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Strong correspondence between gillnet catch per unit effort and hydroacoustically derived fish biomass in stratified lakes

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Summary

1) Sampling of lake fish assemblages is a challenging task in fish science and the information obtained strongly depends on the choice of sampling gear. The use of more than one sampling technique is generally preferred in order to achieve a comprehensive view on fish assemblage structure. Therefore, knowledge of whether catches between fishing gears are comparable is crucial.
2) We compared catches in benthic multi-mesh gillnets with fish biomass estimates obtained by vertical hydroacoustics in 18 European lakes strongly varying in morphometry and trophic status. Separate analyses were conducted for different depth strata and for several fish-length thresholds to account for depth- and size-selective gillnet catches.
3) Gillnet catches and hydroacoustically obtained fish biomass estimates were significantly correlated. The strength of correlations was independent of the fish-length thresholds applied, but varied across different depth strata of the lakes, with the strongest correlations occurring in the shallow strata.
4) The results support the applicability of vertical hydroacoustics for the quantification of fish biomass in stratified lakes. Survey designs combining hydroacoustics with limited gillnetting at sampling dates shortly one after the other, the latter for the purpose of inventory sampling only, are a cost-effective strategy for sampling fish assemblages in lakes. However, gillnet sampling does not provide reliable fish density estimates in very deep lakes with separate, pelagic-dwelling fish assemblages.

Key words: vertical hydroacoustics, lakes, gillnets, fish sampling, biomass estimates

Introduction

Representative sampling of lake fish assemblages is a challenging task in fish science and management. The information obtained on the fish stock depends strongly on the choice of sampling method (Jackson & Harvey, 1997; Jurvelius, Kolari & Leskelä, 2011). Therefore, use of more than one sampling technique is generally preferred in order to achieve a comprehensive overview of the abundance, species composition, size structure and spatio-temporal distribution patterns of fish (Kubečka *et al.,* 2009). Furthermore, application of multiple gears may balance the fact that species caught as well as species size may vary with the gear type used (Bethke *et al.*,1999; Prchalová *et al.*, 2009b).

The efficiency of passive types of sampling gear such as gillnets largely depends on the activity of the fish and estimates of fish abundance are accordingly indirect (Hamley, 1975). In contrast, fish sampled by active gear types such as trawls or hydroacoustics can be linked to the volume or area sampled thus producing quantitative fish abundance estimates (Kubečka *et al.*, 2012). However, local regulations or limited resources often set strict limits to the choice of sampling gears as well as the intensity of sampling. Thus, knowledge of whether catches between fishing gears are comparable is crucial.

Fish assemblages in European lakes are nowadays primarily sampled by multi-mesh gillnets using standardized sampling designs (Appelberg *et al.*,1995; CEN (European Committee for Standardization), 2005). Catches by gillnets are used in both basic (Helland *et al.*, 2007) and applied research, for example the assessment of ecological status of lakes from their fish assemblages required by the European Water Framework Directive (WFD; European Union, 2000) (Søndergaard *et al.*, 2005; Diekmann *et al.*, 2005). However, representative gillnet sampling requires considerable effort with subsequent catch processing time and is therefore quite expensive (Dahm *et al.*, 1992; Van Den Avyle *et al.*, 1995). Furthermore, information on fish assemblage composition based on gillnet catches is relative and may not entirely correspond with absolute fish densities (Linløkken & Haugen, 2006; Prchalová *et al.*,

2011) because of the species and size selectivity and the saturation effect of the nets depending on the number of fish entangled in the meshes (Olin *et al.*, 2004; Prchalová *et al.*, 2011). In most situations, gillnets are considered to be destructive as they kill most individuals entangled in the meshes if the nets are left for several hours in water at high temperatures or rapidly lifted from deep areas to the surface. As a result, the possibility that gillnets may have negative impact on fish population size cannot be excluded. In consequence, some European countries (e.g. U.K., Ireland, Belgium, Netherlands) often limit intensive use of gillnet sampling because of low acceptance by the public and the recreational fisheries community (Winfield *et al.*, 2009). This limitation hampers or even prevents scientific samplings of lake fish assemblages according to the European gillnet standard.

Recently, modern hydroacoustic equipment, a sophisticated active fishing technology which has evolved rapidly during recent times (Simmonds and MacLennan, 2005), has frequently been applied to sample fish assemblages particularly in large deep lakes. A combination of non-destructive fish sampling such as hydroacoustics combined with limited gill netting is highly encouraged (Winfield *et al.*, 2009; Harrison *et al.*, 2010) and is likely to become more important in the future (Kubečka *et al.*, 2012). Currently, data from concurrent gillnet catches (e.g. species composition, relative species abundance) are used for the verification and interpretation of acoustic data because even state-of-the-art echosounders cannot yet distinguish between fish species. The combination of hydroacoustics and gillnets has frequently been applied in research on conservation of fish species (Winfield *et al.*, 2009; Harrison *et al.*, 2010), fish stock assessments (Mehner & Schulz, 2002; Deceliere-Vergès & Guillard, 2008) and fish behaviour (Helland *et al.*, 2007).

However, previous comparisons of abundance data derived from gillnets and hydroacoustics in the same lake have shown very inconsistent and sometimes contrasting results. Peltonen *et al.* (1999) could not detect any significant correlation between gillnet catch per unit effort

(CPUE) and areal fish abundance estimates obtained by hydroacoustics. Likewise, Dennerline, Jennings & Degan (2012) were unable to model a significant relationship between acoustically-derived fish abundances and gillnet catches even after accounting for environmental co-variables. Mehner & Schulz (2002) observed a significant correlation between gillnet and hydroacoustic fish abundances only if the smallest and largest fish were excluded from the analysis, and Elliott & Fletcher (2001) recorded a strong correlation only for large pelagic fish >20 cm. Even in a recently published multi-lake study on 14 Alpine lakes, no significant correlation between fish biomass estimates derived from hydroacoustics and gillnets could be detected (Achleitner, Gassner & Luger, 2012). Obviously, the correspondence between gillnet catches and hydroacoustically obtained fish abundances is weak and/or complex due to differences in size selectivity of the gears or differences in sampling intensity and date of sampling in different lake habitats.

