Vestnik zoologii, **48**(2): 137–148, 2014
DOI: 10.2478/vzoo-2014-0014

Ecology

UDC 594.1:591.157(28)

THE STUDY OF AGE-RELATED VARIABILITY OF PIGMENTATION PATTERNS OF THE SHELLS OF *DREISSENA POLYMORPHA* (BIVALVIA, DREISSENIDAE) FROM DIFFERENT PARTS OF IT'S RANGE

V. V. Pavlova

I. D. Papanin Institute for biology of inland waters Russian Academy of Sciences,
Borok, Yaroslavskaya Region, 152742 Rossija
E-mail: vera@ibiw.yaroslavl.ru

The Study of Age-Related Variability of Pigmentation Patterns of the Shells *Dreissena polymorpha* (Bivavia, Dreissenidae) from Different Parts of it's Range. Pavlova, V. V. — Traditionally, shells of *Dreissena polymorpha* Pallas, 1771 mussels are studied as a whole by the investigation of population variability of coloration. However, shell surface is divided into zones by the lines of growth delay called annual rings, and mussel shell coloration is an array of patterns in the consequent age zones. In the present paper traditional term "pattern type" is expanded by its relation to definite shell zone; pattern types change along with annual ring formation. The pattern is considered not as a holistic feature but rather a sequence of states realized during the mussel's growth. Frequencies of some pattern types showed to be age dependent. Geographic variability of pattern sequences was found. High diversity of pattern sequences' arrays observed in populations may reflect wide adaptation potential of zebra mussels.

Key words: zebra mussel, shell coloration, pattern type, age-related variability.

Изучение возрастной изменчивости окраски раковин моллюска *Dreissena polymorpha* (Bivavia, Dreissenidae) из различных частей ареала. Павлова В. В. — Традиционно при анализе популяционного разнообразия рисунка раковины моллюсков *Dreissena polymorpha* Pallas, 1771 рассматриваются как единое целое. Однако поверхность раковин разделяется на зоны годовыми кольцами (линиями задержки роста), и окраска створки моллюска представляет собой совокупность рисунков на последовательных возрастных зонах. В данной работе общепринятое понятие «тип рисунка» дополняется представлением о приуроченности его к определенной возрастной зоне, о смене типов рисунка при образовании годовой линии. Впервые рисунок рассматривается не как целостная характеристика, а в виде последовательности состояний, реализующихся в процессе роста моллюска. Выявлена возрастная зависимость частот встречаемости некоторых типов рисунка. Возрастные последовательности типов рисунка подвержены географической изменчивости. Отмеченное высокое разнообразие наборов последовательностей в популяциях может являться отражением широчайших адаптационных возможностей дрейссен.

Ключевые слова: дрейссена, окраска раковин, тип рисунка, возрастная изменчивость.

Introduction

Diversity of shell coloration was revealed for many species of both terrestrial and aquatic mollusks. However, dreissenids are the only freshwater mussels which have strikingly variable pigmentation patterns.

Traditionally, description of pigmentation patterns on dreissenid shells includes the discrimination of simple elements and their combinations and evaluation of their occurrence frequencies in populations. This approach was firstly applied by G. I. Biochino for *D. polymorpha* (Biochino, 1990). This approach is used by A. A. Protasov also (Protasov, Gorpinchuk, 1997).

G. I. Biochino studied a particular shell as a uniform image. She attributed every shell in a sample to one of five coloration types according to prevalent pattern (Biochino, 1990). Opposite to that, A. A. Protasov described all characters of shell coloration including background color and elements of pattern which appear individually or in various combinations (Protasov, Gorpinchuk, 1997; Protasov, 2000). By this approach the quantity of phenotypes in population may reach 80 (Protasov, Gorpinchuk, 1997).

Dreissenids have the structures on the outer shell surface, known as "annual rings", representing the zones of growth delay. Visual analysis showed that pattern replacement occurs by the annual ring formation. This phenomenon was noted earlier (Marsden et al., 1996; Protasov, Gorpinchuk, 1997), however neither of schemes described above took it into consideration (Biochino, 1990; Protasov, Gorpinchuk, 1997). Our approach operates the shell not as a whole but as a combination of successive age zones carrying certain pigmentation pattern. We suppose that pattern change during the shell's growth caused by switching of mode of mantle cells that are responsible for pigment formation; when studying pigmentation we should take into account these cells' mechanism of functioning. Such idea was applied by S. O. Sergievskiy with co-workers (1995) for investigation of pigmentation of gastropod *Littorina*. Based on this scheme we worked out our's.

The aim of the present work is to analyze the pigmentation variability of *D. polymorpha* from different parts of its range taking into account successive pattern change during the mussel growth.

Material and methods

Diversity of pigmentation pattern of zebra mussel *Dreissena polymorpha* from some water bodies in Europe and America was studied (table 1). Sampling was carried out by dredge, bottom trawl, rarely by hand. All samples were presented by the subspecies *D. polymorpha polymorpha* except for the sample from Malaya Zhemchuzhnaya Banka (northwest part of Caspian), which consisted of specimens of *D. p. polymorpha* and forms intermediate between this subspecies and *D. p. andrusovi* (Logvinenko, Starobogatov, 1968). Only the latter ones were included in the analysis under the designation «*D. p. andrusovi*».

Mussels were preserved in ethanol (96 %). In laboratory, they were anatomized, the shells were cleaned from tissues, sludge and fouling, and air dried. Only right valves were analyzed since lateral asymmetry of pigmentation is typical for zebra mussel (Protasov, Gorpinchuk, 1997).

Every shell was considered as a sequence of age zones carrying a certain pattern. One zone has one pattern type, as there is no pattern change on its area. Thus, in this paper, p a t t e r n t y p e i s t h e c h a r a c t e r s o f p i g m e n t a t i o n o f s e p a r a t e a g e z o n e o f t h e s h e l l , c a u s e d b y c h r o m a t o p h o r e ' s w o r k i n a c e r t a i n m o d e t h a t i s u n c h a n g e a b l e w i t h i n t h e w h o l e a r e a o f t h i s z o n e. The part of shell of one age carries one pattern type. The older is the mussel the more pattern types its shell has.

