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ICHTHYOLOGY

Impact of the Alien Species *Mnemiopsis leidyi* A. Agassiz, 1865 on Fish of the Caspian Sea

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Abstract—The data of long-term ecological studies (1999–2014) are used for assessing the impact of a new Caspian invader *Mnemiopsis leidyi* A. Agassiz, 1865 on marine and anadromous fish species. The introduction of the ctenophore and its massive development in the Caspian Sea have mainly affected planktophagous fish, especially the most abundant species anchovy sprat (*Clupeonella engrauliformis* Borodin, 1904) and sturgeons (Family Acipenseridae). *Mnemiopsis leidyi* is one of the main negative factors preventing the restoration of the populations of Caspian fishes, especially anchovy tyulka. The critical state of the resources of the spawning parts of sturgeon populations (Family Acipenseridae) has been reinforced as a result of the massive development of *M. leidyi*.

Keywords: Caspian Sea, tyulka, invader, comb jelly, zooplankton, meroplankton

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INTRODUCTION

In 1999, with the help of underwater video recording, a new Caspian species was detected which was identified as a ctenophore *Mnemiopsis leidyi*. Afterwards, the abundance of this short-cycle eurybiont species grew explosively as a result, on the one hand, of weak competition with native species and, on the other hand, the absence of predators and parasites in the new habitat.

From 1999 to 2009, the population abundance of *Mnemiopsis leidyi* A. Agassiz, 1865 grew abruptly (235–385 fold) in the Caspian Sea, which greatly affected all the links in the food pyramid of the ecosystem. In particular, 3 years later, after the first official record of the invader in a new habitat, i.e., in 2002, the zooplankton abundance decreased 4–10 fold relative to that in 1995. In 2000–2009, in the zooplankton samples taken in the Middle and Southern Caspian, the endemic species *Eurytemora grimmi* Sars G.O., 1897 and *E. minor* Behning, 1938 ceased to be encountered. In addition, in summer, larvae of mollusks (meroplankton) disappeared in the areas of maximum density of *Mnemiopsis*, which entailed the disappearance of the mollusk *Mytilaster lineatus* Gmelin, 1791 in the southeastern Caspian Sea.

Our goal was to analyze the impact of the invader *Mnemiopsis leidyi* on the marine and anadromous fish species of the Caspian Sea.

MATERIALS AND METHODS

Data from long-term monitoring studies (2000–2014) were collected and processed by the staff of the Caspian Scientific and Research Institute of Fish Industry. During the 15 years of our studies, over 700000 specimens of *Mnemiopsis* have been analyzed.

The material was collected in sea regions with depths from 2 m (Northern Caspian) to 790 and 1025 m (Derbent and South Caspian hollows) [5]. We used Jedi, Apstein, and IKS nets for zooplankton collection. In sites with depths less than 50 m, *Mnemiopsis* was caught totally from the bottom to the surface. In the warm time, *Mnemiopsis* was caught only in the upper most productive layer (0–50 m), while in winter and spring seasons, during homothermia, it was caught in a layer of 0–100 m. Hydrological, hydrochemical, and ichthyological data were collected simultaneously.

RESULTS AND DISCUSSION

Long-term studies (2000–2009) showed that the center of the *Mnemiopsis* population is formed in particular areas of the sea: open, central part of the Northern Caspian, coastal part of the Middle Caspian, and southeastern shallow waters of the Southern Caspian. All the above regions of the sea serve as the main nursery and feeding grounds for the largest part of commercial species of marine, migratory, and semimigratory fish, mainly pertaining to families Asipenseridae, Clupeidae, and Cyprinidae [4].

