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GENETIC AND MORPHOLOGICAL VARIABILITY OF A BIVALVE *ANADARA KAGOSHIMENSIS* (TOKUNAGA, 1906) AS PROBABLE COMPONENTS OF ITS ADAPTIVE SUCCESS IN THE AZOV AND BLACK SEA REGION

© 2025 **E. Slynko[1,2], V. Ryabushko[2], A. Kozhara[3], I. Voroshilova[3], A. Slynko[1], A. Baimukhambetova[1], V. Pashaev[1], and A. Mironovsky[4]**

[1]Russian Biotechnological University, Moscow, Russian Federation
[2]A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
[3]Papanin Institute for Biology of Inland Waters Russian Academy of Sciences, Borok, Russian Federation
[4]Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russian Federation
E-mail: *elena.slynko.76@mail.ru*

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An invasive population of a bivalve of the genus *Anadara* inhabiting the Kerch Strait of the Sea of Azov was investigated using methods of molecular genetics and multivariate morphometric analysis. These molluscs are highly successful invaders in the Azov–Black Sea region and have a significant effect on local biocenoses which underpins the relevance of this study. The aim of the work was to identify *Anadara* molluscs of the Kerch Strait down to the species level and analyze their genetic and phenotypic heterogeneity, with regard to their adaptability and invasion success. It was confirmed that the investigated population belongs to the species *Anadara kagoshimensis* (Tokunaga, 1906). Morphometric variability in 6 shell characters and polymorphism in a fragment of the cytochrome oxidase I gene in this population were examined. The genetic diversity in our sample appeared to be not lower than in some native populations of this species. At the same time, the analysis of morphological variations gives reason to believe that there are multiple ontogenetic channels in the individual development of the studied population of *A. kagoshimensis*. It is suggested that this condition contributed to the adaptive success of the ark shell in the Azov–Black Sea basin.

Keywords: *Anadara kagoshimensis*, cytochrome oxidase I, Black Sea, Kerch Strait, alien species, adaptation, genetic diversity

Since the second half of the 20th century, the Mediterranean basin, which includes the Sea of Azov and the Black Sea, is an arena for the mass distribution of alien molluscs. A significant part of these species is so-called Lessepsian migrants that penetrated the Mediterranean basin from the southeast *via* the Suez Canal. A prominent place in this category is occupied by *Anadara kagoshimensis* (Tokunaga, 1906): a large bivalve of the family Arcidae Lamarck, 1809, which noticeably affected benthic communities of the marine shelf during its expansion throughout the basin. This species is listed among 100 most dangerous invaders of the Mediterranean basin [Streftaris, Zenetos, 2006] and waters

of Russia [Soldatov et al., 2018]. It is mentioned along with successful invasive species: the rapa whelk *Rapana venosa* (Valenciennes, 1846), the Pacific oyster *Magallana gigas* (Thunberg, 1793), and the sand clam *Mya arenaria* Linnaeus, 1758 [Orlenko, 1994; Pereladov, 2013; Streftaris, Zenetos, 2006].

The current area of the anadara invasion outside its native range covers the Mediterranean, Marmara, and Black seas, the Sea of Azov (waters of Bulgaria, Romania, Ukraine, Russia, Georgia, and Turkey), and the Atlantic coast of Spain and France [Bañón et al., 2015]. Its introduction from the Indo-Pacific into recipient water bodies is usually associated with repeated unintentional transfer of free-swimming larvae *via* ballast water. The mollusc was first registered outside its native range in 1968 in the Black Sea [Kiseleva, 1992]; just a year later, it was recorded in the Adriatic Sea [Ghisotti, 1973]. The finds were initially identified as *Scapharca* cfr. *cornea* (Reeve, 1844) [accepted name *Anadara cornea* (Reeve, 1844)], *Scapharca inaequivalvis* (Bruguière, 1789) [accepted name *Anadara inaequivalvis* (Bruguière, 1789)], and *Cunearca cornea-inaequivalvis* [accepted name *Anadara inaequivalvis* (Bruguière, 1789)] [Ghisotti, 1973; Ghisotti, Rinaldi, 1976; Gomoiu, 1984; Ivanov, 1991; Kiseleva, 1992]. According to the results of genetic analysis [Krapal et al., 2014; Lee, Kim, 2003; Tanaka, Aranishi, 2014], molluscs noted in European waters under these species names should be attributed to *A. kagoshimensis*. However, V. Anistratenko and co-authors [2014], who studied the conchological variability of the Sea of Azov–Black Sea anadara, concluded that the nature and boundaries of these variations correspond to those of *A. inaequivalvis* from the type habitat: the Coromandel Coast (India).

Due to various adaptations, primarily to hypoxic environmental conditions, and wide ecological plasticity, this *Anadara* species can inhabit highly eutrophic waters; at the same time, the mollusc is found in areas characterized by a significant range of salinity [Anistratenko, Khaliman, 2006]. Forming settlements with high abundance and biomass, it acts as an ecosystem engineer creating the core of the consortium [Bondarev, 2020]. Already by 2013, in some areas of the Kerch Strait, the anadara has become one of the most common zoobenthic species [Revkov, 2016]. However, while competing for a substrate, *A. kagoshimensis* is capable of effective displacing of native species, chiefly representatives of the genus *Cerastoderma* Poli, 1795 [Anistratenko, Khaliman, 2006; Öztürk, 2021]. In the Azov–Black Sea basin, this species is also known to have a high morphological variability of both the shell and the soft body [Anistratenko et al., 2014; Finogenova et al., 2012].

