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Estimating whole-lake fish catch per unit effort

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ABSTRACT

The European standard for gillnet sampling to characterize lake fish communities stratifies sampling effort (*i.e.*, number of nets) within depth strata. Nets to sample benthic habitats are randomly distributed throughout the lake within each depth strata. Pelagic nets are also stratified by depth, but are set only at the deepest point of the lake. Multiple authors have suggested that this design under-represents pelagic habitats, resulting in estimates of whole-lake CPUE and community composition which are disproportionately influenced by ecological conditions of littoral and benthic habitats. To address this issue, researchers have proposed estimating whole-lake CPUE by weighting the catch rate in each depth-compartment by the proportion of the volume of the lake contributed by the compartment. Our study aimed to assess the effectiveness of volume-weighting by applying it to fish communities sampled according to the European standard (CEN), and by a second whole-lake gillnetting protocol (VERT), which prescribes additional fishing effort in pelagic habitats. We assume that convergence between the protocols indicates that volume-weighting provides a more accurate estimate of whole-lake catch rate and community composition. Our results indicate that volume-weighting improves agreement between the protocols for whole-lake total CPUE, estimated proportion of perch and roach and the overall fish community composition. Discrepancies between the protocols remaining after volume-weighting may be because sampling under the CEN protocol overlooks horizontal variation in pelagic fish communities. Analyses based on multiple pelagic-set VERT nets identified gradients in the density and biomass of pelagic fish communities in almost half the lakes that corresponded with the depth of water at net-setting location and distance along the length of a lake. Additional CEN pelagic sampling effort allocated across water depths and distributed throughout the lake would therefore help to reconcile differences between the sampling protocols and, in combination with volume-weighting, converge on a more accurate estimate of whole-lake fish communities.

1. Introduction

Fish are regarded as effective indicators of the ecological status of aquatic ecosystems (Karr, 1981). In a healthy lake, fish typically occupy all major habitats (*i.e.*, littoral, profundal, limnetic) and a wide spectrum of trophic niches ranging from primary consumers (*i.e.*, herbivores) and detritivores through to tertiary consumers (*i.e.*, piscivores). Different fish species prefer and tolerate different physico-chemical regimes meaning that changes in fish community composition can reflect shifting ecological state (*e.g.*, Mehner et al., 2005). Fish are generally long-lived and therefore depict environmental effects integrated over several years (Harris, 1995). They also play a key role in structuring the lake ecosystem as they control zooplankton and benthic macroinvertebrate communities, which in turn regulates primary production (Carpenter et al., 1985). In addition to fisheries and lake management questions, lake fish also provide a convenient subject for research into community ecology (Boit et al., 2012), resilience theory (Ibelings et al., 2007) and ecosystem functioning (Holmlund and Hammer, 1999).

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Despite the useful information that can be gained from quantifying the composition of lake fish communities, all methods for surveying these animals in medium to large lakes carry some sort of bias. In order to use fish as an effective bioindicator or for community ecology research, a measure of the fish community must be clearly defined that acknowledges, accommodates, or accounts for these biases. Gillnetting has been widely adopted across Europe as a means of survey lake fish communities as it requires minimal infrastructure and expertise, and can be deployed throughout all major habitats of a lake. The accepted biases of gillnetting are that it tends to under-represent less-active (Backiel and Welcomme, 1980) and long, slender species such as char, pike and eels (Olin et al., 2009), over-represents the proportion of species with spines or rigid appendages (*e.g.*, perch, pikeperch; Prchalová et al., 2008), and that its size-selective (Prchalová et al., 2009), such that each mesh size most efficiently catches a particular size of fish.

For the purpose of tracking broad ecological changes in a lake through time, the influence of most gillnetting biases can be minimized by consistently surveying with the same mesh sizes and the same level of replication throughout a lake. However, comparisons *among* lakes may be affected by the way a gillnetting protocol accommodates differences in lake morphometry. Deeper lakes have a higher proportional volume of pelagic water and the heterogeneity in the distribution of fish populations throughout the lake increases with lake size and depth. Sampling protocols need to accommodate these differences in order to achieve an accurate representation of whole-lake fish communities. The distribution of sampling effort throughout the volume of a lake is particularly important when the focus of the sampling program is to determine the quantity of fish *i.e.*, biomass, abundance, community composition.

The European standard for sampling fish in lakes using multi-mesh gillnets "... provides a whole-lake assessment for species occurrence, quantitative relative fish abundance and biomass expressed as Catch Per Unit Effort (CPUE), and size structure of fish assemblages in temperate lakes" (Scope p5; Comité Européen de Normalisation, 2005; hereafter refered to as the CEN protocol). Numerous important contributions have been made to understanding factors influencing whole-lake fish communities which were based in data collected by the CEN gillnetting protocol. Mehner et al. (2005) used data collected according to the protocol to identify that fish community composition is strongly influenced by lake morphometry and primary productivity in 67 lakes across north-east Germany. Diekmann et al. (2005) extended this analysis using the same set of lakes to show that these lakes cluster into three groups represented by indicator species vendace (*Coregonus albula*), bream (*Abramis brama*) and smelt (*Osmerus eperlanus*). Brucet et al. (2013) investigated the influence of geographic and anthropogenic factors on lake fish communities using CEN gillnetting data collected in 1632 lakes across Europe. They similarly showed that lake morphometry and primary productivity shaped fish diversity, density and body size. Several fish-focused indices of biological integrity have also been developed based on, and for application with, data collected under the CEN protocol (Argillier et al., 2013; Launois et al., 2011; Lyche-Solheim et al., 2013).

Scientific contributions based on the CEN protocol are becoming increasingly common as the database of surveyed lakes increases in spatial and temporal extent. It is therefore important to understand the methodological idiosyncrasies of the protocol in order to appropriately interpret the results of research based on this method. Alexander et al. (2015) recently highlighted that characterisation of lake fish based on data collected according to the CEN protocol is strongly selective towards species in benthic habitats. Other authors have also commented on the heavy benthic emphasis of the protocol and advocated additional sampling effort in pelagic waters to better represent fish communities throughout the lake (Achleitner et al., 2012; Deceliere-Vergès and Guillard 2008; Diekmann et al., 2005; Jeppesen et al., 2006; Lauridsen et al., 2008). Mehner et al. (2005) accommodated the uneven distribution of sampling effort among habitats under the CEN protocol by weighting whole-lake CPUE based on the volumetric contributions of the littoral, benthic and pelagic habitats. They estimated the volume of these habitat-compartments by treating each lake as an ideal cone. Lake maximum depth formed the cone height and the lake surface area forming the area of the base, from which the circumference could be derived. Lauridsen et al. (2008) expanded on this approach, dividing benthic and pelagic habitats into smaller compartments based on depth strata used to allocate netting effort in the CEN protocol. They identified that estimates of whole-lake CPUE are strongly influenced by the morphometry of a lake. They also showed that the proportion of netting effort between benthic and pelagic habitats influences perceived relationships between fish communities and ecological conditions such as nutrients. The risk with applying a volume-based adjustment to CEN protocol data is that estimates of pelagic fish community come only from a single position, the deepest point of the lake, and therefore overlook spatial variability in this habitat. The CEN protocol acknowledges that horizontal variation of pelagic fishes is not adequately sampled under the protocol and, since pelagic waters constitute the vast majority of the volume of a lake, inaccurate or unrepresentative estimates of pelagic fishes will be magnified by the volume-based correction.

A second whole-lake gillnetting protocol for fish communities has been developed and extensively applied in the lakes of eastern France which also aims to provide whole-lake estimates of fish abundance, biomass and community composition (Degiorgi, 1994; Degiorgi et al., 1993a,b; 2001). This protocol prescribes gillnets that simultaneously sample from the lake surface to the lake floor. Nets are longest on the vertical axis so the protocol is hereafter referred to as the vertical netting or VERT protocol. Sampling effort under the VERT protocol is allocated among littoral and deep-water habitats. Littoral habitats (depth < 5 m) are defined according to the habitat architecture of a site (*e.g.*, macrophytes, boulders, sediment). Up to five deep-water (*i.e.*, depth > 5 m) habitat compartments are defined according to the maximum depth of the lake (see methods section for more details). Alexander et al. (2015) compared the CEN and VERT protocols for characterizing lacustrine fish communities (based on raw catch data) and suggested that the larger net area and spatial replication of pelagic nets under the VERT protocol results in a more accurate estimate of fish communities throughout an entire lake.

This paper builds on the results of Alexander et al. (2015) and aims to determine if application of a volume-based weighting of whole-lake CPUE reconciles differences in fish density, biomass and community composition between the CEN and VERT protocols. We assume that a reduction of the differences between the protocols with volume-weighting indicates convergence towards a true estimate of whole-lake catch rate and community composition (*i.e.*, towards the 'true picture' of the fish community; *sensu* Kubečka et al., 2009).

We also aim to investigate the claim by numerous researchers that the CEN protocol does not adequately represent pelagic communities by setting pelagic nets only at the deepest point of the lake. We used VERT nets distributed throughout the lake to test for the presence of spatial gradients in the pelagic fish community. The results of this analysis will guide allocation of additional CEN pelagic netting effort to best represent the whole-lake fish communities.

2. Methods

2.1. Fish sampling

Lacustrine fish communities were surveyed in 18 lakes distributed across eastern France, Switzerland and northern Italy (Fig. 1). Lakes ranged widely in surface area (0.8–582 km^2), maximum depth (18–372 m), volume (5.2–79,017 gigaliters; GL) and altitude (194–1797 m above sea level). See Table 1 in Alexander et al. (2015) for details of lake morphometry. Data for Lake Garda became available subsequent to publication of Alexander et al. (2015). Physical characteristics of Lake Garda are altitude = 65 m, surface area = 370 km^2, maximum depth = 346 m, mean depth = 136 m, volume = 50,372 GL. Fish communities were surveyed in each lake according to two whole-lake gillnetting protocols: the CEN multimesh gillnetting standard (hereafter CEN protocol; Appelberg, 2000; Comité Européen de Normalisation, 2005) and the vertical gillnetting protocol (or VERT protocol; Degiorgi et al., 1993a, 2001).

The CEN protocol prescribes horizontally-oriented gillnets consisting of twelve contiguous mesh panels, each 1.5 m high by 2.5 m wide, of mesh sizes 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55 mm (measured knot-to-knot; overall net dimensions 1.5 × 30 m). Nets sampling benthic habitats were randomly stratified within depth strata with replication provided in the protocol based on maximum depth and area of a lake. The CEN protocol states that the decision to set benthic nets deeper than 75 m is at the discretion of the operator. Nets sampling pelagic habitats consisted of contiguous mesh panels 6 m high and 2.5 m wide following the same series of mesh sizes as the benthic nets but excluding the 5 mm panel. Pelagic nets were deployed in the same depth strata to 75 m deep in the column of water above the deepest point of a lake.

