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Change in Species Composition and Distribution of Algae in the Coastal Waters of Western Japan

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1. Introduction

Estuarine and coastal ecosystems are sensitive to human activities that lead to nutrient pollution, excess or insufficient sedimentation, and other types of pollution. The effects of climate change are particularly noticeable in these shallow ecosystems, and increases in non-native species and gelatinous zooplankton such as jellyfish can have harmful effects on fisheries. With climate change related to human activities well under way (IPCC, 2007), there is a need to assess the impacts of these changes on estuaries and coastal waters. Growing awareness of climate change has stimulated considerable recent interest in the possible shifting of biological events in marine ecosystems and the ecological consequences of these shifts. It has been suggested that enhanced stratification caused by an increase in surface water temperature decreases nutrient supply, leading to a decrease in primary productivity throughout a large area of the North Pacific Ocean (Ono et al., 2002; Watanabe et al., 2005). It has also been reported that the timing and magnitude of phytoplankton blooms have changed markedly, affecting the dynamics of zooplankton and fisheries resources (e.g., Edwards & Richardson, 2004; Chiba et al., 2008). Impacts on estuarine and coastal ecosystems remain unclear, however, because of the difficulty in distinguishing the effects of global warming from those of other anthropogenic factors. Although phytoplankton are major primary producers in most aquatic ecosystems, benthic primary production, such as macroalgae, can be often substantial and even dominant in shallow waters. *Sargassum* algal beds are highly productive and offer habitats for numerous marine animals. The decline and qualitative change of *Sargassum* beds in western Japan, which may be caused by global warming, and their impact on coastal ecosystems and fisheries that rely on them is of great concern. In last two decades, macroalgal beds composed of *Sargassum* and kelp (mainly *Ecklonia*) have been degrading or declining along the coast of the Kyushu and Shikoku areas in western Japan, which has southern temperate climate characteristics. It is estimated that the mass disappearance of local kelp and *Sargassum* beds in these regions totals several thousand hectares and more than 40% of the total macroalgal beds surveyed in the early 1990s. Degradation of macroalgal beds in these areas has coincided with increased

water temperatures and grazing pressures by herbivorous animals (fish and sea urchins). Shifts of flora from temperate to subtropical components, accompanied by quantitative changes in macroalgal beds, have also been observed in many areas of western Japan.

Subtropical *Sargassum* species such as *S. duplicatum* and *S. carpophyllum* have begun to appear in many *Sargassum* beds in the Kyushu and Shikoku regions, sometimes becoming more dominant by replacing temperate species. These subtropical species exhibit an annual life cycle trait and develop their stocks only between winter and spring. This seasonality is attributable to the growth characteristics of the species in which shoot growth is triggered by cooler temperatures and is advantageous for avoiding active grazing by herbivorous animals during warmer seasons. Subtropical *Sargassum* species also have high regenerative ability at their holdfasts, which allows them to grow in severely turbulent conditions during which grazing activity is restricted. These eco-physiological characteristics of subtropical *Sargassum* species contrast greatly with those of their temperate counterparts and are well adapted to an environment with high grazing pressure from herbivorous animals. The quantitative and qualitative changes in macroalgal beds will extend to cooler regions in Japan if coastal water temperatures continue to increase. Monitoring and continuous surveying of coastal areas are needed in addition to countermeasures to protect biological and fisheries production against the coastal environmental changes induced by global warming.

Several species of dinoflagellates produce toxins responsible for paralytic shellfish poisoning (PSP). When these dinoflagellates bloom, their toxins accumulate in mussels and oysters that ingest them. Outbreaks of PSP in mussels and oysters caused by *Alexandrium*, *Gymnodinium catenatum* Graham, and *Pyrodinium bahamense* Plate var. *compressum* (Böhm) Steidinger, Tester & Taylor are currently a serious problem from both an economic and a food hygiene point of view. The occurrence of toxic *Alexandrium* blooms has increased in frequency, and these species are widely distributed in the coastal waters of Europe, North America, Japan, the Philippines, Australasia, India, and Argentina (Hallegraeff, 1995). Extensive taxonomic, physiological, and ecological studies have resulted in the recognition of some 10 species of the genus *Alexandrium* that are toxic or presumed toxic (Balech, 1995; Yoshida & Fukuyo, 2000). In Japan, *A. catenella* (Whedon & Kofoid) Balech, and *A. tamarense* (Lebour) Balech are the major *Alexandrium* species causing PSP. Appearances of the toxic tropical dinoflagellate species *A. tamiyavanichii* have been confirmed in the Seto Inland Sea since the 1990s, although it remains unclear whether global warming is directly responsible. Rising winter water temperatures in the Seto Inland Sea in Japan have occurred in response to progressing global warming caused by the massive exhaustion of carbon dioxide and the decomposition of the ozone layer related to civilization and industrialization (Yamamoto, 2003; Takahashi & Seiki, 2004; Wanishi, 2004; Tarutani, 2007).

Our purpose is to present and summarize some of the evidence of the impact of global warming on the coastal waters of western Japan. In this chapter, we discuss three topics that are closely related to global warming: 1) recent trends in environmental changes—mainly in surface water temperature (Section 2-1), 2) the degradation of macroalgal beds composed of algal genus *Sargassum* and kelp and their replacement by subtropical *Sargassum* species (Section 2-2), and 3) the new invasion of tropical species that cause harmful microalgal blooms and its settlement in the introduced area (Section 2-3).

2. Potential climate change effects on environmental characteristics in the coastal ecosystems of western Japan

2.1 Long-term changes in water temperature in the coastal waters of western Japan

According to the *Global Warming Projection*, published by the Japan Meteorological Agency (2008), the sea surface temperature (SST) around Japan has increased 0.8–1.7°C over the past 100 years (1900–2007). The SST around Japan is projected to increase, and the long-term SST trends for the 21st century predicted using the North Pacific Ocean General Circulation Model (Sato et al., 2006) are increases of 2.0–3.1°C and 0.6–2.1°C per century under scenarios A1B and B1, respectively. The findings for near-shore areas were not included in this report, however, and the impacts of global warming on environmental factors in these waters remain unclear. In this section, we take the Seto Inland Sea as an example of the coastal waters of western Japan and discuss recent trends in water temperature.

2.1.1 Site description

The Seto Inland Sea is the largest semi-enclosed coastal sea in Japan, surrounded by Honshu (the main island of Japan), Shikoku, and Kyushu Islands (Fig. 1). It is 500 km long, has an average depth of 30 m, and contains more than 700 small islands. The region of the Seto Inland Sea is meteorologically referred to as the Seto Inland Climate Zone. The annual average temperature and precipitation are 15°C and 1,000–1,600 mm, respectively. The watershed land covers 68,000 km^2, which corresponds to about 18% of the total land area of Japan. This region is one of the most industrialized areas in Japan. At present, approximately 35 million people—about 18% of the total population of Japan—live within the watershed, and the marine environment has been significantly affected by their activities.

Although the Seto Inland Sea is enclosed, phenomena in the Pacific Ocean can strongly influence its marine environment thorough two boundary regions, the Kii and Bungo Channels. Off the southeastern coasts of Kyushu, Shikoku, and Honshu, the Kuroshio Current flows northeastward. This current corresponds to the northeastern part of the subtropical ocean gyre that circulates clockwise in the North Pacific and transports a large amount of water and heat to the coast of Japan. The current path shows significant interannual variations off the southern coast of Japan (e.g., Kawabe, 2005; see Fig. 1) and strongly influences the thermal conditions and nutrient environment in the Seto Inland Sea, especially around the Kii and Bungo Channels.

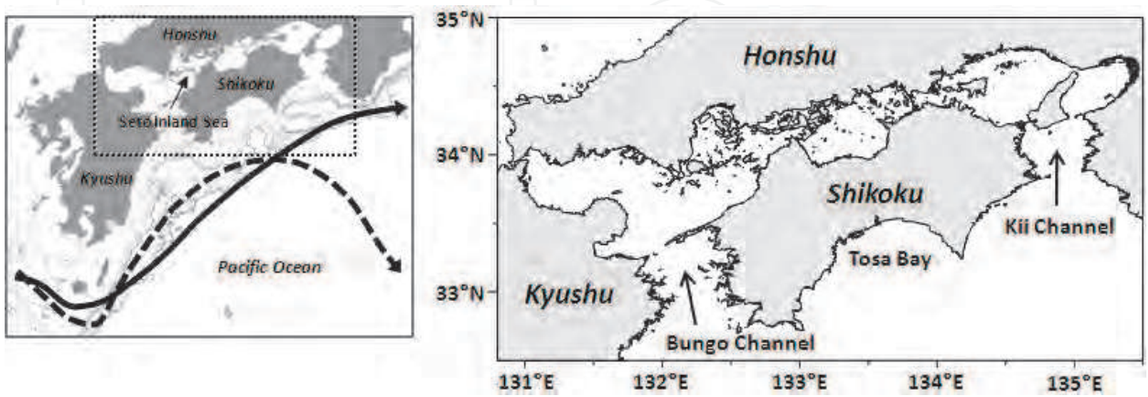


Fig. 1. Maps of the Seto Inland Sea and the typical Kuroshio Current path off the southern coast of Japan (left). The dashed and solid lines in the left panel represent the typical offshore (large meandering) and near-shore (non-large meandering) path, respectively.

The Seto Inland Sea has extremely high productivity per unit area of fishery products, which is the largest among comparable semi-enclosed coastal seas worldwide (e.g., Chesapeake Bay, Baltic Sea, North Sea, Mediterranean Sea; Takeoka, 2002). This high productivity is related to the extremely complex and semi-enclosed geography of the sea and the presence of essential nutrients supplied from the many rivers around the sea in sufficient amounts for the growth of phytoplankton. In recent decades, decreasing fishery production in the Seto Inland Sea has become recognized as a serious problem (Yamamoto 2003; Tarutani et al., 2009).