The objectives of this work were to clarify the species affiliation and analyze the genetic and phenotypic polymorphism of this common invasive mollusc in the Azov–Black Sea basin in the context of its adaptive capabilities and invasive success.

MATERIAL AND METHODS

For molecular genetic analysis, 15 mature anadara specimens measuring 37 to 41 mm in length were sampled in the Kerch Strait in 2018. Immediately after delivery of live molluscs to a laboratory, those were removed from their shells, and samples were taken from the leg tissues fixed in 96% ethanol. Total DNA was isolated using the innuPREP DNA Mini Kit (Analytik Jena, Germany). Amplification of the mitochondrial gene fragment of the first subunit of cytochrome oxidase (COI), approximately 630 base pairs (bp), was performed using COI-4L primer (a forward one) 5’-GGTGTGTGTTTAAGATTTCACA-3’ [Lee, Kim, 2003] and HCO2198 primer (a reverse one) 5’-TAAACTTCAGGGTGACCAAAAAATCA-3’ [Folmer et al., 1994]. Ready-to-use lyophilized PCR mixtures (master mixes) for DNA amplification, in a volume of 20 μL, served as amplification mixtures.

The master mixes contained all the components required for a single reaction, including hot start Taq DNA polymerase, deoxyribonucleotides, and electrophoresis dye (manufactured by a research and production company "Genlab," Moscow, Russia). The polymerase chain reaction was carried out according to the protocol: +94 °C, 2 min 30 s; 35 cycles (+94 °C, 30 s; +58 °C, 1 min; +72 °C, 1 min; +72 °C, 10 min). PCR products were sequenced in both forward and reverse directions at "Evrogen" (Moscow). The resulting haplotypes have been deposited in the NCBI (National Center for Biotechnology Information) international database (https://www.ncbi.nlm.nih.gov/) under accession numbers MK992370 – MK992374.

The nucleotide sequences were viewed applying the MEGA6 software [Tamura et al., 2013]. To compare the sequences obtained with the sequences available in the NCBI database [2025], the BLAST program [Johnson et al., 2008] was used. Calculations of genetic variability parameters and neutrality tests [Fu, 1997; Tajima, 1989] were performed involving the DNASP 5.10 software [Librado, Rozas, 2009] and Arlequin ver 3.1 [Excoffier, Lischer, 2010].

The median network of COI haplotypes was constructed in the Network v. 10.2.0.0 program by the median joining [Bandelt et al., 1999]. During the analysis, the following *A. kagoshimensis* nucleotide sequences from the NCBI database were additionally used: MF426975 – MF426984, KM267562 – KM267563, KT266828, ON716108, AB854409 – AB854417, AB854403 – AB854408, AB854359 – AB854402, KF417435 – KF417440, KJ490940, and KJ490941. To construct the median network, all nucleotide sequences were shortened to 450 bp in accordance with the shortest fragment length presented in the international database for other invasive populations.

To analyze morphological variability in the same 15 molluscs that were used in the genetic analysis, 6 characters were measured (Fig. 1, Table 1).

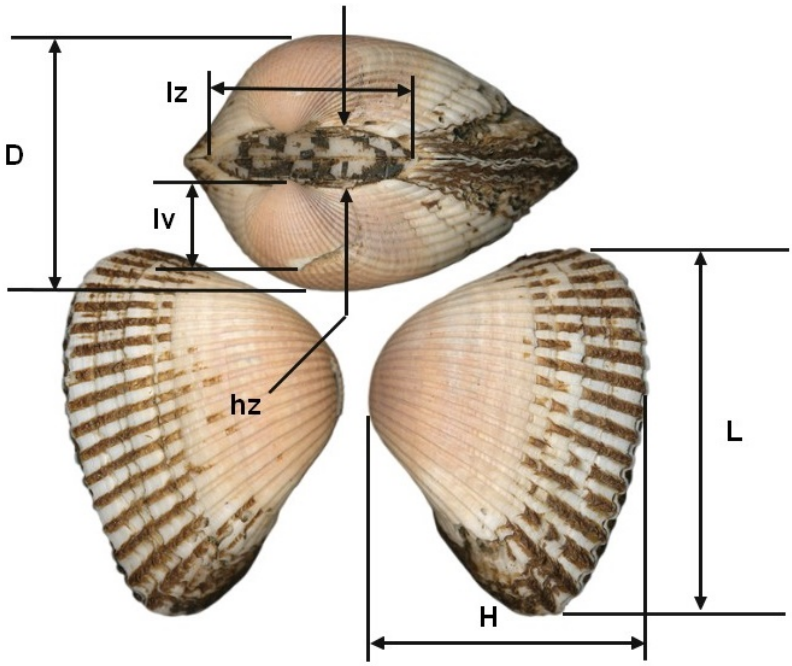

Fig. 1. Scheme of measurements of *Anadara kagoshimensis* specimens: L, shell length; H, shell height; D, shell width; lz, ligament length; hz, ligament width; lv, width of the top of the shell

Table 1. Absolute values of measurements of the characters for 15 *Anadara kagoshimensis* individuals

Specimen number	Measurements, mm					
	L	H	D	lz	hz	lv
1	41	33	28	25	4	13
2	41	32	27	21	4	9
3	40	31	28	21	5	11
4	39	32	27	23	4	11
5	40	31	26.5	20	5	9
6	38	28	26	21	4	12
7	34	28	25	17	5	10
8	40	31	26	19	5	12
9	39	31	27	20	5	11
10	38	31	27	18	4	10
11	37	29	25	19	4	11
12	39	32	28.5	23	5	13
13	37	31	24	20	4	10
14	37	30	25	19	4	12
15	38	32	27	18	5	9

Note: designation of the characters is the same as in Fig. 1.

