

The Caspian Lake: History, biota, structure, and function

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Abstract

The elongate, endorheic Caspian Lake has a north–south orientation and its main freshwater inflow, the Volga River, enters at the shallow north end. Two deep basins occupy its central and southern regions. These facts lead to horizontal differences in temperature, salinity, and ecology. Nutrient levels and primary production are low. Historically, lake level has fluctuated by ~6 m, but on the geological timescale, fluctuations of >200 m have occurred. The lake formed in the late Miocene, first went through a long shrinking phase, expanded to three times its present size in the late Pliocene, and repeatedly rose and fell throughout the Pleistocene, with corresponding freshenings and salinizations. The lake surface has remained below sea level since the last pleniglacial. This dynamic history led to the assemblage of a set of euryhaline biota of Tethyan and freshwater origin, besides Baltic elements, that invaded with glacial meltwater. Endemism is as high as in Lake Baikal, but typical marine groups are absent. Because the lake is oxygenated to the bottom, its biota show a vertical zonation, but without a true abyssal community, suggesting catastrophic episodes of deep anoxia.

The Caspian “Sea,” the largest continental water body on earth, is situated in west Asia, east of the Caucasus and north of the Elburz Mountains. It is noted for its production of sturgeon, for its oil and gas resources, and for problems caused by its recent rise in water level, in contrast with the drying out of Aral Lake, its eastern neighbor. Problems include the flooding of townships, oil fields, agricultural areas, radioactive and toxic waste sites; pollution of the Volga, Ural, and Kura Rivers; and destruction of the spawning grounds of sturgeon, signalling a forthcoming collapse of the world caviar market (Dumont 1995).

The Caspian is the endorheic terminus of the Volga River, which contributes >80% of its total inflow, $237 \text{ km}^3 \text{ yr}^{-1}$ on average (Butorin 1979), with a range of 200–450 km^3 . The Kura River is second in line and discharges only $16.8 \text{ km}^3 \text{ yr}^{-1}$; the Ural River is third, with a discharge of $8.1 \text{ km}^3 \text{ yr}^{-1}$. Lake surface area, situated below sea level, is close to $400,000 \text{ km}^2$ and lake volume is $\sim 78,000 \text{ km}^3$, or ~40% of the world's continental surface water.

Here, I attempt to provide insight into the nature of the Caspian ecosystem, including its eventful past. I outline gaps in our knowledge and suggest research for the future.

Origin and history

Caspian history (Table 1) falls in two parts: (1) a Miocene stage, determined by tectonic events associated with the closing of the Tethys Sea, and (2) a Pleistocene stage, determined by glaciation cycles and the genesis of the modern Volga River (for details, see Atamuradov 1994; Kaplin 1995; Kosarev and Yablonskaya 1994; and Mordukhai-Boltovskoi 1979).

In stage one, the Tethys Sea had evolved into the brackish Sarmatian Lake, composed of the present Black Sea and south Caspian, when the collision of the Arabian peninsula with west Asia pushed up the Elburz-Kopet Dag and Cau-

casus Mountains, setting definitive south and west boundaries to the Caspian basin (Fig. 1). This orogenic movement continued throughout the Pontian, with the site of the present south Caspian sagging and disconnecting from the Black Sea. In the late Pontian, a mountain arch rose across the south basin and divided it in the Khachmas and Lenkoran Lakes (or early Balakhan). In the Balakhanian stage, continued sagging made this land bridge subside again, and a re-united Balakhan Lake was fed by the Paleo-Volga, Paleo-Kura, and Paleo Amu-Darja Rivers. This period of restriction to the south basin was reversed during the Akchagyglan ($3\text{--}2 \times 10^6 \text{ yr B.P.}$) when the lake expanded to more than three times its present area and established the first of a series of contacts with the Black Sea and with Lake Aral. Erosion gulleys in the Karakum Desert (Ali-Zade 1961, 1967) suggest that glacial meltwater from central Asia contributed much to this transgression. The lake surface was at +50 m, but its bottom had probably not yet sunk to its present position, such that its water volume may have been modest. A recession of this lake, Akchagyl, completed stage one.

Stage two began with the Apscheron transgression ($2\text{--}0.7 \times 10^6 \text{ yr B.P.}$), the first of a series of at least 11 high and low stands (Table 1). Lake level sank deeper at each repeat, to reach sea level in the late Khvalyn recession but even after that, the drop continued, with highs of -20 m and lows of -120 m . The rapid fluctuations of the Khazar, Khvalynsk, and New Caspian stadials were evidently linked to glaciation cycles, and probably involved *jokulhaups*, i.e. the sudden emptying of meltwater lakes accumulating at the foot of retreating glaciers in Russia. Such an event may have accounted for the capture of the Kama by the Volga at the end of the Dniepr-Riss glaciation, which almost doubled the size of the Volga catchment (Fortunatov 1979). More *jokulhaups* may have occurred during the Wurm III deglaciation ($12,000\text{--}15,000 \text{ yr B.P.}$), when a giant meltwater lake, Mologa-Sheksna, formed in the upper Volga at the site of the present Rybinsk Reservoir. It evacuated partly to the Baltic-White Sea, partly to the Caspian. One unresolved question is why, in spite of such major inputs of freshwater and an enlarged Volga drainage basin, did the level of the Caspian

