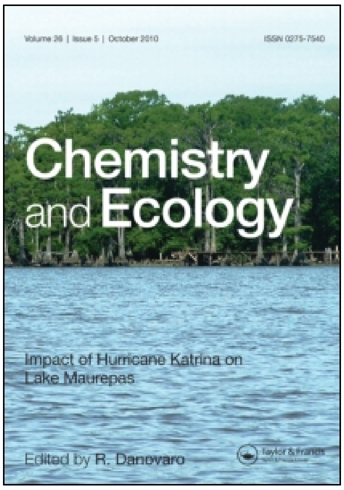

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Spatial and temporal distribution of macronutrients and phytoplankton before and after the invasion of the ctenophore, *Mnemiopsis leidyi*, in the Southern Caspian Sea

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Spatial and temporal distribution of macronutrients and phytoplankton before and after the invasion of the ctenophore, *Mnemiopsis leidyi*, in the Southern Caspian Sea

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The spatio-temporal distribution of nutrients and phytoplankton along the Iranian coast of the Southern Caspian Sea (CS) was investigated by comparing two different periods, namely Phase I (1996–1997), representing the period before the introduction of the ctenophore, *Mnemiopsis leidyi*, into the system, and Phase II (2005), the period after the introduction. The results showed that nutrient concentrations (with the exception of dissolved silicate) in the subsurface water were significantly higher during Phase II ($p < 0.001$), which may be attributed to vertical mixing and the presence of the ctenophores. Long-term data collected from 1994 to 2005 also confirmed these results. As with most other marine ecosystems, the Bacillariophyta (diatoms) was found to be the most dominant phytoplankton group. However, during Phase II (i.e. after the introduction of the ctenophores), a significant increase in the abundance of the Cyanophyta was recorded, especially during summer and autumn. The average abundance of phytoplankton after the introduction of the ctenophores was significantly higher (4.2 fold, $p < 0.05$). Similar trends have been observed in the Narragansett Bay and in the Black, Azov and North Caspian Seas, all of which were related to the predation on zooplankton (the primary consumer of the phytoplankton) by the ctenophores.

Keywords: nutrients; phytoplankton; invasive species; ctenophores; Caspian Sea; Iran

1. Introduction

The Caspian Sea (CS) is well known for its rich resources such as huge oil and natural gas reserves, high biological diversity and its traditional fishery, particularly involving the caviar-producing sturgeons. The CS is surrounded by Russia, Kazakhstan, Turkmenistan, Iran, and Azerbaijan (Figure 1). With a volume of 78,000 km^3 and a surface area of 3.8×10^5 km^2, it is the largest inland water body on earth [1].

Nutrient inputs into the CS are mainly contributed by the Volga, Ural, Terek, Sulak, Samur and the Kura Rivers in the northern and western regions. The main inflow is from the Volga River (average of 86%), which discharges into the northern basin [2,3], where it carries more than 80% of the biogenic and organic compounds [4]. Leonov and Stygar [5] reported that the waters

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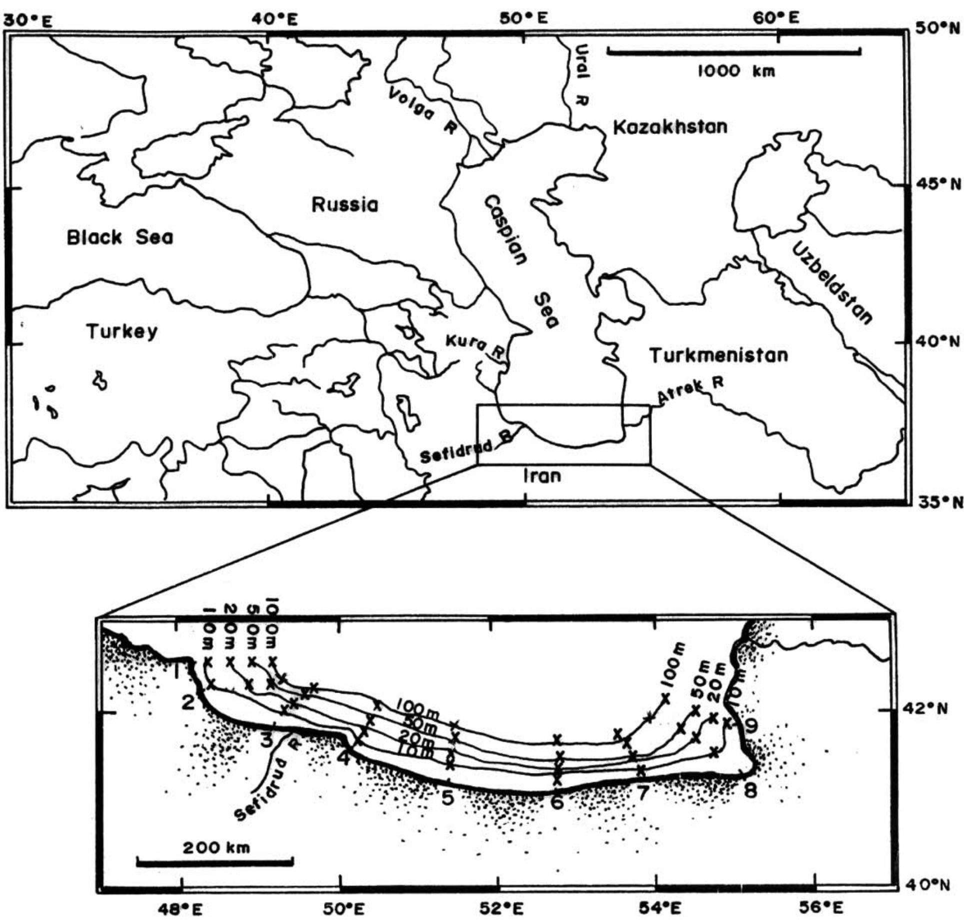