In this study, we sampled fish assemblages in 18 natural European lakes located in different ecoregions using standardized benthic multi-mesh gillnetting (CEN, 2005) and vertical downward-looking hydroacoustics. Ours is, to our knowledge, the largest dataset published comparing fish abundance estimates obtained from these two types of sampling gears. The aim of our study was to test the correspondence between fish biomass caught per unit effort (BPUE) from gillnets and area-related fish biomass derived from hydroacoustics. Separate analyses were conducted for different depth strata and for several fish-length thresholds to account for depth- and size-selective gillnet catches. We hypothesized that correspondence between gears improves using standardized sampling techniques and considering the entire lake as a single sample unit by pooling catches from all gillnets and reflected energy from fish from all hydroacoustic transects in contrast to the above cited tests where single gillnets or hydroacoustic transects within lakes were treated as sample units.

Methods

Study lakes

We analysed fish sampling data from 18 natural lakes located in seven European countries. The study sites covered a latitudinal range of 15 degrees and were located in lowland up to mountain regions (Fig. 1 & Table 1). The lakes differed substantially in surface area (0.25 - 5.45 km^2) and had very different shapes representing circular, elongated and branched lake surface types. All lakes except Lake Fussing (Denmark) were thermally stratified during summer. The mean depth of most lakes varied between 3.8 and 13.6 m and maximum depth between 7.8 and 35.0 m. However, three very deep lakes with mean depth > 30 m and maximum depth > 70 m were sampled additionally (Table 1). The trophic status of the lakes based on the total phosphorus concentration ranged from oligotrophic to hypertrophic (Table 1).

Gillnet sampling

Fish assemblages were sampled consistently across all countries following a stratified random design accredited as the European standard (EN 14757) for sampling fish with multi-mesh gillnets in lakes (CEN, 2005). Sampling took place between 2005 and 2010. In all lakes, the same type of benthic multi-mesh gillnets (type NORDEN) was used. The nets, made of non-coloured, monofilament nylon, were each 30 m long and 1.5 m high (= 45 m^2) and consisted of 12 panels of 2.5 m each with mesh sizes ranging from 5 to 55 mm knot to knot (bar mesh size). The mesh sizes followed a geometric series (43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 5, 35, 29 mm) with an almost constant ratio between two adjacent different mesh sizes of approximately 1.25. Depending on lake area and maximum depth, pre-determined numbers of nets were set randomly within different lake depths. The different depth zones of a lake were divided into a maximum of eight layers and these are termed depth strata (CEN, 2005): lake surface to 2.99 m depth, 3-5.99 m, 6-11.99 m, 12-19.99 m, 20-34.99 m, 35-49.99 m, 50-74.99 m, ≥ 75 m (all depths measured relative to surface). Fish assemblages were sampled between summer and autumn (end of July – mid-October, Table 1) to maximize catch efficiency of the gillnets before the usual reduction of lake temperatures in the epilimnion to <15°C. In accordance with the standard, the gillnets were set overnight to ensure that the activity peaks of the fish during dusk and dawn were included (Prchalová *et al.*, 2009b). Weighting of the gillnet catches after retrieval was not necessary, because all nets were soaked for approximately twelve hours.

The captured fish were determined to species level, measured to the nearest mm total length (TL) and weighed to the nearest g (fresh mass, FM). For the Danish lakes, individuals were pooled according to species, counted and total FM was measured. For the Swedish lake, individual fish lengths were available with pooled FM. Biomass per unit effort (BPUE) was calculated as the average biomass of fish (kg FM) caught by one net during one night. Additionally, depth-strata specific BPUE values were calculated by summing up the FM of all fish caught within a given stratum and dividing it by the number of nets set in that stratum. The gillnet catches were also used to calculate an overall length-mass relationships (LMR) by including all fish from all lakes, independently of their taxonomy, for which information of individual length and individual mass was available. We refrained from developing lake-specific LMR to limit the potential sources of variability in the analyses. Catches from pelagic gillnets, deployed as only a single vertical row at the deepest part of the lakes, were not considered in this study because they were inconsistently used among the countries.

Hydroacoustics

Data collection

Hydroacoustic fish monitoring did not follow an established standard protocol because such a protocol does not yet exist for European waters (Kubečka *et al.*, 2009; Winfield *et al.*, 2011). However, earlier studies have demonstrated that hydroacoustic equipment from different manufacturers operated by different expert teams produce comparable fish density estimates (Mehner *et al.*, 2003; Wanzenböck *et al.*, 2003). Most lakes were sampled by hydroacoustics on dates within the time period of the corresponding gillnet surveys. Only in Lakes Fussing and Fiolen were hydroacoustics performed two and eight weeks after the gillnetting, respectively. Four expert teams collected the data, all using vertical downward-looking split-beam echosounders. The Danish and U.K. lakes were insonified with a Biosonics-DT-X echosounder (Biosonics Inc., U.S.A) equipped with a DT-200-0615-033 transducer. In all other lakes, Simrad EK60 systems (Simrad Kongsberg Maritime AS, Norway) equipped with one of three types of transducers (ES120-7C, ES70-11, ES70-11C) were used. The echosounders operated at frequencies of 200 kHz (Biosonics), 120 kHz and 70 kHz (Simrad) (Table 1) using pulse durations between 256 μs and 512 μs and sample intervals of 2-5 pulses s^{-1} depending on local lake conditions. Transmission power ranged between 80 and 500 watt. Calibration of the systems was undertaken on a regular basis according to the operator manuals using standardized targets.

Acoustic measurements on fish populations can be affected by the sound frequency and pulse duration (Knudsen, Larsson & Jakobsen, 2006; Godlewska *et al.*, 2011) but it has been shown that parameters lying within the range of this study produce unbiased fish biomass estimates (Guillard, Lebourges-Dhaussy & Brehmer, 2004; Godlewska *et al.*, 2009, 2011). Nevertheless, we analysed the effects of the different sound frequencies and pulse durations on the reliability of the fish density estimates using the Sawada index N_v (Sawada, Furusawa & Williamson, 1993) (cf. 2.3.2; 2.4).

For the majority of the lakes the survey designs consisted of non-overlapping, parallel transects. In case where a zig-zag design was used or if transects crossed each other, a representative subset of transects covering all parts of the lake was selected for post processing. This allowed us to generate an approximately parallel survey design for all lakes. The hydroacoustic sampling effort was determined *a priori* following the approach of Aglen (1983) by calculating the degree of coverage, defined as the ratio between the surveyed distance, i.e. the cumulative length of the hydroacoustic transects (km), and the square root of the lake area (km^2). As a general guide, the degree of coverage should be at least 3.0 and preferably near to or above 6.0.

