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**Surfing the biomass size spectrum: some remarks on
 history, theory, and application**

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Draft

Abstract

Charles Elton introduced the 'pyramid of numbers' in the late 1920s but this remarkable insight into body-size dependent patterns in natural communities lay fallow until the theory of the biomass size spectrum was introduced by aquatic ecologists in the mid-1960s. They noticed that the summed biomass concentration of individual aquatic organisms was roughly constant across equal logarithmic intervals of body size from bacteria to the largest predators. These observations formed the basis for a theory of aquatic ecosystems, based on the body size of individual organisms, that revealed new insights into constraints on the structure of biological communities. In this review we discuss the history of the biomass spectrum and the development of underlying theories. We indicate how to construct biomass spectra from sample data, explain the mathematical relations among them, show empirical examples of their various forms, and give details on how to statistically fit the most robust linear and nonlinear models to biomass spectra. We finish by giving examples of biomass spectrum applications to production and fisheries ecology, and offering recommendations to help standardize use of the biomass spectrum in aquatic ecology.

Keywords: Size spectrum, Models, Aquatic, Food webs

28 **Introduction**

29 The abundance of organisms in nature has been of interest to science since Ecology emerged as
30 a formal discipline of study. Elton (1927) introduced the “pyramid of numbers” to describe the
31 commonly observed fact that there is an inverse relationship between the abundance of organisms and
32 their size. He proposed that this pattern arises because predators typically feed on prey smaller than
33 themselves since they cannot engulf organisms that are too large and cannot feed efficiently on
34 organisms that are too small. He further speculated that these tendencies, combined with higher
35 population growth rates at the base of food chains, naturally organize communities into levels of
36 increasingly larger and rarer organisms. However there are limits to food chain length because prey
37 densities near the top of the food web are too low “for it to be worthwhile for a carnivore to eat that
38 food” and thus “carnivores tend to be ... less strictly confined to one habitat than herbivores” (Elton
39 1927). These are remarkable insights that form the basis for the field of trophic ecology that emerged
40 after Elton’s book was published, but particularly after Lindeman (1942) outlined the basic theory of
41 energy flow through communities organized into trophic levels.

Glossary

Size spectra are discrete or continuous representations of the relationships that link either numerical abundance or biomass concentration to body size.

The biomass spectrum is estimated biomass concentration in successive logarithmic size bins, with $\log_2$ and $\log_{10}$ the most common bases used to define the bins. The equivalent abundance spectrum is the numerical concentration of individuals in logarithmic bins. Linear slopes of ~ 0 and ~ -1 are commonly observed for these spectra respectively. In this paper we will refer to the biomass concentration spectrum as the *biomass spectrum* and the numerical abundance spectrum as the *abundance spectrum*.

The normalized spectrum is estimated biomass (or abundance) in logarithmic size bins, where the biomass (or abundance) value for each bin is divided by the linear width of the bin. Linear slopes of ~ -1 and ~ -2 are commonly observed for these spectra respectively. Normalization is carried out to correct for the distortion in the underlying biomass (or abundance) distribution due to logarithmic binning in which bins increase in width in proportion to body size. In this paper we will refer to the *normalized biomass spectrum* or the *normalized abundance spectrum*.

Linear size bins are those in which the upper bin boundary equals the lower boundary *plus* a constant. Their width is the difference between the upper and lower boundaries.

Logarithmic size bins are those in which the upper bin boundary equals the lower boundary *times* a constant. Their *linear* width is the difference between upper and lower boundaries expressed in unlogged units. Their *logarithmic* width is the difference between boundaries expressed in log units.

The focus on body size that stimulated Elton's (1927) observations on the organization of communities largely disappeared as trophic ecologists shifted their attention to species, their interactions, and the concept of trophic levels. It was not until the 1960s that ecologists returned to body size as the principal representation of organisms in studies of food web structure and function (Platt 1985), particularly in aquatic ecosystems and especially through the work of T.R. Parsons, his student R.W. Sheldon, and their colleagues (Parsons 1969; Sheldon et al. 1972). These workers introduced the concept of particle size spectra and the biomass spectrum, which revealed broad regularities in the size structure of aquatic communities, and proposed an underlying ecological/physiological theory to account for the observed patterns. The size spectrum displays a measure of total abundance or biomass in logarithmically equal intervals of body size. Among the many patterns revealed is an inverse relationship between abundance and size that closely parallels the pyramid of numbers proposed by Elton (Trebilco et al. 2013). Furthermore Elton's (1927) conjectures about factors accounting for the decreasing abundance of progressively larger organisms figured prominently in much of size spectrum theory (Kerr and Dickie 2001). The focus of size spectrum studies has been on individual organisms where ecological interactions happen (Gilljam et al. 2011) without any reference to taxa except indirectly as individuals of similar size may also belong to similar taxa.

The use of body size as the representation of organisms in community studies is based on the empirical evidence that many of the most important ecological and physiological processes such as metabolic rate, somatic growth rate, diet breadth, rate of population increase, population abundance, and gross growth efficiency scale with body size (Peters 1983; Kerr and Dickie 2001). This is not to say that species interactions should be ignored but rather to say that a history of ecological studies predominantly on species may have missed some important insights into constraints on community structure (Trebilco et al. 2013). In fact there are different empirical traditions in size-based community studies by terrestrial and aquatic ecologists with the former tending to examine patterns between mean

body sizes of species populations and their abundances, not necessarily in the same community (White et al. 2007), while the latter have studied communities in a given location and characterized them by the sizes of individual organisms with little reference to species. On the other hand the theory of body size distributions in aquatic communities is sometimes based on individual organisms (Platt and Denman, 1977) and sometimes on feeding groups comprising various species of similar body size and similar diets (Thiebaut and Dickie 1993).

In this paper we present an overview of the history, theory, logistics, and applications of biomass spectra in aquatic ecology. We will briefly mention other size-based approaches and theories when they are relevant, but our principal objective is to focus on the biomass spectrum as it has been studied in freshwater and marine ecosystems.

History

In response to a growing perception that there was a need for a more “adequate quantitative expression of [plankton] community structure” than was possible through previous taxonomic and chemical studies, or measures of total primary and secondary production, Parsons and co-workers (Parsons 1969) proposed the use of ‘particle size spectra’ as a new ecological tool that could reveal patterns in plankton community structure and productivity not previously detectable. This approach was facilitated by automated instruments capable of counting and sizing plankton particles, and Sheldon and Parsons (1967) demonstrated the use of a Coulter Counter to measure the number and volumes of suspended particles, ranging from 4 μm nanoplankton to 1024 μm macroplankton, in seawater samples from Saanich Inlet, British Columbia. They determined that the most informative way to present the data was to represent size as the diameter of a sphere that had the same volume as the particle (ESD – equivalent spherical diameter), classify the sizes into a geometric series of intervals (lower boundaries differ by a factor of two; 2-4, 4-8 etc.), and plot this on a $\log_2$ -scaled abscissa against particle

concentration (ppm by volume, equivalent to $\text{mg}\cdot\text{L}^{-1}$ biomass assuming specific gravity of 1) on a linearly-scaled ordinate (Sheldon 1969; Fig. 1a). This is the biomass spectrum, sometimes termed the ‘Sheldon Spectrum’.

Sheldon et al. (1972) greatly extended the empirical basis of the biomass spectrum by surveying areas of the temperate and tropical Atlantic and Pacific oceans at different seasons and different depths using a Coulter Counter to measure concentrations of planktonic particles (living individuals and organic particles) from roughly 0.6 to 100 μm ESD. They documented considerable variation in biomass spectrum shape and total particle concentration but when spectra were organized by geographic region a tendency for roughly equal biomass concentration of particles in logarithmically equal size ranges was observed, particularly for tropical and temperate ocean sites. Although there were clear peaks and valleys in two biomass spectra extended to 4000 μm ESD by the addition of zooplankton data from the same sites (Fig. 1b), on average the pattern of roughly equal biomass held. Sheldon et al. (1972) speculated further by adding published data on the size (converted to ESD) and biomass of larger individuals such as fish and whales to their plankton biomass spectrum and hypothesized that “to a first approximation, roughly equal concentrations of material occur at all particle sizes within the range from 1 μm to about $10^6 \mu\text{m}$, i.e. from bacteria to whales”. This prophetic statement led to decades of empirical and theoretical research on the biomass spectrum that, as we describe below, revealed fundamental insights into the ecology of aquatic food webs and the subtle balances among body size-dependent processes such as population growth rates, physiological and ecological efficiencies, and predation rates that must exist for the hypothesis to be true.

Studies that followed Sheldon et al. (1972) provided biomass spectrum data that broadly supported their prediction of roughly equal biomass concentration in logarithmically equal size categories of individuals. As far as we are aware the first biomass spectra for freshwater communities were published by Sprules et al. (1983) and Sprules and Knoechel (1984) for pelagic phytoplankton and

zooplankton in a wide variety of inland lakes of Ontario (Fig. 1c). The two major biomass peaks corresponding to phytoplankton and zooplankton are evident, and while biomass concentration varies among size intervals, the heights of the peaks are similar. Sprules and Munawar (1986) and Sprules et al. (1988) also presented biomass spectra for the St. Lawrence Great Lakes in the normalized format (discussed below). Gaedke (1992) used a wide range of careful laboratory techniques to determine the sizes and concentrations of all individuals from bacteria to crustacean zooplankton sampled weekly during the growing season at a 147-m deep site in Lake Constance, a pre-alpine meso-eutrophic lake in Germany. The mean biomass spectrum, averaged over all dates and sample depths, showed three distinct biomass peaks corresponding to major trophic groups but biomass per size grade differed by less than 1.5 orders of magnitude across the whole spectrum (Fig. 1d). This was clearly consistent with the prediction of roughly equal biomass per logarithmic size grade. Gaedke's biomass spectrum format differed from Sheldon et al.'s (1972) by using carbon rather than length as a measure of size, and by using a log rather than linear scale for the ordinate (Fig. 1d).

