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Geographical distribution of red and green *Noctiluca scintillans*

P. J. HARRISON[1, *], K. FURUYA[2], P. M. GLIBERT[3], J. XU[1], H. B. LIU[1], K. YIN[4], J. H. W. LEE[1], D. M. ANDERSON[5], R. GOWEN[6], A. R. AL-AZRI[7], A. Y. T. HO[8]

[1] *Hong Kong University of Science and Technology, Clear Water Bay, Hong Kong, China*
[2] *Department of Aquatic Bioscience, University of Tokyo, Tokyo 113-8657, Japan*
[3] *University of Maryland Center for Environmental Science, Horn Point Laboratory, Cambridge MD 21613, USA*
[4] *School of Marine Sciences, Sun Yat-Sen University, Guangzhou 510275, China*
[5] *Department of Biology, Woods Hole Oceanographic Institution, Woods Hole MA 02543, USA*
[6] *Fisheries and Aquatic Ecosystems Branch, Agri-Food and Biosciences Institute, Belfast BT9 5PX, UK*
[7] *Department of Marine Science and Fisheries, Sultan Qaboos University, Muscat 123, Sultanate of Oman*
[8] *Agriculture, Fisheries, and Conservation Department, Hong Kong, China*

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Abstract The dinoflagellate *Noctiluca scintillans* is one of the most important and abundant red tide organisms and it is distributed world-wide. It occurs in two forms. Red *Noctiluca* is heterotrophic and fills the role of one of the microzooplankton grazers in the foodweb. In contrast, green *Noctiluca* contains a photosynthetic symbiont *Pedinomonas noctilucae* (a prasinophyte), but it also feeds on other plankton when the food supply is abundant. In this review, we document the global distribution of these two forms and include the first maps of their global distribution. Red *Noctiluca* occurs widely in the temperate to sub-tropical coastal regions of the world. It occurs over a wide temperature range of about 10°C to 25°C and at higher salinities (generally not in estuaries). It is particularly abundant in high productivity areas such as upwelling or eutrophic areas where diatoms dominate since they are its preferred food source. Green *Noctiluca* is much more restricted to a temperature range of 25°C–30°C and mainly occurs in tropical waters of Southeast Asia, Bay of Bengal (east coast of India), in the eastern, western and northern Arabian Sea, the Red Sea, and recently it has become very abundant in the Gulf of Oman. Red and green *Noctiluca* do overlap in their distribution in the eastern, northern and western Arabian Sea with a seasonal shift from green *Noctiluca* in the cooler winter convective mixing, higher productivity season, to red *Noctiluca* in the more oligotrophic warmer summer season.

Keyword: *Noctiluca*; global distribution; distribution map; green *Noctiluca*; dinoflagellate

1 INTRODUCTION

The heterotrophic dinoflagellate *Noctiluca scintillans* Macartney 1810 (syn. *milaris* Suriray 1836) Kofoid and Swezy 1921 is one of the most prominent "red tide" organisms. It is found in all temperate, subtropical and tropical coastal waters (Elbrachter and Qi, 1998) and in most major upwelling regions (Brongersma-Sanders, 1948a, b). Surprisingly, there is one report of its occurrence in 3°C seawater at an ice station off Point Barrow, Alaska (Tibbs, 1967), but it appears to be absent from the Antarctic Ocean. Often on calm days from late spring to early summer surface aggregations generate streaks and patches of bright to dull reddish surface waters in coastal and shoreline areas around the world. Carotenoids are responsible for much of its orange-red color (Balch and Haxo, 1984). *Noctiluca* differs from most other red tide dinoflagellates since it is: 1) relatively large (200–600 μm); 2) phagotrophic with little food preference (phytoplankton, bacteria, small zooplankton, fish eggs, etc.; 3) a raptorial particle feeder or a passive mucoid net filter feeder; 4) has passive buoyancy; 5) has a diploid vegetative cell while other dinoflagellates are haploid, and 6) produces a large number of gametes during its sexual reproduction (Fukuda and Endoh, 2006). This

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* Corresponding author: harrison@ust.hk

neritic, non-toxic, heterotrophic dinoflagellate can often replace copepods as the primary grazer on phytoplankton. *Noctiluca* is less harmful than most HAB species, but fish yields in aquaculture areas are sometimes decreased due to massive blooms of this species (Huang and Qi, 1997).

There is only one species in the genus *Noctiluca* and therefore only the genus will be used throughout and since *Noctuluca milaris* is a synonym for *Noctiluca scintillans* that should no longer be used to avoid confusion. However, there are 2 forms (Fig.1). Red *Noctiluca* is heterotrophic. In contrast green *Noctiluca* contains a photosynthetic symbiont *Pedinomonas noctilucae* and to date this is the only symbiont to inhabit the green form. Green *Noctiluca* can survive without an external food supply via photosynthetic products from its symbiont, but it can also conduct phagotrophy like the red form when the phytoplankton food supply is high (Saito et al., 2006). Interestingly, there is limited overlap in their geographical distributions. Red *Noctiluca* is broadly distributed and is mainly found in temperate and sub-tropical coastal waters. For example, red *Noctiluca* is the most frequent causative organism of red tides in Japan every year (Fisheries Research Agency, 2008). In contrast, the distribution of green *Noctiluca* appears to be much more restricted and is mainly limited to tropical Asian waters and parts of the Arabian Sea, Gulf of Oman and the Red Sea.

This paper reviews the global distribution of red and green *Noctiluca* and provides the first global distribution maps of these two forms (Figs.2, 3; Tables 1, 2). In some previous reports, there was no clear assessment with regard to which form was being reported and confusion occurred when the authors used mixed terminology — e.g. 'a red tide of green *Noctiluca*'. In our review, we have noted such cases when they were cited. However, because *Noctiluca* is often highly visible as a red surface layer, it has been casually reported in many papers and the grey literature and thus we may have missed some of these very brief reports, especially in the early papers. This review focuses on the factors that influence the distribution of these two forms of

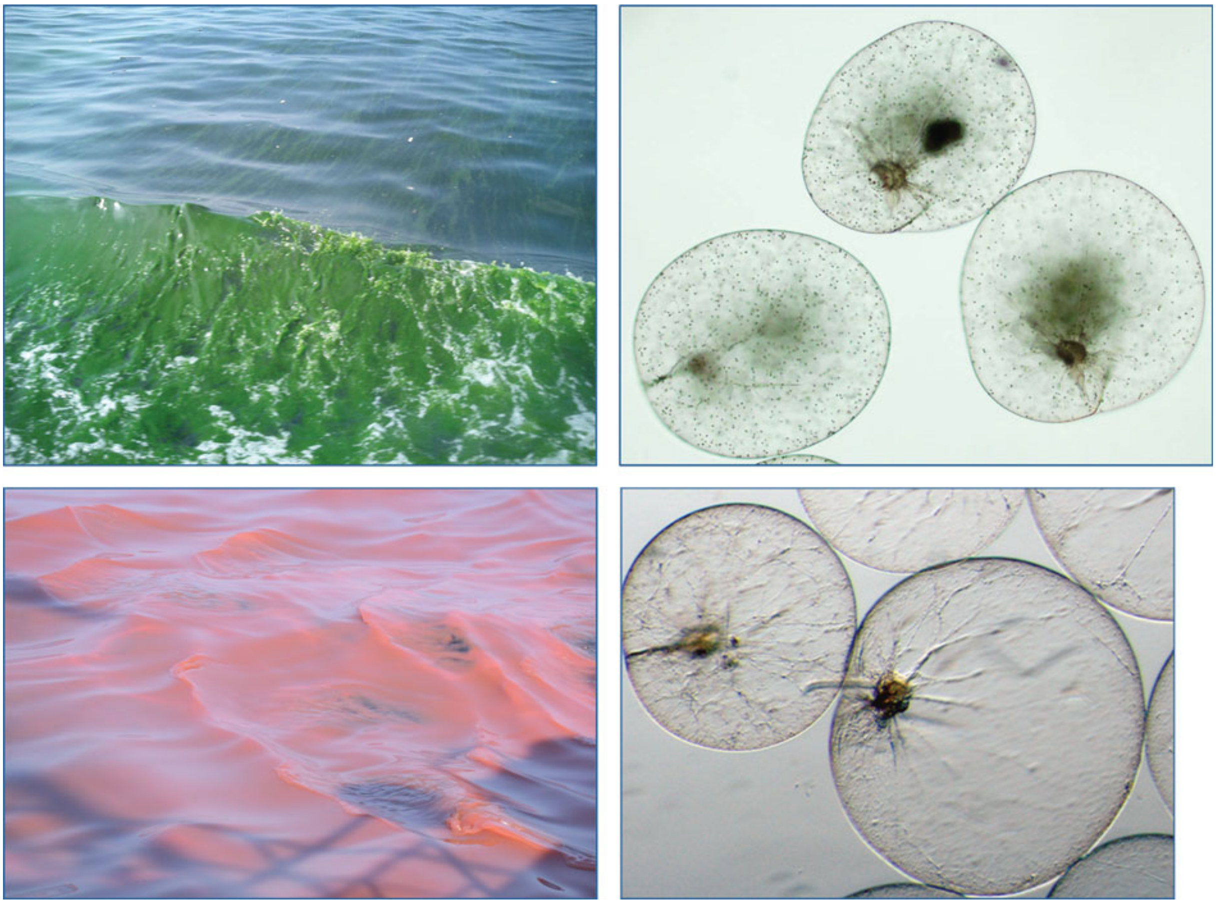

Fig.1 Two forms of *Noctiluca scintillans*: the green form (upper) with the endosymbiont *Pedinomonas noctilucae* and the heterotrophic red form (lower)

