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

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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 \times 10^3 in 1999 to 3.0 \times 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 \sigma_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^\circ\ 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.
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 km² 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](image-url)

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 NH₄ + NO₃ and 16 µM PO₃, 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 (σt) was calculated from seawater temperature and salinity. Water column stability (E) (Sverdrup *et al.* [5]) was calculated as:
\[ E = d\sigma_t dz^{-1} \]  
where \( d\sigma_t dz^{-1} \) is the difference in \( \sigma_t \) 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:

\[ I_d = d\sigma_t dd^{-1} \]

where \( d\sigma_t dd^{-1} \) is the difference in \( \sigma_t \), between Julian day on the first observation in January and day when the maximum \( \sigma_t \) 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 \( (W_E, \text{ m}^2 \text{ s}^{-1}) \) was calculated as the product of wind velocity and fetch (Keddy [6]),

\[ W_E = \sum v_i f_i \]

where \( v_i \) is wind velocity \( (\text{m s}^{-1}) \) from direction \( i \) and \( f_i \) is the corresponding distance over water \( (\text{m}) \). 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° 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 \( \text{(cm)} \) on the occurrence in the maximum standing crop of \textit{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 \textit{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 $1.0 \times 10^2$ cells L$^{-1}$ in 1999 to $3.1 \times 10^5$ cells L$^{-1}$ in 1997. The maximum standing crop of *A. tamarense* ranged from $9.4 \times 10^3$ cells m$^{-2}$ in 1999 to $30 \times 10^6$ 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.

<table>
<thead>
<tr>
<th>Year</th>
<th>Julian Day of maximum standing crop</th>
<th>Tide ratio (cm cm$^{-1}$)</th>
<th>Maximum slope (cm h$^{-1}$)</th>
<th>Water stability ($\sigma$, m$^{-1}$)</th>
<th>Julian Day of maximum density</th>
<th>Daily density increase ($\sigma$d$^{-1}$)</th>
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<td>0.0368</td>
<td>63</td>
<td>0.0196</td>
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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 $1 \times 10^6$ 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.

<table>
<thead>
<tr>
<th>Year</th>
<th>NO$_3$ ($\mu$M m$^{-2}$)</th>
<th>NH$_4$ ($\mu$M m$^{-2}$)</th>
<th>DIN ($\mu$M m$^{-2}$)</th>
<th>PO$_4$ ($\mu$M m$^{-2}$)</th>
<th>NO$_3$:PO$_4$ ($\mu$M M$^{-1}$)</th>
<th>DIN:PO$_4$ ($\mu$M M$^{-1}$)</th>
<th>Chl $a$ (mg m$^{-2}$)</th>
<th>Julian day of maximum standing crop</th>
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<td>7.11</td>
<td>11.4</td>
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3.2 Solar radiation

Solar radiation increased from winter minimum of $8.0 \pm 0.7$ MJ m$^{-2}$ d$^{-1}$ in December to $18.3 \pm 1.4$ 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 $N \pm 45^\circ$ directions with one standard deviation of $2.1 \pm 0.5$ 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$^\circ$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).

![Graph showing seasonal change in sigma-t in 1992.](image)

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

### 3.5 Water stability

Water stability ranged from 0.0155 in 1999 to 0.0782 σt 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:PO₄ 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 NO₃:PO₄ and DIN:PO₄ at the maximum standing crop of *Alexandrium tamarense* during the period from 1992 to 2004.

<table>
<thead>
<tr>
<th>Year</th>
<th>Julian day of Max standing crop</th>
<th>NO₃ (µM m⁻²)</th>
<th>NH₄ (µM m⁻²)</th>
<th>DIN (µM m⁻²)</th>
<th>PO₄ (µM m⁻²)</th>
<th>NO₃:PO₄ (µM µM⁻¹)</th>
<th>DIN:PO₄ (µM µM⁻¹)</th>
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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 × 10³ m² s⁻¹ in 1995 to 305 × 10³ m² s⁻¹ in 2001.
A significant relationship between wind exposure (*W*ₑ) and the maximum
standing crop of cells (SC) was obtained as

\[
\text{Log SC} = -1.1163 + 0.008596 \times Wₑ
\]

\[(p<0.01 \text{ (Fig. 4).})\]

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
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
(Smaya [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 ± 0.0033 σ, 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 σ, m⁻¹). The occurrence of Alexandrium imarense 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 Alexandrium
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.
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