Gaedke (1992) added independent estimates of fish biomass per size grade from yield statistics of commercially-fished species that matched the biomass per size grade of the plankton community, but Sprules and Goyke (1994) were able to collect direct sampling data for all individuals from bacteria to the largest salmonid fish species for the pelagic community of Lake Ontario, Canada/USA (Fig. 1e). The mean biomass spectrum, based on whole lake samples from each of spring, summer and autumn, again showed distinctive biomass peaks corresponding to major trophic groups (large peaks for phytoplankton, zooplankton, the amphipod *Diporeia* at log mass = -2.5, and planktivorous fish with much smaller peaks for bacteria/heterotrophic nanoflagellates and piscivorous fish at the extreme ends of the spectrum). The biomass between peaks was lower than Gaedke (1992) observed (compare Figs. 1d and e, but note the difference in ordinate scalings) and this generated some debate about the adequacy of sample sizes and protocols in constructing biomass spectra (Gaedke 1992) that we discuss

further below. Nevertheless, biomass per size grade in Lake Ontario varied for the most part within two orders of magnitude and thus differed only slightly from Lake Constance.

Schwinghamer (1981) studied benthic invertebrates at a total of six intertidal sites in the Bay of Fundy and an embayment on the Atlantic coast of Nova Scotia 40 km east of the city of Halifax. The resultant biomass spectrum also showed three distinct peaks corresponding to (from smallest to largest particles) bacteria, meiofauna, and macrofauna (Fig. 1f; note the logarithmic ordinate). The regions of low biomass between peaks were not sampling artefacts. Schwinghamer concluded that the physical environment had important effects on benthic organisms by creating habitats for microorganisms on the surface of sediment grains, for meiofauna in the interstices among grains, and for macrofauna that burrow into, or live on, the sediment surface. By superimposing literature-based benthic data from nine other marine habitats around the globe onto the Nova Scotia biomass spectrum Schwinghamer demonstrated high consistency in the size structure of these communities. Biomass per size grade was more variable for the benthic biomass spectrum (by roughly four orders of magnitude across the spectrum) than for the pelagic ones, although peak biomasses varied by only about 1.5 orders of magnitude.

These examples of biomass spectra demonstrated that in open water and benthic sites from marine and freshwater ecosystems biomass spectra have broadly similar form comprising biomass peaks of varying sharpness arranged along a roughly linear trend of slope ~ 0 and separated by particle sizes of lower abundance. Peak biomasses of the various size groupings tend to be within no more than ~ 1.5 orders of magnitude and straight lines fitted to these biomass spectra plotted on log-log or semi-log scales would have slopes near 0 consistent with Sheldon et al.'s (1972) perception that there was at most only a modest decrease in biomass per size grade from bacteria to whales.

As an alternate method of displaying biomass spectra Platt and Denman (1977) proposed the 'normalized biomass spectrum' (NBS) in which biomass concentration per size interval is divided by the

linear width of the interval and displayed on a logarithmic ordinate (Fig. 2). This corrected for the distortion in the underlying biomass (or abundance) spectrum caused by logarithmic bins increasing in width in proportion to body size. A continuous function of normalized biomass versus body mass facilitates the development of theory because it can be integrated over mass. A practical advantage is that normalization standardizes the data so that biomass spectra within which logarithmic intervals are not constant, or among which the width varies, can be analyzed and compared statistically. The NBS is the most common form of aquatic spectrum in the literature and is always presented as a double logarithmic plot typically showing a roughly linear trend of decreasing normalized biomass with increasing size of individuals (Fig. 2). The slope of a linear model fitted to a normalized biomass spectrum is often very close to -1 and this follows mathematically if the biomass spectrum has a slope of 0 (see 'Constructing biomass and abundance spectra' below). However there may be considerable residual variation around the NBS (Fig. 2). The biomass peaks that characterize biomass spectra appear in normalized biomass spectra as slightly curved domes¹ occurring along a linear trend of slope ~ -1 (compare the Lake Ontario biomass spectra in Figs 1e and 2c). This indicates that a simple linear model may not be a complete description of the size distribution of a community, and Boudreau and Dickie (1992) showed that ecological processes controlling patterns of size-dependent abundance *across* all organisms are different from those *within* major trophic or physiological groups, an issue we will consider below under Theory.

The studies referenced above established the basics of the biomass spectrum approach to the study of aquatic communities. What followed was a concerted effort to characterize biomass spectra of many different aquatic communities including small lakes (Ahrens and Peters 1991; Cyr and Pace 1993; Tittel et al. 1998), large temperate lakes (Sprules et al. 1991; Yurista et al. 2014), a large tropical lake

¹ The terms peaks and domes have been used loosely in the biomass spectrum literature but here we use peaks to describe secondary features of biomass spectra and domes to describe their counterparts in normalized biomass spectra.

(Allison 1966), a mountain lake (Rodríguez et al. 1990), a freshwater benthic community (Hanson et al. 1989), the open ocean (Rodríguez and Mullin 1986; Quinones et al. 2003), large marine embayments (Kimmel et al. 2006), the Mediterranean Sea (Vidondo et al. 1997), the Celtic Sea (Warwick and Joint 1987), high latitude oceans (Witek and Krajewska-Soltys 1989), and shallow salt marshes (Quintana et al. 2002). These studies demonstrated the broad similarities as well as the variability in size structure of aquatic communities around the world, and formed the basis for the development of biomass spectrum theories that we now discuss.

Theory

The transfer of energy throughout a food web is governed by a complex of ecological and physiological processes including predation, somatic and population growth, mortality, ingestion, assimilation, egestion, and respiration. Traditional trophic studies of these processes have focussed on species but biomass spectrum approaches are strictly ataxonomic since they are based on individual organisms, represented by their size, among which the real ecological interactions take place (Gilljam et al. 2011). In aquatic food webs this is partially motivated by the fact that gape-limited predation is common; predators tend to eat prey that are small enough to be engulfed whole or at least easily handled. More generally it is well documented that most ecological and physiological processes are strongly body-size dependent (Peters 1983) raising the possibility that the mathematics of size-based food webs would be more tractable, could account for the structural regularities that have been noted across aquatic communities, and could establish a strong predictive theory for size-structured food webs (Kerr and Dickie 2001).

In a first statement of the ecological basis for flat biomass spectra, Sheldon et al. (1972) pointed out that equal particle concentration per logarithmic size interval “can only be maintained if the rate of particle production varies inversely with particle size” but that “subtle interactions between the growth

208 rates and metabolic efficiencies of predators and prey” are also involved. Since most of the energy
209 available to small particles is lost due to ecological inefficiencies when transferred to larger particles,
210 biomass can remain roughly the same only if the turnover rate of large particles is correspondingly
211 lower. Kerr (1974) built on these ideas by equating the production of a prey population to the ration
212 (prey consumed) of a population of predators that were larger in size by a fixed ratio. Part of the
213 predator’s ration supported its metabolism and part its growth, both processes being size dependent.
214 When empirical values of the coefficients of the component processes were used in the final model
215 equation, Kerr (1974) predicted that the standing stock biomass of all prey populations comprising a
216 trophic level should be about 1.2 times that of all their predator populations. He argued that this is
217 broadly consistent with Sheldon et al.’s (1972) observations of flat biomass spectra although for the
218 comparison to be strict the number of logarithmic size intervals must be about the same in the two
219 trophic groups. Sheldon et al. (1977) proposed a very similar model to Kerr’s except they explored the
220 effects of varying predator:prey size ratios and predator growth efficiency (proportion of prey ingested
221 that is converted to predator tissue) on the ratio of biomass standing stocks. Within realistic ranges of
222 the predator:prey size ratio and growth efficiency, Sheldon et al. (1977) predicted that predator
223 standing stocks would be 0.3 - 2 times those of their prey (Fig. 3) which was consistent with
224 observations that biomass per logarithmic size interval was roughly constant (Sheldon et al. 1977).

225 Neither of these models considers the biomass spectrum to operate as a continuum of energy
226 flow from one size interval to the next, but rather across a size gap from a population of small prey to
227 one of large predators. By contrast Platt and Denman (1978) modelled how, in a steady-state
228 normalized biomass spectrum, biomass moved with time through spectral bands (narrow particle mass
229 ranges) from smaller to larger particles. The biomass flux leaving a particular spectral band was
230 dependent on the turnover time (proportional to population growth rate) of the biomass countered by
231 losses to respiration (= metabolism); both processes were particle-mass dependent. Losses to detritus

were originally included but turned out to be numerically unimportant. Using literature values of the various coefficients in the overall model equation indicated that the biomass spectrum had a slope of -0.22 which Platt and Denman (1977) suggested is typical of open ocean examples. While this model deals with the biomass spectrum as continuous, biomass flux was due only to growth and metabolism with no explicit representation of predation. Platt and Denman (1977) viewed their model as somewhat simplified, but purposely so as an initial exploration of their ideas. Silvert and Platt (1978) developed a related time-dependent model showing that normalized biomass in some size interval would move to a larger size interval after a period of time but the ratio of these biomasses would be the same as in the steady state case.