2.1.2 Recent trends in water temperature

The mean seasonal pattern for water temperature in the Seto Inland Sea has a maximum value in late summer (August to September) and a minimum value in late winter (February to March). The pattern differs somewhat spatially: the winter temperature is higher in the areas near the Kii and Bungo Channels, whereas the summer temperature is higher in the western part of the sea. Fig. 2 shows the long-term variations in mean water temperature throughout the Seto Inland Sea, and these variations were extracted from data gathered by the Fisheries Monitoring Program since 1973. After 1989–1990, the mean water temperature at a depth of 10 m generally remained higher than that measured during the 1980s (Tarutani, 2007). Considerable interannual variability is superimposed on long-term warming—for example, in Hiroshima Bay, located in the central part of the Seto Inland Sea, the annual mean temperature of water at 10 m of depth has warmed by about 1.0°C since 1973. The water temperature fluctuations differed seasonally, however. The warming trend was noticeable in autumn-winter, but was weak in spring-summer (Fig. 3). Such warming phenomena have occurred in several of the western coastal waters of Japan (e.g., Tosa Bay, located in the southern part of Shikoku Island; Setou et al., 2004).

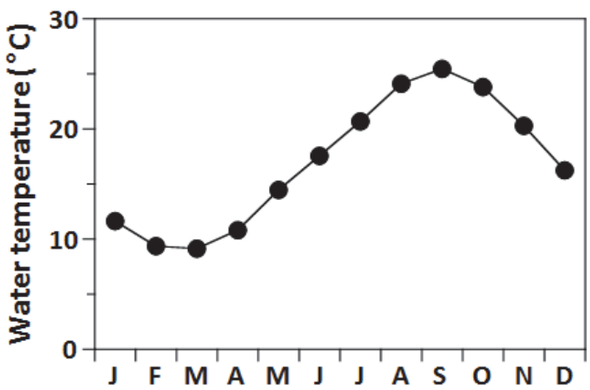


Fig. 2. Seasonal variations in water temperature in Osaka Bay, in the eastern part of the Seto Inland Sea (the mean from 1973 to 2002).

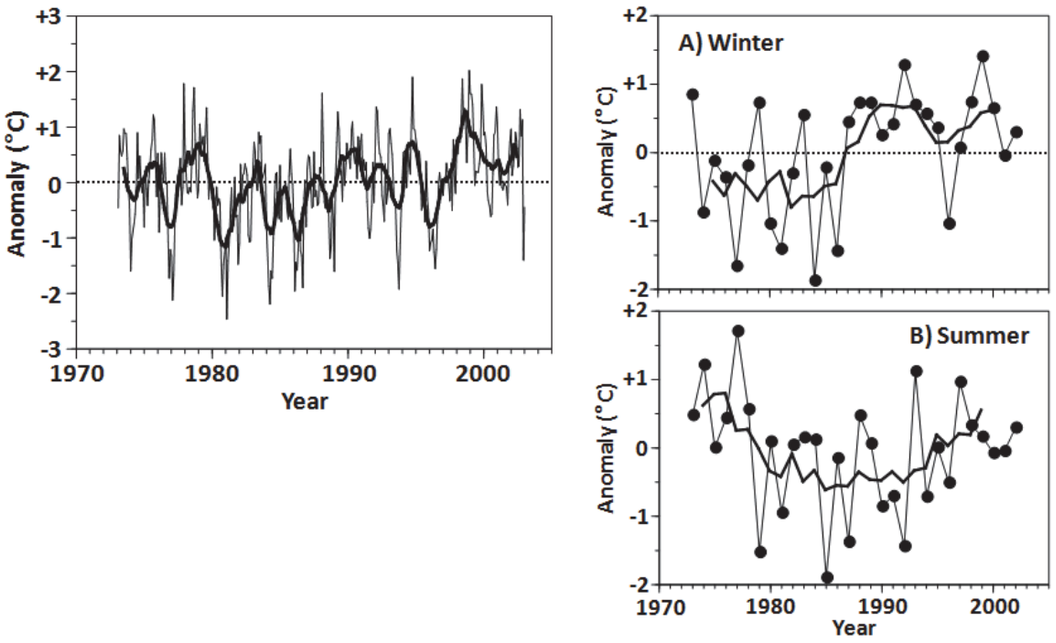


Fig. 3. Long-term variations in water temperature at 10 m depth in the Seto Inland Sea from 1973 to 2002. The thick line in the left panel indicates the running mean from 13 months of data. The right panels are (a) winter and (b) summer data, and the thick lines indicate the running means of 3 years of data.

The seasonality and future trends of water temperatures in the Seto Inland Sea are extremely important because they provide insight into the phenological changes in phytoplankton and macroalgae and may also play a role in regulating nutrient delivery to the sea from the Pacific Ocean. A hydrological modeling study revealed that the rising water temperature in the Seto Inland Sea was caused not only by changes in heat flux at the sea surface but also by changes in open oceanic temperature (Takahashi & Seiki, 2004). This discovery suggests that further detailed investigations of the mechanisms determining both regional atmospheric and oceanic temperature are required to accurately assess the impacts of climate change on hydrology in the Seto Inland Sea.

2.2 Changes in macroalgal vegetation on Japanese coasts

2.2.1 Degradation of macroalgal beds in southern temperate Japan

As mentioned in the introduction, coastal water temperatures have been increasing in Japan since the 1970s. The temperature increase is exerting a large influence on coastal ecosystems both directly and indirectly. Luxuriant macroalgal beds with diverse flora along the Japanese coast reflect variable climatic characteristics (cold and warm temperate to subtropical). These beds, called *Moba* in Japanese, were estimated to cover approximately 201,000 ha during the last research survey conducted between 1989 and 1991 (Environmental Agency & Marine Parks Center of Japan, 1994). In temperate Japan, large brown algae of the genus *Sargassum* and kelps (*Eisenia* and *Ecklonia)* dominate rocky shores and exhibit high productivity (Fig. 4). Along with the seagrass *Zostera* on sandy shores, these algae play important ecological roles as habitats for many marine animals. A recent report has shown that these brown algal beds have become extremely degraded or have

disappeared during the last 20 years, especially in the southern part of temperate Japan (Fig. 5). In the southern area of the Miyazaki Prefecture in Kyusyu, for example, nearly 90% of local *Sargassum* beds have been lost (Aratake et al., 2007). In another case in the Kochi Prefecture, most kelp beds along the coast were lost after 1990 (Hiraoka et al., 2005).

The mass disappearance of local kelp and *Sargassum* beds in these regions is estimated to encompass several thousand hectares and 44.7% of the macroalgal beds reinvestigated after the survey by the Environmental Agency in 1989–1991 (Fujita et al., 2010). In most cases, the disappearance of macroalgal beds has seriously affected local coastal fisheries such as abalone fisheries (Serisawa et al., 2004). The scenery of the seabed after the decrease or loss of these large brown algae is called *Isoyake* (Fig. 6a). *Isoyake* has been known to occur occasionally since the 19th century with the approach of the Kuroshio Current offshore in the Pacific region (Fujita et al., 2010). The recent appearance of *Isoyake* is more frequent, however, and the phenomenon has extended to the entire Japanese coast. In the most remarkable case of *Isoyake*, the only dominant algae are crustose coralline algae on rocks or boulders that frondose macroalgae once occupied. Another common aspect among *Isoyake* regions is increased grazing pressure on algae by herbivorous animals (mainly fish and sea urchins; Fujita et al., 2010). Although it is unconfirmed whether these grazers are the cause of *Isoyake*, they prevent the recovery of frondose macroalgae and surely contribute to the continuity of *Isoyake* conditions.

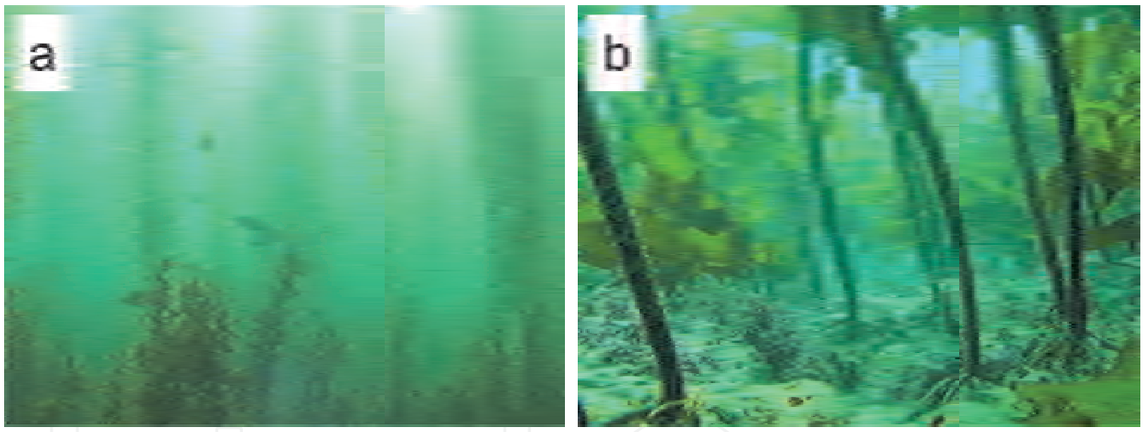


Fig. 4. Brown algal beds in southern temperate Japan. A *Sargassum* bed (a) in Hiroshima Bay, the Seto Inland Sea, and a kelp (*Ecklonia*) bed (b) at Sata-Misaki Peninsula in the Bungo Channel.

2.2.2 Changes in *Sargassum* flora in *Isoyake* areas

Concurrent with *Isoyake* during and after the 1990s, changes in the species composition of *Sargassum* beds that remain in *Isoyake* areas have also been reported in southern temperate Japan (e.g., Fujita et al., 2010). Along the coast of the Kochi Prefecture in the Pacific region, temperate species such as *S. micracanthum* and *S. okamurae* that dominated during the 1970s have been decreasing, and the subtropical species *S. duplicatum* (Fig. 6b) has become a major component of the flora since the 1990s (Hiraoka et al., 2005). In the Miyazaki Prefecture, *Sargassum* flora composed mainly of temperate species in 1970s has contained many subtropical species since 2000 (Aratake et al., 2007). The appearance of subtropical *Sargassum* has also been reported in the *Isoyake* area of Nagasaki, in the western Kyushu region (Fujita

et al., 2010). Subtropical *Sargassum* exhibits annual characteristics in its life cycle that contrast greatly with the perennial characteristics of most temperate species (Fig. 7). Although the perennial species sustain shoots year round, subtropical species in Japan display shoot growth only in winter and spring. After reproduction in early summer, their shoots become senescent, and no visible thalli are observed in autumn (Shimabukuro et al., 2007).

