

Testing and recommending methods for fitting size spectra to data

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Summary

1. The size spectrum of an ecological community characterizes how a property, such as abundance or biomass, varies with body size. Size spectra are often used as ecosystem indicators of marine systems. They have been fitted to data from various sources, including groundfish trawl surveys, visual surveys of fish in kelp forests and coral reefs, sediment samples of benthic invertebrates and satellite remote sensing of chlorophyll.

2. Over the past decades, several methods have been used to fit size spectra to data. We document eight such methods, demonstrating their commonalities and differences. Seven methods use linear regression (of which six require binning of data), while the eighth uses maximum likelihood estimation. We test the accuracy of the methods on simulated data.

3. We demonstrate that estimated size-spectrum slopes are not always comparable between the seven regression-based methods because such methods are not estimating the same parameter. We find that four of the eight tested methods can sometimes give reasonably accurate estimates of the exponent of the individual size distribution (which is related to the slope of the size spectrum). However, sensitivity analyses find that maximum likelihood estimation is the only method that is consistently accurate, and the only one that yields reliable confidence intervals for the exponent.

4. We therefore recommend the use of maximum likelihood estimation when fitting size spectra. To facilitate this, we provide documented R code for fitting and plotting results. This should provide consistency in future studies and improve the quality of any resulting advice to ecosystem managers. In particular, the calculation of reliable confidence intervals will allow proper consideration of uncertainty when making management decisions.

Key-words: abundance size spectrum, biomass size spectrum, bounded power-law distribution, ecosystem approach to fisheries, ecosystem indicators, individual size distribution, truncated Pareto distribution

Introduction

For aquatic ecosystems, size-based indicators are tools for understanding food-web structure and enabling cost-effective monitoring (Shin *et al.* 2005). One indicator, the size spectrum (Sheldon & Parsons 1967; Sheldon, Prakash & Sutcliffe Jr. 1972), has been adopted by several fields in ecology as a method of quantifying the distribution of body size, or other biological or ecological traits, across a community. Size spectra are commonly used to examine fishing impacts at the community or ecosystem level (Rice & Gislason 1996; Bianchi *et al.* 2000; Shin *et al.* 2005; Law, Plank & Kolding 2012; Jacobsen, Gislason & Andersen 2014; Thorpe *et al.* 2015) and have been

more broadly used in analyses of macroecological patterns (Jennings *et al.* 2008; Reuman *et al.* 2008) and dynamical food web models (Blanchard *et al.* 2009; Hartvig, Andersen & Beyer 2011). Despite the widespread use of the size spectrum, its success as a general tool in marine and terrestrial ecology has been hampered by confusion surrounding its definition (White *et al.* 2007) and by methodological inconsistencies in how it is fitted to data (Vidondo *et al.* 1997).

For a fish community, Rice & Gislason (1996) define size spectra as generally being ‘the variation in a community property across the size range of fish in the community’. This allows for different types of spectra, such as the traditional biomass size spectrum (Boudreau & Dickie 1992) the abundance size spectrum (Rice & Gislason 1996) and the diversity size spectrum (Reuman *et al.* 2014).

White *et al.* (2007) give a more specific definition of a size spectrum as the relationship between the number of

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individuals in a body-size class and the average size of that body-size class. Typically, the pattern is linear on logarithmic axes and is quantified by the slope, which ideally should be uniquely defined. However, if the same data set (e.g. individual body masses of fish in a community) is given to two researchers, under current practices it is not clear that they would obtain the same value for the slope of the size spectrum. This is because there are usually choices to be made in determining the slope: (i) how to define the size classes to bin the data, and (ii) how to plot the binned data.

White *et al.* (2007) point out that the size spectrum is, more generally, a frequency distribution or probability density of body sizes of individuals in a community and recommend the term ‘individual size distribution’ (ISD). We adopt this approach because it moves away from the need to define somewhat arbitrary body-size classes. By thinking of body-size data as individual measurements drawn from a probability distribution, we can fit the distribution using likelihood methods (which do not require binning), to give a uniquely defined parameter that is analogous to the size-spectrum slope.

To determine such a parameter requires specifying a probability distribution for the ISD. Size spectra typically exhibit power-law relationships (Platt & Denman 1978; Boudreau & Dickie 1992; White *et al.* 2007; Reuman *et al.* 2008). For example, in community size-spectrum models ‘the number of individuals in each size group is often found to exhibit a power-law relationship with size’ (Andersen & Beyer 2006), and in empirical studies, fitting of straight lines on logarithmic axes implicitly implies the fitting of a power-law relationship (Newman 2005). Therefore, a power-law distribution (or Pareto distribution or Zipf’s law; Newman 2005) is the distribution to be specified; Vidondo *et al.* (1997) recommended thinking about size spectra in such a context. Specifically, we specify a bounded (truncated), rather than the usual unbounded, power-law distribution (see Materials and methods).

Here, we describe and test eight different methods that have been used to fit size spectra. Six of these methods require binning the data in some way, plotting the binned data and fitting a linear regression. The seventh involves no binning and fits a linear regression to all data points, while the eighth involves maximizing the likelihood of a distribution. Using simulated data, we test the accuracy of each method in determining point estimates and confidence intervals for the exponent of the ISD.

Our results first demonstrate that estimated slopes are not always comparable between regression-based methods because the different methods are not estimating the same parameter, even though this may have been assumed or implied in the past. However, for most methods the estimated slopes can be adjusted to provide comparable estimates of the exponent of the ISD. Some methods perform much better than others, but sensitivity analyses show that maximum likelihood estimation is the only method that is consistently accurate, and the only one that yields reliable confidence intervals. We also extend it to deal with data that are only available in binned form.

Therefore, we recommend maximum likelihood estimation, in contrast to previous advice (Vidondo *et al.* 1997). Since this method is computationally more complicated than the

regression-type approaches, in the Data S1 (Supporting Information) we provide fully documented and functionalized R code (R Core Team, 2015) intended to be used by other researchers to reproduce our results and to apply methods to their own data.

Materials and methods

INDIVIDUAL SIZE DISTRIBUTION

Let the random variable X represent the body mass of an individual fish (or other organism). Considering X to come from a bounded power-law (PLB) distribution, the probability density function for X is:

$$f(x) = Cx^b, \quad x_{\min} \leq x \leq x_{\max}, \quad \text{eqn 1}$$

where

$$C = \begin{cases} \frac{b+1}{x_{\max}^{b+1} - x_{\min}^{b+1}}, & b \neq -1, \\ \frac{1}{\log x_{\max} - \log x_{\min}}, & b = -1, \end{cases} \quad \text{eqn 2}$$

x represents possible values of X , \log is the natural logarithm, b is an exponent and x_{\min} and x_{\max} are the minimum and maximum possible values of body mass (with $0 < x_{\min} < x_{\max}$). The normalization constant C is calculated by solving $\int_{x_{\min}}^{x_{\max}} f(x) dx = 1$. Assuming that the body mass of each individual fish is independently distributed according to (1) means that (1) is the ISD. Because of the normalization constant, the ISD describes the shape of the size spectrum independently of the total abundance of fish. The ISD is characterized by the exponent b that needs to be estimated from data. This exponent is expected to be negative, and it can be related to the slope of the size spectrum, though exactly how depends on the method used to estimate the slope (see Results). A steepening slope (e.g. due to selective fishing of larger fish) corresponds to a more negative b .