The cluster analysis and principal component analysis (hereinafter PCA) were performed using the NTSYS 2.02k software package [Rohlf, 1998]. For the canonical discriminant analysis, including determining the probability of an individual's assignment to groups identified by the cluster analysis, the Statistica 6 package was applied. The *a priori* probability of assignment to the group was taken to be proportional to the group size. The calculations involved indices of the ratio of absolute values of measurements to the shell length (L). To assess similarity relationships among individuals, squared multidimensional Euclidean distances (E^2) were determined based on the standardized values of the indices. The cluster analysis of the matrices of morphological distances was performed by the complete linkage. In the PCA, the eigenvectors were calculated using the correlation matrix. The vector length was taken to be equal to 1. When constructing graphs illustrating the PCA results, along with the traditional technique (distribution of individuals in PC1 and PC2 coordinates), an approach known as the ontogenetic channels method was applied [Mina, 2001; Mina et al., 1996, 2010]. Its use in the analysis of the morphological diversity in ecological forms of large African barbs of the *Barbus intermedius* (sensu Banister, 1973) complex [Banister, 1973] and Altai osmans of the genus *Oreoleuciscus* Warpachowski, 1889 showed that each ecological form of the studied fish groups has its own corresponding ontogenetic channel [Mina, 2001; Mina et al., 1996; Mironovsky et al., 2014]. Later, the opposite was shown to be true: the identification of distinct ontogenetic channels in the morphological variability of individuals of a certain population may indicate high ecological plasticity of this population which can mediate the arising of morphological and ecological forms [Dgebuadze et al., 2017, 2020; Mironovsky et al., 2019].

RESULTS

Genetic diversity. In the sample of 15 analyzed specimens of the Kerch Strait anadara, for a 450-bp COI gene fragment, 5 haplotypes were identified differing by 1–2 nucleotide substitutions, which corresponds to difference levels of 0.22 and 0.44%, respectively (Fig. 2). More than half of the individuals

in the sample studied (8 specimens, or 53.3%) were carriers of the H1 haplotype (Table 2). The remaining haplotypes were represented by 1–3 specimens. The variants of nucleotide sequences that we recorded are identical to those from populations in the waters of Japan and South Korea. Two haplotypes, H3 and H4, were registered by us for the first time (Fig. 2, Table 2).

Table 2. Haplotype designations and nucleotide sequence numbers in NCBI

Haplotype	Number in NCBI	Nucleotide sequence numbers from the international database NCBI identical to those in the paper
H1	MK992371	AB854359, AB854381, AB854396, AB854379, AB854369
H2	MK992370	AB854408
H3	MK992373	–
H4	MK992372	–
H5	MK992374	AB854406, AB854370, AB854360

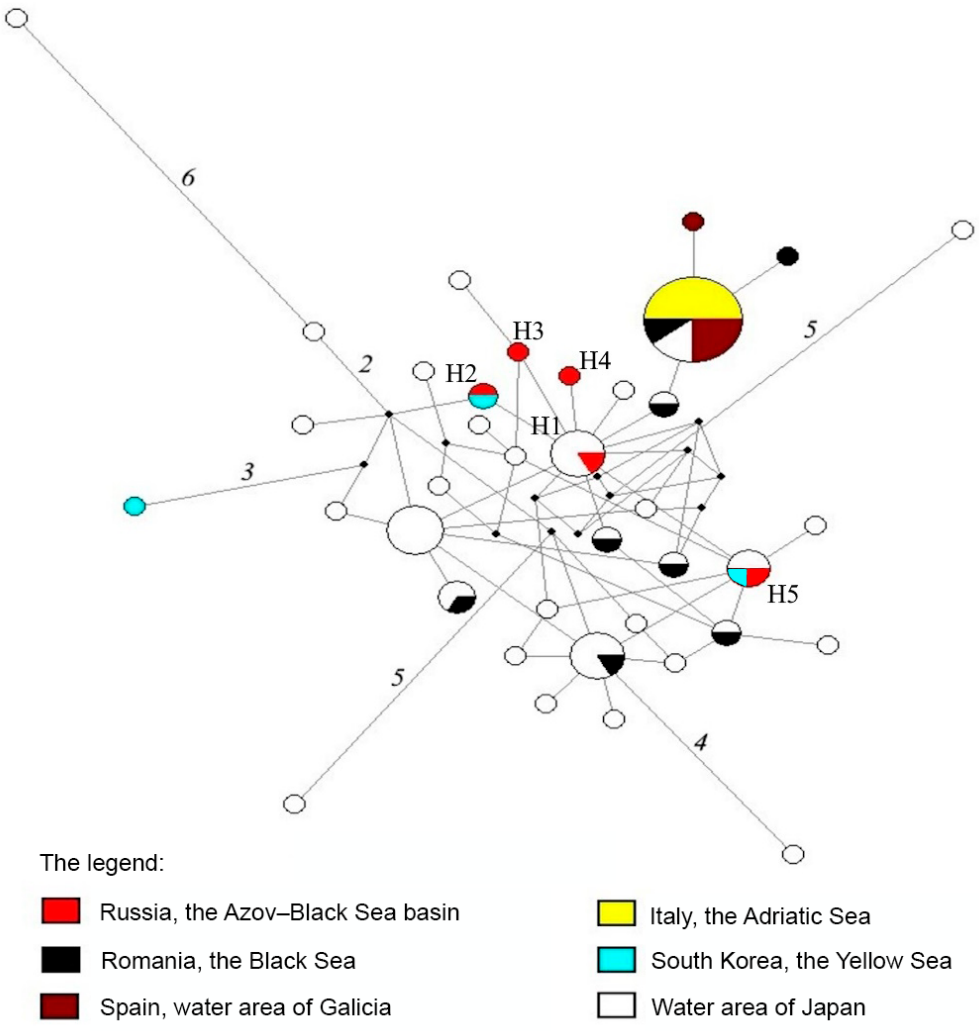

Fig. 2. Median haplotype network of the COI gene fragment (450 base pairs) of *Anadara kagoshimensis*. If the number of mutational substitutions between haplotypes exceeds 1, it is indicated above the segment connecting the haplotypes. The diameter of the circle denoting the haplotype is proportional to its frequency of occurrence. Black dots indicate median vectors – not yet discovered or disappeared sequence variants