Figure 1. The Caspian Sea mapped with five littoral countries (top) and sampling stations in the Southern Caspian Sea – Iranian coast (bottom). The 10, 20, 50 and 100 m labels show the isobaths where the stations are located; numbers show the nine sampled transects. In Phase I we collected samples in all nine transects but in Phase II only in transect 1, 2, 3, 5, 6, and 7.

of the Middle and South Caspian Sea exhibit higher salinity (up to 13 psu) and lower nutrient concentrations. Transport of nutrients from the productive northern basin to the middle is small, and evens less to the southern basin [5]. Nutrient input into the Middle and South basins relies mainly on internal recycling with small contributions from rivers and rainfall (less than 1% for the N and P compounds) [5]. In the Southern CS-Iranian coastal waters (less than 10 m depth), dissolved nutrient concentrations depend upon freshwater influx (such as from the Sefidrud River), which is influenced by meteorological conditions. When some levels of the water column become impoverished in nutrients (due to high phytoplankton activities), available regenerative nutrients are controlled mainly by the vertical mixing [6–8].

During this study, five phytoplankton groups were recorded. The most dominant is the Bacillariophyta (diatom), while the least dominant group is the Euglenophyta. In the North basin, Cyanophyta seems to have increased in abundance during the past decade which may be related to the problem of eutrophication [2]. Pyrrophyta was found to be dominant in the Middle basin. Annual cycle of phytoplankton dominance were found to vary with regions. For example, in the South Caspian Sea (under undisturbed conditions) Bacillariophyta proliferation was followed by Pyrrophyta and Chlorophyta.

During the last two decades of the twentieth century, the ctenophore, *Mnemiopsis leidyi* was reported to have 'invaded' the Black, Azov, Marmara and the Aegean Sea, and recently (late 1999) also the Caspian Sea. *Mnemiopsis leidyi* has tremendous impact on the Caspian ecosystem due to its preying on the herbivorous zooplankton, its high excretion of nutrients and secretion of mucous [4]. Ivanov and Kideys suggested that the introduction of *M. leidyi* into the Caspian Sea had resulted in an increase in phytoplankton abundance [9,10].

Mnemiopsis leidyi can be found in its native habitats of the temperate to subtropical regions along the Atlantic coasts of North and South America such as in Narragansett, Chesapeake, and Biscayne Bay as well as in the Gulf of Mexico. The seasonal abundance of *M. leidyi* seems to be influenced by temperature, salinity, food availability and predators [11]. In the CS, with its subtropical conditions and moderate salinity, the temporal distribution of *M. leidyi* is similar to that of Chesapeake Bay and the Sea of Azov.

It should be noted that most studies on the physico-chemical parameters and phytoplankton in the CS have focused on the fertile waters of the North CS [10] but relatively few studies have been done for the Southern CS.

The main objective of this study is to compare nutrient levels and phytoplankton abundance during two periods, namely 1996–1997 (Phase I, representing the pre-invasion ecosystem) and 2005 (Phase II as a post-invasion ecosystem) in the Iranian coast of the Southern CS. A link between nutrient concentrations and phytoplankton abundance will be established.

2. Materials and methods

2.1. *Sampling and environmental parameters*

Four cruises were carried out in the Southern CS on board the R/V *Gilan* during the four seasons of the year. During Phase I (1996–1997) (representing the pre-invasion ecosystem), samples were taken during spring (2–20 May 1996), summer (1–22 August 1996), autumn (9–27 November 1996) and winter (5–28 February 1997). During Phase II (2005) (representing a post-invasion ecosystem), sampling was carried out in winter (10–25 February 2005), spring (8–22 May 2005), summer (25 July–9 August 2005), and autumn (14–28 November 2005). Samplings were carried out at 36 stations (nine transects) during Phase I and 24 stations (six transects) during Phase II (Figure 1). Along each transect, four stations were located at depths of 10, 20, 50 and 100 m.

In addition, seasonal data collected during a long-term study (although at a smaller scale) along the coast (10 m depth) were also considered. The nutrient and biological data used during the long-term study were adopted from: EACS for data from 1994 to 1995 (288 samples) [6,7]; from Laloei for data from 1998 to 1999 (72 samples) [12]; from Hashemian for data from 2000 to 2003 (72 samples) [13] and from Tabari for the 2004 data (380 samples) [14].

Water samples were taken using a 2-litre Ruttner sampling bottle at subsurface layer (30–50 cm). Water temperature was measured using a reverse thermometer (Hydrobios, Kiel-Holtenau, Germany) while salinity was determined using a salinometer (GM65, Moscow, Russia). The samples for nutrient analysis were frozen at −20 °C and taken ashore to the laboratory at EACS (Ecological Academy of Caspian Sea) and FRG (Fishery Research of Gilan) Centre. Inorganic nutrients (phosphate, ammonia and nitrate) were measured with a spectrophotometer system using standard analytical protocol [15–17]. Silicate was measured according to [18]. Dissolved inorganic nitrogen (DIN) in this context represents the sum of nitrate, nitrite and ammonia. Total nitrogen and phosphorus were obtained following the persulphate digestion procedure of [19]. Dissolved organic nitrogen (DON) was calculated as the difference between total nitrogen and DIN concentrations in the filtrate, and dissolved organic phosphorous (DOP) as total phosphorus minus the dissolved inorganic phosphorus concentration [20]. The detection limits for ammonia, nitrate, total nitrogen, phosphate, total phosphorous, and silicate determination were 0.02, 0.30, 0.30, 0.02, 0.025 and 0.20 μM, respectively.

