Wind driven occurrence of the marine dinoflagellate *Alexandrium tamarense* in a shallow coastal water

A. Murata & S. Taguchi
Faculty of Engineering, Soka University, Japan

Abstract

Occurrence and bloom of dinoflagellate *Alexandrium tamarense* were examined with environmental factors at the central station in a semi-enclosed shallow bay during the period from 1992 to 2004. Vegetative cells of *A. tamarense* occurred distinctively between 70 and 141 Julian days every year. The maximum standing crop of *A. tamarense*, integrated for a water column (0 to 20 m), always occurred after the occurrence of maximum water density at the bottom layer which was formed by upwelled water from the outside of the bay. The maximum standing crop of *A. tamarense* ranged from 9.4×10^3 in 1999 to 3.0×10^6 cells m^{-2} in 1992. Winter standing stock of nutrients was not related with the variability in the standing crop of *A. tamarense*. Tidal change and speed were not identified to be related with the variability in the standing crop although the maximal tidal change was almost 4 m due to the physical structure of the bay. When a water column was well mixed and water stability was the minimum of 0.0155 σ_t m^{-1} as observed in 1999, the standing crop of *A. tamarense* was exceptionally suppressed. The variability in the standing crop was significantly related with the wind exposure (m^2 s^{-1}) estimated from the fetch (m) and wind velocity (m s^{-1}) from North $\pm 45^{o}$ directions ($p < 0.01$). The size of standing crop might be controlled by the physical force. *Alexandrium tamarense* may take a survival strategy to utilize (1) the upwelling as a stirring-up mechanism for resting cysts from the bottom sediments, (2) the stratification of water column to sustain cell division, and (3) wind exposure to enhance the accumulation of cells.

Keywords: N:P ratio, regenerated nutrients, toxin, wind exposure, water stability.

WIT Transactions on Ecology and the Environment, Vol 169, © 2013 WIT Press
www.witpress.com, ISSN 1743-3541 (on-line)
doi:10.2495/CP130061

1 Introduction

Dinoflagellate *Alexandrium tamarense* occurs usually at the similar time of year in a shallow coastal water (Anderson and Rengefors [1]) although their abundance is not necessarily responsible for a total phytoplankton biomass. As one of shallow water coastal waters, Kure Bay is located at the east side of Hiroshima Bay, Japan (Fig. 1). Kure Bay, known as a part of Hiroshima Bay, is intensively utilized for aquaculture of shellfish (Asakawa *et al.* [2]). Kure Bay is connected with Hiroshima Bay through a relatively wide (>1.5 km width), deep (>20 m depth) Kure Channel at the north end and with the Seto Inland Water through two narrow (0.5 km width), shallow (<10 m depth) Onto seto and Hayase seto Channels at the south end. Daily water exchange provided mainly by a westerly current in the Seto Inland Water and a tidal change through channels is limited to about 20% of water volume in Kure Bay (Kimura [3]). The maximum tidal height reaches almost 4 m. The surface area is 51 km^2 with a mean water depth of 20 m. Only one runoff to Kure Bay is Nikou River from the east side of bay. Annual contribution of freshwater to the water volume of Kure Bay is less than 1% of which two third is contributed by the annual amount of precipitation due to well-protected from riverine runoff (Kimura [3]). During the occurrence of *A. tamarense*, river runoff and precipitation are seasonally low in comparison to a following rainy season. Winter standing stock of nutrients could control a dynamics of spring phytoplankton in temperate coastal water assuming no intermediate supply of nutrients within a system. Maximum standing stock of ammonium + nitrate and phosphate integrated throughout a 20 m water column

