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Mollusc biodiversity in late Holocene nearshore environments of the Caspian Sea: A baseline for the current biodiversity crisis

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ABSTRACT

The Caspian Sea is an evolutionary island whose rich and endemic fauna have evolved in partial isolation over the past two million years. Baseline studies of pre-20th Century communities are needed in order to assess the severity of the current Caspian biodiversity crisis, which mostly involves invasive species. An inventory of late Holocene shelly assemblages (c. 2000–2500 cal yr BP) from outcrops in and around Great Turali Lake (Dagestan, Russia) shows a diverse nearshore community consisting of 24 endemic Caspian species, two invasive species and two Caspian native species that lived in a shallow embayment with mesohaline salinities of circa 5–13 psu (parts per thousands). This pre-crisis Holocene Caspian mollusc community serves as a baseline against which modern mollusc diversity measurements can be evaluated. Examination of faunas from similar environments living today and in the past illustrates the dramatic changes in nearshore communities during the 20th Century. Our study identifies a habitat that may have served as a refuge, but that is currently under threat from invasive species. The severity of the Caspian biodiversity crisis is comparable with other well-known biodiversity crises in semi-isolated ecosystems such as the cichlid fish communities of Lake Victoria, Africa.

1. Introduction

The biggest inland water body on Earth is the Caspian Sea, with a surface area of 371,000 km^2. It is an anomalohaline lake, whose water level and salinity regimes are determined by a balance of runoff and evaporation (Kosarev and Yablonskaya, 1994; Krijgsman et al., 2019). The Caspian Sea can be subdivided into three basins: the northern, middle and southern Caspian basin. Each basin is characterized by its own temperature, depth, salinity and ecology features and faunas. The Caspian Sea is disconnected from the open ocean, and various rivers contribute to the inflow of fresh water to the basin. Most of the water (80%) derives from the Volga River, resulting in a strong north-south salinity gradient in the lake (Kostianoy et al., 2005). Near the mouth of the river the salinity is 0 psu, the average of the rest of the basin is around 11–13 psu (practical salinity unit: dissolved salts in parts per thousand (‰)). Currently, the Caspian Sea water level is 27 m below global sea level (Arpe et al., 2018).

The Caspian Sea has a volatile history of large-scale and rapid lake level change (Badyukova and Kalashnikov, 2009; Fedorov, 1978; Ignatov et al., 1993; Kaplin and Selivanov, 1995; Kosarev and Yablonskaya, 1994; Krijgsman et al., 2019; Kroonenberg et al., 2007, 2000; Rychagov, 2002; Svitoch, 2014; Varuschenko et al., 1987; Yanina, 2012), which greatly affected the extent of the lake. During the last major high-stand in the Late Pleistocene lake levels rose up to 50 m above global sea level (77 m above current Caspian Sea water level), and an overflow gateway existed north of the Caucasus towards the Black Sea (early Khvalynian transgression: Chepalyga, 2007; Yanina, 2014). The major cause of the transgression event was the surface runoff increase from the catchment area during the period of deglaciation (Arslanov et al., 2016; Sorokin et al., 2018). In contrast, at the

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time of the last big regression in the early Holocene (the Mangyshlak regression: Bezrodnykh and Sorokin, 2016; Yanina, 2014) the level of the Caspian Sea was about 100 m below the global sea level (73 m below the current Caspian Sea water level). The extreme lowstand of the Mangyshlak has been ascribed to the colder, more continental climatic conditions during the Boreal (Arslanov et al., 2016). During the late Holocene two additional minor highstands were reached; −25 m (compare to −27 m of present-day Caspian Sea) around 2600 cal yr BP, and −26 m during the Little Ice Age (Kroonenberg et al., 2007). The Derbant regression during the Warm Medieval period corresponded to a lowstand of around 32 m (Kroonenberg et al., 2007).

Coinciding with those huge changes, the Caspian endemic fauna has undergone a protracted series of diversifications and extinctions during the Quaternary, including several major turnover events (Krijgsman et al., 2019; Nevesskaja, 2007; Svitoch and Yanina, 2001; Yanina, 2014). The last natural turnover event of the Caspian Sea biota concurred in the early Holocene during the Mangyshlak regression (Krijgsman et al., 2019: 10–8 ka) when the Khvalynian fauna became replaced by the late Holocene Novocaspian fauna. The pre-20th Century Novocaspian faunas (< 7 ka) are characterized by the abundance of endemic cardiid and dreissenid bivalve species (of the genera *Didacna*, *Monodacna*, *Adacna*, *Hypanis* and *Dreissena*) and endemic hydrobiid gastropod species (*Clathrocaspia*, *Laevicaspia*, *Turricaspia* and *Abeskunus*) (Logvinenko and Starobogatov, 1969; Sorokin et al., 2018; Svitoch, 2014; Svitoch and Yanina, 2001; Wesselingh et al., 2019; Yanina, 2011). Three species (*Cerastoderma glaucum*, *Cerastoderma* sp. A [non *C. rhomboides*] and *Ecrobia grimmi*; nomenclature after Wesselingh et al., 2019) established in early Holocene times and lived alongside the endemic Caspian species ever since. *Cerastoderma glaucum* and *C.* sp. A were probably introduced by humans and are still considered invasive in the Caspian Sea basin, but *Ecrobia grimmi* is considered native (Wesselingh et al., 2019).

During the 20th Century a major biodiversity crisis unfolded in the Caspian Sea (Kosarev and Yablonskaya, 1994; Latypov, 2015). The introduction of a number of euryhaline marine invasive species impacted the Caspian fauna profoundly as shown by observational time series (Kosarev and Yablonskaya, 1994) and boxcore data (Leroy et al., 2018). Highly adaptive and competitive marine species, which were in part introduced as food source for fish stock, thrived in the mesohaline Caspian environment and outcompeted most endemic species (Karpinsky, 2010). As a result, the diverse endemic Caspian mollusc communities became replaced by species-poor communities dominated by invasive species (Latypov, 2015; Leroy et al., 2018; Wesselingh et al., 2019). Dense populations of invasive species like *Mytilaster minimus*, *Abra segmentum* and *Cerastoderma* spp. and the native species *Ecrobia grimmi* now dominate the coastal faunas (Karpinsky et al., 2005; Latypov, 2015; Leroy et al., 2018; Mamaev, 2002). Several species of the endemic Caspian fauna are presently considered extinct, and for several other species presumed to be alive no living specimens have been recorded in the past decades (examples in Kosarev and Yablonskaya, 1994; Wesselingh et al., 2019). Beach collecting around the middle Caspian Basin at the Great Turali Lake (Russia, 2003), Sarvan (northern Azerbaijan, 2015) and Bautino (Kazakhstan, 2017) yielded fresh material of only a limited number of Caspian endemic species, such as *Theodoxus pallasi*, *Didacna baeri*, *D. trigonoides*, *D. parallela*, *Adacna laeviuscula*, *A. vitrea* and *Hypanis plicata* (personal observations: FPW, SV and VA). Although this suggests that some endemic species still live in the coastal zone, the restricted amount of living endemic species implies a major decline in diversity.

A proper insight into the severity of the Caspian biodiversity crisis is hampered because (1) the taxonomy of Caspian groups is poorly resolved (Neubauer et al., 2018; van de Velde et al., 2019; Wesselingh et al., 2019), (2) recent expeditions failed to recover living material for the majority of the species, and (3) a lack of pre-20th Century baseline inventories. Here, we report a fauna from shallow-water Novocaspian (Holocene) deposits from several outcrops around the Great Turali Lake (Fig. 1) located south of Makhachkala along the middle Caspian coast of Dagestan (Russia). The Turali fauna provides a baseline for the pre-crisis nearshore Caspian community, which serves as a reference point for comparison with present-day communities. By investigating the depositional environment and documenting the composition of the fauna we aim to provide a habitat-constrained biodiversity baseline for the composition of shallow-water mollusc faunas prior to the drastic alterations that took place in the 20th Century.

2. Study area

2.1. Geographic context

The middle Caspian Basin is a deep (maximum depth 788 m), well-mixed basin with only minor summer water stratification resulting in rather uniform salinities across the entire depth range. Salinities are typically about 11–13 psu, apart from deltaic areas of rivers draining the north-eastern Caucasus where salinities can be locally depressed. The coastal morphology of the western shore of the middle Caspian Basin is largely determined by wave-action, rapid sea-level change, tectonic uplift, as well as local input of terrigenous erosive products from the Caucasian hinterlands. During the Novocaspian stage the Caspian Sea-level rose several meters above the current level twice; approximately 2600 cal yr BP and during the Little Ice Age (Kroonenberg et al., 2007). These highstands produced extensive coastal deposits along the entire Caspian Sea, including the record treated herein. Our material was collected in and around the Great Turali Lake, which was a bay on the west coast of the middle Caspian Basin at the time (Kroonenberg et al., 2007, 2000). During the 2600 cal yr BP highstand the bay became gradually more isolated from the sea by an eastward growing series of barriers, fed by episodic northwards longshore drift and extensive wave action. After an intervening lowstand the final closure occurred during the Little Ice Age highstand (Kroonenberg et al., 2007).

