Oceanological and Hydrobiological Studies

International Journal of Oceanography and Hydrobiology

Volume 49, No. 4, December 2020
pages (391-397)

ISSN 1730-413X
eISSN 1897-3191

First recorded bloom of *Akashiwo sanguinea* (Dinophyceae) from the Cochin backwaters, a tropical estuarine system along the South Eastern Arabian Sea

by

Twinkle Sathish, Lathika Cicily Thomas, Aishwarya, Niya Benny, K.B. Padmakumar*

DOI: **10.1515/ohs-2020-0034**
Category: **Original research paper**
Received: **February 22, 2020**
Accepted: **May 18, 2020**

Department of Marine Biology, Microbiology and Biochemistry, School of Marine Sciences, Cochin University of Science and Technology (CUSAT), Kochi-16, Kerala, India

Abstract

Akashiwo sanguinea, a cosmopolitan red tide-forming dinoflagellate, is reported for the first time as a bloom from the Cochin estuary along the South Eastern Arabian Sea. Monthly sampling showed the continuous presence of *A. sanguinea* with occasional blooms. Blooms of *A. sanguinea* with the highest abundance of 2.8×10^5 cells l^{-1} were observed during the monsoon season (June 2019) with chlorophyll *a* of 17.2 mg m^{-3}. The bloom period was characterized by higher concentrations of nitrate (26 μmol l^{-1}) and phosphate (3.8 μmol l^{-1}). Routine monitoring of the bloom region showed the survival of the *Akashiwo sanguinea* population in the temperature (26 to 30°C) and salinity (22 to 24 PSU) range indicating its eurythermal and euryhaline characteristics.

Key words: *Akashiwo sanguinea*, Dinoflagellate, Harmful Algal Blooms, Cochin estuary, South Eastern Arabian Sea

* Corresponding author: kbpadmakumar@gmail.com

DE GRUYTER

online at www.oandhs.ug.edu.pl

Introduction

Akashiwo sanguinea (Hirasaka) G. Hansen and Moestrup is a well-known red tide-forming dinoflagellate that occurs in coastal marine ecosystems with varying salinity owing to its euryhaline nature. The tolerance to salinity fluctuations makes the species capable of thriving in different environmental conditions (Matsubara et al. 2007; Phlips et al. 2011; 2012; Park et al. 2013; Badylak et al. 2014a,b). *Akashiwo sanguinea* is a cosmopolitan species and has been observed in the form of blooms in many coastal and estuarine areas around the world, including the North Eastern Pacific and South Pacific (Fukuyo et al. 1990; Cai et al. 2006; Park et al. 2013; Kiefer & Lasker 1975; Robinson & Brown 1983; Horner et al. 1997; Gómez-Aguirre 1998; Cloern et al. 2005; Rines et al. 2010; Du et al. 2011; White et al. 2014; Hallegraeff 1991; Kahru et al. 2004). *A. sanguinea* has also been reported from the North Atlantic, the Mediterranean, the South-West Atlantic and from the Gulf of Mexico (Bochstahler & Coats 1993; Badylak & Phlips 2004; Phlips et al. 2011; 2012; O'Boyle & McDermott 2014; Gómez & Boicenco 2004; Feyzioğlu & Öğüt 2006; Domingos & Menezes 1998; Melo et al. 2007; Koening et al. 2014; Harper & Guillen 1989; Robichaux et al. 1998; Badylak et al. 2014a,b).

A. sanguinea is relatively large and lives as single cells. In the cross-section, the cell is ovoid and strongly dorso-ventrally compressed. The cingulum is approximately central and slightly descending. The epicone is bluntly rounded and the hypocone is bilobed with incised sulcus. The cell contains a large number of elongated yellow or brown chloroplasts, which radiate from the cell center. Like most dinoflagellates, it has two flagella, one wrapped around the equator of the cell in a groove and the other extending beyond the cell to facilitate its movement in water (Hargraves 2011). Reproduction takes place primarily by the asexual process via binary fission (Lalli & Parsons 1993), however, the sexual process through formation of isogametes also occurs occasionally (Silva & Faust 1995).

