

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	47	1	87-101	1999
---	----	---	--------	------

Werner ULRICH

Nicholas Copernicus University in Toruń Department of Animal Ecology
 Gagarina 9, 87-100 Toruń; Poland e-mail: ulrichw @ cc.uni.torun.pl

THE DENSITY – WEIGHT AND THE BIOMASS – WEIGHT DISTRIBUTION CAN BE GENERATED BY THE SPECIES – WEIGHT DISTRIBUTION TOGETHER WITH DENSITY FLUCTUATIONS: EVIDENCE FROM MODEL SPECIES DISTRIBUTIONS IN THE HYMENOPTERA

ABSTRACT: This paper tests the hypothesis that the density – weight distribution of species assemblages may be generated alone by underlying weight dependent density fluctuations by constructing several model species – weight and density – weight distributions. The simulations revealed that indeed even a slight dependence of density fluctuation on body weight generated typical density – weight distributions with upper density boundaries and triangular shapes. Other ecological explanations, such as metabolic constraints or arguments based on fractal geometry, may therefore not be necessary to explain the pattern. In a second step of analysis the density – weight relationship was combined with various species – weight distributions (computed over \log_2 weight classes) to show that in nearly all parameter settings steadily rising biomass distributions with a decline only towards the largest weight classes result. The generality of the equal biomass hypothesis is therefore rejected. A general model is developed to explain several of the patterns in density – weight and species – weight plots assuming only underlying weight dependent speciation and extinction rates and weight dependent density fluctuations.

KEY WORDS: Hymenoptera, density – weight distribution, species – weight distribution, biomass – weight distribution, density fluctuation

1. INTRODUCTION

Recently the species – weight (SWD), biomass – weight (BWD), and the density – weight (DWD) distributions have gained a lot of attention (May 1978, 1986, Lawton 1989, 1990,

Currie 1993, Currie and Fritz 1993, Gaston 1993, Blackburn and Gaston 1996, Novotny and Kindlmann 1996, Cyr et al. 1997, Scharf et al. 1998, Ulrich 1999a).

It has been found that the numbers of arthropod species per logarithmic weight class (often approximated by size classes) often can be described by log-normal or truncated normal distributions with a positive skewness (Van Valen 1973, May 1978, Novotny and Kindlmann 1996). Several hypotheses have been proposed to explain the pattern (see Novotny and Kindlmann 1996 for a review), and the log-normality seems to be generated by weight dependent speciation and extinction rates (Dial and Marzluff 1988, Maurer et al. 1992). The positive skewness, however, that means the long tail at the site of larger sizes, is not well understood and needs further theoretical explanation.

The DWD of animal communities or taxa normally follows power functions (Damuth 1981, Currie 1993, Currie and Fritz 1993). This relation has been found in various taxa such as birds (Nee et al. 1991), mammals (Damuth 1981), zoobenthic communities (Strayer 1986, Cyr et al. 1997), and various arthropod groups (Currie and Fritz 1993, Ulrich 1999a). The slope of the global function ranges around -0.9 with large terrestrial communities having slightly steeper slopes (-0.92 versus -0.89 ; Cyr et al. 1997). The theoretical reasoning of Griffiths (1992) pointed to a general slope value of -1.0 . Local communities or narrow taxa did not show such a clear relationship; the slopes appear to be less steep (around -0.5 or less) or even no density – weight relationship was observed (Gaston 1988, Currie and Fritz 1993, Ulrich 1999a). However, this pattern is in accordance with expectation, because fewer species and a narrower range of weight classes should lower the statistical significance of the fits and show a greater variance.

The value of the slope is normally related to metabolic rates (Peters 1983, Griffiths 1992), because individual metabolic rates scale approximately with a slope of -0.75 to body weight. While this argument may be applicable to endotherms, in the case of the ectothermic arthropods the wide range of slopes and the differences between local and global density – weight relationships point to other explanations (Blackburn et al. 1992).

A second feature of the density – weight functions is the so called triangular form (Blackburn et al. 1992, Currie 1993). This means that the smallest species are normally not the most abundant ones but range at intermediate levels. This pattern results in a roughly triangular shape of the density – weight curve (Figure 7). The cause of this pattern is not well understood. Lawton (1989, 1990) argued that underrepresentation of small rare species in samplings or literature compilations and overrepresentation of “tourists” in local assemblages may result in biases towards intermediate sized species and densities. On the other hand, Currie (1993) supposed that stochastic effects are the reason for the triangular pattern. In random samples from simulated density – weight distributions he found patterns very similar to the observed ones.

The DWDs seem also to define upper density boundaries of the species (Blackburn et al. 1992, Scharf et al. 1998, Ulrich 1999a). Blackburn et al. assumed that the upper limit may be defined by the commonest species which are resource limited and concluded that the upper line should have a slope of -0.75 . Such a slope is predicted if the metabolic argument holds. Ulrich, however, when studying natural hymenopteran communities, found that such upper

boundaries may better be described by second order polynomial functions and supposed that the limit defines the upper boundary of stability for each population. The upper density limit may therefore be related to the density fluctuations of the species.

Early studies on aquatic systems (Sheldon et al. 1972) and vertebrate communities (Damuth 1981) suggested that the distribution of biomass among various weight classes in natural communities is rather equal (the so called "equal biomass hypothesis"). Recent work on benthic systems (Strayer 1986), on birds (Maurer and Brown 1988) and tropical arthropod guilds

(Stork and Blackburn 1993), however, suggested a steady rise of biomass towards larger weight classes or at least an asymptotic relationship. The reasons for these contrasting results are not well understood.

The aim of the present study is to analyze the conditions under which natural DWDs and BWDs appear. To do so, simulations with fluctuating model populations as well as comparisons with natural assemblages are undertaken. The simulations indicate that both, the density – weight and the biomass – weight relationship, are generated alone by weight dependent density fluctuations in combination with normal or log-normal SWDs.

2. METHODS

2.1. DENSITY – WEIGHT DISTRIBUTION

The starting point of the present analysis is the hypothesis that random density fluctuations of the species of a certain assemblage alone can generate density – weight distributions with a negative slope and a triangular form. To test this hypothesis model communities were constructed in which the species were divided into 24 binary weight classes. 7 different SWDs (log-normal, normal, Poisson, beta, linear, equal, and random) and 2 types of DWD (power and linear) were combined under various parameter settings to study the resulting BWDs. The properties and functions of the above distributions are given in general statistic textbooks. Normal and log-normal relationships are most often found in nature (Novotny and Kindlman 1996). The beta distribution was

included because of its convex form. Poisson, normal and log-normal distributions are characterized by concave shapes.

The species of these model assemblages were allowed to fluctuate at random between 0 and an upper boundary, which was defined either by a power function ($\text{Density} = \text{const. Weight}^{\text{slope}}$) or by a linear relationship ($\text{Density} = \text{factor Weight} + \text{intercept}$). Therefore, the model assumes that smaller species have a greater tendency for larger density fluctuations than larger ones. Ten slope values between 0 (no weight dependence of density fluctuation) and -0.9 were tested. The linear dependence was tested with 10 factor values between 0 and -0.01 . The slope values and the resulting density fluctuations are given in Table 1.

Table 1: Density fluctuations of the species of a model community generated by a power function with $y = 10 \text{ weight}^{\text{slope}}$ and a linear function with $y = 100 + \text{factor} \cdot 100$. The values of 10 and 100 are chosen to obtain realistic upper densities similar to observed ones.