In our sample, the nucleotide diversity and the number of haplotypes and nucleotide substitutions are somewhat lower, while the values of haplotype diversity are not lower than in several samples from native populations (Table 3).

Table 3. Indices of genetic diversity of the mitochondrial COI gene fragment in the invasive population of *Anadara kagoshimensis* of the Kerch Strait (Azov–Black Sea basin) and in samples from its native area

Population	*n*	h	Hd	π (%)	Ns
The Kerch Strait (Azov–Black Sea basin)	15	5	0.71 ± 0.11	0.16 ± 0.04	4
The Yellow Sea*	20	6	0.45 ± 0.14	0.19 ± 0.15	9
Water area of Japan*, min/max (8 samples)	14/36	7/15	0.65 ± 0.09 / 0.93 ± 0.02	0.22 ± 0.16 / 0.59 ± 0.36	7/17

Note: *n*, number of studied specimens; h, number of haplotypes; Hd, haplotypic diversity; π, nucleotide diversity; Ns, number of nucleotide substitutions between the sequences of individuals in the studied populations. *, data from [Tanaka, Aranishi, 2014].

The neutrality test values are negative, while their discrepancies with theoretically expected values are not significant ($p > 0.02$).

Morphological variability. On the dendrogram showing phenetic relationships of *A. kagoshimensis* individuals in terms of the set of considered characters, four clusters can be provisionally identified: **A**, **B**, **C**, and **D** (Fig. 3).

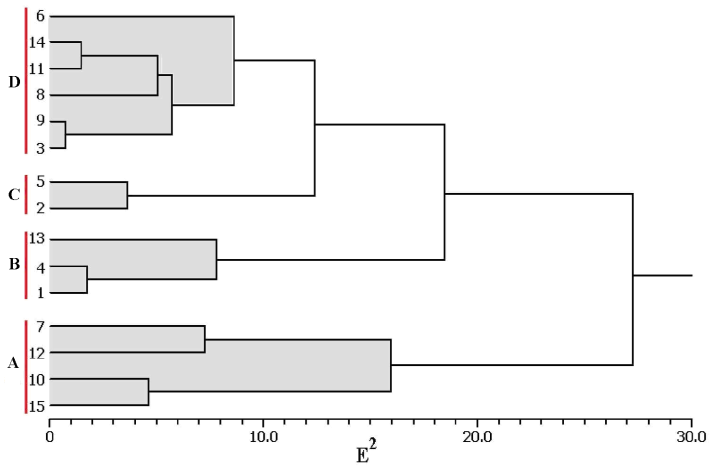

Fig. 3. A dendrogram of the similarity of *Anadara kagoshimensis* individuals of the Kerch Strait according to the set of morphological characters; 1–15, numbers of individuals; A–D, designations of clusters; E^2, squared Euclidean distance

These preliminary identified groups were subjected to the discriminant analysis. Its results showed that in the coordinates of the first two discriminant functions, individuals of the groups corresponding to four clusters of the dendrogram in Fig. 3 are clearly separated from each other (Fig. 4).

Calculations showed as follows. The posterior probability (*i. e.*, considering the determined values of the discriminant functions) of assigning each analyzed individual to a group corresponding to one of the dendrogram clusters in Fig. 3 tends to 1. The probability of erroneous assigning any individual to one of the clusters is noticeably lower than the significance level of $p = 0.05$ accepted in most biological studies (in most cases, the level of $p = 0.01$ as well) (Table 4).

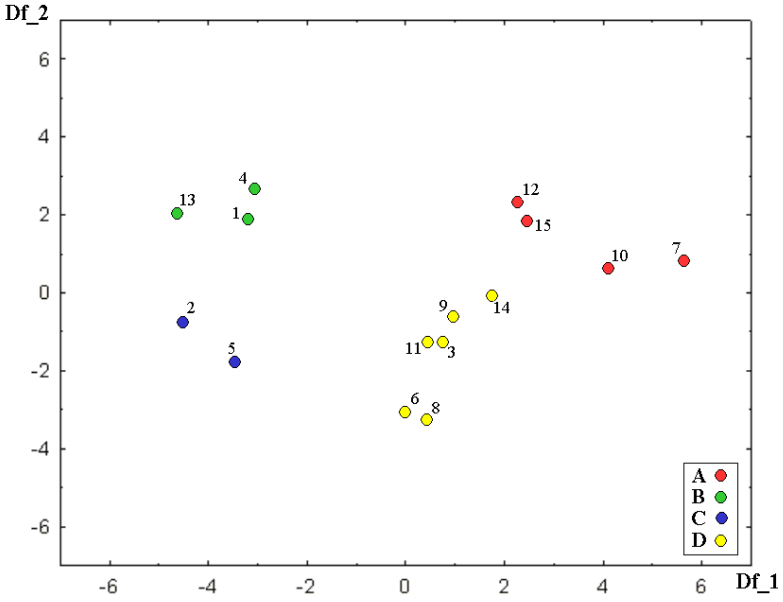

Fig. 4. Distribution of *Anadara kagoshimensis* individuals of the Kerch Strait in coordinates of the first (Df_1) and second (Df_2) discriminant functions. Numbering of individuals and group designations are the same as in Fig. 3