The taxon was first reported as *Gymnodinium sanguine* on the coast of Japan as a red tide-forming organism (Hirasaka 1922) and later, based on its morphological, ultrastructural, and phylogenetic relationship with a large assemblage of gymnoid-type dinoflagellates, it was renamed as *Akashiwo sanguinea* (Hirasaka) G. Hansen and Moestrup (Daugbjerg et al. 2000). Even though *Akashiwo sanguinea* is not associated with toxic production, blooms of these species were reported to coincide with depletion of dissolved oxygen and mortality of fish and shellfish in various parts of the world (Hirasaka 1922; Hallegraeff 1993; Robichaux et al. 1998; Wu et al. 2000). The inclusion of *A. sanguinea* as a harmful algal bloom (HAB) is based on various observations of adverse effects of these blooms on invertebrates, fish and bird communities through the formation of hypoxic conditions due to high respiratory oxygen demand of phytoplankton and accompanying bacterial communities (Diaz 2001; Diaz & Rosenberg 2008; Murray et al. 2015).

As most of the reports on *Akashiwo sanguinea* blooms come from temperate climate zones, this paper reports the first record of the *A. sanguinea* bloom along the tropical estuarine waters of Cochin (South Eastern Arabian Sea), thus delineating the dynamics of its population with temporal variability based on the main environmental parameters.

Materials and methods

The study was carried out along the Cochin estuary (09°57′51″N; 76°16′56″E; Fig. 1), which is located on the southwest coast of India and is connected with the Arabian Sea through two inlets at Cochin and Azhikode. It is the second largest estuarine system in India, fed by six river discharges, more than 60% of which occur during the summer monsoon (June–September), 10–25% during the winter monsoon (November–December) and the remainder during the rest of the year.

Monthly sampling of dinoflagellates was conducted in the study area for a period of 12 months, from November 2018 to October 2019. Hydrobiological characteristics of the study area were also determined during the study period. Surface water temperature (SWT) was measured using a precision mercury thermometer with an accuracy of ± 0.01°C. Salinity was measured using a hand-held refractometer (RHS-10 ATC). Measurements of pH were taken using a portable pH meter (pHep®, Europe, accuracy ± 0.01), calibrated with standard buffers prior to field sampling. The Secchi disc was used to measure the euphotic column depth. Dissolved oxygen was estimated using modified Winkler's method (Winkler 1888). Nutrients such as nitrate and phosphate were estimated using standard procedures (Grasshoff et al. 1983). Chlorophyll *a* was measured spectrophotometrically using a Hitachi U-2900 UV/VIS spectrophotometer following the acetone extraction method (Parsons et al. 1984). Phytoplankton samples were collected by filtering ~50 l of surface water through a 20 µm mesh bolting silk and preserved in 3% neutralized formaldehyde solution. Qualitative and quantitative

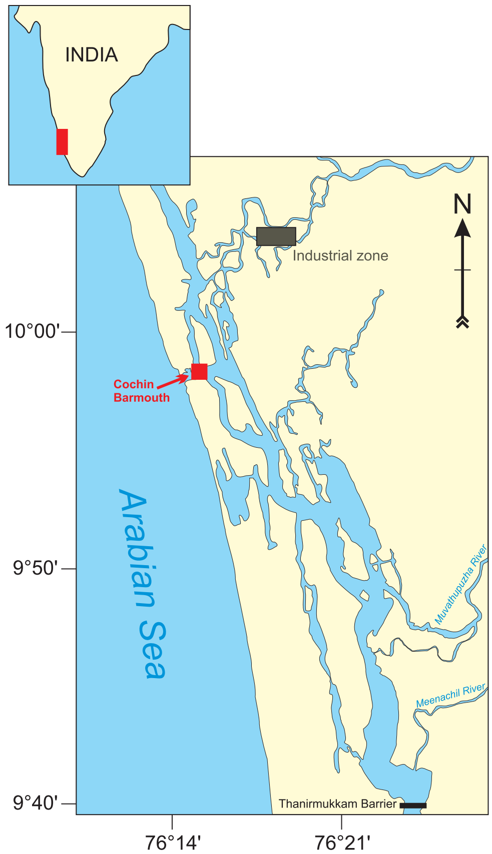

Figure 1

Study area with the sampling location in the Cochin estuary (southwest coast of India)