We use a bounded rather than unbounded ($x_{\max} \rightarrow \infty$) distribution for several reasons. By definition, the unbounded distribution assumes that individuals can, and occasionally will, attain extremely large body masses, even though such body masses are unrealistic. In related tests of the distribution of the mean body masses of species, the bounded power law had overwhelmingly more support than the unbounded power law (Reuman *et al.* 2008) – real biological data inherently have an upper bound. Also, ecological surveys are often designed to sample a specific range of body sizes, leading to size spectra being fit across a finite range (e.g. Dulvy *et al.* 2004; Trebilco *et al.* 2015), so a bounded distribution is being implicitly assumed (even though for most methods the distinction cannot be made). Finally, Graham *et al.* (2005), for example, calculated size-spectra slopes that estimated b to be between -0.24 and -0.20 . Such values of $b > -1$ are only possible for bounded, and not for unbounded (e.g. Edwards 2008), power-law distributions.

For a community of n individuals, the abundance density function, $N(x)$, is

$$N(x) = nf(x) = nCx^b, \quad x_{\min} \leq x \leq x_{\max}. \quad \text{eqn 3}$$

This leads to the biomass density function, $B(x)$, that describes how biomass is distributed with respect to body mass:

$$B(x) = xN(x) = nCx^{b+1}, \quad x_{\min} \leq x \leq x_{\max}. \quad \text{eqn 4}$$

This is the equation for the biomass size spectrum (Boudreau & Dickie 1992) and allows calculation of the total biomass of all individuals with body mass $\leq x$ (see Appendix S1); see also Vidondo *et al.* (1997).

Some studies (e.g. Dulvy *et al.* 2004; Daan *et al.* 2005; Boldt *et al.* 2012) used length to represent size, and calculated the slope of the

length size spectra. Thus, body mass x in (1) would be replaced by length l , but our results regarding the calculation of slopes and the exponent b still hold. There is no direct length-based equivalent to the biomass size spectrum (4); calculating (4) would require first converting lengths to body masses, via species-specific allometric relationships (e.g. Shin *et al.* 2005; Trebilco *et al.* 2015).

SIMULATED DATA

We simulate a data set that consists of individual body masses of $n = 1000$ fish. Define x_i to be the body mass (g) of fish i , where $i = 1, 2, 3, \dots, n$. The 1000 simulated values are independently drawn from the PLB distribution (1) using the inverse method (see Appendix S1), with $x_{\min} = 1$, $x_{\max} = 1000$ and the exponent $b = -2$. The exponent $b = -2$ comes from the Sheldon, Prakash & Sutcliffe (1972) conjecture (Andersen & Beyer 2006), and theoretical and empirical estimates are often close to this value (e.g. Platt & Denman 1978; Boudreau & Dickie 1992; Gaedke 1992; San Martin *et al.* 2006). Other values of x_{\max} , b and n are tested later.

We use seven methods that have previously been used to estimate the slope of a size spectrum, and one that estimates the exponent b directly. We test each method on the simulated data set to obtain an estimated slope. Motivated by other ecological contexts, similar approaches were taken by White, Enquist & Green (2008) and Edwards (2008) to test methods used to fit unbounded power-law distributions ($x_{\max} \rightarrow \infty$ in (1)), though only three of the eight size-spectra methods tested here were investigated, and neither study investigated confidence intervals, as we do here.

We then estimate b for 10 000 simulated data sets to determine the accuracy of each method and the reliability of confidence intervals. Our overall aim is to investigate whether the different methods, which sometimes differ by seemingly minor details, give consistent results. We acknowledge that authors themselves may be aware of any differences, but this is not necessarily apparent from published studies. For clarity, we describe each method in the Results section in conjunction with the figure that arises from applying it to simulated data.

Results

For each method in turn (summarized in Table 1), we prescribe a name, describe the method, plot the results and give the estimated slope for the simulated data set of 1000 values. The slope is what is usually reported, but we explain how it can be an estimate of b , $b + 1$ or $b + 2$, depending upon the method used. Thus, slopes cannot be interpreted as comparable if derived from different methods. Figure 1 is a standard histogram of the simulated data set; the y -axis has a break because so many of the counts end up in the first bin (size interval), since the data are power-law-distributed.

Llin (LOG-LINEAR) METHOD

The Llin (log-linear) method involves binning the data into bins of constant width, plotting $\log(\text{count of the number of individuals within a size interval})$ against the mid-point of the size interval and then using linear regression to estimate the spectrum slope. Essentially, the histogram in Fig. 1 gets replotted as Fig. 2a with the counts plotted on a logarithmic y -axis and the mid-points of each bin on the x -axis. Such a method was used by Daan *et al.* (2005) to analyse changes in the North Sea fish community. Note that they (and Dulvy *et al.* 2004, Boldt *et al.* 2012 and Trebilco *et al.* 2015) subtracted the mid-point of the full range of data, $(x_{\max} - x_{\min})/2$, off the mid-points of all size intervals, in order to centre the size classes around zero. But such a constant shift does not affect the calculated value of the slope, and so for simplicity we omit it in this manuscript.

Applying the Llin method to our simulated data set estimates a slope of -0.0156 . We used eight bins, but two are empty (Fig. 1) and so do not appear on the logarithmic scale of

Table 1. Brief description of methods used to estimate the slope of a size spectrum. Two of the example references use a different logarithmic base for the regression fit to that stated, but this does not affect the estimated slope (see text).