It was shown (Sergievskiy et al., 1995) that mussel pigmentation is determined by disposition and mode of work of chromatophore cells and pigments they produce. These investigators described seven modes of functioning of chromatophores and the same number of pigmentation variations (table 2).

Zebra mussel has six types of functioning of chromatophores: 0, 1, 2, 3 a, 3 b, 3 d. Moreover, pigmentation diversity is increased as the chromatophore cells are able to operate in different modes in different parts of mantle edge, e. g. in the upper region — alternating mode with skew synchronization, in the lower region —

T a b l e 1. Sampling sites and number of studied mussels

Т а б л и ц а 1. Места сбора проб и количество обработанного материала

Water body	Coordinates	Number of mussels
Volga River, the Rybinsk Reservoir (6 locations)*	58°25' N, 38°20' E	634
Volga River, the Gorky Reservoir (5 locations)*	57°29' N, 41°21' E	436
Lake Plescheevo	56°44' N, 38°50' E	51
The Kama Reservoir	57°56' N, 56°42' E	93
Lake Forelevoe (near Kaliningrad)	54°43' N, 20°30' E	218
Northern Dvina River	64°31' N, 40°37' E	77
The Chograi Reservoir (Kalmykia)	45°34' N, 44°18' E	78
RR–1 supply channel (Kalmykia)	46°06' N, 41°57' E	48
Lake Sharony (Kalmykia)	47°53' N, 44°50' E	83
Ahtuba River	48°41' N, 45°12' E	34
Northwest Caspian:		
Malaya Zhemchuzhnaya Banka	45°02' N, 48°18' E	240
Belinskiy Bank	45°48' N, 48°52' E	20
Danube River (Serbia)	44°50' N, 20°31' E	124
The Perućica Reservoir (Serbia)	43°58' N, 19°21' E	186
Lake Erie (USA)	41°48' N, 82°59' W	43
Lake Michigan (USA)	43°11' N, 86°26' W	98
T o t a l		2463

* Coordinates of center of water body are given.

Table 2. Mode of chromatophore cells work according to parametric system of mollusk shell pigmentation description (Sergievskiy et al., 1995) and designations of pattern types in zebra mussel (after Biochino, 1990 and Protasov, Gorpinchuk, 1997)

Таблица 2. Режимы функционирования хроматофоров согласно параметрической системе описания окраски раковин моллюсков (Сергиевский и др., 1995) и соответствующие им обозначения типов (или элементов) рисунка раковин дрейссен (по схемам: Биочино, 1990 и Протасов, Горпинчук, 1997)

Mode of chromatophore cells functioning (after Sergievskiy et al., 1995)		Shell pigmentation	Designations (after Biochino, 1990)	Designations (after Protasov, Gorpinchuk, 1997)
1) Functioning of all chromatophores in one constant mode — monochrome shell coloration		Dark coloration without pattern	OO	D_2
2) Functioning of some of chromatophores in one constant mode		Longitudinal stripes	RR	I, E
3) Functioning of chromatophores in alternating mode with periodic synthesis delay. Different types of synchronization of pigment cell work:	a) unstable synchronization;	Irregular spots	—	L
	b) single-phase synchronization;	Transversal stripes	AA	G
	c) antiphase synchronization;	“Chessboard”	Not registered in zebra mussel	
	d) skew synchronization.	Broken/zigzag lines	CC	F, H, J, K
Absence of chromatophores or their inactivity (this mode was not designated by Sergievskiy with co-authors; we use character «0»).		Depigmentation	DD	C_2

alternating mode with single-phase synchronization. Traditionally, such complex pattern of dreissenid mussels is described dividing it into simple elements. We used the same approach.

Pigmentation pattern of dreissenid shells is composed of transversal and longitudinal elements that are designated as follows:

Transversal elements (we use designations proposed by G. I. Biochino (1990), with additions):

A — regular arcuate pattern along the whole shell height (3 b type by Sergievskiy et al.,1995);

C — zigzag pattern along the whole shell height (3 d);

AC — intermediate pattern between A and C: the upper shell half carries zigzag, the lower — arcs (combination of 3 b and 3 d); variations of this element:

- ACs — regular arcs along the nearly whole shell height, curves are only on the uppermost part of the shell;
- ACi — regular arcs along the nearly whole shell height, curves are only on the lowest part of the shell;
- Ad — arcs with teeth in the middle;

D — light shell without pattern; this type was put to transversal elements conditionally (0 type).

Longitudinal elements:

R — radial lines (2 type); variations of this element:

Rd — single light radial line;

Ro — single dark radial line;

Rm — multiple thin radial lines, light and dark alternately;

F — border between different elements running longitudinally.

Pattern type is an ensemble of elements and their enumeration is the designation of pattern type.

For the description of pattern type sequences, age of mussels was determined by annual rings and mussel length distribution in a sample. Sequence of pattern types from age 0+ was revealed (fig. 1). After 3+ age change of pattern types was not registered, therefore the record was made till this age.

Data from individual shells were summarized. Frequencies of pattern types in age zones 0+, 1+, 2+, 3+ were obtained for every sample. Term “age zone …+” designates shell parts of mussels of different ages formed at this age, e. g., phrase “age zone 0+” means shells of underyearlings (0+) and shell parts before the first annual ring (age of 1 year) of older mussels. “Age zone 1+” means shell area after the first annual ring in yearlings (1+) and shell parts between the first and the second annual rings (age of 2 years) of older mussels etc.

Frequencies of different pattern types were determined both in different age zones separately and in total, summarizing data for all zones. Spearman rank correlation coefficient was used for the analysis of relation between number of pattern types and geographic latitude and between pattern type frequencies and age.

