

Fishes of the Caspian Sea: zoogeography and updated check-list

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Geographic distribution of some 350 taxa from the Caspian and Black Sea basins were analyzed with regard to recent taxonomy, phylogeny, endemism and ecological classification. A check-list of the Caspian Sea fishes (taxa from families down to subspecies) is provided. Eighty species and subspecies permanently occur or occasionally recorded from the North Caspian while 33–35 species and subspecies being only distributed in the Middle and South Caspian. Forty-four species are common for the two ecoregions. A comparison of the Caspian and the Black Sea fish faunas and their historical evolution is given with special respect to palaeogeography and palaeohydrology of the basin.

Key words: Caspian Sea, fishes, evolution, zoogeography, taxonomic composition

INTRODUCTION

The Black, Azov, Caspian and Aral seas, remnants of the intracontinental Paratethys basin, possess a spectacular diversity of the biota. The term “Paratethys” was coined by Laskarev (1924) to designate the string of epicontinental basins originally stretching from the Alps to what was the Aral Sea that has been separated from the rest of the Tethys by the uplift of the Alpine-Caucasian mountain chain since the Early Oligocene. Many groups of aquatic organisms including fishes have radiated in this region (e. g. Mordukhai-Boltovskoi, 1979; Dumont, 1998). Diversification in the Paratethys has been traditionally linked to isolation events from the Mediterranean and the Atlantic and Indian Oceans resulted in restricted marine, brackish lacustrine, and freshwater lacustrine environments, and induced the evolution of endemic species and higher taxa among molluscs, ostracods, fish, and other groups of animals (e. g. Băcescu, 1940; Zenkevich 1963; Starobogatov, 1970, 1994; Bănărescu, 1991; Jones & Simmons, 1996, 1997; Dumont, 2000).

It has been debated in literature if the Caspian Sea is really a sea though freshened, or just a giant lake. Dumont (1998) presents

arguments for this water body being a true lake and not a sea. However, the Caspian biotic diversity clearly reflects its relationship to the Caspian geological history as an isolated basin of the world ocean, and also a complex process of immigration from the Mediterranean and Atlantic Ocean.

Physical environment of the Caspian Sea

A number of publications summarise much of the literature about the geomorphological structure and hydrology of the Caspian Sea, e.g. Kosarev & Yablonskaya (1994), Mandych (1995), Golubev (1997), Mamaev (2002), Reid & Orlova (2002), Coad (2008). Below we briefly overview only those features which has the most significant impact on recent diversity and distribution of fishes – salinity and its gradient, depth, seafloor morphology, and temperature – in two major ecoregions of the Caspian Sea (for the ecoregions, see Bogutskaya, 2007 and Naseka & Bogutskaya, 2007).

The Caspian Sea lies between 47°13' and 36°34'35'' north latitude and between 46°38'39'' and 54°44'19'' east longitude. Statistics for the Caspian Sea (Mamaev, 2002): surface area approximately

390,000 km², water volume 78,700 km³, coastal length 7,000 km, average depth 208 m (184 m by other sources), maximum depth 1,025 m. The Caspian Sea catchment area is about 3.5 million km². The length of the Caspian (north-south) is approximately 1,200 km. The greatest breadth of the Caspian from east to west is 466 km; in the region of the Absheron Peninsula, its breadth is only 204 km. The average breadth of the Caspian from the west to the east is 330 km. These figures vary to a considerable extent for the sea level is changing. The Caspian Sea's size varied during the Quaternary Period. During the glacial epoch the sea decreased because of the decline of flow throughout the basin. However, during the post-glacial Khvalyn transgression its level was approximately 50 m higher than oceanic levels, or 75 m higher than current levels. At that time waters of the Caspian Sea spread far north and occupied the entire Caspian Lowland; the area of the sea was nearly two times as large as it is now. The highest water level, -22 m, was reached about 38,000 years ago, but may have been as low as -64 m. The water level averages -27.66 m over the past 2,500 years (Dumont, 1998). Early in the last century (up to 1929), the sea level fluctuated around -26.2 m, later decreasing to -29.0 m in 1977 and to -29.02 m in 1978 (Kosarev & Yablonskaya, 1994). In 1978 a rapid rise began, the level reaching -27.0 m by 1994. Since 1995 some regression has been observed in the sea level.

The huge basin of the Caspian Sea is morphologically split into three parts: 1) a northern shallow part (less than 10 m), separated from the middle by a line passing from the estuary of the Terek River to the Mangyshlak Peninsula; 2) a middle part, with an average depth of 200 m and a maximum depth of 790 m; and 3) the southern and deepest section, with a maximum depth of 980–1025 m and average depth equal to 325 m.

The northern part of the Caspian Sea is on the margin of the Pre-Caspian synclorium of the Eastern European platform. South of this geological feature and divid-

ing the North and Middle Caspian is the Mangyshlak Threshold, which is structurally connected to the submerged Karpinski Ridge on the western coast and to the Mangyshlak mountains of the eastern coast. The North Caspian Sea is thus bordered in the south by a traverse from Chechen' Island to the Tyub-Karagan Cape, and Mangyshlak Bay. The eastern part of the Precaspian [Prikaspiiskaya Nizmennost'] Lowland is also included. This area represents the former shallow bays of the Caspian Sea, which were covered by water to a greater or lesser extent until the beginning of the 20th century; since 1930–1945 the area has dried completely. However, the coastline is again changing due to recent water level increases. The ecoregion also includes the entire Volga Delta. The place of separation of the Buzan branch is regarded as the area where the Volga Delta begins. From there the Volga River is split into a dense network of arms and anabranches. The Volga River delta is one of the largest deltas in the region. The numerous arms, anabranches, island, and sand ridges (Baer's hillocks) occupy an area of more than 13,000 km². Within the limits of the Volga River are a great number of lakes. These are the so-called ilmens and polois of the Volga Delta; their number totals around 1,000. Ilmens of the delta are relatively more resistant, and partly retain water even during dry periods, whereas polois exist only during spring floods. In total, the Northern Caspian covers about 80,000 km². It is relatively shallow, averaging about 5–6 m in depth. The Ural Furrow is a slightly deeper (8–10 m) structure extending the Ural River trend across the shallow northeast shelf. Being much shallower than the Middle and South Caspian, the Northern Caspian contains only 1% of the Caspian's total volume. The Volga River contributes up to 82% of the inflow. Salinity in the North Caspian varies markedly, from 0.1 parts per thousand (ppt) at the mouth of the Volga and Ural rivers to up to 10–11 ppt near the Middle Caspian. The size and position of the mixing zone varies with the

volume of Volga River outflow and sometimes covers almost the whole area of the northern Caspian Sea (Katunin, 1986).

The Middle and South Caspian are naturally separated from the shallow Northern Caspian. The Middle Caspian floor has a heterogeneous geological structure. The Derbent Depression, the western portion of the shelf, and the continental slope are part of the marginal synclinorium trough of the Great Caucasus. The Apsheron Rift (or Threshold) dividing the South and the Middle Caspian is a structure formed as a continuation of folded structures of the Great Caucasus, part of the alpine fold region. The continental slope, shelf, and the bottom of hollows are prominent in the deep parts of the sea in the Middle and South Caspian, and submarine ridges are prominent in the South Caspian. Thus, in terms of geomorphology the Middle Caspian is a hollow, bounded by the Mangyshlak Rift in the north and by the Apsheron Rift in the south. According to some authors, the deep-water part of the Caspian is a combination of three hollows. The deepest is the Derbent hollow with a flat bottom that is slightly inclined to the southwest. The shelf is the narrowest (up to 11 km) and the continental slope is the steepest (up to 1°) around Derbent and Divichi. The shelf expands to the south, and the continental slope becomes declivous. Tectonic uplifts in the form of banks and islands line the shelf around the Apsheron Peninsula. The average depth of the Middle Caspian is 215 m. The shelf occupies 56% of the area of the Middle Caspian; its edge lies at approximately 100 m in depth. In the South Caspian which is separated from the Middle Caspian by the Apsheron Rift, forty-six percent of the area lies on the shelf at depths up to 100 m. The shelf of the western coast south of the Apsheron Peninsula has many banks, islands, and mud volcanos. The most dissected part of the eastern shelf is the one adjoining Cheleken. South of Cheleken is Ogurchinskii Island, Ulski Bank, and Gryaznyi Volcano. The continental slope in the South

Caspian is very steep, with the eastern slope running deeper and wider than the western slope. The deepwater South Caspian hollow is bounded by depths of 800–900 m: in the north it appears to project between two submarine ridges. To the south the undulations gradually disappear and the bottom levels off over most of the hollow. Between the hollow and the Apsheron Rift are two ridges that extend in a south-southwest direction, and reach 200–250 m above the water level. The middle and southern parts of the sea have only small fluctuations of salinity; surface salinity is about 12.6 to 13.5 ppt, increasing from north to south and from west to east. There is also a slight increase in salinity with depth (0.1 to 0.2 ppt) observed in all regions of the sea. The Karabogaz Gol which is situated on the eastern coast of the Caspian Sea and bites deep into the hinterland is hypersaline.