The samples for phytoplankton analysis were collected in 0.5 litre bottles and preserved by adding buffered formaldehyde to yield a final concentration of 2%. The samples were let to settle for at least 10 days following which they were concentrated to about 30 ml by sedimentation and centrifugation [21]. A subsample of 0.1 ml was analysed using a Sedgewick–Rafter counting cell under a light microscope (Nikon, AFX-DX, Japan) (coverslip 24 × 24 mm and with magnifications of 100, 200, 400×) [22–24]. Phytoplankton taxonomic identification was carried out following [25–29]. The volume of each cell was estimated based on the procedure as suggested in [17,22,23]. Finally, the volume values were converted to 1 m^3 biomass. Phytoplankton diversity was calculated using the Shannon-Weaver diversity index [24,30].

2.2. *Statistical analyses*

For all data sets, the null hypothesis of homogeneity of variances (Levene's test) could be rejected. Seasonal and annual differences in chemical and biological variables were tested by one way ANOVA followed by the Duncan's test as well as T-test. The relationship between variables was studied by Pearson's correlation analysis. Statistical analyses were carried out at a significant level of $\alpha = 0.05$ [31].

3. Results

During Phase I (1996–1997), water temperature in the study area was found to vary with seasons, with values of 13.3–25.0° C during spring; 17.9–28.9° C during summer; 15.8–18.7° C during autumn and 9.9–13.7° C during winter. A similar trend was observed during Phase II (2005). Water temperature was also found to increase in the direction from west to east. Salinity values varied from 11.33 to 13.16 psu during Phase I and 10.82 to 13.51 psu during Phase II.

Nitrate concentrations were found to be significantly higher during Phase II, compared to Phase I ($p < 0.001$). The highest nitrate concentration was recorded in spring followed by a significant decline in summer. The highest nitrate concentrations were 5.90 μM and 9.50 μM during Phase I and Phase II, respectively. The difference in ammonium concentrations between the two sampling periods was found to be significant ($p < 0.05$). The mean ammonium concentration during Phase II was almost 1.5-fold higher than during Phase I (Table 1). The lowest ammonium concentration was recorded in spring and summer (Phase I) and spring (Phase II) due to the proliferation of phytoplankton. Ammonium concentration increased towards summer and peaked in autumn, most probably due to the high remineralisation of organic compounds after the spring development period. As with the other nitrogen compounds, ammonium concentration varied significantly with the seasons for both periods ($p < 0.001$). The difference in the mean DIN concentrations among seasons were also found to be significant ($p < 0.05$) for both sampling periods. During spring of Phase I, DIN concentrations were lower than 1.00 μM. In autumn and winter, high DIN concentration spread evenly across the Southern CS with a mean of 1.16 μM and 2.66 μM respectively. During Phase II, mean DIN concentrations were at least three-fold higher than those observed in Phase I ($p < 0.001$) (Tables 1 and 2). This study also observed that concentrations of DON vary with seasons for both sampling periods ($p < 0.05$). During Phase I, the lowest DON concentrations were recorded in summer and the highest in winter. During Phase II however, the lowest value was recorded in autumn and the highest in summer. It was observed that during the two main sampling periods, more than 90% of the total nitrogen was made up of DON (except in summer of Phase I). During Phase I of the study, the DON concentrations along the Iranian

Table 1. Descriptive statistics for the nutrient concentrations (μM) (mean ± SD) at different seasons between two sampling periods during Phase I (1996–1997) and Phase II (2005) in the southern Caspian Sea – Iranian coast.

		Phase I					Phase II				
Factors		Spring	Summer	Autumn	Winter	Annual	Spring	Summer	Autumn	Winter	Annual
NH_4^+	Mean	0.95	0.52	0.56	1.71	0.978	0.70	1.39	2.90	1.77	1.46
	SD	1.31	0.37	0.73	0.98	0.979	0.50	1.22	1.75	0.78	1.28
	n	36	36	36	36	144	29	30	23	25	107
NO_3^-	Mean	1.62	0.58	0.61	0.95	0.93	1.91	2.13	1.80	1.82	1.96
	SD	1.54	0.41	0.42	0.92	1.02	1.70	1.53	0.41	0.52	1.35
	n	36	36	36	36	144	29	30	23	25	107
DIN	Mean	2.70	1.10	1.16	2.66	1.95	2.61	3.54	4.71	3.68	3.43
	SD	2.14	0.57	0.65	1.53	1.60	1.67	2.35	2.00	0.94	2.00
	n	36	36	36	36	144	29	30	23	25	107
DON	Mean	37.4	10.4	33.1	41.8	30.7	47.4	52.4	44.6	44.6	48.5
	SD	22.1	8.1	22.8	23.6	23.4	9.8	9.0	8.1	7.4	9.4
	n	36	36	36	36	144	29	30	23	25	107
DIP	Mean	0.38	0.33	0.34	0.62	0.42	0.60	0.77	1.07	0.62	0.74
	SD	0.27	0.26	0.17	1.23	0.66	0.30	0.46	0.40	0.19	0.39
	n	36	36	36	36	144	29	30	23	25	107
DOP	Mean	0.64	0.75	0.39	0.67	0.61	0.98	1.20	1.36	0.86	1.10
	SD	0.52	0.6	0.23	1.24	0.74	0.52	0.60	0.43	0.56	0.56
	n	36	36	36	36	144	29	30	23	25	107
DSi	Mean	10.6	7.0	8.4	6.5	8.11	7.9	6.1	10.5	9.3	7.80
	SD	5.1	4.2	4.9	2.7	4.61	2.3	2.2	2.7	2.4	2.82
	n	36	36	36	36	144	29	30	23	25	107

SD, standard deviation; *n*, number of samples.

