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REVIEW ARTICLE

Harmful algal blooms and environmentally friendly control strategies in Japan

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Abstract

The presence and status of harmful algal blooms (HABs) in Japan are reviewed, revealing a decrease in red tides; however, toxic blooms are found to be increasing in western Japan. Environmentally friendly control strategies against HABs are also compared with integrated agricultural pest management. Very high densities (10^5–10^8 CFU/g) of algicidal and growth-inhibiting bacteria were found in biofilm on seagrass and seaweed surfaces and in surrounding coastal seawater. The situation in freshwater ecosystems is similar to coastal seas for toxic cyanobacterium, *Microcystis aeruginosa*, and aquatic plants. These findings offer new insights into the ecology of influential bacteria and harmful algae, suggesting that protection and restoration of native seagrasses and seaweeds in coastal marine environments should be implemented to suppress HABs. Diatom blooms were successfully induced with bottom sediment perturbation to prevent the occurrence of harmful flagellates such as *Chattonella* spp. and *Alexandrium catenella* in the Seto Inland Sea; however, this method requires robust and reproducible verification. "*Sato-Umi*" is a helpful concept for HAB control in the sea and freshwater ecosystems when adequately managed by people (e.g., appropriate bottom perturbation; protection and restoration of seaweeds, seagrasses, and aquatic plants; application of polycultures of fish, seaweeds, etc.).

Keywords Harmful algal bloom · Environmentally friendly strategy · Diatom · Sediment perturbation · Algicidal bacteria · Seagrass bed · Aquatic plant · *Sato-Umi*

Introduction

The sea covers approximately 70% of the Earth's surface. The sea was the birthplace of life and is home to an array of marine life comprising well over a million species. Humans receive numerous ecosystem services from the sea, including provisions (e.g., food, water, and energy), regulations (e.g., climate, erosion and flood control, pollination, and decomposition), cultural activities (e.g., recreation, physical and mental health benefits, aesthetic, etc.), and support (e.g., species habitat, maintenance of genetic diversity, etc.; Millennium Ecosystem Assessment 2007). Converting the benefits of the ocean into direct monetary values is difficult; however, Constanza et al. (1997) evaluated the total annual ecosystem services on Earth at ~ 33.3 trillion USD, of which the ocean's contribution was estimated to be ~ 20.9 trillion USD. Because these values suffer from such wide ranges of uncertainty, they are assumed to be underestimated. As the total annual human productivity is estimated to be ~ 18 trillion USD per year (Constanza et al. 1997), the importance of the oceans is self-evident.

The coastal area of the ocean, which is considered to be the area of shallow sea to the intertidal zone where ebb and flow tides are observed to a water depth of approximately 200 m, is rich in marine life with high levels of biodiversity and biological productivity (Yanagi 2006). Terrestrial regions bordering such coastal areas generally have high population

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density, thereby causing anthropogenic environmental issues such as inflow of pollutants resulting in eutrophication from a variety of human activities, a crucial factor in the occurrence of harmful algal blooms (HABs) (Anderson et al. 2002; Imai et al. 2006a; Heisler et al. 2008).

Since ancient times, Japanese people have utilized a wide variety of aquatic organisms from the sea, rivers, lakes, etc., for food. The variety of seafood in Japan is extensive, and unique recipes and preservation methods have been developed over time. According to the United Nations Food and Agriculture Organization (UNFAO), Japan's per-capita supply of seafood is the largest in the world, and with a population of more than one hundred million people, more fish are consumed in Japan, per capita, than anywhere else in the world.

Seafood is supplied by fisheries from pelagic, offshore, coastal, and aquaculture sources. In particular, the aquaculture industry, with its controllable and methodical production, plays a crucial role in stabilizing supplies. The aquaculture industry produced 23% (1.03 million t) of total production and 32% (486.1 billion JPY) of the monetary value of fisheries in 2018 (MAFF 2020); however, since aquaculture industries operate in relatively calm coastal bay areas, harmful red tides have recurrently plagued the fish and shellfish industries.

The most common organisms responsible for harmful red tides are raphidophytes, dinoflagellates, and diatoms. Harmful flagellates usually kill fish and bivalves, whereas diatoms can cause bleaching of the cultured red alga nori *Neopyropia yezoensis*. It is estimated that a single red tide incident can result in economic damage valued at greater than 1 billion JPY (Itakura and Imai 2014; Imai 2017a).

This review summarizes the occurrence of HABs in the coastal waters of Japan. In terms of preventive strategies, we present feasible and environmentally friendly measures. Furthermore, the concepts of preventive strategies are compared with those of pest control in the agricultural field, which have long been studied extensively in literature. The environmentally friendly, preventive strategies against HABs discussed in this review are also considered to be an integral part of the *Sato-Umi* concept (Yanagi 2008). Additionally, concerning the prevention of toxic cyanobacterial blooms in freshwater ecosystems, we examined a recent discovery of cyanobactericidal bacteria that attach to and inhabit the surface of aquatic plants in great abundance, and proposed a preventive strategy through the effective utilization of aquatic plants.

Occurrence of HABs in Japan

Phytoplankton are floating microalgae that perform photosynthesis and play an essential role as primary producers in the food webs of the marine ecosystem, thus ultimately supporting the production of seafood for human consumption. However, some species of phytoplankton proliferate rapidly, causing harmful "red tides" that are detrimental to marine life (Okaichi 2004; Imai et al. 2006a; Itakura and Imai 2014; Sakamoto et al. 2021), while other species have toxins in their cells that are transferred and amassed in higher-level organisms (e.g., bivalves) through the food web. Such accumulation of toxins, and the potential resulting death of higher-order predators such as fish, birds, marine mammals, and humans, have caused significant problems in the bivalve aquaculture industries, human health, and the environmental conditions (Imai et al. 2006a; Anderson 2017; Trainer et al. 2020; Wells et al. 2020; Sakamoto et al. 2021).

The phenomenon of such increases in the population of algal species is referred to be "blooms." Algae that adversely affect human and marine life are known as harmful algae (HA), and the proliferation of HA results in harmful algal blooms (HABs) (Hallegraeff 1993). HABs can be classified into four types according to their causative species (Hallegraeff 1993; Imai et al. 2006a): (1) biomass blooms, which occur when harmless phytoplankton species proliferate into a large amount of organic matter, and upon death, dissolved oxygen is consumed, causing anoxia in seawater and death of marine life; (2) noxious red tides, which occur when deleterious phytoplankton species form red tides and cause mass mortality of marine life, particularly fish and bivalves in aquaculture; (3) toxic blooms, which are caused when poisonous microalgal species are transferred to higher trophic levels of marine and terrestrial life (including humans) through food webs, deleteriously affecting the higher-level organisms; (4) harmful diatom blooms, which occur when common diatom species form red tides during nori (seaweed) aquaculture, entirely consuming seawater nutrients and reducing the quality, and therefore value, of nori products. Red tides are a phenomenon where the discoloration of seawater results from the growth and accumulation of phytoplankton, and three types of HABs except for toxic blooms can usually be characterized by the term "red tides." However, as even toxic phytoplankton species can increase to levels that cause discoloration of seawater (albeit very rarely), this may also be called a "red tide" (Yamamoto et al. 2009a, 2017).