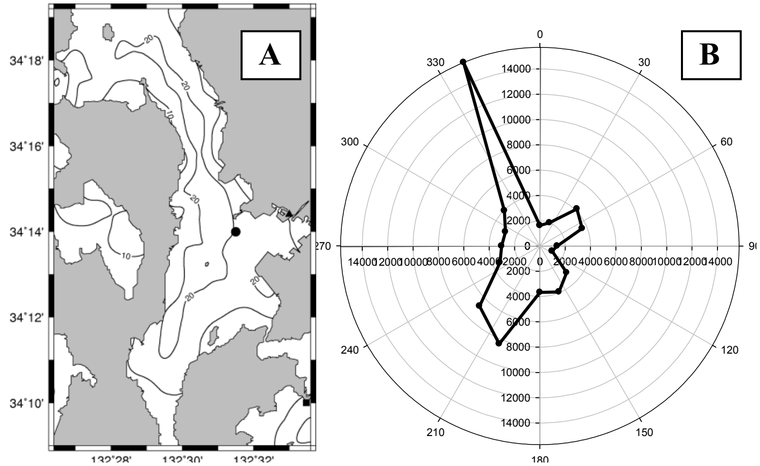

Figure 1: A: map of sampling station, St. 21 (circle) with contour of water depth (m). Locations of Kure Meteorological Observatory (triangle) and Hiroshima Fisheries and Ocean Technologies Center (square) are indicated. B: fetch distribution (m) at St. 21.

of Kure Bay in winter are 180 μM $NH_4 + NO_3$ and 16 μM PO_3, respectively (Hiroshima [4]). The present study analyzed decadal data sets of the oceanographic investigation at the central station St. 21 with a water depth of 20 m (34 °14.0'N, 132°31.5'E) in Kure Bay and the meteorological observation at Kure Meteorological Observatory (34°14.4'N, 132°33.0'E) during the period from 1992 to 2002 (Fig. 1A).

In the present study we show that wind can be a primary force to control the size of bloom of *Alexandrium tamarense* in the semi-enclosed shallow water system such as Kure Bay based on a part of the monitoring program in Hiroshima Bay provided by the Fisheries and Ocean Technologies Center, Hiroshima Prefecture.

2 Materials and methods

2.1 Vegetative cell density of *Alexandrium tamarense*

Water samples (100 mL) for the vegetative cell density measurements were collected monthly usually between 1000 am and 1400 pm by Van Dorn water bottles (4 L) at depths of 0, 2, 5, and 10 m at St. 21 (Fig. 1A). Occasionally water samples were also collected at 19 m, one meter above the bottom. *Alexandrium tamarense* was mainly identified and enumerated. The concentrated 1−mL suspensions were pipette into a counting chamber (5608-C, Rigo-Sha, Japan) and enumerated immediately on a light microscope (BX50F4, Olympus, Japan). The minimum detection limits were ten cells per L.

2.2 Solar radiation and wind direction and velocity

Monthly mean of daily solar radiation (MJ m^{-2} d^{-1}) and hourly mean wind direction and velocity (m s^{-1}) were obtained at Hiroshima Meteorological Observatory (34°23.9'N, 132°27.7'E) and Kure Meteorological Station (34°14.4'N, 132°33.0'E), respectively (Meteorological Agency of Japan 1992–2004). Although monthly mean solar radiation was not available from Kure Meteorological Station, little significant difference was assumed based on the analysis of radiation hours between two locations. Wind directions were recorded every 22.5°.

2.3 Temperature and salinity

Seawater temperature and salinity were measured from a surface layer to 19 m using a Salinity, Temperature, and Depth profiler (STD; SCL208-DK, Alec Electronics, Japan) at the time of water sampling from 1992 to 2004.

2.4 Water density, water-column stability, and daily increase rate of maximum water density

Water density (σ_t) was calculated from seawater temperature and salinity. Water column stability (E) (Sverdrup *et al.* [5]) was calculated as:

$$E = d\sigma_t \, dz^{-1} \qquad (1)$$

where $d\sigma_t \, dz^{-1}$ is the difference in σ_t between 0 m and 20 m. Choice of depth was based on the occasional occurrence of cells at 20 m depth.

Daily increase rate of maximum water density (I_d) at 20 m was calculated as:

$$I_d = d\sigma_t \, d\mathrm{d}^{-1} \qquad (2)$$

where $d\sigma_t \, d\mathrm{d}^{-1}$ is the difference in σ_t between Julian day on the first observation in January and day when the maximum σ_t disappeared at 20 m depth.

