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ABUNDANCE, BIOMASS AND DENSITY BOUNDARIES IN THE HYMENOPTERA: ANALYSIS OF THE ABUNDANCE – WEIGHT RELATIONSHIP AND DIFFERENCES BETWEEN FOREST AND OPEN LANDSCAPE HABITATS

ABSTRACT: The density – weight distributions of the hymenopteran species in a beech forest on limestone and a dry meadow on limestone near Göttingen (FRG) were studied. Species and density distributions (logarithmic size classes) turned out to follow normal and log-normal distributions with the meadow having the more narrow shape. Upper weight classes accumulated more total biomass m^{-2} than lower ones, resulting in a rejection of the equal biomass hypothesis in the case of the Hymenoptera. An analysis of the density – weight relationship revealed an upper density boundary for the hymenopteran species which can be defined by second order polynomial functions. Mean and upper densities of small hymenopteran species ranged well below their boundaries, with an asymptotic relationship between distance from the boundary and species weight. The area defined by the boundaries may mark the area of stability; exceeding the species specific boundary was always followed by a marked decline or even a collapse of population density.

KEY WORDS: Hymenoptera, weight, biomass, density, boundedness, species – weight class distribution, density – weight distribution

1. INTRODUCTION

In the last decade the relationship between density and weight (often approximated by the body size) of animals in terrestrial and aquatic ecosystems has gained growing attention (Lawton 1989, 1990, Basset and Kitching 1991, Griffiths 1992, Currie 1993,

Currie and Fritz 1993, Gaston 1993, Blackburn and Gaston 1996, Cyr et al. 1997 and literature therein). Previous studies on aquatic systems resulted in the so called “equal biomass hypothesis” (Peters 1983, Maurer and Brown 1988), which states that the dis-

tribution of biomass is roughly constant over logarithmic weight classes of the species. However, recent studies on tropical forest arthropods could not confirm the generality of this assumption (Stork and Blackburn 1993). Instead, it was found that larger species contribute more to the total biomass of a given area or community than smaller species and that this relation can be described by double log functions. Data for arthropods of temperate regions are missing.

A second reasoning combines the weight with the density of a species. It had been found that for most aquatic and terrestrial ecosystems the relationship between weight and density of a species also follows double log functions with a negative slope (Damuth 1987, Nee et al. 1991, Currie 1993, Currie and Fritz 1993, Gaston 1993). This general slope appears to be slightly steeper in terrestrial systems (around -0.92) than in aquatic ones (-0.89) (Cyr et al. 1997). But within taxonomic groups the slope values are generally smaller and for invertebrates values of -0.5 to -0.6 (terrestrial and aquatic) have been found (Currie and Fritz 1993, Cyr et al. 1997). Generally, it was observed that extending the span of weights pronounces the relationship between density and weight. Within narrow taxonomic groups often only weak relationships exist (Strayer 1986, Morse et al. 1988, Gaston and Lawton 1988, Nee et al. 1991), or even no dependence could be detected (Gaston 1988, Tokeshi 1990).

Currie (1993) simulated density-weight relationships and found that statistical effects may account for such a pattern simply because of the underlying species-weight distribution. The author argues also that the observed "triangular"

density-weight distribution in limited taxonomic groups, with lower densities at the low and high ends of weight and a maximum density in the middle range of weight may be explained simply by the underlying species-weight class distribution in combination with the sampling method.

All of these studies used fixed densities to compare the parameters. To decide whether observed distributions are the result of the underlying statistics or whether they show any ecological constraints acting on the populations it seems necessary to study other parameters, especially the population fluctuations as well. If the observed distributions hold at all observed densities it is likely that they can be interpreted in an ecologically meaningful way. A second step then has to include density fluctuations into models of species-weight distributions. It seems an interesting task to see whether the different forms of the density-weight relationship (between narrower and wider taxonomic grouping) still appear if one includes the density dynamics of populations.

In this study I will analyze the density-weight distribution in the Hymenoptera by including the density fluctuations of the species. The study compares the distribution in two habitats, a forest and an open land site (a dry meadow) to answer the following questions. What are the shapes of the abundance-weight relations and are they equal in different habitats? Are there upper density boundaries of the species? Does the equal biomass hypothesis hold for the Hymenoptera and is there a general pattern in assembling the size classes of the faunas?

Throughout the text the term density refers to individuals m^{-2} , weight stands

for dry weight per specimen, and the term biomass is used to refer to the total dry weight of a species or a community

of a given area (species-biomass and community biomass).

2. METHODS

During 1980 and 1987 the hymenopteran fauna in a beech forest on limestone (the Göttingen forest, FRG, a Melico Fagetum subassociation *Lathyrus vernus*) has been intensively sampled with ground photo eclectors. Ulrich (1998) gives a detailed account of the study area, the sampling procedures, the densities and the species composition. Individuals of all species were measured (Ulrich 1999c) and the weight was calculated using the formula developed in Ulrich (1998): $B \text{ (mgDW)} = 0.52493 \times \text{thorax volume (mm}^3\text{)}$ ($r = 0.97$; $p < 0.001$).

In total 720 species of Hymenoptera were detected; the mean annual biomass m^{-2} was 68 mgDW.

The second sampled habitat was a dry meadow (Gentiano Koelerietum) on limestone (the Drakenberg near Göttingen, FRG). In 1986 and 1988 this meadow was sampled also using ground photo eclectors (Ulrich 1999a). The sorting and measuring procedures were the same as in the beech forest. A total of 475 species of Hymenoptera were found; the mean annual biomass m^{-2} was 132 mgDW.

3. RESULTS

3.1. SPECIES DISTRIBUTION AND BIOMASS

A sorting of the species into binary weight classes revealed for the species of both habitats species distributions which are shown in Figure 1. On the dry meadow the species numbers – weight class plot is best fitted by a log-normal distribution (mean $[m] = 6.75$, variance $[s] = 0.16$, $p < 0.001$). In the case of the forest a normal distribution gave the best fit with $m = 8.5$ and $s = 0.52$ ($p < 0.01$). In the forest the highest number of species is contained in the classes with 0.18 to 0.36 mgDW (108 species). The highest mean density instead is found in the species with a weight around 0.0224 mgDW (70 ind. m^{-2}) (Figure 1). On the dry meadow the highest number of species

(85) and the highest mean densities (242 ind. m^{-2}) are found in the weight class with 0.0448 mgDW.