Slope	Power function		Factor	Linear dependence	
	Max. density fluctuation of the			Max. density fluctuation of the	
	smallest species	largest species		smallest species	largest species
0	10.00	10.00	0.000	100.00	100.00
-0.1	19.29	7.31	-0.001	100.00	50.00
-0.2	37.22	5.34	-0.002	100.00	25.00
-0.3	71.81	3.91	-0.003	100.00	12.50
-0.4	138.53	2.86	-0.004	100.00	6.25
-0.5	267.26	2.09	-0.005	100.00	3.13
-0.6	515.61	1.53	-0.006	100.00	1.57
-0.7	994.74	1.12	-0.007	100.00	0.78
-0.8	1919.10	0.82	-0.008	100.00	0.39
-0.9	3702.41	0.60	-0.009	100.00	0.20

2.2. BIOMASS – BODY WEIGHT DISTRIBUTION

If the density – weight distribution has the form

1. $D = a W^z$ with D and W – density and weight of a species (a – constant, z – slope), and dividing the weight axis into logarithmic classes we get:

2. $D_{\text{total}} = \sum D_i = \sum (a \sum W_i^z)$ with W_i runs over all species per weight class.

In each weight class are $f(i)$ species, defined by the species – weight distribution. The biomass per weight class (B_i) is the product of the mean species biomass / weight class and the number of species in that class, therefore

$$3. B_i = D_i W_m = a W_m \sum W_i^z$$

$D_i = \sum W_i^z$ is approximately given by $D_i = f(i) W_m$. Thus, the total biomass per weight class is

$$4. B_i = a f(i) W_m^{(1+z)}$$

The biomass – weight distribution is therefore a function of the species – weight distribution and the slope z of the density – weight relationship. Formula 4 was used to compute biomass – weight plots using 7 different SWDs (log-normal, normal, Poisson, beta, linear, equal, and random) and three slope values z (-0.2 , -0.5 , -0.9).

2.3. TEST WITH REAL COMMUNITIES

The above model and Formula 4 were tested using two real terrestrial communities. These are the well studied Hymenoptera of the Göttingen beech forest and the dry meadow Drakenberg

(FRG). Ulrich (1998, 1999b) gave detailed accounts of the fauna, the sampling methods and the habitats. The SWD of the Göttingen forest can well be described by a normal distribution (720

species, 16 binary-logarithmic weight classes ranging from $1.4 \cdot 10^{-6}$ to $2.3 \cdot 10^{-2}$ g), the Drakenberg function follows a log-normal distribution (475 species; 15 weight classes; $8.2 \cdot 10^{-7}$ to $1.6 \cdot 10^{-2}$ g) (Ulrich 1999a) (Figure 4). In the Göttingen forest (7 years of study) the real density fluctuations ranged between

1 and over 1000-fold; a slight, but statistically not significant dependence on body weight could be detected ($R^2 = 0.09$, n.s.). This weight dependence follows a power function with a slope of -0.24 (Figure 1).

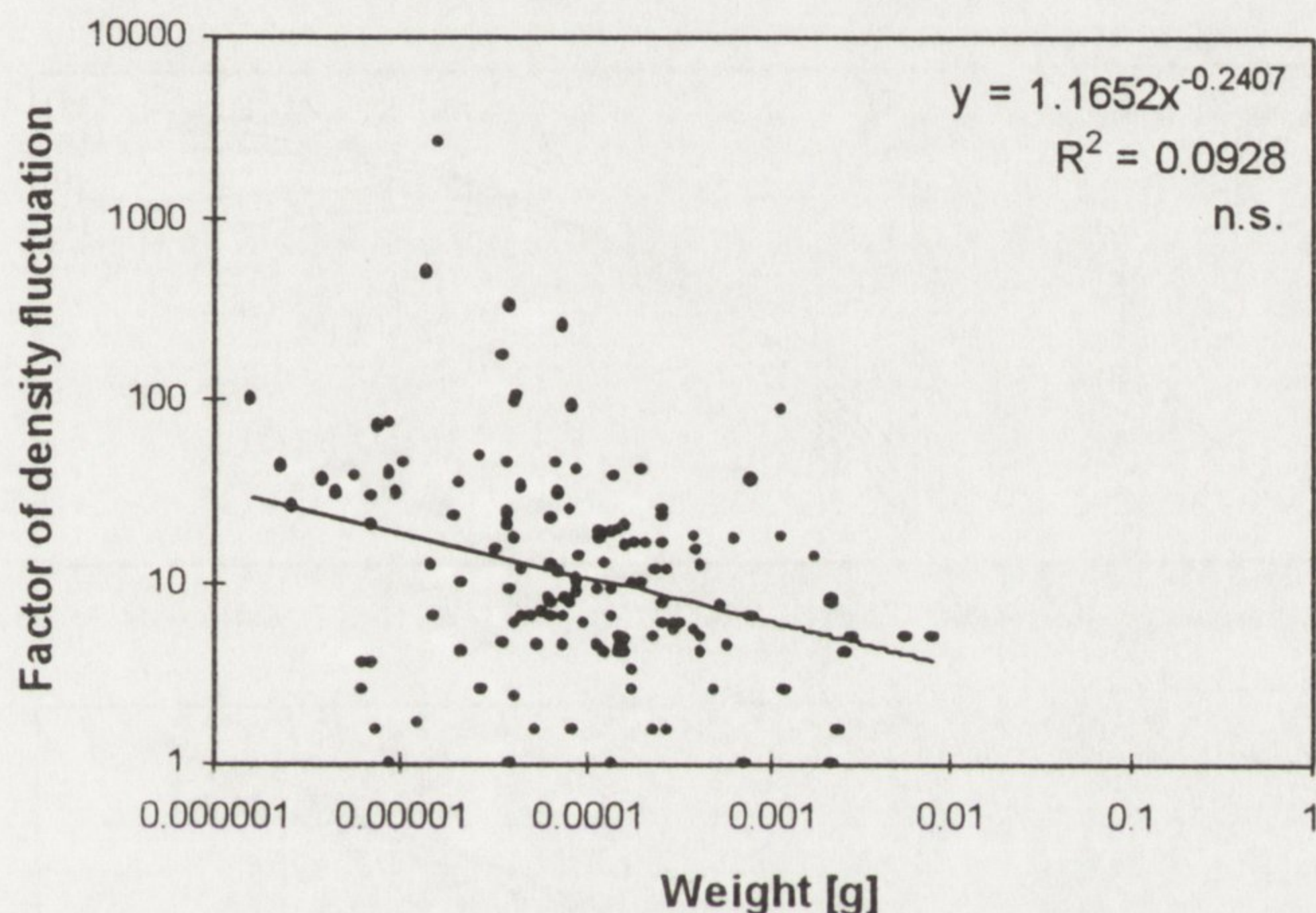


Fig. 1. Relationship between density fluctuation and body weight of the Hymenoptera of the Göttingen forest (FRG). The factor of density fluctuation is the quotient of max. and min. density during seven study years (Ulrich 1998, 1999a). R^2 – Variance explanation; n.s. – not significant.