We decided to use only night-time hydroacoustic data as fish are usually better detected by hydroacoustics during darkness when individuals are more dispersed in the open water (Appenzeller & Leggett, 1992; Mehner, Kasprzak & Hölker, 2007b). This pattern was also confirmed in five of the study lakes where both daytime and night-time data were analysed (M. Emmrich, unpublished). Echoes were recorded at an average boat speed of 1.88 m s^{-1} (SD: 0.44) which equals 6.77 km h^{-1} (range: 2.6-8.6 km h^{-1} (mean per lake)) and stored in a digital format on laptop computers.

Data post-processing

All raw files were converted with a base threshold of -100 dB and a minimum single target size of -80 dB into a format compatible to be processed with the Sonar5-Pro software (Version 6.01; Balk & Lindem, 2011). The analysis of the hydroacoustic data was kept as standardized as possible and was carried out by the same individual researcher. For each transect, the bottom line was automatically detected by the Sonar5-Pro software using pre-defined settings based on the authors' experience and subsequently manually corrected if necessary. All files were additionally checked for the presence of unwanted non-fish echoes (e.g. air bubbles, submerged macrophytes, debris accumulation, ropes from gillnets/buoys, fake bottom echoes) which were manually deleted from the echograms.

Sonar5-Pro software was also used to calculate total mean volumetric backscattering strength (S_v in decibels (dB)) from the fish echoes. To estimate fish biomass, echo integration (sv/ts scaling) was used. All chosen hydroacoustic transects of a lake were merged into a single file and analysed together. We did not divide the transects into horizontal segments (elementary distance sampling units, EDSU) to avoid high numbers of empty cells with no backscattered echo energy. Furthermore, the small variability of our sampling designs can create geostatistical variance patterns due to spatial autocorrelation, a problem that is avoided if S_v is calculated for the entire insonified water volume.

Calculations of S_v and areal fish biomass excluded water layers from surface down to 2 m because for the Danish and U.K. lakes shallower parts were not recorded during field campaigns. This exclusion functioned further as a tradeoff to reduce the effects of possible avoidance reactions of fish from the vessel, to consider the transducer depth, and to account for the upper blind zone (near-field of the transducer) that gives unreliable fish echoes, but still insonifying some volume of surface water. For the comparison of fish biomass in the upper depth stratum defined by the gillnet standard (0-2.99 m; CEN, 2005), we applied the fish biomass detected in 2-3 m depth to the upper meters (0-1 m and 1-2 m). Echoes from fish close to the lake bottom cannot always be distinguished from the bottom echo such that the bottom margin was set to 0.3 m (lower blind zone).

In addition to the analysis covering the entire water volume, depth strata of the merged hydroacoustic files were analysed separately to identify for which depths benthic gillnet catches corresponded with hydroacoustic estimates. It has been recommended to estimate fish biomass from *in situ* target strength data in defined depth strata with homogeneous fish species and size structure (Parker-Stetter *et al.*, 2009). However, for a direct, depth-specific comparison we used the same depth strata that have been *a priori* defined according to the gillnet standard (CEN, 2005). Homogeneous size distributions of single echo detections (SED) could be confirmed for the upper depth strata in most lakes. However, with increasing thickness of the depth strata applied only in the deeper lakes, slightly more non-homogeneous patterns in SED size distributions were observed (M. Emmrich, unpublished).

The hydroacoustic data were also checked for reliable estimates of *in situ* target strength using the Sawada index N_v (number of fish per acoustic sampling volume) (Sawada *et al.*, 1993). The index serves as a diagnostic tool for identification of volumes with very high fish densities. If $N_v > 0.1$, data were interpreted with appropriate caution.

For the conversion of the echo target strength (TS in decibel, dB) into fish total length (TL in cm), the relationship of Love (1971) was used, adjusted to the different sound frequencies (f) of 70 kHz, 120 kHz and 200 kHz.

$$TS = 19.1*\log(TL)-0.9*\log(f)-62$$

By applying this general conversion formula, we avoided introducing additional uncertainty into the comparison of biomass between both fishing gears. For the conversion of the hydroacoustic fish lengths into fish biomass, we used the length-mass relationships (LMR) calculated from the pooled gillnet catches from all lakes (cf. 3.1), because gillnet catches from all lakes (except Montriond) were dominated by the same species (Table 1).

We further tested whether certain fish size thresholds affected the correspondence between the two sampling gears. Previous studies have shown that small fish are not effectively caught with multi-mesh gillnets (Olin, Malinen & Ruuhijärvi, 2009; Prchalová *et al.*, 2009b) because of the small ratio between diameter and mesh size for the smallest meshes, which reduces the stretchability of the meshes and the catchability of small fish (Hamley, 1975), and the saturation effect of the gillnets at high densities of small fish. Therefore, stronger correspondence between gillnet catches and hydroacoustically derived fish abundance might be achieved if small fish are excluded from the comparison (Mehner & Schulz, 2002).

To evaluate the effect of variable lower fish sizes on the analysis, we selected TS thresholds (SED/Amp mode) of -58/-64 dB, -52/-58 dB and -47/-53 dB which equal fish TL of approximately 2 cm, 4 cm and 8 cm according to the TS-TL relationship of Love (1971). For these small fish, the correspondence between fish TL and TS was similar for all three sound frequencies. As also very large fish are not effectively caught with multi-mesh gillnets having a maximum mesh size of 55 mm knot to knot (Psuty & Borowski, 1997), we also tested a maximum size threshold of 60 cm equivalent to TS values > -30 dB. The 60 cm threshold was the upper size range representing 99.9% of all fish caught by the nets.

To account for a potential modification of LMR by exclusion of small fish, an additional LMR for fish ≥ 8 cm was calculated and integrated into the Sonar5-Pro software for the conversion of the hydroacoustically detected fish echoes into fish biomass. The effect of applying a minimum fish-length threshold of 2 cm and 4 cm or a maximum fish-length threshold of 60 cm on LMR was marginal due to small number of fish with minimum and maximum size in the gillnet catches.

Statistics

BPUE values and hydroacoustically derived areal fish biomasses were $\log_{10}(x+1)$ transformed to meet assumptions of bivariate normality and homogeneity of variances. S_v values (in dB) did not need to be transformed as they are already on a log-scale and fulfilled the assumptions for parametric test statistics. Pearson product moment correlations were calculated to test for the linear relatedness of gillnet BPUE with either hydroacoustic S_v or areal fish biomass (kg ha^{-1}).