Upper and lower right photos are by K. Furuya and the lower left photo is by J. Li (from GEOHAB, 2010)

Fig.2 Map of the global distribution of red *Noctiluca scintillans* derived from Table 1

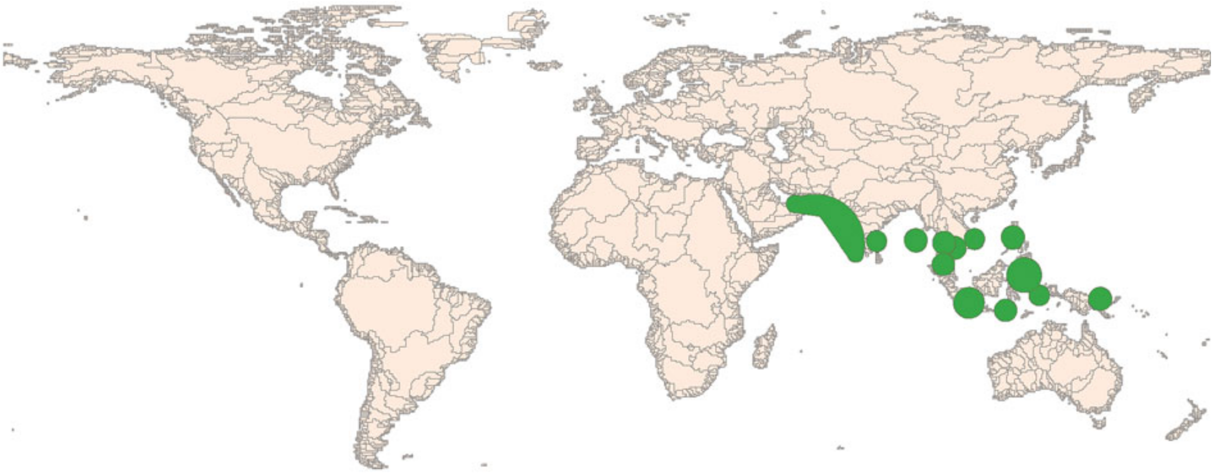

Fig.3 Map of the global distribution of green *Noctiluca scintillans* derived from Table 2

Noctiluca in various geographical regions such as temperate waters of Europe, the Black Sea, Australia and northern Asia for red *Noctiluca* and sub-tropical/tropical waters of southern Asia and the Arabian Sea for green *Noctiluca*. A review of *Noctiluca*'s chemical composition, grazing, growth rates and population dynamics is in progress. The previous review by Elbrachter and Qi (1998) covered many different aspects of *Noctiluca*, but its distribution was only briefly covered.

2 RED *NOCTILUCA*

2.1 Northern Europe, Mediterranean, Black Sea and West Africa

Red *Noctiluca* has been extensively studied in the German Bight in the North Sea (Schaumann et al., 1988; Hesse et al., 1989; Uhlig and Sahling, 1990, 1995; Kirchner et al., 1996; Fock and Greve, 2002). Spring time peaks in abundance occur from March/April to late June, with an abrupt 'crash' in the population in August, often within a few hours (Uhlig and Sahling, 1990). Diatom blooms often follow *Noctiluca* blooms due to the release and regeneration of nutrients when it dies. A very small population is maintained over winter, despite the low water temperatures of <5°C and even to 0°C (Uhlig and Sahling, 1995). Abundance maxima have been observed on a 3 year cycle in the German Bight over a 20 year period (Uhlig and Sahling, 1990). The abundance peaks about ~10^4–10^5 cell/L and, generates a gelatinous and mucilaginous consistency in the surface water of the patch. In the Dutch North Sea, the seasonal cycle and abundance levels are

Table 1 Reported occurrences of red *Noctiluca scintillans* from the literature with cell numbers, water quality (WQ) data such as salinity (*S*), temperature (*T*), dissolved oxygen (DO), light (LT), and nutrients (N.D. indicates no WQ data)

Region	Site	Latitude	Longitude	Sampling date	Cells# in Bloom (*100 cell/L)	WQ data	Reference
North Sea	German Bight, Helgoland Roads	53°30′–55°00′N	6°00′–9°00′E	1968–1988		N.D.	Uhlig and Sahling (1990)
North Sea	German Bight, Helgoland	53°30′–55°00′N	6°00′–9°00′E	1974–1982		N.D.	Greve and Reiners (1988)
North Sea	German Bight	53°–55°N	6°–9°E	April 23–July 23, 1979; May 23–July 17, 1984	0–480	*T*, *S*	Fock and Greve (2002)
North Sea	Southern Bight	50°–54°N	1°–6°E	1993, 1994		*T*, *S*	Schaumann et al. (1998)
SW North Sea	Mouth of Thames estuary	51°–53°N	0°–2°E			*T*, *S*, Nutrients	Weston et al. (2008)
North Sea	German Bight	53°–55°N	6°–9°E				Hesse et al. (1989)
North Sea	SW German Bight	54°–55°N	6°–9°E	July/Aug., 1984	150	*T*, *S*, Nutrients	Schaumann et al. (1988)
North Sea	Helgoland Roads	53°30′–55°00′N	6°00′–9°00′E	1974–1995		*T*	Heyen et al. (1998)
Dutch coastal, North Sea	Meetpost Noordwijk	52.267° N	4.300° E	1984–1985		*T*	Daan (1987)
North Sea	Dutch coast, North Sea	53°–55°N	6°–9°E	Jan., 1976–1985		*S*, Nutrients	Zevenboom et al. (1991)
North Sea	Helgoland and German Bight	53°30′–55°00′N	6°00′–9°00′E	16-year study			Uhlig and Sahling (1985)
NW Spain	Central Cantabrian coast, Bay of Biscay	43°35′–43°43′N	5°53′–6°05′W	April 27–28, 1995	390–11 380	*T*, *S*	Quevedo et al. (1999)
Bay of Biscay	Mouth of the Gironde estuary	45°30′N	2°00′W	May 2–10, 1995	70	*T*, *S*	Sautour et al. (2000)
Bay of Biscay	Grid of 267 stations	43.32°–46.12°N	1.29°–4.31°W	May 2–16, 2004	up to 100	*T*, *S*, LT	Albaina and Irigoien (2007)
Southern Bay of Biscay		41°30′–45°N	1°–10°W	March 30–April 22, 2004	100–1 000	*T*, *S*	Cabal et al. (2008)
Black Sea		41°–46°N	28°–41°E	April, 1989		*T*	Uysal (2002)
Black Sea, Romanian shelf		45°05′21″N	30°02′27″E	1959–1965 and 1970–1986	0.1–1 677	N.D.	Porumb (1992)
NW Black Sea	Danube Delta	45°27′N	29°42′45″E	July, 1995	2 640		Scheffel and Weisse (1997)
Southern Black Sea		40°–44°N	28°–42°E	1996–1999		*T*, *S*, DO	Kideys and Romanova (2001)
NW & NE Black Sea		41°–46°N	28°–41°E	1959–1996		Nutrients	Kideys et al. (2000)
NW Black Sea	Bulgarian, Romanian, Ukrainain	42°30′–46°30′N	28°00′–33°00′E	1960–2005		*T*, Nutrients	Oguz and Velikova (2010)
Northern Adriatic basin	Gulf of Trieste.	42°00′–44°00′N	13°30′–15°00′E	June, 1999 to July, 2002	0–589	*T*, *S*	Umani et al. (2004)
Northern Adriatic		42°00′–44°00′N	13°30′–15°00′E	Summers of 1988, 1989, 1991			Degobbis et al. (1995)
Turkey	Izmit Bay	40.6°–41.0°N	29.0°–30.0°E				Koray et al. (1992)
Turkey	Sea of Marmara	39°30′–41°30′N	26°00′–30°00′E	Sep., 2001–Aug., 2002	2 170	*T*, *S*	Yilmaz et al. (2005)
NE Marmara Sea	Izmit Bay	40.6°–41.0°N	29.0°–30.0°E	Oct., 2001–Sep., 2002	1 110–1 260	*T*, *S*	Isinibilir et al. (2008)