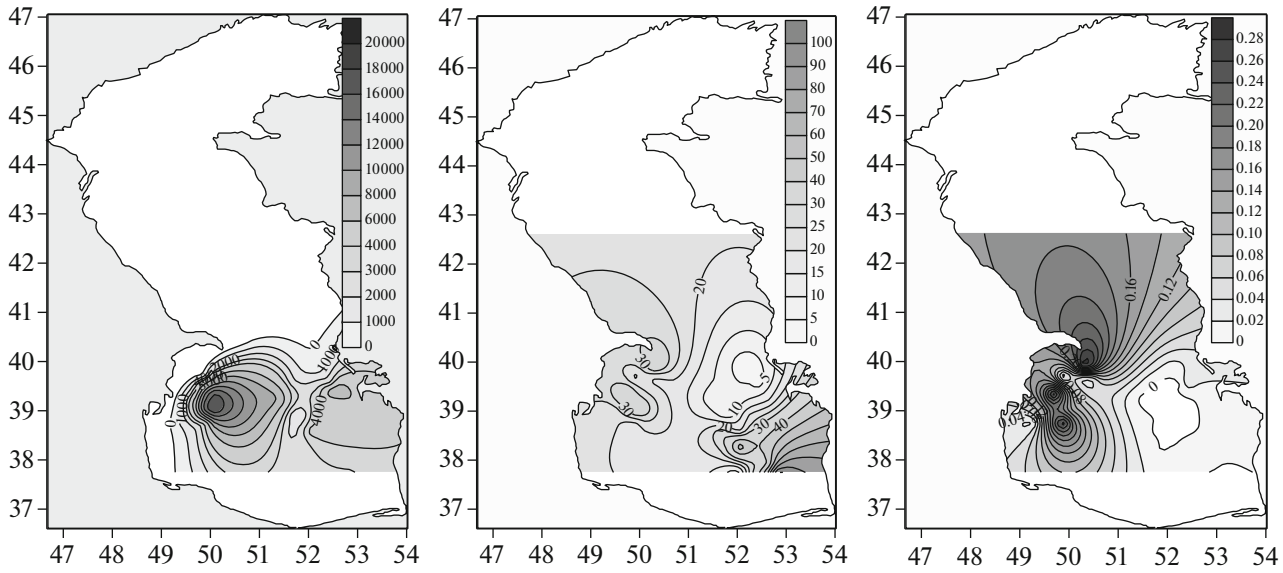

Fig. 1. Map of the distribution of *Mnemiopsis leidyi* and its main food resources in the Caspian Sea in January, 2002: (a) *Mnemiopsis leidyi*, ind./m^3; (b) zooplankton, g/m^3; and (c) meroplankton, ind./m^3.

The maximum abundance of *Mnemiopsis leidyi* was recorded in the eastern shallow waters of the Southern Caspian (Fig. 1). In 2005, the maximum density of ctenophore reached 269 ind./m^3 [4]. This well-heated shallow water area serves as the main nursery and feeding ground for the South Caspian schools of sturgeon (Family Acipenseridae), Caspian roach (*Rutilus rutilus caspicus* Yakovlev, 1870), freshwater bream (*Abramis brama* Linnaeus, 1758), common carp (*Cyprinus carpio* Linnaeus, 1758), and other valuable species of fish from the Cyprinidae family.

The largest abundance of ctenophore was recorded in the sites with depths of 15 to 25 m at the western coast of the Middle Caspian, between 42° and 44° N. In 2005, it reached 306 ind./m^3 [4]. It is noteworthy that this is a very productive region in terms of fisheries, since the rivers Terek and Sulak flow into this part of the sea, carrying out a huge amount of organic substances and nutrients into the sea.

In the summer, from July, *Mnemiopsis* was found in the sites with depths from 14 to 27 m in the central part of the Northern Caspian far away from the shore. This place serves as the feeding ground for the mature part of the populations of the North Caspian sturgeons such as starry sturgeon (*Acipenser stellatus* Pallas, 1771) and Danube sturgeon (*A. gueldenstaedtii* Brandt, 1833). The ctenophore was not encountered in the eastern part of the Northern Caspian.

Correlation analysis revealed that the biomass of *Mnemiopsis* is most closely connected with the biomass of zooplankton ($r = 0.72$) and meroplankton, in particular, larvae of mollusks ($r = -0.50$). This is also confirmed by the distribution maps of *Mnemiopsis leidyi* and its main food resources, i.e., the distribution of the ctenophore corresponds to the seasonal distribution of zooplankton and meroplankton (Fig. 1) [3].

Mnemiopsis actively grazes on zooplankton. After its introduction into the Caspian Sea, it had a considerable impact on the trophic web and fish populations in the sea. In 2000, at the stage of *Mnemiopsis* naturalization, zooplankton of the South Caspian was represented by 22 species; in 2002 it consisted of only nine species.