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Table 1. Summary of the evolution of the Caspian Lake since the late Miocene.

| Major stages (years B.P.) | Substages (years B.P.) | Major events |
|---|---|---|
| Phase I | | |
| Miocene (ends circa 5×10^6) | Late Sarmation ($>7 \times 10^6$) | Caspian and Black Sea united |
| | Pontian ($>7 \times 10^6$) | |
| Pliocene ($5-2 \times 10^6$) | Early | Tectonic sagging; orogenesis sets limits to south basin |
| | Late | Low mountain Kilyazi–Krasnovodsk (K-K) range isolates middle from south basin |
| Phase II | | |
| Pleistocene (2×10^6 –present) | Balakhianian ($6-3 \times 10^6$) | K-K range subsides; a single lake in southern basin |
| | Akchagylian ($3-2 \times 10^6$) | Sudden major transgression to 50 m asl; connections with Black and Aral Lakes |
| Pleistocene (2×10^6 –present) | Apsheronian ($2-07 \times 10^6$) | Second major transgression to 50 m asl |
| | Baku ($5-4 \times 10^5$) | Transgression to around sea level |
| | Early Khazar ($3-2.5 \times 10^5$) | Transgression to 20 m asl; modern Volga basin formed |
| | Late Khazar ($1.4 \times 10^5-9 \times 10^4$) | Transgression to around sea level |
| | Early Khvalyn ($7 \times 10^4-10^4$) | Transgression to a maximum level of 50 m asl; several substages |
| | Late Khvalyn ($2 \times 10^4-10^4$) | Maximum level now equal to sea level; several substages |
| | Neocaspian (9×10^3 –present) | Four high stands, but maximum lake level only -20 m |

continue sinking? Studies of sediment cores from the deep basins will be needed to resolve this question.

Historic fluctuations and water balance

The Caspian has continued to fluctuate to the present but with amplitudes limited to ~ 6 m, and a mean level of 27.66 m below sea level across the past 2,500 years (Varuschenko 1987). Such fluctuations can be evidenced from written accounts and from shore markers like the town walls of Derbent (Fig. 1). Historical transgressions occurred in the 14th, 17th, and early 19th, centuries. These correlated well with periodic changes in the course of the Amu-Darja River.

From about A.D. 1840 to 1930, the Caspian stood at -26 m; between 1930 and 1977, a drop of >3 m occurred. In 1978, a rapid rise began, approaching the -26 m mark, but stabilizing and possibly reversing after 1995. Because coastal industries and townships had greatly expanded in the intervening half century, this rise is causing great economic damage, pollution, and an upsurge of interest in the causes of the fluctuations. Strange as this may seem, there is no consensus about these causes (Rodionov 1994). The reason for the uncertainty becomes clear when examining the water balance (δL) of the lake:

$$\delta L = R + P + G - E - KBG,$$

where R is river discharge, P is precipitation on the lake, G is groundwater inflow, E is evaporation, and KBG is outflow to the Kara Bogaz salt pan.

While it is easy to determine river discharge and on-site precipitation, there are problems in evaluating lakewide evaporation, the single largest loss factor, because of differences in local climate. Furthermore, groundwater inflow is uncertain. It is traditionally entered as a constant ($4 \text{ km}^3 \text{ yr}^{-1}$), but estimates vary up to $60 \text{ km}^3 \text{ yr}^{-1}$ (Rodionov 1994). Correlations between Volga discharge and lake level in the current century have been low (Kosarev and Yablonskaya 1994), while climate-driven changes in evaporation may have been cancelled out by the appearance of an oil film on

the water or by increased inflow of groundwater via the Karakum Desert since its large-scale irrigation with Amu-Darja water. Increased air humidity, a result of the evaporation of Amu-Darja water from the cotton fields of Uzbekistan, depressing evaporation, has also been postulated. The conclusion (Rodionov 1994) is that, while Volga inflow dominates the water balance, the measurement errors in other factors of the budget are too large to enable one to isolate noise from signal.

Physical and chemical characteristics

Many of the lake's particularities arise from the fact that it is north–south oriented. The Volga is at its north end, and its surface stretches over $>10^\circ$ latitude, spanning climate zones from continental to Mediterranean (Fig. 1). In addition, there is a gradient in aridity between its wet western and dry eastern shores. Here, straddling $41^\circ 30' \text{N}$, the evaporation pan of Kara Bogaz may hold up to 35 km^3 of water when full.

Lake bathymetry reveals a deep south (max. 1,025 m), a deep central (max. 788 m), and a shallow (max. 20 m) north basin. These parts are subequal in area, but differ strongly in volume (Fig. 1), with the fresher northern third representing only 0.5% of the lake's volume. Most freshwater from the Volga (total ions $200-400 \text{ mg liter}^{-1}$) (Zenin et al. 1979) enters the lake through the western delta and flows south along the west coast. Because of the shallowness of this area, rapid mixing with lake water produces a gradient in salinity of up to 1‰ per km (Fig. 2); isohalines shift with season and Volga discharge, but roughly reach 11–12‰ at the edge of the zone. Farther south, little increase in salinity occurs, with the highest values in the southeast rarely reaching 13.5‰, with an average of 12.8‰ (i.e. about one-third seawater).