To be continued

Table 1 Continued

Region	Site	Latitude	Longitude	Sampling date	Cells# in Bloom (*100 cell/L)	WQ data	Reference
Western Sweden	Gullmarsfjorden	58°19′N	11°32′E	Oct., 1996		*T*, LT	KiØrboe et al. (1998)
North Wales	Menai Strait, Gwynedd	53°14′5″N	4°03′18″E	June and Sep.		N.D.	Lucas (1982)
West France	Brittany	48.72°N	3.56°E	July, 1967			Le Fèvre and Grall (1970)
Russia	Glubokoye Lake	67.67°N	45.87°E				Polishchuk and Ghilarov (1981)
France	Ban-yuls-sur-mer	42.48°N	3.12°E			N.D.	Métivier and Soyer–Gobillard (1988)
Greek	Coastal waters	31.00°N	22.00°E	2000–2004			Nikolaidis et al. (2005)
Plymouth	The Bay of Douarneney (BD)	(BD) 48°18.5′N,	5°13′W	July August 1995 & June 1957		N.D.	Nicol (1958)
	The Bay of Concaneau (BC)	(BC) 47°51′N,	3°58′W				
Sagami Bay, central Japan	Stn. W	35°09′30″N	139°09′25″E	April 12–July 22, 2003	20 000	*T*, *S*, Nutrients	Baek et al. (2009)
Japan	Eastern Seto Inland Sea	34°28′N	134°24′W	May, 1992–Dec., 1997	0–40	*T*, *S*, LT	Tada et al. (2004)
Japan	Eastern Seto Inland Sea	34°28′N	134°24′W	May, 1995–Dec., 1998	0–126	Nutrients	Pithakpol et al. (2000)
Japan	Ie-shima Islands, Seto Inland Sea	34°35′N	134°30′E	July 17–Aug. 11, 1997	0–3.45	N	Nakamura (1998)
Japan	Sagami Bay	35°09′49″N	139°10′33″E	Monthly 1997 to 2004	0–6 000	*T*, *S*	Miyaguchi and Hirata (2006)
Japan	Ariake Sound	33°00′–32°30′N	130°00′–130°30′E	Autumn 2002, 2003 and 2004		N.D.	Nakamura and Hirata (2006)
Japan	Mikawa Bay	34.8°N	137.1°E	1979–1990		N.D.	Yamamoto et al. (1997)
Japan	Awazi Island, Hyogo Prefecture,	34.30°N	135°E	April, 2004		N.D.	Fukuda and Endoh (2006)
Korea	Saemangeum dyke	35°46′33″N	126°28′56″E	Mar., May, July & Oct., 2007 & 2008	1.73–158.3		Lee et al. (2009)
Korea	Pusan Harbor	35°05′N	129°05′E	Oct.1990 and Jan., Apr. July 1991		*T*, *S*, DO, Nutrients	Hong et al. (1994)
SW East Sea, Korea	Ulleung Basin (UB)	35°–38.5°N	129–133°E	Autumn (2000 and 2001) and Spring (2001)		*T*, *S*	Kang et al. (2004)
Korea	Chinhae Bay	34°59′–35°01′N	128°30′–128°40′E	Feb.–Sep., 1993	35–826	*T*, *S*, DO	Kang et al. (1996)
Southern Korea	Jinhae Bay	34°40′–35°02′N	128°29′–128°45′E	Aug., 1979–1983			Lee (1985)
Western Korea	Kyeonggi Bay, Inchon Dock	37°28′30″N	126°37′30″E	Dec., 1989–Dec., 1991		*T*, *S*, DO	Kim and Lee (1994)
South coast of Korea	Jangmok Bay	34°59′N	128°40′E	July–Sep., 2003		*T*, *S*, DO	Jang et al. (2010)
Korea	Deukryang Bay	34°27′–34°40′N	127°–127°10′E	July and Sep., 1992 & Jan., and Mar., 1993		*T*, *S*	Han et al. (1995)

To be continued

Table 1 Continued

Region	Site	Latitude	Longitude	Sampling date	Cells# in Bloom (*100 cell/L)	WQ data	Reference
Yellow Sea	Mid-Eastern Yellow Sea	36°00′–37°00′N	124°00′–127°00′E	April, 1987–June, 1988		N.D.	Hwang and Choi (1993)
China	Southern Yellow & East China seas	22°–36°N	116°–132°E	1933–2004		N.D.	Tang et al. (2006)
China	Zhujiang (Pearl) River estuary	21°48′–22°27′N	113°03′–114°19′E	Apr., 2005–Sep., 2006			Fang et al. (2009)
China	Zhejiang coastal, Bohai Sea	21°48′–39°00′N	100°00′–120°00′E	After 2002			Lin et al. (2010)
China	Bohai Bay	37°50′–39°20′N	117°30′–119°00′E	Jul. 26 & Aug. 20, 2006			Sun et al. (2010)
Bohai Sea, China	Bohai Bay	37°50′–39°20′N	117°30′–119°00′E	1978–1981	10 000	Nutrients, DO	Zou et al. (1985)
South China Sea		20°00′–25°00′N	100°00′–120°00′E	1980–2003		N.D.	Wang et al. (2008)
South China Sea	Dapeng Bay	22°34′–22°37′N	114°15′–114°20′E				Qi et al. (1993)
South China Sea	Dapeng Bay	22°34′–22°37′N	114°15′–114°20′E	March, 1990–June, 1992	2–2 800	*T*, *S*	Huang and Qi (1997)
East China Sea	Changjiang (Yangtze) River	29°00′–32°30′N	122°00′–123°20′E	Aug. 3–22, 2000		*T*, *S*, DO	Chen et al. (2003)
East China Sea	Changjiang (Yangtze) River	29°00′–32°30′N	122°00′–123°20′E	1968–1997		Nutrients	Yan et al. (2003)
South China	Guangdong & Hong Kong	15°00′–25°00′N	100°00′–123°00′E	1998		*T*, DO, Nutrients	Qi et al. (2004)
Hong Kong	Tolo Harbor	22°15′–22°35′N	114°10′–14°20′E	July 30 and Aug. 1, 1991		*T*, DO	Tang et al. (1994)
				Jan. 24 and 25, 1992 .			
Hong Kong	Tolo Harbor	22°15′–22°35′N	114°10′–114°20′E	August, 1969–July, 1971	28 000	*T*, *S*	Fung and Trott (1973)
Hong Kong		22°00′–23°00′N	113°30′–114°30′E	1983–1998		Date form AFCD	Yin (2003)
Hong Kong	Six regions	22°15′–22°35′N	114°10′–114°20′E	1975–1986		N.D.	Wong (1989)
Kowloon Peninsula, Hong Kong	Junk Bay	22°10′–22°30′N	114°10′–114°20′E	Three times a month from 1997 to 1998		N.D.	Lu and Hodgkiss (2004)
NE Hong Kong	Tolo Harbour and Mirs Bay	22°00′–22°30′N	114°10′–115°00′E	July, 2003 & June, 2005	0–1 200	*T*, *S*	Liu and Wong (2006)
Hong Kong	Deep Water Bay	22°15′–22°35′N	114°10′–114°20′E	June, 1971		*T*	Morton and Twentyman (1971)
NE Hong Kong	Tolo Harbour	22°15′–22°35′N	114°10′–114°20′E	1976–1986		*T*, *S*, Nutrients, LT, DO	Lam and Ho (1989)
Gulf of Thailand		5°00′–13°30′N	99°00′–106°00′E	1981–1987		*T*, *S*, Nutrients, LT, DO	Suvapepun (1989)
Gulf of Thailand		5°00′–13°30′N	99°00′–106°00′E	1988–1995, 17 blooms		N.D.	Cheevaporn and Menasveta (2003)
Vietnam		21°01′N	105°52′E	1993			Lam and Hai (1996)
SE India	Gulf of Mannar, Keezhakkarai	8°46′–9°14′N	78°09′–79°14′E	Oct., 2008			Edward et al. (2009)
southern Kerala coast, India	South of Trivandrum	8°19′N	76°30′E		> 9 000	*T*, *S*, Nutrients	Sahayak et al. (2005)
Orissa Coast, India	Rushikulya River, Bay of Bengal	12°22′N	85°02′E	April, 2005	2 380	*T*, *S*, DO, Nutrients	Mohanty et al. (2007)

To be continued

Table 1 Continued

Region	Site	Latitude	Longitude	Sampling date	Cells# in Bloom (*100 cell/L)	WQ data	Reference
Indonesia	Jakarta Bay	6°00′–6°20′S	106°2′–107°00′E	Since 1976 at least		N.D.	Maclean (1989)
Gulf of Mexico & Caribbean		15°–33°N	88°–115°E	1987–1992	1 570–22 070	N.D.	Gomez-Aguirre (1998)
California	La Jolla, near San Diego	32.89°N	117.24°W	April, 1995		N.D.	Franks (1997)
Southern California	San Diego	32.89°N	117.24°W	March, 1976	0–0.1	*T*	Kimor (1979)
Eastern California	Guaymas & Mazatlan	23°13′–29°55′N	106°25′–110°59′W				Cortés-Altamirano et al. (1995)
Southern California	Scripps Pier	32.867°N	117.257°W	April 22–29, May 13–20, 1982	0–0.1	N.D.	Balch and Haxo (1984)
Mexico	Veracruz	19°11′N	96°10′W	May & Nov., 1996, Mar. May & Oct., 1997			Figueroa-Torres and Weiss-Martinez (1999)
Mexico	Gulf of Mexico	16°00′–32°00′N	88°00′–112°00′W				Ochoa et al. (2002)
The United States	Chesapeake Bay	37°00′–39°00′N	76°00′–77°00′W	1984–2002		*S*, LT, Nutrients	Marshall et al. (2006)
Coos Bay, Charleston, Oregon.& Friday Harbor, Washington		(CB) 43°21′10″N (FH) 48°32′10″N	124°19′50″W 123°00′19″W			LT	Johnson and Shanks (2003)
NSW, Australia	Sydney Harbour (Port Jackson)	35°58′S	151°00′E	1993–1996		N.D.	Tong et al. (1998)
NSW, Australia	Port Hacking near Sydney	34°06′S	151°12′E	March, 1997–1998	0.01–0.05	*T*, *S*, Nutrients	Dela-Cruz et al. (2002)
NSW, Australia	Botany Bay & Port Hacking	32°–36°S	151°–152°E	Monthly July 1996–June 1997	63–2 200	*T*, *S*, DO	Murray and Suthers (1999)
NSW, Australia	Port Stephens	27°–33°S	152°–156°E	Jan. 1997		*T*	Oke and Middletor (2001)
SE Australia		31°00′–35°00′S	150°00′–152°00′E	Sept. & Nov., 1998; Feb. & Mar., 1999		*T*, *S*, DO, Nutrients	Dela-Cruz et al. (2003)
NE Australia	Moreton Bay	27°30′S	153°1′E	May–Sept., 1996		N.D.	Heil et al. (1998)
NSW, Australia		30°05′–32°05′S	152°–153°05′E	Nov., 1998 and Jan., 1999	0–0.1	*T*, Nutrients	Dela-Cruz et al. (2008)
Australian coastal waters	Cairns, Port Lincoln & Port Esperance	Cairns (16°57′S, 145°45′E) Lincoln (34°42′S, 135°52′E) Esperance (43°19′S, 147°4′E)		2008		*T*	Hallegraeff et al. (2008)
Australian coastal waters		10°00′–50°00′S	110°00′–160°00′E	1944–2005		*T*, *S*, Nutrients	Thompson et al. (2009)
Tasmania	Huon Estuary	40°00′–45°00′S	144°00′–149°00′E	1996–2005		*T*	Thompson et al. (2008)
NE New Zealand		35°–37°N	174.5°–175.5°E	Oct., 1996 & Jan., 1997		*T*, *S*	Walker et al. (2000)
NE coast of New Zealand	Hauraki Gulf	35°–37°N	174.5°–175.5°E	Sep. 13–27, 1996, Oct. 18–29, 1996,	>10 in late spring	*T*, Nutients	Hall et al. (2006)