Name	Brief description	Example reference(s)
Llin	Log-linear transform. Plot linearly binned data on log-linear axes then fit regression of $\log(\text{count in bin})$ against mid-point of bin.	Daan <i>et al.</i> (2005)
LT	Log-transform. Plot linearly binned data on log-log axes then fit regression of $\log(\text{count in bin})$ against $\log(\text{mid-point of bin})$.	Rice & Gislason (1996), Boldt <i>et al.</i> (2012)
LTplus1	Log-transform plus 1. Plot linearly binned data on \log_{10} - \log_{10} axes then fit regression of $\log_{10}(\text{count}+1)$ against $\log_{10}(\text{mid-point of bin})$.	Dulvy <i>et al.</i> (2004), Graham <i>et al.</i> (2005)
LBmiz	Logarithmic binning as done by <code>mizer</code> . Bin data using \log_{10} bins (but with largest bin the same arithmetic size as the penultimate bin), and regression of $\log(\text{count in bin})$ against $\log(\text{lower bound of bin})$.	Scott <i>et al.</i> 's (2014) <code>mizer</code> R package
LBbiom	Logarithmic binning and then fit biomass size spectrum. Bin sizes using \log_2 bins then fit regression of $\log_{10}(\text{biomass in bin})$ against $\log_{10}(\text{mid-point of bin})$.	Maxwell & Jennings (2006), Jennings, de Oliveira & Warr (2007), Trebilco <i>et al.</i> (2015)
LBNbiom	Logarithmic binning with normalization and then fit biomass size spectrum. Bin sizes using \log_2 bins, then fit regression of $\log_{10}(\text{biomass in bin divided by bin width})$ against $\log_{10}(\text{mid-point of bin})$.	Blanchard <i>et al.</i> (2005), Roy, Platt & Sathyendranath (2011)
LCD	Logarithmic plotting of $1-F(x)$, that is one minus the cumulative distribution. Rank data from largest (rank 1) to smallest (rank n), fit regression of $\log(\text{rank}(x)/n)$ against $\log x$.	Vidondo <i>et al.</i> (1997), Rogers, Blanchard & Mumby (2014)
MLE	Maximum likelihood estimate. No binning or plotting necessary. Calculate the maximum likelihood estimate of the parameter b . Data and fitted distribution can be plotted on a rank/frequency plot.	Arim <i>et al.</i> (2011), Robinson & Baum (2016)

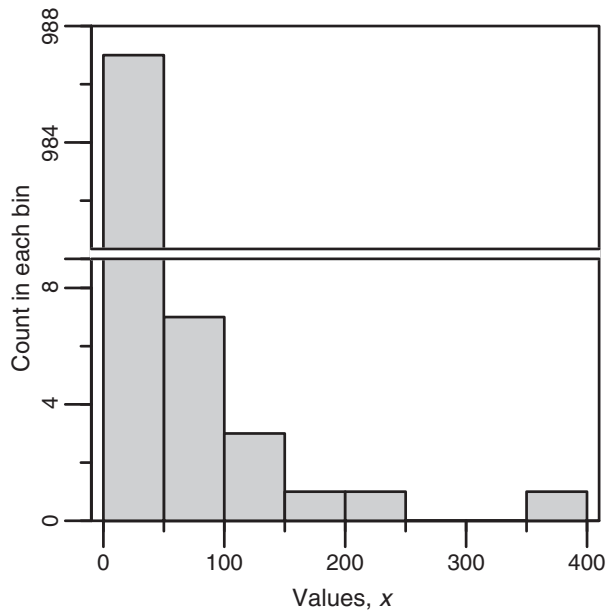


Fig. 1. Standard histogram of a random sample of 1000 values from a bounded power-law distribution (1) with $b = -2$, $x_{\min} = 1$ and $x_{\max} = 1000$. Histogram shows the number of counts within each of the eight equally sized bins. Note the break in the y -axis to clearly show all the counts.

Fig. 2a. The use of log-linear axes suggests an exponential distribution, and so the slope cannot be related to b .

LT (LOG-TRANSFORM) METHOD

The LT (log-transform) method involves binning the data into bins of constant width, plotting $\log(\text{count within a size interval})$ against $\log(\text{mid-point of the size interval})$ and then using linear regression to estimate the spectrum slope. Thus, the only difference to the Llin method is the logging of the values on the x -axis. Such a method was used on length-based data from groundfish trawl surveys by Rice & Gislason (1996) for the North Sea and Boldt *et al.* (2012) for the eastern Bering Sea. Figure 2b shows the result of applying the LT method to the simulated data set, using the same eight bins (and thus counts), as in Figs 1 and 2a. The LT method estimates a slope of -2.64 , which is an estimate of b because of the logarithmic axes (White, Enquist & Green 2008).

LTplus1 (LOG-TRANSFORM PLUS 1) METHOD

The LTplus1 (log-transform plus 1) method is similar to the LT method, except that the count in each bin is increased by one. Dulvy *et al.* (2004) and Graham *et al.* (2005) used it to examine the effects of fishing intensity on coral-reef fish communities in Fiji. Their choice of \log_{10} axes, rather than \log axes as for the LT method, does not affect the slope (this is true for all regression-based methods – see Appendix S1). Consequently, $\log_{10}(\text{count} + 1)$ within a size interval) is plotted against $\log_{10}(\text{mid-point of the size interval})$, and a linear regression is fitted. Adding one to the count avoids bins with zero counts not appearing in the plots and not contributing to the

regression calculation, as occurred in Fig. 2a,b for the Llin and LT methods. For the LTplus1 method, Fig. 2c has eight points (one for each bin), and the slope of the regression is -2.33 , which is an estimate of b . Adding one to the counts has estimated b closer to the true value of $b = -2$, compared to the LT method's estimate of -2.64 .

LBMiz (\log_{10} BINNING PLOTTED ON \log AXES USED IN `mizer`) METHOD

The LBMiz method involves binning the data using bins that have equal width on a \log_{10} scale (e.g. bin breaks of 1, 10, 100, 1000), but with the largest bin set to the same arithmetic width as the penultimate bin. It then involves plotting and fitting the regression of $\log(\text{count within a size interval})$ against $\log(\text{lower bound of the size interval})$. It was used in the R package `mizer` (Scott, Blanchard & Andersen 2014), which simulates the potential consequences of various fishing patterns using an approach based on the McKendrick–von Foerster equation and calculates resulting size spectra. The user specifies the number of bins, and the lower bounds of the lowest and highest bins. For our simulated data, we know the minimum and maximum values of the data and can derive the bin breaks (see Appendix S1). Our estimated slope is -1.11 . For logarithmically spaced bin breaks, as used here except for the largest bin, the slope estimates $b + 1$ (Appendix A of White, Enquist & Green 2008), such that this method essentially estimates $b = -2.11$. Repeating the LBMiz method using the mid-point of bins (as per the other binning methods), rather than the minimum, estimates $b = -2.13$, suggesting that the LBMiz method's use of minima is not important.

