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Vitrinidae (*Mollusca*, *Gastropoda*) of Poland. Their density and related problems

[With 4 Tables and 17 Figures]

Abstract. Basing on a rich material collected in 14 sites both in mountains and lowlands of Poland, the writer analyses 5 species of the *Vitrinidae*: *Vitrina pellucida* (O. F. MÜLLER), *Semilimax semilimax* (FÉRUSSAC), *S. kotulai* (WESTERLUND), *Eucobresia nivalis* (DUMONT et MORTILLET), *Eucobresia diaphana* (DRAPARNAUD). Density of populations, yearly fluctuation in density and individual rate of growth are studied.

In contradistinction to the crop-damaging slugs and to the Roman snail — the knowledge of Central European forest-floor gastropods is largely restricted to their taxonomy and geographical distribution. Many fundamental data concerning their biology are lacking. It is only for few species that we know the time of egg deposition, the time of hatching, the growth rate or life-span. Initial research of the density phenomena was done already by OEKLAND (1929, 1930) but our knowledge in this field to date has been scanty. In Poland the relevant investigations were initiated by DROZDOWSKI and continued by DZIĘCZKOWSKI (see below). The population dynamics have not yet been studied. Preliminary observations by a number of authors indicate that for this sort of study the *Vitrinidae* constitute an object both difficult and promising because of their irregular occurrence both in time and space. I think my findings confirm this view.

MATERIAL, TERRITORY, METHODS

This paper deals with 5 vitrinid species to be found in Poland, viz.: *Vitrina pellucida* (O. F. MÜLLER 1774), *Semilimax semilimax* (FÉRUSSAC 1802), *Semili-*

max kotulai (Westerlund 1883), *Eucobresia nivalis* (Dumont et Mortillet 1852), *Eucobresia diaphana* (Draparnaud 1805).

The paper is based on the data concerning the density of *Vitrinidae*, obtained at different places and times in several studies. Their distribution in the country is shown in Fig. 1, their list is as follows.

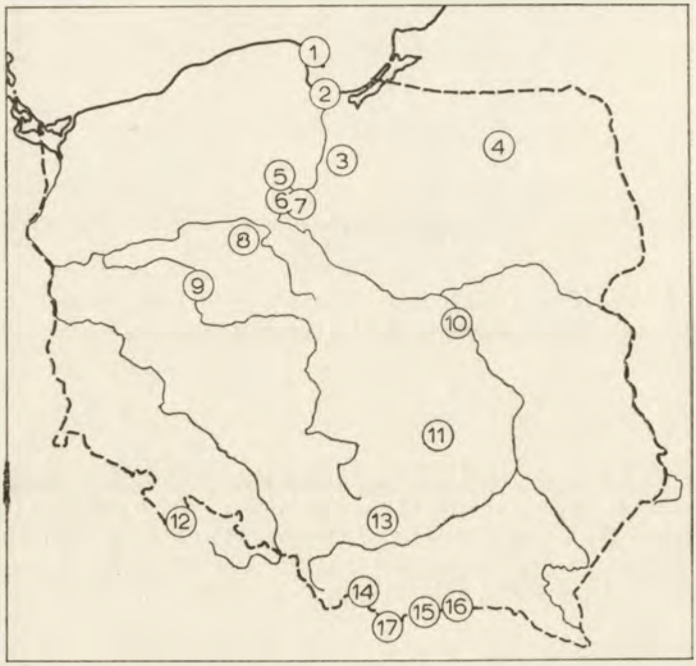


Fig. 1. Location of the sites investigated. 1. Kuźnica in Hel (Umiński, Focht 1979). 2. Bąsak (Drozdowski 1963a). 3. The island of Lake Klasztorne (Drozdowski 1966). 4. Lake Łuknajno (this paper). 5. Wierzchlas (Drozdowski 1958). 6. Luszkowo (Drozdowski 1968). 7. Płutowo (Drozdowski 1961). 8. Steppe vegetation sanctuary Folusz (Drozdowski 1963b). 9. Mt. Góra Moraska near Poznań (Dzięczkowski 1974). 10. Sękocin near Warszawa (Skrzypczak, Umiński 1979). 11. Sanctuary Świnia Góra (Dzięczkowski 1971). 12. Mt. Śnieżnik Kłodzki (this paper). 13. Ojców (Dzięczkowski 1972). Mt. Babia Góra (Dzięczkowski 1972). 15. Pieniny Mts. (Dzięczkowski 1972). 16. Krynica (Umiński 1979). 17. Tatra Mts. (Dzięczkowski 1972, Umiński 1975).

1. In the years 1963–1965 in the valley Dolina Kościeliska, Tatra Mts. 3 sites were examined (elevations of 980 m, 1240 m and 1420 m), populated with *Vitrina pellucida, Semilimax kotulai* and *Eucobresia nivalis* (Umiński 1975).

2. In the years 1964–1965 2 sites on the mountain Śnieżnik Kłodzki (50°10′N, 16°50′E) populated with *Semilimax kotulai* and *Eucobresia diaphana* were examined. Both the sites were situated at an elevation of 1180 m ±10 m on a slope between the mountain lodge of the Polish Society for Tourism (PTTK) and a valley running NW towards the mountain resort Międzygórze. Both of them were in a well-head area where the soil is damp or wet throughout most

of the year. One site, referred to as the "*Picea* site", was situated in a dense, pure *Picea* stand, aged about 60. The ground was in a deep shadow so that the herb layer was very scanty. The other site, referred to as the "*Salix* site", was at the bottom of a grassy slope. It was an elongated patch, some 60 m long and 20 m wide, crossed by a network of small, unstable streams, covered with rich herbaceous vegetation and with *Salix* thickets. The lower end of this patch gets narrower to form the bed of a stream. On both the sites a square frame of 1/16 m² was used. Living snails were hand-sampled from the vegetation, leaf-litter, soil surface and the upper 2 cm layer of soil. In 1964 from July through November samples consisting of 10 frames were taken 4 times from each site. In 1965 from May through October samples of 24 frames were taken 5 times. On both the sites *Eucobresia diaphana* live probably 2 years, they hatch in spring and die out in the second autumn of their life, after oviposition (UMIŃSKI, unpublished).

3. In the years 1970–1973 and again in 1976 a site in the Hel peninsula, close to the summer resort Kuźnica in forest section 12 H n, populated by *Vitrina pellucida* (UMIŃSKI, FOCHT 1979) was investigated.

4. In 1976 2 sites in the Beskidy Mts., near the mountain resort Krynica (49°26'N, 20°54'E, elevation 1000 m ±10 m), populated by *Vitrina pellucida, Semilimax kotulai* and *Eucobresia nivalis* (UMIŃSKI 1979) were investigated.

5. In 1976 5 sites in the forest of Sękocin, some 20 km south of Warszawa (SKRZYPCZAK, UMIŃSKI 1979) were investigated. One of them, the site in a pure *Alnus* stand, with the strongest *V. pellucida* population was investigated again in October 1977 and 4 times in 1978. In each case, 20 frames of 1/16 m² were taken.

6. In 1978 on the eastern shore of Lake Łuknajno (53°49'N, 21°41'E) an area along the shoreline was studied; it was about 70 m wide. It included a dry, grassy moraine hill, the grassy lakeward slope of that hill, an *Alnus* forest on low, flat ground and the muddy lake bottom, several meters of which were exposed in summer when the water level was low. Samples were taken with a square frame of 0.05 m² area.