Table 4. Posterior probability of assigning *Anadara kagoshimensis* individuals to one of the dendrogram clusters (see Fig. 3)

Specimen of a group	Group A	Group B	Group C	Group D
A(7)	$p > 0.999$	$p < 0.001$	$p < 0.001$	$p < 0.001$
A(10)	$p > 0.999$	$p < 0.001$	$p < 0.001$	$p < 0.001$
A(12)	$p > 0.990$	$p < 0.001$	$p < 0.001$	$p = 0.003$
A(15)	$p > 0.999$	$p < 0.001$	$p < 0.001$	$p < 0.001$
B(1)	$p < 0.001$	$p > 0.999$	$p < 0.001$	$p < 0.001$
B(4)	$p < 0.001$	$p > 0.999$	$p < 0.001$	$p < 0.001$
B(13)	$p < 0.001$	$p > 0.999$	$p < 0.001$	$p < 0.001$
C(2)	$p < 0.001$	$p < 0.001$	$p > 0.999$	$p < 0.001$
C(5)	$p < 0.001$	$p < 0.001$	$p > 0.999$	$p < 0.001$
D(3)	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p > 0.999$
D(8)	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p > 0.999$
D(9)	$p = 0.005$	$p < 0.001$	$p < 0.001$	$p > 0.990$
D(11)	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p > 0.999$
D(14)	$p = 0.013$	$p < 0.001$	$p < 0.001$	$p > 0.990$
D(6)	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p > 0.999$

Note: the letters indicate the groups corresponding to the dendrogram clusters; the digits in parentheses are the numbers of the individuals.

All considered above gives good reason to assume that the division of 15 *Anadara* specimens into 4 morphologically distinct groups is not just an accident, but an objective reflection of the morphological heterogeneity of the population.

The results of the analysis of variation among the studied individuals using the PCA correspond to those described above (Fig. 5, Table 5).

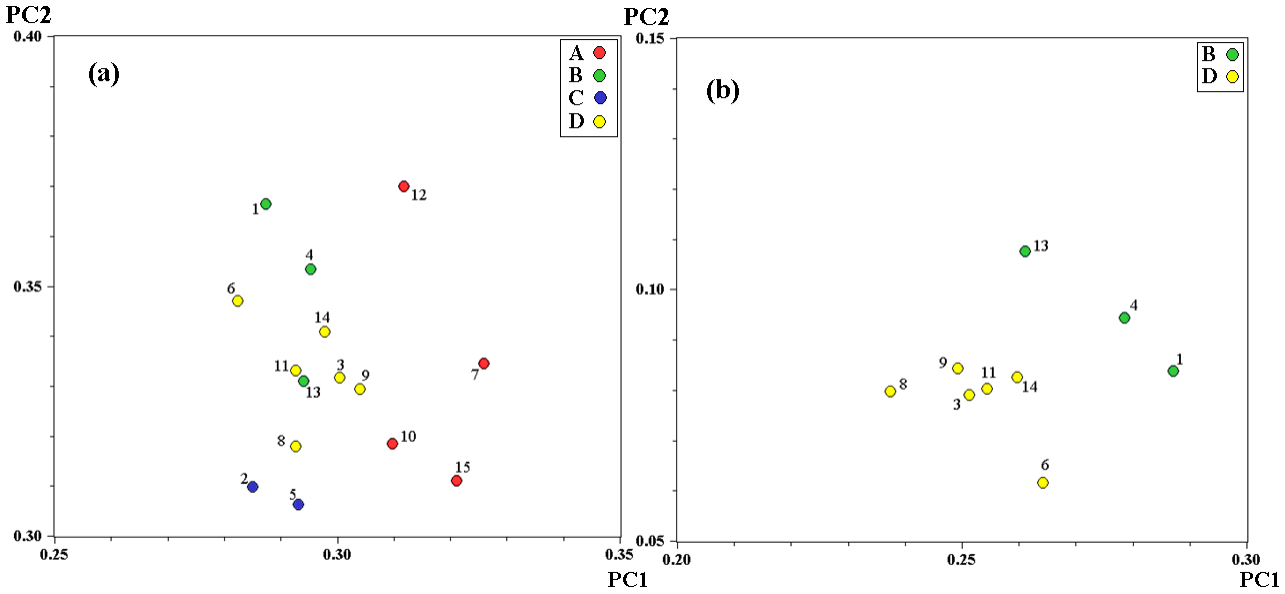

Fig. 5. Distribution of *Anadara kagoshimensis* individuals of the Kerch Strait in coordinates of the principal components: **a**, principal component analysis of 15 individuals of clusters A, B, C, and D; **b**, principal component analysis of 9 individuals of clusters B and D. Numbering of individuals and group designations are the same as in Figs 2 and 3

Table 5. Eigenvalues of the principal components and factor loadings of characters in principal component analysis of variability of *Anadara kagoshimensis* of the Kerch Strait

Character	Fig. 5a (15 specimens)		Fig. 5b (9 specimens)	
	PC1	PC2	PC1	PC2
H	0.442	0.116	0.207	0.745
D	0.607	0.301	0.175	–0.373
lz	–0.215	0.670	0.647	0.062
hz	0.625	–0.157	–0.658	–0.033
lv	0.014	0.650	0.274	–0.549
λ	1.77	1.63	2.01	1.41
Explained variance, %	35.30	32.61	40.16	28.3

Note: λ, eigenvalues of the principal components. Other designations are the same as in Figs 3–5.