Water temperature in the Caspian Sea varies considerably with latitude. This difference is greatest (about 10°C) in the winter when temperatures in the north are 0–0.5°C near the ice and 10–11°C in the south. Freezing temperatures are found in the north and in shallow bays along the eastern coast. The water temperature of the west coast is generally 1–2°C higher than along the east coast. In the open sea, the water temperatures are higher than those near the coast by 2–3°C in the Middle Caspian and by 3–4°C in the southern part of the sea.

Palaeogeography

The border between the Mediterranean and Paratethyan bioprovinces was dynamic; in extreme cases, the Mediterranean completely invaded the Paratethys (as in some periods of the Early Miocene), or Paratethyan waters drained into the dry Mediterranean basin, as it is supposed for some intervals in the Messinian. Thus the history of the Paratethyan basins has been an involved story of opening and closing connections (towards each other and the Medi-

terranean), catastrophic transgressions, and episodes of desiccation (Schulz et al., 2005).

There is a big number of publications discussing palaeogeography and palaeohydrology of the Caspian Sea, some most recent are those by Benson (1976), Nevevskaya et al. (1986), Rögl (1998, 1999), Meulenkamp et al. (2000), Vasiliev et al. (2004, 2005), Popov et al. (2004, 2006). Palaeontological data were widely used in publications discussing the Caspian fauna composition and its evolution, e. g. those by Starobogatov (1994), Dumont (1998, 2000), Aladin & Plotnikov (2000), Reid & Orlova (2002). We are not intending to provide a full review of the issue but try below to emphasize some aspects which may be critical for understanding of the Caspian fish fauna transformation through the history of the Paratethys.

During the Mesozoic and early Cenozoic, the Eurasian and African continents were separated by a large oceanic basin called the Tethys. Global plate tectonic processes caused a northward motion of the African plate with respect to Eurasia and led to continental collision and the gradual closure of the Tethys Ocean. These tectonic movements generated the elevation of the Alpine–Himalayan mountain belt, which started to act as an E–W striking barrier since the beginning of the Oligocene. Consequently, the Tethys Ocean evolved into two different domains, the Mediterranean basin to the south and the Paratethys to the north. The Mediterranean remained an open marine basin because the connection to the Atlantic guaranteed the exchange of water masses and organisms, permitting a direct biostratigraphic correlation to the world's oceanic record. The Paratethys became semi-isolated with brackish to fresh water environments that led to the development of endemic faunas and different biozonations. In addition, ongoing tectonics caused a fragmentation of the Paratethys into various subbasins, which were affected by a continuous changing of the water surface extent and of the water connections between subbasins and the Mediterranean

and Indian Ocean. The Paratethys region is divided into a western and eastern Paratethys, which are separated from each other by the Carpathian mountain range. The western Paratethys formed in the back (to the north and west) of the Alpine–Carpathian belt and comprises the Pannonian and Transylvanian basins (Austria, Hungary and NW Romania). The eastern Paratethys developed in the Alpine–Carpathian foredeep and consists of the Dacian, Euxinian and Caspian basins. The Black Sea and the Caspian Sea are the actual brackish water remains of this ancient water mass.

Throughout its past, short episodes of abrupt salinity rises as a result of saline infusions from neighbouring marine waters were followed by a slow return to brackish conditions. The first isolation event of the Paratethys, indicated by the appearance and abundance of endemic molluscs, took place in the late Early Oligocene (Rupelian, Kiscellian, Solenovian). The second such Paratethys-wide isolation event happened during the late Early Miocene (Burdigalian, Ottangian, Kozahurian), and the third in the late Middle Miocene (Serravallian in the Mediterranean, Sarmatian s. str. in the Central Paratethys, Volhynian in the Eastern Paratethys) (Schulz et al., 2005; Popov et al., 2004, 2006). During the late Miocene, the continental Eastern Paratethyan basin evolved into the Sarmatian which developed 9–9.9 million years ago (Mya) (Semenenko, 1987; Steininger et al., 1996) into the slightly brackish Pontian basin. The most usual correlation proposes correspondence of the Maeotian with the Middle–Upper Tortonian, and Pontian with the entire Messinian (Iljina & Nevevskaja, 1979; Rögl, 1998). This correlation was supported by absolute age data (Chumakov, 1993): 9.3 Mya for the lower boundary of the Maeotian, 8.0–8.4 Mya for the Lower/Upper Maeotian boundary, 7.1 Mya for the Maeotian–Pontian boundary, and 5.2–5.3 Mya for upper boundary of the Pontian (Popov et al., 2006). However, the Neogene chronology of the eastern Paratethys is poorly defined.

Ages of stages can easily vary by more than 1 or 2 million years between different basins and different studies: a good example is the Pontian Stage for which estimates of the duration vary from 3.0 Mya to 0.3 Mya (Vasiliev et al., 2004). The Early Pontian basin was strongly enlarged, especially by transgression along its northern and eastern margins. Deep-water environments existed only in the Black Sea and South Caspian depressions. Based on the prevailing brackish fauna, the salinity of the basin was low, but it did not fall under 5–8 ppt (Popov et al., 2004). A pronounced regression started at the beginning of the Late Pontian (Portaferrian and Babadzhanian), and the Ciscaucasian Strait was closed, separating the Caspian Basin from the Euxinian Basin. The eastern lake-sea became restricted to the recent Middle and South Caspian depressions, including the Kura Gulf. This fall in sea level approximately corresponded in time with a drastic sea level drop in the Mediterranean (5.7–5.6 Mya). The salinity of Late Pontian Lake remained at the level of 10–15 ppt, however in Babadzhan Lake, due to higher climate aridity, it probably increased up to 15–30 ppt or even higher (Aladin, 1989; Aladin & Plotnikov, 2000). Babadzhan Lake existed for about 1 million years (Aladin & Plotnikov, 2000) or less (Popov et al., 2004) and undergone a drastic further regression. This basin, Balakhanian, which occupied the South Caspian depression and the Kura Gulf, also known as the Reservoir of the Productive Series, played a key role in the history of the Caspian biota (reviewed by e.g. Tarasov, 2001). Most authors suppose that this basin was saline or hypersaline (about 100 ppt or higher) and traditionally, since Mordukhai-Boltovskoi (1960), it has been accepted that the Caspian Pontian biota experienced a bout of extinctions. However, a group of well-known experts on the palaeo-history of Paratethys (Popov et al., 2004) supposes that the Balakhanian basin was freshwater.

The drastic regression during the Balakhanian was followed by a major (the larg-

est one in the history of the Eastern Paratethys) transgression (Akchagylia, around 3.4–1.8 Mya) which resulted in an inflow of oceanic water, probably from the Persian Gulf (Zenkevich, 1963). It is commonly supposed that this oceanic influence had a devastating effect on the brackish water fauna of Pontian origin in the Caspian basin, but only a minor effect on the Kujalnician (Black Sea) basin though the brackish-water Akchagilian basin was connected with the Euxinian depression through the Kuma-Manych Straight. However, recent data show that the salinity at the beginning of the Akchagilian was about 20–25 ppt and then decreased to 5–12 ppt due to large inflow of fresh waters.

The successive basins since about 1.8 Mya (Apsheron, Baku, Khazar, and Khvalyn) that followed the Akchagilian basin were also brackish water reservoirs and experienced large water level and salinity changes (Aladin & Plotnikov, 2000). Caspian and Euxinian basins had repeated interconnections through Pleistocene (Svitoch, 1991) until, probably, as recently as Late Khvalynian (Badyukova, 2005).