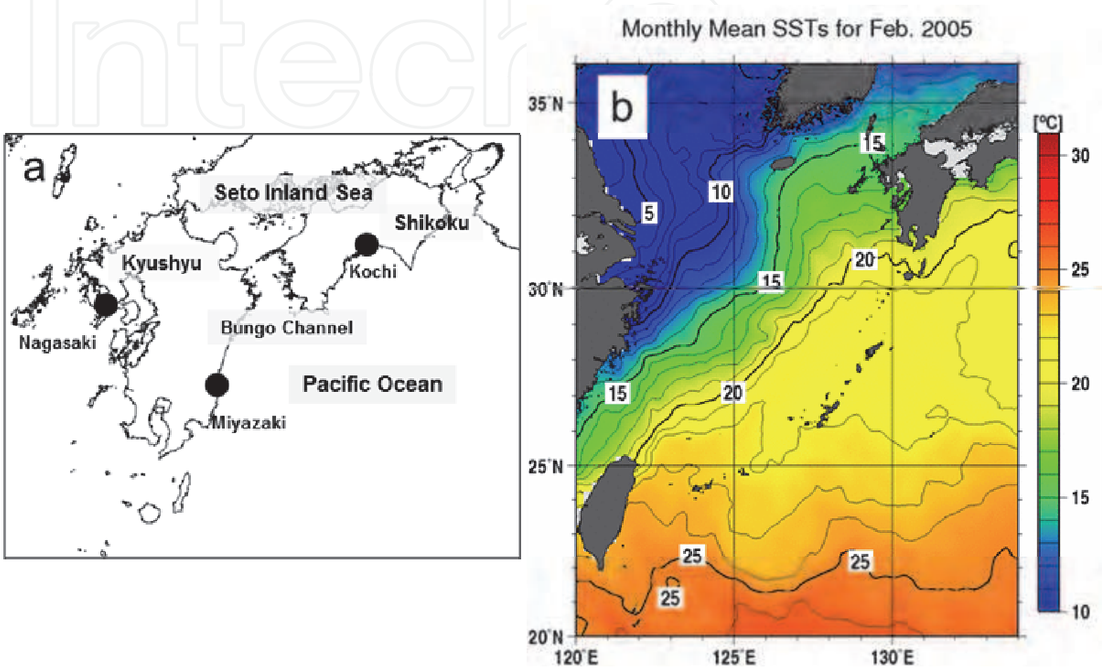


Fig. 5. Places cited in the text (a) and surface water temperature in winter (Feb. 2005) in the southern sea area of Japan (b) from the website of the Japan Meteorological Agency (2011).

To understand the physiological mechanism of subtropical *Sargassum* seasonality, we examined growth characteristics against variable temperatures for several common subtropical *Sargassum* species under experimental culture conditions. The results showed that the optimum temperature range for shoot growth in these species is 16–21°C, a range that coincides with winter coastal water temperatures in southern temperate Japan (see Fig. 5). Shoot development was inhibited above 24°C (Fig. 8), which is the average summer-autumn temperature in the field (Yoshida et al., 2009). This finding suggests that a drop in winter water temperature triggers shoot growth in subtropical *Sargassum*. On the contrary, the optimum temperature range for shoot growth is wider for temperate species. Even at summer temperatures (25°C), the shoots of many temperate species exhibit smooth growth (Haraguchi et al., 2005; Yoshida et al., 2008). These data seemed contradictory—a warmer temperature suppresses the growth of subtropical species more than it suppresses the growth of temperate species. Such a growth characteristic seems to be advantageous, however, because it allows subtropical species to escape grazing pressure by herbivorous animals. For example, the feeding activity of rabbit fish (*Siganus fuscescens*), a common herbivorous fish in warm temperate Japan, is temperature dependant. It grazes brown algae intensively under warmer temperatures (>25°C), whereas grazing activity is low below 20°C and almost stops at 15°C (Yamauchi et al., 2006). Owing to their growth characteristics,

subtropical species can develop shoots during winter when the herbivorous fish is inactive. On the contrary, temperate species are defenseless and vulnerable to grazing by these fish owing to the year-round growth pattern of their stands.

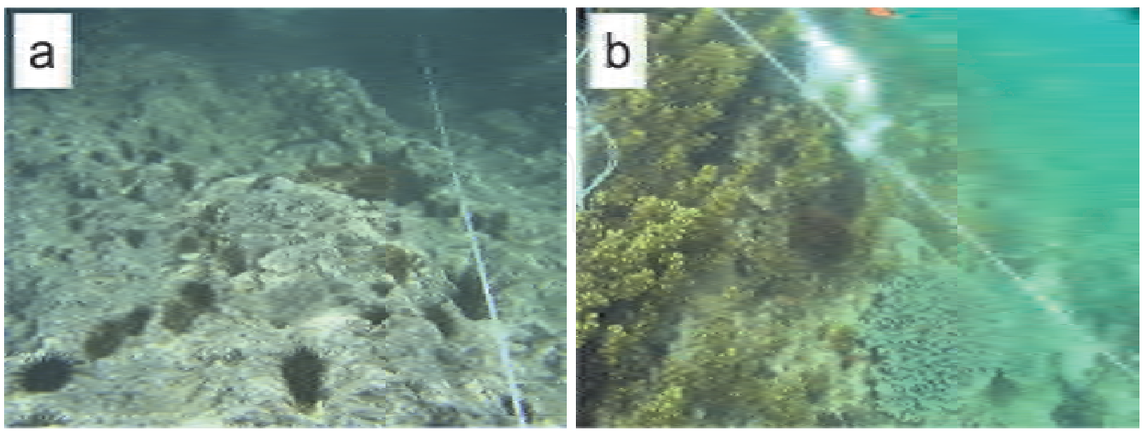


Fig. 6. *Isoyake* (a) and subtropical *Sargassum duplicatum* with co-occurring corals (b). Both were photographed at Ainan, Ehime Prefecture, in the Bungo Channel.

Another advantageous characteristic of subtropical species revealed by our study is their high regenerative ability, which enables them to develop stands under high grazing pressure. A high frequency of new budding production from holdfasts is observed in several subtropical species (e.g., *S. carpophyllum*) when the holdfasts are experimentally excised from their thalli (Fig. 9a). On the contrary, less or no budding occurs in the excised holdfasts of temperate species—e.g., *S. yamamotoi*, one of major species in warm temperate regions. Many subtropical *Sargassum* can develop stands in specific environments with relatively severe physical turbulence—for example, strong surge or frequent sand movement (Fig. 9b). Holdfasts of subtropical *S. carpophyllum* can endure being buried in sand for several months, and after reappearing, they can generate new thalli. Less grazing occurs in such severe environments, and even when grazing does occur, the high regenerative ability of subtropical species allows them to grow despite physical damage.

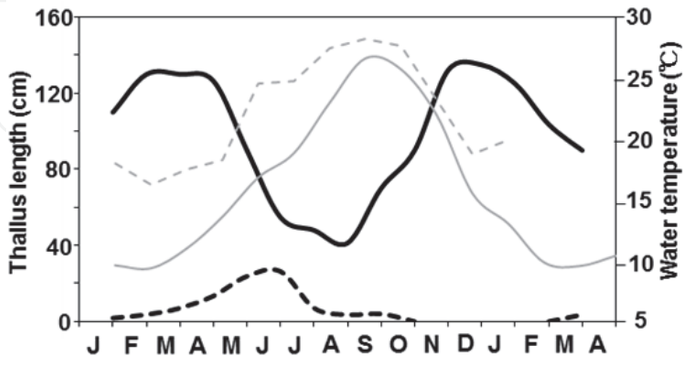


Fig. 7. Schemes of seasonality of temperate and subtropical *Sargassum*. The bold, solid line indicates seasonal growth of temperate *S. fulvellum* (from Yoshida et al., 2008), and the bold dotted line indicates subtropical *S. duplicatum* (from Shimabukuro et al., 2007). The thin solid and dotted lines indicate water temperature in their habitats, respectively.

2.2.3 Mechanisms of the changes and human countermeasures

Although many factors (e.g., nutrient depletion, change in food web structure related to overfishing of predators) are possible contributors to *Isoyake*, the increase in coastal water temperature is one of the most plausible (Fujita et al., 2010). In the past few decades, the mean yearly surface temperature along the warm temperate Japanese coast has increased 0.5°C to 0.7°C (e.g., Serisawa et al., 2004; Shimabukuro et al., 2007). Although extreme rises in summer temperature could cause physiological damage to macroalgae, long-term monitoring also indicates that the temperature increase has been larger in winter than in summer (Hiraoka et al., 2005; Shimabukuro et al., 2007). Rising water temperature in autumn and winter allows herbivorous animals to be active for longer periods. An increase in grazing by these animals may be the most potent cause for the ousting of temperate large brown algae in warm temperate regions. It has been reported that when grazing pressure increases, shallow coastal seabeds shift from being macroalgal dominated to being coral- or coralline algal dominated in tropical and subtropical regions (Lapointe et al., 1997). Are subtropical *Sargassum* extending their distribution in temperate regions of Japan? Some past records indicate that the subtropical species are minor but original members of the coastal flora once dominated by temperate species in southern temperate Japan (Aratake et al., 2007). As the result of environmental change over several decades, subtropical *Sargassum* ecologically adapted to high grazing pressure and has been becoming conspicuous, replacing major temperate species that are more sensitive to grazing (Yoshida et al., 2009).

