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Benthic macroinvertebrates of the northern Caspian Sea during recent rises in water-level

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Abstract. Data on benthic macroinvertebrates of the northern Caspian Sea in 1980–1991 were collected by the Caspian Fishery Research Institute. During the initial period of the water-level rise, the main trends in benthic macroinvertebrates were increases in the biomass of the main groups and decreases in the relative abundance of species of Mediterranean origin. There was no significant alteration in species composition. The increased abundance was due to improved trophic conditions and a decrease in the numbers of benthos-feeding fish. Some decrease in the relative abundance of species of marine origin was related to a decrease in water salinity.

Key words: benthic macroinbertebrates, Caspian Sea, salt lakes, water-level rise, zoobenthos

Introduction

The Caspian Sea, like many lakes in arid regions, has undergone marked changes in the water-level. In the first half of the 20th century, the water-level fell and by 1977 had reached 28.9 m below ocean level. In 1978, however, the water-level began to rise and by 1991 had risen 1.8 m. At present (1998), the level of the Caspian Sea has risen 2.2 m. This level was attained in 1997 and has been more or less stable since then.

The unique biological resources of the Caspian Sea, as well as its significant social and economic values, have attracted close public and scientific attention in recent years. Explorations of its benthic communities have revealed large numbers of endemic species, and spatial irregularity and significant long-term fluctuations in the abundance of benthic invertebrates (Birstein, 1945; Vinogradov, 1955, 1959; Saenkova, 1959; Osadchikh, 1963, 1968; Romanova, 1960, 1963; Yablonskaja, 1975). Many studies identified a significant correlation between the abundance of benthic taxa and elements of the hydrological regime, particularly salinity, river outflow volume, and flood periodicity etc. (Yablonskaja et al., 1974; Osadchikh, 1980; Yablonskaya and

Osadchikh, 1996). Changes in key environmental factors followed the fall in water-level in the period 1930–1970s and significantly influenced benthic communities (Osadchikh, 1988; Yablonskaya and Osadchikh, 1996). Likewise, recent rises in water-level have apparently caused significant ecosystem changes. Unfortunately, these recent changes are less well known because of difficulties in the support of scientific research.

The main objective of the present paper is to evaluate the state and dynamics of benthic macroinvertebrates in the northern Caspian Sea during the initial period of recent rises in water-level (between 1980 and 1991).

Materials and methods

Data were obtained in the northern Caspian Sea in 1980–1991 during the course of standard June hydrobiological observations by the Caspian Fishery Research Institute (KaspNIRH) (Figure 1). Benthos at depths of 2 to 10 m was investigated. Bottom samples were collected using an "okean" bottom sampler of 0.1 m^2 gape size. Sample collection and treatment was made using standard methods (Anon., 1983). A total of 1400 quantitative benthic samples was collected and analysed.

Results

Northern Caspian as a whole

In the period 1980–1991, benthic communities of the northern Caspian comprised 110 species of aquatic invertebrates (Table 1). The largest number of species (50) recorded were amphipod species. Polychaetes comprised 6 species, leeches 3, bivalves 22, gastropods 2, ostracods 10, Cumacea 14, Mysidacea 8, Isopoda, Cirripedia and Decapoda, 1 species. Species of Turbellaria, Nematoda, Oligochaeta, Chironomidae and Trichoptera were not identified.

A number of the species recorded (70 taxa) was found during the whole period of the investigation. Other species were represented only occasionally and without any noticeable trends.

Bivalve molluscs formed the greatest part (75 per cent) of benthic macroinvertebrate biomass in the northern Caspian (Table 2). The abundance of Annelida, crustaceans and chironomids was much lower (12, 12, and 1 per cent, respectively). *Mytilaster lineatus* and *Abra ovata* were the dominant bivalves. Oligochaetes dominated the Annelida. Among crustaceans,

Figure 1. Areas in the Caspian Sea investigated. 1, western part of the northern Caspian Sea; 2, eastern part of the northern Caspian Sea.

Table 1. Species composition of benthic macroinvertebrates in the northern Caspian Sea in 1980–1991

Species	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Turbellaria indet.	+	+	+	+	+	+	+	+	+	+	+	+
Nematodes indet.	+	+	+	+	+	+	+	+	+	+	+	+
Polychaeta *Hypania invalida* (Grube)	+	+	+	+	+	+	+	+	+	+	+	+
Hypaniola kowalewskii (Grimm)	+	+	+	+	+	+	+	+	+	+	+	+
Manayunkia caspica Annenkova	+	+	+	+	+	+	+	+	+	+	+	+
Nereis diversicolor O.F.Muller	+	+	+	+	+	+	+	+	+	+	+	+
Fabricea sabella (Ehrenberg)	–	–	+	+	+	+	+	+	+	–	–	+
Parnypania brevispinis (Grube)	+	–	–	–	–	–	–	+	+	+	–	–
Oligochaeta indet.	+	+	+	+	+	+	+	+	+	+	+	+
Hirudinea												
Caspiobdella tuberculata Epstein	–	–	–	+	–	–	–	–	+	–	–	–
Archaeobdella esmonti Grimm	+	+	+	+	+	+	+	+	+	+	+	+
Piscicola caspica Salensky	+	–	+	+	+	–	+	+	+	+	–	+
Bivalvia												
Abra ovata (Phil.)	+	+	+	+	+	+	+	+	+	+	+	+
Cerastoderma Iamarcki (Reeve)	+	+	+	+	+	+	+	+	+	+	+	+
Dreissena polymorpha polymorpha (Pall.)	+	+	+	+	+	+	+	–	+	–	+	–
D.p.andrusovi (Andr.)	+	+	+	+	+	+	+	+	+	+	+	+
D.rostriformis (Desh.)	+	–	+	–	+	+	+	+	+	+	+	+
Didacna trigonoides (Pall.)	+	+	+	+	+	+	+	+	+	+	+	+
D.profundicola Logv.et Star.	–	–	–	–	–	–	–	+	–	–	–	–