The forest is characterized by a more equal density distribution than the dry meadow. The weight classes between 0.0028 and 3 mgDW (10 classes) of the beech forest have roughly equal densities. On the dry meadow the densities immediately fall from the peak towards higher and lower weight classes. These trends follow power functions with slopes of -0.84 and 1.02 , respectively.

The biomass-weight distribution of the beech forest can also be described by a peaked function (a log-normal distribution gave the best fit) with the highest

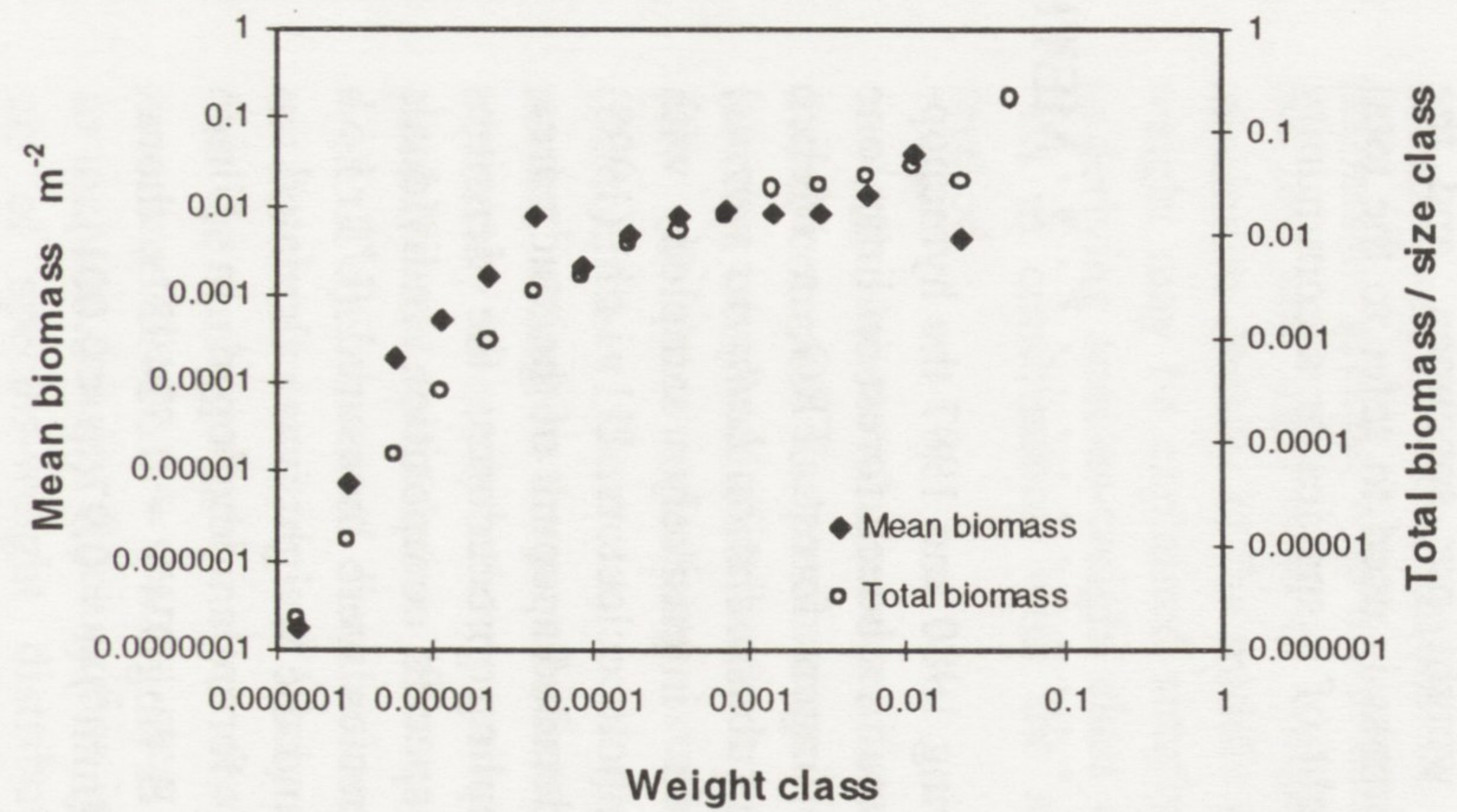
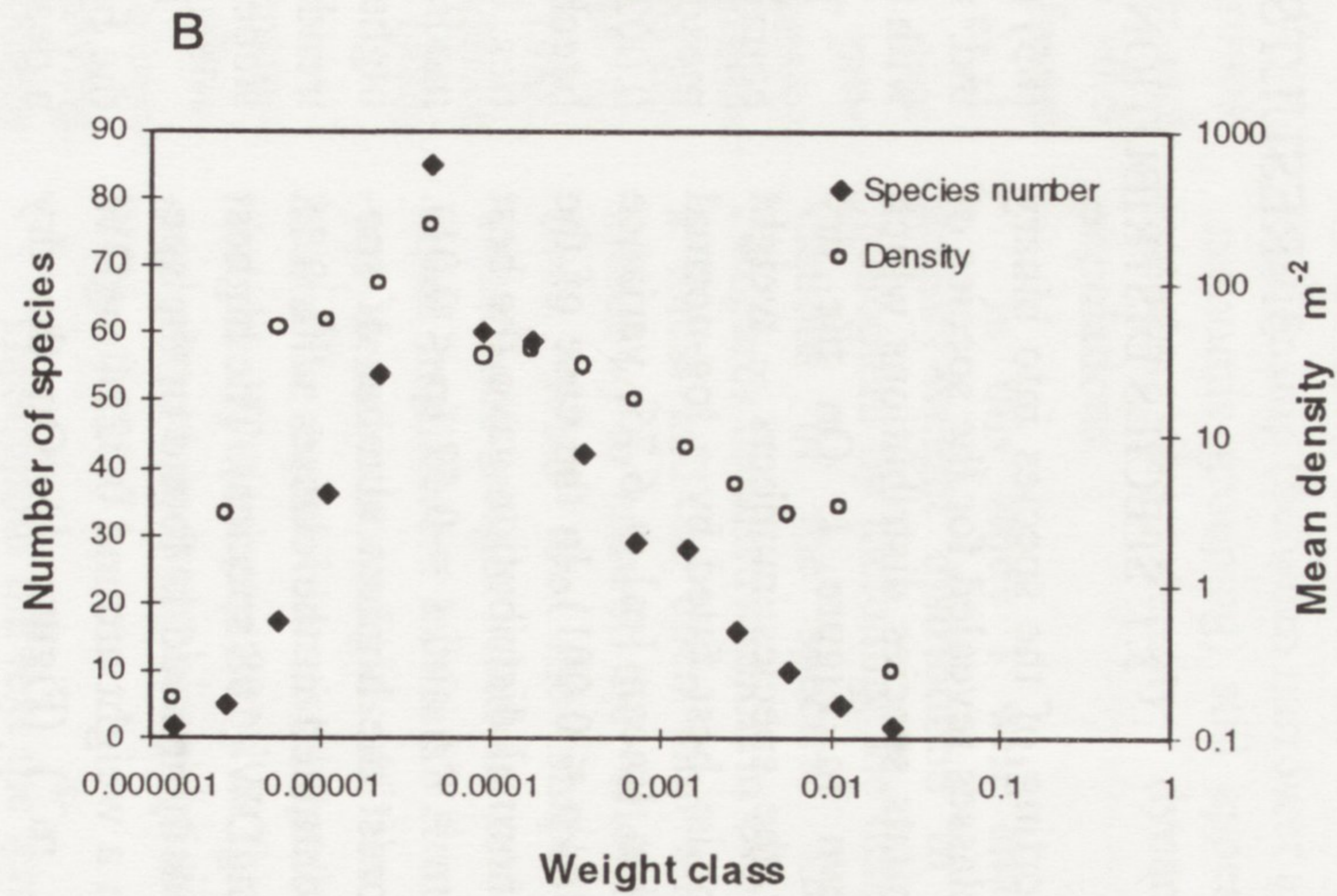
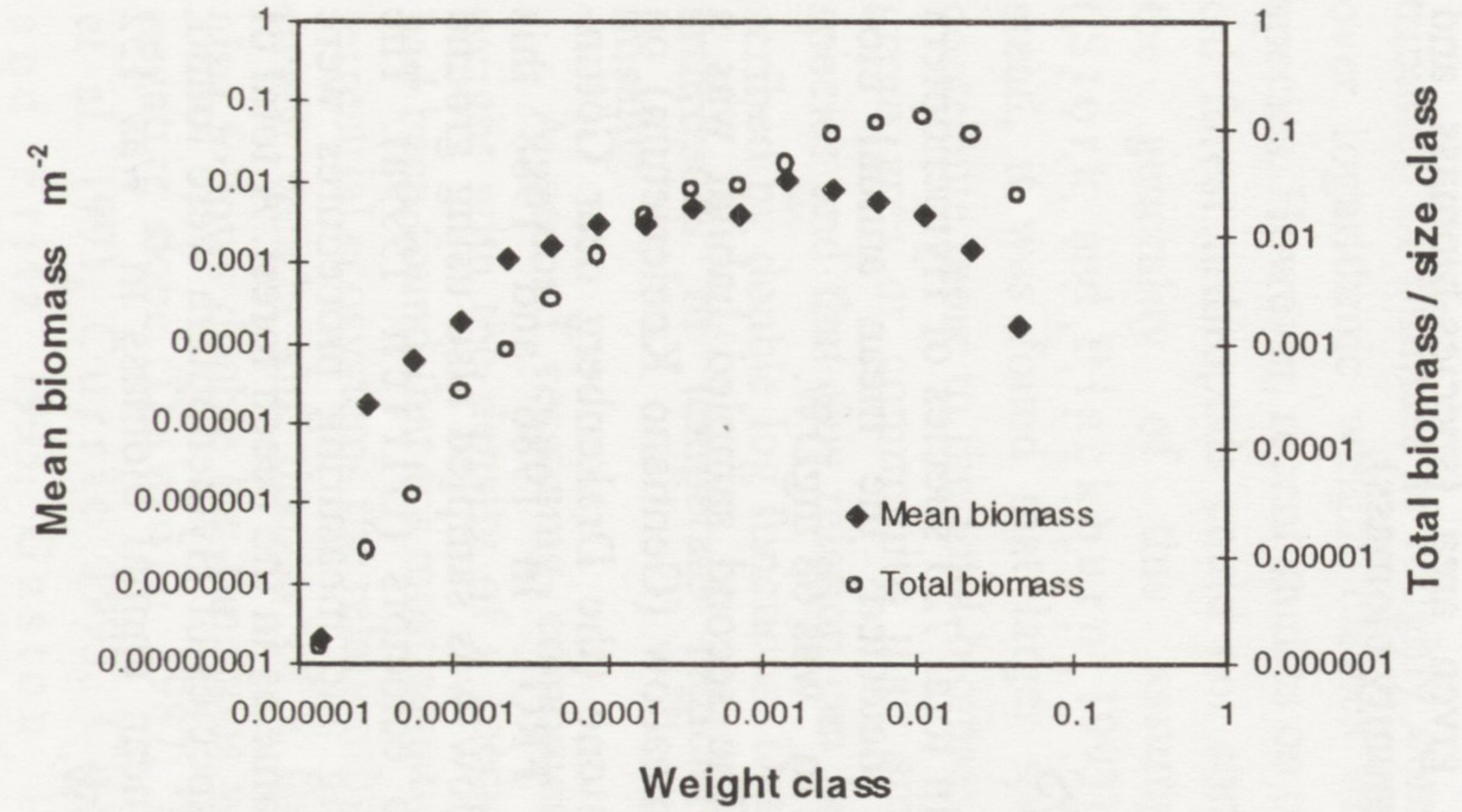
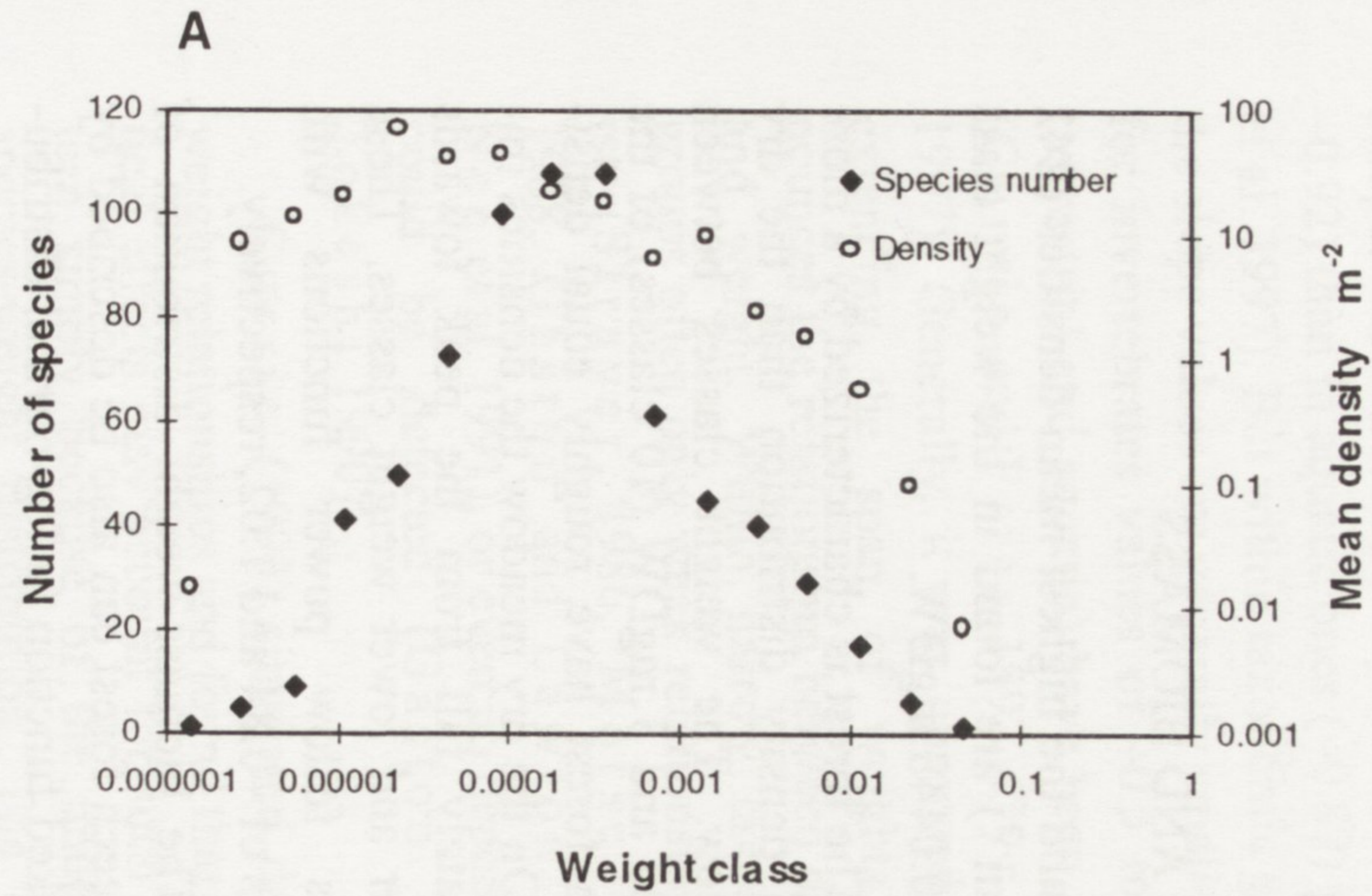