Table 2. Statistical analysis (T-test) of the nutrients (by season) between two sampling periods during Phase I (1996–1997) and Phase II (2005) in the Southern Caspian Sea – Iranian coast.

Factors	Spring 1996 versus Spring 2005	Summer 1996 versus Summer 2005	Autumn 1996 versus Autumn 2005	Winter 1997 versus versus Winter 2005	1996–1997 versus 2005
NH_4^+	NS	+(∗∗∗)	+(∗∗∗)	NS	+(∗∗∗)
NO_3^-	NS	+(∗∗∗)	+(∗∗∗)	+(∗∗∗)	+(∗∗∗)
DIN	NS	+(∗∗∗)	+(∗∗∗)	+(∗∗)	+(∗∗)
DON	+(∗∗)	+(∗∗∗)	+(∗∗)	NS	+(∗∗∗)
DIP	+(∗∗∗)	+(∗∗∗)	+(∗∗∗)	NS	+(∗∗∗)
DOP	+(∗∗)	+(∗∗∗)	+(∗∗∗)	NS	+(∗∗∗)
DSi	−(∗∗)	NS	NS	+(∗∗∗)	NS

NS, non-significant; ∗∗, significant (0.05); ∗∗∗, significant (0.01); (+) means increase from Phase I to Phase II; (−) means decrease from Phase I to Phase II.

coast of the CS was found to decrease from west to east (except during summer). Throughout the year, the DON concentrations were always in excess of 20 μM, except during summer when lower values of less than 15 μM were recorded. During Phase II, the DON concentrations were generally higher with values of more than 30 μM. The DIP concentrations nearly doubled during Phase II (Table 1). During Phase II, the DIP concentrations varied with seasons but not so during Phase I. During Phase II the minimum concentration of DIP was recorded in spring and maximum in autumn ($p < 0.05$). The DOP concentrations were found to be significantly higher during Phase II (Table 1). Like DIP, DOP concentrations also showed no seasonal dependency during Phase I, but fluctuated with seasons during Phase II, with a minimum in winter and maximum in autumn ($p < 0.05$). The present study observed no significant difference in the concentrations of dissolved silicate (DSi) between the two sampling periods (Table 2). However, differences in DSi concentration among seasons were found to be significant ($p < 0.05$). During Phase I, the minimum and maximum DSi concentrations were recorded in winter and spring, respectively, while during Phase II, the minimum value was recorded in summer and maximum in autumn.

Tables 1 and 2 summarise the statistical analysis for nutrient concentrations during Phase I and Phase II. Based on average annual values, all nutrients (except DSi) showed significantly higher concentrations during Phase II. The mean values of DON, DOP and DIP were significantly higher in spring, summer and autumn of Phase II compared with the same seasons during Phase I, while inorganic nitrogen was significantly higher in summer, autumn and winter of Phase II (NH_4^+ only in summer and autumn) (Table 2).

Table 3 elaborates how the mean annual values of nutrient concentrations vary from the shallower stations (10 m depth) to the offshore stations (100 m depth). During Phase I, it was found that the mean annual nutrient concentrations did not vary significantly with station depth. However, significant differences among the nine transects were observed for DON, DOP, DIP and DSi. The transects along the west coast, especially those near the Sefidrud River, recorded higher DON and DOP concentrations but no significant difference was recorded for NO_3^-, NH_4^+, and DIN. During Phase II of the study it was observed that the mean annual nutrient concentrations were not influenced by water depth or transect ($p > 0.05$). The long-term measurements of the nutrient concentrations (1994–2005) showed similar trends, although with some exception (Figure 2). Higher concentration for all nutrients (except for NH_4^+ and DSi) was recorded during 2000–2005 (Figure 3).

The phytoplankton abundance in the Southern CS during Phase I and Phase II displayed a strong seasonal variability (Figure 4). During spring and autumn, high phytoplankton abundance was recorded which may be a consequence of the upwelling of nutrient-rich water from the bottom layer. Phytoplankton abundance was found to decline sharply during summer and winter.

Table 3. Spatial variability of nutrient concentrations (NH_4^+, NO_3^-, DIN, DON, DIP, DOP, DSi, μM) at subsurface water from inshore (10 m depth) to offshore (100 m depth), during Phase I (1996–1997) and Phase II (2005) in the Southern Caspian Sea Iranian coast; mean annual values ±SD are reported.