LBbiom (\log_2 BINNING WITH BIOMASS IN EACH BIN PLOTTED ON \log_{10} AXES) METHOD

The LBbiom method involves binning the individual fish into size intervals that have equal width on a \log_2 scale, and then plotting and fitting the regression of $\log_{10}(\text{biomass within a size interval})$ against $\log_{10}(\text{mid-point of the size interval})$, as used by Maxwell & Jennings (2006) for data on benthic invertebrates in the North Sea and Jennings *et al.* (2007) for theoretical work and analyses of fish data from bottom trawl surveys. Trebilco *et al.* (2015) used it (with \log_2 - \log_2 axes) to examine the role of habitat complexity on the size structure of the rockfish-dominated fish community in kelp forests off Haida Gwaii, Canada. So in contrast to the above methods based on number of fish in each bin, this method uses the total biomass in each bin and is effectively fitting the biomass spectrum rather than the ISD, though these are related via (3) and (4). Maxwell & Jennings (2006) and Jennings, de Oliveira & Warr (2007) used bin breaks at integer powers of two that spanned their data, and so we set bin breaks at 1, 2, 4, 8, Vidondo *et al.* (1997) described how early instruments measured numbers of particles within \log_2 size classes, and such binning was adopted by later scientists (even when sizes could be individually measured). We obtain an estimated *biomass* size-spectrum slope of -0.0937 . The biomass size spectrum (4) has exponent $b + 1$

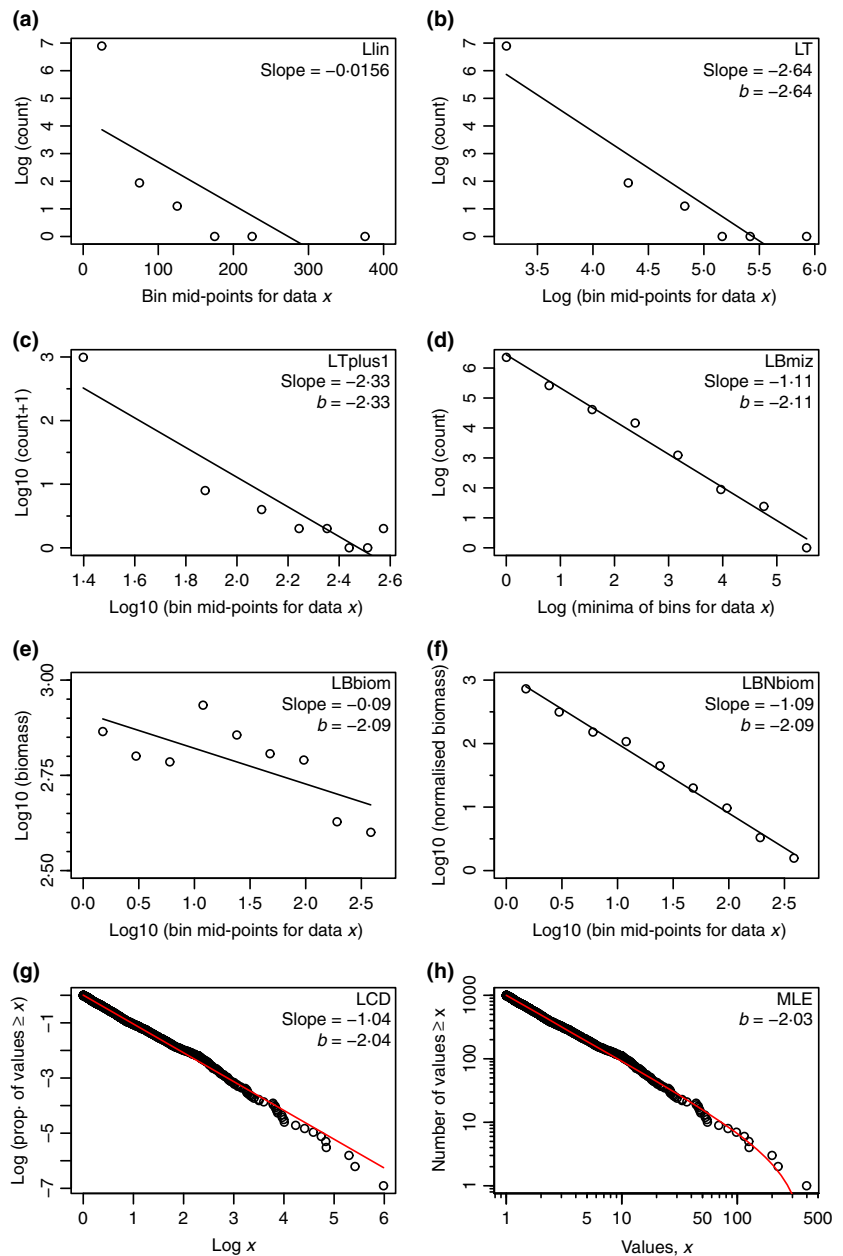


Fig. 2. Results from using eight methods (Table 1) to estimate the slope or exponent of size spectra from the simulated data set of 1000 values shown in Fig. 1. The estimated slope and/or the estimated value of the ISD exponent b is given for each method in panels (a–h), with lines showing the resulting fitted size spectra.

and, since logarithmically spaced bins mean the slope is the exponent plus one (White, Enquist & Green 2008), the slope is estimating $b + 2$, giving $b = -2.09$.

LBNbiom (log₂ BINNING WITH NORMALIZED BIOMASS IN BINS PLOTTED ON log₁₀ AXES) METHOD

The LBNbiom (log-binning with normalization using biomass) method is the LBbiom method but with the biomass in each bin normalized by dividing it by the bin width, that is plotting and fitting the regression of log₁₀(biomass within a size interval divided by the width of that size interval) against log₁₀(mid-point of the size interval). Blanchard *et al.* (2005) used it to analyse groundfish survey data from the Celtic Sea, and Roy, Platt & Sathyendranath (2011) used it (with log-log axes) to investigate temporal changes in the slope of the

normalized phytoplankton biomass size spectrum for a location in the North Atlantic Ocean. Platt & Denman (1977, 1978) introduced the idea of dividing the total biomass in a size class by the width of that size class. For our simulated data set, using the same bin breaks as for the LBbiom method, the estimated biomass size-spectrum slope is -1.09 . This correctly estimates the biomass size spectrum (4) exponent $b + 1$ because of the normalized counts (White, Enquist & Green 2008), giving $b = -2.09$.

LCD (LOG CUMULATIVE DISTRIBUTION) METHOD

The LCD (log of the cumulative distribution) method requires no binning because it plots all data points. Body masses are ranked from largest (rank 1) to smallest (rank n), and log(rank(x)/ n) against log x is plotted, with one point for

each body mass x . A regression is fitted to estimate the slope. Note that $\text{rank}(x)/n$ is the fraction of values $\geq x$, which is estimating $P(X \geq x) = 1 - F(x)$, where $F(x)$ is the probability distribution function (Grimmett & Stirzaker 1990) or cumulative distribution function (Bolker 2008), and the resulting slope is approximately $b + 1$ (see Appendix S1). Vidondo *et al.* (1997) recommended this method (for the unbounded power law), and it was recently used by Rogers, Blanchard & Mumby (2014) to investigate vulnerability of coral-reef fisheries in The Bahamas. Figure 2g demonstrates this method for our data set, yielding an estimated slope of -1.04 , giving $b = -2.04$.