Fig. 1. Number of species, densities, and biomass in different binary weight classes of the Hymenoptera of the Göttingen forest and the Drakenberg. Total biomass refers to the sum of biomass of all species in a given weight class. Biomass and weight are given in g. A – Göttingen forest, B – Drakenberg.

biomass m^{-2} in the weight class around 3 mgDW and a decline towards the five largest classes. The largest weight class is missing on the dry meadow; the mean biomass steadily rises towards the highest weight classes and 54% of the total mean biomass of the Hymenoptera on the dry meadow is assembled in the upper three classes. The distribution can readily be described by a second order polynomial function: $\ln B = -0.203 (\ln(X))^2 - 2.668 \ln(X) - 12.684$ ($R^2 = 0.893$, $p < 0.01$) [B denotes the biomass, X the weight class].

In the beech forest the upper three weight classes count only for 12% of total mean biomass, the mean biomass m^{-2} is more equally distributed among the weight classes, and the distribution takes the form: $\ln B = -0.246 (\ln(X))^2 - 3.429 \ln(X) - 16.362$ ($R^2 = 0.896$, $p < 0.01$).

Another aspect is the amount of biomass which each species contributes to the total hymenopteran biomass in a given habitat. In Figure 2 the weight of each species is plotted against the mean annual biomass m^{-2} of this species. The strong positive correlations indicate again that larger species contribute more to the total biomass than smaller species. This

relation holds for all three strata of the beech wood (ground, herb layer and canopy) and the two strata of the dry meadow (ground, herb layer).

The biomass distribution is not equal between the strata. In the forest habitat the ground living Hymenoptera weigh around $22 \text{ mgDW } m^{-2} a^{-1}$, the canopy living species reach half of this value and the species which find their hosts in the herb layer weigh only $1.1 \text{ mgDW } m^{-2} a^{-1}$. However, the regression slope of the herb layer species is steepest (Figure 2), indicating a very unequal biomass distribution. On the other hand, the biomass distribution of the canopy species is the most equal.

The Drakenberg meadow has not only a more diverse and abundant hymenopteran fauna than the Göttingen fauna, the species also reach a higher total biomass (Figure 2 and Ulrich 1999a). This holds especially for the species associated with the herb layer. The slopes of the regression in Figure 2 are comparable to the beech forest with the exception of the ground living species, which have a more uneven biomass distribution.

3.2. DENSITY – WEIGHT DISTRIBUTION

The density – weight plots for both habitats are shown in Figure 3. Larger species have lower densities than smaller species. But this relationship turned out to be comparably weak. In none of the strata does the variance explanation exceed 10% and in the ground living Hymenoptera of the Drakenberg meadow there even is no trend detectable. The slopes of the regressions range between -0.17 and -0.38 and are lower than the slopes reported for arthropods in the literature (Currie and Fritz 1993).

The plots define a rather sharp upper density limit for the Hymenoptera, a fact that has up to now only been described in vertebrates (Damuth 1981, 1987, Peters and Raelson 1984), pond invertebrates (Blackburn et al. 1992) and tropical beetles (Blackburn et al. unpubl., cited after Gaston 1993). In other studies with limited taxonomic groups such boundaries were much lesser defined (Gaston 1988, Morse et al. 1988, Maurer and Brown 1988).