2.2. Sample sites

Nine samples from five localities are treated in this paper (Figs. 1, 2). Four of these localities are positioned along the Great Turali Lake (Ozero Bol'shoye Turali in Russian) and one at the Sulfat Canal that links the lake with the Caspian Sea. The localities are situated on a coastal strip some 25 km southeast of the city of Makhachkala. Locality Turali-1 (47°41′20″E, 42°49′54″N) is an approximately 50 m long cliff exposure along the east bank of the Great Turali Lake. Sample M0222 was taken there. Locality Turali-2 (47°41′43″E, 42°49′04″N) consists of a number of very slightly westward-dipping layers that are exposed in the shore zone and just below the water table on the south-eastern margin of the Great Turali Lake, south of the Sulfat Canal outlet. Samples M0204, M0205 and M0216 derive from these deposits. The third locality Turali-3 (47°42′22″E, 42°49′13″N) comprises a series of outcrops along the south bank of the Sulfat Canal. Samples M0202 and M0203 were collected there. Turali-4 and Turali-5 represent single sediment layers and these are not illustrated in Fig. 2. Turali-4 (47°41′33″E, 42°48′51″N) is a flat grey-yellow silt layer of at least 50 cm thickness with molluscs outcropping on the southern beach of the Great Turali Lake. Samples M0220 and M0221 were collected there within a few meters from each other. Turali-5 (47°41′43″E, 42°49′08″N) is a single shell-bearing sand layer exposed in the shore zone at and just below the water table hundred-meter north of Turali-2. Sample M0215 was taken there.

3. Materials and methods

For each sample about 1 kg of sediment was washed through a 1 mm-sieve. Molluscs were identified to the species level and the total of individuals for each species was counted. For bivalves, all valves and

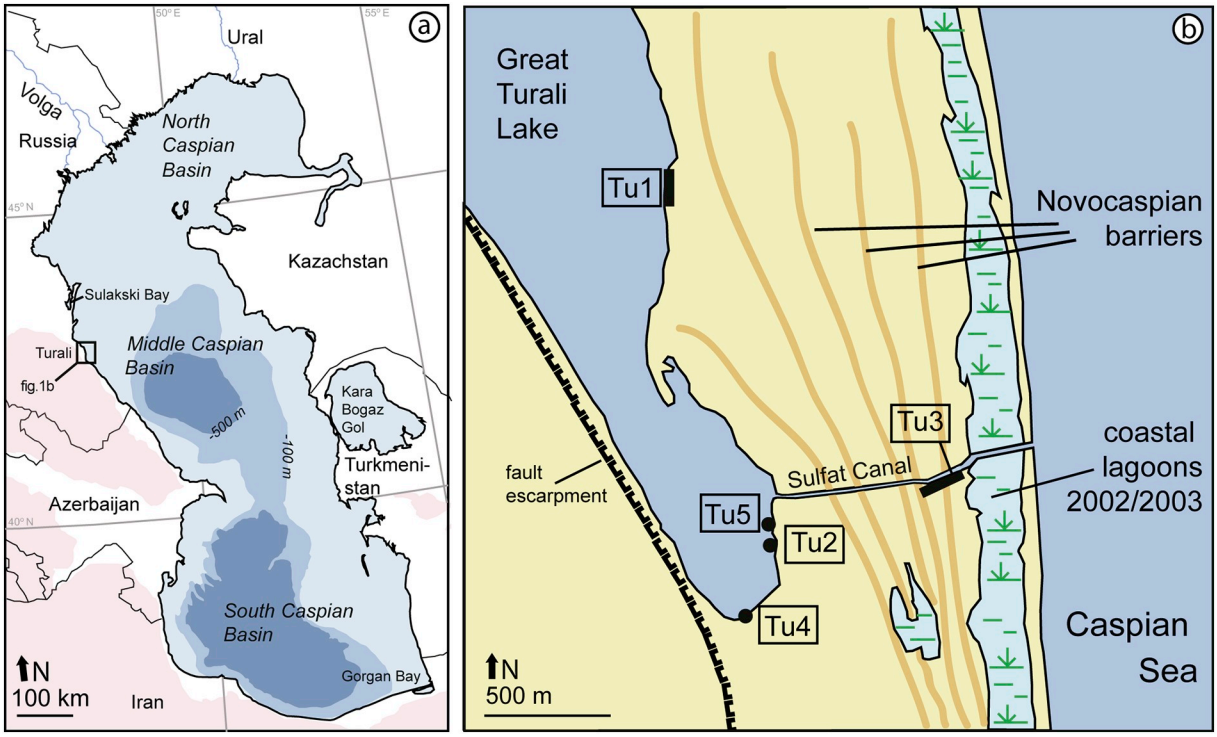

Fig. 1. Geographic context of study site. (a) Map of the Caspian Sea. Source bathymetry: Kostianoy et al. (2005): Fig. 1 (p. 7). (b) Location of the outcrops treated in this paper. Tu1-Tu5 represent outcrops Turali 1-5. Brown ridges are Holocene Novocaspian beach barriers (see Kroonenberg et al., 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fragments containing a hinge were counted. One valve was counted as half an individual, whereas for gastropods, a fragment with a protoconch was considered one individual. Final counts were rounded up to the next integer. We follow the gastropod taxonomy of Neubauer et al. (2018) and Wesselingh et al. (2019). The generic classification of Pontocaspian hydrobiids is subject of current studies and nomenclature might further be updated as a result in the near future. For bivalves, we used Kijashko in Bogutskaya et al. (2013), Wesselingh et al. (2019) and van de Velde et al. (2019). Cases in which we deviate are argued below.

To assess the taphonomic fidelity of the fauna, we examined preservation characteristics of the molluscs. Samples were checked for dissolution, abrasion, coloration and fragmentation. Paired bivalves, which indicate in-situ samples, were noted.

To reconstruct the Holocene environment of Turali, we used the published information on species' preferred environmental conditions (salinity ranges, habitat and depth ranges) collected by van de Velde et al. (2019). Additional ecological characteristics were assembled from literature data and personal observations for *Adacna vitrea*, *Cerastoderma* cf. *glaucum*, *Cerastoderma* sp. A and *Monodacna albida*, *Didacna baeri*, *D. eichwaldi*, *D. parallela*, *D. protracta*, *D. pyramidata*, *D. trigonoides*, *Abeskunus exiguus*, *Laevicaspia conus* and *Clathrocaspia gmelinii*.

Stable isotope data derive from Vonhof et al. (2004). Radiocarbon data were previously published by Kroonenberg et al. (2007). The software Calib version 5 was used to calibrate ^{14}C ages to calendar years BP. To correct for reservoir ages, the marine calibration curve Marine 04 was used (Hughen et al., 2004). We used R version 3.5.2 (R Core Team, 2018) and the package 'iNext' 2.0.19 (Chao et al., 2014; Hsieh et al., 2016) to perform rarefaction analyses to estimate the representativeness of the samples (Raup, 1975). Land snails and reworked species were excluded from this analysis.

The following abbreviations are used: LV = left valve, RV = right valve, RGM = collections of Fossil Mollusca, Naturalis Biodiversity Center collection, formerly Rijksmuseum Geologie en Mineralogie, Leiden, The Netherlands.

4. Results

4.1. Geology and age

Five facies are described in the studied outcrops (Table 1). Facies I (beach-berm shingle) and II (highstand/regressive shoreface and bay fill) dominate the sections. Other facies include lagoonal (Facies III), lagoonal to restricted embayment (Facies IV) and paleosol (Facies V).

Section Turali-1 contains two successive coarsening-up units, with beach settings migrating over bay fill deposits. A lagoonal interval is found in between the two coarsening-up units. The lower unit comprises a lower interval of eastwards-dipping bay fill (facies IIb, Fig. 2-a) overlain by beach-berm shingle (facies I, Fig. 2-b). Although the contact between the two intervals appears to be sharp, increasing pebble lines along the clinoforms at the top of the lower interval in the southern part of the outcrop indicate that the contact may become gradual laterally. The upper unit comprises three intervals. The lower interval (facies IIb, Fig. 2-c) is a body of sand with shells, including paired *Didacna trigonoides* and *Adacna laeviuscula*, dispersed or lined along eastward-dipping foresets. This sand layer has an undulating top, forming a palaeorelief with height differences of about 70 cm. A single ^{14}C age of 2240–2390 cal yr BP was measured from a paired *Didacna trigonoides* (specimen HV#10a; Table 2). Within a depression in the northern half of the outcrop a 20 cm-thick succession (Fig. 2-d) of deformed laminated silts and sands is found (attributed to facies III, IVa and IVb, lagoonal deposits). In the silts and silty sands small paired *Cerastoderma* are common. The ^{14}C ages of *Cerastoderma* from two silt layers (2000–2140 cal yr BP and 2060–2240 cal yr BP) indicate that the different lagoonal layers are of approximately the same age and only a few hundred years younger than the top of underlying sequence I. The lagoonal interval grades laterally into the base of massive gravel beds (Fig. 2-e) assigned to facies I (beach-berm shingle). The shingle grades laterally into more sand-dominated deposits, possibly a gradation into facies IIb (fill), which overlays the lagoonal interval. Finally, a coarse-grained pebble lag (Fig. 2-f) is found on top of the section that may