2.5 Nutrient concentrations

Water samples for nutrient analyses were collected by Van Dorn bottles (4 L) at 0, 5, and 19 m during the same period as the STD measurements. The concentrations of nitrate, ammonium, and phosphate were determined using an autoanalyzer (TRAAC800, Bran+Lubbe, Germany).

2.6 Wind exposure and tidal height

Wind exposure (W_E, $m^2 \, s^{-1}$) was calculated as the product of wind velocity and fetch (Keddy [6]),

$$W_E = \sum v_i f_i \qquad (3)$$

where v_i is wind velocity ($m \, s^{-1}$) from direction i and f_i is the corresponding distance over water (m). The corresponding distance over water, *i.e.* fetch was calculated from the ocean map obtained from the Japan Coast Guard made in 2006. Sixteen lines radiating at 22.5^{o} intervals from St. 21 were drawn on Kure Bay perimeter. The distance to the adjacent shoreline along each line was determined to the nearest 26 m (0.5 mm on the ocean map).

Tidal heights were recorded hourly at Kure Meteorological Station by Meteorological Agency of Japan. Tidal ratio was calculated for the maximum to minimum tidal height (cm) on the occurrence in the maximum standing crop of *Alexandrium tamarense*. The steepest slope of tide change between two consecutive sets of low and high tides was estimated at the maximum standing crop because the tide fluctuates twice a day in the present study area.

2.7 Statistical analysis

The standing stocks of nitrate, ammonium, and phosphate and standing crop of *Alexandrium tamarense* were calculated by integrating the value from the surface to 20 m. Relationship between the standing crop and the environmental data was analyzed based on either 24 h mean in the observation day, one day earlier day, and two days earlier day, or monthly mean on the observation month, one month earlier month and two months earlier month. The linear relationships were examined by using a model II regression analysis (Law and Archie [7]).

3 Results

3.1 Cell density with chlorophyll *a*

Vegetative cells of *Alexandrium tamarense* were detected from February to June every year. The occurrence of maximum cell density ranged from 60 Julian days in 1999 to 95 Julian days in 1993 (Table 1). The maximum cell density ranged from 1.0×10^2 cells L^{-1} in 1999 to 3.1×10^5 cells L^{-1} in 1997. The maximum standing crop of *A. tamarense* ranged from 9.4×10^3 cells m^{-2} in 1999 to 30×10^6 cells m^{-2} in 1992 (Fig. 2). The maximum standing crop of chlorophyll *a* occurred 61 days on the average earlier than those of *A. tamarense* (Table 2).

Table 1: Ratio of high and low tide, maximum slope of tide change between a consecutive high and low tide on date at the maximum standing crop of *Alexandrium tamarense*, water stability and the disappearing date on the maximum water density, and the daily water density increase rate at 20 m depth.

Year	Julian Day of maximum standing crop	Tide ratio (cm cm^{-1})	Maximum slope (cm h^{-1})	Water stability (σ_t m^{-1})	Julian Day of maximum density	Daily density increase ($\sigma_t d^{-1}$)
1992	108	3.61	-25.7	0.0370	68	0.0118
1993	132	2.39	-24.7	0.0435	95	0.0087
1994	118	6.49	-65.8	0.0527	94	0.0152
1995	121	4.66	-56.8	0.0564	94	0.0152
1996	141	4.40	-54.2	0.0674	64	0.0118
1997	108	3.57	-42.3	0.0563	60	0.0136
1998	112	2.35	-37.2	0.0782	60	0.0138
1999	70	1.91	-16.7	0.0155	69	0.0100
2000	91	2.06	-30.4	0.0351	70	0.0143
2001	113	4.22	-57.2	0.0459	62	0.0102
2002	105	4.77	-62.2	0.0339	60	0.0129
2003	85	3.61	-48.0	0.0294	84	0.0066
2004	106	2.36	-36.6	0.0368	63	0.0196

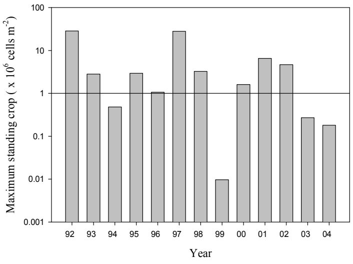

Figure 2: Maximum standing crop of *Alexandrium tamarense* ($\times 10^6$ cells m^{-2}) at St. 21 during the period from 1992 to 2004. A horizontal line indicates 1×10^6 cells m^{-2} as a reference.