Analysis of 15 specimens of the four previously identified clusters revealed that 4 specimens of cluster **A** and 2 specimens of cluster **C** are isolated from other ones (Fig. 5a). The distributions of individuals of clusters **B** and **D** overlap (see Fig. 5a). Let us, however, take into account that with incomplete separation of several sets (groups) in the coordinates of the principal components, individuals of the non-separated groups may become isolated at the next step of the analysis, when the already isolated groups are excluded from consideration. Let us exclude from analysis 4 specimens of cluster **A** and 2 specimens of cluster **C** and repeat the PCA for 9 specimens of clusters **B** and **D**. It is obvious that clusters **B** and **D** are clearly separated (Fig. 5b).

When using the discriminant analysis, one cycle of calculations was enough to sort 15 studied individuals into 4 clusters, and one graph was enough to visualize the results. When applying the PCA, two cycles and graphs were required. This fact is quite understandable if we take into account that PC1,

PC2… are the axes of the greatest variance between all individuals of the analyzed sample, without *a priori* division into groups, while the discriminant functions Df1_, Df_2… are the axes of the greatest differences between the centroids of **already specified** groups, previously identified by the cluster analysis.

For further consideration, it is important to note that two isolated clusters are clearly separated, each cluster by one of the two principal components: cluster **A**, by PC1, and cluster **C**, by PC2 (see Fig. 5a). The distributions of clusters **B** and **D** overlap both by PC1 and PC2 (see Fig. 5b). The division is clear and unambiguous only by the **combination** of the first two principal components: PC1 and PC2 (see Fig. 5b).

Thus, in the space of the considered characters, the studied specimens form 4 well-differentiated groups. Such heterogeneity can be interpreted differently reflecting several situations. One of them is a change in morphological proportions as the molluscs grow due to ontogenetic allometry. In this case, distances between clusters to one degree or another reflect the differences between individuals of various size groups. Specifically, positive allometry was revealed for the dependence of the anadara shell height and its width (convexity) on the length: $H = 0.730 \times L^{1.037 \pm 0.0184}$ and $D = 0.473 \times L^{1.103 \pm 0.022}$, respectively [Zhavoronkova, Zolotnitsky, 2014]. Although the molluscs in our sample differ little in the absolute size of their shells, this hypothesis requires verification.

Another possible situation is the presence of epigenetically determined channels (creodes) in the ontogeny of individuals of the analyzed *A. kagoshimensis* population. Creodes serve as attractors for the trajectories of individual development and are realized in the phenotype in the form of morphologically distinguishable groups of individuals. Each creode corresponds to a separate cluster.

The so-called ontogenetic channel method allows us to distinguish these two fundamentally different situations. The pattern is as follows. The values of one of the principal components reflecting the morphology of individuals are plotted on the ordinate axis (Y) of the graphs, and the parameter reflecting absolute sizes of individuals (in our case, it is the shell length, L, in mm) is plotted on the abscissa axis (X) [Mina et al., 1996]. This approach helps in estimating the ratio of differences mediated by allometric growth and differences related to polymorphism. In other words, it helps in separating differences of size groups in a single, monomorphic population from differences of morphological subunits of a polymorphic population. The results of this approach are shown in Fig. 6.

The distribution of specimens of cluster **A** along the ordinate axis (PC1) is clearly separated from the distribution of specimens of the other three clusters. So, each specimen of cluster **A** is morphologically different from all comparable-sized specimens of the other clusters of the sample (Fig. 6a).

It follows from the above that the observed isolation of 4 individuals of cluster **A** cannot be explained by the size difference: this is not allometry, but evidence of morphological subdivision of the population. The section highlighted in Fig. 6a by shading is usually considered in studies of this issue as an ‘ontogenetic channel’: a two-dimensional projection of the region of the multidimensional space of characters where individual ontogenetic trajectories are located [Mina, 2001; Mina et al., 1996]. Thus, there are grounds for a completely justified assumption that the development of individuals of cluster **A** occurs in a separate ontogenetic channel (see Fig. 6a).

Along the ordinate axis (here, it is no longer PC1, but PC2 of 15 specimens), two molluscs of cluster **C** also differ from all the same-sized ones (see Fig. 6b). The short size range and small number of individuals do not yet allow us to claim that it is an independent ontogenetic channel, but the phenetic isolation of this group can hardly be unambiguously explained by the effect of allometry.

