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Crustacean Fauna of the Aral Sea and its Relation to Ichthyofauna During the Modern Regression Crisis and Efforts at Restoration

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The regression and salinization of the Aral Sea, largely caused by water diversion for irrigation, is among the most severe ecological disasters of the 20th century, and has had severe health and economic consequences for the local population. Introductions of alien species to enhance commercial fisheries before the regression had already impacted the ecology of this system. Crustaceans made up about one-quarter of the original metazoan species and constituted the principal food for native and introduced fish. From 1960 on, crustaceans were recorded at numerous fixed sampling stations, including thanatocoenoses (dead animals from sediment cores). We use this previously unpublished information to document changes in species abundance and discuss their causes in the context of species interactions and changes to physical and chemical parameters. Competition from alien crustaceans led to declines in or even extinction of some native species, but eventually severe salinization became the main detriment, and resulted in the complete collapse of commercial fisheries. This seriously hurt a critical trade, which provided the principal protein source for the local population. We document how comparatively modest conservation efforts enabled the northern Small Aral Sea to partially recover and commercial fishing to resume.

Key words: Conservation, Fisheries, Long term monitoring, Saline lake, Introduced species.

BACKGROUND

The regression of the former Aral Sea is one of the most serious human caused environmental disasters in recent times, affecting both the aquatic fauna and the surrounding human population (Micklin 2007 2016; Micklin et al. 2020). Until the middle of the 20th century, the Aral Sea was a semistable, brackish water lake with a diverse fauna. Fisheries played a central part in the area's economy and food supply, yielding 44,000 tons of fish per year before 1960. The Aral Sea regressed in area during the latter part of the 20th century due to water diversion for irrigation; this led the water to become increasingly salinized, had catastrophic consequences for the biota (Figs. 1–3), and led to the complete collapse of commercial fisheries (Aladin et al. 2004; Chen 2018 2020). The virtual desiccation of the lake system also caused multiple health problems for the local human population. One example is dust particles, sometimes contaminated with pesticides or other chemicals, sent into the air from the large salt pans (Jensen et al. 1997; Small et al. 2001; Erdinger et al. 2004; Crighton et al. 2003 2011; Indoitu et al. 2015; O'Hara et al. 2000; Whish-Wilson 2002). The break up of the former USSR exacerbated the problems, which went largely unmanaged until very recently.

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Geography and climate combined to make the Aral Sea an ecologically complex system. The original Aral Sea was an endorheic saline lake, and the fourth largest lake in the world. The history of the area prior to 1960 was described in the Encyclopedia Britannica (2020), and by Krinovogov (2014), Krivonogov et al. (2014), Micklin et al. (2014) and Zonn et al. (2009). The Aral receives two rivers, the Syr Darya in the northeast and the Amu Darya in the south (Figs. 1, 2A). The average depth is 16 m, but reaches 69 m in places along the western coast. The water has an average salinity at 10.3 ppt, but a much higher proportion of divalent ions than in the ocean. Salinity and temperature range was mostly stable, but variable conditions existed due to freshwater inflow near the river deltas or where high temperatures could cause local fluctuations (Bortnik and Cistayevaya 1990; Kosarev 1975; Zenkevich 1963). In some shallow regions and bays salinity could increase to > 50 ppt (Dengina 1959; Husainova 1960). A similar locally increased salinity is also known in the nearly isolated Garabogazköl Bay in the Caspian Sea. Finally, small, adjacent isolated and hypersaline water bodies interacted faunistically with the Aral itself through wind or animal mediated dispersal of organisms.

Unlike the Caspian Sea, the Aral Sea is faunistically almost completely isolated, because no natural or artificial waterways connect it to other water bodies (Micklin et al. 2020). Good scientific studies of the Aral Sea started with the monograph by Berg (1908). The fauna was virtually undisturbed until the middle of the 20th century, when the first planned and accidental species introductions occurred. Since 1960, physical, chemical and biological changes were all monitored by scientists from the former USSR and the later CIS countries (Aladin and Potts 1992; Aladin et al. 2019). These records provide a chronology of the chemical, physical and biological events during the ecological disaster, but major parts remain unpublished. The records are particularly on Crustacea, which are a primary food source for both native and introduced fish.

The modern anthropogenic regression began in 1961 (Fig. 2). Due to large scale irrigation projects and a natural low flow period, the water supply in the two rivers began to decline, causing a decrease in area and

Fig. 1. Map of Central Asia with the Aral Sea and its affluent rivers (modified from www.freeworldmaps.net).

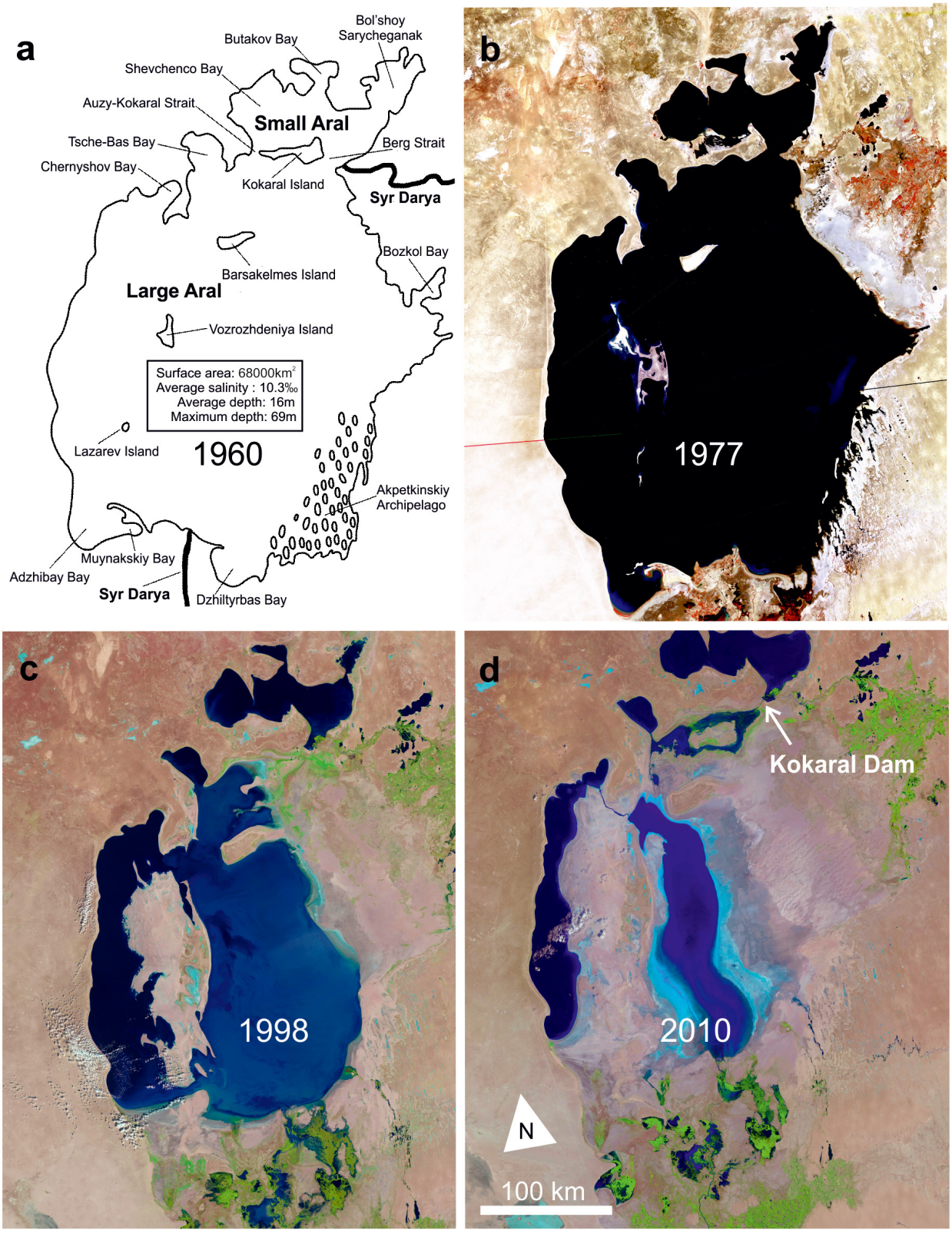

Fig. 2. The original Aral Sea around 1960 (a) and NASA Landsat images (b–d) documenting the modern regression (source NASA); separation of the northern Small Aral and the southern Large Aral had occurred by 1998; in 2010 the continued regression resulted in fragmentation of the Large Aral into several hypersaline water bodies; in contrast, construction of the Kokaral Dam (d) now preserves the water level in the Small Aral and allows it to gradually increase.