Water temperatures show the same north–south gradient, caused by a synergism of climate and depth. In summer, when strong thermoclines develop down to 60–80 m, gradients are insignificant because the shallow northern basin

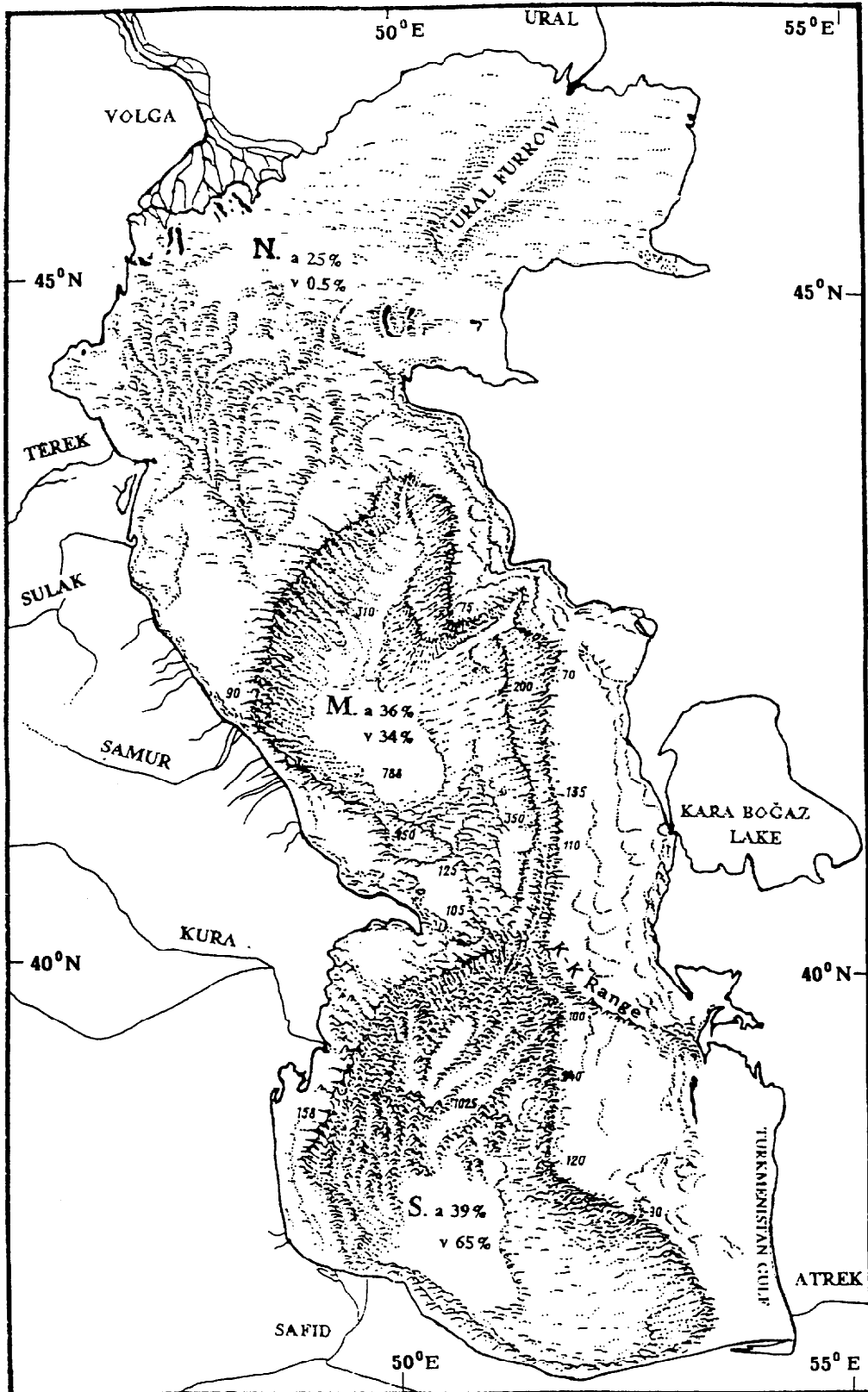


Fig. 1. Bathymetric and contour map of the Caspian. North (N), middle (M), and south (S) basins, with relative surface area (a) and volume (v); K-K range, the underwater Kilyazi-Krasnovodsk mountain chain.

