1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2024, том 9, № 4, с. 26–34
https://marine-biology.ru

UDC 597.556.331.1-027.63(262.5)

PHENOMENON OF THE "LARGE" HORSE MACKEREL APPEARANCE IN THE BLACK SEA: VERSIONS AND PROOFS

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Received by the Editor 18.06.2024; after reviewing 02.08.2024;
accepted for publication 10.09.2024; published online 19.11.2024.

The paper provides an overview of literature data and results of the authors' own investigations on the phenomenon of a sudden mass appearance of a "large" ("giant") form of the horse mackerel (*Trachurus*, Carangidae) (LM) in the Black Sea in the late 1940s and its unexpected disappearance in the mid-1960s. This phenomenon was of great interest and attracted attention of many researchers hypothesizing that it was a new source of information for understanding processes of the organisms' adaptation and important issues of microevolution and speciation. Different approaches to the study of this fact are analyzed, including determination of the LM origin and clarification of its taxonomic status. On their basis, three mutually exclusive versions are proposed. According to the first one, the LM is a new species of the Mediterranean origin; according to the second one, it is an ecomorph of *Trachurus mediterraneus ponticus*; and according to the third one, it is a hybrid of *T. mediterraneus mediterraneus* and *T. mediterraneus ponticus*. Based on the investigation on thermal resistance of isolated muscles and serological analysis of tissue proteins, Yu. Altukhov and co-authors identified the LM as an independent species of the Mediterranean (and, possibly, Atlantic) origin which appeared in the Black Sea because of a sudden expansion of its range after a sharp increase (outburst) in abundance. The main evidence for the Black Sea origin of the LM is the fact as follows: all stages of its life cycle, *i. e.*, reproduction, growth of juveniles, feeding, and wintering of adults, occur in the Black Sea; moreover, its large specimens were known earlier. Belonging of the Black Sea "small" horse mackerel and LM to the same species was confirmed by the electrophoretic studies on protein composition of their blood serum. The idea of the hybrid origin of the LM was first proposed by I. Dobrovolov based on an investigation of electrophoretic spectra of nonspecific muscle esterases in *T. mediterraneus ponticus* and *T. mediterraneus mediterraneus*. According to our data, the third version of the LM origin seems more probable than other ones. Occurrence of *T. mediterraneus mediterraneus* in the Black Sea and its hybridization with *T. mediterraneus ponticus* are manifestations of the mediterranization; this process has intensified due to increasing anthropogenic load on the ecosystem of Azov–Black Sea Basin and ongoing disruption of freshwater balance resulting from overregulation of river flows and sea salinization. None of three versions can be refuted or confirmed by molecular genetic methods, since there is currently no LM in the Black Sea. Thus, the phenomenon of the "large" horse mackerel appearance in the Black Sea is still unexplained.

Keywords: Black Sea "large" horse mackerel, versions, Mediterranean origin, Black Sea origin, hybrid origin

The "large" ("giant") horse mackerel unexpectedly appeared in enormous abundance in the Black Sea in the late 1940s and suddenly disappeared in the early 1960s, and this phenomenon aroused great interest of many researches. In relatively short period, about 10–15 years, dozens of articles were published discussing its origin, systematics, morphology, biology, physiology, and biochemistry,

as well as characteristics of behavior and migrations, stock assessment, and prospects for its fishery. Such attention was due to at least two factors. The first one seemed to be related to high economic importance of the “large” horse mackerel as a valuable food object. In this regard, accurate estimates of total stock were supposed to serve as a necessary condition for organization of rational exploitation and forecasting. Commercial fishing of the “large” horse mackerel began in 1953, and about 15 thousand tons were caught already in 1956. To compare, maximum catches of the main commercial fish of the Black Sea, the European anchovy *Engraulis encrasicolus* (Linnaeus, 1758), did not exceed 16 thousand tons in the 1950s. Thus, the “large” form prevailed in the Black Sea fishery with the stock that was estimated to be 2–3 million tons [Tikhonov, 1959]. The second factor governing the interest of researchers was as follows: studies of the “large” horse mackerel were supposed to provide new information for better understanding of the organism adaptation, microevolution, and speciation. To date, there is no common concept on the origin of the “large” form, reasons for its occurrence in the Black Sea, and relationships with the Black Sea horse mackerel.