Apart from the investigations listed above, data from DROZDOWSKI (1958, 1961, 1963a and b, 1966, 1968) and from DZIĘCZKOWSKI (1971, 1972, 1974) have been used. In order to compare the results obtained by different writers, using different frame sizes, mean densities per one frame were turned into densities per 1 m². The standard error of the mean densities per 1 m² computed in this way was estimated by the formula:

$$SEy = \sqrt{SEx^2 k},$$

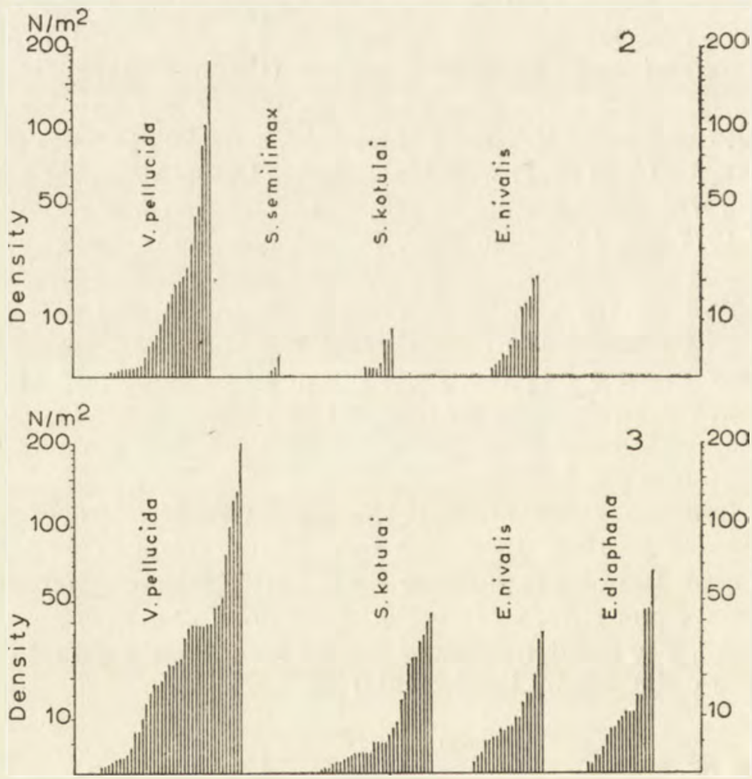
where SEy = standard error of mean density per 1 m², SEx = standard error of mean density per frame, k = reciprocal of frame area in m².

Determining the modal value of shell diameter presented some difficulty, when the sample examined was small, and measurements taken to the nearest 0.1 mm. In such cases measurements were pooled in classes 0.3 mm wide so as to find the most numerous class possible. The middle value of such most numerous class was taken as the modal value. The shell diameter considered is always the biggest shell diameter.

Since the area sampled per year never reached 1% of the total site area, it was always assumed that the disturbing effect of sampling on the habitat and the snail populations could be neglected.

DENSITY

One of the main purposes of this study was to obtain rough estimates of what the densities of vitrinid populations in Poland are. The densities noted by other authors are summarized in tables I and II. In these studies a particular value obtained was often meant to describe to some extent the site examined, to be an instantaneous picture of the local gastropod fauna. The sampling was



Figs. 2–3. Densities of *Vitrinidae*, noted in Poland. Each bar represents one result (see text). Fig. 2 — data after Drozdowski and Dzięczkowski (see Tables I and II). Fig. 3 — own data. Site at Lodowe Źródło, Tatra Mts., 980 m omitted (see Figs. 7 and 8).

Table I. Densities of *Vitrinidae* in the mountain Fagetea of Poland. Data after DZIĘCZKOWSKI 1972. Samples have been taken with a square-frame of 0.04 m² area. The standard error could not be computed exactly, if the original counts were not published

Mountain range	Sample number and site	Date of sampling	No. of frames taken	*E. nivalis* density N/m²	*E. nivalis* standard error	*E. kotulai* density N/m²	*E. kotulai* standard error	*E. semilimax* density N/m²	*E. semilimax* standard error
Pieniny Mts.	1. The right bank of the stream Pieniński Potok	9–11 Aug. 1962	50	3.5	0.3	0	—	0	—
	2. ,,	7 Aug. 1965	25	2.0	0.4	0	—	0	—
	3. Zagroń	5–6 Aug. 1962	25	6.0	0.63	1.0	0.2	0	—
	4. Zagroń by Mała Dolina	7 Aug. 1962	25	13.0	0.85–1.1	1.0	0.2	0	—
Tatra Mts.	5. The valley Dolina Strążyska	2–6 Aug. 1963	50	14.0	0.65–1.0	0	—	0	—
	6. ,,	6 Oct. 1965	25	16.0	0.85–1.1	0	—	0	—
	7. ,,	19 Aug. 1966	25	20.0	0.95–1.6	0	—	0	—
	8. "Na Grześkówkach"	6 Aug. 1963	25	6.0	0.5	2.0	0.2	0	—
	9. The valley "Ku Dziurze"	8 Aug. 1963	25	5.0	0.4	0	—	0	—
	10. The valley of the stream Biały Potok	20 Oct. 1965	25	21.0	0.85–1.2	1.0	0.2	0	—
Babia Góra	11. below the Czarna Hala	8–12 Jul. 1964	50	3.5	0.3	8.0	0.37	0.5	0.1
	12. ,,	30 Jul. 1965	50	2.5	0.25	6.0	0.4–0.55	3.0	0.3
	13. SW of the Czarna Hala	14 Jul. 1964	25	1.0	0.2	1.0	0.2	1.0	0.1
	14. banks of the stream Potok Cylów	17 Jul. 1964	25	0	—	6.0	0.5–0.65	0	—

Table II. Density of *Vitrina pellucida* in Poland

Locality	Site	Date of sampling	Frame area m²	Density N/m²	Standard error	Source
Wierzchlas	1. *Impatiens* – *Carex*	29 Oct. 1955	0.25	0.5	0.25	Drozdowski 1958
	2. *Mercurialis*	,,	,,	5.0	1.4	
	3. *Oxalis* – *Majanthemum*	,,	,,	1.8	0.56	
Płutowo	1. Forested gorge, in litter	not precised	0.25	31.8	5.2	Drozdowski 1961
	2. Forested gorge, in moss	1954	,,	47.6	8.3	
	3. Grassy hillside	1959	,,	20.0	5.6	
	4. Forested hillside		,,	89.0	10.3	
	5. Meadow, at the foot of 3		,,	114.4	27.4	
	6. Meadow, at the foot of 4		,,	16.8	4.3	
	7. Fallow land "A"		,,	178.0	34.8	
	8. Fallow land "B"		,,	1.0	0.5	
	9. Rye field		,,	0.8	0.4	
	10. Alfalfa field		,,	7.2	1.5	
	11. Pasture		,,	21.2	5.4	
Bąsak	Young *Alnus* stand	Jul.–Aug. 1957–1958	,,	43.6	2.9	Drozdowski 1963a
Folusz	Steppe vegetation	May and Aug. 1962	,,	11.8	1.0	Drozdowski 1963b
Island on the Lake Klasztorne	*Ulmus* forest with *Acer*	not given	,,	23.6	3.0	Drozdowski 1966
Luszkowo	1. Forested gorge	summer 1963	,,	9.3	1.8	Drozdowski 1968
	2. Dry hillside steppe vegetation	summer 1964	,,	18.4	3.0	
Świnia Góra	1. Dentario glandulosae Fagetum with *Abies alba*	Aug. 1961	0.04	1.5	–	Dzięczkowski 1971
	2. with *Allium ursinum*	May 1966	,,	14.0	–	