Table 1 summarizes the types of issues caused by HABs of major causative species in Japanese coastal waters. The damage inflicted by red tides is primarily confined to aquacultures, where various HAB species have resulted in mass mortality of fish and bivalves, and seaweed bleaching. In bivalve aquaculture, many toxic phytoplankton species can poison shellfish, and the resultant shipping restrictions have had significant economic repercussions (Suzuki 2017). Ciguatera fish poisoning (CFP) occurs when humans eat toxified fish that have accumulated toxins of toxic dinoflagellates attached to seaweed via direct consumption or food

Table 1 Major types and causative organisms of HABs in Japanese coastal sea

Category	Causative organism	Remark
Fish kill	Raphidophyceae	
	Chattonella antiqua	Largest impact on yellowtail
	C. marina	
	C. ovata	
	Heterosigma akashiwo	Serious damage in Kagoshima Bay
	Dinophyceae	
	Karenia mikimotoi	Killing mollusks, crustaceans, etc.
	Margalefidinium polykrikoides	Killing mollusks, crustaceans, etc.
	Dictyochophyceae	
	Pseudochattonella verruculosa	Blooming at low temperature (< 15 °C)
Bivalve kill	Dinophyceae	
	Heterocapsa circularisquama	Introduced from southern China
Biomass bloom	Dinophyceae	
	Noctiluca scintillans	Most frequent red tides in the world
	Gonyaulax polygramma	Massive damage (807 million JPY) in 1994
Nori (*Neopyropia*) bleaching	Bacillariophyceae	Blooms in nori aquaculture season
	Eucampia zodiacus	
	Coscinodiscus wailesii	
	Rhizosolenia imbricata	
	Asteroplanus karianus	
	Chaetoceros spp.	
	Skeletonema spp.	
	Thalassiosira spp.	
	Dinophyceae	
	Akashiwo sanguinea	
Paralytic shellfish poisoning (PSP)	Dinophyceae	
	Alexandrium catenella (group I)	Formerly *Alexandrium tamarense*
	Alexandrium pacificum (group IV)	Formerly *Alexandrium catenella*
	Gymnodinium catenatum	
Diarrhetic shellfish poisoning (DSP)	Dinophyceae	
	Dinophysis fortii	Mixotroph feeding *Mesodinium*
	D. acuminata	
	D. caudata	
	Prorocentrum lima	Epiphytic dinoflagellate to seaweeds
Ciguatera fish poisoning (CFP)	Dinophyceae	
	Gambierdiscus toxicus	Epiphytic dinoflagellate to seaweeds

web interactions (Yasumoto et al. 1977; Adachi 2016). In addition, the damage to marine life inflicted by red tides is complicated, as larval mortality of important species will remain unnoticed until poor catches are observed in subsequent fishing seasons. It was reported that red tides of the harmful raphidophyte *Heterosigma akashiwo* killed a large quantity of juvenile sockeye salmon that had descended to Puget Sound from lakes on the west coast of the USA en route to the Arctic Sea, having a deleterious effect on returning resources (Rensel et al. 2010). As described above, various harmful algae have an array of adverse effects on marine life and human beings.

Noxious red tides

The following are the major red-tide-causing plankton species that have caused large-scale mortality of marine life in coastal areas of Japan: *Chattonella* spp. (*C. antiqua*, *C. marina*, and *C. ovata*) belonging to Raphidophyceae have inflicted the greatest damage to farmed fish, especially yellowtail *Seriola quinqueradiata*. The dinoflagellate *Karenia mikimotoi* is the second most important killer of fish in the region. *Heterocapsa circularisquama* is a unique dinoflagellate that selectively kills bivalves, which usually graze phytoplankton. *Cochlodinium polykrikoides* (currently called

Margalefidinium polykrikoides) is the most violent red tide dinoflagellate in neighboring Korea. *Heterosigma akashiwo* (Raphidophyceae) and *Noctiluca scintillans* (Dinophyceae) are other important species creating red tides with high frequency.

Aquaculture, especially fish culture, is a key industry in the coastal areas of western Japan, where the incidence of red tides is widespread, including those driven by harmful species. Figure 1 shows the long-term changes in red tide frequencies, and correlated fishery damage, for the Seto Inland Sea and coastal areas of Kyushu (Fisheries Agency 2020a; b). In the Seto Inland Sea, the number of red tides increased linearly during the period of high economic growth from the 1960s to the mid-1970s. In this era of progress, industrial production flourished under the new industrial city initiative, and populations concentrated in large cities; and as a result, increasing volumes of industrial and domestic wastewater were discharged into the coastal seas, increasing pollution and eutrophication. Untreated human waste was dumped directly into the Seto Inland Sea as recently as the 1960s, further accelerating eutrophication. Annual red tide cases peaked in 1976 (299), and the highest number of mortalities of farmed yellowtail (14.2 million) due to the *Chattonella* red tide was recorded in 1972, inflicting an estimated ~ 7.1 billion JPY in economic damage. The Law Concerning Special Measures for Conservation of the Environment of the Seto Inland Sea was enacted in 1973 in reaction to this historical *Chattonella* red tide. This legal regulation, in conjunction with new wastewater treatment measures, was effective at improving water quality (especially nutrient levels), and decreasing the incidence of red tides in the Seto Inland Sea (Imai et al. 2006a). Since then, the number of red tides has decreased to ~ 100 per year, and an even further decline has been recorded since 2015, with just 58 recorded cases in 2019; however, fishery production is also declining in the Seto Inland Sea, and it has been suggested that water quality (namely nutrient levels) may have been over-improved to a state of oligotrophication (Yamamoto 2003).

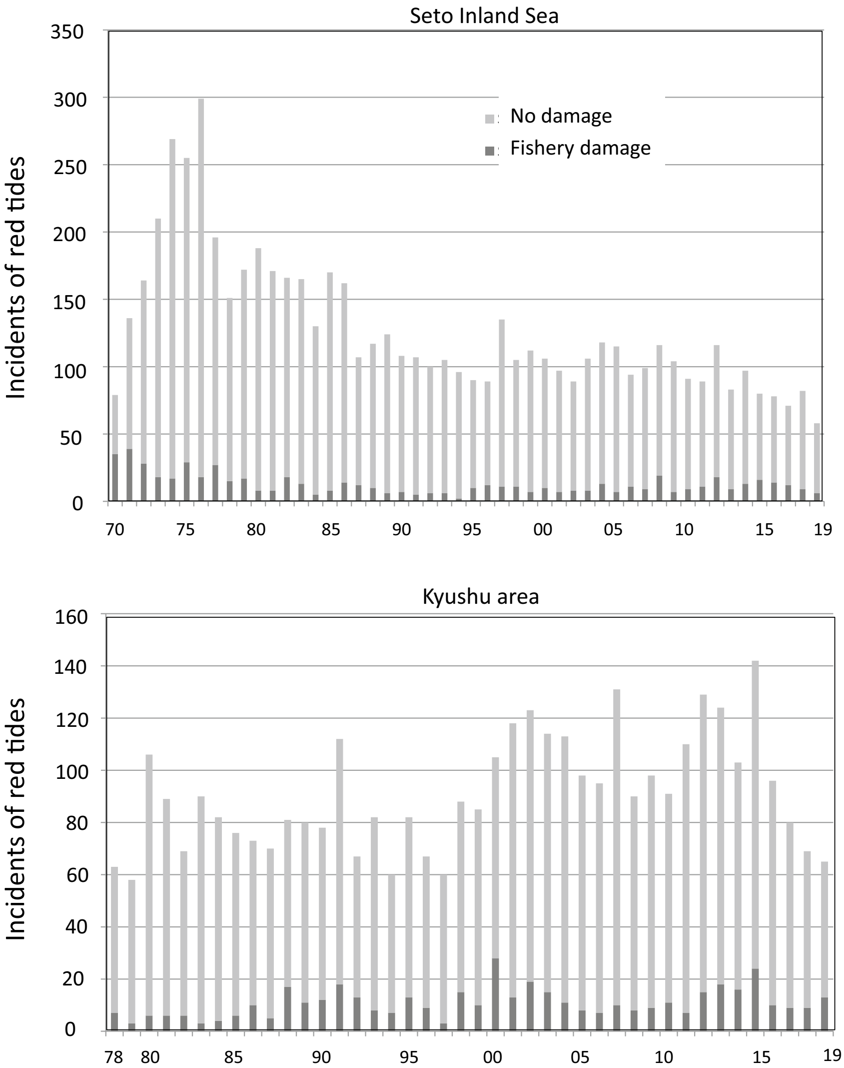

Fig. 1 Occurrences of red tides in Seto Inland Sea from 1970 to 2019 (Fisheries Agency 2020a) and the Kyushu area from 1978 to 2019 (Fisheries Agency 2020b)