Table 2: Standing stock of nitrate, ammonium, DIN, and phosphate, and ratios of NO_3:PO_4 and DIN:PO_4 in January and the maximum standing crop of chlorophyll *a* and its date during the period from 1992 to 2004.

Year	NO_3 (μM m^{-2})	NH_4 (μM m^{-2})	DIN (μM m^{-2})	PO_4 (μM m^{-2})	NO_3:PO_4 (μM M^{-1})	DIN:PO_4 (μM μM^{-1})	Chl *a* (mg m^{-2})	Julian day of maximum standing crop
1992	16.5	43.7	60.2	53.7	0.27	1.12	40.0	66
1993	119	60.1	180	16.2	7.35	11.1	106	34
1994	121	34.4	133	9.37	12.9	16.6	44.3	6
1995	69.1	82.5	150	12.7	5.44	11.8	51.3	66
1996	85.8	1.58	87.4	5.23	16.4	16.7	130	38
1997	114	7.67	122	12.7	8.98	9.62	60.0	99
1998	90.1	3.63	93.7	11.3	7.97	8.23	79.9	35
1999	47.1	26.7	73.9	10.8	4.36	6.84	115	36
2000	65.1	36.9	102	9.03	7.21	11.3	96.4	6
2001	120	56.6	177	13.0	9.23	13.7	145	66
2002	62.5	57.6	120	7.58	8.25	15.7	73.6	60
2003	100	43.7	144	12.1	8.27	12.1	68.7	37
2004	73.2	46.8	120	10.3	7.11	11.4	66.0	63

3.2 Solar radiation

Solar radiation increased from winter minimum of 8.0 ± 0.7 MJ m^{-2} d^{-1} in December to 18.3 ± 1.4 MJ m^{-2} d^{-1} (mean ± one standard deviation) in May. When solar radiation reached 10 MJ m^{-2} d^{-1}, the vegetative cells were usually appeared in a water column.

3.3 Wind direction and velocity

Within a scale of day, high winds from the direction between NW and NE prevailed usually during night whereas sluggish winds between SW and SE prevailed during day during the occurrence of *Alexandrium tamarense*. During 72 h prior to date at the maximum standing crop of *A. tamarense*, mean winds from N ± 45° directions with one standard deviation of 2.1 ± 0.5 m s^{-1} prevailed (42.4%) out of four quarters of wind direction. The faster than 7.0 m s^{-1} of the maximum velocity of winds was observed from NNW winds; 7.1 m s^{-1} in 1993 and 8.1 m s^{-1} in 2001, respectively.

3.4 Temperature and salinity

Surface water temperature usually started increasing in March to higher than 15°C in April. Surface salinity also usually started decreasing in March to lower than 32.25 PSU. High density water was usually upwelled in February and gradually mixed with low density water but limited to the bottom layer as a pycnocline was developed. Data obtained in 1992 were shown as examples for a temporal change in the vertical distribution of water density (Fig. 3). A general trend in the temporal distribution was similar to one in 1992 except for 1999 as described in a section of water stability. The disappearing date on the maximum water density at 20 m was observed between 60 and 95 Julian days (Table 1). The disappearing date on the maximum water density at 20 m was always earlier than the maximum standing crop of *Alexandrium tamarense* (Table 1).

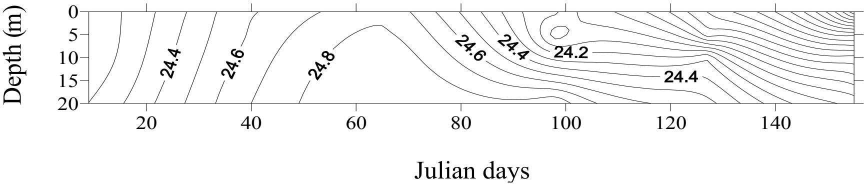

Figure 3: Seasonal change in sigma-t in 1992. Only values higher than 24.2 σ_t were labeled.