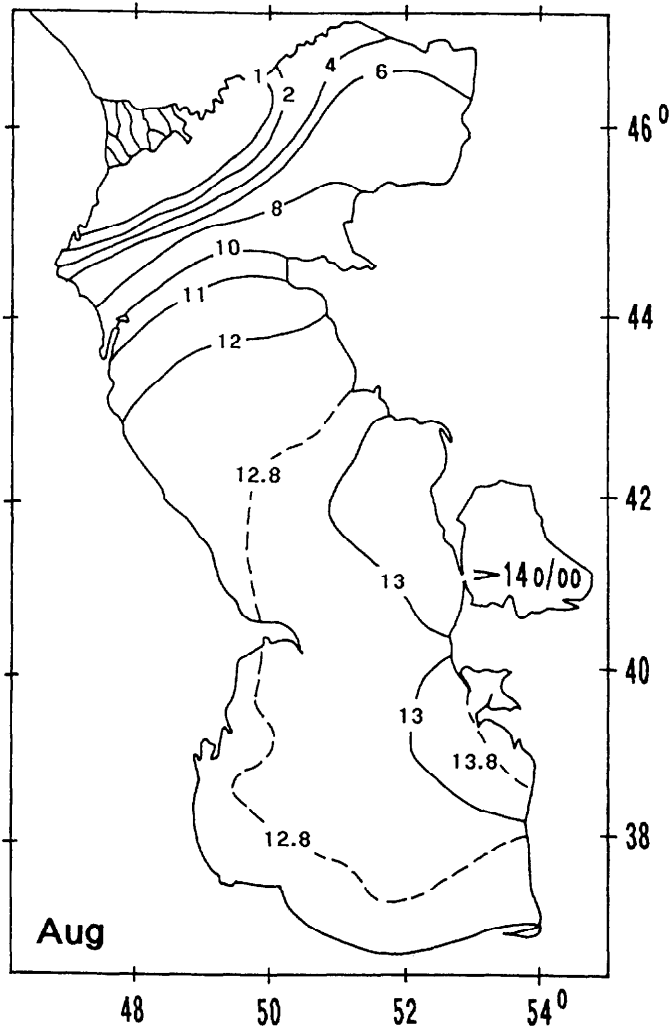


Fig. 2. The north-south salinity gradient of the Caspian is especially steep in the north; maximum salinity is found in the south-east. In Kara-Bogaz Lake, salinity fluctuates from 14‰ to saturation.

heats up rapidly such that the middle basin is then slightly cooler than both other zones (Fig. 3a). During winter, however, the north cools strongly, whereas the middle and south basins, because of their volume and warmer climate, remain warmer. The south basin never cools below 10°C, while the north and the littoral shelves typically freeze for several months during winter (Fig. 3b).

The synergy between salinity and temperature sets up vertical currents that explain why, unlike the Black Sea, it remains oxygenated to the bottom (*see below*).

The north zone is dimictic and well oxygenated. Oxygenation is better along the west than along the east coast because of the cyclonic flow of water, which drives north shelf water south in the west, and south basin water north in the east. In the middle and south basins there is a persistent stratification (Fig. 4), with values at the bottom depending on the severity of winter. During cold winters (e.g. 1968–1969), the middle basin cools sufficiently to mix to the bottom and reach 5–6 mg liter⁻¹. During mild winters, this does

not occur, however, and oxygen may decrease to 1–3 mg liter⁻¹ (Kosarev and Yablonskaya 1994). In the south basin, deep oxygenation is maintained by a salinity-temperature-driven convective mixing, which has to overcome a saline stratification (the increase from surface to bottom in the middle and south basins may reach 0.1–0.4‰). Sinking water is probably produced in winter, as well as in summer, by two mechanisms (Kosarev 1985). In summer, evaporation increases surface density, and heavy water “slides down,” predominantly along the walls of the trough. In winter, freezing produces a heavier saltwater layer underneath the ice, with a similar result on density. Figure 5 shows that the surface area of this “slow” deep oxygenation zone is about one-third of total lake surface. This reoxygenation proceeds at a slow pace, but is normally sufficient to compensate a low consumption per unit volume at great depths. The risk of deep anoxia, however, is directly proportional to Volga discharge. During the early decades of this century, increased freshwater discharge caused a high lake level and a slight decrease in surface salinity (Bruyevich 1937). This sufficiently reduced the production of heavy surface water to cause deoxygenation of the bottom of the middle and south basins, with the appearance of hydrogen sulfide. The drop in level between 1930 and 1977 reversed this, but the present rise could revive bottom deoxygenation (Bordovsky 1986). Such incidences of deep meromixis probably occurred during all past high lake stands; they may account for the absence of an endemic abyssal community (*see below*).

Nutrients

Most nutrients enter the Caspian with the Volga. Until the 1950s, peak in discharge fell in April–June in the Volga, but currently a chain of dams regulates the river. These dams store and recycle part of the nutrients (dissolved and particulate) and result in a sharp drop of phosphorus and silicate load to the lake. Since the late 1970s, however, agricultural and domestic runoff has restored nutrient input to levels that now even exceed the pre-damming period, except in the case of Silica.

The Volga delta (area of 10,000 km²), which is largely covered by macrophytes, buffers nutrient outflow. Up to 70% of dissolved inorganic phosphorus and 50% of dissolved inorganic nitrogen is temporarily stored here, and when exported, most of it is in organic, particulate form, which slowly remineralizes as it is taken south by the current. This influx has almost doubled since the 1970s (Kattunin 1989).

Nutrient levels in the Caspian are low, even in the north, where inorganic phosphate levels are on average 0.12–0.8 μM (but 90% of the phosphorus here, 2–2.5 μM, is in organic form) (Baydin and Kosarev 1986). Nitrogen as well is largely present in organic form (10–250 μgN liter⁻¹). Nitrates reach 0.5 μM in spring and summer and 7–10 μM in winter. Silica shows a strong seasonal cycle, decreasing from 60 μM in winter to <20 μM in summer, when diatoms bloom. Relatively little of this spills over to the middle, and even less to the south basin, which relies on internal recycling and small contributions from rivers and rainfall. Sur-