To be continued

Table 1 Continued

Region	Site	Latitude	Longitude	Sampling date	Cells# in Bloom (*100 cell/L)	WQ data	Reference
				Nov. 26–Dec. 7, 1996, Jan. 26–Feb. 5, 1997			
NE coast of New Zealand	Hauraki Gulf	35°–37°N	174.5°–175.5°E				Chang et al. (2003)
NE coast of New Zealand	Hauraki Gulf	35°–37°N	174.5°–175.5°E	Oct.–Dec., 2002			Chang et al. (2008)
Brazil	Rio de Janeiro & Cabo Frio	23°–25°S	41°–44°W	Jan. & Feb., 2002		*T*	KiØrboe (2003)
South Africa	St Helena Bay, Cape Columbine	32.0°–35.0°S	18.0°–20.0°W	Feb. 20–27, 1995		*T*, *S*, Nutrients	KiØrboe et al. (1998)
Red Sea	Al Shuqayq coast, SW Saudi Arabia	19°65′N	42°18′E	2004–2006	0–30 000	*T*, *S*, DO, Nutrients	Mohamed and Mesaad (2007)
Gulf of Guinea	Nigerian coast	3°00′N	4°00′E				Akin-Orida et al. (2006)
SW coast of India	Mangalore	7°00′–13°00′N	70°00′–77°00′E	May, 1993			Nayak and Karun (2000)
Arabian Sea	SW coast of India	7°00′–13°00′N	70°00′–77°00′E	Sep.–Oct., 2004		*T*, *S*, DO, Nutrients	Joseph et al. (2008)
Arabian Sea		7°00′–13°00′N	70°00′–77°00′E	Feb. 20–Mar. 11, 2004		*T*, *S*, Nutrients	Prakash et al. (2008)
NE Arabian Sea	Pakistan's shelf and adjacent waters	23°–26°N	62°–69°E	Jan. 19–June 20, 1977		*T*, *S*	Saifullah and Chaghtai (1990)
Arabian Sea	Gulf of Oman	18°00′–26°00′N	52°00′–60°00′E	Feb., 2004–Feb., 2006		*T*, *S*, DO, Nurients	Al-Azri et al. (2010)
Northern Arabian Sea	Gulf of Oman	18°00′–26°00′N	52°00′–60°00′E			*T*	Gomes et al. (2009)

similar to the German Bight (Kat, 1979; Zevenboom et al., 1991). Abundance decreases by an order of magnitude offshore with a tendency for marked concentrations in frontal areas (Hesse et al., 1989).

A long time series near Helgoland in the North Sea revealed a similar seasonal abundance pattern, but the abundance was much less than in the German Bight (Uhlig and Sahling, 1985). Using a multivariate statistical approach, Heyen et al. (1998) detected a high correlation between the winter SST and summer abundance which involved the timing of the predators *Pleurobrachia pileus* and *Sagitta*. *Noctiluca* has been found on the west coast of Norway up to 62°N (Tangen, 1979). In the southern part of the North Sea off London, Weston et al. (2008) observed that *Noctiluca* occurred after the diatom spring bloom and was responsible for the grazing pressure on the flagellate community.

In 1967, Le Fevre and Grall (1970) studied a large *Noctiluca* bloom off the western coast of Brittany and concluded that a surface convergence produced by an outflow of coastal water probably contributed to the bloom. *Noctiluca* has frequently been observed in the western English Channel (Boalch, 1987) and associated with tides (Holligan, 1979). In the southern region of the Bay of Biscay, *Noctiluca* has been shown to be dominant in the spring and associated with frontal structures where it exerts heavy predation pressure on eggs of the copepod *Acartia clausi* (Quevedo et al., 1999; Cabal et al., 2008). *Noctiluca* food vacuoles containing toxigenic *Dinophysis* and *Pseudo-nitzschia* have been reported in samples from the Galician Rias Baixas (NW Spain) and it was suggested that *Noctiluca* may act as a vector of phycotoxins to higher trophic levels or transport to natural shellfish beds (Escalera et al., 2007). In coastal waters off the Gironde estuary and the west coast of Spain, *Noctiluca* was dominant during the spring (Fraga and Sanchez, 1979; Sautour et al., 2000). It has been recorded off the northwest African upwelling region off Mauretania and Senegal (Margalef, 1973; Elbrachter, unpubl. results) and even the Red Sea (Brongersma-Sanders, 1948a).

Table 2 Reported occurrences of green *Noctiluca scintilans* from the literature with cell numbers, water quality (WQ) data such as salinity (*S*), temperature (*T*), dissolved oxygen (DO), light (LT) and nutrients (N.D. indicates no WQ data)

Region	Site	Latitude	Longitude	Dates of Bloom	Cells # in Bloom (100 cell/L)	WQ data	Reference
Manila Bay, Philippine	Western Manila Bay	14°35′N	120°59′E	N.D.	N.D.	Nutrients	Hansen et al. (2004)
Manila Bay	Off Limay	14°35.78′N	120°36.08′E	N.D.	N.D.	N.D.	Furuya et al. (2006b)
Vietnam	Van Phong-Ben Goi Bay	12.5°N	109°W	Feb., 1995	55	*S*, DO, Nutrients	Lam and Hai (1996)
Vietnam	Upwelling south coast	11°15′N	108°47″W				
Southeast Borneo	Halmahera Island & Celebes Sea	1°00′–3°00′N	122°00′–128°00′E	N.D.	N.D.	N.D.	Sweeney (1978)
Indonesia	Jakarta Bay	5°10′–6°10′S	106°20′–107°03′E	Nov., 1975; May, 1976; Jan. May, 1977; Jan. Nov., 1978 Jul. Jul., 1979; Jul., 1986; Feb. May Jun. Jul., 1987	6–53	N.D.	Adnan (1989)
Indonesia	Jakarta Bay	5°10′–6°10′S	106°20′–107°03′E	1993	32×10^4	N.D.	Praseno and Wiadnyana (1996)
Indonesia	Ambon Bay	3°47′55″S	128°15′	1995	1.3×10^4	N.D.	Praseno and Wiadnyana (1996)
Indonesia	Ambon Bay	3°47′55″S	128°15′	May, 1994–Apr., 1995	1.4×10^5	*T*, *S*, Nutrients	Sidabutar et al. (1996)
Bostrem By, Sek Harbor & Larlar Island, New Guinea	Sek & Karkar Islands	4°32′–4°41′S	145°44′–145°58′E	N.D.	N.D.	N.D.	Sweeney (1971)
Western Gulf of Thailand	Gulf of Thailand	12°40′–13°30′N	100°00′–101°00′E	1985 throughout the year, 1981–1987 Jan.–Feb.	N.D.	N.D.	Suvapepun (1989)
Gulf of Thailand	Chonburi & Bangpakong River mouth	13°18′–13°27′N	100°50′–101°00′	Jul.–Aug., 2002 & Feb.–Jun., 2003	18.7×10^3 (Max)	*S*, *T*, Nutrients	Sriwoon et al. (2008)
Gulf of Thailand	Chonburi	13°18′–13°27′N	100°50′–101°00′	Jun., 2003; Oct., 2003; Apr., 2004, Jun., 2004; Jul., 2004	1.0×10^5	*S*, DO, *T*, Nutrients	Lirdwitayaprasit et al. (2006)
Gulf of Thailand	Inner Gulf of Thailand	12°40′–13°30′N	100°00′–101°00′E	N.D.	N.D.	N.D.	Menasveta (2000)
Gulf of Thailand	Chao Praya River mouth, Bangkok	13°45′N	100°35′E	Aug., 1989; Jan., 1990	N.D.	N.D.	Okaichi et al. (1991)
Gulf of Thailand	Sichang Island	12°40′–13°30′N	100°00′–101°00′E	N.D.	N.D.	N.D.	Piyakarnchana et al. (1986)
Penang, Malaysia	Penang harbor	5°25′N	100°15′E	N.D.	N.D.	N.D.	Endo (1918)
India	Off Calicut	11°25′N	75°77′E	Dec., 1952; Mar., 1953	N.D.	*S*	Subrahmanyan (1954)
east India	Kalpakkam	12°34′N	80°10′E	Oct., 1988	$(0.3–2.5)\times10^4$	*T*, *S*, DO, Nutrients	Sargunam et al. (1989)
India	Goa,	15°20′–15°40′N	73°30′–73°50′E	Sep., 1973; May, 1977; Feb.–Apr., 1987	5.1×10^3	DO, Nutrients	Devassy et al. (1979)
Goa, India	Zuari & Mandovi estuary	15°24′5″–15°26′	73°48′E	Feb., 1987	32 250	*S*, DO, *T*, Nutrients	Devassy (1989)
India	Port Blair Bay	11°38′705″N	92°42′513″E	Jun.–Jul., 2000	$(1.5–2.3)\times10^4$	*T*, Nutrients	Eashwar et al. (2001)