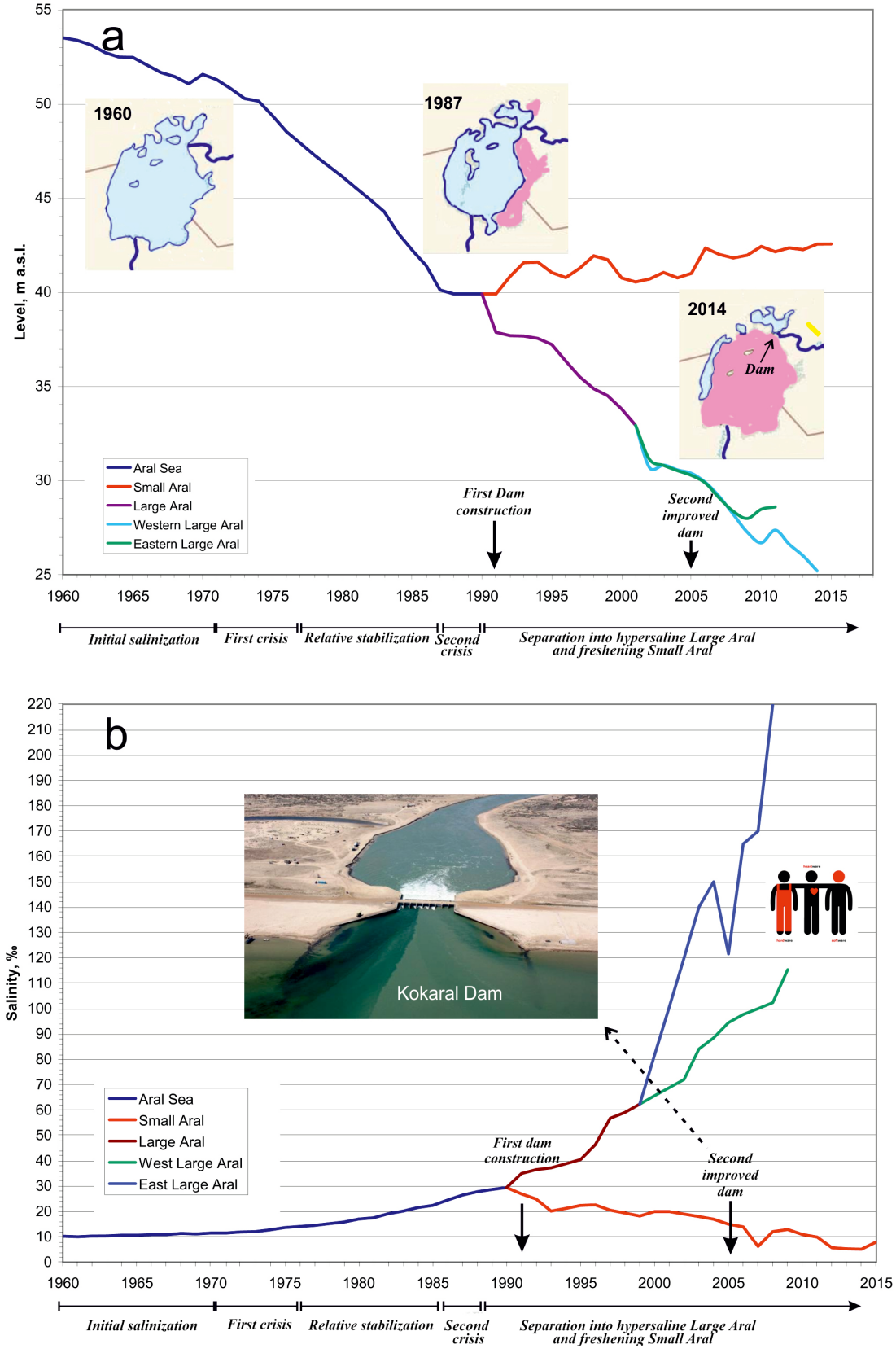

Fig. 3. Changes to water level (a) and salinity (b) in the Aral Sea during the modern regression; m.a.s.l, metres above sea level; salinity given in parts per thousand; inserted images show the concomitant decrease in surface area and the Kokaral Dam (Redrawn from data in Micklin 2014).

an increase in salinity (Bortnik and Chistyaeva 1990). By the late 1980s, both the Berg Strait and the Auzy-Kokaral Strait in the north had dried up, creating two separate water bodies with very different hydrologies (Fig. 3). The northern Small Aral (3200 km^2) was then receiving water only from the Syr Darya, but it retained a positive water balance. Surplus water began to spill into the southern Large Aral, but this and inflow from the Amu Darya were insufficient to stem the ongoing desiccation and salinization (Aladin et al. 1995). The Large Aral is now fragmented into a western part, the former Tschebas Bay, and an extensive eastern part (Bortnik and Chistyaeva 1990). The western part is shrinking. The eastern part still receives irregular inflow from the Amu Darya and oscillates in size, but may also be facing complete desiccation.

In 1992 a primitive dam was built across the Berg Strait. This caused the water level to increase and salinity to decline in the Small Aral (Fig. 3), enabling fisheries to resume (Chen 2018 2020). In 2004–2005 the World Bank financed a new and improved structure, the Kokaral Dam (Fig. 3). This supports the continued preservation of the Small Aral and the gradual restoration of its lost biodiversity (Aladin 1991 2014; World Bank 2014), but also raises the question of whether the reconstituted water body should remain a single, ecologically homogenous entity, or if future restoration projects should aim to diversify habitats that facilitate biodiversity. Such decisions require a detailed knowledge of the faunal history.

Here we report on changes to the crustacean fauna in the Aral Sea from 1960 to the present. We put special emphasis on crustacean-fish relationships, including planned species introductions with the purpose of enhancing commercial fisheries. We document that even before the modern regression, species introductions (of both crustaceans and fish) caused displacement of native forms and dramatic disturbance of food webs. Eventually, all faunistic changes depended entirely on the progressing salinization. We end by using our data to predict how different restoration projects could affect the Aral Sea crustacean fauna to the benefit of fisheries and the human population in the area.

MATERIALS AND METHODS

We summarize investigations into the aquabiological and hydrological conditions of the Aral Sea over an approximately 60-year period. Due to the long time span and the multiple research teams involved, the sampling methodology vary. *Hydrochemical data* used and illustrated here derive from previously published studies. Water samples were obtained as described by Chechko (2015). For further details see Micklin (2007), Micklin et al. (2014) and references therein.

Zooplankton and benthos sampling

Sampling took place at a large number of fixed stations covering the entire Aral Sea system (Figs. 4, 5). Plankton was most commonly collected using Juday and Apstein nets while a Petersen bottom sampler was used for benthic sampling (Baker et al. 1977; Skjoldal et al. 2019; RECO 2020; WRiMS 2020) Plankton was sampled across the entire water column, from the bottom to the surface. For the benthos, the number of sample repeats varied based on substrate hardness, with one or two samples taken on the soft bottom and five on solid ground. A piston bottom sampler was used in the shallower areas to collect plankton and benthos. In addition, plankton and benthos samples were sometimes collected by divers using a Borok plankton net (Dyjachenko 1963) and a shark mouth ("closing jaw" type) bottom sampler, both constructs of the I. D. Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok, Russia (Mathnet.ru 2020). All collected zooplankton and zoobenthos samples were fixed in formalin before being analyzed. We present the faunistic results for all native and introduced crustacean species within the period of investigation, organized as a time series that illustrates faunistic changes. We depict the occurrence through time of selected crustacean species at the fixed sampling stations.

Thanatocenoses

The invertebrate composition from the recent past was analyzed using samples of thanatocoenoses (dead organisms) found in the dried bottom substrate and dried layers of sea grass. These samples provided data on Ostracoda, Branchiopoda and Malacostraca. The samples were collected from shallow holes dug in the hardened muddy ground of the former bottom. Data analysis was conducted using samples dated to 1960, 1965, 1970, 1975, 1980, 1985 and 1990–2011. Dating of these dried samples was based on known coastline positions. *Physiological data and salinity tolerances* used to discuss crustacean faunistic changes are based on Vinogradov and Bobovich (1970) and Aladin (1996).

Data analysis and storage

After the collapse of the USSR, notes and journals concerning sampling and sample processing that survived with the Aral branch of the Kazakh Research Institute of Fishery (KazNIIRKH) were transferred

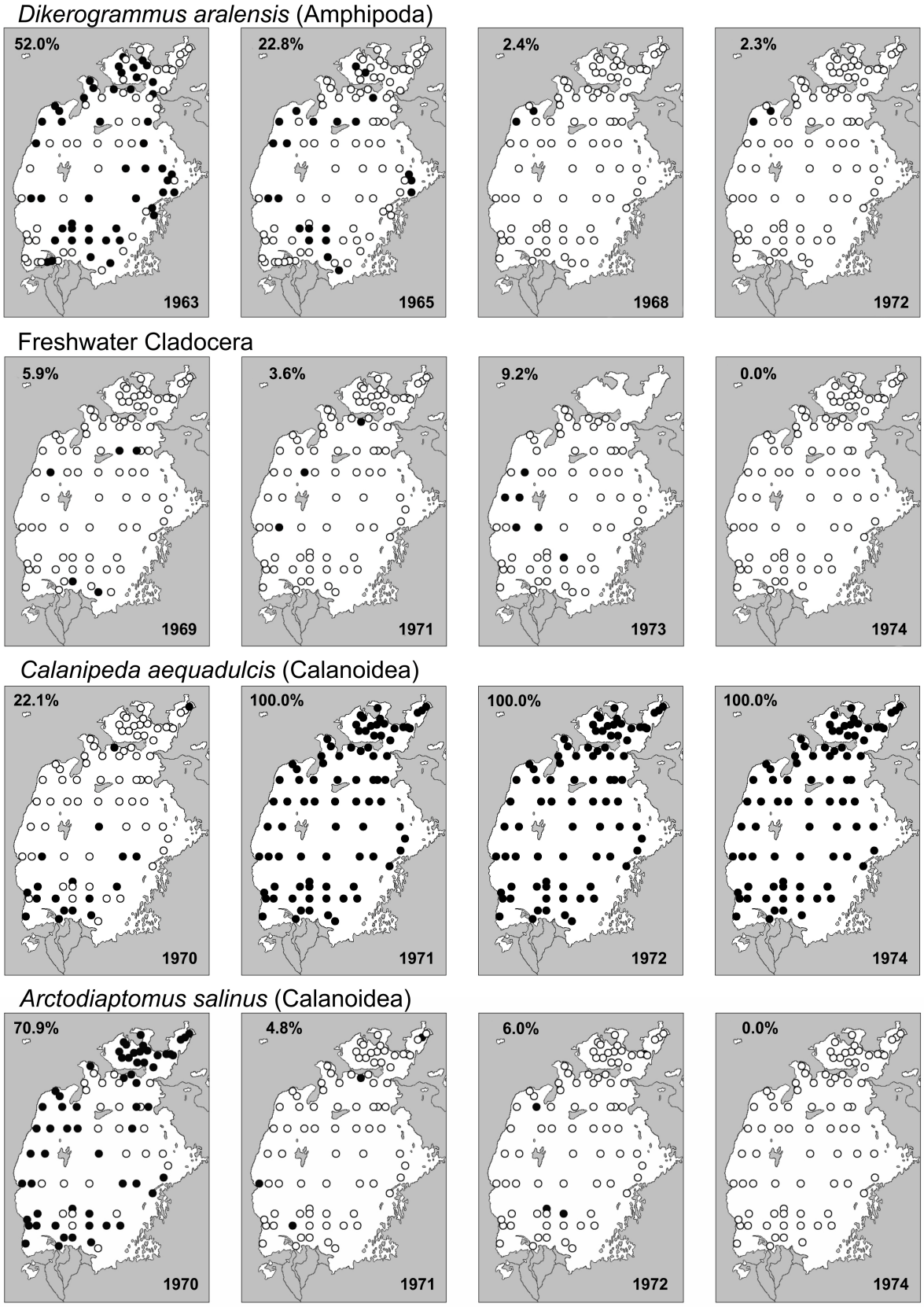

Fig. 4. Occurrence of selected crustacean species at fixed sampling stations during the study period; filled circles = species present; percentages are of the number of stations where the species was found.