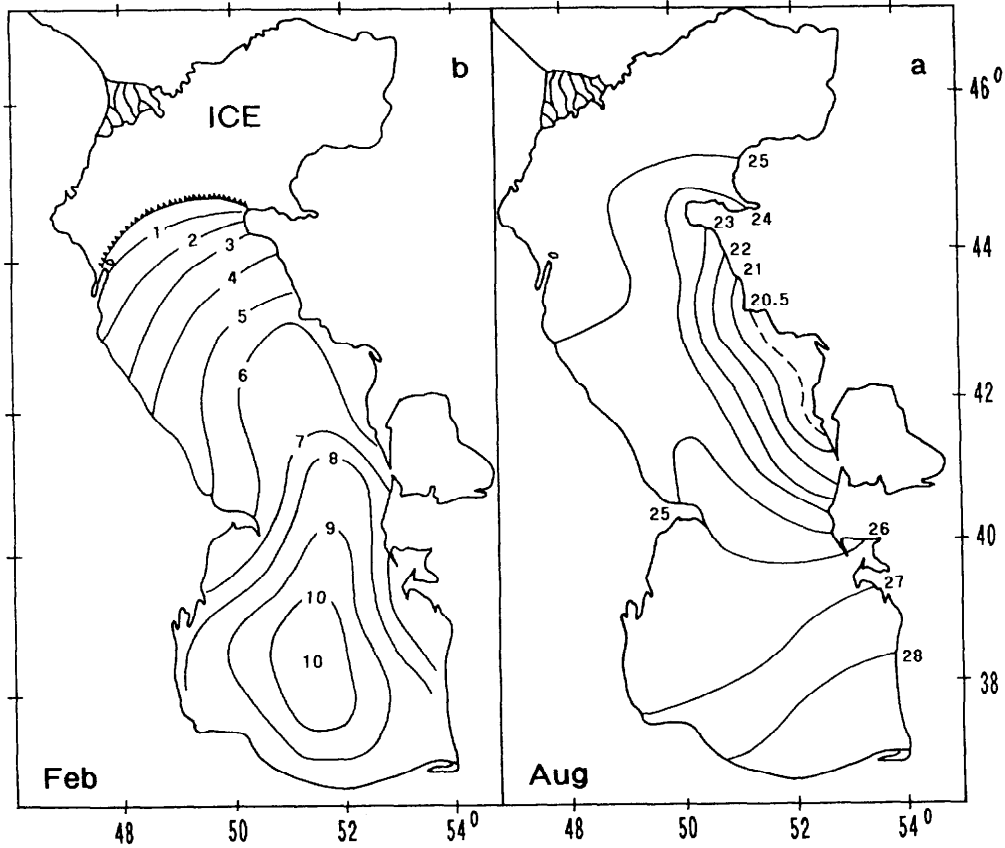


Fig. 3. Surface water temperatures in the Caspian in summer and winter.

face inorganic phosphate levels are on average $0.3\text{--}0.4\ \mu\text{M}$ in the middle basin (max. of $2.0\ \mu\text{M}$) and $0.2\text{--}0.3$ (max. of $0.7\ \mu\text{M}$) in the south. Phosphorus depletion in the south basin is almost permanent, because photosynthesis there continues throughout winter. Phosphorus increases with depth owing to release by organic compounds or excretion by biota. In particularly severe winters, a bottom layer anomaly may occur at great depths; at such times, extremely low phosphate concentrations occur, and this has been interpreted

as proof of the sinking of heavy surface water that is depleted in phosphate.

Nitrate in the middle and south basins reaches up to $2\ \mu\text{M}$ but is depleted to $0.2\text{--}0.3\ \mu\text{M}$ in summer. Ammonia follows an antiparallel course and is at a minimum in winter ($0.1\text{--}0.7\ \mu\text{M}$) and maximum in summer ($10\text{--}14\ \mu\text{M}$). Organic nitrogen is even higher ($7\text{--}130\ \mu\text{M}$), but needs clarification whether it resides in the living, dead, or dissolved fractions.

A situation of particular interest was revealed by a comparison of vertical profiles of phosphate and nitrate in the middle and south basins in 1934, when lake levels had started receding, and in 1983, when they were rising again (Kosarev and Yablonskaya 1994, using data of Bruyevich 1937 and Bordovsky 1896). Because of poor deep circulation in the 1930s, phosphorus accumulated in the abyssal zone, whereas nitrate first increased with depth (with a zone of accumulation between 200 and 400 m and a nitrite transition zone at 50–100 m), but then declined at greater depths, where reducing conditions prevailed (Fig. 6). In 1983, the picture was quite different; phosphate had changed little, but nitrate increased to the bottom, a reflection of the (now) oxidizing nature of deep waters.

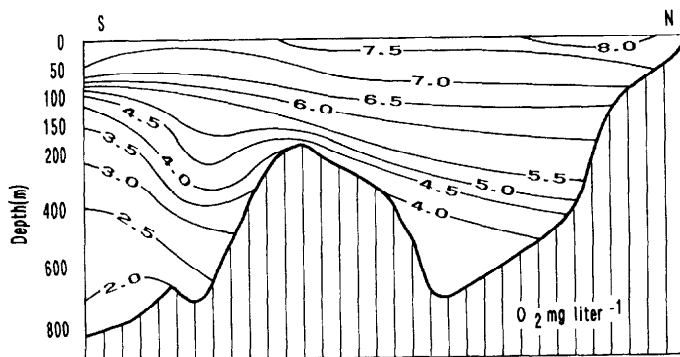


Fig. 4. Vertical distribution of dissolved oxygen in winter during the 1980s. Oxygen has always been present to the bottom in modern times, but during the 1930s, near-bottom values in the south dropped to near zero (modified from Kosarev and Yablonskaya 1994).