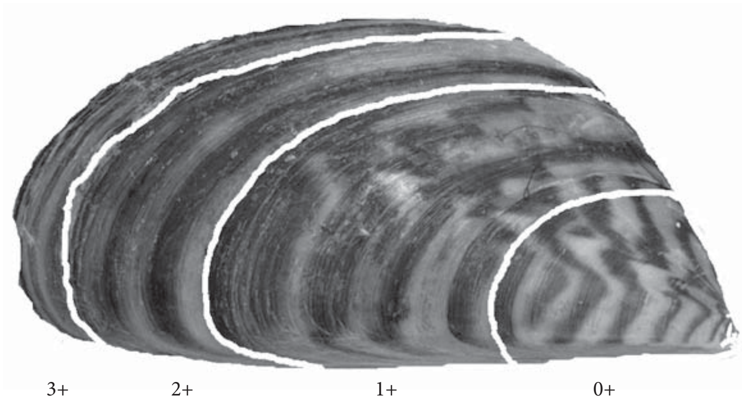

Fig. 1. Change of pattern types on zebra mussel shell.
The present shell has four age zones (0+, 1+, 2+, 3+). The pattern sequence is C–AC–A–A.

Рис. 1. Смена типов рисунка на раковине *D. polymorpha*.
Данная створка имеет четыре возрастные зоны (0+, 1+, 2+, 3+). Запись последовательности типов имеет вид C–AC–A–A.

Similarity between populations was estimated following Zhivotovskiy (1982) (r_{Zhiv} index). The significance of differences between populations was determined using χ^2 criterion (Lakin, 1980). Correlation between population similarity and geographic distances between them were estimated using Mantel test: GenAlEx 6 (Peakall, Smouse, 2006); significance level was determined using 9999 permutations.

Diversity of sequences of pattern types was estimated for whole samples, for mussels of all ages. For every population share of individuals carrying different sequences was calculated.

Results

Change of pattern type during mussel growth is typical for zebra mussel but no pattern change was revealed in 3.9 % of 2+ mussels and 0.9 % of 3+ mussels. Pattern types in adjacent age zones may be either the same or different (e.g. in shell with sequence AC–AC–A–A pattern remains the same by switch from 0+ to 1+ and from 2+ to 3+ and changes by switch from 1+ to 2+). The share of specimens with either constant or changing patterns varies between samples. On average pattern remains the same in 16.6 % of individuals by switch from 0+ to 1+, in 32.5 % of individuals by switch from 1+ to 2+, in 65.9 % of individuals by switch from 2+ to 3+. Thus, pattern types in older age zones tend to be more stable than in the younger.

Total frequencies of pattern types

In total, 16 pattern types were found in zebra mussel (fig. 2, table 3).

Pattern types C, AC, Ad, A are the main types present in all populations (all other types are secondary). Total frequency of main types varied from 73.8 to 100 % across different samples. Pattern was presented only by basic types in 6 from 26 samples (4 locations in the Rybinsk Reservoir, in Ahtuba River and in Belinskiy Bank). The maximum diversity (8–9 pattern types) in *D. p. polymorpha* was found in samples from the Kama and Chograi Reservoirs, from the Danube River and Lake Michigan. Very high variability was obtained in «*D. p. andrusovi*» from Malaya Zhemchuzhnaya Banka (MZhB) (14 pattern types).

Average within-sample pattern diversity in *D. p. polymorpha* is 6 pattern types. There is no significant correlation between number of pattern types in the sample and geographic latitude ($R = -0.37$, $p > 0.05$) (fig. 3).

Mean intersample similarity r_{Zhiv} is 0.892 ± 0.05. Minimal value was found in pair Danube River — Lake Michigan (0.441), maximal value — for two samples from the Gorkiy Reservoir (0.996). Correlation between r_{Zhiv} and geographic distance between locations is statistically significant ($R_M = -0.45$; $p = 0.002$).