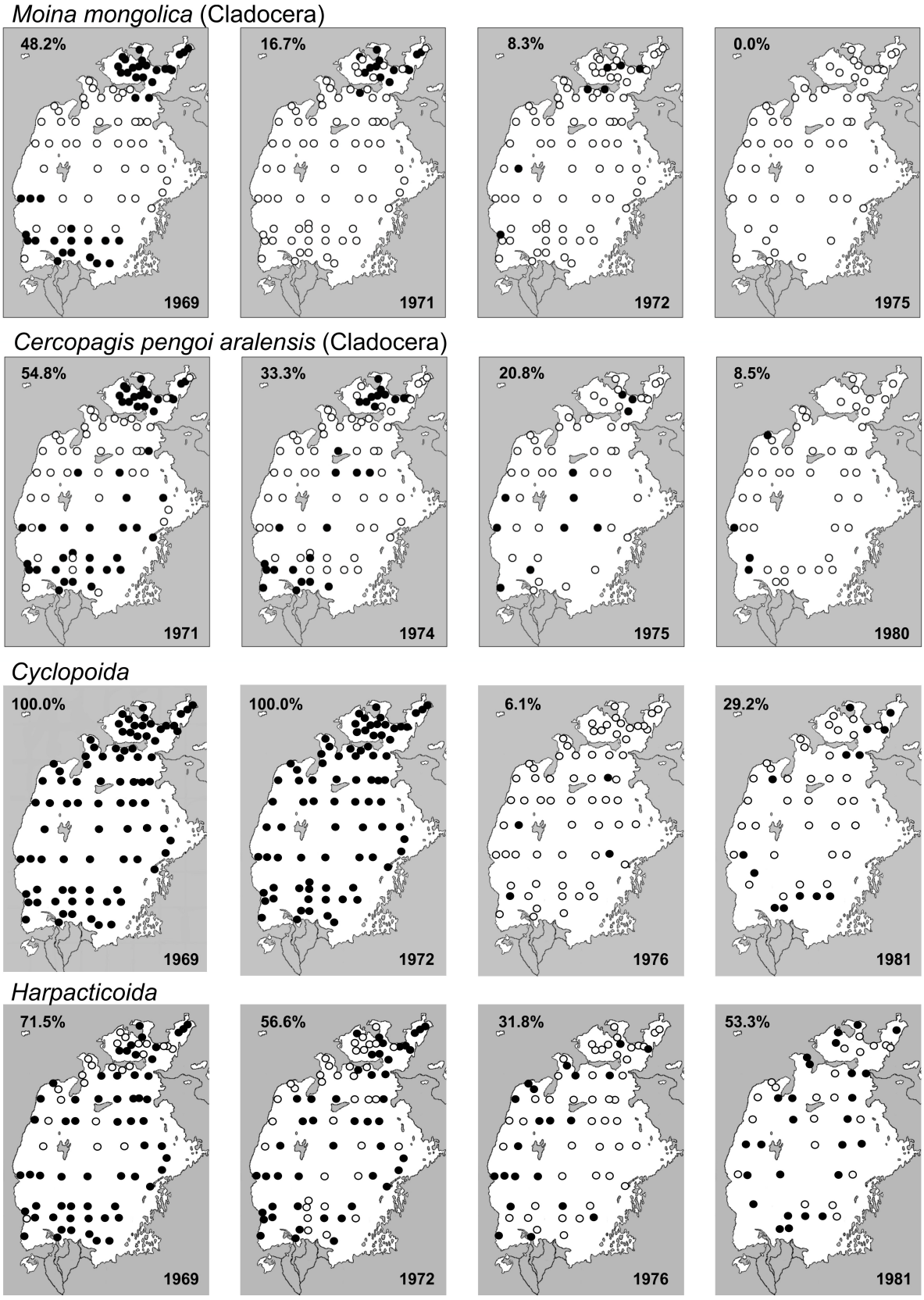

Fig. 5. Occurrence of selected crustacean species at fixed sampling stations during the study period; filled circles = species present; percentages are of the number of stations where the species was found.

to and safeguarded at the ZIN (Zoological Institute Russian Academy of Sciences). The information was since returned and is stored in the Republic of Kazakhstan office of the IPA CIS (Inter-Parliamentary Assembly of the Member States of the Commonwealth of Independent States). The database is not yet available on the Internet, but is free for on site personal use.

Literature data

Mordukhai-Boltovskoi (1972 1974) provided important results for the period before the modern crisis. Some additional information was also published concerning the early part of the crisis, but mostly in Russian, often in hard to access sources not electronically available, and mostly without an English abstract (Andreev 1989; Andreeva 1989; Andreev and Andreeva 1988; Kortunova 1968 1975; Kortunova et al. 1972; Husainova 1958 1960; Karpevich 1975; Kazakhbaev 1974; Lukonina 1960a). Our account is also based on these valuable sources.

RESULTS

As with most water bodies, crustaceans of all kinds constituted a key component of the fauna in the original Aral Sea, both as primary consumers of photosynthetic organisms and as other parts of the food web in both the plankton and the bottom fauna. Table 1 (native species), table 2 (introduced species) and table 3 (parasites) document the faunistic changes from 1960 onwards. Tables 1–3 also provide the taxonomic data. Changes in selected crustacean species at the fixed sampling stations are detailed in figures 4 and 5. Table 4 lists major events and their implied causes.

Native crustacean fauna

The native, free-living crustacean fauna (Table 1) comprised 56 species and subspecies: Anostraca (1), Cladocera (18), Copepoda (30), Ostracoda (11) and Malacostraca (1) (Fig. 6a, d, e). This fauna comprised freshwater species, Ponto-Caspian brackish-water species, marine species, and representatives of the fauna from saline continental water bodies of the arid zone.

Halobiontic cladocerans

These comprised species from three orders and nine families. The open sea contained Ponto-Caspian species belonging to the Onychopoda: *Cercopagis pengoi aralensis*, *Evadne anonyx*, *Podonevadne camptonyx*, *P. angusta* and *P. trigona*. Of these, only *E. anonyx* and *P. camptonyx* occurred consistently all over the sea, except for the portions diluted from freshwater inflow. Being extremely rare, *P. trigona* was not reported before 1981. Three anomopod species occurred throughout the Aral Sea, but none commonly: *Ceriodaphnia reticulata*, *Coronatella rectangula* sensu lato and *Moina mongolica*. Population explosions occasionally took place, primarily in *M. mongolica*, but this species eventually declined and was gone by 1973.

Freshwater cladocerans

Some nine species were always restricted to areas with low salinity. Eight were ctenopodes: *Diaphanosoma brachyurum*, *Moina micrura*, *Chydorus sphaericus*, *Bosmina longirostris*, and *Ceriodaphnia cornuta*, *C. pulchella, Daphnia longispina* and *Daphnia galeata*. *Diaphanosoma galeata*, was first found in the 2nd half of the 1990s in the diluted zone of the Small Aral (Stuge 2001; Stuge and Saduakasova 2005). The only onychopod was *Polyphemus pediculus*.

Anostraca

The only representative was the brine shrimp *Artemia*, which inhabits hypersaline continental water bodies. In the past, parthenogenetic *Artemia* clones were sometimes locally encountered in the Aral, but only in its most saline regions such as small shallow bays and lagoons with 52 ppt salinity on the eastern coast of the Large Aral (Aladin and Filippov 1993). *Artemia* was first found in the Large Aral, when the salinity in its open part reached ~58 ppt (Musaev et al. 2012). By the 2000s it became the dominant planktonic crustacean (Marden et al. 2012) in the residual and fragmented water bodies, and it now seems to be the only crustacean in the shallow eastern part (Aladin and Plotnikov 2008).

Free-living copepods

The original fauna comprised 31 species, representing three orders and 10 families (Calanoida 2 spp; Cyclopoida 14 spp; Haparcticoida 15 spp). These represented both euryhaline, brackish water and freshwater species with some being widely distributed and a few being endemic to the Aral Sea.

Two species of *Calanoida* (Diaptomidae) occurred. The large phyto-detritophagous *Arctodiaptomus salinus* (Fig. 6d) was found throughout the Aral (Behning 1934 1935), but by the early 1960s it declined catastrophically in numbers due to predation by introduced planktophagous fish (smelt and herring). The freshwater *Phyllodiaptomus blanci* occurred only in highly diluted areas near the deltas of the Amu Darya

and Syr Darya.

Cyclopoida

Of the 14 free-living species, the widely distributed and euryhaline *Halicyclops rotundipes aralensis* belongs to the marine fauna, while the remaining 13 species are widespread freshwater forms. Nine inhabit only areas with low salinity: *Cyclops strenuus*, *Diacyclops bisetosus*, *Eucyclops macrurus*, *E. serrulatus*, *Macrocyclops albidus*, *M. fuscus*, *Microcyclops bicolor*, *Thermocyclops dybowskii* and *Tropocyclops prasinus*. *Mesocyclops leuckarti* and, less often, *Cyclops vicinus* and *Thermocyclops crassus*

Table 1. Free-living crustaceans of the Aral Sea (native and naturally introduced)

