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Taylor's power law and fixed-precision sampling: application to abundance of fish sampled by gillnets in an African lake

Meng Xu, Jeppe Kolding, and Joel E. Cohen

Abstract: Taylor's power law (TPL) describes the variance of population abundance as a power-law function of the mean abundance for a single or a group of species. Using consistently sampled long-term (1958–2001) multimesh capture data of Lake Kariba in Africa, we showed that TPL robustly described the relationship between the temporal mean and the temporal variance of the captured fish assemblage abundance (regardless of species), separately when abundance was measured by numbers of individuals and by aggregate weight. The strong correlation between the mean of abundance and the variance of abundance was not altered after adding other abiotic or biotic variables into the TPL model. We analytically connected the parameters of TPL when abundance was measured separately by the aggregate weight and by the aggregate number, using a weight–number scaling relationship. We utilized TPL to find the number of samples required for fixed-precision sampling and compared the number of samples when sampling was performed with a single gillnet mesh size and with multiple mesh sizes. These results facilitate optimizing the sampling design to estimate fish assemblage abundance with specified precision, as needed in stock management and conservation.

Résumé : La loi de puissance de Taylor (LPT) décrit la variance de l'abondance d'une population comme étant une fonction de puissance de l'abondance moyenne pour une espèce ou un groupe d'espèces. En utilisant des données de capture sur une longue période (1958–2001) obtenues de manière cohérente avec des filets de mailles variées dans le lac Kariba en Afrique, nous avons démontré que la LPT décrit de manière robuste la relation entre la moyenne temporelle et la variance temporelle de l'abondance de l'assemblage de poissons capturés (peu importe l'espèce), que l'abondance soit mesurée sur la base du nombre d'individus ou de la masse cumulative. La forte corrélation entre la moyenne de l'abondance et la variance de l'abondance ne changeait pas après l'intégration d'autres variables abiotiques ou biotiques dans le modèle de LPT. Nous avons relié de manière analytique les paramètres de la LPT pour l'abondance mesurée sur la base de la masse cumulative et sur la base du nombre d'individus, en utilisant une relation de mise à l'échelle masse–nombre. Nous avons utilisé la LPT pour déterminer le nombre d'échantillons requis pour l'échantillonnage à précision fixe et comparé le nombre d'échantillons quand l'échantillonnage était réalisé avec des filets de taille de maille unique et avec des filets de différentes tailles de maille. Ces résultats facilitent l'optimisation des plans d'échantillonnage pour estimer l'abondance d'assemblages de poissons à une précision prédéterminée à des fins de gestion et de conservation des stocks. [Traduit par la Rédaction]

Introduction

Quantifying fluctuations in population abundance is important for the estimation, exploitation, and regulation of fish stocks. For example, different fishing strategies (e.g., minimum size versus balanced harvesting) affect the variability of harvested marine fish stocks differently (Hsieh et al. 2006; Anderson et al. 2008; Cohen et al. 2012; Law et al. 2012, 2015; Fujiwara and Cohen 2014). Sampling is expensive and determining the desired number of samples in fixed-precision sampling of fish stocks relies on accurate description of fluctuation scaling of abundance (Mouillot et al. 1999).

Measuring the distribution and fluctuation of fish abundance in space and time presents theoretical and practical challenges to ecologists and fishery managers. Representative sampling depends on available fishing methods, which have varying selectivity. For example, in small water bodies, such as lakes and reservoirs, sampling is usually carried out with stationary gillnets. Gillnet selectivity allows small and large fishes to escape, so gillnet samples from a single mesh size misrepresent the size composition of fish communities. To reduce this selection bias, multiple mesh sizes have been implemented experimentally and operationally (European Standard 2005; Gray et al. 2005; Prchalová et al. 2009; Emmrich et al. 2012). The temporal fluctuation of fish sample abundance from multimesh gillnets has not been thoroughly investigated.

Traditionally, researchers used the coefficient of variation (CV, i.e., the temporal standard deviation divided by the temporal mean) of a time series to quantify the temporal fluctuation of fish species abundance (Mehner and Schulz 2002; Hsieh et al. 2006; Anderson et al. 2008). Recently, Fujiwara and Cohen (2014) argued that CV was "not appropriate to measure fish population instability", since the CV varies for different values of the mean abundance. They proposed using the mean–variance scaling of population density to describe fish abundance fluctuations.

Using fish data from long-term sampling with multimesh gillnets in Lake Kariba, we test and confirm a mean–variance scaling pattern of sampled fish assemblage abundance, Taylor's power law (TPL; Taylor 1961), at various levels of sampling years, mesh sizes, species counts, and collectively (definitions of mean and variance are given in Materials and methods). TPL describes the sample variance of population abundance of a single or a group of species as approx-

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imately a power-law function of the corresponding sample mean of population abundance: variance = $a_1(\text{mean})^{b_1}$. Equivalently,

$$\text{(1)} \qquad \log(\text{variance}) = \log a_1 + b_1 \cdot \log(\text{mean})$$

where $a_1 > 0$ and b_1 are parameters estimated from the data. The equality signs in eq. 1 and the power law are approximate, since sampling variability will affect the sample mean and the sample variance.

TPL has many forms. A temporal TPL depicts the power-law relationship between the temporal variance of species abundance and the temporal mean abundance (where mean and variance are calculated over multiple time periods) (Taylor and Woiwod 1980). A spatial TPL examines the relationship between the spatial mean and the spatial variance of species abundance (where mean and variance are calculated over multiple locations; Taylor et al. 1980). TPL has been confirmed for thousands of biological taxa and many nonbiological quantities (Eisler et al. 2008). TPL's slope b_1 falls between 1 and 2 often but not always in other empirical studies (Anderson et al. 1982; Keil et al. 2010) and here. Extensive empirical support (Taylor et al. 1978, 1980, 1983; Taylor and Woiwod 1980, 1982; Taylor 1984) made TPL a "law" in ecology.

In fisheries science, Elliott (1986) studied TPL for migratory trout populations at different age groups and argued that "TPL parameters were not only species specific but also life-stage specific." Baroudy and Elliott (1993) confirmed TPL using acoustic estimates of pelagic fishes. Both studies focused on the spatial TPL. Cohen et al. (2012) and Fujiwara and Cohen (2014) found support for TPL in theoretical fisheries models under specific, but not universal, conditions. Further empirical investigation of fisheries is required to illuminate when the temporal TPL is, or is not, valid in nature.

In addition to its theoretical importance in quantifying fluctuations of ecological populations, TPL aids fixed-precision sampling design, such as in pest control for agricultural crops (Overholt et al. 1994) and fish stock sampling (Mouillot et al. 1999). In summary, when TPL (eq. 1) holds, the number N of samples necessary to obtain a desired precision C is reached when the empirical plot of $\log(T_N)$ (logarithmic cumulative abundance from N samples) against $\log(N)$ (logarithmic number of samples; N = 1, 2, 3, …) intersects with the stopping line:

$$\text{(2)} \qquad \log T_N = \frac{\log\left(\dfrac{C^2}{a_1}\right)}{b_1 - 2} + \frac{b_1 - 1}{b_1 - 2} \times \log N$$

Appendix A gives a detailed derivation of eq. 2 and explains its use.

Here we formulate and test a temporal TPL between the annual mean and the annual variance (calculated over multiple night settings in a year) of aggregate fish sample assemblage abundance (measured in number or weight of individuals, regardless of species) caught using multiple mesh sizes in a gillnet sampling over four decades. The annual means and variances were fitted across various variables to construct different versions of temporal TPL, including a temporal–hierarchical TPL, where the annual variance was supposed to be a power-law function of the annual mean across years. To our knowledge this work is the first empirical analysis of the temporal–hierarchical TPL of fish samples at multiple time scales.

Based on the Lake Kariba sampling data, the specific aims of this work were to study (*i*) the empirical validity of a temporal TPL under various environments classified by abiotic and biotic factors (i.e., years, mesh sizes, and species counts); (*ii*) the effect of these abiotic and biotic variables on the form and parameters of TPL; (*iii*) the analytic connection between TPL parameters when different measures of abundance were used; and (*iv*) the use of TPL and the implications of single or multiple gillnet mesh sizes for the efficiency of a fixed-precision sampling plan.

Materials and methods

Site description

Lake Kariba on the Zambezi River between Zambia and Zimbabwe (16°28′S to 18°04′S, 26°42′E to 29°03′E) is the world's largest human-made hydroelectric reservoir by volume (180 km³). Water filling of the reservoir started in December 1958 and completed in September 1963 (Kolding et al. 2003). Lake Kariba has a surface area of 5580 km² and is divided into five basins (refer to online Supplementary Fig. S1[1]). In addition to hydropower, it supports an important fishery for the local community and has become a tourist attraction for angling and leisure.

Since the impoundment, fish species diversity has gradually increased in the lake from natural fish invasion and human introductions (Karenge and Kolding 1995; Kolding et al. 2003; Zengeya and Marshall 2008). In 1976, only 27 species were regularly found in basin 5 (Sanyati basin, closest to the dam wall) using a poisoning sampling program (Mitchell 1976). Presently 50 different fish species have been observed in the lake, five of which are introduced, but seven of the species have been reported just once (Kolding et al. 2003). Several species previously thought to be restricted to the upper stream of the Zambezi River, including *Sargochromis giardi*, *Marcusenius macrolepidotus*, *Labeo cylindricus*, and *Barbus poechii*, were spotted in Lake Kariba as early as the 1960s. Among the introduced species are *Limnothrissa miodon*, *Oreochromis niloticus*, and *Oreochromis macrochir*. While the two former are important parts of the present fishery, *Oreochromis macrochir* is only found occasionally (Kolding et al. 2003; Zengeya and Marshall 2008).

Sampling method

In the long-term gillnet sampling data analyzed here, fishes were caught from 1958 to 2001 at the Lakeside station of basin 5 (Supplementary Fig. S1[1]) with a consistent gillnet sampling design. Multiple panels of multifilament gillnets with height 2 m and hanging ratio 0.5 were used for sampling. Each panel (mostly 45.7 m long, but with some variation in length) was of a unique mesh size ranging from 25 to 200 mm. During the earlier years, the sampling was carried out sporadically (Kenmuir 1984), and no sampling was performed in 1959. Since 1976, gillnet fishing was conducted almost weekly except in 1981, when no sampling was performed. On a sampling date, a fleet carrying a total of 12 panels of unique gillnet mesh sizes (rarely were multiple panels of a single mesh size used on the same date) set the nets at 1500 and retrieved the nets at 0800 on the next day. For each individual fish caught, its species, fork length, weight, sex, and gonadal maturity status were recorded. Small fish species in large numbers were not always individually recorded, and therefore their weights were occasionally missing from the data set. No single cut-off value was set to determine whether to weigh a fish or not.

Data filtering, analysis, and deposition

For consistency, we selected and analyzed data with uniform catching effort (45.7 m panel length) using bottom-set and multifilament net of 12 distinct mesh sizes from 38 to 178 mm (with a constant increment of about 12.5 mm) at the Lakeside station of basin 5 (Kolding et al. 2003). We defined a setting as the single usage of a panel of a unique mesh size on a given sampling date. The aggregate number and the aggregate weight of all fish (regardless of species) caught within each setting were used to mea-

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0009.

sure fish assemblage abundance. All weights, whether of individual fish or aggregated fish, are reported in grams (g). In our analysis, the aggregate fish abundance (in absolute weight or absolute number, not in relative percentages) of a setting is the smallest unit of the abundance variable. The total number and the total weight were attributes of the setting, not of individual fish. The increment of mesh size was small enough to treat mesh size as a continuous variable, so the sampling theory of simple random sampling (applied to settings) was appropriate for analysis, rather than the sampling theory of clustered random sampling applicable to individual fishes (Nelson 2014).

Settings that caught no fish were kept in the analysis to account for fishing effort, and the corresponding fish abundance, under either measure, was equal to 0. In the data, 1585 individual fishes did not have weight records. These fishes were kept in the analysis when "number" was used to measure fish abundance and omitted when "weight" was used to measure fish abundance. 41 unidentified (species unknown) individual fishes were excluded from both the descriptive statistics (Supplementary Table S1[1]) and the analysis of TPL.

In summary, we started with 229 907 records of individual fishes captured by gillnets of 16 mesh sizes. Each record contained the following fields: station, species, fishing gear, mesh size (mm), setting type, number of fish (1 or 0), length of individual fish (cm), weight of individual fish (g), sex, and gonadal stage. We excluded 62 858 records from the original data because of the selection criteria and the exclusion of unidentified fish. This data filtering left us with exactly 167 049 records from 12 mesh sizes. A summary of these records is available in Supplementary Table S1[1]. Our analysis is based on the fish caught in gillnets, not on the entire fish populations in the lake. We did not correct for gillnet selectivity to avoid introducing additional bias in the data.

Testing TPL

The temporal mean and the temporal variance of sampled fish abundance were calculated across all settings of one mesh size in a given year, using total number and total weight per setting separately. A mean measures the average abundance of fish caught per setting in a given year using a unique mesh size. A variance measures the intersetting variation of fish abundance in a given year using a unique mesh size. Therefore, a unique combination of mesh size and year corresponded to one pair of mean and variance. If any combination of mesh size and year contained fewer than 15 settings, the corresponding mean and variance were not calculated, and that combination was excluded from our analysis (Taylor et al. 1988). To generate finite log(mean) and finite log(variance) for the testing of TPL, only positive-valued means and positive-valued variances were used in the analysis. The number of fish species was counted within each combination of year and mesh size used for analysis.

To test TPL, we plotted log(variance) as a function of log(mean) and fitted a least-squares linear regression (eq. 1) and a least-squares quadratic regression (Taylor et al. 1978)

$$\text{(3)}\qquad \log(\text{variance of abundance}) = \log a_2 + b_2 \log(\text{mean of abundance}) + c_2\,[\log(\text{mean of abundance})]^2$$

using number and weight separately as abundance measure. When the null hypothesis that $c_2 = 0$ was rejected because the 95% confidence interval (CI) of c_2 did not contain 0, then the log(mean)–log(variance) relationship was significantly nonlinear ($P < 0.05$). When the null hypothesis that $c_2 = 0$ was not rejected, and when the 95% CI of b_1 did not contain 0, then TPL (eq. 1) was not rejected as a description of the mean–variance relationship for sampled fish abundance under the corresponding measure. We judged it unnecessary to fit terms of higher order than quadratic because visual inspection of the scatterplots gave no hint of a cubic or other nonlinear relationship (Figs. 1–3, Supplementary Fig. S3[1]).

We first tested TPL using eqs. 1 and 3 for log(mean)–log(variance) pairs from all combinations of years and mesh sizes, then repeated the tests separately at each level of the sampling year, mesh size, and species count (number of species in the sample or species richness). For example, in year 1962, all pairs of mean and variance from 1962 (across all mesh sizes) were plotted on the log–log scale and fitted by the regressions; for mesh size 178 mm, all pairs of mean and variance with mesh size 178 mm (across years) were plotted on the log–log scale and fitted by the regressions; when species count was 10, all pairs of mean and variance from combinations of years and mesh sizes with 10 species were plotted on the log–log scale and fitted by the regressions. If the number of pairs of finite log(mean) and finite log(variance) was fewer than five at any level of a factor, the corresponding level was not tested against TPL (Taylor et al. 1988). Since TPL was tested at each level of a single variable simultaneously, we adjusted the significance level of individual regression using the Bonferroni method (Bonferroni 1936) to avoid multiple comparison problems.

To compare the goodness of fit with TPL between multimesh sampling and single-mesh sampling, when TPL was not rejected, we used the Welch two-sample *t* test of unequal variance (Welch 1947) to compare the goodness-of-fit statistics (i.e., adjusted coefficient of determination (adj. R^2) and root mean square error (RMSE)) from two sets of linear regressions by year (across multiple mesh sizes) and by mesh size (for a single mesh size, across years).

After TPL was confirmed for fish abundance measured by number and by weight separately, we studied the connection between the parameters of TPL estimated using these two measures. We showed that given a weight–number allometry of aggregate fish abundance (equivalent to "density–mass allometry"; Damuth 1987), the slope and intercept of TPL estimated by weight can be approximated analytically from those estimated using numbers of fishes through the delta method (Oehlert 1992). We found the analytic formula that connects TPL parameters under different measures and confirmed it against aggregate abundance for each mesh size in the Results. A detailed derivation of the formula is in Appendix A.

In this work, log = $\log_{10}$, significance level $\alpha = 0.05$ unless specified otherwise, and P denotes the P value of a hypothesis test. Every CI here is a 95% CI calculated assuming a normal distribution resulting from the central limit theorem. Where appropriate, Bonferroni corrections are applied to multiple comparisons.

Testing robustness of TPL

We examined the influences of year, mesh size, and species count on the temporal fluctuation of abundance and TPL using multiple linear regressions (MLRs). MLRs added to eq. 1 the covariates of year, mesh size, and species count and possibly their interactions with or without log(mean), depending on the complexity of the model. We built all possible 36 MLRs, including seven additive-effect models, 21 two-way interaction models, seven three-way interaction models, and one four-way interaction (or saturated) model. For each abundance measure (number or weight), we fitted the same 36 models when mesh size was treated as a numerical variable and again as a categorical variable. Numerical mesh size was centered at its mean. We listed the top ten MLRs ranked by their Akaike information criterion (AIC) and calculated the point and interval estimates of the intercept and coefficient of log(mean) in each model (Supplementary Tables S5–S8[1]). Year and species count were numerical variables, and year was centered at its mean. For each abundance measure, we compared the parameter estimates of TPL with the corresponding parameter estimates of MLRs when mesh size was treated as numerical and as categorical separately.

Linear and quadratic regressions, MLRs, and the model statistics (including the coefficient of determination R^2, adj. R^2, and AIC)

Fig. 1. Scatterplot matrices showing bivariate relationships among five variables: log(mean), log(variance), species count, mesh size, and year. Abundance was quantified by (*a*) number and (*b*) weight (g). Except for 1962, every year from 1958 to 1970 and 1981 was eliminated from the mean–variance calculations and therefore was missing from the figure because of limited settings (<15) or absence of sampling activity. Axes are labeled in the diagonal boxes that run from the lower left corner to the upper right corner of each panel. For example, in panel (*a*), in the box in the first row, second column, the horizontal axis is labeled “Mesh” and the vertical axis is labeled “SpeciesCount”. Labels “LogMeanNum”, “LogMeanWgt”, “LogVarNum”, and “LogVarWgt” represent log(mean of aggregate number), log(mean of aggregate weight), log(variance of aggregate number), and log(variance of aggregate weight), respectively.