3.5 Water stability

Water stability ranged from 0.0155 in 1999 to 0.0782 σ_t m^{-1} in 1998 (Table 1). Water stability in 1999 was the lowest in the present study although water temperature and salinity in 1999 were within the range of the inter-annual variability in spring when *A. tamarense* usually occurs.

3.6 Tide

A ratio of tide heights at low and high tides in two consecutive sets at the maximum standing crop of *Alexandrium tamarense* ranged from 1.9 in 1999 to 6.5 in 1994 (Table 1). There was no relationship between the ratio and the maximum standing crop. Positive slopes of tide change were observed in 1992, 1993, 1997, and 1999 whereas negative slopes were obtained in other years (Table 1). The maximum slope of tide change between a consecutive high and low tide ranged from 17 cm h^{-1} to 66 cm h^{-1} with a mean and one standard deviation of 43 ± 16 cm h^{-1} (Table 1). There was no relationship between the slope and the maximum standing crop except for a coincident minimum value of the maximum standing crop at the minimum slope in 1999.

3.7 Nutrients

Nitrate and ammonium standing stock in January ranged from 16.5 μM m^{-2} in 1992 to 121 μM m^{-2} in 1994 (Table 2). Standing crop of nitrate + ammonium (=dissolved inorganic nitrogen, DIN) and phosphate in winter ranged from 60.2 μM m^{-2} in 1992 to 180 μM m^{-2} in 1993 (Table 2). This was resulted in a ratio of DIN:PO_4 ranging from 1.12 to 16.7. Standing stocks of all nutrients decreased with seasons and the minimum standing stock was usually observed around the maximum standing crop of *Alexandrium tamarense* (Table 3), after the maximum standing crop of chlorophyll *a* (Table 2). After March the standing stock of ammonium increased from 12 ± 6 μM m^{-2} before 1998 to 26 ± 8 μM m^{-2} after 1999. The relative abundance of ammonium in DIN also increased from 58 ± 15% before 1998 to 82 ± 5% after 1999 (Table 3).

Table 3: Standing stock of nitrate, ammonium, DIN, and phosphate and ratios of NO_3:PO_4 and DIN:PO_4 at the maximum standing crop of *Alexandrium tamarense* during the period from 1992 to 2004.

Year	Julian day of Max standing crop	NO_3 (μM m^{-2})	NH_4 (μM m^{-2})	DIN (μM m^{-2})	PO_4 (μM m^{-2})	NO_3:PO_4 (μM μM^{-1})	DIN:PO_4 (μM μM^{-1})
1992	108	23.4	16.0	39.4	2.90	8.01	13.1
1993	132	10.1	10.4	20.6	3.41	2.98	5.88
1994	118	7.50	18.8	26.3	4.18	1.79	19.0
1995	121	5.02	19.4	24.4	3.16	1.59	7.70
1996	141	7.54	6.71	14.3	4.24	1.78	3.92
1997	108	4.56	4.66	9.22	3.44	1.32	2.67
1998	112	4.52	10.7	15.2	1.80	2.52	8.41
1999	70	3.98	15.4	19.4	4.60	0.865	4.08
2000	91	6.22	28.9	35.1	3.54	1.76	9.87
2001	113	5.21	36.2	41.4	2.78	1.81	14.6
2002	105	4.25	31.5	35.8	1.60	2.66	22.3
2003	85	7.01	20.1	27.1	3.89	1.80	6.97
2004	106	5.48	22.4	27.9	2.35	2.33	11.9

3.8 Wind exposure

Fetch ranged from 1.0 km at ESE to 15.7 km at NNW direction (Fig. 1B. Most fetches were shorter than 5 km. Wind exposure from the direction between NW and NE ranged from 53×10^3 m^2 s^{-1} in 1995 to 305×10^3 m^2 s^{-1} in 2001. A significant relationship between wind exposure (W_E) and the maximum standing crop of cells (SC) was obtained as

$$\text{Log SC} = -1.1163 + 0.008596\, W_E \tag{4}$$

(p <0.01 (Fig. 4).)

