

SEASONAL CHANGES IN THE AGE STRUCTURE OF A LAND MALACOCENOSIS (GASTROPODA), WITH NOTES ON CLUSTERED DISTRIBUTION OF SELECTED SPECIES

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ABSTRACT: Comparison of quantitative samples taken in consecutive seasons of the year in a forest malacocenosis in SW Poland revealed considerable changes in the snail density per unit area; the structure of the malacocenosis remained roughly constant throughout the year. *Acicula polita* (Hartm.), *Columella edentula* (Drap.), *Discus perspectivus* (Mühlf.), *Alinda biplicata* (Mont.) and *Helicodonta obvolvata* (O. F. Müll.) show aggregated distribution only during a part of the year.

KEY WORDS: terrestrial malacocenoses, quantitative studies, age structure, aggregated distribution

INTRODUCTION

There exists an array of papers dealing with quantitative aspects of land malacocenoses (e.g. DROZDOWSKI 1968, DYDUCH 1980, DYDUCH-FALNIEWSKA & TOBIS 1989, DZIĘCZKOWSKI 1966, 1972, 1974, 1975, 1988, OEKLAND 1929, 1930, POKRYSZKO 1993, UMIŃSKI 1983, UMIŃSKI & FOCHT 1979, VALOVIRTA 1968, WALDÉN 1978, 1981, WÄREBORN 1970, 1982); they are based on samples taken in various seasons of the year. On the other hand, many data suggest that the age structure and population density, especially in small species of a short life span, may undergo considerable

seasonal fluctuations (DZIĘCZKOWSKI 1972, HELLER et al. 1997, POKRYSZKO 1987, 1990, UMIŃSKI 1975, 1979, 1983). If this were true, data on the structure of different malacocenoses sampled in different seasons would not be comparable. The main objective of this study was to find out, based on a single malacocenosis, to which degree the age structure and population density, and thus the whole structure of the community, change during a year. As a side effect, some data on clustered distribution of some common species have been accumulated, which are also discussed.

MATERIAL AND METHODS

The samples were taken in a nature reserve Muszkowicki Las Bukowy (SW Poland; described in detail in KUŹNIK-KOWALSKA 1998, this volume), from October 1993 till October 1994, from a patch of beech, ash, alder and hornbeam. Each month four surface samples were taken of a total area of 1 m², according to the modified OEKLAND's (1930, KUŹNIK 1997)

method. Each sample was sorted three times: immediately after bringing it to the laboratory, and then twice after drying and sieving the material through sieves of 1 × 1 and 0.5 × 0.5 cm mesh. Only living individuals were taken into account. Since the comparison of two sampling methods applied to land malacocenoses revealed differences between

these methods, depending on the season and species (KUŹNIK 1997), in the summer months (June, July, August) volume samples were taken parallelly, as described in KUŹNIK (1997).

Ten species (*Acicula polita* (Hartmann, 1840), *Columella edentula* (Draparnaud, 1805), *Acanthinula aculeata* (O. F. Müller, 1774), *Ena montana* (Draparnaud, 1801), *Discus perspectivus* (Mühlfeld, 1818), *Alinda biplicata* (Montagu, 1803), *Perforatella bidentata* (Gmelin, 1791), *P. incarnata* (O. F. Müller, 1774), *P. vicina* (Rossmässler, 1842), *Helicodonta obvoluta* (O. F. Müller, 1774)), that were the most constant in the samples,

are considered in the paper; those that appeared only sporadically or rarely have been omitted.

For each of these species its relative abundance (A%) and frequency in the series of samples (F%) were calculated; based on frequency each was classified in a constancy class (MÖRZER-BRUIJNS, after DZIĘCZKOWSKI 1988).

In order to construct the species-age pyramids, the three samples of each season were pooled, resulting in a joint sample of 3 m² for the spring, summer, fall and winter.

Chi square test was used in order to estimate the degree of clustering of spatial distribution.

RESULTS AND DISCUSSION

The number of snails of each species found in each season in the surface samples is presented in Tables 1, 3, 6 and 8. Lists of species with division into adults and juveniles, frequency in the series of samples, relative abundance and constancy class, for both surface and volume samples, are given in Tables 2, 4, 5, 7 and 9. For species-age pyramids see figures 1–4.