MLE (MAXIMUM LIKELIHOOD ESTIMATE) METHOD

The MLE (maximum likelihood estimate) method directly estimates the parameter b using a standard statistical likelihood approach (e.g. Hilborn & Mangel 1997; Bolker 2008). It finds the value of b that maximizes the likelihood function for the given data set. In the context of *unbounded* power-law distributions, it has been tested (e.g. Newman 2005; Edwards 2008; White, Enquist & Green 2008) and used (together with other methods) by Arim *et al.* (2011) on body-size data from ponds in Uruguay. The bounded power-law distribution was recently used by Robinson & Baum (2016) to analyse visual-census data from coral-reef fish communities around Kiritimati (Christmas Island). The MLE for b requires numerical maximization of the log-likelihood function (Page 1968; Edwards 2011; see Appendix S1). The MLEs for x_{\min} and x_{\max} are the minimum and maximum observed values, respectively (Edwards *et al.* 2012). For our data set, the MLE for b is -2.03 .

The MLE method does not require any plotting to estimate b . To visualize the resulting fit, in Fig. 2h we show a rank/frequency plot which gives, on logarithmic axes, the rank of x (the number of values $\geq x$) against the value of x (e.g. Edwards *et al.* 2007). We label axes using actual values (rather than log values) for easier interpretation of the results; the points in Fig. 2g,h are essentially the same with the axes defined differently. The fitted PLB model (red curve) is calculated across the range of x values as $(1 - F(x))n$ using the MLE value for b and characterizes the *abundance size spectrum* based on (3); see Appendix S1. It is not linear because we have used the MLE method to explicitly fit a bounded power-law distribution; the fit from the LCD method in Fig. 2g is linear because that method implicitly assumes an unbounded power-law distribution.

SUMMARY OF METHODS APPLIED TO THE SIMULATED DATA SET

Overall, the *slopes* differ considerably between methods, from -2.64 to -0.02 . But the slopes cannot be directly compared because they are estimating different quantities. Translating the slopes into estimates of b means that five of the methods estimate b in the range $(-2.11, -2.03)$, just below the true value of $b = -2$.

While some of the above differences in what each method calculates will have been appreciated by some authors, it is not

always clear that subtle methodological differences are important. For example, Daan *et al.* (2005) initially talk about the 'slope of the log-linear size spectrum of the total fish community' (i.e. the Llin method) and then mention Rice & Gislason (1996) as having shown that the spectrum slope for a North Sea fish community had steepened over time. However, Rice & Gislason (1996) used the LT method. Thus, spectrum slopes were being defined using different methods and so cannot be considered comparable.

REPEATED SIMULATIONS – ACCURACY OF THE METHODS

The above results depend on the single simulated data set of $n = 1000$ random numbers drawn from the PLB distribution (1). To build a more detailed picture of the accuracy of each method, we now repeat the above calculations on 10 000 independent simulated samples (a number recommended by Crawley 2002), each containing 1000 values drawn randomly from the PLB distribution (still with $b = -2$, $x_{\min} = 1$ and $x_{\max} = 1000$). So for each method we obtain 10 000 estimates of b (or slope for the Llin method). For the MLE method, x_{\min} and x_{\max} are explicitly estimated as the minimum and maximum data values, respectively, for each of the 10 000 samples.

The resulting estimates of b are shown in the blue histograms in Fig. 3, with summary statistics in Table 2. The Llin method gives a narrow range of slopes that are just below zero, which is intuitive when looking at the scales of the axes in Fig. 2a. The distribution of estimates of b for the LT and LTplus1 methods are fairly wide and highly biased (Fig. 3b,c), with 99% and 82%, respectively, of the estimates being below the true value of $b = -2$ (Table 2).

For the remaining five methods, the means and medians of the estimates are all within 0.01 of the true value of b (Table 2), with Lbmiz having 47% of the estimates below the true value, which is the closest any of the methods get to the desired value of 50% (equally likely to be above or below the true value). The Lbmiz, Lbbiom and LBNbiom methods show similar distributions, with the LCD and then MLE methods having progressively narrower distributions. Thus, overall, the final five methods appear to be fairly accurate, with MLE showing the least variation.

The shaded gold histograms in Fig. 3 show the same analyses but with $x_{\max} = 10\,000$ (rather than $x_{\max} = 1000$). Such a 10 000-fold range of body sizes can be observed for coral-reef fishes (Robinson & Baum 2016). The results for the MLE method remain essentially unchanged from the $x_{\max} = 1000$ results, while the accuracy of some of the other methods is diminished. For example, for the LBNbiom method the distribution of estimated b values shifts to the right in Fig. 3f, such that only 20% (rather than 45%) of the estimated values fall below the known value of -2 . See Appendix S1 for full details.

CONFIDENCE INTERVALS

The previous results estimate b using the different methods. Bolker (2008) states that such types of best-fit estimates require