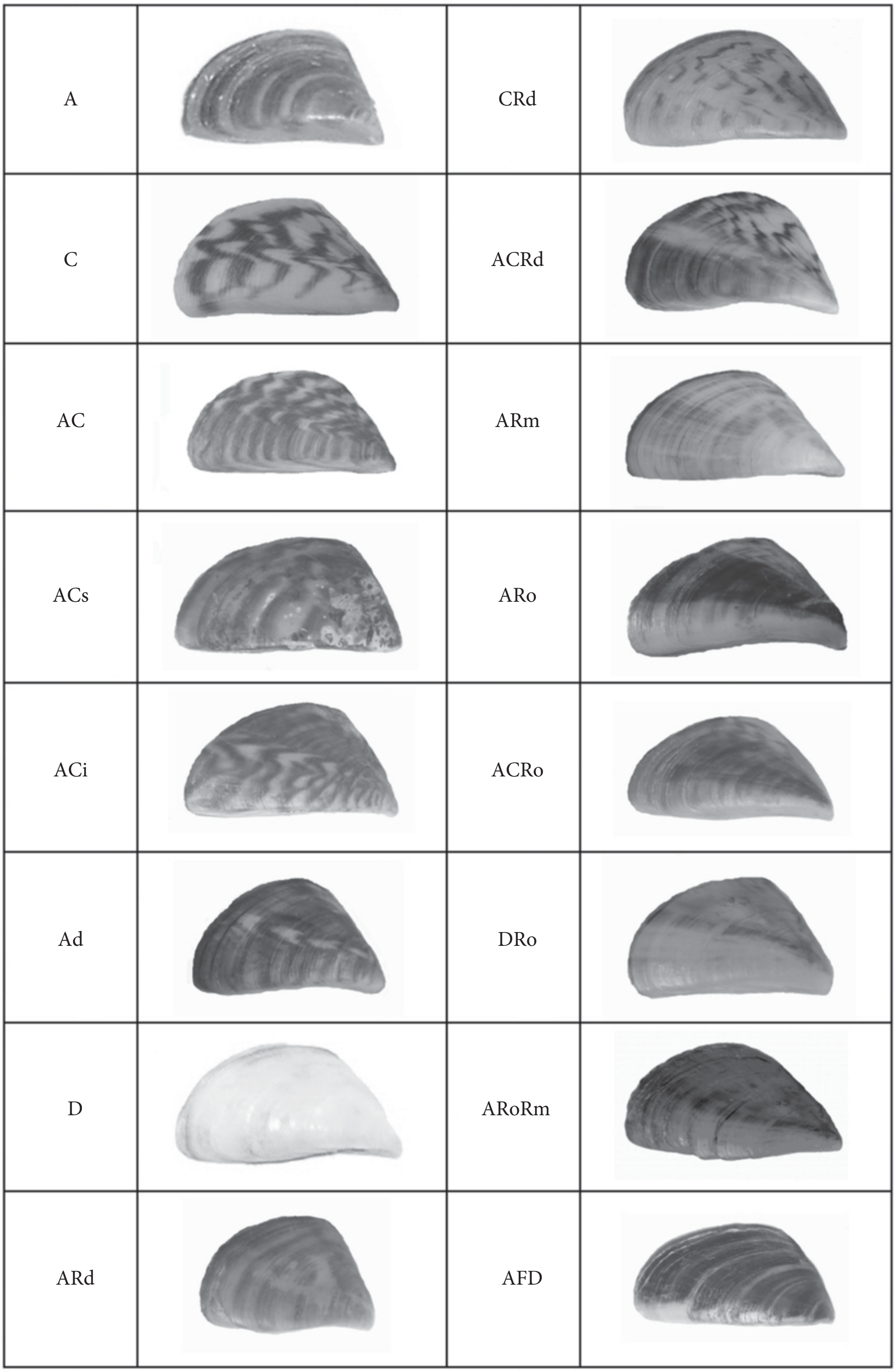

Fig. 2. Pattern types on zebra mussel shells.

Рис. 2. Типы рисунка на раковинах *D. polymorpha*.

Table 3. Frequency of occurrence of pattern types in zebra mussel populations

Таблица 3. Встречаемость типов рисунка в популяциях *D. polymorpha*

Pattern type	Frequency, N (%) of samples	Share in different samples, min–max, %
C	26 (100.0)	5.5–58.5
AC	26 (100.0)	5.2–50.0
Ad	26 (100.0)	0.5–37.6
A	26 (100.0)	0.5–67.1
ACs	16 (61.5)	0.2–5.6
ACi	13 (50.0)	0.4–5.2
D	8 (30.8)	0.5–9.1
AFD	1 (3.9)	1.3
ARd	4 (15.4)	0.5–2.5
CRd	5 (19.2)	0.3–2.4
ACRd	2 (7.7)	0.5–0.9
ARm	4 (15.4)	0.6–9.4
ACRo	1 (3.9)	0.2
DRo	1 (3.9)	2.1
ARo	3 (11.5)	1.7–1.9
ARoRm	3 (11.5)	0.2–3.5

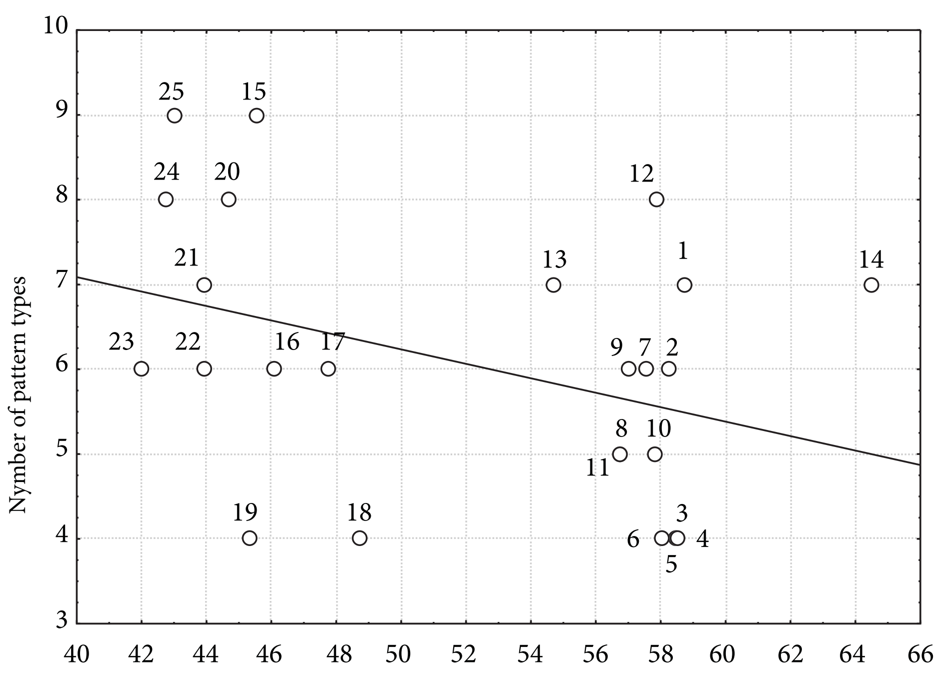

Fig. 3. Latitudinal variability of the number of pattern types. Samples: 1–6 — the Rybinsk Reservoir; 7–10 — the Gorky Reservoir; 11 — Lake Plescheevo; 12 — the Kama Reservoir; 13 — Lake Forelevoe; 14 — Northern Dvina River; 15 — the Chograi Reservoir; 16 — RR–1 channel; 17 — Lake Sharony; 18 — Ahtuba River; 19 — Belinskiy Bank; 20 — Danube River; 21, 22 — the Perućica Reservoir; 23 — Lake Erie; 24, 25 — Lake Michigan.

Рис. 3. Изменение количества типов рисунка с географической широтой. Обозначения выборок: 1–6 — Рыбинское вдхр.; 7–10 — Горьковское вдхр.; 11 — оз. Плещеево; 12 — Камское вдхр.; 13 — оз. Форелевое; 14 — р. Северная Двина; 15 — Чограйское вдхр.; 16 — канал РР–1; 17 — оз. Шароны; 18 — р. Ахтуба; 19 — Белинский банк; 20 — р. Дунай; 21, 22 — вдхр. Перучица; 23 — оз. Эри; 24, 25 — оз. Мичиган.