Examining red tide occurrences and fishery damage in the Kyushu area, the eutrophication and subsequent recovery of water quality are unclear, as in the case of the Seto Inland Sea (Fig. 1). Prior to 2000, annual red tide occurrences greater than or equal to 100 had been recorded only twice; however, this threshold was exceeded 10 times in the 16 years from 2000 to 2015, and case numbers have showed a decreasing trend since then.

Table 2 presents the major fishery damage caused by red tides in Japanese coastal waters. Mortality caused by *Chattonella* spp. is the most prominent in both scale and frequency. Significant fishery damage caused by *Chattonella* has been a frequent occurrence since 1972, although no fishery damage exceeding 100 million JPY per year was reported in the Seto Inland Sea from 1990 to 2002. In 2003 and 2004, however, damage amounted to 1.3 billion JPY and 390 million JPY, respectively (totals include the damages inflicted by the dinoflagellate *M. polykrikoides*). Later, in the Yatsushiro Sea of Kyushu, *Chattonella* red tides caused 3.3 billion JPY and 5.3 billion JPY in 2009 and 2010, respectively, along with the fish kill of yellowtail.

The harmful dinoflagellate *K. mikimotoi* caused huge damage of 4.6 billion JPY due to the red tide in Kumano-Nada in 1984, shocking people involved in aquaculture industries. Since 1979, *K. mikimotoi* has continuously caused damage due to mortality of cultured fish and shellfish in the Seto Inland Sea. It was notable in 2012 that amberjack, red sea bream, yellowtail, abalone, etc., were killed with losses amounting to 1.5 billion JPY (1.2 billion JPY along the coast of Ehime Prefecture) in the Bungo Channel, western Seto Inland Sea. In 2017, about 600 million JPY of damage was caused, mainly to tiger puffer (*Takifugu rubripes*) and yellowtail, etc., in the Kyushu area, mainly in Imari Bay. Other notable damages to the aquaculture industries include: the 1992 mass die-offs of pearl oyster *Pinctada fucata* (3.0 billion JPY) in Ago Bay, the oyster *Crassostrea gigas* (3.9 billion JPY) in Hiroshima Bay in 1998 due to *H. circularisquama*, and the yellowtail kill due to *M. polykrikoides* in the Yatsushiro Sea resulting in total damage of 4.0 billion JPY in 2000. Diatom red tides have caused bleaching damage in nori aquaculture as well, and in the winter of 2000, the Ariake Sea experienced a 13.6 billion JPY decrease in production compared with the previous year. Therefore, there is an urgent social need for preventive strategies to decrease the frequency of such red tides.

The occurrence of red tides is related to the unique physiological, ecological, and lifecycle characteristics of the causative species, as well as the local environmental characteristics of the aquatic area (Imai 2012). Extensive monitoring data are necessary to best understand the mechanisms behind their occurrence and build an accurate predictive model, which requires targeted investigations into each species for every location, with the hope that the development of scientifically based strategies will contribute to the prevention, control, and eradication of HABs.

Toxic blooms

In the coastal waters of Japan, bivalve mollusks such as oyster *Crassostrea* spp., scallop *Mizuhopecten yessoensis*, and mussels *Mytilus* spp. are the most abundant aquaculture products, supporting livelihoods and supplementing

Table 2 Extensive economic damage to aquaculture (≥ 1 billion JPY) caused by HABs (red tides) in the coastal sea of western Japan. Data partially modified from Itakura and Imai (2014)

Year	Area	HAB species	Damaged organism	Economic loss (billion JPY)
1972	Harima-Nada	*Chattonella* spp.	Yellowtail	7.1
1977	Harima-Nada	*Chattonella* spp.	Yellowtail	2.7
1978	Harima-Nada	*Chattonella* spp.	Yellowtail	3.3
1984	Kumano-Nada	*Karenia mikimotoi*	Yellowtail, noble scallop, etc.	4.6
1991	Aki-Nada, etc.	*Karenia mikimotoi*	Red sea bream	1.5
1992	Ago Bay	*Heterocapsa circularisquama*	Pearl oyster	3.0
1995	Kagoshima Bay	*Heterosigma akashiwo*	Yellowtail, amberjack, etc.	1.0
1998	Hiroshima Bay	*Heterocapsa circularisquama*	Oyster	3.9
2000	Yatsushiro Sea	*Margalefidinium polykrikoides*	Yellowtail, amberjack, Japanese pufferfish, etc.	4.0
2000–2001	Ariake Sea	Diatoms	Nori (*Neopyropia*)	> 10
2003	Harima-Nada	*Chattonella* spp.	Yellowtail, amberjack	1.3
2009	Yatsushiro Sea Ariake Sea	*Chattonella* spp.	Yellowtail	3.3
2010	Yatsushiro Sea	*Chattonella* spp.	Yellowtail	5.3
2012	Bungo Channel	*Karenia mikimotoi*	Amberjack, red sea bream, etc.	1.5

diets. Moreover, shellfish on tidal flats, such as Manila clam *Ruditapes philippinarum*, offer recreational opportunities to interact with the sea through shellfish gathering.

In Japanese coastal waters, the main poisonings of useful bivalves have been reported to cause paralytic shellfish poisoning (PSP) and diarrhetic shellfish poisoning (DSP) (Fukuyo 2000; Imai and Itakura 2007; Kamiyama 2017; Suzuki 2017). When toxin concentrations exceeded permitted levels, shipping restrictions were self-imposed to prevent toxic bivalves from entering the market (Iioka 2017). DSP problems are caused by the dinoflagellate genus *Dinophysis*, being most commonly observed in northeast Japan. Surprisingly, DSP problems rarely occur in western Japan, even where the same *Dinophysis* species proliferate to much higher cell densities in the Seto Inland Sea (Imai et al. 2006a; Imai and Itakura 2007). Regarding the PSP problems in western Japan, sporadic and small-scale poisonings of Manila clams have occurred because of *Alexandrium pacificum* (formerly named *A. catenella*) in the Kii Channel, Bungo Channel, Kagoshima Prefecture, etc. (Imai et al. 2006a). Since the early 1990s, oysters and Manila clams have frequently been poisoned by *Alexandrium catenella* (group I; formerly named *Alexandrium tamarense*) in Hiroshima Bay, Harima Nada, Osaka Bay, Ise Bay, Mikawa Bay, etc. (Itakura et al. 2002; Ishida and Sonda 2003; Imai et al. 2006a). Abundant cysts have also been confirmed in the seafloor sediment in these areas (Yamaguchi et al. 1995a, b, 2002; Kotani et al. 1998; Ishikawa et al. 2007; Yamamoto et al. 2009b), and it was concluded that this species has been completely established in the Seto Inland Sea and Mikawa Bay. Outbreaks of PSP were historically restricted to the Tohoku and Hokkaido areas but have recently been observed in the Seto Inland Sea, particularly in Osaka Bay (Table 3). The driver for this expanding distribution is the presence of cysts and/or temporary cysts of *A. catenella* (group I) that are simultaneously carried from the waters of northeastern Japan to the Seto Inland Sea when bivalve culture seedlings (mainly oysters) are transported (Nagai 2007). Microsatellite markers have been developed using population genetic methods and molecular techniques, confirming the spread of toxic *A. catenella* (group I) (Nagai 2007; Nagai et al. 2007). As a result, possible cases in which the distribution of HABs expands with the transfer of aquatic seedlings have been suggested (Nagai et al. 2007; Matsuyama et al. 2010).