After 1999, in the course of *M. leidyi* naturalization, endemic species such as *Eurytemora grimmi* and *E. minor* disappeared from the zooplankton community in the Middle and Southern Caspian [9], while they had been quite abundant before the *Mnemiopsis* invasion. In 2014, the most abundant zooplankton species was *Acartia* sp., which constituted up to 91% of the total zooplankton abundance and 98% of the total biomass. It became the basic food resource of *Mnemiopsis* (Fig. 2a). As a result of the introduction of the ctenophore, the abundance of zooplankton fell, depending on the region, by 4- to 10-fold from 1999 to 2002 [9].

Since 2000, there has been a steady trend towards a reduction in the biomass of zoobenthos representatives such as Bivalvia or Polychaeta, which have a planktonic stage during larval development (Fig. 2b). In particular, in the eastern shelf of the Southern Caspian, the mollusk *Mytilaster lineatus* previously abundant in zoobenthos (≤52 g/m^2) ceased to be present in the samples [9].

In addition, *Mnemiopsis leidyi* is an active grazer on ichthyoplankton. In its gastrovascular cavity, we found fish larvae and eggs of sprats (genus *Clupeonella*),

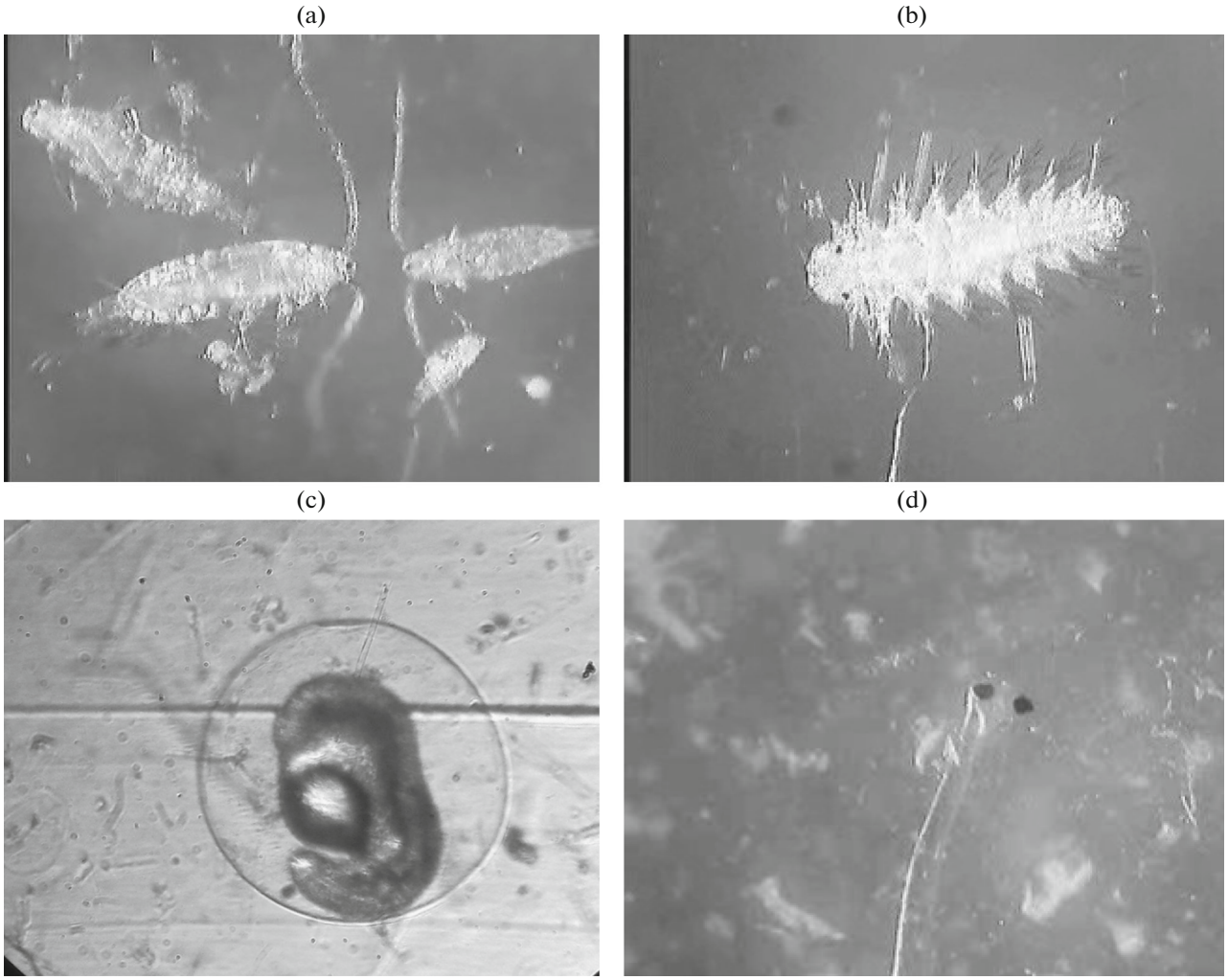

Fig. 2. *Acartia* sp. (a), larva of the ragworm (*Hediste diversicolor*) (b), spawn of the Caspian tyulka (genus *Clupeonella*), (c) and larva of the anchovy sprat (*Clupeonella engrauliformis*) (d) in the gastrovascular cavity of *Mnemiopsis leidyi* (A.M. Kamakin's photo).

shads (genus *Alosa*), and other fishes which have pelagic eggs (Figs. 2c, 2d).

Therefore, *Mnemiopsis leidyi* can affect fish populations directly via eating their eggs and larvae and indirectly through food competition.