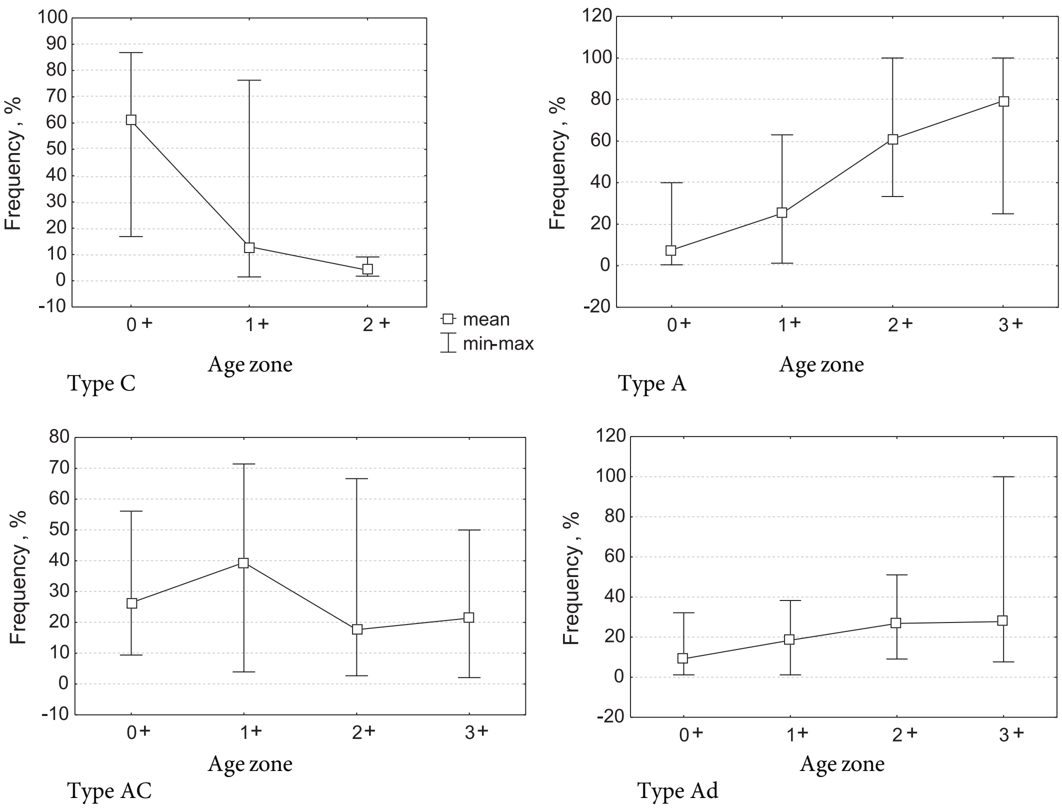

Fig. 4. Frequences of main pattern types at different age zones on zebra mussel shells.

Рис. 4. Частоты основных типов рисунка на различных возрастных зонах раковин *D. polymorpha*.

Frequencies of pattern types on different age zones

General regularities

The highest pattern diversity was revealed in early age zones, the lowest — in 3+ zone. In 0+ age zone 11 pattern types were found in *D. p. polymorpha* and 12 in «*D. p. andrusovi*»; in 1+ zone 14 and 10 pattern types, respectively; in 2+ and 3+ zones — 11 and 6 pattern types in *D. p. polymorpha* («*D. p. andrusovi*» was presented only by young mussels).

Some pattern types have been shown to be age-related. Type C is specific for early age zones, only one individual had this type in 3+ zone (fig. 4). Correlation between frequency of this type and the age is 0.83 ($p < 0.05$). The frequency of type A rises as age increases ($R = 0.83$, $p < 0.05$). Age-dependence of frequencies of types AC and Ad is weaker (R is 0.25 and 0.52, respectively, $p < 0.05$).

Regularity of age alteration of main types C, AC, Ad, A described above is basic in *D. polymorpha* and is obtained in all samples (fig. 5).

Mean intersample similarity of pattern on separate age zones decreases from 0+ to 3+ (r_{Zhiv} is 0.856 ± 0.006, 0.856 ± 0.006, 0.780 ± 0.012, 0.730 ± 0.020, respectively).

Local characteristics

Figure 5, *a* shows the most typical pattern types distribution on age zones. It is typical for all samples of *D. p. polymorpha* from the Rybinsk and the Gorkiy Reservoirs and from Lake Forelevoe, the Perućica Reservoir and the Danube River. Frequencies of secondary types did not exceed 8.9 % in these samples.

Population from Lake Plescheevo is evidently different from the Upper Volga basin samples despite of it is the source of penetration of zebra mussel in the lake (Bakanov, 1992). The most prominent difference is the frequency of type Ad on age zones from 0+ to 2+ which is the highest among all samples (it achieved 51.1 %). Occurrence of type C on age zone 0+ is one of the lowest. Similarity of populations from Lake Plescheevo on the one hand and from the Rybinsk and the Gorkiy Reservoirs on the other in 0+ varies from 0.799 до 0.934 (differences between sample from Lake Plescheevo and any sample from two reservoirs are statistically significant; χ^2 is 7.5–37.7, number of degrees of freedom is 1–2, $p < 0.05$). However, the similarity of mussel samples from different locations in two reservoirs is 0.894–1.000. Upper Volga populations show more likeness to geographically distant populations from Lake Forelevoe and the Kama Reservoir (r_{Zhiv} is 0.939–0.994 and 0.881–0.950, correspondingly) than to populations from nearby Lake Plescheevo.

Sample from the Northern Dvina River is the only where type C is prevalent not only