The aim of this paper is to systematize and generalize versions of the “large” horse mackerel origin and its appearance in the Black Sea.

History of research and versions of origin. A short period of the “large” horse mackerel occurrence in the Black Sea has the following chronology. In spring 1948, aggregations of large fish occupying an area of about 800 sq mi were noted from the aircraft searching for marine biological resources (fish and dolphins) off the coast of Georgia [Biologiya i promysel, 1955]. It turned out to be the “large” horse mackerel, 50 cm in length. Next year, it appeared in catches off the Caucasian coast. In 1950, the “large” form spread along the Caucasian coast and southern coast of the Crimea up to the Cape Chersonesus and occurred in the Sea of Azov [Biologiya i promysel, 1955; Tikhonov, 1958, 1959]. Meanwhile, a part of a population wintered off the southern coast of the Crimea. In 1952, the “large” horse mackerel was found off the Anatolian coast and also in the northwestern Black Sea: off the coasts of Romania and Bulgaria. In 1954–1955, only single specimens were recorded in the Black Sea: in the Bosphorus, Sea of Marmara, and Dardanelles [Nümann, 1956]. At the same time, in 1953–1954, the “large” form spread throughout the Black Sea and covered open deepwater areas.

However, since 1955, the range of the “large” horse mackerel was shrinking. This process was accompanied by a decrease in its abundance as a result of natural mortality and fishing and also due to absence of abundant generations. In 1963, total stock dropped by at least 20–25 times compared to that of 1956. Since 1965, the statistics of fishery has no differentiation of the Black Sea horse mackerel into “small” and “large” ones because of extremely low abundance of the second form.

The occurrence of the “large” form in the Black Sea caused debates on its taxonomic status and origin. To date, there are three main versions of the Black Sea “large” horse mackerel origin: Mediterranean, Black Sea, and hybrid ones.

Version of the Mediterranean origin of the “large” horse mackerel. The first to propose this version was Yu. Aleev. Based on similarity in body shape and growth rate of the “large” horse mackerel and horse mackerel from the Mediterranean Sea, the researcher considered that the “large” form is a migrant from the Mediterranean Basin and suggested to name it the Mediterranean horse mackerel [Aleev, 1952]. Later, after detailed investigations of the genus *Trachurus*, he concluded that the “large” horse mackerel was a local herd of *Trachurus mediterraneus ponticus*, along with other three herds (northern, eastern, and southwestern ones), and identified it as a southern herd [Aleev, 1957]. He tended to associate rapid growth of the “large” horse mackerel with more favorable water temperature off the Anatolian coast and better nutritional conditions.

Yu. Altukhov supported the version of the Mediterranean origin. With his co-authors, he applied cytophysiological (thermal resistance of isolated muscles) and biochemical (serological analysis of tissue proteins) techniques for studying the relationship between the “large” horse mackerel and the Black Sea

"small" one [Altukhov, 1962a, b, 1967; Altukhov, Apekin, 1963; Altukhov, Mikhalev, 1964]. Based on results, these researchers drew conclusions about the level of differences between the species, and B. Ushakov's concept served as the ground. According to it, thermal resistance of tissues is the species criterion of poikilotherms [Ushakov, 1959]. However, in subsequent studies, differences in thermal resistance were registered not only on the level of species and populations, but also on the level of smaller groups representing different taxonomic ranks, with fish included [Yablokov, 1987]. Yu. Altukhov searched for evidence for the Mediterranean origin of the "large" horse mackerel and even for the Atlantic one. He attempted to explain its mass appearance in the Black Sea by a sudden range expansion resulting from a sharp increase in the species abundance.