The Great East Japan Earthquake, and the accompanying tsunami, struck the Pacific coast of Tohoku and Hokkaido on 11 March 2011. The tsunami caused significant seabed turbulence, and cysts of the toxic dinoflagellate *A. catenella*

Table 3 Cases of PSP in Japan. Data modified from Imai and Itakura (2007)

Date	Locality (City/Town, Prefecture)	Poisoned shellfish	Patients (mortalities)
July 1947	Toyohashi, Aichi	Manila clam	12 (1)
May 1961	Ohfunato, Iwate	Farrer’s scallop	20 (1)
February 1962	Miyazu, Kyoto	Oyster (aquaculture)	42 (0)
January 1979	Senzaki, Yamaguchi	Oyster (aquaculture)	16 (0)
April 1979	Asahikawa, Hokkaido	Blue mussel	3 (1)
May 1982	Ohfunato, Iwate	Sea squirt	2 (0)
June 1987	Kagoshima, Kagoshima	Manila clam	1 (0)
April 1989	Ohfunato, Iwate	Scallop	5 (0)
		Blue mussel	1 (0)
July 1989	Shimokita, Aomori	Blue mussel	6 (1)
May 1991	Nanae, Hokkaido	Scallop	1 (0)
April 1996	Nobeoka, Miyazaki	Blue mussel	2 (0)
March 1997	Tamanoura, Nagasaki	Oyster (nature)	26 (0)
February 1998	Yawatahama, Ehime	Oyster (nature)	4 (0)
April 2008	Kaizuka, Osaka	Blue mussel	3 (0)
May 2013	Osaka, Osaka	Blue mussel	2 (0)
May 2015	Tochigi	Scallop	4 (0)
March 2016	Hannan, Osaka	Manila clam	2 (0)
March 2016	Sennan, Osaka	Manila clam	1 (0)
	Sakai, Osaka	Blue mussel	3 (0)
	Hyogo (Seto Inland Sea)	Blue mussel	1 (0)
	Hyogo (Seto Inland Sea)	Japanese geoduck	1 (0)
March 2019	Misaki, Osaka	Blue mussel	2 (0)

(group I) were suspended in the water column from the bottom sediment (Kamiyama et al. 2014). After that, cysts tended to settle more slowly than sand grains due to their lower specific gravity, concentrating on the surface layer of seafloor sediment in Sendai (Kamiyama et al. 2014), Kesennuma (Ishikawa et al. 2015), and Funka Bays (Natsuike et al. 2014). As a result, large-scale blooms of *A. catenella* (group I) started to occur in Kesennuma Bay on the Pacific coast of the Tohoku region (Ishikawa et al. 2015). Despite the fact that shellfish toxification of PSP toxins had once been rare in Kesennuma Bay, contamination of scallops with PSP toxins has now become common (Tanabe and Kaga 2017).

The expansion of the scale of blooms due to *A. catenella* (group I) is noteworthy in Osaka Bay (Fig. 2), with an apparent increasing trend since 1994 (Yamamoto et al. 2017). A high-density red tide of 72,400 cells mL^{-1} occurred in April 2007 at the Sakai Dejima Fishing Port in Osaka Prefecture, and another of 14,000 cells mL^{-1} was confirmed in Yodo River (Yamamoto et al. 2009a, 2011, 2013). These events revealed that *A. catenella* (group I) not only causes toxification of bivalve mollusks by PSP toxins with low cell densities, but if conditions are suitable, this species can cause red tides and kill various forms of marine life (Yamamoto et al. 2009a). Until now, bivalve toxification was limited to marine species, but blooming in Yodo River was the first documented case to detect accumulation of PSP toxins in brackish water clams *Corbicula japonica* (Yamamoto et al. 2011). In the past, when eutrophication was prominent in Osaka Bay, diatoms were always predominant, while flagellates were relatively scarce due to lower growth rates. However, recently, it has been documented that diatoms can consume seawater nutrients, cease growth after nutrient depletion, and disappear from the water column. Theoretically, *Alexandrium catenella* (group I) can utilize the available nutrients after the disappearance and/or decrease of diatoms and thus form exceptionally high-density blooms, eventually leading to red tides (Yamamoto et al. 2017).

Mouse assays have been employed as the official method for monitoring toxin contamination of bivalves by toxic plankton (Iioka 2017; Suzuki 2017). However, since many countries consider the mouse assay to be a violation of animal welfare, instrumental analysis of toxin levels has gained support. According to a notification from the Ministry of Health, Labor, and Welfare, dated March 6, 2015, instrumental analyses have been adopted as the official method for measuring DSP toxins (okadaic acid and dinophysis toxins), with a regulated value of 0.16 mg okadaic acid (OA) per kg of edible part of bivalves. Consequently, yessotoxin and pectenotoxin, previously detected by mouse assay, are excluded from instrumental analyses (Iioka 2017).

A major advancement in the field of DSP studies was made with the successful culturing and maintaining of the toxic dinoflagellate genus *Dinophysis* (Park et al. 2006; Nagai et al. 2008, 2020). Chloroplasts of the ciliate *Mesodinium rubrum* were found to be derived from cryptophytes by kleptoplasty (Gustafson et al. 2000), and it became possible to culture *M. rubrum* alongside the prey of cryptophytes as feed and the chloroplast source (Yih et al. 2004). The first culture was achieved for mixotrophic *D. acuminata* (Park et al., 2006), and subsequent successful cultures of important species including *D. fortii*, *D. infundibulum*, *D. caudata*, *D. tripos*, etc., and investigations on toxin production and chloroplast characteristics have been carried out (Kamiyama et al. 2010; Nishitani et al. 2010; Nagai et al. 2020).

The relationship between *Dinophysis* spp. and the DSP toxicity of bivalves displays a number of enigmas. In the coastal waters of western Japan, such as the Seto Inland Sea, DSP problems did not occur even when the causative species *D. fortii* was detected at sufficiently high densities (Imai and Itakura 2007; Nishitani et al. 2016). In Mutsu Bay in northern Japan, toxification of scallops was less likely when *D. fortii* populations increased in the surface and shallow waters, whereas an increase observed in the deeper layers near the sea bottom led to toxicity levels exceeding regulation levels (Nishitani et al. 2016). In Mutsu Bay, scallops reared in the upper layers are reported to be less toxic than those in the deep layers (Tanaka et al. 1985). Therefore, monitoring *Dinophysis* populations in deep waters is critical

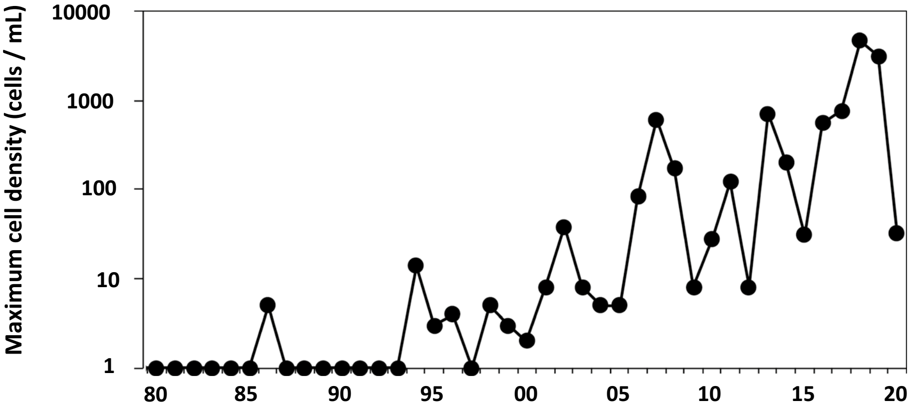

Fig. 2 Annual changes in maximum cell density of toxic dinoflagellate *Alexandrium catenella* (group I; formerly *A. tamarense*) in Osaka Bay, eastern Seto Inland Sea, 1980–2020

for predicting scallop toxification in aquaculture. The elucidation of the mechanism of toxification of scallops by deep populations of *D. fortii* is eagerly awaited from a practical point of view.