To predict areal fish biomass from given BPUE values, ordinary least squares (OLS) regression was used with gillnet BPUE as the independent variable and hydroacoustically derived areal fish biomass as the dependent variable. We chose OLS regression instead of model II regression (e.g. major axis regression), because we aimed to predict areal fish biomasses from gillnet catches (BPUE). In this case, OLS regression can be used in model II situations, because it produces fitted values with the smallest error (Legendre & Legendre, 1998). However, as the independent variable (BPUE) was also measured with an unknown error term, we did not calculate reliability estimates (95% confidence intervals). Furthermore, the regression lines presented cannot be used to predict gillnet catches (BPUE) from quantitative fish biomass estimates derived from hydroacoustics. Intercepts of the regression lines were tested for a significant deviation from zero to determine whether zero catches in gillnets also resulted in the prediction of zero fish biomass from hydroacoustics.

To test the effects of the different sound frequencies and pulse durations on the reliability of fish density estimates (expressed by the Sawada index N_v), we used a generalized linear model (GLM) with N_v as the response variable and sound frequency and pulse duration as factors. Calculations were made using the R statistical software package version 2.10.0 (R Development Core Team, 2009).

Results

Benthic gillnet catches

In total, 455 nets caught 21 067 fish representing 35 species from 15 families. Mean number of fish caught in the lakes was 1170 individuals (SD: 1093; range: 152-3534). The number of species per lake caught by gillnets ranged between 3 and 14. Perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* (L.)) dominated the catch in most lakes (Table 2) and also dominated the overall gillnet catch (perch: 59.6% of number and 39.3% of biomass; roach: 24.5% of number and 30.7% of biomass). Mean size of fish caught was 11.3 cm (SD: 6.4) and 38.5 g (SD: 150.3) with a maximum individual TL of 88.0 cm and an FM of 6229 g. Minimum TL of fish caught was 2.0 cm. However, very small (2-4 cm) and very large (> 60 cm) fish were rarely caught (n = 8 and n = 15, respectively). The overall numerical proportion of fish < 8 cm TL in the gillnet catches was 37.9%, but differed between the lakes (0-74.9%).

BPUE values of single nets ranged between 0-11.15 kg net^{-1} night^{-1} (mean 1.79 kg; SD: 2.16). The proportion of empty nets in a lake ranged between 0 and 37.5%. In 14 out of 18 lakes, the maximum depth-specific average BPUE values were observed in the two shallowest strata (0-5.99 m).

The length-mass relationship (LMR) for all fish captured in the 18 lakes was

FM (g) = 0.00956 TL (cm) $^{3.033}$ (r^2 = 0.96; P < 0.001; n = 15 804).

After removing fish < 8 cm from the data set the LMR changed into

FM = 0.00762 TL $^{3.116}$ (r^2 = 0.97; P < 0.001; n = 10 199).

Hydroacoustics

Mean total S_v averaged -62.8 dB (SD: 10.5) by applying a minimum length threshold of ≥ 2 cm TL, -61.1 dB (SD 8.3) for the fish TL threshold ≥ 4 cm and -62.1 dB (SD: 8.4) for the fish TL threshold ≥ 8 cm. Hydroacoustically derived areal fish biomass averaged 88.4 kg ha^{-1} (SD: 150.7) for fish ≥ 2 cm, 79.7 kg ha^{-1} (SD: 131.1) for fish ≥ 4 cm and 68.3 kg ha^{-1} (SD: 109.1) for fish ≥ 8 cm, and biomass ranged between 1.3 and 318.2 kg ha^{-1} (only lakes with a Sawada index N_v < 0.10). Depth-strata specific fish biomass ranged between 0 and 378.3 kg ha^{-1}. There was a tendency towards higher fish biomass in the shallow strata relative to deep depth strata, although not as strong as observed in the gillnet catches. Particularly in deep lakes, a comparatively high fish biomass was observed at depths down to 35 m. A high Sawada index (N_v > 0.10) was found in three lakes (Nordborg, Loweswater, Rostherne Mere) after applying a TS threshold of -58 dB (2 cm long fish), but it remained high in only one lake (Nordborg) after the TS threshold was raised to -52 dB (4 cm long fish) (Table 3). However, removal of these lakes from the dataset did not significantly influence the correlation strength and therefore we kept all lakes in the analyses. Furthermore, N_v was not influenced by the use of different sound frequencies (GLM: t = -1.58; P = 0.14) or pulse durations in our dataset (GLM: t = -1.27; P = 0.22), suggesting unbiased comparison of the hydroacoustically obtained fish biomass estimates.

Comparison hydroacoustics – gillnet BPUE

We found a highly significant overall correlation between total S_v and BPUE across the 18 lakes (*r* = 0.80, *P* < 0.001; Fig. 2) with similar correlation strengths for all fish length thresholds tested (*r* = 0.77 – 0.80, *n* = 18, all *P* < 0.001; Table 3). When split into five successive depth strata (0-2.99 m, 3-5.99 m, 6-11.99 m, 12-19.99 m, 20-34.99 m), we found a significant correlation between S_v and BPUE for the shallowest strata for all fish length thresholds (Table 3). In stratum 3 (6-11.99 m), a significant correlation was only observed if fish echoes from fish < 8 cm TL were ignored. In deeper strata (≥ 12 m), S_v was not at all correlated with BPUE (all *P* > 0.47). These results indicate that length thresholds had no impact on the correlation, whereas lake depth contributed substantially to the overall correspondence between the two types of sampling gear.

The importance of lake depth was confirmed when the reflected fish echo energy was converted into areal fish biomass (kg ha^{-1}). The OLS regression between gillnet BPUE and areal fish biomass derived from hydroacoustics was not significant (r^2 = 0.19, *F* = 3.82, *P* = 0.07, *n* = 18). However, OLS became significant if the three very deep lakes were excluded (y = 3.698 x - 0.198, r^2 = 0.52, *F* = 14.18, *P* = 0.002, *n* = 15, Fig. 3a). The intercept of this OLS (-0.198) did not differ from zero (*t* = -0.40, *P* = 0.70). A gillnet BPUE of 2 kg net^{-1} $night^{-1}$ corresponds to a fish biomass of 36.8 kg ha^{-1}. However, for gillnet catches > 6 kg net^{-1} $night^{-1}$, area-related fish biomass derived from the regression line was very high (> 840 kg ha^{-1}).