Taxa	species	native	before 1961	1961–1970	1971–1980	1981–1990	Small Aral		Large Aral	
(#) = species in found in family							1991–2000	After 2000	1991–2000	after 2000
BRANCHIOPODA										
Anostraca										
Artemiidae (1)	*Artemia parthenogenetica* Bowen et Sterling, 1978	no	–	–	–	–	–	–	↑	+
Cladocera										
Sididae (1)	*Diaphanosoma brachyurum* Lievin, 1848	yes	+	+	↓	–	↑	+	–	–
Chydoridae (2)	*Chydorus sphaericus* s.l. (O.F. Müller, 1785)	yes	+	↓	–	–	↑	+	–	–
	Coronatella rectangula s.l. (Sars, 1861)	yes	+	↓	–	–	↑	+	–	–
Bosminidae (1)	*Bosmina longirostris* (O.F. Müller, 1785)	yes	+	↓	–	–	↑	+	–	–
Ilyocryptidae (1)	*Ilyocryptus agilis* Kurz, 1878	?	?	?	?	?	↑	+	–	–
Daphniidae (5)	*Daphnia longispina* (O.F. Müller, 1776)	yes	+	+	↓	–	↑	+	–	–
	D. galeata G.O. Sars, 1864	?	?	?	?	?	↑	+	–	–
	Ceriodaphnia reticulate (Jurine, 1820)	yes	+	+	↓	–	↑		–	–
	C. cornuta G. Sars, 1885	yes	+	↓	–	–	↑	+	–	–
	C. pulchella G. Sars, 1862	yes	+	↓	–	–	↑	?	–	–
Moinidae (2)	*Moina mongolica* Daday, 1888	yes	+	+	↓		↑	+	+	↓
	M. micrura Kurz, 1874	yes	+	?	?	–	↑?	+?	–	–
Polyphemidae (1)	*Polyphemus pediculus* s.l. (Linnaeus, 1761)	?	?	?	±	–	–	?	–	–
Podonidae (4)	*Evadne anonyx* G. Sars, 1897	yes	+	+	+	↓	↑	+	–	–
	Podonevadne camptonyx (G. Sars, 1897)	yes	+	+	+	↓	↑	+	–	–
	P. angusta (G. Sars, 1902)	yes	+	+	+	↓	↑	+	–	–
	P. trigona (G. Sars, 1897)	?	?	?	±	?	?	?	–	–
Cercopagididae (1)	*Cercopagis pengoi aralensis* M.-Boltovskoi, 1971	yes	+	+	+	–	–	–	–	–
COPEPODA										
Calanoida										
Diaptomidae (2)	*Arctodiaptomus salinus* (Daday, 1885)	yes	+	+	↓	–	–	–	–	–
	Phyllodiaptomus blanci (Guerne et Richard, 1896)	yes	+	+	?	?	?	↑	–	–
Pseudodiaptomidae (1)	*Calanipeda aquaedulcis* Kritchagin, 1873	no	–	+	+	+	+	+	↓	–
Cyclopoida										
Cyclopidae (14)	*Halicyclops rotundipes aralensis* Borutzky, 1971	yes	+	+	+	+	+	↓	+	–
	Diacyclops bisetosus (Rehberg, 1880)	yes	+	+	↓?	–?	–	↑	–	–
	Megacyclops viridis (Jurine, 1820)	yes	+	+	+	+	+	?	?	–
	Cyclops strenuus s.l. Fischer, 1851	yes	+	+	↓	–	–	↑?	–	–
	C. vicinus Uljanin, 1875	yes	+	+	↓	–	–	↑	–	–
	Eucyclops macrurus (G.O. Sars, 1863)	yes	+	+	↓	–	–	↑?	–	–
	E. serrulatus (Fischer, 1851)	yes	+	+	↓	–	–	↑?	–	–
	Macrocyclops albidus (Jurine, 1820)	yes	+	+	↓	–	–	↑?	–	–
	M. fuscus (Jurine, 1820)	yes	+	+	↓	–	–	↑?	–	–
	Mesocyclops leuckarti s.l. (Claus, 1857)	yes	+	+	↓	–	↑	+	–	–

Table 1. (Continued)

Taxa	species	native	before 1961	1961–1970	1971–1980	1981–1990	Small Aral		Large Aral	
(#) = species in found in family							1991–2000	After 2000	1991–2000	after 2000
	Microcyclops bicolor (G.O. Sars, 1863)	yes	+	+	↓	–	–	↑?	–	–
	Thermocyclops crassus (Fischer, 1853)	yes	+	+	↓	–	–	↑?	–	–
	Th. dybowski (Lande, 1890)	yes	+	+	↓	–	–	↑?	–	–
	Tropocyclops prasinus (Fischer, 1860)	yes	+	+	↓	–	–	↑?	–	–
	Apocyclops dengizicus (Lepeshkin, 1900)	no	–	–	–	–	–	–	–	↑
Harpacticoida										
Ectinosomatidae (1)	*Halectinosoma abrau* (Kritchagin, 1873)	yes	+	+	+	?	+	?	–	–
Diosaccidae (3)	*Schizopera aralensis* Borutzky, 1971	yes	+	+	+	↓?	?	?	+	–
	S. jugurtha (Blanchard et Richard, 1891)	yes	+	+	+	↓?	?	+?	–	–
	S. reducta Borutzky, 1971	yes	+	+	+	↓?	?	+?	–	–
Ameiridae (2)	*Nitocra lacustris* (Schmankewitsch, 1875)	yes	+	+	+	+	+	+?	+?	+?
	N. hibernica (Brady, 1880)	yes	+	+	+	+?	+	?	–	–
Canthocamptidae (1)	*Mesochra aestuarii* Gurney, 1921	yes	+	+	+	?	+	?	–	–
Laophontidae (1)	*Onychocamptus mohammed* (Blanchard et Richard, 1891)	yes	+	+	+	?	+	?	–	–
Cletodidae (4)	*Cletocamptus retrogressus* Schmankewitsch, 1875	yes	+	+	+	+	+	+?	+	+
	C. confluens (Schmeil, 1894)	yes	+	+	+	+	+	+?	+?	+?
	Limnocletodes behningi Borutzky, 1926	yes	+	+	↓	–	–	+?	–	–
	Enhydrosoma birsteini Borutzky, 1971	yes	+	+	+	?	?	?	–?	–
Nannopodidae (1)	*Nannopus palustris* Brady, 1880	yes	+	+	?	?	+	+?	–	–
Darcythompsoniidae (1)	*Leptocaris brevicornis* (Van Douwe, 1905)	yes	+	+	+	?	?	?	–	–
Leptastacidae (1)	*Paraleptastacus spinicauda trisetosus* Noodt, 1954	yes	+	+	+	+	?	?	?	–
OSTRACODA										
Darwinulidae (1)	*Darwinula stevensoni* (Brady et Robertson, 1870)	yes	+	+	↓	–	?	↑?	–	–
Candonidae (1)	*Typhlocypris* (*Typhlocypris*) *marchica* (Hartwig, 1899)	yes	+	+	↓	–	?	↑?	–	–
Cyprididae (4)	*Cyclocypris laevis* (O.F. Müller, 1776)	yes	+	+	↓	–	?	↑?	–	–
	Plesiocypridopsis newtoni (Brady et Robertson, 1870)	yes	+	+	↓	–	?	↑?	–	–
	Cyprinotus salinus (Brady, 1868)	no	?	?	?	?	+	+?	?	–
	Eucypris mareotica (Fischer, 1855)	no	–	–	–	–	+	+?	+	+
Cytherideidae (1)	*Cyprideis torosa* (Jones, 1850)	yes	+	+	+	+	+	+	+	↓?
Leptocytheridae (1)	*Amnicythere cymbula* (Livental, 1929)	yes	+	+	↓	–	?	↑?	–	–
Hemicytheridae (1)	*Tyrrhenocythere amnicola donetziensis* (Dubowsky, 1926)	yes	+	+	↓	–	?	↑?	–	–
Limnocytheridae (3)	*Limnocythere dubiosa* Daday, 1903	yes	+?	–	–	–	–	–	–	–
	Limnocythere inopinata (Baird, 1850)	yes	+	+	↓	–	?	↑?	–	–
	Galolimnocythere aralensis Schornikov, 1973	yes	+	+	↓	–	?	↑?	–	–
Loxoconchidae (1)	*Loxoconchissa* (*Loxocaspia*) *immodulata* (Stepanaitys, 1958)	yes	+	+	↓	–	?	↑?	–	–
MALACOSTRACA										
Amphipoda										
Gammaridae (1)	*Dikerogammarus aralensis* (Uljanin, 1875)	yes	+	+	↓	–	–	–	–	–

+, present; -, absent; ↓, disappeared; ↑, appeared. Occurrence based sampling at standard stations and shown for selected species and species groups in figures 1 and 2; s.l., species sensu lato.

were found not only in the diluted areas, but also at "normal" salinity. The widely distributed and euryhaline *Megacyclops viridis* occurred at even up to 50 ppt salinity. Throughout the Aral Sea, except for strongly salinized areas, the most numerous cyclopid was *Mesocyclops leuckarti* (Fig. 6c). *Halicyclops rotundipes aralensis* was also present throughout the Aral, but always in low numbers.

Harpacticoida occurred with 15 euryhaline, brackish and marine species from eight families: *Halectinosoma abrau*, *Schizopera aralensis*, *S. jugurtha*, *S. reducta*, *Nitocra lacustris*, *N. hibernica*, *Leptocaris brevicornis*, *Mesochra aestuarii*, *Laophonte mohammed*, *Cletocamptus retrogressus*, *C. confluens*, *Limnocletodes behningi*, *Nannopus palustris*, *Enhydrosoma birsteini* and *Paraleptastacus spinicauda trisetosus*). Three of these were endemic to the Aral Sea: *Schizopera aralensis*, *S. reducta*, and *Enhydrosoma birsteini*. Another three (*Nitocra lacustris*, *Cletocamptus retrogressus*, *C. confluens*) are euryhaline and found in continental hypersaline waters > 100 ppt (Loffler 1961; Mirabdullayev et al. 2004; Mokievsky and Miljutina

Table 2. Free-living crustacean introduced by man

Taxa	Species	Before 1961	1961–1970	1971–1980	1981–1990	Small Aral		Large Aral	
						1991–2000	after 2000	1991–2000	after 2000
COPEPODA									
Calanoida									
Pseudodiaptomidae	*Calanipeda aquaedulcis* Kritchagin, 1873	–	↑	+	+	+	+	↓	–
MALACOSTRACA									
Mysida									
Mysidae	*Paramysis* (*Mesomysis*) *intermedia* (Czerniavsky, 1882)	+	+	+	–	–	↑	–	–
	Paramysis (*Serrapalpisis*) *lacustris* (Czerniavsky, 1882)	+	+	+	–	–	↑?	–	–
	Paramysis (*Metamysis*) *ullskyi* Czerniavsky, 1882	–	+	+	–	–	↑?	–	–
Decapoda									
Palaemonidae	*Palaemon elegans* Rathke, 1837	+	+	+	+	+	+	↓	–
Panopeidae	*Rhithropanopeus harrisii tridentata* Maitland, 1874 Only in Large Aral	–	↑	+	+	–	–	↓	–

+, present; -, absent; ↓, disappeared; ↑, appeared. Occurrence based on sampling at standard stations and shown for selected species and species groups in Figs. 1 and 2; s.l., species sensu lato. Taxonomic naming issues are discussed in the text.