Most authors (e.g. Băcescu, 1940; Bănărescu, 1991; Dumont, 2000) have concluded that the primary Miocene basins, the Sarmatian and Pontian Lakes, played a decisive role in initializing the radiation of most Ponto-Caspian lineages and terms such as “Sarmatian relicts” or “Pontian relicts” are common in the literature when referring to the origins of the local fauna. It is generally believed that taxa of Miocene origin survived in the succeeding Pliocene and Pleistocene basins of the Black and Caspian Seas. However, because both basins experienced at least one major bout of extinction during episodes of high salinity, coupled with several opportunities for subsequent faunal exchange, there is much confusion regarding the evolutionary history of the fauna (Cristescu et al., 2003).

With regard to fishes, a key question is thus the salinity tolerance and salinity preferences of different groups of taxa in

terms of both the extant adaptations and the evolution of ecological characteristics through time. With regard to salinity, four ecological groups are distinguished among the Caspian Sea animals: 1. freshwater forms, inhabiting estuaries and coastal waters with a salinity of 0–2 ppt; 2. coastal and brackish forms, occurring in waters of a salinity ranging from around 2 to 7 ppt (some species may be euryhaline living in a broader range of the salinity); 3. brackish water forms inhabiting waters of a salinity from 3–5 to 10–11 ppt; 4. ‘marine’ forms (mostly of Mediterranean origin) found in waters of a salinity 8–10 ppt and higher (Aladin & Plotnikov, 2000).

Traditionally (since Mordukhai-Boltovskoi, 1960, 1964, 1979; Zenkevich, 1963), the fish species of the Caspian Sea are grouped as *autochthonous*, *freshwater*, *Mediterranean*, and *Arctic*. This grouping is based on a mixture of different criteria, ecological and historical ones, and gives only a very preliminary picture of the fish fauna origin and evolution in the Caspian basin. Besides, our knowledge on the taxonomy and phylogeny of many groups dramatically changed since 1960–80s.

Understanding of endemic radiations, phylogenies and migration of the fauna are among the best tools in the reconstruction of past paleogeographic changes, and vice versa, understanding successive stages in the evolution and fragmentation of the Paratethys basin provide the opportunity to gain new insights into the biotic diversity in general and the phylogeny of different taxa and communities in particular.

Thus, the goal of this paper is to review the Caspian Sea fish fauna composition and zoogeography using the most recent taxonomic and phylogenetic data, both original and taken from literature. Ecological groups of species are discussed. Comparisons between Northern, Middle and South Caspian fish faunas are done as well as a comparison with some fish taxa distributed in the Black Sea.

MATERIAL AND METHOD

The initial database comprised over 2800 taxa (family to subspecies or local “form” of doubtful status) of lampreys and freshwater fishes inhabiting over 200 drainages and lake basins entirely or partially lying within the borders of the former USSR and adjacent countries (see in Naseka & Bogutskaya, 2007).

For the purposes of this study, geographic distribution of some 350 taxa from the Caspian and Black Sea basins were analyzed. The principal sources for these data are material deposited at the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), in Kalmyk State University (Elista), Caucasian Biosphere Reserve (Adler), Natural History Museum (Vienna), Zoological Institute and Museum of Hamburg University, Canadian Museum of Nature (Ottawa) collections, field observations of a number of expeditions to the drainage areas of the Kuban and Western Transcaucasia (2001, 2002), to the Lower Don and Lower Volga (2002), Northern Azov region and the Crimea (2002, 2003), Daghestan (2004), Azerbaijan (2008), and critically analyzed data from extensive existing literature. Some groups have not been revised yet taxonomically or phylogenetically. As a result, the taxonomic assignments given to some fishes are based on preliminary although reasonable assumptions.

Fish taxa are classified according to their tolerance to salt water and mode of life according to Kessler (1877) and Myers (1938, 1949, 1951).

RESULTS AND DISCUSSION

General characteristic of the fish fauna

Indigenous fish fauna of the Caspian Sea basin (including drainages of rivers belonging to it) encompass 159 species and subspecies from 60–62 genera (four to six endemic) of 19 families. Ninety-nine species and subspecies (62%) may be considered

endemic to the basin. The most numerous is the family Cyprinidae (27 genera), then goes Gobiidae (12 genera); other families are much less numerous (1–3 genera).

List of families and genera of the Caspian Sea basin fishes

Petromyzontidae: *Caspiomyzon* Berg, 1906 (endemic), *Eudontomyzon* Regan, 1911, *Lampetra* Bonnaterre, 1788.

Acipenseridae: *Acipenser* Linnaeus, 1758, *Huso* Brandt & Ratzeburg, 1833

Clupeidae: *Alosa* Linck, 1790, *Clupeonella* Kessler, 1877.

Cyprinidae: *Rhodeus* Agassiz, 1832, *Barbus* Cuvier, 1816, *Capoeta* Valenciennes, 1842, *Luciobarbus* Heckel, 1843, *Carassius* Jarocki, 1822, *Cyprinus* Linnaeus, 1758, *Gobio* Cuvier, 1816, *Romanogobio* Bănărescu, 1961, *Abramis* Cuvier, 1816, *Acanthalburnus* Berg, 1916, *Alburnoides* Jeitteles, 1861, *Alburnus* Rafinesque, 1820, *Aspius* Agassiz, 1832, *Ballerus* Heckel, 1843, *Blicca* Heckel, 1843, *Chondrostoma* Agassiz, 1832, *Leucalburnus* Berg, 1916 (endemic or not for may be a synonym of the genus *Telestes* Bonaparte, 1840, M. Kottelat, pers. comm.), *Leucaspis* Heckel & Kner, 1858, *Leuciscus* Cuvier, 1816, *Phoxinus* Rafinesque, 1820, *Pseudophoxinus* Bleeker, 1860, *Rutilus* Rafinesque, 1820, *Scardinius* Bonaparte, 1837, *Squalius* Bonaparte, 1837, *Vimba* Fitzinger, 1873, *Pelecus* Agassiz, 1835, *Tinca* Cuvier, 1816.

Cobitidae: *Cobitis* Linnaeus, 1758, *Misgurnus* La Cèpède, 1803, *Sabanejewia* Vladikov, 1929

Nemacheilidae: *Barbatula* Linck, 1790, *Oxynoemacheilus* Banarescu & Nalbant, 1966, *Paracobitis* Bleeker, 1863.

Siluridae: *Silurus* Linnaeus, 1758.

Exocidae: *Esox* Linnaeus, 1758.

Osmeridae: *Osmerus* Linnaeus, 1758.

Coregonidae: *Coregonus* Linnaeus, 1758, *Stenodus* Richardson, 1836.

Thymallidae: *Thymallus* Cuvier, 1829.

Salmonidae: *Hucho* Günther, 1866, *Salmo* Linnaeus, 1758.

Lotidae: *Lota* Oken, 1817.

Atherinidae: *Atherina* Linnaeus, 1758.

Gasterosteidae: *Pungitius* Coste, 1848.

Syngnathidae: *Syngnathus* Linnaeus, 1758.

Cottidae: *Cottus* Linnaeus, 1758.

Percidae: *Gymnocephalus* Bloch, 1793, *Perca* Linnaeus, 1758, *Sander* Oken, 1817.

Gobiidae: *Anatirostrum* Iljin, 1930 (endemic), *Babka* Iljin, 1927 (earlier considered a synonym or a subspecies of *Neogobius*), *Benthophiloides* Beling & Iljin, 1927 (including *Asra* Iljin, 1941, endemic of the Caspian Sea which may be a distinct genus), *Benthophilus* Eichwald, 1831, *Caspiosoma* Iljin, 1927, *Chasar* Vasilieva, 1996 (endemic of the Caspian Sea but may be a synonym of *Ponticola*), *Hyracanogobius* Iljin, 1928 (endemic; a synonym of *Knipowitschia* by some authors), *Knipowitschia* Iljin, 1927, *Mesogobius* Bleeker, 1874, *Neogobius* Iljin, 1927, *Ponticola* Iljin, 1927 (earlier considered a synonym or a subspecies of *Neogobius*), *Proterorhinus* Smitt, 1899.