The VERT protocol prescribes vertically-oriented nets that simultaneously sample from the lake surface to the lake floor. Mesh sizes used by nets under this protocol were 10, 15, 20, 30, 40, 50, 60 mm. Mesh columns were 2 m wide, with the length of the vertical axis (*i.e.*, height) of the net corresponding to water depth. Mesh columns for nets sampling littoral habitats (to 5 m depth) were attached to the same float and lead lines with adjacent columns separated by 2 m gaps. For deep-set nets, each mesh column was deployed as a separate net but as close together as practical. Netting effort under the vertical netting protocol was distributed among littoral and pelagic habitats. Littoral habitats (<5 m deep) were mapped prior to the fish sampling event and reflected dominant substrate composition (*i.e.*, leaf litter, silt, sand, cobble, boulders, bedrock), vegetation (living/dead, floating, emergent or submerged macrophytes) or proximity to an in- or outflowing river or stream (see Table 2 in Alexander et al., 2015 for more detail). Deep habitats were defined according to the maximum depth of a lake ($Z_{\max}$). These included two sublittoral zones (5–10 m; 10 m–$0.3Z_{\max}$) and three deep zones ($0.3Z_{\max} - 0.6Z_{\max}$; $0.6Z_{\max} - 0.9Z_{\max}$; $0.9Z_{\max} - Z_{\max}$). Some deep habitats were not present in the lake if $Z_{\max}$ was less than 40 m. Three replicate batteries of all mesh-nets should be set within each habitat category.

Fish abundance and biomass were adjusted for net area and soak time with the result expressed in number of fish per square meter of net per 14 h soak time (abundance per unit effort; NPUE) and grams of fish (wet weight) per square meter of net per 14 h soak time (biomass per unit effort; BPUE). In this paper, NPUE and BPUE are collectively referred to as catch per unit effort (CPUE) or catch rate. Unless otherwise specified, biomass and abundance always refer to the effort adjusted values.

Whole-lake CPUE was calculated as global CPUE (*sensu* Alexander et al., 2015) for both CEN and VERT protocols. Global CPUE sums the soak-time corrected abundance or biomass across all nets set in a lake and divides by the summed net area of all nets set in the lake. Whole-lake CPUE calculated as global CPUE describes the average catch rate across every square meter of net set in the lake. This approach is most appropriate where the surface area of nets varies between netting actions, such as among actions for the VERT protocol and between CEN benthic and pelagic nets.

2.2. Volume-weighted CPUE

The process of calculating volume-weighted whole-lake CPUE divided the lake into depth-based compartments and weighted the whole-lake CPUE for each species by their catch rates in each depth-compartment and the volumetric contribution of the compartment (*i.e.*, the volume of the compartment as a proportion of the volume of the lake). Compartments were defined according to the depth strata used in each gillnetting protocol to allocate netting effort (Fig. 2). The volume of the compartments were calculated in ArcMap v10.1 based on depth contours of digitized nautical charts (Garda), generated using a triangular irregular network based on acoustic bathymetric mapping (Remoray, Saint Point) or from available digital bathymetric maps (remaining lakes; Swisstopo (Art. 30 GeoIV): 5704 000 000/Vector200©2010, reproduced with permission from Swisstopo/JA100119). The volume-weighted CPUE therefore reflects the catch rate across the entire volume of the lake.

When adjusting CPUE based on the CEN data, benthic habitats were defined with an upper boundary of 3 m from the lake floor. For example, the volume of the 6–12 m benthic compartment was calculated as the planar surface area of the lake floor between the 6 m and 12 m depth contours multiplied by a height of 3 m. This height differs from Mehner et al. (2005) who defined benthic habitats as 1.5 m high, corresponding with the height of the benthic nets. We extended the height of benthic habitats to 3 m to acknowledge that vertical movement of fishes means that the volume of water being fished by benthic nets extends higher than the height of the net. Defining benthic habitats as 1.5 m above the lake floor also severely limits the volumetric contribution of this habitat with whole-lake weighting, particularly in large lakes.

Replication and net areas in each compartment are provided for CEN and VERT protocols in Appendix A Tables A1 and A2, respectively. Net replication occasionally deviated from that recommended by the protocol due to lost, damaged, stolen drifted or malfunctioning (excluded) nets, or where weather conditions prohibited safely setting the required number of nets, particular VERT nets in the deepest parts of a lake. There were four instances where no VERT nets were set within a depth-habitat. The volumes of these habitat-compartments were subtracted from the total lake volume when calculating proportional volumes for volume-weighting.

2.3. Statistical analyses

2.3.1. Total CPUE and common species

The level of agreement in whole-lake CPUE, and the relative abundance and biomass (*i.e.*, proportion of total CPUE) of the three most abundant taxa, perch (*Perca fluviatilis*), whitefish (*Coregonus* sp) and roach (*Rutilus* sp), between CEN and VERT protocols was quantified using the r^2 from a Pearson's correlation for each measured aspect of the fish community as quantified by each protocol. A high r^2 indicated that protocols ranked each lake in a similar manner relative to other lakes and that the magnitude of difference between lakes was similar between protocols. An increase in r^2 with volume-weighting therefore indicated increased agreement in estimates of whole-lake CPUE between the protocols. This metric is most informative to assess the benefit of volume-weighting for the purposes of ecological assessments (*e.g.*, comparison to reference/natural conditions within a lake typology) and ecological analyses (*e.g.*, regressions to determine the influence on whole-

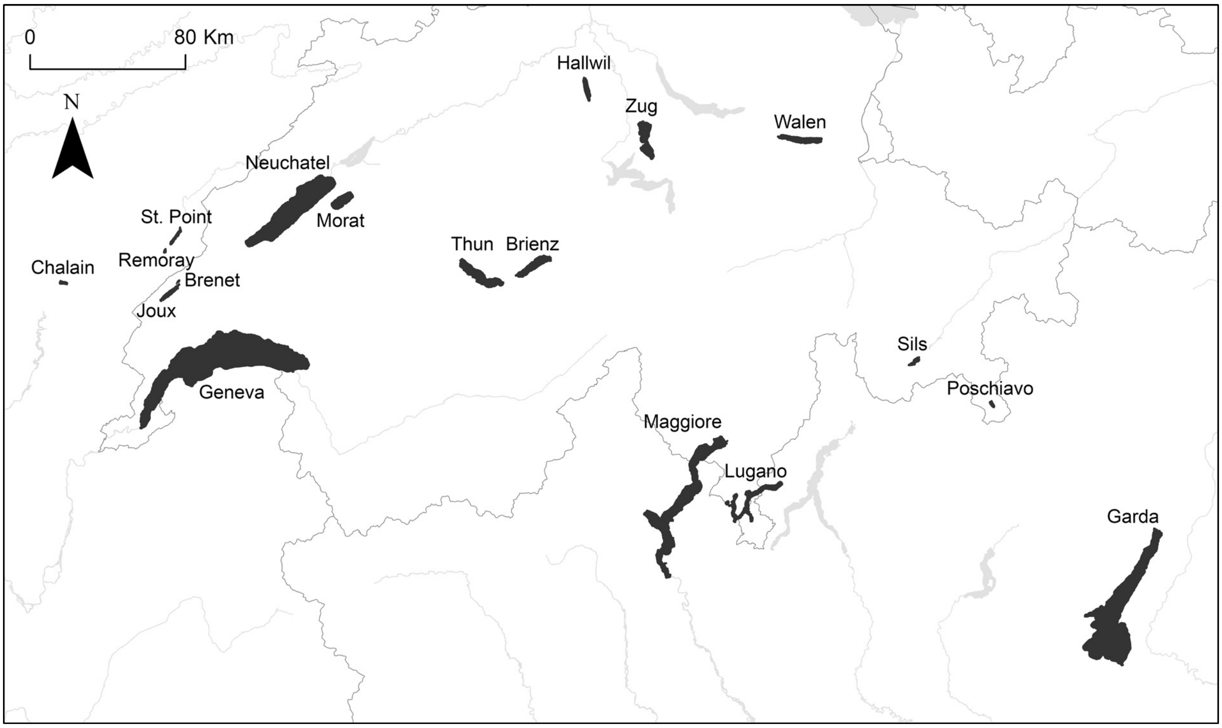

Fig. 1. Map of sampled lakes across Switzerland, eastern France and northern Italy.

Table 1
Volume-weighting improved agreement between the CEN and VERT protocols for total NPUE (number/m^2/14 h) and BPUE (g/m^2/14 h), both in terms of r^2 (coefficient of determination for Pearson's correlation) and 1:1 agreement (*i.e.*, slope → 1, intercept → 0 determined by major axis regression). Volume-weighting also improved agreement between the protocols in the proportion of perch and roach, however results for whitefish were less clear. Estimates of CPUE were log transformed to achieve normality prior to analysis. Asterisks indicate where slope and intercept varied significantly from 1 and 0, respectively.

Response	Metric	Treatment	Slope	Intercept	r^2
Total	NPUE	Raw	0.88	-1.90^{**}	0.66
		Volume-weighted	0.94	-0.92^{*}	0.83
	BPUE	Raw	1.53^{**}	-2.11^{**}	0.74
		Volume-weighted	1.01	0.02	0.82
Perch	NPUE	Raw	2.82^{**}	-7.97^{*}	0.44
		Volume-weighted	1.09	−0.60	0.68
	BPUE	Raw	2.08^{**}	-4.74^{**}	0.66
		Volume-weighted	0.97	−0.23	0.62
Whitefish	NPUE	Raw	0.97	1.23^{**}	0.63
		Volume-weighted	0.84	$0.88^{\dagger}$	0.64
	BPUE	Raw	1.24	−0.44	0.76
		Volume-weighted	0.89	0.25	0.54
Roach	NPUE	Raw	1.85	−2.38	0.32
		Volume-weighted	1.07	−0.22	0.83
	BPUE	Raw	1.68†	$-2.58^{\dagger}$	0.49
		Volume-weighted	1.00	−0.42	0.73

† $p < 0.1$.
* $p < 0.05$.
** $p < 0.01$.

lake fish community of natural and anthropogenic factors). The closeness to 1:1 agreement of estimates of whole-lake CPUE and proportion of common species between the protocols with volume-weighting was also tested by focusing on the change in coefficients of major axis regression. Major axis regression was used because both X and Y variables are measured with unknown level of error (Legendre and Legendre, 1998). A slope of 1 and intercept of 0 indicated that estimates obtained by the two protocols did not systematically deviate from equivalence across the range of observed values. Significance was determined using the major axis regression equivalent of ANCOVA (see also Emmrich et al., 2010, who used a similar technique to compare lake fish density estimates based on hydroacoustics and pelagic trawling). Prior to analysis, all CPUEs were tested for normality using a Shapiro test and log-transformed where necessary. Major axis regression was carried out using packages "lmodel2" (version 1.7-2) and "smatr" (version 3.4-3; Warton et al., 2012). As a final step, linear regression analysis was used to determine which aspects of lake morphometry (maximum depth, surface area or volume) best explained (based on AIC) the magnitude of change in CPUE with volume-weighting. All analyses were conducted in R (R Core Team, 2014).

2.3.2. Community composition

We also determined whether volume-weighting significantly increased the similarity of estimates of fish community composition between the CEN and VERT protocols. Fish community

Table 2
Linear regression models of (a) abundance (NPUE; number/m^2/14 h), and (b) biomass (BPUE; g/m^2/14 h) of limnetic fishes *versus* setting depth (*i.e.*, depth of the water column at net-setting locations in each lake) and distance along the length of the lake. n indicates the number of vertical net batteries (*i.e.*, 7 mesh-nets set together) used in the analysis.