Table 3. Parasitic crustaceans of the Aral Sea (native and naturally introduced)

Taxa	Species	Native	before 1961	1961–1970	1971–1980	1981–1990	Small Ara after 2000		Large Aral after 2000	
Copepoda										
Cyclopoida										
Ergasilidae	*Ergasilus sieboldi* Nordmann, 1832	yes	+	+	?	–	–	+?	–	–
Lernaeidae	*Lernaea cyprinacea* Linnaeus, 1758	yes	+					+?		
	Lamproglena pulchella Nordmann, 1832	yes	+	+	?	?	–	+?	–	–
Caligoida										
Caligidae	*Caligus lacustris* Steenstrup et Lütken, 1861	yes	+	+	?	–	–	+?	–	–
Lernaeopodidae	*Achtheres percarum* Nordmann, 1832	no	–	↑	+	–	–	+?	–	–
Branchiura										
Argulidae	*Argulus foliaceus* (Linnaeus, 1758)	yes	+	+	?	?	–	+	–	–

+, present; -, absent; Occurrence based on regular sampling at standard stations.

2011; Shadrin 2012; Carrasco and Perisinotto 2012).

Ostracoda

The native fauna comprised 11 species from eight families of the Podocopida: Five are freshwater forms: *Darwinula stevensoni*, *Typhlocypris marchica*, *Cyclocypris laevis*, *Limnocythere inopinata* and *Loxoconchissa* (*Loxocaspia*) *immodulata*. The remaining species are brackish and marine: *Plesiocypridopsis newtoni*, *Cyprideis torosa*, *Amnicythere cymbula*, *Tyrrhenocythere amnicola donetziensis*, *Limnocythere dubiosa* and *Galolimnocythere aralensis*. The most common ostracod, *Cyprideis torosa*, is found from fresh to hyperhaline waters and occurs in the Aral as the "*amphiosmotica*" form of freshwater origin, which is a robust osmoregulator with salinity tolerance up to 104 ppt (Aladin 1989a).

Two additional ostracods in Cyprididae, *Cyprinotus salinus* and *Eucypris mareotica*, are not listed in Mordukhai-Boltovskoi (1974), and were apparently only recently autointroduced to the Aral Sea. These euryhaline and widespread marine species were first found in 1995 in the Gulf Bolshoy Syrycheganak of the Small Aral (Aladin et al. 2004).

Malacostraca

The only original malacostracan was the euryhaline gammarid amphipod *Dikerogammarus aralensis*, widespread in the Ponto-Caspian fauna province (Mordukhai-Boltovskoi 1974). In the salinized gulfs of the Caspian Sea, it is numerous at a salinity of 50 ppt (Behning 1937). In the Aral Sea it was found throughout the entire salinity gradient.

Parasitic crustaceans

The original fauna contained only seven parasitic crustaceans (Table 3), all infecting fish by means of their free-swimming larvae: from Cyclopoida *Ergasilus sieboldi*, *Lernaea cyprinacea*, *L. esocina* and *Lamproglena pulchella*; from Caligoida *Caligus lacustris* and *Achtheres percarum*; and from Branchiura *Argulus foliaceus*.

Introduced crustaceans

Six alien species of free-living crustaceans were introduced either intentionally or accidentally during initiatives to enhance commercial fisheries (Fig. 6;

Table 4. Major changes to Crustacea and fish in the Aral Sea during the modern regression

Time	Period	Physical and chemical factors	Main changes to Crustacea and fish
Pre 1961	Before regression	Native semi-stable state	Introduction of alien crustaceans (Mysida, Calanoida, Caridea) Introduction of planktivorous fish (smelt and herring) Introduced fish caused decline of the calanoid *Arctodiaptomus salinus* and of some cladocerans Massive deaths of planktivorous fish due to starvation
1961–1971	Initial salinization	Slow salinity increased to 11.5 ppt	Changes to crustacean fauna mostly due to introduced species Introduced caridean spread and displaced native amphipod Introduced calanoid displaced native calanoid Mud crab introduced and naturalized Freshwater cladocerans started to decline
1971–1976	First crisis	Salinity passed 12–13 ppt	All freshwater crustaceans disappeared
1976–1987	Relative stabilization		Euryhaline cyclopoids, calanoids, and cladocerans dominated Only 16 species of free-living copepods remained Only two cladoceran species relatively common Mud crab and shrimp remained stable populations Plaice introduced and became only valuable species for fisheries
1987–1990	Second crisis	Salinity passed 27–32 ppt	Ponto-Caspian crustaceans disappeared All cladocerans disappeared Only one ostracod species remained Introduced Calanipeda aquaedulcis only widespread planktonic copepod Introduced mud crab and shrimp only benthic crustaceans
Post 1990	Separation of Large and Small Aral	Large Aral became hypersaline Small Aral partially restored due to dam	Small Aral: many native crustaceans and fish reappeared; fisheries rebounded Large Aral: Artemia only common crustacean; all fish disappeared

Table 2). Several of these crustaceans and some of the introduced fish caused ecological disturbance even before the area regression became serious: the introduction of the shrimp *Palaemon elegans* led to the disappearance of the native gammarid *Dikerogammarus aralensis*; the introduced calanoid *Calanipeda aquaedulcis* largely replaced the native *Arctodiaptomus salinus* although the latter was already seriously declining, while the introduction of herring caused a serious decline in all crustacean zooplankton.

Palaemon elegans, a caridean shrimp, was the first crustacean to become naturalized in the Aral Sea

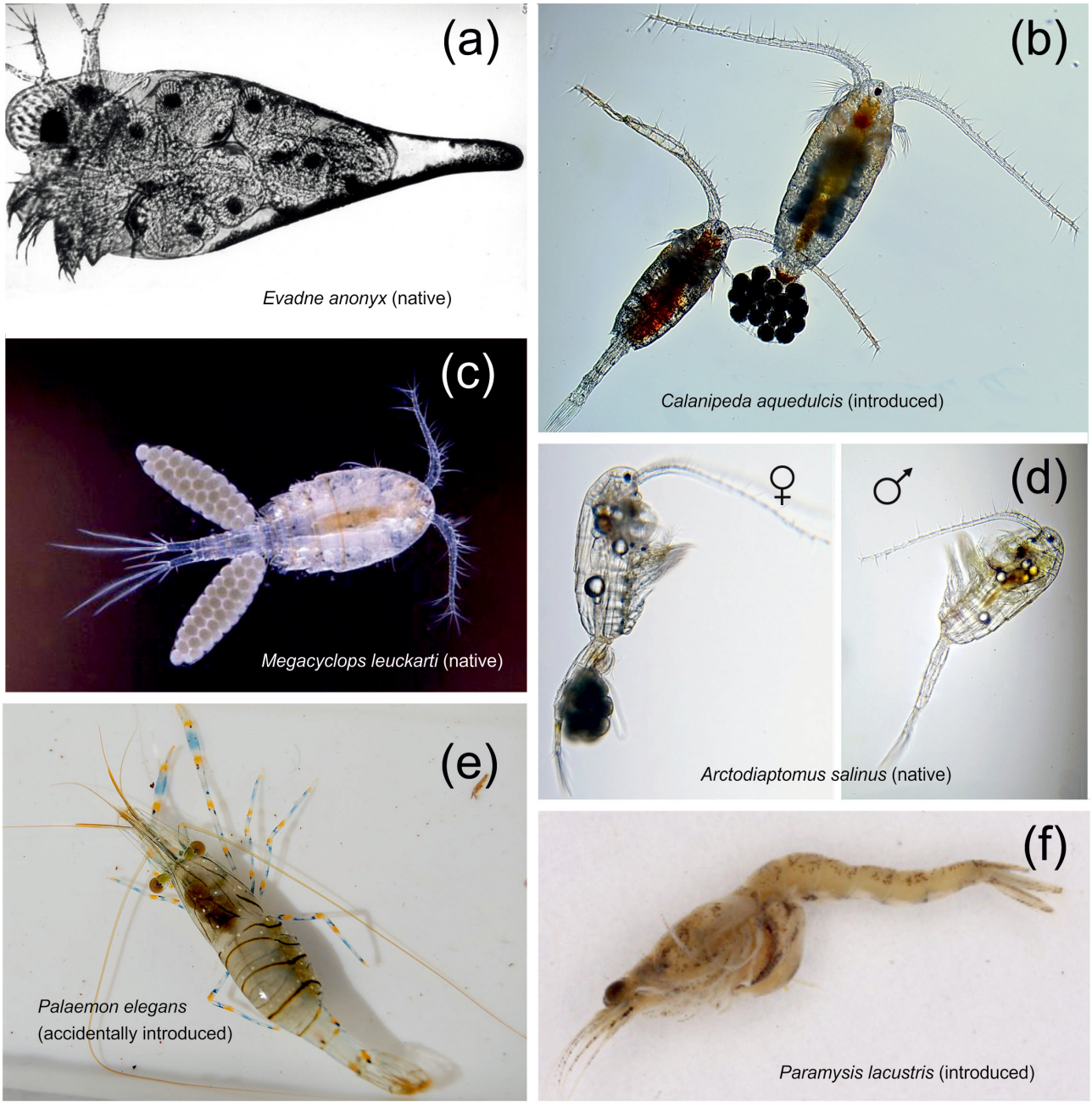

Fig. 6. Selected native and invasive crustaceans from the Aral Sea: (a) *Evadne anonyx* (native), (b) *Calanipeda aquedulcis* (planned introduction), (c) *Megacyclops leuckarti* (native), (d) *Arctodiaptomus salinus* (native), (e) *Palaemon elegans* (accidentally introduced), (f) *Paramysis lacustris* (planned introduction). *Calanipeda aquedulcis* and *P. lacustris* were both introduced to become a food resource for commercially important fish. Further explanation in text (photo credits: a, NV Aladin, b, AN Khanaychenko Russian Academy of Sciences with permission; c, Dr. Ulrich Hopp, Germany, with permission; d, LS Svetlichny, National Academy of Sciences of Ukraine with permission; e, from Wikimedia Commons; f, T Lipinskya, National Academy of Sciences of Belarus with permission)

(Fig. 6e). It was accidentally introduced during the unsuccessful attempt to acclimatize two species of mullets intended for commercial fisheries. First found in 1957, the shrimp spread throughout the entire water body.