To be continued

Table 2 Continued

Region	Site	Latitude	Longitude	Dates of Bloom	Cells # in Bloom (100 cell/L)	WQ data	Reference
India	Port Blair Bay & Minnie Bay	11°38′705″N	92°42′513″E	Dec., 2002	17 111	*T*, *S*, DO, Nutrients	Dharani et al. (2004)
Pakistan	Miani Hor	25°31′N	66°20′E	Dec., 1999; Dec., 2000; Dec., 2001; Feb., 2001	3×10^3–2.4×10^6	SST, *S*	Chaghtai and Saifullah (2006)
				Mar., 2003; Mar., 2004; Nov., 2004; Dec., 2004			
Arabian Sea	Arabian Sea	10°72′–21°N	65°82′–74°78′E	Feb.–Mar., 2004	N.D.	SST, *S*, Nutrients	Prakash et al. (2008)
Oman	Gulf of Oman	24°30′N	58°45′E	Mar., 2003; Mar., 2004; Mar., 2007	1 200–4 000 cell/L	SST, Nutrients	Gomes et al. (2008)
Java Sea	Mouth of the Kumai river	6°5′–6°12′S	108°18′–108°20′E	Mar. 22, 1934	N.D.	*S*, Nutrients	Delsman (1939)
Cambodia	Ream Bay	13°00′N	105°00′E	Mar. 7–20, 1927	N.D.	N.D.	Weill (1929)
Indonesia	Bay of Bima on Sumbawa Island	8°15′S	118°00′E	N.D	N.D.	N.D.	Weber et al. (1890)
Tanzania	Coastal waters	6º18′25″S	34º51′14′E	July, 2003–June, 2004			Lugomela (2007)

Noctiluca has been observed in the Mediterranean Sea (Jacques and Sournia, 1978). In particular, the northern Adriatic Sea is a site for prominent blooms of this species (Fonda-Umani et al., 2004). In 1977, the first recorded *Noctiluca* bloom occurred in the Gulf of Trieste (Fonda-Umani, 1985), and this observation demonstrated its ability to reproduce actively even at low winter temperatures of 6.5°C, possibly due to the development of a new ‘cold’ strain (Fonda-Umani et al., 2004). It has bloomed since 1978 in the northwest Adriatic, south of the Po River due to high nutrient inputs, enhanced stratification from the freshwater and surface heating in the spring (Boni, 1983). A bloom covering much of the Adriatic occurred in 1980 with abundances up to $>10^6$ ind./m^3 (Fonda-Umani et al., 1983; Malej, 1983). After 1988, the phosphate concentration decreased sharply due to the banning of phosphorus in detergents by the Italian government and there was a shift from this red tide species to the mucilaginous phenomena with low *Noctiluca* abundance (Degobbis et al., 1995). Since 1997, *Noctilica* blooms have reappeared with abundances ~10^3 to 10^4 ind./m^3 and are highest in areas near the Po River where plankton productivity and stratification are high (Fonda-Umani et al., 2004). Over an 18 year time series, Fonda Umani et al. (2004) found no significant relationship between *Noctiluca* abundance and total phytoplankton or diatoms alone. However there was a negative relationship with net zooplankton biomass, indicating a possible competition for food resources. *Noctiluca* is one of the HAB species that commonly occurs in coastal waters off Greece, especially in Thermaikos and Amvrakikos Bays (Nikolaidis et al., 2005; Chalaris, 2010) and in Izmir Bay in the Agean Sea (Koray et al., 1992).

Noctiluca is very common in the spring in the Sea of Marmara, a small basin that connects the Mediterranean and the Black Sea and plays an important role in the top-down control of the zooplankton community (Yilmaz et al., 2005; Isinibilir et al., 2008). *Noctiluca* exhibited two prominent peaks in abundance in November and May and its abundance was inversely correlated to chl-*a* (Isinibilir et al., 2008).

Severe eutrophication of the Romanian littoral waters in the western Black Sea is linked to the explosive development of *Noctiluca* starting about 1980 (Polishchuk et al., 1981; Porumb, 1989, 1992; Bologa et al., 1995). *Noctiluca* occurs along the Bulgarian coast, particularly in Novorossiysk Bay (Selifonova, 2000). It also dominates along the entire Turkish Black Sea coast, including the Bosphorus Junction of the Sea of Marmara (Uysal, 2002; Uysal and Sur, 1995), but is less abundant in the eastern Black Sea. Mean densities were about 1 000 to 6 000 ind./m^3 in the 1970s and increased by 8–10 times in the 1980s. According to Vinogradov and Grinberg (1979), *Noctiluca* accounted for about 40% of the fresh weight of the plankton biomass. Even though surface water temperatures are only 1–3°C in the winter, a small population was maintained and thought to feed on the existing small amount of plankton (Porumb, 1992). The key factor for the rapid increase in abundance in the spring is the presence of food (mainly diatoms) and calm conditions and during this time *Noctiluca* is present throughout the photic zone. However, in the main basin of the Black Sea, the gelatinous zooplankton are dominated by the ctenophores *Pleurobrachia pileus* and *Mnemiopsis leidyi* and the scyphozoan *Aurelia aurelia* (Kideys et al., 2000; Kideys and Romanova, 2001). In a recent synthesis paper by Oguz and Velikova (2010) for the Bulgarian and Ukranian areas, the biomass of *Noctiluca* was reported to be ~100 mg/m^3 during the pristine stage in the 1960s and early 70s. However, it rapidly increased by one order of magnitude to ~1 000 mg/m^3 during the late 1970s due primarily to the high phytoplankton biomass. Starting in the 1980s, relatively high biomass of *Noctiluca* coincided with cold SST years (1985, 1993, 2003) and vice versa for warm years in the mid 1990s when biomass was 10% of the cold years.

There have also been recent reports of *Noctiluca* off the coast of Nigeria (Nwankwo, 1997; Akin-Oriola et al., 2006). Further investigation along the coast of other west African countries is warranted.

2.2 Northern Asia (Japan, eastern Russia, Korea and northern China)

The first scientific study on *Noctiluca* in Japan was made by Nishikawa in 1900 and for a review of HABs in Japan, see Fukuyo et al. (2002). In the Seto Inland Sea of Japan, *Noctiluca* is one of the most common red tide species occurring over the last few decades (Kuroda, 1995; Kondo et al., 2004; Tada et al., 2004). Tada et al. (2004) found that the stability of the water column in late spring to early summer appeared to promote the increase in the abundance of *Noctiluca* up to ~4 000 cell/L (i.e. ~4–5 g C/m^2, assuming 0.35 μg C/cell). When it is abundant (only ~200–400 ell/L), its biomass is often several times higher than that of calanoid copepods (Nakamura, 1998). During summer, its cells are larger, possibly due to a lack of food and its disappearance was related to water temperatures >25°C (Nakamura, 1998).

The relationship between a bloom of *Noctiluca* and environmental factors has also been investigated in Sagami Bay, near Tokyo, from 1997 to 2004 (Miyaguchi et al., 2006; Baek et al., 2009). A stepwise multiple linear regression analysis showed that wind direction and rainfall were significantly correlated with the variation in the abundance of *Noctiluca*. They suggested that the bloom formation could be separated into three phases: 1) initial increase in *Noctiluca* when optimal hydrographic and biological factors occurred; 2) stratification during low winds and rainfall; and 3) development of swarmer cells that can grow into vegetative cells. Another recent study in Sagami Bay, concluded that the reduction in phytoplankton abundance (mainly diatoms) was mainly controlled by *Noctiluca* grazing, while an overall increase in phytoplankton (non-diatoms) was stimulated by nutrient loading from freshwater (Baek et al., 2009). In Ariake Sound and Mikawa Bay in western Japan, wind was reported to play an important role in the aggregation of the surface layer blooms (Nakamura and Hirata, 2006; Yamamoto et al., 1997). *Noctiluca* was reported to possibly damage the fishery off Kyushu (near Nagasaki) by consuming large amounts of fish eggs (Enomoto, 1956).

Noctiluca has been observed frequently in the far eastern coast of Russia (Konovalova, 1989) and the Sea of Japan, in Patrokl Bay (Peter the Great Bay) where it has reached up to 10^4 to 10^5 cell/L in June and July (Orlova et al., 2002). There are also several earlier reports of its occurrence in this bay in the early 1900s (Ostroumov, 1924; Tagatz, 1933).

In southern Korea, in Pusan Harbor and Chinhae Bay, *Noctiluca* has been shown to be very abundant in April where it can make up to 90% of the total zooplankton abundance in Chinhae Bay (Kim et al., 1993; Hong et al., 1994; Kang et al., 1996). In Jangmok Bay, on the south coast of Korea, the summer abundance oscillates with temperature (Jang et al., 2010). They found that peaks of abundance up to ~100 ell/L occurred when water temperature was <25°C, but quickly declined to <10 cell/L when the temperature reached >28°C. Mesozooplankton abundance strongly correlated with *Noctiluca* density, suggesting that it is a strong competitor with mesozooplankton for food resources.

The first documented HAB event in China was caused by *Noctiluca* and *Skeletonema costatum* in Zhejiang coastal waters near Shanghai, in 1933 (Fei, 1952). For a review of HABs in China, see Yan et al. (2002). In the early 1980s, *Noctiluca* occurred in Bohai Bay, northern China, from July to Sept and it was one of the top three red tides in this bay (Zou et al., 1985). *Noctiluca* and *Skeletonema costatum* were dominant red tide species in the southern part of the Yellow Sea and the East China Sea off the mouth of the Changjiang (Yangtze) River, especially before 2000 (Chen et al., 2003; Yan et al., 2003; Tang et al., 2006; Xu, 2009).