3. RESULTS

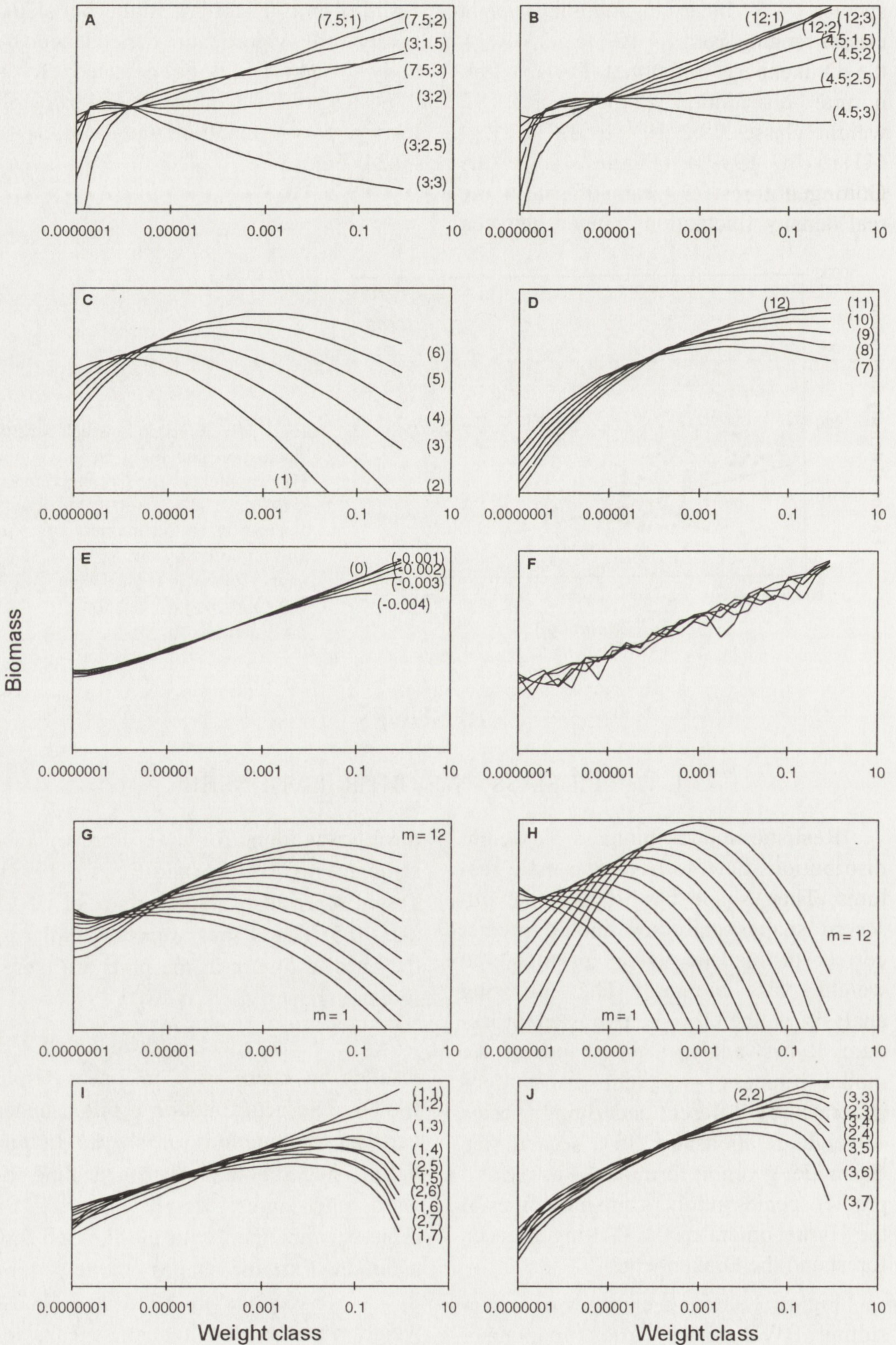
3.1. THE BIOMASS – WEIGHT RELATIONSHIP

Realistic model biomass – weight distributions have to have two main features. Their shape has to resemble observed shapes and they should predict correct or realistic values of total and weight class biomass. The following analysis is therefore a two step procedure. It first analyzes the shapes of the model biomass – weight distributions generated by different underlying species – weight relationships. In a second step the model given in formula 4 was used to predict species numbers and biomasses of the Hymenoptera of the Göttingen beech forest and the Drakenberg.

Figure 2 shows the shapes of the resulting BWD under various parameter values of the underlying SWDs. They are obtained with a DWD-slope of -0.9 , the

mean value found for larger terrestrial assemblages (Currie and Fritz 1993). Tested were also slope values of -0.2 and -0.5 . The shapes are very similar to the ones in Figure 2; the plots are therefore not shown.

The linear, equal, and random SWD resulted in every case in linear rising BWDs. The beta function resulted under various combinations of shapes in initially rising functions with a decline towards the largest weight classes. The same was obtained with the Poisson distribution. Extreme shapes (mode = 1 or 2) gave a decline in biomass in most weight classes; more realistic means resulted in peaked or steadily rising functions.



Log-normal and normal SWD are most often found in nature. They are therefore the most interesting ones. Log-normal distributions resulted with modes above the fourth weight class and various variances in steadily rising or peaked functions. The higher the mode the more pronounced was the trend towards a steady rise. At modes below the fourth weight class (out of 24) – that means more extreme shapes – peaked functions or – at even more extreme values – a steady decline was observed. However, under some parameter settings (mode between 3 to 4) a roughly constant biomass distribution appeared (Figure 2).

Normal SWD gave peaked functions with an initial rise and a decline in the upper weight classes (Figure 2). The higher the variance, the more narrow was the shape of the resulting BWD. Extreme parameter settings (modes below the 3rd weight class) resulted however in declining BWDs. In none of the parameter settings a constant biomass distribution was observed.

Which of the tested SWDs give realistic species number and biomass estimations when applied to real communities? Figure 3 shows parameter ranges under which the computed BWDs and the underlying SWDs predict both, the correct total species number and the total biomass of the Hymenoptera of the Göttingen beech forest and the dry meadow Drakenberg. Linear, random or equal SWDs gave in none of their parameter combinations realistic values. They are

therefore omitted. A Poisson distribution was also not able to predict both variables at the same time (Figure 3). The beta distribution resulted in every case in a too high biomass. However, normal and log-normal SWDs and the resulting BWDs correctly predicted in both populations the species number and the biomass at the same time.

Figure 4 shows plots of the observed and the predicted values for each weight class of the Hymenoptera. The Figure proves that the model given in Formula 4 is able to predict not only the total values but also the values in each weight class and the shape of the BWD. In the case of the Drakenberg the model predictions for total values differ only slightly from the real values ($S_{\text{pred.}} = 539$, $S_{\text{real}} = 475$, $W_{\text{pred.}} = 160$ mg, $W_{\text{real}} = 132$ mg). For the Göttingen forest the predicted total biomass is too high ($W_{\text{pred.}} = 120$ mg, $W_{\text{real}} = 68$ mg), the species number slightly too low ($S_{\text{pred.}} = 659$, $S_{\text{real}} = 720$).

The Drakenberg distributions are best fitted with a DWD slope of -0.22 , a value near the observed one ($z = -0.17$, Ulrich 1999a). For the forest species the real slope ($z = -0.23$) resulted always in too high biomass predictions. The best fit was obtained with a slope of -0.9 , the mean value in ectothermic terrestrial assemblages (Currie and Fritz 1993).

The above analysis reveals that it is possible to predict the total biomass of a population combining the SWD (normal or log normal) and a power function DWD. It is necessary to know the total

Fig. 2. Simulation of the biomass – body weight class distribution in model populations combining various species – weight distributions and a density weight distribution with the function: $y = 1000 \text{ weight}^{-0.9}$. The intercept (1000) is arbitrary and has of course no influence on the shape of the function. The slope also had only minor influence on the shape of the resulting functions. A, B – log-normal distribution with (mean; variance); C, D – Poisson distribution with (mean); E: linear and equal (bold) distributions with (slope); F – random distributions; G, H – normal distribution (m: mean) and s (variance) = 0.3 (G) and s = 0.5 (H); I, J – beta distribution with (shape one, shape two).