Table 1. Continued

Species	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
D.barbotdemarnyi (Grimrn)	+	+	+	+	+	+	+	+	+	+	+	+
D.longipes(Grimm)	+	+	+	+	–	–	+	+	+	+	+	–
D.parallella Bog.	+	+	+	+	+	+	+	+	+	+	+	+
D.protracta (Eichw.)	–	+	+	–	–	–	+	+	+	–	–	+
Hypanis vitrea (Eicnw.)	+	+	+	+	+	+	+	+	+	+	+	+
H.laeviuscula (Eichw.)	+	+	+	+	+	+	+	+	+	+	+	+
H.plicata Eichw.	+	–	+	+	+	–	–	+	+	+	+	+
H.angusticostata (Borcea)	+	+	+	+	+	+	+	+	+	+	+	+
H.caspia (Eichwald)	+	+	+	+	+	+	+	+	–	–	–	–
H.minima (Ostr.)	+	+	–	–	–	+	+	+	–	–	+	–
H.albida Logv.et Star.	+	+	+	+	+	+	+	+	+	+	+	+
Mytilaster lineatus (Gmel.)	+	+	+	+	+	+	+	+	+	+	+	+
Pisidium sp.	–	+	–	–	–	–	+	–	–	–	–	–
Unio sp.	–	–	+	–	+	–	–	–	–	–	–	–
Anodonta sp.	–	–	–	–	+	–	–	–	–	–	–	–
Gastropoda												
Pyrgulidae gen sp.	+	+	+	+	+	+	+	+	+	+	+	+
Theodoxus pallasi Ldh.	+	+	+	+	+	+	+	+	+	+	+	+
Cirripedia												
Balanus improvisus Darwin	+	+	+	+	+	+	+	+	+	+	+	+
Amphipoda												

Table 1. Continued

Species	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Axelboeckia spinosa (G.O.Sars)	+	+	–	–	–	+	–	–	–	–	–	+
Amathillina cristata Grimm	+	+	+	+	+	+	+	+	+	+	+	+
A.spinosa (Grimm)	–	–	–	–	–	–	–	–	–	–	–	–
Am.Pusilla G.O.Sars	–	–	–	–	–	–	+	–	–	–	–	–
Cardiophilus baeri G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
Dikerogammarus caspius (Pallas)	+	+	+	+	+	+	+	+	+	+	+	+
D.haemobaphes (Eichwald)	+	+	+	+	+	+	+	+	+	+	+	+
Gammarus pauxillus Grimm	+	+	+	+	+	+	+	+	+	+	+	+
G.warpachowskyi G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
G.ischnus Stebbing	+	+	+	+	+	+	+	+	+	+	+	+
G.placidus Grimm	–	–	–	–	–	–	–	–	–	–	+	–
Gammaracantus loricatus caspius Grimm	–	–	–	+	–	+	+	–	–	+	–	–
Gmellina costata Grimm (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
G.pusilla G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
G.branchiura Derzh. et Pjat.	–	+	–	–	–	–	–	+	–	+	–	–
G.laeviuscula G.O.Sars	–	+	–	–	–	–	–	–	–	–	–	–
Gmelinopsis tuberculata G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
Iphigenella andrussovi (G.O.Sars)	–	+	+	+	+	+	+	+	+	+	+	–
Niphargoides caspius (Grimm)	+	+	+	+	+	+	+	+	+	+	+	+
N.corpulentus G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
N.compactus G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+

Table 1. Continued

Species	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
N.spinicaudatus Car.	+	+	+	+	+	+	+	+	+	+	+	+
N.quadrimanus G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
N.aequimanus G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
N.derzhavini Pjatakova	+	+	+	+	+	+	+	+	–	+	+	+
N.robustoides (Grimm)	+	+	+	+	+	+	+	+	+	–	+	–
N.deminutus (Stebbing)	–	–	–	–	–	–	–	+	–	–	–	–
N.obesus (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
N.motasi Car.	–	–	–	–	–	–	–	–	–	–	–	–
N.paradoxus (Derzhavin)	–	–	–	–	–	+	–	–	–	+	+	–
N.abbreviatus (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
N.macrurus (Sars)	+	+	+	+	+	+	+	+	+	+	+	+
N.compressus (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
N.similis (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
N.maeoticus (Sowinsky)	–	–	–	–	–	–	–	+	+	–	–	–
Derzhavinella macrochelata Birstein	–	–	–	–	–	+	–	–	–	–	–	–
Pontoporeia affinis microphtalma Grimm	–	–	–	–	–	–	+	–	+	+	+	–
Pseudalibrotus caspius (Grimm) G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
P.platyceras (Grimm) G.O.Sars	–	–	+	+	+	–	+	+	–	+	–	+
Pandorites platycheir (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
P.podoceroides (Grimm)	+	+	+	+	+	+	+	+	–	+	+	+
Gammaridee gen. sp.	+	+	–	+	+	+	+	+	+	+	+	+