The biota

The Caspian has had flora and fauna of mixed origin throughout its history. High lake levels corresponded to a

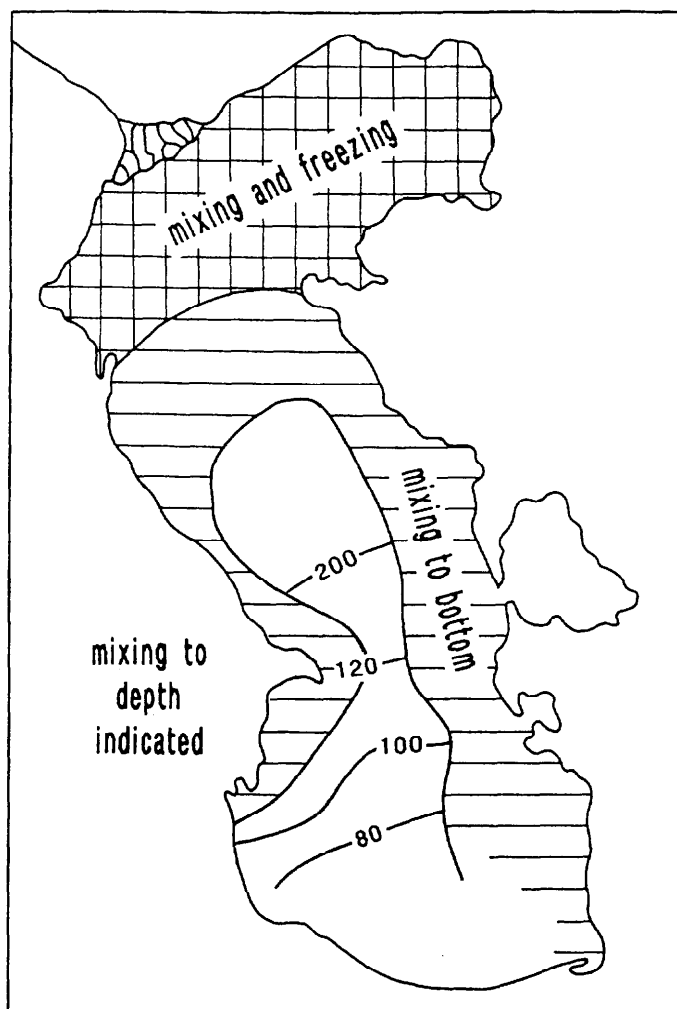


Fig. 5. Horizontal zoning of winter mixing across the Caspian. The north zone mixes and freezes annually; the shelf zones mix but do not freeze. The deep central and south troughs mix to depths that strongly decrease from north to south, and deep reoxygenation here depends on heavy water sliding down the edges of the troughs.

low salinity and contacts with the Black Sea. Low levels interrupted that contact, i.e. salinity increased. As other ancient lakes (Brooks 1950), the Caspian has been a focus of speciation. Adaptive radiation has occurred in many groups, and endemism at the species level often reaches 80%. Endemism in the Caspian thus even rivals that of Lake Baikal (Mordukhai-Boltovskoi 1979). For example, of 124 species of molluscs, 119 are endemic or shared only with the Black Sea and Lake Aral (Starobogatov 1994)—all onychopod cladocerans, all Cumacea, and most mysids, amphipods, and decapods are (sub)endemic. Crustaceans are so species-rich among the more than 950 metazoan species recorded from the lake (Kasymov 1987), that Zenkevitch (1963) called the Caspian “the Crustacean Sea.” Among *Pisces*, all 35 species of gobiids, 18 species of clupeids, and all 5 sturgeon species are endemic or shared with the Black Sea only.

A characteristic of Caspian biota is its euryhalinity, with

species of freshwater origin tolerant of salinities up to $\sim 13\text{‰}$ and species of marine origin tolerant of salinities down to $\sim 13\text{‰}$ being almost equally well represented. Stenoionic marine groups (e.g. cephalopods, echinoderms, and chaetognaths) are completely absent. Caspian endemics began being selected for euryhalinity since Miocene times, and fall into four groups: (1) species whose ancestors lived in the Tethys Sea (e.g. sturgeons, gobiids, and clupeids) and are of marine ancestry; (2) species whose ancestors lived in the brackish Sarmatian or Pontic Lakes, (e.g. the onychopod flock), of which six species are shared with the Black Sea and three with Lake Aral (Mordukhai-Boltovskoi 1966); (3) opportunistic freshwater species that mainly inhabit the northern Caspian, including most Rotifera, the non-onychopod Cladocera, and most cyprinid fish; and (4) recent invaders of northern (Baltic and White Seas) origin, a small but significant group (~ 14 species) that shows little or no sign of speciation. The latter group arrived while Lake Mologa-Sheksna united the Volga with northward running rivers such as the Sukhona and includes the copepods *Limnocalanus grimaldii*, several mysids, the Caspian salmon, and the Caspian seal, *Phoca caspica*. This seal, the top predator of the Caspian, is close to if not identical with the Baltic *Phoca hispida*.