Water depth	NH_4^+	SD	NO_3^-	SD	DIN	SD	DON	SD
Phase I								
10 m	1.38	0.64	1.00	0.94	2.38	1.35	32.1	14.81
20 m	0.98	0.50	1.07	0.68	1.96	0.93	32.7	14.92
50 m	0.66	0.18	0.70	0.23	1.41	0.52	28.2	13.76
100 m	0.92	0.65	0.94	0.46	1.96	1.13	28.3	12.57
	DIP	SD	DOP	SD	DSi	SD		
10 m	0.42	0.05	0.63	0.11	9.30	2.14		
20 m	0.36	0.06	0.50	0.21	7.90	2.19		
50 m	0.32	0.05	0.60	0.26	7.50	1.76		
100 m	0.38	0.12	0.54	0.16	7.70	2.56		
Phase II								
10 m	1.90	1.05	2.62	0.59	4.52	1.31	49.2	3.72
20 m	1.83	0.56	1.76	0.28	3.59	0.83	49.0	7.19
50 m	1.37	0.12	2.02	1.26	3.39	1.36	46.1	2.92
100 m	1.98	0.53	2.31	0.22	4.29	0.57	43.9	2.20
	DIP	s.d.	DOP	s.d.	DSi	s.d.		
10 m	0.69	0.13	1.03	0.45	8.96	0.85		
20 m	0.80	0.08	1.04	0.24	8.18	0.24		
50 m	0.72	0.12	1.13	0.19	8.40	1.08		
100 m	0.66	0.09	1.17	0.11	7.06	2.66		

SD, standard deviation.

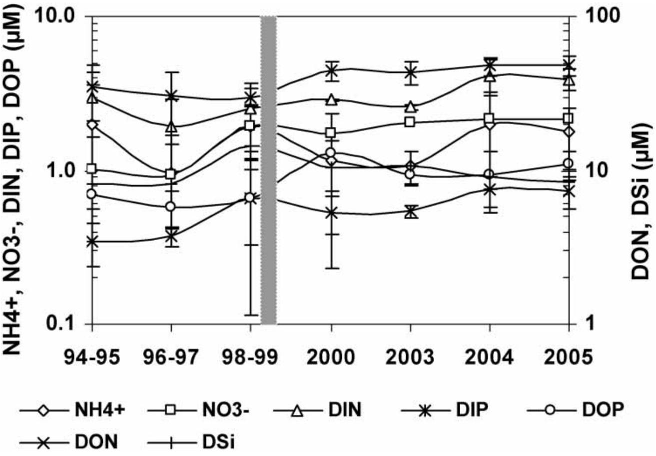

Figure 2. Long-term trend of nutrient concentrations (NH_4^+, NO_3^-, DIN, DON, DIP, DOP, DSi, μM) from 1994 to 2005 in the Iranian coastal area of the Caspian Sea: mean annual values ± STD. The grey bar indicates the time when the ctenophores have been introduced to the area.

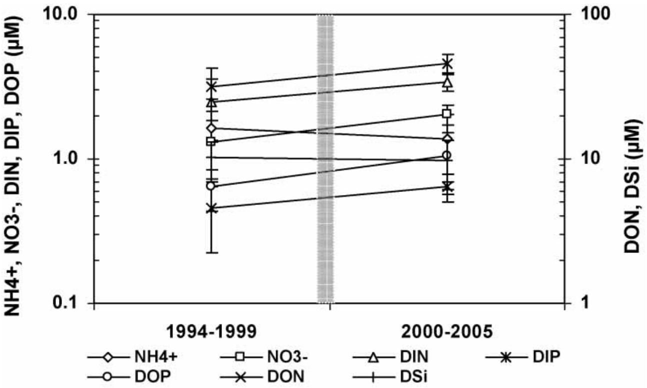

Figure 3. Long-term annual distribution of nutrients (NH_4^+, NO_3^-, DIN, DON, DIP, DOP, DSi, μM) before the introduction of the ctenophores (1994–1999) and after (2000–2005) in the Iranian coastal area of the Caspian Sea: mean annual values ± SD. The grey bar indicates the time when the ctenophores were introduced to the area.

The average abundance of phytoplankton during Phase II was significantly higher (4.2 fold, $p < 0.05$) than during Phase I (about 55000 cells.l^{-1} during Phase II compared to about 13000 cells.l^{-1} during Phase I). Bacillariophyta (diatoms) was the dominant group (59–62%) during both sampling periods (Figure 5a, b). The overall composition of the phytoplankton changed during Phase II. During Phase I, Cyanophyta formed only about 4% of the total phytoplankton, but increased to the 25% during Phase II. Cyanophyta also increased both in terms of number of taxa (from 5 to 11) and overall abundance (from 700 to 9400 cells.l^{-1}). The reverse trend was observed for the other two groups. Chlorophyta made up about 13% of the phytoplankton abundance during Phase 1 and this decreased to 6% in Phase II. The decrease was from 7 to 1% for Euglenophyta.

During Phase I, the Bacillariophyta (diatoms) represented 90% of the phytoplankton abundance in spring, 81% during summer, 92.5% in autumn and 79% in winter. During Phase II, the dominance of Bacillariophyta declined slightly, with percentage composition of 79% (spring), 48% (summer), 47% (autumn) and 43% (winter). Consequently, the seasonal abundance for the two other main groups increased in Phase II as compared to Phase I (Pyrrophyta: 10%, 7%, 3% and