Mysids

In 1958–1960 relict Ponto-Caspian species of mysids were introduced from the Don River delta as a possible new food source for commercially harvested fish (Fig. 6f). About 90% of the specimens consisted of *Paramysis* (*Serrapalpisis*) *lacustris*, the remaining part being *P.* (*Mesomysis*) *intermedia* and few *P.* (*Paramysis*) *baeri* (Karpevich 1960b). The first batches perished when they were transported from fresh water to the small Aral to a salinity of ~10 ppt, but in 1959–1960 new introductions were successful in the diluted bay near the mouth of the Syr Darya. The mysids spread throughout the Aral, but only *P. lacustris* and *P. intermedia* became established. To accelerate the naturalization, mysids were also transported in 1964 into the Large Aral near the Amu Darya delta, from where expansion continued. By the second half of the 1960s, *P. intermedia* had invaded all nonsalinized littoral areas, and replaced *P. lacustris*. The latter remained only near the Syr Darya mouth and eventually disappeared altogether. In 1965, *Paramysis* (*Metamysis*) *ullskyi* appeared independently in the mouth of the Syr Darya, having penetrated from reservoirs on the river, where it was introduced in 1963.

Calanoida

The native calanoid *Arctodiaptomus salinus* had dwindled by the early 1960s. To remediate this, the Mediterranean-Atlantic *Calanipeda aquaedulcis* (Pseudodiaptomidae) was introduced in 1965–1970 as an alternative food source for introduced plantivorous fish (Fig. 6b). The specimens came from the Kuban estuaries and the Taganrog Bay of the Sea of Azov and were released in the southern part of the Large Aral, in diluted bays and at the mouth of the Amu Darya. By 1970 *C. aquaedulcis* had spread into the open waters, and in 1971 it even began to dominate the zooplankton throughout the entire Aral Sea, including areas with salinity up to 15–18 ppt. Within a single year, the native *A. salinus* decreased even more and has not been seen in the Aral since 1974.

Mud crabs and parasites

In 1970, the mud crab *Rhithropanopeus harrisii tridentata* (Panopeidae) and the parasitic copepod *Achtheres percarum* (Lernaeopodidae) were accidentally introduced into the Large Aral. The source larvae in water bags containing *Calanipeda aquaedulcis*. In 1976, *R. harrisii* had become established in the Large Aral, but it never penetrated to the Small Aral. *Achtheres percarum* appeared on pike perch, *Sander lucioperca* (L., 1758), in the late 1970s.

Modern Regression

Eventually salinity increase became the main cause for changes in the Aral Sea crustacean fauna (Fig. 2). Based on physical and biological changes, we divide the modern regression into four periods (Fig. 3, Table 4). The initial period (1961–1971) was dominated by changes due to introduced species. The first crisis period (1971–1976) ended with the disappearance of all brackish and fresh water species due to salinization. The following (1976–1987) period had relatively stable conditions for the surviving, halophilic organisms. Finally, the second crisis period (1987–1990) saw the most dramatic salinity increase, accompanied by the disintegration of the Aral Sea into several separate water bodies and the extinction of the majority of metazoan species, including most crustaceans. After 1990, the development must be described separately for northern Small Aral and the southern Large Aral. Main changes to crustaceans and ichthyofauna are summarized in Table 4 and details for selected species appear in figures 4 and 5.

Initial salinization (*1961–1971*): During this decade the desiccation was slow and average salinity increased only 1.5 ppt, reaching 11.5 ppt in 1971 (Fig. 3). The crustacean faunal changes were occasionally drastic, but primarily associated with species introductions.

First crisis (*1971–1976*): Desiccation and salinization accelerated, and from 1974 the inflow from the rivers was dramatically reduced, further deteriorating the situation. Salinity initially increased only slowly with few if any faunistic changes, but a dramatic change happened when it reached 12–13 ppt and all freshwater cladocerans disappeared completely (Plotnikov and Aladin 2011, Plotnikov et al. 1991). *Ceriodaphnia reticulata* disappeared before 1971, followed by *Coronatella rectangula* by 1974. By 1975 only four cladoceran species remained (*Evadne anonyx*, *Podonevadne camptonyx*, *P. angusta* and *Cercopagis pengoi aralensis*), all belonging to the saline Ponto-Caspian fauna province.

Relative stabilization (*1976–1987*): The salinization caused the fauna of free-living cyclopid copepods to decrease from 22 to 16 species. After the freshwater *Mesocyclops leuckarti* disappeared, the

most numerous cyclopoid was the euryhaline and more salinity halotolerant *Halicyclops rotundipes aralensis*. The number of harpacticoid species also declined, but the more euryhaline ones survived.

Of the cladocerans that survived the first crisis, *Cercopagis pengoi aralensis* was the most salinity sensitive, becoming rare and then, from 1981, absent. *Podonevadne camptonyx* was now the most numerous cladoceran, with *Evadne anonyx* being less widely distributed and present in smaller numbers. Since 1971, the recent invading planktonic copepod *Calanipeda aquaedulcis* had become numerous and replaced *Arctodiaptomus salinus*. The euryhaline cyclopoid *Halicyclops rotundipes aralensis*, although present all over the sea, decreased in numbers everywhere. *Diacyclops bisetosus* was only occasionally observed.

Second crisis (*1987–1990*): By 1987 salinity had reached 27 ppt. Many remaining species could not survive beyond the 27–32 ppt range (Plotnikov and Aladin 2011), and with continued salinity increase the crustacean fauna entered a "second crisis period", entailing another fast decrease in diversity (Plotnikov et al. 1991).

The last remaining Ponto-Caspian crustaceans disappeared; by this time they were represented only by the Podonidae. *Evadne anonyx* disappeared by 1988, when salinity reached 28 ppt, and by 1990, *Podonevadne* was gone (Aladin 1989b). The thanatocenoses from 1985 and 1990 (Aladin 1991) showed changes in the ostracod fauna. The carapaces of *Amnicythere cymbula*, *Tyrrhenocythere amnicola donetziensis* and *Galolimnocythere aralensis* could no longer be found. Of the aboriginal and benthic ostracods, only *Cyprideis torosa* survived the crisis. After this crisis, the now much depleted crustacean fauna entered a period of relative stabilization.

Post 1990: The cladoceran *Podonevadne camptonyx* reappeared in 1991 in the Small Aral, apparently from dormant eggs (Plotnikov 2016). It was only absent in Butakov Bay, where the salinity remained higher. From 1991–1996 no new changes were observed in the composition of the crustacean fauna. The copepod *Calanipeda aquaedulcis* was still the most widespread species in both the Small and the Large Aral, while the cyclopid *Halicyclops rotundipes aralensis* was uncommon. Benthic crustaceans were represented only by the shrimp *Palaemon elegans* and (only in the Large Aral) the mud crab *Rhithropanopeus harrisii tridentata* (see Filippov 1995).

The small Aral Sea: Following separation of the two water bodies, water from the Syr Darya flowed only to the Small Aral. This, and especially the restrained outflow due to the new dam, combined to raise the water level, causing a significant salinity decrease, and the formation of a large freshwater zone. The effect on both crustacean and fish fauna was almost immediate. In 2016, the planktonic crustacean fauna had increased, including recolonizing fresh- brackish water species (Plotnikov et al. 2016), including the cladocerans *Bosmina longirostris*, *Chydorus sphaericus*, *Diaphanosoma brachyurum*, *Ceriodaphnia reticulata* and *Podonevadne angusta*, *Evadne anonyx* and the copepods *Phyllodiaptomus blanci*, *Cyclops vicinus*, *Mesocyclops leuckarti* and *Megacyclops viridis*. The intentionally introduced *Calanipeda aquedulcis* remained present, and is now again common after a decline in the 1990s. Mysids immigrated from the lower Syr Darya, with *Paramysis intermedia* now found in Shevchenko Bay. Other species are known or suspected to be returning (Tables 1, 2).

Post 1990 - The hypersaline Large Aral: After the separation, the salinity in the Large Aral accelerated and, upon reaching 47–52 ppt in the second half of the 1990s, the fauna reflected this condition. In 1998, the dominant zooplankton species had disappeared, including *Calanipeda aquaedulcis* and *Halicyclops rotundipes aralensis*. Most truly marine harpacticoids also disappeared, and only three aboriginal and high salinity (> 100 ppt tolerant species may now remain: the presence of *Cletocamptus retrogressus* is documented, but there is no information on *C. confluens* and *Nitocra lacustris* (Mirabdullayev et al. 2004; Mokievsky and Miljutina 2011). The ostracod *Cyprinotus salinus* disappeared before 2002, while the very salinity tolerant *Cyprideis torosa* remained in the western part in 2005 (Zavialov 2012).

During hypersalinization there were temporary species invasions. The cladoceran *Moina mongolica* reappeared in 1996, but was gone again by 2002 (Mirabdullayev et al. 2004; Aladin and Plotnikov 2008). The halophilic copepod *Apocyclops dengizicus* appeared in the western Great Aral in 2004 and seems to have become established (Mirabdullayev et al. 2007). Carapaces of the invasive and euryhaline ostracod *Eucypris mareotica* were frequently found in thanatocenoses in 2005 (Aladin and Plotnikov 2008). *Artemia* appeared in 1998, when salinity in the open parts reached ~58 ppt (Musaev et al. 2012). The shallow eastern Large Aral salinized more strongly than the deeper western part. In some years, it dries out completely, and its crustacean fauna now comprises only *Artemia* (Aladin and Plotnikov 2008).

DISCUSSION

Native crustacean fauna

Compared to the similarly saline Caspian Sea, the native Aral Sea had a much poorer fauna, with both fewer species and the absence of several major taxa. Absent were species of the Centropagidae and Temoridae (Copepoda) and the cladocerans *Apagis* (Cercopagidae), *Cornigerius*, *Caspievadne* and *Pleopis* (Podonidae). One species of *Cercopagis* (Cercopagididae) occurred. The only native malacostracan was the amphipod *Dikerogrammus aralensis*, contrasting with a rich and diverse malacostracan fauna in the Caspian (Birstein et al. 1968; Mordukhai-Boltovskoi 1974).

Natural and accidental introductions

The isolation of the Aral Sea basin limited the number of species invasions to a few from the local area and anthropogenic causes, whether accidental or planned. This differs from the Caspian Sea, where many alien species were brought in by ships in ballast or as biofouling after navigable canals connected the inflowing Volga to the Black and Baltic Seas (Aladin et al. 2004).

Branchiopoda

The halobiontic cladoceran *P. trigona* was not recorded until 1981. It most likely invaded from the Ponto-Caspian Sea with introduced fish or invertebrates (Aladin and Andreev 1984). The halobiontic cladoceran *Ilyocryptus agilis* was previously (Nikolsky and Pankratova 1934) found in the nearby Lake Sudochye system. Although this lake is separated from the Amu Darya delta the species spread, probably naturally, to the Aral Sea. *Artemia* was always present in the general area, but occurred in the Aral Sea itself only after salinization reached sufficient levels (Arashkevich et al. 2009).