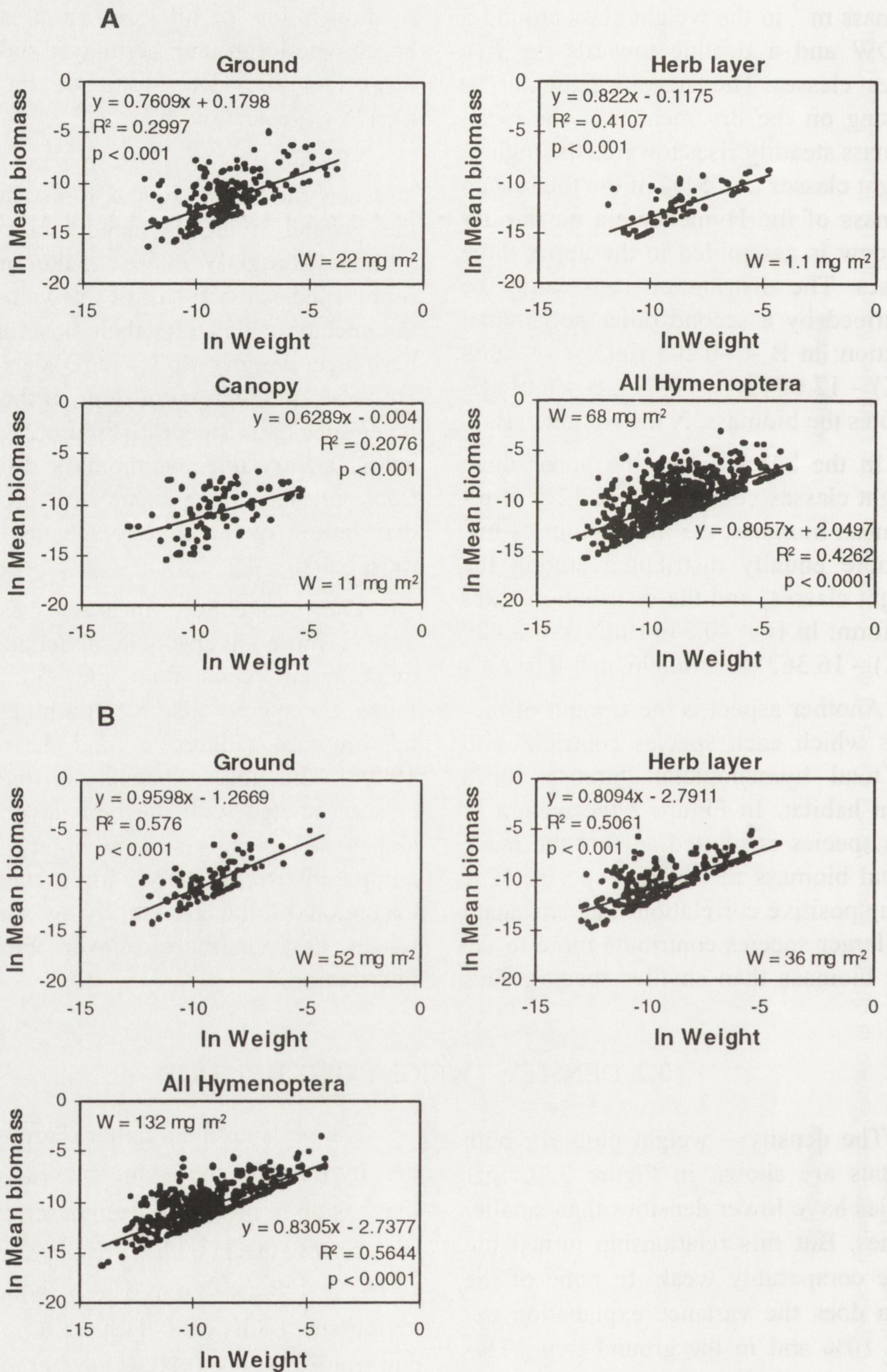


Fig. 2. Annual biomass / species [g] versus weight of the species [g] (natural logarithms). W denotes the total annual mean biomass of the hymenopteran species in each of the strata. A – Göttingen forest, B – Drakenberg. The sharp lower line is formed by species of which only one individual was found. The equation gives the linear regression between In mean biomass and In weight (R^2 – variance explanation, p – significance level).