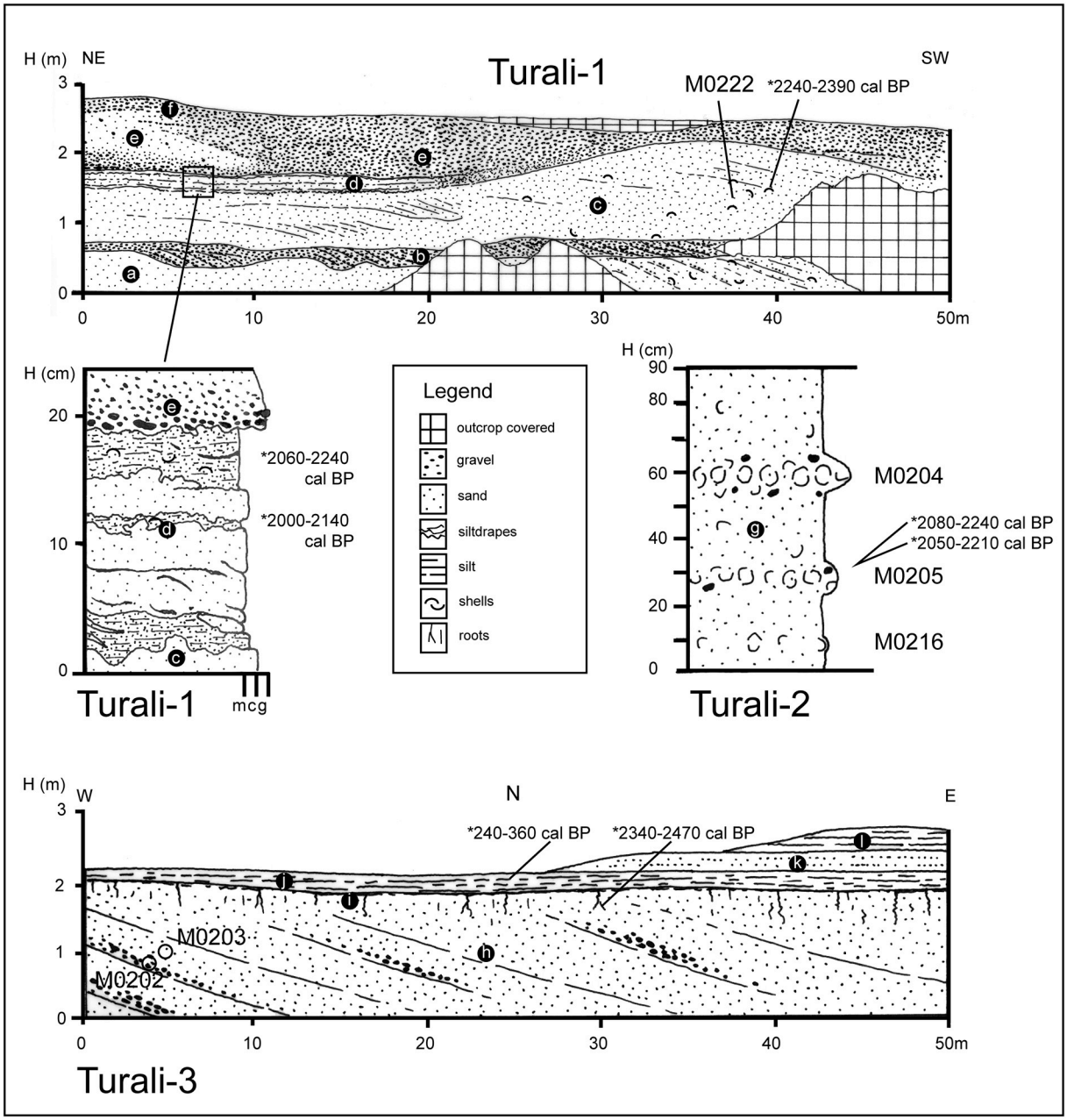

Fig. 2. Schematic representation of sections Turali 1-3. Asterisks (*) denote calibrated ^{14}C ages BP. Small case letters refer to sedimentary units: a. eastwards-dipping bay fill, b. eastwards-dipping bay fill, c. sand with shells along eastward-dipping foresets, d. deformed laminated silts and sands, e. massive gravel beds, f. coarse-grained pebble lag, g. slightly dipping sand layers with shells, h. low-angle clinoforms with pebbles and shells, i. stratified silt stone, lagoonal, j. silt layer with shells, k. Aeolian interval, l. stratified silt stone, lagoonal.

represent ablation of and soil formation in the underlying gravel interval.

Section Turali-2 is formed by slightly dipping layers outcropping on the floor of the lake. The stratigraphic thickness is only 90 cm, and the succession is assigned to facies IIb (Fig. 2-g). The sands and shell layers have a very low-angle westward dip (< 5°). The shell beds yield abundant paired, in-situ bivalves dominated by *Didacna eichwaldi*. The lower boundary of the shelly intervals is not sharply delimited. The fauna is comparatively diverse and well-preserved, but minor amounts of abraded specimens and fragments as well as some pebbles indicate the proximity of physical disturbance. These specimens and fragments either originated from proximal wash-over events or are the result of reworking of an underlying transgressive layer by bioturbation. Two paired *D. eichwaldi* specimens in the lower shell bed yield ^{14}C ages of 2080–2240 cal yr BP and 2050–2210 cal yr BP, respectively. The section in Turali-2 may therefore be the lateral equivalent of the upper sequence of Turali-1.

Section Turali-3 (Sulfat Canal) contains two units. The lower circa two-meter unit is a single unit assigned to facies IIb (shoreface, Fig. 2-h). Low-angle clinoforms with occasional pebbles and often abraded shells and shell fragments are present. Some concentrations of worn *Dreissena elata* and *Clessiniola variabilis* are present. Root traces, dispersed organic matter as well as dispersed, slightly decalcified terrestrial snails are found in the upper 30–50 cm indicating soil formation after deposition (< 2600 cal yr BP). This lower unit is overlain by three thin layers, assigned to facies IV, II and IV, respectively. The lower silt layer of the upper interval (Fig. 2-j) contains abundant and well-preserved paired subadult *Cerastoderma* as well as *Ecrobia grimmi*. A shell of

Table 1
Sedimentary facies in the Novocaspian (Holocene) deposits near Turali.

Facies	Colour	Lithology	Sedimentary structures	Details	Interpretation
I	Grey-yellow	Poorly sorted gravel with variable amounts of coarse-grained sands	Sediment can be matrix or clast-supported, bedding poorly and irregularly developed	Pebbles (1–8 cm), grey to orange brown durable calcilutite, flattened, irregularly oriented or slightly imbricate	Beach-berm shingle
II	Yellowish	Fine to coarse grained poorly to reasonably sorted sand	Low-angle dipping foresets with sometimes imbricated gravel and shell accumulations present, top sets and bottom sets rarely found	Dispersed shells and pebbles	
IIa	Yellowish	Sands medium-coarse grained	Foresets dipping seaward, well defined	Abraded shells and shell fragments, often with a mixture of colours, dispersed and concentrated along clinoforms, plugs of flat (ø < 2 cm), imbricate carbonate pebbles occur	Eastward prograding shore face during lake-level fall
IIb	Yellowish	Sands mostly fine to medium grained	Foresets dipping landwards or undulating (possibly including hummocky cross stratification), somewhat irregularly developed, locally stacked low-angle dipping foresets with cross stratification, foresets grade laterally into facies iic	Shells and shell fragments on foresets or dispersed in sediment, sometimes abraded but well-preserved, include paired bivalves (sometimes in butterfly preservation)	Washover lobes of beach barriers formed by storms during lake-level rise and highstand interfingering with bay floor successions
IIc	Grey-yellow	Fine-grained sand to silt	Subhorizontal massive or poorly stratified	Dispersed well-preserved molluscs, including pairs of *monodacna* and *dreissena*, shell beds with in-situ *didacna* dominated faunas	Shallow bay floor
III	Yellowish-white	Fine to medium grained, well sorted sand	More or less horizontal layering		Lagoon, possibly with substantial input of windblown sands.
IV		Silt to fine grained silty sand		Paired subadult and juvenile *Cerastoderma*	See: IVa, IVb
IVa		Silt to medium grained sand	Massive silt to slightly irregularly layered silt-medium grained sand laminae	Shells, mostly well-preserved, paired subadult and juvenile *Cerastoderma* and *Ecrobia grimmi*	Restricted embayment or lagoon with storm-induced sand layers
IVb		Fine-medium grained silty sands	Silt drapes, sometimes overlaying wave ripples	Few dispersed shells, mostly of *Cerastoderma*	Restricted embayment or lagoon lacking storm-induced sand layers
V	Grey-purple-black	Sand or partially flat-lying gravel with loam		Sand with root fragments and dispersed organic matter, gravel with root traces and some organic matter, dispersed pulmonate (terrestrial) snails	Soil developed in sandy/gravelly substrate

Table 2
Radiocarbon ages.
(Compiled from Kroonenberg et al., 2007).

Sample	Species	Sample site	^{14}C age (yrs uncal. BP)	Calendar age (cal. BP)
HV#06	*Cerastoderma* sp. A	Turali-3	525 ± 33	240–360
HV#08	Indet. pulmonate terrestrial snail	Turali-3	2603 ± 33	2340–2470
HV#09	*Cerastoderma* sp. A	Turali-1	2370 ± 40	2060–2240
HV#10a	*Didacna trigonoides*	Turali-1	2517 ± 41	2240–2390
HV#11	*Cerastoderma* sp. A	Turali-1	2322 ± 37	2000–2140
M0205#1	*Didacna eichwaldi*	Turali-2	2373 ± 38	2080–2240
M0205#2	*Didacna eichwaldi*	Turali-2	2366 ± 30	2050–2210

Fig. 3. Paired *Didacna eichwaldi* (Turali-2, sample M0205) exposed just below the water table of the Great Turali Lake. Width of the shells approximately 2 cm.
Photograph SBK, 2002.