Palaemon elegans

This caridean is naturally distributed in coastal areas of the Atlantic, Baltic, Mediterranean, Black and Azov Seas (Borisov 2012). It has a salinity tolerance of 5 to > 62 ppt (Plotnikov 2016) and is a good osmoregulator, and therefore also invaded the Caspian Sea (Karpevich 1975). Its main food is detritus, aquatic plants and benthic invertebrates (Mordukhai-Boltovskoi 1974). The frequency increase of *P. elegans* correlates with the decline of the native amphipod *D. aralensis* (Malinovskaya 1961; Mordukhai-Boltovskoi 1972), which disappeared in 1973 before salinization became significant. We therefore suggest that *P. elegans* predation was a primary cause of this decline.

Mud crabs

The accidentally introduced *Rhithropanopeus harrisii* occurs naturally in the Gulf of Mexico and along the Atlantic coast of North America. It is a good osmoregulator (Bayly 1972); tolerates salinities > 56 ppt; and occurs in freshwater, rivers mouths and true marine habitats (Borisov 2012). It has invaded the Mediterranean Sea, Black Sea, Azov Sea, parts of the Baltic Sea and the Caspian Sea. The effect of this invader on the Aral Sea fauna has been negligible, although it may have provided a new food resource for wading birds. In contrast, Kotta et al. (2018) recently demonstrated how introduction of *Rhithropanopeus harrisii* to the Baltic caused a surprising ecological change from a bottom-up to a strong top-down controlled ecosystem, with a decline in benthic invertebrate biomass but an increase in pelagic nutrients and phytoplankton. This emphasizes how the effect of an alien invader can vary critically with the ecology of the receiving ecosystem.

Planned introductions of fish and crustaceans

Aladin et al. (2019) treated the Aral Sea ichthyofauna, so here we discuss only events closely associated with the crustacean fauna. The native ichthyofauna consisted of freshwater fish that migrated into the rivers for reproduction, since eggs and fry could not develop in saline conditions (Ermakhanov et al. 2012). In the 20th century, non-native fish (herring, plaice, and cyprinids) and crustaceans (mysids and calanoids intended as fish food) were artificially introduced to enhance fisheries. In addition, the accidentally introduced *Palaemon elegans* also became a food source for bottom foraging fish. The introduction of cyprinids and plaice, *Platichthys flesus* (L., 1758), were a success, while the other attempts had either no effect or caused ecological disruption such as *P. elegans* displacing *D. aralensis*.

Effect of introduced fish

The big sand smelt, *Atherina boyeri caspia* (Eichwald, 1838), became accidentally established in the Aral during unsuccessful attempts to introduce mullets from the Caspian Sea. The Baltic herring (*Clupea harengus membras* Valenciennes, 1847) was intentionally introduced in 1954–1956, with

catastrophic results. The herrings increased rapidly in number, causing heavy predation on native zooplankton, which was previously consumed mainly by sticklebacks (*Pungitius platygaster* Kessler, 1859) and juvenile fish. All large sized crustacean zooplankton (*Arctodiaptomus salinus*, *Moina mongolica*, *Cercopagis pengoi aralensis*, *Ceriodaphnia reticulata*) declined and virtually disappeared, and during the winter of 1960–1961 this caused massive deaths among the introduced fish due to starvation (Pankratova 1935, Osmanov 1961; Karpevich 1975; Kortunova and Lukonina 1970; Kortunova 1975). In the original Aral Sea, sticklebacks seem to have had a relatively minor ecological role, since they were not numerous and do not forage for zooplankton in deeper waters, but if introduced to small, shallow waters they will normally almost completely eradicate planktonic crustaceans (JM personal observation). Another, unexpected change was recently described from the Baltic coast of Sweden, where a decreased predation by larger fish caused a 50-fold increase in stickleback numbers. As a result, the former predator dominated system changed to prey dominance, because the small, but very numerous sticklebacks now prey upon the juveniles of larger species (Eklöf et al. 2020).

Introduction of mysids and calanoids

The three introduced mysids species are all detritophageous from brackish and marine waters in the Ponto-Caspian region. They were selected as potential fish food due to their fertility and better salinity tolerance (up to 17–20 ppt) than most of the native crustaceans (Daribaev 1967; Karpevich 1958a b 1960a b 1975; Bokova 1960). We conclude that *Paramysis intermedia* became established because it tolerates the relatively cold temperatures that can prevail in the Aral Sea (Karpevich and Bokova 1970). The quick demise of *P. baeri* was either due to being introduced in insufficient numbers or to an intolerance of low temperatures. Unfavourable thermal conditions may explain the eventual disappearance of *P. lacustris*, but fish predation may also have been a contributing factor for this large and less mobile mysid (Karpevich and Bokova 1970; Kortunova 1968 1970). The native calanoid, *Arctodiaptomus salinus*, is widely distributed in saline continental waters of the Palaearctic. It is monocyclic (one generation per year) and has low fertility (4–12 eggs) (Lukonina 1960b; Kortunova 1975). *Calanipeda aquaedulcis* was introduced to compensate for the decline of *A. salinus*, because it is much more fertile (six generations per year) and tolerates a wider salinity range (0.5–56 ppt) (Gubareva and Svetlichny 2011). Eventually the alien calanoid replaced both *A. salinus* and *Moina mongolica* in the plankton (Plotnikov 2016). Salinity increase cannot explain the disappearance of *M. mongolica*, which can tolerate up to > 80 ppt (Aladin 1996).

Plaice: a saviour for fisheries

Plaice (flounder gloss) was successfully introduced after other commercially important fish had seriously declined because of increasing salinity (Ermakhanov et al. 2012; Lim 1986). Fishermen from Denmark, where plaice fishing is important, gave valuable technical advice as part of the Joint Danish-Kazakhstani environmental project "From Kattegat to the Aral Sea", 1996–2008 (KSC 2020). The biologically and technically well founded introduction meant that plaice became the only asset for commercial fisheries in the Aral during the 1990s.

Introduced crustaceans and ichthyofauna

The planned introduction of alien mysids for fish food seems not to have had the desired effect. The accidental introduction of the caridean shrimp negatively affected the native fauna of gammarids, but there is no record that it affected the fish fauna. The planned introduction of the calanoid *Calanipeda aquaedulcis* displaced local planktonic crustaceans, but had no effect on the planktivorous fish, which just changed to the new food source. The native fish were unaffected by the decline in zooplankton, since they utilized other food sources, but eventually almost all fishery, whether on native or introduced species, ceased in the Aral itself due to salinization (Ermakhanov et al. 2012). Most initiatives to improve fisheries occurred without any coordination with the diversion of water for agricultural irrigation (see chapters in Micklin et al. 2014). Without the regression, the species introductions might have led to a stable but much changed fauna.

Parasitic crustaceans

Many of the parasitic crustaceans in the Caspian Sea were absent from the native Aral Sea fauna. This includes the ergasilid copepod *Thersitina gasterostei*, whence the sticklebacks were free from this parasite. It is remarkable that no parasitic crustaceans were introduced along with alien fish hosts. The only introduced parasite, *Achtheres percarum*, entered as larvae in transport bags. This and the similar pathway for mud crab larvae emphasizes the danger of transporting any alien species to a new habitat.

Among the parasitic crustaceans, *Ergasilus sieboldi*, *Argulus foliaceus*, *Caligus lacustris* and *Achtheres percarum* are euryhaline, but infestation

by *Lernaea cyprinacea*, *L. esocina* and *Lamproglena pulchella* occurs only in fresh water (Osmanov 1967 1971; Osmanov and Yusupov 1985), and during salinization these parasites began to disappear. Increased consumption of their larvae by introduced planktophagous fish may also have been a factor (Osmanov et al. 1976; Osmanov and Yusupov 1985). From the mid-1970s salinity increase had caused the disappearence of all native fish along with their crustacean parasites from the Aral itself (Osmanov and Yusupov 1985), but both groups persisted in the inflowing rivers and the diluted floodplains and delta lakes (Ermakhanov et al. 2012). The Syr Darya crustacean parasites may therefore help repopulate the reconstituted Small Aral, but there are no recent parasitological studies investigating this.

In its native range the introduced mud crab *P. harrisii* is frequently infested by the parasitically sterilizing rhizocephalan *Loxothylacus panopei* (Gissler, 1884). Rhizocephalans are not commonly introduced alongside with their hosts (Thresher et al. 2000), but a notable exception is a *P. harrisii* population infested with this parasite in the eastern Mediterranean (Øksnebjerg 2000). For the Aral Sea, *P. harrisii* entered as larvae, and this prevented the simultaneous introduction of the parasite due to the nature of the rhizocephalan life cycle (Høeg 1995; Glenner 2001).

Crisis and partial recovery

Recovery of the Small Aral fauna

No introductions took place after the dam construction, so most species must have entered naturally from the Syr Darya and lakes in its lower reaches. Some crustaceans perhaps also reappeared by hatching from dormant eggs. We explain the even earlier reappearance of *Podanevadne* to a somewhat decreasing salinization when the Small and Large Aral became separated. The decreased salinity and the abundance of crustaceans for food explain why commercial fisheries are now rebounding, even though they have not reached the catches obtained in the original Aral Sea (Chen 2018 2020). With timely action, the Aral system has therefore proven to be rather resilient. The list of crustaceans now recorded in the Small Aral (Plotnikov et al. 2016) is probably incomplete, because some infrequent species may well have escaped notice, but the marine copepod *Halicyclops rotundipes aralensis* was never numerous and may have disappeared completely due to decreasing salinity.

Demise of the Large Aral

The extreme salinization during the 1990s caused the loss of many species, but also the appearance of crustaceans, which must have derived from resting stages from other hyperhaline waters in the general region. The result is a now much poorer fauna with new dominant species such as *Eucypris mareotica*, *Apocyclops dengizicus* and especially *Artemia*.