Borgmann (1982) developed the concept of particle-size conversion efficiency, ϵ , which was the gross production efficiency of a predator trophic group scaled to the predator:prey body mass ratio. He showed that using ϵ greatly facilitated estimation of the productivity of one size group of individuals from knowing that for another, and of estimating contaminant concentrations in individuals of a given body size (Borgmann and Whittle 1983).

Thiebaut and Dickie (1992) proposed a biomass spectrum model that was based on a consideration of both physiological processes of individuals and ecological processes of populations. Their work was strongly motivated by Banse and Mosher's (1980) comprehensive study of annual production:mean biomass (P:B) as a function of body mass for a wide range of natural species populations. Banse and Mosher (1980) showed that the linear model fitted to all species data combined had a shallower slope (-0.18) than those for the individual trophic groups (mean = -0.32) (Fig. 4). Thus P:B declined as a function of body size more quickly *within* trophic groups than it did *among* trophic groups. Dickie et al. (1987) and Kerr and Dickie (2001) interpreted this to mean there were two scalings in the production ecology of a population, the less negative one reflecting physiological processes within individuals (approximately equal to the size dependency of metabolic rate of -0.25, Kleiber 1961) and

the more negative one within trophic groups reflecting an ecological scaling of the interactions among predators and prey. This ecological scaling was due to changes in gross production efficiency of a predator population (production per unit of consumed prey) as its members grew in body size and foraged over broader areas seeking larger-bodied or clumped prey in order to meet their daily ration (Dickie et al. 1987). Thiebaut and Dickie (1992) modelled specific production (P/B) of a predator population as a function of normalized prey biomass modified by the product of predator gross production efficiency and the mortality imposed on the prey, all components of the model being body-size dependent and the prey being a fixed fraction of predator size. This model had multiple solutions but Thiebaut and Dickie (1992) assumed the normalized biomass spectrum of a predator to be a parabola based on the results of their within trophic group model. The normalized biomass spectra of successive smaller-bodied prey groups would also be parabolas with the same curvature but shifted vertically and horizontally by fixed amounts (Fig. 5). These periodic structures were reflected in many normalized spectra (Fig. 2) and quantitative tests of these models indicated they fit observations quite well (Thiebaut and Dickie 1993; Sprules and Goyke 1994).

A variety of other theoretical approaches to biomass spectrum analyses have been taken. Zhou and Huntley (1997) modelled marine zooplankton normalized biomass flux from smaller to larger sizes as a balance among individual growth, birth, natural death and predation. Their steady-state analysis indicated that the linear slope of the normalized biomass spectrum equalled the ratio of the intrinsic rate of increase to individual weight-specific growth rate, and they showed how these parameters can be determined if the slope of the normalized biomass spectrum is known. Although similar to Platt and Denman's (1977, 1978) formulations of biomass flux along the biomass spectrum, Zhou and Huntley (1997) explicitly incorporated additional processes controlling the flux (birth, predation) and illustrated how to make inferences about some population dynamic parameters from properties of biomass spectra. Adopting a similar framework, Law et al. (2009) used a carefully parameterized individual-

based model of a predator of a certain size encountering and capturing smaller prey and growing in size as a result. Death was by being eaten or by natural mortality and ‘renewal’ was achieved by replacing any individual leaving a size interval by dying or growing. Elements of the model such as the rate at which predators encounter prey, non-predatory mortality, and prey size selection were based on stochastic processes. Under mass-balance conditions the model showed the total biomass of each log size interval to be constant – just as observed and predicted by Sheldon et al. (1972) – although Law et al. (2009) pointed out that model solutions were sensitive to the choice of parameter values. It is interesting that this *system* state emerged from a stochastic model of *individual* growth and death. Numerical analyses indicated that the abundance spectrum model came to a steady state from initial conditions, but that this state consisted either of a linear trend with a slope of -1.1 if predators fed on a relatively wide range of prey sizes, or of sustained oscillations over time if the prey size range was narrower. Law et al. (2009) pointed out that the domes or wave-like structures emerging from Thiebaut and Dickie’s (1992) model based on trophic levels also emerged from their model of the growth of individuals. Similar time-dependent waves in the biomass spectrum were predicted by Silvert and Platt (1978) but their formulation was so much simpler than Law’s et al. (2009) that direct comparisons are problematic.

Motivated by the work of Anderson and Beyer (2006) and Hartvig et al. (2011), Rossberg (2012) modelled a community comprising many “species” varying in maturation body size, linked through feeding interactions, and expending energy on metabolism and growth. Trophic interaction strengths depended only on predator and prey sizes and reached a maximum at certain ratios of these sizes. Rossberg (2012) found that the equilibrium model corresponded to observed patterns in abundance spectra with slopes of -1 . For a particular parameterization of the model, removing some organisms in a narrow size range, such as a size-selective fisheries might do, caused ‘fronts’ to emanate towards both smaller and larger organisms. These fronts eventually stabilized in the form of trophic cascades of

alternating high and low abundances of size groups along the normalized biomass spectrum (Rossberg 2012). Rossberg (2012) speculated that the periodic modulations of the biomass spectrum he observed and the interpretation of the biomass spectral domes predicted by Thiebaut and Dickie (1992) may be compatible but they are based on quite different mathematical approaches.

The common feature of all of these theories is that they are based on physiological and ecological processes that are consistently observed in nature. Many of the theories predicted a linear normalized biomass spectrum with slope ~ -1 . In our view the future effort should be to seek a comprehensive and common theory of the biomass spectrum addressing such issues as why marine biomass spectra appear more linear than freshwater ones, whether the commonly observed NBS biomass domes are transient or stable features, and whether natural communities have a size-structured equilibrium state to which they return after perturbation (Andersen et al. This Issue).

While our focus in this review is on the aquatic biomass spectrum, there are other approaches to the study of size-based patterns in the abundance of organisms, particularly by terrestrial ecologists, that should be mentioned for completeness. Many studies were based on *species* statistics such as the abundances of mammal species populations as a function of the species mean body sizes (Damuth 1981). Observations could be taken from all over the world (global size-density relationships), from a single region (local size-density relationships), or from single species assemblages in different locations (White et al. 2007; Reuman et al. 2008). Many of these studies dealt with species within a particular trophic group, rather than across the whole range of species in a community, and relationships could often be described by a log-log linear model with a slope close to -0.75 (White et al. 2007). Results from global studies that combine data from species around the world are difficult to interpret since the species are not part of a single food web and hence do not interact. However the -0.75 slope for many species abundance-size relationships is interesting because this is inversely proportional to a commonly observed scaling of 0.75 between metabolic rate and body mass (Kleiber 1961). In his study of

mammalian herbivorous species Damuth (1981) pointed out that the product of metabolic rate per individual for a particular-sized species and the abundance of that species has a coefficient of 0 ($\text{mass}^{0.75} \times \text{mass}^{-0.75} \sim \text{mass}^0$) suggesting that the total energy use of all species populations utilizing a common resource is the same. This was called the “energy equivalence rule” that was formalized into a Metabolic Theory of Ecology by Brown et al. (2004) that described patterns of abundance and energy use in nature attributable to metabolic processes and for which there was empirical support (Enquist et al. 1998). There is overlap between this theory and biomass spectrum theories insofar as metabolic rate figures prominently in both, but while both approaches have been applied to the same data sets (Marquet et al. 2005; Reuman et al. 2008; Gilljam et al. 2011), and a modified metabolic theory applied to a pelagic marine community (Brown and Gillooly 2003; Jennings and Mackinson 2003), we feel a full development of the relationship among these theories, as begun by Rossberg (2013, Section 22.2.6), would be useful. For instance Chang et al. (2014) showed that modifying the Metabolic Theory by using a nonlinear rather than linear relation between trophic level and body size predicted the existence of secondary domes around the linear (= power law, see below) core of abundance spectra as they observed in most plankton community samples from a Taiwanese reservoir. There have been some attempts to utilize both species data and individual body size data in very comprehensive food web analyses (Jonsson et al. 2005) but whether the ecological insight justified the much greater sampling effort to incorporate species data remains an open question.

The focus on body size alone in aquatic biomass spectra means the use of automated survey instruments can greatly reduce the field effort thus allowing for large sample sizes and greater spatial and temporal resolution in addition to the unique insight afforded by a size-based approach. Individual organism size distributions have also been explored in some terrestrial communities but results are not consistent due partly to a paucity of studies and possibly because there is not as strong a relation between trophic level and body size as there is in aquatic communities (White et al. 2007).

With this discussion of the theory of biomass spectra we now address in detail the logistics of constructing biomass spectra, some underlying mathematical relations, and note some of the pitfalls to be avoided.

Constructing biomass and abundance spectra

Perhaps the most basic visualization of the size distribution of organisms in a sample is a frequency histogram showing the numerical concentration of individuals in size classes of equal linear width (Fig. 6*b*). The high abundance of small organisms with a long right tail dropping rapidly to ever decreasing frequencies of larger organisms is very typical of natural communities. Such frequency distributions can be described by a function of body size known as a power law;

(1) $f(x) = ax^{\lambda}$

This is a continuous function that is characterized by a scaling constant, a , and an exponent λ which is typically negative. More precisely it is a probability density function (PDF) of a continuous random variable (x) giving the relative likelihood or probability of x having a particular value (in practice the integral of the function gives the probability of x occurring within an interval). There are various forms of power laws depending on the nature of the data and especially the value of the exponent (White et al. 2008). We will show below that if, in a particular community, the numerical frequency distribution of body size on a linear scale follows a power law with $\lambda = -2$, the normalized biomass spectrum will be linear with a slope of -1 as is commonly observed in nature. Thus we can use such a power law to simulate a typical community of aquatic organisms, draw samples from it (Fig. 6*a*), and compute and compare size spectra in the various forms that appear in the literature. We used a power law with exponent $\lambda = -2$ and $a = 10^{10}$ and a Monte Carlo technique (Blanco et al. 1994) to select a random

sample of 1000 body masses from the distribution. Units are arbitrary so we set the body mass range from 1 to $10^5 \mu\text{g}$ (roughly the range for zooplankton) which gives total organism abundance (integral of the function between the size limits) of $\sim 10^{10} \cdot \text{m}^{-3}$ (typical of an oligotrophic lake), and expressed concentration as $\mu\text{g} \cdot \text{L}^{-1}$. To average out the vagaries of the random sampler, and to produce spectra as close as possible to mathematical expectation, we replicated the sample 10,000 times, each time ordering the masses from smallest to largest, and then computed the mean mass for each sorted position to give the final sample. Because of the long right tail in power law distributions there are inevitably many size intervals that are empty or contain few organisms which can affect the fitting of statistical models and the clarity of graphical presentations. We use the full sample of 1000 body masses to estimate parameters of fitted power functions, but for all graphs and for linear model fitting we use only size bins containing at least two observations.