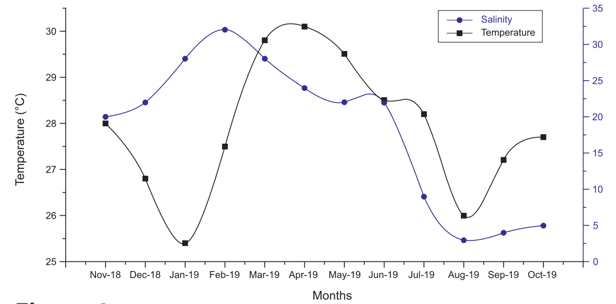

Figure 2

Distribution of surface water temperature and salinity in different months

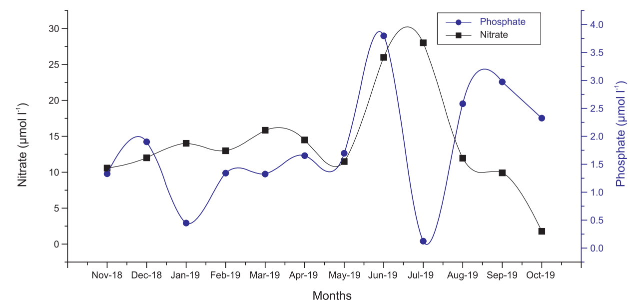

Figure 3

Distribution of nitrate and phosphate concentrations in different months

analysis of phytoplankton samples were carried out using a Sedgewick-Rafter Counting Cell under a Leica DM2500 microscope following standard identification keys (Tomas 1997).

Results

Physicochemical parameters

The surface water temperature (SWT) varied from 25.4°C to 30°C with an average of 27.8°C. SWT peaked in April, while the minimum value was recorded in January. Salinity varied from 3 to 32 PSU, the average value was 18.2 PSU. The maximum salinity was recorded in February and the minimum in August (Fig. 2). The water was turbid, with only small changes in transparency (0.61 to 0.81 m). The maximum surface concentration of nitrate was determined in June and July (26 to 28 µmol l^{-1}), while the lowest in October (1.8 µmol l^{-1}). The maximum surface phosphate concentration was recorded in June (3.8 µmol l^{-1}) and the lowest in July (0.13 µmol l^{-1}; Fig. 3).

Akashiwo sanguinea morphology and abundance

The cells were pentagonal in shape with a broad epicone and a bilobed hypocone (Fig. 4). The epicone and hypocone were nearly equal in length with a groove extending into the hypocone. The size of *A. sanguinea* ranged from 42 to 52 µm in length and 37 to 46 µm in width. Some cells were well pigmented, while others were colorless or pale yellow. Morphological variations of *A. sanguinea* were also recorded during the study.

Major blooms of *A. sanguinea* were observed in December, April and June (Fig. 5). In December, the surface chlorophyll *a* concentration was 11.2 mg m^{-3} and *A. sanguinea* contributed about 73% to the dinoflagellate community. In April, the surface chlorophyll *a* concentration was 24.2 mg m^{-3} and *A. sanguinea* contributed over 91% to the dinoflagellate community. Even though the abundance of *A. sanguinea* was observed in a wide range of temperature and salinity, its intense bloom was observed in June (2.85×10^5 cells l^{-1}), with an average surface water temperature of 28.5°C and salinity of 22 PSU (Figs 6 and 7). The chlorophyll *a* concentration in the area was 17.2 mg m^{-3}.