Environmentally friendly strategies against HABs

The occurrence of red tides and fishery damage has a long history. Mass mortality of farmed pearl oyster caused by *K. mikimotoi* was recorded in Gokasho and Ago Bays in Mie Prefecture in 1933 (Oda 1935). Since the mass mortality of cultured fish and bivalves caused by harmful red tides increased in scale and frequency in the 1960s with urbanization, various countermeasure techniques were investigated and proposed until the 1980s (Shirota 1989). However, regarding physicochemical countermeasures, few technologies have been applied except for clay spraying. This is because of no considerations regarding the scale or economic cost and the lack of careful attention to the environments (Imai 2017b).

Grazing of red tide plankton by zooplankton (copepods and protozoa) and bivalves has previously attracted significant attention and has been studied for the extermination of red tides; however, zooplankton tend to avoid grazing harmful plankton species (Uye and Takamatsu 1990; Mikhail 2007). Considering the abundance of copepods and calculated grazing rates, their capacity for removal of red tide plankton was estimated to be at most a few percent of the causative phytoplankton population per day, thus deemed impractical (Uye 1986). Heterotrophic dinoflagellates, such as the genera *Gyrodinium* and *Polykrikos*, appear and graze upon the raphidophytes *Chattonella* spp., and the dinoflagellate *K. mikimotoi* in coastal seas at the final stages of their blooms (Nakamura et al. 1992, 1996; Matsuyama et al. 1999). This has also been confirmed in laboratory experiments (Nakamura et al. 1992). However, cultivating and preparing large quantities of heterotrophic dinoflagellates to control red tides in the sea is also impractical.

Filter feeding of red tide phytoplankton by bivalves was once eagerly awaited in the pertinent aquaculture industries. In the northern part of Hiroshima Bay, the Seto Inland Sea, where oyster farming has been performed extensively, the corresponding amount of filter feeding of suspended matter (phytoplankton and detritus) by cultured oysters was estimated to be 26% of the amount of local primary production on the basis of average annual nitrogen balance (Songsangjinda et al. 2000). Bivalves also show selectivity for plankton as food (Baker et al. 1998). However, although oyster farming has some effect on thinning out phytoplankton communities, it is unlikely that the cultured oysters contribute to the prevention of red tide occurrences. Thus, the frequent occurrence of red tides in Hiroshima Bay suggests that aquacultures of bivalves are ineffective for prevention, and it was further concluded that controlling red tides through grazers is impractical (Imai 2010c).

All strategies for addressing harmful red tides must be practically feasible and environmentally friendly. Table 4 summarizes red tide countermeasures that have been evaluated as effective at the present or as promising in the future. Thus far, indirect strategies have been instrumental in reducing the incidence of red tides. In particular, legal regulations have contributed significantly to water quality improvements, especially in the Seto Inland Sea. With regards to aquaculture technologies, improvement of food quality has reduced water pollution during feeding. At present, stop-feeding (i.e., short-time starvation) is the measure that is most commonly employed to reduce fish mortality during red tides (Ohta 2018). Improving modeling accuracy for forecasting and monitoring red tide occurrences would also be promising for reducing fishery damage in the future (Onitsuka et al. 2016). Regarding direct countermeasures, clay spraying has been the most commonly employed tactic (Kagoshima Prefecture 1982, 2018; Kim 2006; Park et al. 2013). Recently, significant improvements in clay quality, such as an enhancement of the aggregated cohesive ability of red tide plankton, have enhanced its usefulness as an urgent countermeasure tactic (Murata 2017; Seger et al. 2017). Further, a dense seed bed of the toxic dinoflagellate *A. catenella* (group I) was identified in the inner part of Kesennuma Bay, Iwate Prefecture (Ishikawa et al. 2015), and the removal of bottom sediments containing dense cysts of HAB species located within the seed bed (Table 4) is thought to effectively reduce seed populations and prevent toxic blooms in small-scale embayments, such as Kesennuma Bay (Mine et al. 2015).

Biological controls using bacteria (Imai et al. 1993, 1995; Imai and Yamaguchi 2012; Imai 2015) and viruses (Tomaru et al. 2004, 2007; Nagasaki et al. 2006; Nagasaki 2008), or techniques exploiting the ecophysiological characteristics of red tide organisms (e.g., disturbance of thin-layer orientation in *K. mikimotoi*; Miyamura 2017) require further examination for practical use. Biological control methods are expected to be environmentally friendly and feasible.

The red tide countermeasures that are considered to be effective now or promising in the future are summarized in Fig. 3 in association with the stage transition of red tide occurrences. Monitoring is fundamental for enacting appropriate countermeasures before outbreaks, during the early stages and peak period, and until termination.

In the early stages of *K. mikimotoi* red tide initiation, thin-layer orientation has frequently been observed in subsurface layers with high cell densities (Aoki et al. 2017), and the physical disturbance of this thin layer has been proposed to be effective to prevent the development of red

Table 4 Practical and promising countermeasures for HABs. Data modified from Imai (2017a)

- Indirect methods
  - Legal regulation
    - Act on Special Measures Concerning Conservation of the Environment of the Seto Inland Sea, Act on Special Measures Concerning Restoration of the Environment of the Ariake Sea and Yatsushiro Sea, Water Pollution Control Law, Marine Pollution Prevention Law, Regulation Law of Agriculture Chemicals, Sustainable Aquaculture Production Assurance Act, etc.
  - Forecasting by monitoring
    - Regular monitoring, molecular monitoring
    - Improvement of prediction accuracy by data analysis and modeling
  - Fish culture technique
    - Improvement of bait (moist pellet), maintaining proper scale and density of fish, large-scale and deep pen cages
  - Emergency procedures
    - Feeding stop, transfer of net cages (horizontal and vertical)
- Direct methods
  - Physicochemical methods
    - Clay spraying
    - Disturbance of thin-layer orientation of population (*Karenia mikimotoi*, etc.)
    - Removal of bottom sediments containing dense cysts of HAB species located in the seed bed
  - Biological control
    - Algicidal activity: viruses, algicidal bacteria, parasitic protists (dinoflagellates, etc.)
    - Competitive overwhelming: diatoms (diatom growth after germination of diatom resting stage cells in sediments lifted to the euphotic layer with bottom perturbation by submarine tillage)

tides (Miyamura 2017). In the case of *H. circularisquama* red tides, treating frozen bottom sediments collected from red tide areas with algicidal viruses was demonstrated to be an effective preventive measure (Nakayama et al. 2020). Further, perturbation of the bottom sediment for utilizing diatom resting stage cells was proposed to prevent the occurrence of red tides due to harmful flagellates such as *Chattonella* spp. (results discussed below; Imai 2010b; Imai et al. 2017a). The restoration and creation of seaweed and seagrass beds could increase algicidal bacteria from their biofilm in surrounding areas, thereby mitigating HABs (Imai and Yamaguchi 2012; Imai 2015; Imai et al. 2016, 2017b; Inaba et al. 2017). If these strategies are implemented appropriately, they are anticipated to mitigate and significantly reduce the frequency and damage caused by HABs.