We first discuss numerical or biomass frequency distributions of body size based on mass bins of equal *linear* width. The abundance frequency distribution in the simulated community is well described by a power function, as is to be expected, and the exponent $\lambda = -1.89$ is close to $\lambda = -2$ used to generate the data (Fig. 6c). We used the nonlinear function *fitnlm* in MatLab (MatLab 2015) to fit the power function. Alternatively the frequency distribution could be plotted on log-log axes and the exponent estimated as the linear slope, but this is not reliable (White et al. 2008). Since the power function is a continuous function, estimates of the exponent based on binned data will get ever closer to the ‘true’ value as bin width approaches zero. For practical purposes we have used a bin width of $0.2 \mu\text{g}$ that gives reasonable parameter estimates and allows clear graphical visualizations. The simulated biomass frequency distribution is also right-skewed but with an exponent of -0.97 (Fig. 6d). This is close to the expected value of -1 which is one unit larger ($\lambda + 1$) than the exponent of the abundance distribution (Table 1). Biomass is proportional to abundance $\times$ mass, so to convert an abundance frequency distribution (equation 1) to a biomass frequency distribution requires multiplying the right side by x

400 making the exponent $\lambda + 1$. Thus the exponent of the biomass frequency distribution has to be
401 decreased by 1 to get an estimate of the underlying power law size-abundance distribution in the
402 community (Table 1).

403 From the frequency distributions in Figs. 6c and 6d we can draw the important conclusion that
404 size distributions of organisms in nature are in fact strongly asymmetric. This appears to be at odds with
405 Sheldon's observation that organism biomass is roughly constant with body size (Sheldon et al. 1972)
406 but this is simply a matter of how the data are treated. His analysis was based on size bins of equal
407 width on a *logarithmic* scale. Such intervals are narrow for small body sizes, encompassing only a
408 limited part of the size range of these abundant organisms, and become progressively wider with
409 increasing body size, encompassing a large portion of the size range of rare organisms. Our simulation
410 of Sheldon's biomass spectrum for equal $\log_2$ mass intervals confirms the pattern of roughly constant
411 biomass with body mass (Fig. 6e) that is well described by a straight line with slope ~ 0 on log-log axes
412 (Fig. 6f). This is the biomass spectrum. The equivalent abundance spectrum is also linear but with a
413 slope ~ -1 (Fig. 6g) that is one unit more negative than the biomass spectrum as explained above (see
414 also Appendix A in White et al 2008).

415 An issue with logarithmic size intervals is that the biomass or abundance per size interval is
416 dependent not only on the characteristic mass of the interval but also on its width (White et al. 2008).
417 This issue can be avoided by standardizing or "normalizing" biomass or abundance by dividing it by the
418 *linear* width of the size interval and displaying the result on a double logarithmic scale. These are the
419 normalized biomass and normalized abundance spectra (Figs. 6h and 6i) with slopes of ~ -1 and -2
420 respectively, again showing the difference of one unit of slope between biomass and abundance (Table
421 1). The units of the Y-axis of the normalized biomass spectrum are $\mu\text{g}\cdot\text{L}^{-1}\cdot\mu\text{g}^{-1}$ which reduces to L^{-1} giving
422 the illusion of numerical concentration. This would be correct only in the very unlikely case of all mass

values in an interval being equal to the lower boundary (Blanco et al. 1994). Thus it is best to be precise and refer to normalized biomass rather than, for instance, 'abundance' (Fig. 2a).

All of the biomass or abundance spectra so far described are based on binning methods in which body mass measurements are grouped into linear or logarithmic size intervals. Such methods require arbitrary decisions about the bin width which affects parameter estimation, and bins with no observations can make statistical analysis difficult. There are formal procedures for optimizing bin width for robust parameter estimation (Blanco et al. 1994; White et al. 2008), but an alternative is to use a cumulative distribution function (CDF) that can be fit to data without binning thus making use of every individual observation. The Type I Pareto probability distribution is a form of power law that is defined over the range $x_{\text{minimum}} \leq x < \infty$ and with the exponent $\lambda < -1$ (White et al. 2008). The CDF of this function gives the probability that $x \leq X$ (a specified value), and the complement of the CDF ($1 - \text{CDF}$) gives the probability that $x > X$. This has been used for the analysis of biomass frequency distributions (Vidondo et al. 1997, White et al. 2008) and can be fit to a sample of body masses by ordering them from smallest to largest and for each one computing the proportion (= probability) of masses that are larger. The probabilities are displayed on the ordinate and mass on the abscissa of a log-log plot and if the masses are distributed according to a Type I Pareto function, the result is a straight line with slope -1 (Fig. 6j). Least-squares linear regression can be used to estimate the slope, but we show below that maximum likelihood techniques are preferable. This slope can be used to estimate the exponent of the underlying Pareto power law by subtracting one unit from it (Table 1).

To summarize, we simulated the abundance frequency distribution of body mass in linear bins in an aquatic plankton community using a power law with $\lambda = -2$. We then generated a random sample of 1000 observations from this distribution and from these constructed all common forms of histograms and size spectra that have been used to characterize body size distributions in lakes and oceans. The exponent or slopes of the fitted statistical models are 0, -1, or -2 and there are clear relationships among

them (Table 1). These relationships also follow from theory if a -2 power law is used as a starting point to characterize size distributions (Vidondo et al. 1997, Anderson and Beyer 2006). Of course data from actual aquatic communities will not precisely follow the patterns described even if an underlying linear trend of normalized biomass of slope -1 is a reasonable description. Furthermore there is evidence that while linearity may be a reasonable first order approximation to normalized biomass spectra, there can be strong nonlinear secondary patterns that require statistical description. As an example, an abundance spectrum for only zooplankton in Lake Opeongo, Ontario is better described by a quadratic model than a linear one (Fig. 7). This parallels the quadratic domes that have been fitted to the component ecological groups in the complete Lake Ontario spectrum (Fig. 2c). If the cumulative distribution of a sample of body sizes is nonlinear (e.g. dome-shaped) it may be possible to fit a Type II Pareto CDF (Vidondo et al. 1997) although its parameters are less easily interpreted than the simple slope of the complement of a Type I Pareto CDF. We should point out that while the power laws and linear models presented here are good statistical descriptors of the patterns in abundance and biomass spectra predicted by the various theories we discussed above, they do not provide any direct insight into underlying ecological and physiological processes in the communities.

Estimating biomass spectrum parameters

With this clarification about the various forms of biomass spectra we can now describe how the estimation of biomass spectrum parameters is affected by a) units and scaling of the axes, b) use of partial community data, c) sampling effort and its temporal and spatial extent, and d) statistical fitting techniques. We will consider each of these issues separately.

Units and scaling of axes

Sheldon et al.'s (1972) original biomass spectra were based on a size scale of volume doublings (V, 2V, 4V, ...) because the Coulter counter they used measured particle volume. Any such doubling scale is referred to as an 'octave' scale and has the convenient feature that the linear interval width is the same as the lower class boundary. Sheldon (1969) also proposed a related measure of linear size to match length measures typically taken with a microscope. He called this the 'equivalent spherical diameter' or ESD – the diameter of a sphere having the same volume (V) as the particle,

$$(2) \quad ESD = \sqrt[3]{6V/\pi}$$

Since diameter is proportional to the cube root of the volume then diameters scale as $(1V)^{1/3}$, $(2V)^{1/3}$, $(4V)^{1/3}$ or equivalently $V^{1/3} \times (2^{0/3}, 2^{1/3}, 2^{2/3})$. Hence a $\log_2$ scale of lengths is equivalent to a volume doubling scale and this is what Sheldon and coworkers used in their analyses (Fig. 1a).

A major variation in biomass spectrum form among authors is the unit used for individual size. This can range from body length, mass in either fresh (Fig. 1e) or dry units, and in some cases a derived measure of mass such as units of carbon (Fig. 1d) or a measure of energy content such as calories (Boudreau and Dickie 1992). Blanco et al. (1994) showed that both the slope and intercept of a linear model fitted to the normalized biomass spectrum will depend on the measure of individual size. They contrasted biomass spectra based on both volume and linear measures of individual body size showing that the ratio of biomass in adjacent size classes, the logarithmic width of adjacent size classes, and the size units all affected the linear biomass spectrum parameters. The one exception is when the biomass concentration is the same across all mass intervals; in this case the slope of the normalized biomass spectrum is -1 (biomass spectrum slope 0) no matter whether size is measured as length or volume (Blanco et al. 1994). Quinones et al. (2003) constructed plankton biomass spectra from the Atlantic ocean using both volume and carbon units as measures of individual size and found that the mean linear

slope of the NBS using volume units was not statistically different from -1.0 yet that based on carbon units was statistically lower at -1.14. The former value is consistent with Sheldon et al.'s (1977) biomass spectrum model while the latter is more consistent with Platt and Denman's (1978) theory (slope = -1.22) so effects of size units have to be carefully managed in biomass spectrum studies. Carbon is an especially difficult unit because its content per unit volume can change among species and types of organisms.