Table II. (Continuation)

Locality	Site	Date of sampling	Frame area m²	Density N/m²	Standard error	Source
Ojców	1. Fagetum carpaticum	15–18 Aug. 1962	0.04	0.5	0.1	Dzięczkowski 1972
	2. Fagetum carpaticum with *Majanthemum bifolium*	3 Jun.	,,	1.0	0.2	
Morasko		17 Jun. 1966	,,	1.0	0.2	Dzięczkowski 1974
	Galio-Carpinetum	16 Oct. 1966	,,	1.0	0.2	
		29 Jun. 1969	,,	3.0	0.45	
		5 Oct. 1969	,,	6.0	0.65	

often done at different times of the year; sometimes the exact date was lacking; sometimes the published value gave the pooled results of sampling in two consecutive years.

My data result from sampling the same site 4–5 times a year. The densities observed on different occasions were usually widely divergent. In assessing the range of actual densities I think it permissible to regard each of my samplings as a separate result. Hence, from some sites I got a dozen results or so, while in the published data each site is usually described by one value only. All the existing estimates of vitrinid densities in Poland are summarized in Fig. 2 (data by other authors), and in Fig. 3 (my own data). In Fig. 3 the data from Lodowe Źródło, Tatra Mts., 980 m were omitted. The densities noted there are higher than the top values at any other site by one order of magnitude and they no doubt represent a separate problem. The data on the densities of *V. pellucida* and of *S. kotulai* for this site are given in Figs. 7 and 8. A comparison of my results with those obtained by other authors shows a conspicuous difference as regards *S. kotulai* and *E. nivalis*. I have got much more results and have noted much higher densities. This is due to a different way of selecting the sites examined. My sites have been selected after a search for strong and stable vitrinid populations. All the other data for these two species come from Dzięczkowski (1972). His study was aimed at a quantitative analysis of gastropod fauna of mountain Fagetea, and the sites were selected without paying any particular attention to *Vitrinidae*. For *Eucobresia diaphana* the only existing results are mine as nobody has done any quantitative research in the area of the species. On *Semilimax semilimax* the only data available are from Dzięczkowski (1972). On my sites, sampled quantitatively, this species was absent.

When comparing Figs. 2 and 3 a marked resemblance can be noted between the two distributions of the densities noted for *E. nivalis* and the distribution of the densities of *E. diaphana*. This is quite remarkable, as these data come from different areas and different writers. In the genus *Eucobresia* very low densities, viz. of 2 individuals per 1 m^2 or less than that were found only very rarely. The majority of the results were falling within the range of 3–15 individuals per 1 m^2. It should be borne in mind that "density" as presented here is not the actual population density, but the density of animals obtained by the procedure adopted. This "observed density" is a function of the actual population density and the level of the activity of the animals. The lack of very low observed densities in the genus *Eucobresia* could possibly result from a more even response to environmental conditions, than is the case with the other genera. Moreover, this response should be of an "all-or-nothing" nature, i.e. either a vast majority of *Eucobresia* population is active or this majority is in hiding. It follows that the actual population densities should be rather low, usually not in excess of 15 individuals per 1 m^2.

The distribution of the noted densities of *Semilimax kotulai* was just the opposite of what was observed in *Eucobresia*. The numbers were either very low or rather high. Medium values were less frequent. This kind of distribution could result if the following was true:

a) Actual population densities are higher than in the genus *Eucobresia*, attaining the levels of about 25–30 individuals per 1 m^2.

b) With the onset of unfavourable environmental conditions most animals go into hiding very quickly.

c) A small proportion of animals remain active long after the rest went into hiding.

The above interpretation is only a conjecture, and testing it would require much further research. Other regularities than those stated above cannot be ruled out.

As regards *Vitrina pellucida* my own data and the data obtained by other authors show a striking similarity. The number of results, the maximum values (exception made for the site at 980 m in Tatra Mts.), as well as the distribution of the noted densities are quite similar. This comes as no surprise since *V. pellucida* can be found throughout the country, being relatively common in a fair proportion of varied habitats. In my results these are many values in the range of 15–40 individuals per 1 m^2, making the graph bulging while in Fig. 2 there is no such bulge. This is probably due to the fact that, in contradistinction to other authors, I have repeatedly sampled my sites in autumn, when the observed vitrinid densities are the highest.

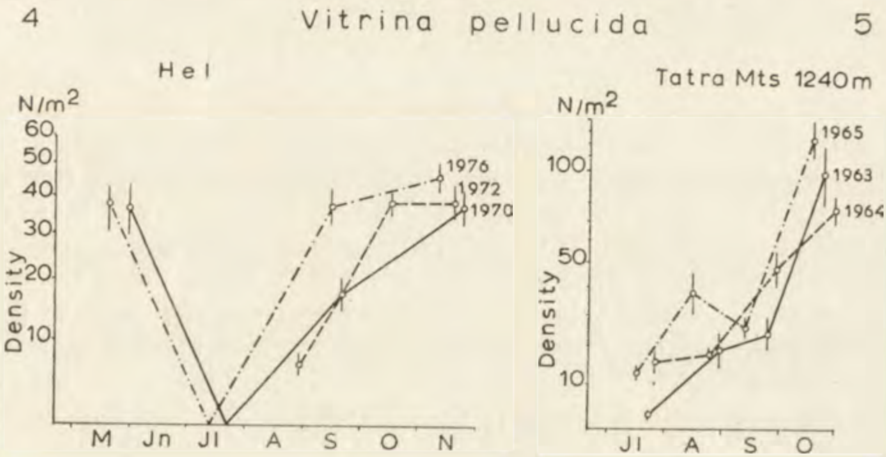
As for the vitrinid populations living in the densities of 0.5/m^2 or less, little can be said at present. Preliminary, not quantifiable results suggest the possibility of such low densities. A repeated search in the upper reaches of Hala Pyszna (Tatra Mts., elevations 1470–1790 m) resulted in 2 specimens of *S. kotu-*

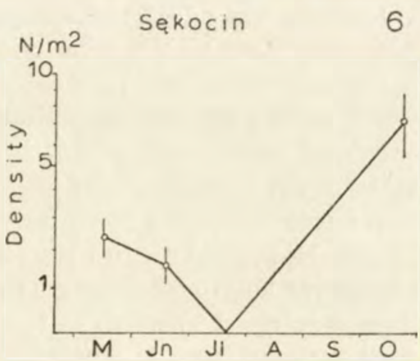
lai found during a total of 13 hours search (UMIŃSKI, unpublished). At such levels of yield per unit effort the cost of reliable density estimates would be enormous.