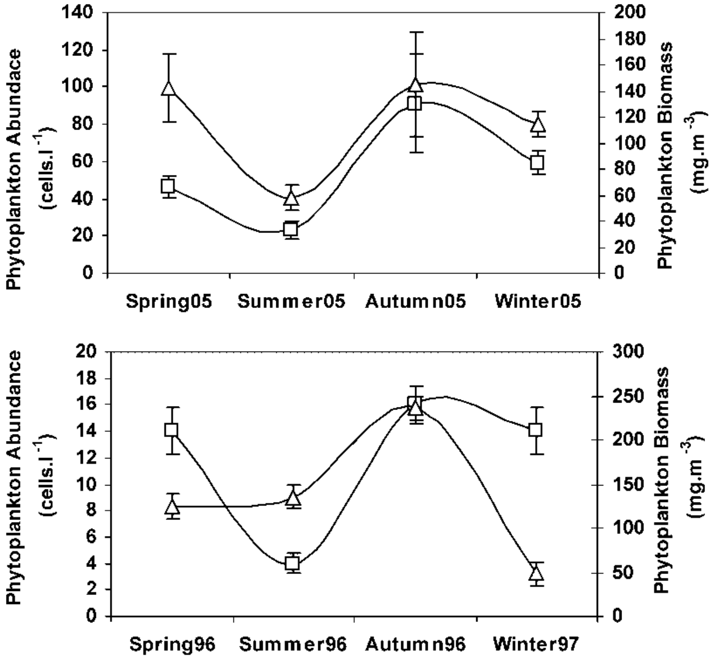

Figure 4. Seasonal variation of abundance and biomass of phytoplankton in the subsurface layer of the Iranian coastal area of the Caspian Sea before and after the introduction of the ctenophores, during Phase I (1996–1997) and Phase II (2005). (Δ represents biomass and □ abundance $\times 10^3$). Mean seasonal values ±SE.

17% to 21%, 40%, 52% and 53%; Cyanophyta: 2.3%, 11.9%, 1.1% and 2.3% to 6.7%, 62.5%, 22.5% and 7.2%) for spring, summer, autumn and winter, respectively. Seasonal abundance of Chlorophyta decreased from 8.7%, 21.8%, 6.2% and 15.6% during Phase I to 5.7%, 4.4%, 3.5% and 12.0% during Phase II for spring, summer, autumn and winter, respectively. This trend was also observed for Euglenophyta but with different percentages.

Although the total phytoplankton biomass during Phase II was similar to Phase I, the contribution of the different groups to biomass changed. During Phase II, on average 52% of the biomass was contributed by Bacillariophyta (compared to 86% during Phase I) whereas Pyrrophyta (dinoflagellates) increased from 7% to 33% (Figure 5c, d).

4. Discussion

Nitrate was found to be the dominant form of inorganic nitrogen in the Southern Caspian Sea. This is consequently due to the presence of high levels of dissolved oxygen and to temperatures favorable for mineralisation of organic compounds at the subsurface layer. Low ammonium concentrations were found because it is the preferred nitrogen form for phytoplankton uptake due to its lower energy requirement [32].

DON concentrations observed during Phase I are comparable to those recorded in the North Caspian by [33]. Higher DON concentrations occurred near the river mouths, such as the Sefidrud River in the west coast (Transect 3). Lower DON concentrations were observed in the east coast and during summer, as the warmer surface water temperature allowed a higher remineralisation of organic compounds. Surface water temperature increased along the transect in the eastern zone. A maximum difference of 4 °C in surface water temperature was recorded between the west and east coast. However, a seasonal fluctuation of DON was not observed during Phase II.

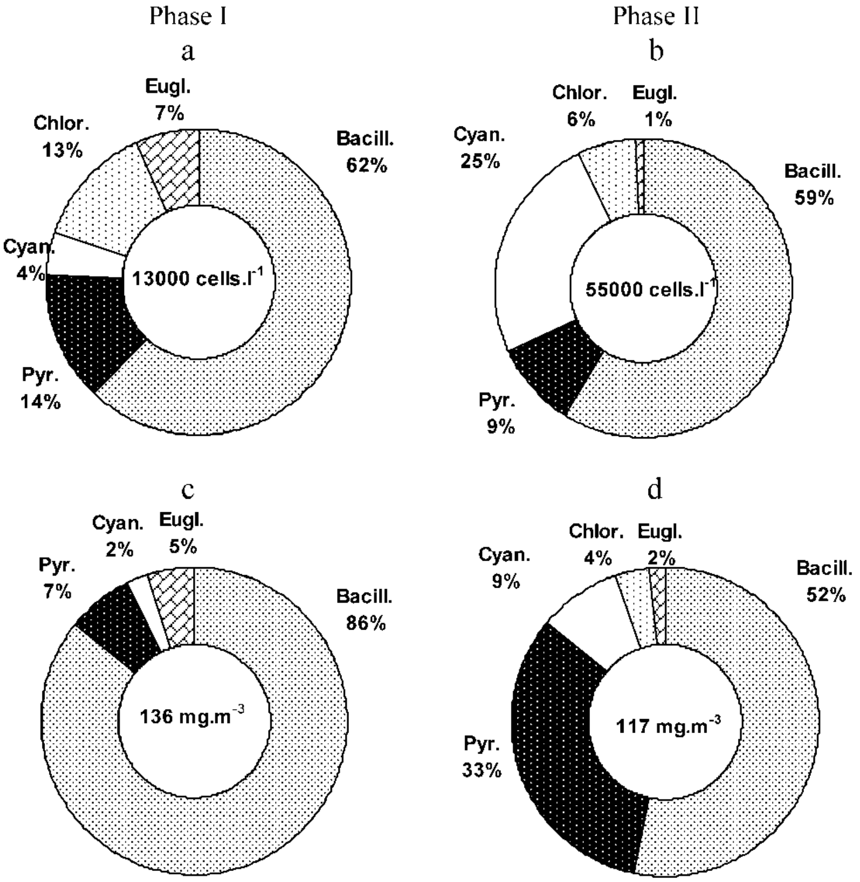

Figure 5. Contribution of different phytoplankton groups to the total (a) abundance in 1996–1997, (b) abundance in 2005, (c) biomass in 1996–1997, and (d) biomass in 2005 of the Iranian coastal area of the Caspian Sea (the groups having a very low contribution to the total were not shown). Bacill. = Bacillariophyta, Pyr. = Pyrrophyta, Cyan. = Cyanophyta, Chlor. = Chlorophyta and Eugl. = Euglenophyta.