Mnemiopsis has a considerable negative impact on planktivorous fishes (sprats and shads), especially on the most abundant species, anchovy sprat *Clupeonella engrauliformis* Borodin, 1904 [8]. Prior to the invasion of *Mnemiopsis*, *Eurytemora grimmi* and *E. minor* were the dominant species and served as the basic food resources for pelagic fishes such as sprats (genus *Clupeonella*) and shads (genus *Alosa*).

The decrease in the abundance of plankton has brought about a corresponding decline in the abundance of planktivorous fishes, especially in warm waters of the Southern Caspian, where *Mnemiopsis leidyi* displays its grazing activity throughout the year. For example, catches of Caspian sprats (genus *Clupeonella*) on the Iranian coast decreased 2.7-fold in 2002 [1, 2]. In the last decade, research catches of *Clupeonella engrauliformis* have become ~10- to 11-fold less than the "pre-ctenofore" period (Fig. 3) [8].

The impact of the invader can be traced from long-term data on catches of yearlings of anchovy sprat as one of the most numerous species of fish in the Caspian Sea. In those years when the abundance of *Mnemiopsis leidyi* increased, the research catches of yearlings of anchovy sprats declined simultaneously. The correlation coefficient (r) between these two factors was 0.40 (Fig. 4).

In the Northern Caspian, the selectivity of *Mnemiopsis*, grazing mainly on meroplankton, largely affected food resources of benthosphagous fishes. In the areas of mass concentration of *M. leidyi*, meroplankton was completely absent [9]. In 2003–2004, this was one of the main reasons for the reduction in the abundance in some species of North Caspian mollusks and barnacles (Cirripedia), resulting in changes

