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BROADENING AND DIVERSIFICATION OF HUNTED RESOURCES, FROM THE LATE PALAEOOLITHIC TO THE LATE MESOLITHIC, IN THE NORTH AND EAST OF FRANCE AND THE BORDERING AREAS

Anne BRIDAULT*

Summary

The question of subsistence changes during the Mesolithic period is debated on the basis of the diachronic analysis of the structure of 60 faunal spectra. The assemblages come from sites located in northern and eastern France and bordering areas (Switzerland, Germany and Luxembourg). Some Ertebølle assemblages from Scania are also included for comparison.

A quantitative analysis of macrofaunal data is carried out. Two criteria are used for comparison: species richness, that is the abundance of taxa represented in an assemblage, and species diversity or evenness. Species richness and diversity are measured by statistical tests of quantitative indices unrelated to sample sizes. It appears that neither broadening of prey spectrum, nor chronological diversification (from late Palaeolithic to late Mesolithic) can be attested in those regions.

A qualitative analysis focuses on birds, fishes, amphibians and micromammals data, species likely to have been food supplies. Results are more subtle: no intensification of birds occurrence is observed in our regions during the periods considered. Bird predation seems to be a random, generalized and probably opportunistic foraging. An increase in the occurrence of fishes, amphibians and micromammals is observed between the early and late stages.

Résumé

Enrichissement et diversification des espèces chassées, de la fin du Paléolithique au Mésolithique final dans le Nord et l'Est de la France et les régions limitrophes.

La question des changements dans le mode de subsistance au cours du Mésolithique est discutée sur la base de l'analyse diachronique de la structure de 60 spectres de faunes provenant de sites du Nord, de l'Est de la France et des régions limitrophes (Suisse occidentale et Allemagne), ainsi que de quelques sites de l'Ertebølle de Scanie.

Une analyse quantitative est pratiquée sur les restes de macrofaune. Deux critères sont utilisés pour comparer les ensembles : d'une part la richesse taxinomique, c'est-à-dire l'abondance des espèces exploitées, d'autre part la diversité taxinomique ou équilibre de répartition de ces espèces au sein des spectres. Dans les deux cas, des indices quantitatifs peu dépendants de la faible taille des échantillons fauniques (propres à ces périodes) sont utilisés conjointement à des procédures de contrôle statistique. Il ressort que l'évolution diachronique (du Paléolithique final au Mésolithique final) n'est marquée ni par un enrichissement en espèces ni par une diversification de la prédation au cours du temps.

Une analyse qualitative a été menée sur les données concernant les "petites espèces" (oiseaux, poissons, amphibiens et micromammifères), ressources susceptibles d'être nouvellement exploitées de façon systématique. Les résultats sont ici plus nuancés : aucune intensification de l'acquisition des oiseaux reposant sur une exploitation spécialisée n'est attestée dans nos régions durant la séquence diachronique envisagée. Une augmentation de l'occurrence des restes de poissons, d'amphibiens et de micromammifères entre les phases anciennes et la phase récente est néanmoins documentée.

Zusammenfassung

Menge und Diversität der Jagdtiere im Spätpaläolithikum und Spätmesolithikum Nord- und Ostfrankreichs sowie angrenzender Gebiete.

Die Frage des Subsistenzwandels während des Mesolithikums wird auf der Basis der zeitlichen Abfolge von 60 Faunenspektren untersucht. Die Ensembles stammen aus Siedlungen in Nord- und Ostfrankreich sowie aus angrenzenden Gebieten (Schweiz, Deutschland). Zum Vergleich werden auch Komplexe der Ertebølle-Kultur Skandinaviens herangezogen.

Die Überreste der Großfauna wurden einer quantitativen Untersuchung unterzogen. Zwei Kriterien wurden zum Vergleich herangezogen: Artenreichtum (Zahl der erkannten Arten) und Artenvielfalt. Es scheint, daß im Arbeitsgebiet zwischen Spätpaläolithikum und Spätmesolithikum weder eine Erweiterung des Beutespektrums, noch eine Diversifikation festgemacht werden kann.

Die Resultate der Kleinsäuger, Vögel, Fische und Amphibien wurden einer qualitativen Auswertung unterzogen. Das Ergebnis ist unspektakulär: während des untersuchten Zeitraumes konnte im Arbeitsgebiet keine Intensivierung der Nutzung von Vögeln festgestellt werden. Sie scheinen nur nebenbei bejagt worden zu sein. Fische, Amphibien und Kleinsäuger kommen in den jüngeren Stationen allerdings häufiger vor als in den älteren.

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Key Words

Hunting economy, Epipalaeolithic, Mesolithic, Species richness, Species diversity, Broad spectrum.

Mots clés

Economie de chasse, Epipaléolithique, Mésolithique, Richesse spécifique, Diversité spécifique, Large spectre.

Schlüsselworte

Jagd, Epipaläolithikum, Mesolithikum, Artenreichtum, Diversifikation, Jagdspektrum.

The research problem

One aspect related to subsistence change from the late Palaeolithic to the late Mesolithic (ca 12,000 bp-6500 bp uncal.), in the North and East of France and the bordering areas will be considered in this paper.

At the end of the sixties, this question has been first addressed by several scholars (Clark, 1967; Binford, 1968; Flannery, 1969). Based mostly on qualitative analyses, they pointed out an increase in the range of resources used by hunters-gatherers, in the Near East as in northern Europe, from the late Palaeolithic or the Mesolithic, depending of the regions. The exploitation of a limited prey spectrum significantly broadened in favour of new animal species, particularly the small ones often called sub-optimal resources (for instance Cohen, 1977 and Binford, 1983), and possibly in favour of plants (Clarke, 1976; Rozoy, 1978: 1040-1041). Flannery (1969) even termed this change "broad spectrum revolution". Since then, this pattern in which all the trophic levels are exploited has been considered as characteristic of Mesolithic economies.

Recent observations on the Kebarian and Natufian modes of subsistence in the southern Levant confirm such a "broad spectrum" exploitation, together with a "specialization towards hunting of certain small species like *Lepus* and *Alectoris*, waterfowl, reptiles and fishes in extremely high proportions and throughout the year" (gazelles being always the main prey) (Pichon, 1984; Tchernov, 1993a: 137-159, 1993b). More balanced results have been drawn from recent analyses of 21 faunal assemblages from sites dating from Stone to Early Iron Age, in the east Baltic area (Zvelebil, 1990): "[...] late Mesolithic groups [...] both combined generalized and specialized resource use strategies" (*op. cit.*: 87). Nonetheless, no clear trend towards more intensive use of small animal species (fish excepted) can be demonstrated for the Mesolithic period.