4 Discussion

Toxic dinoflagellate *Alexandrium tamarense* appears repetitively between February and June every year in Kure Bay although both occurrence and size of the maximum standing crop *A. tamarense* are variable. The variability in the occurrence and size of vegetative cells in a water column could be related with abundance of resting cysts, stirring-up mechanisms of bottom sediment layer, and turbulence of water (Anderson and Wall [8]). Resting cysts have been

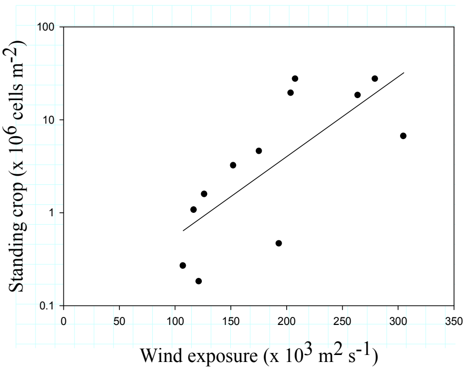

Figure 4: Relationship between the maximum standing crop of *Alexandrium tamarense* (× 10^6 cells m^{-2}) and wind exposure (m^2 s^{-1}).

known to accumulate densely at the first 3 cm of bottom sediments in shallow coastal water with a limited circulation (White and Lewis [9], Turgeon *et al.* [10]) as in a protected Kure Bay (Yamaguchi *et al.* [11]). Upwelling of bottom water through Kure Channel can be one of the stirring-up mechanisms for resting cysts from bottom sediment as suggested by Fanning *et al.* ([12]). When current speed at the surface bottom sediment exceeds 8 cm s^{-1}, the bottom sediment could be stirred up in the simulated experiment in Kure Bay (Hibino and Matsumoto [13]). Along Kure Channel, the southward bottom current could be as fast as 10 cm s^{-1} in comparison with one at St. 21 where the current speed at 7 cm above the bottom never exceeds 8 cm s^{-1} (Hibino and Matsumoto [13]). Duration of steady upwelling in winter and early spring, the stirring-up process, which is indexed by a duration from the initial winter density to the disappearance of the maximum water density at the bottom layer in the present study, can be related with the occurrence and size of pelagic resting cysts and consequently vegetative cells in a water column. The stirring-up mechanism provided by upwelling water is clearly speculative based on the assumption on stable abundance of viable cysts in the bottom sediments (Yamaguchi *et al.* [11]) and little effect of bioturbation on viable cysts (Tsujino *et al.* [14]) but needs to be explored as a possible contributing factor in the dynamics of cyst-forming *A. tamarense.*

Even a stable supply of viable cysts presents in the bottom sediments, anoxia condition at the bottom layer, which occurs during a summer stratification period in Kure Bay (Tsujino *et al.* [14]), may influence on a success in germination in a following year (Anderson *et al.* [15], Kremp and Anderson [16]). Due to anoxia condition a reduction of germination potential and consequently, less successful initiation of new vegetative cells could decrease the size of inoculums of vegetative cells and retard a bloom development. By the disappearing time of maximum water density at the bottom layer, water temperature increases higher than 10°C which is within the optimum temperature window for germination of *A. tamarense* (Anderson and Rengefors [1]). Once the survived resting cysts through unfavorable conditions are re-suspended in a water column, they are ready for the germination and cellular division due to increased radiation and water temperature (Nehring [17]).

Biophysical impairment can primarily influence cellular processes such as cellular division as experimentally shown for dinoflagellates (Berdalet *et al.* [18]). Initiation of stratification is favor for cellular division of *A. tamarense* (Smayda [19]). Once the cell division is underway, the magnitude of tide is not seemed to have a negative effect. As the maximum rate of tide change between high and low tide is at the similar magnitude of swimming speed of dinoflagellates (Berdalet *et al.*[18]), dinoflagellates may maintain their vertical position in a water column to avoid dispersion.