(a) NPUE		Variable treatment			Setting depth		Distance along lake	
Lake	n	NPUE	Depth	Distance	P	R^2	P	R^2
Geneva	33	sqrt(y)	ln(x)	–	0.007^{**}	0.21	0.054	0.115
Neuchatel	14	sqrt(y)	–	$(x)^2$	0.101	0.21	0.047^{*}	0.43
Morat	9	ln(y)	–	–	0.298	0.15	0.0005^{***}	0.85
Saint-Point	9	sqrt(y)	–	–	0.127	0.3	0.772	0.01
Hallwil	9	ln(y)	–	$(x)^2$	0.037^{*}	0.49	0.015^{*}	0.76
Zug	8	sqrt(y)	ln(x)	–	0.394	0.12	0.788	0.01
Thun	10	sqrt(y)	ln(x)	–	0.659	0.03	0.803	0.07
Brienz	6	ln(y)	ln(x)	–	0.512	0.11	0.135	0.47
Walen	12	sqrt(y)	$(x)^2$	$(x)^2$	0.070	0.45	0.021^{*}	0.58
Maggiore	7	sqrt(y)	ln(x)	ln(x)	0.162	0.35	0.303	0.21
Lugano	12	ln(y)	ln(x)	ln(x)	0.096	0.25	0.900	0.01
Garda	8	–	ln(x)	$(x)^2$	0.264	0.20	0.024^{*}	0.77
(b) BPUE		**Treatment**			**Setting depth**		**Distance along lake**	
Lake	**n**	**BPUE**	**Depth**	**Distance**	**P**	**R^2**	**P**	**R^2**
Geneva	33	sqrt(y)	ln(x)	–	0.364	0.03	0.0001^{***}	0.49
Neuchatel	14	sqrt(y)	–	$(x)^2$	0.173	0.15	0.007^{**}	0.59
Morat	9	sqrt(y)	–	–	0.119	0.36	0.025^{*}	0.53
Saint-Point	9	ln(y)	–	–	0.854	0.01	0.661	0.03
Hallwil	9	–	–	$(x)^2$	0.162	0.26	0.101	0.535
Zug	8	sqrt(y)	ln(x)	–	0.642	0.04	0.795	0.01
Thun	10	sqrt(y)	ln(x)	–	0.891	0.01	0.903	0.01
Brienz	6	ln(y)	ln(x)	–	0.523	0.11	0.246	0.32
Walen	12	sqrt(y)	$(x)^2$	$(x)^2$	0.020^{*}	0.58	0.012^{*}	0.63
Maggiore	7	sqrt(y)	ln(x)	ln(x)	0.747	0.02	0.091	0.359
Lugano	12	ln(y)	ln(x)	ln(x)	0.014^{*}	0.47	0.623	0.02
Garda	8	–	ln(x)	$(x)^2$	0.807	0.01	0.004^{**}	0.89

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

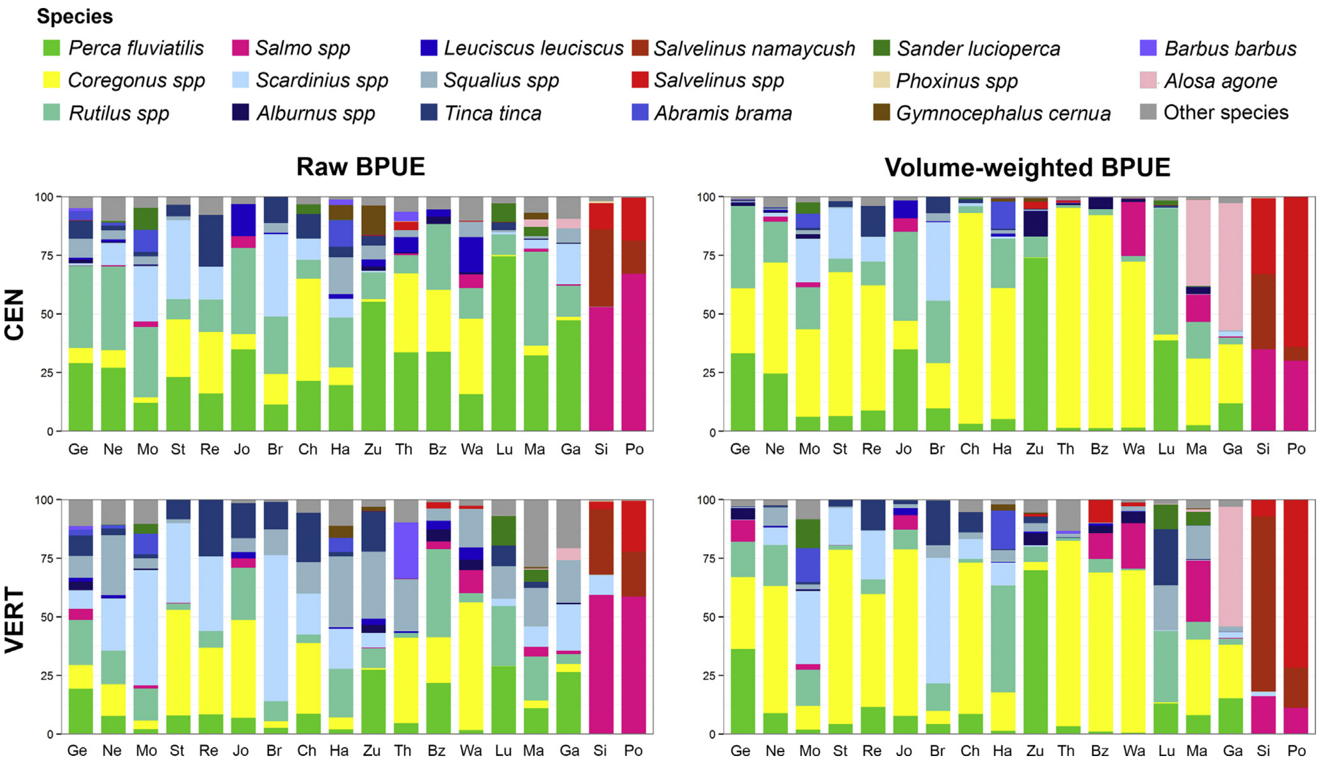

Fig. 2. Hypothetical lake cross-sections showing depth compartments used to allocate gillnetting effort and as the basis for volume-weighting (a) CEN and (b) VERT data. Horizontal extent of each compartment (x-axis) reflects the measured planar surface area of the depth contours.

similarity between protocols in each lake was quantified using Bray–Curtis similarity. A paired *t*-test was used to determine the change in Bray–Curtis similarity with and without volume-weighting. The analysis was conducted on both raw and relativized species catches (*i.e.*, catch for each species divided by the summed CPUE for all species in the lake; also known as relative abundance). Bray–Curtis similarity was calculated using the package “vegan” (version 2.0-10; Oksanen et al., 2013).

2.3.3. Gradients in limnetic fish communities

The distribution of VERT nets set across multiple depths and locations throughout the lake allowed us to explore gradients in the fish community of pelagic waters. The objective of this analysis was to (a) help to explain any differences that remained between CEN- and VERT-estimated fish communities after volume-weighting, and (b) allow us to identify criteria which may be relevant to allocate additional CEN pelagic netting effort. The two explanatory variables considered in the linear regression analysis were the depth of the water column where the net was set (net-setting depth) and distance along the length of a lake. Distance along the length (longest axis) of the lake was defined in the main direction of water flow through the lake *i.e.*, distance of the net-setting location from the main inflow at one end of the lake. Analyses of pelagic fishes were restricted to those caught in the top 20 m of the VERT nets (limnetic zone: well-lit surface waters of a lake away from the shore). Restricting the analysis to limnetic waters (*i.e.*, the section of net from lake surface to 20 m deep) avoided the chance that a higher proportion of a vertical net sampling lower-density profundal waters in deeper parts of the lake might bias the test for horizontal gradients (*e.g.*, a vertical net set in 10 m of water will generally have higher CPUE than one set in 100 m owing to the fact that the latter have a higher proportion of the net sampling aphotic waters). Nets set shallower than 23 m (20 m surface waters, plus an additional 3 m buffer to avoid the influence of benthic habitats) were excluded so that each replicate had the same net surface area ($2\text{ m net width} \times 20\text{ m net height} \times 7\text{ mesh nets} = 280\text{ m}^2$). Chalain, Remoray, Brenet and Joux were excluded from the analysis because insufficient numbers of vertical nets were set in water deeper than 23m ($n \leq 5$ net batteries) to be able to conduct a meaningful regression analysis. Dependent and independent variables were test for normality using a Shapiro test and log or square root transformed where necessary. Quadratic models were considered based on inspection of residuals of the linear model and accepted if they increased R^2.

3. Results

3.1. Total CPUE

Volume-weighting whole-lake CPUE increased agreement (increased r^2 and reduced deviation from unity *i.e.*, slope → 1, intercept → 0) between protocols for estimates of biomass and abundance (Table 1; Fig. 3). Volume-weighting significantly decreased whole-lake estimates of total CPUE for both protocols in all lakes. Volume-weighted total CPUEs ranged from 3.1% to 97.6% of the raw (un-weighted) estimates. Volume-weighting had a greater influence on CEN than VERT data with a higher minimum, maximum and mean change in CPUE as a proportion of the raw CPUE across lakes for both biomass (CEN: range = 20.6–96.8%, mean change = 73.7%, paired *t*-test: $t = 8.14$, df = 17, $p < 0.001$; VERT: range = 13.1–89.7%, mean change = 55.8%, paired *t*-test: $t = 6.04$, df = 17, $p < 0.001$) and abundance (CEN: range = 19.6–96.9%, mean change = 76.8%, paired *t*-test: $t = 5.44$, df = 17, $p < 0.001$; VERT: range = 2.4–89.0%, mean change = 51.6%, paired *t*-test: $t = 6.93$, df = 17, $p < 0.001$). Regression analyses and model selection based on AIC indicated that, among three metrics of lake morphometry (surface area, maximum depth and lake volume), the extent of change in CPUE with volume-weighting in each lake was best explained by its maximum depth (CEN NPUE: $F = 15.86$, df = 16, $p < 0.01$, $R^2 = 0.5$; CEN BPUE: $F = 35.22$, df = 16, $p < 0.00$, $R^2 = 0.69$; VERT NPUE: $F = 6.9$, df = 16, $p < 0.05$, $R^2 = 0.3$; VERT BPUE: $F = 17.23$, df = 16, $p < 0.001$, $R^2 = 0.52$).

3.2. Common species

Volume-weighting consistently improved agreement between protocols in the proportion of abundance contributed by common species (Table 1; Fig. 4); while improvements for biomass were less clear (Table 1; Fig. 5). Volume-weighting shifted estimates of the abundance and biomass contribution of common species in different directions. The proportion of whitefish increased for both protocols in all lakes with volume-weighting (with the exception of biomass and abundance in Lake Zug under CEN), while the proportion of fish community contributed by perch and roach decreased in most lakes. The mean increase in the proportion of total fish abundance contributed by whitefish was 440.4% for CEN (paired *t*-test: $t = -2.98$, df = 17, $p < 0.01$) and 235.7% for the VERT protocol (paired *t*-test: $t = -3.52$, df = 17, $p < 0.01$), while the mean increase in biomass was 633.2% for CEN (paired *t*-test: $t = -5.37$, df = 17, $p < 0.001$), and 163.3% for VERT protocol (paired *t*-test: $t = -5.26$, df = 17, $p < 0.001$). The proportion of abundance and biomass contributed by perch decreased in most lakes. Shifts in the proportion of perch were strongest for CEN data where proportion of perch in biomass decreased in 14 of the 16 lakes where the species was recorded (mean decrease = 60.8%, paired *t*-test: $t = 3.35$, df = 17, $p < 0.01$) and abundance decreased in 12 lakes (mean decrease = 59.2%, paired *t*-test: $t = 2.97$, df = 17, $p < 0.01$). The decrease in proportion of perch was less pronounced for VERT data (biomass mean decrease = 40.4%, paired *t*-test: $t = -0.136$, df = 17, $p = 0.89$; abundance mean decrease = 48.1%, paired *t*-test: $t = 1.51$, df = 17, $p = 0.15$). The proportion of roach was also lower with volume-weighting in the majority of lakes: CEN abundance decreased in 9 of 16 lakes (mean decrease = 65.2%, paired *t*-test: $t = -0.18$, df = 17, $p = 0.86$), and biomass decreased in 13 lakes (mean decrease = 49.2%, paired *t*-test: $t = 1.17$, df = 17, $p = 0.26$); VERT abundance decreased in 11 lakes (mean decrease = 53.0%, paired *t*-test: $t = 0.22$, df = 17, $p = 0.83$), and biomass in 11 lakes (mean decrease = 46.7%, paired *t*-test: $t = 0.76$, df = 17, $p = 0.46$).