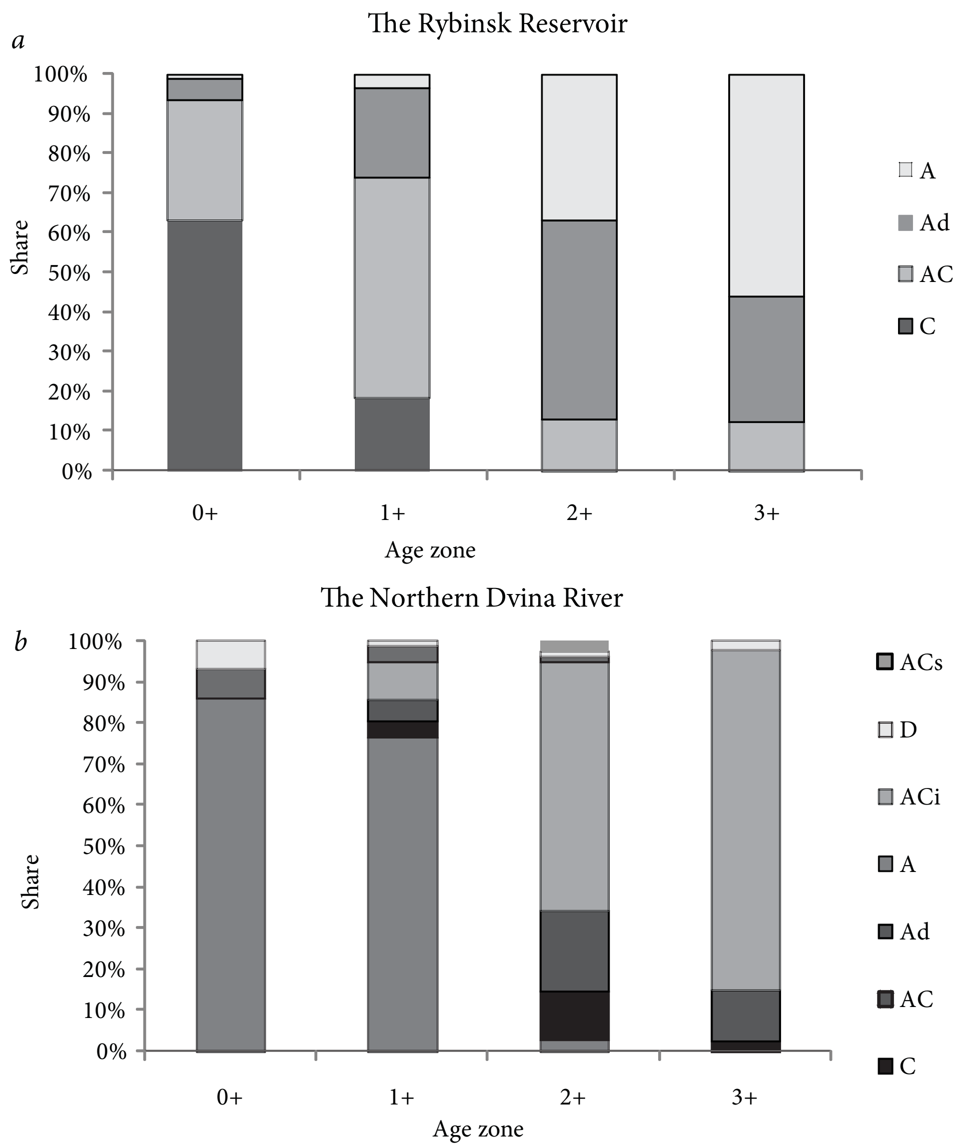

Fig. 5. Examples of fluctuation of pattern type frequencies in zebra mussel populations.

Рис. 5. Распределение частот типов рисунка в популяциях *D. polymorpha*.

in 0+, but also in 1+ (85.7 and 76.3 %, correspondingly) (fig. 5, *b*).

High frequency of type A in early age zones is typical for many populations (Belinskiy Bank, MZhB, RR–1 channel, the Chograi and Kama Reservoirs, Lakes Erie and Michigan). It rises 40 % in 0+ (Lake Erie), in 1+ varies from 31.1 to 63.0 %, on older shell zones is 72.1–100 %. In the samples mentioned low frequency of type AC is characteristic as well; it does not exceed 33.3 % at different ages. The portion of secondary types is high, it reaches 18–20 % (in samples from RR–1 channel and the Chograi Reservoir). In the population of «*D. p. andrusovi*» (MZhB) total frequency of secondary types is 31.9 % in 0+ and 20.2 % in 1+. Unique types ACRo and DRo were found in this population.

Specific feature of samples from Lake Sharony and the Ahtuba River is a high share of type AC. Unlike other samples, this type is frequent in not only 0+ and 1+ age zones (up to 56.1 and 60.0 %), but also in 2+ and 3+ (up to 66.7 и 50.0 %).

Thus, the differences between zebra mussel populations are manifested in changes of frequencies of main types C, AC, Ad and A with the age. The secondary types show weak age dependence.

Age-related sequences of pattern change

Pattern types substitute each other during the zebra mussel growth. Change of pattern types is not chaotic. Usually the pattern changes from zigzag to arched as mussel grows. Figuratively, lines of pattern "are straightened" (fig. 1). As the sequence of types it is encoded as C–AC–Ad–A. Some stages in this row may be absent, while others may be repeated, but the general order of types change from zigzag to arch is always present. Inverted order is extremely rare and may be considered an aberration. The pattern type A may be considered as "final": this pattern does not change after its realization. Some shells carrying this type from 0+ and during the whole ontogenesis were found.

The diversity of pattern types determines the variety of sequences in population. For example, the greatest variety of sequences (25 at age 1+) was revealed in the sample of "*D. p. andrusovi*", in which the number of pattern types is the greatest. In *D. p. polymorpha* samples number of sequences do not exceed 13; it is 6–8 in those ones where only main pattern types were revealed.

The array of sequences in population consists of a big amount of rows among which one or two are dominant (fig. 6).

Comparison of sequences arrays has shown that the most similar were populations from the Rybinsk, Gorkiy, Kama and Perućica Reservoirs, from Lake Forelevoe and Danube

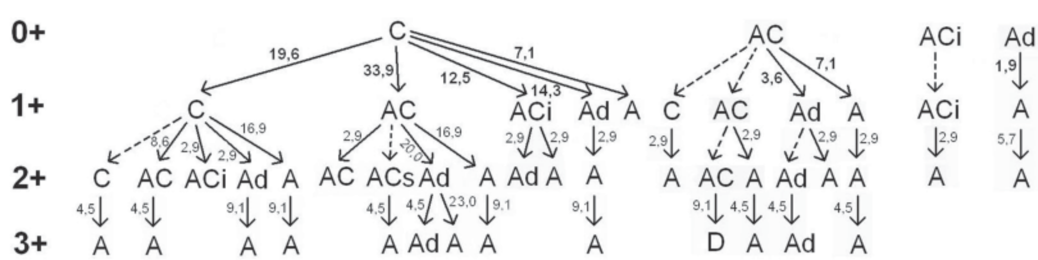

Fig. 6. Scheme of pattern change in zebra mussel population (by the example of the Perućica Reservoir). Data for mussels of ages from 1+ to 3+ are aggregated.