Artemia in the Large Aral

The complexity of the Aral Sea system makes it an excellent example of the zoogeography and dispersal of the halobiontic *Artemia*. The introduction occurred from latent eggs, presumably by aeolian means or by bird transfer from other nearby high-salinity waters (Aladin and Filippov 1993; Aladin et al. 2004; Reynolds et al. 2015; Rogers 2014). Such transfer may be critical to the long-term survival of this species in arid regions, where any locality may be short lived (Green and Figuerola 2005; Figuerola and Green 2002; Figuerola et al. 2005). Charalambidou and Santamaria (2005) suggested from field evidence that the fast digestion of wading birds allows for the transport of ingested resting eggs. This was verified for anostracans in general by the experimental study of Rogers (2014), which also demonstrated that this method, unlike spreading by wind, favours directed transport to habitable new locations. Rogers (2015) furthermore discussed how patchy distribution and bird transfer to virgin habitats might together forge the evolution of *Artemia* clones. Undoubtedly, *Artemia* dispersal by resting eggs has always occurred in the Aral area, but before the 20th century, salinity in the sea itself remained too low for development. The phyto-detritophagous copepod *Calanipeda aquaedulcis* would also have been a fierce competitor for food, and planktivorous fish would quickly have exterminated any emerging *Artemia* (Musaev et al. 2012). Disappearance of fish and high salinity created the conditions for the establishment of *Artemia* (Arashkevicha et al. 2009). The genus is now harvested commercially for export, and this industry could be increasingly important in this otherwise economically depressed region. Nonetheless, problems remain for this industry in terms of both reliable water supply to the *Artemia* sites, logistics and economical factors (Marden et al. 2012). In many arid areas of the World, brine shrimps are also an important food source for birds, and the heavily increased *Artemia* populations could be such a novel resource. This underlines the often neglected, but important connection between conservation efforts in terrestrial and aquatic systems (Abell and Harrison 2020). Unfortunately, we are

unaware of any recent studies on the avian ecology in the Aral Sea area.

Future of the Aral Sea

The Small Aral

Further perspectives on the Aral Sea crustacean fauna depend primarily on salinity, and this in turn depends on future changes to existing dams or construction of new ones to retain inflowing water. A further salinity decrease in the Small Aral may negatively affect marine species and the fauna of saline continental water bodies. Salinity decrease could threaten *Palaemon elegans* but would also favour a return of the amphipod *Dikerogammarus aralensis*. Extinction is also likely for cladocerans of the Podonidae, the copepods *Calanipeda aquaedulcis*, *Halicyclops rotundipes aralensis* and all freshwater intolerant harpacticoids. Lower salinity would on the other hand allow for the re-establishment of all ostracods, except *Limnocythere aralensis*, and all freshwater tolerating copepods (Plotnikov et al. 2016). A project has been proposed for an additional dam in the neck of Bolshoy Sarycheganak Bay (Fig. 7). The dam would have a spillway into the main Small Aral and be fed by a channel from the Aklak control structure, diverting part of the Syr Darya flow (Micklin et al. 2020). If realized, the Small Aral will become a cascade of two water bodies. The novel dammed in bay would have a very low salinity (< 2 ppt) and be inhabited by freshwater species immigrating from the Syr Darya, while marine and brackish organisms would disappear. The main part would remain brackish, allowing at least some halophilic species to remain. An alternative project suggests to elevate the existing Kokaral Dam, causing the entire Small Aral to increase in area and remain a single brackish water body, with a diluted zone only in the vicinity of the Syr Darya delta (Micklin 2016; Micklin et al. 2020; Plotnikov et al. 2016). Clearly, any new project must take into serious consideration the predicted changes to biodiversity and make a choice that also best benefits fisheries and thereby the surrounding human population.

The Large Aral

The absence of any permanent water inflow

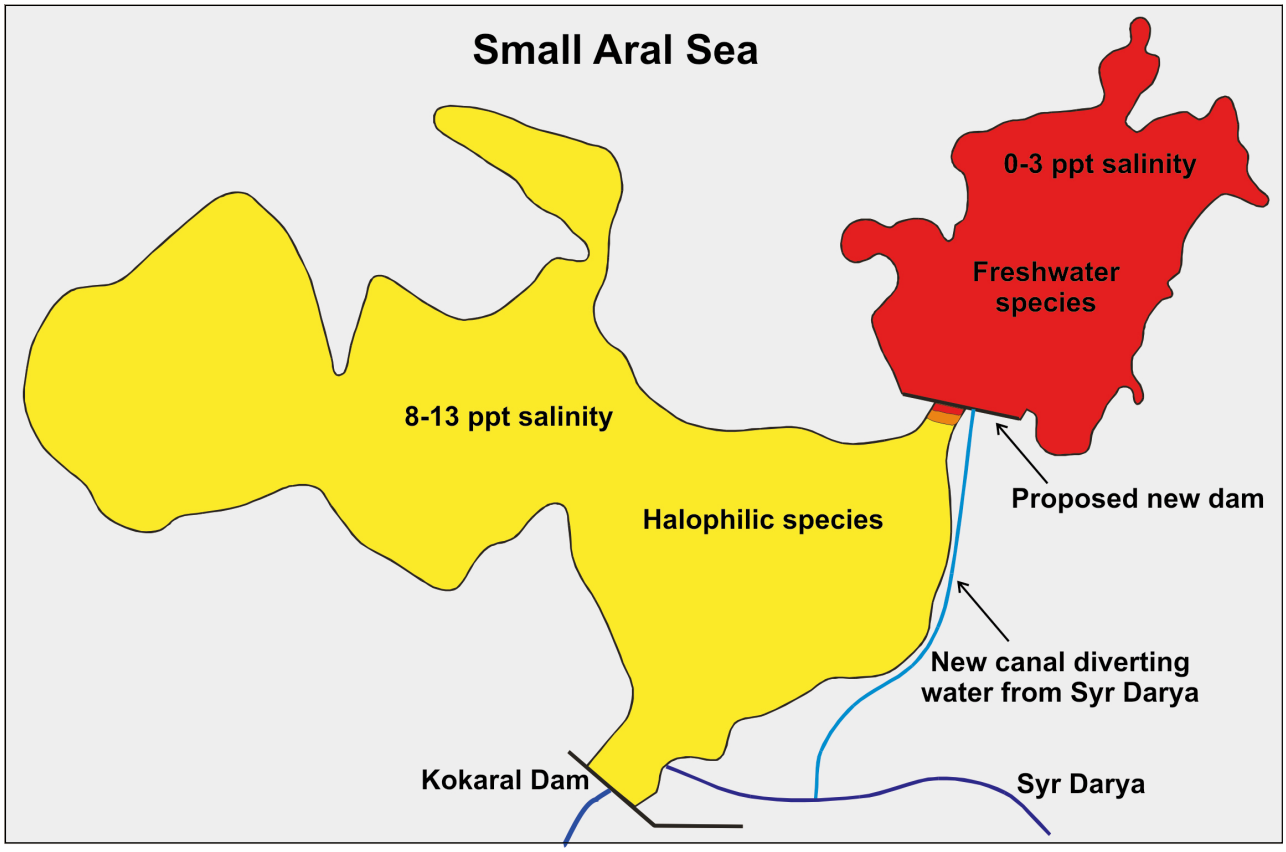

Fig. 7. Future of the Small Aral Sea. A new dam would divide the Small Aral Sea into two basins with different salinities and resulting faunas. The canal feeding the new, northern basin could have several different courses with only one shown here. See details in text and Micklin et al. (2020).

from the Amu Darya means that stabilization of the water level or decrease in salinity is impossible. With no action taken to arrest salinization in the western parts, the decline in biodiversity will continue and soon cause the extinction of the ostracod *Cyprideis torosa* and eventually also *Eucypris mareotica*. The harpacticoids *Cletocamptus confluens*, *Nitocra lacustris*, *C. retrogressus* and the cyclopid *Apocyclops dengizicus* are more salinity tolerant and will remain for some time. But eventually *Artemia* will be the only crustacean present (Plotnikov et al. 2016), and when its salinity tolerance (350 ppt) is exceeded, the western Large Aral will resemble the Dead Sea, with no metazoan life at all (Oren et al. 2010). The crustacean fauna of the eastern Large Aral might be restored, but only if it again receives a reliable inflow from the Amu Darya (Fig. 2). At present, such discharge happens only irregularly and not every year, and the outflow from the Small Aral presently evaporates in vain on the salt pan without ever reaching Large Aral waters. Another concern may be opposition to any re-flooding after the discovery of rich natural gas fields under the former seabed in Uzbekistan.

CONCLUSIONS

The isolated situation of the Aral makes it a rare site for studying how species originally invaded naturally and interacted to become and a unique ecosystem. Anthropogenic species introductions, whether accidental or planned, and the virtual breakdown of the ecology happened within the last half of the 20th century and were therefore well documented (Micklin 2007 2016; Micklin et al. 2014 2020). We have described changes to the important crustacean fauna and shown that they were caused by changes in physical and chemical factors, interactions among native and introduced crustaceans, and predation by introduced fish. The changes did not occur gradually following the salinity increase, but occurred stepwise and often catastrophically, when species met an introduced predator or a physiological barrier. Such a nonlinear pattern is now also expected for species extinctions in general due to climate change (Sunday 2020; Trisos et al. 2020). This implies that an observed, slow extinction rate does not by itself guard against sudden, catastrophic changes. On the other hand, the restoration projects for the Aral Sea have demonstrated that a relatively small effort can very rapidly result in a naturally occurring, partial restoration of the fauna, especially with respect to crustaceans and fish (Micklin and Aladin 2008; Micklin et al. 2014). We have also highlighted the consequences of future restoration projects on crustacean fauna. This should inform attempts to protect other threatened salines lakes such as Lake Balkhash in Kazakhstan, Lake Urmia in Iran and the Great Salt Lake in the U.S.A. (Aladin et al. 2020; Stone 2021). The Aral Sea is ecologically unique, and its affluent rivers economically crucial for the human population in the two adjacent countries for both fisheries and agriculture. Cotton and rice are now the prevalent crops and require copious amounts of water. Unfortunately, most of the diverted water never reaches the crops; they could, however, be saved by implementing properly designed and maintained irrigation systems (Dukhovny et al. 2008). This calls for internationally coordinated restoration and management projects in the area (Cosens et al. 2018) coupled with full cooperation with the local population, as emphasized by Kim (2018).

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Authors' contributions: Problem defined by Aladin and Plotnikov; Data sampling by ladin and Plotnikov. Data Analysis by ALL authors; Write the paper ALL authors.

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Availability of data and materials: The information has now been returned and is stored in the office of the IPA CIS in the Republic of Kazakhstan (IPA CIS, Inter-Parliamentary Assembly of the Member States of the Commonwealth of Independent States). The database is not yet Internet available but free for on site personal use.

Consent for publication: We declare that All authors hereby consent for publication. This letter is sent CC to all authors.

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