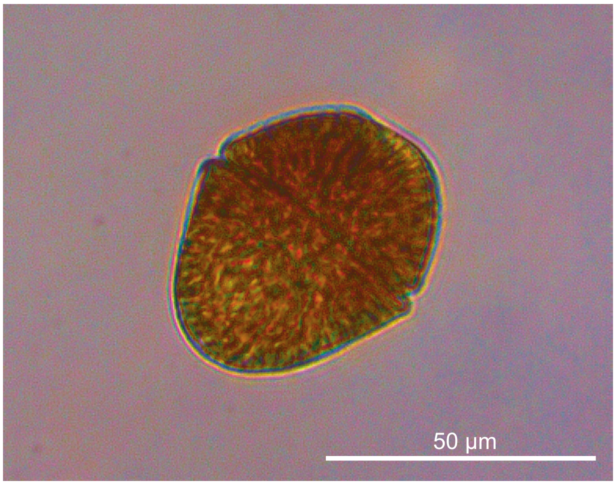

Figure 4

LM of *Akashiwo sanguinea*

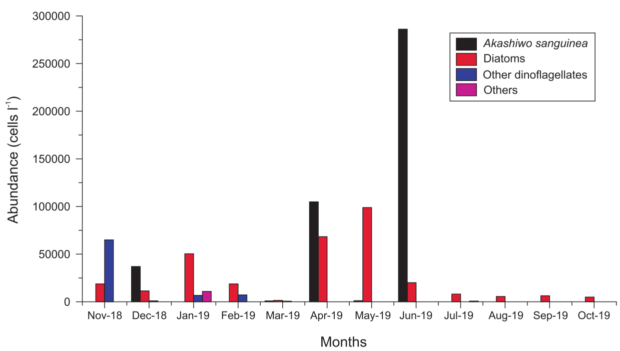

Figure 5

Monthly abundance of four groups of phytoplankton, i.e. *Akashiwo sanguinea*, diatoms, other dinoflagellates and other taxa (Others)

The phytoplankton community was dominated by centric diatoms (> 70%). *Thalassiosira* spp., *Chaetoceros* spp., *Skeletonema costatum, Odontella mobiliensis* etc.

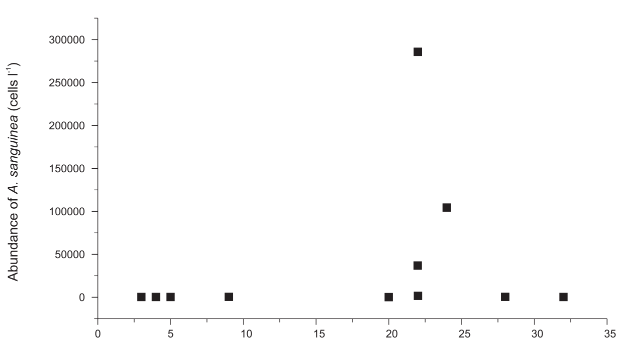

Figure 6

Distribution of *Akashiwo sanguinea* in relation to salinity

were the major Centrales present. Pennate diatom representatives included *Navicula* sp., *Pseudo-nitzschia* sp., *Cylindrotheca closterium* etc. Apart from *A. sanguinea*, the dinoflagellate community consisted of *Protoperidinium* sp., *Tripos tripos* and *Gymnodinium* sp.

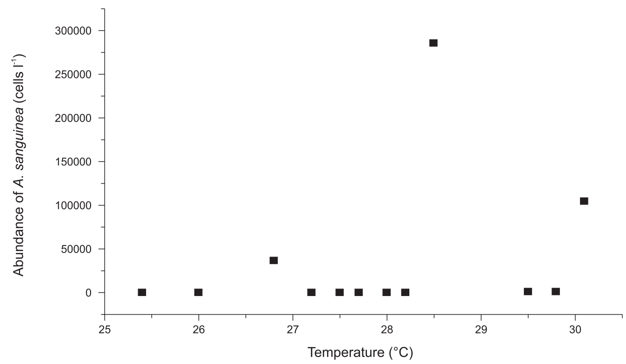

Figure 7

Distribution of *Akashiwo sanguinea* in relation to surface water temperature

Discussion

Blooms of *Akashiwo sanguinea* were previously observed mainly in temperate waters, including the California coast, the New Jersey coast in the U.S.A., Esquimalt in Canada, the Black Sea, Venice, Liverpool Bay and the Ariake Sea in Japan (Martin 1928; Voltolina 1975; Voltolina et al. 1986; Voltolina 1993; Horner et al. 1997; Gómez & Boicenco 2004; Matsubara et al. 2007; Rines et al. 2010). However, due to their eurythermal nature, their occurrence has also been reported from subtropical and tropical ecosystems of Brazil and Hong Kong Bay (Matsubara et al. 2007; Domingos & Menezes 1998; Lu & Hodgekiss 2004). The present report on *A. sanguinea* blooms from the Cochin estuary indicates the expansion of the species to tropical ecosystems, where it plays a major role in the microalgal community structure.

The Cochin estuary is exposed to significant fluctuations in salinity due to the large inflow of freshwater from discharging rivers and terrestrial input during monsoon seasons.