If gillnet catches and hydroacoustics data were limited to the upper two strata (0 to 5.99 m), the OLS regression was significant as well (y = 4.090 x – 0.896, r^2 = 0.66, *F* = 31.14, *P* < 0.001, *n* = 18). In this case, the deepest lakes did not deviate from the overall regression line (Fig. 3b). The intercept was significantly different from zero (*t* = -2.16, *P* = 0.05). A gillnet BPUE of 2 kg net^{-1} $night^{-1}$ corresponds to a fish biomass of 11.4 kg ha^{-1} for the shallow depth stratum. At high gillnet catches (> 7 kg net^{-1} $night^{-1}$), area related fish biomass derived from the regression model was again very high (> 620 kg ha^{-1}).

Discussion

To our knowledge, our study is the first to show a strong significant correlation between gillnet catch data and fish biomass estimates obtained by hydroacoustics collected from a series of lakes varying strongly in morphometry and trophic status. By applying entire lakes as sample units, we found a strong log-linear correspondence between backscattered echo energy (S_v) from fish and average biomass caught by the gillnets (kg fish net^{-1} night^{-1}). After converting the reflected fish echo energy into areal fish biomass (kg ha^{-1}), the significant relationship with gillnet BPUE persisted if the three very deep lakes were excluded. The strength of correlations was independent of the fish-length thresholds applied, but varied across the different depth strata of the lakes.

The observed discrepancy in correlation strength between the use of S_v and converted areal fish biomass demonstrates complications arising from conversion of the echo target strength into fish total length and the further conversion of fish length into fish biomass. These calculations include two steps of uncertainty, particularly regarding large fish echoes. Typically, abundances of large fish are low, such that the few large fish echoes do not contribute substantially to the total back-scattered echo energy. However, the conversion of S_v into a biological unit (kg fish ha^{-1}) can produce high fish biomass estimates from the few large fish because their SEDs contribute to the S_v scaling. The occurrence of a few very large fish can be detected by hydroacoustics, but may go undetected by gillnets (Psuty & Borowski, 1997), thereby weakening the relationship between the hydroacoustic estimates of fish biomass and gillnet BPUE.

According to the results of earlier studies, correspondence of fish abundance estimates between gillnets and hydroacoustics generally seemed weak (Peltonen *et al.*, 1999; Dennerline *et al.*, 2012), particularly in deep lakes (Jurvelius *et al.*, 2011; Achleitner *et al.*, 2012). However, these studies compared fish catches by gillnets with hydroacoustically obtained fish densities in single lakes where fish catches between individual nets can be highly variable both horizontally (area) and vertically (depth) (Prchalová *et al.*, 2009a; Deceliere-Vergès *et al.*, 2009) or they sampled fish assemblages by different gears at different seasons where different fish assemblages might be sampled by both gears (Winfield, Fletcher & James, 2007; Bobori & Salvarina, 2010). Therefore, combination of data from several gillnets and hydroacoustic transects sampled at short time intervals and by considering the entire lake as a sample unit, as in our study, reduces the effect of high temporal and spatial variability of fish samplings and thus substantially improves between-lake comparability.

Nevertheless, the strength of correspondence between the two types of gear declined in the deeper strata of the lakes. However, although the power of the statistical correlation was reduced for these analyses due to the smaller sample sizes (12 and 6 lakes, respectively), we suggest that the weaker correspondence was primarily the result of less precise biomass estimates of pelagically living fish from benthic gillnets (*cf.* Deceliere-Vergès *et al.*, 2009; Achleitner *et al.*, 2012). At low productivity, the hypolimnion of European stratified lakes is occupied by stenothermic coldwater species of the order Salmoniformes (Beier, 2001; Guillard *et al.*, 2006; Mehner *et al.*, 2007a). The majority of these species are truly pelagic although a few have benthic morphs (Kahilainen *et al.*, 2011). Therefore, they are underrepresented in benthic multi-mesh gillnet catches (Deceliere-Vergès & Guillard, 2008), and their relative abundance estimates from pelagic gillnets are less accurate even if the sampling effort is higher than a single vertical row of pelagic nets per lake according to the CEN standard (Achleitner *et al.*, 2012). However, these fish are reliably detected by vertical hydroacoustics, because the sound transmitted and hence the volume of water sampled increase with increasing water depth. Precision of biomass estimates is even higher by conducting night-time hydroacoustics because many pelagic fish perform diurnal vertical migration and disperse more evenly in the pelagic area at night (Appenzeller & Leggett, 1992; Mehner *et al.*, 2007b).

In contrast, fish biomass in shallow or highly productive deep lakes is highest in strata close to the surface, particularly if environmental conditions at greater depths are less favourable for the fish population (Draštík *et al.*, 2009). Consequently, the highest fish catches by multi-mesh gillnets usually appear in the upper depth strata (Lauridsen *et al.*, 2008; Prchalová *et al.*, 2009a; this study). The ratio between the open-water and near-benthic volume of these lakes is often low, hence, catches in benthic gillnets are representative for the fish assemblage in these strata. Furthermore, diurnal horizontal migrations of fish between onshore and offshore shallow strata (Lewin, Okun & Mehner, 2004; Pekcan-Hekim *et al.*, 2005) are covered by gillnet catches because the nets are set overnight and there catch the fish during their migration and activity peaks at dusk and dawn (Prchalová *et al.*, 2010). Nevertheless, the very strong correspondence between hydroacoustically and gillnet derived fish biomass particularly for the shallow depth strata was not expected, since previous studies have revealed that vertical, downward-looking hydroacoustics underestimates fish abundance in shallow waters (Knudsen & Sægrov, 2002; Draštík *et al.*, 2009). For example, in two of the study lakes no fish > 8 cm were detected by hydroacoustics in the upper depth strata, whereas a few individuals were caught by gillnets. Accordingly, the negative regression intercept for fish biomass estimates from the shallow depth strata (0-5.99 m) was significantly different from zero, indicating that fish biomass in these strata may be underestimated by vertical hydroacoustics even after adding fish biomass from the layer beyond the nearfield dead zone of the transducers (2-3 m) to the upper blind zone (0-2 m). However, our data also indicate that if fish are more abundant, vertical hydroacoustics can produce fish biomass estimates that strongly correspond with benthic gillnet catches, even for shallow lake depth strata.

