First report on *Noctiluca scintillans* blooms in the Red Sea off the coasts of Saudi Arabia: consequences of eutrophication

OCEANOLOGIA, 49 (3), 2007.
pp. 337–351.

KEYWORDS
Dinoflagellates
Noctiluca scintillans
Red Sea

Zakaria A. Mohamed[1,2,*]
Ibrahim Mesaad[2]

[1] Botany Department,
Faculty of Science, Sohag University,
Sohag – 82524, Egypt

[2] Department of Biological Sciences,
Faculty of Science, King Khalid University,
Abha – 9004, Saudi Arabia;

e-mail: mzakaria_99@yahoo.com

*corresponding author

Received 11 June 2007, revised 30 July 2007, accepted 14 August 2007.

Abstract

Blooms of *Noctiluca scintillans* are reported for the first time in the Red Sea off the south-western coasts of Saudi Arabia. During the present study, surface water samples were collected weekly on the coasts of the Al Shuqayq region from February to April 2004–2006. The abundance of *N. scintillans* correlated negatively with most nutrients, as well as the cell densities of diatoms and dinoflagellate species. Microscopic examination of live cells from *Noctiluca* blooms showed the presence of some species of diatoms and dinoflagellates within the *Noctiluca* body – confirmation of its grazing on these microalgae. The presence of a *Noctiluca* bloom in the coastal waters off south-western Saudi Arabia could be linked indirectly to water eutrophication by an increase in prey abundance. The physico-chemical properties of Red Sea coastal waters should therefore be monitored regularly in order to minimize the formation of harmful algal blooms, which may affect all food web levels, including the human level.

The complete text of the paper is available at http://www.iopan.gda.pl/oceanologia/

1. Introduction

Noctiluca scintillans Macartney is a large heterotrophic dinoflagellate that is widely reported as a 'red tide' organism in temperate, tropical and polar waters (Elbrachter & Qi 1998). *N. scintillans* forms blooms with a 'tomato soup' colour and a bioluminescence that lights up the wakes of boats and breaking waves on beaches (Dharani et al. 2004). It has been suggested that the formation of *N. scintillans* blooms is regulated by hydrographical and biological factors (Elbrachter & Qi 1998). Miyaguchi et al. (2006) have also suggested that bloom formation by *N. scintillans* can be resolved into a three-step process: (i) an initial increase in the abundance of *N. scintillans*, attributable to an increase in optimum hydrographical and biological factors (temperature, salinity, water stability and chlorophyll *a*), (ii) *N. scintillans* are then accumulated by the convergence of seawater as a result of low rainfall and wind, and (iii) swarmer-effects, which enhance bloom formation, as suggested by Sato et al. (1998). The availability of phytoplankton prey is an important factor affecting the abundance of *N. scintillans* (Elbrachter & Qi 1998). *N. scintillans* blooms were found to occur after diatom blooms (Kiørboe et al. 1998, Tiselius & Kiørboe 1998, Dela-Cruz et al. 2003). Although *Noctiluca* does not produce toxins, it is categorized as a harmful alga on the basis of mass mortalities of finfish in farms associated with oxygen depletion, gill clogging and high ammonia levels (Okaichi & Nishio 1976). More recently, it has been reported that *N. scintillans* may act as a vector of phycotoxins to higher trophic levels by feeding on toxigenic microalgae (Escalera et al. 2007).

An intense bloom of *N. scintillans* was first noticed in the Red Sea off the Al Shuqayq region, south-western Saudi Arabia, during the first week of February 2004. This bloom imparted light of a vivid green colour to the coastal waters. To our knowledge, the present study is the first to report on an *N. scintillans* bloom in the Red Sea. Since the occurrence of *Noctiluca* blooms is not a common phenomenon in Saudi Arabian coastal waters, this study describes some of the environmental factors that prevailed in the region of the *N. scintillans* bloom in the Red Sea off the south-western coast of Saudi Arabia.

2. Material and methods

2.1. Sampling

Sampling was carried out on the coasts of the Al Shuqayq region, south-western Saudi Arabia (19°65′N, 42°18′E), where a sudden intense bloom of *N. scintillans* was observed. Sampling sites were close to the shoreline rain drains that discharge rain water into the sea. Surface water samples were taken from onboard a fishing vessel using clean plastic buckets once a week during the presence and absence of an *N. scintillans* bloom from 2004 to 2006. Water samples were taken in calm weather and at low tide (0.5–1.3 m). Part of the water sample was preserved immediately in 2% formaldehyde. The water samples were transported to the laboratory in an icebox for chemical and biological analysis.

2.2. Measurement of physical and chemical parameters

Temperature, salinity, pH and dissolved oxygen were measured in situ with a thermometer, salinometer, pH meter (WTW Digi 88) and O_2-meter, respectively. Concentrations of nutrients – ammonium, nitrate, phosphate and silicate – were determined in GF/C filtered water samples by the standard analytical methods as approved by the American Public Health Association (APHA) (1995). All chemical variables were determined in triplicate.