Table 1. Continued

Species	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Zemovia volgensis Deahavin	–	–	–	–	–	–	–	+	+	–	+	–
Corophium nobile G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
C.chelicorne G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
C.curvispinum G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
C.robustum G.O.Sars	+	+	+	+	–	+	+	+	+	+	+	+
C.mucronatum G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
C.sipinulosum G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
C.monodon G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
Cumacea												
Caspiocuma campylaspoides (G.O.Sais)	+	+	+	+	+	+	+	+	+	+	+	+
Pseudocuma cercaroides G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
Pterocuma pectinata (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
P.sowinskyi (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
P.rostrata (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
Stenocuma gracilis (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
S.graciloides (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
S.tenuicauda (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
Schizorhynchus bilamellatus (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
Sch.Eudorelloides (G.O.Sars)	+	+	+	+	+	+	+	+	+	+	+	+
Sch.Scabriusculus G.O.Sars	+	+	+	+	+	+	+	+	+	+	+	+
Sch.Knipowitchi (Derzhavin)	+	+	+	+	+	+	+	+	+	+	+	+

Table 1. Continued

Species	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Volgocuma telmatophora Derzhavin	+	+	+	+	+	+	+	+	+	+	+	+
Carinocuma birsteini	+	+	+	–	+	+	+	–	–	+	+	–
Mysidacea												
Paramysis baery Czemiavsky	+	+	+	+	+	+	+	+	+	+	+	+
P.ullskyi Czerniavsky	+	+	+	+	+	+	+	+	+	+	+	+
P.lacustris Czern.	+	+	+	+	+	+	+	+	+	+	+	+
P.intermedia (Czem.)	+	+	+	–	+	+	+	+	+	–	–	–
P.loxolepis G.O.Sars	–	–	–	–	–	–	–	–	–	–	–	–
P.kessleri G.O.Sars	–	+	–	–	–	–	+	–	+	–	+	+
Limnomysis benedeni Czerniavsky	–	+	+	+	–	+	–	–	–	–	+	+
Caspiomysis knipowitschi G.O.Sars	–	+	–	–	+	+	+	+	+	–	–	–
Isopoda												
Jaera sarsi caspica Kesselyak	+	+	+	+	+	+	+	+	+	+	+	+
Decapoda												
Rhithropanopeus harrisii (Gould)	+	+	+	+	+	+	+	+	+	+	+	+
Chironomidae indet.	+	+	+	+	+	+	+	+	+	+	+	+
Trichoptera indet.	–	–	+	+	+	–	+	+	–	+	+	–

Table 2. Biomass of main benthic macroinvertebrate components in the northern Caspian in 1980–1991, gm^{-1}

Species	Year												Average	Average
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1980–1991	1960–1979
Nereis	2.60	2.80	2.30	4.60	3.90	3.60	3.20	2.80	4.80	4.70	4.90	2.20	3.53	2.90
Ampharetidae	0.80	1.00	1.60	1.20	0.70	1.20	1.20	1.70	1.10	1.00	1.10	1.90	1.21	0.50
Oligochaeta	4.70	4.60	6.10	4.30	5.20	7.00	5.70	9.70	6.70	9.40	7.90	6.60	6.49	3.20
Other	0.00	0.00	0.04	0.06	0.03	0.04	0.02	0.02	0.02	0.03	0.03	0.04	0.03	0.02
Annelida	8.10	8.40	10.04	10.16	9.83	11.84	10.12	14.22	12.62	15.13	13.93	10.74	11.26	6.62
D.p.polymorpha	5.30	1.90	2.40	1.70	0.70	0.06	0.10	—	0.70	—	0.50	—	1.11	—
D.p.andrusovi	1.00	1.00	0.80	0.70	0.70	2.10	1.40	8.10	2.70	3.00	1.60	3.90	2.25	2.60
H.vitrea	0.90	3.60	2.60	3.20	2.30	4.00	2.20	1.50	4.00	4.80	3.40	4.00	3.04	1.70
H.angusticostata	2.90	6.00	6.10	9.80	7.90	9.00	10.50	9.10	14.10	12.00	8.80	11.00	8.93	3.20
D.trigonoides	4.50	9.60	7.10	8.70	11.50	19.30	12.90	5.90	5.50	8.10	3.50	4.50	8.43	9.20
D.barbotdemarnyi	1.10	8.10	0.80	0.70	4.00	5.90	2.50	9.90	0.60	2.30	3.10	2.80	3.48	—
C.lamarcki	1.10	1.30	3.40	1.90	0.10	0.50	0.40	0.70	0.50	0.40	0.30	0.60	0.93	2.10
M.lineatus	7.70	14.00	6.50	39.50	12.50	21.30	39.50	35.80	33.50	41.90	27.70	2.90	23.57	12.70
A.ovata	10.00	9.90	9.70	9.30	4.40	9.70	9.60	6.30	7.50	21.10	29.70	9.30	11.38	12.60
Other	3.20	3.00	1.60	4.90	2.60	2.70	15.20	13.00	1.60	11.90	6.20	6.40	6.03	1.30
Mollusca	37.70	58.40	41.00	80.40	46.70	74.56	94.30	90.30	70.70	105.50	84.80	45.40	69.15	45.40