Indigenous fish fauna of the Caspian Sea proper (the sea, lagoons and river deltas) including those species which are only occasionally found in the sea includes 115 species and subspecies from 52 genera and 15 families (Table).

The most numerous is the family Gobiidae (35 species from 12 genera), then goes Cyprinidae (32 species and subspecies from 22 genera) and Clupeidae (22 species and subspecies from two genera). The number of Caspian species and subspecies, 115, is markedly less than that in the Black and Mediterranean seas with about 200 and 550 species and subspecies, respectively. Endemic for the sea are at least two genera, *Caspiomyzon*, *Anatirostrum*, but we suppose that *Hyracanogobius* and *Chasar* should be also considered as distinct genera until a phylogenetic study is done, that lifts the number of endemic genera up to four. The number may be five if *Asra* is accepted as a separate genus. At species level, endemic are 73 species and subspecies (63.5% of the total number).

Table. List of indigenous fish taxa known to occur in the Caspian Sea (e, endemic for the Caspian; +, present/recorded in North and Middle+South Caspian; other abbreviations explained in text).

Taxon	Ecological group	Whole Caspian Sea	North Caspian	Middle and South Caspian
PETROMYZONTIDAE		+	+	+
Caspiomyzon Berg, 1906		e	+	+
<i>C. wagneri</i> (Kessler, 1870)	anadr	e	+	+
ACIPENSERIDAE		+	+	+
Acipenser Linnaeus, 1758		+	+	+
<i>A. gueldenstaedtii</i> Brandt & Ratzeburg, 1833	anadr	+	+	+
<i>A. nudiiventris</i> Lovetsky, 1828	anadr	+	+	+
<i>A. persicus</i> Borodin, 1897	anadr	e	+	+
<i>A. ruthenus</i> Linnaeus, 1758	fluv	+	+	+
<i>A. stellatus</i> Pallas, 1771	anadr	+	+	+
Huso Brandt & Ratzeburg, 1833		+	+	+
<i>H. huso</i> (Linnaeus, 1758)	anadr	+	+	+
CLUPEIDAE		+	+	+
Alosa Linck, 1790		+	+	+
<i>A. braschnikowi braschnikowi</i> (Borodin, 1904)	marine	e	+	+
<i>A. braschnikowi agrachanica</i> (Mikhailovskaya, 1941)	marine	e	+	+
<i>A. braschnikowi autumnalis</i> (Berg, 1915)	marine	e		+
<i>A. braschnikowi grimmi</i> (Borodin, 1904)	marine	e		+
<i>A. braschnikowi kisselevitschi</i> (Bulgakov, 1926)	marine	e		+
<i>A. braschnikowi nirchi</i> (Morozov, 1928)	marine	e		+
<i>A. braschnikowi orientalis</i> (Mikhailovskaya, 1941)	marine	e		+
<i>A. braschnikowi sarensis</i> (Mikhailovskaya, 1941)	marine	e		+
<i>A. caspia caspia</i> (Eichwald, 1838)	marine	e	+	+
<i>A. caspia aestuarina</i> (Berg, 1932)	marine	e	+	
<i>A. caspia knipowitschi</i> (Iljin, 1927)	marine	e		+
<i>A. caspia persica</i> (Iljin, 1927)	marine	e		+
<i>A. caspia salina</i> (Svetovidov, 1936)	marine	e	+	
<i>A. curensis</i> (Suvorov, 1907)	marine	e	+	+
<i>A. kessleri</i> (Grimm, 1887)	anadr	e	+	+
<i>A. saposchnikowii</i> (Grimm, 1885)	marine	e	+	+
<i>A. sphaerocephala</i> (Berg, 1913)	marine	e	+	
<i>A. volgensis</i> (Berg, 1913)	anadr	e	+	+
Clupeonella Kessler, 1877		+	+	+
<i>C. caspia</i> Svetovidov, 1941	marine	e	+	
<i>C. engrauliformis</i> (Borodin, 1904)	marine	e	+	+

Table (continued).

Taxon	Ecological group	Whole Caspian Sea	North Caspian	Middle and South Caspian
<i>C. grimmi</i> Kessler, 1877	marine	e		+
<i>C. tsarchalensis</i> (Borodin, 1896)	estuarine	e	+	
CYPRINIDAE		+	+	+
Acheilognathinae		+		+
Rhodeus Agassiz, 1832		+		+
<i>Rhodeus</i> sp.	fluv	e		+
Barbinae		+	+	+
Barbus Cuvier, 1816		+		+
<i>B. cyri</i> De Filippi, 1865	fluv	e		+
Capoeta Valenciennes, 1842		+		+
<i>C. gracilis</i> (Keyserling, 1861)	fluv	+		+
Luciobarbus Heckel, 1843		+	+	+
<i>L. brachycephalus caspius</i> (Berg, 1914)	fluv&anadr	+	+	+
<i>L. capito capito</i> (Gueldenstaedt, 1773)	fluv&anadr	+	+	+
Cyprininae		+	+	+
Carassius Jarocki, 1822		+	+	
<i>C. carassius</i> (Linnaeus, 1758)	fluv	+	+	
<i>C. gibelio</i> (Bloch, 1782)	fluv	+	+	
Cyprinus Linnaeus, 1758		+	+	+
<i>C. carpio</i> Linnaeus, 1758	fluv&semi-anadr	+	+	+
Gobioninae		+	+	
Gobio Cuvier, 1816		+	+	
<i>G. volgensis</i> Vasil'eva, Mendel, Vasil'ev, Lusk & Lusková, 2008	fluv	e	+	
Romanogobio Bănărescu, 1961		+	+	
<i>R. albipinnatus</i> (Lukasch, 1933)	fluv	e	+	
Leuciscinae		+	+	+
Abramis Cuvier, 1816		+	+	+
<i>A. brama</i> (Linnaeus, 1758)	semi-anadr	+	+	+
Alburnus Rafinesque, 1820		+	+	+
<i>A. alburnus</i> (Linnaeus, 1758)	fluv	+	+	
<i>A. chalcoides</i> (Gueldenstaedt, 1772)	anadr	e	+	+
<i>A. hohenackeri</i> Kessler, 1877	fluv	+		+
Aspius Agassiz, 1832		+	+	+
<i>A. aspius</i> (Linnaeus, 1758)	semi-anadr	+	+	

Table (continued).

Taxon	Ecological group	Whole Caspian Sea	North Caspian	Middle and South Caspian
<i>A. aspius taeniatus</i> (Eichwald, 1831)	anadr	e		+
Ballerus Heckel, 1843		+	+	+
<i>B. ballerus</i> (Linnaeus, 1758)	fluv&semi-anadr	+	+	
<i>B. sapa</i> (Pallas, 1814)	fluv	+	+	+
Blicca Heckel, 1843		+	+	
<i>B. bjoerkna bjoerkna</i> (Linnaeus, 1758)	fluv&semi-anadr	+	+	
<i>B. bjoerkna transcaucasica</i> Berg, 1916	fluv&semi-anadr	e		+
Chondrostoma Agassiz, 1832		+	+	
<i>Ch. variable</i> Jakovlev, 1870	fluv	+	+	
Leucaspis Heckel & Kner, 1858		+	+	+
<i>L. delineatus</i> (Heckel, 1843)	fluv	+	+	
Leuciscus Cuvier, 1816		+	+	
<i>L. idus</i> (Linnaeus, 1758)	fluv&semi-anadr	+	+	
<i>L. leuciscus</i> (Linnaeus, 1758)	fluv	+	+	
Rutilus Rafinesque, 1820		+	+	+
<i>R. caspicus</i> (Yakovlev, 1870)	semi-anadr	e	+	+
<i>R. kutum</i> (Kamensky, 1901)	anadr	e	+	+
<i>R. rutilus</i> (Linnaeus, 1758)	fluv	+	+	
Scardinius Bonaparte, 1837		+	+	
<i>S. erythrophthalmus</i> (Linnaeus, 1758)	fluv&semi-anadr	+	+	
Squalius Bonaparte, 1837		+	+	
<i>S. cephalus</i> (Linnaeus, 1758)	fluv	+	+	
<i>S. orientalis</i> (Nordman, 1840)	fluv	+	+	
Vimba Fitzinger, 1873		+	+	+
<i>V. persa</i> (Pallas, 1814)	anadr	e	+	+
Pelecinae		+	+	+
Pelecus Agassiz, 1835		+	+	+
<i>P. cultratus</i> (Linnaeus, 1758)	fluv&semi-anadr	+	+	+
Tincinae		+	+	
Tinca Cuvier, 1816		+	+	
<i>T. tinca</i> (Linnaeus, 1758)	fluv	+	+	
COBITIDAE		+	+	
Cobitis Linnaeus, 1758		+	+	
<i>C. melanoleuca</i> Nichols, 1925	fluv	+	+	

Table (continued).