A. sanguinea was observed to survive in salinity ranging from 22 to 24 PSU and its abundance peaked (2.85×10^5 cells l^{-1}) in June when salinity was 22 PSU (Fig. 6). The euryhaline character of *A. sanguinea* was established by Matsubara et al. (2007), who observed the growth of the species in salinity between 10 and

40 PSU. Another study on phytoplankton populations in the Indian River lagoon in Florida also showed the persistence of *A. sanguinea* over a wide range of salinity from 10 to 30 PSU (Phlips et al. 2012), thereby indicating its ability to thrive in a wide range of salinity. In the later phase of the monsoon season (July–August), the *A. sanguinea* cell density declined (9×10^2 cell l^{-1}) as the salinity dropped to the fresh water level (3 PSU). The inhibition of *A. sanguinea* growth in response to the rapid decline in salinity was previously reported by Shikata et al. (2008). The sudden drop in salinity could have resulted in the decline of *A. sanguinea* abundance during this period.

A. sanguinea shows a preference for water temperature between 10°C and 30°C, with the optimal growth at 25°C (Matsubara et al. 2007). In the present study, however, the blooms of *A. sanguinea* were observed in a temperature range of 26 to 30°C (Fig. 7), suggesting that the species in the Cochin estuary shows the maximum growth in the upper range of temperature, i.e. above 25°C, and its eurythermal nature likely contributes to its success in the ecosystem.

Changes in the nutrient availability affect the dynamics of *A. sanguinea* blooms and are positively correlated with total phosphorus and total nitrogen concentrations (Badylak et al. 2014a). The maximum cell density of *A. sanguinea* (2.85×10^5 cells l^{-1}) in the Cochin estuary was observed during the period of elevated nitrate and phosphate concentration (26 μmol l^{-1} and 3.8 μmol l^{-1}, respectively) in June (Fig. 3). Similar observations on the relationship between the increase in nutrient levels and the increase in *A. sanguinea* were observed in the British Columbia coastal waters (Robinson & Brown 1983), as well as in the tropical estuarine waters of northeastern Brazil (Koening et al. 2014).

In addition to these physicochemical factors, the success of *Akashiwo sanguinea* in a wide range of estuaries throughout the world is also associated with the extracellular mucus production. It has been observed that *A. sanguinea* produces large amounts of mucilage, with up to 50% of the photosynthate excreted through the pores in the cell surface (Smayda 2002; Badylak et al. 2014b). According to Smayda (2002), the mucus excretion by these dinoflagellates changes the physical and chemical structure of the water column, as well as reduces the turbulence of the water column, favoring the bloom formation. The excretion of mucus by algae has certain advantages, as it increases the nutrient availability, helps to compete with other phytoplankton species and reduces grazing losses (Reynolds 2006). In some cases, however, a large amount of mucilage is also said to have a negative effect on other planktic, pelagic and benthic organisms, compared to other mucus-producing algal species (Shumway 1990; Buskey & Hyatt 1995; Liu & Buskey 2000; Botes et al. 2002). Blooms of *A. sanguinea* were also associated with fish mortality in certain parts of the world (Lassus 1988; Hallegraeff 1993; Robichaux et al. 1998; Wu et al. 2000). The discoloration of surface water as a result of the accumulation of carotenoids (Cantonati et al. 2003) has attracted the attention of scientists and tourists due to the bloom-forming potential of the species.

A. sanguinea is a well-known bloom forming dinoflagellate that occurs all over the world and has been associated with upwelling systems as well as with climate change and the related water column stratification (Kudela et al. 2010). The study reports the occurrence of *A. sanguinea* along the Cochin estuary and determines its dynamics with seasonal changes based on parameters such as salinity, temperature and nutrient concentrations. The recurring blooms and continuous presence of *A. sanguinea* can be attributed to its euryhaline and eurythermal characteristics, which can be further linked to changes in physicochemical characteristics as well as microalgal community structure. Since the bloom of *A. sanguinea* is closely related to the increase in nutrient concentrations, particularly nitrate and phosphate, the impact of anthropogenic eutrophication on the expansion of the species to tropical estuarine waters cannot be neglected.