In the spring (March, April, May) the total number of individuals per 3 m² was 299 (Table 1), juveniles constituting 57.52%. *A. biplicata*, *D. perspectivus* and *A. polita* constituted the highest percentage (together 88.29%). In the summer (June, July, August) the respective value was 666 (Table 3), 63.21% being juveniles. Like in the spring, the dominants were *A. biplicata*, *D. perspectivus* and *A. polita*, of high (9–100%) constancy. Together they accounted for 78.52% collected individuals. In the summer, the number of individuals per 30 l litter was 429 (Table 5), 67.59% being juveniles. Again the same three species dominated, amounting jointly to 80%. In the fall (September, October, November) 510 individuals were found per 3 m² (Table 6), with 50.59% juveniles. The dominant species, which were the same as in the previous seasons, constituted jointly 88.63% malacocenosis, with the constancy of 100%. In the winter (December, November, January) the respective value was 373, with 54.69% juveniles (Table 8), dominant species as above, forming 82.84% and being 100% constant.

Apart from the differences in the number of individuals between the summer surface and volume samples (666 and 429, respectively), resulting from incomparability of the two methods (KUŹNIK 1997), the density per 3 m² in the spring and winter was decidedly lower than in the summer and fall. Comparison of tables 2 and 9 with tables 4 and 7 reveals that, except *P. bidentata* and *E. montana* which are more numerous in the spring samples, all the species in the summer/fall samples are considerably more numerous than in the winter/spring. Thus, estimates of snail

density should be made in the same season in order to be comparable.

Contrary to the density, the general structure of the malacocenosis remains unchanged: the same species dominate and they constitute almost the same proportion of the community. The percentage of juveniles of all species taken together is also similar between the seasons.

Species-age pyramids (Figs 1a–e) indicate that, though the total proportion of juveniles remains almost unchanged, there are species whose age structure changes seasonally. In the spring all species except *A. polita* were characterized by the prevalence of adult individuals; in the summer the situation was similar, except the considerable increase in the proportion of juvenile *C. edentula*. This species is known to reproduce mainly in June (POKRYSZKO 1990). The fall diagram shows an increased proportion of adult *A. biplicata* and *A. polita*, and does not differ significantly from the winter diagram. Comparisons of the structure of malacocenoses sampled in different seasons seem thus acceptable, albeit with the reservation that there are species whose life cycle results in rather rapid fluctuations in the proportion of mature and immature individuals (cf. HELLER et al. 1997, KUŹNIK-KOWALSKA 1998, this volume, POKRYSZKO 1990). The division into juveniles and adults adopted in the species-age pyramids reflects the actual population dynamics in a much coarser way than a division into several age classes based on e.g. the number of whorls and often applied in life cycle studies, and this is probably the main reason why results obtained in different malacocenoses and different seasons can be rather safely compared.

Tables 10–14 illustrate the degree of clustering of occurrence of selected species. The comparison of actual and expected values of snail distribution among the samples indicates that none of the studied species displayed a clustered occurrence throughout the year. *A. biplicata* was distributed in this way during 8

Table 1. Quantitative list of snails found within 3 m² – spring

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	<i>Alinda biplicata</i>	14	11	13	11	5	16	6	10	15	17	4	7
2	<i>Discus perspectivus</i>	13	10	9	5	7	4	6	7	7	6	4	3
3	<i>Acicula polita</i>	4	6	7	4	9	6	2	5	6	2	2	1
4	<i>Acanthinula aculeata</i>	1	0	0	0	3	0	0	0	0	0	0	0
5	<i>Columella edentula</i>	2	0	0	0	3	2	0	0	0	0	0	0
6	<i>Perforatella incarnata</i>	0	0	0	0	0	0	0	0	2	1	0	0
7	<i>Perforatella bidentata</i>	3	3	0	0	0	0	3	0	0	0	0	0
8	<i>Perforatella vicina</i>	0	0	0	0	0	0	0	0	0	1	0	0
9	<i>Ena montana</i>	1	2	1	2	1	0	0	0	0	1	0	0
10	<i>Helicodonta obvolvata</i>	0	0	0	0	1	0	0	0	2	0	0	0