Taxon	Ecological group	Whole Caspian Sea	North Caspian	Middle and South Caspian
Misgurnus La Cepède, 1803		+	+	
<i>M. fossilis</i> (Linnaeus, 1758)	fluv	+	+	
Sabanejewia Vladykov, 1929		+		+
<i>S. aurata</i> (De Filippi, 1863)	fluv	e		+
<i>S. caspia</i> (Eichwald, 1838)	fluv	e		+
<i>S. caucasica</i> (Berg, 1906)	fluv	e		+
SILURIDAE		+	+	+
Silurus Linnaeus, 1758		+	+	+
<i>S. glanis</i> Linnaeus, 1758	fluv&semi-anadr	+	+	+
ESOCIDAE		+	+	+
Esox Linnaeus, 1758		+	+	+
<i>E. lucius</i> Linnaeus, 1758	fluv&semi-anadr	+	+	+
COREGONIDAE		+	+	
Stenodus Richardson, 1836		+	+	
<i>S. leucichthys</i> (Gueldenstaedt, 1772)	anadr	e	+	+
SALMONIDAE		+	+	+
Salmo Linnaeus, 1758		+	+	+
<i>S. caspius</i> Kessler, 1877	fluv&anadr	e		+
<i>S. ciscaucasicus</i> Dorofeyeva, 1967	fluv&anadr	e	+	+
LOTIDAE		+	+	
Lota Oken, 1817		+	+	
<i>L. lota</i> (Linnaeus, 1758)	fluv	+	+	
ATHERINIDAE		+	+	+
Atherina Linnaeus, 1758		+	+	+
<i>A. caspia</i> Eichwald, 1831	marine	e	+	+
GASTEROSTEIDAE		+	+	+
Pungitius Coste, 1848		+	+	+
<i>P. platygaster</i> (Kessler, 1859)	fluv&estuarine	+	+	+
SYNGNATHIDAE		+	+	+
Syngnathus Linnaeus, 1758		+	+	+
<i>S. caspius</i> Eichwald, 1838	marine	e	+	+
PERCIDAE Cuvier, 1816		+	+	+
Perca Linnaeus, 1758		+	+	
<i>P. fluviatilis</i> Linnaeus, 1758	fluv	+	+	

Table (continued).

Taxon	Ecological group	Whole Caspian Sea	North Caspian	Middle and South Caspian
Sander Oken, 1817		+	+	+
<i>S. lucioperca</i> (Linnaeus, 1758)	fluv&semi-anadr	+	+	+
<i>S. marinus</i> (Cuvier, 1828)	marine	+		+
<i>S. volgensis</i> (Gmelin, 1788)	fluv&semi-anadr	+	+	
GOBIIDAE		+	+	+
Anatirostrum Iljin, 1930		e		+
<i>A. profundorum</i> (Berg, 1927)	marine	e		+
Babka Iljin, 1927		+	+	+
<i>B. macrophthalma</i> (Kessler, 1877)	marine	e	+	+
Benthophiloides Beling & Iljin, 1927		+		+
<i>B. brauneri</i> Beling & Iljin, 1927	marine&estuarine	+		+
<i>B. turcomanus</i> (Iljin, 1941)	marine	e		+
Benthophilus Eichwald, 1831		+	+	+
<i>B. abdurahmanovi</i> Ragimov, 1978	marine&estuarine	e	+	+
<i>B. baeri</i> Kessler, 1877	marine	e	+	+
<i>B. casachicus</i> Ragimov, 1978	marine	e		+
<i>B. ctenolepidus</i> Kessler, 1877	marine	e		+
<i>B. granulatus</i> Kessler, 1877	marine&estuarine	e	+	+
<i>B. grimmi</i> Kessler, 1877	marine	e		+
<i>B. kessleri</i> Berg, 1927	marine	e	+	+
<i>B. leobergius</i> Berg, 1949	marine	e	+	+
<i>B. leptcephalus</i> Kessler, 1877	marine	e		+
<i>B. leptorhynchus</i> Kessler, 1877	marine	e		+
<i>B. macrocephalus</i> (Pallas, 1787)	marine&estuarine	e	+	+
<i>B. mahmudbejovi</i> Ragimov, 1976	marine&estuarine	e	+	+
<i>B. pinchuki</i> Ragimov, 1982	marine	e		+
<i>B. ragimovi</i> Boldyrev & Bogutskaya, 2004	marine	e		+
<i>B. spinosus</i> Kessler, 1877	marine	e		+
<i>B. svetovidovi</i> Pinchuk & Ragimov, 1979	marine	e		+
Caspiosoma Iljin, 1927		+	+	
<i>C. caspium</i> (Kessler, 1877)	marine&estuarine	+	+	
Hyrceanogobius Iljin, 1928		e	+	+
<i>H. bergi</i> Iljin, 1928	marine&estuarine	e	+	+
Knipowitschia Iljin, 1927		+	+	+
<i>K. caucasica</i> (Berg, 1916)	marine&estuarine	+	+	

Table (continued).

Taxon	Ecological group	Whole Caspian Sea	North Caspian	Middle and South Caspian
<i>K. iljini</i> Berg, 1931	marine	e		+
<i>K. longicaudata</i> (Kessler, 1877)	marine&estuarine	+	+	+
Mesogobius Bleeker, 1874		+	+	+
<i>M. nigrnotatus</i> (Kessler, 1877)	marine	e		+
<i>M. nonultimus</i> (Iljin, 1936)	marine	e	+	+
Chasar Vasilieva, 1996		e	?	+
<i>Ch. bathybius</i> (Kessler, 1877)	marine	e	?	+
Neogobius Iljin, 1927		+	+	+
<i>N. caspius</i> (Eichwald, 1831)	marine	e	+	?
<i>N. pallasii</i> (Pallas, 1814)	marine&estuarine &fluv	e	+	+
<i>N. melanostomus affinis</i> (Eichwald, 1831)	marine&estuarine &fluv	e	+	+
Ponticola Iljin, 1927		+	+	+
<i>P. goebelii</i> (Kessler, 1874)	marine	e	?	+
<i>P. gorlap</i> (Iljin, 1949)	marine&estuarine &fluv	e	+	+
<i>P. syrman eurystomus</i> (Kessler, 1877)	marine&estuarine	e	+	+
Proterorhinus Smitt, 1899		+	+	+
<i>Proterorhinus</i> sp. (Lower Volga tube-nose goby)	fluv&estuarine	e	+	
<i>P. nasalis</i> (De Filippi, 1863)	marine	e	+	+

Reported in the Caspian Sea are about 28 non-indigenous species from 18 genera of 14 families, as given below.

Acipenseridae: *Acipenser baerii baicalensis* Nikolsky, 1896, *Acipenser baerii chatys* Drjagin, 1948.

Polyodontidae: *Polyodon spathula* (Walbaum, 1792).

Anguillidae: *Anguilla anguilla* (Linnaeus, 1758).

Engraulidae: *Engraulis encrasicolus* (Linnaeus, 1758).

Cyprinidae: *Ctenopharyngodon idella* (Valenciennes, 1844), *Hemiculter leucisculus* (Basilevsky, 1855), *Carassius auratus* (Linnaeus, 1758), *Pseudorasbora parva* (Tem-

minck & Schlegel, 1846), *Aristichthys nobilis* (Richardson, 1845), *Hypophthalmichthys molitrix* (Valenciennes, 1844).