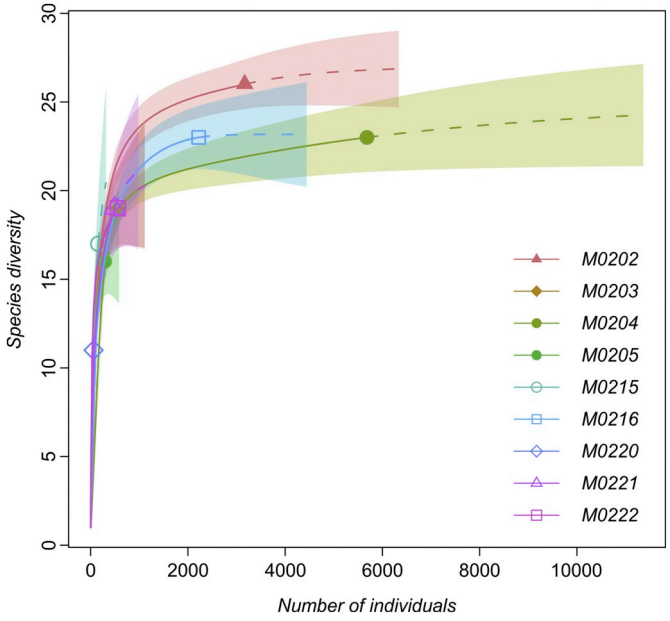

Fig. 4. Rarefaction curves of the Turali samples with 95% confidence interval and extrapolated species richness for double sample size.

the former yielded a ^{14}C age of 240–360 cal yr BP. The three upper beds appear to represent mostly lagoonal facies with possibly a short Aeolian interval (Fig. 2-k) developed in the Middle Ages and thus overlie the older Novocaspian deposits with a hiatus comprising approximately 1800 yrs.

Turali-4 and Turali-5 are single layers cropping out along the banks of the Great Turali Lake for which no age data are available. Locality

Table 3
Turali species list with mollusc counts per sample. Species indicated with (n) are native species, (i) are invasive, and species indicated with (r) are reworked.

	M0202	M0203	M0204	M0205	M0215	M0216	M0220	M0221	M0222
Cerastoderma cf. *glaucum* (n)(i)	2.5	1.0	1.5	0.5	1.0	2.0	0.0	1.5	59.0
Cerastoderma sp. A (n)(i)	14.5	6.5	752.0	73.5	32.5	263.0	1.0	3.0	36.5
Adacna laeviuscula	29.0	0.5	22.5	0.0	0.5	4.0	0.0	5.0	15.5
Adacna vitrea	115.5	5.5	42.0	2.5	0.0	11.0	5.5	64.5	18.0
Hypanis plicata	29.0	3.0	93.5	2.0	0.5	13.0	1.0	8.5	2.5
Monodacna albida	11.0	26.0	57.0	10.5	4.0	20.0	1.5	7.0	4.0
Monodacna caspia	14.5	7.0	27.0	2.5	2.0	7.0	0.0	2.0	2.0
Monodacna semipellucida	7.5	3.0	6.5	6.0	0.0	4.5	0.0	0.5	11.5
Didacna eichwaldi	178.5	11.5	332.0	9.5	2.5	96.0	0.5	0.0	0.0
Didacna baeri	12.5	5.5	18.0	7.0	1.0	7.5	0.0	0.0	0.0
Didacna barbotdemarnyi	2.5	0.0	1.0	0.0	0.0	0.0	0.0	9.0	9.5
Didacna parallela	17.0	0.0	18.5	0.0	0.0	4.0	0.0	0.0	3.5
Didacna protracta (r)	1.0	0.0	0.0	1.0	0.0	0.5	0.0	0.0	0.5
Didacna pyramidata	3.5	0.0	0.0	0.0	1.5	2.0	0.0	0.5	1.0
Didacna trigonoides	13.5	1.5	32.0	2.0	10.0	8.5	0.0	2.5	17.5
Dreissena caspia	215.0	53.5	15.5	5.5	5.0	24.5	2.0	14.5	51.0
Dreissena elata	1598.0	248.5	3089.0	83.5	38.5	1313.0	37.5	251.0	174.0
Dreissena grimmi	7.5	3.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0
Theodoxus pallasi (n)	104.0	7.0	663.0	51.0	35.0	244.0	1.0	12.0	49.0
Abeskunus brusinianus	11.0	0.0	75.0	0.0	1.0	28.0	0.0	0.0	0.0
Abeskunus exiguus	25.0	0.0	26.0	1.0	0.0	16.0	0.0	0.0	1.0
Abeskunus sp. indet.	5.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Clessiniola variabilis	61.0	18.0	300.0	16.0	12.0	110.0	3.0	2.0	26.0
Ecrobia grimmi (n)	126.0	57.0	65.0	15.0	3.0	33.0	2.0	89.0	55.0
Laevicaspia sieversii	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Laevicaspia kolesnikoviana	1.0	3.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Laevicaspia conus	9.0	0.0	9.0	0.0	0.0	2.0	0.0	1.0	0.0
Clathrocaspia gmelini (r)	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Turricaspia spica	553.0	88.0	33.0	0.0	4.0	5.0	2.0	13.0	17.0
Turricaspia sp. indet	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Pulmonata sp. indet.	14.0	2.0	9.0	1.0	3.0	2.0	0.0	4.0	2.0

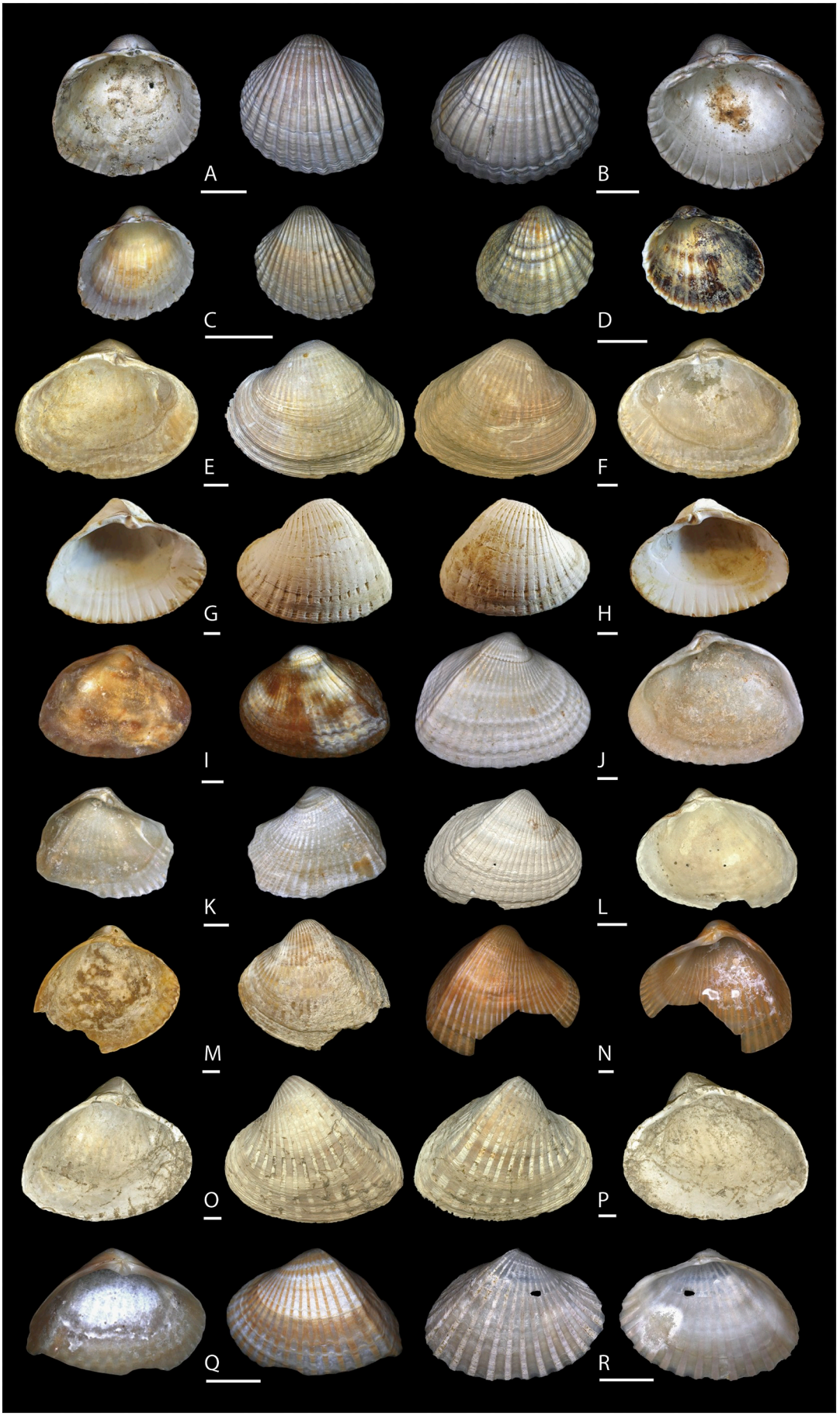

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Fig. 5. Late Holocene Novocaspian bivalve species from Turali, with indication of sample and collection number. LV displayed on the left, RV on the right. **A–B** *Cerastoderma* sp. A [non *C. rhomboides* (Lamarck, 1819)] **A** M0215, RGM.961896 **B** M0215, RGM.962391 **C–D** *Cerastoderma glaucum* (Bruguière, 1789) **C** M0216, RGM.962390 **D** M0216, RGM.962389 **E–F** *Didacna baeri* (Grimm, 1877) **E** M0204, RGM.962379 **F** M0204, RGM.962380 **G–H** *Didacna eichwaldi* (Krynicki, 1837) **G** M02-05, RGM.961900 **H** M02-05, RGM.961900 **I–J** *Didacna parallela* (Bogachev, 1932) **I** M0202, RGM.962383 **J** M0202, RGM.962384 **K–L** *Didacna protracta* (Eichwald, 1841) **K** M0202, RGM.962386 **L** M0222, RGM.962385 **M–N** *Didacna pyramidata* (Grimm, 1877) **M** M0202, RGM.962387 **N** M0222, RGM.962388 **O–P** *Didacna trigonoides* (Pallas, 1771) **O** M0215, RGM.962378 **P** M0215, RGM.962377. **Q–R** *Didacna barbotdemarnii* (Grimm, 1877) **Q** M0222, RGM.962420 **R** M0221, RGM.962421. Scale bars 5 mm.