Table 2. Selected snail species collected from 3 m² – spring

No.	Species	total	juveniles	adults	A%	F%	C
1	<i>Alinda biplicata</i>	129	76	53	43.14	100.00	V
2	<i>Discus perspectivus</i>	81	56	25	27.09	100.00	V
3	<i>Acicula polita</i>	54	13	41	18.06	100.00	V
4	<i>Acanthinula aculeata</i>	4	3	1	1.34	16.66	I
5	<i>Columella edentula</i>	7	6	1	2.34	25.00	II
6	<i>Perforatella incarnata</i>	3	2	1	1.00	16.66	I
7	<i>Perforatella bidentata</i>	9	6	3	3.01	25.00	II
8	<i>Perforatella vicina</i>	1	0	1	0.33	8.33	I
9	<i>Ena montana</i>	8	8	0	2.67	50.00	III
10	<i>Helicodonta obvolvata</i>	3	2	1	1.00	16.66	I
	Total	299	172	127	99.98		

Table 3. Quantitative list of snails found within 3 m² – summer

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	<i>Alinda biplicata</i>	30	13	27	15	9	29	40	28	32	12	24	25
2	<i>Discus perspectivus</i>	25	22	18	11	18	12	17	15	13	3	11	1
3	<i>Acicula polita</i>	5	10	0	4	3	3	5	5	6	3	13	16
4	<i>Acanthinula aculeata</i>	2	2	1	0	3	4	4	0	1	1	0	0
5	<i>Columella edentula</i>	4	4	2	1	6	6	10	4	9	3	0	0
6	<i>Perforatella incarnata</i>	2	3	1	0	0	0	0	0	2	1	1	0
7	<i>Perforatella bidentata</i>	11	4	12	3	4	5	0	0	4	0	0	0
8	<i>Perforatella vicina</i>	1	0	0	0	1	1	1	0	0	0	0	0
9	<i>Ena montana</i>	3	0	0	0	6	4	0	0	2	0	0	0
10	<i>Helicodonta obvolvata</i>	0	0	0	0	0	0	0	0	4	0	0	0

Table 4. Selected snail species collected from 3 m² – summer

No.	Species	total	juveniles	adults	A%	F%	C
1	<i>Alinda biplicata</i>	284	205	79	42.64	100.00	V
2	<i>Discus perspectivus</i>	166	108	58	24.92	100.00	V
3	<i>Acicula polita</i>	73	24	49	10.96	91.66	V
4	<i>Acanthinula aculeata</i>	18	7	11	2.70	66.66	IV
5	<i>Columella edentula</i>	49	33	16	7.36	83.33	V
6	<i>Perforatella incarnata</i>	10	9	1	1.50	50.00	III
7	<i>Perforatella bidentata</i>	43	24	19	6.46	58.33	III
8	<i>Perforatella vicina</i>	4	3	1	0.60	33.33	II
9	<i>Ena montana</i>	15	7	8	2.25	33.33	II
10	<i>Helicodonta obvolvata</i>	4	1	3	0.60	8.33	I
	Total	666	421	245	99.99		

Table 5. Quantitative list of species found in 30 l. litter – summer

No.	Species	total	juveniles	adults	A%
1	<i>Alinda biplicata</i>	190	138	52	44.29
2	<i>Discus perspectivus</i>	107	80	27	24.94
3	<i>Acicula polita</i>	18	8	10	4.19
4	<i>Acanthinula aculeata</i>	50	27	23	11.65
5	<i>Columella edentula</i>	28	15	13	6.53
6	<i>Perforatella incarnata</i>	1	1	0	0.23
7	<i>Perforatella bidentata</i>	27	16	11	6.29
8	<i>Perforatella vicina</i>	0	0	0	0.00
9	<i>Ena montana</i>	8	5	3	1.86
10	<i>Helicodonta obvolvata</i>	0	0	0	0.00
	Total	429	290	139	99.98