Use of partial community data

The original prediction that organism biomass per logarithmic size interval is roughly constant from bacteria to whales (Sheldon et al. 1972) is obviously based on observations from a whole food web even though its genesis came from studies of narrower particle size ranges (Fig. 1). It is clear from the biomass spectra in Fig. 1 that almost any relation between concentration and size could exist depending on the particular size range analyzed. For most size ranges corresponding to major trophic groups the pattern comprises peaks with biomass concentration declining on either side (Fig. 1). It is only when the whole community is examined that a general pattern is observable – namely that even though there is variation in biomass among size intervals the overall trend in biomass concentration is roughly flat, equivalent to a normalized biomass spectrum with a slope ~ -1 (Fig. 2). It should be clear that the perception of pattern could strongly depend on the body size range over which observations are taken. For instance in the few freshwater normalized biomass spectra based on size measurements of all pelagic individuals from picoplankton to fish the slope is very close to -1 (Sprules 2008, Lakes Ontario and Malawi; Yurista et al. 2014, Lake Superior), but for smaller inland lakes abundance spectra based on zooplankton only ranged from linear to unimodal to bimodal and are poorly described by linear models (Cyr and Pace, 1993). They pointed out that the greater range of pattern is due to the narrow range of body sizes covered compared to a whole community biomass spectrum. Similarly Gaedke (1992) noted

that while the whole plankton community in Lake Constance was well described by a normalized biomass spectrum with a slope of -1 , the subset of herbivores (ciliates, rotifers, and most crustaceans) had a slope of only -0.74 indicating that biomass declines less steeply with size for this subgroup (Fig. 2a). We caution against comparisons of biomass spectra that vary in the size range of individuals sampled.

Biomass spectrum parameters may vary among major habitats. The linear slopes of normalized biomass spectra from bacteria to zooplankton in inland lakes varied considerably in value (-0.75 to -1.0) and explained variance (coefficient of determination 84 to 97 %) (Ahrens and Peters 1991) whereas those covering the same organisms from offshore Atlantic Ocean sites varied much less (-0.96 to -1.01 and 97 to 99%) (Quinones et al. 2003). Quinones et al. (2003) also noted that normalized biomass spectra from pelagic marine communities appear to more closely fit an overall -1 linear model with less obvious secondary structure than is the case for lakes (compare Fig. 2b to Figs 2a, c and d) speculating that marine heterotrophs may feed on broader ranges of trophic levels than freshwater ones. This raises the possibility that feeding interactions in marine food webs may be different from those in freshwater webs in a manner that affects NBS structure which has been discussed in the Theory section above.

Sampling effort and spatial and temporal extent

The range of the sizes of individuals in a whole aquatic community from bacteria to whales or large fish varies enormously, and the sampling procedures required for accurate abundance estimates have to be suited to each size range. Gaedke (1992) determined that the sample volume required to obtain roughly 50 individuals per log size class varied from 10 m^3 for large predatory zooplankton such as *Leptodora* to $0.1\text{ }\mu\text{l}$ for bacteria. Sampling and counting techniques have biases such as the difficulty of seeing small particles under microscopes, the efficiency with which individuals take up stain to

enhance visibility, the filtering efficiency and selectivity of different plankton meshes (Pace 1986), and net selectivity and hydroacoustic calibration for fish. To evaluate the rigour of any sampling technique it is best to process multiple replicate samples and then to use efficiency criteria that have to be met before particles in a certain size range are retained in the analysis. Observations could be eliminated if particles are not observed in a minimum fraction of replicate samples, or if their counting error as gauged by the coefficient of variation is too high (García et al. 1994). It is especially important to ensure robust estimates of the concentration of individuals at the extremes of biomass or abundance spectra since errors there could strongly influence any model fitted to the data (Fig. 8). Formal statistical identification of outliers or those observations with an undue influence on a fitted regression model using, for instance, Cook's Distance (Quinn and Keough 2003) is recommended. The most difficult task is to assess individuals in size ranges that fall between the upper limit of one sampling technology and the lower limit of the next. On the suspicion that gaps of near zero biomass between major size groupings of individuals in previously published biomass spectra were methodological artifacts, Gaedke (1992) paid particular attention to these regions in characterizing the Lake Constance biomass spectrum (Fig 1d). The variation in biomass per size interval in Lake Constance is roughly 1.5 orders of magnitude which is not atypical of the ranges seen for the other biomass spectra (Fig. 1) suggesting that regions of lower biomass are basic features of the size structure of aquatic ecosystems and not sampling artifacts. Yurista et al. (2014) show that the Lake Superior normalized biomass spectrum is continuous across the range from small zooplankton to large fish and argue that the large sample sizes made possible by electronic survey instruments such as plankton counters and acoustics permit more rigorous assessments of biomass spectrum structural details. These issues with sampling technologies are not unique to biomass spectrum studies but play perhaps a particularly large role because of the variety of technologies required to sample individual organisms differing by many orders of magnitude in body size.

Estimation of the parameters of a linear model fitted to an abundance or normalized biomass spectrum based on binned data depends on both the total sample size of individuals and the width of the logarithmic interval chosen as demonstrated by Blanco et al. (1994) and White et al. 2008 using Monte Carlo techniques (Fig. 9). The solution to the problem for total sample size involves a combination of the practical limits to the sampling effort and consideration of the minimum number of observations required in a size interval as discussed in the paragraph above. For interval width there has to be a balance between intervals so narrow that abundance estimates are based on too few individuals, and intervals so wide that structural details of the normalized abundance spectrum are hidden. As an example, Gaedke (1992) displays the Lake Constance biomass spectrum on both $\log_2$ and $\log_{10}$ scales showing that the broad spectral features appear in both but that considerable detail is lost in the $\log_{10}$ biomass spectrum. A practical alternative that eliminates concerns about interval width is to use a cumulative distribution function that requires no binning (Fig. 6j).

Temporal and spatial variability in the size structure of a given aquatic community can occur as species go through seasonal development from small- to large-bodied stages, as predator-prey cycles oscillate through a season, and as community dynamics vary across the spatial extent of larger lakes and oceans. Shapes of biomass spectra can provide a useful indicator of this variability in community structure. For instance Mullaney and Suthers (2013) observed a peak in the normalized zooplankton biomass spectrum sampled from a coastal eddy, but the peak was absent from adjacent East Australian Current water. They speculated that these large zooplankton could support the early development of fish larvae entrained in the eddy. Gaedke (1992) documented seasonal variability in the slopes of models fitted to linear Lake Constance plankton biomass spectra that was due to varying environmental conditions throughout the season. She pointed out that there is a size-dependency of response time to perturbations so that bacteria and small phytoplankton can change quickly in abundance compared to larger organisms leading to temporary changes in the slope of the biomass spectrum. If the purpose of a

study is to compare the ‘typical’ or ‘near steady-state’ size structure of aquatic communities then spectrum data should be averaged over such short-term or transient dynamics – ideally over long enough time periods to average out the variability in the largest, slowest growing organisms and large enough spatial scales to include all major environmental variability. Sprules et al. (1991) studied the Lake Michigan complete biomass spectrum from bacteria to large fish at nine onshore-offshore transects located around the periphery of the lake in both spring and summer and captured both spatial and temporal variability in community size structure (Fig. 10). Zooplankton biomass (large central peak) was consistently greater on the west shore (Figs. 10a and c) than the east shore (Figs. 10b and d) and phytoplankton biomass increased from northeast to southeast (Figs. 10a, and 10c). Spatially averaging the biomass spectra highlights the seasonal differences showing a large phytoplankton bloom (left peak) with relatively low zooplankton biomass in the spring (Fig. 10e) changing to lower phytoplankton and greater zooplankton biomasses by summer (Fig. 10f).

Statistical fitting techniques

As we will discuss under Applications below, the ordinary least squares (OLS) regression slope and intercept (= value of Y when X is 0) of the linear normalized biomass spectrum are often used in studies of the effects of external forces such as fish exploitation or lake productivity on community size structure. However, using a combination of theory, empirical data, and Monte Carlo techniques Gómez-Canchong et al. (2013) found strong correlations between the slope and intercept of the NBS indicating they do not represent independent features of the size-structured community. This is because, in linearly size-structured communities with a normalized biomass spectrum slope <0 and organism sizes made relative to the minimum size, the following holds:

(3) $N = -a/b$

614

615 where N is total abundance (number per unit area or volume), a is the intercept, and b is the slope.

616 Given the generally strong correlation between abundance spectrum intercepts and slopes, Gómez-

617 Canchong et al. (2013) recommended that at least two of total abundance, intercept, and slope be used

618 when characterizing the abundance spectrum. Although Blanco et al. (1994) described a procedure for

619 determining the most robust estimate of the OLS intercept given the nominal value used to represent

620 the size intervals (lower or upper size class limit, geometric or arithmetic mean of size class), its

621 correlation with slope weakens its utility. An alternate approach to avoid the correlation is to rescale

622 the mid-point of the size range of individuals to 0 and use the corresponding 'height' (abundance or

623 normalized biomass) and the (unchanged) OLS slope as descriptors (Fig. 11). These parameters are

624 uncorrelated, the former depending mostly on total abundance and the latter a measure of the relative

625 abundances of small and large individuals (Daan et al. 2005). In addition, the OLS intercept may lie well

626 outside the range of body sizes defining the spectrum, whereas 'height' will occur at the midpoint of the

627 size range of organisms in a study.