Table 2. Continued

Species	Year												Average	Average
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1980–1991	1960–1979
Gammaridae	2.90	3.50	1.40	2.50	2.80	3.00	3.60	2.40	2.60	2.10	1.90	2.20	2.58	2.10
Corophiidae	6.00	2.80	1.40	3.80	1.90	3.80	2.80	4.90	3.10	2.70	2.00	2.10	3.11	2.00
Cumacea	1.00	1.40	2.60	1.60	1.30	2.10	1.20	1.70	2.20	2.50	1.80	1.90	1.78	1.00
R.harrisii	1.50	0.70	0.30	0.70	0.40	0.60	0.90	0.40	0.60	0.40	0.30	0.10	0.58	0.00
B.improvisus	1.20	1.10	1.60	3.30	1.20	2.10	3.50	4.70	7.10	3.60	6.30	0.90	3.05	0.00
Other	0.05	0.01	0.05	0.06	0.10	0.04	0.05	0.04	0.08	0.02	0.10	0.05	0.05	0.04
Crustacea	12.65	9.51	7.35	11.96	7.70	11.64	12.05	14.14	15.68	11.32	12.40	7.25	11.14	5.14
Chironomidae	0.80	0.60	2.20	0.80	0.50	0.20	0.40	2.70	1.10	0.20	0.10	0.60	0.85	0.20
Total	59.25	76.91	60.59	103.32	64.73	98.24	116.87	121.36	100.10	132.15	111.23	63.99	92.40	57.36

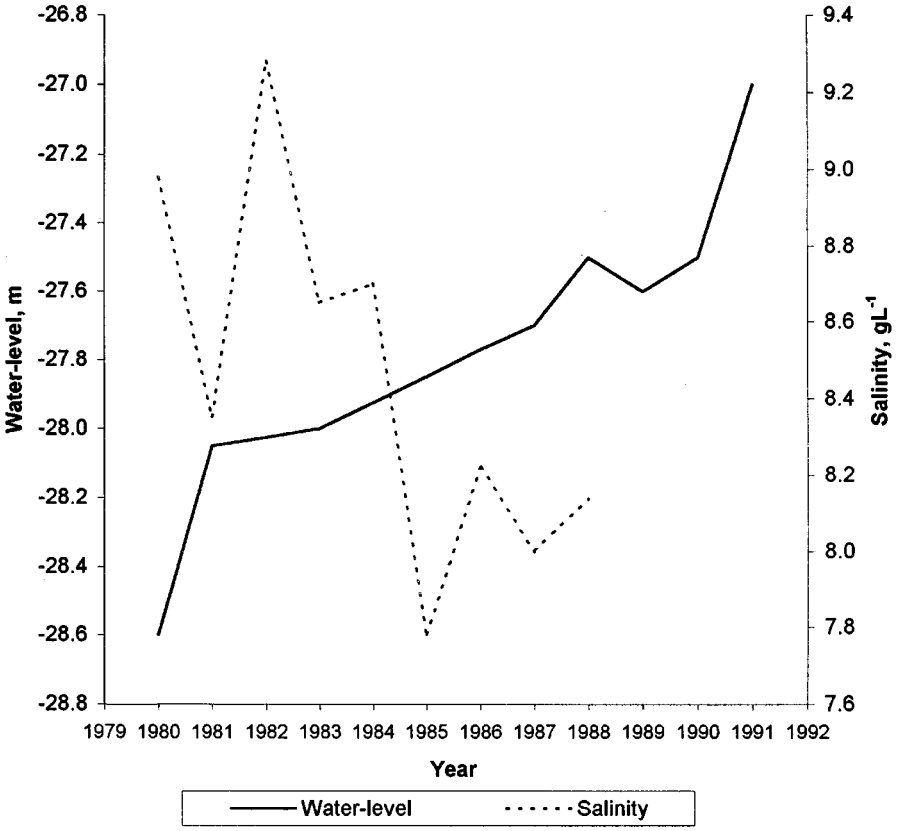

Figure 2. Sea-level and salinity in the northern Caspian Sea in the period 1980–1991. After Katunin (1992) and Latypov et al. (1991).

Corophiidae and Gammaridae dominated in the first half of the 1980s, Cirripedia in the second half.

The total biomass of bivalves fluctuated widely during the period of investigation: from 38 g m^{-2} in 1980 to 106 g m^{-2} in 1989 (Table 2). Changes were generally determined by changes in the biomass of the dominant species, *M. lineatus*, which underwent significant but irregular fluctuations in abundance. The biomass of *Abra ovata*, *Hypanis vitrea* and *H. angusticostata* increased slightly near the end of 1980, while *Dreissena polymorpha polymorpha* and *Cerastoderma lamarcki* decreased in abundance. Overall, the quantity of bivalves has increased significantly during the period of investigation.

Total Annelida biomass varied from 8.1 g m^{-2} in 1980 to 15.2 g m^{-2} in 1989. At the end of the period of investigation, the abundance of Oligochaetes rose considerably while the biomass of *Nereis diversicolor* increased slightly.