N. Revina and T. Saf'yanova supported the version of the Mediterranean origin as well. Based on Yu. Altukhov's data on significant immunological and cytophysiological differences between the "small" and "large" forms and also considering the lack of abundant recruitment of the "large" horse mackerel herd over several years, these researchers suggested that its mass occurrence could result from an outburst outside the Black Sea [Revina, Saf'yanova, 1966a, b]. A possible reason for this phenomenon could be a response to climate change, in particular, intensification of oceanographic processes in the North Atlantic in the 1950s covering the Mediterranean Sea [Izhevsky, 1964]. In the opinion of these authors, the "large" horse mackerel might be a Mediterranean and even Atlantic migrant.

Version of the Black Sea origin of the "large" horse mackerel. V. Tikhonov adhered to the version of the Black Sea origin [Biologiya i promysel, 1955; Tikhonov, 1958, 1959]. His position was based on data of W. Nümann [1956]: according to the latter one, the "large" horse mackerel was noted by Turkish fishermen engaged in fishing off the coasts of Bulgaria, the Crimea, and Georgia since ancient times. Moreover, he relied on facts that all stages of this fish life cycle, *i. e.*, reproduction, growth of juveniles, feeding, and wintering of adults, occur in the Black Sea. Another evidence was the absence of the "large" form in the Mediterranean Sea. According to V. Tikhonov, the "large" horse mackerel was not widespread earlier because of its low abundance. To confirm, he referred to a work of S. Zernov [1913] who recorded the capture of a 40 cm long horse mackerel off the Caucasian coast.

A study of protein composition of the blood serum for six horse mackerel species of two genera, *Trachurus* and *Decapterus*, from the Black, Mediterranean, and Red seas by electrophoresis method revealed no differences between the Black Sea "small" and "large" forms [Golovko, 1964; Kulikova, 1968; Shulman, Kulikova, 1966].

Investigating morphological, ecological, and behavioral characteristics of the Black Sea horse mackerel, R. Shaverdov concluded as follows: the Black Sea "small" and "large" forms were the ecotypes of *T. mediterraneus ponticus* that differed in terms of nutritional conditions alone [Shaverdashvili, 1976; Shaverdov, 1964]. In his opinion, the horse mackerel as the facultative predator was an active migrant, grew faster, and, consequently, became larger during the years of elevated abundance of its main food object, the European anchovy.

Based on results on the variability of plastic traits, Yu. Slynko and co-authors [2018] defined the "large" and "small" horse mackerel as distinct in-population morphological forms that differed in feeding type.

Version of the hybrid origin of the "large" horse mackerel. A Bulgarian researcher I. Dobrovolov analyzed electrophoretic spectra of nonspecific muscle esterase of the Black Sea *T. mediterraneus ponticus*, Mediterranean *T. mediterraneus mediterraneus*, and "large" horse mackerel and proposed the version of the hybrid origin of the latter one [Dobrovolov, 1988, 2000; Dobrovolov, Manolov, 1983]. In accordance with it, the "large" horse mackerel is the result of hybridization of the Black Sea and Mediterranean subspecies that could occur in both the Marmara and Black seas. Its truly large size, high growth rate, noticeable abundance, and other ecological advantages over the Black Sea horse mackerel, in opinion of the author, are due to heterosis effect which is most prominent among the first-generation (F_1) hybrids and quickly disappears in subsequent generations.