Salmonidae: *Oncorhynchus gorbuscha* (Walbaum, 1792), *Oncorhynchus keta* (Walbaum, 1792), *Oncorhynchus kisutch* (Walbaum, 1792), *Oncorhynchus (Rhabdofario) mykiss* (Walbaum, 1792), *Salmo salar* Linnaeus, 1758.

Mugilidae: *Liza aurata* (Risso, 1810), *Liza haematocheilus* (Temminck & Schlegel, 1845), *Liza saliens* (Risso, 1810).

Poeciliidae: *Gambusia affinis* (Baird et Girard, 1853), *Gambusia holbrooki* Girard, 1859.

Gasterosteidae: *Gasterosteus aculeatus* Linnaeus, 1758.

Moronidae: *Morone saxatilis* (Walbaum, 1792).

Mullidae: *Mullus barbatus* Linnaeus, 1758.

Scombridae: *Scomber scombrus* Linnaeus, 1758.

Channidae: *Channa argus* (Cantor, 1842).

Scophthalmidae: *Psetta maeotica* (Pallas, 1814).

Pleuronectidae: *Platichthys flesus* (Linnaeus, 1758).

Only few species have been established, such as *Pseudorasbora parva*, *Hemiculter leucisculus*, *Liza aurata*, *Liza saliens*, *Gambusia* (probably two species), *Gasterosteus aculeatus*. Some species are questionably established but numerous in the basin due to stocking, such as *Aristichthys nobilis*, *Hypophthalmichthys molitrix*, *Ctenopharyngodon idella*. The Indian carps (Cyprinidae) *Cirrhinus mrigala*, *Labeo rohita* and *Catla catla* are being reared in aquaculture stations and are potential escapees into the natural environment (Gilkolaei, 2007, cited from Coad, 2008).

Non-indigenous species are not included in the zoogeographical discussion below.

Distribution of species and subspecies in North, Middle and South Caspian

Analyzing distribution of fishes, we found no significant difference between the Middle Caspian and the South Caspian (Naseka & Bogutskaya, 2007).

As it can be seen from the Table, 80 species and subspecies permanently occur or occasionally recorded from the North Caspian while 33–35 species and subspecies being only distributed in the Middle and South Caspian. Forty-four species are common for the two ecoregions.

A more prominent picture can be drawn when the fluvial species, which are rarely met in the sea occurring only in deltas and freshened coastal shallows, are excluded from calculations. Freshwater and fluvial are 25 species – *Acipenser ruthenus*, *Rhodeus* sp., *Barbus cyri*, *Capoeta gracilis*, *Carassius*

carassius, *Carassius gibelio*, *Gobio volgensis*, *Romanogobio albiginnatus*, *Ballerus sapa*, *Alburnus alburnus*, *Alburnus hohenackeri*, *Chondrostoma variable*, *Leucaspis delineatus*, *Leuciscus leuciscus*, *Rutilus rutilus rutilus*, *Squalius cephalus*, *Squalius orientalis*, *Tinca tinca*, *Cobitis melanoleuca*, *Misgurnus fossilis*, *Sabanejewia aurata*, *Sabanejewia caspia*, *Sabanejewia caucasica*, *Lota lota*, *Perca fluviatilis*. When these species are excluded, the number of species inhabiting the sea falls to 90. Among them, 17 occur only in the North Caspian and 25 (may be 27) – only in the Middle and South Caspian. Forty-eight species (including three species with questionable distribution) inhabit or migrate through all three major partitions of the sea.

Ecological groups of fishes

Classification introduced by Kessler (1877) is based on criteria of physical habitats and the presence/absence of migrations between them; he grouped the Aral-Ponto-Caspian fishes into *marine*, *fluvial*, 'of various waters' ["raznovodnyye"], *anadromous* and *semi-anadromous*. This classification concerns tolerance to salt water by indication only. It is worth emphasizing that dealing with the Aral-Caspian fishes any author realized well that no one species is true marine for salinity in these water bodies hardly exceeds 13.7 ppt in most areas. A term *marine* reflects the geomorphology of the water body rather than its salinity. We slightly modified the classification adding a category 'estuarine' and combinations of the categories (see Table).

Most of the 25 fluvial freshwater species mentioned above belong to the families Cyprinidae and Cobitidae which are *primary division families* sensu Myers (1938, 1951) (i.e. those families whose members are strictly intolerant of salt water, both currently and historically). Lotidae and Percidae are *secondary division families* (i.e. those families which are supposed to be of marine origin but contain members that now live in

fresh water). *Acipenser ruthenus* may be also classified as 'fluv/semi-anadr' for it historically had a semi-anadromous form. Eleven species currently have semi-anadromous forms, most of them belong to primary division families (Cyprinidae, Siluridae, Esocidae) while two – to a secondary division family Percidae. Distribution of the fluvial species reflects zoogeographical delineation between river drainages rather than zoogeography of the sea.

Semi-anadromous fishes (14 species and subspecies) keep spawning in fresh water (limnetic waters, 0.5 ppt and less) but forage in oligohaline water (around 0.5–5 ppt). There is only one endemic (questionable) subspecies, *A. aspius taeniatus*, that is restricted by the Middle and South Caspian; all other taxa inhabit the North Caspian or the whole sea being distributed in areas adjacent to large river mouths, especially the Volga River delta.

Seventeen species and subspecies are anadromous; they spawn in rivers, often much farther upstream than semi-anadromous fishes, and forage all over the sea undertaking long-distance migrations. However, Caspian fishes of this group are not strictly diadromous sensu Myers because they migrate between fresh and oligohaline-mesohaline waters rather than between fresh and true sea (euhaline) water. They belong to the primary division families Cyprinidae and Coregonidae, and to Petromyzontidae, Acipenseridae and Salmonidae; origin of the latter three families are still debated in literature (for Acipenseridae see discussion in Artyukhin, 2008). Degree of endemism is high in this group, 11 from 17 (64%). Most anadromous species, especially those from the family Cyprinidae and Salmonidae, are (historically were) much more numerous in the Middle and South Caspian being rare or occasional migrants in the North Caspian (entering the Volga).

Sixteen species are classified as 'estuarine' mostly inhabiting deltaic areas and adjacent coastal shallows, some of them being distributed also in lower reaches of riv-

ers and/or open marine habitats. Most species – 14 – belong to the family Gobiidae. This group contains those species which can be classified as vicarious sensu Meyers, i. e. strictly or preferably freshwater or oligohaline species of primarily marine families. Eleven species (69%) from this group are endemic for the Caspian Sea.

Strictly 'marine' or almost marine (mostly inhabiting the open sea, benthic or pelagic waters) form a largest group of species from the secondary division families Clupeidae (19 species and subspecies), Atherinidae (1 species), Syngnathidae (1 species), Percidae (1 species) and Gobiidae (22 species). All species but one (43 from 44) are endemic for the basin. Many species of this group are tolerant for the whole range of Caspian salinity though some clearly prefers the upper part of the range, up to 13.7 ppt in South Caspian, and historically could even occur and spawn in areas with higher salinity such as the former Mertvy Kultuk [= Zaliv Tsesarevicha, Zaliv Komsomolets] and Kaydak bays. For example, *Alosa caspia salina* was known to spawn in the Mertvy Kultuk Bay at a salinity of up to 32.2 ppt and its larvae were found in areas with salinity up to 45.6 ppt, and *Alosa braschnikowi* was reported in the Kaydak Bay at a salinity of 47.7 ppt (Svetovidov, 1952).

The data presented above clearly confirm and even emphasize a well known fact that some Clupeidae and Gobiidae represent in the Caspian Sea examples of adaptive diversification. However, taxonomy and phylogeny of the Caspian taxa can not be understood without a comparison with the Black Sea 'paired' taxa. Each of these groups – *Alosa*, *Clupeonella*, benthophilin and neogobiin gobies within the Paratethys limits – meets the definition of species flocks sensu Greenwood (1984) – a geographically circumscribed, monophyletic taxon characterized by marked radiation. This was specifically underlined for the Benthophilinae by Neilson & Stepien (2009). Below we try to briefly analyse the most recent data on taxonomy and phylogeny of some taxa in

the Caspian and the Black Sea to show their relationships and the supposed degree of differences in order to roughly estimate the degree (and relative age) of their divergence.