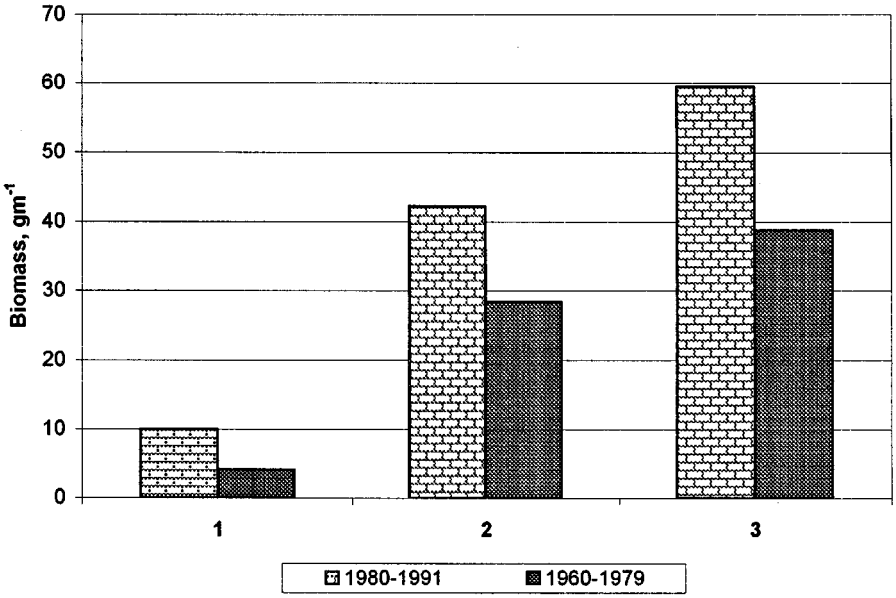

Figure 3. Biomass of benthic invertebrates of different origin in the western part of the northern Caspian. 1, freshwater species; 2, brackish-water species; 3, marine-derived Mediterranean species.

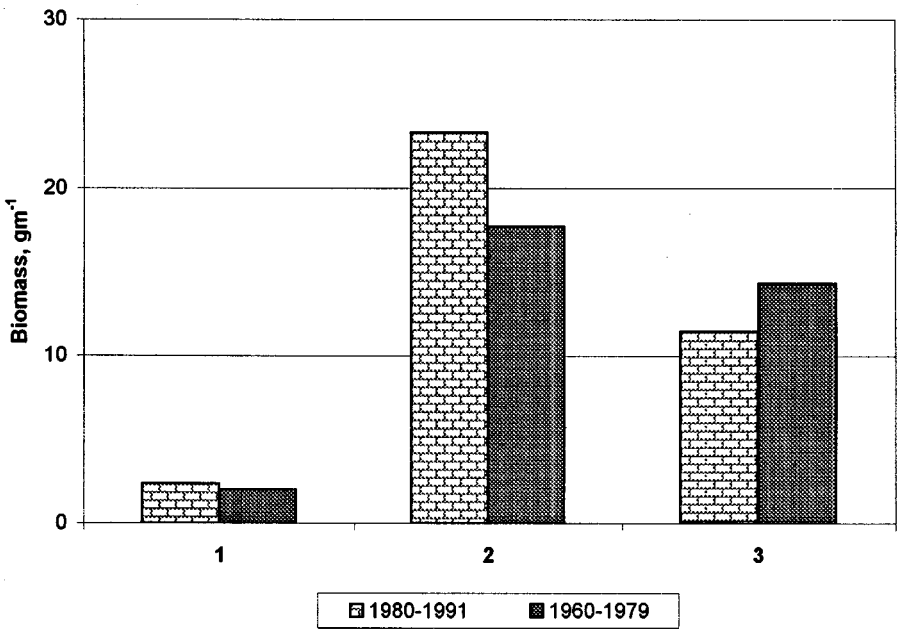

Figure 4. Biomass of benthic invertebrates of different origin in the eastern part of the northern Caspian. Explanations as in Figure 3.

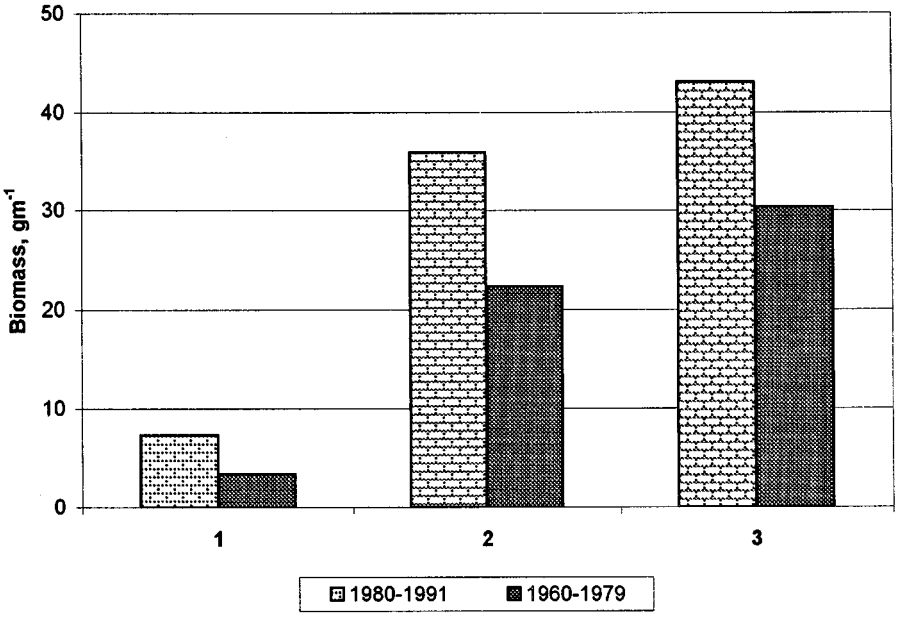

Figure 5. Biomass of benthic invertebrates of different origin in the northern Caspian. Explanations as in Figure 3.

As a result, total Annelida biomass increased markedly between 1980 and 1991.

Crustacean biomass varied from 5.4 g m^{-2} in 1982 to 9.9 g m^{-2} in 1980, the biomass of Chironomidae from 0.1 g m^{-2} in 1990 to 2.7 g m^{-2} in 1987. No trend was discerned in the abundance of these groups in 1980–1991, but maximum biomass values were noted in the second half of the period of investigation.