In this study, we obtained an overall DIP: DOP ratio of 1:2. In the North Caspian Sea, this ratio is 1:18 [33] probably due to the intense discharge from large rivers like the Volga. The low DIP: DOP ratio in the Southern Caspian Sea suggests a low influence of the small rivers in the area.

According to [33], the diatoms are the most abundant and widespread phytoplankton group throughout the Caspian Sea. In the North Caspian Sea, Chlorophyta and Cyanophyta were found to be the next most abundant groups after Bacillarophyta. In the Middle (including the Eastern) and South Caspian Sea, however, Pyrrophyta (dinoflagellates) dominates all year round. Roohi et al. in their survey during 2003–2004 [34] reported that Bacillariophyta (diatoms) was the dominant phytoplankton group (mean of total phytoplankton and number of taxa) along the Iranian coast of the Southern Caspian Sea. During a study from 1962 to 1974, the total number of phytoplankton taxa recorded was 449 (Table 4), decreasing to 414 in the North, 225 in the Middle and 71 in the South. This may be due to the absence of large rivers (such as Volga River) in the South. The phytoplankton composition observed during Phase I was quite similar to that observed in the Middle and South Caspian Sea by [33], which reported that Bacillariophyta had highest cell abundance and biomass, followed by Pyrrophyta (dinoflagellates). In comparison to the spring bloom (Figure 4), the autumn phytoplankton showed higher values of abundance and biomass in both sampling periods as Kasymov and Bagirov already reported [35]. During

Table 4. Number of phytoplankton taxa recognised at subsurface water during Phase I (1996–1997) and Phase II (2005) in the Southern Caspian Sea Iranian coast. Only the five main groups of phytoplankton in the Caspian Sea are shown.

Phytoplankton Groups	Iranian coast Phase I	Iranian coast Phase II	Caspian Sea*
Bacillariophyta	25	45	164
Pyrrophyta	11	16	39
Cyanophyta	5	11	102
Chlorophyta	5	17	139
Euglenophyta	4	7	5
Total	50	96	449

*Kosarev and Yablonskaya 1994 [33].

Phase II, Cyanophyta was the second most dominant group after the Bacillariophyta. The Shannon-Weaver index of phytoplankton species was significantly higher during Phase II (1.85 bits/cell) as compared to Phase I (1.25 bits/cell).

Phytoplankton needs a wide variety of nutrients to grow. Two particularly important ones are nitrogen and phosphorous. Phytoplankton also needs nutrients in a well-defined ratio. In most of the oceans and seas nitrogen is first depleted and growth is said to be nitrogen limited. The Southern CS is nitrogen limited [36]. An increase in phytoplankton abundance and biomass during spring can take place as a combined result of nutrient upwelling and increase in temperature. In autumn, however the increase may be a combined result of summer thermocline breakdown (which induces nutrient upwelling) and optimum temperature (17.30 °C).

During Phase I, as a result of vertical mixing (which normally occurs in winter) the inorganic nitrogen concentrations increased during spring but declined in summer, probably due to increase in phytoplankton growth. During autumn, no significant change in inorganic nitrogen concentrations was observed even though there was vertical mixing. This probably happened because the increase in inorganic nitrogen concentrations was accompanied by an increase in phytoplankton growth. Observations during Phase I showed that inorganic nitrogen compound correlated negatively with phytoplankton growth. On the contrary, DON correlated positively with phytoplankton growth. Similar observations were reported for the long-term study (1994–1999) and this was associated with the undisturbed condition of the CS. A different scenario was observed during Phase II, where it was found that the inorganic nitrogen concentrations increased from spring to autumn, but decreased slightly in winter. This increase from spring to autumn may be the result of nutrients being released from the mucus of the ctenophores into the surrounding water. During Phase II, there was no correlation between the phytoplankton abundance and DIN.

The mean concentrations of DIP and DSi were found to be almost stable and no correlation was found between phytoplankton abundance and the concentration of these nutrients during both sampling periods.

Vollenweider [37] clearly demonstrated the destructive and harmful effects of nutrient enrichment on the coastal environment. Leonov and Stygar [5] reported that there is an extensive development of industrial areas, particularly on the northern coast of the CS. The situation in the Southern CS near the Iranian coast is quite different. The input of nutrients is mostly limited to biotransformation and vertical mixing with minimal contribution from river discharge and atmospheric precipitation [5]. EACS and CSN reported that advection transport of nutrient rich waters from the North CS by water current is minimal because water circulation in this area is formed in the deep zone and is not able to affect the inshore areas [6,38].

Biological transformation which generally occurs in the Southern CS – Iranian coast seems to be the main factor affecting the increase in nutrient concentrations within the study area. Yearly surface water temperatures of the coastal waters of the Iran, which range from 10.0 to 28.9 °C, is typical of a subtropical region. The mean salinity value recorded in the present study (12.40 psu) is comparable to that reported by [33] (12.50–13.40 psu) for the Eastern and South CS. The range in temperature and salinity values for the Iranian coastal waters makes them for favourable to the growth of ctenophores throughout the year. Shiganova [39] reported that the factors limiting *M. leidyi* growth in the North CS are salinities below 2 psu and the water temperatures lower than 4 °C. The distribution of ctenophores in the Southern CS shares a lot of similarities with that observed in Chesapeake Bay and the Sea of Azov, probably due to the resemblance in weather and salinity conditions between these places. The long-term data from the Southern CS – Iranian coast revealed that the abundance of the ctenophores is strongly affected by seasons, with the highest values recorded in summer and the mid-autumn months [34,40]. The introduction of the ctenophores into the CS seems to have a much more severe impact on the ecosystem as compared to the other systems such as the Black Sea, due to the enclosed nature of CS that hinders water exchange with the open ocean [41,42].