Acknowledgements

This study was carried out as part of the *Seed Money for New Research Initiatives* (SMNRI) program under the State Plan Grant (2017-18) of Cochin University of Science and Technology (CUSAT), Kerala, India.

References

Badylak, S. & Phlips, E.J. (2004). Spatial and temporal patterns of phytoplankton composition in a subtropical lagoon, the Indian River Lagoon, Florida, USA. *J. Plankton Res.* 26: 1229–1247.

Badylak, S., Phlips, E.J. & Mathews, L.A. (2014a). *Akashiwo sanguinea* (Dinophyceae) blooms in a sub-tropical estuary: an alga for all seasons. *Plankton Benthos Research* 9: 147–155.

Badylak, S., Phlips, E.J., Mathews, L.A. & Kelley, K. (2014b). *Akashiwo sanguinea* (Dinophyceae) extruding mucus from pores on cell surface. *Algae* 29: 1–5.

Bochstahler, K.R. & Coats, D.W. (1993). Spatial and temporal aspects of mixotrophy in Chesapeake Bay dinoflagellates. *J. Eukaryot. Microbiol*. 40: 49–60.

Botes, L., Smit, A.J. & Cook, P.A. (2002). The potential threat of algal blooms to the abalone (*Haliotis midae*) mariculture industry situated around the South African coast. *Harmful Algae* 2: 247–259.

Buskey, E.J. & Hyatt, C.J. (1995). Effects of the Texas (USA) brown tide alga on planktonic grazers. *Marine Ecology Progress Series* 126: 285–292.

Cai, Y., Zhang, H. & Xiang, Y. (2006). Discussion on the causes of *Gymnodinium sanguineum* red tide in the red tide monitoring area of Xiangshan Port. *Ocean Dev. Manage.* 5: 116–118.

Cantonati, M., Tardio, M., Tolotti, M. & Corradini, F. (2003). Blooms of the dinoflagellate *Glenodinium sanguineum* obtained during enclosure experiments in Lake Tovel (N.Italy). *Journal Limnology* 62(1): 79–87.

Cloern, J.E., Schraga, T.S., Lopez, C.B. & Knowles, N. (2005). Climate anomalies

generate an exceptional dinoflagellate bloom in San Francisco. *Geophys. Res. Lett.* 32: 1–5.

Daugbjerg, N., Hansen, G., Larsen, J. & Moestrup, Ø. (2000). Phylogeny of some of the major genera of dinoflagellates based on ultra structural and partial LSU rDNA sequence data, including the erection of three new genera of unarmored dinoflagellates. *Phycologia* 39: 302–317.

Deng, Y., Hu, Z., Zhan, Z., Ma, Z. & Tang, Y. (2015). Differential expressions of an HSP70 gene in the dinoflagellate *Akashiwo sanguinea* in response to temperature stress and transition of life cycle and its implications. *Harmful Algae* 50: 57–64.

Diaz, R.J. (2001). Overview of hypoxia around the world. *Journal of Environmental Quality* 30: 275–281.

Diaz, R.J. & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science* 321: 926–929.

Domingos, P. & Menezes, M. (1998). Taxonomic remarks on planktonic phytoflagellates in a hypertrophic tropical lagoon (Brazil). *Hydrobiologia* 369/370: 297–313.

Du, X., Peterson, W., McCulloch, A. & Liu, G. (2011). An unusual bloom of the dinoflagellate *Akashiwo sanguinea* of the central Oregon USA, coast in autumn 2009. *Harmful Alage* 10: 784–793.

Feyzioğlu, A.M. & Öğüt, H. (2006). Red tide observations along the Eastern Black Sea Coast of Turkey. *Turk. J. Bot*. 30: 375–798.

Fukuyo, Y., Takano, H., Chihara, M. & K. Matsuoka. (1990). *Red tide organisms in Japan, An illustrated taxonomic guide.* Uchida Rokakuho, Tokyo.

Gómez-Aguirre, S. (1998). Red tide occurrences recorded in Mexico from 1980–1992. *Serie Zoology* 69: 13–22.

Gómez, F. & Boicenco, F. (2004). An annotated checklist of dinoflagellates in the Black Sea. *Hydrobiologia* 517(1–3): 43–59.