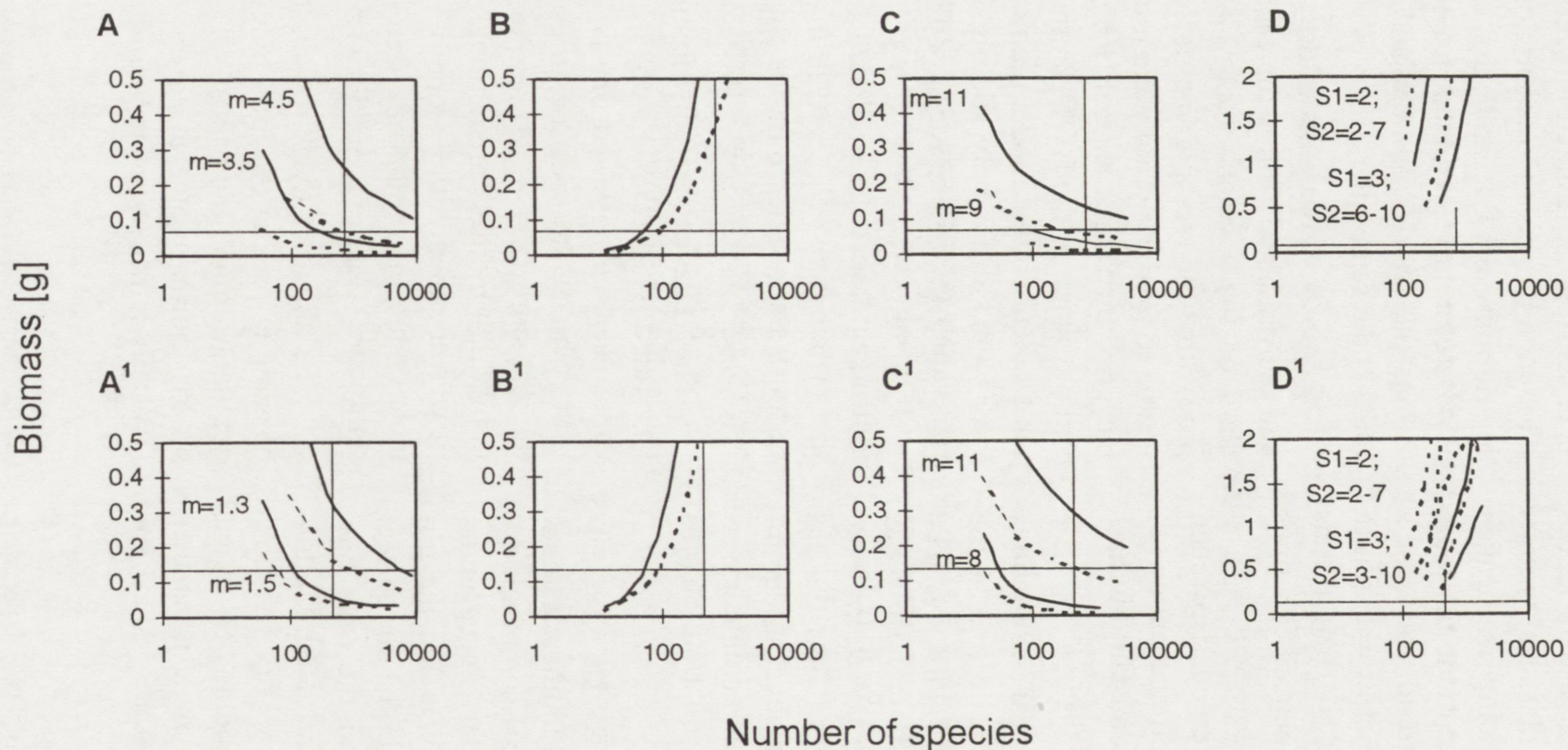


Fig. 3. Testing normal (C, C¹), log-normal (A, A¹), Poisson (B, B¹), and beta functions (D, D¹) to predict species numbers and total population biomass in the Hymenoptera of the Göttingen forest (A – D) and the dry meadow Drakenberg (A¹ – D¹). The areas between the solid and the interrupted lines indicate the parameter ranges with which realistic predictions were obtained. Other combinations of parameters gave unrealistic predictions and are not shown. The vertical and horizontal solid lines mark the real values. m – modal weight class, $S1, S2$ – shape 1 and 2 of the beta distribution.

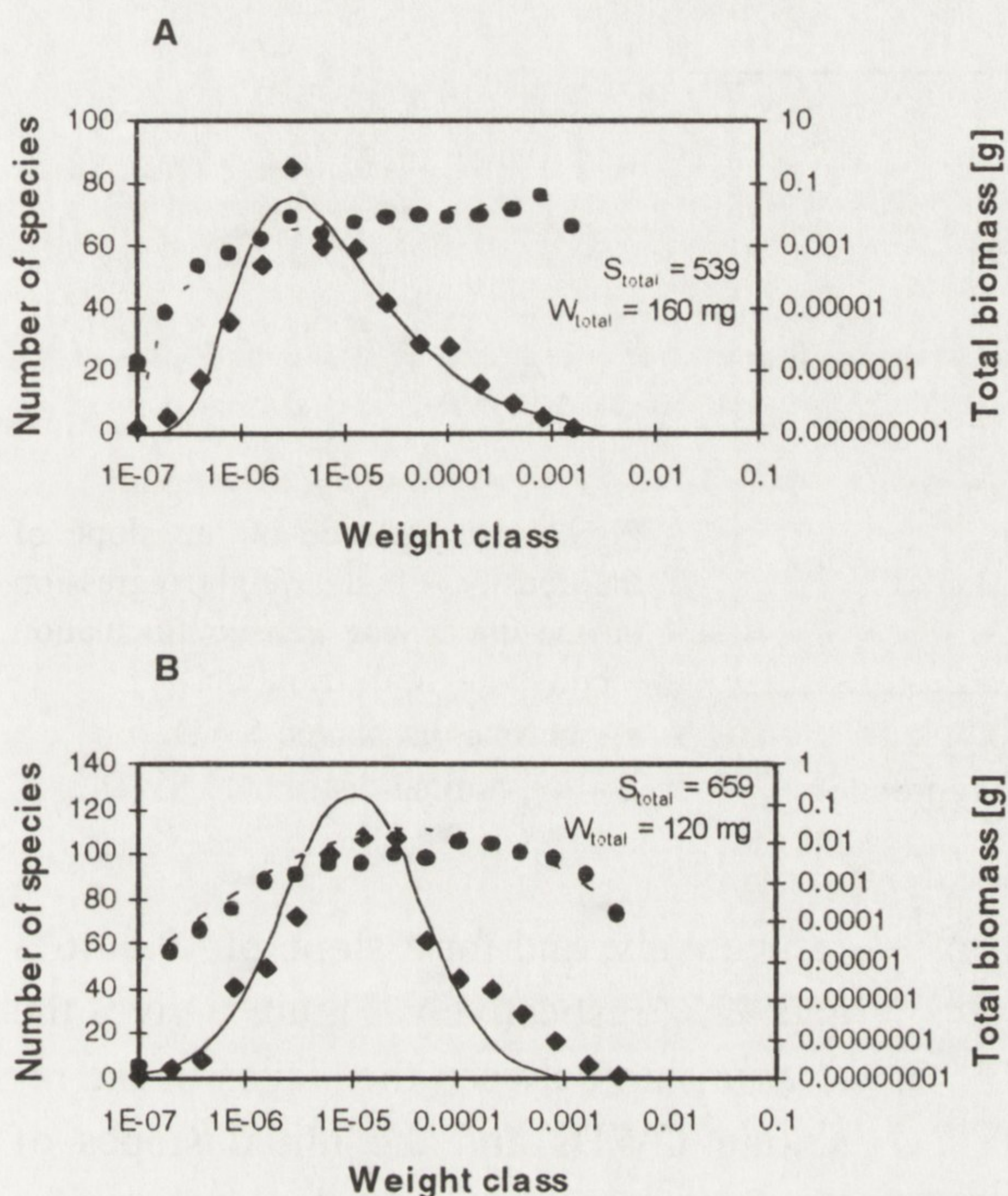


Fig. 4. Comparing real species and biomass distributions with the ones derived by underlying normal and log normal distributions.