Table 6. Quantitative list of snails found within 3 m² – autumn

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	<i>Alinda biplicata</i>	17	17	21	26	23	10	27	21	5	0	30	8
2	<i>Discus perspectivus</i>	4	10	10	12	25	8	4	2	6	9	5	2
3	<i>Acicula polita</i>	9	8	7	7	20	9	22	15	0	0	2	2
4	<i>Acanthinula aculeata</i>	0	0	2	0	3	0	0	0	0	0	0	0
5	<i>Columella edentula</i>	0	0	0	2	5	0	0	0	2	0	0	0
6	<i>Perforatella incarnata</i>	4	5	1	2	4	0	0	0	2	0	0	0
7	<i>Perforatella bidentata</i>	0	0	0	0	3	0	0	0	3	0	0	0
8	<i>Perforatella vicina</i>	2	0	0	0	1	0	0	0	0	0	0	0
9	<i>Ena montana</i>	1	0	0	0	2	1	2	0	1	0	0	0
10	<i>Helicodonta obvolvata</i>	6	1	0	0	3	0	0	0	0	0	0	0

Table 7. Selected snail species collected from 3 m² – autumn

No.	Species	total	juveniles	adults	A%	F%	C
1	<i>Alinda biplicata</i>	250	145	105	49.02	91.66	V
2	<i>Discus perspectivus</i>	97	54	43	19.02	100.00	V
3	<i>Acicula polita</i>	105	17	88	20.59	83.33	V
4	<i>Acanthinula aculeata</i>	5	2	3	0.98	16.66	I
5	<i>Columella edentula</i>	9	4	5	1.76	25.00	II
6	<i>Perforatella incarnata</i>	18	16	2	3.53	50.00	III
7	<i>Perforatella bidentata</i>	6	2	4	1.18	16.66	I
8	<i>Perforatella vicina</i>	3	2	1	0.59	16.66	I
9	<i>Ena montana</i>	7	6	1	1.37	41.66	III
10	<i>Helicodonta obvolvata</i>	10	4	6	1.96	25.00	II
	Total	510	252	258	99.97		

Table 8. Quantitative list of snails found within 3 m² – winter

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	<i>Alinda biplicata</i>	11	19	22	15	22	16	11	21	15	6	9	12
2	<i>Discus perspectivus</i>	11	7	8	8	7	11	4	3	3	5	8	2
3	<i>Acicula polita</i>	8	5	6	7	1	0	1	4	13	0	7	2
4	<i>Acanthinula aculeata</i>	0	0	0	0	0	0	0	0	0	0	0	1
5	<i>Columella edentula</i>	8	3	0	0	2	1	0	0	1	5	6	3
6	<i>Perforatella incarnata</i>	0	0	0	0	1	0	0	0	2	0	0	0
7	<i>Perforatella bidentata</i>	3	7	0	0	9	2	0	0	3	0	0	0
8	<i>Perforatella vicina</i>	0	0	0	0	1	0	0	0	0	0	0	0
9	<i>Ena montana</i>	0	0	0	0	1	1	0	0	1	3	0	0
10	<i>Helicodonta obvolvata</i>	0	0	0	0	0	0	0	0	0	0	0	0

Table 9. Selected snail species collected from 3 m² – winter

No.	Species	total	juveniles	adults	A%	F%	C
1	<i>Alinda biplicata</i>	177	110	67	47.45	100.00	V
2	<i>Discus perspectivus</i>	78	41	37	20.91	100.00	V
3	<i>Acicula polita</i>	54	15	39	14.48	83.33	V
4	<i>Acanthinula aculeata</i>	1	1	0	0.27	8.33	I
5	<i>Columella edentula</i>	29	18	11	7.77	66.66	IV
6	<i>Perforatella incarnata</i>	3	3	0	0.80	16.66	II
7	<i>Perforatella bidentata</i>	24	12	12	6.43	41.66	III
8	<i>Perforatella vicina</i>	1	0	1	0.27	8.33	I
9	<i>Ena montana</i>	6	4	2	1.61	33.33	II
10	<i>Helicodonta obvolvata</i>	0	0	0	0.00	0.00	
	Total	373	204	169	99.99		