Earlier studies have suggested that correspondence between hydroacoustics and gillnet derived fish abundances can be improved if analyses are limited to the size range of fish that both gears sample efficiently (Mehner & Schulz, 2002; Dennerline *et al.*, 2012). In general, acoustic fish length distributions are wider than those obtained by net fishing gears

(Emmrich *et al.*, 2010; Jurvelius *et al.*, 2011). Consequently, removal from the analysis of fish from the lower and upper end of the size spectrum might improve the comparability and correspondence of fish abundance estimates (Mehner & Schulz, 2002). In our analyses, however, application of varying fish size thresholds did not significantly affect the results. Although numerical dominance of small, newly hatched fish may characterise fish assemblages in lakes during spring and summer, intermediate-sized fish are dominant in late summer/early autumn, when sampling took place, due to reduced abundance of small fish by growth and high mortality over the seasons. Consequently, based on our hydroacoustic observations, fish of 2-4 cm total length which are most likely one-summer old recruits, contributed on average only 12.2% to the total biomass. Likewise, very large fish contributed on average only 5% to the standing biomass because of their low overall abundance. These calculations further indicate that total biomass of fish is a less variable descriptor than numerical abundance for lake fish assemblages. Accordingly, correspondence between gears is usually stronger in biomass comparisons (Mehner *et al.*, 2003; Emmrich *et al.*, 2010). This is no limitation since information on trophic interactions and energy budgets of lakes requires biomass estimates of trophic variables (Jeppesen *et al.*, 1998), and the correspondence between trophic state or productivity of lakes and their fish assemblages is usually also stronger for biomass than for abundance units (Hanson & Leggett, 1982; Garcia *et al.*, 2006).

Although our data fit best to linear models, the general log-linear relationship between gillnet CPUE and absolute fish biomass may become biased at very high fish densities (Linløkken & Haugen, 2006; Prchalová *et al.*, 2011). Maximum catch capacity of the standardized benthic multi-mesh gillnets has been estimated to 11 kg net^{-1} (Prchalová *et al.*, 2011). During our samplings, only three out of 455 nets caught more than 10 kg fish, suggesting that our gillnet catch data were not strongly biased by saturation effects. However, we cannot exclude the possibility that the linear pattern might change if more lakes with very high fish densities are included. Our regression lines for the prediction of fish biomass from relative gillnet catches also suggested reduced reliability at high fish densities, because an average gillnet catch of > 6 kg net^{-1} $night^{-1}$ predicts areal fish biomasses > 600 kg ha^{-1} which are rarely observed in stratified natural European lakes.

The results of our comparative approach are encouraging and support the more frequent application of vertical hydroacoustics for the quantification of fish biomass in stratified lakes. Survey designs combining hydroacoustics and limited gillnetting at sampling dates with short time intervals, the latter for inventory sampling only (i.e. apportionment of species data from gillnet catches to hydroacoustic data) rather than CPUE calculations, offer a cost-effective strategy for sampling lake fish assemblages. This approach is particularly appropriate because gillnetting can create ethical problems or conflicts with interests of local recreational fisheries.

In turn, standardized gillnet sampling by benthic nets in moderately deep lakes may be used to roughly predict areal fish biomasses according to our regression equations. Whether the equation derived for the upper depth strata can be applied to shallow, polymictic lakes as well deserves further studies. Furthermore, gillnet sampling seems not to provide sufficiently reliable relative fish density estimates in very deep lakes with separate, pelagic dwelling fish assemblages irrespective of whether the full set of benthic nets is used or is supplemented with pelagic nets required to sample fish in deep lakes (>10 m maximum depth) even if the sampling effort is higher than proposed by the European gillnet standard EN14757 (CEN, 2005; Deceliere-Vergès & Guillard, 2008; Achleitner *et al.*, 2012). To comply with the requirement for quantitative information on pelagic lake fish assemblages (Lauridsen *et al.*, 2008), representative sampling should be conducted using active sampling gears which are more efficient and give more accurate estimates on fish abundance (Haakana & Huuskonen, 2008; Jurvelius *et al.*, 2011). It has already been demonstrated that catches from these gears are comparable to those obtained by hydroacoustics if sampling systems are sufficiently developed (Emmrich *et al.*, 2010).

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Table 1 Characteristics of the study lakes including latitudinal (Lat) and longitudinal (Long) coordinates (WGS84), altitude (Alt (m a.s.l.)), area (km^2), mean depth (Z_{mean} (m)), maximum depth (Z_{max} (m)) and total phosphorus concentration (TP ($\mu g\ L^{-1}$)). In addition, sound frequencies of the hydroacoustic systems (Freq (kHz)), number of hydroacoustic transects (n Tr), degree of coverage (DoC), number of benthic gillnets (n GN) and sampling month of gillnetting are given

Country	Lake	Lat	Long	Alt	Area	Z_{mean}	Z_{max}	TP	Freq	n Tr	DoC	n GN	month
Denmark	Fussing	56.4705	9.8722	18	2.17	12.6	28.1	40	200	11	3.8	17	August
	Nordborg	55.0575	9.7638	6	0.54	5.0	7.8	241	200	12	3.1	13	September
France	Aiguebelette	45.5555	5.7985	374	5.45	30.7	71.0	10	70	12	5.3	58	October
	Aydat	45.6641	2.9861	837	0.56	8.0	15.0	20	70	11	6.9	24	September
	Bouchet	44.9091	3.7906	1200	0.43	15.0	28.0	27	70	6	5.7	24	September
	Montriond	46.2090	6.7283	1060	0.33	9.0	19.7	14	70	9	3.7	16	September
	Pavin	45.4956	2.8875	1196	0.45	45.0	96.0	20	70	9	6.9	32	September
Germany	Glindow	52.3568	12.9284	33	1.95	4.9	14.3	139	120	18	4.7	24	September
	Grienerick	53.1067	12.8873	56	0.87	4.3	14.1	37	120	8	4.0	24	September
	Roofen	53.1087	13.0397	59	0.57	9.0	19.1	17	120	18	5.6	24	September
Italy	Ghirla	45.9166	8.8222	415	0.25	11.0	14.0	24	120	17	7.3	16	October
	Mergozzo	45.9561	8.4643	204	1.82	45.6	73.0	6	120	12	7.0	32	October
Norway	Longumvatnet	58.4880	8.7529	32	1.00	9.6	35.0	10	70	19	3.9	32	August
	Nøklevann	59.8751	10.8748	163	0.79	11.3	33.0	5	70	17	4.1	32	August
	Temse	58.3835	8.6370	15	0.62	5.0	10.0	16	70	6	3.4	24	September
Sweden	Fiolen	57.0827	14.5331	226	1.56	3.8	10.0	13	70	9	4.5	24	July
UK	Loweswater	54.5830	-3.3562	125	0.60	8.4	16.0	13	200	12	5.6	17	August
	Rostherne Mere	53.3542	-2.3858	27	0.48	13.6	31.0	180	200	13	7.2	22	August