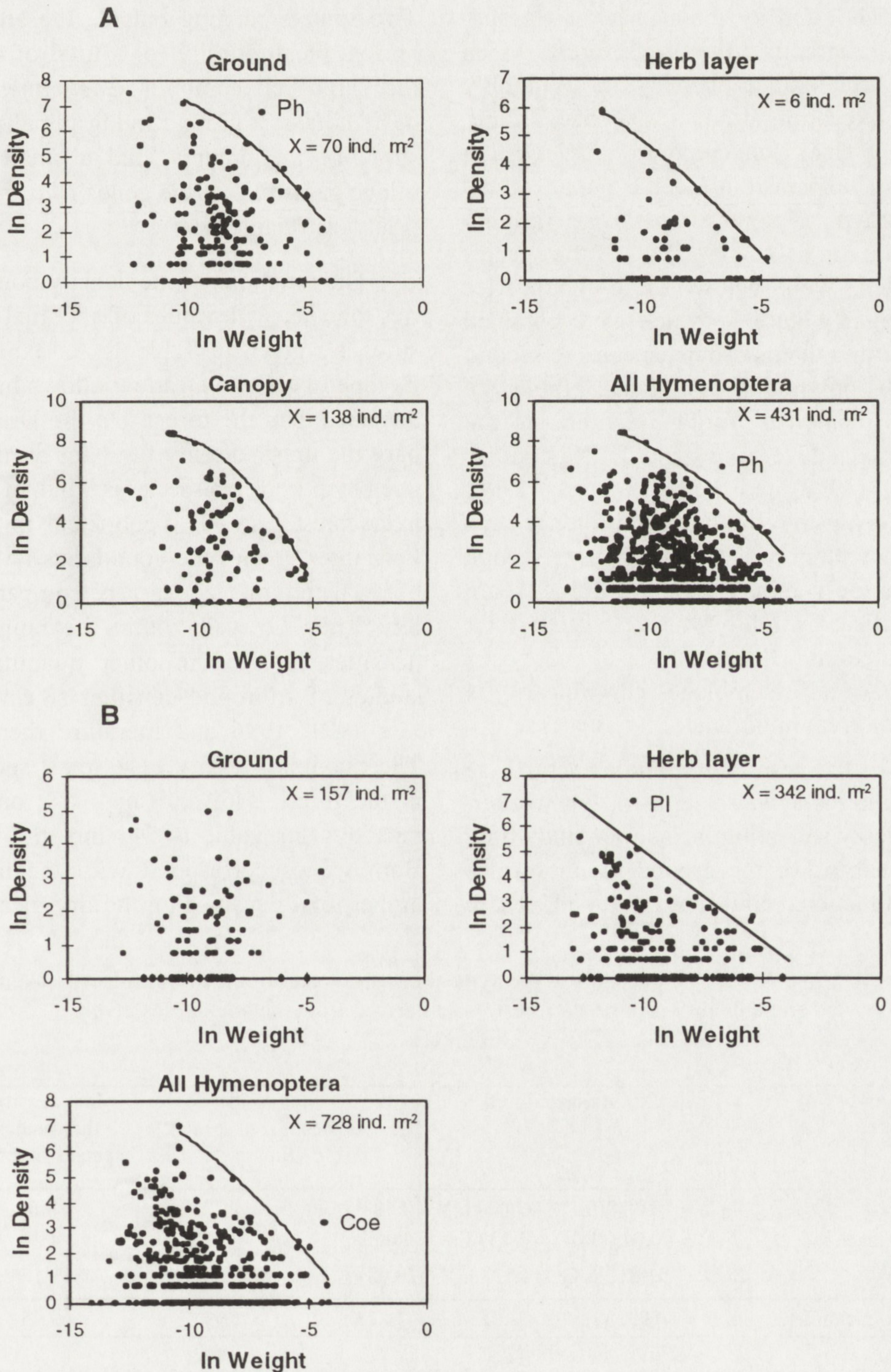


Fig. 3. Density of the hymenopteran species (ind. m^{-2}) versus their weight [g]. X denotes the mean annual density in each of the strata. The boundary lines are computed with the functions given in Table 1. The functions given refer to the regression between density and weight. A – Göttingen forest, B – Drakenberg. For the Göttingen forest Ph refers to the ichneumonid *Phygadeuon ursini*, for the Drakenberg Pl denotes *Platygaster td2* and Coe – *Coelichneumon desinatorius*.

The density boundaries are especially marked in the beech forest, which had been studied over 7 years. With only one exception (from a total of 720 species) (the ichneumonid *Phygadeuon ursini*, a parasitoid of the pupae of the common dipteran *Cheilosia fasciata* (Hövmeyer 1992) all of the species ranged well below these boundaries given in Figure 3, which were obtained by fitting the outermost species to second order polynomial functions (Table 1). This method of fitting is similar to the method developed by Blackburn et al. (1992) and Scharf et al. (1998) but with the important difference that even with few data points most second order polynomial terms in Table 1 are significant at the 5%-level. From their simulations Blackburn et al. supposed that in real assemblages curvilinearity is not of great importance.

In the case of the Drakenberg these boundaries are also defined, but weaker, probably reflecting the shorter study time (2 years). For the ground living species no functions could be obtained at all.

Two species ranging outside the area of normal mean density (of a total of 475): the large ichneumonid *Coelichneumon desinatorius*, a ground living pupal parasitoid of Lepidoptera, and a small gall midge parasitoid of the genus *Platygaster* (Platygastridae).

The functions of the density boundaries together with values of maximal densities are given in Table 1. As expected the open land site meadow allows higher densities than the forest. On the Drakenberg the upper density limit for a middle sized hymenopteran species is 9 ind. m⁻² a⁻¹; in the forest this value is only 2 ind. m⁻² a⁻¹. For larger species the boundaries lie well below 1 ind. m⁻² a⁻¹ and are comparably low. They lie well within the range of densities reported in other quantitative studies of arthropod densities (Schafer 1991, 1996 and literature therein). The maximal density of a small species in the forest is 69 ind. m⁻² a⁻¹; on the meadow this value is 544 ind. m⁻² a⁻¹. Both values correspond with the much higher total densities on the dry meadow

Table 1. Upper values for densities of the hymenopteran species of the dry meadow Drakenberg and the Göttingen beech forest. Data derived from the boundaries given in Figure 3.

Stratum	Göttingen forest	Max. density of a mean sized species (ind.m ⁻²)	Max. density of the smallest species (ind.m ⁻²)
Ground	$\ln D = -0.084 (\ln X)^2 - 2.024 \ln X - 9.58$	1.42	18.64
Herb layer	$\ln D = -0.023 (\ln X)^2 - 1.133 \ln X - 9.06$	0.11	4.34
Canopy	$\ln D = -0.181 (\ln X)^2 - 4.123 \ln X - 20.08$	0.98	19.17
All Hymenoptera	$\ln D = -0.0938 (\ln X)^2 - 2.313 \ln X - 10.73$	1.99	69.45
Drakenberg			
Ground	not possible		
Herb layer	$\ln D = -0.7099 \ln X - 4.47$	2.56	111.83
Canopy	—		
All Hymenoptera	$\ln D = -0.04 (\ln X)^2 - 1.5087 \ln X - 6.99$	9.08	544.48

D – Densities (ind.m⁻²); X – Weight [g]
 Bold parameters are significant at the 5%-level.

and are also not extraordinarily high (Ulrich 1999a).

Of course, the functions are obtained by fitting mean density values (mean values of seven [Göttingen forest] and 2 [Drakenberg] years of study) and it may therefore be that they are results of the computational process: if there are more species in middle ranking weight classes the chance of having species with a high density is greater than in less species rich weight classes. The triangular shape may therefore only be a stochastic effect. The simulations of Currie (1993) resulted in similar shapes but with less marked limits and indeed were mainly caused by underlying species-weight distributions. It is therefore necessary to test whether the boundaries are due to stochastic effects or have more "ecological" causes. For this task I compared the boundaries of the species of the beech forest with their real upper densities (max. densities during seven years of study) and analyzed the pattern.

Most of the species fluctuated more or less in density, and 18% of the species had density fluctuations of more than factor 10 (up to more than factor 1000) (Ulrich 1998). But individual computations for each species showed that only 25 of them (3.5% from a total of 720) reached in one of the years their upper density limit as defined in Figure 3 (Figure 4).