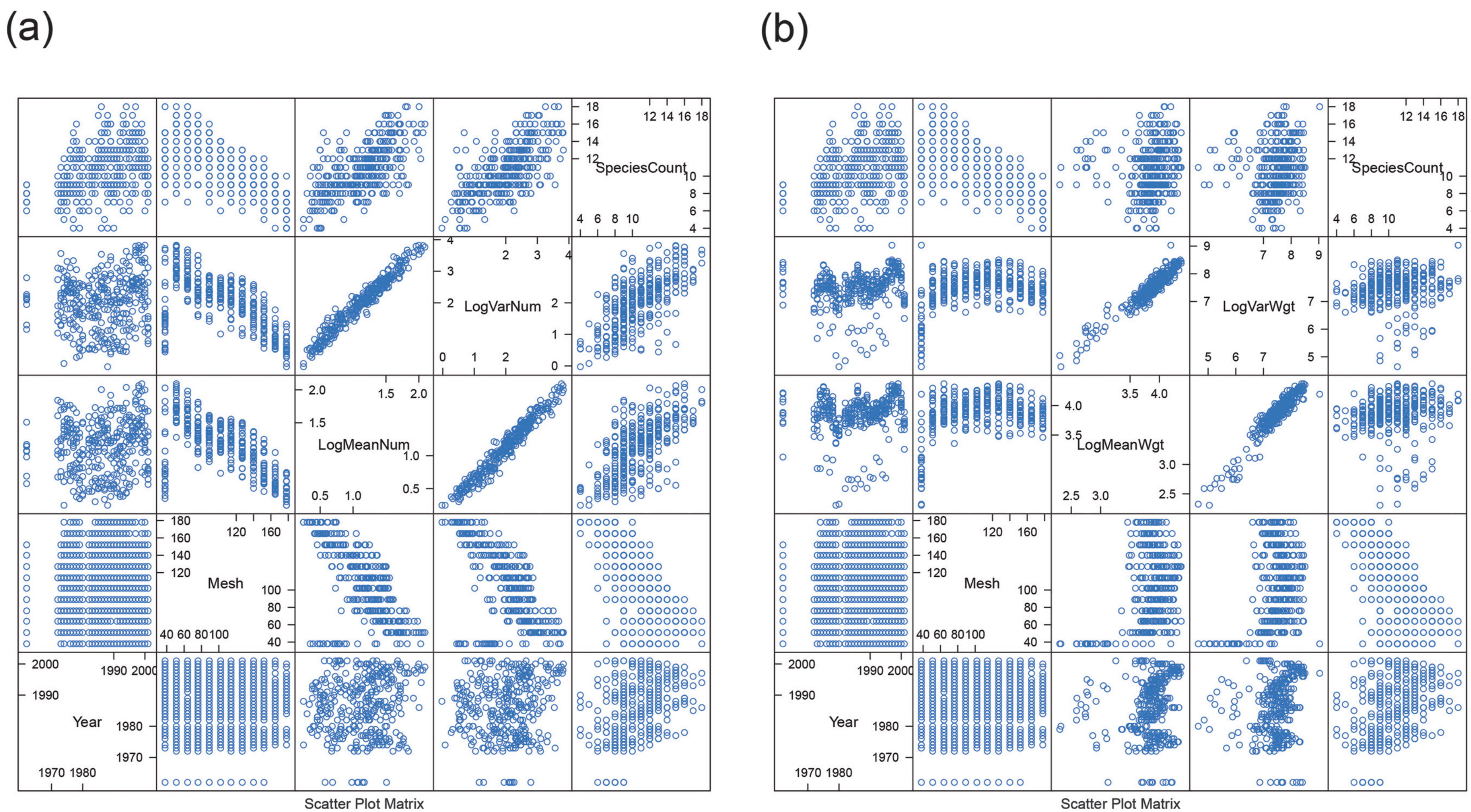

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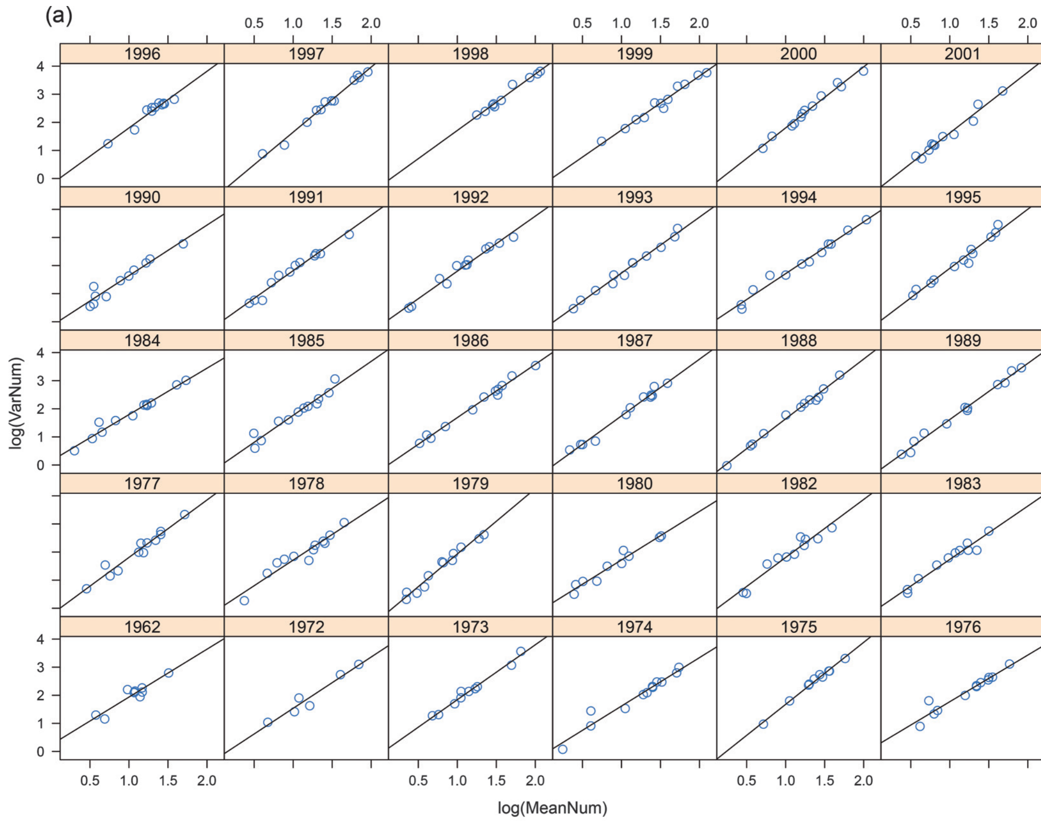
Fig. 2. Log(variance) as a function of log(mean) for each year (across mesh sizes (mm)) when fish abundance was measured by (*a*) number and (*b*) weight (g) separately. Each circle represents a pair of log(mean) and log(variance) from a unique combination of year and mesh size (mm). Solid lines are the least-squares linear regression lines fitted in each year. Axis labels are defined as in Fig. 1. In each panel, the scales of measurement alternate, for the vertical axes, between the left and right sides, and for the horizontal axes, between the top and the bottom.



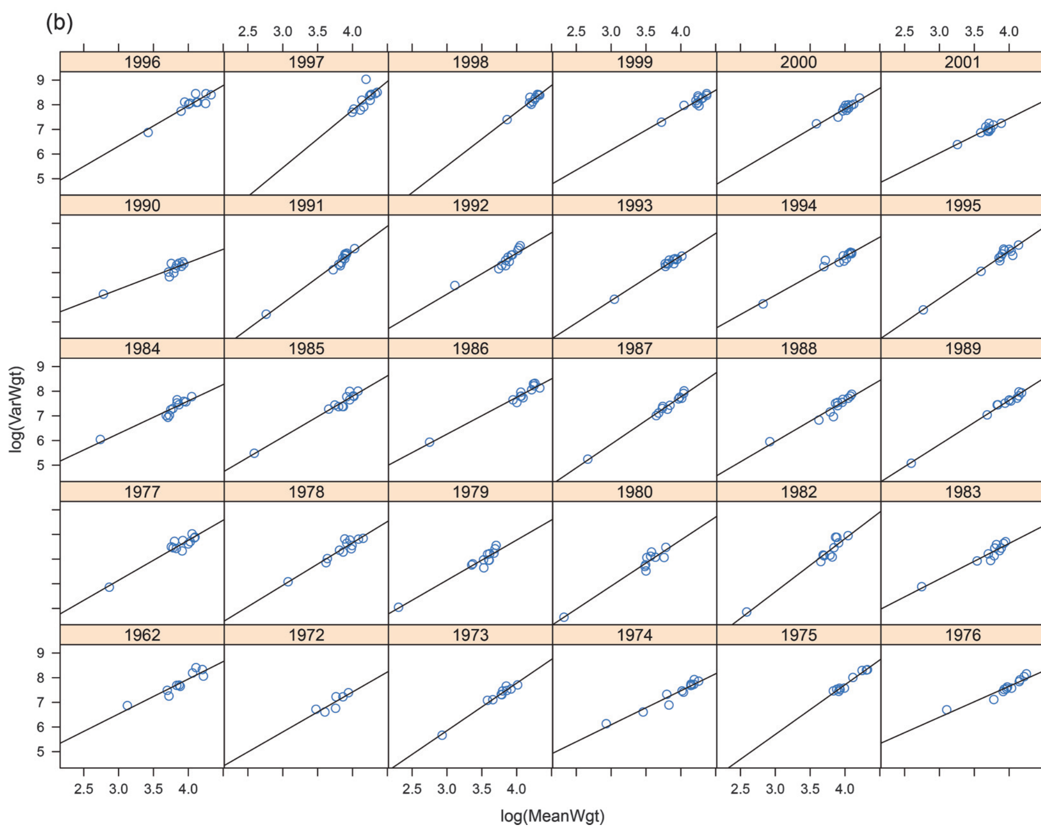
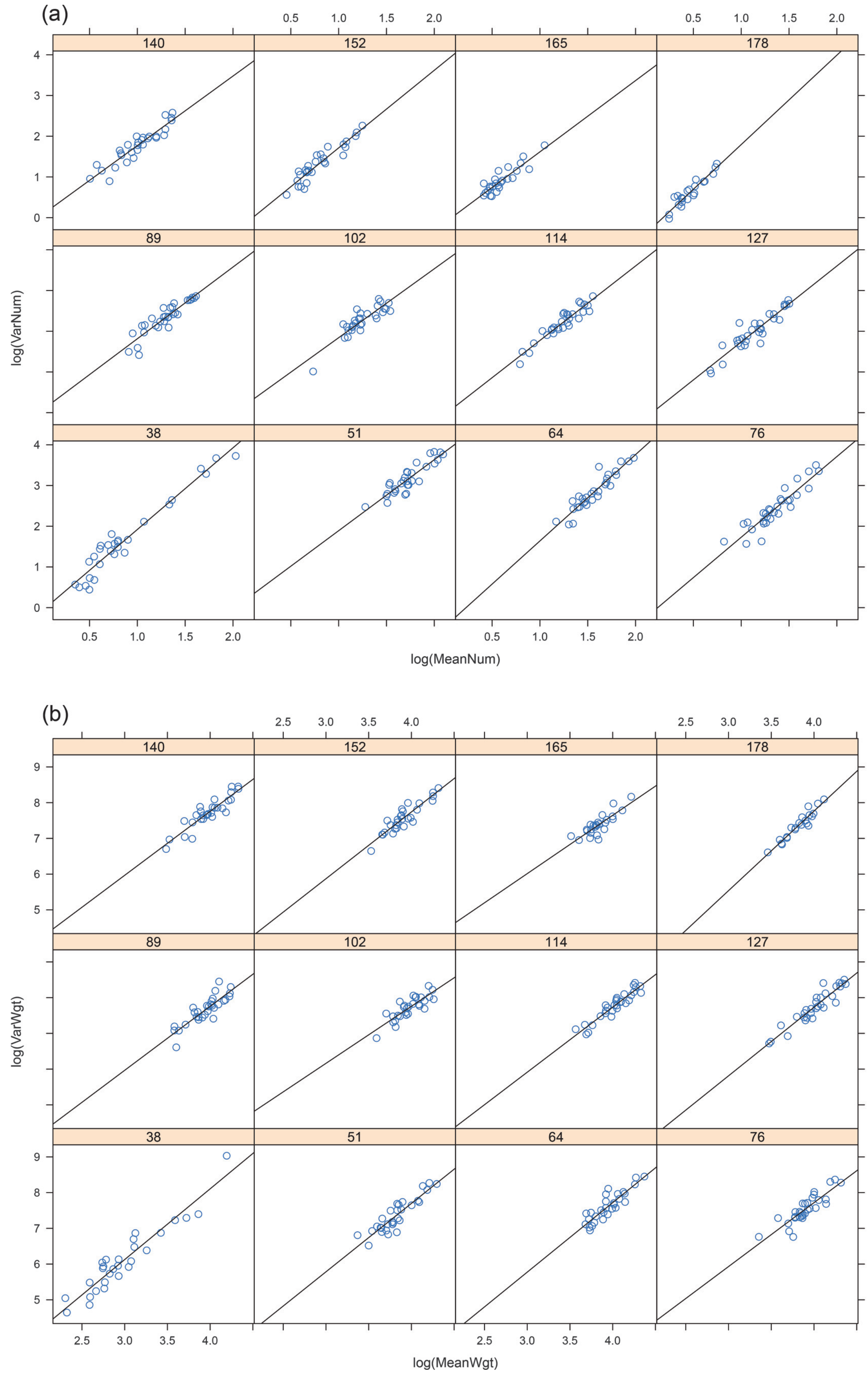


Fig. 3. Log(variance) as a function of log(mean) by mesh size (mm) (across years) when fish abundance was measured by (*a*) number and (*b*) weight (g). Circles and solid lines are defined in the legend of Fig. 2. Axis labels are defined in Fig. 1.



were computed using R 3.2.0 packages "qpcR" and "nlme" (R Core Team 2015).

Fixed-precision sampling design using TPL

We analyzed the stopping line of the number of samples in fixed-precision sampling (with precision level C = 0.1) following Green (1970) using the Lake Kariba gillnet sample abundance (in number) when TPL was tested separately by year (across mesh sizes) and by mesh size (across years). In both cases, a sample and the number of samples were defined respectively as a setting and the number of settings. In each sampling year, TPL parameters estimated in that year (Supplementary Table S2[1]) were used to construct the intercept and slope of the fixed-precision stopping line (eq. 2). When accumulating fish abundance from samples in a year (calculating T_N) on each sampling day, we randomized the order of mesh sizes in which the sample was selected. For each mesh size, the stopping line was calculated using the TPL parameters estimated for that mesh size (Supplementary Table S3[1]). Fish abundance from samples was accumulated following the chronological order within the year. For each year and for each mesh size separately, the number of samples was estimated when the log–log plot of accumulated abundance against number of samples intersected with the corresponding stopping line (eq. 2), at which the precision of C = 0.1 was reached.

We then compared the number of samples obtained per mesh size and per year using the analysis of variance (ANOVA) and Bartlett's test (Bartlett 1937). Sample variances of the required number of samples per mesh size and per year were calculated among the 12 mesh sizes and among the 30 sampling years, respectively. ANOVA tested the hypothesis that the mean number of samples required to reach precision 0.1 by single-mesh sampling and by multimesh sampling was identical. Bartlett's test examined the homoscedasticity (equality of variance) of the number of samples between single and multimesh samplings.

Results

Descriptive statistics

Fish caught in gillnets mostly belonged to the families of Characidae, Cichlidae, Mochokidae, and Schilbeidae, totaling 38 species. In the selected data, 70 322 699 g of 167 049 individual fishes were collected during the 42 years of sampling between 1958 and 2001 (excluding 1959 and 1981). In descending order, the four species with at least 10 000 individuals each were *Hydrocynus vittatus* (45 215), *Sargochromis codringtonii* (33 551), *Synodontis zambezensis* (16 510), and *Oreochromis mortimeri* (15 171). The three species with at least 10 000 000 g each were *Sargochromis codringtonii* (14 612 229 g), *Hydrocynus vittatus* (14 005 228 g), and *Mormyrus longirostris* (12 014 314 g). The larger the mesh size, the bigger individual fish in weight (g) (Supplementary Fig. S2[1]). When individuals were aggregated by setting (regardless of species), the average number of fish per setting declined as mesh size increased, except when mesh was 38 mm, while the average aggregate weight of fish per setting peaked at mesh size 127 mm (6631 g per setting) and decreased when mesh size was smaller or larger (except when mesh size was 64 mm; Supplementary Table S1[1]). Minimum and maximum numbers of species per setting were 1 and 14, respectively.

Bivariate relationships between each pair of five variables (log(mean), log(variance), species count, mesh size, and year) are shown in Fig. 1. Whether fish abundance was measured by number (Fig. 1*a*) or by weight (Fig. 1*b*), the clearest linear relationship was between log(mean) and log(variance). Each pair of mean and variance was calculated within each combination of a year and a mesh size, then all mean–variance pairs were pooled from all years and all mesh sizes. No systematic trend over the years of log(mean) and log(variance) was found using either abundance measure (Fig. 1). As the number of species increased, the mean and variance increased for fish number but remained stable for fish weight (Fig. 1).

Confirmation of TPL

Least-squares regressions fitted to finite log(mean) and finite log(variance) from all combinations of years and mesh sizes (row 2 and column 3 in Fig. 1*a*, 1*b*) yielded significantly positive slopes ($b_1 > 0$ in eq. 1) and insignificant nonlinearity ($c_2 \approx 0$ in eq. 3; Table 1).

Under each abundance measure (weight and number), TPL (eq. 1) and its quadratic generalization (eq. 3) were tested by the least-squares linear and quadratic regressions at each level of year, mesh size, and species count separately.

When regressions were fitted per year (Supplementary Table S2[1]), 1971 was eliminated because it contained fewer than five pairs of finite log(mean) and finite log(variance), under either abundance measure. Using numbers of fish to measure abundance, the slope b_1 of TPL (eq. 1) was significantly positive in each year (and remained significant after Bonferroni correction), ranging from 1.4764 (1976) to 2.4527 (1997). The quadratic coefficient c_2 (eq. 3) was significantly different from 0 in 1995 only (c_2 = 1.3025 and P = 0.0022) and was not significantly different from 0 after Bonferroni correction (P > 0.05/30 = 0.0017). Using weights to measure abundance, b_1 was again significantly positive in all years and remained significant after Bonferroni correction, while c_2 differed significantly from 0 in 1984 (c_2 = 1.4601, P = 0.0035), 1996 (c_2 = −2.7131, P = 0.0005), and 1997 (c_2 = −24.2884, P = 0.0002) and remained significantly negative in 1995 and 1997 after Bonferroni correction. Under either measure, TPL described the mean–variance relationship of sampled fish abundance well (Fig. 2).

Similarly, TPL was tested at each of the 12 mesh sizes (Supplementary Table S3[1]). For fish number, slope b_1 was significantly positive for each mesh size before and after Bonferroni correction, ranging from 1.3408 (178 mm) to 2.0762 (38 mm), while c_2 was not significantly different from 0 for any mesh sizes except size 38 mm (c_2 = −0.7500, P = 0.0059), which was not significantly different from 0 after Bonferroni correction. For fish weight, b_1 was significantly positive for each mesh size before and after Bonferroni correction, with point estimates between 1.0893 (76 mm) and 2.0022 (152 mm), while c_2 was significantly different from 0 for mesh size 38 mm only (c_2 = 0.5647, P = 0.0071), which was not significantly different from 0 after Bonferroni correction. TPL described the mean–variance relationship well except when mesh size was 38 mm (Fig. 3), for which the observed nonlinearity between log(mean) and log(variance) for fish weight may be due to a single outlying point.

In general, the adj. R^2 of the linear relationship between log(variance) and log(mean) was larger for each year (across all mesh sizes) than for each mesh size (across all years) under both abundance measures (Fig. 4). The Welch (1947) two-sample t test showed that when abundance was measured by fish number, the mean of adj. R^2 of linear regressions by year was significantly higher than that by mesh size. The t test did not reject the null hypothesis that the means of RMSE from the two sets of linear regressions were equal. When abundance was measured by fish weight, the set of linear regressions by year yielded significantly higher mean adj. R^2 and lower mean RMSE than those from the set of linear regressions by mesh size. These comparisons suggested that fish caught by multiple mesh sizes (TPL by year; Fig. 2) conformed to TPL better than those caught by any single mesh size (TPL by mesh size; Fig. 3) under both abundance measures.

We examined whether species richness affects the validity and interpretation of TPL. For each combination of year and mesh size, the number of species of sampled fish was counted. The means and variances of fish assemblage abundance (regardless of species) from each year and each mesh size were grouped by species count, using fish number and fish weight separately (Supplementary Fig. S3[1]). Although the maximum number of species in any one setting was 14, the pooled number

Table 1. Parameter estimates of least-squares linear (eq. 1) and quadratic (eq. 3) regressions fitted to log(mean) and log(variance) lumped from all combinations of years and mesh sizes, in number and weight separately.

	TPL (eq. 1)			Generalized TPL (eq. 3)			
	b_1	$\log(a_1)$	adj. R^2	c_2	b_2	$\log(a_2)$	adj. R^2
Number	1.8774 (1.8200, 1.9348)	−0.2313 (−0.2874, −0.1751)	0.9552	−0.1059 (−0.2460, 0.0342)	2.0689 (1.8091, 2.3286)	−0.3024 (−0.4120, −0.1929)	0.9553
Weight	1.4794 (1.4068, 1.5520)	1.5830 (1.3192, 1.8468)	0.9047	−0.0561 (−0.1888, 0.0766)	1.8494 (0.9713, 2.7275)	0.9843 (−0.4560, 2.4246)	0.9064

Note: 95% confidence intervals (CIs) (in parentheses) follow the corresponding regression point estimates. TPL, Taylor's power law.

of species over all settings with a given combination of year and mesh size (which we call the species count) ranged as high as 18. TPL was tested at each value of the species count except when species count was 18, where only three pairs of log(mean) and log(variance) were available. In the analyzed samples, the number of species for each mesh size in a year ranged from four to 17. For fish number, at each species count except four and 17, linear regressions yielded significantly positive b_1 (before and after Bonferroni correction), ranging from 1.5411 (species count = 12) to 2.2325 (species count = 16). Without the Bonferroni correction, the coefficient c_2 of the quadratic term was significantly different from 0 only when the species count was 12 ($c_2 = 0.8454$, $P = 0.0050$); with the Bonferroni correction, this c_2 was not significantly different from 0. For fish weight, at each species count except four, five, and 17, linear regressions yielded significantly positive b_1 (before and after Bonferroni correction), ranging from 1.1596 (species count = seven) to 2.3518 (species count = six), and c_2 was significantly different from 0 (before and after Bonferroni correction) only when the species count was seven ($c_2 = 2.5358$, $P = 0.0010$). Insignificant linear regressions under both measures were probably due to limited numbers of pairs of mean and variance (six pairs when species count was four and five pairs when species count was five or 17). The adj. R^2 of each fitted linear regression was high when the species count was intermediate and low when the species count was small or large, under both measures (Supplementary Fig. S4[1]). Since the number of finite log(mean)–log(variance) pairs was greatest at medium species counts and smallest at extreme species counts (Supplementary Table S4[1]), the effect of species counts on the strength of TPL was confounded with the number of samples and could not be interpreted ecologically.