2.3. Counts of *Noctiluca* and other phytoplankton

Samples were concentrated through a sieve (100 μm mesh) and transferred to a 100 cm^3 cylinder. The *Noctiluca* cells were counted using an S-tray under an Olympus dissecting microscope in this fraction; other phytoplankton species were counted with a Sedgwick-Rafter counting chamber and an Olympus binocular microscope in the < 100 μm size fraction. The density was calculated for natural taxonomic units (cells, colonies or filaments) per litre of the original sample. Cell diameters of 50 randomly chosen cells of *N. scintillans* were measured from each sample under the dissecting microscope. Microalgal prey items in an *N. scintillans* body were examined primarily in whole *Noctiluca* cells under the microscope. The dinoflagellate and diatom species within the *Noctiluca* body were counted in a gentle homogenate of 50 *Noctiluca* individuals. The taxonomic identification of the phytoplankton was carried out according to Hasle & Syversten (1997) for diatoms and Steidinger & Tangen (1997) for dinoflagellates.

2.4. Statistical analysis

Differences in environmental variables in the presence and absence of an *N. scintillans* bloom were determined by one-way ANOVA ($P < 0.05$). Spearman rank correlation coefficients were used to measure the degree of association between the count of *N. scintillans*, and the counts of other phytoplanktonic species and physico-chemical variables of seawater.

Table 1. Phytoplankton densities (cells dm^{-3}) in Red Sea surface water off the south-western coast of Saudi Arabia in the presence and absence of a *Noctiluca scintillans* bloom

Species	7 February bloom	14 February bloom	21 February bloom	28 February bloom	14 March bloom	28 March bloom	14 April bloom	28 April bloom
Dominant dinoflagellates								
Noctiluca scintillans	$2.5\times10^6\pm2^*$	3000±44	$3\times10^6\pm2.3^*$	35±6	$2.7\times10^6\pm1.6^*$	12±4	0	0
Alexandrium sp.	33±2	830±32	21±4	730±14	31±6	920±24	110±11	130±2
Ceratium sp.	45±6	62±4	30±5	60±7	12±3	71±13	80±9	100±11
Dinophysis acuta	62±4	810±21	45±6	880±24	19±3	800±32	900±34	850±45
Prorocentrum sp.	71±8	110±12	13±3	92±11	11±4	150±16	200±21	220±31
Others	21±2	29±3	15±2	33±4	23±3	22±2	18±1	25±8
Dominant diatoms								
Thalassiosira rotula	1200±32	$9\times10^4\pm0.2^*$	1300±64	$11\times10^4\pm0.3^*$	1500±24	720±31	240±15	40±8
Nitszchia sigma	30±4	50±5	60±8	50±4	31±3	10±4	0	0
Pseudonitzschia sp.	52±5	57±6	53±7	70±6	33±5	21±5	0	0
Chaetoceros sp.	113±22	187±11	165±12	173±9	193±8	22±7	0	0
Others	34±5	55±4	28±5	79±3	35±6	68±8	62±6	56±7
Chlorophyta								
Dunaliella tertiolecta	830±53	9540±67	870±52	7650±51	810±28	650±13	485±26	510±33
Others	25±7	78±6	38±9	56±6	36±7	63±5	58±6	47±4

*SD is the value $\times\,10^3$.

3. Results

The results of the field study showed that an intense sudden bloom of *N. scintillans* had been observed on 6 February 2004 in the Red Sea off the Al Shuqayq coasts, south-western Saudi Arabia (Table 1). This bloom persisted for three days, then suddenly disappeared. In the course of time, the bloom reappeared twice, during February and March 2004 and 2005, eventually waning in the April of these years. Blooms were absent during 2006, even though the physico-chemical properties of the seawater in this year did not differ significantly from those of 2004 and 2005 (Figs. 1, 2). The largest number of *N. scintillans* cells (3×10^6 cells dm^{-3}) was recorded in the third week of February 2004 and 2005 (Table 1). During this study,