Several factors have been proposed to explain the change of subsistence behaviour:

– the ecological transformation at the end of the Pleistocene brought a new composition of the fauna and a new seasonality of resources that led human groups to adopt a new mode of subsistence (in particular Clark, 1980);

– an ecological factor together with a demographic increase that led to a reduction of the size territory exploited by each human group and then to a decrease in resources, driving hunters to diversify their subsistence (Binford, 1983);

– the settled way of life, for instance during the Natufian, that created an overuse of the traditional animal resources (mainly large game). Hunters-gatherers were then driven to rely on much less energetical resources (Tchernov, 1993a and b).

This problem being less well documented for the temperate regions of Europe, I shall then examine if such a broadening and diversification of subsistence did occur in some regions of temperate Europe between the late Palaeolithic and the late Mesolithic.

The methods

Our discussion will be based on the analysis of the structure of faunal spectra. Questions to be considered can be formulated as follow: 1) are the faunal spectra generalized or specialized? 2) how are the species distributed? 3) is the structure of the prey spectra stable through time?

Due to the disparity between the data of the macrofauna compared to the data of the other taxa, two types of analysis have been carried out:

– a rather qualitative one focuses on birds, fishes, amphibians and micromammals⁽¹⁾, likely to be resources exploited by Mesolithic groups⁽²⁾.

⁽¹⁾ Only three species have been considered: *Sciurus vulgaris*, *Erinaceus eurapaeus*, *Talpa europaea* (see Bridault, 1993 for further explanations).

⁽²⁾ There are methodological problems when one wants to include those taxa in an overall quantitative analysis: first they are likely to be intrusive in the anthropic levels, some taphonomic analysis exist but are not systematic (Mourer-Chauviré, 1983 on birds remains; Noe-Nygaard, 1983 on fish remains and Bailon, 1993 for amphibians in Middle Neolithic deposits), second the quantitative data are very uneven from one site to another, third their abundance in the spectrum is strongly linked to the sample size and the degree of preservation of the bones.

Molluscs remains being rather scarce in the regions studied and data being very uneven, this category has not been included in the observations.

– a quantitative analysis has been made on macro-faunal data⁽³⁾. In this case, faunal spectra will be compared on the basis of two distinct but complementary concepts recently revisited by several archeologists (Cruz-Uribe, 1988; Leonard and Jones, 1989; Mc Cartney and Glass, 1990):

- species richness, that is the abundance of taxa represented in an assemblage. It will be mesured here as:

$(S-1)/\log_n N$ (after Margaleff, 1958, cited by Bobrowski and Ball, 1989),

where S is the number of species in an assemblage and N the total number of identified specimens. The higher the value, the richer the spectrum and thus the broader the exploitation of resources (fig. 1).

- species diversity will be measured after Grayson (1984: 160), by the reciprocal of Simpson's index:

$$1/\sum p_i^2, \text{ with } p_i = n_i/N,$$

n_i being here the number of identified specimens of the i species, and N the total of NISP. "This index represents the number of equally common species in a given absolute sample of species; the higher the value, the more evenly distributed" the NISP across species (Grayson, 1984: 160), and thus the more diversified the acquisition of the resources (fig. 1).

Spectra with both high richness and diversity values would reflect generalised economies of subsistence (Leonard and Jones, 1989).

Comparisons of the distributions of richness and diversity indices are then carried out by chronocultural stages and statistically tested two by two. Similar comparisons are made on the small species data.

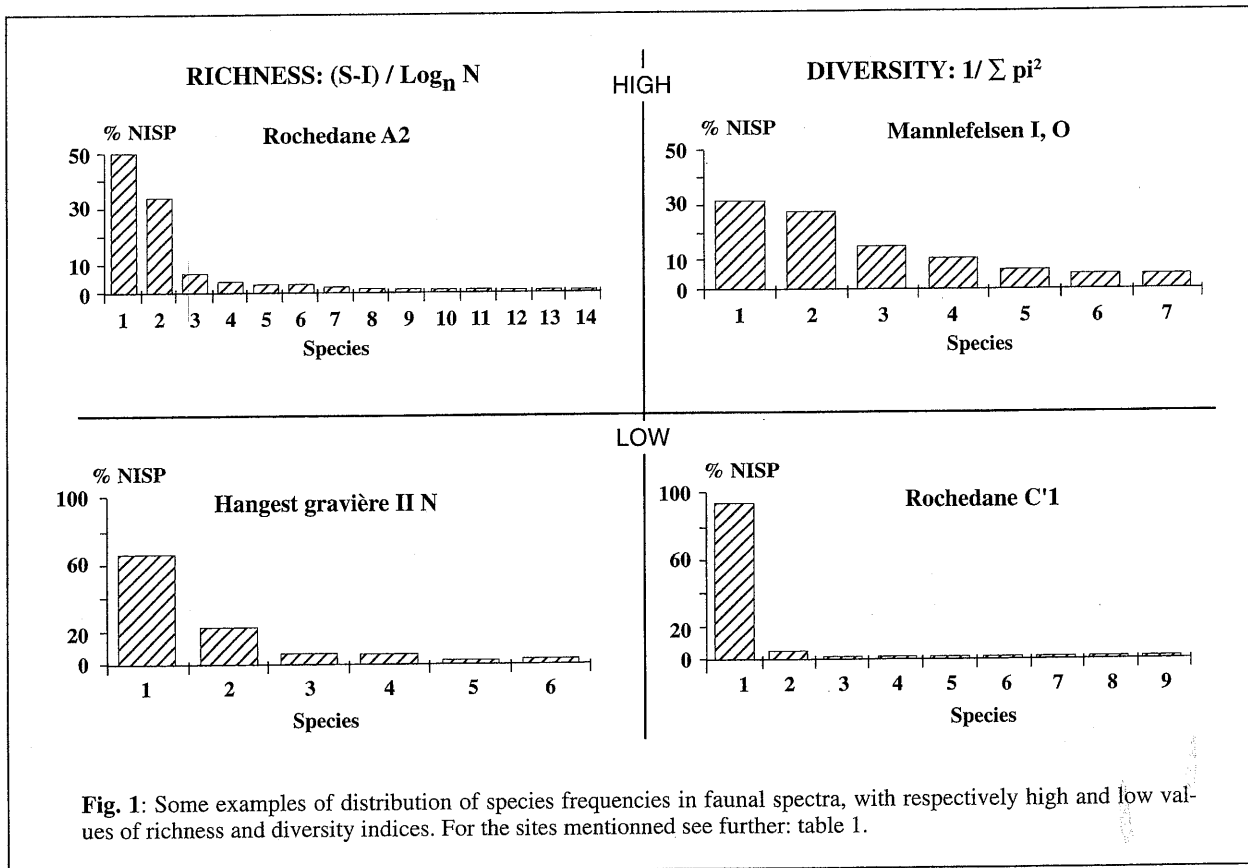


Fig. 1: Some examples of distribution of species frequencies in faunal spectra, with respectively high and low values of richness and diversity indices. For the sites mentioned see further: table 1.

⁽³⁾ *Emys orbicularis* included (for more precisions see Bridault, 1993: Chapter 7).