TPL parameters using weight and number measures and empirical test of their connection

In a given setting, suppose the aggregate weight of fish caught (denoted by "wgt") behaves as a power-law function of the corresponding aggregate number of fish caught (denoted by "num") with exponent β and coefficient α:

$$\text{(4)} \qquad \text{wgt} = \alpha(\text{num})^{\beta}$$

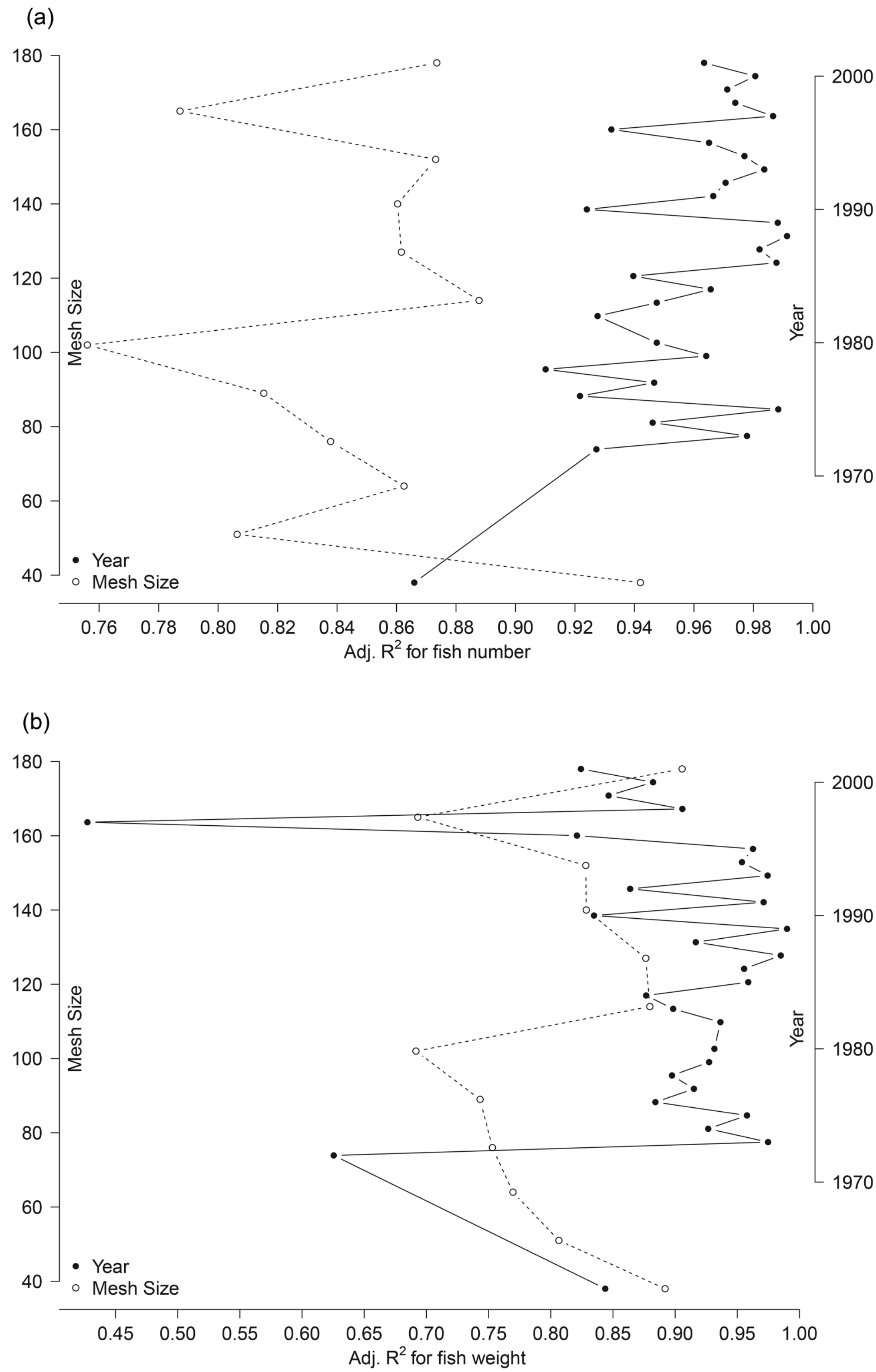
Also suppose that the exponent and coefficient of TPL were b_w and a_w, respectively, when abundance was measured by weight ($\mathrm{Var}(\text{wgt}) = a_w\,[E(\text{wgt})]^{b_w}$) and were b_n and a_n, respectively, when abundance was measured by number ($\mathrm{Var}(\text{num}) = a_n\,[E(\text{num})]^{b_n}$). Here E and Var denote the mean and variance, respectively, of the corresponding variable. Then

$$\text{(5)} \qquad b_w = 2 + \frac{b_n - 2}{\beta} \ \text{and} \ a_w = \alpha^{\frac{2-b_n}{\beta}}\beta^2 a_n$$

Appendix A gives the background and derivation of this equation. We used aggregate abundance by mesh sizes to test eqs. 4 and 5. To test eq. 4, we fitted linear regressions to independent variable log(num) and dependent variable log(wgt) across all settings for each mesh size separately (Supplementary Fig. S5[1]). Parameters of eq. 4 on log–log scale under each mesh size were significantly nonzero ($P < 0.0001$), and their point estimates are listed in Table 2. No clear nonlinear relationship was observed between log(num) and log(wgt) in Supplementary Fig. S5[1] and nonlinear regression was not fitted.

Next, we predicted parameters of TPL for weight using eq. 5 and compared them with the corresponding parameters of TPL estimated directly from observations of fish weight. We found that for all mesh sizes except 76 mm, the predicted TPL slope and intercept fell inside the corresponding 95% CIs estimated from

Fig. 4. Comparisons of adj. R^2 of fitted linear regressions when log(mean)–log(variance) pairs were grouped by year (across all mesh sizes (mm) used in each year) and by mesh size (mm) (across all years in which the mesh size was used). Fish abundance was measured by (*a*) number and (*b*) weight (g).



data. When mesh size was 76 mm, neither predicted slope nor intercept (eq. 5) was included in the corresponding 95% CI estimated from data. In this case, the predicted TPL slope was 2.3243 standard deviations greater than the slope point estimate, while the predicted TPL intercept was 2.4269 standard deviations less than the intercept point estimate. The discrepancy for mesh size 76 mm was marginal and did not disprove the systematic agreement of TPL parameters found in other mesh sizes. Equation 5 thus provides an approximate analytic connection of TPL parameters under different abundance measures of the same fish sample.

Table 2. Parameters of weight–number power law and Taylor's power law (TPL) using number and weight separately for each mesh size.

	Weight–number power law (eq. A4)			TPL: Fish number (eq. A5)		TPL: Fish weight (g) (eqs. A6 and A10)				
Mesh size (mm)	Slope (β)	Intercept ($\log(\alpha)$)	No. of data points	Slope (b_n)	Intercept ($\log(a_n)$)	Slope (b_w, eq. A6)	Predicted slope (b_w, eq. A10)	Intercept ($\log(a_w)$, eq. A6)	Predicted intercept ($\log(a_w)$, eq. A10)	No. of data points
38	1.0232	1.9383	973	2.0762	−0.1060	1.9694 (1.7516, 2.1873)	2.0745	0.2837 (−0.3319, 0.8992)	−0.2304	30
51	0.9572	2.1423	1266	1.4412	0.4735	1.4044 (0.9573, 1.8514)	1.4162	1.7908 (0.1876, 3.3939)	1.6862	30
64	0.9101	2.4843	1229	1.8009	−0.1697	1.3665 (0.8612, 1.8718)	1.7812	1.9276 (0.0562, 3.7989)	0.2920	30
76	0.9346	2.5981	1242	1.6954	−0.0189	1.0893 (0.5943, 1.5844)	1.6741	3.0116 (1.1939, 4.8292)	0.7691	30
89	0.9231	2.7184	1242	1.4196	0.2345	1.4187 (0.9021, 1.9352)	1.3712	1.8306 (−0.0873, 3.7485)	1.8742	30
102	0.9281	2.7796	1240	1.5991	0.0665	1.4437 (0.9502, 1.9372)	1.5680	1.7331 (−0.1089, 3.5751)	1.2024	30
114	0.9239	2.8593	1223	1.7160	−0.1101	1.5742 (1.1902, 1.9581)	1.6926	1.2285 (−0.2233, 2.6804)	0.7001	31
127	0.9439	2.9201	1215	1.4322	0.1446	1.4540 (1.0620, 1.8459)	1.3985	1.6857 (0.2012, 3.1702)	1.8510	30
140	0.9329	3.0155	1143	1.4342	0.0785	1.4237 (0.9751, 1.8724)	1.3935	1.7864 (0.1034, 3.4694)	1.8471	30
152	0.9383	3.1160	1042	1.8610	−0.2673	2.0022 (1.4982, 2.5063)	1.8519	−0.3243 (−2.1746, 1.5259)	0.1390	30
165	0.9418	3.2354	873	1.6967	−0.2166	1.2552 (0.3567, 2.1538)	1.6780	2.3986 (−0.8966, 5.6939)	0.7733	27
178	1.0285	3.3115	690	1.3408	−0.1815	1.8821 (1.0924, 2.6718)	1.3591	0.1357 (−2.7369, 3.0084)	1.9654	24

Note: Parameter estimates of TPL by mesh size (across years) using fish number and weight are from Supplementary Table S3[1].

Robustness of TPL

The linear relationship between log(mean) and log(variance) of fish abundance (TPL, eq. 1) was not destroyed when year, mesh size, and species count were introduced as covariates in the MLR models, whether fish number or fish weight was used to measure abundance.

When mesh size was treated as a numerical variable, the coefficient of log(mean) was significantly nonzero in each of the 36 MLRs when abundance was measured by number, with all CIs falling between 1.2012 and 2.3243 (Supplementary Material, Fig. S6*a*; Table S5[1]). This range contained the CI of b_1 (1.8200, 1.9348) in TPL when all temporal means and temporal variances were pooled. We use the notation "$X1 \times X2$" to mean that $X1$, $X2$, and their interaction were included in the model. Among the three two-way interaction models where log(mean) interacted with a single factor (log(var) = log(mean) × (year), log(var) = log(mean) × (mesh size), log(var) = log(mean) × (mesh size), also called analysis of covariance (ANCOVA)), only year had significant effect on b_1, which increased as year increased. The coefficient of log(mean) was again significant in each of the 36 MLRs when abundance was measured by weight, with all CIs falling between 1.1855 and 2.5517 (Supplementary Material, Fig. S6*b*; Table S7[1]), again containing the CI of b_1 (1.4068, 1.5520) in TPL. Three ANCOVA models did not indicate any significant effect of year, mesh size, or species count on b_1.

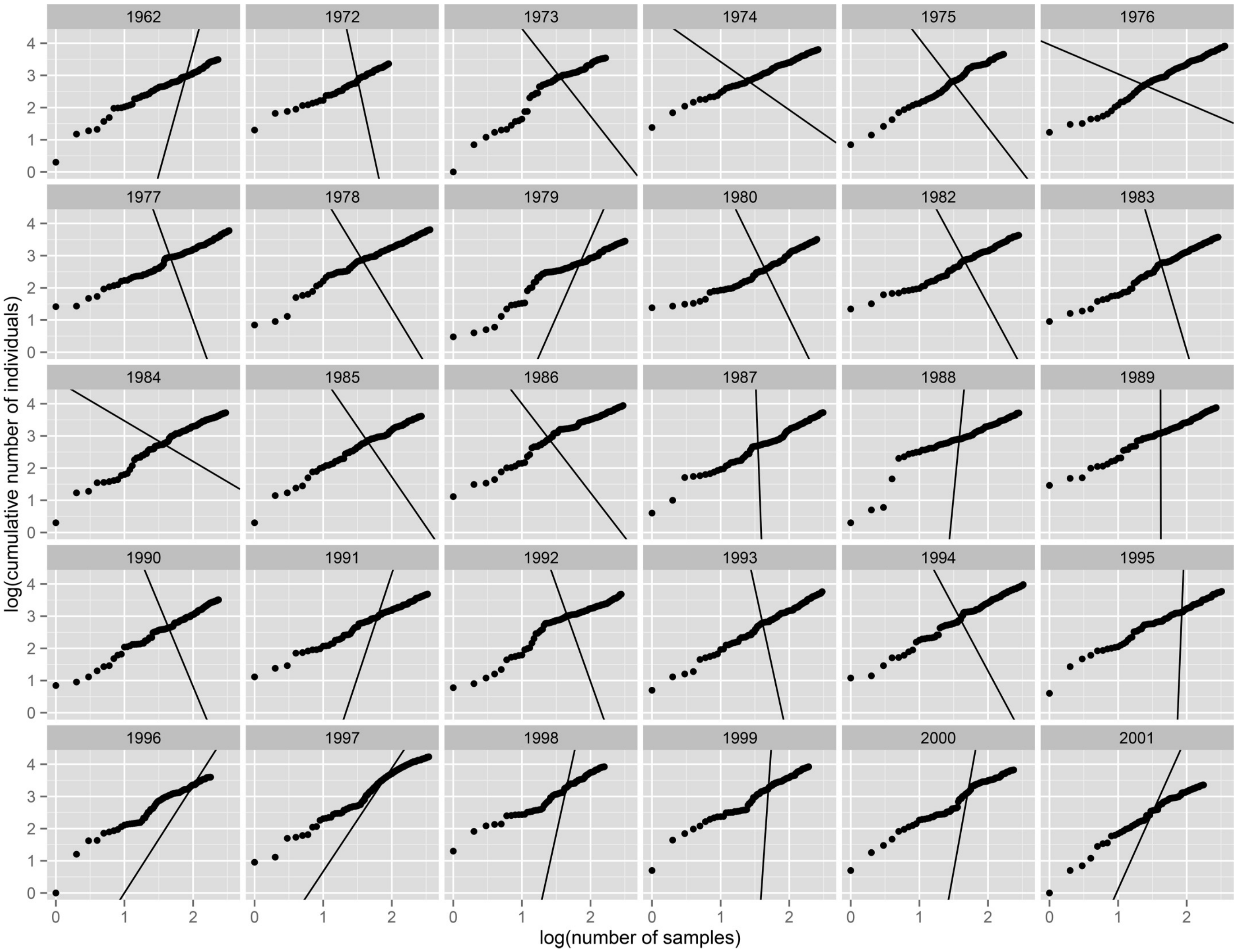
When mesh size was treated as a categorical factor, under either abundance measure, the coefficient of log(mean) was significantly nonzero in all but three of the 36 MLRs. Those three MLRs were log(var) = log(mean) × (mesh size) × (species count), log(var) = log(mean) × (mesh size) × (species count) + year, and log(var) = log(mean) × (mesh size) × (species count) × (year). When abundance was measured by number, the CIs of the significant coefficient of log(mean) fell between 1.1833 and 2.3467 (Supplementary Material, Fig. S6*c*; Table S6[1]), containing the CI of b_1 (1.8200, 1.9348) in TPL when lumping all temporal means and temporal variances. In the three ANCOVA models, b_1 was affected by year only. When abundance was measured by weight, the CIs of the significant coefficient of log(mean) fell between 1.2396 and 2.3683 (Supplementary Material, Fig. S6*d*; Table S8[1]), again containing the CI of b_1 (1.4068, 1.5520) in TPL. None of the single factors in ANCOVA models significantly affected b_1.

Regardless of whether mesh size was treated as a continuous variable or categorical factor, for each MLR, the adj. R^2 for number was higher than the corresponding adj. R^2 for weight (Supplementary Tables S5–S8[1]). MLR models did not indicate that the effect on TPL's slope of any single factor (i.e., year, mesh size, or species count) was stronger than the others. Regardless of the variable type of mesh size and abundance measure, the saturated model including all variables and their interactions (log(var) = log(mean) × (year) × (mesh size) × (species count); Supplementary Material[1], fm36 in Tables S5 and S6 and fmw36 in Tables S7 and S8) was not the best model in terms of AIC. The ten MLRs with the smallest AIC, under each combination of abundance measure and mesh size variable type, are listed in the Supplementary Tables S5–S8[1].

TPL and sampling efficiency

When sampling within each year (across mesh sizes), the mean and the variance of the number of samples needed for a 0.1 sampling precision level were 46.47 and 350.74, respectively (Fig. 5). When sampling using each mesh size (across years), the mean and the variance of the number of samples required to reach a 0.1 precision level were 42.75 and 230.20, respectively (Supplementary Fig. S7[1]). ANOVA did not reject the hypothesis that the mean required number of samples obtained per year and per mesh size was identical (P = 0.5450). Bartlett's test did not reject the hypothesis that the required number of samples from each year and from each mesh size had equal variance (P = 0.4239). No significant difference in the magnitude or the spread of the required number

Fig. 5. Log(cumulative number of individuals) against log(number of samples) in each sampling year. The straight solid line in each panel is the fixed-precision stopping line (eq. 2) with C = 0.1 from each year, which used TPL's parameters listed in Table S2[1]. Each solid circle gives the logarithmic number of settings and the logarithmic cumulative sum of individual fishes from these settings. On a sampling day, settings were accumulated from 12 randomly ordered mesh sizes. Where the solid circles intersect the straight line, the number of samples reaches C = 0.1.



of samples was observed between single-mesh and multimesh sampling.

Discussion

Effects of multimesh gillnets

We found that the linear relationship between log(variance) and log(mean) posited by TPL (eq. 1) was tighter when TPL was tested for each of 30 years (each year included 12 mesh sizes; Fig. 2) than when TPL was tested for each of the 12 mesh sizes (each mesh size was used in 30 years; Fig. 3), whether abundance was measured by number or by weight. The most likely explanation is that in most years considered individually (Fig. 2), the mean abundance varied over at least an order of magnitude with different mesh sizes (i.e., the x coordinates generally ranged over at least one whole unit on the $\log_{10}$ scale), whereas for most mesh sizes considered individually (Fig. 3), the mean abundance often varied over little more than half an order of magnitude over different years (i.e., the x coordinates generally ranged over much less than one whole unit on the $\log_{10}$ scale). Using gillnets of widely varying mesh sizes increased the range of variation of mean abundance relative to interannual variation for a given mesh size and therefore reduced the standard error of the estimated slope of TPL, increasing its precision. This effect is a simple consequence of the formula for the standard error of the regression slope, which is inversely proportional to the population standard deviation of the x coordinate.

It is well known that multimesh gillnet fishing increases the range of fish body sizes caught and the range of fish abundance from one sample to another and is therefore recommended by the 2005 European Standard for sampling fish in lakes (European Standard 2005). However, our data were based on 12 mesh sizes increasing in approximately arithmetical progression from 38 to 178 mm with an increment of approximately 12.5 mm (Supplementary Table S1[1]), whereas the multimesh sampling recommended by the European Standard is based on 12 mesh sizes increasing in geometrical progression from 5 to 55 mm to reduce overlap of catches in larger mesh sizes (Baranov 1948). It seems likely, but remains to be demonstrated empirically, that multimesh sampling with geometrically increasing mesh sizes will follow the temporal TPL, as we found for Lake Kariba fish samples.

Factors affecting TPL

MLRs revealed the effects of the sampling year, mesh size, and species count on the log(mean)–log(variance) relationship (eq. 1).

We found that the form of TPL remained valid despite experimental and biological influences, although its parameters depended on the model structures and variable types. These findings suggested that the form of TPL is likely to be general and independent of many biological or experimental variables.

The ANCOVA compares parameters of the same scaling pattern estimated from multiple conditions and treatments. Taylor et al. (1988) argued that ANCOVA (which they called "analysis of parallelism") should be used as the main statistical tool to study intraspecific differences of TPL slopes under different conditions. ANCOVA has been applied to study whether the TPL parameters of a single species differed between different seasons and growing stages (Van Den Berg and Cock 1995; Ali et al. 1998; Sétamou et al. 2008). Models of exploited fishery populations analyzed by Fujiwara and Cohen (2014) showed that TPL need not be universal under all possible circumstances. Accounting for the changes in TPL parameters and for variations in the success of TPL itself remains an empirical and a theoretical challenge to ecologists.

Number and weight of fish both obey TPL

We confirmed TPL using number and weight as two abundance measures separately and found an approximate, but empirically supported, analytical formula (eq. 5) that relates the parameters of TPL under these two measures when Damuth's law (density–mass allometry, DMA) or a weight–number power law (eq. 4) holds. Our empirical and theoretical results showed that the form of TPL did not depend on the abundance measure used.

Traditionally, the abundance of a species has been measured by a count of total number of individuals within a community or a count of individuals per unit area (Taylor et al. 1978, 1980). But some clonal animal and plant species cannot be counted in individuals (Damgaard 2009), though their abundance can be measured by weight. Our finding that TPL describes fluctuation in weights as well as in numbers extends the scope of TPL to species for which the number of individuals is not well defined.

Sampling effort of single- and multimesh gillnet samplings

TPL has been applied to find the size of samples required to assess changes in marine fish stocks to a desired precision (Mouillot et al. 1999) and fish populations' risk of extinction (Mellin et al. 2010). In the Lake Kariba data examined here, measuring abundance by number, we found that the required number of samples did not differ significantly between single-mesh and multimesh sampling. To compare properly the sampling effort required for single-mesh and multimesh sampling, identical number of panels should be used for distinct mesh sizes and for a unique mesh size.