628 Blanco et al. (1994) point out that the X and Y variates of a normalized biomass size spectrum

629 are not independent since the former is mass (w) and the latter is a function of $1/w$ thus violating a

630 primary assumption of OLS linear regression analysis. Nevertheless this regression technique is the

631 most common way of characterizing the parameters of normalized biomass spectra in the literature, and

632 if it is to be continued should be supplemented with more statistically reliable methods. More reliable

633 methods are presented by White et al. (2008) who used Monte Carlo techniques to contrast a variety of

634 techniques for estimating the exponent of a power-law frequency distribution (equation 1) used to

635 simulate the distribution of body masses in a community. They compared fitting OLS regressions to

636 abundance spectra based on linear, logarithmic, and normalized logarithmic binning of individual sizes,

637 OLS regressions fitted to a Pareto cumulative distribution, and maximum likelihood estimation (MLE)

techniques. The evidence indicates that binning approaches such as the normalized biomass spectrum lead to inaccurate and variable estimates of the exponent or slope, the cumulative Pareto slope gives better estimates, and the MLE estimate of the exponent of the Type I Pareto probability density function is the most robust approach. White et al. (2008) provide the formula and MatLab code for this MLE estimate. The Pareto Type I function is defined over a range from the minimum value of the variate to infinity, whereas in natural communities there is always a maximum size of organism. White et al. (2008) indicate that if this maximum is at least $100 \times$ the minimum, as is often the case, the MLE estimate is reasonable. Finally, normalized biomass spectra do not necessarily follow a strict power function (simple straight line on log-log abundance versus size plots) as is evidenced by the often observed secondary domes in NBS (Fig. 2c). In these cases it should be determined whether nonlinear models such as quadratic functions for domes in normalized biomass spectra, or a Type II Pareto function for nonlinear cumulative distributions, provide significant statistical improvement over linear models.

Applications

Productivity

There is evidence that parameters of the biomass spectrum respond to changes in ecosystem productivity in a relatively consistent manner. Plankton community normalized biomass spectra in eutrophic systems tend to have flatter slopes (Fig. 12) and higher y-intercepts (linear model) or greater curvature and higher peaks (quadratic model) than oligotrophic ones (Sprules and Munawar 1986; Ahrens and Peters 1991; Zhang et al. 2013). This shows that increasing productivity results in a greater abundance of large plankton individuals relative to small ones and a higher overall total abundance (Quintana et al. 2002; Finlay et al. 2007). By contrast, Emmrich et al. (2011) showed for fish assemblages in north German lakes that NBS slopes were shallower in deeper, less nutrient-rich lakes

due to higher abundances of large predatory fish. Thus different patterns in NBS parameters may depend on the trophic group studied. Residual variation around linear NBS models for plankton communities has also been shown to be higher in more productive systems suggesting that systems with greater nutrient inputs (benthic, littoral, rivers, etc.) show greater departure from the theoretical steady state, possibly due to higher throughput of energy in these systems (Sprules and Munawar 1986). On the other hand, some researchers have found that NBS parameters for plankton (Gamble et al. 2006) and complete pelagic communities (Sprules 2008) are not sensitive indicators of increasing productivity. This discrepancy does not appear to be a result of limited productivity ranges, lack of temporal and spatial averaging of biomass spectra, or the type of biomass spectrum model used (e.g. biomass, abundance, mass or length). Thus, many aquatic communities respond in a predictable manner to changes in productivity, and this is captured by the normalized biomass spectrum parameters, while others do not. It may be that the community biomass spectrum is not sensitive enough to external perturbations and that metrics with greater resolution are needed to define consistent effects of productivity on the size distribution of aquatic communities.

Indicator of environmental perturbations

The sensitivity of the biomass spectrum to environmental perturbations has been of particular interest to researchers. Biomass spectra reflect ecological processes governing the biomass distribution and energy flow in aquatic ecosystems (Trebilco et al. 2013) so anthropogenic and natural disturbances that disrupt these processes should be captured by the shape of a community biomass spectrum. Duplisea and Kerr (1995) demonstrated that a natural perturbation to the demersal fish community on the Scotian Shelf was reflected in their normalized biomass spectrum. They did this by recording γ -values (closely related to curvature) of quadratic domes (Thiebaut and Dickie 1992, 1993) fitted to normalized biomass spectra averaged over many sites for individual years and displaying their variation

around the mean value of γ for the 22-year sampling period (Fig. 13). 1976 stood out as an unusual year that was characterized by an anomalously large biomass of squid. Yvon-Durocher et al. (2011) used an outdoor freshwater mesocosm experiment to show how the abundance spectrum of planktonic communities could be affected by climate change. A 4°C increase in temperature caused the abundance of small individuals to increase and larger ones to decrease which was reflected by a statistically significant steepening of the linear abundance spectrum slope and a lowering of the y-intercept.

Much research has been directed toward using the biomass or abundance spectrum as an indicator of exploited fish communities (Rice and Gislason 1996; Blanchard et al. 2005; Sweeting et al. 2009). The abundance spectra of fish communities subjected to intense fishing pressure tend to have significantly steeper slopes and lower mid-point heights (y-intercept of centered abundance spectrum) than communities exposed to low fishing intensity (Zwanenburg 2000; Daan et al. 2005). The steepening of the abundance spectrum slope reflects the removal of large fish from the system and possibly a release in predation pressure on smaller prey fish while the lower height of the abundance spectrum indicates an overall reduction in the abundance of the community (Blanchard et al. 2005; Daan et al. 2005). Even in systems with relatively low harvesting due to subsistence fishing, an abundance spectrum was sensitive enough to show decreasing slopes and decreased heights indicating loss of larger fish and overall reductions in fish abundance respectively as harvesting increased (Fig. 14) (Dulvy et al. 2004; Graham et al. 2005). Hence, abundance and biomass spectra have the potential to be used as an indicator of fisheries exploitation and have already been used as a tool to gain insight into management practices of fishery resources through evaluation of fishing moratoria (Zwanenburg 2000; Jiang et al. 2009) and trawling practices (Sweeting et al. 2009). Moreover, the Ecosystem Approach to Fisheries Management (EAFM) by the European Union (EU) adopted conservation of community size-structure into their Marine Strategy Framework Directive (EU 2008). They recognized the importance of size-based methods, such as the Large Fish Indicator (LFI) (the proportion by weight of fish individuals

greater than a length threshold defined for large fish) (Greenstreet et al. 2010), as conservation tools because they can summarize the size structure of whole communities (Fung et al. 2013). This allows conservation efforts to focus on energy flow and structural elements of food webs (size and abundance) rather than single species (EC 2010, Fung et al. 2013). Recently, fisheries researchers have been developing size-based models that simulate the impacts of different types of fishing practices on fish communities to determine optimal harvest methods that minimize negative effects on their abundance and size structure (Andersen and Pedersen 2010; Blanchard et al. 2014; Jacobsen et al. This Issue; Kolding et al. This Issue).

Despite these successful applications, there is some evidence that the biomass spectrum may not reflect changes in community structure even when systems are undergoing large shifts in species composition. Sprules (2008) constructed annual normalized biomass spectra for zooplankton in Lakes Erie and Ontario from 1991-1997 during a period when these lakes were undergoing large changes in species composition and abundance that should have directly or indirectly affected zooplankton in these lakes (e.g. lake trout decline, invasion of sea lamprey, zebra mussels and *Bythotrephes*, stocking of Pacific salmon, etc.). However, he found that there were no differences among the biomass spectra across years for each lake. In the same paper Sprules constructed normalized biomass spectra for the whole pelagic community (phytoplankton, zooplankton and fish) for Lake Ontario, Canada and Lake Malawi, Tanzania and showed there was no difference in slopes between the two lakes despite large differences in geological age, species composition, and climate. He suspects that regularities in normalized biomass spectra are likely a result of the species-independent ecological and physiological limits on the movement of energy through size-structured communities that Peters (1983) and others have helped identify. It may be that transient responses of aquatic communities to disturbance are 'pulled back' to a common steady state by these limits.