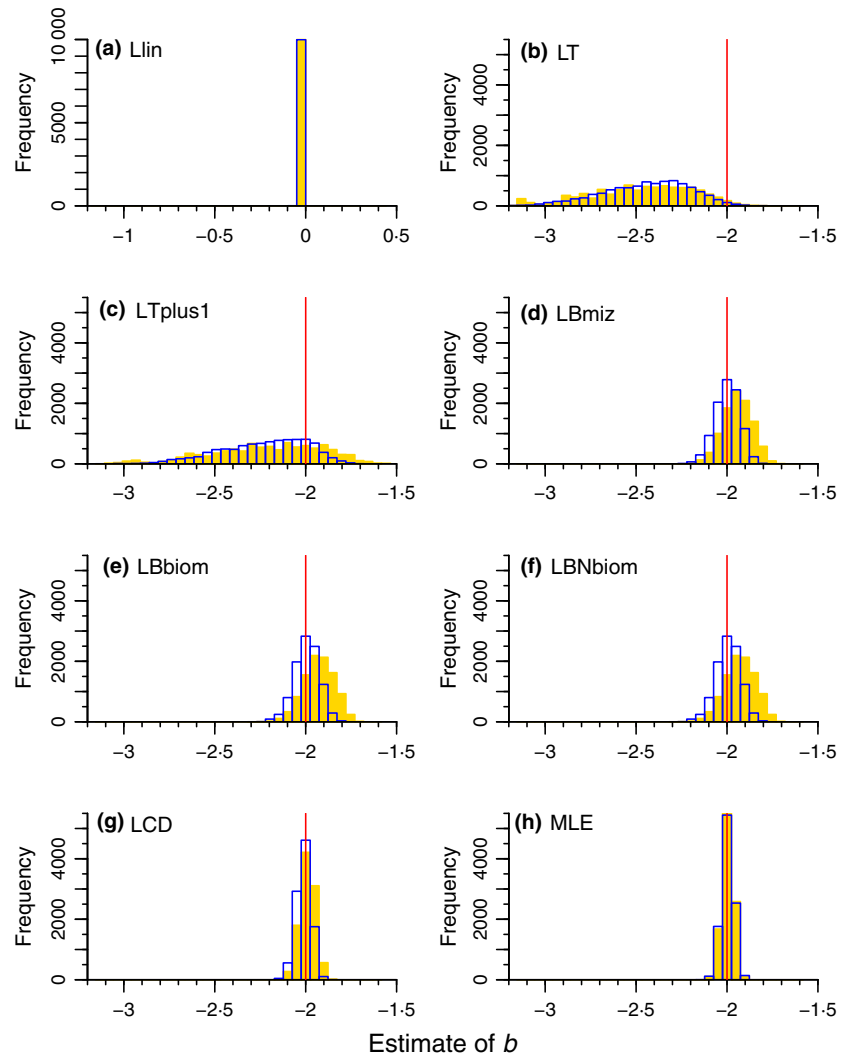


Fig. 3. Histograms (in blue) of estimated exponent b for 10 000 simulated data sets, each of which contains 1000 independent random numbers drawn from a bounded power-law distribution with $b = -2$, $x_{\min} = 1$ and $x_{\max} = 1000$. Each panel (a–h) uses the method from the corresponding panel in Fig. 2. The vertical red lines indicate the known value of $b = -2$. Shaded gold histograms show results when setting $x_{\max} = 10\,000$. Axis scales are the same for all panels except (a), which gives estimates of slope since the Llin method does not estimate b .

some measurement of uncertainty to be meaningful. However, uncertainty of slopes has only been occasionally calculated in previous studies (e.g. Rice & Gislason 1996; Graham *et al.* 2005), a situation that is ‘particularly unsettling’ (Rice 2000). Therefore, we now construct confidence intervals of b for each method and test how well they perform.

For the regression-based methods, a confidence interval for the slope can be calculated (e.g. Crawley 2002) using the R command `confint`. The confidence interval for b can then be obtained by subtracting one or two as appropriate for each method (see Table 2). For the MLE method, a 95% confidence interval for b can be calculated using the profile likelihood test (Hilborn & Mangel 1997).

By definition, 95% of the 95% confidence intervals should contain the true value of the estimated quantity. To see whether this holds, for each method we compute a confidence interval for b for each of the 10 000 simulated data sets (with $x_{\max} = 1000$) and see what percentage of a method’s intervals contain the true value of $b = -2$. This percentage is the ‘observed coverage’ and should ideally equal the ‘nominal coverage’ of 95% (Bolker 2008).

Figure 4 shows the resulting confidence intervals for subsamples of the 10 000 simulated data sets; we use subsamples

for clarity (see Appendix S1). For each method, the true value of b is shown as a vertical red line, and each confidence interval is coloured grey if it encompasses the true value and blue if it does not. Thus, we would expect 95% of the intervals to be grey and 5% to be blue. The resulting percentage (the observed coverage) based on all 10 000 confidence intervals is indicated for each method.

Figure 4a shows that the confidence intervals of the slope for the Llin method never include the true value of b . The confidence intervals of b for the LT and LTplus1 methods are so wide that they essentially always include the true value (Fig. 4b,c); such intervals are therefore not of practical use. For the Lbmiz, Lbbiom and LBNbiom methods, the confidence intervals include the true value of b only 90% of the time (Fig. 4), thereby overstating their reliability. For the LCD method, only 6% of the confidence intervals include the true value of b because the intervals are very narrow (Fig. 4g). Intuitively, such narrow intervals can be inferred from Fig. 2g – the regression line is being fitted to all $n = 1000$ points, and there is clearly not a large possible range in the slope (compared to, say, Fig. 2e). Thus, the very narrow confidence intervals from the LCD method give a misleading impression of accuracy.

For the MLE method, 95% of the confidence intervals include the true value of b (Fig. 4h). The intervals are of a relatively consistent width, which is an intuitively desirable property that is lacking for the other methods.

With $x_{\max} = 10\,000$, the observed coverage declines from 90% to 84% (LBmiz method) and 74% (LBbiom and LBNbiom methods) and remains at 6% for the LCD method and at the desired 95% for the MLE method (see Appendix S1).

Table 2. Summary statistics for each method for the 10 000 simulations of 1000 samples from (1), corresponding to the blue histograms ($x_{\max} = 1000$) in Fig. 3. The second column indicates how the fitted slope can be translated into an estimate of b , though for the MLE method b is estimated directly. Statistics relate to the resulting estimates of b (or slope for Llin method), with the final column giving the percentage of simulations for which the estimate is below the true value of $b = -2$. See the end of the Results for the MLEbin method

Method	Slope represents	5% quantile	Median	Mean	95% quantile	Percentage below -2
Llin	–	–0.02	–0.01	–0.01	–0.01	0
LT	b	–2.88	–2.42	–2.44	–2.09	99
LTplus1	b	–2.66	–2.20	–2.23	–1.90	82
LBmiz	$b + 1$	–2.11	–2.00	–2.00	–1.89	47
LBbiom	$b + 2$	–2.11	–1.99	–1.99	–1.89	45
LBNbiom	$b + 1$	–2.11	–1.99	–1.99	–1.89	45
LCD	$b + 1$	–2.08	–2.01	–2.01	–1.95	59
MLE	b	–2.05	–1.99	–2.00	–1.94	44
MLEbin	b	–2.05	–2.00	–2.00	–1.94	46