3.3. Community composition

Volume-weighting significantly increased the similarity of the fish community composition between the two protocols. The increase in similarity was stronger for abundance-based community composition (NPUE: $t = 7.5$, df = 17, *p*-value < 0.001, mean difference in Bray–Curtis similarity between CEN and VERT community composition with volume-weighting = 0.31; Fig. 6a), than fish community composition based on biomass (BPUE: $t = 3.8$, df = 17, *p*-value < 0.01, mean difference = 0.14; Fig. 6b). For abundance-based community composition, the similarity between the two protocols became more similar with volume-weighting in all lakes. In terms of biomass-based community composition, volume-weighting improved the similarly between CEN and VERT protocols in most lakes but slightly reduced the similarity in Lakes Saint Point, Morat, Lugano and Joux (mean decrease in Bray–Curtis similarity = 0.06). In the same analysis based on relativized fish community composition (*i.e.*, relative species abundances), volume-weighting also increased the average similarity of the fish community composition between the two protocols, however the difference was significant only for abundance (NPUE: $t = 2.23$, df = 17, *p*-value < 0.05, mean difference = 0.077;

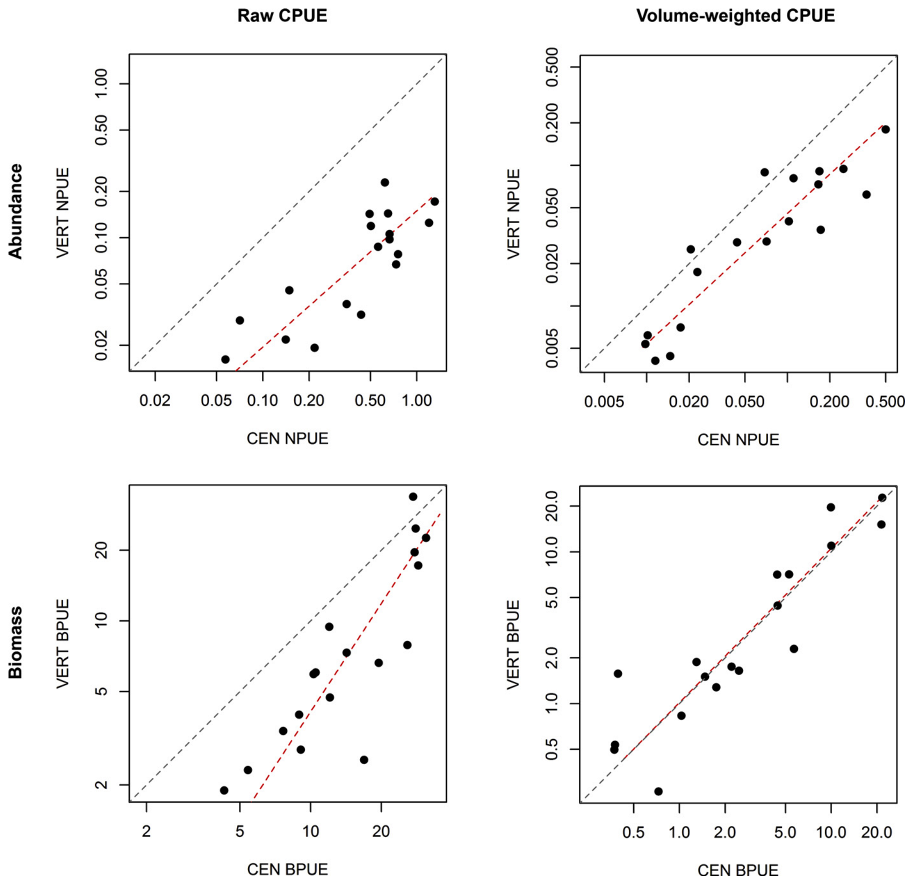

Fig. 3. Volume-weighting whole-lake CPUE brought estimates between protocols closer to unity (1:1 agreement) and increased r^2 values from correlation analysis. Dashed red line indicates line of best fit and dashed grey line represents 1:1 agreement. CPUE is expressed as number of fish or weight in grams/m^2 net surface area/14 h soak time for NPUE and BPUE respectively.

BPUE: $t = 1.69$, df = 17, p-value = 0.110, mean difference = 0.069). Appendix B Figs. B1 and B2 show the relative abundance and biomass of the most common species in each lake.

3.4. Gradients in limnetic fish communities

We identified significant relationships between the limnetic fish community and depth of the water at the net setting location and distance along the length of the lake (*i.e.*, distance from inflow) in multiple lakes (Table 2). Gradients in fish communities *along the lake* were stronger (higher R^2) and more common (occurring in five of twelve lakes tested; Fig. C1, in Appendix C) than those with water column depth (occurring in only two lakes; Fig. C2). Heatmaps showing the two-dimensional distribution of biomass for CEN and VERT data within CEN depth strata for a selection of lakes are also provided in the appendix (Fig. D1).

4. Discussion

Weighting whole-lake catch per unit effort by volume-based compartments increased the correlation between protocols reflecting improved agreement in the rank–order and the magnitude of differences among lakes for fish biomass and abundance. Volume-weighting whole-lake CPUE also increased 1:1 agreement between estimates of CPUE (*i.e.*, direct numerical comparison of estimates within each lake) between the protocols. In addition, volume-weighting generally increased agreement between the protocols in the proportion of common species, perch and roach, and increased the similarity in fish community composition among lakes as estimated by the two protocols. Convergence in whole-lake CPUE and community composition between the two protocols suggests that volume-weighted estimates better represent the fish community of a lake than a CPUE based on the raw (unweighted) data. This suggests that application of a volume-based adjustment in large lakes provides an estimate of whole-lake CPUE that is less influenced by idiosyncrasies of a particular sampling protocol and therefore more appropriate for community- and macro-ecological research, such as to determine the effects of natural variables and anthropogenic conditions on whole-lake fish communities.

The increased influence of pelagic fish communities with volume-weighting resulted in lower estimates of CPUE in all lakes for both protocols. CPUE calculated on raw catch data is influenced by the distribution of netting effort among littoral, benthic and pelagic habitats (and the characteristics of the fish community in each habitat). Fish density is generally higher in littoral and shallow benthic than pelagic habitats (Lauridsen et al., 2008), however the former habitats occupy only a small proportion of the volume of a large lake. Application of volume-weighting therefore tends to reduce the influence of littoral and shallow benthic habitats, while increasing the contribution of pelagic habitats, which constitute a high proportion of the lake volume, but generally support fewer fish per volume of water (Achleitner et al., 2012). The increased importance of pelagic habitats in whole-lake CPUEs is reflected in the increased proportion of whitefish (*Coregonus* spp.) in the fish community with volume-weighting for every lake under both CEN and VERT protocols, particularly in terms of biomass. Since whitefish predominantly occupy pelagic waters, the consistent increase of these taxa with volume-weighting reinforces that pelagic habitats are under-represented in raw estimates of whole-fish communities for both protocols. It is also worth noting that agreement between

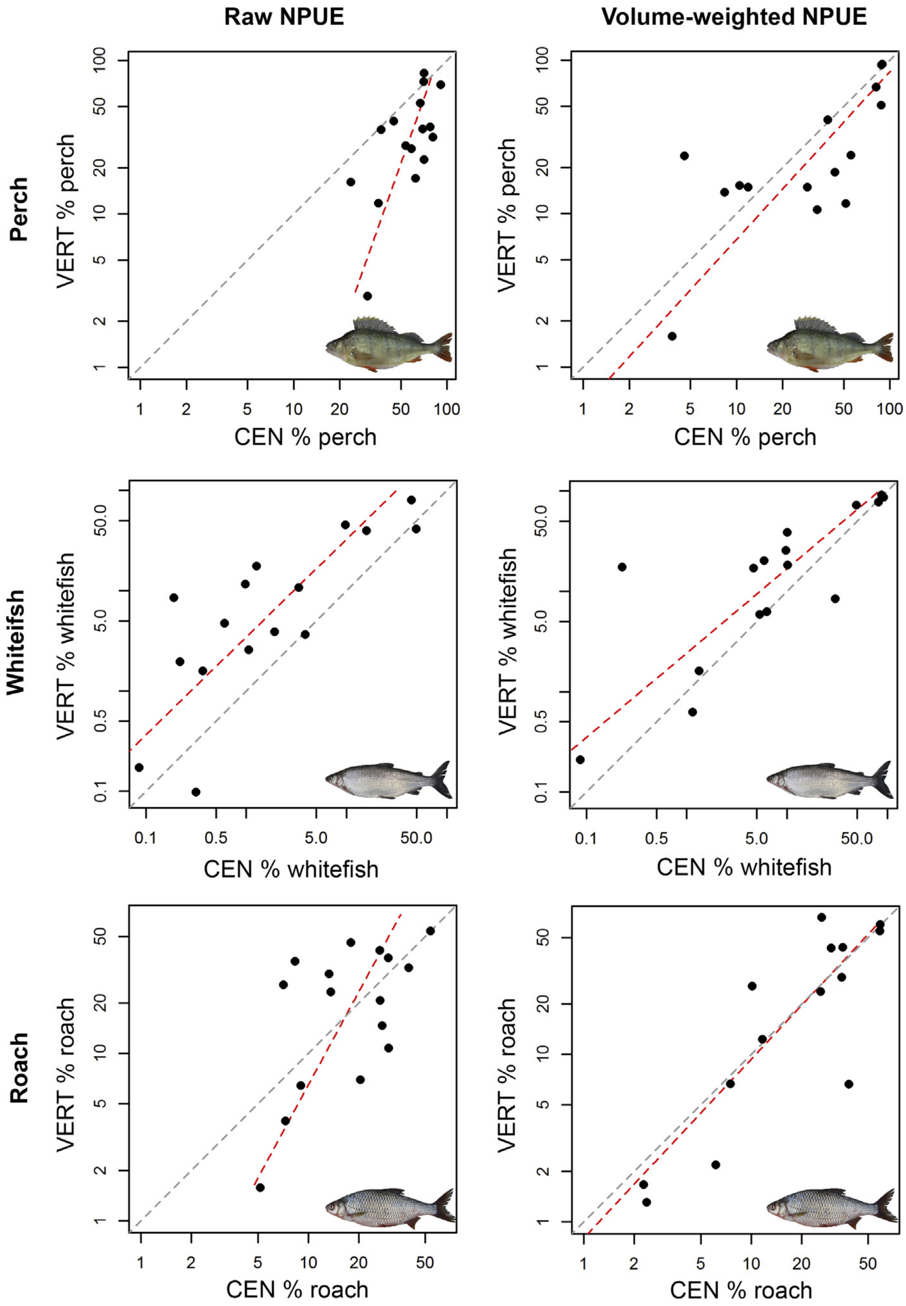

Fig. 4. Volume-weighting generally improved agreement between the protocols in the proportion of abundance (NPUE; number/m^2/14 h) contributed by the common species perch, whitefish and roach.

protocols among lakes in the proportion of whitefish by biomass actually decreased with volume-weighting, probably reflecting the inaccurate estimate of pelagic fish communities throughout the lake that is provided by the CEN protocol. The increased importance of the pelagic community with volume-weighting is further shown by the corresponding decrease in the proportion of perch and roach, predominantly littoral and shallow benthic species, with volume-weighting in the majority of lakes. Deceliere-Vergès and Guillard (2008) also showed a similar reduction of total CPUE when pelagic catches were included in estimates of lake CPUE based on CEN netting data from French lakes. This effect was particularly strong in deep lakes which have a higher proportional volume of less-productive, profundal waters.