Table 2 Species richness (SR) and the two dominant species (numerical abundance) in the benthic gillnet catches

Lake	SR	Abundance (%)
Fussing	6	PEF (84.0) RUR(13.3)
Nordborg	9	RUR (43.0) GYC (18.1)
Aiguebelette	12	RUR (48.3) PEF (38.4)
Aydat	7	RUR (52.0) PEF (31.0)
Bouchet	11	RUR (68.4) PEF (9.2)
Montriond	7	PHP (59.7) LES (21.6)
Pavin	6	PEF (75.5) SAU (10.8)
Glindow	9	PEF (45.3) RUR (24.3)
Grienerick	11	PEF (52.5) RUR(32.9)
Roofen	11	PEF (71.7) RUR (23.0)
Ghirla	6	PEF (57.0) RUR (28.4)
Mergozzo	14	RUR (60.4) GYC (15.0)
Longumvatnet	4	PEF (55.8) SCE (43.0)
Nøklevann	6	PEF (73.0) RUR (22.2)
Temse	5	PEF (94.7) CO sp. (3.8)
Fiolen	4	PEF (62.6) RUR (25.2)
Loweswater	4	PEF (99.1) ESL (0.4)
Rostherne Mere	3	PEF (84.6) RUR (15.3)

Species codes (scientific names): CO sp. (*Coregonus* sp.), ESL (*Esox lucius* L.), GYC (*Gymnocephalus cernuus* L.), LES (*Leuciscus souffia* RISSO), PEF (*Perca fluviatilis* L.), PHP (*Phoxinus phoxinus* (L.)), RUR (*Rutilus rutilus* (L.)), SAU (*Salvelinus umbla* L.), SCE (*Scardinius erythrophthalmus* (L.))

Table 3 Correlation between the log (x+1)-transformed mean volumetric backscattering strength (S_v in dB) and log (x+1)-transformed catches from benthic multi-mesh gillnets (BPUE (kg net^{-1} night^{-1})) for five depth strata and the total lake. Depth strata were defined according to the European standard for sampling fish in lakes with multi-mesh gillnets. Given are target strength (TS) and Sv thresholds and the corresponding range of fish lengths (LR) included in the analyses, Pearson's correlation coefficient (*r*) and the corresponding *P*-value. Significant correlations ($P \leq 0.05$) are highlighted in bold. Note: The number of lakes included in the correlation analyses was 18 (depth strata 1-3), 12 (depth stratum 4) and 6 (depth stratum 5). Asterisks indicate analyses where lakes with a Sawada index N_v > 0.10 were included

TS/S_v thresholds (dB)	LR (cm)	Depth stratum	*r*	*P*
-58/-64	2 - ∞	1 *	**0.714**	**<0.001**
		2 *	**0.681**	**0.002**
		3 *	0.405	0.095
		4	0.182	0.550
		5	-0.226	0.666
		total *	**0.797**	**<0.001**
-52/-58	4 - ∞	1	**0.753**	**<0.001**
		2	**0.654**	**0.003**
		3 *	0.430	0.074
		4	0.217	0.474
		5	-0.224	0.668
		total	**0.788**	**<0.001**
-47/-53	8 - ∞	1	**0.749**	**<0.001**
		2	**0.624**	**0.006**
		3	**0.482**	**0.043**
		4	0.195	0.522
		5	-0.187	0.720
		total	**0.774**	**<0.001**
-47/-53	8 - 60	1	**0.753**	**<0.001**
		2	**0.631**	**0.005**
		3	**0.592**	**0.01**
		4	0.182	0.551
		5	-0.187	0.720
		total	**0.769**	**<0.001**

Fig. 1 Geographical location (closed circles) of the 18 lakes distributed across seven European countries (grey-coloured) whose fish assemblages were sampled by vertical hydroacoustics and standardized benthic multi-mesh gillnets.

Fig. 2 Scatter plot of log(x+1)-transformed benthic multi-mesh gillnet catches (kg net^{-1} $night^{-1}$) and mean total volumetric backscattering strength (S_v in decibel (dB)) from hydroacoustics for 18 European lakes. The correlation was highly significant (Pearson's $r = 0.80$; $P < 0.001$). The used TS/S_v threshold was -52/-58 dB which corresponds to fish ≥ 2 cm according to Love's equation (1971).

Fig. 3 Scatter plots and ordinary least square regression lines between log(x+1)-transformed benthic multi-mesh gillnet catches (kg net^{-1} $night^{-1}$) and log(x+1)-transformed areal fish biomass (kg ha^{-1}) derived from hydroacoustics for the entire depth range analysed (surface to bottom; a) and for the upper depth stratum (0-6 m; b). The three deepest lakes (white circles) were excluded from the regression analysis for the entire depth range (a) but remained in the analysis of the shallow depth stratum (b). Given are the regression equation and the coefficient of determination (r^2). The used TS/S_v threshold was -52/-58 dB which corresponds to fish ≥ 2 cm according to Love's equation (1971).