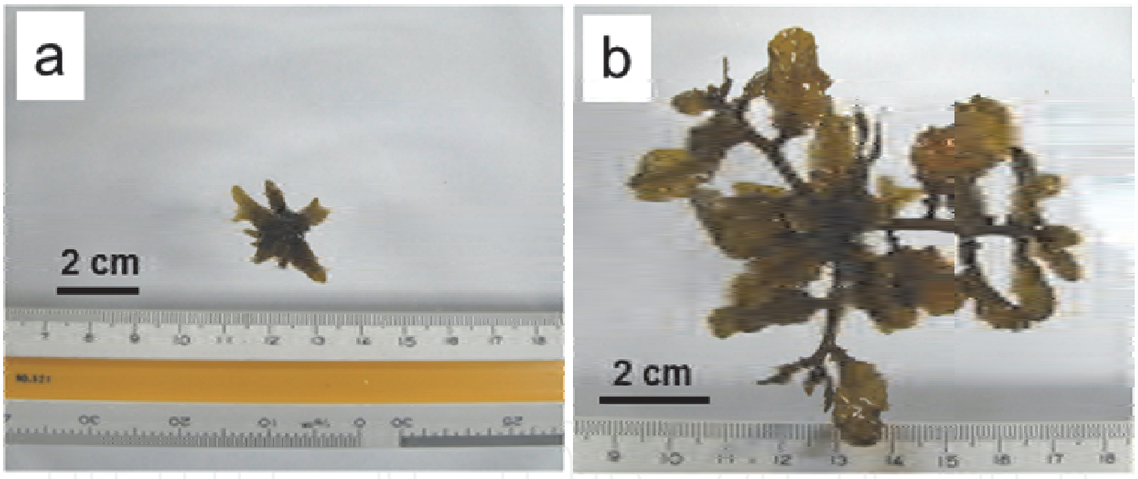


Fig. 8. Growth of subtropical *Sargassum duplicatum* cultured in a laboratory under (a) 24°C, and (b) <18°C.

The mass disappearance of macroalgae in warm temperate coastal Japan has had serious effects on coastal biological productivity, and countermeasures to sustain coastal fisheries are needed. It is well known that physical defense of *Moba* against grazing by using nets or cages and removing herbivores is often effective for recovering macroalgal beds in *Isoyake* areas (Fujita et al., 2010). Another possible countermeasure that protects fisheries production is the exploitation of productivity of the new vegetation of subtropical *Sargassum*. Because subtropical *Sargassum* species have characteristics that differ from those of temperate ones—e.g., seasonality, habitat, stand structure—the ecological roles they could play in the coastal ecosystem should be evaluated (Fujita et al., 2010).

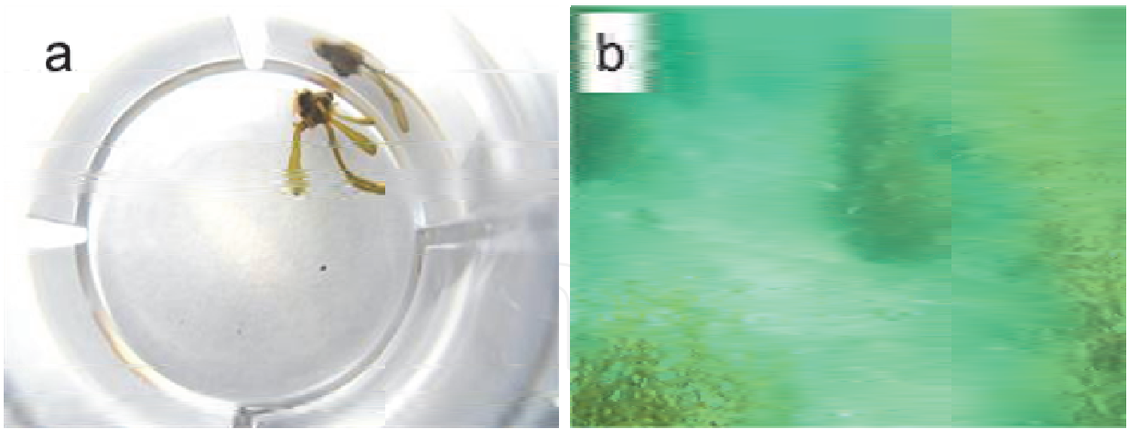


Fig. 9. (a) Regeneration of new buddings from an excised holdfast of *Sargassum carpophyllum*, and (b) a *Sargassum* habitat buried in sand (Kushima, Miyazaki Prefecture).

If coastal water temperature continues to increase as predicted, quantitative and qualitative change in macroalgal beds will extend to cooler regions in Japan. To recognize these changes as soon as possible, fixed survey stations around the Japanese coast have been established for a long-term national monitoring project (e.g., Biodiversity Center of Japan, 2011). One of the most interesting survey points is in the channels between the Pacific regions and the Seto Inland Sea in southern Japan. In the Bungo Channel, a gradient in winter seawater temperature ranges between 6°C and 8°C within ca. 200 km. Within this distance, both luxuriant brown algal beds and *Isoyake* with subtropical *Sargassum* and corals are observed (Yoshida et al, 2009), as shown in Figs. 4 and 6. Ecological and oceanological surveys in this transition zone, or ecotone, between temperate and subtropical areas will provide valuable information about the mechanisms of global warming effects on coastal ecosystems.

2.3 Appearance of a tropical harmful algal bloom species in temperate Japanese coastal waters

The first appearance of *A. tamiyavanichii* was confirmed in a towing plankton net sample at Aburatsubo in Sagami Bay, Japan, in 1988 (Ogata et al., 1990). After that, *A. tamiyavanichii* bloomed for the first time at Shioya Bay in Okinawa Prefecture, Japan, in 1997 and again in 1998, and an outbreak of PSP was confirmed in green muscles fed *A. tamiyavanichii* (Koja et al., 2001). This record is the first of toxification of shellfish caused by this species in Japan. The appearance of *A. tamiyavanichii* was also confirmed in the Seto Inland Sea in 1997 when 6.6 MU g^{-1} of PSP from the edible part of Japanese oysters in Uchinoumi, Tokushima Prefecture (Sato et al., 2001) and 8.8 MU g^{-1} of PSP from muscles and 5.0 MU g^{-1} of PSP from arch shells at Tsuta-cho in Kagawa Prefecture were detected in 1999 (Yoshimatsu et al., 2000)—the first record of PSP outbreaks attributed to this species in the Seto Inland Sea. In 2001, *A. tamiyavanichii* blooms were confirmed in almost all areas of the Seto Inland Sea, and 2.4 MU g^{-1} of PSP was detected in manila clams (Tanada et al., 2003).

The blooming of this species has often been observed not only the Seto Inland Sea but also around the Tsushima, Gotou, and Amami Islands (Fig. 10). This species has also been collected in the Gulf of Mexico, the Straits of Malacca in Malaysia (Usup et al., 2002), the Gulf of Thailand (Fukuyo et al., 1988), and Manila Bay in the Philippines (S. Sakamoto, personal communication). Research has provided some information on the morphology and

the ultrastructure of vegetative cells (Phanichyakarn et al., 1993; Wisessang et al., 1993; Balech 1994; Nagai et al., 2003), life cycle (Nagai et al., 2003; Nagai et al., 2008), growth characteristics and toxin production (Kodama et al., 1988; Fukuyo et al., 1989; Ogata et al., 1990; Nagai et al., 2008; Oh et al., 2009), phylogenetic position (Usup et al., 2002), and distribution (Fukuyo et al., 1988) of this species and toxin accumulation in mussels that feed on it (Wisessang et al., 1991; Hashimoto et al., 2002).

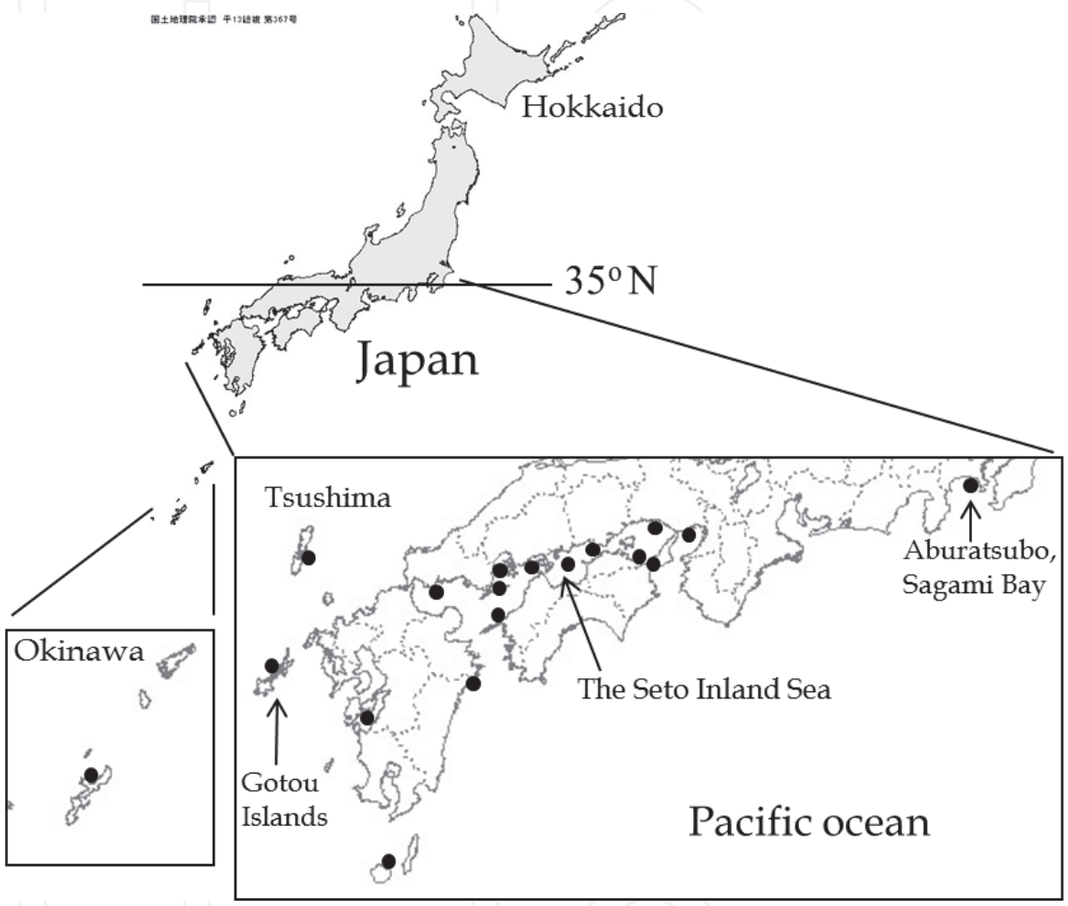


Fig. 10. Occurrences of the toxic dinoflagellate *Alexandrium tamiyavanichii* in Japanese coastal waters. Note that until now, the distribution has been limited in areas south of the northern latitude of 35°C.

item	vegetative cells (μm)	planozygotes (μm)	item	cysts (μm)
length	30-60	50-70	long diameter *	45-75
width	35-65	50-75	short diameter*	35-60
			height	40-60

Table 1. Measurements of cell sizes of *Alexandrium tamiyavanichii* in culture (n=50). *, They were measured from the upper side.