Earlier, we applied an ecological approach involving studies of the relationship between populations and changes in their structure, external (physical and geographical conditions and biotic factors), spatial, and temporal ones, with shifts in external conditions [Yablokov, 1987] and also put forward the version of the hybrid origin of the “large” horse mackerel [Zuyev, Melnikova, 2003]. Considering possible reasons for the occurrence of the “large” form in the Black Sea, we reviewed the hydrological situation in the region in the 1940s. Specifically, data on long-term changes (1923–1985) in the Black Sea hydrological regime were analyzed, namely total river flows [Gidrometeorologiya i gidrokhimiya morei SSSR, 1991]. As known [Samodurov, Ivanov, 1998], river flow is the main component of freshwater balance in the Black Sea. It determines the intensity of water exchange with the Sea of Marmara *via* the Bosphorus due to two opposite directional flows: the surface one transferring water with lower salinity from the Black Sea and the bottom one transferring saline Mediterranean water to the Black Sea. An increase in river flow to the Black Sea during high-water years leads to a rise in thickness of the upper desalinated layer and, accordingly, to weakening of the lower Bosphorus flow, whilst a decrease in river flow during low-water years is accompanied by weakening of the upper Black Sea current and a gain in the lower Bosphorus flow. In low-water years, 2–2.5 times more Mediterranean Sea water usually penetrates into the Black Sea with the lower Bosphorus flow as compared to the long-term mean value [Bogdanova, 1972]. Such years are the most favorable for the invasion of flora and fauna representatives from the Mediterranean Sea into the Black Sea.

The analysis of mean annual volumes of total river flows into the Black Sea Basin over more than 60 years showed as follows: 1943 was the most low-water year (Fig. 1). Specifically, total volume of river flow constituted only 69.5% of the long-term mean one and 46.6% of the maximum registered in 1941. Thus, hydrological conditions in 1943 were the most favorable for penetration of the Mediterranean horse mackerel *T. mediterraneus mediterraneus* into the Black Sea over a long period of time.

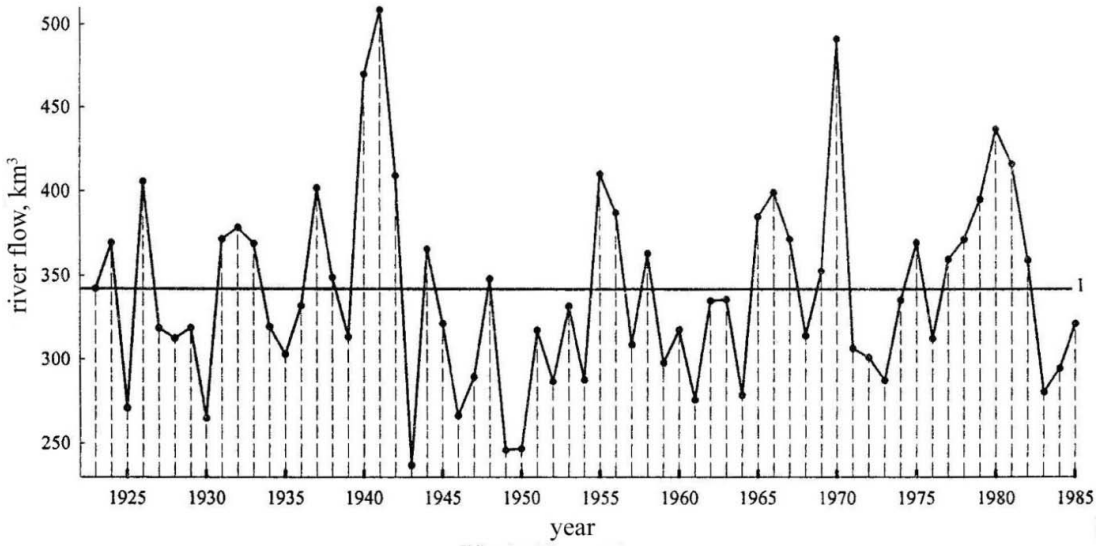

Fig. 1. Long-term dynamics of river flow in the Black Sea Basin (1, the long-term mean value of river flow [Gidrometeorologiya i gidrokhimiya morei SSSR, 1991])

Рис. 1. Многолетняя динамика речного стока в бассейне Чёрного моря (1 — среднемноголетнее значение речного стока [Gidrometeorologiya i gidrokhimiya morei SSSR, 1991])

Interestingly, the study of the age composition for the “large” horse mackerel population confirmed its appearance in the Black Sea in 1943 [Tikhonov, 1959]. We suggest as follows: in 1943, a mass migration of *T. mediterraneus mediterraneus* to the Black Sea occurred; it was accompanied by crossing of *T. mediterraneus mediterraneus* and *T. mediterraneus ponticus* and, accordingly, by formation

of hybrids. A similar process of intraspecific hybridization of the Sea of Azov anchovy (*Engraulis encrasicolus maeoticus* Pusanov & Zeeb, 1926) and the Black Sea anchovy (*Engraulis encrasicolus ponticus* Alexandrov, 1927) resulted from *E. encrasicolus ponticus* penetration into the Black Sea in the post-glacial period [Zuyev, Skuratovskaya, 2023].