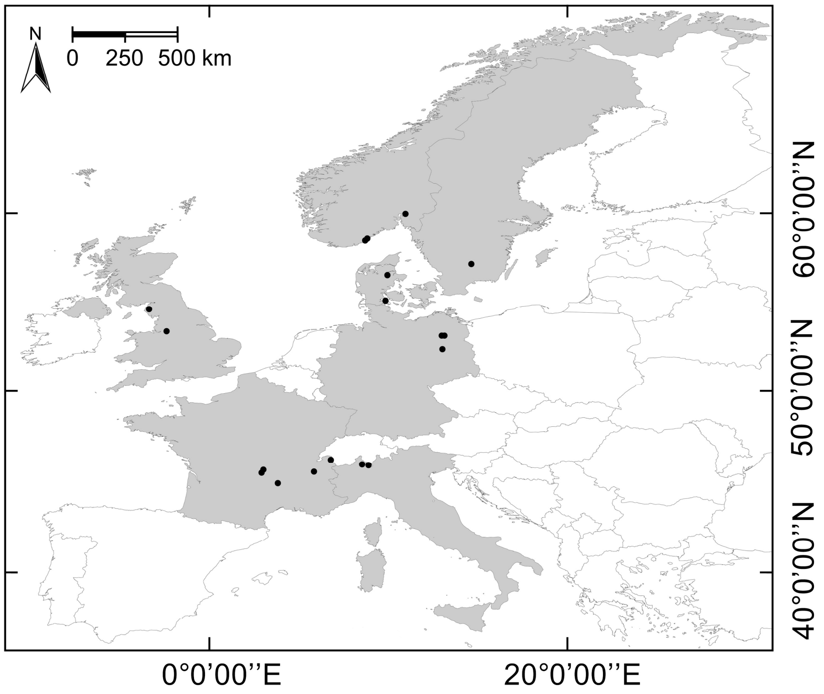


Figure 1

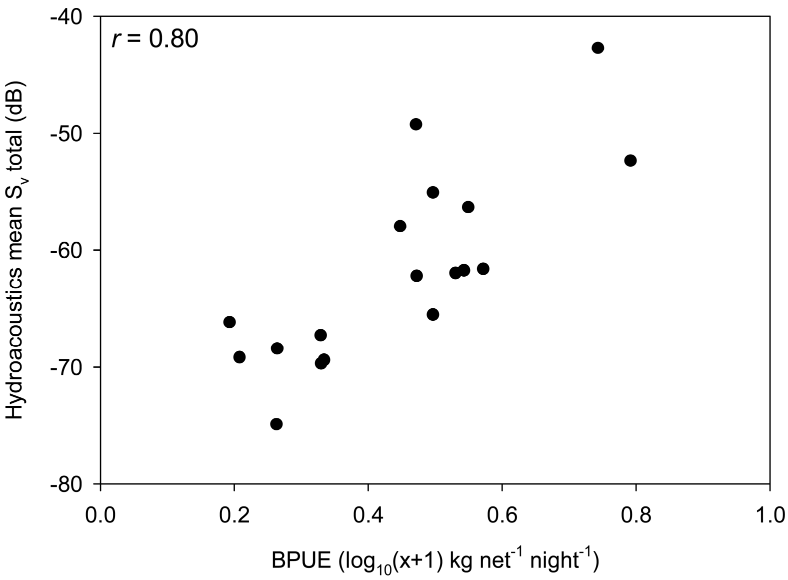
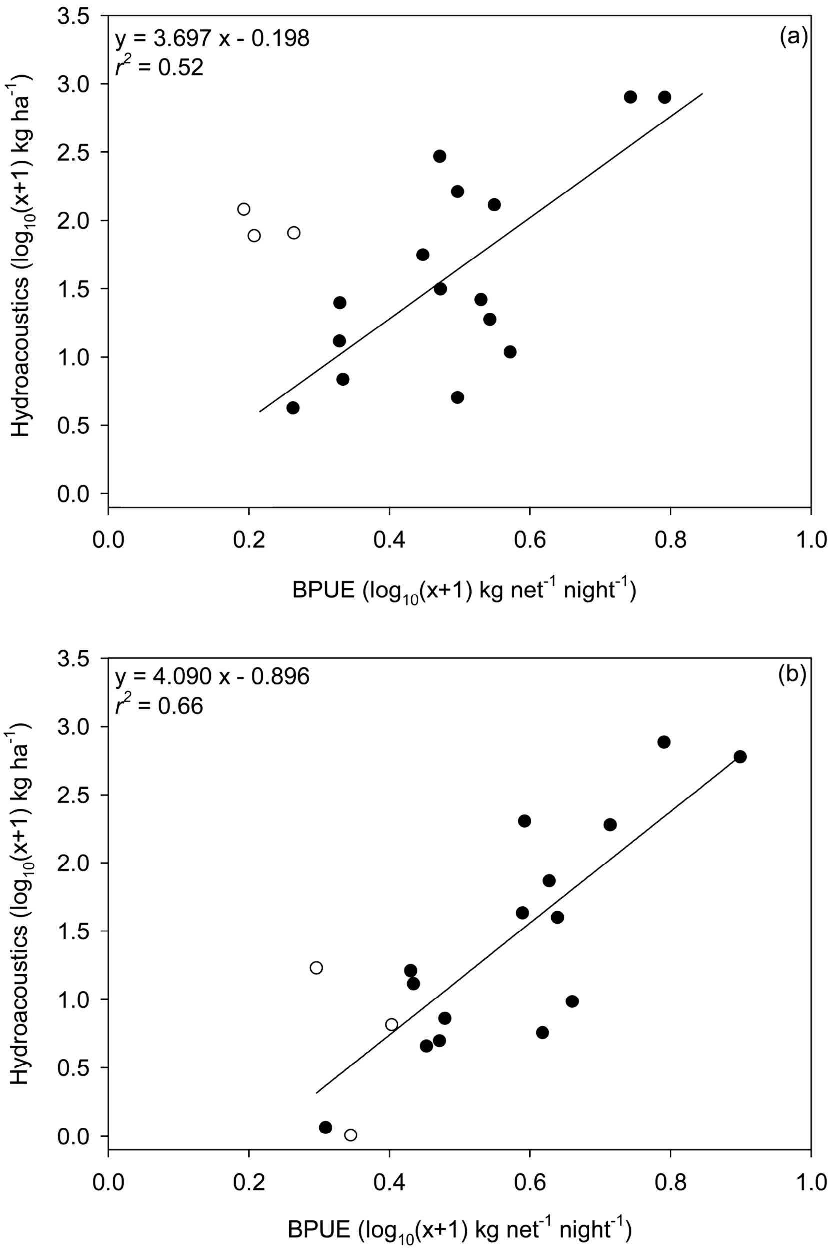


Figure 2



y = 3.697 x - 0.198
r² = 0.52
(a)
Hydroacoustics (log10(x+1) kg ha-1)
BPUE (log10(x+1) kg net-1 night-1)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0.0
0.2
0.4
0.6
0.8
1.0
y = 4.090 x - 0.896
r² = 0.66
(b)
Hydroacoustics (log10(x+1) kg ha-1)
BPUE (log10(x+1) kg net-1 night-1)

Figure 3