Lastly, a group of 20th-century introductions was intentionally (e.g. the polychaete *Nereis succinea*; Nikitin 1953) or unintentionally caused by man. The Lenin Canal between Don and Volga, which opened the Caspian to maritime navigation in 1954, promptly led to invasions by Mediterranean biota, especially of fouling cirripids and marine molluscs (e.g. *Mytilaster lineatus*). Some of these drove endemic species (e.g. the bivalve *Dreissena caspia*) to extinction. Other endemic species escaped through the canal, often developing in an explosive manner elsewhere (e.g. the zebra mussel *Dreissena polymorpha*). The damming of the Volga and other rivers facilitated the upstream dispersal of Caspian onychopods, mysids, and amphipods (Mordukhai-Boltovskoi 1966).

The pelagic community

In the phytoplankton, more than 450 species of algae have been recorded (~ 70 abundant), with brackish and freshwater species dominant, and diatoms being the most abundant group. Cyanobacteria have become abundant in the north in the present decade, a sign of eutrophication. Phytoplankton development is highest in the north, opposite the Volga, with biomasses of $0.1\text{--}5\text{ mg liter}^{-1}$ in the top meters; however, these values drop by one order of magnitude in the middle and by two orders in the south. In addition, the east of the lake has a standing crop of only about one-tenth that of the west. Strong seasonal and local differences also occur, with the largest part of the deep lake's surface never reaching $>0.1\text{ mg liter}^{-1}$ in algal biomass.

Primary production has been studied by Salmanov (1968, 1985). Except in the turbid north, photosynthesis is inhibited in the subsurface, with maximum rates at 4–8 m. At 20 m, values decrease to 20–25% of the maximum. The euphotic zone is up to 70 m wide, but viable phytoplankton cells occur down to 100–150 m.

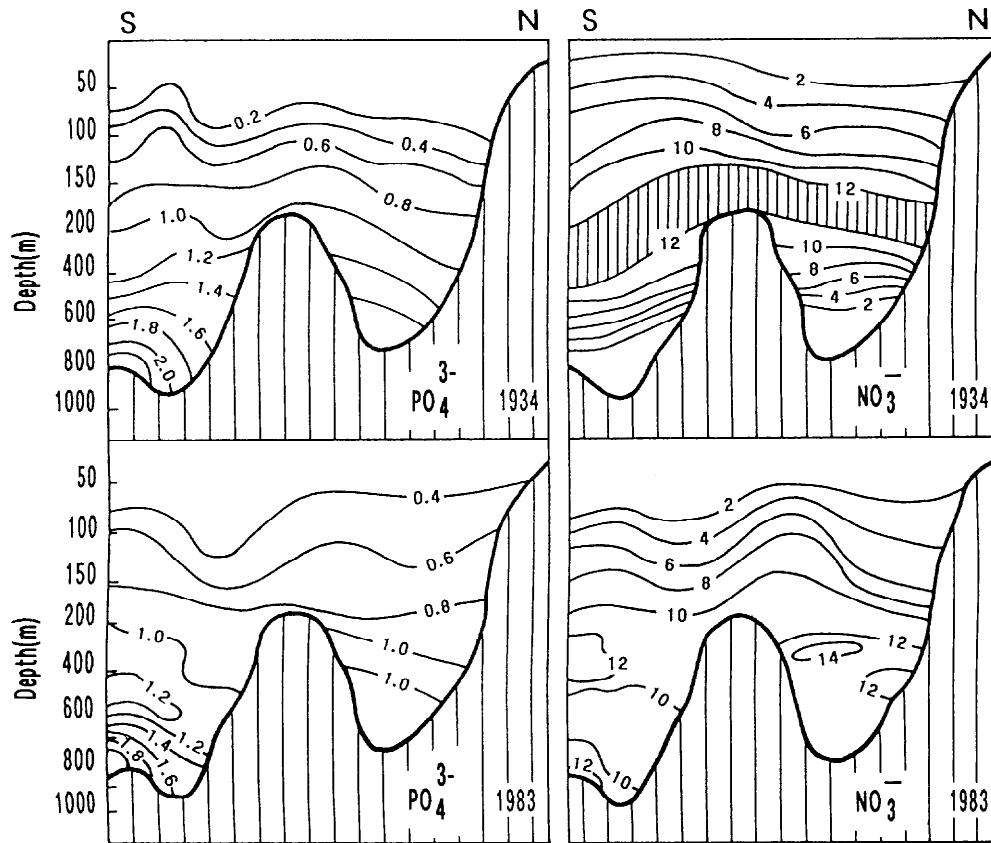


Fig. 6. Vertical distribution of P and N (in μM) in the middle and south basins during falling (1934) and rising (1983) lake levels. Phosphate profiles remained stable, but during the 1930s there was a nitrate maximum between 200 and 400 m, followed by an abyssal decrease due to reducing conditions; in the 1980s, there was good deep oxygenation, and nitrate kept increasing to the bottom (modified from Kosarev and Yablonskaya 1994).