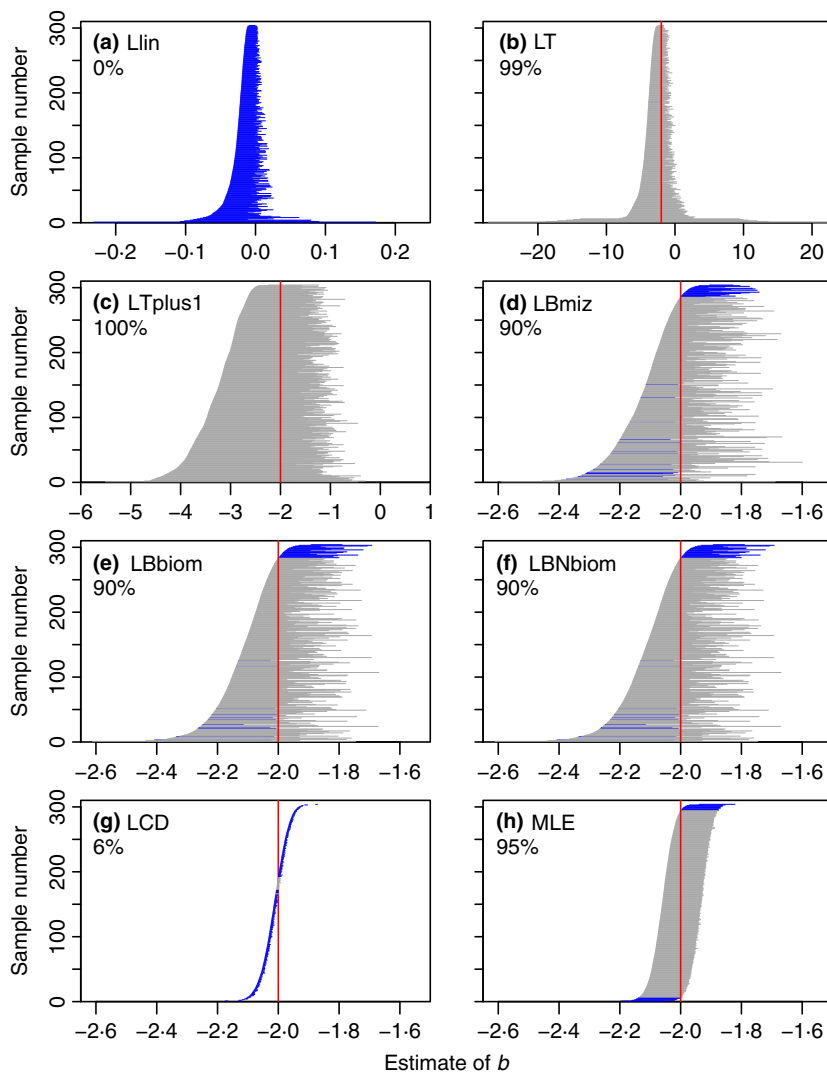


Fig. 4. Confidence intervals (horizontal lines) of b obtained for each method (panels a–h) for subsamples of the 10 000 simulated data sets (with $x_{\max} = 1000$) used in Fig. 3. For each numbered subsample on the y -axis, the 95% confidence interval of b obtained using the respective method is plotted as a horizontal line, which is coloured grey if the interval includes the true value of $b = -2$ (given by the vertical red line) or blue if it does not. Simulations are sorted in ascending order of their lower bound. The percentage for each method gives the observed coverage, namely the percentage of all 10 000 simulated data sets for which the 95% confidence interval contains the true value of b ; by definition, this should ideally be 95%. Horizontal axes are the same for (d–h), and (a) shows confidence intervals of the slope.

Thus, overall we find the MLE method to be the only one that produces reliable estimators of the uncertainty of b .

SENSITIVITY ANALYSES – ROBUSTNESS OF THE MLE METHOD

In the Appendix S1, we modify the MLE method to fix x_{\max} across the 10 000 data sets rather than estimating it individually for each data set, which gives only minor numerical differences in results. We also repeat our main simulations with $b = -2.5$, $b = -1.5$ and $b = -0.5$ instead of $b = -2$, and with a ten-fold increase in sample size to $n = 10\,000$. The conclusions for most methods are sensitive to the value of b or n (e.g. the LBNbiom method performs worse with $b = -2.5$). However, only the conclusions for the MLE method are robust – estimates of b are accurate and confidence intervals are reliable (observed coverage of 94% or 95%), unlike for other methods. We also find our results and conclusions are not dependent on the seed used for the random-number generator.

MLEbin METHOD FOR BINNED DATA

Sometimes data (or model output, Thorpe *et al.* 2015) are only available in binned form. We extend the MLE method for such data sets to give the MLEbin method (adapted from Edwards *et al.* 2007 and Edwards 2011; see Appendix S1). We test it using the same 10 000 simulated data sets as earlier, but first binning each data set (using bin breaks at 1, 2, 4, 8, ...) and then applying the method to the counts in each bin. The MLEbin method appears as accurate as the MLE method (Table 2 and Fig. 5). Sensitivity analyses (e.g. regarding binning) will be conducted in future work. Researchers can adapt our code for their particular data sets and also investigate different binning protocols for data that require binning when being collected.

Discussion

We have expanded upon White *et al.*'s (2007) recommendation to think of size spectra in terms of ISDs, because it places such work in the context of probability densities. Our results show that the slopes of size spectra arising from commonly used methods cannot be interpreted as equivalent since they do not all directly estimate the exponent b of the ISD and that the methods estimate b with different levels of accuracy. We recommend the MLE method for estimating b and its confidence intervals, since only its performance was robust under sensitivity analyses. This is in contrast to Vidondo *et al.*'s (1997) recommendation to use the LCD method over the MLE method (based on unpublished simulations for unbounded power laws).

The MLE method avoids binning and regression. Binning in general can be problematic (e.g. if a data set has no body masses <10 g but the lowest bin is defined as 8–16 g), and the choice of bin widths can affect the estimated slope (Vidondo *et al.* 1997). Regression-based methods are problematic because the intercept and the slope implicitly determine x_{\min} , which can erroneously be greater than some data values (James, Plank & Edwards 2011). They also assume that the

errors in the logarithmic counts for each bin have the same variance, which may not be justified. Although regression can be understood in a likelihood context, this is different to explicitly using a likelihood-based method (Edwards *et al.* 2012).

However, researchers are used to seeing biomass size spectra in the form of log–log plots of the normalized biomass in logarithmic bins, as in Fig. 2f. Thus, we recommend presenting results as the two plots in Fig. 6 – a biomass size spectrum and an abundance size spectrum, with the MLE estimate for b (and bounds of the 95% confidence interval) used in (4) for biomass and (3) for abundance. Only the abundance plot would be appropriate for length data.

Rice (2000) called for an objective way to determine whether differences among values of a community metric are meaningful. The calculation of reliable confidence intervals for b will allow this. Furthermore, quantifying the uncertainty in b should improve the quality of advice to fisheries or ecosystem managers, because without uncertainty numerical results can give a misleading impression of accuracy. Uncertainty can be accounted for when investigating changes in b (e.g. using weighted linear regression) that could represent steepening of the size spectra in response to fishing.