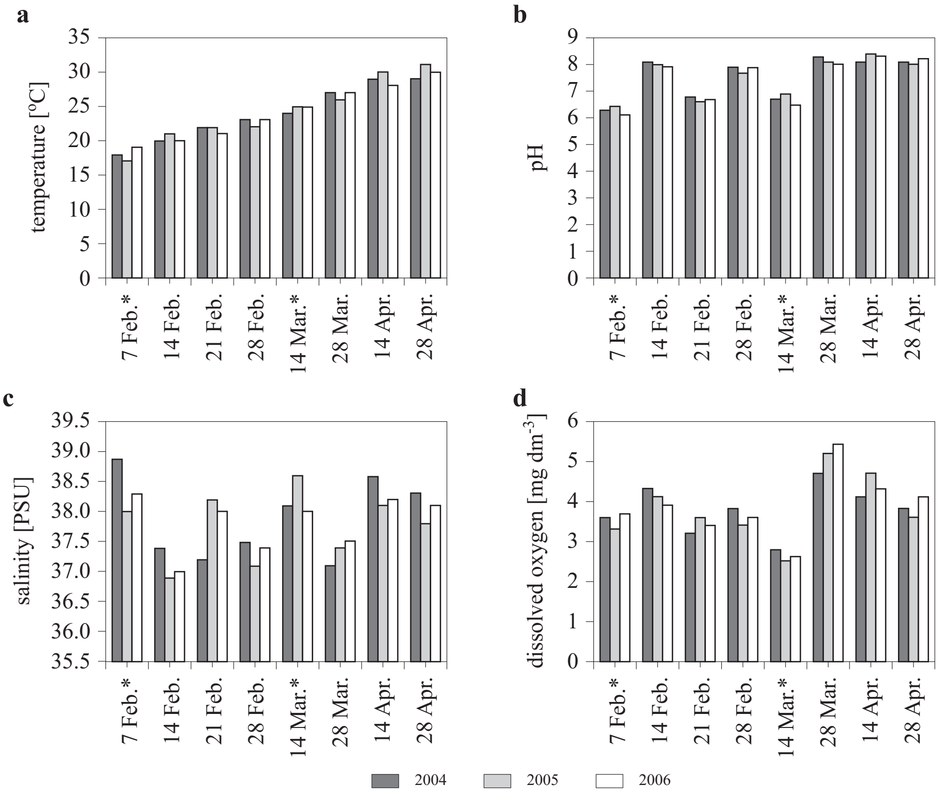

Fig. 1. Physico-chemical characteristics of Red Sea surface water off the south-western coast of Saudi Arabia in the presence and absence of *Noctiluca scintillans* blooms during 2004, 2005 and 2006. Temperature (a), pH (b), salinity (c) and dissolved oxygen (d). An asterisk (*) by the sampling date implies the presence of blooms during this period

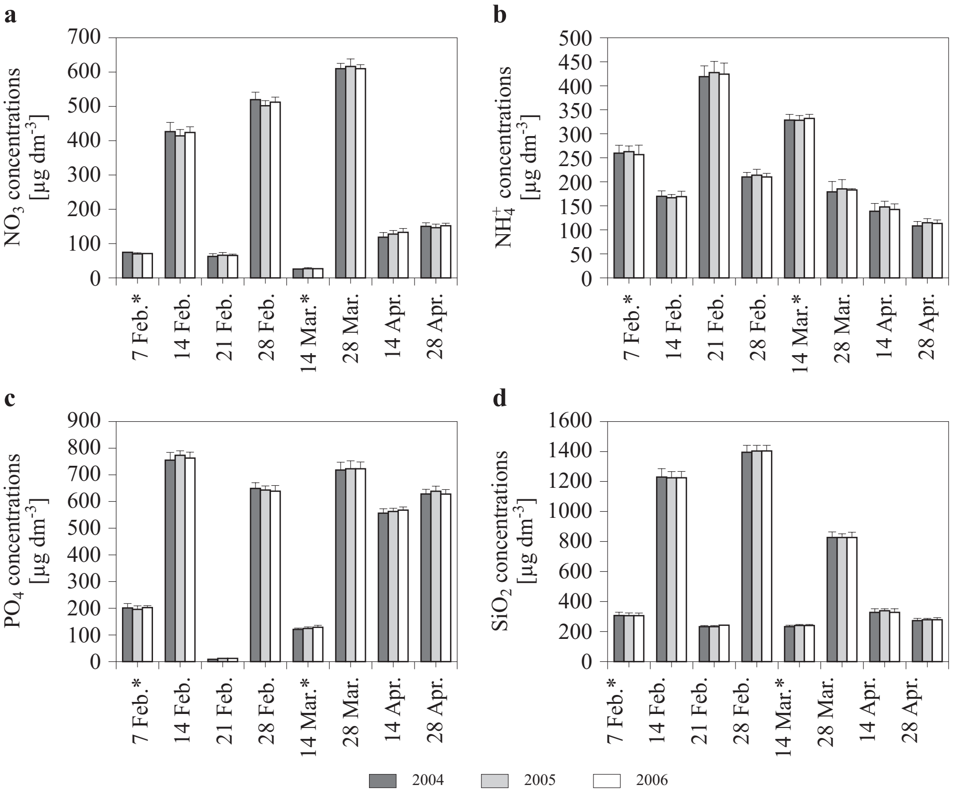

Fig. 2. Chemical characteristics of Red Sea surface water off the south-western coast of Saudi Arabia in the presence and absence of *Noctiluca scintillans* blooms during 2004, 2005 and 2006. $NO_3{}^-$ (a), $NH_4{}^+$ (b), PO_4 (c) and SiO_2 (d). An asterisk (*) by the sampling date implies the presence of blooms during this period

the *N. scintillans* cells constituting the blooms were small in size (270 –380 μm) (Fig. 3).

No significant differences in temperature, pH, salinity and dissolved oxygen of surface seawater were observed (ANOVA test) between the blooming and non-blooming periods of *N. scintillans* ($P > 0.05$). However, a slight decrease in pH and dissolved oxygen did occur during the *Noctiluca* blooms (Fig. 1). With regard to nutrients, the cell number of *N. scintillans* correlated negatively with the nitrate, phosphate and silicate concentrations ($r = -0.5{:}-0.97$), but positively with the ammonium concentration ($r = 0.9$). In contrast, the abundance of other phytoplankton, including diatoms, dinoflagellates and green algae, correlated positively ($r = 0.4 - 0.9$) with nitrate, phosphate and silicate, but negatively with ammonia ($r = -0.9$) (Fig. 2).