Relatively low variability in both the duration of occurrence of maximum water density water (73 ± 14 Julian days) and the daily density increase rate of bottom water ($0.0126 \pm 0.0033\ \sigma_t\ d^{-1}$) may be related with characteristic physical structure of long Kure Channel at the NNW direction of Kure Bay. The earliest occurrence of the maximum standing crop of *Alexandrium tamarense* but exceptionally low standing crop due to a lack of subsequent development of the population observed in 1999 is likely to relate with the least water stability ($0.0155\ \sigma_t\ m^{-1}$). The occurrence of *Alexandrium tmarense* in Hiroshima Bay has been reported to relate with North wind (Yamamoto *et al.* [20]). Kure Bay is much smaller than Hiroshima Bay and well protected by nine mountains in comparison to widely opened Hiroshima Bay. The present analysis of wind exposure indicates a significant relationship between the maximum standing crop of *A. tamarense* and wind from direction between NW and NE. Similar observation on meteorological accumulation of cells has been observed on *Aureococcus anaphagefferens* (MacIntyre *et al.* [21]) and *Alexandreium minutum* (Lenning *et al.* [22]). Even the effective wind exposure as suggested by MacIntyre *et al.* [21] is considered, the general conclusion is not changed.

Upwelled high density water through Kure Channel to the central water of Kure Bay might play a role in stirring-up of resting cysts of *Alexandrium tamarense* from the bottom sediments. Once moderate water stability is formed, the vegetative cells of *A. tamarense* appear and accumulate in a water column. Variability in the maximum standing crop of *A. tamarense* is most likely controlled by the wind exposure.

Increases of absolute standing stock (more than 100%) and relative abundance of ammonium in DIN (140%) on the maximum standing crop of *Alexandrium tamarense* observed since 1999 may induce possible reverse effects on the occurrence of *A. tamarense* in Kure Bay. Standing stock of ammonium has been known to increase further during summer stratification period causing anoxic condition at the bottom layer. With excess anoxic condition, resting cysts are most vulnerable without a successful mandatory dormancy. This may reduce a size of seed stock in the following year. It is too early to conclude but it would be worthwhile to monitor the occurrence of low standing crop in relation to a degree of anoxic condition in the preceding year.

Acknowledgements

We could not complete this paper without the help provided by numerous people, especially Hiroshi Hattori, Hiroaki Saito, and Ichiro Yasuda. We appreciate Haili Wang for his excellent assistance in data analysis on Sigma Plot and Surfer. This manuscript was prepared during a sabbatical leave at the Scripps Institution of Oceanography (ST). All support provided by Greg Mitchell was appreciated. This study was partly supported by a Sasagawa Scientific Research Grant (19-704M) awarded to AM from the Japan Science Society.

References

[1] Anderson, D. M. and Rengefors, K., Community assembly and seasonal succession of marine dinoflagellates in a temperate estuary: The importance of life cycle events. *Limnol. Oceanogr.* 51, pp. 860–873, 2006.

[2] Asakawa, M., Miyazawa, K. and Noguchi, K., Studies on paralytic shellfish poison (PSP) toxification of bivalves in association with appearance of *Alexandrium tamarense*, in Hiroshima Bay, Hiroshima Prefecture. *J. Food Hrg. Soc. Japn* 34, pp. 50–54, 1993.

[3] Kimura, T., Freshwater input to Hiroshima Bay. *Suisan Zoshoku* 22, pp. 110–119, 1975. (In Japanese.)

[4] Hiroshima, Annual report of Hiroshima Prefecture Fisheries Experimental *Station 1992–2004*. Hiroshima Prefecture, Hiroshima, 1992–2004. (In Japanese.)

[5] Sverdrup, H.U., Johnson M.W. and Fleming, R.H., The oceans, Prentice-Hall, 1942.

[6] Keddy, P.A., Quantifying within-lake gradients of wave energy: Interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. *Aqa. Bot.* 14, pp. 41–58, 1982.

[7] Laws, E. A. and Archie, J. W., Appropriate use of regression analysis in marine biology. *Mar. Biol.* 65, pp. 13–16, 1981.