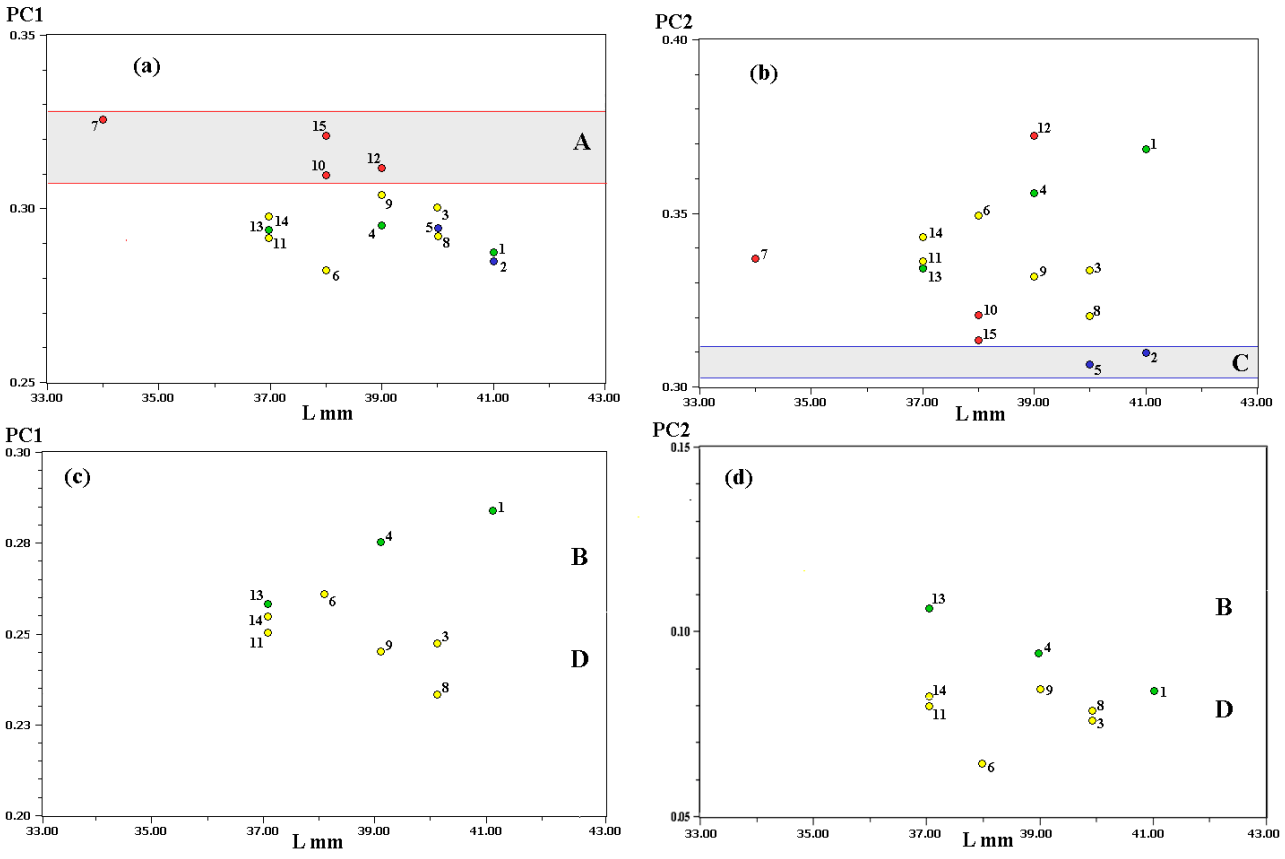

Fig. 6. Ontogenetic channels of *Anadara kagoshimensis* individuals of the Kerch Strait: **a**, individuals of cluster A, PC1 to the principal component analysis (PCA) of variability of 15 individuals of the studied sample; **b**, individuals of cluster C, PC2 to the PCA of variability of 15 individuals of the studied sample; **c**, individuals of clusters B and D, PC1 to the PCA of variability of 9 individuals of clusters B and D; **d**, individuals of clusters B and D, PC2 to the PCA of variability of 9 individuals of clusters B and D. Numbering of individuals and group designations are the same as in Figs 2–4

In Fig. 6c and 6d, the ordinate axes show the values of PC1 and PC2 of the PCA not for all 15 individuals studied, but only for 9 molluscs of clusters **B** and **D**. Obviously, the distributions of the compared groups slightly overlap, and, despite the almost complete coincidence of the size ranges, we would mistakenly come to a conclusion about just a tendency for the isolation of the channels analyzed. The graph in Fig. 5b helps to avoid such an error: there, clusters **B** and **D** are clearly separated, with a pronounced hiatus in the **combination** of PC1 and PC2. Thus, we do not deal with a tendency, but with a complete separation of the ontogenetic trajectories of these groups in the multidimensional space of the initial characters.

Let us summarize the results of the analysis of morphological variability:

1. Multivariate analysis of the variability of the sampled individuals shows that the studied population is heterogeneous and is divided into several clearly distinct groups based on the set of characters considered.
2. Analysis of the ratio of morphological differences of specimens of the identified groups with differences in their absolute sizes does not provide grounds for concluding that the identified differences are allometric in nature.

3. The above provides reasonable grounds to believe that there are several ontogenetic channels in the morphogenesis of individuals of the studied population of *A. kagoshimensis*. At the moment, the presence of such channels can be discussed at the level of a hypothesis, and its confirmation requires further research involving additional material.

DISCISSION

The presented results clearly indicate that all analyzed individuals belong to one species known both from the native range (Indo-Pacific region) and the area of invasion (waters of Spain, Italy, and Romania). The reduction in genetic diversity is not as significant as, for example, in the case of the rapa whelk and the Pacific oyster [Chandler et al., 2008; Slynko et al., 2018]. In the Azov–Black Sea basin, these invasive mollusc species (the anadara, the rapa whelk, and the Pacific oyster) have a similar origin (Indo-Pacific region), although the scenarios for their distribution are different.

In the case of the Pacific oyster, there was a deliberate introduction from the Sea of Japan and European oyster nurseries [Slynko et al., 2018]. Its low genetic diversity may be due to both intense inbreeding under mariculture conditions and the poor genetic diversity of donor populations. The low genetic diversity observed in the rapa whelk populations could be driven by the founder effect in the absence of repeated invasions. Apparently, as assumed by M. Pereladov [2013], there is a high mortality rate of both adult individuals attached to the surface of vessel bottoms and larvae in ballast water during long-term transportation.