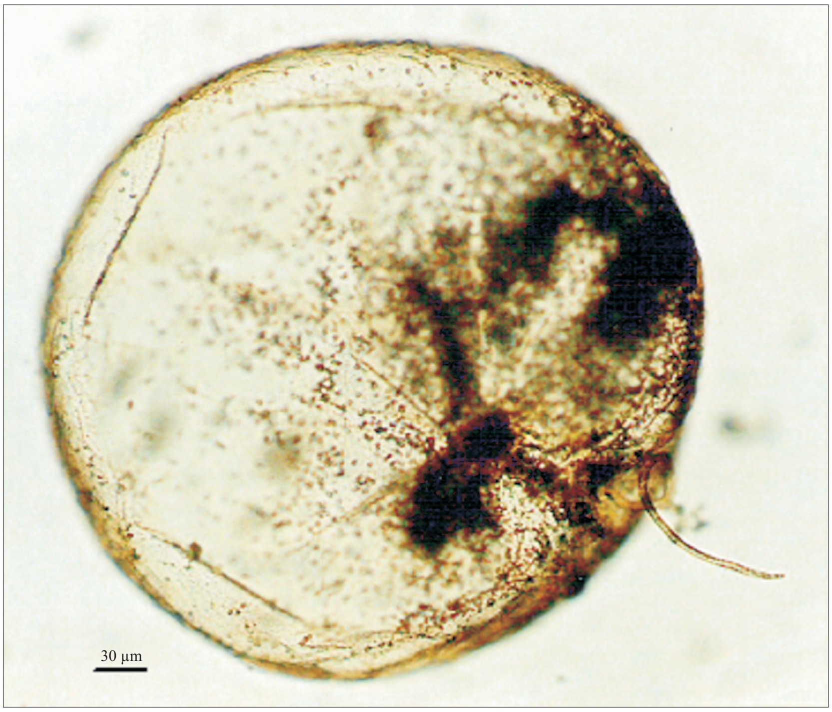

Fig. 3. Photomicrograph of *Noctiluca scintillans* forming blooms in the Red Sea off the south-western coast of Saudi Arabia. The bar represents a length of = 30 μm

The cell number of *N. scintillans* correlated negatively with the cell numbers of the diatom *Thalassiosira rotula*, the green alga *Dunaliella tertiolecta*, and all the dinoflagellate species (*Alexandrium* sp., *Ceratium* sp., *Dinophysis* sp., *Prorocentrum* sp.) ($r = -0.4{:}-0.99$). These species were abundant in the absence of an *N. scintillans* bloom, but their densities decreased sharply upon the appearance of an *N. scintillans* bloom (Table 1). On the other hand, *N. scintillans* blooms did not significantly affect the cell numbers of *Chaetoceros* sp., *Nitzschia* sp. or *Pseudonitzschia* sp. ($P > 0.05$).

Microscopic examination of live *Noctiluca* cells collected during the blooms revealed the presence of microalgal species, including diatoms and autotrophic dinoflagellates. The largest cell density of microalgae within the *Noctiluca* body was represented by the green alga *Dunaliella tertiolecta*, the diatom *Thalassiosira rotula* and *Pseudonitzschia* sp., whereas the dinoflagellate species represented the lowest cell density of the algal prey in the *Noctiluca* body (Fig. 4). On the other hand the total cell density of the prey within the *Noctiluca* body differed significantly in the *Noctiluca* cells in the presence and absence of the bloom. The statistical analysis of variance (ANOVA) did not reveal any significant differences in the physico-chemical

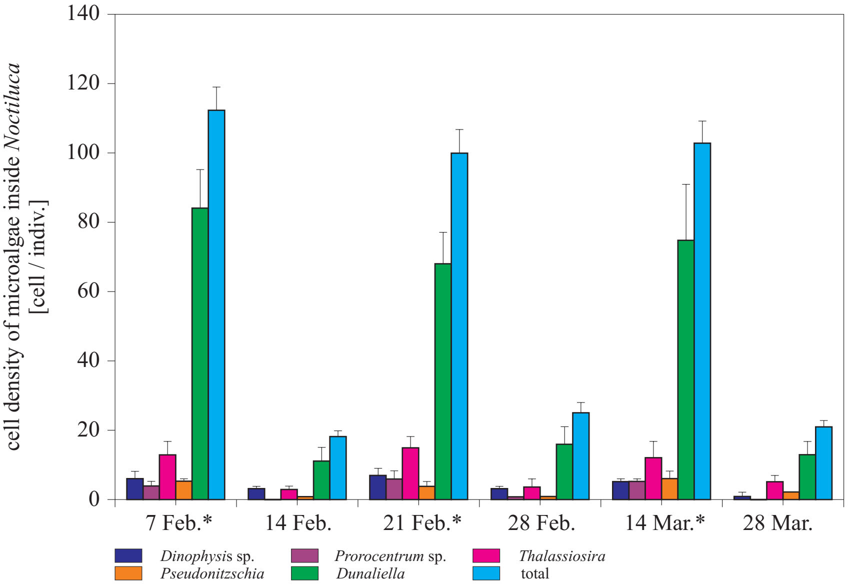

Fig. 4. Variation in cell density of microalgae (cells/*Noctiluca* individual, mean of 50 readings) in the food vacuoles of *Noctiluca scintillans* taken from the Red Sea off the south-western coast of Saudi Arabia during 2004. An asterisk (*) by the sampling date implies the presence of blooms during this period

parameters or the abundance of *N. scintillans* and other phytoplankton between 2004 and 2005 (Figs. 1, 2).