[8] Anderson, D. M. and Wall, D., Potential importance of benthic cysts of *Gonyaulax temarensis* and *G. excavate* in initiating toxic dinoflagellate blooms. *J. Phycol.* 14, pp. 224−234, 1978.

[9] White, A. W. and Lewis, C. M., Resting cysts of the toxic, red tide dinoflagellate *Gonyaulax excavate* in Bay of Fundy sediments. *Can. J. Fish. Aquat. Sci.*, 39, pp. 1185–1194, 1982.

[10] Turgeon, J., Cembella, A.D., Therriault, J-C. and Beland, P., Spatial distribution of resting cysts of *Alexandrium* spp. in sediments of the lower St. Lawrence estuary and the Gaspe coast (eastern Canada), In, *Toxic Marine Phytoplankton* (eds) E. Graneli, B. Sundstrom, L. Edler and D. M. Anderson, Elsevier, New York, pp. 238–243, 1990.

[11] Yamaguchi, M., Itakura, S. and Imai, I., Vertical and horizontal distribution and abundance of resting cysts of the toxic dinoflagellate *Alexandrirum tamarense* and *Alexandrium catenella* in sediments of Hiroshima Bay, the Seto Inland Sea, Japan. *Nippon Suisan Gakkaishi* 61, pp. 700−706, 1995.

[12] Fanning, K. A., Carder, K. L. and Betzer, P. R., Sediment resuspension by coastal waters: a potential mechanism for nutrient recycling in the ocean's margins. *Deep-Sea Res.* 29, pp. 953–965, 1982.

[13] Hibino T. and Matsumoto H., Distribution of fluid mud layer in Hiroshima Bay and its seasonal variation. *Engineering* B 62, pp. 348–359, 2006.

[14] Tusijino, M., Arima, S., Kamiyama, T. and Uchida, T., Macrobenthos and meiobenthos communities in relation to the bottom environment in Kure Bay of Seto Inland Sea. *Bull. Fish. Environ. Inland Sea* 2, pp. 49–56, 2000. (in Japanese)

[15] Anderson, D. M., Taylor, C. D. and Armbrust, E. V., The effects of darkness and anaerobiosis on dinoflagellate cyst germination. *Limnol. Oceanogr.* 32, pp. 340–351, 1987.

[16] Kremp, A. and Anderson, D. M, Factors regulating germination of resting cysts of the spring bloom dinoflagallate *Scrippsiella hangoei* from the northern Baltic Sea. *J. Plank. Res.*, 22, pp. 1311–1327, 2000.

[17] Nehring, S., Recruitment of planktonic dinoflagellates: importance of benthic resting stages and resuspension events. *Int. Revue Ges. Hydrobiol.* 70, pp. 55–60, 1996.

[18] Berdalet, E., Peters, F., Koumandou, V. L., Roldan, C., Gaudayol, O. and Estrada, M., Species-specific physiological response of dinoflagellates to quantified small-scale turbulence. *J. Phycol.* 43, pp. 965−977, 2007.

[19] Smayda, T. J., Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.* 42, pp. 1137–1153, 1997.

[20] Yamamoto, T., Hashimoto, T., Tarutani, K. and Kotani, Y., Effects of winds, tides and river water runoff on the formation and disappearance of the *Alexandrium tamarense* bloom in Hiroshima Bay, Japan. *Harmful Algae* 1, pp. 301–312, 2002.

[21] MacIntyre, H. L., Lomas, M. W., Cornwell, J., Suggett, D. J., Gobler, C. J., Koch, E. W. and Kana, T. M., Mediation of benthic-pelagic coupling by microphotobenthos: an energy- and material-based model for initiation of blooms of *Aureococcus anophagefferens*. *Harmful Algae* 3, pp. 403–437, 2004.

[22] Lenning, K. V., Vila, M., Maso, M., Garces, E., Angles, S., Sampedro, N., Morales-Blake, A. & Camp, J., Short-term variations in development of a recurrent toxic *Alexandrium minutum*-dominated dinoflagellate bloom induced by meteorological conditions. *J. Phycol.* 43, pp. 892–907, 2007.