According to the law of maximum development of the heterosis effect, the first-generation (F_1) hybrids should highly exceed the subsequent ones in terms of viability, endurance, and productivity. To confirm, we carried out a comparative analysis of viability of different hybrid generations. We concentrated on indicators of viability providing the "large" horse mackerel an advantage in struggle for survival: its growth rate, maximum size, and population fecundity.

We suggested that *T. mediterraneus mediterraneus* penetrated from the Mediterranean Sea into the Black Sea in 1943, and its population included all age classes. The lifespan of the Mediterranean horse mackerel is 7–8 years, and its maturity occurs in the 2nd year [Dobrovolov, 1988]. Accordingly, the appearance of F_1 hybrids might be expected annually over 6 to 7 years (1943 to 1949–1950). With life expectancy of 17–18 years [Revina, Saf'yanova, 1966a, b; Saf'yanova, Revina, 1960], F_1 hybrids could live until 1967–1968. Considering the fact that F_1 hybrids reach maturity at the age of 4, the appearance of the second-generation (F_2) hybrids should have been expected no earlier than in 1947. So, only the first four "large" horse mackerel generations (those of 1943–1946) were regarded as F_1 hybrids. Starting from the generation born in 1947, the "large" horse mackerel population included F_1 and F_2 hybrids; since the early 1950s, it could cover representatives of more than two genetically different hybrid generations in which shares of F_1 and F_2 hybrids consistently decreased.

In accordance with the law of heterosis effect attenuation resulting from crossing of genetically different hybrid generations, there should have been a drop in viability of succeeding generations of the "large" horse mackerel. R. Shaverdov studied growth of the "large" form representing generations of the 1950s and concluded as follows: growth rates for the "large" and "small" horse mackerel were similar [1964]. However, by that time, the "large" horse mackerel was a totality of genetically different hybrid generations that varied significantly in viability, namely in growth rate. This is how, in our opinion, the "paradox of Shaverdov" can be explained.

According to the version of the hybrid origin of the "large" horse mackerel against the backdrop of the law of heterosis effect attenuation, starting from the generation of 1947 (the year when F_2 hybrid appeared in the population), the differentiation of specimens by viability could be observed. Therefore, certain attention should be paid to detection of the "middle" ("intermediate") form differing from the "large" one by lower growth rate, smaller size of specimens, lower fecundity, a special type of population abundance dynamics, and even body shape (Fig. 2). Importantly, the "middle" form was initially registered in 1947, and this corresponded to the appearance of F_2 hybrids.

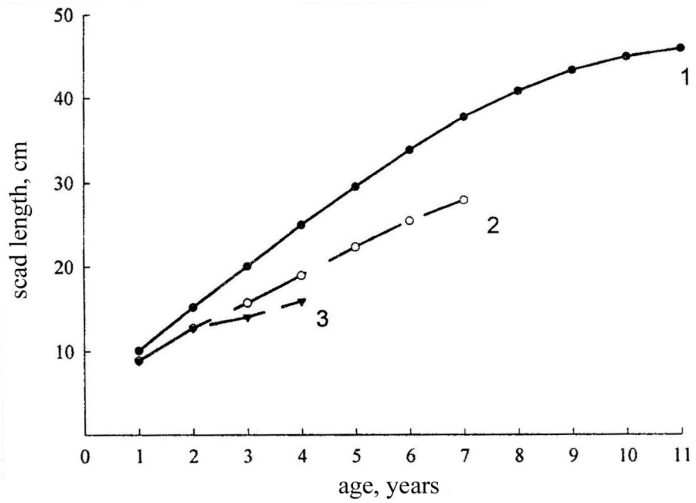

Fig. 2. Growth of different forms of the horse mackerel in the Black Sea: 1, the "large" horse mackerel; 2, the "middle" one; 3, the "small" one [Tikhonov, 1959]