4. Discussion

The present study reports for the first time on the occurrence of an *N. scintillans* bloom in Red Sea coastal waters off Saudi Arabia. This bloom occurred almost at the same time and place during 2004 and 2005; this is consistent with reports of *Noctiluca* blooms elsewhere in the world (Uhlig & Sahling 1990, Huang & Qi 1997, Pithakpol et al. 2000, Miyaguchi et al. 2006). But the blooms were absent during 2006, in spite of the non-significant difference in the physico-chemical properties of seawater between 2006, and 2004 and 2005. Therefore, it was unlikely that the disappearance of this bloom from Saudi coastal waters during 2006 was due to the Saudi government's restrictions imposed on the coasts, leading to a decreased input of anthropogenic pollution into seawaters. It could have been the result, however, of the advection of *Noctiluca* blooms by prevailing winds and currents to other regions not sampled during the present study. These advective processes are often strong enough to transport organisms over large distances, as observed by Tester et al. (1991), who found that an outbreak of the toxic dinoflagellate, *Gymnodinium breve*, in North Carolina had been transported by several major current systems from the south-western coast of Florida, nearly 1000 km away. Dela-Cruz et al. (2003) also reported that *Noctiluca* cells were advected southward with the East Australian Current over hundreds of kilometres. Hence, these authors concluded that the spatial variability in the abundance of *Noctiluca* must also be partly attributed to advective processes rather than to local growth alone. On the other hand, the non-significant difference in the physico-chemical variables of Red Sea surface waters in the study region during 2004, 2005 and 2005 may have been due to the cyclic discharge of rainwater stored in ponds close to the sampling sites.

The temperature (18–29°C) and salinity (37.1–38.9 PSU) recorded during the present study lie in the optimal ranges for *N. scintillans* (10–28°C and 28–36 PSU, respectively) (Huang & Qi 1997, Tada et al. 2004, Miyaguchi et al. 2006). Our results showed a decrease in the pH and DO of the seawater during *Noctiluca* blooms. The reduction in pH during the *Noctiluca* bloom periods is attributable to the generation of carbon dioxide by the respiratory activity of *N. scintillans* (Dharani et al. 2004), but the decrease in DO to large-scale respiration on the part of *Noctiluca* (Venugopal et al. 1979, Sargunam et al. 1989).

It is unlikely that the reduction in macronutrient concentrations ($NO_3{}^-$, $PO_4{}^{-3}$, SiO^2) in the bloom area during the present study was due to consumption by *N. scintillans*, owing to its heterotrophic nature. But the high concentrations of nutrients initially available at the water surface are exhausted by the autotrophic phytoplankton on which *Noctiluca* may feed (Sahayak et al. 2005). This hypothesis is confirmed by the results of the present study, where these nutrients correlated positively with the growth of autotrophic phytoplankton (e.g. diatoms, coccoid green algae, dinoflagellates). However, the diversity and species composition of microplankton in the Al Shuqayq region of the Red Sea are low compared to those of the microplankton in the northern Gulf of Aqaba, Red Sea (Al-Najjar et al. 2007).

Previous studies have reported that upwelling events along coasts deliver relatively high amounts of nutrients, which trigger diatom blooms (Hallegraeff & Jeffrey 1993, Ajani et al. 2001, Dela-Cruz et al. 2002) and subsequently *Noctiluca* blooms (Dela-Cruz et al. 2002). On the other hand, the high concentration of ammonia in the bloom area during the present study may have been due to autochthonous nutrient generation by *Noctiluca* cells (Montani et al. 1998), which contain high levels of ammonia in their vacuoles (Elbrachter & Qi 1998).

Cell size was used as an indicator of the condition of *Noctiluca* because it is a product of the culture conditions (Hanslik 1987, Qi & Li 1994, Buskey 1995). The smaller the cell size (340–450 μm), the better the nutritional conditions, whereas the larger the cell size (400–1200 μm), the poorer the nutritional conditions (Murray & Suthers 1999, Dela-Cruz et al. 2003). Accordingly, the small size (270–380 μm) of *N. scintillans* cells constituting the blooms in the Red Sea during the present study reflects a good nutritional status for its growth.