Yearly fluctuations in density

THE SUMMER DECLINE – *VITRINA PELLUCIDA*

The pattern of yearly fluctuations in density was particularly clear in Kuźnica in the Hel (UMIŃSKI, FOCHT 1979). The course of changes in 1970, 1972 and in 1976 was almost the same (Fig. 4). In spring the density was high. In the summer it declined, reaching zero or very low values. In the autumn the density was high again, often higher than it used to be in spring. Still, it was not the case that either the summer decline was due to mortality, or the autumn rise to natality, because *V. pellucida* live here one growing season or one year





Figs. 4–6. Seasonal changes in density in *Vitrina pellucida*. The "summer decline" type. Points show mean density per 1 m². Vertical lines show 2 standard errors on either side of the mean. Fig. 4 – Kuźnica, Hel peninsula. Life-span 1 year. Fig. 5 – Hala Pyszna, Tatra Mts., 1240 m. Life-span 2 years. Fig. 6 – Sękocin near Warszawa in 1978. Life-span 1 year.

at the most (7–12 months). The animals hatch in April or early in May; in the autumn, fully grown and mature, they oviposit and the vast majority of them die out. Single individuals happen to live as long as till the successive April. In other words, the numerous spring individuals and the numerous autumn individuals represent the very same age group (cohort) which has disappeared from the research area in the summer, to reappear in the autumn. Such a pattern can only result from migration, either horizontal or vertical. It is beyond any reasonable doubt that a horizontal migration (the snails wandering out of the site and coming back) can be ruled out. The sampling was done in an *Alnus* forest aged about 80 with rather lush under-storey and undergrowth. The same habitat extended all around for 50 m to 300 m and was surrounded by habitats entirely unsuitable for snails: bare coastal sand-dunes on one side and dry pine forest growing on old sand dunes on the three other sides. The only plausible explanation is that the snails must dig into the soil deeper than 2 cm, as the soil was searched down to that depth. The ability to dig is nothing particular among snails. In *Vitrinidae* it has not yet been reported, but I have already found myself an individual of *Eucobresia diaphana* inside a small, obviously self-made, burrow. The summer drought period has been regarded (Umiński, Focht 1979) as the environmental factor, forcing the animals to hide. This theory is in agreement with data on the rate of individual growth, i.e. with the ratio of increase in shell diameter to the time lapse (see below).

A pattern of yearly changes in density, strikingly similar to those of Hel, was found in Hala Pyszna (Tatra Mts., 1840 m). This site was sampled during the whole investigation from July through late October, hence the diagram (Fig. 5) is corresponding only to the right arm of the Hel diagram (Fig. 4). Still, the curves of all the 3 years are very similar to each other as well as to the curves obtained in Hel. It should be borne in mind that the population at Hala Pyszna has a two-year life cycle (Umiński 1975) and at any time consists of two cohorts. The summer decline means that both this-year individuals, aged 2–3 months, of 1–2 mm shell diameter (*sd*) and one-year-olds aged at least 14 months, of 3–4 mm *sd*, go into hiding simultaneously. This reaction is therefore not restricted to any particular age or developmental stage. One may conjecture that it is not controlled by any internal clock, but each time imposed upon the animals by environmental conditions. What these environmental conditions are was made open to doubt by the data of 1978 from Sękocin near Warszawa (Fig. 6). The course of events here has been almost the same as in Kuźnica, Hel or in Hala Pyszna, Tatra Mts., 1240 m. But the summer of 1978 was extremely wet, with rainfall well over long-term average, evenly distributed in time, without any trace of a summer drought period. In the studied area the groundwater-table was close to the ground level. Migration can rather safely be ruled out. The alder grove where samples were taken from is about 500 m long and 100 m wide, quite homogenous in its character throughout. The population of *V. pellucida* here must have gone into hiding in July, to emerge in the autumn.

Similarly, on the site of Lake Łuknajno in May and October 1978 *V. pellucida* was found, albeit at very low densities of 0.8–0.9/m². In July rainfall and ground-water-table were much the same as in Sękocin. No *V. pellucida* were found in 100 square frames of a total area of 5 m². The populations of Sękocin and of Lake Łuknajno are both one-year-lived as was the one of Kuźnica in Hel. Both have displayed an unquestionable summer decline under unquestionably no-drought conditions.

The agent causing the snails to hide remains to be found. In the case of *V. pellucida* one might think of high temperature. This species obviously tolerates, if not prefers outright, low temperatures. In the Tatra Mts. I have repeatedly observed in October and November fully active animals, creeping among snow patches, and even under snow cover. The data from the northern part of this species' area are discordant. LOHMANDER (1938) who drew on the collection of Ch. H. LINDROTH concluded that in Iceland *V. pellucida* is found from June through November, with the top density of the young in July, the top density of the adults in August. This conclusion is based on materials collected by a non-quantitative procedure, but I do not see any reason to doubt it is correct. According to WALDÉN (in litt.) in the north of Sweden *V. pellucida* can be found all year long. In the vicinity of Stigstuv on the Hardangervilla plateau (60°18′N, 7°41′E) SOLHØY (in print) sampled 9 times from 15 May through 14 October 1971. The lowest number of *V. pellucida* was noted on July 2nd, and none at all were found on July 26th. It was a model case of the summer decline.

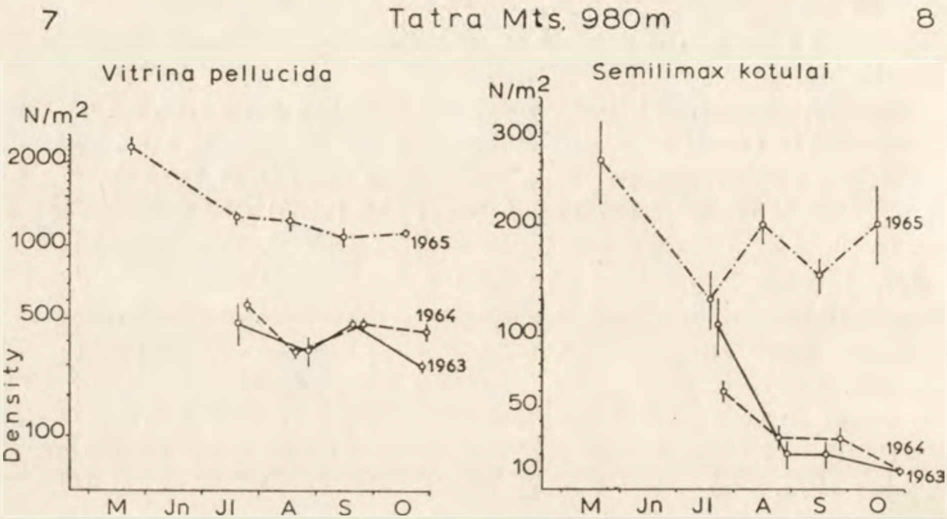
As for the causative agent, the meteorological data do not offer any easy conclusion. The first decade of July was the warmest period of this summer, and rather dry at that, but the second decade was cold with the biggest amount of rainfall this summer (SOLHØY l.c.).

THE SURVIVORSHIP CURVE – SITE AT LODOWE ŹRÓDŁO

The only site, where yearly changes in density approach theoretical expectations is the one at Lodowe Źródło (Tatra Mts., 980 m) where both *V. pellucida* and *S. kotulai* live one year, hatching in spring (UMIŃSKI 1975). Yearly changes in the density of *V. pellucida* in 1965 (Fig. 7) make up a typical survivorship curve, susceptible to the classical interpretation: a steep decline (high mortality) of very young animals, and a much slower decline (lower mortality) among older ones. In 1963 and 1964 some external factors must have disturbed this pattern, but still these curves resemble the one of 1965 much more than those with a typical summer decline. On the site at Lodowe Źródło there is not only no detectable summer decline in density but neither is there any summer arrest in the rate of individual growth in *V. pellucida*.