Limitation and summary of current study

Although multiple mesh sizes were used during sampling, gillnet catches were still selective as fish smaller than those caught in the smallest mesh size escaped capture (Kolding et al. 2016). Consequently, unless population data that reflect all fish species and sizes become available, our results should not be used to infer some aspects of fish biology such as differences between species in catchability and behavior. For this reason, we analyzed aggregate fish abundance instead of individual species abundance. Results of this work could profitably be reexamined using data on the fish population estimated by using a wider range of gillnet mesh sizes or other fishing techniques (e.g., electrofishing) or by correcting the selectivity bias using catching probability models (Rudstam et al. 1984; Kolding et al. 2016).

In summary, we found that TPL robustly described the temporal fluctuation of freshwater fish assemblage abundance (regardless of species), measured by aggregate number and aggregate weight separately. The use of multiple gillnet mesh sizes strengthened the mean–variance relationship of fish abundance described by TPL, and the correlation between mean and variance was not destroyed after adding the year, mesh size, and species count into TPL (eq. 1). However, the parameters of TPL did depend on how abundance was measured, the variable type of mesh size, and model complexity. A weight–number power-law relationship of fish stocks analytically connected the parameters of TPL when fish abundance was measured by number with the parameters of TPL when fish abundance was measured by weight. The stopping line analysis with TPL shed practical light on the design of efficient fixed-precision fish sampling program with gillnets, which can benefit fishery management and conservation.

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Appendix A

Fixed-precision sampling design using Taylor's power law (TPL)

Here we summarize how Mouillot et al. (1999, p. 23) and European Standard (2005, p. 17) used the standard error of the mean to calculate desired number of samples N in a sampling program with fixed precision C and discuss how TPL parameters can be used to determine N.

Supposing abundance has sample mean m, sample variance v, and sample standard deviation s (with $v = s^2$), the standard error of the mean is defined to be SEM = $s/N^{1/2}$. The precision C is defined to be C = SEM/m = CV/$N^{1/2}$. The manager or the designer of sampling determines the value of C in advance, requiring, for example, C = 0.1 or C = 0.5 if the goal is to estimate the mean with a precision of 10% or 50%, respectively. A formula of Karandinos (1976) used by Mouillot et al. (1999, p. 23) and European Standard (2005, p. 17) is

$$\text{(A1)} \qquad N = v(Cm)^{-2}$$

Equation A1 follows immediately from the definitions of C and SEM: Cm = SEM = $sN^{-1/2}$, so $(Cm)^2 = vN^{-1}$, which is equivalent to $v(Cm)^{-2} = N$. By expressing the number of samples N as a function of the desired precision C, eq. A1 shows that the necessary number of samples N is inversely proportional to the square of the desired precision C. For example, when v and m are fixed, increasing the desired precision by a factor of five, from 50% to 10%, multiplies the necessary number of samples N by a factor of 25. Managers could use this formula to balance the desire for precise estimation of the mean abundance against the cost of more sampling.

To apply eq. A1 in sampling, it is desirable to express the variance v as a function of the mean m. For example, when the power-law form, $v = a_1 m^{b_1}$, of TPL holds, then, as Mouillot et al. (1999) noted, $N = v(Cm)^{-2} = a_1 m^{b_1}(Cm)^{-2} = a_1 m^{b_1-2} C^{-2}$. Therefore

$$\text{(A2)} \qquad \log N = \log a_1 - 2 \log C + (b_1 - 2) \log m$$

Equation A2 provides a method of calculating the number of samples N necessary to achieve a fixed precision C at a given mean m. When $b_1 = 2$, N depends on the intercept of TPL ($\log(a_1)$) and the fixed precision (C) only and is independent of m: $\log N = \log a_1 - 2 \log C$. So the number of samples N required to achieve a fixed precision C can be derived directly from $N = a_1/C^2$. Equation A2 also shows that when $b_1 > 2$, a larger m corresponds to a greater N; thus, more sampling effort is needed. When $b_1 < 2$, a larger m corresponds to a smaller N; thus, less sampling effort is needed.

When $b_1 \neq 2$, eq. A2 can be transformed to a formula relating N and the total abundance T_N of the N samples of average abundance m ($T_N = m \times N$). After replacing m in eq. A2 with T_N/N and algebraic simplifications

$$\text{(A3)} \qquad \log T_N = \frac{\log\left(\frac{C^2}{a_1}\right)}{b_1 - 2} + \frac{b_1 - 1}{b_1 - 2} \times \log N$$

Equation A3 was derived by Green (1970, eq. 7 therein) and was used as a stopping line criterion to attain fixed-precision sampling. In practice, a researcher samples abundance data, records and plots the accumulated total number of individuals T_N against the number of samples N, and stops sampling when the empirical curve of $\log(T_N)$ as a function of $\log(N)$ intersects with eq. A3. At that point, the fixed precision C is reached (see figure 1 in Green 1970). When $0 < b_1 < 1$ or $b_1 > 2$, the slope of eq. A3 is positive; when $1 < b_1 < 2$, the slope of eq. A3 is negative.

Theory to relate fish number and fish weight in TPL

Suppose that TPL holds when fish abundance is measured by numbers, and suppose that TPL holds when fish abundance is measured by aggregate weight. In this section, we show that these two suppositions are mathematically consistent under certain circumstances and that the parameters of TPL using number and weight are connected analytically. The connecting link is a weight–number power law, which is mathematically equivalent to and can be analytically derived from the well-known density–mass allometry (DMA) or "Damuth's law" in ecology (Damuth 1987; Brown and Maurer 1989).

Suppose DMA held with parameters c and d:

$$\text{sample abundance} = c(\text{average individual body mass})^d, \qquad c > 0$$

In our data, sample abundance was the total number of fish caught in a single setting (denoted by "num"), and average individual weight (g) can be calculated as the sum of weight (g) of individual fish caught in a single setting (denoted by "wgt") divided by the corresponding "num". In this case, DMA can be written as

$$\text{num} = c\left(\frac{\text{wgt}}{\text{num}}\right)^d$$

After simple algebraic manipulations, this equation becomes

$$\text{wgt} = c^{-\frac{1}{d}}(\text{num})^{1+\frac{1}{d}}$$

Define $\alpha = c^{\left(-\frac{1}{d}\right)}$ and $\beta = 1 + \frac{1}{d}$. We call the following eq. A4 the weight–number power law.

$$\text{(A4)} \qquad \text{wgt} = \alpha(\text{num})^{\beta}$$

Denote the mean and variance by E and Var, respectively, and suppose num follows TPL:

$$\text{(A5)} \qquad \text{Var(num)} = a_{\text{n}}\,[E(\text{num})]^{b_{\text{n}}}$$

Here E and Var were calculated from all settings within a single level of a grouping factor (sampling year, mesh size, or species count; see Results, Confirmation of TPL). Subscript n of a and b refers to "number." Suppose also that the aggregate fish weight per setting follows TPL:

$$\text{(A6)} \qquad \text{Var(wgt)} = a_{\text{w}}\,[E(\text{wgt})]^{b_{\text{w}}}$$

The subscript w of a and b refers to "weight". We now express a_{w} and b_{w} in terms of α, β, a_{n}, and b_{n}. From eq. A4

$$\text{(A7)} \qquad \text{Var(wgt)} = \text{Var}[\alpha(\text{num})^{\beta}] = \alpha^2\,\text{Var}[(\text{num})^{\beta}]$$

By Taylor expansion of random variables, we approximate the variance of a power function using the first-order delta method (Oehlert 1992; Cohen and Xu 2015):

$$\begin{aligned}\text{Var}[(\text{num})^{\beta}] &\approx \{\beta\,[E(\text{num})]^{\beta-1}\}^2\,\text{Var(num)}\\ &= \beta^2\,[E(\text{num})]^{2(\beta-1)}\,\text{Var(num)}\end{aligned}$$

From eq. A5

$$\text{(A8)} \qquad \begin{aligned}\text{Var}[(\text{num})^{\beta}] &= \beta^2\,[E(\text{num})]^{2(\beta-1)}\,a_{\text{n}}\,[E(\text{num})]^{b_{\text{n}}}\\ &= \beta^2 a_{\text{n}}\,[E(\text{num})]^{2(\beta-1)+b_{\text{n}}}\end{aligned}$$

Taking expectation on both sides of eq. A4 and using the first-order delta method for the expectation of a power function

$$E(\text{wgt}) = E\,[\alpha(\text{num})^{\beta}] \approx \alpha\,[E(\text{num})]^{\beta}$$

Assuming $\alpha \neq 0$ and $\beta \neq 0$

$$E(\text{num}) \approx \left[\frac{E(\text{wgt})}{\alpha}\right]^{1/\beta}$$

Plugging the above expression into the right side of eq. A8

$$\text{(A9)} \qquad \begin{aligned}\text{Var}[(\text{num})^{\beta}] &\approx \beta^2 a_{\text{n}}\left\{\left[\frac{E(\text{wgt})}{\alpha}\right]^{\frac{1}{\beta}}\right\}^{2(\beta-1)+b_{\text{n}}}\\ &= \alpha^{\frac{2-b_{\text{n}}}{\beta}-2}\,\beta^2 a_{\text{n}}\,[E(\text{wgt})]^{2+\frac{b_{\text{n}}-2}{\beta}}\end{aligned}$$

Equations A7 and A9 therefore yield

$$\text{(A10)} \qquad \text{Var(wgt)} \approx \alpha^{\frac{2-b_{\text{n}}}{\beta}}\,\beta^2 a_{\text{n}}\,[E(\text{wgt})]^{2+\frac{b_{\text{n}}-2}{\beta}}$$

Equation A10 is the derived approximate TPL for fish weight with predicted exponent $b_{\text{w}} = 2 + \frac{b_{\text{n}}-2}{\beta}$ and predicted coefficient $a_{\text{w}} = \alpha^{\frac{2-b_{\text{n}}}{\beta}}\beta^2 a_{\text{n}}$, assuming $\alpha \neq 0$ and $\beta \neq 0$.

A few simple relationships between b_{w} and b_{n} can be derived, assuming $\alpha \neq 0$ and $\beta \neq 0$, from $b_{\text{w}} = 2 + \frac{b_{\text{n}}-2}{\beta}$. First, $b_{\text{w}} = 2$ if and only if $b_{\text{n}} = 2$. Now suppose $\beta > 0$. Then when $b_{\text{n}} > 2$, $b_{\text{w}} > 2$; when $b_{\text{n}} < 2$, $b_{\text{w}} < 2$. Moreover, if $\beta = 1$, then $b_{\text{w}} = b_{\text{n}}$; and conversely, if $b_{\text{w}} = b_{\text{n}}$, then $\beta = 1$. The interpretation of $\beta = 1$ is that wgt and num are strictly proportional to one another. If $\beta \neq 0$

$$b_{\text{w}} - b_{\text{n}} = 2 + \frac{b_{\text{n}} - 2}{\beta} - b_{\text{n}} = (b_{\text{n}} - 2)\left(\frac{1}{\beta} - 1\right)$$

This formula shows that if $0 < \beta < 1$, $b_{\text{w}} > b_{\text{n}} > 2$ when $b_{\text{n}} > 2$, and $b_{\text{w}} < b_{\text{n}} < 2$ when $b_{\text{n}} < 2$. If $\beta > 1$, $b_{\text{w}} < b_{\text{n}}$ when $b_{\text{n}} > 2$, and $b_{\text{w}} > b_{\text{n}}$ when $b_{\text{n}} < 2$.

Taylor's power law and fixed precision sampling: application to abundance of fish sampled by gillnets in an African lake

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Supplementary materials

Relationship between fitted TPL slopes and year, mesh size, and species count

After TPL was tested at each level of sampling year, mesh size, and species count separately, it is natural to ask if the estimates of TPL slope followed any trend with any single variable. In the following regression analysis, the slope estimates $\widehat{b_1}$ were equally weighted among all levels of the corresponding variable.

When TPL was tested for each year, using number as the abundance measure, least-squares linear regression fitted to the slope estimate $\widehat{b_1}$ (as ordinate) and sampling year (as abscissa) yielded a significant slope of 0.0115, meaning that $\widehat{b_1}$ rose by 0.0115 per year. However, the relationship was weak ($R^2 = 0.2262$) as $\widehat{b_1}$ fluctuated widely over the years (Supplementary Fig. S8a). When abundance was measured by weight, linear regression did not show any significant increase or decrease in $\widehat{b_1}$ over the years (Supplementary Fig. S8b).

When TPL was tested for each mesh size, linear regressions did not show any significant relationship between $\widehat{b_1}$ and mesh sizes for either abundance measure (Supplementary Fig. S9).

When TPL was tested at each level of species count, linear regressions did not show any significant relationship between $\widehat{b_1}$ and species counts for either abundance measure (Supplementary Fig. S10).

We conclude that the slope of TPL increased weakly with year of sampling when abundance was measured by number, but bore no consistent relationship otherwise to year, mesh size, and species count. Thus it is empirically defensible to report the slope of TPL without conditioning on the values of these variables.

Supplementary tables S1-S9

Table S1. Mesh sizes (mm) used in Lake Kariba fish sampling and average abundance (in number and weight (g)) of fish per setting. Numbers of settings under different measures differed due to the inclusion (in fish numbers) or exclusion (from fish weights) of individual fishes without weight record.

Mesh size (mm)	Average number of fish per setting	Variance of number of fish per setting	Average weight of fish per setting (g)	Variance of weight of fish per setting (g^2)	Number of settings for fish number	Number of settings for fish weight
38	8	536	1 057	34 851 867	1 034	992
51	32	1511	4 035	48 754 091	1 301	1 290
64	22	715	5 246	71 362 042	1 276	1 256
76	14	636	4 872	59 496 468	1 304	1 265
89	12	351	5 381	73 775 370	1 298	1 267
102	11	279	5 697	76 719 825	1 301	1 266
114	10	257	6 623	97 590 913	1 281	1 234
127	8	196	6 631	113 569 584	1 313	1 240
140	6	110	6 121	91 241 631	1 278	1 160
152	4	44	5 609	64 091 774	1 307	1 080
165	2	14	4 708	35 441 787	1 221	917
178	2	6	4 524	37 806 276	1 175	755

Table S2. Parameter estimates of Taylor's power law (eqn 1) for each year (across mesh sizes), using aggregate number and weight separately. Under either measure, *P* of the regression slope b_1 was less than 0.0001, smaller than the significance level of 0.05/30 (30 years) ≈ 0.0017 adjusted by the Bonferroni method (Dunn 1961). After Bonferroni correction, the quadratic regression c_2 was significantly different from 0 only in 1995 and 1997 and when abundance was measured by weight.

Year	Slope (b_1)				Intercept ($\log a_1$)				$\hat{c}_2$ (eqn 3)		Number of mean-var pairs	Avg settings per mean-var pair
	Number		Weight (g)		Number		Weight (g)					
	Point estimate	95% CI	Point estimate	95% CI	Point estimate	95% CI	Point estimate	95% CI	Number	Weight	Number or weight	Number or weight
1962	2.1490	(1.6501, 2.6479)	1.2842	(0.8576, 1.7108)	-0.2646	(-0.7121, 0.1830)	2.6433	(1.0629, 4.2238)	-0.0333	1.3424	10	35
1972	1.9079	(1.6132, 2.2026)	1.4374	(0.9153, 1.9595)	-0.3730	(-0.6866, -0.0594)	1.5506	(-0.3029, 3.4041)	-0.4694	0.7747	10	18
1973	1.7310	(1.3913, 2.0707)	1.6042	(1.1678, 2.0405)	-0.0709	(-0.4236, 0.2817)	1.0514	(-0.4957, 2.5984)	0.4833	-1.0653	10	25
1974	1.5991	(1.3650, 1.8331)	1.3380	(1.0484, 1.6276)	-0.0287	(-0.3161, 0.2587)	2.0225	(0.8939, 3.1511)	-0.1903	0.3040	12	25
1975	1.7343	(1.4371, 2.0315)	1.3318	(0.9538, 1.7099)	-0.1660	(-0.4997, 0.1676)	2.0430	(0.6091, 3.4768)	-0.4990	0.4430	12	24
1976	1.4764	(1.1700, 1.7828)	1.1611	(0.7703, 1.5519)	0.0710	(-0.2538, 0.3959)	2.6723	(1.2059, 4.1388)	0.3388	0.1774	12	49
1977	1.8553	(1.5277, 2.1829)	1.5641	(1.2092, 1.9190)	-0.1463	(-0.4604, 0.1679)	1.3436	(0.0480, 2.6392)	0.5066	-0.7389	12	45
1978	1.7782	(1.4688, 2.0875)	1.4447	(1.0347, 1.8547)	-0.1437	(-0.4469, 0.1594)	1.6677	(0.1725, 3.1628)	-0.3252	0.2395	12	47
1979	2.2602	(1.8914, 2.6291)	1.5203	(1.2108, 1.8299)	-0.3942	(-0.6551, -0.1333)	1.5103	(0.4788, 2.5418)	-0.8991	0.3282	12	38
1980	1.8130	(1.5213, 2.1047)	1.8462	(1.5427, 2.1498)	-0.1785	(-0.3899, 0.0330)	0.3312	(-0.6696, 1.3321)	-0.8578	0.6403	12	36
1982	1.7978	(1.4594, 2.1362)	1.7488	(1.4607, 2.0369)	-0.1055	(-0.4165, 0.2055)	0.5990	(-0.4237, 1.6217)	-1.0501	0.9558	11	39

1983	1.8785	(1.5314, 2.2256)	1.2239	(0.8542, 1.5936)	-0.2374	(-0.5407, 0.0659)	2.4590	(1.1478, 3.7703)	-0.4047	1.1746	11	39
1984	1.5575	(1.2942, 1.8207)	1.2832	(0.9434, 1.6229)	0.0916	(-0.1501, 0.3333)	2.2655	(1.0558, 3.4751)	0.1845	1.4601	12	39
1985	1.7563	(1.4441, 2.0685)	1.5288	(1.2407, 1.8168)	-0.0667	(-0.3570, 0.2237)	1.6007	(0.5507, 2.6508)	0.8132	0.1655	12	33
1986	1.7342	(1.4969, 1.9715)	1.1995	(0.9181, 1.4808)	-0.2039	(-0.4607, 0.0529)	2.6352	(1.5711, 3.6993)	0.4112	-0.2141	12	45
1987	1.9830	(1.7192, 2.2468)	1.6452	(1.3440, 1.9465)	-0.4363	(-0.6903, -0.1824)	0.8754	(-0.2123, 1.9630)	0.0200	0.2588	12	39
1988	2.0479	(1.7841, 2.3117)	1.4776	(1.1215, 1.8336)	-0.4825	(-0.7424, -0.2226)	1.5303	(0.2210, 2.8396)	0.3731	0.7008	12	35
1989	1.9992	(1.7801, 2.2182)	1.6751	(1.4005, 1.9497)	-0.3785	(-0.6054, -0.1515)	0.8406	(-0.1676, 1.8488)	-0.3617	-0.2105	12	38
1990	1.8368	(1.5398, 2.1337)	1.0317	(0.6630, 1.4004)	-0.1937	(-0.4590, 0.0716)	3.1607	(1.8272, 4.4942)	-0.2976	1.2049	12	23
1991	2.1838	(1.8929, 2.4748)	1.7938	(1.4487, 2.1388)	-0.4272	(-0.6767, -0.1776)	0.4544	(-0.7843, 1.6930)	-0.2453	1.1625	12	44
1992	1.8575	(1.5730, 2.1421)	1.3204	(0.8540, 1.7868)	-0.1474	(-0.3960, 0.1012)	2.2773	(0.6122, 3.9423)	-0.3118	1.3488	12	44
1993	1.9076	(1.6424, 2.1728)	1.4383	(0.9665, 1.9101)	-0.2806	(-0.5299, -0.0312)	1.6658	(-0.0306, 3.3622)	0.0256	-1.1080	12	42
1994	1.7992	(1.5853, 2.0132)	1.4852	(1.1548, 1.8156)	-0.1405	(-0.3679, 0.0869)	1.6063	(0.3981, 2.8145)	-0.0527	-1.0069	12	47
1995	2.0190	(1.7352, 2.3029)	1.7080	(1.3917, 2.0244)	-0.0942	(-0.3669, 0.1785)	0.9415	(-0.2013, 2.0844)	1.3025	-0.3174	12	46
1996	2.4286	(1.9923, 2.8649)	0.8907	(0.4009, 1.3805)	-0.5736	(-0.9378, -0.2094)	3.9430	(2.1808, 5.7052)	-0.3693	-2.7131	12	46
1997	2.4527	(2.1671, 2.7382)	1.4814	(0.2901, 2.6726)	-0.8499	(-1.1754, -0.5244)	1.6772	(-2.9026, 6.2571)	0.8015	-24.2884	12	40
1998	2.1150	(1.8411, 2.3890)	1.7718	(0.8647, 2.6790)	-0.5375	(-0.8406, -0.2343)	0.4578	(-2.9447, 3.8604)	0.0429	0.2795	12	44
1999	2.0333	(1.7385, 2.3280)	1.8941	(1.2499, 2.5383)	-0.3550	(-0.6715, -0.0384)	0.0482	(-2.3589, 2.4554)	-0.2634	-0.8273	12	49
2000	2.0923	(1.7840, 2.4006)	1.5055	(0.7435, 2.2675)	-0.4244	(-0.7226, -0.1263)	1.3771	(-1.3771, 4.1314)	-0.6385	-1.8552	12	48
2001	2.2660	(1.9331, 2.5989)	1.0908	(0.3548, 1.8268)	-0.7646	(-1.0822, -0.4471)	2.8092	(0.1527, 5.4657)	0.5920	-0.2233	11	19

Table S3. Parameter estimates of Taylor's power law (eqn 1) for each mesh size (across years), using aggregate number and weight separately. Under either measure, *P* of the regression slope b_1 was less than 0.0001, smaller than the significance level of 0.05/12 (12 mesh sizes) ≈ 0.0042 adjusted by the Bonferroni method (Dunn 1961). After Bonferroni correction, the quadratic regression c_2 was not significantly different from 0 for any mesh size under either abundance measure.