As promising and practical strategies against red tides, we introduce two biological methods below: The development of seaweed and seagrass beds (utilization of algicidal bacteria; Imai et al. 2002, 2016; Imai 2015; Inaba et al. 2017) and bottom sediment perturbation (utilization of the diatom resting stage cells in bottom sediments; Imai 2010b; Imai et al. 2017a).

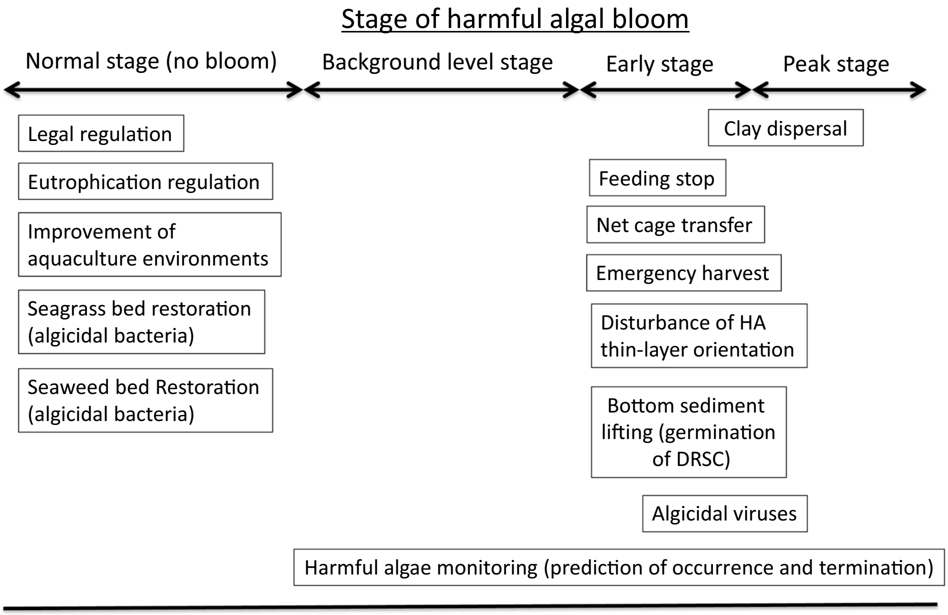

Fig. 3 Possible and/or promising countermeasures against HABs at each stage. HA, harmful algae; DRSC, diatom resting stage cells. Data modified from Imai (2017b)

Algicidal and growth-inhibiting bacteria associated with seaweed and seagrass beds

Algicidal bacteria can attack and kill microalgae, utilizing organic matter to proliferate (Imai 2011). Growth-inhibiting bacteria cause motility reduction and/or cell deformation of microalgae, ultimately leading to death (Inaba et al. 2014). Studies on the distribution of these bacteria have found that they commonly inhabit the coastal waters of Japan, and increase in abundance from peak to termination of red tides, playing a key role in red tide disintegration (Imai et al. 1998a, 2001). In fact, many strains of algicidal and growth-inhibiting bacteria have been isolated from coastal seawaters in Japan and elsewhere around the world (Imai et al. 1993, 1995; Imai and Yoshinaga 2002; Mayali and Azam 2004; Inaba et al. 2014, 2017; Onishi et al. 2014, 2021).

As an example of the processes of algicidal and growth-inhibiting bacteria, Fig. 4 shows various patterns of *C. antiqua*. Since *C. antiqua* does not have a cell wall, its cells can be ruptured by algicidal activities. Various patterns of growth inhibition activities were observed for *C. antiqua*, with observed incidences of spheroidization, elongation, and irregular deformation of cell morphology (Inaba et al. 2014, 2019; Imai et al. 2016). In the case of the thecate dinoflagellates *A. catenella* (group I) and *H. circularisquama*, complete algal kill off is rare, and spherical cells (temporary cysts) are often formed as a result of growth-inhibition activities (Imai et al. 1998b, 2020; Nagasaki et al. 2000;

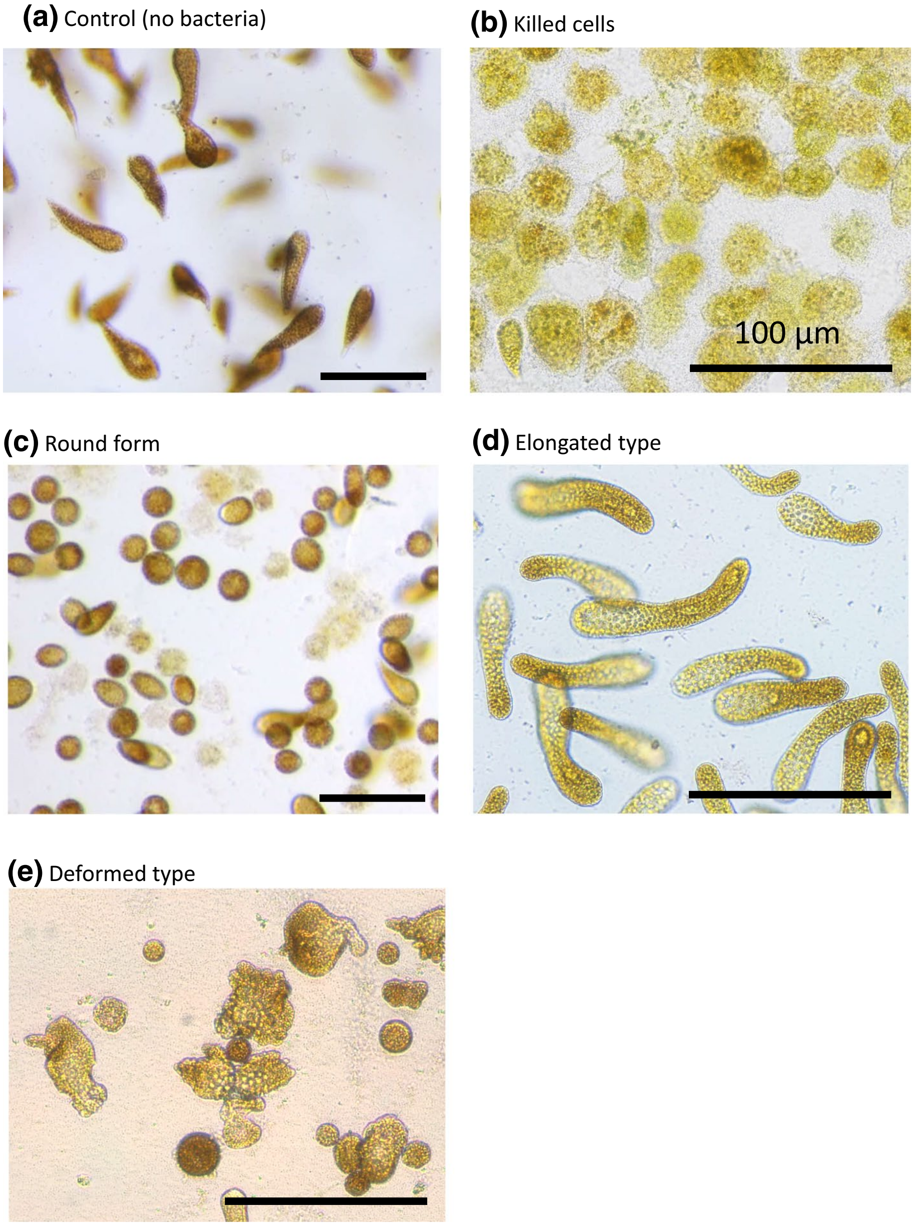

Fig. 4 Representative morphologies of *Chattonella antiqua* during co-culture experiments with algicidal and growth-inhibiting bacteria. **a** Control: no addition of bacteria, **b** killed cells: algicidal activity, **c** round form: growth inhibition by no-motility inducing bacteria, **d** elongated type: growth inhibition by elongation inducing bacteria, and **e** deformed type: growth inhibition by deformation-inducing bacteria. Scale bar: 100 µm. Images acquired from Imai et al. (2016)