Comparison of the Caspian and the Black Sea fish faunas and their evolution

Petromyzontidae. *Caspiomyzon* is the only one absolutely undoubted Caspian endemic genera. There are no indications that any close form existed in the Black Sea basin though the migratory lamprey from the Black Sea is still a poorly known issue (for discussion see Kottelat et al., 2005 and Naseka & Diripasko, 2008).

Acipenseridae. Most authors do not accept an idea that there are distinct Caspian and Black Sea species and subspecies within each 'sturgeon' inhabiting the two basins (e.g. Artyukhin, 2008). However, at least for few cases, there are different opinions. For example, Kottelat & Freyhof (2007) accepted the opinion that *Acipenser persicus* and *A. colchicus* Marti, 1940 are distinct species though commonly considered synonyms or subspecies of the same species. Russian sturgeon *A. gueldenstaedtii* from the Caspian may be different at least on the subspecies level from *A. gueldenstaedtii tanaicus* Marti, 1940 (Sea of Azov) and *A. gueldenstaedtii danubicus* (described as *A. gueldenstaedtii colchicus* nation *danubica* Movchan, 1967) (western Black Sea basin) (taxonomy of Russian sturgeon was reviewed by Podushka, 2003). *Huso huso* from the Caspian Sea was described as a distinct subspecies based on morphological differences as *Huso huso caspicus* Babushkin, 1942. Morphological difference between Caspian and Black Sea beluga sturgeons were earlier described by other authors (Sal'nikov & Malyatskiy, 1934). Movchan (1970) described a Black Sea subspecies of stellate sturgeon, *A. stellatus ponticus* Movchan, 1970. These taxonomic conclusions have been largely ignored by most other authors but need special attention at least for understanding of Caspian and Black Sea lineages within

these species as distinct evolutionary significant units (ESUs).

Clupeidae. Since long time most subspecies and 'forms' of *Alosa* had been considered as belonging to three species – *A. caspia* (puzanok-shads), *A. braschnikowi* (marine shads) and *A. kessleri* (anadromous shads) – distributed in both the Caspian and the Black Sea basins. Then, the Black Sea 'subspecies' were considered as distinct species (see reviews by Bogutskaya & Naseka, 2004 and Kottelat & Freyhof, 2007) – *A. immaculata* Bennett, 1835 (as *A. kessleri pontica* in Svetovidov, 1952), *A. maeotica* (Grimm, 1901) (as *A. brashnikovii maeotica* in Svetovidov, 1952), *A. tanaica* (Grimm, 1901) (as *A. caspia tanaica* in Svetovidov, 1952) with subspecies *Alosa tanaica etemi* Battalgil, 1941, *Alosa tanaica nordmanni* Antipa, 1904, and *Alosa tanaica palaeostomi* (Sadovsky, 1934) of disputed status. Respective paired species of all three groups of shads – puzanok-shads, marine shads and anadromous, or migratory, shads – in the Caspian Sea are much more diverse, and each contains (Table) distinct species and subspecies of the uncertain status. Unfortunately, no recent revision or phylogenetic study has been done on this group of Caspian fishes but morphological differences between them described in a number of detailed publications (as can be seen from a review by Svetovidov, 1952) deserve special attention (Panin et al., 2005) and give reason to suspect that most of them are distinct species if phylogenetic methodology is applied.

There are three species of *Clupeonella* in the Caspian Sea – *C. engrauliformes*, *C. grimmi*, *C. caspia* – and one more species, *C. tscharchalensis*, which was originally described from the Charkhal Lake and then reported from backwaters at Saratov (Borodin, 1905). Both *C. caspia* and *C. tscharchalensis* were earlier considered synonyms of *C. cultriventrif* (Nordmann, 1840). Besides the latter species, there are two more local freshwater species in the Black Sea basin – *C. abrau* Malyatskiy, 1928

(Abrau Lake, Russia) and *C. muhlisi* Neu, 1934 (Apoloyond Lake, Turkey). *Clupeonella engrauliformes* and *C. grimmi*, being typical brackish water marine pelagic tyulkas which commonly occurs over big depths in the Middle and South Caspian.

Cyprinidae. Among anadromous cyprinids the most striking difference of the Caspian fauna from the Black Sea fauna is the presence in the Caspian (and the Aral Sea basin) of two species of the genus *Luciobarbus*. This genus contains over 30 species widely distributed in the Iberian Peninsula, North Africa and Middle East but absent from the Black Sea. Three other anadromous cyprinid species form pairs with the Black Sea – *Rutilus kutum* and *R. frisii* (Nordmann, 1840), *Vimba persa* and *V. vimba* (Linnaeus, 1758), *A. chalcoides* (probably conspecific with *A. chalcoides aralensis* Berg, 1924) and a number of migratory shemayas in different river drainages and lake basins of the Black Sea (*A. danubicus* Antipa, 1909, *A. derjugini* Berg, 1923, *A. istanbulensis* Battalgi, 1941, *A. leobergi* Freyhof & Kottelat, 2007, *A. mandrensis* (Drensky, 1943), *A. mentoides* Kessler, 1859, *A. sarmaticus* Freyhof & Kottelat, 2007, *A. schischkovi* (Drensky, 1943), *A. vistonicus* Freyhof & Kottelat, 2007; for more information on these species see Freyhof & Kottelat, 2007a, 2007b and Kottelat & Freyhof, 2007). The *Alburnus* complex has not been yet phylogenetically studied while the former two pairs of species (formerly pairs of conspecific subspecies) have been analysed using molecular markers. It was shown for *R. kutum* and *R. frisii* (though the taxonomic conclusion was not done) that the latest gene migration between them from the Caspian Sea to the Black Sea occurred on average 250,000–450,000 years ago and migration in the opposite direction took place on average 270,000–480,000 years ago (Kotlik et al., 2008). The authors made a conclusion that the two ‘forms’ maintained refugial populations in both the Black Sea and the Caspian Sea and diverged despite periods of migration between them. These data to-

gether with some clear morphological differences give good reasons for considering *R. kutum* and *R. frisii* as distinct species. Similar data were received for *Vimba* (Hänfling et al., 2009) supporting (not contradicting) the suggestion to rank the Caspian vimba as a separate species *V. persa*.

Salmonidae. Taxonomic status of many subspecies, ‘forms’ and local groups populations of *Salmo trutta* Linnaeus, 1758 in wide sense has been one of the most controversial issues in ichthyology since long time. Some authors supposed that *S. caspius* Kessler, 1877 (South Caspian, Kura and Iranian rivers), *S. ciscaucasicus* Dorofeyeva, 1967 (eastern Middle and North Caspian, rivers from northern Azerbaijan to Volga and Ural, mostly Terek River) and *Salmo labrax* Pallas, 1814 from the Black Sea may represent distinct species (Bogutskaya & Naseka, 2004; Bogutskaya & Dorofeyeva, 2007; Kottelat & Freyhof, 2007). We do not know any publication analysing the time of divergence between the three species. The age of *S. caspius* and *S. ciscaucasicus* divergence can be dated as post-Balaxhanian; *S. caspius* appears to be closer to an ancestor of the both species which was distributed in the restricted Balaxhanian basin (current South Caspian) while *S. ciscaucasicus* may represent a lineage that expanded northwards during the Akchagilian transgression, and gene flow between the lineages became interrupted because of stable using of different rivers for spawning.

Atherinidae and Syngnathidae. Zenkevich (1963) supposed that two ‘marine’ species (names given as *Atherina mochon pontica* and *Syngnathus nigrolineatus*) had the Mediterranean-Atlantic origin and penetrated the Caspian basin from the Black Sea relatively recently, during Khvalynian some 50,000 years ago. However, Tarasov (2001) has a different opinion which is based on published data on differences in morphology, ecology and parasitic fauna of the Caspian and the Black Sea *Atherina*, *Syngnathus* and *Knipowitschia* species; this author estimates the age of divergence as

5.5–6.0 Mya and supposes that holoeuryhaline ancestors of the Caspian species inhabited the Pontic basin (N_{1p}) and survived the Balakhanian salinity crisis. We agree with this opinion and consider *Atherina boyeri* Risso, 1810 and *A. caspia* as distinct species as well as *Syngnathus abaster* Risso, 1827 and *S. caspius*.