Mesh size (mm)	Slope (b_1)				Intercept ($\log a_1$)				$\hat{c}_2$		Number of mean-var pairs	Avg settings per mean-var pair
	Number		Weight (g)		Number		Weight (g)					
	Point estimate	95% CI	Point estimate	95% CI	Point estimate	95% CI	Point estimate	95% CI	Number	Weight	Number or weight	Number or weight
38	2.0762	(1.8883, 2.2641)	1.9694	(1.7516, 2.1873)	-0.1060	(-0.2517, 0.0397)	0.2837	(-0.3319, 0.8992)	-0.7500	0.5647	30	33
51	1.4412	(1.0430, 1.8393)	1.4044	(0.9573, 1.8514)	0.4735	(-0.1234, 1.0704)	1.7908	(0.1876, 3.3939)	-0.5956	-1.0592	30	46
64	1.8009	(1.3982, 2.2035)	1.3665	(0.8612, 1.8718)	-0.1697	(-0.7057, 0.3663)	1.9276	(0.0562, 3.7989)	1.3243	0.4928	30	41
76	1.6954	(1.3230, 2.0679)	1.0893	(0.5943, 1.5844)	-0.0189	(-0.4430, 0.4052)	3.0116	(1.1939, 4.8292)	1.1356	-0.2630	30	41
89	1.4196	(0.9732, 1.8659)	1.4187	(0.9021, 1.9352)	0.2345	(-0.2403, 0.7093)	1.8306	(-0.0873, 3.7485)	-1.2652	-0.6770	30	41
102	1.5991	(1.1872, 2.0109)	1.4437	(0.9502, 1.9372)	0.0665	(-0.3544, 0.4873)	1.7331	(-0.1089, 3.5751)	-1.5110	0.3396	30	41
114	1.7160	(1.3860, 2.0459)	1.5742	(1.1902, 1.9581)	-0.1101	(-0.4411, 0.2209)	1.2285	(-0.2233, 2.6804)	-1.1330	-0.6636	31	40
127	1.4322	(1.0724, 1.7919)	1.4540	(1.0620, 1.8459)	0.1446	(-0.1881, 0.4773)	1.6857	(0.2012, 3.1702)	-0.3766	-0.7241	30	41
140	1.4342	(1.0688, 1.7995)	1.4237	(0.9751, 1.8724)	0.0785	(-0.2123, 0.3692)	1.7864	(0.1034, 3.4694)	0.6396	-0.5567	30	38
152	1.8610	(1.4383, 2.2838)	2.0022	(1.4982, 2.5063)	-0.2673	(-0.5166, -0.0180)	-0.3243	(-2.1746, 1.5259)	-0.7231	-1.5009	30	35
165	1.6967	(1.0098, 2.3837)	1.2552	(0.3567, 2.1538)	-0.2166	(-0.5187, 0.0855)	2.3986	(-0.8966, 5.6939)	1.8385	2.8969	27	33
178	1.3408	(0.2971, 2.3845)	1.8821	(1.0924, 2.6718)	-0.1815	(-0.4909, 0.1280)	0.1357	(-2.7369, 3.0084)	-0.6943	-0.3975	24	30

Table S4. Parameter estimates of Taylor's power law (eqn 1) for each species count (across combinations of years and mesh sizes), using aggregate number and weight separately. Under either measure, except when species count was four, five, or 17, P of the regression slope b_1 was less than 0.0001, smaller than the significance level of 0.05/11 (11 levels of species count other than four, five and 17) ≈ 0.0045 adjusted by the Bonferroni method (Dunn 1961), and the quadratic regression c_2 was significantly different from 0 after Bonferroni correction only when species count was seven under the weight measure.

Species count	Slope (b_1)				Intercept ($\log a_1$)				$\hat{c}_2$		Number of mean-variance pairs		Avg settings per mean-variance pair	
	Number		Weight (g)		Number		Weight (g)							
	Point estimate	95% CI	Point estimate	95% CI	Point estimate	95% CI	Point estimate	95% CI	Number	Weight (g)	Number	Weight (g)	Number	Weight (g)
4	2.0412	(-0.7469, 4.8293)	1.5201	(-0.1105, 3.1508)	-0.3918	(-1.3254, 0.5418)	1.4557	(-4.5425, 7.4539)	-37.5745	-3.3569	6	6	25	25
5	1.7639	(0.7190, 2.8089)	1.2610	(-0.3301, 2.8521)	-0.4053	(-0.8191, 0.0085)	2.2333	(-3.3843, 7.8509)	13.3069	13.7836	5	5	24	24
6	2.1427	(1.5713, 2.7140)	2.3518	(1.7723, 2.9312)	-0.3581	(-0.6259, -0.0903)	-1.5397	(-3.6123, 0.5329)	0.5367	-0.1880	12	12	28	28
7	1.9522	(1.6468, 2.2576)	1.1596	(0.7208, 1.5985)	-0.2944	(-0.5041, -0.0847)	2.7398	(1.1540, 4.3256)	0.3345	2.5358*	22	23	30	29
8	1.8817	(1.7012, 2.0623)	1.6307	(1.3215, 1.9399)	-0.2878	(-0.4262, -0.1494)	1.0111	(-0.1274, 2.1495)	-0.1571	-0.0072	37	36	31	31
9	1.7333	(1.5774, 1.8892)	1.4618	(1.3099, 1.6136)	-0.1272	(-0.2665, 0.0122)	1.6432	(1.0849, 2.2016)	-0.1280	-0.2433	59	60	36	35
10	1.7831	(1.5982, 1.9679)	1.4112	(1.1404, 1.6821)	-0.1616	(-0.3326, 0.0093)	1.8240	(0.8282, 2.8199)	-0.2719	-0.2062	38	37	37	38
11	1.6591	(1.4370, 1.8812)	1.5418	(1.4005, 1.6831)	-0.0333	(-0.2470, 0.1805)	1.3315	(0.8235, 1.8395)	0.1247	-0.0323	42	42	41	41
12	1.5411	(1.3218, 1.7604)	1.3168	(1.1254, 1.5082)	0.1796	(-0.0580, 0.4171)	2.1917	(1.5034, 2.8801)	0.8454*	0.0574	41	41	43	43
13	1.8356	(1.6034, 2.0679)	1.5443	(1.3610, 1.7275)	-0.1871	(-0.4423, 0.0680)	1.3364	(0.6764, 1.9965)	-0.3882	-0.2495	31	31	44	44
14	1.6859	(1.3495, 2.0223)	1.3597	(1.1153, 1.6041)	0.0142	(-0.3699, 0.3984)	2.0314	(1.1504, 2.9123)	0.6481	-0.0274	18	18	46	46
15	1.9308	(1.6344, 2.2272)	1.4825	(1.2126, 1.7525)	-0.2093	(-0.5734, 0.1549)	1.6113	(0.6429, 2.5797)	-0.2169	0.0104	21	21	44	44
16	2.2325	(1.5803, 2.8848)	1.9422	(0.9701, 2.9143)	-0.7412	(-1.6824, 0.2000)	-0.1906	(-3.8282, 3.4469)	-3.1939	1.9083	12	12	47	47
17	1.4404	(-0.3343, 3.2152)	-1.0544	(-2.4680, 0.3592)	0.3741	(-1.9319, 2.6801)	10.7810	(5.6695, 15.8926)	4.9737	10.6324	5	5	43	43

Table S5. Multiple linear regressions (MLRs) fitted to independent variable log(mean) (denoted by "lm") and dependent variable log(variance) (denoted by "lv") for fish number, with covariates year (denoted by "yr"), mesh size (denoted by "ms"), and species count (denoted by "sc"). Mesh size was treated as a numerical variable. MLRs with the 10 smallest AICs (in ascending order) and TPL (fm0) were shown. Intercept was included in every model. Years and mesh sizes were centered on their respective means. "×" means that the connected variables and their interaction are included in the model. ":" represents the interaction between two variables. For example, yr×sc include year, species count, and their interaction, while "yr:sc" is the interaction between year and species count. A list of 352 data points fitted for each model was given in Table S9.

MLR	Coefficient of lm		Intercept		Significance effects ($P < 0.05$)	adj. R^2	AIC
	Point estimate	95% CI	Point estimate	95% CI			
fm30 lv=lm×yr×sc+ms	1.7921	(1.5724, 2.0119)	-0.2265	(-0.4435, -0.0094)	yr>0, ms<0, lm:yr<0, yr:sc<0, lm:yr:sc>0	0.9398	-185.48
fm36* lv=lm×yr×ms×sc	1.8637	(1.4031, 2.3243)	-0.2509	(-0.6847, 0.1829)	ms<0	0.9399	-179.12
fm35 lv=lm+yr×ms×sc	1.6300	(1.5554, 1.7047)	-0.1125	(-0.2286, 0.0035)	yr<0, ms<0, yr:ms>0, ms:sc:yr<0	0.9383	-176.83
fm31 lv=lm×yr×ms	1.7038	(1.6298, 1.7778)	-0.0795	(-0.1463, -0.0127)	yr<0, ms<0, lm:yr>0, yr:ms>0, lm:yr:ms<0	0.9375	-173.12
fm9 lv=lm×yr+ms	1.6975	(1.6295, 1.7654)	-0.0692	(-0.1334, -0.0049)	ms<0, yr<0, lm:yr>0	0.9369	-172.74
fm32 lv=lm×yr×ms+sc	1.6906	(1.6104, 1.7707)	-0.1204	(-0.2363, -0.0044)	yr<0, ms<0, lm:yr>0, yr:ms>0, lm:yr:ms<0	0.9374	-171.86
fm11 lv=lm×yr+ms+sc	1.6872	(1.6138, 1.7606)	-0.1045	(-0.2190, 0.0101)	yr<0, ms<0, lm:yr>0	0.9368	-171.29
fm27 lv=lm×yr+ms×sc	1.6810	(1.6069, 1.7551)	-0.1012	(-0.2158, 0.0134)	yr<0, ms<0, lm:yr>0	0.9369	-170.66
fm24 lv=lm+yr×sc+ms	1.6542	(1.5808, 1.7276)	-0.1226	(-0.2371, -0.0082)	yr<0, ms<0, yr:sc>0	0.9365	-169.64
fm28 lv=lm×ms+yr×sc	1.6476	(1.5693, 1.7259)	-0.1239	(-0.2386, -0.0092)	ms<0, yr<0, yr:sc>0	0.9364	-167.88
fm0 lv=lm	1.8774	(1.8200, 1.9348)	-0.2313	(-0.2874, -0.1751)	none	0.9217	-99.70

*Partitioning sum of squares among variables of fm 36 (sum of squares is listed in the corresponding parenthesis after each variable): lv = lm(223.929) + yr(0.001) + ms(0.738) + sc(0.028) + lm:yr(0.457) + lm:ms(0.078) + yr:ms(0.111) + lm:sc(0.189) + yr:sc(0.001) + ms:sc(0.002) + lm:yr:ms(0.113) + lm:yr:sc(0.000) + lm:ms:sc(0.082) + yr:ms:sc(0.053) + lm:yr:ms:sc(0.034) + error(8.585)

Table S6. Multiple linear regressions (MLRs) fitted to independent variable log(mean) (denoted by "lm") and dependent variable log(variance) (denoted by "lv") for fish number, with covariates year (denoted by "yr"), mesh size (denoted by "ms"), and species count (denoted by "sc"). Mesh size was treated as a categorical variable. MLRs with the 10 smallest AICs (in ascending order) and TPL (fm0) were shown. Intercept was included in every model. Years were centered on their mean. Significant effects of year and species count, if any, were shown. "×" and ":" were defined in Table S5. A list of 352 data points fitted for each model was given in Table S9.

MLR	Coefficient of lm		Intercept		Significance effects ($P <$ 0.05)	adj. R^2	AIC
	Point estimate	95% CI	Point estimate	95% CI			
fm30 lv=lm×yr×sc+ms	1.6925	(1.3797, 2.0053)	0.0318	(-0.3056, 0.3693)	yr>0, ms, lm:yr<0, yr:sc<0, lm:yr:sc>0	0.9400	-176.87
fm36* lv=lm×yr×ms×sc	-0.4493	(-1.6550, 0.7565)	1.8333	(0.7674, 2.8992)	sc<0, lm:sc>0	0.9485	-169.10
fm32 lv=lm×yr×ms+sc	2.1225	(1.8984, 2.3467)	-0.2934	(-0.5084, -0.0784)	sc>0	0.9425	-164.99
fm28 lv=lm×ms+yr×sc	2.0376	(1.8481, 2.2270)	-0.2597	(-0.4631, -0.0563)	yr<0, sc>0, yr:sc>0	0.9392	-164.98
fm9 lv=lm×yr+ms	1.7535	(1.6488, 1.8583)	0.1013	(0.0022, 0.2004)	yr<0, lm:y>0	0.9372	-164.64
fm11 lv=lm×yr+ms+sc	1.7421	(1.6360, 1.8483)	0.0233	(-0.1344, 0.1809)	yr<0, lm:yr>0	0.9373	-164.28
fm24 lv=lm+yr×sc+ms	1.7043	(1.5970, 1.8116)	0.0120	(-0.1460, 0.1699)	yr<0, yr:sc>0	0.9369	-162.20
fm31 lv=lm×yr×ms	2.1094	(1.8845, 2.3344)	-0.1385	(-0.2939, 0.0169)	none	0.9419	-162.19
fm14 lv=lm×ms+sc	2.0686	(1.8819, 2.2556)	-0.2201	(-0.4016, -0.0385)	sc>0	0.9379	-159.22
fm15 lv=lm×ms+yr+sc	2.0848	(1.8967, 2.2730)	-0.2838	(-0.4884, -0.0792)	sc>0	0.9380	-159.10
fm0 logV=logM	1.8774	(1.8200, 1.9348)	-0.2313	(-0.2874, -0.1751)	none	0.9217	-99.70

*Partitioning sum of squares among variables of fm 36 (sum of squares is listed in the corresponding parenthesis after each variable): lv = lm(223.929) + yr(0.001) + ms(1.097) + sc(0.034) + lm:yr(0.392) + lm:ms(0.382) + yr:ms(0.536) + lm:sc(0.065) + yr:sc(0.002) + ms:sc(0.306) + lm:yr:ms(0.251) + lm:yr:sc(0.001) + lm:ms:sc(0.454) + yr:ms:sc(0.397) + lm:yr:ms:sc(0.248) + error(6.309)

Table S7. Multiple linear regressions (MLRs) fitted to independent variable log(mean) (denoted by "lm") and dependent variable log(variance) (denoted by "lv") for fish weight, with covariates year (denoted by "yr"), mesh size (denoted by "ms"), and species count (denoted by "sc"). Mesh size was treated as a numerical variable. MLRs with the 10 smallest AICs (in ascending order) and TPL (fm0) were shown. Intercept was included in every model. Years and mesh sizes were centered on their respective means. "×" and ":" were defined in Table S5. A list of 352 data points fitted for each model was given in Table S9.

MLR	Coefficient of lm		Intercept		Significant effects ($P < 0.05$)	adj. R^2	AIC
	Point estimate	95% CI	Point estimate	95% CI			
fmw35 lv=lm+ms×sc×yr	1.3690	(1.2825, 1.4547)	1.7010	(1.4166, 1.9864)	sc>0, yr<0, ms:yr>0, sc:yr>0, ms:sc:yr<0	0.8420	-108.31
fmw36* lv=lm×yr×ms×sc	1.8610	(1.2294, 2.4932)	-1.0610	(-2.4215, 2.2093)	none	0.8434	-104.80
fmw24 lv=lm+yr×sc+ms	1.4061	(1.3204, 1.4917)	1.6307	(1.3462, 1.9153)	yr<0, sc>0, ms>0, yr:sc>0	0.8284	-82.29
fmw28 lv=lm×ms+yr×sc	1.4725	(1.3456, 1.5995)	1.3799	(0.9260, 1.8338)	yr<0, sc>0, yr:sc>0	0.8289	-82.27
fmw30 lv=lm×yr×sc+ms	1.7455	(1.2559, 2.2352)	0.4016	(-1.3728, 2.1761)	ms>0	0.8284	-79.33
fmw21 lv=lm+yr×sc	1.4763	(1.4043, 1.5482)	1.5313	(1.2520, 1.8106)	yr<0, yr:sc>0	0.8248	-75.88
fmw34 lv=lm×ms×sc+yr	2.0401	(1.5345, 2.5456)	-0.7087	(-2.5631, 1.1457)	ms<0, sc>0, lm:ms>0, lm:sc<0, ms:sc>0, lm:ms:sc<0	0.8266	-75.61
fmw33 lv=lm×ms×sc	2.0454	(1.5391, 2.5517)	-0.6718	(-2.5285, 1.1849)	ms<0, sc>0, lm:ms>0, lm:sc<0, ms:sc>0, lm:ms:sc<0	0.8260	-75.43
fmw6 ln=lm+ms+sc	1.4336	(1.3489, 1.5184)	1.5978	(1.3103, 1.8854)	ms>0, sc>0	0.8231	-73.45
fmw29 lv=lm×yr×sc	1.8556	(1.3673, 2.3440)	0.1522	(-1.6312, 1.9355)	none	0.8250	-73.33
fmw0 logV=logM	1.4794	(1.4068, 1.5520)	1.5830	(1.3192, 1.8468)	none	0.8207	-70.78

*Partitioning sum of squares among variables of fmw 36 (sum of squares is listed in the corresponding parenthesis after each variable): lv = lm(123.870) + yr(0.060) + ms(0.124) + sc(0.131) + lm:yr(0.534) + lm:ms(0.165) + yr:ms(0.028) + lm:sc(0.031) + yr:sc(0.264) + ms:sc(0.031) + lm:yr:ms(0.034) + lm:yr:sc(0.001) + lm:ms:sc(0.088) + yr:ms:sc(0.341) + lm:yr:ms:sc(0.023) + error(11.150)

Table S8. Multiple linear regressions (MLRs) fitted to independent variable log(mean) (denoted by "lm") and dependent variable log(variance) (denoted by "lv") for fish weight, with covariates year (denoted by "yr"), mesh size (denoted by "ms"), and species count (denoted by "sc"). Mesh size was treated as a categorical variable. MLRs with the 10 smallest AICs (in ascending order) and TPL (fm0) were shown. Intercept was included in every model. Years were centered on their mean. Significant effects of year and species count, if any, were shown. "×" and ":" were defined in Table S5. A list of 352 data points fitted for each model was given in Table S9.

MLR	Coefficient of lm		Intercept		Significance effects ($P < 0.05$)	adj. R^2	AIC
	Point estimate	95% CI	Point estimate	95% CI			
fmw35 lv=lm+ms×sc×yr	1.4117	(1.2795, 1.5439)	1.0114	(0.4247, 1.5982)	sc>0, yr<0, sc:yr>0	0.8480	-85.61
fmw28 lv=lm×ms+yr×sc	1.8961	(1.6804, 2.1118)	0.1923	(-0.4295, 0.8140)	sc>0, yr<0, sc:yr>0	0.8389	-84.55
fmw36* lv=lm×yr×ms×sc	0.8435	(-0.6692, 2.3563)	3.2020	(-1.1957, 7.6002)	lm:yr<0	0.8616	-84.00
fmw24 lv=lm+yr×sc+ms	1.5652	(1.4406, 1.6898)	1.1374	(0.7756, 1.4992)	yr<0, sc>0, yr:sc>0	0.8321	-80.17
fmw30 lv=lm×yr×sc+ms	1.8736	(1.3790, 2.3683)	0.0306	(-1.7467, 1.8080)	none	0.8323	-77.80
fmw15 lv=lm×ms+yr+sc	1.9579	(1.7428, 2.1730)	0.0326	(-0.5893, 0.6545)	yr<0, sc>0	0.8346	-76.01
fmw21 lv=lm+yr×sc	1.4763	(1.4043, 1.5482)	1.5313	(1.2520, 1.8106)	yr<0, yr:sc>0	0.8248	-75.88
fmw29 lv=lm×yr×sc	1.8556	(1.3673, 2.3440)	0.1522	(-1.6312, 1.9355)	none	0.8250	-73.33
fmw14 lv=lm×ms+sc	1.9458	(1.7297, 2.1618)	0.1620	(-0.4522, 0.7761)	sc>0	0.8327	-72.97
fmw7 lv=lm+yr+ms+sc	1.5923	(1.4675, 1.7172)	1.0787	(0.7145, 1.4429)	sc>0	0.8279	-72.52
fmw0 logV=logM	1.4794	(1.4068, 1.5520)	1.5830	(1.3192, 1.8468)	none	0.8207	-70.78

*Partitioning sum of squares among variables of fmw 36 (sum of squares is listed in the corresponding parenthesis after each variable): lv = lm(123.870) + yr(0.060) + ms(1.179) + sc(0.158) + lm:yr(0.545) + lm:ms(0.400) + yr:ms(0.385) + lm:sc(0.047) + yr:sc(0.246) + ms:sc(0.227) + lm:yr:ms(0.389) + lm:yr:sc(0.001) + lm:ms:sc(0.415) + yr:ms:sc(0.235) + lm:yr:ms:sc(0.446) + error(8.273)

Table S9. A list of 352 data points used in the fitting of multiple linear regression models in Tables S5-S8. For each unique combination of year and mesh size, the number of settings for fish number and the number of settings for fish weight are identical.