Onishi et al. 2014; Inaba et al. 2017). Most of the algicidal and growth-inhibiting bacteria belong to the Gram-negative α-proteobacteria, γ-proteobacteria, and the phylum Bacteroides (Imai and Yoshinaga 2002; Mayali and Azam 2004; Imai et al. 2006b; Inaba et al. 2017, 2019; Onishi et al 2021).

The action of algicidal bacteria on HAB species can roughly be divided into two types: direct attack (mainly the phylum Bacteroides) and algicidal substance producers (Imai et al. 1993, 1995; Imai 1997; Meyer et al. 2017). When these bacteria start to exhibit algicidal activity, the first step is aggregation at the target algal cells (Imai et al. 1995). The involvement of quorum sensing has been suggested to control algicidal activities, such as producing algicidal substances (Fuqua et al. 1994; Nakashima et al. 2006; Kodama et al. 2017). As the algicidal substances, serine protease (Lee et al. 2000), prodigiosin (Nakashima et al. 2006), isatin (Sakata et al. 2011), and questiomycins (Umetsu et al. 2019), etc., have been reported.

Ecological studies on the relationships between algicidal bacteria and red tides have been carried out in coastal seas. In one such study of a small red tide of *Chattonella* in Harima-Nada, the algicidal bacterium *Cytophaga* sp. J18/M01 increased immediately after the bloom peak, as revealed by the indirect fluorescent antibody method using an antibody that specifically detects this bacterium (Imai et al. 2001). It was also observed that the number of total bacteria (direct counts) increased rapidly immediately after a *Chattonella* red tide (Imai 2013). In *H. akashiwo* red tides, algicidal bacteria also increased after the bloom peak in the coastal waters of Hiroshima Bay, and a predator–prey relationship of abundance was observed (Imai et al. 1998a; Kim et al. 1998; Yoshinaga et al. 1998). Similar relationships were also observed in the South Carolina brackish detention ponds in the USA (Liu et al. 2008). Furthermore, it was reported that a greater proportion of algicidal bacteria were attached to particles such as detritus, than free-living bacteria (Park et al. 2010; Inaba et al. 2014), indicating that colony formation on particles is advantageous for these bacteria to express growth-limiting activities controlled by quorum sensing. Increased numbers of algicidal and growth-inhibiting bacteria following an increase in red tide microalgae were observed to reduce algal numbers rapidly, together with heterotrophic bacteria due to feeding by heterotrophic nanoflagellates (Inaba et al. 2019). The influence of these temporarily predominant bacteria on the environment is thought to be small, making them a more environmentally friendly strategy for controlling HABs.

This research field was broadened to include seaweed beds for surveying algicidal bacteria. At one seaweed bed in Obama Bay, Fukui Prefecture, algicidal bacteria against the red tide raphidophytes *Chattonella* spp. (*C. antiqua*, *C. marina*, and *C. ovata*), *H. akashiwo*, and *Fibrocapsa japonica* were found at high densities despite the absence of these red tide raphidophytes (Imai and Yoshinaga 2002). The distribution of algicidal bacteria was investigated by targeting the raphidophytes *C. antiqua*, *C. marina*, *C. ovata*, *H. akashiwo*, and *F. japonica*, and the dinoflagellates *M. polykrikoides* and *K. mikimotoi* in a natural seaweed bed in Misaki Park, Osaka Prefecture (Imai et al. 2002). Enormous densities of algicidal bacteria were found to inhabit the surface of the green alga *Ulva pertusa*, the red alga *Gelidium* sp., and the brown algae *Sargassum thunbergii* and *S. muticum* (Imai et al. 2002). The densities of algicidal bacteria were as high as 10^5–10^6/g of wet weight seaweed. Among the tested harmful algae, the dinoflagellate *K. mikimotoi* and the raphidophytes *H. akashiwo* and *F. japonica* were very effectively killed by algicidal bacteria isolated from the seaweed bed. Major isolated strains of algicidal bacteria from seaweed beds belonged to α-proteobacteria, γ-proteobacteria, and the phylum Bacteroides, similar to the results obtained in red tide areas (Imai and Yoshinaga 2002; Imai et al. 2006b). A large number of algicidal bacteria were found to attach to the surface of *Ulva pertusa* in polyculture cages of seaweed and fish (Imai et al. 2012), ultimately leading to the successful introduction of *U. pertusa* beds using mobile floating cages to harbor bacteria that inhibit several HAB species (Inaba et al. 2020).

As the next step of the investigation, the seasonal distribution of algicidal bacteria was measured in a seagrass (*Zostera marina*) bed in Hannan, Osaka Prefecture, Japan. From June to October 2006, monthly samples were collected from the seagrass bed (~ 2000 m^2), which was restored naturally near Sennan-Sato-Umi Park (Imai et al. 2009, 2016). A large number of bacteria exhibiting algicidal activity against five species of red tide plankton were confirmed to inhabit the leaf surface of *Z. marina* at densities up to 6.4×10^7 (average of ~ 10^7) colony-forming units (CFU)/g (wet weight; Fig. 5). Calculating the densities of algicidal bacteria that kill at least one species of red tide microalgae, high densities of algicidal bacteria (1×10^7–9×10^7 CFU) were found on 1 g of wet weight leaves of *Z. marina*. Algicidal bacteria were also detected in seawater from the seagrass bed at densities of 10^3–10^4 CFU/mL, and algicidal bacteria density in seawater was highest in the seagrass bed and lowest at the sandy beach. Cell densities of phytoplankton in seawater within the seagrass field were markedly lower than those in the offshore area of Osaka Bay (Imai et al. 2016), and similar decreased densities of phytoplankton have been observed in seagrass beds and surrounding waters elsewhere (Lee et al. 2006; Jacobs-Palmer et al. 2020).