734 ***Predicting production and biomass***

735 Theoretical models developed by Borgmann (1982, 1987) and Thiebaut and Dickie (1992, 1993)
736 that derive the shape of the biomass spectrum using allometric relationships between predators and
737 prey have been used to estimate the production and biomass of various trophic groups (Borgmann et al.
738 1984; Minns et al. 1987; Sprules and Goyke 1994,). Borgmann (1982, 1987) showed that production or
739 biomass can be predicted for any size range of individual organisms if the production or biomass of
740 another size group, the particle-size conversion efficiency (ϵ), and the exponent of the size-dependent
741 turnover rate (n) are known. Sprules et al. (1991) used published values of ϵ and n to predict
742 phytoplankton, zooplankton, and planktivorous fish biomass that conform closely to observations for
743 Lake Michigan, although estimates for piscivorous fish were low because many of these species are
744 stocked. Leach et al. (1987) also used Borgmann's (1982) model to predict potential fish productivity
745 from zooplankton and benthic invertebrate productivity in the St. Lawrence Great Lakes and Lake
746 Winnipeg, and noted that while the technique held promise, refinements of the model and the data
747 used as input were required. Sprules and Goyke (1994) found that predictions of annual zooplankton
748 production in Lake Ontario using Borgmann's model were much lower than measured estimates. The
749 limitations of Borgmann's model may be due to the assumptions that all prey production is consumed
750 by predators, and that ϵ and n are constant throughout the food web. The latter assumptions result in a
751 smooth, even decline in biomass as the sizes of individuals increase (Sprules et al. 1991) and thus does
752 not incorporate the dome structure observed in many normalized biomass spectra (Sprules et al. 1991;
753 Boudreau and Dickie 1992; Sprules 2008). Sprules and Goyke (1994) parameterized Thiebaut and
754 Dickie's (1992) 'dome' model using the normalized biomass parabola for Lake Ontario zooplankton in
755 combination with published parameters of allometric production:biomass functions and found
756 predictions of zooplankton annual production for Lake Ontario were close to independent sampling
757 estimates. Yurista et al. (2014) successfully applied this theory to predict the shape and position of

normalized biomass domes of large predatory zooplankton and planktivorous fish biomass in Lake Superior using the relative positions of phytoplankton and herbivorous zooplankton biomass domes. They also estimated predatory fish standing stock using average shifts of phytoplankton and zooplankton domes and found these estimates to be consistent with 2011 lake-wide measured values. Thus, the biomass spectrum offers a promising tool for fisheries research to estimate the biomass and production of higher trophic levels given more easily obtained information on lower ones. Thiebaut and Dickie's (1992) model may be better suited than that of Borgmann's (1982, 1987) for predicting biomass and production in systems that exhibit a periodic dome structure but there is a need for empirically validating these models in a variety of systems before biomass spectrum estimates can be used for management purposes. We should add one caveat about using biomass spectrum models for making predictions about biomass and production in aquatic communities. Models typically represent steady-state conditions of a system so lack of agreement between model predictions and observed community structure could either reflect limitations of the model or that the community is in a perturbed state. We suggested in the section on 'Estimating Biomass Spectrum Parameters' above that averaging data over spatial and temporal scales gives the best estimate of a system's steady-state structure. If the system is known to be perturbed, an alternative approach is to use models to reconstruct what could be the natural state of the community. This was done by Jennings and Blanchard (2004) who used biomass spectrum theory to estimate what would be the biomass of the heavily fished North Sea fish community in the absence of fisheries exploitation.

Predicting ecological processes

Important ecological interactions and physiological processes in aquatic ecosystems are dependent on body size (e.g. mortality, transfer efficiencies, metabolism and growth) (Kerr and Dickie 2001). Consequently, researchers have been incorporating biomass spectrum theory into models

designed to estimate size-dependent ecological processes. For example, Blanco et al. (1998) predicted respiration of freshwater and oceanic plankton communities using empirical normalized biomass spectra and allometric relationships between body size and respiration. Jennings et al. (2002) quantified trophic transfer efficiencies using a combination of biomass spectrum data and production- and trophic level-body size relationships. Peterson and Wroblewski (1984) derived an equation to estimate mortality rates of fish-sized particles using the normalized biomass spectrum equation developed by Silvert and Platt (1980). Thygesen et al. (2005) used the abundance spectrum model of an aquatic community to calculate the energetics of an individual organism of a given size which was then used to find optimal life history strategies of individuals. Therefore, the biomass spectrum approach appears to be a valuable tool for estimating and predicting ecological processes in size-structured communities and offers an alternative approach to species-specific methods which are more costly and time consuming.

Conclusions and recommendations

Our review of the aquatic biomass spectrum demonstrates that it has strong empirical and theoretical bases that have revealed new insights into constraints on the structure of biological communities. There is remarkable regularity in the size structure of a wide variety of aquatic ecosystems ranging from open oceans to small lakes, and a variety of size-based theories highlight the predominant roles of size-specific metabolic rate and the predator:prey size ratio in determining this regularity. Biomass spectra are based on the individual organism, the level at which ecological interactions take place, and in particular on their body size which is a strong predictor of most of the ecological and physiological processes governing the flow of energy through ecosystems. Taxonomic identity of organisms is not explicit. The overall pattern of the abundance and normalized biomass spectra for a whole community near steady state comprises a linear or near linear “backbone” with a slope close to -1 and a series of domes corresponding to groups of individuals of similar size and

ecological role (autotrophs, primary heterotrophs etc.). The slope can vary among communities that differ, for example, in productivity or in the extent of fish harvesting, but is typically not shallower than -1 on a sustained basis for a whole community of organisms near steady-state. In some communities, such as the open ocean, the domes are not prominent (Rodríguez and Mullin 1986) whereas in others, such as inland lakes, they are more obvious (Gaedke 1992, Yurista et al. 2014). It is likely that these differences are related to ecological characteristics of the ecosystem such as the mean and variance in predator:prey size ratios, the strength of the association between ecological role and body size (i.e. fish-sized zooplankton or vice-versa), and the diet breadth of predators (Quinones et al. 2003). Biomass spectra have successfully been used as indicators of environmental perturbations of community structure, including fishing pressure, and have also been used as a basis for estimating productivity of size groups in lakes and oceans.

Despite the relatively long history of biomass spectrum studies, there has been little attempt to standardize methods so that comparisons among studies, and with predictions from theory, can be made with confidence. We finish with some suggestions below that may help.

Visualizing Spectra

For simplicity, and to facilitate comparison between past and future studies, use the abundance spectrum or the normalized biomass spectrum to visualize results (White et al 2008).

Sample Size.

Estimation of spectrum parameters is strongly dependent on sample size. The goal should be to collect as large a sample of individuals as possible so that abundance in *all* size intervals is rigorously estimated. Be cautious especially of abundance estimates at the upper and lower size ranges for a given sampling technique and utilize criteria such as those described in García et al. (1994), or statistical criteria such as

Cook’s distance, to eliminate observations based on small numbers or those that may distort the outcome of a linear regression model.

Logarithmic Bin Size for Body Size Axis.

Choose the smallest logarithmic bin size for which acceptable estimates of numerical abundance/biomass are available.

Units of Body Size.

Use fresh mass which is equivalent to the volume measurements of many automated survey instruments if specific gravity of unity is assumed. If other units are used, provide a conversion to fresh mass, being careful to report it by size group if it varies.

Models Fitted to Size Spectra.

The primary trend to a full community abundance or normalized biomass spectrum is approximately linear. Secondary patterns, if present, are generally parabolic domes. For some purposes the primary linear trend may be an adequate description. For others, particularly if restricted size ranges are studied, quadratic models, or Pareto Type II models for nonlinear cumulative distributions, should also be fitted and a statistical evaluation made of whether the additional reduction in residual variation is significant.

Estimating Parameters of Linear Spectra

Use both ordinary least squares (OLS) regression and an MLE estimate of the exponent of the Type I Pareto probability density function to obtain complementary estimates of λ , the exponent of the power function underlying linear abundance spectra (Equation 1). When applying OLS methods: (i) use

abundance or biomass spectra data to maintain independence between the dependent and independent variables; (ii) rescale the body size axis so that the new zero is placed at the centre of the logarithmic bin that contains the midpoint of the range of observed body sizes; (iii) report both the OLS estimate of the spectrum slope and the Pareto parameter (λ), recognizing that the OLS procedure provides an estimate of $(\lambda + 1)$ and $(\lambda + 2)$ for the abundance and biomass spectra respectively; (iv) report the intercept, or 'height', at the new zero as well as the nominal body size value (in original units) corresponding to the intercept. When using MLE methods use the formula in White et al. (2008, Table 1) to estimate the exponent of the Type I Pareto function which is a direct estimate of λ .

Full versus Partial Spectra.

Be cautious making inferences about the full community spectrum from observations on restricted body size ranges (e.g. for phytoplankton only, or for phytoplankton plus zooplankton).

Spatial and temporal sampling scales.

If the objective is to characterize the near steady state spectrum of a relatively independent community, it is important to recognize that ecological processes operate at a variety of temporal and spatial scales, typically related to body size. Therefore it is desirable to average over short-term and spatially localized dynamics in order to characterize the near steady state. Ideally this means different sampling regimes for organisms of varying size and turnover time, but in practice samples that reflect the major spatial gradients in the study system and the principal seasons should suffice.

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Figure captions

Figure 1. Examples of biomass spectra. Units and axis scales vary among studies. a) Basic form of a biomass spectrum from Coulter Counter data on a $\log_2$ axis of particle volume (converted to equivalent spherical diameter) and a linear concentration axis in ppm by volume. Redrawn with permission from Sheldon et al. (1972), copyright by the American Society of Limnology and Oceanography, Inc. b) Pacific (upper) and Atlantic Ocean plankton biomass spectra. Redrawn with permission from Sheldon et al. (1972), copyright by the American Society of Limnology and Oceanography, Inc. c) Mean biomass spectrum for phytoplankton and zooplankton for 26 inland lakes of Ontario. Redrawn with permission from Sprules et al. (1983). d) Lake Constance, Germany mean biomass spectrum from bacteria to crustacean zooplankton. Redrawn with permission from Gaedke (1992), copyright by the American Society of Limnology and Oceanography, Inc. e) Lake Ontario Canada/USA mean biomass spectrum from bacteria to large salmonid fish. Redrawn with permission from Sprules and Goyke (1994). f) marine intertidal mean benthic biomass spectrum from Bay of Fundy and Atlantic Ocean sites around Nova Scotia, Canada. Redrawn with permission from Schwinghamer (1981).