Year	Mesh size (mm)	Species Count	Log(mean number)	Log(variance of number)	Log(mean weight)	Log(variance of weight)	Number of settings
1962	102	6	1.1682	2.2628	4.2012	8.3302	26
1962	114	8	1.1419	1.9456	4.2163	8.0642	22
1962	127	9	0.9812	2.2026	4.1095	8.4085	26
1962	140	8	0.5754	1.2965	3.6974	7.4863	21
1962	152	8	0.6892	1.1565	3.8837	7.6508	18
1962	38	7	1.0696	2.1105	3.1254	6.8682	19
1962	51	8	1.5087	2.7937	3.8335	7.6888	27
1962	64	7	1.1695	2.1130	3.7218	7.2555	22
1962	76	9	1.0665	2.0945	3.8681	7.6975	26
1962	89	7	1.0775	2.1510	4.0608	8.1917	22
1972	114	10	1.0743	1.9038	3.7636	7.2270	15
1972	127	6	0.6752	1.0384	3.4757	6.7183	15
1972	51	9	1.8414	3.1003	3.8625	7.2237	15
1972	64	9	1.6064	2.7341	3.9422	7.3908	15
1972	76	9	1.2131	1.6272	3.7572	6.7592	15
1972	89	8	1.0170	1.4145	3.6037	6.6092	15
1973	102	8	1.1479	2.1365	3.7871	7.3090	17
1973	114	7	1.2289	2.2347	3.8575	7.4800	17
1973	127	8	0.9661	1.6972	3.7991	7.4639	16
1973	140	7	1.0460	1.9097	3.9190	7.5424	17
1973	152	6	0.6812	1.2728	3.6583	7.1069	15
1973	165	6	0.6434	1.3498	3.5421	6.9743	16
1973	178	5	0.5797	1.1067	3.3445	6.5123	17
1973	38	9	0.7597	1.3110	2.9303	5.6655	17
1973	51	9	1.8149	3.5628	3.8506	7.6610	17
1973	64	9	1.6949	3.0704	4.0138	7.7078	17
1973	76	11	1.2567	2.3047	3.7786	7.3204	23
1973	89	8	1.0483	2.1356	3.5805	7.0806	23
1974	102	9	1.3972	2.3138	4.1533	7.6899	23
1974	114	8	1.4532	2.4730	4.1919	7.9228	23
1974	127	10	1.4002	2.2809	4.2553	7.8594	23
1974	140	8	1.2797	2.0244	4.1855	7.7293	23
1974	152	9	1.0482	1.5287	4.0178	7.4627	17
1974	165	7	0.6068	0.9103	3.7984	7.3249	18
1974	178	5	0.2467	0.0760	3.4593	6.6085	23
1974	38	10	0.6081	1.4425	2.9296	6.1329	23
1974	51	8	1.7072	2.7970	3.8294	6.8904	23

1974	64	10	1.7366	2.9938	4.1449	7.7379	22
1974	76	12	1.5174	2.4715	4.1421	7.6845	17
1974	89	9	1.3269	2.0904	4.0378	7.4107	17
1975	102	10	1.4370	2.7338	4.1131	8.0081	17
1975	114	11	1.5542	2.8610	4.3223	8.3238	17
1975	127	8	1.4728	2.6492	4.3071	8.3109	17
1975	140	9	1.3672	2.5780	4.2452	8.2932	16
1975	152	7	1.0506	1.7998	3.9916	7.5772	17
1975	165	6	0.7150	0.9714	3.9297	7.5188	17
1975	178	5	0.6179	1.0067	3.6798	7.3497	17
1975	38	12	0.6799	2.3347	2.9754	5.7988	17
1975	51	10	1.7630	3.3083	3.8813	7.5273	31
1975	64	11	1.5619	2.8599	3.9211	7.5725	31
1975	76	9	1.3023	2.3974	3.8327	7.4636	31
1975	89	10	1.2933	2.3622	3.9100	7.4437	31
1976	102	12	1.4927	2.5473	4.1544	7.9117	29
1976	114	9	1.5007	2.6328	4.2470	8.1555	31
1976	127	10	1.3424	2.3099	4.2150	8.0424	26
1976	140	9	1.1971	1.9933	4.1448	7.8411	26
1976	152	8	0.8430	1.4597	3.9620	7.5528	31
1976	165	9	0.7987	1.3374	3.9138	7.4386	31
1976	178	8	0.6185	0.8930	3.9769	7.6169	31
1976	38	9	0.7312	1.8062	3.1041	6.6983	31
1976	51	12	1.7661	3.1116	3.7798	7.1131	30
1976	64	13	1.5473	2.6451	4.0345	7.5765	30
1976	76	12	1.3418	2.3410	3.9270	7.5224	30
1976	89	13	1.3957	2.4499	3.9716	7.6210	30
1977	102	14	1.4071	2.6239	4.0534	8.0231	28
1977	114	9	1.3418	2.4193	4.0963	7.8900	26
1977	127	9	1.1866	1.9758	4.0270	7.7041	21
1977	140	9	1.1249	1.9922	4.0859	7.8605	23
1977	152	5	0.8603	1.3315	3.9116	7.3316	29
1977	165	8	0.7582	1.1500	3.9985	7.6158	30
1977	178	4	0.4559	0.6927	3.8274	7.4303	29
1977	38	12	0.6952	1.5378	2.8662	5.8599	29
1977	51	12	1.7143	3.3348	3.7562	7.4961	31
1977	64	15	1.4077	2.7337	3.9203	7.7536	31
1977	76	15	1.2322	2.3249	3.7819	7.4578	31
1977	89	11	1.1525	2.3148	3.8011	7.7212	30
1978	102	11	1.3860	2.3862	4.0857	7.8102	31
1978	114	9	1.4068	2.3122	4.1530	7.8428	29
1978	127	7	1.2015	1.7003	3.9826	7.4189	27
1978	140	9	1.0086	1.8474	3.9183	7.6441	27
1978	152	8	0.8870	1.7426	3.8888	7.8185	31

1978	165	7	0.6679	1.2435	3.8135	7.3626	30
1978	178	7	0.3748	0.2689	3.6204	6.8540	31
1978	38	13	0.7939	1.6171	3.0755	6.0809	31
1978	51	12	1.6541	3.0496	3.6395	7.0215	30
1978	64	16	1.4723	2.6001	3.9930	7.5504	28
1978	76	14	1.2607	2.0818	3.8653	7.2859	28
1978	89	13	1.2810	2.2426	3.9623	7.7734	24
1979	102	12	1.0479	2.1729	3.7053	7.5551	25
1979	114	9	0.9367	1.7029	3.6741	7.2406	24
1979	127	12	0.8033	1.6516	3.6137	7.2234	18
1979	140	10	0.6284	1.1548	3.5245	6.9687	25
1979	152	8	0.5798	0.7597	3.5288	6.6472	31
1979	165	4	0.4831	0.5357	3.6060	6.9534	31
1979	178	6	0.3468	0.3150	3.5995	6.9618	26
1979	39	11	1.2864	2.4079	3.6421	6.5469	29
1979	51	10	1.2788	2.4722	3.3699	6.8086	29
1979	64	12	1.3418	2.6172	3.6903	7.4175	25
1979	76	13	0.8206	1.6217	3.3551	6.7626	24
1979	89	12	0.9509	1.9473	3.5820	7.1939	20
1980	102	10	1.0963	1.8524	3.7849	7.4766	22
1980	114	7	0.8169	1.4949	3.5666	7.1153	19
1980	127	8	0.6842	0.9632	3.4946	6.7677	29
1980	140	9	0.5051	0.9548	3.4852	6.7020	29
1980	152	8	0.4356	0.9065	3.5088	6.8889	27
1980	165	6	0.4135	0.8401	3.5131	7.0634	29
1980	178	5	0.3889	0.6687	2.9834	6.5555	28
1980	38	11	0.3933	0.4986	2.3238	4.6429	26
1980	51	12	1.5098	2.5723	3.5000	6.5191	25
1980	64	13	1.4880	2.5199	3.7596	7.0657	25
1980	76	12	1.0250	2.0570	3.5796	7.2881	21
1980	89	12	1.0030	1.5918	3.6343	7.0767	22
1982	102	9	1.1913	2.5388	3.8645	7.8892	19
1982	114	9	1.2534	2.4529	4.0439	7.9522	28
1982	127	9	1.0120	1.8236	3.9087	7.6581	29
1982	140	9	0.9009	1.7892	3.8824	7.8829	29
1982	152	6	0.4559	0.5597	3.6864	7.1643	28
1982	165	7	0.4964	0.5265	3.8166	7.0869	28
1982	178	6	0.4898	0.5068	3.7998	7.0689	27
1982	38	9	0.7626	1.5728	2.5896	4.8566	26
1982	51	14	1.5938	2.8631	3.6530	6.8990	26
1982	64	12	1.4132	2.4735	3.7849	7.1604	23
1982	76	11	1.1128	1.9215	3.6990	7.1360	22
1982	89	10	1.2377	2.2359	3.8416	7.4638	25
1983	102	11	1.2249	2.3158	3.9479	7.7059	28

1983	114	9	1.1261	2.0561	3.9204	7.6342	27
1983	127	9	0.9812	1.7908	3.8854	7.4465	27
1983	140	9	0.8330	1.5356	3.7938	7.4472	28
1983	152	10	0.5973	1.0537	3.7849	7.1349	27
1983	165	8	0.4569	0.6627	3.7004	7.2117	28
1983	178	7	0.4436	0.5664	3.6559	7.1358	26
1983	38	11	0.4594	0.5370	2.7451	5.8826	26
1983	51	10	1.5003	2.7456	3.5400	6.9259	23
1983	64	11	1.3468	2.0634	3.7340	6.9430	18
1983	76	11	1.2361	2.0637	3.8605	7.3418	19
1983	89	11	1.0700	1.9692	3.8170	7.5891	22
1984	102	11	1.2286	2.1583	3.9342	7.5885	28
1984	114	10	1.2876	2.2062	4.0485	7.7817	26
1984	127	10	1.0489	1.7525	3.9646	7.5676	28
1984	140	9	0.8281	1.5803	3.8385	7.6521	28
1984	152	9	0.6553	1.1678	3.8376	7.5237	26
1984	165	8	0.5301	0.9406	3.7484	7.2517	22
1984	178	8	0.3010	0.5082	3.6832	7.0116	24
1984	38	12	0.6166	1.5220	2.7378	6.0431	25
1984	51	11	1.7310	3.0137	3.7069	6.9400	22
1984	64	11	1.6120	2.8525	3.7282	7.0227	20
1984	76	12	1.2323	2.1161	3.7787	7.2980	17
1984	89	14	1.1923	2.1355	3.8654	7.4509	15
1985	102	12	1.1377	2.0265	3.9178	7.7759	24
1985	114	12	1.1903	2.0866	4.0205	7.7916	25
1985	127	13	1.0654	1.8842	4.0787	8.0032	25
1985	140	12	0.9405	1.6061	3.9601	7.6514	25
1985	152	11	0.8129	1.5560	3.9597	7.9935	25
1985	165	10	0.5911	0.8668	3.8012	7.3737	25
1985	178	6	0.5099	0.5956	3.8544	7.3799	26
1985	38	11	0.4960	1.1274	2.5907	5.4830	26
1985	51	17	1.5357	3.0621	3.6587	7.2741	25
1985	64	12	1.4588	2.5704	3.7462	7.4394	24
1985	76	13	1.3062	2.1793	3.8690	7.3756	21
1985	89	13	1.3255	2.3541	4.0112	7.8104	22
1986	102	14	1.5237	2.6945	4.2475	8.2204	26
1986	114	13	1.5175	2.4889	4.3317	8.1341	26
1986	127	12	1.3417	2.4190	4.2611	8.3212	26
1986	140	11	1.1978	1.9635	4.2147	8.0591	26
1986	152	9	0.8476	1.3687	4.0659	7.8017	28
1986	165	9	0.6612	0.9518	4.0021	7.5394	27
1986	178	4	0.5166	0.7719	3.9468	7.6498	27
1986	38	14	0.6070	1.0669	2.7506	5.9331	27
1986	51	18	2.0035	3.5384	4.0916	7.7346	27

1986	64	15	1.7010	3.1706	4.0595	7.9625	23
1986	76	14	1.4892	2.6319	4.0554	7.7921	18
1986	89	15	1.5745	2.8266	4.2412	8.2981	23
1987	102	12	1.4197	2.7939	4.0464	8.0140	28
1987	114	11	1.2830	2.4203	4.0402	7.9099	27
1987	127	9	1.1127	2.0367	3.9675	7.6886	28
1987	140	10	1.0586	1.7936	4.0122	7.7145	28
1987	152	9	0.6655	0.8505	3.8087	7.2689	25
1987	165	9	0.4771	0.7295	3.7401	7.3837	25
1987	178	5	0.3358	0.5367	3.7340	7.3010	25
1987	38	13	0.5016	0.7269	2.6653	5.2434	25
1987	51	15	1.5895	2.9101	3.6472	7.0089	25
1987	64	16	1.3947	2.4625	3.6812	7.1150	20
1987	76	13	1.3783	2.4841	3.8448	7.4287	17
1987	89	13	1.3737	2.4162	3.9831	7.7532	20
1988	102	12	1.2405	2.1887	3.9601	7.5477	25
1988	114	10	1.3071	2.3161	4.0960	7.8772	25
1988	127	9	1.1953	2.0606	4.0783	7.8035	25
1988	140	8	1.0035	1.7787	3.9687	7.6682	25
1988	152	9	0.7193	1.1175	3.8931	7.5440	24
1988	165	7	0.5740	0.7372	3.8339	6.9663	23
1988	178	4	0.2467	-0.0263	3.6260	6.8305	24
1988	38	15	0.5502	0.6800	2.9217	5.9535	22
1988	51	16	1.6927	3.1969	3.7875	7.1571	22
1988	64	17	1.4863	2.7072	3.8643	7.5071	19
1988	76	16	1.3902	2.3055	3.8937	7.4149	15
1988	89	13	1.4216	2.4112	4.0459	7.7151	20
1989	102	14	1.2272	2.0208	3.9407	7.5147	25
1989	114	11	1.1946	2.0473	3.9970	7.6326	25
1989	127	12	1.2240	1.9411	4.1134	7.7196	25
1989	140	9	0.9608	1.4650	4.0241	7.6027	25
1989	152	8	0.6704	1.1323	3.8386	7.4488	17
1989	165	9	0.5408	0.8407	3.8278	7.4451	20
1989	178	8	0.3802	0.3802	3.6844	7.0392	18
1989	38	13	0.4983	0.4418	2.5956	5.0788	17
1989	51	16	1.9176	3.4606	4.0025	7.6458	17
1989	64	14	1.7924	3.3500	4.1409	7.9730	17
1989	76	16	1.7065	2.9251	4.1387	7.8106	17
1989	89	14	1.6132	2.8622	4.1784	7.9366	15
1990	102	8	1.0640	1.8365	3.8152	7.1780	18
1990	114	10	0.8893	1.4630	3.7147	7.0212	20
1990	127	9	0.9976	1.6287	3.9182	7.4358	20
1990	140	9	0.7091	0.8954	3.7909	6.9884	29
1990	152	8	0.5689	0.9082	3.7557	7.3727	30

1990	165	7	0.5477	0.6299	3.9018	7.2561	29
1990	178	4	0.5019	0.5477	3.9355	7.3555	28
1990	38	12	0.5482	1.2548	2.7819	6.1251	22
1990	51	13	1.6956	2.7728	3.7280	6.8303	26
1990	64	13	1.3669	2.5987	3.8004	7.1236	23
1990	76	12	1.2695	2.2319	3.8342	7.3108	26
1990	89	9	1.2188	2.0943	3.8651	7.3809	30
1991	102	12	1.0866	2.1085	3.9106	7.7395	30
1991	114	10	1.0267	2.0055	3.9174	7.7882	30
1991	127	9	0.9576	1.7729	3.8887	7.5668	29
1991	140	10	0.8153	1.6503	3.8911	7.7557	24
1991	152	9	0.6070	0.7604	3.8253	7.2803	24
1991	165	8	0.5041	0.7665	3.8411	7.4013	24
1991	178	8	0.4376	0.6595	3.8611	7.5917	24
1991	38	11	0.7217	1.3910	2.7618	5.3160	23
1991	51	13	1.7191	3.1071	3.7227	7.1156	22
1991	64	11	1.3490	2.4229	3.8037	7.3349	23
1991	76	12	1.2908	2.4206	3.8954	7.6920	22
1991	89	11	1.2756	2.3473	4.0303	7.9745	23
1992	102	11	1.1027	2.0162	3.8423	7.4968	24
1992	114	10	1.1222	2.0289	3.9383	7.7222	24
1992	127	10	1.1409	2.1901	4.0309	8.0021	23
1992	140	9	0.9927	1.9957	4.0503	8.0913	27
1992	152	10	0.7718	1.5348	3.8762	7.6275	27
1992	165	7	0.4135	0.5430	3.7431	7.1563	25
1992	178	7	0.3786	0.4867	3.7845	7.2941	26
1992	38	13	0.8671	1.3490	3.1130	6.4789	23
1992	51	15	1.7211	3.0139	3.8424	7.2820	21
1992	64	15	1.5389	2.7986	3.8940	7.4494	19
1992	76	14	1.4115	2.6684	3.9223	7.7126	27
1992	89	12	1.3658	2.5943	4.0169	7.9023	27
1993	102	13	1.1427	2.1002	3.8093	7.3501	26
1993	114	11	1.1461	2.0929	3.9145	7.5634	27
1993	127	11	1.0382	1.6515	3.9003	7.3640	27
1993	140	11	0.8904	1.3569	3.8951	7.5420	28
1993	152	9	0.6677	1.1128	3.8207	7.3698	28
1993	165	10	0.4771	0.7634	3.7759	7.3627	28
1993	178	6	0.3840	0.4660	3.7800	7.2515	28
1993	38	15	0.9011	1.6660	3.0469	5.9198	28
1993	51	16	1.7188	3.3208	3.8343	7.5077	23
1993	64	17	1.6830	3.0246	4.0148	7.6681	20
1993	76	17	1.5077	2.6488	3.9503	7.5530	27
1993	89	15	1.3215	2.3382	3.9383	7.5205	29
1994	102	14	1.4629	2.4655	4.0948	7.7703	29