Archeological stages	n°	Sites	Richness	Rank	Diversity	Rank	NISP	References
ca 8000-6500 BP uncal. Late Mesolithic (“à trapèzes”)	1	Birsmatten H1	2.364	2	2.686	28	373	Schmid, 1963
	2	Liesbergmühle VI	2.162	5	3.478	12	650	Stampfli, 1980
	3	Birsmatten H2	2.083	7	3.155	19	514	Schmid, 1963
	4	Chataillon 6-7	1.039	45	3.244	16	47	Chaix, 1983
	5	Falkenstein Höhle sup.	0.826	49	2.594	31	127	Boessneck, 1978
	6	Felsdach Inzighofen sup.	1.289	32	5.301	3	495	Boessneck, 1978
	7	Jägerhäus-Höhle 6	1.084	41	3.077	21	40	Boessneck, 1978
	8	Jägerhäus-Höhle 7ab	2.084	6	5.397	2	75	Boessneck, 1978
	9	Jägerhäus-Höhle 7c	1.689	16	1.871	46	63	Boessneck, 1978
	10	Larchant	1.497	26	1.91	45	209	Bridault & al., 1993
	11	Loschbour	1.716	15	3.33	14	33	Cordy, 1982
	12	Mannlefelsen H	0.994	46	2.323	35	56	Bridault, 1993
	13	Schötz 7	1.158	37	1.161	52	2371	Stampfli, 1979
	14	Tchäppperfels	1.996	9	5.127	4	55	Stampfli, 1971
	15	Zwingen	1.555	20	2.354	34	329	Büttiker <i>et al.</i> , 1986
ca 9000-8000 BP uncal. Middle Mesolithic	16	Acquigny	0.791	50	2.998	23	157	Bridault, 1993
	17	Birsmatten H3	1.717	14	2.836	24	338	Schmid, 1963
	18	Birsmatten H4	2.025	8	3.065	22	614	Schmid, 1963
	19	Falkensteinhöhle inf.	1.201	34	3.871	11	143	Boessneck, 1978
	20	Felsdach Inzighofen inf.	1.417	28	3.43	13	283	Boessneck, 1978
	21	Hangest gravière II N.	1.06	43	2.008	42	112	Bridault, 1993
	22	Hohen Viecheln	2.315	3	3.184	18	1545	Gehl, 1961
	23	Jägerhaus-Höhle 8d	1.381	29	2.184	37	77	Boessneck, 1978
	24	Jägerhaus-Höhle 8e	1.529	21	4.411	10	187	Boessneck, 1978
	25	Jägerhaus-Höhle 8f	1.111	40	3.313	15	222	Boessneck, 1978
	26	Jägerhaus-Höhle 10	1.418	27	4.983	5	34	Boessneck, 1978
	27	La Grande Rivoire B3	1.798	13	2.719	26	149	Bridault <i>et al.</i> , 1991
	28	La Grande Rivoire C	1.077	42	4.529	8	41	Bridault <i>et al.</i> , 1991
	29	La Grande Rivoire D	1.135	39	3.154	20	82	Bridault <i>et al.</i> , 1991
	30	La Vieille Eglise 6A	1.513	23	2.081	38	102	Ginestet & coll., 1984
	31	Mannlefelsen I	0.588	52	2.074	39	30	Bridault, 1993
	32	Mannlefelsen J	0.844	48	1.947	43	35	Bridault, 1993
33	Mannlefelsen L	1.504	24	2.599	30	54	Bridault, 1993	
34	Mannlefelsen O	1.674	17	4.596	7	36	Bridault, 1993	
35	Rochedane A2	2.25	4	2.818	25	504	Bridault, 1993	
36	Tribsees	1.944	10	4.771	6	277	Lehmkuhl, 1988	
37	Bedburg Königshoven	1.146	38	1.468	50	450	Street, 1990	
ca 10,000-9000 BP uncal. Early Mesolithic & Epipalaeolithic	38	Birsmatten H5	1.381	29	2.667	29	77	Schmid, 1963
	39	La Vieille Eglise 7A	0.91	47	2.243	36	27	Ginestet & coll., 1984
	40	Mannlefelsen Q	1.642	19	1.82	47	71	Bridault, 1993
	41	Rochedane A3	1.891	12	2.704	27	336	Bridault, 1993
	42	Rochedane A4	1.498	24	1.664	49	406	Bridault, 1993
ca 10,800-10,000 BP uncal. Epipalaeolithic	43	La Vieille Eglise 8A	1,059	44	2,042	41	17	Ginestet & coll., 1984
	44	Mannlefelsen R	1,668	18	4,481	9	11	Bridault, 1993
ca 12,000-10,800 BP uncal. Epipalaeolithic & Late Palaeolithic	45	Bettelküche 5*	2,396	1	6,009	1	65	Boessneck, 1978
	46	Mannlefelsen S	1,518	22	2,532	33	52	Bridault, 1993
	47	Freydières*	1,29	31	1,145	53	493	Bouchud <i>et al.</i> , 1973
	48	Rochedane B	1,907	11	1,31	51	914	Bridault, 1993
	49	Rochedane C'1	1,196	35	1,143	54	805	Bridault, 1993
	50	Neumülhe	1,172	36	3,236	17	167	Stampfli, 1979
	51	Petersfels P1 AH2*	0,784	51	2,045	40	164	Albrecht <i>et al.</i> , 1983
	52	Petersfels P3 AH2*	0,52	54	1,945	44	319	Albrecht <i>et al.</i> , 1983
	53	Petersfels AH2/3*	1,253	33	2,567	32	54	Albrecht <i>et al.</i> , 1983
	54	Rochedane D1*	0,528	53	1,808	48	44	Bridault, 1993