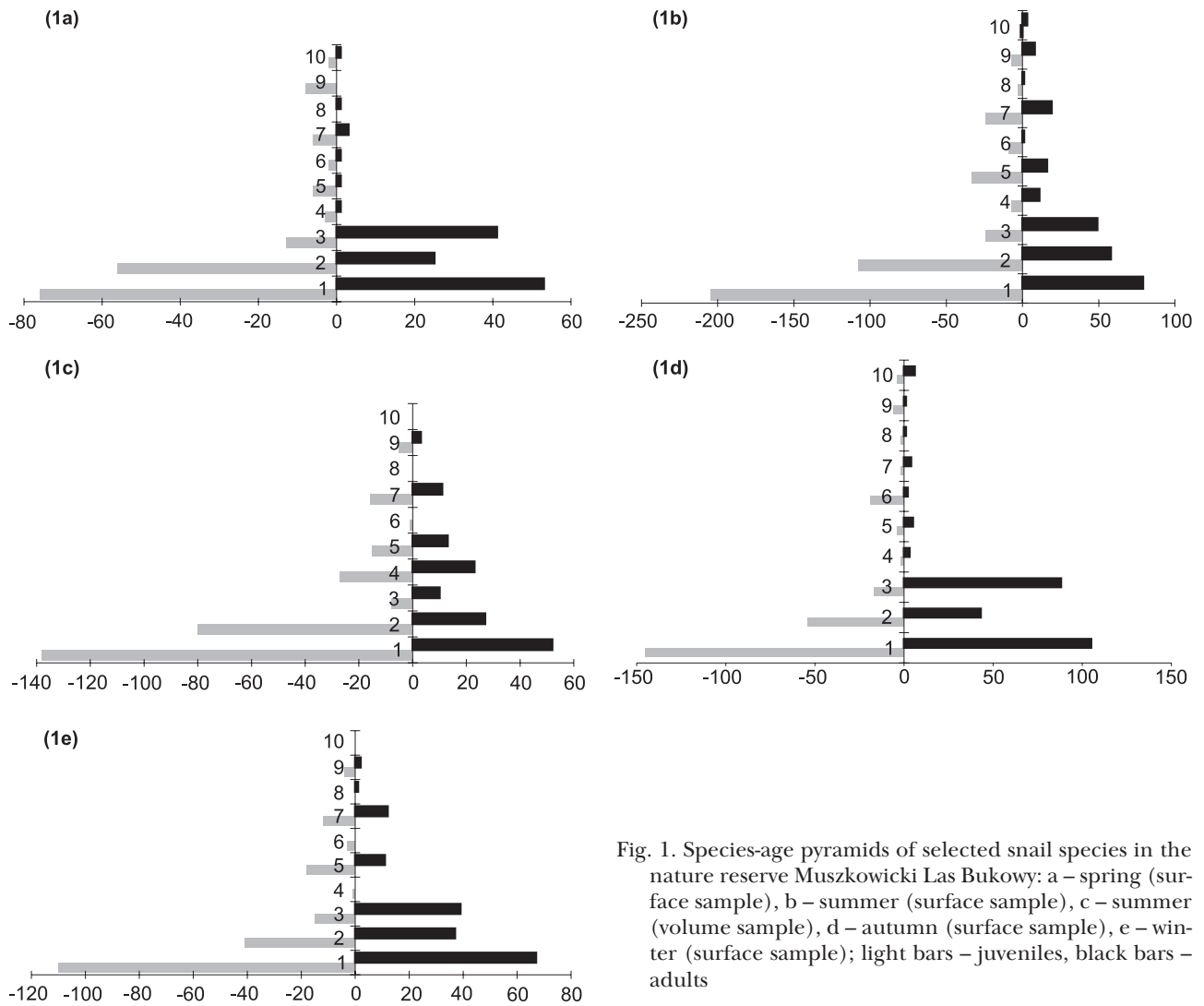


Fig. 1. Species-age pyramids of selected snail species in the nature reserve Muszkowicki Las Bukowy: a – spring (surface sample), b – summer (surface sample), c – summer (volume sample), d – autumn (surface sample), e – winter (surface sample); light bars – juveniles, black bars – adults

Table 10. *Alinda biplicata* (Mont.)

Months	Expected	Observed	χ^2	df	P
October	11.25	7/16/22/0	5.133	3	<0.000
November	10.75	5/0/30/8	49.000	3	<0.000
December	16.75	11/19/22/15	4.104	3	<0.250
January	175.00	22/16/11/21	4.400	3	<0.221
February	10.50	15/6/9/12	4.286	3	<0.232
March	12.25	14/11/13/11	0.551	3	<0.907
April	9.25	5/16/6/10	8.081	3	<0.044
May	10.75	15/17/4/7	10.860	3	<0.012
June	21.25	30/13/27/15	10.200	3	<0.017
July	26.50	9/29/40/28	18.755	3	<0.000
August	34.25	32/12/24/25	20.167	3	<0.000
September	20.25	17/17/21/26	2.704	3	<0.439
October	20.25	23/10/27/21	7.839	3	<0.049

Table 11. *Acicula polita* (Hartm.)