Gobiidae. The genus *Benthophilus* now includes 20 species, 16 from which occur only in the Caspian basin (Boldyrev & Bogutskaya, 2004, 2006). Based on morphological characters and distribution the species can be divided into four groups. First group includes five species: *B. leptorhynchus*, *B. grimmi*, *B. svetovidovi*, *B. kessleri*, and *B. granulatus*. Second group is the largest and contains nine species: *B. mahmudbejovi*, *B. durrelli* Boldyrev & Bogutskaya, 2004, *B. abdurahmanovi*, *B. magistri*, *B. leobergius*, *B. stellatus* (Sauvage, 1874), *B. nudus* Iljin, 1927, *B. macrocephalus*, and *B. casachicus*. Third group contains four species: *B. ctenolepidus*, *B. leptocephalus*, *B. ragimovi*, and *B. pinchuki*. Fourth group includes only two species: *B. spinosus* and *B. baeri*. Some assumptions can be done based upon the most evident polarities of some morphological structures. Thus, the most ancestral type of dermal ossification is apparently that one with no differentiation into different types of ossicles when all of them resemble modified ctenoid scales being embedded into skin with only posterior edge exposed outside. Specialization included differentiation into tubercles and granules with subsequent reduction of both tubercles and granules or enlargement of tubercles and decrease of the number of granules. If this hypothesis is true, so the first group is the most ancestral one and the second one diverged from it; the third and the fourth groups are probable derivatives of the second group.

Species of the presumably ancestral group occur only in the Caspian Sea, with four species having comparatively limited geographical distribution in Middle Caspian at depths up to 200 m (*B. leptorhynchus*, *B. svetovidovi*, *B. grimmi*) or in

coastal waters (*B. kessleri*) with water salinity of 10–14 ppt while a single species only, *B. granulatus*, is widely spread in both fresh and brackish waters (up to more than 20‰) of coastal waters of almost the whole sea, but prefers highly freshened waters of river deltas and lower reaches. The second group is the only one distributed now out of the Caspian Sea and adopted to highly freshened or pure fresh waters. Three Caspian species display undoubted phenotypic affinity to the species from the Pontic basin – *B. mahmudbejovi* and *B. durrelli*, *B. abdurahmanovi* and *B. magistri*, *B. leobergius* and *B. stellatus*. *Benthophilus nudus* from the Black Sea is also close to the latter pair. Similar to the first group, species of the third and fourth groups include species distributed only in the Caspian Sea and clearly confined to deeper waters (30–300 m) of the Middle and South Caspian.

These data give reasons to propose two opposing models, the origin of species via late Miocene vicariance events for the Black Sea/Caspian lineages vs. late Pliocene through Holocene dispersal events for lineages of the Black Sea basin. Both hypotheses suggest that the extant high diversity of endemic Caspian *Benthophilus* species reflects the continuity of the fauna since late Miocene-Pliocene and a complex process of speciation to specific conditions of the “brackish water sea”. They are different in explaining the historical reasons of the fewness of *Benthophilus* in the Black Sea basin. The vicariance model suggests that the Pontic fauna of *Benthophilus* experienced a high rate of extinctions due to Pleistocene climatic and hydrologic changes that produced dramatic transformations in the Black Sea basin. The few survivors retreated into the estuarine, lacustrine or riverine habitats along the margins of the Black Sea where they are represented now by 4–5 species. The dispersal model suggests relatively recent colonization events during periods of major transgression when brief contacts between the Caspian and the Black seas allowed faunal exchange, for example, in the

late Pliocene (between Akchagylian and Kuyalnikian basins), during the Apsheronian transgression of the Pleistocene, or throughout the Pleistocene. Both hypotheses suggest that the ancestor of *Benthophilus* inhabited Pontian basin about 7.1–5.8 Mya with some other “Pontic relicts” and survived the Balakhanian regression. Nielson & Stepien (2009) provide the estimated age for the node of tribe Neogobiini (*Neogobius*) + tribe Benthophilini (*Benthophilus* + *Caspiosoma*) as 9.18 Mya.

Quite recently, Neilson & Stepien (2009) provided the first comprehensive phylogenetic and biogeographic analysis of ‘neogobiini’ and ‘benthophilini’ (tadpole gobies) based on sequences from two mitochondrial and two nuclear genes with maximum parsimony, likelihood, and Bayesian approaches. Their data provided a solid basis for recognizing the subfamily Benthophilinae, which encompasses both the ‘neogobiini’ and tadpole gobies, and genetically diverges from other Gobiidae subfamilies including (non-monophyletic) Gobiinae and Gobinellinae. Benthophilinae contains three tribes: Neogobiini (*Neogobius*), Ponticolini (containing the genera *Mesogobius*, *Proterorhinus*, *Babka*, and *Ponticola* elevating the latter two from subgenera and removing them from the formerly paraphyletic *Neogobius*), and Benthophilini. Within Ponticolini, *Proterorhinus* and *Mesogobius* comprise the sister clade of the *Ponticola* and *Babka* clade.

Neilson & Stepien (2009) further discussed the evolutionary scenario of gobiids. They suppose that the Black and Caspian Sea basins contain an endemic Sarmatian fauna of gobies. There are two main clades, the gobiine-benthophilines (or transverse gobiids) and the pomatoschistines (or sand gobies), that have probably been distinct for at least 40 million years. The transverse gobiids include *Mesogobius*, *Neogobius*, *Proterorhinus*, *Chasar*, *Anatirostrum*, *Benthophiloides*, *Benthophilus* and *Caspiosoma* while the sand gobies include *Knipowitschia* and *Hyracanogobius*. The Sarmatian fauna was separated from the Atlantic-Mediterranean

fauna with the isolation of the Paratethys during the late Miocene and only the partial flooding of the Mediterranean from the Paratethys in the early Pliocene allowed Sarmatian gobies to spread westwards. Within the Ponto-Caspian basin, evolution of species flocks was favoured by basin subdivisions and rejoinings. The benthophilines may be a monophyletic group from these events. Their data made it possible to calculate approximate divergence times among lineages of Benthophilinae. The initial separation of the Black and Caspian Sea basins 5 Mya coincides with the diversification of most Neogobiini + Ponticolini genera (*Neogobius*, *Babka*, *Mesogobius*, *Ponticola*, and *Proterorhinus*), as well as diversification within Benthophilini (separation of *Benthophilus* and *Caspiosoma*). In addition to older divergences within Ponto-Caspian taxa, several recent separation events are identified such as several radiation events which occurred 1–2 Mya among the Ponticolini during the midst of the Pleistocene glacial cycles or Pleistocene-aged divergences of the two subspecies of *Neogobius melanostomus* (*N. m. melanostomus* in the Black Sea and *N. m. affinis* in the Caspian Sea).

CONCLUSIONS

Though the lack of Ponto-Caspian invertebrate species from Pliocene deposits in the bottom sediments of the Caspian Sea has sometimes been interpreted as evidence for a mass extinction, implying a discontinuity of the fauna in the Caspian Sea and a subsequent repopulation by lineages from the Black Sea, the presented data provide good reasons for a conclusion that the role of freshwater or slightly brackish coastal habitats as refugia along the basin margins during regressions of the sea was very important. This appears to be true even for the Balakhanian crisis. The conclusion supports hypotheses of other authors on a significant role of freshened coastal refugia in allowing lineage survival during intermittent pulses of high salinity (Tarasov, 2001; Cristescu et al., 2003).

The different divergence times discussed for some groups above (late Miocene, Pliocene and Pleistocene) support a scenario of repeated colonization and vicariance events in all group of fishes throughout the history of the Ponto-Caspian basin. One should also suppose to find different phylogeographical patterns in lineages with contrasting life history strategies. It is therefore probable that most of the taxa, which currently inhabit the both basins, represent pairs of evolutionary significant units, subspecies (probable distinct species) and species evolved under prolonged geographical isolation and exposed to different selective forces which has provoked their morphological and physiological differentiation. Besides, there are examples of intra-basin isolations and divergences including divergence in salinity preferences. Although there is a widespread opinion that Ponto-Caspian endemics are very euryhaline, there is evidence that their 'euryhalinity' is overestimated and most species groups (complex species sensu earlier authors) consist of distinctive evolutionary lineages (species or ESUs) demonstrating marked regional or intraspecific variation in their salinity tolerance.

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