Turali-4 comprises a single fine-grained sandy silt layer with dispersed molluscs. The layer contains very poorly developed bedding planes. Given the location farthest from the shore and close to the escarpment that bounded the landward side of the Novocaspian deposits, this layer may be among the oldest Novocaspian intervals. It is considered to represent a (relatively shallow) bay floor infill. Locality Turali-5 is a poorly delimited shelly sand layer, and like Turali-2 located below the water table.

4.2. Taphonomy

The degree of preservation varies within the samples. Samples M0202 and M0203 are dominated by abraded (polished) fragments and specimens. Within most other samples the majority of shells have retained fine sculptural details, and paired bivalves were observed (Fig. 3), but a few abraded specimens were found too. These abraded specimens were either induced by storm events or result from reworking by bioturbation from underlying layers. In rare cases Late Pleistocene fossil species were found in these samples. Both Khvalynian and Khazarian (Late Pleistocene) units crop out very close to the study site. The land snails were either introduced in the layers during post-depositional soil formation or reworked floating material.

4.3. Faunal composition and taxonomy

All studied material is listed in Table 3. The sample represents 28 identifiable aquatic mollusc species, of which two (*Cerastoderma* cf. *glaucum*, *Cerastoderma* sp. A) are invasive, and two (*Ecrobia grimmi* and *Theodoxus pallasi*) are native species sensu Wesselingh et al. (2019); the remainder are endemic Caspian species. The rarefaction curve is nearly saturated for the largest three samples, suggesting that our samples represent an appropriate estimate of the true richness (Fig. 4). Pictures of all species are shown in Figs. 5–7.

The endemic Caspian fauna contains several endemic species complexes (Logvinenko and Starobogatov, 1969; Neubauer et al., 2018), and identifications can be difficult. This is mainly caused by the poorly studied variability of mollusc characteristics (Anistratenko et al., 2017) and by the lack of data concerning the type material of almost all Caspian species (Anistratenko et al., 2019, 2018; Vinarski and Kantor, 2016). First steps in revising the Pontocaspian gastropod fauna are in progress (Neubauer et al., 2018; van de Velde et al., 2019; Wesselingh et al., 2019). Here, we discuss some of the taxonomic uncertainties in the Turali fauna.

4.3.1. Bivalves

We are not entirely certain about the distinction and identity of the two *Cerastoderma* species in the Turali samples (Fig. 5A–D). Two forms that coincide with the species as reported by Wesselingh et al. (2019) are *C. glaucum* (Fig. 5C–D) and *Cerastoderma* sp. A (Fig. 5A–B). The latter species is typically more convex, thick-shelled, has more regularly spaced ribs often with regularly developed scales and these ribs usually extend well to the anterior and posterior margins. *Cerastoderma glaucum* in the Turali samples is much thinner shelled, ribs are lower and fade towards the edges of the shells. A marked difference exists in the degree of symmetry of the shell, with *C. glaucum* being stronger inequilateral. Also, the number of ribs differs slightly. The length/height (L/H) ratio also differs, but that may (partly) result from differences in the shell size of the measured specimens (all *C. glaucum* valves being larger than *C.* sp. A). Without conducting more elaborate morphometric analyses based on a broader range of Pontocaspian material, we feel it premature to introduce a new name. Several names have been used for specimens similar to *C.* sp. A as reported here (see Wesselingh et al., 2019).

The common *Didacna* species (*D. trigonoides*, *D. eichwaldi*, *D. baeri* and *D. barbotdemarnii*) in the Turali material have closely resembling morphologies and a large shell shape variability. The distinguishing characters proposed by Nevesskaja (2007) were found to apply to the studied material with slight modifications (Supplementary Table S1). *Didacna trigonoides* is convex, thin-shelled, high and has an acute posterior ridge (often a double ridge on juvenile stages) and flat, relatively few ribs (12–20 anterior ribs). *Didacna baeri* has a rounded shape, relative low shell with more numerous ribs (19–22 anterior ribs). The posterior keel is not well developed and distinct only near the umbo. The general shell shape resembles that of *D. eichwaldi*, but the latter species has slightly fewer ribs (typically 18–20 anterior ribs), is more convex, has a more projecting beak and a more distinct posterior ridge. Finally, *D. barbotdemarnii* can resemble juvenile and subadult specimens of *D. trigonoides* but the former has slightly more ribs (16–20 + anterior ribs versus 12–20 on *D. trigonoides*) that are low and broad, is broader and flatter with a relatively low beak and the posterior ridge is poorly pronounced.

There still exists uncertainty about the amount and definition of species within the genus of *Monodacna* (Wesselingh et al., 2019). In our material we distinguish three types: *Monodacna albida*, *M. caspia* and *M. semipellucida* (Fig. 6; G–L). They can all be recognized as *Monodacna* species by their single cardinal tooth and lack of a posterior keel. *Monodacna caspia* (Fig. 6; I–J) is a highly variable species, but can be identified by the thick, sturdy, relatively convex shell and the regularly spaced, almost flat ribs. Interspaces are narrower than the ribs. The beak is almost centrally located and slightly curved towards the anterior margin. *Monodacna albida* (Fig. 6; G–H) can be distinguished by its wedge-shape shell outline and its low flat ribs that are irregularly spaced. The location of the beak is in the centre of the shell. *Monodacna semipellucida* (Fig. 6; K–L) can be distinguished from *M. albida* by being relatively thin-walled. Moreover, the shell is lower, often elliptical and bears a very characteristic, very thin, tuberculate cardinal tooth. The ribbing is weak and the beak is located towards the anterior margin.

We are uncertain about the identity of *Dreissena elata* (Fig. 6; O–P). The shells are morphologically similar to the Palearctic *D. polymorpha*, even though Caspian shells are in general lower, thicker and are often wider. The habitats of genuine *D. polymorpha* and the Caspian *D. elata* are apparently non-overlapping, with the former restricted to habitats of fresh water up to 2 psu in the Volga delta and adjacent rivers, while the latter occurred in the coast of the Caspian Sea in salinities of 7–13 psu (Orlova et al., 2005). However, the *D. elata* populations disappeared in the second half of the 20th Century. They were outcompeted by *Mytilaster minimus*, thereby impeding a molecular taxonomic assessment. If *D. elata* is confirmed as a separate species, it might well be extinct.

4.3.2. Gastropoda

The Turali sample of *Theodoxus pallasi* contains a remarkable variation of colour patterns and shapes (Fig. 7; K, L). Colour varieties range from dotted specimens to zig-zag coloured specimens, and the general shape varies from ovate to elongate. The latter shape is often attributed