2.3.1 Morphological characteristics of *A. tamiyavanichii*

Vegetative cells of *A. tamiyavanichii* are yellow-brown and contain numerous chloroplasts (Nagai et al., 2003). This species forms long chains that often contain more than 200 cells during the early and middle exponential growth phases under laboratory conditions (Fig. 11a). Cell chains separate into smaller chains or even single cells in the stationary phase. Vegetative cells are 30–60-µm long and 35–65-µm wide, and the sizes drastically change in response to culturing (Table 1). The cell is round to subpentagonal in the ventral view and usually more wide than long. The first apical plate has a ventral pore at the posterior portion of the right anterior margin with the fourth apical plates (Fig. 11b). The most typical characteristic of this species is that the sulcal anterior plate has a triangular or rectangular anterior expansion, and the anterior and posterior portions are delimited by a transverse rib, but the two parts are inseparable (Balech, 1994; see Fig. 11b).

2.3.2 Toxin composition in *A. tamiyavanichii*

Vegetative cells of *A. tamiyavanichii* collected from the Tokushima Prefecture (eastern Seto Inland Sea) in 1999 showed PSP toxicity, of which 83 mol% was accounted for by gonyautoxin (GTX) 2, GTX3, and GTX4 with fluorescent high-performance liquid chromatography analysis. Its specific toxicity was 112.5 fmol cell^{-1}, and 1 MU was equivalent to 7,200 cells (Hashimoto et al., 2002). The toxic component of the Aburatsubo strains from Sagami Bay, Japan, was dominated by the highly potent carbamate toxin GTX4 (37–45 mol%; Ogata et al., 1990). The toxic composition observed in samples from the Tokushima Prefecture was closely related to that of strains isolated from the Gulf of Thailand (Ogata et al., 1990; Wisessang, et al., 1991). The toxic components of *A. tamiyavanichii* clonal strains, isolated from the Seto Inland Sea, showed that *N*-sulfocarbamoyl (C-) 2 and GTX4 were the main toxins, and C3+4, GTX2+3, GTX5, neo-saxitoxin (neo-STX), and STX were minor components (Oh et al., 2009). The percentages of the main toxins (C2 and GTX4) are closely related to those of *A. tamarense* and *A. catenella*. Potent toxic components including GTX2+3 and STX existed at higher concentrations than was the case with *A. tamarense* and *A. catenella*, however. Additionally, the average toxicity of *A. tamiyavanichii* was higher than that of *A. tamarense* and *A. catenella*. Toxic components detected from several shellfish, including the mussel *Mytilus galloprovincialis*, the Pacific oyster *Crassostrea gigas*, and the ark shell *Scapharca broughtonii* after the large-scale bloom of *A. tamiyavanichii* in the eastern Seto Inland Sea in early December 1999 were similar to those detected in *A. tamiyavanichii* plankton cells (Hashimoto et al., 2002), and the PSP toxicity in the shellfish that were higher than regulation levels (4 MU g^{-1}) were seen when the abundance of *A. tamiyavanichii* in the bloom was greater than 30 cells mL^{-1} (Yoshimatsu et al., 2000; Sato et al., 2001; Tanada et al., 2003).

2.3.3 Sexual reproduction in *A. tamiyavanichii* under laboratory conditions

In one study, encystment through sexual reproduction was observed in 54 pairs (39.7%) of 136 pairs of *A. tamiyavanichii*, which included 16 that were self-crossing, using 16 clonal strains under laboratory conditions (Nagai et al., 2003). Neither planozygote formation nor encystment was confirmed in any of the self-crossings. These results clearly show that *A. tamiyavanichii* is heterothallic—i.e., compatible strains of an opposite mating type are required for sexual reproduction. Crossing experiments have been carried out in a modified f/2 medium (made up with 1/6 nitrate and phosphate, 1/3 metals and 1/10 vitamins; see

Nagai et al., 2004) using a sexually compatible mating pair under the same conditions used in growth experiments. Vegetative cells in the mixed culture at 25°C grew exponentially, and the growth reached a peak (2,400 ± 200 cells mL^{-1}) on day 8, with density thereafter decreasing gradually owing to an increase in the number of planozygotes and resting cysts (Fig. 12). Suspected gametes began to appear in the culture 2–3 days after the crossing experiment started (see Fig. 12). These cells were morphologically indistinguishable from gametes (hologamy), but the swarming of single vegetative cells, which make an association of sexual mating behaviour as seen in *A. tamarense*, were often observed in the early and middle exponential growth phases.

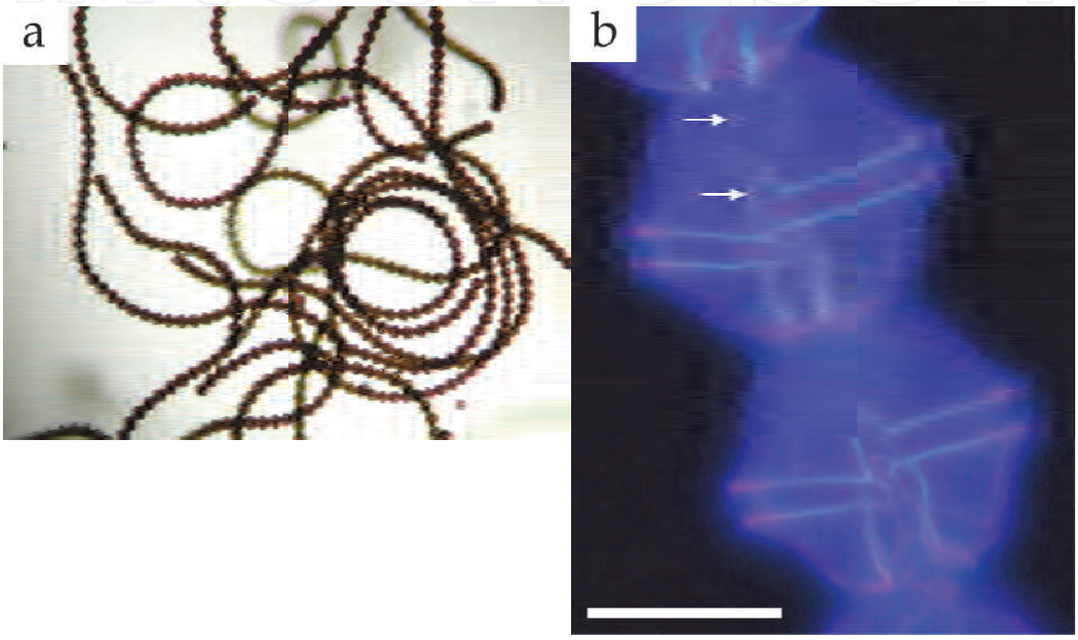


Fig. 11. Vegetative cells of *Alexandrium tamiyavanichii*. (a) A long chain consisting of more than 200 cells. (b) Vegetative cells stained with calcofluor-white. Arrows indicate a ventral pore and a transverse rib. Scale bar is 25 μm. Observation in (a) was made using a Nikon TE-300 light microscope (Tokyo, Japan) and in (b) using an epifluorescence microscope under ultraviolet and blue light excitation.

Pairs of fusing gametes were isolated in the wells of a microplate with 1 mL of the culture medium to observe the sequence of zygotes. The gametes swam rapidly and made contact with each other bilaterally (gametes remained side by side; Fig. 13a), and the couplets swam helicoidally with rotation due to the almost perpendicular orientation of their longitudinal flagella, as reported in *A. pseudogonyaulax* (Biecheler) Horiguchi ex Yuki et Fukuyo by Montresor (1995). The length of this phase was variable, and a couplet was observed swimming for more than 1 hour before conjugation, whereas others started fusing sooner and formed a planozygote (Fig. 13b, c). Conjugation took place through the progressive engulfment of one gamete by the other, which consequently increased in size (see Fig. 13c). Sexual reproduction was by conjugation of isogametes, although the cell length of one mating gamete was often up to 1.2–1.3 times longer than that of the other. Plasmogamy was completed 60–80 min after conjugation started and produced a planozygote with one

transverse and two longitudinal flagella (Fig. 13d). There was no trace of thecal plates near the newly formed zygotes, and only the thecal plates of the gamete that engulfed the other gamete appeared to be maintained as the zygotic thecal plates.