A – Dry meadow Drakenberg, B – Göttingen beech forest. Functions of best fits: A – log-normal (mode = 6.7; variance = 0.4), B = 63 $W^{-0.22}$; B – normal (mode = 8.25; variance = 0.55), B = 61 $W^{-0.9}$. Also given are the predicted species numbers and the biomass. S_{total} – Total number of species predicted, W_{total} – Total biomass predicted. ♦ – Number of species; • – Total biomass.

number of species, which can also be inferred with the SWD, the constant 'a' and the slope 'z' of the DWD. The latter slope is similar to the slope of the density

fluctuation – weight distribution (see below). The constant 'a' can be inferred from a DWD plot.

3.2. THE SPECIES – WEIGHT RELATIONSHIP

To derive species – weight plots 100 species each of the model communities with normal and log-normal SWDs (the other SWD distributions were omitted because of their inability to predict bio-

mass and species numbers simultaneously) were allowed to fluctuate at random in the boundaries given by the power function relationship between density fluctuation and weight (parameter

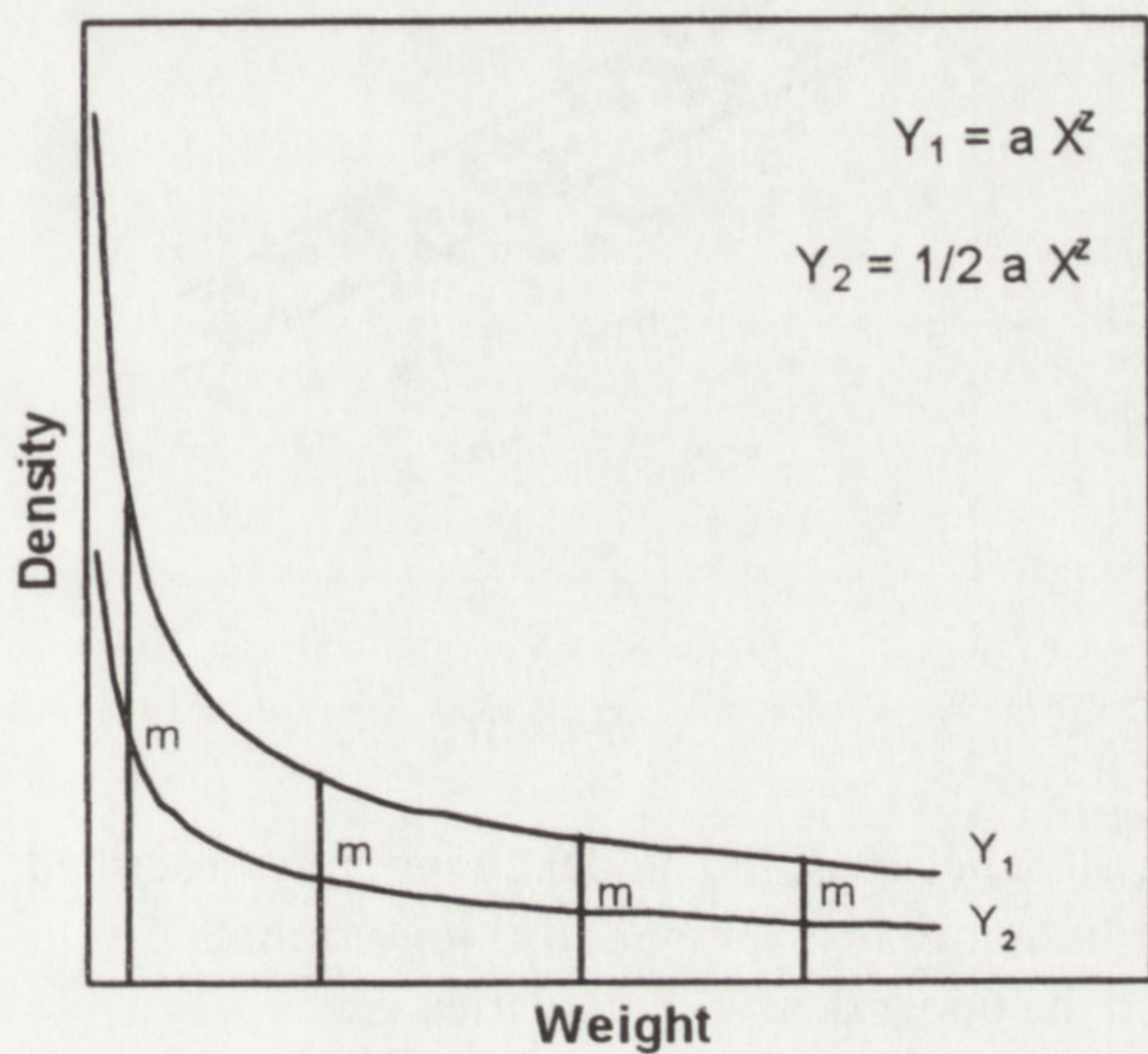


Fig. 5. Random density fluctuations of species of various weight classes (upper power function (Y_1); the span indicated by solid straight lines) result in a DWD (Y_2) through the resulting mean (m) densities with a slope (z) similar to the underlying density fluctuation – weight distribution (Y_1).