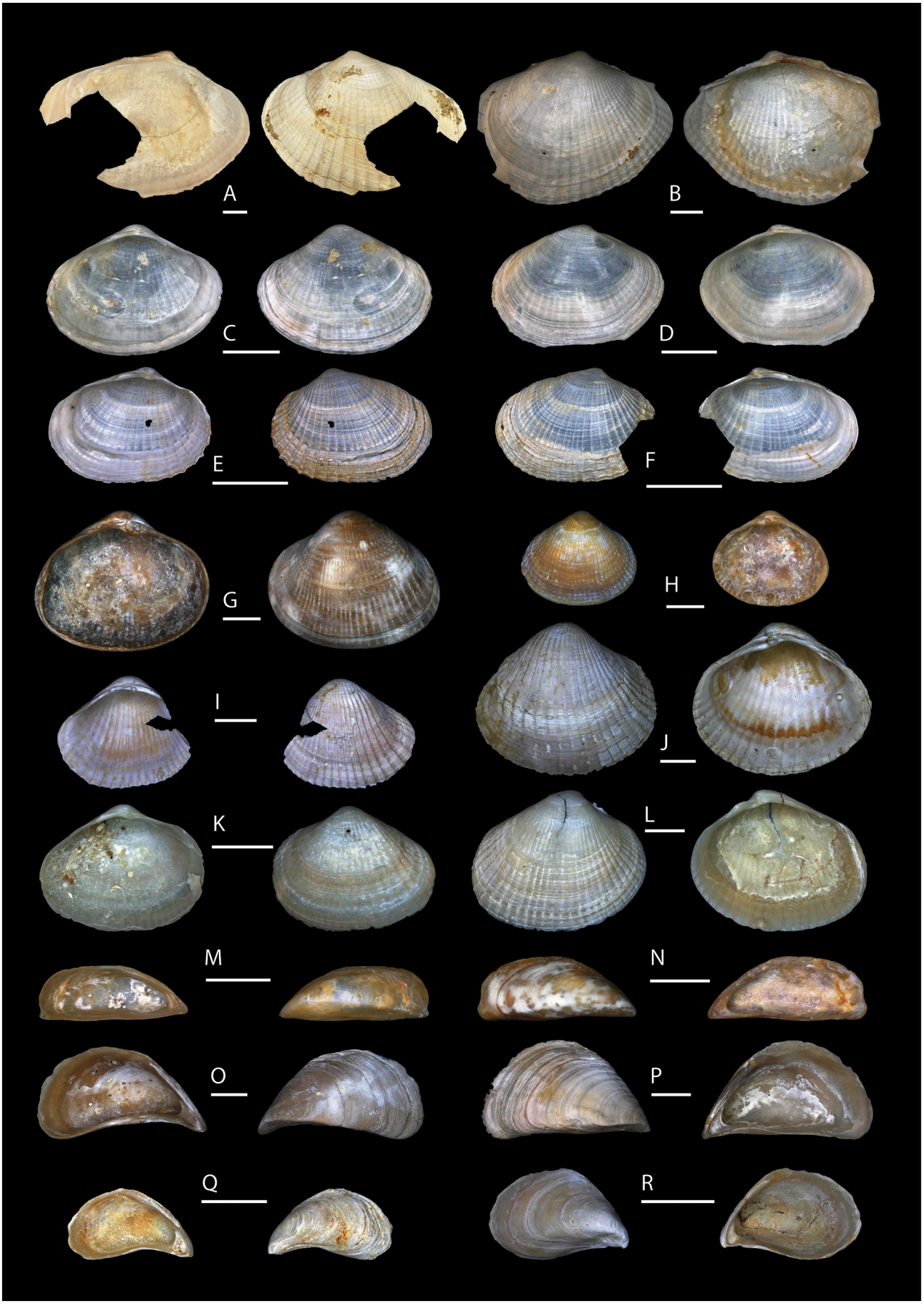

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Fig. 6. Late Holocene Novocaspian bivalve species from Turali, with indication of sample and collection number. LV displayed on the left, RV on the right. **A–B** *Adacna laeviuscula* (Eichwald, 1829). **A** M0222, RGM.962359 **B** M0222, RGM.962358 **C–D** *Adacna vitrea* (Eichwald, 1829) **C** M0221, RGM.962360 **D** M0221, RGM.962361 **E–F** *Hypanis plicata* (Eichwald, 1829) **E** M0221, RGM.962362 **F** M0221, RGM.962363 **G–H** *Monodacna albida* (Logvinenko & Starobogatov, 1967) **G** M0202, RGM.962364 **H** M0202, RGM.962365 **I–J** *Monodacna caspia* (Eichwald, 1829) **I** M0204, RGM.962367 **J** M0205, RGM.962368 **K–L** *Monodacna semipellucida* (Logvinenko & Starobogatov, 1967) **K** M0222, RGM.962369 **L** M0222, RGM.962370 **M–N** *Dreissena caspia* (Eichwald, 1855) **M** M0222, RGM.962371 **N** M0202, RGM.962372 **O–P** *Dreissena elata* (Andrusov, 1897) **O** M0203, RGM.962375 **P** M0221, RGM.962376 **Q–R** *Dreissena grimmi* (Andrusov, 1890) **Q** M0203, RGM.962374 **R** M0202, RGM.962373. Scale bars 5 mm.

to *T. schultzii* (Fig. 7; L), but in our material we see intermediate forms as well. A recent molecular approach suggests that all forms from the Caspian Sea might be conspecific with the Armenian *T. major* Issel, 1865 (Sands et al., 2019).

The identification of *Abeskunus* species was difficult because different species concepts have been proposed (Logvinenko and Starobogatov, 1969; Neubauer et al., 2018). Here, we distinguish two species, *Abeskunus brusinianus* (Fig. 7I–J) and *Abeskunus exiguus* (Fig. 7M). The former species involves a considerable morphological variability as to the height of the spire and two morphs were found (Fig. 7I–J). Further taxonomic study is required to assess whether the two shapes of *A. brusinianus* represent ecomorphs or distinct species.

Shells of *Clessiniola variabilis*, *Ecrobia grimmi*, *Laevicaspia conus* and *L. sieversii* contain a wide range of variability too. Sometimes it is difficult to distinguish one species from other, e.g. *L. conus* and *L. sieversii*, and molecular and/or more in-depth morphological and anatomical studies are required. In some cases, morphological variation seems to be very well defined. For example, modern specimens of *Turricaspia spica* fit well in shape and size with the extensive specimens from Turali (Fig. 7; G).

4.4. Palaeoecology

Ecological data for mollusc species is given in Table 4. The majority of the Turali fauna represents salinities between 5 and 13 psu, indicating a lower to upper mesohaline environment. The upper salinity tolerance of *Monodacna caspia* has previously been reported as 8 psu (van de Velde et al., 2019), but personal observations of species present in the middle and southern Caspian Sea indicate an upper salinity tolerance of 12–13 psu instead. All species are able to live within the depth range of 0 to 50 m on a silty sandy to muddy lake floor. The abundance of *Theodoxus*, a grazer of microalgae, confirms the fauna lived within the photic zone. Direct evaluation of vertical distribution of species inhabiting the Caspian Sea (Kolesnikov, 1947; Tarasov, 1996; Tarasov and Chepalyga, 1996) supports the conclusion about a shallow environment for the Novocaspian Turali molluscs. A similar composition of faunal communities (the absence of deep-dwelling forms) can be observed along the Dagestan shore today. This corresponds well with shallow bay and barrier facies from where the faunas were collected. No species that inhabit depths over 30 m such as *Didacna profundicola*, Clathrocaspia spp., Ulskia ulskii, Turricaspia elegantula, *T. dimidiata* and Andrusovia spp. were found.

The samples represent washover-bay floor transitions between 2000 and 2400 cal yr BP and the presence of paired bivalves in almost all samples shows that these faunas were mostly in situ. The faunal composition (species group ratios) is similar in the samples. The most abundant species is *Dreissena elata* (52% of all individuals, the species occurs in all samples), followed by *Cerastoderma* sp. A, *Theodoxus pallasi* (each accounts for 9% of the total abundance, both occur in all samples). The common occurrence of the grazing gastropod *T. pallasi* in all samples indicates shallow environments in the photic zone.

5. Discussion

5.1. Novocaspian mollusc biodiversity and palaeoenvironment

The Turali fauna contains a snapshot of a pre-20th Century mollusc fauna from shore and shallow bay environments in the western-middle Caspian Basin. The palaeoenvironment (depth, depositional energy, temperature) is constrained by the sedimentary facies and ecological preferences of the species. The Turali setting represents a semi-open shallow bay with beach ridges partially isolating the bay from the main Caspian Sea (Fig. 8). The differences in the palaeoenvironment are minimal between individual sites and there are no strong dissimilarities regarding facies, age, mollusc diversity and palaeoenvironment that are not in concordance with the general results. The sedimentary succession represents mostly transitional settings between beach barriers and bay floor environments of around 2000–2400 cal yr BP and the palaeoecology of the mollusc faunas fits with such environments. Sclerochronological analyses of stable isotope ratios in the molluscs shows strong seasonal changes in oxygen and carbon isotope values, which are generally in line with seasonal changes in temperature and salinity in the nearby Caspian Sea today (Vonhof et al., 2004). The setting resembles that of the Sulakski Bay north of Makhachkala (Dagestan).

In total, we encountered 28 identifiable species: 24 are Pontocaspian endemics, two species are native, and two are invasive. Of the 24 endemics, only two species were found as reworked species. The Turali fauna is dominated by *Dreissena elata*, *Cerastoderma* sp. A and *Theodoxus pallasi*. Common species are *Turricaspia spica*, *Didacna eichwaldi*, *Clessiniola variabilis*, *Dreissena caspia*, *Ecrobia grimmi*, *Adacna vitrea*, *Monodacna albida*, *Hypanis plicata* and *Abeskunus brusinianus*. The invasive species (*Cerastoderma* spp.) are common but not dominant.

The species composition indicates a palaeo-water depth between 0 and 50 m, even though the majority of species prefer the shallowest parts of these depths and sedimentary structures indicate very shallow depositional depths. The salinity range varies between 5 and 13 psu. These estimated salinity ranges overlap with the current salinity in the middle Caspian basin (11–13 psu). Caspian Sea levels around 2600 cal yr BP were very similar to today's Caspian Sea level (around −25 m versus −27 m today: Kroonenberg et al., 2008), hence it is likely that salinity regimes were similar to today's salinity.

5.2. Holocene versus Pleistocene faunas

The Turali faunas have aspects in common with other Late Pleistocene Caspian communities. Thirteen bivalve species and 24 gastropod species were identified at a Hyrcanian (c. 107 ka) outcrop at Selitrennoye (Russia): 99% of the individuals belong to endemic species (van de Velde et al., 2019). The Selitrennoye assemblage is dominated by the same three families as the Turali assemblages: Cardiidae, Dreissenidae and Hydrobiidae. The authors estimated palaeosalinities between 5 and 8 psu (it might be slightly higher as the estimate was partially based on an erroneous upper salinity tolerance of 8 psu for *Monodacna caspia*, while our current observations show a limit of 12–13 psu instead). Half of the species (14 out of 28) found at Turali are also found at Selitrennoye. The genus *Didacna* shows a completely different species composition on both sites, illustrative for the rapid turnover of *Didacna* species in particular (Nevesskaja, 2007).