2.3 Southern Asia (South China Sea)

In Hong Kong waters, one of the first records of *Noctiluca* was in the southern waters in 1971 (Morton and Twentyman, 1971; Fung and Trott, 1973). *Noctiluca* is now the most common red tide species in Hong Kong (Wong, 1989; Qi et al., 1993; Yin, 2003; Lu and Hodgkiss, 2004), especially in Tolo Harbour (Lam and Ho, 1989; Yin, 2003; Liu and Wong, 2006). A two-year study in Tolo Harbour, a semi-enclosed bay in NE Hong Kong, revealed that blooms occurred during winter and early spring (Dec–April) and the highest density was 10^5 cell/L (Liu and Wong, 2006). Blooms usually appear first in Mirs Bay (beyond the mouth of Tolo Harbour) and then higher densities occur in the harbor later, suggesting that an increase in the abundance in Mirs Bay may have been limited by food and water currents and mixing. Although no significant correlations have been found between chl-*a* and *Noctiluca* abundance, high chl-*a* was correlated with the presence of small cells, suggesting active growth of *Noctiluca* (Liu and Wong, 2006). In the harbor, *Noctiluca* feed on a variety of phytoplankton and microzooplankton (diatoms, dinoflagellates, copepod eggs and small ciliates). Its abundance has been shown to decline when temperatures were >25°C and after a heavy rain (Liu and Wong, 2006). A recent monthly survey over 3 years in Hong Kong coastal waters (Chen unpubl. results) revealed that *Noctiluca* blooms occurred in the eastern waters of Hong Kong (Port Shelter) in winter to early spring every year, similar to Tolo Harbour. In contrast, about 40 km west in the western waters of Hong Kong near the Zhujiang (Pearl) River estuary, blooms were observed much later (May). Yin (2003) provided a comprehensive review of the influence of seasonal monsoons and oceanographic processes on the occurrence and distribution of *Noctiluca* in Hong Kong waters.

In Dapeng Bay, a semi-enclosed bay near the border between Hong Kong and mainland China, blooms of *Noctiluca* have occurred from March to June when temperatures ranged from 16°C to 28.6°C (Huang and Qi, 1997). A *Noctiluca* bloom also occurred in November off Shanwei, about 200 km northeast of Hong Kong (Qi et al., 2004). The highest densities (~10^4 cell/L) occurred over a narrower range of 19–25°C and surface temperatures of ~30°C appeared to be its lethal temperature during summer. It is not known how *Noctiluca* survives over summer, although water temperatures at depth could reduce temperature stress. It has been observed to be concentrated at convergence areas in the northwestern part of the bay. During heavy rain events when salinity decreased by >4, the population declined rapidly. Therefore, ideal conditions appear to be calm conditions without wind and rain and weak tidal currents during a neap tide (Huang and Qi, 1997). *Noctiluca* constitutes >50% of the red tides in Dapeng Bay and was probably utilizing the high primary productivity in the bay.

Based on an analysis of existing data bases for the South China Sea during 1980–2003, Wang et al. (2008) reported that red *Noctiluca* dominates in the northern region, while *Pyrodinium bahamense* dominates in the southern and eastern regions. It has been reported in northern Vietnam (Cat ba and Halong Bay area) (Chu, pers. comm.) and Indonesian waters (Adnan, 1989). Green *Noctiluca* occurs in other parts of the South China Sea and this will be discussed later.

In the Bay of Bengal, off the Orissa Coast of eastern India near the Rushikulya River, a bloom (3×10^5 cell/L) of red *Noctiluca* was observed in April 2005 (Mohanty et al., 2007) when surface temperature was 28.5°C (but cooler than normal due to the upwelling season). This is much higher than the optimum range of 19–25°C previously reported for Hong Kong and the northern part of the South China Sea. It occurred along with *Trichodesmium erythraeum*, *Ceratium furca*, *C. tripos*, and 19 species of diatoms that were supported by nutrients from the upwelling. On the southern Kerala coast off Trivandrum (8°19′N, 76°30′E) a very large bloom (~10^6 cell/L) of red *Noctiluca* occurred in Sept during very calm seas and was accompanied by various species of diatoms and *Ceratium* sp. and low nutrients (Sahayak et al., 2005). A bloom of red *Noctiluca* was reported off the southwest coast of India near Mangalore (8°N and 76°E) during calm weather and low nutrients (Joseph et al., 2008) and further north off Mangalore (13°N and 75°E) by Nayak and Karunasagar (2000) and Venugopal et al. (1979). Off Goa (15°N, 73°W), red *Noctiluca* was observed during calm weather in Sep. 1973 and during May 1977, the latter bloom followed a large bloom of *Trichodesmium erythraeum* and co-occurred with a mixed diatom bloom (Devassy, 1989).

2.4 Northeastern Pacific and Northwest Atlantic

Red *Noctiluca* has been observed off Alaska (Lutz and Incze, 1979) and even in very cold waters off Point Barrow Alaska (Tibbs, 1967). It also occurs in several inlets in British Columbia (Quayle, 1969), in the San Juan Island (coast of Washington) (Fredrickson and Strom, 2009), and off La Jolla, California (Kofoid and Swezy, 1921; Smayda, 1974; Holmes and Williams, 1967). A very large bloom occurred from Santa Barbara to the Mexican border after heavy rains in 1995 (Howard, 1996).

Further south along the Baja California coast, *Noctiluca* frequently occurs along with *Myronecta rubra* (previously *Mesodinium rubrum*), especially in Bahia Concepcion during autumn and winter (Cortes-Altamirano et al., 1995a, b; Altamirano et al., 1996; Garate-Lizarraga et al., 2001; Ochoa et al., 2002). During this period, winter mixing occurs and brings up nutrients for phytoplankton which serve as food for *Noctiluca*. Blooms of up to 4×10^3 cell/L can occur when water temperature ranges from 18–21°C. In Mazatlan Bay, Mexico, a red tide of both the toxic dinoflagellate *Gymnodinium catenatum* and *Noctiluca* occurred in Jan. 2000 (Alonso-Rodriguez et al., 2005). *Noctiluca* was observed to actively graze on *G. catenatum* and may act as a 'biocontrol' mechanism for toxic blooms.

Noctiluca has been noted off the eastern coast of the USA in the vicinity of Chesapeake Bay, but it has never been very dominant in that region (Marshall, 1976; Marshall et al., 2006). It occurs in Florida waters and the Gulf of Mexico (Buskey, 1995; Gomez-Aguirre, 1998; Figueroa-Torres and Weiss-Martinez, 1999) as well as in the Caribbean (Ferraz-Reyes et al., 1979; Gomez-Aguirre, 1998). Further south, off northeastern Venezuela (off Sucre State), *Noctiluca* was noted along with *Gonyaulax tamerensis* and *Cochlodinium* sp. (Reyes-Vasquez et al., 1979). It has been observed on the east coast of South America, off Brazil (Odebrecht et al., 1995), off Uruguay (Mendez, 1993) and off Argentina (Balech, 1988). On the west coast of South America it blooms off Peru (Brongersma-Sanders, 1948b) and off Chile (Elbrachter and Qi, 1998).

2.5 Australia, New Zealand, Brazil and South Africa

Noctiluca has frequently occurred along the entire southeast coast of Australia between 28°S and 34°S with the highest concentrations occurring downstream of upwelling areas with high diatom abundance (Brongersma-Sanders, 1948a; Jeffery and Carpenter, 1974; Dela-Cruz et al., 2008). However, it is much less abundant in estuaries, suggesting that these red tides are a coastal/continental shelf phenomenon (Murray and Suthers, 1999; Ajani et al., 2001). High concentrations (>100 cell/L) occur in spring and again in late summer with low concentrations (<5 cell/L) in mid summer and winter. Cells appear to be larger, but in poor nutritional state, in summer (Murray and Suthers, 1999). The peaks in abundance were not correlated with temperature since the water temperature was 16°C in spring and 22°C in summer, but *Noctiluca* was absent when temperatures were >27°C.

A comprehensive physical-biological interaction investigation was conducted off the SE coast of Australia to resolve whether *Noctiluca* blooms were enhanced by sewage inputs from Sydney (Tong et al., 1998) and other cities or from nutrients derived from upwelling (Dela-Cruz et al., 2002, 2003, 2008). They showed that upwelling was the dominant mechanism that stimulated diatom blooms that in turn stimulated *Noctiluca* growth during the austral spring and late summer. The highest abundances occurred where upwelling was the strongest. However, the peaks of *Noctiluca* abundance were only ~80 cell/L (Dela-Cruz et al., 2008). Small cells were associated with the upwelling area, indicating that these cells were actively growing due to a good food supply of diatoms. *Noctiluca* was most abundant when water temperatures were between 19–24°C, which is the water temperature between 32.5°S and 35°S in austral spring and summer. Cells were advected southward with the East Australian Current (EAC) and thus this large scale physical flow field affected its spatial distribution. The highest abundances were recorded south of 31.5°S, where the EAC separates from the coast. The high abundances partly arise from the southward advection and retention of cells and partly from upwelling inshore of the separated EAC driven by cross-shelf boundary layer fluxes (Oke and Middleton, 2001). There have been very few reports of *Noctiluca* north of the EAC separation point where summer temperatures are >25°C (Ajani et al., 2001). Anomalously, high cell numbers occurred during 1997 when a strong El Niño resulted in warmer surface temperatures in winter and thus the growing season of *Noctiluca* was longer than normal.

Hallegraeff et al. (2008) and Hallegraeff (2010) examined long term data sets and found that *Noctiluca* was present in the Sydney region during 1860 to 1950 and then it expanded southward during 1980–1993 and reached Tasmania in 1994–2005. The first observations of its occurrence in Queensland, West Australia and South Australia were reported in 2008 (Hallegraeff et al., 2008). These observations suggest that *Noctiluca* may have extended its range very significantly in the last few decades, although this may be partially due to an increase in the number of observations.