Months	Expected	Observed	χ^2	df	P
October	1.75	1/3/0/3	3.857	3	<0.277
November	1.00	0/0/2/2	4.000	3	<0.261
December	6.50	8/5/6/7	0.769	3	<0.857
January	1.50	1/0/1/4	6.000	3	<0.112
February	5.50	13/0/7/2	18.363	3	<0.000
March	5.25	4/6/7/4	1.285	3	<0.732
April	5.25	9/6/2/5	4.809	3	<0.186
May	2.75	6/2/2/1	5.363	3	<0.147
June	4.75	5/10/0/4	10.684	3	<0.013
July	4.00	3/3/5/5	1.000	3	<0.801
August	9.50	6/3/13/16	11.474	3	<0.009
September	7.75	9/8/7/7	0.355	3	<0.949
October	16.50	20/9/22/15	6.121	3	<0.105

Table 12. *Columella edentula* (Drap.)

Months	Expected	Observed	χ^2	df	P
June	2.75	4/5/1/1	4.636	3	<0.200
July	6.5	6/2/13/5	10.000	3	<0.018
August	3	9/0/0/3	18.000	3	<0.000
October	1.25	5/0/0/0	15.000	3	<0.001

Table 13. *Discus perspectivus* (Mühlf.)

Months	Expected	Observed	χ^2	df	P
October	10.00	12/11/1/16	12.200	3	<0.006
November	5.50	6/9/5/2/	4.545	3	<0.208
December	8.75	11/7/8/8	1.057	3	<0.787
January	6.25	7/11/4/3	6.200	3	<0.102
February	4.50	3/5/8/2	4.666	3	<0.198
March	9.25	13/10/9/5	3.540	3	<0.315
April	6.00	7/4/6/7	1.000	3	<0.801
May	5.00	7/6/4/3	2.000	3	<0.572
June	19.00	25/22/18/11	5.789	3	<0.122
July	15.50	18/12/17/15	1.354	3	<0.716
August	7.00	13/3/11/1	14.857	3	<0.002
September	9.00	4/10/10/12	4.000	3	<0.261
October	9.75	25/8/4/2	33.718	3	<0.000

Table 14. *Helicodonta obvoluta* (Müll)

Months	Expected	Observed	χ^2	df	P
September	1.75	6/0/1/0	14.143	3	<0.003

months (Table 10), *A. polita* and *C. edentula* (Tables 11, 12) during 3 months, *D. perspectivus* during 2 months (Table 13) and *H. obvolvata* only during 1 month (Table 14). The fact that each of the five species showed a clustered distribution during different months suggests that the distribution-affecting factors vary between species. Besides the association between snail distribution and some plant species (DYDUCH-FALNIEWSKA & TOBIS 1989 and literature therein) little is known about the reasons for clustered distribution in apparently even habitats. Possible reasons are reproduction (clustered distribu-

tion of newly hatched juveniles from the same clutch), aggregation at unevenly distributed food sources or in good hiding places during frost or drought. The problem requires an approach that would consider preferences of particular species and age classes.

ACKNOWLEDGEMENTS

I would like to express my sincerest thanks to Dr. hab. BEATA M. POKRYSZKO for her helpful suggestions and help in translation of this paper.