5.3. Comparison with Caspian biodiversity of today

Latypov (2015) studied invertebrates from the Sulakski Bay, where a number of stations down to 4 m water depth were sampled during 1994–2001. He did not report salinities, but these may have been slightly lower than in the adjacent Caspian Sea because the bay itself

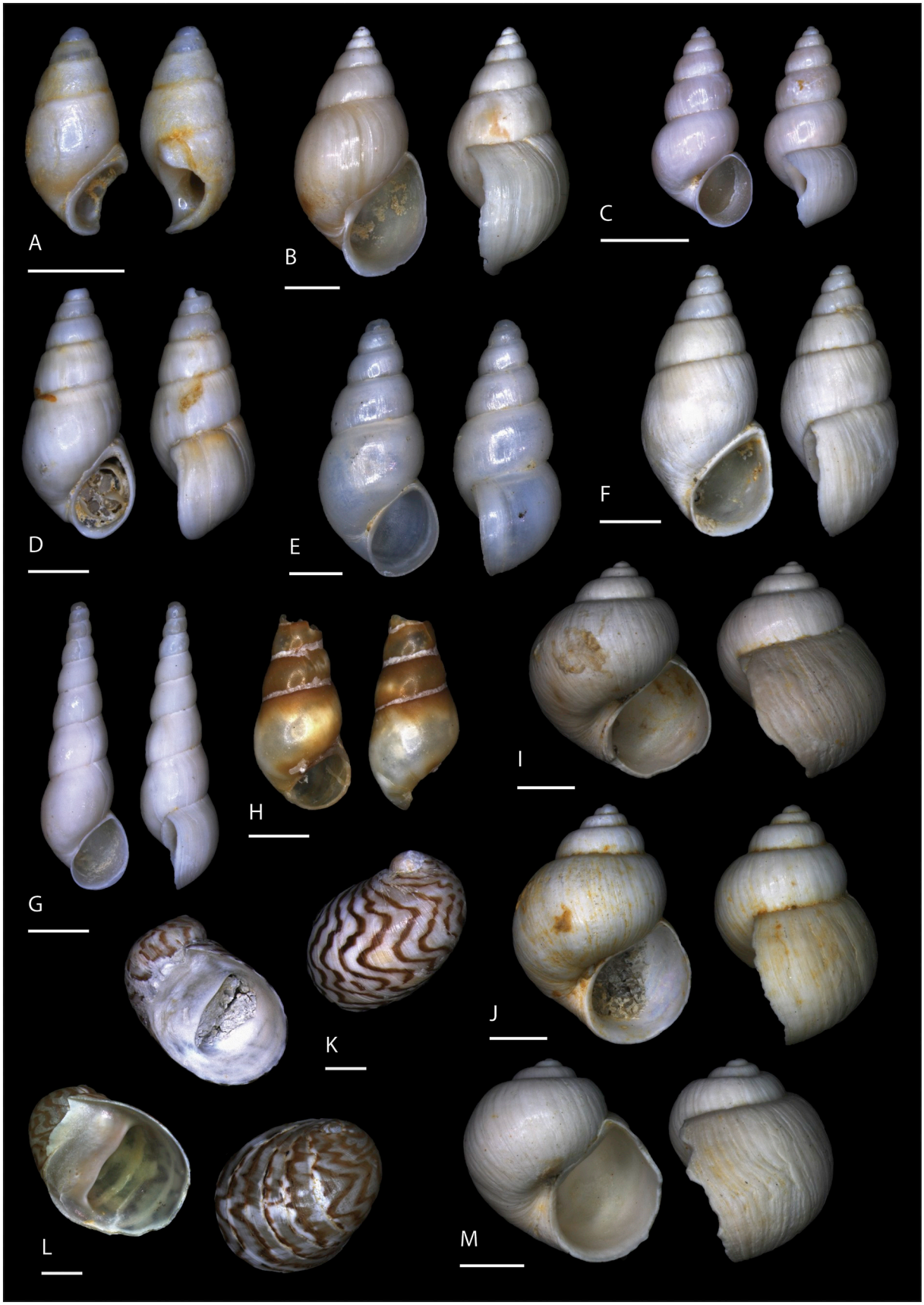

Fig. 7. Late Holocene Novocaspian gastropod species from Turali, with indication of sample and collection number. A *Clathrocaspia gmelinii*: M0203, RGM.1309848 B *Clessiniola variabilis*: M0204, RGM.1309864 C *Ecrobia grimmi*: M0202, RGM.1309863 D *Laevicaspia sieversii*: M0204, RGM.1309849 E *Laevicaspia kolesnikoviana*: M0221, RGM.1309850 F *Laevicaspia conus*: M0204, RGM.1309851 G *Turricaspia spica*: M0202, RGM.1309858 H *Turricaspia* sp. indet. M0222, RGM.962401. I *Abeskunus brusinianus*: low morph, M0204, RGM.962355 J *Abeskunus brusinianus*: high morph, M0204, RGM.962355 K *Theodoxus pallasi*: M0204, RGM.130985, L. *Theodoxus pallasi*: M0220, RGM.1309862, M *Abeskunus exiguus*, M0204, RGM.962357. Scale bars 1 mm.

Table 4
Environmental indicators: optimal living conditions of Turali species.

Species	Origin	Natural salinity ranges (psu)	Environment	Depth (m)
Cerastoderma cf. *glaucum*	Invasive[7]	Min. 5–8[1], 10–23[6]	Caspian Sea.[1]	10–50[1], 5–40[6]
Cerastoderma sp. A [non *C. rhomboides*]	Invasive[7]	Min. 5–8[1], max 12–13	Caspian Sea.[1]	0–40[1]
Adacna laeviuscula	Endemic[1]	Min. 5–8[1], 4–14[1], min. 4[2]	Caspian Sea.[1] Muddy, sandy- mud and, rarely, sandy bottoms.[1]	30–100[1], max. 80–85[2a]
Adacna vitrea	Endemic[1]	Min. 5–8[1], max 12–13	Caspian Sea.[1, 2]	0–40[1], 20 rarely 30[2]
Hypanis plicata	Endemic[7]	4–8[1, 2], max 12–13	Caspian Sea.[1] Silty-sandy, clayey soils, hard aleurites with shell rock.[1]	0–40[1], 0.5–30[1, 2]
Monodacna albida	Endemic[1]	Min. 5–8[1], max 12–13	Middle and southern Caspian Sea.[1,2]	0–150[1, 2], 200–400[3]
Monodacna caspia	Endemic[1]	2–8[1], max 12–13	Northern Caspian Sea.[1] Middle & southern Caspian Sea.[5] Muddy and sandy-mud substrates.[1]	0–40[1], 0–200[2]
Monodacna semipellucida	Endemic[1]	Min. 5–8[1], max 12–13	Middle Caspian Sea.[1]	0–40[1], 0–30[2]
Didacna eichwaldi	Endemic[9]	Min. 3, max. 14[1]	Middle and southern Caspian Sea.[1] Western and eastern Caspian Sea.[4]	7.5–60[1]
Didacna baeri	Endemic[1]	Min. 3, max. 14[1]	Southern Caspian Sea.[1] Southern Caspian Sea and southern part of the middle Caspian Sea.[2, 4]	0–50[1, 6], 0–60[2]
Didacna barbotdemarnii	Endemic[1]	Min. 3, max. 14[1]	Middle and southern Caspian Sea.[1]	0–40[1]
Didacna parallela	Endemic[1]	Min. 3, max. 14[1]	Middle and southern Caspian Sea.[1]	50–100[1], 50–85[2, 6], 200–300[3]
Didacna protracta	Endemic[1]	Min. 3, max. 14[1]13	Middle and southern Caspian Sea.[1, 2, 4]	25–50[1, 2], 25–75[6]
Didacna pyramidata	Endemic[1]	Min. 3, max. 14[1]	South Caspian Sea.[1] Southern and middle Caspian Sea.[2, 4]	35–130[1], 30–100
Didacna trigonoides	Endemic[1]	Min. 3, max. 14[1]	Caspian Sea.[1] Northern Caspian Sea.[2]	5–60[1]
Dreissena caspia	Endemic[1]	Opt. 2–8[1], max 12–13	Caspian Sea.[1, 2]	0–40?[1], 0–35[2]
Dreissena elata	Endemic[1]	Opt. 2–8[1], max 12–13	Middle and southern Caspian Sea.[1]	0–40?[1], 0–35[2], 0–30[7]
Dreissena grimmi	Endemic[1]	Opt. 2–8[1], max 12–13	Middle Caspian Sea.[1, 5, 2]	35–100[1], 45–80[2,5], 200–400[3]
Theodoxus pallasi	Native[7]	Opt. 0–8[1], max 12–13	Caspian Sea.[1] Low salinity seas and large lakes, limans and estuaries.[2]	0–40[1], 0–35[2]
Abeskunus brusinianus	Endemic[1]	Min. 5–8[1], max 12–13	Middle and southern Caspian Sea.[1]	0–200[1]
Abeskunus exiguus	Endemic[1]	Min. 5–8[1], max 12–13	Northern Caspian Sea.[1]	0–40[1]
Clessiniola variabilis	Endemic[1]	Opt. 0–8[1], 5–7[8], max 12–13	Caspian Sea.[1, 3]	0–25[2], > 20[1], 200–300[3]
Ecrobia grimmi	Native[7]	Opt. 2–8[1], max 12–13	Southern Caspian Sea.[1, 3]	> 25[1], 25–40[2]
Laevicaspia sieversii	Endemic[1]	Min. 5–8[1], max 12–13	Caspian Sea.[1, 3]	0–120[1, 2], 200–300[3]
Laevicaspia kolesnikoviana	Endemic[1]	Min. 5–8[1], max 12–13	Southern Caspian Sea.[1]	25–120[1], 25–180[2], 200–400[3]
Laevicaspia conus	Endemic[1]	Min. 5–8[1], max 12–13	Caspian Sea[1, 3]	25–50[1, 2], 200–300[3]
Clathrocaspia gmelinii	Endemic[1]	Min. 5–8[1], max 12–13	Middle and southern Caspian Sea.[1, 2]	35–100[1], 30–81[2],200–300[3]
Turricaspia spica	Endemic[1]	Min. 5–8[1], max 12–13	Northern and middle Caspian Sea.[1, 2]	0–40[1], 0–30[2]

References: [1]Bogutskaya et al., 2013, [2]Logvinenko and Starobogatov, 1969, 3Mirzoev and Alekperov, 2017, 4Nevesskaja, 2007, [5]Starobogatov, 1994, [6]Yanina, 1981, [7]Wesselingh et al., 2019, [8]Chukhchin, 1984, [9]Vinarski and Kantor, 2016.

[a] Our findings point towards shallow foreshore environments.