Figure 2. Examples of normalized biomass spectra. Slopes or equations of ordinary least squares regression are shown. a) Lake Constance, Germany. Regressions are shown for all plankton (solid line) and for herbivores only (dashed line). Although the ordinate is labelled 'abundance' it is actually normalized biomass. Corresponding biomass spectrum is in Fig. 1d. Redrawn with permission from Gaedke (1992), copyright by the American Society of Limnology and Oceanography, Inc. b) A normalized biomass spectrum for the euphotic zone of the North Pacific Ocean central gyre averaged over seasons and including phytoplankton, protozoa, copepods, euphysiids, amphipods, and small fish larvae. Redrawn with permission from Rodriguez and Mullen (1986), copyright by the American Society of

1165 Limnology and Oceanography, Inc. c) Lake Ontario, Canada/USA. Equivalent biomass spectrum in Fig
1166 1e. Dashed line is the linear model for all data, solid lines are quadratic models fitted to individual
1167 plankton groups. Redrawn with permission from Sprules and Goyke (1994). d) A normalized biomass
1168 spectrum from a permanent subtropical shallow lake in north-eastern Argentina including data on pico-,
1169 nano-, micro-, and macroplankton averaged over two sampling dates separated by a year. Redrawn
1170 with permission from Czar et al. (2003). e) Example of an abundance spectrum for phytoplankton and
1171 zooplankton in Lake Superior, Canada/USA. Observations are daytime and are averaged over sampling
1172 sites in 2011 (P. Yurista, US EPA, Duluth, MN, USA, pers. comm.).

1173

1174 Figure 3. Interaction among predator:prey body size (D_c/D_p) and biomass standing stock (S_c/S_p) ratios,
1175 and predator growth efficiency (G_e where capture efficiency $C_e = 1$) according to Sheldon et al. (1977).
1176 The general equation is shown above the graph. Dashed line shows values required for equal standing
1177 stocks of predator and prey populations and solid lines show the range of community structure to be
1178 expected for varying growth efficiencies. Redrawn with permission from Sheldon et al. (1977).

1179

1180 Figure 4. Relationships between specific production (annual production/mean biomass) and body mass
1181 for a variety of trophic groups. Each data point is a population. Solid lines are fitted linear regressions
1182 for each group and the dashed line is the overall regression. Redrawn with permission from Banse and
1183 Mosher (1980), copyright by the Ecological Society of America.

1184

1185 Figure 5. Patterns of normalized biomass spectra predicted from Thiebaut and Dickie's (1992) multiple
1186 spectrum model. The separate normalized biomass domes have the same curvature and equal
1187 displacement along each of the horizontal and vertical axes. Redrawn with permission from Sprules and
1188 Goyke (1994).

1189
1190 Figure 6. Examples of various forms of biomass and abundance spectra for actual lake sampling data or
1191 for a single data set generated from Monte Carlo simulations (see text for details). All regression and
1192 power models fitted using the 'fitnlm' function in MatLab Version R2014b (MathWorks 2015). a) The
1193 Monte Carlo simulated data. b) Abundance frequency distribution of zooplankton across a linear series
1194 of mass intervals. Data are from a 1 km, 2 m deep horizontal tow of an Optical Plankton Counter in Lake
1195 Opeongo, Ontario. c) An abundance frequency distribution with linear mass intervals. d) Biomass
1196 frequency distribution with linear mass intervals. e) Biomass spectrum on a log-linear scaling. f) Biomass
1197 spectrum on a log-log scale. g) Abundance spectrum. h) Normalized biomass spectrum. i) Normalized
1198 abundance spectrum. j) Type 1 Pareto cumulative mass distribution.

1199
1200 Figure 7. A biomass dome for a zooplankton sample from Lake Opeongo, Ontario. Data were collected
1201 with an Optical Plankton Counter towed at a fix depth of 2.5 m for 1.2 km. Data points are the summed
1202 abundances of individual organisms in $\log_2$ mass intervals. The equations and Akaike Information
1203 Criterion (AIC) of a linear (dashed line) and a quadratic (solid line) model fitted to the data using the
1204 non-linear fitting function 'fitnlm' in MatLab Version R2014b are shown (MathWorks 2015). Note that
1205 the quadratic model with the lower AIC is a better fit to the data than the linear one.

1206
1207 Figure 8. Illustration of pruning data points based on low sample sizes. Data are from plankton samples
1208 from the western Mediterranean Sea. Closed circles are retained data points and open circles are those
1209 removed due to excess counting error, or absence from at least one of 15 replicate samples. Solid line is
1210 a linear model fitted to retained points and dashed line is that fitted to all original data points; least
1211 squares linear regressions and explained variance are shown. Redrawn, with permission, from García et
1212 al. (1994), copyright by Scientia Marina.

1213
1214 Figure 9. Effects of sample size (line style denotes number of individuals) and the ratio of upper:lower
1215 logarithmic size class boundaries (higher ratio = fewer, wider size classes) on estimations of the
1216 normalized abundance spectrum slope. Each distribution of slopes is based on 1000 random samples
1217 selected from a simulated spectrum of slope -2 (equivalent to a flat biomass spectrum) in a community
1218 with 10^{12} individuals m^{-3} and particle sizes equivalent to bacteria to small zooplankton. Sample size of
1219 100 individuals for a ratio of 3.0 is missing because there were too many size classes with no individuals.
1220 Redrawn, with permission, from Blanco et al. (1994), copyright by Scientia Marina.

1221
1222 Figure 10. Spatial and temporal variability in biomass spectra from Lake Michigan, Canada/USA.
1223 Samples are from the following parts of the lake; a) northwest, b) northeast, c) southwest, and d)
1224 southeast. Mean biomass spectra for the whole lake are from sampling trips in e) late May (spring), and
1225 (f) late August to early September (summer). Redrawn with permission from Sprules et al. (1991).

1226
1227 Figure 11. Lake Ontario normalized biomass spectrum plotted with a) the original size axis with dashed
1228 lines showing $X = 0$ and the corresponding intercept, and b) the size axis rescaled so its mid-point is at 0
1229 with dashed lines showing the new $X = 0$ and the corresponding 'height'. In each case the equation of
1230 the fitted least squares linear regression is shown. This transformation of the body mass axis can be
1231 used to remove the correlation between the slope and intercept in linear normalized biomass spectra so
1232 that they are independent parameters reflecting the size distribution and overall particle abundance
1233 respectively.

1234
1235 Figure 12. Relation between normalized spectrum slope and measures of ecosystem productivity for
1236 the North Pacific Gyre (0), inland lakes (3) and various St. Lawrence Great Lakes. Ranges (vertical lines),

1237 medians (cross bars), or single observations (circles) are shown. Redrawn with permission from Sprules
1238 and Munawar (1986).

1239

1240 Figure 13. Each point is the gamma value ($\approx$ curvature) for a quadratic model fitted to the mean
1241 normalized demersal fish biomass size spectrum based on 48 depth strata samples from the Scotian
1242 Shelf for a single year. Values are shown for the years from 1970 to 1991. The arrow indicates the
1243 gamma value for the mean spectrum for the 22-year period. Note the unusually low value in 1976
1244 (circled) which was a year with high squid biomass. Drawn using data from Duplisea and Kerr (1995).

1245

1246 Figure 14. Effects of increasing fishing intensity (persons km^{-1} of reef) on abundance spectrum
1247 parameters for coral reef fish communities across ten fishing grounds along the northwestern coast of
1248 Kadavu Island, Fiji. Abundance spectra were fish number in linear length intervals vs interval midpoint
1249 on log-log axes after scaling the centre of the length axis to zero. Each data point represents the mid-
1250 length height (closed circles) or slope (open circles) of a linear regression fitted to the abundance
1251 spectrum for each of the 10 fishing grounds. Lines are linear regressions of the height (solid line) or
1252 slope (dashed line) vs log fishing intensity ($F_{9,69} = 15.78$ $p < 0.01$, $F_{9,69} = 3.20$ $p < 0.01$ respectively).
1253 Drawn using data from Graham et al. (2005).

Table 1. Values of the exponents (power models) or slopes (linear models) for various size spectra if the actual abundance frequency distribution of body sizes follows a power law with exponent λ . For each type of size spectrum these values indicate how the fitted model parameter has to be modified in order to estimate the actual exponent of the abundance-size distribution (e.g. subtract 1 from the abundance spectrum slope).

Size spectrum model	Exponent or slope
Abundance frequency histogram (power)	λ
Biomass frequency histogram (power)	$\lambda+1$
Biomass spectrum (linear)	$\lambda+2$
Abundance spectrum (linear)	$\lambda+1$
Normalized biomass spectrum (linear)	$\lambda+1$
Normalized abundance spectrum (linear)	λ
Type I Pareto probability density function (power)	λ
Cumulative Pareto distribution (linear)	$\lambda+1$

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

(a) Table of data

Mass (μg) (lower boundary)*	Interval Midpoint (on $\log_2$ scale)	Abundance (No. L^{-1}) = number per size interval	Biomass ($\mu\text{g L}^{-1}$) = Σ mass per size interval	Normalized Biomass (L^{-1})	Normalized Abundance ($\text{No. L}^{-1} \mu\text{g}^{-1}$)
(a)	(b)	(c)	(d)	(d/a)	(c/a)
1	0.5	500	693.6	693.6	500.00
2	1.5	250	694.0	347.0	125.00
4	2.5	124	687.1	171.8	31.00
8	3.5	63	696.8	87.1	7.88
16	4.5	31	685.7	42.9	1.94
32	5.5	16	707.3	22.1	0.50
64	6.5	8	722.7	11.3	0.13
128	7.5	4	760.6	5.9	0.03
256	8.5	2	837.8	3.3	0.01

* Lower boundary equals interval width for $\log_2$ scale only

Figure 6 (1)

Figure 6(2)

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Figure 12

Figure 13

Figure 14