The changes in the density of *S. kotulai* (Fig. 8) run a markedly similar course, with a high number of the young, rapidly declining in spring and early summer, contrasted with lower numbers and slower decline in late summer and autumn (the diagrams do not show that the whole population dies out rather quickly at the onset of winter).

The site at Lodowe Źródło (the name means "Ice Spring") is on the low banks of this spring in which the water-table is almost stable throughout the year. Hence the soil is always moist, the water filtering in from the main basin and from several run-off streams of the spring. Even during long spells of hot



Figs. 7–8. Seasonal changes in density. The "mortality curve" type. Site at Lodowe Źródło, Tatra Mts., 980 m. Points show mean density per 1 m². Vertical lines show 2 standard errors on either side of the mean. Notice the numbers recorded here! Fig. 7 — *Vitrina pellucida*. Fig. 8 — *Semilimax kotulai*.

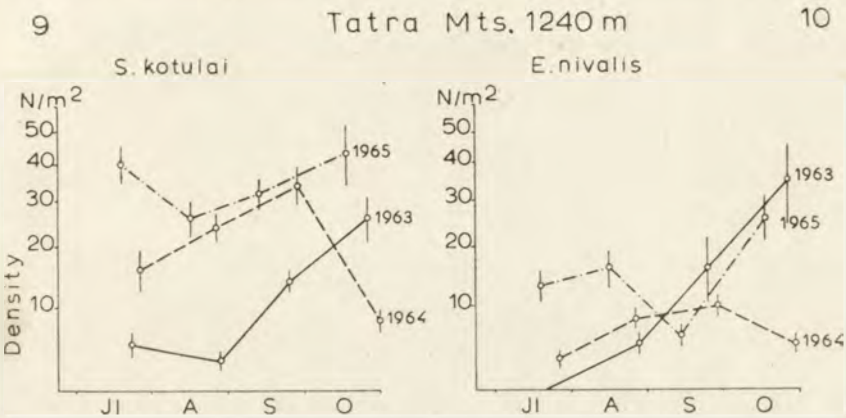
weather with no rainfall, the soil here does not dry out. On the other hand, the basin itself, even abstraction made from the streams, is a water-mass of about 60 m³ at a temperature never exceeding 7°C which obviously influences the temperatures of its closest vicinity. The vitrinids at Lodowe Źródło live in a peculiar habitat of a higher and more stable humidity and lower summer temperatures than are met with in the surrounding habitats.

OTHER MODELS

1. Hala Pyszna. In the Hala Pyszna (Tatra Mts., 1240 m) there are, besides *V. pellucida,* relatively numerous populations of *S. kotulai* and *E. nivalis.* The patterns of changes in density in these species are somewhat similar to each other and different from those in *V. pellucida* (Figs. 9, 10 and 5). A typical summer decline, almost the same in all the 3 species, has been observed in 1963. In 1964 the curves of *S. kotulai* and *E. nivalis* were very similar, with the top density late in September and a steep decline towards the end of October, completely different from that of *V. pellucida.* In 1965 the curves of these 2

species were again similar to each other, but different from those of the preceding year, and from that of *V. pellucida*. These results imply that *S. kotulai* and *E. nivalis* are much more similar to each other as regards their requirements and responses than either of them is to *V. pellucida*.

2. Siwe Sady. The data from the site at Siwe Sady (Tatra Mts., 1420 m), give the number of animals sampled during two periods of searching, of 15 minutes' duration each. This procedure has been adopted because the terrain prevented the use of a square-frame. The site was not big enough to permit more sampling without undue disturbance to the habitat and the snail population. These data (Fig. 11) enable, at most, a very rough estimate of yearly chan-



Figs. 9–10. Seasonal changes in the density in 2 vitrinid species at Hala Pyszna, Tatra Mts., 1240 m. Points show mean density per 1 m². Vertical lines show 2 standard errors on either side of the mean. Fig. 9 — *Semilimax kotulai*. Fig. 10 — *Eucobresia nivalis*.

ges in density. Here, similarly as in Hala Pyszna (Tatra Mts., 1240 m) there was no summer decline of *S. kotulai* or *E. nivalis*, or of *V. pellucida*, either.

On this site a comparison of the data of the years 1964 and 1965 is most instructive. The pattern of changes in these two years is fundamentally different. On the other hand, the changes in density of the 3 studied species within one year run a remarkably similar course. A possible interpretation: at higher elevations the direct influence of harsh climatic conditions is strong enough to suppress the subtler differences between species.

3. Krynica. 2 sites near Krynica were examined. They were both situated in a shallow gully, the bed of a periodic stream, about 30 m away from each other. In the upper site *V. pellucida* was very scarce in May, its numbers reached maximum in late August, than dropped again (Fig. 12). This species has here a life-span of one year, beginning in spring (Umiński 1979). Hence the autumn decrease in observed numbers may result from a decrease in actual numbers. On the other hand, the increase in observed numbers, particularly

that from July through August could be due merely to a higher level of activity, since it took place long after the hatching period. The observed density of *S. kotulai* was growing steadily from a minimum in May to a maximum in October. This species lives here two years (Umiński 1979), so two cohorts (age groups) are present at any time. Still, every May one cohort hatches and every winter one cohort is dying out. Also in this case the changes in observed density must be different from those of actual density. Here too, the observed density is a measure of the above-ground activity of this species. In *E. nivalis* the observed density remains fairly stable throughout most of the season. The steep rise in October results from a rise in actual density because the youngest cohort hatches in early autumn (possibly in early September).

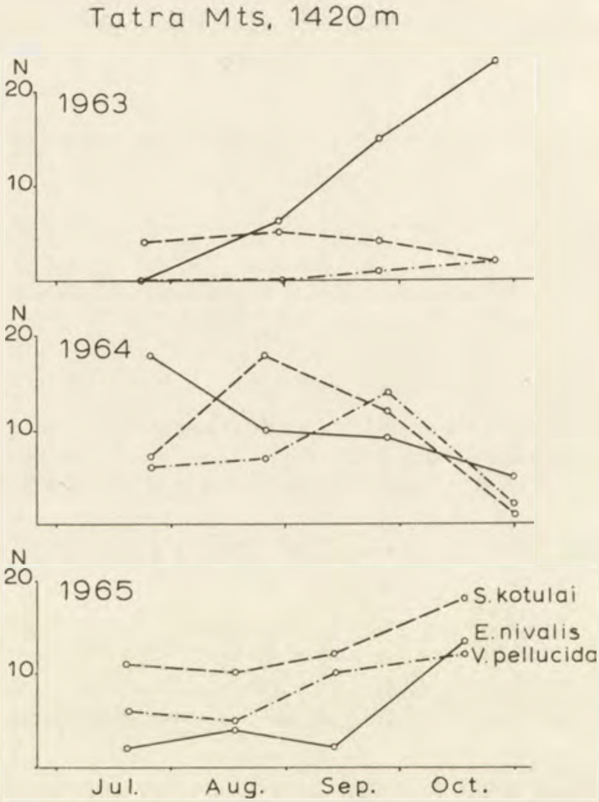
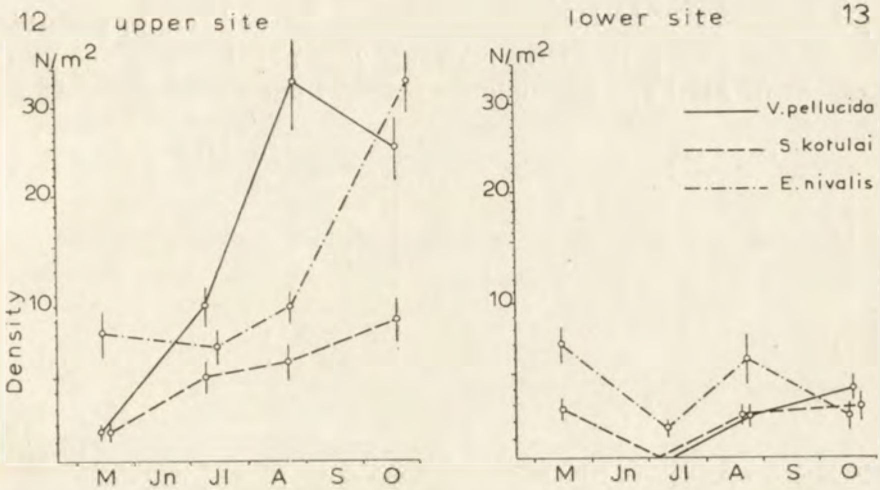


