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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 ($\sim 9\,\mathrm{mg\,m^{-3}}$) 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.

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 ($\sim$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 ($1.8\,\mathrm{y^{-1}}$) 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* ($\sim 900\,\mathrm{g\,m^{-2}}$ 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]).

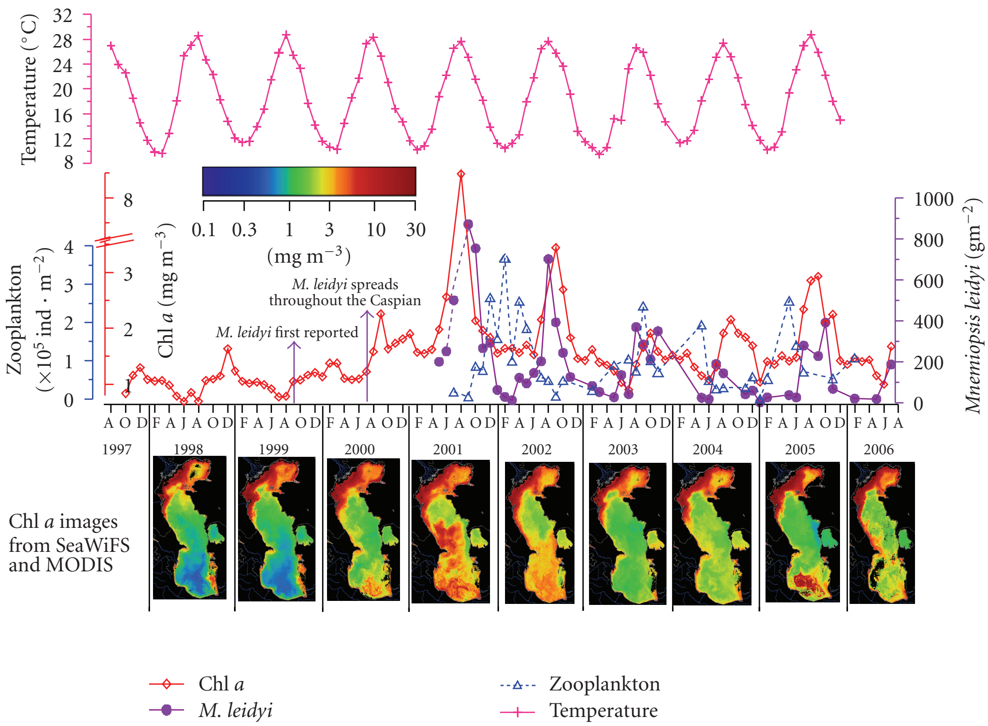

FIGURE 1: Spatiotemporal distribution of Chl *a* concentration (mg m^{-3}, note the broken scale here), zooplankton abundance (ind · m^{-2}), *Mnemiopsis leidyi* biomass (g m^{-2} values for June and August 2001 are from Shiganova et al. [7]), and sea surface temperature (°C) obtained from NOAA in the Caspian Sea. Note the strong difference in Chl *a* distributions (as seen from satellite during a warm period, September) before (1998 and 1999) and after *Mnemiopsis leidyi* impact (2001 and 2006) in the lower section of the figure.

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

	Before *M. leidyi*	Period (reference)	After *M. leidyi**	Period
Zooplankton Abundance (×10^5 ind · m^{-2})	5.1 ± 3.7	1994 summer [8]	0.19 ± 0.19	2001 summer
	2.8 ± 1.3	1995 autumn [8]	0.55 ± 0.42	2001 autumn
	3.1 ± 2.2	1996 summer [8]	0.52 ± 0.26	2002 summer
	4.6 ± 1.9	1996 autumn [8]	0.28 ± 0.10	2002 autumn
Phytoplankton abundance (×million cells m^{-3})	14.9	1962 summer [9]	108 ± 99	summer-autumn 2001
	17.2	1975 summer [9]	—	—
	8.8	1976 summer [9]	34 ± 71	summer-autumn 2002

* 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.

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 doi://10.1155/2007/85642 for methods and statistical analyses). Phytoplankton cell abundance was also much higher between 2001 and 2002, compared to years when *M. leidyi* was absent (see Table 1). Chl *a* concentrations during the cooler months fell when *M. leidyi* levels had also decreased.

Inorganic nutrient concentrations were reported to be low according to a few available publications in the southern Caspian Sea [20, 21]. However, it was also noted that Iranian lagoons and coastal regions have been steadily polluted with anthropogenic sources (fertilisers and pesticides used in agriculture and increased nutrient load of river flows due to deforestation of woodland) since the early 1980s [22–24]. Thus, simultaneous rises in nutrient concentrations and *M. leidyi* biomass might also have contributed to increases in Chl *a* values.

Unfortunately, it is difficult to assess the impacts of eutrophication and climate on phytoplankton and zooplankton abundance in the Caspian Sea due to a limitation in data availability. In the Black Sea, Oguz [25] suggested that severity of winters in 1992 and 1993 could cause an abrupt decrease of mesozooplankton and *M. leidyi* when fish stocks were at the lowest level and phytoplankton biomass was very high. Bilio and Niermann [13] also emphasized the possible effects of hydrological and meteorological regimes in the northern hemisphere on phyto and mesozooplankton changes. However, the relatively warm and stable temperature regime in the region [25](see also Figure 1) is unlikely to explain Chl *a* variations observed herein.

The reduction in herbivory due to extremely low levels of zooplankton is a possible factor determining enormous levels of Chl *a* observed in the SeaWiFS data. High turnover of nitrogen and phosphorus by *M. leidyi* excretion [26] would also contribute to this consistently high phytoplankton growth. If the relation between *M. leidyi* and phytoplankton (Chl *a*) is compared in two different seas, the Caspian and Black Seas; it is observed that *M. leidyi* reached $\sim$2 times higher maximum biomass ($2000\,\mathrm{g\,m^{-2}}$ in 1990) in the Black Sea [5] than in the Caspian Sea, while Chl *a* concentrations were $\sim$10 times lower in the former sea (basin-scale Chl *a* $\sim 1\,\mathrm{mg\,m^{-3}}$ [27]) than the latter. Small size composition of *M. leidyi* and the dominance of juvenile ctenophores [6, 28] might have played a role in faster removal of zooplankton [3, 6] from the Caspian Sea leading to high phytoplankton biomass. In addition, distinct hydrological, physical, chemical (e.g., nutrients originating from anthropogenic and natural sources), and biological characteristics might have also led to differences in Chl *a* concentrations in these two seas.

There have been a large number of very marked changes in planktonic systems around the World in recent decades [29]. While there is clearly a level of speculation in the approach of using correlation to infer the cause and impacts of such changes, correlation analysis has been widely used before and has certainly provided compelling evidence for gelatinous zooplankton having a variety of ecosystem effects [30, 31], some of which have been confirmed experimentally, for example, in mesocosm manipulations [32]. Certainly invasive species have caused profound ecological and economic problems in many ecosystems around the world. One of these species, *M. leidyi,* might have contributed to elevated Chl *a* levels in the Caspian Sea, associated with the effects of eutrophication.

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