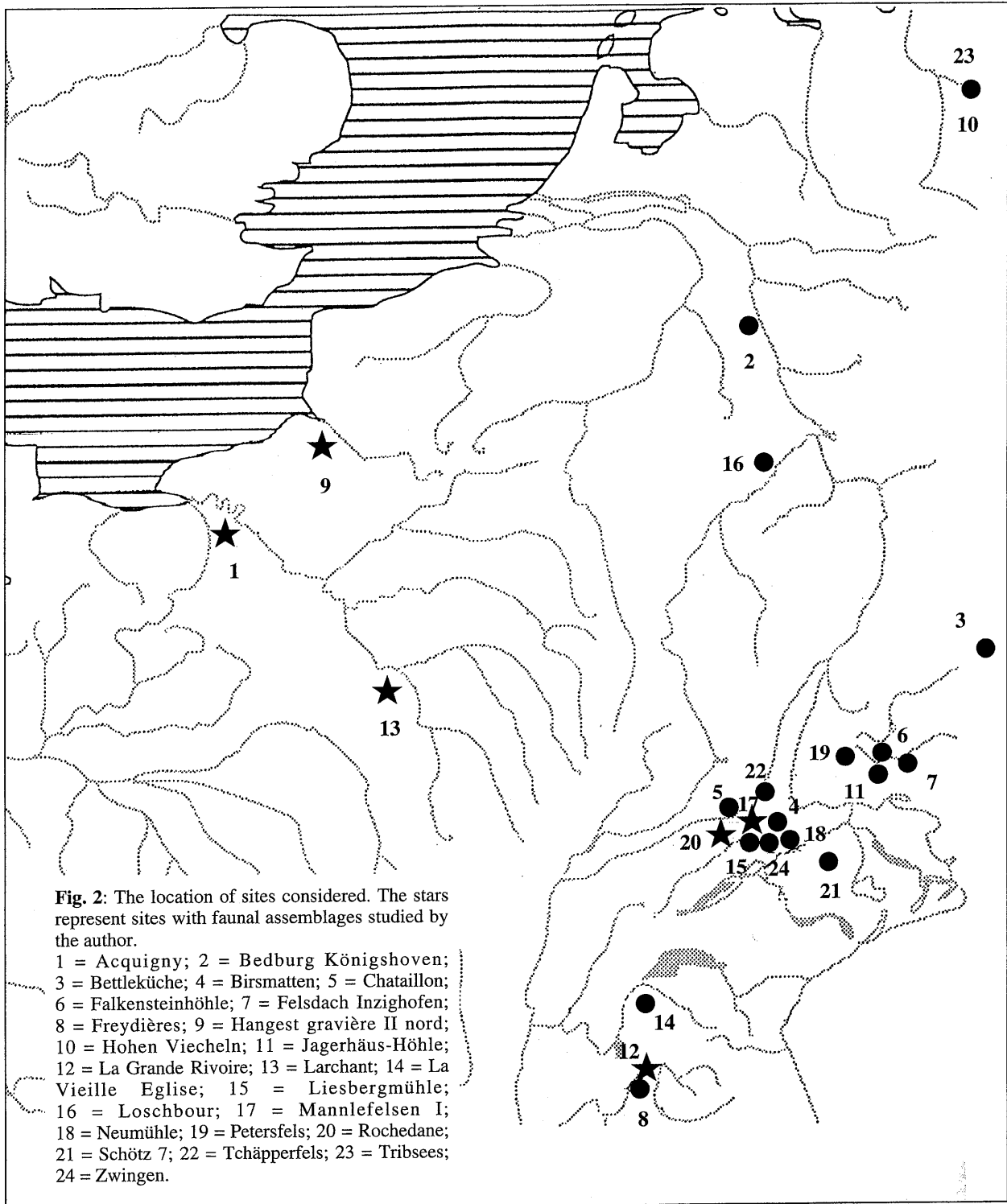


Table 1: Species richness values, diversity values and ranks calculated for the 54 faunal assemblages presented by chronological stages. * Magdalenian. For species richness and diversity indices see in the text.

Study area

The data chosen for this study consist of 54 faunal assemblages from sites located in northern, eastern France and neighbouring areas (Switzerland, Germany and Luxembourg), studied and published by various archaeozoologists (fig. 2; tab. 1). About twenty of them have been recently studied by the present author for a doctoral thesis (Bridault, 1993, 1994). Six more Ertebølle assemblages from Scania (Jonsson, 1988) are taken into account for comparison in some cases, Ertebølle assemblages being considered to be characteristic of "broad spectrum economies". These data cover the chronocultural sequence bounded by the late Palaeolithic and the late Mesolithic included.

Results

Richness, diversity and sample size

First of all, a measure of control is carried out in order to determine if the values of richness and diversity for the 54 assemblages are linked to sample size. The null hypothesis

is statistically tested with a non parametric test, the Spearman rank correlation. Sample sizes are ranging between 30 and 2371⁽⁴⁾ (tab. 1), with a mean of 203 and a standard deviation of 403.

– for species richness, the correlation is not significant at the 0.1 level (fig. 3)

– for species diversity, the correlation is not significant at the 0.5 level (fig. 4).

Indices values being weakly associated to sample size, the null hypothesis can be accepted (with a higher risk for species richness) and the analysis of the structure of faunal spectra can be carried out.

A broadening of the macrofauna prey spectra?

The curve richness indices of the 54 studied assemblages arranged in decreasing rank are almost continuous.

⁽⁴⁾ Two samples counting less than 30 identified specimens are nonetheless included in the analysis, because they are dated from the Dryas III, a very poorly documented chronological stage.

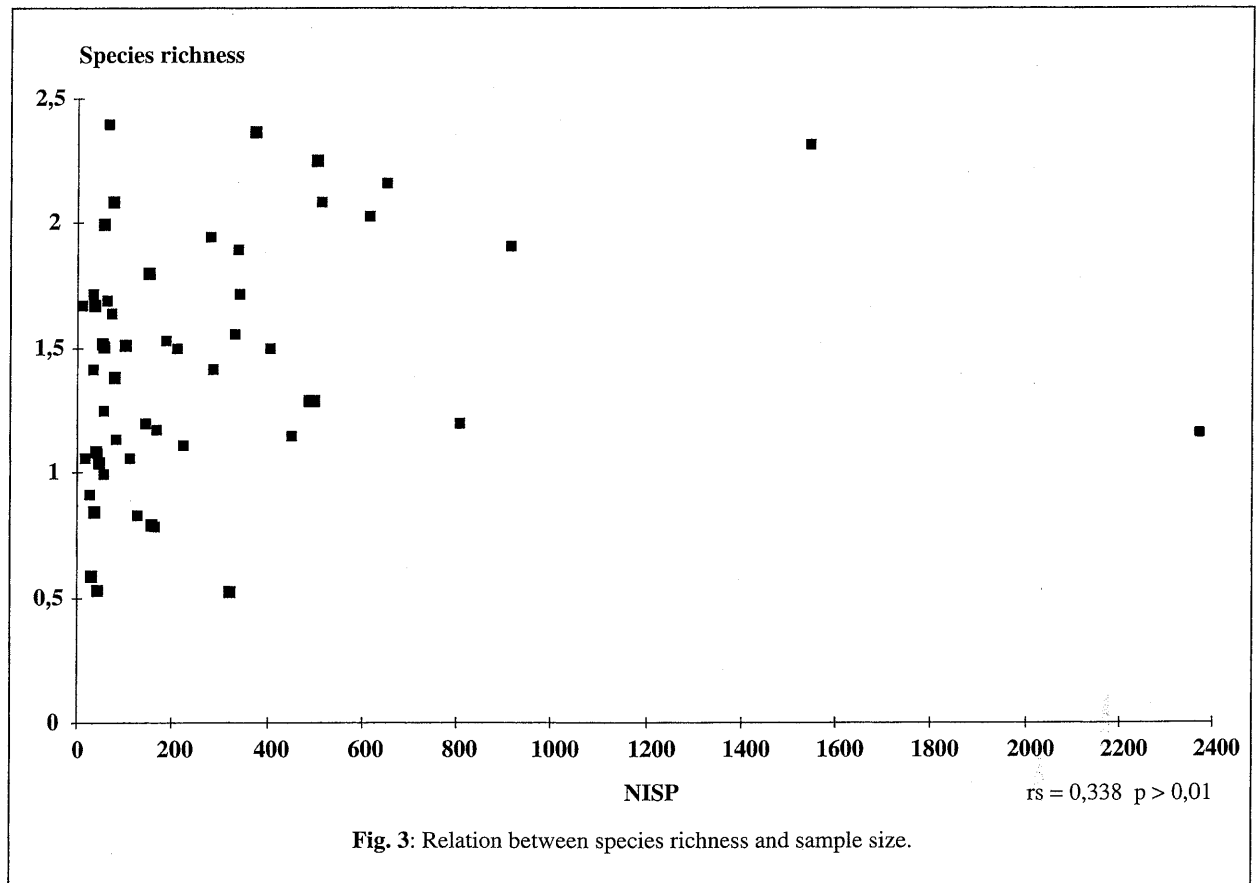


Fig. 3: Relation between species richness and sample size.