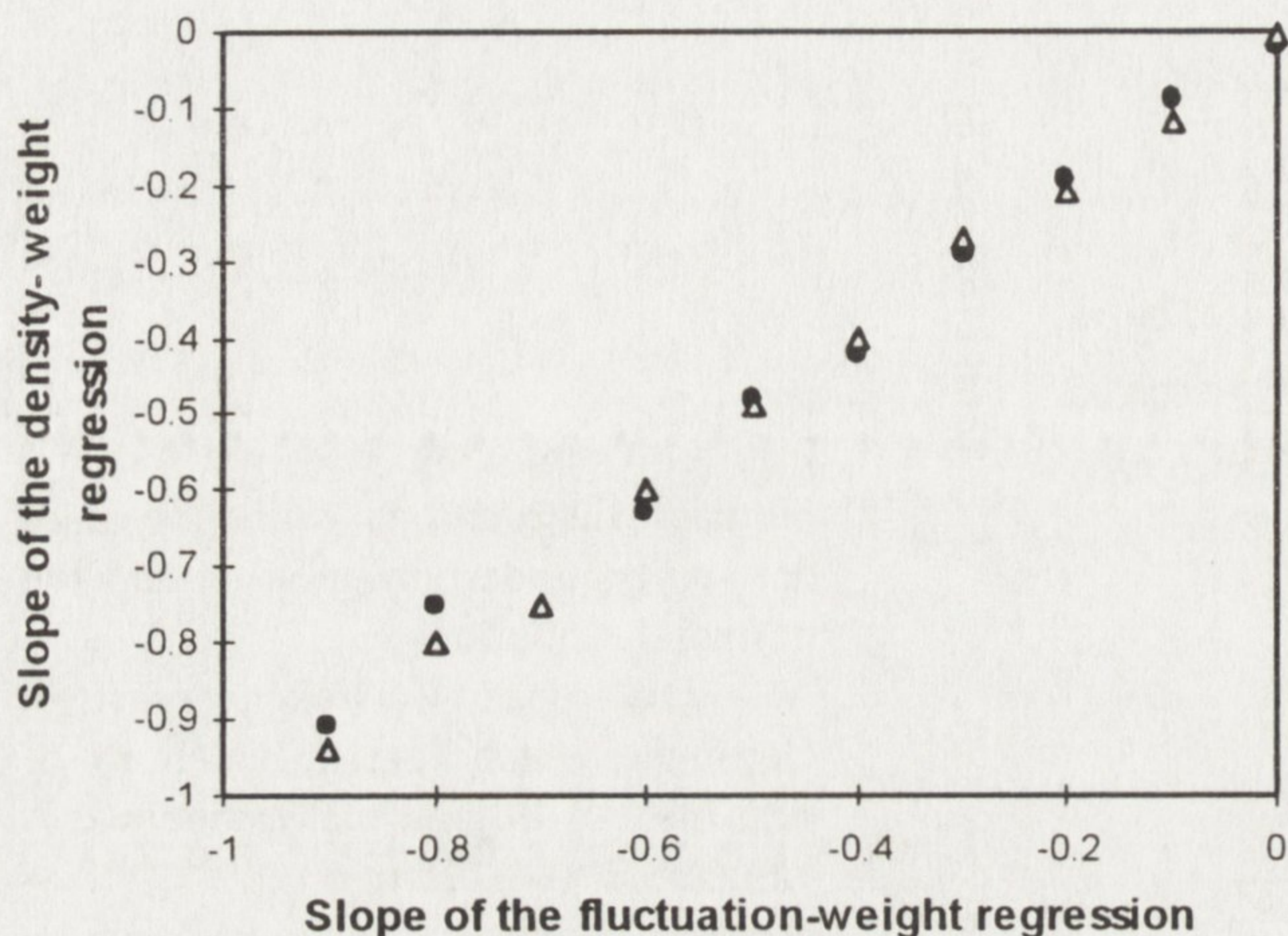


Fig. 6. Dependence of the slope of the density – body weight regression on the underlying density fluctuation – body weight distribution.
 • – normal distributed SWD,
 Δ – log-normal distributed SWD.

values like in Table 1). 50 replicates for each population and parameter value resulted in very similar DWDs. Figure 7 shows therefore only two typical replicates with a slope of -0.5 (power function) and a normal and a log-normal SWD. Without weight dependence of the density fluctuations (slope = 0) 74% (normal distribution) and 73% (log-normal) of the resulting DWDs showed a typical triangular form (the criterion was that none of the smallest 5% of species had the highest density). For a slope value of -0.2 this was the case in 69% and 54%,

respectively, and for a slope of -0.5 46% and 42%, respectively. Figure 6 gives the relationship between the slopes of the resulting DWDs and the initial slopes of the fluctuation – weight distributions for all tested slope values.

Several conclusions can be drawn:

1. As expected, an equal fluctuation – weight distribution did not generate any density – weight dependence in the model populations. However, a triangular shape appeared.

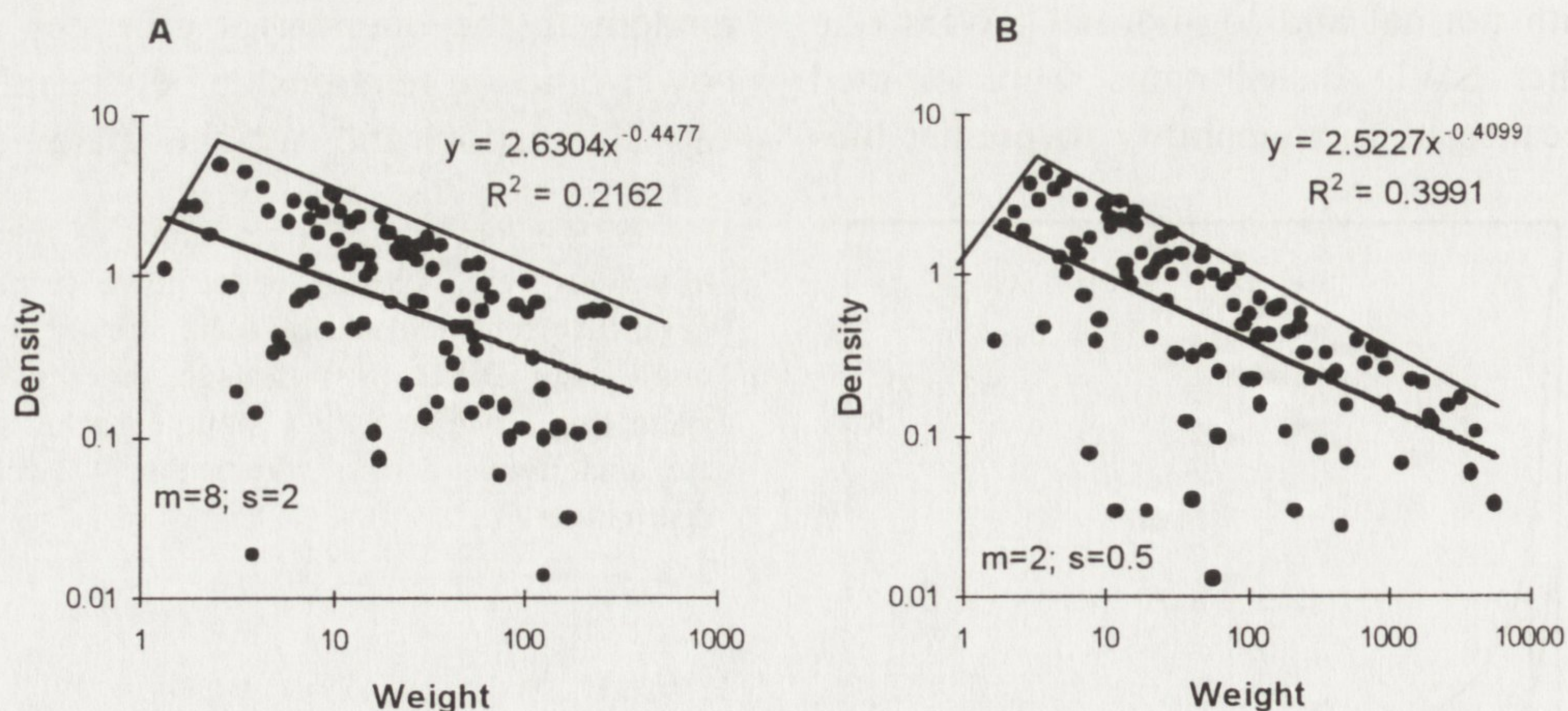


Fig. 7. Relationship between density and body weight in 100 species of the model community described in the methods section. The species – weight distribution in A is normal, in B log-normal.

M – mean, s – variance. Marked are also the upper density boundaries.

2. Even a small dependence of species density fluctuation on species weight resulted in every case in plots similar to the one in Figure 7. The stronger the initial dependence the steeper was the slope of the density – weight function (Figure 6). This is of course a simple outcome of the mathematical properties of the model (Figure 5). Because the function fittings rely on least square procedures and the pattern of density fluctuation of each weight class is normally distributed, the slopes of the two power functions (the underlying and the generated) are similar (Figure 5, 6). Interestingly however, exactly the same similarity was observed in

the Hymenoptera of the Göttingen forest (the Drakenberg Hymenoptera were only studied for two years). The slope of the density fluctuation – weight distribution was -0.24 (Figure 1), the slope of the DWD 0.23 (Ulrich 1999a).