Fig. 11. Seasonal changes in the density of *Vitrinidae* at Siwe Sady, Tatra Mts., 1420 m. Points show the number of animals taken during 2 periods of 15 minutes' search.

The data from the lower site at Krynica differed from those of the upper one in many ways (Fig. 13). The level of observed density of all 3 species was much lower. The pattern of changes was different. All the 3 species displayed here a marked "July decline". Besides, from August through October the changes in numbers of *V. pellucida* and *E. nivalis* were opposite to those at the upper site. Striking differences in the density of snails between neighbouring sites are common knowledge. The two sites at Krynica provide evidence that even the observed pattern of density changes can differ much on adjacent sites with no detectable differences in habitat.

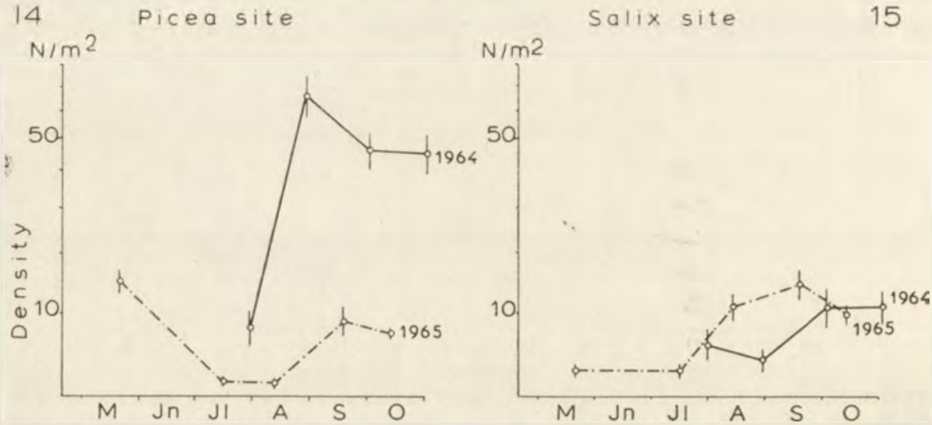


Figs. 12–13. Seasonal changes in the density of *Vitrinidae* on two sites (elevation 1000 m) near Krynica, Beskidy Mts. Points show mean density per 1 m². Vertical lines show 2 standard errors on either side of the mean. The life-span of *Vitrina pellucida* was 1 year, of *Semilimax kotulai* — 2 years, of *Eucobresia nivalis* — 3 years. Fig. 12 — upper site. Fig. 13 — lower site.

4. Śnieżnik Kłodzki. Of *S. kotulai* single individuals were found occasionally; they do not warrant any conclusions as to density changes. *Eucobresia diaphana* was more numerous by a factor of 20. Similarly as in the Krynica case, marked differences between the two sites have been found. On the *Picea* site (Fig. 14) the pattern of density changes closely resembles the model with a July decline, high density in spring and particularly high in autumn. The material was not rich enough to assess the slight decline in late autumn. The decline from August through September 1964 was significant at 5% level, but that of October 1965 was not. On these sites *E. diaphana* live 2 years, hatching in June and dying out late in the autumn of the following year (Umiński, unpublished). Hence two cohorts are always present in *E. diaphana* population. The observed autumn decline can not be due to the dying out of the older cohort as it occurs much too early. At the *Salix* site the changes in apparent density have not been very orderly (Fig. 15). Still, in both years the density was rather low in July, i.e. just after hatching of the this-year cohort. In both years the density in September and October was rather high. The pattern of changes on these two sites resembled to some extent the model with a July decline, but there were marked differences between sites. These were presumably due to the influence of microclimatic and microhabitat factors.

Individual rate of growth

The rate of growth of individual animals measured as ratio of shell diameter (*sd*) increment to the time lapse, was regarded as a possible measure of the animals' well-being and, indirectly, of judging whether or not the ambient conditions are favourable. For this kind of consideration, the data on *V. pellucida* from Kuźnica in Hel were particularly relevant. This population is one-year-lived, hence except in April every sample consisted of one cohort only. All animals



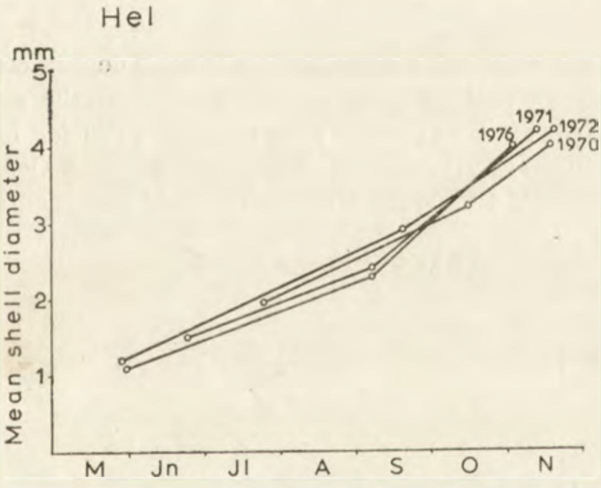
Figs. 14–15. Seasonal changes in the density of *Eucobresia diaphana* on two sites at Mt. Śnieżnik Kłodzki, 1180 m. Points show mean density per 1 m². Vertical lines show 2 standard errors on either side of the mean. Fig. 14 — the "*Picea* site". Fig. 15 — the "*Salix* site".

here grew at a similar rate, without significant accelerations or retardations. In all samples the differences in *sd* between the biggest and the smallest specimens were small and *sd* distribution usually close to normal (Umiński, Focht 1979, Fig. 2[1]). Any skewness of distribution was small and found solely in November samples; only in these samples modal and median *sd* values were higher than the mean (Table III). Mean *sd* values make a very impressive picture (Fig. 16) as the curves for 4 years of study are strikingly similar. *V. pellucida* in Hel grow rather slowly from spring through September. Then the curves rise rapidly; in late autumn the snails grow much faster. Because in July live specimens have been sampled only once, it is not known whether the rate of growth does change at this time and to what extent. The low initial rate of growth has been regarded (Umiński, Focht 1979) as related to the summer decline in apparent density and both have been attributed to the summer drought period. It was presumed that the animals, when in hiding, stopped all activity, something which resulted also in the retardation of growth. The

[1] The graph showing live *V. pellucida* of May, 1976 was erroneously placed 1 mm high.