Noctiluca has been observed as far south as the Huon Estuary, Tasmania (Thompson et al., 2008; 2009). The strengthening of the EAC may also explain its ~1 700 km southward movement from Moreton Bay over the last several decades (Wood, 1964; Dela-Cruz et al., 2002, 2003) and its recent arrival in southern Tasmania.

In late spring, *Noctiluca* has reached densities of >1 000 œll/L but declines in late summer on the northeast continental shelf of New Zealand in the area of Hauraki Gulf (Chang et al., 2003; Hall et al., 2006). In the same area in the austral spring of 2002, *Noctiluca* occurred along with a nearly mono-specific bloom of *Karenia concordia* (Chang et al., 2008). In the Hauraki Gulf, dead cells of *Noctiluca* were observed with *K. concordia* cells inside. However outside the Gulf, there were no *Karenia* cells and healthy *Noctiluca* had diatoms, larvae of several marine organisms and a few cysts of *Alexandrium catenalla* inside (Chang et al., 2005). In the spring of 1999, pink blooms (~10^6 cell/L) of *Noctiluca* were observed in Wellington Harbour at the bottom end of the north island and were noticeably different than the usual orange-red blooms along the northeast coast of the north island and the Hauraki Gulf.

Noctiluca has been observed in the autumn in the South Atlantic off Brazil at 32°S (Cassino Beach) and off the Benguela upwelling system, South Africa. *Noctiluca* is one of the important microzooplankters in upwelling areas probably because of the high abundance of diatoms, its usual preferred food source. It has been observed on several occasions in the southern Benguela upwelling system (Horstman, 1981; Painting et al., 1993; KiØrboe et al., 1998; Pitcher et al., 2000). Upwelling-induced diatom blooms (mainly *Chaetoceros* sp.) have been shown to be terminated by aggregate formation with most of the aggregates colonized by *Noctiluca* that fed upon the diatoms in the aggregates (KiØrboe et al., 1998). Blooms have also occurred in bays near Capetown (Grindley and Heydorn, 1970; Grindley and Taylor, 1971).

2.6 Arabian Sea

Red *Noctiluca* has been observed in the Arabian Sea in the Indus shelf region of Pakistan (Saifullah and Chaghtai, 1990) and on both the east and west coasts of India (Subrahmanyan, 1954; Devassy, 1989) and it geographically overlaps with green *Noctiluca* but they appear in different seasons or in different water masses as discussed below.

In the coastal waters of the northern part of the Arabian Sea bordering Pakistan, red *Noctiluca* occurs during a short period in late winter (February and March) when water temperatures are 22–24°C. Compared to the Baluchistan shelf west of Karachi, the blooms are more frequent off the Indus Delta shelf due to eutrophication and the subsequent higher productivity in this area (Saifullah and Chaghtai, 1990).

3 GREEN NOCTILUCA

While red *Noctiluca* has a fairly broad global distribution (Fig.1; Table 1), the green form appears to be restricted to the western tropical Pacific and the Indian Ocean (Fig.3; Table 2) The difference between the two forms is the presence (green) or absence (red) of the photosynthetic prasinophyte endosymbiont *Pedinomonas noctilucae*.

Green *Noctiluca* is one of the most recurrent bloom species in the Southeast Asian waters, and has been expanding its distribution during the last two decades (Furuya et al., 2006a). The duration and bloom intensity of green *Noctiluca* blooms have been increasing in Manila Bay, the upper Gulf of Thailand, and Jakarta Bay (Furuya et al., 2006a) and large blooms have been observed via satellite in NW Arabian Sea and the Gulf of Oman (Gomes et al., 2008). Green *Noctiluca* exhibits two nutritional modes according to laboratory studies on isolated clones: one requiring an external food supply and the other depending on photosynthesis. The latter grows photoautotrophically for many generations, but it also feeds on food particles. Phagotrophy promotes faster vegetative growth than autotrophy, and provokes sexual reproduction (Furuya et al., 2006a).

Recent field studies show that bloom formation of green *Noctiluca* depends on active phagotrophy (Sriwoon et al., 2008) and that it survives primarily on photoautotrophy under food-limited conditions (Furuya, unpubl. results). These observations lead to the hypothesis that progressive eutrophication in Southeast Asia provides a competitive advantage to green *Noctiluca* over co-existing species by increasing food availability (Furuya, pers. comm.). Furthermore, once it becomes dominant, its active grazing is expected to prevent population growth of co-existing phytoplankton. In addition, *Noctiluca* may have some impact on other HABs by grazing on them (Hansen et al., 2004).

The distribution of green *Noctiluca* appears to be quite restricted to the coastal waters in Southeast Asia and the Indian Ocean. The northern boundary in the western Pacific appears to be at Bashi Channel, and the Vietnamese coast. The eastern boundary is in Papua New Guinea, while the southern boundary is uncertain as there are no reports as yet from Australian waters. The distribution of green *Noctiluca* extends westward into the Indian Ocean over to the west coast of Oman.

In the Philippines, the main bloom forming dinoflagellate species changed over time in Manila Bay. Until the 1990's, *Pyrodinium bahamense* v. *compressum* was dominant (Furio and Gonzales, 2002), but since 2001, green *Noctiluca* has become dominant (Borja and Furio, unpubl.; Azanza and Miranda, 2001). In the Philippines, it is present most of the year and large blooms occur from Feb. to April in Manila Bay (Jacinto et al., 2006), off Manila (Hansen et al., 2004), off Limay (Furuya et al., 2006b; Azanza et al., 2001), and in the entire Manila Bay where the highest chl-*a* concentrations were >500 μg/L (Furuya et al., 2006b). The increasing eutrophication in the bay also produces large amount of diatoms such as *Chaetoceros* sp. and *Skeletonema costatu*m which may provide a good food supply for *Noctiluca* (Furuya et al., 2006b; Chang et al., 2009).

In Vietnam, green *Noctiluca* is widely distributed along the coast from 10°N to 16°N and 106°W to 109°W (Lam et al., 1997). Very large blooms (5×10^6 cell/L) of green *Noctiluca* occur in spring in Van Phong-Ben Goi Bay at 12.5°N and 109°15′W (Lam and Hai, 1996; Lam et al., 1997), and further south along other parts of the Cambodian and Vietnamese coasts, especially off Binh Thuan Province (Weil, 1929; Hai et al., 2010). Hai et al. (2010) observed that green *Noctiluca* occurs in the upwelling waters of the south central coast of Vietnam, after colonies of *Phaeocystis globosa* disintegrate. *Noctiluca* reportedly fed on the individual cells that were released from the colonies.

The first report of green *Noctiluca* was in the Dutch Indies (Weber and Weber-van Bosse, 1890). *Noctiluca* occurs in eastern Indonesia as far east as Papua New Guinea, and northern Papua New Guinea and Borneo in September and October (Sweeney, 1976), Bostrem Bay, Sek Harbour and Karkar Islands near Papua New Guinea (Sweeney, 1971). Blooms (~10^6 cell/L) occur in Jakarta Bay throughout the year and are likely due to increasing eutrophication (Delsman, 1939; Praseno and Adnan, 1978, Adnan, 1989, 1992; Praseno and Wiadnyana, 1996). It has also been recorded in Ambon Bay (Sidabutar et al., 1996), and Baie de Bima (Weber and Weber-van Boise, 1890).

In the upper Gulf of Thailand, since the first record in 1957, the frequency and intensity of green *Noctiluca* blooms have been increasing over the past 2 decades (Pollution Control Department, 2003). The situation is similar in Jakarta Bay. Progressive eutrophication of these bays is well documented in Manila Bay (Chang et al., 2009), Gulf of Thailand (Cheevaporn and Menasveta, 2003; Wattayakorn, 2006), and Jakarta Bay (Adnan, 1992). Several studies in Thailand have documented the occurrence of green *Noctiluca* on the western coast of the middle and upper Gulf of Thailand (Suvapepun, 1989), Chonburi and Bangpakong River mouth (Sriwoon et al., 2008; Lirdwitayaprasit et al., 2006), inner Gulf (Menasveta, 2000), Chao Praya River mouth (Okaichi et al., 1991) and Sichang Island (Piyakarnchana et al., 1986). Green *Noctiluca* often occurs along with *Ceratium furca*, *Trichodesmium erythraeum* and various diatom species (Suvapepun, 1989; Cheevaporn and Menasveta, 2003). Blooms occur seasonally with larger blooms in the western part of the Gulf of Thailand from May to September during the SW monsoon and clockwise circulation in the upper gulf. Low abundance occurs from November to February during the NE monsoon in the western part of the gulf when counter-clockwise circulation occurs (Lirdwitayaprasit et al., 2006; Sriwoon et al., 2008). High densities are observed during the summer rainy season, especially during calm days after heavy rain (Sriwoon et al., 2008).

There are only a few early reports of green *Noctiluca* in Malaysia off Penang (Endo, 1918; Peters, 1926).

Green *Noctiluca* was reported off the South Andaman Island in Port Blair Bay and Minnie Bay (11°39′N, 92°43′E) for the first time in June and July of 2000 when its abundance reached 2×10^4 cell/L and chl-*a* was 18 mg/m^3 (Eashwar et al., 2001). It bloomed with *Ceratium* spp. Rainfall appeared to supply nutrients for a small bloom of diatoms, but when the nutrients became depleted, the *Noctiluca* bloom declined. In December 2002, when water temperatures were ~29–30°C and nutrients were very low, *Noctiluca* reached ~10^4 cell/L (Dharani et al., 2004). It has been observed in several localities on the east coast of India, off Calicut (Subrahmanyan 1954) and off Kalpakkam in October (Sargunam et al. 1989). Despite very low nutrients, cells reached 4×10^4 cell/L and chl-*a* was 28 mg/m^3 when water temperatures were ~30°C. There were very few diatoms during the peak of the *Noctiluca* bloom.