The lower CPUE with volume-weighting, caused by the increased influence of pelagic communities, must be considered when interpreting ecological patterns based on volume-weighted data as deeper lakes will naturally have a lower whole-lake catch rate. One option to accommodate this effect is to restrict ecological assessments to within lake typological classes defined by depth (as recommended in the Water Framework Directive; Council of the European Communities, 2000). However, boundaries between typological classes are arbitrary, while the gradient among lake types is continuous and incremental. An alternative is to focus on the residuals of a regression between volume-weighted whole-lake CPUE and lake depth. This would identify which lakes support a higher or lower fish density relative to other lakes for with similar morphometry and could provide a useful foundation for ecological assessments and research across a wide range of lake sizes and depths. A further alternative, particularly applicable to the VERT protocol, is to sum fish biomass or abundance throughout the water column and weight whole-lake catches based on the average depth-integrated catch and the proportional surface area of each depth

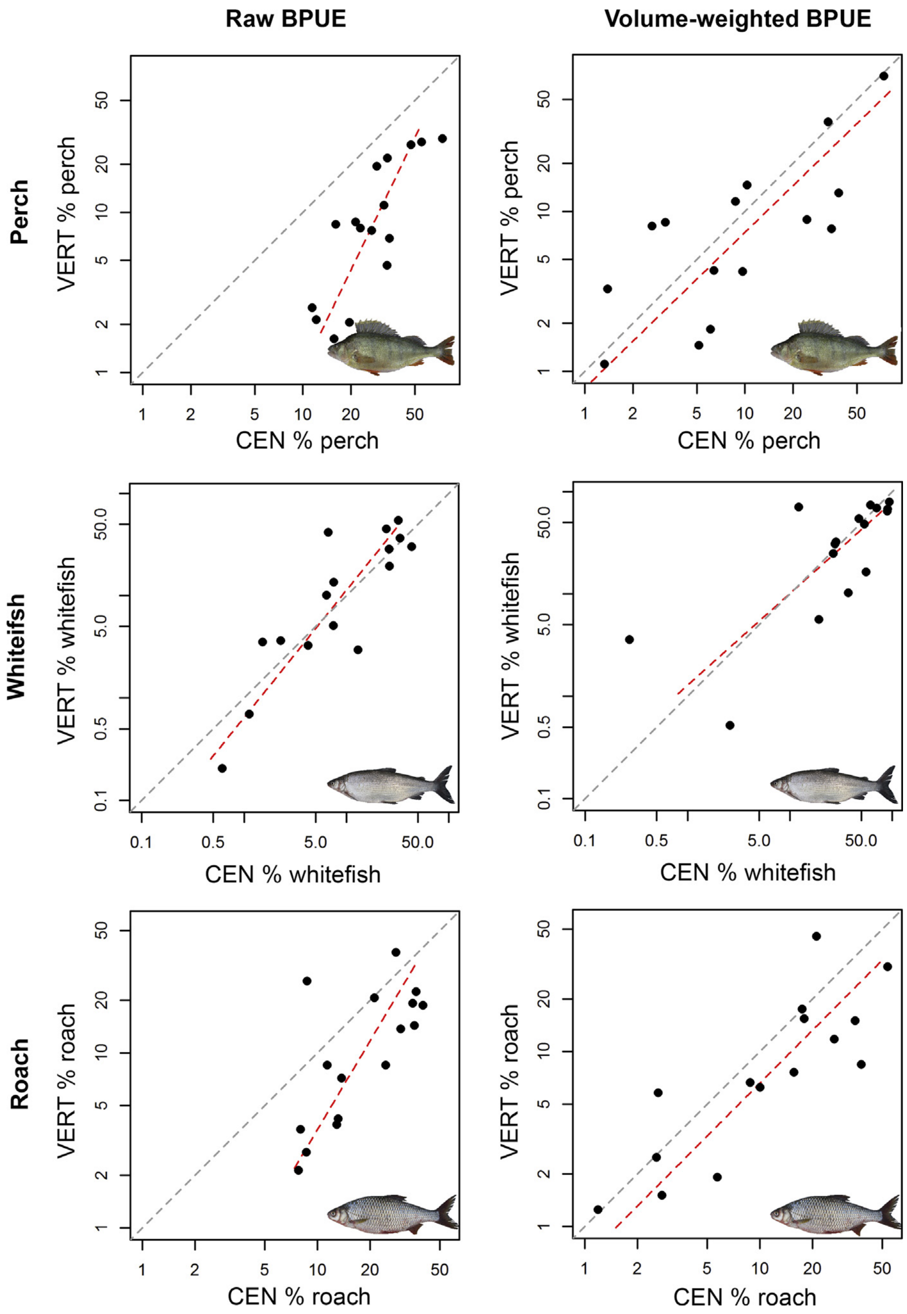

Fig. 5. Volume-weighting generally improved agreement between the protocols in the proportion of biomass (BPUE; g/m^2/14 h) contributed by the common species perch and roach. Volume-weighting actually decreased r^2 between the protocols for the proportion of biomass contributed by whitefish.

strata. The resulting fish weight (or abundance) per area of lake (*e.g.*, kg/ha) could be more relevant for comparisons to fishery catch statistics, which are usually reported in similar units (*e.g.*, Gerdeaux et al., 2006).

4.1. Benefits of volume-weighted whole-lake CPUE

In addition to reducing the influence of the previously-described mismatch between the sampling effort among habitats and their volumetric representation within the lake, several other benefits are associated with calculating volume-weighted estimates of whole-lake fish communities. Volume-weighting can reduce the influence of extreme lake morphometry, such as particularly steep or weakly sloping sides, on estimates of fish communities under sampling protocols that allocate a fixed amount of effort within depth strata. The allocation of net-sampling effort recommended by the CEN protocol was developed to reflect the volumetric contribution of each depth strata in an average lake (Comité Européen de Normalisation, 2005). The CEN protocol recommends that "to achieve a better estimate of the total fish abundance in lakes with extreme morphometry, the volume of each depth stratum should be calculated, and the number of [benthic] gillnets used at each stratum should be distributed in relation to the volume of each stratum" (Comité Européen de Normalisation, 2005, p7). In lakes where this was not adequately achieved in the field, volume-weighting offers the opportunity to adjust the whole-lake catch rate *post-hoc* in order to achieve ecologically representative estimate of whole-lake fish communities. This approach was tested by Lauridsen et al. (2008) in two Danish lakes where they concluded that whole-lake CPUE is highly sensitive to the morphometry of

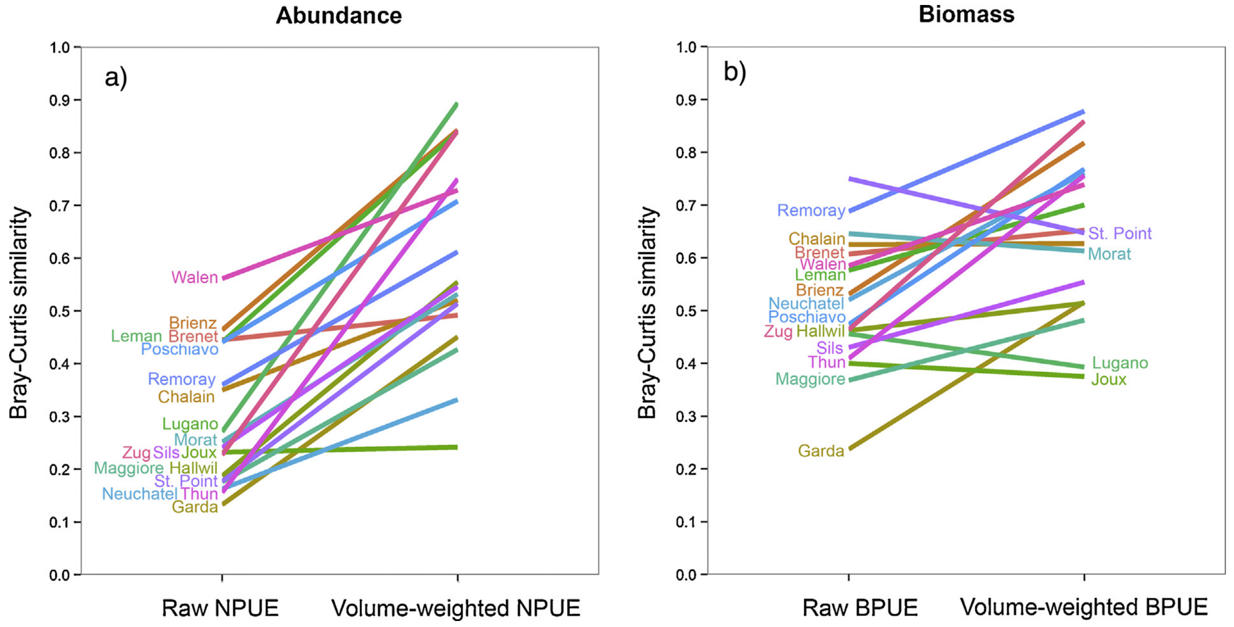

Fig. 6. Volume-weighting significantly improved Bray–Curtis similarity between the fish community sampled by the CEN and VERT protocol in each lake, based on (a) abundance (NPUE; number/m^2/14 h), and (b) biomass (BPUE; g/m^2/14 h). Volume-weighting increased similarity between protocols in lakes listed on the left side of each panel and decreased similarity in those listed on the right.

the lakes. Note however, that allocating sampling effort according to the volumetric contribution of each habitat is not necessarily the best approach to provide a true and precise representation of whole-lake fish communities. Sampling effort should rather be allocated according to the heterogeneity of the fish community with the objective of achieving an accurate estimate of the fish community within each compartment. Volume-weighting can then be applied to adjust whole-lake CPUE based on the catch in each compartment and the volumetric contribution of the compartment. See assumptions and improvements (Section 4.2) for further discussion.

Volume-weighting can also be used to overcome the effects of whether or not an operator elects to set benthic nets deeper than 75 m. The CEN protocol deems that the decision to set nets deeper than 75 m is at the discretion of the operator and should be determined on a case-by-case basis. While some authors have identified that deep-set nets add no information (Achleitner et al., 2012), raw estimates of whole-lake CPUE will be influenced by whether or not these nets are included in the sampling program. Inclusion of nets set deeper than 75 m will almost certainly decrease un-weighted whole-lake estimates of CPUE due to the relatively lower productivity of these waters. In cases where operators choose to not set deep nets because they believe that either no fish live there or that the fish community in compartments below 75 m are the same as those in shallower compartments, these assumptions can be integrated into the calculation of volume-weighted estimates.