REFERENCES

- DROZDOWSKI A. 1968. Badania ilościowe nad ślimakami (Gastropoda) zadrzewionego parowu i kserotermicznego stoku koło Luskowa (pow. Świecie nad Wisłą). *Fragm. Faun.* 14: 159–181.
- DYDUCH A. 1980. Ślimaki lądowe (Gastropoda terrestria) wybranych zbiorowisk roślinnych Puszczy Białowieskiej i Puszczy Niepołomickiej. *Ochrona Przyrody* 43: 223–272.
- DYDUCH-FALNIEWSKA A., TOBIS H. 1989. Spatial structure of a gastropod community in the litter of a beech forest of Dentario-glandulosae fagetum in the Tatra Mountains. *Folia Malacologica* 3: 55–72.
- DZIĘCZKOWSKI A. 1966. Badania ilościowe nad ślimakami rezerwatu Puszczykowskie Góry w Wielkopolskim Parku Narodowym. *Przyroda Polski Zachodniej* 7 (1963): 65–74.
- DZIĘCZKOWSKI A. 1972. Badania ilościowe ślimaków buczyn południowo-zachodniej Polski. Studium ekologiczno-faunistyczne. *Prace Komisji Biologicznej PTPN* 35: 1–90.
- DZIĘCZKOWSKI A. 1974. Badania nad strukturą zespołu ślimaków (Gastropoda) lasu grądowego (*Galio-Carpinetum*) w Morasku pod Poznaniem. *Badania fizjograficzne nad Polską zachodnią*, ser. C, 27: 25–51.
- DZIĘCZKOWSKI A. 1975. Badania ilościowe mięczaków i ich znaczenie dla różnych dziedzin wiedzy. *Prace Komisji Naukowej Polskiego Towarzystwa Gleboznawczego* 3: 133–142.
- DZIĘCZKOWSKI A. 1988. Zespoły ślimaków (Gastropoda) zbiorowisk leśnych Polski. Studium ekologiczne. *Prace Komisji Biologicznej PTPN* 68: 1–109.
- HELLER J., SIVAN N., HODGSON A. N. 1997. Reproductive biology and population dynamics of an ovoviparous land snail, *Lauria cylindracea* (Pupillidae). *J. Zool.* 243: 263–280.
- KUŹNIK E. 1997. Comparison of two methods of quantitative sampling applied in studies on land malacocenoses (Gastropoda: Pulmonata). *Malak. Abh.* 18: 263–270.
- KUŹNIK-KOWALSKA E. 1998. Life cycle and population dynamics of *Alinda biplicata* (Montagu, 1803) (Gastropoda: Pulmonata: Clausiliidae). *Folia Malacologica* 6: 33–37.
- OEKLAND F. 1929. Methodik einer quantitativen Untersuchung der Landschneckenfauna. *Arch. Moll.* 61: 121–136.
- OEKLAND F. 1930. Quantitative Untersuchungen der Landschneckenfauna Norwegens. I. *Zeitschr. Morph. Ökol. Tiere* 16: 748–804.
- POKRYSZKO B. M. 1987. European *Columella* reconsidered (Gastropoda: Pulmonata: Vertiginidae). *Malak. Abh.* 12: 1–12.
- POKRYSZKO B. M. 1990. The Vertiginidae of Poland (Gastropoda: Pulmonata: Pupilloidea) – a systematic monograph. *Ann. Zool.* 48: 133–257.
- POKRYSZKO B. M. 1993. Fen malacocenoses in Dovrefjell (S Norway). *Fauna norv.*, Ser. A 14: 27–38.
- UMIŃSKI T. 1983. Vitrinidae (Mollusca, Gastropoda) of Poland. Their density and related problems. *Ann. Zool.* 37: 290–311.
- UMIŃSKI T., FOCHT U. 1979. Population dynamics of some land gastropods in a forest habitat in Poland. *Malacologia* 18: 181–184.
- VALOVRTA I. 1968. Land molluscs in relation to acidity on hyperite hills in Central Finland. *Ann. Zool. Fennici* 5: 245–253.
- WALDÉN H. W. 1978. An introductory survey of the mollusc fauna in oligotrophic oak woods in the Stenungsund area (SW Sweden), with regard to the effect of airborne deposition of sulphuric acid and heavy metals. *Terrestra Kontrollundersökningar i Stenungsund Rapport Nr. 8*. Naturhistoriska Museet, Göteborg.
- WALDÉN H. W. 1981. Communities and diversity of land molluscs in Scandinavian woodlands. I. High diversity communities in taluses and boulder slopes in SW Sweden. *J. Conch. London* 30: 351–372.
- WAREBORN I. 1970. Environmental factors influencing the distribution of land molluscs of an oligotrophic area in southern Sweden. *Oikos* 21: 285–291.
- WAREBORN I. 1982. Environments and molluscs in a noncalcareous forest area in southern Sweden. Dept. of Animal Ecol., Univ. of Lund. Dissertation.

received: May 29th, 1998

accepted: September 18th, 1998