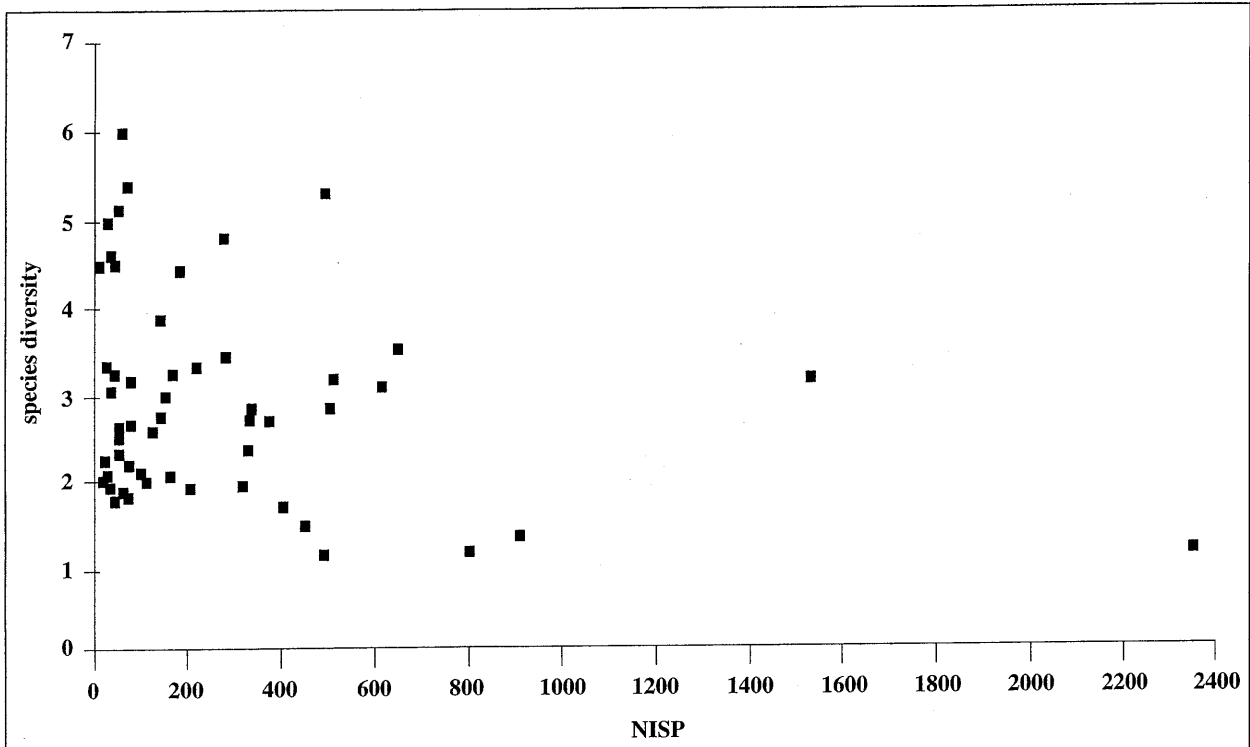


Fig. 4: Relation between species diversity and sample size.

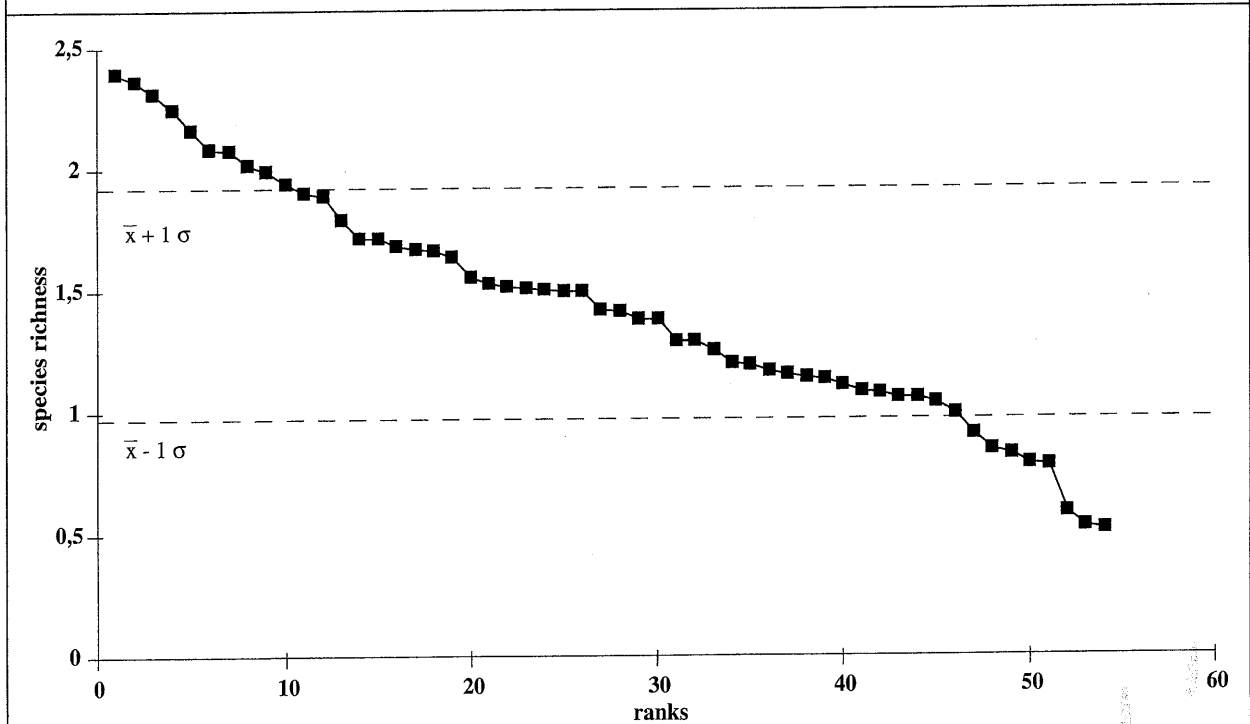


Fig. 5: Faunal assemblages ranked by species richness. Dotted lines are $\bar{x} \pm 1\sigma$. Lilliefors test: maximum deviation = 0.7518, the normality is not rejected (the reject would be done with a risk > 20%).