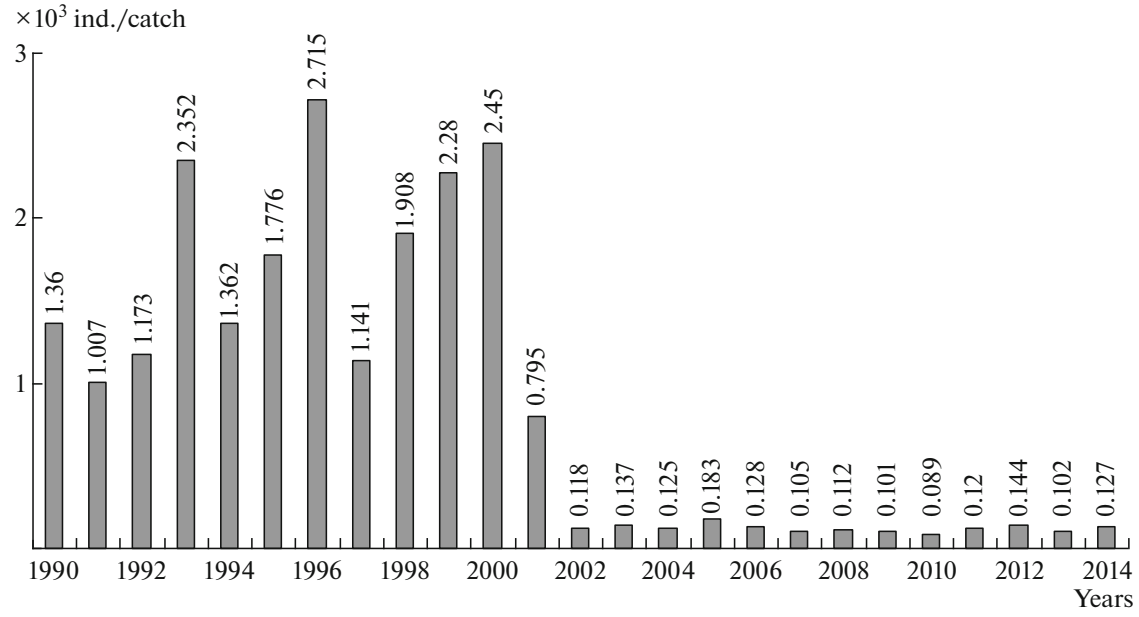

Fig. 3. Long-term dynamics of research catches of yearlings of anchovy sprats (*Clupeonella engrauliformis*) (from [8]).

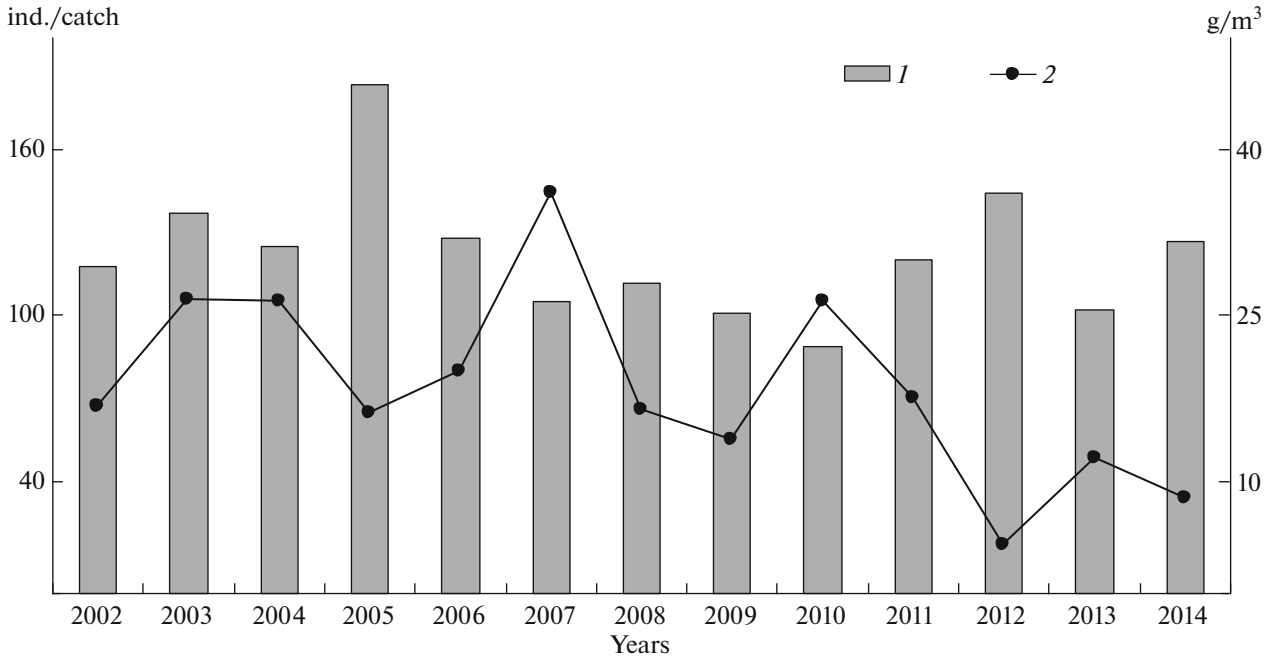

Fig. 4. Long-term fluctuations in research catches ((*1*) ind./catch) of yearlings of anchovy sprat (*Clupeonella engrauliformis*) and average biomass ((*2*) g/m^3) of *Mnemiopsis leidyi* in the Caspian Sea.

in the trophic conditions for fish feeding on mollusks, i.e., vobla, bream, carp and sturgeon.