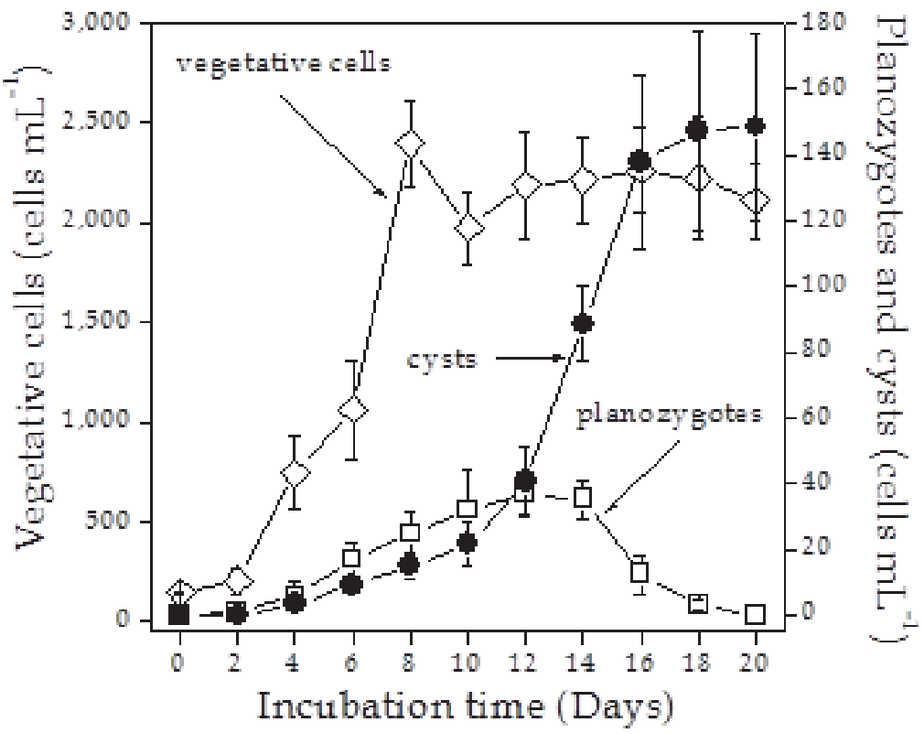


Fig. 12. Encystment of an *Alexandrium tamiyavanichii* batch culture at 25°C. Time-course measurements were carried out to observe the sexuality and the encystment process in 1.9 mL of modified f/2 medium in Iwaki 24-well microplates (Chiba, Japan) under an irradiance of 100–150 µmol m^{-2} s^{-1} provided by cool-white fluorescent lamps with a 12:12 h light:dark cycle (Nagai et al., 2003, 2008). The culture medium contained 1/6 nitrate and phosphate, 1/3 metals, and 1/10 vitamins. Two compatible strains of AT0112T06 and AT0112F06 were mixed and incubated for 20 days. A portion of the *Alexandrium* culture (100 µL) was sampled every 2 days, and the numbers of vegetative cells, planozygotic cells, and resting cysts were counted using a microscope.

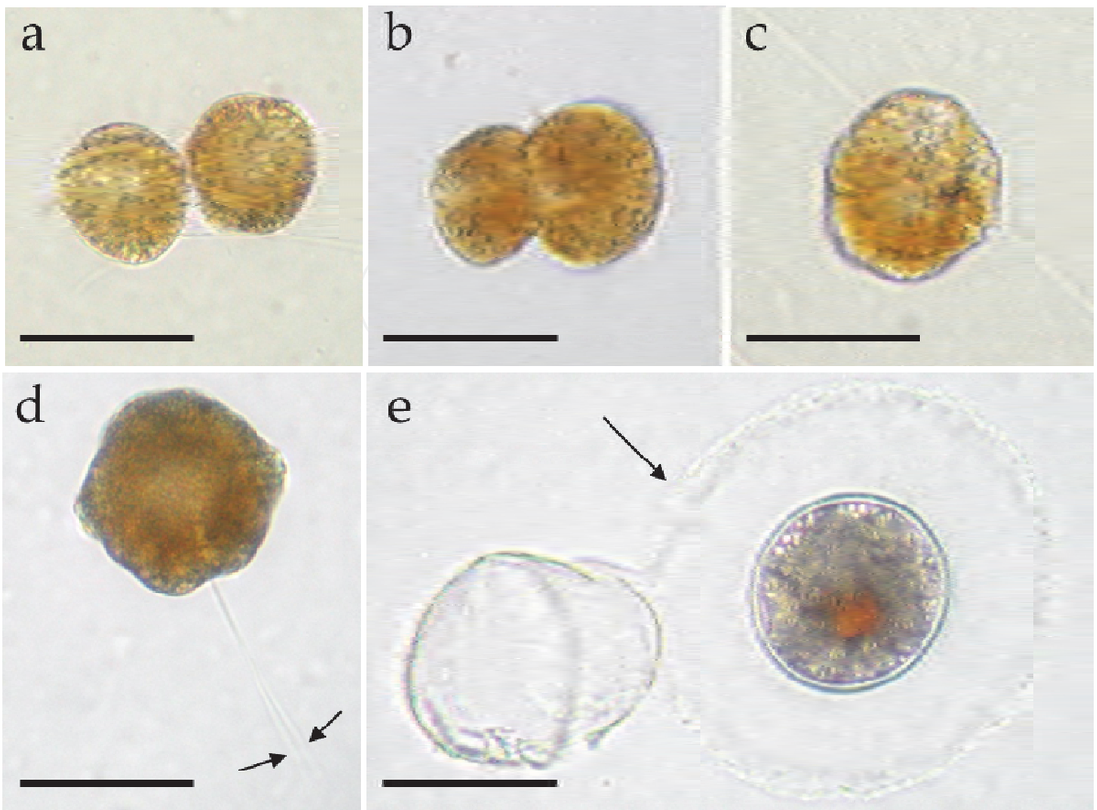


Fig. 13. Life cycle stages of *Alexandrium tamiyavanichii* obtained in the sexual reproduction experiment described in Fig. 12 (Nagai et al., 2003). Scale bars are 50 µm (all at the same magnification). (a) Mating pair of isogametes entwined by their flagella (initial contact phase). (b) Conjugating gametes. (c) Completion of conjugation in which one gamete engulfs the other. (d) Planozygote with two longitudinal flagella indicated by arrows. (e) Threshing during encystment and resting cysts covered with transparent mucilaginous matter indicated by arrows. Observation was made using a Nikon TE-300 light microscope (Tokyo, Japan).

Planozygotes were typically a more blackish color compared with vegetative cells and tended to swim more slowly; therefore, they were readily distinguishable. Planozygotes were 50–70-µm long and 50–75-µm wide and larger than vegetative cells (see Table 1). In the transformation process of planozygotes to hypnozygotic cysts, a small number of planozygotes failed to thresh, but most succeeded and after 2–3 days the cysts were covered with transparent mucilaginous matter as seen in *A. tamarense* and *A. catenella* reported by Turpin et al. (1978), Yoshimatsu (1981), and Nagai et al. (2004) (Fig. 13e). Cysts were vertically compressed (Fig. 14a, b) or spherical (Fig. 14c, d) and 45–75-µm long, 35–60-µm wide, and 40–60-µm high. Scanning electron microscopy clearly showed that the surface of *A. tamiyavanichii* cysts was smooth and lacked paratabulation (see Fig. 14). The density of planozygotes increased gradually until day 12 (74 ± 13 cells mL^{-1}) and then decreased on day 14 owing to transformation into cysts. The period from planozygote formation to transformation into cysts depended on the individual planozygote and varied from 2 to approximately 10 days. Cyst formation was observed on day 4 and encystment continued

exponentially until day 16, with density slightly increasing until the end of the incubation (150 ± 30 cysts mL^{-1}; see Fig. 12).

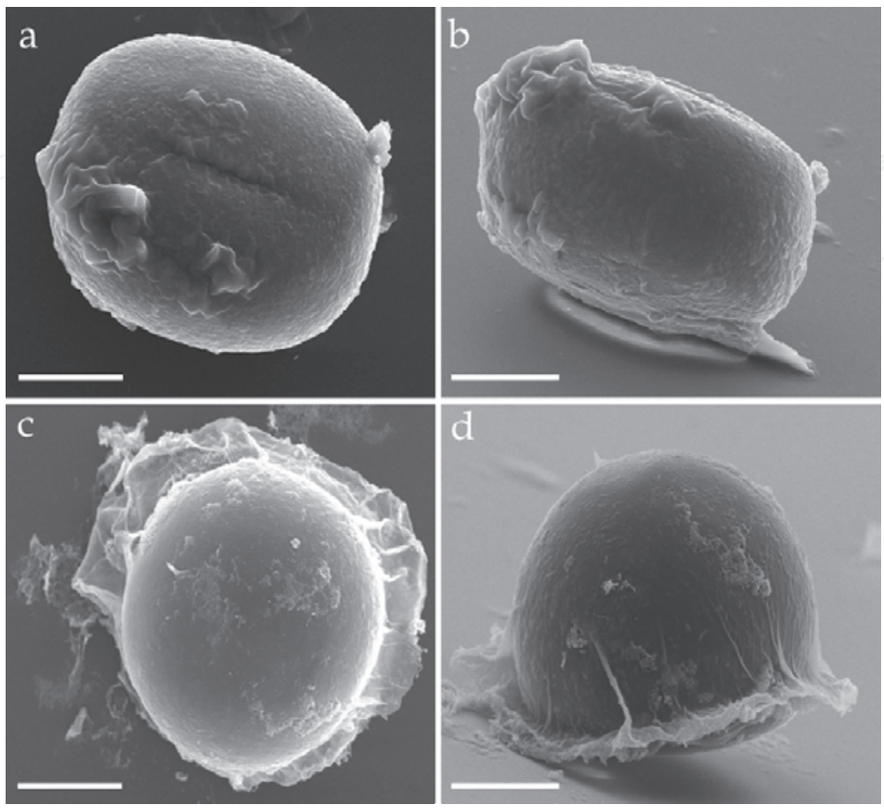


Fig. 14. Scanning electron microscopic observations of resting cysts in *Alexandrium tamiyavanichii* (Nagai et al., 2003). Scale bars are 20 μm (all at the same magnification). (a) Vertically compressed cyst without any paratabulation on the surface (view from above). (b) Side view of the cyst shown in (a). (c) Spherical cyst covered with transparent mucilaginous material (viewed from above). (d) Side view of the cyst shown in (c).

2.3.4 Effect of temperature on vegetative growth and sexual reproduction in *A. tamiyavanichii* and *A. tamarense* under laboratory conditions

Vegetative growth in *A. tamiyavanichii* has been observed at temperatures ranging from 20°C to 32.5°C, and the culture strains survived briefly at 17.5°C and 35°C but died quickly at 15°C (Fig. 15a). Optimum growth was seen around 27.5–30°C, and the growth rates were 0.71–0.76 divisions day^{-1} (Fig. 15b). The maximum yield of vegetative cells ranged from 300 ± 41 cells mL^{-1} at 20°C to 3,513 ± 452 cells mL^{-1} at 30°C, and the yields were highest at 27.5–30°C (see Fig. 15a). The effect of temperature on growth rate tended to be very similar to that for the maximum yield of vegetative cells. Encystment was observed at temperatures between 20°Cand 32.5°C and cyst yields ranged from 7.0 ± 2.6 cysts mL^{-1} at 20°C to 148 ± 28 cysts mL^{-1} at 25°C (Fig. 15c). The cyst yield was highest at 25°C and significantly higher than that at temperatures between 20°C and 32.5°C (*t*-test, $P < 0.005$–0.001). Cyst formation (cyst yield/maximum yield of vegetative cells × 100 [%]) ranged from 0.1 ± 0.1% at 32.5°C to 6.2 ± 1.1% at 25°C (data not shown).