The negative relationship between the abundance of *N. scintillans* and that of some of the phytoplanktonic species during the present study is indicative of predation by *N. scintillans* on these species. These results are in agreement with those obtained by Dharani et al. (2004), who reported a negative relationship between *Noctiluca* and other phytoplankton in Indian coastal waters. Other studies have shown that *Noctiluca* requires a relatively high quantity of its phytoplankton prey to support optimal growth (Lee & Hirayama 1992, Kiørboe & Titelman 1998, Kiørboe 2003). During the diatom bloom *N. scintillans* increased, but it decreased when the algal biomass was low (Nakamura 1998). Diatom clearance rates by *N. scintillans* ranged between 0.1 and 0.35, which suggests that *N. scintillans* is an important mesozooplankter. The rich supply of nutrients brought in by the upwelling events increases the concentrations of dissolved inorganic nitrogen in the water column to concentrations well above ambient levels (Pritchard et al. 2000). Rapid population growth of *Noctiluca* has been recorded following phytoplankton blooms (Painting et al. 1993, Hayward et al. 1995). An increase in *Noctiluca* abundance has also been linked to increasing eutrophication, possibly caused indirectly by an increase in prey abundance (Porumb 1992).

The disappearance and re-appearance of *N. scintillans* blooms in Red Sea waters during the present study may have been due to *Noctiluca* cells sinking after a complete feed to assimilate food and then re-floating by the virtue of the vacuoles. *Noctiluca* cells are normally positively buoyant owing to their large cell vacuole (Elbrachter & Qi 1998). When the cells are well fed, they tend to sink until digestion and defecation have taken place (Uhlig & Sahling 1990, Kiørboe & Titelman 1998). The sated cells frequently undergo cell division (reproduce) and are consequently smaller than starved cells (Buskey 1995), which are irreversibly damaged and no longer divide (Uhlig & Sahling 1990).

Many studies have reported that *Noctiluca* is able to prey on other phytoplankton (Kiørboe & Titelman 1998, Jakobsen & Tang 2002, Sun 2003, Fonda-Umani et al. 2004, Escalera et al. 2006). In the present study, microscopic examination of live *Noctiluca* cells collected during the blooms showed the presence of diatoms (*Thalassiosira rotula* and *Pseudonitzschia* sp.), dinoflagellates (*Dinophysis* sp. and *Prorocentrum* sp.), and the green alga *Dunaliella tertiolecta* in the food vacuoles of *Noctiluca*, which suggests that *N. scintillans* feeds on these species. Most of these algae, particularly *Pseudonitzschia* and the autotrophic dinoflagellates, are known to produce toxins that can cause a fish kill or can accumulate in shellfish, causing poisoning in humans if they consume such contaminated seafood (Reguera et al. 1993, Blanco et al. 1998). Such potentially toxic phytoplankton found in the *Noctiluca* body may be transferred to higher food web levels, as suggested by Escalera et al. (2007). Although *Noctiluca* cannot be grazed by bivalves because of its large size (200–1000 μm), it can certainly be eaten by large fish. So, if these toxins are not assimilated and detoxified by *Noctiluca*, they will damage most fish, or accumulate in fish tissues (Moroño et al. 2003, Kwong et al. 2006), again causing poisoning in humans if they consume such contaminated fish (Reguera et al. 1993, Blanco et al. 1998). In addition, *Noctiluca* blooms are implicated in the reduction of Mn and Fe associated with bacteria and phytoplankton (Schoemann et al. 1998) and may therefore play an important role in nutrient fluxes.

In conclusion, the results of our study, along with those of previous studies (e.g. Painting et al. 1993, Hayward et al. 1995), show that *Noctiluca* blooms usually occur after eutrophication-induced phytoplankton blooms. A *Noctiluca* bloom can be indirectly linked to increasing eutrophication by an increase in prey abundance. Therefore, this organism and other potentially harmful algae, along with physico-chemical parameters, should be regularly monitored in Red Sea coastal waters, in order to discover the factors triggering such harmful algal blooms, which could affect all food web levels, including the human level.

Acknowledgements

The authors would like to thank the Saudi navy and coastguard for facilitating sample collection.

References

Ajani P., Hallegraeff G. M., Pritchard T. R., 2001, *Historic overview of algal blooms in marine and estuarine waters of New South Wales, Australia*, Proc. Linn. Soc. NSW, 123, 1–22.

Al-Najjar T., Badran M., Richter C., Meyerhoefer M., Sommer U., 2007, *Seasonal dynamics of phytoplankton in the Gulf of Aqaba, Red Sea*, Hydrobiologia, 579 (1), 69–83.

APHA, 1995, *Standard methods for the examination of water and wastewater*, 19th edn., Am. Publ. Health Assoc. (APHA), Washington, DC.

Blanco J., Moroño A., Pazos Y., Maneiro J., Marino J., 1998, *Trends and variations of the abundance of main PSP and DSP producing species in the Galician rias: Environmental and biological influences*, [in:] *Harmful algae*, B. Reguera, J. Blanco, M. L. Fernández & T. Wyatt (eds.), Xunta de Galicia & IOC UNESCO, Santiago de Compostela, Spain, 204–207.

Buskey E. J., 1995, *Growth and bioluminescence of Noctiluca scintillans on varying algal diets*, J. Plankton Res., 17 (1), 29–40.