1994	114	13	1.3034	2.1362	3.9849	7.4662	29
1994	127	12	1.2080	2.0548	4.0476	7.7542	29
1994	140	9	1.0015	1.6617	3.9745	7.6825	27
1994	152	9	0.5822	1.1370	3.7178	7.4984	27
1994	165	9	0.4307	0.6063	3.6972	7.2448	28
1994	178	8	0.4033	0.7899	3.5454	7.1366	28
1994	38	14	0.7991	1.6508	2.8248	5.7314	27
1994	51	16	2.0359	3.6307	4.0774	7.7729	26
1994	64	18	1.7984	3.2584	4.0775	7.8262	25
1994	76	16	1.5821	2.7637	4.0203	7.5697	24
1994	89	16	1.5483	2.7655	4.0969	7.8092	28
1995	102	12	1.1772	2.1969	3.8654	7.4804	28
1995	114	11	1.2426	2.0821	4.0512	7.6999	27
1995	127	13	1.2948	2.4250	4.1343	8.1202	28
1995	140	11	1.0593	1.9660	4.0276	7.8699	16
1995	152	11	0.7590	1.3740	3.9001	7.7587	17
1995	165	6	0.5673	1.1505	3.8792	7.6547	17
1995	178	7	0.5263	0.9374	3.9341	7.8965	16
1995	38	11	0.7959	1.4862	2.7684	5.4906	15
1995	51	14	1.5283	3.0177	3.5973	7.0527	16
1995	64	15	1.6173	3.4597	3.9213	7.9539	16
1995	76	13	1.5869	3.1703	3.9999	7.9449	17
1995	89	12	1.2738	2.5726	3.8545	7.5989	17
1996	102	13	1.2288	2.4400	4.0226	8.0588	17
1996	114	11	1.2933	2.3990	4.1348	8.1001	16
1996	127	10	1.4526	2.6560	4.3262	8.4031	18
1996	140	8	1.2928	2.5227	4.2525	8.4483	18
1996	152	9	1.0719	1.7315	4.2476	8.0503	18
1996	165	9	1.0653	1.8355	4.1899	8.0667	18
1996	178	8	0.7304	1.2385	4.1178	8.0926	17
1996	38	15	1.3337	2.5335	3.4235	6.8752	15
1996	51	17	1.5805	2.8193	3.8962	7.7397	18
1996	64	15	1.4453	2.6783	3.9475	8.1101	19
1996	76	14	1.4237	2.6275	4.0026	8.0177	18
1996	89	13	1.3836	2.6881	4.1047	8.4509	18
1997	102	11	1.2998	2.4269	4.0190	7.8262	18
1997	114	12	1.4103	2.7283	4.2614	8.4145	18
1997	127	11	1.4921	2.7660	4.3541	8.5031	16
1997	140	11	1.3565	2.4531	4.3281	8.4512	16
1997	152	11	1.1778	2.0030	4.2534	8.1816	16
1997	165	9	0.8884	1.1902	4.1135	7.7841	16
1997	178	8	0.6081	0.8800	3.9949	7.6941	15
1997	38	18	1.8237	3.6713	4.1938	9.0324	16
1997	51	15	1.9577	3.7935	4.1334	8.1860	16

1997	64	16	1.8478	3.5931	4.2716	8.4222	16
1997	76	15	1.7818	3.5014	4.2463	8.3651	16
1997	89	14	1.5258	2.7615	4.1610	7.9112	16
1998	102	13	1.4780	2.5562	4.2100	8.0166	16
1998	114	13	1.4643	2.6579	4.2704	8.2939	16
1998	127	12	1.4529	2.6152	4.2969	8.4185	16
1998	140	11	1.3582	2.3889	4.3305	8.3872	16
1998	152	12	1.2488	2.2613	4.3168	8.4088	16
1998	165	10	1.2110	2.2338	4.2138	8.0564	16
1998	178	8	1.2033	2.2157	4.3087	8.4566	16
1998	38	12	2.0286	3.7252	3.8627	7.3977	16
1998	51	15	2.0631	3.8140	4.1857	8.0754	16
1998	64	14	1.9288	3.5938	4.2601	8.2304	16
1998	76	15	1.7076	3.3470	4.1907	8.3019	16
1998	89	15	1.5630	2.7811	4.2310	8.1221	16
1999	102	13	1.5402	2.4967	4.2608	7.9553	20
1999	114	11	1.4253	2.6923	4.2451	8.3547	20
1999	127	11	1.5035	2.6756	4.3711	8.3808	20
1999	140	12	1.2928	2.1698	4.2439	8.0818	19
1999	152	10	1.1886	2.0929	4.2520	8.2838	19
1999	165	10	1.0487	1.7774	4.2168	8.1661	20
1999	178	10	0.7453	1.3263	4.0456	7.9745	18
1999	38	12	1.7186	3.2848	3.7226	7.2933	20
1999	51	16	2.0925	3.7649	4.2968	8.2430	20
1999	64	15	1.9817	3.6784	4.3708	8.4503	20
1999	76	13	1.8117	3.3526	4.3155	8.2794	20
1999	89	15	1.5945	2.8158	4.2265	8.0358	20
2000	102	14	1.2122	2.3114	3.9671	7.7506	17
2000	114	10	1.2430	2.4239	4.0484	7.9962	16
2000	127	11	1.1973	2.1887	4.0249	7.8799	17
2000	140	10	1.1106	1.9486	4.0523	7.8557	16
2000	152	8	1.0811	1.8728	4.0930	7.9822	16
2000	165	10	0.8261	1.5039	4.0084	7.9774	15
2000	178	6	0.7085	1.0744	3.9005	7.4973	16
2000	38	10	1.6646	3.4125	3.5897	7.2291	16
2000	51	13	1.9985	3.8249	4.2100	8.2712	16
2000	64	13	1.7143	3.2682	4.1247	8.0208	16
2000	76	12	1.4556	2.9387	3.9823	7.8585	15
2000	89	13	1.3444	2.5780	4.0225	7.7741	18
2001	102	11	0.7333	1.0110	3.5922	6.8662	20
2001	114	9	0.7915	1.1902	3.6912	6.9715	19
2001	127	8	0.8070	1.1835	3.6926	6.9233	16
2001	140	7	0.7690	1.2283	3.7028	7.0384	18
2001	152	7	0.6410	0.7033	3.6651	7.1038	17

2001	165	8	0.5643	0.7951	3.7350	7.0083	15
2001	178	5	0.7084	1.0799	3.6854	7.0511	16
2001	38	11	1.3617	2.6429	3.2574	6.3846	17
2001	51	12	1.6778	3.1170	3.7738	7.1772	16
2001	64	10	1.3024	2.0427	3.8871	7.2482	18
2001	76	9	1.0536	1.5670	3.7094	6.9172	14
2001	89	10	0.9103	1.4931	3.7121	7.2446	19

Supplementary figures S1-S10

Figure S1

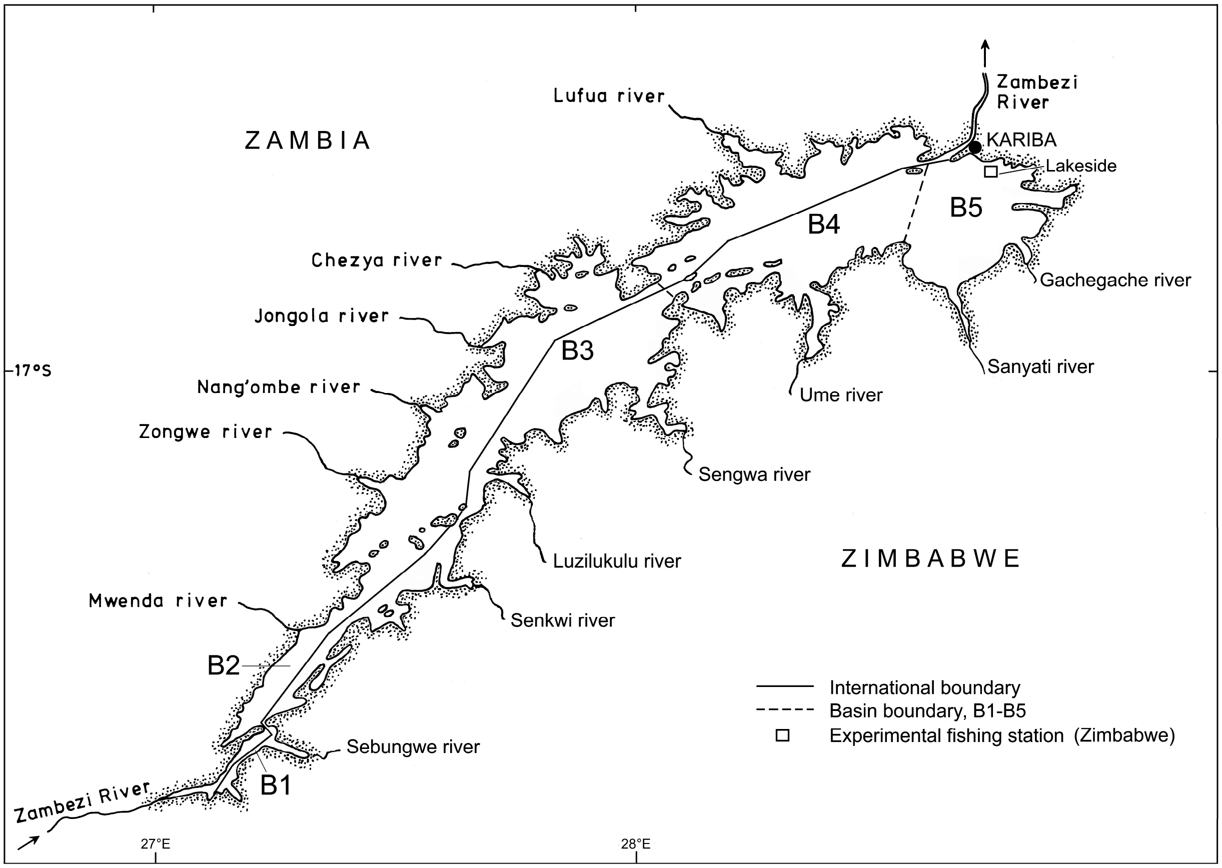


Figure S1. Map of man-made Lake Kariba on the Zambezi River between Zambia and Zimbabwe, and the location of the Lakeside gillnet sampling site (open square) in basin 5 near Kariba town.

Figure S2

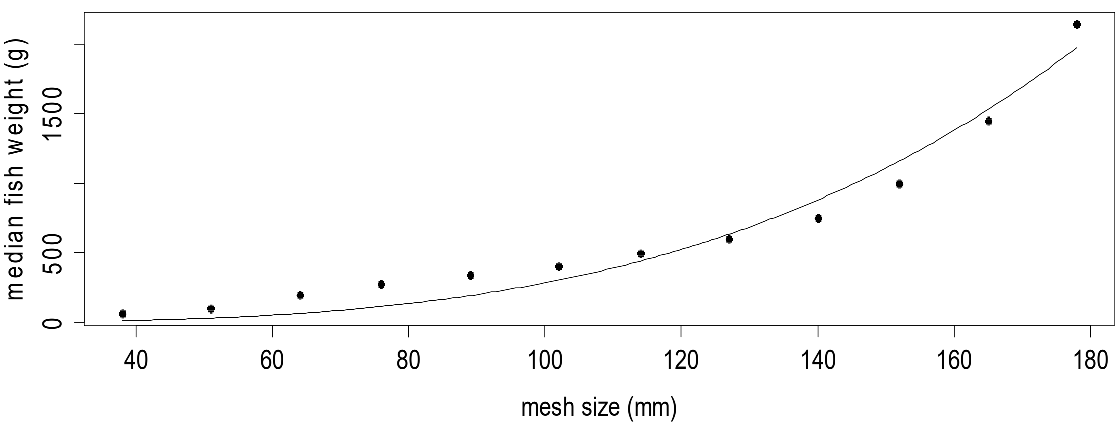
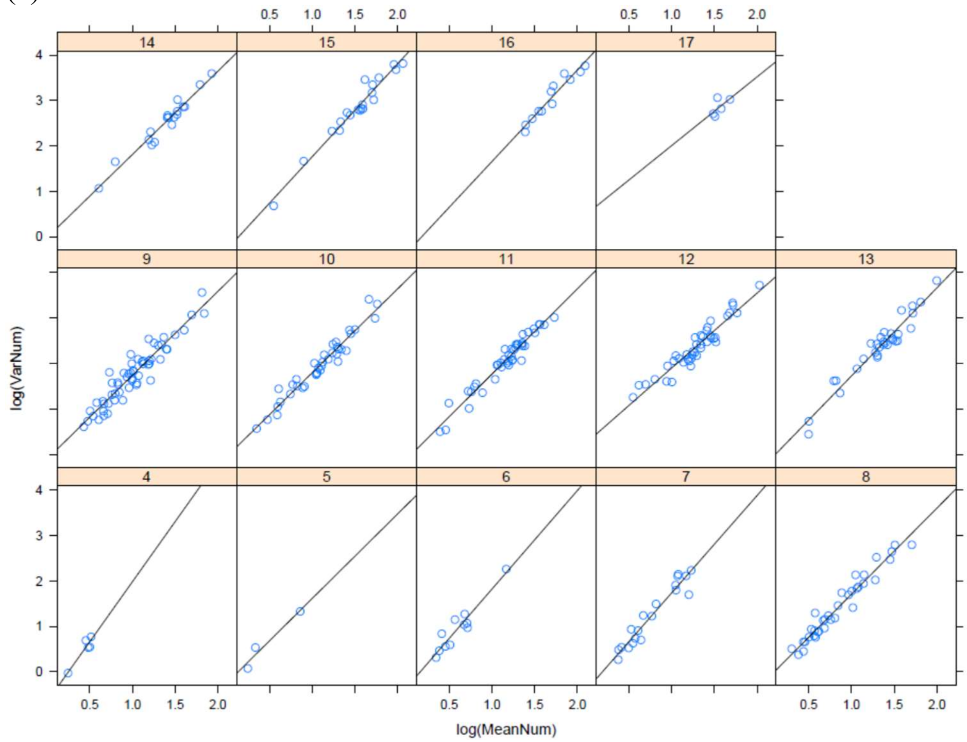


Figure S2. Median individual fish weight (g) against mesh size (mm). The solid curve is the least-squares nonlinear regression curve: median fish weight = 5.0450×10^{-5} $(2.8600\times10^{-8}, 1.0087\times10^{-4})$ × [mesh size]$^{3.3740\ (-0.0003,\ 6.7483)}$. In parentheses, the CI follows the point estimate of corresponding parameter. Regression parameters were estimated using the "nls" function in R 3.2.0 (R Core Team 2015).

Figure S3

(a)



(b)

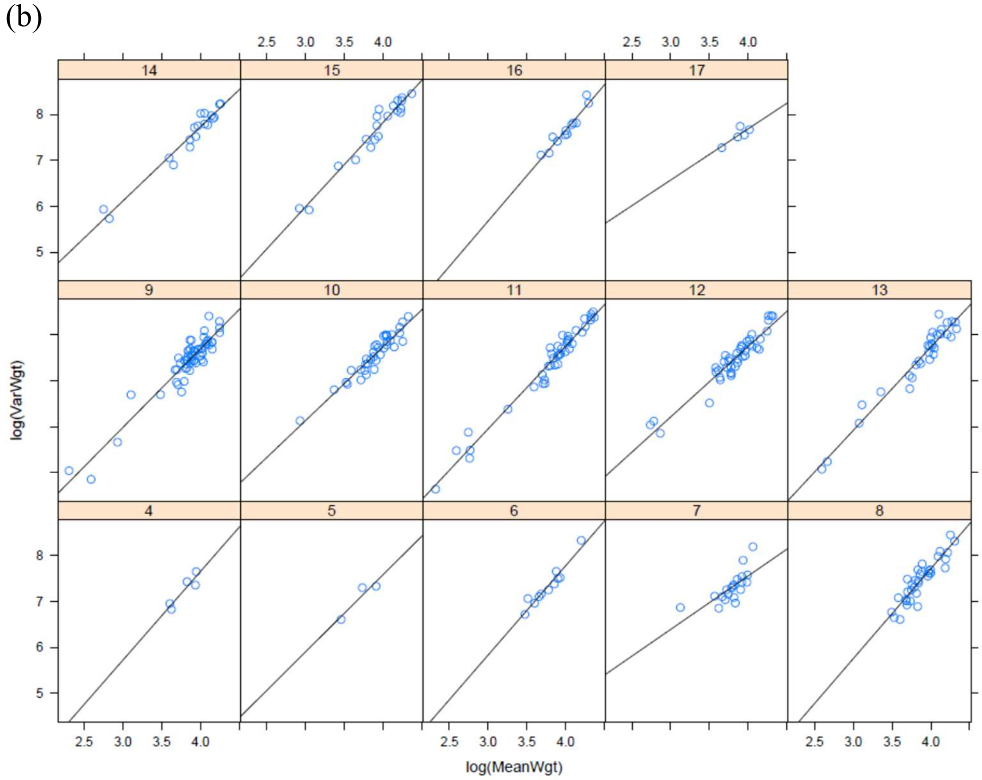


Figure S3. Log(variance) as a function of log (mean) by species count (across all combinations of years and mesh sizes [mm]) when fish abundance was measured by number (a) and weight (g) (b). Blue circles and black solid lines are defined in the legend of Fig. 2.

Figure S4

(a) (b)

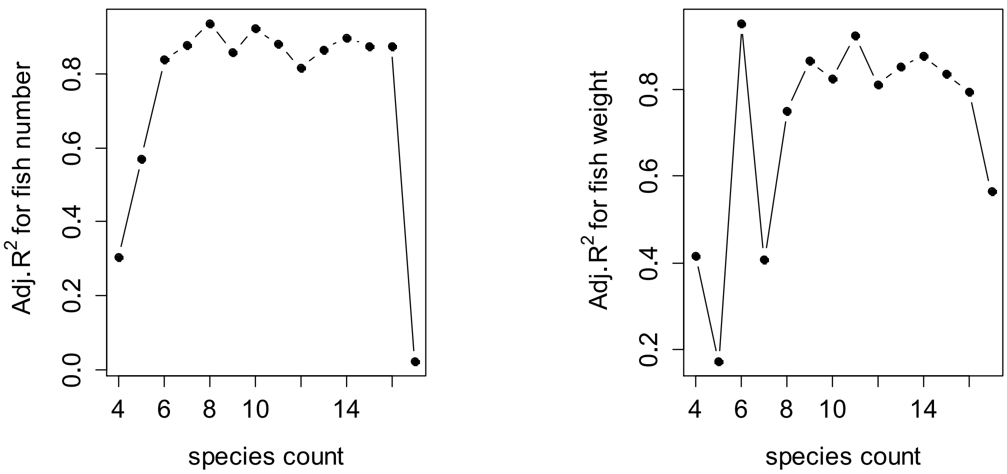


Figure S4. Adj. R^2 of fitted linear regressions when log(mean)-log(variance) pairs were grouped by species counts (across all mesh-size × year combinations). Fish abundance was measured by number (a) and weight (g) (b).

Figure S5

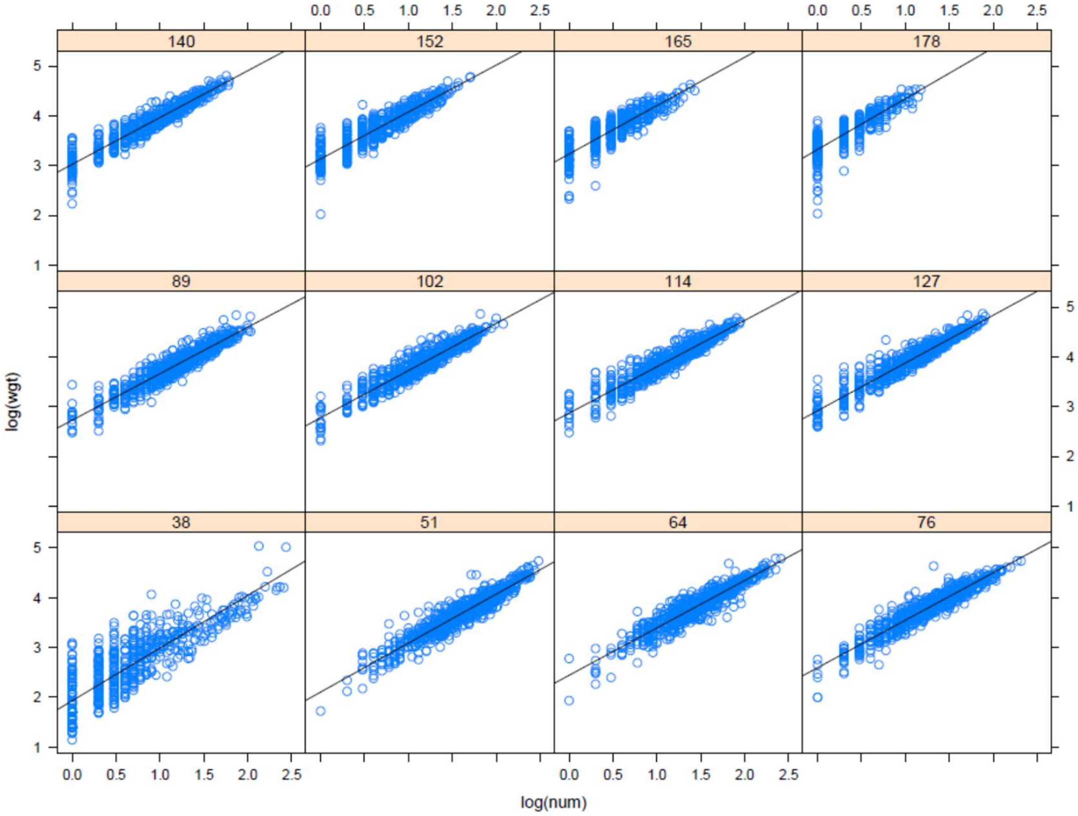


Figure S5. Log(aggregate weight [g] of fish per setting) as a function of log(number of fish per setting) for each mesh size (mm) separately. Solid black lines are least-squares linear regression lines showing the weight-number power law (eqn A4). Regression statistics were reported in Table 2.