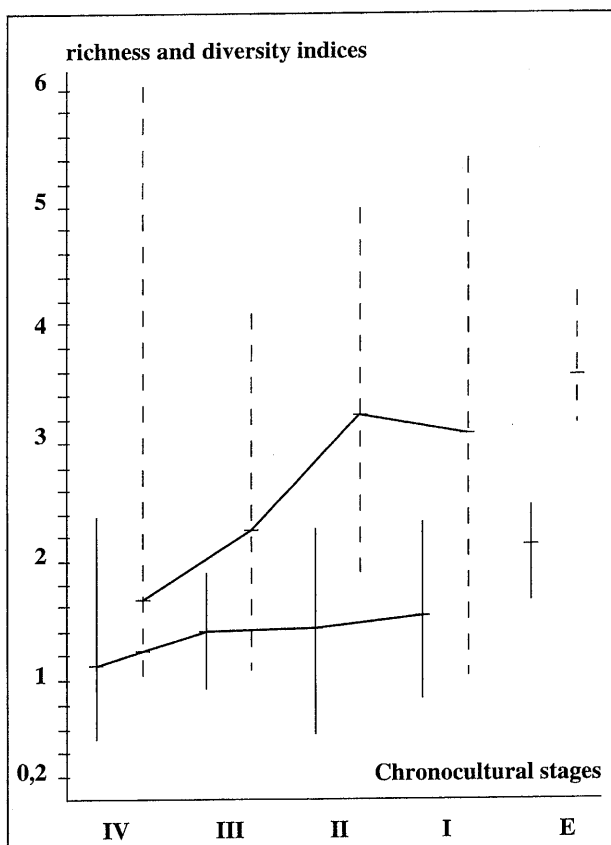


Fig. 6: Comparison of richness indices (continuous line) and diversity indices (dotted line) by chronocultural stages. Means and ranges are represented. IV = late Palaeolithic; III = Early Mesolithic and Epipalaeolithic; II = Middle Mesolithic; I = Recent Mesolithic; E = Ertebolle of Scania (Ageröd-complex, Arlov I, Lödesborg, Segebros, Skateholm I, Skateholm II).

Richness values range from 2.4, for the richest spectrum, to 0.5, for the lowest (tab. 1, fig. 5). According to the Lilliefors non parametric test, the normality of this distribution cannot be rejected (this would be done with a risk > 20%). The majority of the values is thus contained between 0.96 and 1.92 (mean ± 1σ). It means that no distinct groups of faunal spectra (more or less rich) can be discriminated, the values ranging in a continuum.

A comparison of the richness values by chronocultural stage is now carried out. Four chronocultural stages are distinguished: late Palaeolithic, early Mesolithic and Epipalaeolithic (noted early Mesolithic in the figures), middle Mesolithic and late Mesolithic (fig. 6). The Kolmogorov-Smirnov statistic test is used to compare the four distributions two by two. In any case (including the comparison between our late Mesolithic and the Ertebolle assemblages), the null hypothesis can be accepted at the 0.5 level (tab. 2).

Within the limits of the studied sample, significant differences between the chronocultural stages cannot then be proved. Even though more or less rich spectra of hunted fauna are found (*cf. supra*), no broadening of prey spectra (macrofauna) can be attested from the late Palaeolithic to the late Mesolithic. Rich spectra are found from the late Palaeolithic as less rich ones are found in the recent stage.

A diversification of the macrofauna prey spectra?

The 54 diversity indices are arranged in decreasing rank (fig. 7), but unlike the previous case this distribution cannot be compared with a normal law. According to the Lilliefors test, the normality can be rejected with a low risk of error (between 1% and 5%).

Table 2: Kolmogorov-Smirnov test on the species richness of the faunal assemblages grouped by chronocultural stages. Stage I = late Mesolithic (n = 15); Stage II = Middle Mesolithic (n = 21); Stage III = Early Mesolithic and Epipalaeolithic (n = 12), Stage IV = late Palaeolithic (n = 6)

Stages	II	III	IV	Ertebolle
I	T = 0.2 T < 0.459 at the 0.5 level T < 0.551 at the 0.1 level Ho not rejected	T = 0.333 T < 0.526 at the 0.5 level T < 0.631 at the 0.1 level Ho not rejected	T = 0.5 T < 0.656 at the 0.5 level T < 0.787 at the 0.1 level Ho not rejected	T = 0.533 T < 0.656 at the 0.5 level T < 0.787 at the 0.1 level Ho not rejected
II		T = 0.190 T < 0.492 at the 0.5 level T < 0.589 at the 0.1 level Ho not rejected	T = 0.452 T < 0.629 at the 0.5 level T < 0.754 at the 0.1 level Ho not rejected	
III			T = 0.5 T < 0.68 at the 0.5 level T < 0.815 at the 0.1 level Ho not rejected	