Figure 4 contains all species with maximal densities of more than 1 ind. $m^{-2} a^{-1}$ by plotting the difference of max. density minus boundary density against the weight. The interesting fact appears, that small species did not reach their limit despite of their high density fluctuations. In larger species the maximal density reaches asymptotically the boundary. Only 10 species had maximal densities well above (more than 10 ind. m^{-2}) their limit, all of them (with the exception of *Phygadeuon ursini*) medium sized species. These species are listed in Table 2. The maximal densities of them, their boundary densities, and the densities in the year following the maximum are given. The following generation of *P. ursini* could not be checked because the study ended in 1987 but the data in Hövemeier (1992) indicate a marked decline in density. The populations of six of the ten species collapsed in the year after their peak (the population of *Synopeas gw1* collapsed in the second year; in 1985 it reached 77 ind. m^{-2}). Three species also declined and reached densities near their boundaries.

Only five of the 720 hymenopteran species of the Göttingen forest (*Synopeas gw1*, *Omphale gw2*, *Eumacepolus grahami*, *Phygadeuon ursini*, *Cratichneumon rufifrons*) exceeded their boundary density in one of the years and had even higher densities in the following year

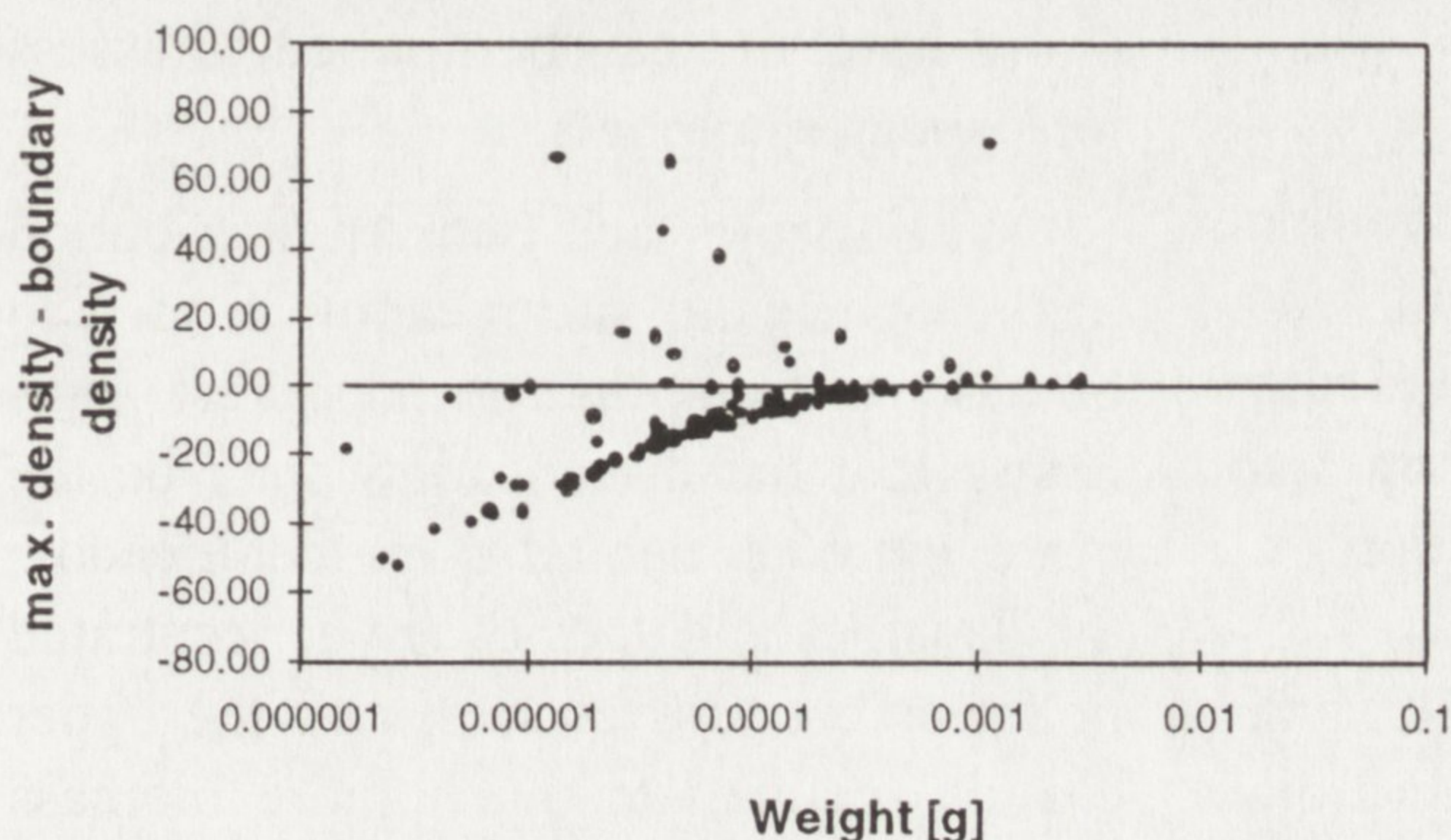


Fig. 4. Difference between max. density and boundary density (as defined in Table 1 with the function for all Hymenoptera) versus weight. Plotted are all species of the Göttingen forest with max. densities above 1 ind. m^{-2} . The straight line marks the zero deviation from the boundary density.

Table 2. Maximal densities (ind.m⁻²) and densities in the following years of all hymenopteran species in the Göttingen forest with maximal densities more than 10 ind.m⁻² above their boundary density. The boundary densities are defined in Table 1 (function for all Hymenoptera).

Species	Boundary density	Max. density	Difference	Year of max. density	Density in the next year	Year
<i>Synopeas gw1</i>	30	658	627	1984	not found	1986
<i>Phygadeuon ursini</i>	1	72	70	1987	–	–
<i>Eretmocerus mundus</i>	33	99	66	1983	<1	1984
<i>Tetrastichus brachycerus</i>	18	83	65	1984	not found	1985
<i>Mesopolobus gw1</i>	19	64	45	1985	3	1986
<i>Omphale gw2</i>	13	50	37	1985	13	1986
<i>Gastrancistrus walkeri</i>	24	39	16	1984	<1	1985
<i>Tetrastichus ?charoba</i>	20	34	14	1982	<1	1983
<i>Charitopes gastricus</i>	5	20	14	1986	6	1987
<i>Tetrastichus luteus</i>	8	19	11	1984	9	1985

(from a total of 4320 combinations = 0.11%). The first three species are parasitoids of gall inducing Cecidomyiidae.