Dela-Cruz J., Ajani P., Lee R., Pritchard T., Suthers I., 2002, *Temporal abundance patterns of the red tide dinoflagellate Noctiluca scintillans along the south-east coast of Australia*, Mar. Ecol. Prog. Ser., 236, 75–88.

Dela-Cruz J., Middleton J. H., Suthers I. M., 2003, *Population growth and transport of the red tide dinoflagellate, Noctiluca scintillans, in the coastal waters off Sydney Australia, using cell diameter as a tracer*, Limnol. Oceanogr., 48 (2), 656–674.

Dharani G., Abdul Nazar A. K., Kanagu L., Venkateshwaran P., Kumar T. S., Ratnam K., Venkatesan R., Ravindran M., 2004, *On the recurrence of Noctiluca scintillans bloom in Minnie Bay, Port Blair: Impact on water quality and bioactivity of extracts*, Curr. Sci. India, 87 (5), 990–994.

Elbrachter M., Qi Y. Z., 1998, *Aspects of Noctiluca (Dinophyceae) population dynamics*, [in:] *Physiological ecology of harmful algal blooms*, D. M. Anderson, A. D. Cambella & G. M. Hallegraeff (eds.), Springer, London, 662 pp.

Escalera L., Pazos Y., Moroño A., Reguera B., 2007, *Noctiluca scintillans may act as a vector of toxigenic microalgae*, Harmful Algae, 6 (3), 317–320.

Fonda-Umani S., Beran A., Parlato S., Virgilio D., Zollet T., De Olazabal A., Lazzarini B., Cabrini M., 2004, *Noctiluca scintillans (Macartney) in the Northern Adriatic Sea: long-term dynamics, relationships with temperature and eutrophication, and role in the food web*, J. Plankton Res., 26 (5), 545–561.

Hallegraeff G. M., Jeffrey S. W., 1993, *Annually recurrent diatom blooms in spring along the New South Wales coast of Australia*, Aust. J. Mar. Freshw. Res., 44 (2), 325–334.

Hanslik M., 1987, *Nahrungsaufnahme und Nahrungsverwertung im Meeresleuchttierchen Noctiluca miliaris*, Ph. D. thesis, University Bonn.

Hasle G. R., Syversten E. E., 1997, *Marine diatoms*, [in:] *Identifying marine phytoplankton*, C. R. Tomas (ed.), Acad. Press, St. Petersburg, FL, 5–385.

Hayward T. L., Cayan D. R., Franks P. J. S., Lynn R. J., Mantyla A. W., McGowan J. A., Smith D. E., Schwing F. B., Venrick E. L., 1995, *The state of the California Current in 1994–1995, a period of transition*, CalCOFI Rep., 36, 19–39.

Huang C., Qi Y., 1997, *The abundance cycle and influence factors on red tide phenomena of Noctiluca scintillans (Dinophyceae) Dapeng Bay, the South China Sea*, J. Plankton Res., 19 (3), 303–318.

Jakobsen H. H., Tang K. W., 2002, *Effects of protozoan grazing on colony formation in Phaeocystis globosa (Prymnesiophyceae) and the potential costs and benefits*, Aquat. Microb. Ecol., 27 (3), 261–273.

Kiørboe T., 2003, *High turnover rates of copepod fecal pellets due to Noctiluca scintillans grazing*, Mar. Ecol. Prog. Ser., 258, 181–188.

Kiørboe T., Tiselius P., Mithell-Innes B., Hansen J. L. S., Visser A. W., Mari X., 1998, *Intensive aggregate formation with low vertical flux during an upwelling-induced diatom bloom*, Limnol. Oceanogr., 43 (1), 104–116.

Kiørboe T., Titelman J., 1998, *Feeding, prey selection and prey encounter mechanisms in the heterotrophic dinoflagellate Noctiluca scintillans*, J. Plankton Res., 20 (8), 1615–1636.

Kwong R. W. M., Wang W-X., Lam P. K. S., Yu P. K. N., 2006, *The uptake, distribution and elimination of paralytic shellfish toxins in mussels and fish exposed to toxic dinoflagellates*, Aquat. Toxicol., 80 (1), 82–91.

Lee J. K., Hirayama K., 1992, *Effects of salinity, food level temperature on the population growth of Noctiluca scintillans Macartney*, Bull. Fac. Fish. Nagasaki Univ., 71, 163–167, (in Japanese with English abstract).

Miyaguchi H., Fujiki T., Kikuchi T., Kuwahra V. S., Toda T., 2006, *Relationships between the bloom of Noctiluca scintillans and environmental factors in the coastal waters of Sagami Bay, Japan*, J. Plankton Res., 28 (3), 313–324.

Montani S., Pithakpol S., Tada, K., 1998., *Nutrient regeneration in coastal seas by Noctiluca scintillans, a red tide-causing dinoflagellate*, J. Mar. Biotech., 6 (4), 224–228.

Moroño A., Arévalo F., Fernández M. L., Maneiro J., Pazos Y., Salgado C., Blanco J., 2003, *Accumulation and transformation of DSP toxins in mussels Mytilus galloprovincialis during a toxic episode caused by Dinophysis acuminata*, Aquat. Toxicol., 62 (4), 269–280.