Table III. Shell diameter of *Vitrina pellucida* from Hel peninsula. Data from Umiński and Focht (1979). See also Fig. 16

Year	Date	Mean mm	Standard deviation	Standard error	Median value	Modal value	No. of individuals
1970	25 Jul.	1.95	0.16	0.037	2.0	2.0	19
	15 Oct.	3.2	0.42	0.067	3.2	3.2	39
	18 Nov.	4.0	0.42	0.063	4.1	4.1	44
1971	23 Jun.	1.5	0.18	0.013	1.5	1.4	198
	7 Sep.	2.4	0.30	0.042	2.5	2.4	51
	13 Nov.	4.2	0.45	0.039	4.3	4.4	132
1972	29 May	1.2	0.21	0.034	1.2	1.2	37
	20 Sep.	2.9	0.34	0.082	2.9	2.9	17
	20 Nov.	4.2	0.38	0.063	4.3	4.5	36
1976	31 May	1.1	0.13	0.021	1.2	1.2	38
	7 Sep.	2.3	0.36	0.058	2.4	2.3	39
	3 Nov.	4.0	0.34	0.050	4.1	4.1	47



Figs. 16. Growth rate of *Vitrina pellucida* individuals at Kuźnica in Hel. Points show mean shell diameter for all animals collected at a given time. For the sake of clarity, statistical characteristics were omitted (see Table III).

main evidence in favour of this claim is inherent in the data from the site at Lodowe Źródło, Tatra Mts., 980 m (Table IV, Fig. 17). The rate of growth there from July through August was high. On this site there was no summer decline in density and no retardation of growth either, something which could imply some interrelation of both phenomena. The curves of growth, obtained at Lodowe Źródło are shifted in time in comparison to those from Kuźnica in Hel. In Hel the period of rapid growth was only beginning in September. At the Lodowe Źródło by the end of September — early October the snails have already

Table IV. Shell diameter of *Vitrina pellucida* from the Tatra Mts., site at Lodowe Źródło, elevation 980 m. Data from Umiński (1975). See also Fig. 17

Year	Date	Mean mm	Standard deviation	Standard error	Median value	Modal value	No. of individuals
1963	21 Jul.	2.5	0.38	0.028	2.5	2.5	178
	27 Aug.	3.7	0.74	0.087	3.6	3.4	72
	23 Sep.	4.6	0.73	0.104	4.8	4.9	49
	24 Oct.	4.6	0.74	0.133	4.6	4.8	31
	25 Nov.	4.2	0.75	0.265	4.3	4.3	8
1964	25 Jul.	2.7	0.37	0.046	2.8	2.9	63
	25 Aug.	3.6	0.52	0.087	3.6	3.6	36
	26 Sep.	4.3	0.63	0.060	4.4	4.4	110
	29 Oct.	4.4	0.70	0.097	4.5	4.5	52
1965	22 May	1.25	0.11	0.007	1.3	1.25	213
	18 Jul.	2.0	0.28	0.025	2.0	2.1	121
	15 Aug.	2.6	0.42	0.038	2.6	2.6	117
	13 Sep.	3.4	0.65	0.063	3.4	3.4	107
	16 Oct.	4.2	0.93	0.092	4.5	4.5	103

had attained maximum size and stopped growing. The curve of 1965, the only one covering May as well, is progressively steeper in the successive sections up to September. A similar curve of growth of *V. pellucida* has been obtained near Krynica (Umiński 1979, Fig. 2). From May through October 1976 during 3 consecutive periods of 1.6 month each the mean *sd* increments were 40 %, 71 %

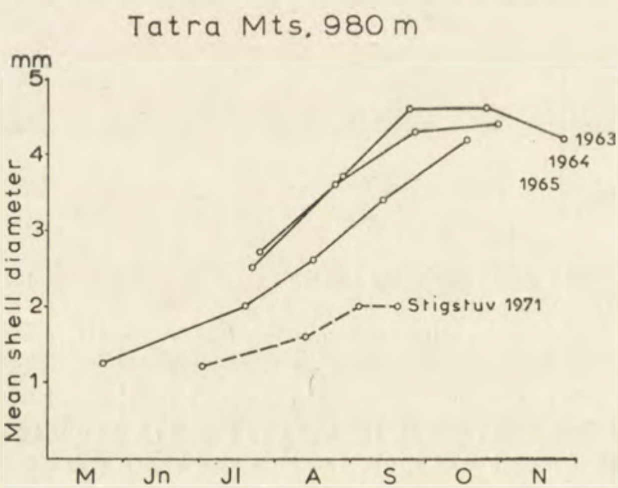


Fig. 17. Growth rate of *Vitrina pellucida* individuals at Lodowe Źródło, Tatra Mts., 980 m. Points show mean shell diameter for all animals collected at a given time. For the sake of clarity, statistical characteristics were omitted (see Table IV). For comparison the growth rate of the youngest cohort of 1971 at Stigstuv is shown here, too (broken line; data from Solhøy).

and 100% of the initial value, respectively. Very interesting in this context are the already quoted results of SOLHØY which come from Stigstuv. The vegetational period is very short; it lasts from late May through middle September. The curve in Fig. 17 gives data on the youngest cohort, hatched this year (it was the most numerous and the only clearly discernible one). Even there it was plainly visible that older and bigger animals grow faster, in spite of their displaying but a small difference in age and size. The arrest of their growth at 2.0 mm *sd* in September may have indicated the beginning of hibernation, although it is not clear what factor could bring it about. Mean daily temperatures at that time have still been within the range of 5–9°C which is not bad for this area. From June through August mean daily temperatures fall mostly in the range of 6–13 °C (SOLHØY l.c.).

As for *V. pellucida,* there is little doubt that the rate of growth increases with age and size, that the bigger they are the faster they grow, until they are close to the final size. As for the rate of growth of *Eucobresia nivalis* some data were obtained near Krynica (UMIŃSKI 1979, Fig. 2). The snails live there three years, so in every sample 2 or 3 cohorts have been represented, but these could be discerned and separated. The rate of growth of this-year young, hatched probably in early September, could not be determined. One year-olds grew in spring, did not grow in summer and grew again in autumn. In their third year the animals still grew in spring, in July they attained the final size and stopped growing. It should be noted that in the second year of life the rate of growth in autumn is higher than it was in spring. This is in accord with the rule for *V. pellucida* that the bigger the snail is, the faster it grows. After their second winter, in spring, the rate of growth is lower than it was in autumn. The three known periods, when *E. nivalis* grow look in the diagram as if they were sections of the curve for *V. pellucida* (Fig. 17) cut by the second summer and the second winter of their life. The slow growth of one-year-olds in spring would correspond to the initial slow growth in *V. pellucida*. The highest rate of growth – of one-year-olds in autumn – would correspond to the steepest part of the curve for *V. pellucida*. Finally, the slow growth of two-year-olds in spring corresponds to the time when *V. pellucida* gradually stop growing while being close to the final size.