The higher genetic diversity in the anadara invasive populations is mediated by the fact that both in the Atlantic and in the Mediterranean basin, they are permanently replenished with individuals from the native range due to the significantly increased cargo turnover with the Indochina countries [Ulman et al., 2017; Zenetos et al., 2010]. Surprisingly, the Kerch Strait sample does not contain haplotypes that are most common in populations from waters of Spain, Italy, and Romania. At the same time, there are haplotypes identical to those from the native range, but absent from the above-mentioned European populations. A relatively large number of haplotypes (13) in the Black Sea (5 in the Kerch Strait, and 8 in the waters of Romania) is likely to result from the absence of two effects, the founder one and the bottleneck one, during the invasion. The obtained data suggest that in the case of the anadara, we observe multiple expansion [Wilson et al., 2009]. However, applying the Tajima's test (*D*) and Fu's test (*Fs*) on our material, this hypothesis cannot be verified, since the test results are statistically insignificant.

Most ecological studies on the Black Sea anadara highlight stability and even prosperity of its populations [Anistratenko, Khaliman, 2006; Ivanov, 1991; Revkov, 2016; Revkov, Scherban, 2017; Zolotarev, Zolotarev, 1987]. In the area of its invasion, the mollusc demonstrates a wide range of salinity, respiratory, and trophic adaptations. A logical question arises: what ensures its adaptive success? A high level of morphological divergence of populations of this species in the northwestern Black Sea has been previously noted [Finogenova et al., 2012]. In this case, according to the classical concepts of I. Schmalhausen [1982] and A. Rasnitsyn [1987], multiple stable channels of ontogenetic development should be formed acting as attractors and ensuring pronounced morphological differentiation at the definitive stages. Apparently, this is exactly the pattern we observe when analyzing the morphological variability of the Kerch Strait anadara (the Sea of Azov). A similar pattern of subdivision by morphometric features was recently revealed for the anadara of the Black Sea and Sea of Azov [Mirzoeva, Zhukov, 2021]. The authors interpreted the clusters obtained after excluding dimensional variability as ecomorphotypes,

the formation of which contributes to more successful adaptation of molluscs to a heterogeneous environment. Despite the use of different terminology, we are likely to be talking about the same phenomenon: intrapopulation divergence related to the diversity of biotopes colonized by this species. The obtained results of the study of the anadara morphological variability are obviously preliminary and require further research.

Conclusions. Based on the analysis of the nucleotide sequences of the COI mtDNA gene fragment, it was possible to confirm that *Anadara kagoshimensis* (Tokunaga, 1906), originating from the Pacific basin, inhabits the Sea of Azov waters, namely the Kerch Strait. It is quite likely that we are dealing with repeated expansion with a classic anthropogenous type of distribution. The success of the introduction seems to be partly associated with the ability of this mollusc to form multiple trajectories of individual development in population ontogenesis, apparently corresponding to different ecological forms.

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ГЕНЕТИЧЕСКАЯ И МОРФОЛОГИЧЕСКАЯ ИЗМЕНЧИВОСТЬ МОЛЛЮСКА *ANADARA KAGOSHIMENSIS* (TOKUNAGA, 1906) КАК ВЕРОЯТНЫЕ СОСТАВЛЯЮЩИЕ АДАПТИВНОГО УСПЕХА ЭТОГО ВИДА В АЗОВО-ЧЕРНОМОРСКОМ РЕГИОНЕ

Е. Е. Слынько[1,2], В. И. Рябушко[2], А. В. Кожара[3], И. С. Ворошилова[3], А. Ю. Слынько[1], А. С. Баймухамбетова[1], В. Ш. Пашаев[1], А. Н. Мироновский[4]

[1]ФГБОУ ВО «Российский биотехнологический университет (РОСБИОТЕХ)», Москва, Российская Федерация

[2]ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН», Севастополь, Российская Федерация

[3]ФГБУН «Институт биологии внутренних вод имени И. Д. Папанина РАН», Борок, Российская Федерация

[4]Институт проблем экологии и эволюции имени А. Н. Северцова РАН, Москва, Российская Федерация

E-mail: *elena.slynko.76@mail.ru*

Методами молекулярно-генетического и многомерного морфометрического анализа исследована инвазийная популяция двустворчатого моллюска рода *Anadara*, обитающая в Керченском проливе Азовского моря. Моллюски этого рода являются весьма успешными вселенцами в Азово-Черноморском бассейне, оказывая значительное влияние на местные биоценозы, что определяет актуальность исследования. Задачей работы было уточнить видовую принадлежность и проанализировать генетический и фенотипический полиморфизм анадары в Керченском проливе в контексте её адаптивных возможностей и инвазионного успеха. Подтверждена принадлежность исследованной популяции к виду *Anadara kagoshimensis* (Tokunaga, 1906). Для представителей этой популяции изучена изменчивость 6 морфометрических признаков раковины и полиморфизм фрагмента гена цитохромоксидазы I. Генетическое разнообразие в исследуемой выборке оказалось не ниже, чем в некоторых нативных популяциях анадары. Анализ морфологической изменчивости даёт основания полагать, что в индивидуальном развитии особей рассматриваемой популяции *A. kagoshimensis* имеет место несколько каналов онтогенеза. Высказано предположение, что это обстоятельство способствовало адаптивному успеху анадары в Азово-Черноморском бассейне.

Ключевые слова: *Anadara kagoshimensis*, цитохромоксидаза I, Чёрное море, Керченский пролив, чужеродный вид, адаптация, генетическое разнообразие