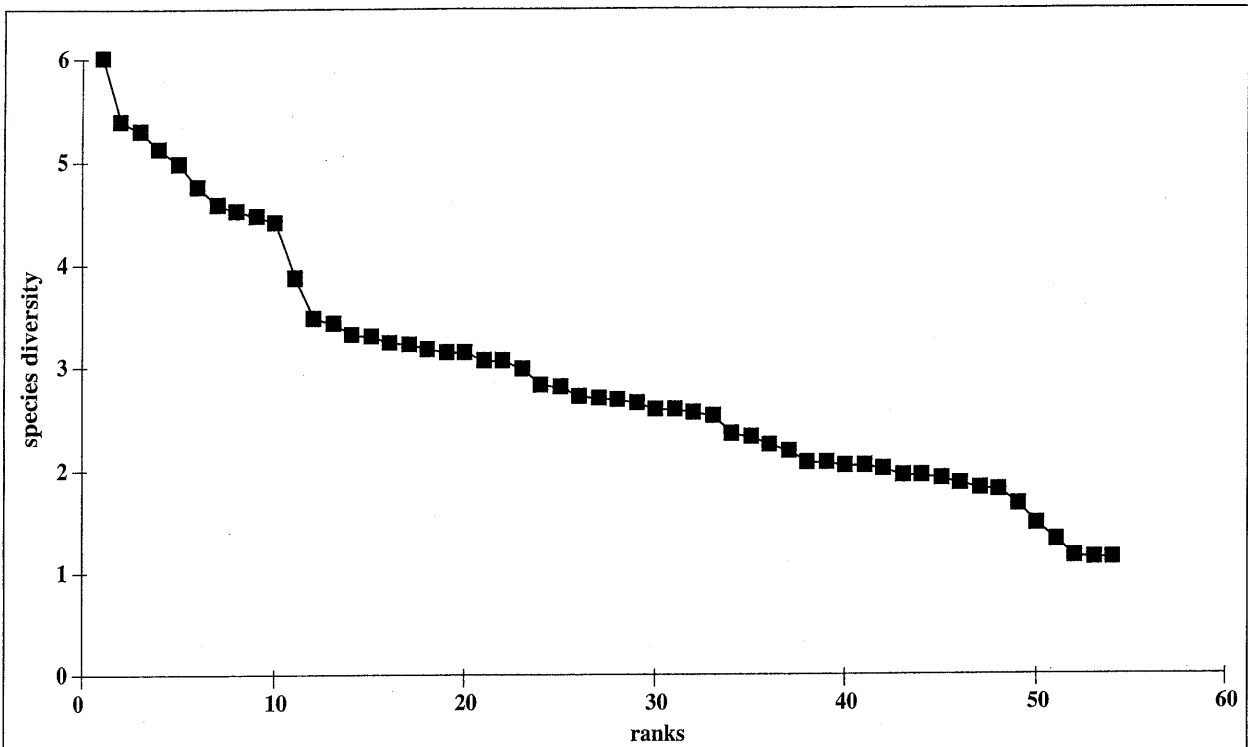


Fig. 7: Faunal assemblages ranked by species diversity.
Lilliefors test: maximum deviation = 0.1243, the normality is rejected with a risk between 1% and 5%.

Stages	II T= 0.2	III T = 0.383	IV T = 0.5	Table 3: Kolmogorov-Smirnov test on the species diversity of the faunal assemblages grouped by chronocultural stages. Stage I = late Mesolithic (n = 15); Stage II = Middle Mesolithic (n = 21); Stage III = Early Mesolithic and Epipalaeolithic (n = 12), Stage IV = late Palaeolithic (n = 6)
I	T < 0.459 at the 0.5 level T < 0.551 at the 0.1 level Ho not rejected	T < 0.526 at the 0.5 level T < 0.631 at the 0.1 level Ho not rejected T = 0.547	T < 0.656 at the 0.5 level T < 0.787 at the 0.1 level Ho not rejected T = 0.595	
II		T > 0.492 at the 0.5 level T < 0.589 at the 0.1 level Ho not rejected at the 0.1 level	T < 0.629 at the 0.5 level T < 0.754 at the 0.1 level Ho not rejected	
III			T = 0.166 T < 0.68 at the 0.5 level T < 0.815 at the 0.1 level Ho not rejected	

The profile of the curve is different from the previous one, showing two groups of points separated by a step:

- one high rank group of values (between 6 and 4.4) consisting of ten faunal spectra in which neither a single species nor a group of taxa predominates. Each chronocultural stage is represented in this sample,

- the other group of values comprises the 44 other prey spectra, less diversified (values between 3.8 and 1.1). Some of the assemblages are dominated by a single species. Here again, all the chronocultural stages are represented.

The statistical comparison of diversity indices by chronocultural stage shows that in nearly any case the null

	Ertebolle	Late Meso	Middle Meso	Early Meso	Late Paleo.
BIRDS					
Ertebolle					
Late Meso.					
Middle Meso.					
Early Meso.					
Late Paleo.					
FISHES					
Ertebolle					
Late Meso.					
Middle Meso.					
Early Meso.					
Late Paleo.		↗			
AMPHIBIANS					
Ertebolle					
Late Meso.					
Middle Meso.					
Early Meso.		↗			
Late Paleo.					↘
MICROMAMMALS*					
Ertebolle					
Late Meso.					
Middle Meso.					
Early Meso.		↗	↗		
Late Paleo.					↘

Fig. 8: Comparisons of the percentages of occurrences of the "small taxa" in the faunal assemblages, by chronocultural stages.

* *Sciurus vulgaris*, *Erinaceus europaeus*, *Talpa europaea* only.

Hatched areas indicate that the comparison of percentages is statistically significant at the 0.5 level, rising arrows indicate a significant increase of occurrences, descending arrows indicate a significant decrease.

hypothesis can be accepted at the 0,5 level (at the 0,1 level in one case) (fig. 6, tab. 3). Therefore, once again, if a dichotomy is found between more and less diversified prey spectra, it is not chronological. A diversification of the subsistence during the Mesolithic cannot then be proved, on the basis of these data.

The other potential resources

If, as it is suggested, birds, fishes and possibly amphibians⁽⁵⁾ and micromammals have been newly and frequently exploited by Mesolithic hunters-gatherers, these taxa should then be frequently attested in the archaeological sites. If their exploitation was intensified during the sequence, their bone remains should be more frequent in the recent levels (taphonomic conditions being similar).

A comparison of the chronocultural evolution of the frequencies of occurrences of each taxonomic category is conducted in order to clarify the problem of small species exploitation in our study areas (tab. 4). The percentages of occurrence in each chronocultural stage are tested two by two in order to determine if the differences observed are statistically significant.

– None of the taxa displays a similar diachronic evolution, even if birds and fishes patterns on the one hand, amphibians and micromammals on the other hand can be lumped together (fig. 8).

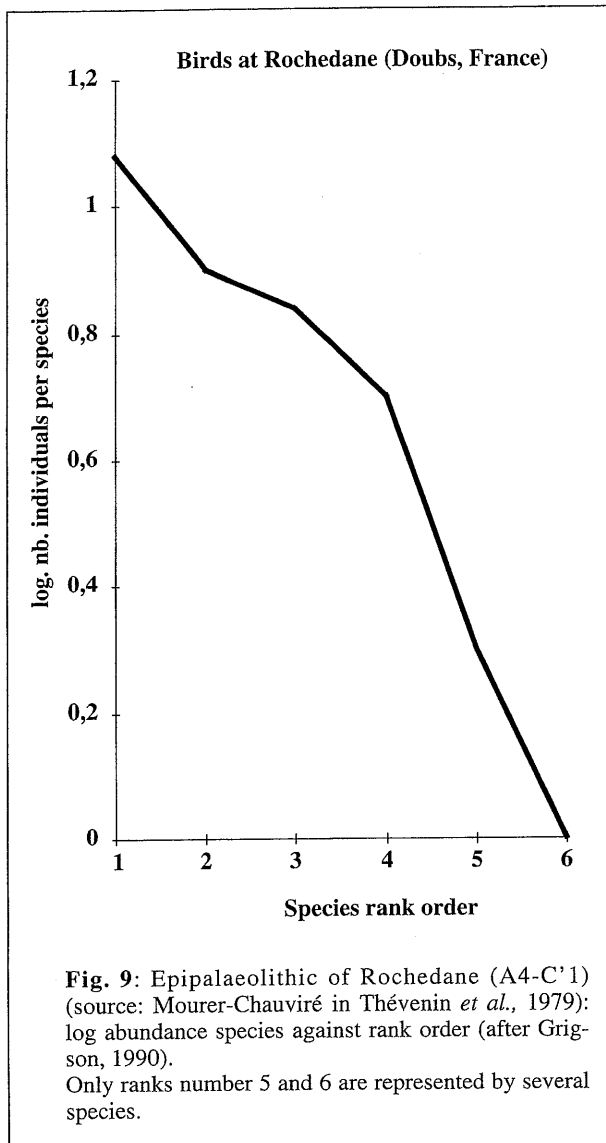
– It also appears that an increase in bird occurrences cannot be supported. The significant differences are to be found with the Ertebølle assemblages (as for fishes). This would rather sign cultural or economic differences than chronological ones.