On the southeast coast of India near the southern tip of India at Palk Bay (9°16′N and 79°12′E), Prasad (1953; 1958) was one of the first to observe green *Noctiluca* that was reported to be associated with fish kills.

On the west coast of India, both the red and green *Noctiluca* has been reported. Possibly the first report of green *Noctiluca* was made by Subramanyan (1954) in the eastern Arabian Sea and he described the symbiotic green flagellate as *Protoeuglena noctiluca*. Over 30 years later, Katti et al. (1988) observed a large bloom of ~10^6 cell/L in January in the eastern Arabian Sea off Mangalore (13°N, 75°W). Off the coast of Goa, Devassy (1989) observed two red *Noctiluca* blooms in 1973 and 1977 and then, in February 1987, a bloom of green *Noctiluca* occurred along with *Ceratium*, providing evidence that red and green *Noctiluca* can occur in the same waters, but during different seasons. Similarly, in the more oligotrophic offshore coastal waters of the northwest Arabian Sea bordering Pakistan, red *Noctiluca* was observed mainly during the winter NE monsoon upwelling season when water temperatures were 22–26°C (Saifullah and Chaghtai, 1990). In contrast, green *Noctiluca* was observed for the first time in the early 2000s, in eutrophic inshore waters with dense mangrove vegetation during winter months (Chaghtai and Saifullah, 2006). Off Pakistan, red and green *Noctiluca* both occur during the winter months when water temperatures are lower, but green *Noctiluca* occurs in more eutrophic inshore waters, while red *Noctiluca* occurs on more oligotrophic offshore waters. The Gulf of Oman is a third example of the co-occurrence of red and green *Noctiluca* in the same area, but in different seasons (red mainly in February to April and green in August–September). In the Gulf of Oman (from Khasab to Sur) red *Noctiluca* bloomed every year between January and May from 1978 up to 1998 when water temperatures were 23–27°C and was tentatively linked to fish kills (Thangaraja et al., 2007). Then in 1999, green *Noctiluca* occurred for the first time in August and September and the bloom intensity has been increasing since then. It occurs along with *Trichodesmium* sp. and *Ceratium* sp. (Thangaraja et al., 2007). It is worth mentioning that the red and green colour of the blooms in the same area does not necessarily indicate the co-occurrence of the red and green *Noctiluca* in the Gulf of Oman, since a reddish color could indicate the dying stage of the green *Noctiluca* (Al-Azri, unpubl. data).

Recent studies in the eastern Arabian Sea confirm that both red and green *Noctiluca* occur in the same waters, but in different seasons. A large scale oceanographic study was conducted in 2004 between 10°N to 22°N along the west coast of India (Parab et al., 2006; Prakash et al., 2008). This area is dominated by seasonally reversing monsoons. In the southern part of the west coast of India during the southwest summer monsoon in September/October when heavy rains increase stratification and reduce the supply of nutrients to the surface, red *Noctiluca* occurs. In contrast in the NE Arabian Sea, during the northeast winter monsoon, convective mixing brings up nutrients and increases primary productivity of diatoms and dinoflagellates and followed by green *Noctiluca* blooms along with *Trichodesmium* with water temperatures of about 26–28°C (Parab et al., 2006; Prakash et al., 2008).

Al-Azri et al. (2010) reported red *Noctiluca* at two stations along the southern coast of the Gulf of Oman. During late winter and early spring, it was about 25% of the total phytoplankton biomass, but surprisingly it occurred in April, June, August and even in October, but no water temperatures were given. Al-Azri et al. (2007) examined the relationship between environmental conditions and the occurrence of red *Noctiluca*. Bloom formation started in early winter and reached a maximum in spring, but brief peaks occurred in June and September when water temperatures were 25–29°C.

The use of satellite data in conjunction with shipboard sampling has yielded a clearer picture of winter blooms of green *Noctiluca* in the northwestern Arabian Sea. Satellite data were very useful since green *Noctiluca* made up a large portion of the total Chl biomass, however, only surface blooms are detected by satellites (Gomes et al., 2008). Their satellite altimetry data suggested a strong coupling between green *Noctiluca* blooms and mesoscale cold-core eddies which bring nutrients to the surface in the Gulf of Oman. They suggest that the winter time diatom blooms during the northeast monsoon are short-lived contradicting the earlier view that diatom blooms dominated during the NE winter monsoon. A shift appears to have occurred in recent years, where the diatom bloom has been replaced by large blooms of green *Noctiluca* from late January to March when convective mixing is strong and water temperatures are <26°C (Dwivedi et al., 2006). Green *Noctiluca* is often associated with *Trichodesmium* after March during the beginning of the spring intermonsoon season in the offshore regions of the eastern and western Arabian Sea as well as along the northwest coast of India and in the Gulf of Oman. During this time, NO_3 was <1 μmol/L, while NH_4 was high, indicating active grazing or atmospheric deposition of NH_4 which has been documented to have increased substantially in recent years (Duce et al., 2008). A bloom of *Trichodesmium* frequently followed the *Noctiluca* bloom. Gomes et al. (2008) concluded that green *Noctiluca* clearly appeared to be associated with colder waters in the north and was rarely seen in warmer water >26°C off the southwest coast of India where *Trichodesmium* bloomed, especially during May to Sept. It remains to be resolved which factors such as water temperature, nutrient concentrations, stratification, and grazing are responsible for the recent appearance of large scale green *Noctiluca* blooms in the NE and NW Arabian Sea.

Given the intensity of oceanographic cruises in the Arabian Sea during the JGOFS program (e.g., Baars, 1994; Krishnaswami and Nair, 1996; Smith et al., 2001; Burkill, 1999), this is a region of the world where the recent increase in green *Noctiluca* has been frequently documented. Both the warming of Eurasia due to climate change (Goes et al., 2005) and the increasing use of anthropogenic sources of nitrogen in the past several decades in Asia and globally (e.g. Seitzinger et al., 2002, 2005; Glibert et al., 2006; Duce et al., 2008), have led to changes in phytoplankton biomass and community structure. Blooms of *Noctiluca* now occur in regions that are <24°C, high in concentrations of ammonium, and undersaturated with respect to oxygen (Parab et al., 2006). Mesoscale eddies may contribute to the dispersal of these blooms in the Arabian Sea (Gomes et al., 2008). The expansion of green *Noctiluca* has now reached the coastal waters of Tanzania during the northeast monsoon period (Lugomela, 2007).

In the Red Sea off the southwest coast of Saudi Arabia where water temperatures range from 18–29°C and salinity from 37–39, blooms of red *Noctiluca* are common and microscopic examination revealed that red *Noctiluca* was grazing on diatoms and some dinoflagellates. Green *Noctiluca* was reported for the first time during February 2004 and 2005 when temperature was <25°C (Mohamed and Mesaad, 2007).

4 CONCLUSION

4.1 Factors associated with the distribution of red *Noctiluca* (Fig.2; Table 1)

Red *Noctiluca* occurs over a wide temperature range, normally 10°C to 25°C in temperate regions, but as low a 3°C off Alaska and up to 29–30°C off the SW coast of India. This suggests that different temperature strains probably exist. It occurs in upwelling and other productive areas and may also be linked to eutrophication since it requires a good food supply of mainly diatoms in order to maintain its high growth rate. It appears to grow in the water column and the 'apparent bloom' occurs at the very end as a highly visible thin red layer on the surface where it may disintegrate quickly. Therefore the highly visible 'apparent bloom' at the surface actually signals the end of the bloom. Red *Noctiluca* may be concentrated at the shoreline in bays by the wind, or at convergences to produce a very high abundance. Heavy rains may cause a sharp decrease in the population. It is interesting that it often blooms with *Ceratium* sp. which is mixotrophic and also an active grazer. *Trichodesmium* often follows a *Noctiluca* bloom.

4.2 Factors associated with the distribution of green *Noctiluca* (Fig.3; Table 2)

Green *Noctiluca* occurs mainly in tropical waters in SE Asia and the Arabian and Red Seas. Both red and green *Noctiluca* can occur at the same site but in different seasons. Green *Noctiluca* occurs during the winter convective mixing season (NE monsoon) when productivity is high in the Arabian Sea. In contrast, red *Noctiluca* may occur during the more oligotrophic summer (SW monsoon) season when water temperatures are nearly 30°C. Green *Noctiluca* is now common in the northern Arabian Sea, Gulf of Oman and it recently been observed off Tanzania.

4.3 General trends in the occurrence of *Noctiluca*

Overall, *Noctiluca* is a HAB species that is increasing globally. Although in some regions this may be, at least in part, a function of increasing observations and awareness, in other regions, such as southeast Asia, this is not the case. There are examples of range expansion of red *Noctiluca* along the west coast of Australia (Hallegraeff, 2008, 2010) and green *Noctiluca* expanding from the Arabian Sea westward to Tanzania (Gomes et al., 2008; Lugomela, 2007). Plankton dynamics have changed and are changing due to climate change and increasing eutrophication. *Noctiluca* may be a coastal or offshore manifestation of eutrophication in some areas, since an increase in nutrients provides an increase in phytoplankton, its main food supply as a grazer.

Optical detection of *Noctiluca* blooms has been reported recently in Belgian waters using sensors mounted on ships and airplanes and detection by satellites may be possible in the future (Mol et al., 2007). A strong optical signature suggests that remote mapping of these blooms should be possible. A detection algorithm was proposed based on a combination of a high reflectance threshold with a sharp increase in reflectance in the range 520–580 nm. Remote detection in the future will provide better coverage of *Noctuluca's* spatial and temporal distribution in the future.

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