Murray S., Suthers I. M., 1999, *Population ecology of Noctiluca scintillans Macartney, a red-tide-forming dinoflagellate*, Mar. Freshwater Res., 50 (3), 243–252.

Nakamura Y., 1998, *Biomass, feeding and production of Noctiluca scintillans in the Seto Inland Sea, Japan*, J. Plankton Res., 20 (11), 2213–2222.

Okaichi T., Nishio S., 1976, *Identification of ammonia as the toxic principle of red tide of Noctiluca miliaris*, Bull. Plankton Soc. Jpn., 23 (2), 75–80.

Painting S. J., Lucas I. M., Peterson W. T., Brown P. C., Hutchings L., Mitchell-Innes B. A., 1993, *Dynamics of bacterioplankton, phytoplankton and mesozooplankton communities during the development of an upwelling plume in the southern Benguela*, Mar. Ecol. Prog. Ser., 100, 35–53.

Pithakpol S., Tada K., Montani S., 2000, *Nutrient regeneration during Noctiluca scintillans red tide in Harima Nada, the Seto Inland Sea, Japan*, Proc. 15th Ocean Eng. Symp., 20–21 January 2000, J. Soc. Nav. Archit. Jpn., 127–134.

Porumb F., 1992, *On the development of Noctiluca scintillans under eutrophication of Romanian Black Sea waters*, [in:] *Marine coastal eutrophication*, R. A. Vollenweider, R. Marchetti & R. Viviani (eds.), Elsevier, London, 907–918.

Pritchard T. R., Lee R., Ajani P., Rendell P., Black K., 2000, *How do ocean outfalls affect nutrient patterns in coastal waters of New South Wales, Australia*, J. Coastal Res., 34 (Spec. iss.), 96–109.

Qi S., Li D., 1994, *Unequal cell division of Noctiluca scintillans*, Oceanol. Limnol. Sinica, 25, 158–61, (in Mandarin).

Reguera B., Bravo I., Marcaillou-Le Baut C., Masselin P., Fernandez M. L., Miguez A., Martinez A., 1993, *Monitoring of Dinophysis spp. and vertical distribution of okadaic acid on mussel rafts from Ria de Pontevedra (NW Spain)*, [in:] *Toxic phytoplankton blooms in the sea*, T. J. Smayda & Y. Shimizu (eds.), Elsevier, Amsterdam, 553–558.

Sahayak S., Jyothibabu R., Jayalakshmi K. J., Habeebrehman H., Sabu P., Prabhakaran M. P., Jasmine P., Shaiju P., Rejomon G., Thresiamma J., Nair K. K. C., 2005, *Red tide of Noctiluca milliaris off south of Thiruvananthapuram subsequent to the 'stench event' at the southern Kerala coast*, Curr. Sci. India, 89 (9), 1472–1473.

Sargunam C. A., Rao V. N. R., Nair K. V. K., 1989, *Occurrence of Noctiluca bloom in Kalpakkam coastal waters, East coast of India*, Indian J. Mar. Sci., 18 (4), 289–290.

Sato S. M., Suzuki M., Hayashi H., 1998, *The density of homogeneous population of cells controls resetting of the program for swarmer formation in the unicellular marine microorganism Noctiluca scintillans*, Exp. Cell Res., 245 (2), 290–293.

Schoemann V., De Baar H. J. W., De Jong J. T. M., Lancelot C., 1998, *Effects of phytoplankton blooms on the cycling of manganese and iron in coastal waters*, Limnol. Oceanogr., 43 (7), 1427–1441.

Steidinger K. A., Tangen K., 1997, *Dinoflagellates*, [in:] C.R. Tomas (ed.), *Identifying marine phytoplankton*, Acad. Press, St. Petersburg, FL, 387 –584.

Sun J., Liu D., Wang Z., Shi X., Li R., Zhu M., 2003, *Microzooplankton herbivory during red tide-frequent-occurrence period in spring in the East China Sea*, Chin. J. Appl. Ecol., 14 (7), 1073–1080.

Tada K., Pithakpol S., Montani S., 2004, *Seasonal variation in the abundance of Noctiluca scintillans in the Seto Inland Sea, Japan*, Plankton Biol. Ecol., 51 (1), 7–14.

Tester P. A., Stumpf R. P., Vukovic F. M., Fowler P. K., Turner J. T., 1991, *An expatriate red tide bloom: Transport, distribution, and persistence*, Limnol. Oceanogr., 36 (5), 1053–1061.

Tiselius P., Kiørboe T., 1998, *Colonization of diatom aggregates by the dinoflagellate Noctiluca scintillans*, Limnol. Oceanogr., 43 (1), 154–159.

Uhlig G., Sahling G., 1990, *Long-term studies on Noctiluca scintillans in the German Bight population dynamics and red tide phenomena 1968–1988*, J. Sea Res., 25 (1–2), 101–112.

Venugopal P., Haridas P., Madhupratap M., Rao T. S. S., 1979, *Incidence of red water along South Kerala coast*, Indian J. Mar. Sci., 8, 94–97.