Рис. 2. Рост ставриды разных форм в Чёрном море: 1 — крупная ставрида; 2 — средняя; 3 — мелкая [Tikhonov, 1959]

Similar biological differentiation was found in generations of the “large” horse mackerel in 1957, 1958, 1962, and 1963 [Revina, Saf’yanova, 1966b]. Within each of them, two groups of specimens were determined. Those were similar in growth rate, maximum size, life expectancy, and age of maturity. However, in contrast to previous generations, those were significantly smaller and less abundant which fully complied with the law of heterosis effect attenuation.

Meanwhile, admitting the version of the hybrid origin, many other phenomena can be explained as well: a drop in fecundity in succeeding generations, dramatic reduction in commercial catches within a short period of time, “biological transformation” of the “large” horse mackerel into a “small” one, *etc.* The abovementioned facts result from the heterosis effect attenuation. Thus, the most abundant generations, those of 1945–1949, included mainly F_1 hybrids, with a very small share of F_2 ones in which the heterosis effect was most pronounced. A decline in population abundance of the “large” horse mackerel in the 1950s reflected a decrease in a share of fast-growing and larger F_1 hybrids with higher absolute fecundity and their replacement by smaller and, correspondingly, less fecund F_2 hybrids in which the heterosis effect was less pronounced.

At the same time, a decline in total abundance of F_1 hybrids and in fecundity and growth rate of F_2 hybrids resulted in a noticeable decrease in the population recruitment. Consequently, there was a sharp increase in the mean age of the “large” horse mackerel exploited population. Within 1953–1963, the mean age of commercially caught fish gradually rose from 4.7 to 12.9 years, and this led to a dramatic reduction in catches. In 1957, catches of the “large” form dropped by more than 3 times compared to those in previous year.

Nevertheless, a decrease in abundance of subsequent generations of hybrids is not the only reason for a decline in recruitment of the “large” horse mackerel population. Interestingly, in 1955 and 1956, very high spawning intensity and abundance of juveniles were recorded [Saf’yanova, Revina, 1960]. The second reason for disappearance of the “large” form is the occurrence of significant changes in its biology, since those result not only in a decrease of growth rate and size of specimens, but also in reduction in lifespan and fluctuations in the age of maturity, *i. e.*, a complete “biological transformation” of the “large” horse mackerel into a “small” one.

Naturally, the question arises whether the Mediterranean horse mackerel migration into the Black Sea and its hybridization with the Black Sea horse mackerel occurred throughout the whole history of the Mediterranean–Black Sea Basin, over the last 5–7 thousand years (since the last opening of the Bosphorus), or only once, in 1943. There is no definite answer. However, considering evidences for the “large” form appearance in various areas of the sea in different periods, it can be assumed as follows: processes of crossing might have occurred in the past, but their scale was obviously not so significant. The question could be answered properly after clarification of the taxonomic status of specimens. At the same time, the belonging of large specimens to *Trachurus trachurus* seems to be very doubtful: this species is sporadic in the Black Sea and is registered only in waters adjacent to the Bosphorus, while its occurrence off the coasts of Georgia and Crimea remains questionable [Svetovidov, 1959]. Literature data on the “large” horse mackerel confirm its appearance in various areas of the sea: off the Crimean and Caucasian coasts and off the coasts of Georgia, Turkey, and Romania.

It is noteworthy as follows. The registration of an 11-year-old horse mackerel specimen, 44 cm in length, in 1979 [Dobrovolov, Manolov, 1983] also could not clarify this issue, for it might belong to fast-growing F_2 hybrids related to the generation of 1968 or to hypothetical F_1 hybrids that might appear after a possible migration of the Mediterranean horse mackerel into the Black Sea during low-water years: 1949 and 1950.