The increase in nutrient concentrations during Phase II can be related to the internal recycling of nutrients released from the mucus of the ctenophores into the surrounding waters, as reported by Shiganova for the North Caspian Sea [4]. During Phase II, land-based nutrient input from such rivers as the Sefidrud is low due to various external factors such as reported in [43,44], which further confirmed the above discussion.

NH_4^+ concentrations during Phase II of the study were positively correlated with abundance of the ctenophores [14]. According to [4], a reliable correlation exists between the maximum abundance of the ctenophores and the concentration of ammonium nitrogen. In a study conducted in 2001-02 [4] it was found that stations with higher NH_4^+ concentration (0.80–0.95 μM) also reported high population of ctenophores. This was due to the fact that one of the main products of ctenophores excretion is ammonium nitrogen. The NH_4^+ concentrations found in this study were comparable to the data reported by [4].

DON was also found to be positively correlated to the abundance of ctenophores [14]. The increase in DON concentration after the introduction of the ctenophores could be due to increase in phytoplankton and ctenophores populations and vertical mixing. Bronk [45] suggested that on the average 25–41% of the DIN (NH_4^+ and NO_3^-) taken up by phytoplankton reentered the oceanic, coastal and estuarine waters in the form of DON. Ctenophores were also found to release large amounts of DON [43]. This is reflected in the fact that the highest DON concentrations were recorded in summer during the ctenophores bloom as reported by [34,40]. These results agree with Deason and Smayda who observed that ctenophores excrete nutrients into the water especially at high temperatures [46]. Thus, the increase in DON concentrations after the introduction of the ctenophores was most probably caused by the excretion from ctenophores especially in summer when the river flow was greatly reduced due to the high rate of evaporation and uptake for irrigation. Furthermore, the maximum DON concentrations were observed in the central and eastern zones, about 10 to 20 km from the shore, which received little influence in terms of land-based nutrient input. The formation of a thermocline during summer reduced nutrient upwelling from the underlying layers. The organic and inorganic nitrogen forms increase in the area where ctenophores dwell [4]. Nitrogen excretion has been used to evaluate the importance of ctenophores in nutrient recycling [11]. In this study, the concentration of total nitrogen increased at least 1.5 times after the introduction of the ctenophores. This increase was particularly high in summer and autumn (3 to 4 times) during the ctenophores bloom (Table 1).

According to Kremer, ctenophores release DIP [11]. It was therefore suggested that the introduction of the ctenophores, together with vertical mixing in the Southern CS can explain the increase in DIP concentration (which was found to be higher in Phase II by a factor of 1.7) observed in this study. A positive correlation was also observed between DIP and the ctenophores abundance [14]. As with the DON distribution, high DOP concentrations were observed near the mouth of the Sefidrud River in the west coast, before the introduction of the ctenophores. However, after the introduction of the ctenophores the difference was nullified by the input from mucus secretion as well as due to the reduction in flow and nutrient loading from the Sefidrud River.

A number of studies widely claim that the anthropogenic input and invasion by alien species such as the ctenophores can play an integral part in altering the phytoplankton community in terms of biomass and dominant taxa [40,42,47–50]. For example, Shiganova [4] reported that, under field and experimental conditions, the increase in phytoplankton abundance (in particular the diatoms) was related to the presence of ctenophores, since the ctenophores have been shown to directly affect nutrient concentrations. Roohi et al. [34] compared spatial distribution of ctenophores, phytoplankton, zooplankton and nutrients (DON and DOP) from 2003 to 2004 in the Southern CS – Iranian coast. The study found that an increase in phytoplankton (Bacillariophyta and Cyanophyta); nutrients and a decline in zooplankton abundance were related to presence of the ctenophores. The study also noted that the ctenophores were found widespread in the CS – Iranian coast and that their abundance and biomass declined in winter and late spring. The increase in phytoplankton abundance and diversity during Phase II can be attributed to the preying of zooplankton by the ctenophores, which in addition contributed to the increase in nutrient concentrations through their mucus secretion. A similar increase in phytoplankton abundance due to the predation on zooplankton by ctenophores had been reported by [46] during 1972–1977 in Narragansett Bay, Rhode Island, USA and in the North Caspian Sea [4]. The lower total phytoplankton biomass recorded despite the increase in abundance during Phase II indicates the dominance of smaller size phytoplankton during this period. The general structure of the phytoplankton diversity is given in [36].

5. Conclusions

In general, the study found that nutrient concentrations (except DSi) and phytoplankton abundance and diversity in the subsurface water of the Southern CS were significantly higher after the introduction of the ctenophore, *M. leidyi*. Data collected from 1994 to 2005 also showed an overall increase in nutrient concentrations (except NH_4^+ and DSi). Most nutrient concentrations show clear seasonal variations during both sampling periods. In addition, increase in nutrient concentrations seem to be influenced by vertical mixing and by the increase in ctenophores population in summer during Phase II. In conclusion, the study suggests that the introduction of the ctenophores into the Southern CS resulted in an increase in the amount of nutrients through their secretion and excretion, which stimulates the overall phytoplankton growth. Due to its enclosed nature and with moderate temperature and salinity, the CS is extremely susceptible to anthropogenic impact and presence of alien species. Further research on the impact of invasive species on the CS ecosystem should be carried out even though recovery is in progress in the area.

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