Finally, volume-weighting also provides a means by which to reduce the influence of any deviations from the protocol-recommended replication among habitats that commonly arise when conducting large scale field campaigns. For example, since pelagic waters generally contain a lower density of fishes than littoral habitats (*e.g.*, Lauridsen et al., 2008), if in one year (or in one lake) fewer nets are set in pelagic waters than a protocol recommends, the resulting estimate of CPUE for the lake will likely be higher for that year (or lake). Similar effects would follow for estimates of fish community composition. Such problems can be avoided if CPUE is weighted by the volumetric contribution and catch rate of each depth-based compartment.

4.2. *Assumptions and improvements*

A challenge of volume-weighting, and the design of sampling protocols in general, is that one needs to define appropriate boundaries for each habitat or water mass within the lake in order to prescribe sufficient sampling effort to obtain an accurate estimate of the fish community within each compartment. Volume-weighting can then be applied to adjust whole-lake CPUE based on the catch in each compartment and the volumetric contribution of the compartment. The ideal scenario is to delineate such compartments based on observed transitions in the distribution of the fish community. Compartment boundaries should therefore reflect shifts in the density and variability of fish communities, *i.e.*, changes in the amount of fish and the amount of sampling effort required to return a reliable estimate of the fish community within the compartment. Unfortunately, such clear transitions, if observed, are unlikely to remain stable in a lake through time. They are even less likely to be consistent across lakes of a wide range of latitudes, altitudes, depth, area, productivity, anthropogenic influence *etc.*, which is required for adoption in a sampling standard or protocol for broad-scale application. The vertically-oriented whole water column nets used by the VERT protocol overcome this issue on the vertical axis, meaning that sampling effort just needs to be allocated appropriately on the horizontal axis. Volume-weighting the data from the CEN protocol is more open to error in this regard, because the height of the benthic compartments (*i.e.*, the habitat of fish caught in the CEN benthic nets) must be arbitrarily defined. Thus, the habitat transitions used to allocate netting effort for both protocols remain an assumption of these methods should be further tested to determine their influence on the estimates of whole-lake CPUE.

It should also be noted that the different physical characteristics of nets used by the two gillnetting protocols (particularly differences in mesh sizes and net-spacing) mean that, even with volume-weighting, perfect agreement is unlikely. Volume-weighting reduces the influence of disproportionate sampling effort among depth-habitats, however the interaction between fish morphometry and behaviour with the physical characteristics of gillnets must still be acknowledged when interpreting the results of gillnet sampling using either the CEN or VERT protocols.

4.3. Additional pelagic netting effort

Research is ongoing to determine the applicability of the CEN protocol for sampling lakes outside of Nordic countries where it was originally developed (Appelberg 2000; Appelberg et al., 1995). Any modifications to the protocol should be in the form of *additional* netting effort (rather than changes to the core of the protocol) in order to retain comparability to existing monitoring datasets. Ideally, method development and testing should be conducted across lakes varying widely in depth, area, latitude and altitude. Existing studies suggest that modification of the CEN protocol is necessary to accommodate the full variation of lake morphometry and fish communities across Europe. Deceliere-Vergès and Guillard (2008), Deceliere-Vergès et al. (2009) and Specziár et al. (2009), emphasise the need for better representation of fish communities in the pelagic zone for assessments of biological integrity. Diekmann et al. (2005), Jeppesen et al. (2006), Lauridsen et al. (2008) and Achleitner et al. (2012) echo the calls for increased netting effort in pelagic habitats.

We used spatially-replicated pelagic VERT gillnets to investigate the claims of previous authors regarding the need for addition pelagic netting effort. We hoped that this analysis could also provide guidance on how to allocate additional CEN pelagic netting effort. We showed that indeed pelagic fish communities in large lakes are not uniformly distributed. The presence of significant gradients in multiple lakes were associated with distance along the length of the lake and depth of the water column where the net was set. This suggests that spatial replication of pelagic gillnets distributed throughout the lake is essential to capture horizontal heterogeneity in pelagic fish community and produce an accurate estimate of whole-lake catch per unit effort.

5. Conclusions

For research or management requiring an estimate of whole-lake fish communities, volume-weighting estimates of abundance or biomass surveyed according to either CEN or VERT protocols provides an estimate of whole-lake CPUE that is less influenced by an uneven distribution of netting effort throughout the volume of a lake. Volume-weighting is therefore most important where the distribution of sampling effort throughout a lake does not match the volumetric contribution of the different habitats. This is often the case in large and deep lakes, and those with complex morphometry (*i.e.*, where hypsographic curves strongly deviate from those of the lakes where the protocol was developed). When considering volume-weighting for data collected under the CEN protocol, additional spatial replication in the pelagic zone across multiple water depths and along the length of the lake is critical for large and deep lakes in order to accommodate horizontal heterogeneity and provide a more representative estimate of pelagic and therefore whole-lake fish communities.

Acknowledgements

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Appendix A.

Table A1
Distribution of CEN netting effort among depth compartments in each lake. Replication of benthic nets in compartments deeper than 75 m is not shown.

	Number CEN benthic nets per compartment (area each net = 45 m^2)							Number CEN pelagic nets per compartment (area each net = 165 m^2)					
Lake	000–003 m	003–006 m	006–012 m	012–020 m	020–035 m	035–050 m	050–075 m	000–006 m	006–012 m	012–020 m	020–035 m	035–050 m	050–075 m
Brenet	5	3	5	3	–	–	–	2	2	–	–	–	–
Brienz	8	11	10	10	9	6	7	2	2	2	2	2	2
Chalain	7	8	8	9	8	–	–	2	2	2	4	–	–
Garda	19	20	16	18	14	14	10	4	4	4	4	2	2
Hallwil	10	11	9	8	6	6	–	2	2	2	2	2	–
Joux	7	4	9	8	3	–	–	2	2	2	–	–	–
Geneva	19	21	20	19	18	12	18	8	8	8	16	1	16
Lugano	8	10	11	7	11	6	5	4	4	4	4	4	4
Maggiore	20	19	15	20	16	13	11	4	4	2	4	4	4
Morat	10	10	12	9	9	6	–	2	2	2	6	2	–
Neuchatel	20	21	20	20	20	18	12	4	4	4	4	4	4
Poschiavo	8	6	6	6	5	4	8	2	2	2	2	2	2
Remoray	8	7	9	6	2	–	–	2	2	2	–	–	–
Saint-Point	10	10	10	9	5	4	–	2	2	2	2	2	–
Sils	10	8	12	14	10	6	7	2	2	2	2	2	2
Thun	10	11	10	10	10	6	6	2	2	2	2	2	2
Walen	11	9	10	10	11	6	6	2	2	2	2	2	2
Zug	9	9	9	10	10	6	6	2	2	2	2	2	–

Table A2
Distribution of VERT netting effort among depth compartments in each lake. Thresholds between depth compartments are 5 m, 10 m, $0.3Z_{max}$, $0.6Z_{max}$ and $0.9Z_{max}$ (where Z_{max} is the maximum depth of the lake). See Alexander et al. (2015) for more details.

	Number VERT nets per compartment (net area varies)						Area VERT nets per compartment (m^2)					
Lake	Littoral	Sublittoral	Deep sublittoral	Min pelagic	Med pelagic	Max pelagic	Littoral	Sublittoral	Deep sublittoral	Min pelagic	Med pelagic	Max pelagic
Brenet	29	4	–	–	3	1	763	392	–	–	504	224
Brienz	41	3	4	2	0	2	1092	294	1708	3010	0	7070
Chalain	33	3	–	4	4	3	833	252	–	714	1260	1274

Table A2 (*Continued*)

Lake	Number VERT nets per compartment (net area varies)						Area VERT nets per compartment (m^2)					
	Littoral	Sublittoral	Deep sublittoral	Min pelagic	Med pelagic	Max pelagic	Littoral	Sublittoral	Deep sublittoral	Min pelagic	Med pelagic	Max pelagic
Garda	36	3	7	1	1	0	924	252	4566	1454	3992	0
Hallwil	27	3	1	4	5	2	798	210	180	1334	2666	1346
Joux	16	0	–	4	2	2	518	–	–	784	658	854
Geneva	115	7	28	9	4	2	3360	588	15834	15354	13116	8230
Lugano	41	3	11	4	0	1	1043	210	6944	5670	0	4186
Maggiore	39	3	6	2	1	0	1148	252	2988	4860	4116	0
Morat	27	3	–	6	3	3	672	350	–	1904	1568	1820
Neuchatel	56	3	12	4	3	1	1568	308	4942	4900	5712	2002
Poschiavo	35	1	4	4	2	2	1036	70	1008	2250	2010	2338
Remoray	25	4	–	2	5	4	672	378	–	364	1582	1618
Saint-Point	28	4	2	1	5	3	728	364	336	364	2368	1708
Sils	31	4	4	6	2	3	840	350	854	2590	716	2956
Thun	28	1	6	4	2	1	784	126	2492	5574	4830	3122
Walen	16	0	5	4	3	3	490	0	1566	4144	5076	6066
Zug	49	2	7	1	2	1	1344	212	3036	1490	4222	2692

Appendix B.

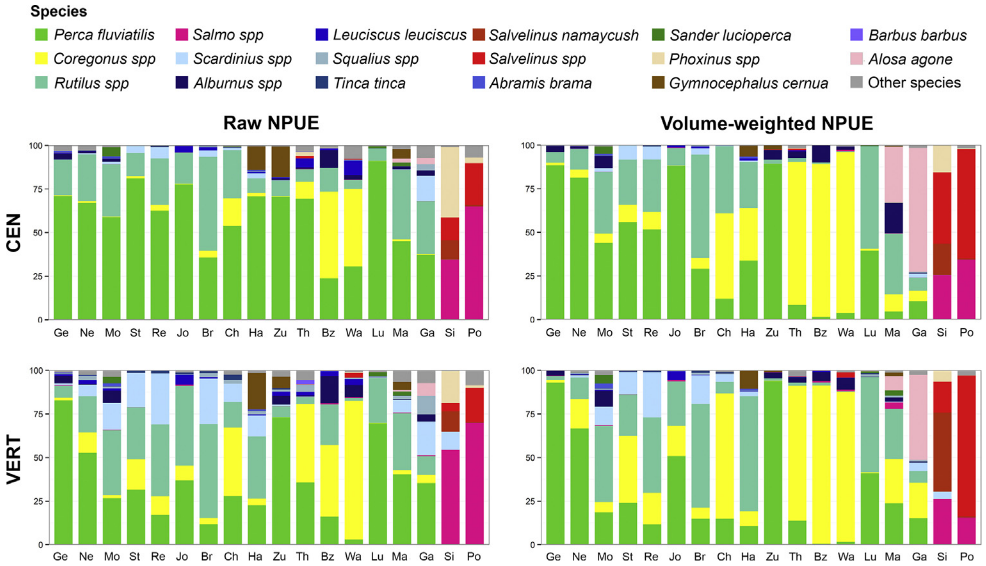

Fig. B1. Abundance-based species composition (NPUE; number fish/m^2/14 h) for raw data and with volume-weighting in each lake.