The total biomass of benthic macroinvertebrates of the northern Caspian varied from 56.5 g m^{-2} in 1980 to 128.1 g m^{-2} in 1989, mostly reflecting changes in bivalve abundance. Overall, some increase in total biomass was observed in the 1980s, an increase more obvious in the western part of the northern Caspian.

Comparison of our data with those for 1960–l979 (Table 2) revealed that almost all major groups of benthic invertebrates had a higher biomass in the 1980s than in the period 1960–1979. Even minimum values for worm and crustacean biomass in the 1980s were higher than average values for the period 1960–1979 (6.6 and 5.1 g m^{-2}, respectively). Nevertheless, the average biomass of some mollusc species remained at former levels in the 1980s (*Dreissena polymorpha andrusovi*, *Didacna trigonoides*, *A. ovata*) or even

lower (*C. lamarcki*). Average total biomass of benthic macroinvertebrates in 1980–1991 appear to be 1.6 times higher than in 1960–1979.

Differences in the structure of benthic macroinvertebrate communities in different parts of the northern Caspian

The western and eastern parts of the northern Caspian differed significantly in terms of the abundance of benthic invertebrates, the relative biomass of different species, and long-term fluctuations in these.

The western part was characterised by the high productivity of benthic communities. Average benthic biomass in 1980–1991 was 121.8 g m^{-2} (Table 3). In the 1980s, an increased biomass of molluscs and Annelida was recorded in this region while no obvious trends were revealed in the abundance of crustaceans and Chironomidae.

The eastern part of the Sea, on the other hand, was characterised by a lower productivity of benthic communities. Average biomass in 1980–1991 was only 36.6 g m^{-2} (Table 4). The only obvious trend in benthic communities was an increase in Annelida abundance. The biomass of molluscs, crustaceans and Chironomidae changed irregularly between years.

In both the western and eastern parts, the largest fraction of benthic macroinvertebrate biomass comprised bivalve molluscs. In the west, *M. lineatus* dominated except in 1991 when *A. ovata* dominated. The abundance of *A. ovata* and *H. vitrea* increased during the 1980s and peaked at the end of the period of investigation. *Dreissenia polymorpha polymorpha*, was found in considerable numbers at the beginning of the 1980s, but then gradually disappeared from the benthos. Simultaneous1y, the number of *D. polymorpha andrusavi* increased.

In the east, the dominant mollusc was *Didacna trigonoides*. Occasionally, *Hypanis angusticostata angusticostata* and *Abra ovata* also had high biomasses. During the period of investigation *D. trigonoides* and *A. ovata* decreased slightly in abundance, while *D. polymorpha andrusovi*, *H. angusticostata* and *H. vitrea* increased in abundance.

The abundance of the Annelida grew in both parts of the northern Caspian in the 1980s. In the western part, this was mainly due to Oligochaeta. In the east, *Nereis diversicolor* formed the largest part of annelidan biomass. Its abundance continued to increase markedly during the early 1990s.

Among crustaceans, Gammaridae dominated the west in the first half of the 1980s. In the second half of the 1980s, Cirripedia dominated. Overall, crustacean abundance was higher in the second half of the period under study than in the first half. In the east, Corophiidae dominated, but its biomass varied irregularly. The abundance of the Gammaridae and Cumacea increased slightly during the study period.

Table 3. Biomass of main benthic macroinvertebrate components in the western part of the northern Caspian in 1980–1991, gm^{-1}

Species	Year												Average	Average
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1980–1991	1960–1979
Nereis	2.40	2.70	1.60	4.70	3.80	2.80	2.80	2.50	4.40	4.70	4.30	1.20	3.20	3.10
Ampharetidae	1.10	1.30	2.50	1.80	1.00	1.30	1.60	2.30	1.40	1.30	1.50	2.70	1.70	0.60
Oligochaeta	6.40	6.00	8.70	5.60	6.80	9.00	7.30	12.70	8.70	12.90	11.10	8.00	8.60	3.80
Other	0.05	0.03	0.07	0.09	0.04	0.06	0.04	0.02	0.03	0.05	0.05	0.06	0.05	0.03
Annelida	9.95	10.03	12.87	12.19	11.64	13.16	11.74	17.52	14.53	18.95	16.95	11.96	13.55	7.53
D.p.polymorpha	8.10	3.00	3.80	2.70	1.00	0.10	0.20	—	1.10	—	—	—	1.70	—
D.p.andrusovi	1.00	0.80	0.40	0.80	0.70	2.10	1.60	11.50	3.80	3.90	2.30	3.20	2.70	2.50
H.vitrea	1.40	5.30	4.00	4.80	4.00	5.80	2.90	1.90	5.60	6.50	4.70	4.70	4.30	2.20
H.angusticostata	3.20	6.90	8.10	11.80	10.80	9.10	13.00	12.90	19.90	15.90	9.80	9.60	10.90	6.60
D.trigonoides	1.80	6.10	2.00	7.30	13.30	15.10	14.70	7.20	5.60	7.00	2.00	2.40	7.00	6.00
D.barbotdemarnyi	1.60	12.60	1.30	1.10	6.10	9.00	3.70	14.30	0.90	3.60	4.80	4.20	5.30	4.70
C.lamarcki	1.60	1.60	5.00	2.60	0.20	0.70	0.50	1.00	0.80	0.60	0.30	0.60	1.30	3.00
M.lineatus	11.80	21.90	10.10	60.80	19.00	32.40	58.10	51.80	51.40	65.70	43.20	4.40	35.90	19.40
A.ovata	9.80	9.80	6.90	10.00	5.70	12.60	13.20	8.90	11.10	30.50	41.40	13.60	14.50	13.30
Other	4.80	4.10	2.50	7.30	7.20	3.80	16.50	31.20	2.40	18.70	11.30	10.50	10.00	2.90
Mollusca	45.10	72.10	44.10	109.20	68.00	90.70	124.40	140.70	102.60	152.40	119.80	53.20	93.60	60.60