Figure S6

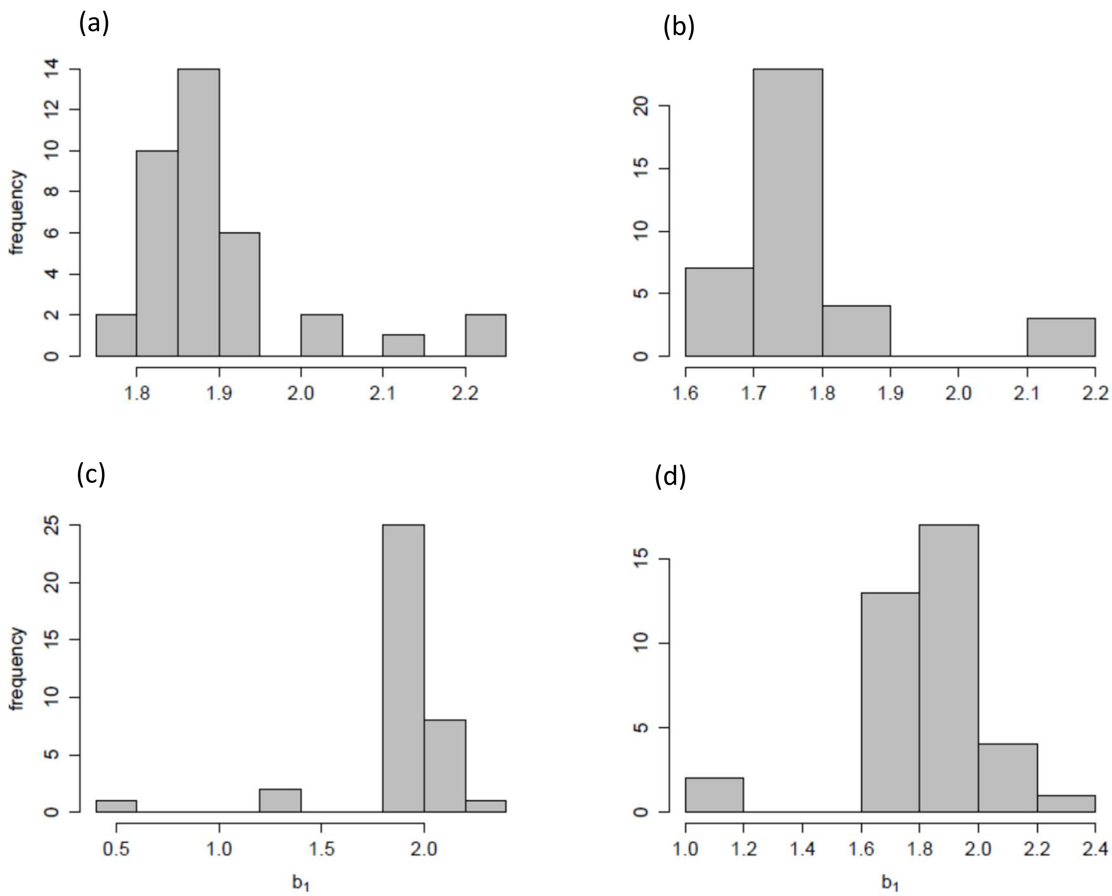


Figure S6. Frequency distributions of estimates of the coefficient of log(mean) from all possible 36 multiple linear regressions (MLRs). Fish abundance was measured by number (a, c) and weight (g) (b, d). Mesh size (mm) was treated as a numerical variable (a, b) and as a categorical variable (c, d).

Figure S7

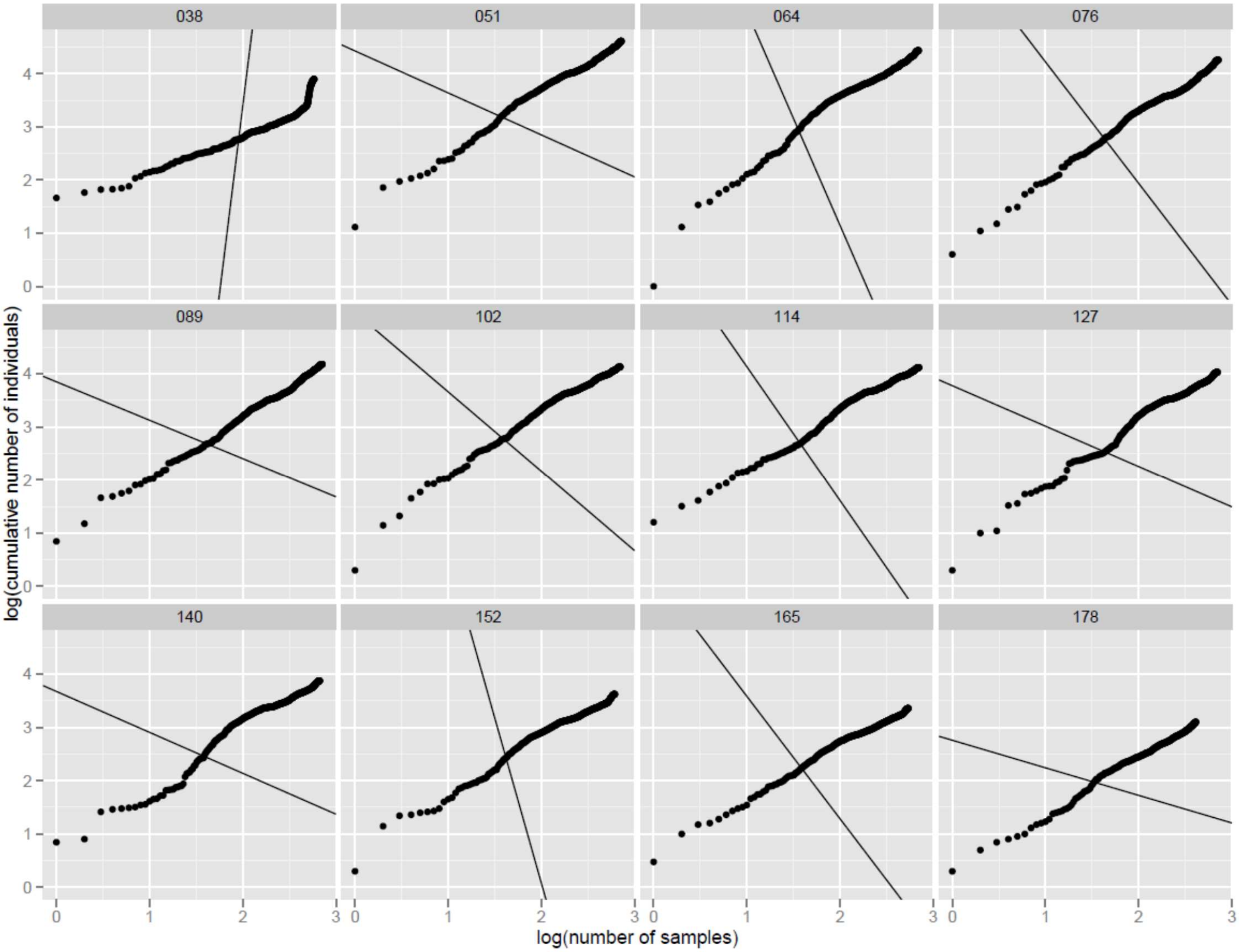
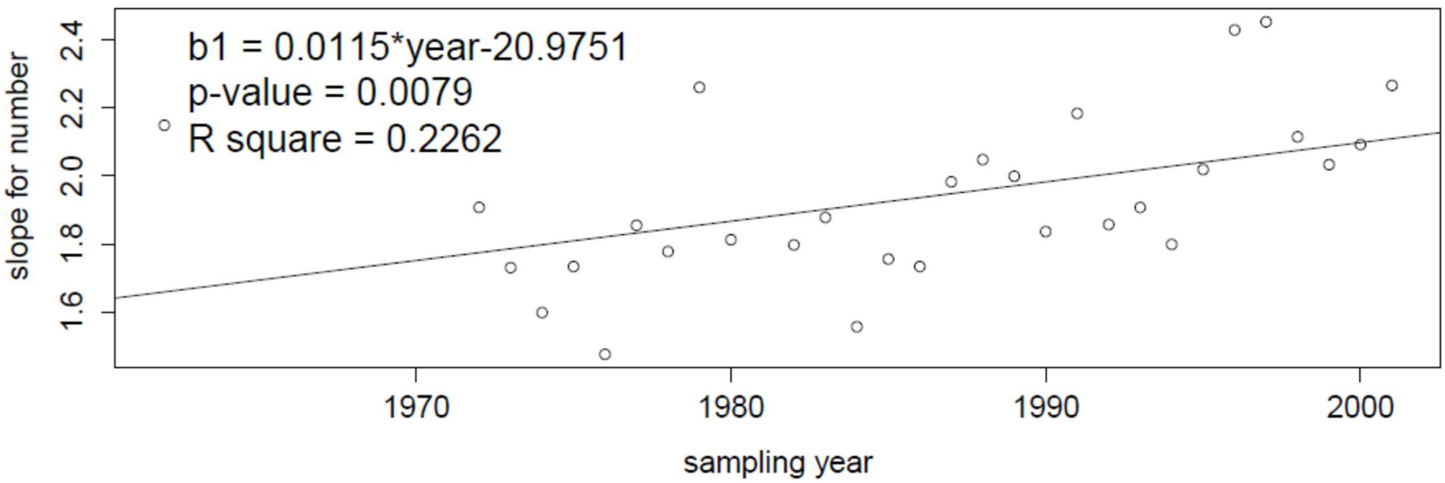


Figure S7. Log(cumulative number of individuals) against log(number of samples) for each mesh size. Straight solid lines, solid circles, and intersection points are defined in the legend of Fig. 5. For each mesh size, settings were accumulated in chronological order.

Figure S8

(a)



(b)

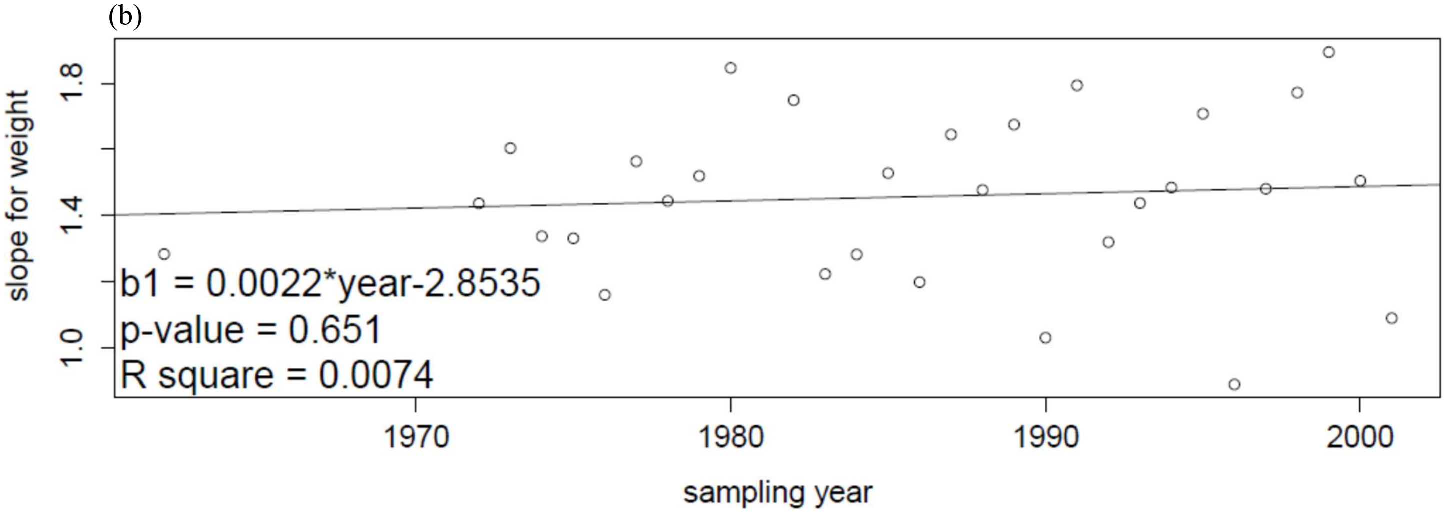
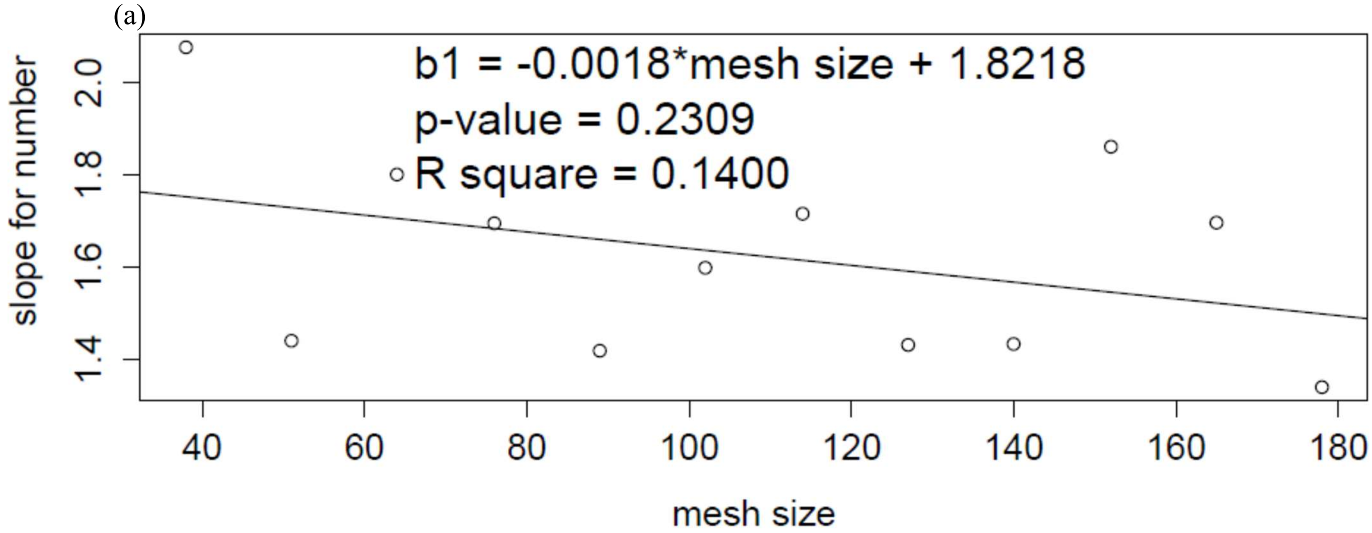


Figure S8. Estimates of TPL's slope (b_1 in eqn 1) against sampling year using number (a) and weight (b) as abundance measure separately. Least-squares linear regression equations and the corresponding P and R^2 are shown in the plot.

Figure S9

(a)



(b)

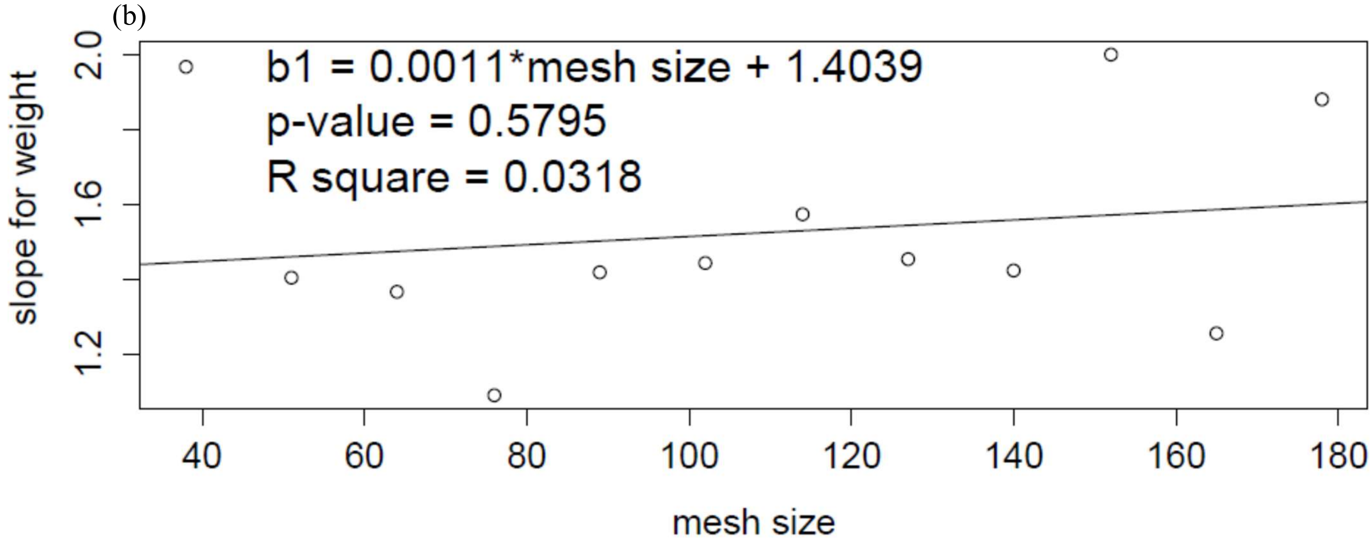


Figure S9. Estimates of TPL's slope (b_1 in eqn 1) against mesh size using number (a) and weight (b) as abundance measure separately. Least-squares linear regression equations and the corresponding P and R^2 are shown in the plot.

Figure S10

(a)

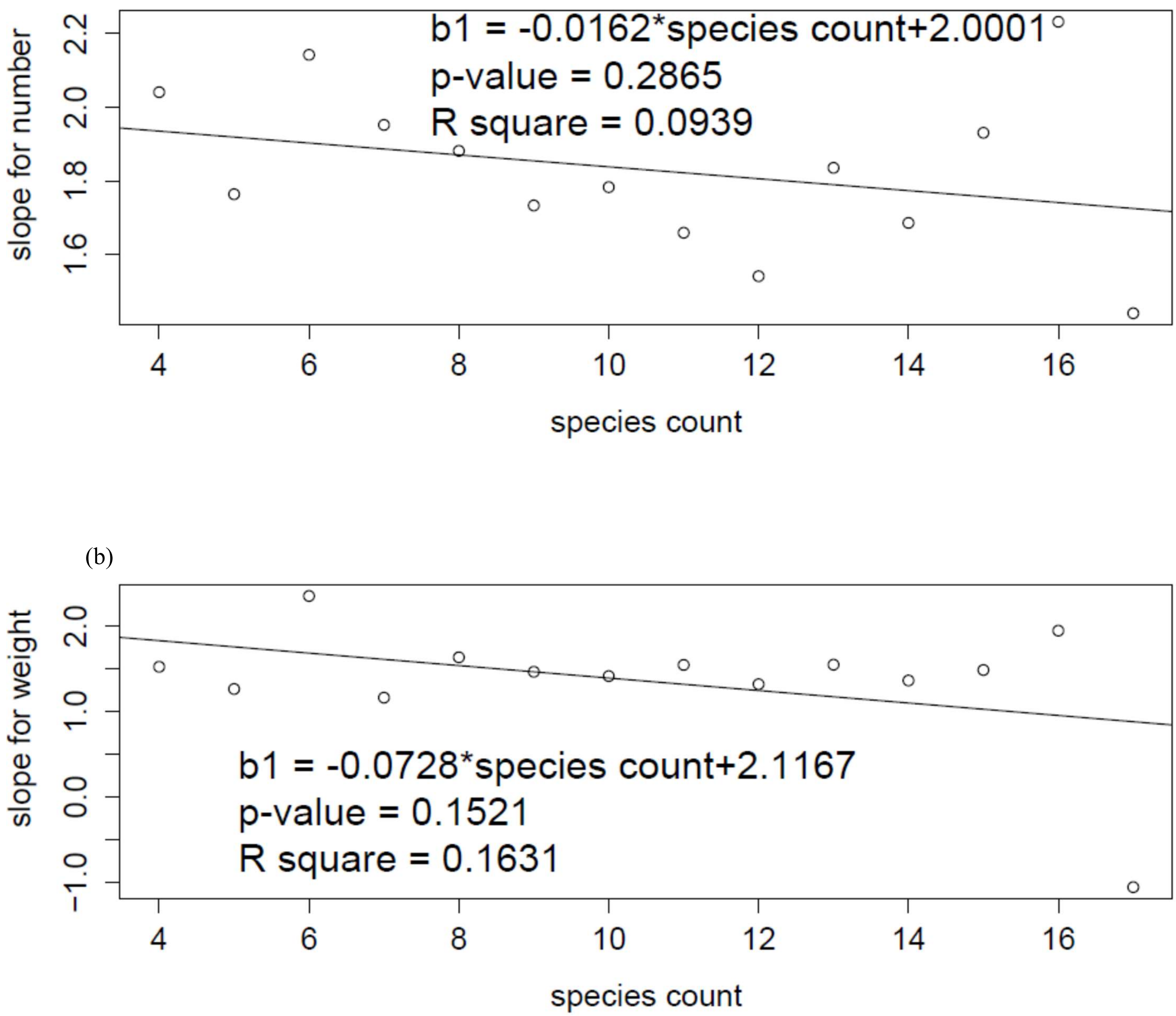


Figure S10. Estimates of TPL's slope (b_1 in eqn 1) against species count using number (a) and weight (b) as abundance measure separately. Least-squares linear regression equations and the corresponding P and R^2 are shown in the plot.