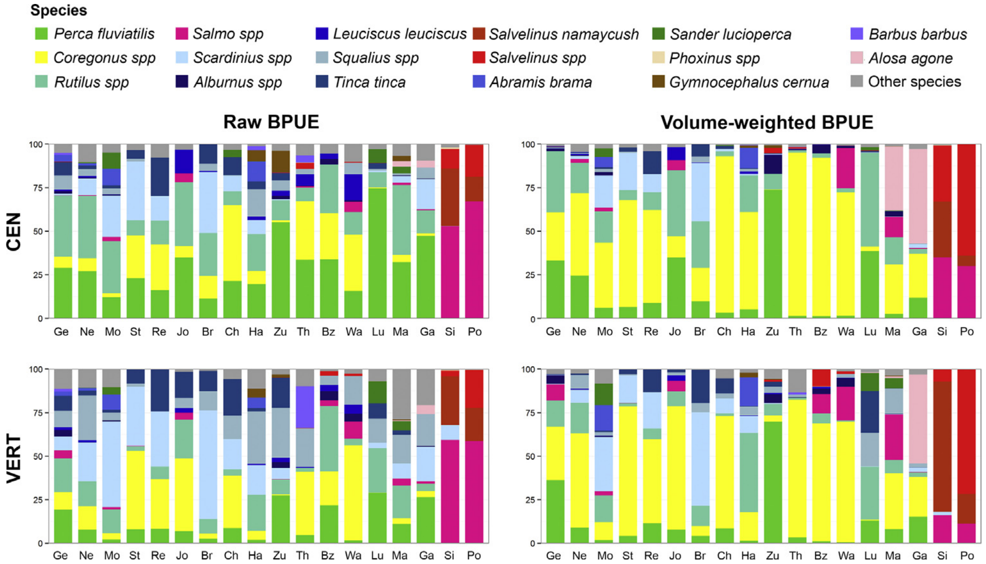

Fig. B2. Biomass-based species composition (BPUE; biomass in g/m^2/14 h) for raw data and with volume-weighting.

Appendix C.

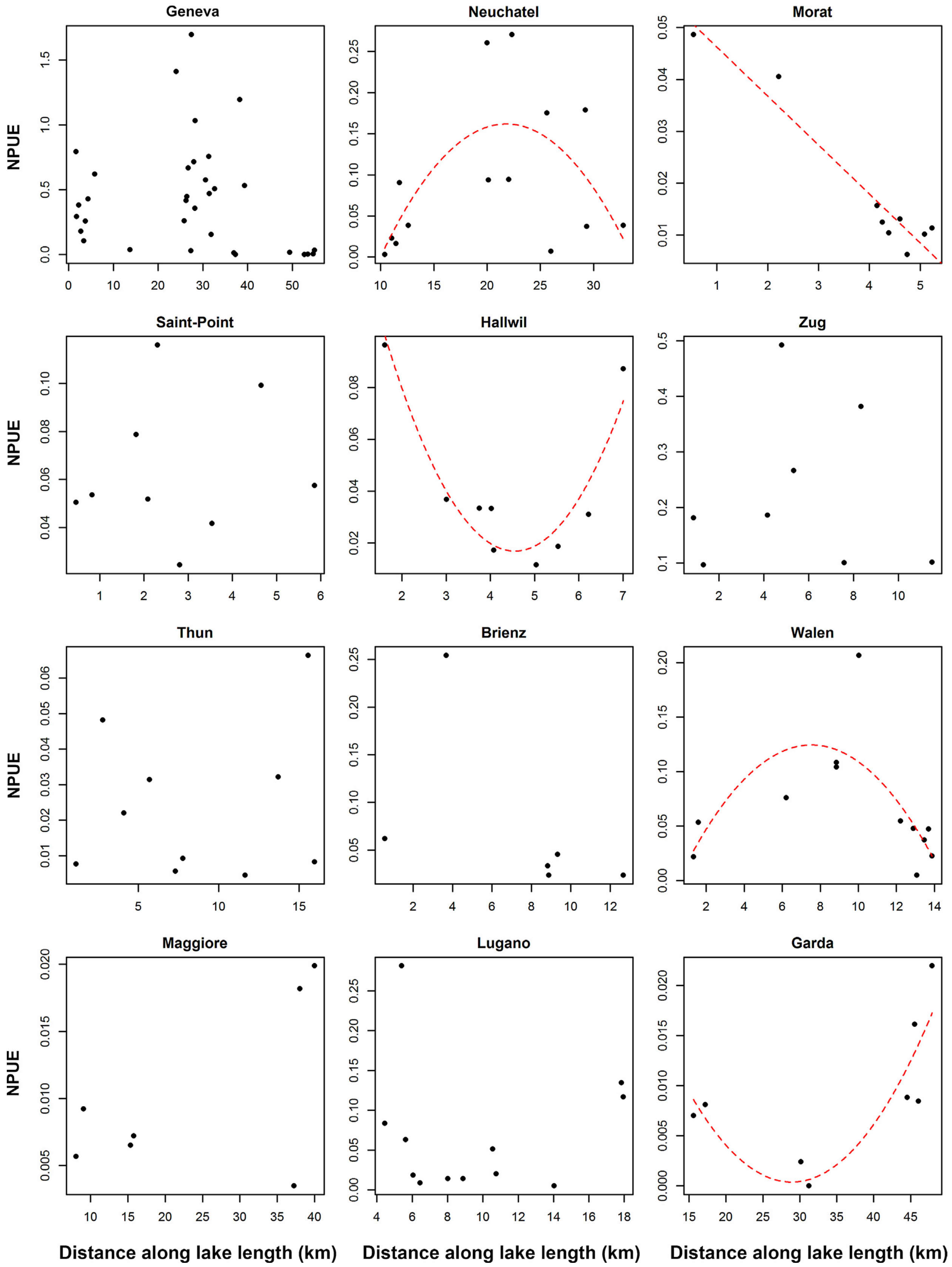

Fig. C1. Relationship between NPUE of limnetic fishes (number/m^2/14 h) and distance along the length of the lake. Plots show fish caught in the upper 20 m section of vertical net batteries (*i.e.*, 7 mesh-nets) set at sites deeper than 23 m (incorporating 3 m buffer to exclude benthic species). Dashed red lines of best fit are shown for lakes with a significant relationship between abundance and distance along the lake. Regression statistics are provided in Table 2.

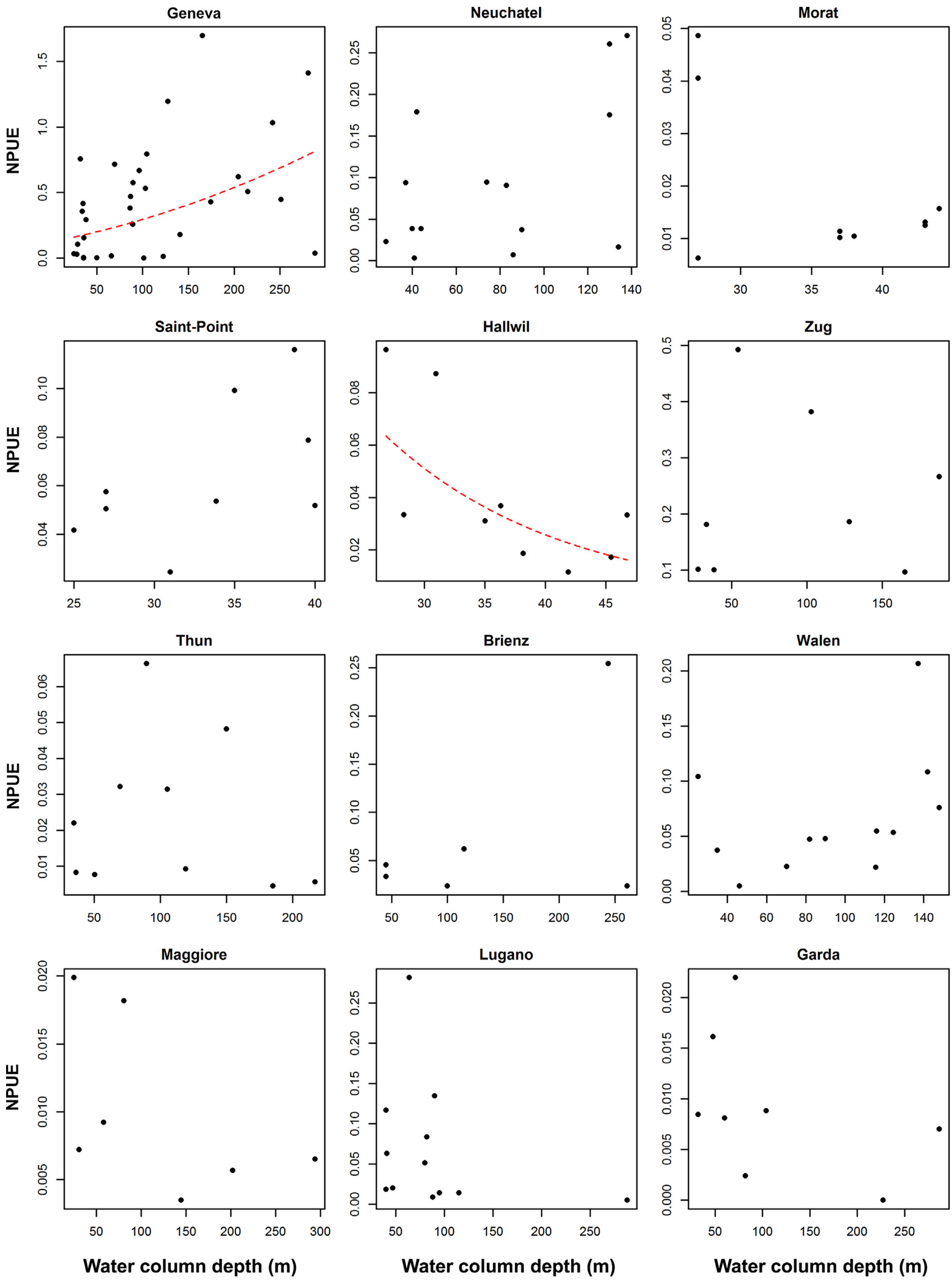

Fig. C2. Relationship between NPUE of limnetic fishes (number/m^2/14 h) and the depth of the water column at net-setting locations in each lake. Plots show fish caught in the upper 20 m section of vertical net batteries (*i.e.*, 7 mesh-nets) set at sites deeper than 23 m (incorporating 3 m buffer to exclude benthic species). Dashed red lines of best fit are shown for lakes with a significant relationship between abundance and the depth of water beneath the net. Regression statistics are provided in Table 2.

Appendix D.