Table 3. Continued

Species	Year												Average	Average
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1980–1991	1960–1979
Gammaridae	4.20	5.10	1.90	3.70	4.10	4.00	4.70	3.30	3.70	2.50	2.30	2.40	3.50	2.90
Corophiidae	6.90	1.80	1.20	3.90	1.80	3.40	2.50	5.00	3.40	1.70	1.40	0.90	2.80	1.70
Cumacea	1.30	1.60	3.90	2.40	1.70	2.80	1.50	2.10	2.90	3.20	2.20	2.50	2.30	1.20
R.harrisii	1.00	0.40	0.20	0.50	0.50	0.60	1.20	0.50	0.80	0.30	0.20	0.10	0.53	—
B.improvisus	1.80	1.40	0.70	4.10	1.60	2.60	4.80	6.80	10.60	4.90	9.70	1.30	4.19	—
Other	0.06	0.03	0.08	0.10	0.20	0.06	0.06	0.06	0.10	0.03	0.02	0.10	0.08	0.05
Crustacea	15.26	10.33	7.98	14.70	9.90	13.46	14.76	17.76	21.50	12.63	15.82	7.30	13.45	5.85
Chironomidae	1.30	0.90	3.40	1.30	0.70	0.30	0.60	4.00	1.70	0.30	1.30	0.90	1.39	0.30
Total	71.61	93.36	68.35	137.39	90.24	117.62	151.50	179.98	140.33	184.28	153.87	73.36	121.82	74.28

Table 4. Biomass of main benthic macroinvertebrate components in the eastern part of the northern Caspian in 1980–1991, gm^{-1}

Species	Year												Average	Average
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1980–1991	1960–1979
Nereis	3.20	2.80	3.50	4.40	4.00	5.10	4.10	3.70	5.60	4.70	5.90	4.00	4.25	2.40
Ampharetidae	0.20	0.40	0.10	0.20	0.20	0.90	0.20	0.40	0.50	0.40	0.20	0.30	0.33	0.20
Oligochaeta	1.30	2.00	1.40	1.90	1.90	2.90	2.20	2.80	3.00	3.10	2.30	3.80	2.38	2.00
Other	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.01	0.01	0.02	0.00			
Annelida	4.70	5.20	5.00	6.50	6.10	8.90	6.50	6.90	9.10	8.20	8.40	8.10	6.97	4.60
D.p.polymorpha	—	—	—	—	—	—	—	—	—	—	—	—	0.00	—
D.p.andrusovi	1.00	1.40	1.50	0.40	0.50	2.10	0.90	0.60	0.80	1.40	0.40	5.50	1.38	1.90
H.vitrea	0.10	0.60	0.10	0.40	0.40	0.70	0.80	0.80	1.00	1.80	0.80	3.00	0.88	0.90
H.angusticostata	2.30	4.30	2.70	5.90	2.70	8.90	5.20	1.00	3.50	5.10	4.80	11.40	4.82	2.70
D.trigonoides	9.00	15.70	16.10	11.20	8.00	27.40	9.30	3.20	5.40	10.10	6.30	8.70	10.87	7.80
D.barbotdemarnyi	—	—	—	—	—	—	—	—	—	—	—	—	0.00	—
C.lamarcki	0.30	0.80	0.60	0.70	0.00	0.01	—	0.00	0.01	—	—	—	0.20	0.60
M.lineatus	0.00	0.02	0.00	0.01	—	0.01	—	0.00	—	—	—	0.00	—	
A.ovata	10.40	10.10	14.50	8.00	1.80	4.10	2.00	0.50	1.00	4.70	8.70	0.60	5.53	11.30
Other	0.90	0.70	0.50	0.40	0.90	0.30	1.10	0.10	0.30	0.02	0.09	0.05	0.45	0.10
Mollusca	24.00	33.62	36.00	27.01	14.30	43.52	19.30	6.20	12.01	23.12	21.09	29.25	24.12	25.30

Table 4. Continued

Species	Year												Average	Average
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1980–1991	1960–1979
Gammaridae	0.50	0.70	0.30	0.30	0.40	1.10	1.10	0.50	0.60	1.20	1.10	1.90	0.81	0.80
Corophiidae	4.20	4.60	1.80	3.70	2.20	3.00	3.50	4.50	2.30	4.50	3.20	4.50	3.50	2.60
Cumacea	0.60	0.90	0.40	0.30	0.50	0.80	0.60	0.70	1.00	1.30	1.10	0.80	0.75	0.80
R.harrisii	2.30	1.20	0.50	1.00	0.40	0.60	0.20	0.09	0.20	0.80	0.70	0.01	0.67	—
B.improvisus	0.20	0.60	3.00	1.80	0.30	1.00	0.80	0.04	0.50	1.20	0.10	0.20	0.81	—
Other	0.00	0.00	0.00	0.01	0.02	0.02	0.01	0.02	0.03	0.01	0.04	0.02	0.02	0.02
Crustacea	7.80	8.00	6.00	7.11	3.82	6.52	6.21	5.85	4.63	9.01	6.24	7.52	6.56	4.22
Chironomidae	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.01	0.03	0.00	0.03	0.01	0.20
Total	36.50	46.83	47.00	40.62	24.22	58.96	32.01	18.96	25.75	40.36	35.73	44.90	37.65	34.14

In both the western and eastern parts, fluctuations of total biomass in the 1980s were closely related to changes in bivalve biomass. In the west, total biomass grew from 69 g m^{-2} in 1980 to 179 g m^{-2} in 1989. In the east, total biomass did not change significantly and bivalve abundance showed no clear trends.