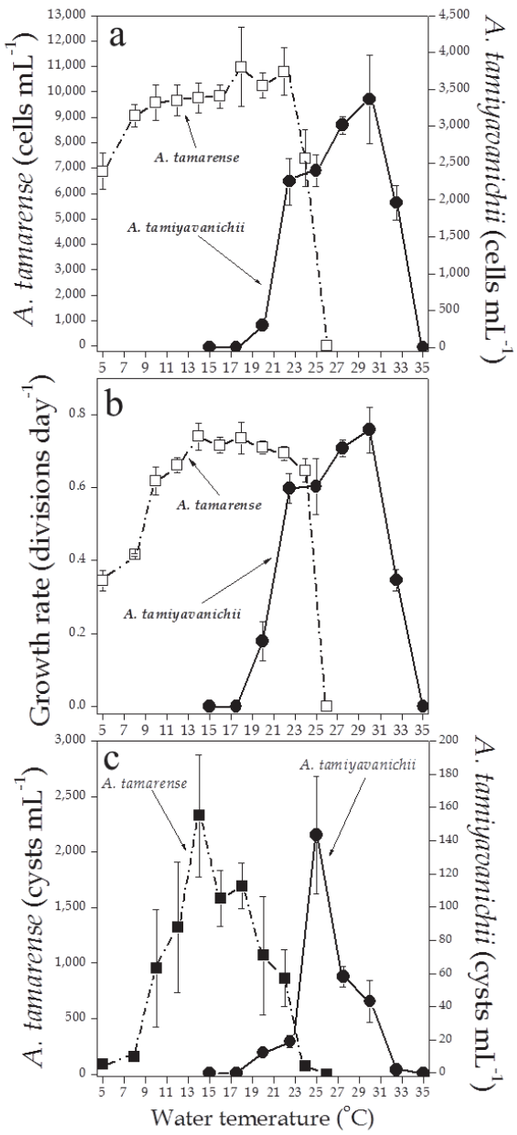


Fig. 15. Effect of temperature on vegetative growth and resting cyst formation in *Alexandrium tamiyavanichii* and *A. tamarense* under laboratory conditions. (a) Maximum yields of vegetative cells at each temperature. (b) Growth rates of vegetative cells at each temperature. (c) Maximum yields of resting cysts at each temperature. Effect of temperature on vegetative growth was investigated at nine temperatures between 15°C and 35°C in *A. tamiyavanichii*, and 11 temperatures between 5°C and 26°C in *A. tamarense* under the conditions described in Fig. 12 (except temperature). Two compatible strains of AT0104H15 and AT0104H26 were used to study *A. tamarense*. After pre-incubation, both strains were mixed at each temperature setting and incubated for 20 days (*A. tamiyavanichii*) and 30 days (*A. tamarense*). Five wells of each were used for counting motile cells and cysts, and the maximum yields of vegetative cells and cysts. The number of vegetative cells counted using the microscope, and the growth rates (divisions day^{-1}) in the exponential growth phase were calculated using the method of Guillard (1973).

In Japanese coastal waters, the toxic dinoflagellate *A. tamarense* was reported mostly along the northern Pacific coast, such as in the Hokkaido and Tohoku regions, until the 1980s (Uchida et al., 1980; Fukuyo, 1982; 1985; Sekiguchi et al., 1986). Since the 1990s, however, *A. tamarense* has become a conspicuous species in southwestern Japan (Yamamoto & Yamasaki, 1996; Kotani et al., 1998), especially in Hiroshima Bay (Asakawa et al., 1995; Yamaguchi et al., 1995; Itakura et al., 2002; Yamaguchi et al., 2002). In laboratory cultures of *A. tamarense* isolated from Hiroshima Bay, vegetative growth was observed at temperatures ranging from 5°C to 24°C, and the maximum yields of motile cells ranged from 6,880 ± 716 cells ml^{-1} at 5°C to 10,980 ± 1,553 cells ml^{-1} at 18°C. No growth was seen at 26°C (see Fig. 15a, b). The growth rate ranged from 0.34 ± 0.03 divisions day^{-1} at 5°C to 0.74 ± 0.04 divisions day^{-1} at 14°C and 18°C (see Fig. 15b), and the rates at 5°C and 8°C were remarkably lower than those at the other temperatures. The range of growth rates between 10°C and 24°C was 0.62–0.74 divisions day^{-1}. Encystment was observed at temperatures ranging from 5°C to 24°C using compatible strains with different mating types, and cyst yields ranged from 68 ± 34 cysts ml^{-1} at 24°C to 2,326 ± 551 cysts ml^{-1} at 14°C (see Fig. 15c). The cyst yields at 5°C, 8°C, and 24°C were remarkably lower than those at the other temperatures. The cyst yield at 14°C was significantly higher than that at temperatures between 10°C and 22°C (*t*-test, $P < 0.05$–0.001). Cyst formation (cyst yield/maximum yield of vegetative cells × 100 [%]) ranged from 0.9 ± 0.5% at 24°C to 23.8 ± 5.1% at 14°C. The effect of temperature on cyst formation tended to be similar to that for cyst yield. Cyst formation at 14°C was also significantly higher than that at temperatures between 10°C and 22°C (*t*-test, $P < 0.05$–0.001; data not shown, but see Nagai et al., 2004). Therefore, the optimal temperature for encystment of *A. tamarense* strains from Hiroshima Bay is approximately 14°C.

2.3.5 Effect of temperature on germination of resting cysts in *A. tamiyavanichii* under laboratory conditions

Experiments have been conducted to examine the germination physiology of resting cysts obtained from laboratory cultures of *A. tamiyavanichii* under laboratory conditions after storage at nine temperatures ranging from 5°C to 30°C for several months in darkness. The experiments were conducted at 25°C or at each temperature at which the resting cysts had been stored. In the experiment at 25°C, the first excystment (germination) was confirmed on day 7 because the cysts had been stored in darkness at 17.5°C to 30°C (3.3–10.8% germination success—i.e. germinated cysts/total cysts × 100 [%]), and germination was confirmed at all temperatures except 5°C on day 15 (4.2–91.2%). Germination success was higher than 60% at temperatures between 10°C and 17.5°C (Fig. 16a). After day 30, germination success at 10°C continued to be approximately 50%, but >80% at 15°C to 27.5°C. Germination success at 30°C increased after day 51, and high germination success (>80%) was observed after that. No germination was confirmed at 5°C throughout the experiment, however. At 7.5°C, germination was seen only on day 15 (4.2%) and day 30 (9.0%). In the germination experiment at each temperature at which cysts were stored in darkness, successful germination was observed at ≥17.5°C, but not at <15°C (Fig. 16b). High germination success (79.4–96.6%) was observed at 20°C, 27.5°C, and 30°C after day 64. At 17.5°C, germination was confirmed after day 79, but no vegetative growth was seen after germination. Accordingly, the optimum temperature for storage in darkness and germination in resting cysts in *A. tamiyavanichii* is around 25°C, and this species has no dormancy period, or if it does, it would be within 1 week. A germination experiment was carried out at 25°C to examine the germination potential of resting cysts after 3 months of storage in darkness at each temperature, and germination was observed on day 2, although

germination success was low (0.8–8.8%). After that, active germination was confirmed in the resting cysts stored at 15–25°C, with germination success >70% on day 6 (Fig. 16c).

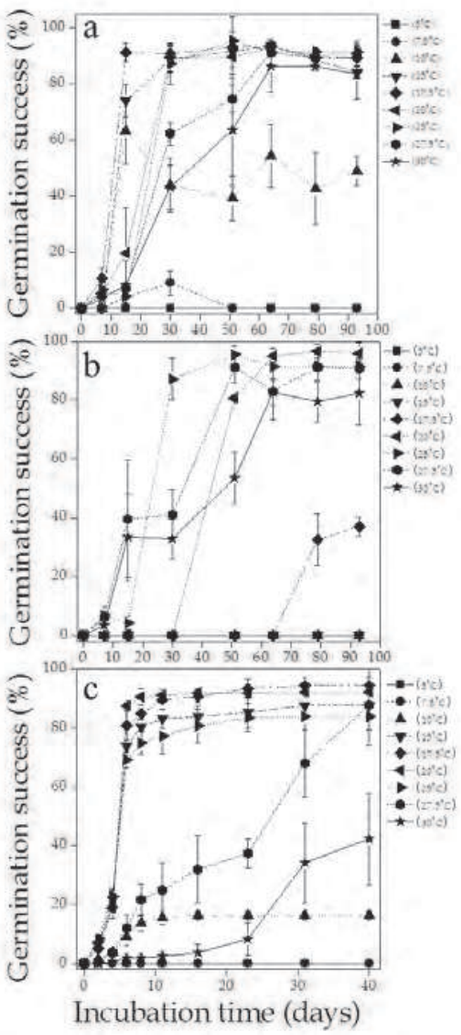


Fig. 16. Effect of temperature on germination in resting cysts of *Alexandrium tamiyavanichii* under laboratory conditions. Cysts were produced under appropriate incubation conditions at 25°C by mixing two compatible strains of AT0112T06 and AT0112F06 as described in Fig. 12. Resting cysts were harvested 3 weeks after the start of the encystment experiment. Cysts were stored in darkness at nine temperatures between 5°C and 30°C to investigate the period of mandatory dormancy of cysts. Some of the cysts (14–65 cysts) were picked up on days 7, 15, 30, 51, 64, 79, and 93 days and incubated at 25°C (a) and at the same temperature at which they had been stored (b). One month after incubation under the light conditions described in Fig. 12, the number of germinated cysts, dead cysts, and total cysts were measured under an inverted microscope. The percentage of germination success was calculated (germinated cysts/total cysts × 100 [%]).Resting cysts stored at the nine temperatures for 90 days were incubated under appropriate light conditions at 25°C (c). Germination success was calculated every 2–9 days for 40 days.