We can only partially determine the consequences of our results for previous conclusions. For example, Dulvy *et al.*

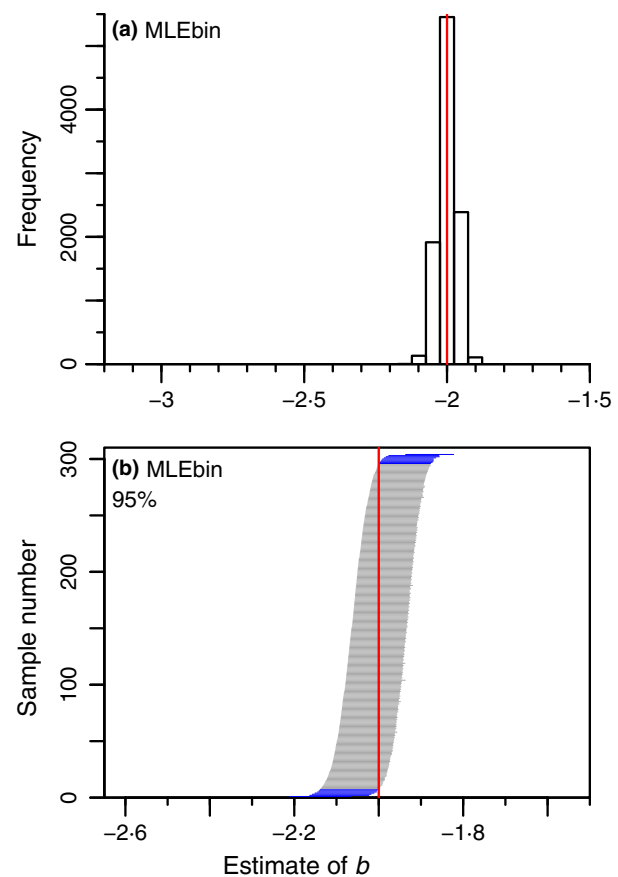


Fig. 5. Testing of the MLEbin method on binned versions of each of the simulated data sets; (a) as in Fig. 3 and (b) as in Fig. 4. Confidence intervals range in width from 0.114 to 0.145, only marginally wider than the range of 0.114 to 0.143 for the MLE method.

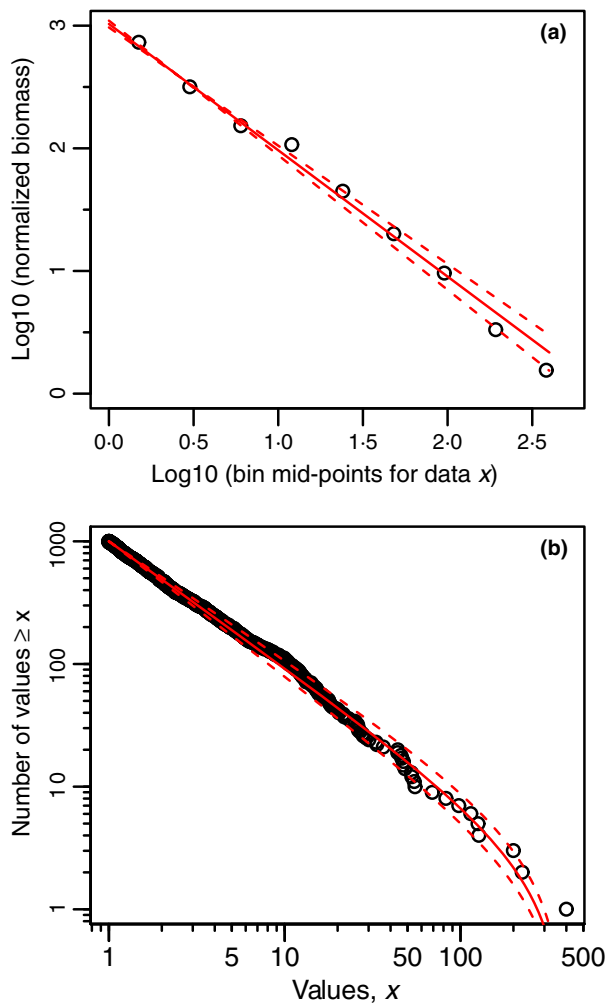


Fig. 6. Suggested plots of (a) biomass size spectrum from (4), and (b) abundance size spectrum from (3), fitted using the maximum likelihood estimate -2.03 of the exponent b (red solid lines). Data are from Fig. 2. For the biomass size spectrum, data are binned and normalized as for the LBNbiom method (Blanchard *et al.* 2005). Dashed lines are from using the lower and upper bounds (-2.10 and -1.96) of the 95% confidence interval of b .

(2004) found a significant relationship between size-spectrum slopes and fishing intensity across 13 fishing grounds. The slopes were all between -0.04 and -0.01 , derived using the LTplus1 method. However, Fig. 3c suggests that such a small change in size-spectrum slope could be an artefact of the LTplus1 method. In general, previously calculated slopes must be interpreted with respect to the method used.

We have used a bounded power-law distribution for the ISD since power laws are commonly used models for size spectra (Platt & Denman 1978; Boudreau & Dickie 1992; Andersen & Beyer 2006). However, we echo Vidondo *et al.*'s (1997) warning that there will be data sets for which power-law distributions are not appropriate. Dynamic models of size spectra in marine communities predict non-power-law size distributions at the level of individual species (Hartvig, Andersen & Beyer 2011; Jacobsen, Gislason & Andersen 2014; Law, Plank & Kolding 2014), although the aggregate community ISD may be closer to a power law (Andersen & Beyer 2006). We have

compared different methods for estimating the exponent b on the common assumption that the ISD is a power law. In applications, the validity of this assumption could be investigated using goodness-of-fit tests and Akaike Information Criteria (e.g. Edwards *et al.* 2007; Edwards 2011).

We have not considered measurement errors here – these may dominate sampling errors when the sample size is sufficiently large. The likelihood method can be explicitly adapted to account for measurement errors using the convolution approach of Koen & Kondlo (2009). Further simulations could test how well all methods cope with data that are subject to measurement error. To account for measurement resolution (e.g. if body masses are recorded to the nearest gram, then a 10 g mass really represents a true body mass in the range 9.5–10.5 g), the MLEbin method can be used. Our current results (and R code) have application in ecology beyond size spectra, since power-law distributions arise in several areas (White, Enquist & Green 2008).

Our take-home messages are as follows: (i) size spectra should be formally expressed in terms of individual size distributions, (ii) the MLE method should be used to estimate the ISD exponent b and its confidence intervals, and (iii) there is no need to bin data, but if data are only available in binned form, then the MLEbin method can be used and tested. We hope that these will be adopted and applied in size-spectra research. To facilitate this, we have formalized the mathematics used to analyse size spectra, tested the methods and provided usable R code for researchers.

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Data accessibility

This paper uses simulated data. All results can be completely reproduced from our R code (R version 3.1.0), which is uploaded as Data S1. We have functionalized and documented the code with the aim of it being used by researchers for their own data (e.g. to produce an equivalent Fig. 6). Furthermore, to share future enhancements the code is available at <https://github.com/andrew-edwards>.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Extended mathematical derivations and explanations, plus extra numerical results including sensitivity analyses.

Data S1. Archive of all R code used in this paper, equivalent to release version 1.0.0 of the code available at <https://github.com/andrew-edwards>. See `README.md` (viewable in a Markdown editor or any standard text editor) to get started.