Virtually no data are available on secondary production. By composition, the zooplankton differs greatly from that of other ancient lakes. The north basin, populated by numerous rotifers and daphniid cladocerans, behaves like an ordinary shallow lake, but the middle and south basins present unique features (Bening 1938; Kudryelina 1959). Unlike other ancient lakes where the pelagic zooplankton is dominated by one (rarely two) calanoids (Dumont 1994), the Caspian has at least three calanoids (*Heterocope caspica*, *Limnocalanus grimaldii*, and *Eurytemora grimmii*). This is because the lake offers opportunities for vertical segregation that are not available in lakes such as Tanganyika and Kivu, which have thick anoxic hypolimnia, or in Baikal, which is too cold throughout. Thus, the northern invaders *Limnocalanus* and *Eurytemora* consistently occur below the thermocline. That this is not primarily by predator (mainly clupeid) avoidance is suggested by the fact that in periodic cold coastal upwellings, these species are plentiful. Recently, two additional species of Black Sea origin, *Calanipeda aquaedulcis* and *Acartia clausi*, invaded the epilimnion.

Pelagic invertebrate predation is also strongly stratified vertically (Zenkevich 1963). The pelagic amphipods *Pseudalibrotus platyceras* and *P. caspius* occur below the thermocline, the former even down to 700 m; with four semi-

pelagic mysids (*Mysis amblyops*, *microphthalma*, *caspia*, *macrolepis*) of subarctic origin, they constitute a typical deep-lake biocenosis that lives at constant low temperatures and avoids being eaten by pelagic (clupeid) or semipelagic (sturgeon) fish. *M. amblyops* occurs from 50-m depth to the very bottom. All others have more restricted, partly complementary, and conspicuously broad ranges (*M. caspia*, 40–390 m; *M. macrolepis*, 250–425 m; *M. microphthalma*, 400 m–bottom). Their biomass may equal or even exceed that of the copepods–cladocerans. Planktonic predation (on ciliates?) above the thermocline is dominated by endemic onychopods with extravagant body shapes; all species appear to swarm throughout the lake (Mordukhai-Boltovskoi 1966; Mordukhai-Boltovskoi and Rivier 1987) and are themselves preyed upon by pelagic kilka (clupeids). How these related onychopods can continue to co-exist is an unsolved problem. Specialization on particular food items comes to mind as an isolating mechanism, but based on sizes, only two groups, the polyphemids and cercopagids, can be separated. All *Cornigerius* and related genera are <1 mm in size, whereas *Cercopagis* species are >1 and up to 2.5 mm long. With such a broad overlap, either yet undiscovered specializations must exist or the number of taxa has been grossly overestimated, as suggested by Aladin (1995).

Research on cyclomorphosis, inducible predator evasion morphologies, and population genetics is needed on these onychopods, which also stand out by an extreme scarcity of males. Males occur in *Cercopagis*, but none are known in *Cornigerius*, *Podonevadne*, and *Caspievadne*, and obligate parthenogenesis has been proposed but not experimentally demonstrated by Mordukhai-Boltovskoi and Rivier (1987).

The benthic community

In ancient lakes, the benthos is where most biodiversity is found (Martens et al. 1994) and, with >450 species on record, the Caspian is no exception to this rule. Horizontal (salinity and temperature dependent) and vertical (temperature and predation dependent) zonation is common, and complex patterns of distributions have been recognized. In molluscs, Starobogatov (1994) identified 12 zones, each with a specific community. Deep waters were conspicuously impoverished. Among crustaceans, the cumacean *Schizorhynchus eudorelloides* occurs between 214 and 700 m, and the mysid *Paramysis loxolepis* occurs between 600 and 750 m. More information on the deep benthos would be beneficial since it is striking that deep-living associations always occur over wide intervals, and none are typically abyssal. This suggests, as indicated earlier, that recurrent episodes of anoxia wiped out whatever fauna had evolved on the very lake bottom.

Biomass is concentrated in the top 75 m (Romanova and Osadchik 1965), and the receding lake level of 1930–1977 caused it to decline dramatically. Mollusc standing crop fell by a factor of 4–10, and there were repercussions at the level of mollusc-eating benthic fish, such as gobiids, sturgeon, and *robla* (*Rutilus rutilus caspicus*). Estimates for the north basin, $4\text{--}5 \times 10^6$ t, dropped to $0.9\text{--}2.2 \times 10^6$ t in 1935–1956, after which a recovery occurred.

Conclusion: A lake, not a sea

The Caspian is truly unique among aquatic ecosystems, not only by its volume, but first and foremost by its longitudinal zones of salinity, depth, and climate. These three zones combine independently to produce three basins that are more different from each other than are many individual lakes. The dimictic north behaves like a temperate shallow lake. The central basin is still largely dimictic. The south, but for a delicate salinity-driven mechanism of reoxygenation, would rapidly revert to a meromictic basin, comparable to the Black Sea. Here, however, meromixis only set in at the start of the Holocene, when the then Pontic Lake became united with the Mediterranean Sea and acquired a number of typical marine traits, including many truly marine biota. But the biota of the Caspian basins are all euryhaline, and typical marine groups are lacking. Furthermore, intralacustrine speciation within that euryhaline gene pool produced a level of endemism comparable to that of other ancient lakes (e.g. Lake Baikal), suggesting similar mechanisms of speciation.

I conclude that, except for its sheer size, there are no arguments (except political ones) to call the Caspian a sea.

Not only has it never been connected to the world ocean, but even when united with the Black Sea, that was at a time when the Pontic basin still contained a true lake itself.

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