In our conviction, the invasion of the Mediterranean horse mackerel into the Black Sea and its hybridization with the Black Sea horse mackerel are not accidental, but reflect the mediterranization. This process has intensified due to increasing anthropogenic load on the Black Sea ecosystem,

ongoing disruption of freshwater balance because of the overregulation of river flows and sea salinization, and climate warming. The probability of the “large” horse mackerel invasion into the Black Sea may become higher in future.

Unfortunately, it is impossible to confirm or refute any version by molecular genetic methods due to the current absence of the “large” form in the Black Sea. Therefore, despite the existence of these versions, the origin of the “large” horse mackerel and reasons for its appearance in the Black Sea remain unexplained.

This work was carried out within the framework of IBSS state research assignment “Biodiversity as the basis for the sustainable functioning of marine ecosystems, criteria and scientific principles for its conservation” (No. 124022400148-4).

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ФЕНОМЕН ПОЯВЛЕНИЯ КРУПНОЙ СТАВРИДЫ В ЧЁРНОМ МОРЕ: ВЕРСИИ И ДОКАЗАТЕЛЬСТВА

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В статье обсуждаются литературные данные и результаты собственных исследований авторов, посвящённых объяснению феномена внезапного массового появления в Чёрном море в конце 1940-х гг. и столь же неожиданного исчезновения в середине 1960-х гг. крупной («гигантской») формы ставриды (род *Trachurus*, Carangidae) (КС). Данный феномен вызвал огромный интерес и привлёк внимание многих авторов как возможный источник новых сведений для познания процессов и путей адаптации организмов, а также проблем микроэволюции и видообразования. Проведён анализ разных подходов к изучению этого явления, включая выяснение происхождения и таксономического статуса КС. На их основе были предложены три взаимоисключающие версии. Согласно первой, КС является новым видом средиземноморского происхождения, согласно второй — экоморфой *Trachurus mediterraneus ponticus*, согласно третьей версии — гибридом *Trachurus mediterraneus mediterraneus* и *T. mediterraneus ponticus*. В результате анализа теплоустойчивости изолированных мышц и серологического исследования тканевых белков Ю. П. Алтухов с соавторами выделили КС в самостоятельный вид, имеющий средиземноморское (и даже, возможно, атлантическое) происхождение, и указали, что его массовое появление в Чёрном море произошло из-за внезапного расширения ареала вследствие резкого увеличения (взрыва) численности. Основные аргументы в пользу черноморского происхождения КС заключаются в том, что все этапы её жизненного цикла — размножение, рост молоди, нагул и зимовка взрослых особей — проходят в Чёрном море, а крупные экземпляры были известны и ранее. Принадлежность мелкой черноморской ставриды и КС к одному виду подтверждена результатами электрофоретических исследований белкового состава сыворотки крови этих форм. Версию гибридного происхождения КС первым предложил И. Доброволов после изучения электрофоретических спектров неспецифических мышечных эстераз *T. mediterraneus ponticus* и *T. mediterraneus mediterraneus*. В соответствии с нашими исследованиями, третья версия происхождения КС кажется более вероятной, чем другие. Проникновение *T. mediterraneus mediterraneus* в Чёрное море и её скрещивание с *T. mediterraneus ponticus* — это проявление процесса медитерранизации, усилившегося в результате возрастающего антропогенного воздействия на экосистему Азово-Черноморского бассейна, а также продолжающегося нарушения баланса пресных вод из-за зарегулирования речного стока и осолонения моря. Ни одна из трёх версий не может быть опровергнута или доказана молекулярно-генетическими методами ввиду отсутствия в настоящее время КС в Чёрном море. Таким образом, феномен появления крупной ставриды в Чёрном море остаётся необъяснённым.

Ключевые слова: черноморская крупная ставрида, версии, средиземноморское происхождение, черноморское происхождение, гибридное происхождение