2.3.6 Difference in life cycle strategies of *A. tamiyavanichii* and *A. tamarense*

A. tamiyavanichii grows at temperatures ranging from 20°C to 32.5°C and the optimum temperatures for growth are 27.5–30°C (see Fig. 15). *A. tamiyavanichii* cannot survive below 15°C, however, demonstrating the growth physiology of a typical tropical microalgal species (Ogata et al., 1990; Nagai et al., 2008). Actively swimming vegetative chains of this species have been confirmed around 15°C in the Seto Inland Sea at the end of blooms in the middle of December (Yoshimatsu et al., 2000; Tanada et al. 2003; Nagai et al. 2008), suggesting a higher tolerance for low water temperatures in natural populations than in laboratory cultures. Anderson & Wall (1978), Anderson & Morel (1979), and Itakura & Yamaguchi (2001) have emphasized the importance of *Alexandrium* cysts as the seed population for overwintering, bloom initiation, and cyst dispersal within estuaries and near-coastal waters—i.e., the geographical spread of the population. Hallegraeff (1998) has also pointed out the role of dinoflagellate cysts in settling and spreading over a wider distribution through transportation either in ship's ballast water or associated with the movement of shellfish stocks from one area to another. *A. tamiyavanichii* produces resting cysts at temperatures of 20–32.5°C in laboratory cultures, and the optimal temperature for encystment is 25°C (see Fig. 15). Interestingly, this temperature is slightly lower than the optimal temperature for vegetative growth (see Fig. 15). Conversely, resting cyst production in *A. tamarense* is observed at temperatures of 5–24°C in laboratory cultures (see Fig. 15). The optimal temperature for encystment is around 14°C, and cyst formation is ca. 25%. Accordingly, these data clearly indicate that *A. tamiyavanichii* produces resting cysts at remarkably higher temperatures and does not produce resting cysts at high density compared with *A. tamarense*. In the coastal areas around Hokkaido in Japan, *A. tamarense* usually appears in early spring when the water temperature is 1–3°C (start of blooming) but appears when waters temperatures reach 8–10°C in western Japan. *A. tamarense* has a vegetative stage that usually lasts for <4 months in the water column (Itakura et al. 2002; Nagai et al. 2007), although the duration of the vegetative stage varies with the water temperature as well as with the pattern of annual water temperature fluctuation. This species disappears in the water columns when the water temperature exceeds ca. 15–16°C, clearly indicating an adaptation to cold waters (Itakura et al., 2002; Nagai et al., 2007; Shimada et al., 1996, 2010).

It is assumed that in the annual life cycle of *A. tamarense*, to appear for a limited time as vegetative populations in the water column in a year and to endure the most unsuitable season (high water temperatures), the organism has developed a survival strategy that produces high amounts of resting cysts at the end of blooms (Itakura et al., 2002; Nagai et al., 2007). Conversely, *A. tamiyavanichii* is a typical tropical species that blooms in stable environmental conditions—i.e., little fluctuation in annual water temperature. Therefore, no preparation is necessary to survive adverse environmental conditions (e.g., unsuitably cold winter season) through the production of high amounts of resting cysts as seen in *A. tamarense*. Regarding germination, *A. tamiyavanichii* also cannot germinate at temperatures below 20°C, and although occasional germination was observed at this temperature, the organism did not grow. *A. tamiyavanichii* loses the ability to germinate when kept at the temperatures below 10°C in darkness even for a week or so, even though the resting cysts look alive. Conversely, resting cysts of *A. tamiyavanichii* have high potential for germination, even when kept in darkness for more than 3 months at relatively high temperatures of 20–30°C (see Fig. 16). Thus, we can conclude from the results of these laboratory experiments that *A. tamiyavanichii* is the species with the life cycle strategy that adapts to tropical

environmental conditions, thereby resulting in limited distribution, until now, in areas south of a northern latitude of 35 degrees.

2.3.7 Environmental conditions that allow the appearance of *A. tamiyavanichii* in the Seto Inland Sea

In the Seto Inland Sea, the first appearance of *A. tamiyavanichii* has been observed in middle and late August when water temperature rises to around 28°C, and the species has grown up to 30 cells mL^{-1} by late autumn (Yoshimatsu et al., 2000). Tropical species cannot survive at water temperatures lower than 15°C, and they die when temperatures drop below 15°C (Ogata et al., 1990; Nagai et al., 2008). Vegetative populations of this species are not found in middle December, therefore (Fig. 17). We speculate that this species produces durable resting cysts when growing in water columns as vegetative populations, perhaps in November-December when its abundance reaches its maximum, and resting cysts overwinters in surface sediments as seed populations between December and early June, during which it cannot survive as vegetative populations (<15°C). Accordingly, this life cycle characteristic enables this species to appear for 6–7 months a year in the water column. *A. tamiyavanichii* begins to germinate next in the middle of June, when the bottom water temperature exceeds 20°C, and swims out as a vegetative population in water columns. These characteristics strongly suggest that cysts play an important role in prolonged overwintering in surface sediments as a seed population in temperate Japanese coastal waters. Also, the fact that planozygotes have been observed in sea water samples collected from the Seto Inland Sea during *A. tamiyavanichii* blooms in 2001 and that appearances of this species have since been observed often not only in the Seto Inland Sea but also around Tsushima and Gotou Islands imply that they may have gained a niche and become settled in this coastal area. Moreover, *A. tamiyavanichii* might be transferred to other areas of Japan by natural and human-assisted dispersals, expanding its distribution.

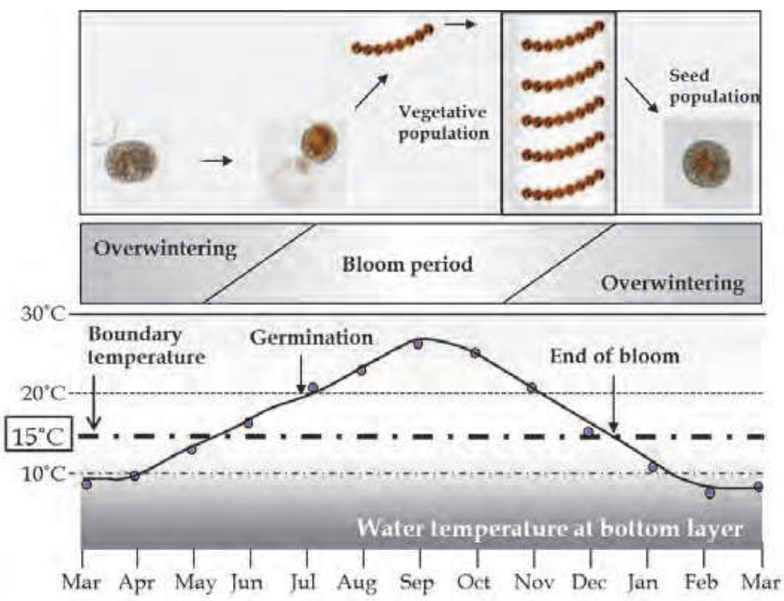


Fig. 17. A conceptual diagram showing the relationship between bottom water temperature and bloom mechanism in *Alexandrium tamiyavanichii* in the Seto Inland Sea. The solid line shows the change in water temperature in Hiroshima Bay (see Fig. 10).

But why does *A. tamiyavanichii* bloom during September–December and not during August–September in western Japan? We have investigated cyst abundance in the surface sediments collected from several locations in the Tokushima Prefecture region of the eastern Seto Inland Sea just after the dense bloom and carried out a germination experiment using 10 g of wet sediments with seawater under appropriate incubation conditions for germination and vegetative growth. No germinated cells were detected, however. We speculate, therefore, that *A. tamiyavanichii* is undetectable in July or August if the resting cysts germinate and begin blooming when the water temperature exceeds 20°C in mid-June (see Fig. 17), because cyst abundance is too low to grow to detectable levels in July-August. Occurrences of bloom in this species, resulting in PSP outbreaks in shellfish, are recognized as a new biological threat in western Japan. We have begun investigating the origin of the Japanese population of this species using highly polymorphic genetic markers (Nishitani et al., 2009).

3. Conclusion

The increase in atmospheric carbon dioxide concentrations caused by human activities has influenced the change of world's ocean environments such as increasing water temperature, decreasing sea ice, and causing acidification (Tadokoro et al., 2008). It has been suggested that enhanced stratification, caused by the increases in the surface layer temperature, is decreasing the nutrient supply from the subsurface layer hindering the primary productivity over a large area of the North Pacific Ocean, resulting in the changes of marine ecosystems in primary productivities and seasonal succession in phytoplankton (Ono et al., 2002), zooplanktons (Aoyama et al., 2008), fish (Tian et al., 2006; Shida et al., 2007; Masuda, 2008) and coral (Nojima & Okamoto, 2008). In this chapter, we demonstrated the influence of water temperatures on the changes of habitat of microalgal species or the Isoyake phenomena and the introduction of a toxic phytoplankton from tropical regions to Japanese coastal waters. Thus, effects of global warming on marine ecology have been studied with high research activities. In future, it is highly possible that the influence of global warming on marine ecosystems will be more prominent, therefore, continuous efforts for environmental and biological monitoring would be crucial.

4. Acknowledgement

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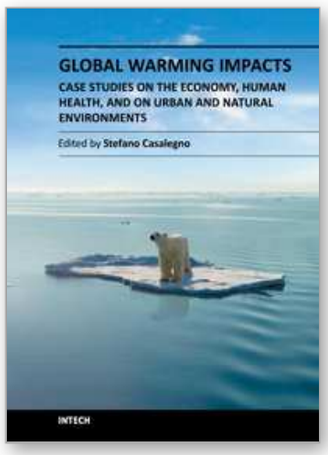
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This book addresses the theme of the impacts of global warming on different specific fields, ranging from the regional and global economy, to agriculture, human health, urban areas, land vegetation, marine areas and mangroves. Despite the volume of scientific work that has been undertaken in relation to each of each of these issues, the study of the impacts of global warming upon them is a relatively recent and unexplored topic. The chapters of this book offer a broad overview of potential applications of global warming science. As this science continues to evolve, confirm and reject study hypotheses, it is hoped that this book will stimulate further developments in relation to the impacts of changes in the global climate.

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