Grasshoff, K., Ehrhardt, M., Kremling, K. & Almgren, T. (1983). *Methods of seawater analysis.* Verlag Chemie., Weinheim.

Hallegraeff, G.M. (1991). *Aquaculturists guide to harmful Australian microalgae.* CSIRO Division of Fisheries, Hobart.

Hallegraeff, G.M. (1993). A review of harmful algal blooms and their apparent global increase. *Phycologia* 32(2): 79–99.

Hargraves, P.E. (2011). *Akashiwo sanguinea. Protists of the Indian River Lagoon*. Smithsonian Institution. URL: http://www.sms.si.edu/IRLSPEC/Akashi_sangui.htm.

Harper, D.E. & Guillen, G. (1989). Occurrence of a dinoflagellate bloom associated with an influx of low salinity water at Galveston Texas, and coincident mortalities of demersal fish and benthic invertebrates. *Contrib. Mar. Sci*. 31: 147–161.

Hirasaka, K. (1922). Red tides appearing in the spring (Honnen Shunkini Okoreru *Akashiwo*). *Zool. Magazine* 34: 740–748.

Horner, R.A., Garrison, L. & Plumley, F.G. (1997). Harmful algal blooms and red tide problems on the U.S. west coast. *Limnology and Oceanography* 42: 1076–1088.

Kahru, M., Mitchell, G., Diaz, A. & Miura, M. (2004). MODIS detects a devastating algal bloom in Paracas Bay, Peru. *EAS Trans A.G.U*. 85: 493–509.

Kiefer, D.A. & Lasker, R. (1975). Two blooms of *Gymnodinium splendens* an unarmored dinoflagellate. *Fish Bull*. 73: 675–678.

Koening, M.L., Flores Montes, M.J., Leca, E. & Tiburcio, A. (2014). New record of *Akashiwo sanguinea* (Dinophyta) in the tropical estuarine waters of Northeastern Brazil (Western Atlantic). *Braz. J. Bio*. 74: 191–198.

Kudela, R.M., Horner-Devine, A.R., Banas, N.S., Hickey, B.M., Peterson, T.D. et al. (2010). Multiple trophic levels fuelled by recirculation in the Columbia River plume. *Geophysical Research Letters* 37: L18607.

Lassus, P. (1988). *Planctontoxiqueet plankton d'eaux rouges sur lescôtes Européennes.* Brest: Institut Français de Recherche pour l'Exploitation de la Mer.

Lalli, C.M. & Parsons, T.R. (1993). Biological Oceanography: an Introduction. *Elsevier Butterworth-Heinemann* 2: 42–45.

Liu, H. & Buskey, E.J. (2000). The exopolymer secretions (EPS) layer surrounding *Aureoumbra lagunensis* cells affects growth, grazing and behaviour of protozoa. *Limnology and Oceanography* 45: 1187–1191.

Lu, S.H. & Hodgkiss, I.J. (2004). Harmful algal bloom causative collected from Hong Kong waters. *Hydrobiologia* 512: 231–238.

Martin, G.W. (1928). Dinoflagellates from marine and brackish waters of New Jersey. *Uni. Iowa Stud. Nat. Hist*. 12: 1–32.

Matsubara, T., Nagasoe, S., Yamasaki, Y., Shikata, T., Shimasaki, Y. et al. (2007). Effects of temperature, salinity, and irradiance on the growth of the dinoflagellate *Akashiwo sanguinea. Journal of Experimental Marine Biology and Ecology* 342: 226–230.

Melo, S., Bozelli, R.L. & Esteves, F.A. (2007). Taxonomic remarks on planktonic phytoflagellates in a hypertrophic tropical lagoon (Brazil). *Braz. J. Biol*. 67: 475–483.

Murray, S.A., Kohl, G.S., Farrell, H., Spiers, Z.B., Place, A.R. et al. (2015). A fish kill associated with a bloom of *Amphidinium carterae* in a coastal lagoon in Sydney, Australia. *Harmful Algae* 49: 19–28.

O'Boyle, S. & McDermott, G. (2014). Observations of a thin near surface layer in an estuarine environment: an exceptional bloom of the dinoflagellate *Akashiwo sanguinea* in the Lee estuary (Lough Mahon). Co. Cork, in September 2010. *Deep-Sea Res*. 101(2): 244–248.