– For the three other taxa (fishes, amphibians and micromammals), a significant increase of their occurrence appear in our study areas between the late Palaeolithic or the early Mesolithic and the late Mesolithic. This trend is nonetheless sometimes discontinuous since a significant decrease of amphibians and micromammals frequencies of occurrence can be observed between the late Palaeolithic and the early Mesolithic. A similar decrease of fish occurrence have been observed by Le Gall (1993) in southern France between the Epipalaeolithic and the beginning of the middle

Table 4: Birds, fishes, amphibians and micromammals remains in the faunal assemblages studied (after various sources). * *Rana sp.* and *Bufo sp.*; ** *Sciurus vulgaris*, *Erinaceus europaeus*, *Talpa europaea* only. Nsp = number of species; NISP = number of identified specimens.

⁽⁵⁾ See Bailon (1993) for frog (*Rana temporaria*) consumption at Chalain-3 (Jura, France), in a middle neolithic level.

Archeological stages	n°	Sites	Birds		Fisches		Amphibians*		Micromammals**	
			Nsp	NISP	Nsp	NISP	Nsp	NISP	Nsp	NISP
ca 8000-6500 BP uncal. Late Mesolithic (“à trapèzes”)	1	Birsmatten H1	4	10	?	14	?	24		
	2	Liesbergmühle VI	?	19	?	186	?	6	1	1
	3	Birsmatten H2	10	16	?	22				
	4	Chataillon 6-7			4	27				
	5	Falkensteinhöhle sup.			4	>67	1	2	2	5
	6	Felsdach Inzighofen sup.	8	11	5	40	1	2	1	14
	7	Jägerhäus-Höhle 6	1	3					1	1
	8	Jägerhäus-Höhle 7ab								
	9	Jägerhäus-Höhle 7c	2	2	?	2	0		1	2
	10	Larchant			1	2	1	3	1	2
	11	Loschbour								
	12	Mannlefelsen H								
	13	Schötz 7	?	3			?	12		
	14	Tchäpperfels							1	1
	15	Zwingen	4	5	?	2				
ca 9000-8000 BP uncal.	16	Acquigny								
	17	Birsmatten H3	3	7	?	2				
Middle Mesolithic	18	Birsmatten H4	5	6	?	3	?	2		
	19	Falkensteinhöhle inf.	3	4						
	20	Felsdach Inzighofen inf.	3	8	4	173	1	4	2	20
	21	Hangest gravière II N.	3	5			+	?		
	22	Hohen Viecheln	20	103	3	132				
	23	Jägerhaus-Höhle 8d	1	1					1	1
	24	Jägerhaus-Höhle 8e			?	5			1	2
	25	Jägerhaus-Höhle 8f	2	3	?	3			1	3
	26	Jägerhaus-Höhle 10								
	27	La Grande Rivoire B3	1	1					+	?
	28	La Grande Rivoire C					+	?	+	?
	29	La Grande Rivoire D	+	?					+	?
	30	La Vieille Eglise 6A								
	31	Mannlefelsen I								
	32	Mannlefelsen J								
	33	Mannlefelsen L								
34	Mannlefelsen O									
35	Rochedane A2			4	?					
36	Tribsees	9	19	1	15					
ca 10,000-9000 BP uncal. Early Mesolithic & Epipalaeolithic	37	Bedburg Königshoven								
	38	Birsmatten H5	1	1	?	2				
	39	La Vieille Eglise 7A	1	1						
	40	Mannlefelsen Q								
	41	Rochedane A3			4	?				
42	Rochedane A4			4	?					
ca 10,800-10,000 BP uncal Epipalaeolithic	43	La Vieille Eglise 8A	?	3						
	44	Mannlefelsen R								
ca 12,000-10,800 BP uncal. Epipalaeolithic & Late Palaeolithic	45	Bettelküche 5*					1	156	2	15
	46	Mannlefelsen S								
	47	Freydières*	16	87			1	122	1	?
	48	Rochedane B	8	?	4	?				
	49	Rochedane C'1	5	?	4	?				
	50	Neumühle	1	7						
	51	Petersfels P1 AH2*	1	7						
	52	Petersfels P3 AH2*								
	53	Petersfels AH2/3*								
	54	Rochedane D1*								



Mesolithic (ca 10500 bp - 9000 bp uncal.), followed later by a resumption of fishing activity around 7000 bp (uncal.).

Another general pattern emerges from the quantitative data: the faunal assemblages encompass few different species of each taxonomic category, each species being represented by a limited number of bone remains (tab. 4). This pattern neither evokes a specialized predation nor a storage as it is often observed in Scandinavian sites (Rowley-Conwy and Zvelebil, 1989; Grigson, 1990), but a rather random, generalised and probably opportunistic foraging (Grigson, 1990) (fig. 9).

Conclusion

It has been shown that the diachronic evolution of the macrofauna exploitation is structurally stable: between 12000 and 6500 bp, neither broadening, nor diversification can be attested in these regions. More important, our recent results confirm Rozoy's observations that hunters used to rely on the highest ranked preys (more often red deer and wild boar) (Rozoy, 1978; Bridault, 1993, 1994). Prey choice was also turned, in the case of red deer, towards adult animals (Bridault, *ibid.*). Epipalaeolithic-Mesolithic economies of subsistence are generalized in the sense that people exploited a rather broad spectrum of different species living in different habitats. These economies are also specialized in the sense that the base of subsistence relies on few high ranked species and that preys are often individually selected on age criteria. By these features our Mesolithic economies are very similar to the Ertebølle, as to the Natufian (Tchernov, 1993 a and b).

The very preliminary results of the observations carried out on the "small species" data are more subtle. In particular, it seems that the significant differences are found between Epipalaeolithic-Mesolithic from temperate Europe and Ertebølle Mesolithic from Scania. Developing more detailed analyses of these taxa (including systematic taphonomic evaluation) is nonetheless required to determine their economic status. Despite their low quantitative importance (measured by NISP, as by MNI or by meat weight, see Rozoy, 1978 for this last criterion), their economic role could actually have been of great relevance either as substitution resources (*cf. supra*) or buffering resources (Halstead and O'Shea, 1989). Two questions will be addressed during the next years:

- Were birds, fishes, amphibians and micromammals exploited in order to maintain a constant bulk of food resources? In such a case a whole year round predation is expected,
- or were they rather exploited seasonally or during times of shortage? In this case, in what season, and were they stored?

More comparative analysis, particularly with assemblages from northern Europe, together with an appropriate methodology should bring more relevant informations.

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