3. The overall form of the generated DWDs is very similar to real distributions. Especially marked is an upper density boundary which had been found in several studies on natural assemblages (Blackburn et al. 1992, Ulrich 1999a). The lower densities vary to a greater extent, also a feature of real distributions.

4. DISCUSSION

The present analysis shows that the DWD and BWD together with their characteristic features can be derived from two basic distributions: the species – weight distribution and the dependence of species density fluctuation on species weight. It seems therefore not necessary to involve metabolic arguments (Damuth 1981, Peters 1983, Peters & Wassenberg 1983), or arguments based on fractal geometry (Morse et al. 1985, Shorrocks et al. 1991). This is not to say that both arguments should be rejected. Especially in endothermic vertebrates metabolic constraints may act in shaping assemblages. However, population dynamics have to be taken into account when inferring density – weight relationships. Such studies are up to now missing (Damuth 1981, Strayer 1986, Nee et al. 1991, Cyr et al. 1997). The present study shows that even a slight dependence can generate a DWD with a negative slope, a typical upper density boundary, and a triangular form. In the case of the Hymenoptera of

the Göttingen forest, the relationship between density fluctuation and body weight proved to be not significant; however it generated realistic DWDs. It may therefore be that such dependencies have been overlooked in other studies.

If the above model holds the DWD should have nearly the same slope as the fluctuation – weight power function. In the case of the Hymenoptera of the Göttingen forest this was indeed the case. It is tempting to reverse this argument. A DWD with a given slope may indicate a dependence of species density fluctuation on weight with a similar slope. DWDs are more easy to measure and may therefore serve as a measure of density fluctuations as well.

It may be argued that deriving the DWD from density fluctuations is similar to the question of what was first, the chicken or the egg. However, density fluctuations are a more fundamental feature of populations than density – weight distributions. Additionally, it is not possible to derive a fluctuation – weight rela-

tionship out of the DWD concept without assuming also weight dependent variances.

A second main result of the above analysis is that in natural populations the biomass is not evenly distributed among weight classes irrespective of the underlying species distribution. All of the tested species – weight distributions resulted in steadily rising or peaked biomass distributions. Only a log-normal distribution with a very low mode (between 3 and 4; that means in the lower 15% of weight classes) resulted in some variance settings (variance between 2 and 3) in a roughly constant biomass distribution. Such extreme shapes seem to be uncommon in nature. Dial and Marzluff (1988) analyzed 46 animal assemblages and found that in only 17% of them most species were found in the lower 15 % of weight classes. 13% (all vertebrates) were most species rich in the

lowest weight class, a feature that resulted in the present analysis always in a constant decline of biomass. Only 4% of the assemblages examined by Dial and Marzluff would therefore be candidates for an equal biomass distribution. The generality of the equal biomass hypothesis has therefore to be rejected, but there may be some communities for which the theory holds.

Unimodal normal and log-normal species – weight distributions, which are most often found in nature (Novotny and Kindlmann 1996), generated in most parameter combinations rising BWDs with a decline towards the largest weight classes. Extreme parameter settings resulted in steadily rising functions or unrealistic shapes (Figure 7). Strayer (1986), Maurer and Brown (1988) and Stork and Blackburn (1993) found similar distributions in studies of lacustrine benthic communi-

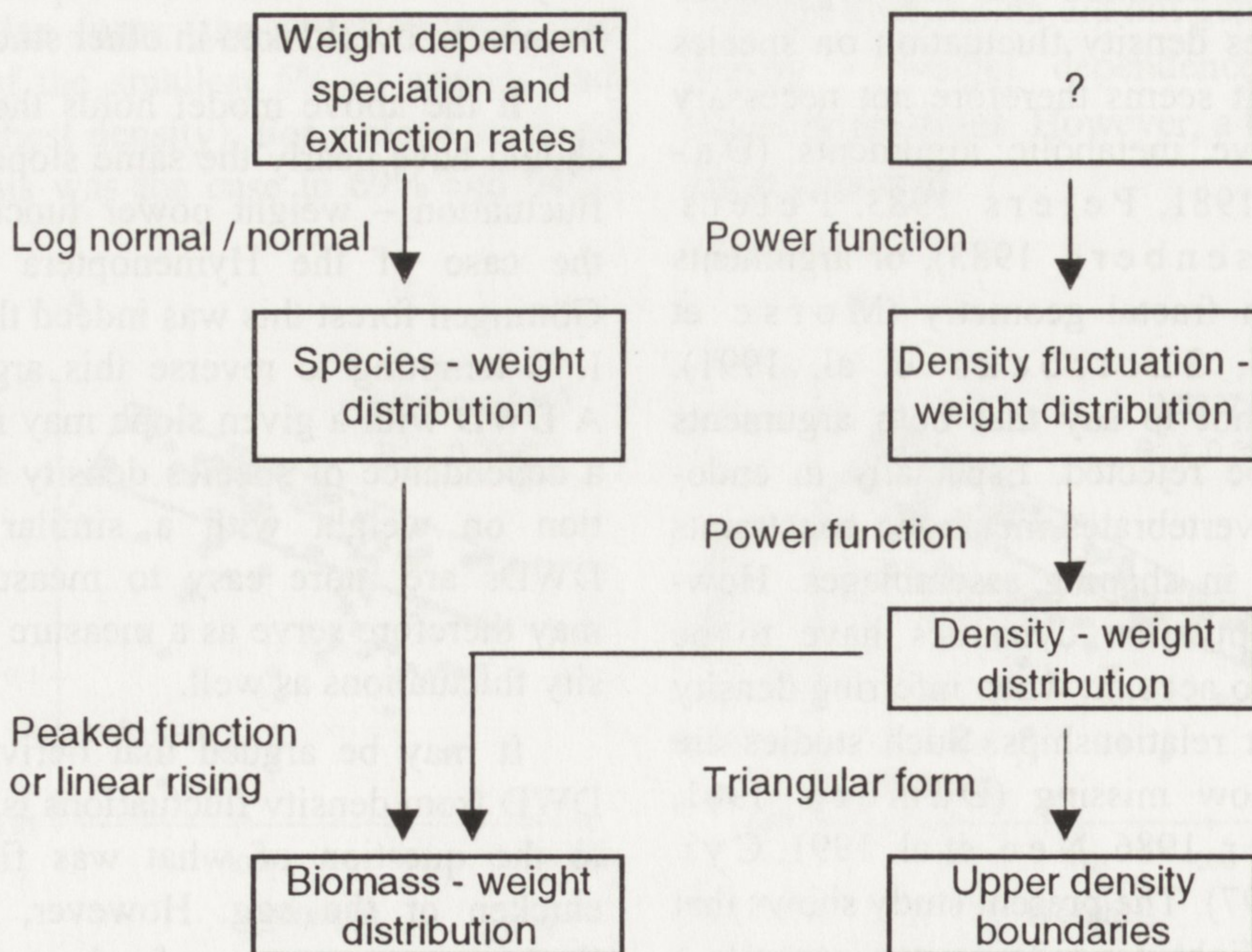


Fig. 8. Model to describe the dependence of different distributions on two basic ecological processes, the speciation/extinction rates and an unknown distribution which leads to size dependent density fluctuations. Further explanations in the text.

ties, terrestrial birds and tropical forest arthropods. Stork and Blackburn (1993), following Lawton (1989), assumed that the rising biomass may be an outcome of the sampling procedure because lower weight classes may have been undersampled or overlooked. The present study indicates that a rising biomass towards upper weight classes should be a property of most animal assemblages.

