Research Letter

Increased Chlorophyll Levels in the Southern Caspian Sea Following an Invasion of Jellyfish

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A significant correlation was observed between satellite derived chlorophyll a (Chl a) concentrations and the biomass of the invasive comb jellyfish Mnemiopsis leidyi in the southern Caspian Sea. By consuming the herbivorous zooplankton, the predatory ctenophore M. leidyi may have caused levels of Chl a to rise to very high values (≈9 mg m⁻³) in the southern Caspian Sea. There might also be several other factors concurrent with predation effects of M. leidyi influencing Chl a levels in this region, such as eutrophication and climatic changes which play major roles in nutrient, phytoplankton, and zooplankton variations. The decrease in pelagic fishes due to overfishing, natural, and anthropogenic impacts might have provided a suitable environment for M. leidyi to spread throughout this enclosed basin.

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The Caspian Sea is the largest inland water body in the world sustaining large stocks of small commercially important zooplanktivorous, pelagic fish. In such ecosystems, a consistent, significant decrease in numbers of grazing zooplankton would be expected to result in a decrease in pelagic fish stocks and their predators.

Mnemiopsis leidyi is a highly fecund comb jelly feeding extensively on zooplankton. The main diet of this ctenophore in the southwestern Caspian Sea was found to be copepods (~45%) during May 2000–March 2001 [1], as found previously in the Black Sea [2]. Predation impacts of M. leidyi on zooplanktic prey organisms have been previously demonstrated in its native waters, the western Atlantic [3], and in introduced regions [4, 5]. Furthermore, a recent study based on feeding experiments in the Caspian Sea suggested that the predation pressure of M. leidyi alone would be sufficient to suppress available stocks of zooplankton within a short period (1 day in summer and 3–8 days during winter/spring) [6] and thus would allow phytoplankton biomass to increase.

In the late 1990s, M. leidyi was transported into the Caspian Sea [5], possibly in ballast water [5] and spread throughout the Caspian Sea within a few years [1, 5, 7, 10]. Overfishing, eutrophication, and climatic changes (such as global warming) have been suggested as triggering factors of the blooms of jellyfish in both native and introduced waters [11–14]. Native predators (e.g., goby species [15]) of M. leidyi in the Caspian Sea did not appear to be as efficient as B. ovata, which feeds almost exclusively on M. leidyi [16], in the Black Sea, in consuming M. leidyi biomass [17].

At the end of the 1991–2000 period, in which relatively good recruitment and high spawning-stock biomass of anchovy kilka were recorded, fishing mortality (1.8 y⁻¹) peaked in 1999 [15], which might have made kilka fish stocks vulnerable to external stress. Following the period of intensive overfishing and peak levels of M. leidyi (~900 g m⁻² in 2001), a sharp decrease in fish catch data was observed [5]. M. leidyi has already been suggested as the primary reason for the dramatic recruitment failure of anchovy kilka from 2001 to 2004 in the Caspian Sea [15]. Other possible factors in the decline in kilka stocks could be related to natural (release of toxic gases by the activation of seismic plates [15], oil seeps from mud volcanoes [18]) and anthropogenic sources (e.g., oil leakage from petroleum industry [19]).
Despite the substantial decreases in zooplanktivorous fish and still available phytoplankton biomass (inferred from Chl \(a\) levels), sharp declines in the zooplankton abundance, particularly in late summer-early autumn, could be related to predation by \(M.\) leidyi in our study (see Figure 1). When the surface waters cooled in winter, \(M.\) leidyi biomass decreased substantially and a limited recovery of zooplankton abundance was observed. The average zooplankton abundance in the summers and autumns of 2001 and 2002 was one order of magnitude lower compared to the period before \(M.\) leidyi invasion (see Table 1).

Before the \(M.\) leidyi invasion, the minimum and maximum monthly composite Chl \(a\) levels in the southern Caspian were in October 1997 and in December 1998, respectively, (see Figure 1) but when \(M.\) leidyi spread into the Caspian, Chl \(a\) levels gradually increased and reached extremely high levels in August 2001 contemporaneous with the highest recorded \(M.\) leidyi biomass and the lowest zooplankton abundance (see Figure 1). According to statistical analyses, in addition to there being a significant, positive linear relationship between levels of \(M.\) leidyi and Chl \(a\) (Pearson test, \(r = +0.6, t = 4.5, df = 40, P = .000005\)), there was also a significant change in the seasonal cycle of Chl \(a\) concentration, that is, the peak occurred in winter-spring before \(M.\) leidyi invaded and in late summer afterwards (see Figure 1 and also see supplementary material available at

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**Table 1:** Zooplankton (>100 \(\mu\)m) and phytoplankton quantities before and after \(Mnemiopsis leidyi\) invasion in the southern Caspian Sea (±standard deviation).

<table>
<thead>
<tr>
<th></th>
<th>Before (M.) leidyi</th>
<th>Period (reference)</th>
<th>After (M.) leidyi*</th>
<th>Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooplankton Abundance ((\times10^5 \text{ ind} \cdot \text{m}^{-2}))</td>
<td>5.1 ± 3.7</td>
<td>1994 summer [8]</td>
<td>0.19 ± 0.19</td>
<td>2001 summer</td>
</tr>
<tr>
<td></td>
<td>2.8 ± 1.3</td>
<td>1995 autumn [8]</td>
<td>0.55 ± 0.42</td>
<td>2001 autumn</td>
</tr>
<tr>
<td></td>
<td>3.1 ± 2.2</td>
<td>1996 summer [8]</td>
<td>0.52 ± 0.26</td>
<td>2002 summer</td>
</tr>
<tr>
<td></td>
<td>4.6 ± 1.9</td>
<td>1996 autumn [8]</td>
<td>0.28 ± 0.10</td>
<td>2002 autumn</td>
</tr>
<tr>
<td>Phyttoplankton abundance ((\times\text{million cells} \cdot \text{m}^{-3}))</td>
<td>14.9</td>
<td>1962 summer [9]</td>
<td>108 ± 99</td>
<td>summer-autumn 2001</td>
</tr>
<tr>
<td></td>
<td>17.2</td>
<td>1975 summer [9]</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>8.8</td>
<td>1976 summer [9]</td>
<td>34 ± 71</td>
<td>summer-autumn 2002</td>
</tr>
</tbody>
</table>

*Present study (see methods in Supplementary Material). [8]: from Mazandaran region, the zooplankton sampling and analyses methods were the same as in the present study; [9]: from Southern Caspian Sea.
Invasive species have caused profound ecological and economic effects, some of which have been confirmed experimentally, for example, in mesocosm manipulations [32]. Certainly approaches of using correlation to infer the cause and impacts have also contributed to elevated Chl $a$ levels in the Caspian Sea, associated with the effects of eutrophication.

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REFERENCES