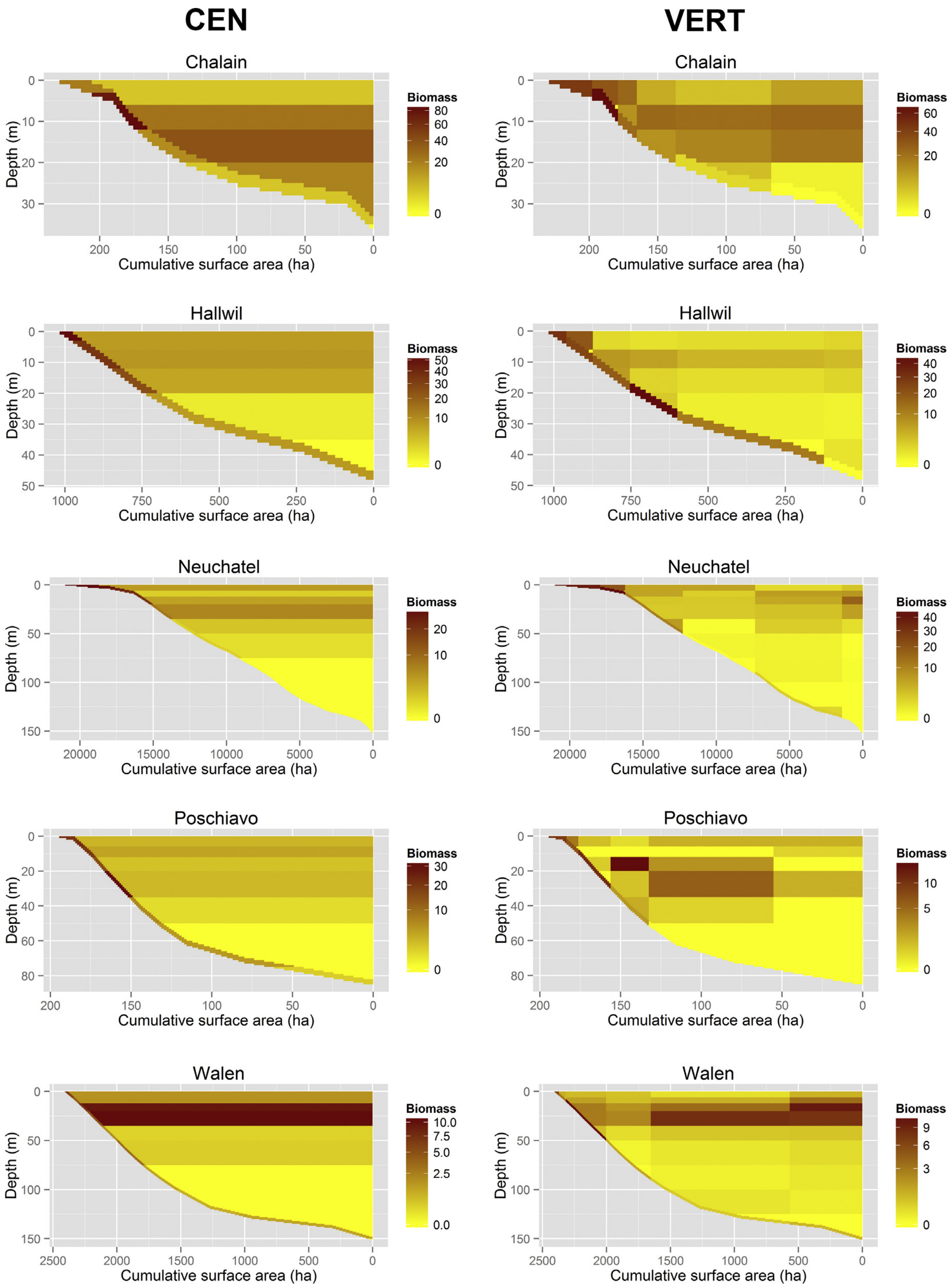

Fig. D1. Heatmaps show the distribution of biomass (BPUE; g/m^2/14 h) throughout a depth-based lake cross-section according to the CEN and VERT protocols. Vertical net data partitioned into CEN depth strata to facilitate comparison. Benthic habitats have an arbitrary height of 3 m. Note that color scale is square root transformed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

References

Achleitner, D., Gassner, H., Luger, M., 2012. Comparison of three standardised fish sampling methods in 14 alpine lakes in Austria. Fish. Manag. Ecol. 19, 352–361.

Alexander, T.J., Vonlanthen, P., Periat, G., Degiorgi, F., Raymond, J.-C., Seehausen, O., 2015. Evaluating gillnetting protocols to characterize lacustrine fish communities. Fish. Res. 161, 320–329.

Appelberg, M., 2000. Swedish standard methods for sampling freshwater fish with multi-mesh gillnets. Fiskeriverket Inf. 1.

Appelberg, M., Berger, H.-M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., Rask, M., 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air Soil Pollut. 85, 401–406.

Argillier, C., Caussé, S., Gevrey, M., Pédron, S., De, B., ortoli, J., Brucet, S., Emmrich, M., Jeppesen, E., Lauridsen, T., Mehner, T., 2013. Development of a fish-based index to assess the eutrophication status of European lakes. Hydrobiologia 704, 193–211.

Backiel, T., Welcomme, R.L., 1980. Guidelines for Sampling Fish in Inland Waters, EIFAC Technical paper 33. FAO, Rome.

Boit, A., Martinez, N.D., Williams, R.J., Gaedke, U., 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. Ecol. Lett. 15, 594–602.

Brucet, S., Pédron, S., Mehner, T., Lauridsen, T.L., Argillier, C., Winfield, I.J., Volta, P., Emmrich, M., Hesthagen, T., Holmgren, K., Benejam, L., Kelly, F., Krause, T., Palm, A., Rask, M., Jeppesen, E., 2013. Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures. Freshw. Biol. 58, 1779–1793.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. Bioscience 35, 634–639.

Comité Européen de Normalisation, 2005. Water Quality—Sampling of Fish with Multi-Mesh Gillnets (CEN 14757). European Committee for Standardization, Brussels.

Council of the European Communities, 2000. Directive 2000/60/EC of the European Parliament and the Council of 23rd October 2000 Establishing a Framework for Community Action in the Field of Water Policy (OJ L 327, 22/12/2000 p. 1–72).

Deceliere-Vergès, C., Argillier, C., Lanoiselée, C., De, B., ortoli, J., Guillard, J., 2009. Stability and precision of the fish metrics obtained using CEN multi-mesh gillnets in natural and artificial lakes in France. Fish. Res. 99, 17–25.

Deceliere-Vergès, C., Guillard, J., 2008. Assessment of the pelagic fish populations using CEN multi-mesh gillnets: consequences for the characterization of the fish communities. Knowl. Manag. Aquat. Ecosyst. 389, 1–16.

Degiorgi, F., 1994. Ètude de l'Organisation Spatiale de l'Ichtyofaune Lacustre-Prospection Multisaisonnière de 6 Plan d'Eau de l'Est de la France à l'Aide de Filets Verticaux. Université de Besançon Besançon, France.

Degiorgi, F., Grandmottet, J.P., Chanteloube, P., Pardon, C., Rousselet, A., Suat, J.F., Vandelle, J.P., 1993a. Relations entre la topographie aquatique et l'organisation spatiale de l'ichtyofaune lacustre: définition des modalités spatiales d'une stratégie de prélèvement reproductible. Bull. Fr. Pisc. 329, 199–220.

Degiorgi, F., Grandmottet, P.J., Raymond, J.C., Rivier, J., 2001. Échantillonnage de l'ichtyofaune lacustre: engins passifs et protocole de prospection. In: Gerdeaux, D. (Ed.), Gestion Piscicole des Grands Plans d'Eau. Quae, Paris, pp. 151–182.

Degiorgi, F., Guillard, J., Grandmottet, P.J., Gerdeaux, D., 1993b. Les techniques d'étude de l'ichtyofaune lacustre utilisée en France: bilan et perspectives. Hydroécol. Appl. 5, 27–42.

Diekmann, M., Brämick, U., Lemcke, R., Mehner, T., 2005. Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities. J. Appl. Ecol. 42, 901–909.

Emmrich, M., Helland, I.P., Busch, S., Schiller, S., Mehner, T., 2010. Hydroacoustic estimates of fish densities in comparison with stratified pelagic trawl sampling in two deep, coregonid-dominated lakes. Fish. Res. 105, 178–186.

Gerdeaux, D., Anneville, O., Hefti, D., 2006. Fishery changes during re-oligotrophication in 11 peri-alpine Swiss and French lakes over the past 30 years. Acta Oecol.-Int. J. Ecol. 30, 161–167.

Harris, J.H., 1995. The use of fish in ecological assessments. Aust. J. Ecol. 20, 65–80.

Holmlund, C.M., Hammer, M., 1999. Ecosystem services generated by fish populations. Ecol. Econ. 29, 253–268.

Ibelings, B.W., Portielje, R., Lammens, E., Noordhuis, R., van, den, B., erg, M.S., Joosse, W., Meijer, M.L., 2007. Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. Ecosystems 10, 4–16.

Jeppesen, E., Pekcan-Hekim, Z., Lauridsen, T., Søndergaard, M., Jensen, J., 2006. Habitat distribution of fish in late summer: changes along a nutrient gradient in Danish lakes. Ecol. Freshw. Fish 15, 180–190.

Karr, J.R., 1981. Assessment of biotic integrity using fish communities. Fisheries 6, 21–27.

Kubečka, J., Hohausová, E., Matěna, J., Peterka, J., Amarasinghe, U.S., Bonar, S.A., Hateley, J., Hickley, P., Suuronen, P., Tereschenko, V., Welcomme, R., Winfield, I.J., 2009. The true picture of a lake or reservoir fish stock: a review of needs and progress. Fish. Res. 96 (1), 1–5.

Launois, L., Veslot, J., Irz, P., Argillier, C., 2011. Selecting fish-based metrics responding to human pressures in French natural lakes and reservoirs: towards the development of a fish-based index (FBI) for French lakes. Ecol. Freshw. Fish 20, 120–132.

Lauridsen, T.L., Landkildehus, F., Jeppesen, E., Jørgensen, T.B., Søndergaard, M., 2008. A comparison of methods for calculating Catch Per Unit Effort (CPUE) of gill net catches in lakes. Fish. Res. 93, 204–211.

Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam.

Lyche-Solheim, A., Feld, C., Birk, S., Phillips, G., Carvalho, L., Morabito, G., Mischke, U., Willby, N., Søndergaard, M., Hellsten, S., Kolada, A., Mjelde, M., Böhmer, J., Miler, O., Pusch, M., Argillier, C., Jeppesen, E., Lauridsen, T., Poikane, S., 2013. Ecological status assessment of European lakes: a comparison of metrics for phytoplankton, macrophytes, benthic invertebrates and fish. Hydrobiologia 704, 57–74.

Mehner, T., Diekmann, M., Brämick, U., Lemcke, R., 2005. Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. Freshw. Biol. 50, 70–85.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. 2013. vegan: Community Ecology Package. R Package Version 20-10.

Olin, M., Malinen, T., Ruuhijärvi, J., 2009. Gillnet catch in estimating the density and structure of fish community—comparison of gillnet and trawl samples in a eutrophic lake. Fish. Res. 96, 88–94.

Prchalová, M., Kubečka, J., Říha, M., Litvín, R., Čech, M., Frouzová, J., Hladík, M., Hohausová, E., Peterka, J., Vašek, M., 2008. Overestimation of percid fishes (Percidae) in gillnet sampling. Fish. Res. 91, 79–87.

Prchalová, M., Kubečka, J., Říha, M., Mrkvička, T., Vašek, M., Jůza, T., Kratochvíl, M., Peterka, J., Draštík, V., Křížek, J., 2009. Size selectivity of standardized multimesh gillnets in sampling coarse European species. Fish. Res. 96, 51–57.

Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Specziár, A., Erős, T., György, Á.I., Tatrai, I., Bíró, P., 2009. A comparison between the benthic Nordic gillnet and whole water column gillnet for characterizing fish assemblages in the shallow Lake Balaton. Ann. Limnol.-Int. J. Limnol. 45, 171–180.

Warton, D.I., Duursma, R.A., Falster, D.S., Taskinen, S., 2012. Smatr 3—an R package for estimation and inference about allometric lines. Methods Ecol. Evol. 3, 257–259.