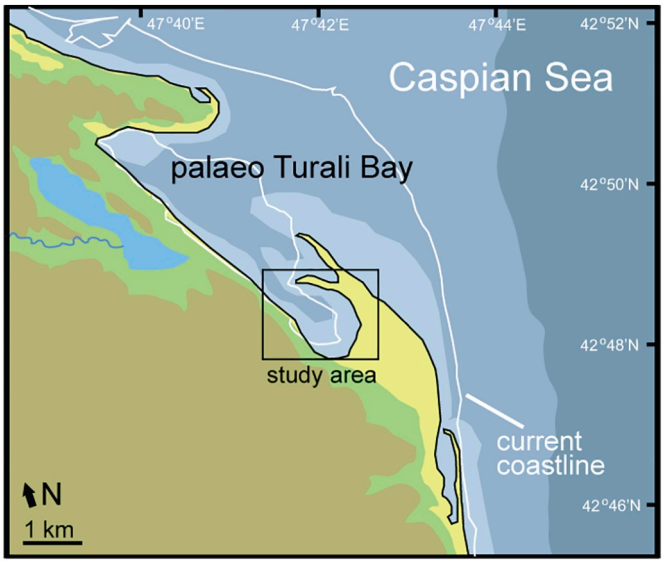

Fig. 8. Reconstruction of Turali Bay, c. 2300 cal yr BP. The palaeocoastline is approximatly based on the estimated lake level reconstructed for the time of deposition.

Fig. 9. Box core residue (sample M0267, c. 2 km off shore Turali at a water depth of 9.4 m) separated into the dark Novocaspian (left) and light 20th Century (right) fractions defined in the text. Largest shell c 1.5 cm across.

borders on the Terek River delta. Otherwise Sulakski Bay yields an almost identical environment as the Turali settings (shallow open bay in the proximity of beach barriers). Latypov (2015) reported a predominant *Abra-Cerastoderma* community dominated by three invasive species *A. segmentum*, *M. minimus* as well as *C. glaucum* (which likely includes *C.* sp. A). He only reported seven Pontocaspian species from

Table 5
Overview of mollusc species biomass abundances (mg/m2), collected at the environmental monitoring programme of the North-East Caspian Sea (2005–2016). Macrozoobenthos samples were taken with van Veen grab sampler (0.1 m^2), Petersen Dredger (0.025m^2) and tubular dredger (0.002m^2) along four sites: Kashagan, Aktote, Kalamkas sites and the oil field pipe route in the North-East Caspian Sea. From: North Caspian Operating Company (NCOC, 2018).

Species	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Theodoxus pallasi (Lindholm, 1924)	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.15
Clathrocaspia gmelinii (Clessin & Dybowski in Dybowski, 1887)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
Clathrocaspia sp.	8.95	0.00	0.00	5.16	3.36	6.68	6.52	5.94	3.30	3.18	4.97
Laevicaspia conus (Eichwald, 1838)	0.00	0.00	0.00	0.79	0.52	0.00	0.00	0.00	0.00	0.00	0.00
Turricaspia andrussowi (Dybowski & Grochmalicki, 1915)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
Turricaspia uralensis (Logvinenko and Starobogatov, 1969)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Abeskunus brusinianus (Clessin & Dybowski in Dybowski, 1887)	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.00	0.00	0.00
Abeskunus sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00
Gyraulus eichwaldi (Clessin & Dybowski in Dybowski, 1887)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
Mytilaster minimus (Poli, 1795)	0.00	0.00	0.99	3.28	1.29	0.53	0.00	0.09	0.00	0.00	0.15
Adacna minima (Ostroumov, 1907)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Adacna vitrea (Eichwald, 1829)	23.64	9.52	17.82	24.60	5.94	1.34	0.28	4.28	7.49	5.51	12.13
Cerastoderma glaucum (Bruguière, 1789)/*C.* sp. A[a]	0.00	0.00	0.74	2.38	3.88	29.95	58.92	81.12	59.71	78.83	71.49
Didacna trigonoides (Pallas, 1771)	60.06	28.57	49.50	67.86	63.31	32.35	20.11	18.44	22.99	21.69	25.88
Didacna protracta (Eichwald, 1841)	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.58
Didacna pyramidata (Grimm, 1877)	0.00	0.00	0.00	0.00	2.33	0.00	0.00	0.00	0.00	0.00	0.00
Didacna sp.	0.64	0.00	0.50	0.40	0.00	0.00	0.00	0.00	0.00	0.09	0.44
Monodacna albida (Logvinenko & Starobogatov, 1967)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.15
Monodacna colorata (Eichwald, 1829)	58.79	61.90	75.74	90.48	67.70	26.47	11.90	21.59	38.06	31.93	42.98
Monodacna caspia (Eichwald, 1829)	7.99	0.79	25	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.00
Monodacna sp.?	0.32	0.00	6.93	0.00	0.26	0.27	0.57	0.61	0.00	0.09	1.61
Abra segmentum (Récluz, 1843)	38.98	75.40	77.48	89.29	91.21	96.52	96.03	92.92	86.72	89.76	95.32
Dreissena caspia (Eichwald, 1855)	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dreissena polymorpha s.l. (Pallas, 1771)	61.02	29.37	19.06	58.73	52.45	11.76	0.00	0.44	0.00	0.09	0.29
Bivalvia gen. et sp. indet.	16.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15

[a] Status based on Wesselingh et al. (2019).

extensive sampling efforts. The sampling design is not entirely clear and differs from our Turali approach, yet the numbers reported and the presence of small amounts of species in Latypov's analyses indicate that today's richness is more than three times as low and that communities now are dominated by invasive species and natives instead of endemic species.

A similar division has been observed in grab samples taken offshore Turali (samples taken by FPW): (1) Novocaspian shells and fragments with darker grey-blue-brown colour and extensive surface wear and (2) light coloured specimens with preservation of fine surface details and often presence of colouration and/or organic remains representing the 20th Century assemblage (Fig. 9). The separation of the shelly residue allows a basic comparison. The fresh-looking fauna component there is dominated by the native *C.* sp. A and *E. grimmi* and the invasive *A. ovata* and *M. minimus*. Only some fresh specimens of the Pontocaspian *Clessiniola variabilis* were found. The older fraction of the sample represents pre-20th Century Novocaspian species such as *Dreissena caspia* and *D. elata*, *Didacna baeri*, *D. barbotdemarnii* as well as Caspian hydrobiid species.

The dominance by invasive species in modern assemblages is not restricted to the middle Caspian Basin as is shown by a faunal inventory from nearshore settings in Gorgan Bay in Iran (Leroy et al., 2018) in the southern basin. Three samples taken between 5.2 m and 8.6 m water depth contained only nine species (n = 226). The samples are also dominated by the native species *Ecrobia grimmi*, ancient invasive *Cerastoderma glaucum/C.* sp. A and the 20th Century invasive *Abra segmentum* that make up 97% of the total abundance. Fresh-looking shells of endemic species (five species) made up only 3%.

The impact of recent invasions on the Caspian fauna is shown in observational time series such as those of the environmental monitoring programme (2005–2016) of the North Caspian Operating Company (NCOC, 2018). It shows the species richness and biomass of the north-eastern Caspian Sea benthic communities (NCOC, 2018; summary in Table 5) as well as the current distribution of native and foreign mollusc species. In total, the NCOC monitoring provided 21 endemic Pontocaspian mollusc species and 3 marine invasive species (*Mytilaster minimus*, *Cerastoderma glaucum* [which likely includes *C.* sp. A] and *Abra segmentum*). The marine invasive species of this ten year record make up half the biomass (49%), and *Monodacna colorata*, which originated in the Black Sea Basin, accounts for another 20%, leaving 29% of the biomass for endemic Caspian species. *Abra segmentum*, which accounts for 34% of the total biomass, was introduced as a food source for fish (Malinovskaya and Zinchenko, 2011). As opportunistic euryhaline species *A. segmentum* outcompeted the native Pontocaspian species (Karpinsky, 2010). Invasive species make up 10% of the specimen numbers in the Turali faunas while they represent almost 70% of the biomass in the modern north-eastern Caspian assemblage. The endemic Pontocaspian fauna has formed over a long period of time and never had to face competition of marine species before (Kostianoy et al., 2005). The introduction of new marine invasive species, intentionally or accidentally, is expected to have a very strong and adverse impact on the native Pontocaspian fauna.

5.4. Refuges

Beach collections from the Great Turali Lake and later at Sirvan (Azerbaijan) and Bautino (Kazakhstan: all alongside the middle Caspian Basin) delivered fresh material of a number of Pontocaspian endemic bivalves: *Adacna vitrea*, *A. laeviuscula*, *Didacna protracta*, *D. trigonoides*, *D. barbotdemarnii* and *Hypanis plicata*. It concerns specimens with often paired valves, preserved colour patterns and organic remnants. This indicates that these bivalve species still live alongside the invasive species within the foreshore habitats. For several of the species only deeper habitats have been mentioned before: for example, *Adacna laeviuscula*, has been reported from depths ranging between 35 m and 100 m (Bogutskaya et al., 2013; Logvinenko and Starobogatov, 1969). The foreshore habitats merit further exploration as they may comprise a refuge for a particular set of Pontocaspian species. Within the Black Sea similar foreshore habitats have been invaded by *Anadara inaequivalvis/kagoshimensis*, *Mya arenaria* and *Rapana venosa*. Such species may have the ability to seriously impact the Caspian foreshore assemblages and further marginalize endemic species in case they might be introduced there.

6. Conclusions

The studied Holocene Turali fauna represents a snapshot of a pre-20th Century crisis middle Caspian open bay to shoreface mollusc community. Comparisons with present-day data are qualitative, but indicate the loss of many endemic Caspian species and a very large turnover in such communities. However, it is likely that a foreshore community still exists where alongside immigrant species a number of endemic Caspian species still thrive. This foreshore habitat is in need of further investigations as it may be threatened by further invasive species.

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