Numbers denote the percentage of individuals possessing the given sequence at the given age. Dotted lines denote the pattern change not revealed in the mussels of current age but revealed in older ones.

Рис. 6. Последовательности смены рисунка в популяции *D. polymorpha* (на примере вдхр. Перучица). Объединённая схема для моллюсков возрастов 1+ – 3+.

Цифрами обозначены частоты встречаемости особей (в процентах), у которых отмечена данная последовательность в данном возрасте. Пунктиром обозначены переходы, не отмеченные в текущем возрасте, но выявленные у моллюсков старших возрастов.

Table 4. Sequences of pattern types for zebra mussel populations

Таблица 4. Последовательности смены типов рисунка в популяциях *D. polymorpha*

Water body	Main sequences	Secondary sequences
The Rybinsk Reservoir	C–AC–Ad C–AC–A–A	C–C–AC–A AC–AC–Ad–A AC–A–A–A
The Gorky Reservoir	C–AC–Ad C–AC–A–A	AC–A–A C–Ad–A AC–Ad–A
The Kama Reservoir	– « –	C–Ad–A
Lake Forelevoe	– « –	AC–Ad–Ad AC–A–A C–AC–AC–Ad
Northern Dvina River	C–C–A–A	C–C–Ad–A C–C–Ad–Ad
Lake Sharony	C–AC AC–A AC–AC	AC–Ad C–A
The Chograi Reservoir	C–Ad C–AC C–A	AC–A Ad–A
RR–1 channel	C–A C–AC–A	AC–Ad
Ahtuba River	C–A C–AC–AC	AC–AC–AC
Malaya Zhemchuzhnaya Banka, *"D. p. andrusovi"*	Ad–A D–ARm C–A AC–A	AC–A C–A ARd–A DRo–A ARo–AC
Belinskiy Bank	C–A	C–AC–A C–Ad–A
Danube River, the Perućica Reservoir	C–AC C–AC–Ad–A C–AC–A–A	C–Ad
Lake Erie Lake Michigan	?–A–A–A ?–Ad–A–A	

Note. «?» means damaged shell zones where no pattern can be recognized.

River. They are different only in secondary frequencies (table 4).

The specific feature of the Northern Dvina population is the predominance of C–C sequence when 0+ is changed by 1+.

Pattern types change C–A is typical by the switch from 0+ to 1+ for south water bodies. The highest frequency of this sequence is found in samples from the Ahtuba River and Belinskiy Bank. It was also noted in MZhB, Chograi Reservoir, Lake Sharony and RR–1 channel.

The set of sequences in «*D. p. andrusovi*» is specific, it includes unique rows D–Arm, ARd–A, DRo–A and ARo–AC.

Main sequences of pattern types in North American samples of zebra mussel were failed to be obtained since upper pigmented layer of the shells was eroded on anterior shell part in many individuals. Nevertheless it was noted that the most frequent sequences beginning from 1+ age zone are A–A–A and Ad–A–A, and that is similar to populations from the South Volga basin.

Therefore, fast "straightening" of pattern lines (from C to A in 1+ age zone, without intermediate stages) occurs in southern zebra mussel populations from the Volga River basin; "straightening" is slower in northern ones (through intermediate types AC and Ad in 1+ – 2+ age zones); in the most northern sample (the Northern Dvina River) type C is obtained during the longest period and "straightening" begins from 2+ zone.

Discussion

Mussel shell pigmentation is determined by the operation of mantle chromatophore cells. Pattern appears as a result of functioning of these cells in a certain mode (Sergievskiy et al., 1995; Boettiger et al., 2009). Factors that induce growth delay (slowdown of shell secretion by mantle cells) may also affect pigmentation-responsible cells altering mode of their functioning. Such factors are reduced or elevated temperature, spawning and others (L'vova, 1980; Allen et al., 1999; Karatayev et al., 2006).

Obviously, chromatophores' functioning is influenced by environmental conditions. Interpopulation differences in frequencies of pattern types and their sequences found in *D. polymorpha* (fig. 5, table 3) confirm it. Apparently, degree of population similarity is also determined by the intensity of gene flow between them. For example, differences in pattern types frequencies between Upper Volga reservoirs are low since constant gene exchange occurring between them through veligers. Population from nearby Lake Plescheevo possesses dissimilar pattern types frequencies, that is caused by isolation (there is no stable interconnection between Upper Volga populations and one from Lake Plescheevo).

It was noted earlier that pattern variability in zebra mussel is geographic-related (Biochino, 1994; Protasov, 2000). It was shown that frequency of arched pattern (type A) in southern population in Europe is higher than in northern. Our results support this and specify that it is happening due to appearance of type A on younger shell zones in southern populations. Consequently, type A is found in a larger number of mussels as it is final type. It is assumed that phenotypes are differentially adaptive to the environmental conditions (Yablokov, Larina, 1985). For example, Protasov with co-authors (1997) revealed that individuals of *D. polymorpha* with arched pattern were more resistant to hypoxia, than specimens with zigzag pattern.

Described age-relation of pattern variability in dreissenid shells allows assuming that the highest adaptability to several factors develops successively during the ontogenesis. Observed diversity reflects enormous adaptation resources of dreissenid populations: an individual is best adapted to a certain factor at a certain age. As a result, the population possesses adaptive potentials to wide range of conditions, even if they change constantly. Pattern diversity may serve as explanation for high adaptability of zebra mussel and its success as invasive species.

Despite of variability of the pattern types sequences, "straightening" of pattern lines is specific for most of mussels. The most curved lines (type C) are typical for mussels at early stages; older age zones of most of individuals carry regular arched pattern lines (type A). Probably, skew synchronization of chromatophore cells work (Sergievskiy et al., 1995) forming type C is connected with intense mussel growth. Growth rate slows with age, and possibly stabilization of chromatophores' work in a single-phase mode occurs when all cells of mantle edge switch simultaneously and arched pattern occurs.

This general regularity does not contradict the conclusion mentioned above on the variety of adaptive possibilities of populations since deviations exist. First of all, initial pattern type is not always C. Pattern type variability in age 0+ is one of the highest in populations. In some cases the initial type is A and it is also "final", and hence persists during the whole ontogenesis. Moreover, succession of transition from C to A differs in populations (table 3).