Compared to 1960–1979, the average biomass of all major groups of benthic macroinvertebrates in the west increased considerably (Table 3). The average value for total biomass was 1.5 times higher for 1980–1991 than for 1960–1979. Changes in the abundance of groups in the east were insignificant. However, a smaller biomass of bivalves and a slightly greater biomass of crustaceans and Annelida occurred. The relative abundance of different macroinvertebrate groups did not change compared to the previous period in both parts of the northern Caspian.

Discussion

The investigation indicated that no benthic macroinvertebrate species disappeared or appeared for the first time in the northern Caspian during the period of study. Thus species composition remained constant despite marked changes in environmental factors in 1980–1991 (Figure 2). Even so, the abundance of certain species fluctuated considerably during the initial stages in the rise in water-level. Moreover, total biomass increased gradually in the 1980s, as it did earlier when the water-level fell in the 1950s–1970s (Yablonskaya and Osadchikh, 1996). However, the increase in biomass before and during the present rise can be attributed to different factors. Thus in the 1950–1970s, the increase in benthic productivity was due mainly to an increase in the biomass of alien species from the Mediterranean. Their increase followed an increase in sa1inity as water-levels fell. At the same time, a decrease in the amounts of nutrients and suspended organic matter in the River Volga outflow occurred in the 1950s–1980s (Yablonskaya et al., 1974), and this led to a decrease in primary production and zooplankton biomass in the northern Caspian. The absence of a corresponding decrease in benthic biomass indicates that the changes in trophic conditions did not seem to influence benthic communities in that period.

In 1989, total phosphorus inflow from rivers was 2.6 times and nitrogen 1.5 times greater than in the 1960s. Simultaneously, there was a considerable increase in organic matter inflow, from 1.6 to 2.9 millions ton per flood (Katunin et al., 1994), and this led to increased productivity of the ecosystem and improved trophic conditions for the benthos. As a result, in the 1960s biomass of all groups of benthic invertebrates increased. Characteristically, this increase occurred mostly in the western part of the northern Caspian, i.e.

in the region directly influenced by the outflow from the River Volga. Notably, the stock of benthic-feeding fish (particularly sturgeon) greatly decreased in the 1980s; from 1980 to 1995, catches decreased from 25,000 to 2,500 ton (Ivanov, 1996). This decrease in predator pressure clearly favoured the development of benthic communities.

The increased average biomass for 1980–1991 compared to 1960–1979 was higher for freshwater and brackish species than for marine-derived species (Figures 3–5). This apparently reflected the effect of decreased salinity on benthic communities in the 1980s.

The decreased biomass of *Dreissenia polymopha polymorpha* and the replacement of this subpecies by *D. polymopha andrusovi* seems paradoxical given the lower salinity in the 1980s, since the latter is more halotolerant. Changes in the biomass of other bivalves are more easily interpreted and are probably related to reduced oxygen levels in near-bottom waters. *Cerastoderma lamarcki* is not tolerant of low oxygen concentrations, and this is not favoured by the significantly lowered oxygen content of near-bottom waters following falls in water-level (Katunin et al., 1994). It competes with *Abra ovata* and relative biomasses have changed markedly from year to year in response to environmental changes, particularly those in dissolved oxygen concentration (Romanova, 1979). When water-levels rise, *A. ovata* has a competitive advantage as it is less demanding with regard to oxygen content.

Data for 1991 clearly differ from those for other years when benthic biomass had decreased to values typicla of those for the period prior to water-level rise (62.6 g m^{-2}). This was mainly due to the marked fall in the abundance of *A. ovata* and *M. lineatus* in the deep-water zone. At the same time, an extensive development of these bivalves took place in the central Caspian. Perhaps this was because the unusually high velocity of currents from floods in 1991 carried bivalve larvae from the northern Caspian to central regions where they settled down and developed (the velocity of the flood wave fall in 1991 was 6 cm day^{-1} as opposed to 2.8 cm day^{-1} in 1990).

The abundance of Oligochaeta in the northern Caspian is closely related to the silt concentration in sediments. As noted, there was a significant increase in the inflow of organic matter into the lake the the 1990's – from 1.6 to 2.9×10^6 ton per flood (Katunin, 1992), and this probably led to increased organic matter in sediments. Characteristically, in the 1980's, the increased *N. diversicolar* biomass occurred in the eastern part only, where the impact of low salinity was less, whereas Oligochaeta abundance grew in both eastern and western parts of the northern Caspian.

Overall, the main trends in the biomass of benthic macroinvertebrates in the northern Caspian during the initial rise in water-level rise grew for the main benthic group and but there was a relative decrease in the abundance

of marine-derived Mediterranean species. However, no noticeable change in species composition took place. The rise in the abundance of the benthic fauna followed improved trophic conditions and a fall in predator pressure. Some decrease in the relative abundance of marine-derived species was related to lower salinity.

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