4. DISCUSSION

The species distribution along weight classes is not well understood, but has practical implications because a detailed knowledge of the distribution would allow the total number of species in a given biome or in the world to be assessed (May 1978, 1986). The data presented here for the Hymenoptera indicate for both habitats log-normal or normal distributions. A recalculation of the data in Hövemeyer (1996) for the dipteran fauna of the same dry meadow also resulted in a log-normal distribution (12 size classes, $m = 5.75$, $s = 0.14$). Novotny and Kindlmann (1996) analyzed 16 arthropod taxa and found that

most of them are best fitted by normal or log-normal distributions and the “automobilistic” examples of Gaston (1993) also point in this direction. It would be of great interest to see whether the above reported distributions and parameters generally hold and can be applied to assess total species numbers.

The species and density distribution in the open land site meadow tended to be more unequal than in the forest, indicating that the dry meadow may be the more extreme habitat. On the meadow the densities and species are concentrated in fewer biomass classes, and the upper classes accumulate much more biomass

than in the forest. This contrasts with the higher annual species numbers on the meadow (Ulrich 1999a), and the higher diversity (Ulrich in prep.). In both habitats the data are not consistent with the equal biomass hypothesis (Maurer and Brown 1988).

The above results can be compared with the data of Stork and Blackburn (1993) obtained for the arthropod fauna in a tropical lowland rain forest in Indonesia. Their biomass classes ranged over six magnitudes of order and their plots of total biomass against biomass class of the species resulted in power functions with slopes around 1.0. A ten-fold increase in size would therefore result in a 10 fold increase in total biomass. The hymenopteran fauna of the temperate beech forest and the dry meadow studied here do not fit in such a distribution, but can be described by second order polynomial functions. On the dry meadow a 10 fold increase in size results in a roughly three-fold increase in total biomass. However, Stork and Blackburn dealt with all arthropods. Therefore, large arthropods other than Hymenoptera, (Coleoptera, Orthoptera or spiders) may well account for the steady rise in biomass. The authors also reported a decline in mean species size from canopy to soil. In the beech forest no such differences were found. The mean weight of a canopy living parasitoid species is 0.55 mgDW; in the herb layer the mean weight is 0.89 mgDW, and at the ground 0.95 mgDW. However, the differences between the strata are not significant (Kruskal Wallis non parametric ANOVA, $p = 0.08$).

The most important result of the present study is the finding that from density-weight plots upper density boundaries for the Hymenoptera can be inferred. Gaston (1993) discussed two

hypotheses explaining such upper boundary lines in mammals: metabolic constraints and concatenations of the underlying frequency distributions of size and abundance. In the following I will outline a third explanation.

The studies on mammalian and tropical beetle density boundaries and the explanations of the patterns assume roughly stable species densities. "Stochastic" explanations which assume that the patterns are caused by underlying distributions also used fixed densities. However, this study shows that even when high density fluctuations are taken into account the boundaries – defined by mean abundances – held. Any explanation has therefore also to deal even with extreme (factor 100 or more) density fluctuations. The boundaries may therefore be caused by ecological factors rather than being an effect of statistics or physiology. One can speculate that these factors may force the species to range inside an "allowed" area of density. These density areas (defined by the boundary functions) may mark the range in which the species can fluctuate without a following collapse in density. Thus, they define the range of stability. Exceeding the boundaries is followed by a decline or even a collapse of the population in the next generation. This is exactly the pattern found: species with higher densities than defined by the boundary returned nearly always to densities at or below this threshold. It is interesting that the densities of larger species ranged near their boundary, whereas small species had mean densities well below their threshold. This behavior also fits into the above explanation because in the beech forest under study small species had higher density fluctuations than larger ones (Ulrich 1999b). Having low mean densities may thus be a strategy to avoid

too high abundances (and latter population collapses) caused by stochastic fluctuations.

The comparatively low densities of small species are the cause of the so called triangular form which had been observed in many density-weight curves (Gaston 1993). Gaston assumed that this form may be caused by the species-biomass distribution involved. The above argument, on the other hand, draws attention to the stability of populations. Simulations with fluctuating populations (Ulrich 1999b) showed that realistic density-weight distributions with negative slopes may indeed be generated alone by the underlying species-weight class distribution together with a negative (linear or power function) density fluctuation-weight distribution.

Theoretical considerations related with models on population regulation emphasized that there are outer limits of density between which the densities may wander but rarely exceed them. This so called "boundedness" (Chesson 1978, Chesson and Ellner 1989) plays a crucial role in several distribution-free tests on density dependent regulation (Pollard et al. 1987, Reddingius and Den Boer 1989, Den Boer and Reddingius 1989, Crowley 1992). A serious shortcoming of these concepts is the fact that it proved to be very difficult to obtain empirical values for upper and lower limits of density (Crowley 1992).

The above developed method may serve to reach at upper density limits. Further studies on other arthropod groups and guilds are necessary to prove whether the boundaries can generally be described by polynomial functions and whether these functions have similar parameters. It is also necessary to analyze the role of the boundary in detail, especially whether it acts like a repellent (Pollard et al. 1987) or marks the upper boundary of a strange attractor band (Crowley 1992) that means an area to which densities return after exceeding them.

The above argument can in fact be combined with the explanation that underlying distributions result in the observed patterns. Such a reasoning would combine the concepts of density dependence with species abundance and biomass relationships. It is tempting to speculate that the boundary as defined above also acts like a limit for density dependence. Densities above this limit would therefore always be regulated in a density dependent manner; densities below may or may not be regulated anyway. Further studies on other populations have to confirm these hypotheses.

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5. SUMMARY

The density – weight distributions of the hymenopteran species in a beech forest on limestone and a dry meadow on limestone near Göttingen (FRG) were studied.

Species – weight class distributions turned out to follow normal (forest habitat) and log-normal distributions (dry meadow) (Figure 1). Upper size classes accumulated more total biomass m^{-2}

than lower ones, resulting in a rejection of the equal biomass hypothesis in the case of the Hymenoptera (Figures 1, 2).

An analysis of the density – weight relationship revealed an upper density boundary for the hymenopteran species, which can be defined by second order polynomial functions (Table 1, Figure 3). Mean and upper densities of small parasitoid

species ranged well below their boundaries, with an asymptotic relationship between distance from the boundary and species weight (Table 2, Figure 4). The area defined by the boundaries may mark the area of stability; exceeding the species specific boundary was always followed by a marked decline or even a collapse of population density.

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