Park, J., Jeong, H.J., Yoo, Y.D. & Yoon, E.Y. (2013). Mixotrophic dinoflagellate red tides in Korean waters: distribution and ecophysiology. *Harmful Algae* 30S: S28–S40.

Parsons, T.R., Maita, Y. & Lalli, C.M. (1984). *A manual of chemical and biological methods for seawater analysis.* Pergamon Press, Oxford.

Phlips, E.J., Badylak, S., Christman, M., Wolny, J., Brame, J. et al. (2011). Scales of variability of harmful algae blooms in the Indian River, Florida, USA. *Harmful Algae* 10: 277–290.

Phlips, E.J., Badylak, S., Hart, J., Haunert, D., Lockwood, J. et al. (2012). Climatic influences on autochthonous and allochthonous phytoplankton blooms in a subtropical estuary, St Lucie Estuary, Florida USA. *Estuaries and Coasts* 35: 335–352.

Reynolds, C.S. (2006). *Ecology of phytoplankton.* Cambridge University Press, Cambridge.

Rines, J.E.B., McFarland, P.L., Donaghay, P.L. & Sullivan, J.M. (2010). Thin layers and species-specific characterization of the phytoplankton in Monterey Bay, California USA. *Continental Shelf Research* 30: 66–80.

Robichaux, R.J., Dortch, Q. & Wrenn, J.H. (1998). Occurrence of *Gymnodinium sanguineum* in Texas and coastal waters Characteristics and Causes of Texas Marine Strandings In R. Zimmerman (Ed.), NMFS 143, *NOAA Technical Report* (pp. 19–25).

Robinson, M.G. & Brown, L.N. (1983). A recurrent red tide in a British Columbia Coastal Lagoon. *Can. J. Fish. Aquat. Sci*. 40: 2135–2143.

Shikata, T., Nagasoe, S., Oh, S., Matsubara, T., Yamasaki, Y. et al. (2008). Effects of down- and upshocks from rapid changes of salinity on survival and growth of estuarine phytoplankters. *J. Fac. Agr. Kyushu. Univ*. 53: 81–87.

Shumway, S.E. (1990). A review of the effects of algal blooms on shellfish and Aquaculture. *Journal of the World Aquaculture Society* 21: 65–104.

Silva, E.S. & Faust, M.A. (1995). Small cells in the life history of dinoflagellates (Dinophyceae): a review. *Phycologia* 34: 396–408.

Smayda, T.J. (2002). Turbulence, water mass stratification and harmful algal blooms: an alternative view and frontal zones as "pelagic seed banks". *Harmful Algae* 1: 95–112.

Tomas, C.R. (1997). *Identifying Marine diatoms and dinoflagellates*. Academic press, New York.

Voltolina, D. (1975). The phytoplankton of the lagoon of Venice: November 1971–November 1972. *Pubbl. Staz. Zool. Napoli*. 39: 206–340.

Voltolina, D. (1993). The origin of recurrent blooms of *Gymnodinium sanguineum* (Hirasaka) in a shallow lagoon. *Journal of Experimental Marine Biology and Ecology* 168: 217–222.

Voltolina, D., Beardall, J. & Foster, P. (1986). *The phytoplankton of Liverpool Bay 1977–1978. Quantitative distributions and seasonal variations.* Nova Hedwig, 43: 11–28.

White, A.E., Watkins-Brandt, K.S., McKibben, S.M., Wood, A.M., Hunter, M. et al. (2014). Large-scale bloom of *Akashiwo sanguinea* in the Northern California current system in 2009. *Harmful Algae* 37: 38–46.

Winkler, L.W. (1888). Die Bestimmung des im Wasser gelösten Sauerstoffes. *Ber. Dtsch. Chem. Ges.* 21: 2843–2853.

Wu, Y.L., Zhou, C.X., Zhang, Y.S., Pu, X.M. & Li, W.H. (2000). Evolution and causes of formation of *Gymnodinium sanguineum* bloom in Yantai Sishili Bay. *Oceanol Limnol Sinica* 32:159–167.

Zhang, J.Z. & Fischer, C.J. (2006). A simplified resorcinol method for direct spectrophotometric determination of nitrate in seawater. *Marine Chemistry* 99(1–4): 220–226.