Figure 8 summarizes the above results into a general model. It hypothesizes that two basic relationships generate various ecological distributions. One basic process, weight dependent speciation and extinction rates, generate species – weight distributions (Maurer et al. 1992) and, together with weight dependent density fluctuations, density – weight and biomass – weight distributions with their typical properties.

The question is what generates weight dependent density fluctuations. Again evolutionary processes may explain the pattern, in this case trends towards *r*- and *K*-selected species. Larger species are more often *K*-selected than smaller ones due to their larger amount of energy use. Such difference can produce

differences in density fluctuations as well (Owen and Gilbert 1989). However, this may be a circular conclusion because one main definition of *r*-selectedness is high density fluctuation. A second explanation again invokes the species – weight distribution. There may be higher density fluctuations in species rich weight classes simply because in these classes there is a higher probability to find such species. Because these species rich weight classes are normally below the median weight class such a distribution would result in fluctuation patterns similar to the ones observed in natural assemblages. In this case all of the mentioned ecological distributions would be reduced to one basic process, the speciation and extinction rate. More theoretical and experimental work is necessary to sustain this hypothesis.

ACKNOWLEDGMENTS: I thank Prof. J. Buszko and Dr. Kartanas for critical and valuable suggestions on the manuscript. The suggestions of an anonymous reviewer greatly improved the methods section. Miss H. Pearson kindly improved my English.

This work was in part supported by a grant of the Deutsche Forschungsgemeinschaft. The author received a scholarship of the Friedrich-Ebert-Foundation.

5. SUMMARY

This paper tests the hypothesis that the density – weight distribution is generated alone by underlying weight dependent density fluctuations. For this purpose model assemblages were constructed with which several species weight and density weight and the resulting biomass – weight distributions could be studied (Table 1, Figure 5). The simulations revealed that indeed even a slight dependence of density fluctuation on weight generated typical density – weight distributions with upper density boundaries and triangular shapes (Figures 6, 7). Other ecological explanations, such as metabolic constraints or arguments based on

fractal geometry, may therefore not be necessary to explain the pattern.

In a second step of analysis the density – weight relationship was combined with various species – weight distributions (computed over \log_2 weight classes) to show that in nearly all parameter settings steadily rising biomass distributions with a decline only towards the largest weight classes result (Figure 2). The generality of the equal biomass hypothesis is therefore rejected.

Only normal or log-normal species – weight distributions were able to predict simultaneously the species weight and the biomass weight distributions in two real communities, the Hymenoptera

of a beech wood and a dry meadow in northern Germany. (Figures 1, 3, 4)

A general model is developed to explain the existence of several of the patterns in density –

weight and species – weight plots assuming only underlying weight dependent speciation and extinction rates and weight dependent density fluctuations (Figure 8).

6. REFERENCES

- Blackburn T. M., Lawton J. H., Perry J. N. 1992 – A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages – *Oikos* 65: 107–112.
- Blackburn T. M., Gaston K. J. 1996 – Abundance – body size relationships: the area you census tells you more – *Oikos* 75: 303–309.
- Currie D. J. 1993 – What shape is the relationship between body mass and population density – *Oikos* 66: 353.
- Currie D. J., Fritz J. T. 1993 – Global patterns of animal abundance and species energy use – *Oikos* 67: 56–68.
- Cyr H., Peters R. H., Downing J. A. 1997 – Population density and community size structure: comparison of aquatic and terrestrial systems – *Oikos* 80: 139–149.
- Damuth J. 1981 – Population density and body size in mammals – *Nature* 230: 699–700.
- Dial K. P., Marzluff J. M. 1988 – Are the smallest organisms the most diverse – *Ecology* 69: 1620–1624.
- Gaston K. J. 1988 – Patterns in the local and regional dynamics of moth populations – *Oikos* 53: 49–57.
- Gaston K. J. 1993 – Comparing animals and automobiles: a vehicle for understanding body size and abundance relationships in species assemblages? – *Oikos* 66: 172–179.
- Griffiths D. 1992 – Size, abundance, and energy use in communities – *J. Animal Ecol.* 61: 307–315.
- Lawton J. H. 1989 – What is the relationship between population density and body size in animals – *Oikos* 55: 429–434.
- Lawton J. H. 1990 – Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space. *Phil. Trans. R. Soc. Lond. B* 330: 283–291.
- Maurer B. A., Brown J. H. 1988 – Distribution of energy use and biomass among species of North American terrestrial birds – *Ecology* 69: 1923–1932.
- Maurer B. A., Brown J. H., Rusler R. D. 1992 – The micro and macro in body size evolution – *Evolution* 46: 939–953.
- May R. M. 1978 – The dynamics and diversity of insect faunas (In: *Diversity of insect faunas*, Eds. L. A. Mound, N. Waloff) – Oxford, pp. 188–204.
- May R. M. 1986 – The search for patterns in the balance of nature: advances and retreats. *Ecology* 67: 1115–1126.
- Morse D. R., Lawton J. H., Dodson M. M., Williamson M. H. 1985 – Fractal dimension of vegetation and the distribution of arthropod body lengths – *Nature* 314: 731–733.
- Nee S., Read A. F., Greenwood J. J. D., Harvey P. H. 1991 – The relationship between abundance and body size in British birds – *Nature* 351: 312–313.
- Novotny V., Kindlmann P. 1996 – Distribution of body sizes in arthropod taxa and communities – *Oikos* 75: 75–82.
- Owen J., Gilbert F. S. 1989 – On the abundance of hoverflies (Syrphidae) – *Oikos* 55: 183–193.
- Peters R. H. 1983 – The ecological implications of body size – Cambridge.
- Peters R. H., Wassenberg K. 1983 – The effect of body size on animal abundance – *Oecologia* 60: 89–96.
- Scharf S. F., Juanes F., Sutherland M. 1998 – Inferring ecological relationships from the edges of scatter diagrams: comparisons of regression techniques – *Ecology* 79: 448–460.
- Sheldon R. A., Prakash A., Sutcliffe Jr. W. H. 1972 – The size distribution of particles in the ocean – *Limnology and Oceanography* 17: 327–340.
- Shorrocks B., Marsters J., Ward I., Evannett P. J. 1991 – The fractal dimension of lichens and the distribution of arthropod body length – *Funct. Ecol.* 5: 457–460.
- Stork N. E., Blackburn T. M. 1993 – Abundance, body size and biomass of arthropods in tropical forest – *Oikos* 67: 483–489.

-
- Strayer D. 1986 – The size structure of a lacustrine zoobenthic community – *Oecologia* 69: 513–515.
- Ulrich W. 1998 – The parasitic Hymenoptera in a beech forest on limestone I: Species composition, species turnover, abundance and biomass – *Pol. J. Ecol* 3: 261–289.
- Ulrich W. 1999a – Abundance, biomass and density boundaries in the Hymenoptera: analysis of the abundance – weight relationship and differences between forest and open landscape habitats – *Pol. J. Ecol.* 47: 73–86.
- Ulrich W. 1999b – The Hymenoptera of a dry meadow on limestone: Species composition, abundance and biomass – *Pol. J. Ecol.* 47: 29–47.
- Van Valen L. 1973 – Body size and numbers of plants and animals – *Evolution* 27: 27–35.

(Received after revising September 1998)