The invasion of the ctenophore into the Caspian Sea has affected all species consuming tyulka: sea herrings (genus *Alosa*), sturgeons, and the Caspian seal (*Pusa caspica* Gmelin, 1788).

According to the data of summer sturgeon surveys, tyulka was very significant in the diet of Russian sturgeon; stellate sturgeon; and, especially, beluga (*Huso huso* Linnaeus, 1758). In the Northern Caspian in the 1990s, i.e., before the introduction of the ctenophore, the degree to which the beluga stomachs were filled with ordinary sprat (*Clupeonella delicatula* Nordmann,

Table 1. Long-term dynamics of the share of Caspian tyulka (*Clupeonella*) in the diet of sturgeon (*Acipenser gueldenstaedtii*) and stellate sturgeon (*Acipenser stellatus*) in summer, % of total mass of stomach content (from [6, 7])

Year	Northern Caspian	Middle Caspian	Southern Caspian	The whole Sea
1988	5.2 9.0	25.2 15.4	13.2 13.0	17.0 13.3
1989	5.1 4.4	35.4 29.7	27.1 28.0	18.8 15.1
1990	3.7 0	65.6 41.8	48.6 15.7	35.3 14.9
1993	3.4 6.4	29.2 4.8	25.3 0	14.3 6.4
1998	46.4 0	0.8 32.8	11.7 7.0	11.7 13.3
1999	2.2 5.5	2.6 0	2.6 0	2.6 1.8
2000	0 1.5	2.6 0	0 0	– –
2001	1.0 0	0 0	0 0	– –
2002	1.0 0	1.6 2.8	1.7 23.8	1.3 0.6

Sturgeon is shown above the line, and stellate sturgeon is shown under the line.

1840) averaged 2.2‰ [9]. After the introduction of the ctenophore, this index decreased to 0.1‰ [6, 7].

The role of tyulka was especially high in the feeding of sturgeons in the middle and southern parts of the sea. In these areas, tyulka constituted 40% in the fish diet. In the diet of sturgeons and stellate sturgeons, the content of tyulka was constantly high in the winter and spring periods and reached 20–40% (see Table 1) [6, 7].

In 2001, after the mass death of Caspian tyulka, its abundance was restored very slowly, owing to the effects of *Mnemiopsis leidyi*, which is still one of the main factors hindering the restoration of the anchovy sprat population.

CONCLUSIONS

Ctenophore *Mnemiopsis* is an active planktophagous species. After introduction into the Caspian Sea, it had a considerable impact on the trophic structure and state of the populations of Caspian fish owing to its high abundance, strong food competition, and direct consumption of fish eggs and juveniles at early stages of development [1, 2]. The ctenophore preferentially grazes on meroplankton. As a result, since 2000 there has been a steady trend towards a reduction in the biomass of zoobenthos species that have a planktonic larval stage in their life cycle. The ctenophore *Mnemiopsis* had negative impact primarily on planktophagous fishes (Caspian tyulka (genus *Clupeonella*) and Caspian Sea herrings (genus *Alosa*)). A reduction in the abundance of plankton brought about a decrease in planktophagous fishes. In the Northern Caspian, the high abundance of *Mnemiopsis leidyi* preferring meroplankton has largely affected the food resources of benthosphagous fishes (vobla, bream, and carp) and sturgeons due to a reduction in the abundance of benthic organisms (bivalve mollusks (Bivalvia) and polychaete (Polychaeta), which have a planktonic larval stage in their life cycle. The decrease in the abundance of Caspian tyulka as a result of food competition with the ctenophore greatly affected the food resources of the Russian sturgeon; stellate sturgeon; and, especially, white sturgeon, since the Caspian sprat have always played a significant role in their diet.

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