Summary

1. Apparent densities in *Vitrinidae* in Poland usually do not exceed:

	individuals/m²
Vitrina pellucida	40
Semilimax kotulai	25
Eucobresia nivalis	15
Eucobresia diaphana	15

Reliable data on *Semilimax semilimax* are still not available.

2. Yearly changes in density can follow different patterns, but one which is common is with a July decline to values close to zero. Very low densities were sometimes noted at other seasons. All these declines apply to apparent density, not to the actual density, and are the result of the animals hiding, not of their mortality. There is some evidence that the snails hide from drought, although the results obtained in Sękocin near Warszawa and near the Lake Łuknajno seem to contradict this. During the July decline in density the animals' growth is largely or completely arrested.

3. On the site at Lodowe Źródło, Tatra Mts., 980 m the environmental conditions are particularly favourable for *V. pellucida* and *S. kotulai*. This results in: (a) Densities higher by an order of magnitude than the highest densities observed anywhere else. (b) Seasonal changes in density approximating a typical invertebrate mortality curve. The conclusion is that what is observed here is the actual density, and its decline is due to mortality, not to the animals hiding. The animals grow here rather rapidly.

4. *S. kotulai* and *E. nivalis* in their environmental requirements and responses are much more similar to each other than either of them is to *V. pellucida*.

5. The rate of growth of *V. pellucida* individuals changes according to a sigmoid curve: young and small animals grow slowly, the rate of growth increasing with the animals' size. When the animals are close to their final dimensions, they gradually stop growing. In a population of *E. nivalis* with a 3 years' life-span growth follows the same course, but there is no growth at all during winter and summer. The growth curve is sigmoid too, but divided into separate spring and autumn sections.

6. As far as *Vitrinidae* are concerned, a single sampling, however extensive, gives no ground to assess their numbers. To get reliable estimates 4–6 samplings, evenly spaced throughout the vegetational period, are needed. A preliminary minimum would be 3 samplings in spring, in July and in autumn.

7. The concept of a "species-age pyramid" (Dzięczkowski 1972) is not applicable to vitrinid populations with one-year life-span. Every population of that sort sampled in spring and presented in this way would prove to be a young, growing population. The same population sampled in autumn would seem to be an old population, declining and dying out.

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STRESZCZENIE

[Tytuł: *Vitrinidae* (*Mollusca, Gastropoda*) Polski. Gęstość populacji i zagadnienia pokrewne]

Na podstawie bogatego materiału zebranego na 14 stanowiskach w Polsce, zarówno w górach, jak i na nizinach, autor omawia 5 gatunków z rodziny *Vitrinidae*: *Vitrina pellucida* (O. F. MÜLLER), *Semilimax semilimax* (FÉRUSSAC), *S. kotulai* (WESTERLUND), *Eucobresia nivalis* (DUMONT et MORTILLET), *Eucobresia diaphana* (DRAPARNAUD). Badana była gęstość populacji, zmiany liczebności w ciągu roku i tempo wzrostu osobników. Wyniki można streścić, jak następuje:

1. Zagęszczenia obserwowane krajowych *Vitrinidae* nie przekraczają zazwyczaj: *Vitrina pellucida* — 40 osobników/m^2, *Semilimax kotulai* — 25 osobników/m^2, *Eucobresia nivalis* — 15 osobników/m^2, *Eucobresia diaphana* — 15 osobników/m^2. Dla *Semilimax semilimax* istniejące dane są jeszcze zbyt skąpe.

2. Sezonowe zmiany liczebności mogą przebiegać rozmaicie, ale szeroko rozpowszechniony jest model z lipcowym spadkiem do zera lub prawie do zera. Niekiedy obserwuje się wielkie spadki w innych porach roku. Tak jedne, jak i drugie, są to zawsze spadki liczebności obserwowanej, nie zaś rzeczywistej, wywołane ukrywaniem się ślimaków, nie zaś śmiertelnością. Wiele przesłanek wskazuje, że ślimaki ukrywają się przed suszą, aczkolwiek wyniki z Sękocina i znad jeziora Łuknajno z 1978 r. wydają się temu zaprzeczać. Z lipcowym spadkiem liczebności wiąże się zwolnienie tempa wzrostu ślimaków.

3. Przy Lodowym Źródle w Tatrach panują warunki szczególnie korzystne dla *Vitrina pellucida* i dla *Semilimax kotulai,* co uwidacznia się w następujących zjawiskach: a) Niezwykle wysokie zagęszczenia obydwu gatunków, o rząd wielkości przekraczających najwyższe zagęszczenia, notowane gdziekolwiek indziej. b) Sezonowe zmiany liczebności zbliżone do typowej krzywej przeżywania. Stąd wniosek, że jest to liczebność rzeczywista, a jej spadek jest wynikiem śmiertelności, nie zaś ukrywania się. Wiąże się z tym wysokie tempo wzrostu ślimaków.

4. *Semilimax kotulai* i *Eucobresia nivalis* pod względem wymagań środowiskowych i sposobu reakcji na warunki zewnętrzne są podobne do siebie nawzajem znacznie bardziej, niż którykolwiek z nich jest podobny do *Vitrina pellucida.*

5. Przebieg wzrostu osobników *Vitrina pellucida* odbywa się według krzywej esowatej: ślimaki młode i małe rosną wolno, im są większe, tym rosną szybciej. Gdy zbliżają się do ostatecznych swoich rozmiarów, tempo wzrostu stopniowo maleje do zera. Wzrost osobników *Eucobresia nivalis* w populacji o trzyletnim cyklu życiowym przebiega według tego samego schematu, ale zatrzymuje się na czas zimy i na czas lata. Krzywa jest również esowata, ale rozdzielona na osobne odcinki wiosenne i jesienne.

6. W odniesieniu do *Vitrinidae* jednorazowe zebranie materiałów ilościowych nie daje podstaw do oszacowania ich liczebności. Do uzyskania wiarygodnej oceny sytuacji niezbędne jest 4–6 prób, zebranych w ciągu całego sezonu wegetacyjnego, dla wstępnej orientacji — co najmniej 3 próby, zebrane wiosną, w lipcu i jesienią.

7. W odniesieniu do jednorocznych populacji *Vitrinidae* nie można stosować „piramidy gatunkowo-wiekowej" Dzięczkowskiego (1972), gdyż każda taka populacja okazałaby się rozwijająca, gdyby próby pobrano na wiosnę, byłaby zaś wygasająca na podstawie prób z jesieni.

РЕЗЮМЕ

[Заглавие: *Vitrinidae* (*Mollusca*, *Gastropoda*) Польши. Плотность популяций и связанные с этим вопросы]

На основании богатого материала, собранного с 14 местонахождений в Польше, расположенных как в горах, так и на низменностях, автор обсуждает 5 видов из семейства *Vitrinidae*: *Vitrina pellucida* (O. F. Müller), *Semilimax semilimax* (Férussac, *S. kotulai* (Westerlund), *Eucobresia nivalis* (Dumont et Mortillet) и *Eucobresia diaphana* (Draparnaud). Была исследована плотность популяций, изменения численности на протяжении года и темп роста особей.

Redaktor pracy — prof. dr J. Nast