Conclusion

Totally, 16 pattern types were found in zebra mussel. The pattern variety in intermediate forms between *D. p. polymorpha* and *D. p. andrusovi* ("*D. p. andrusovi*") is more than that in *D. p. polymorpha*. General regularity of age-related pattern change was revealed: decrease of type C portion and increase of type A portion during the transition from early to older age zones. The rate of this "straightening" grows from north to south.

Author appreciates Yu. V. Gerasimov, I. A. Stolbunov, A. N. Kasyanov, D. D. Pavlov, D. E. Vekhov, E. V. Nikitenko, D. A. Guseva, I. V. Pozdeev, T. F. Nalepa, B. Mickovic for help in mussel sampling.

References

Allen, C. Y., Thompson, B. A., Ramcharan, C. W. Growth and mortality rates of the zebra mussel, Dreissena polymorpha, in the Lower Mississippi River // Can. J. Fish. Aquat. Sci. — 1999. — **56**. — P. 748–759.

Bakanov, A. I. Anthropogenic succession of the benthos of Lake Plescheevo // Factory i processy evtrofikatsii ozera Plescheevo. — Yaroslavl : Yaroslavl State Univ., 1992. — P. 105–121. — Russian : *Баканов А. И.* Антропогенная сукцессия бентоса озера Плещеево.

Biochino, G. I. Polymorphism and geographic variability of Dreissena polymorpha (Pallas) // Microevolutsiya presnovodnykh organismov : Trudy Instituta biologii vnutrennikh vod AN SSSR. — 1990. — Is. 59 (62). — P. 143–158. — Russian : *Биочино Г. И.* Полиморфизм и географическая изменчивость Dreissena polymorpha (Pallas) // Микроэволюция пресноводных организмов.

Biochino, G. I. Polymorphism and geographic variability // Dreissena Dreissena polymorpha (Pall.) (Bivalvia, Dreissenidae): sistematica, ecologiya, practicheskoe znachenie. — Moscow : Nauka, 1994. — P. 56–66. — Russian : *Биочино Г. И.* Полиморфизм и географическая изменчивость.

Boettiger, A., Ermentrout, B., Oster, G. The neural origins of shell structure and pattern in aquatic mollusks // PNAS. — 2009. — **106**. — P. 6837–6842.

Karatayev, A.Y., Burlakova, L.E., Padilla, D.K. Growth rate and longevity of D. polymorpha: a review and recommendation for future study // J. Shellfish research. — 2006. — **25**, N 1. — P. 23–32.

Lakin, G. F. Biometry. — Moscow : Vysshaya shkola, 1980. — 293 p. — Russian : *Лакин Г. Ф.* Биометрия.

Logvinenko, B. M., Starobogatov, Ya. I. Type Mollusca // Atlas bespozvonochnykh Kaspiyskogo morya. — Moscow : Pischevaya promyshlennost, 1968. — P. 308–385. — Russian : *Логвиненко Б. М., Старобогатов Я. И.* Тип Mollusca // Атлас беспозвоночных Каспийского моря.

L'vova, A. A. Ecology of zebra mussel (Dreissena polymorpha polymorpha (Pall.)) // Bentos Uchinskogo vodokhranilischa. — Moscow : Nauka, 1980. — P. 101–119. — Russian : *Львова А. А.* Экология дрейссены (Dreissena polymorpha polymorpha (Pall.)).

Marsden, J. E., Spidle, A., May, B. Review of genetic studies of Dreissena spp. // Amer. Zool. — 1996. — **36**. — P. 259–270.

Peakall, R., Smouse, P. E. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research // Molecular Ecology Notes. — 2006. — **6**. — P. 288–295.

Protasov, A. A. The variability of pigmentation pattern, shell sculpture and shape of Dreissena polymorpha in European and North American parts of modern range // Vestnik zoologii. — 2000. — **34**, N 6. — P. 57–64. — Russian : *Протасов А. А.* Изменчивость признаков рисунка, скульптуры и формы раковин Dreissena polymorpha в европейской и североамериканской частях современного ареала.

Protasov, A. A., Gorpinchuk, E. V. The phenotypic structure of Dreissena polymorpha populations (Pall.) // Gidrobiologicheskiy Zhurnal. — 1997. — **33**, N 2. — P. 21–32. — Russian : *Протасов А. А., Горпинчук Е. В.* О фенотипической структуре популяций Dreissena polymorpha (Pall.).

Protasov, A. A., Sinitsyna, O. O., Gorpinchuk, E. V., Golubkova, E. A. On the adaptivity of the phenotypes in Dreissena polymorpha (Pallas) // Tezisy dokladov Vtorogo syezda gidroecologicheskogo obschestva Ukrainy. — Kyiv, 1997. — P. 180. — Russian : *Протасов А. А., Синицына О. О., Горпинчук Е. В., Голубкова Е. А.* Об адаптивности фенотипов Dreissena polymorpha (Pallas).

Sergievskiy, S. O., Granovich, A. I., Kozminskiy, E. V. Shell pigmentation polymorphism in Littorina saxatilis (Olivi): classification principles // Populatsionnye issledovaniya belomorskikh molluskov : Trudy Zoologicheskogo instituta RAN. — 1995. — **264**. — P. 3–18. — Russian : *Сергиевский С. О., Гранович А. И., Козминский Е. В.* Полиморфизм окраски раковины Littorina saxatilis (Olivi): принципы классификации.

Yablokov, A. V., Larina, N. I. Introduction to population phenetics. New approach to natural populations study. — Moscow : Vysshaya shkola, 1985. — 159 p. — Russian : *Яблоков А. В., Ларина Н. И.* Введение в фенетику популяций. Новый подход к изучению природных популяций.

Zhivotovskiy, L. A. The indices of population variability of polymorphic features // Fenetika populatsiy. — Moscow : Nauka, 1982. — P. 38–44. — Russian : *Животовский Л. А.* Показатели популяционной изменчивости по полиморфным признакам.

Received 22 November 2011
Accepted 21 November 2012