The distribution of algicidal and growth-inhibiting bacteria against *H. akashiwo* and *A. catenella* (group I) was investigated by collecting seagrasses (*Z. marina* and *Z. japonica*), seaweed (*U. lactuca*), and seawater samples from various locations in Puget Sound on the west coast of the USA (Inaba et al. 2017). The densities of effective (algicidal and

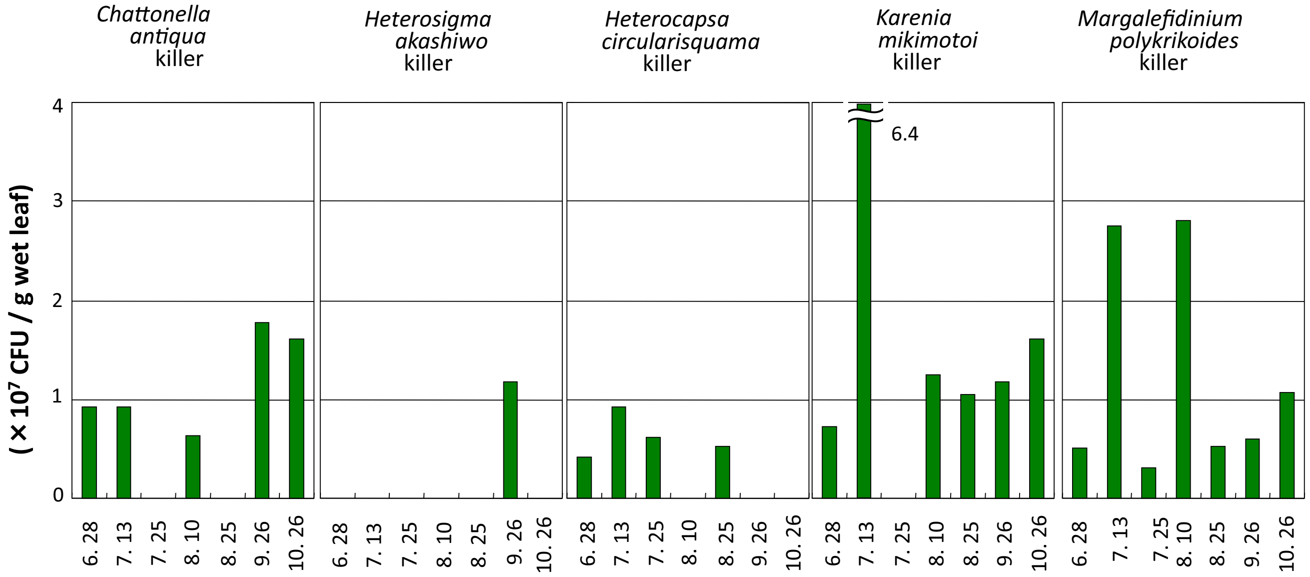

Fig. 5 Seasonal changes in densities of algicidal bacteria against five species of red tide plankton inhabiting the biofilm on the surface of seagrass *Zostera marina*. Seagrass samples were collected from the coast of Misaki Town, Osaka Prefecture, in 2006. Data partly modified from Imai et al. (2016)

growth-inhibiting) bacteria were found to reach a maximum of 10^8 cells/g (wet weight) on *Z. marina*, similar to those observed in Osaka Bay. Additionally, the obtained effective bacteria also belonged to α-proteobacteria, γ-proteobacteria, and the phylum Bacteroides in Puget Sound as well. Sakami et al. (2017) investigated the distribution of algicidal bacteria of three *Alteromonas* strains (S, K, D) in seagrass beds and external seawaters of the Seto Inland Sea. The analyzed *Alteromonas* strains were found more abundantly on the *Z. marina* leaves and in the seawater within the seagrass bed, as compared with the external seawater. Seagrass beds are thus presumed to be the source of these algicidal bacteria (Sakami et al. 2017). The influence of algicidal bacteria in a seagrass (*Z. marina*) bed and the capability of *C. antiqua* to control blooms were examined in a laboratory microcosm experiment (Inaba et al. 2019), revealing that bacterial communities in seawater collected from the seagrass bed and *Z. marina* biofilm suppressed artificial *Chattonella* blooms in the presence of their natural competitors (heterotrophic bacteria) and predators (heterotrophic nanoflagellates).

The distribution of algicidal bacteria in coastal waters is summarized in Table 5, revealing that seaweed and seagrass beds are hotspots of bacteria capable of killing and/or inhibiting the growth of harmful algae. It is further assumed that these bacteria are continuously supplied from seaweed and seagrass beds to the surrounding waters, thus restoration and creation of seaweed and seagrass beds could be a practical and environmentally friendly measure to prevent HABs. Seaweeds and seagrasses could be beneficial not only by harboring these bacteria but also through water quality restoration via the uptake of excess nutrients, releasing allelochemicals that negatively affect the growth of HAB species, and some algal species are of commercial importance. An example application is the mixed aquaculture of fish and seaweed discussed above (Fig. 6). In this regard, applying the recently revealed ability of seaweed and seagrass beds to suppress HABs would be an ideal system from the viewpoint of bioremediation, as the habitat of these bacteria is prepared by the seaweeds and seagrasses (biostimulation), and proliferating bacteria are continuously supplied from their surfaces to the surrounding seawater (bioaugmentation). Probably the most significant advantage is that the costs of maintaining seaweed and seagrass beds are negligible.

Utilization of diatoms

It is empirically well known that diatoms are scarce in the water column when red tides occur due to harmful flagellates such as *Chattonella* spp., *H. akashiwo*, and *K. mikimotoi* (Itakura et al. 1996; Onitsuka et al. 2011; Shikata et al. 2011; Imai 2012; Nishi et al. 2012); however, many diatom resting stage cells are deposited on the bottom sediments of coastal seas (Imai et al. 1990; Itakura et al. 1997, 1999), and require light for germination and revival (Imai et al. 1996; Itakura 2000). Therefore, if the diatom resting stage cells in sediments are suspended from the seafloor into the water column of the euphotic layer, it is presumed that the vegetative cells of diatoms, which are generated through germination and rejuvenation from the resting stage cells, can consume nutrients in the water, proliferate, and overwhelm

Table 5 Summary of published studies on algicidal or growth-inhibiting bacteria targeting HAB species investigated in seaweed and seagrass beds. Data modified from Inaba et al. (2017)

Sampling site	Year	Source	Target HAB species	Maximum density of AB and GIB	Method	Remark	Ref.
Osaka Bay, Seto Inland Sea	1999	*Ulva* sp.	*Heterosigma akashiwo*	1.4×10^3 MPN/g	MPN	Green alga	Imai et al. (2002)
			Fibrocapsa japonica	1.2×10^4 MPN/g	MPN		
			Karenia mikimotoi	7.0×10^4 MPN/g	MPN		
		Gelidium sp.	*H. akashiwo*	2.6×10^5 MPN/g	MPN	Red alga	
			F. japonica	1.3×10^6 MPN/g	MPN		
			K. mikimotoi	4.9×10^5 MPN/g	MPN		
		Seawater	*H. akashiwo*	1.6×10^2 MPN/mL	MPN	Seaweed bed	
			F. japonica	4.3×10^2 MPN/mL	MPN		
			K. mikimotoi	4.3×10^3 MPN/mL	MPN		
Shimo-Haya Bay, Wakayama	2002–2003	Seawater	*H. akashiwo*	2.0×10^2 MPM/mL	MPN	Aquaculture pond with *Ulva pertusa*	Imai et al. (2012)
			Chattonella antiqua	1.0×10^2 MPN/mL	MPN		
			F. japonica	1.4×10^2 MPN/mL	MPN		
			K. mikimotoi	2.2×10^4 MPN/mL	MPN		
		Ulva pertusa	*H. akashiwo*	2.0×10^2 MPN/g	MPN	Aquaculture pond with *Ulva pertusa*	
			C. antiqua	8.0×10^2 MPN/g	MPN		
			F. japonica	1.9×10^5 MPN/g	MPN		
			K. mikimotoi	1.1×10^6 MPN/g	MPN		
	2003	*Ulva pertusa*	*H. akashiwo*	4.7×10^4 CFU/g	Bacterial isolation and co-culture	Aquaculture pond with *Ulva pertusa*	
			C. antiqua	9.4×10^4 CFU/g			
			F. japonica	2.3×10^5 CFU/g			
			K. mikimotoi	8.0×10^5 CFU/g			
			Heterocapsa circularisquama	1.9×10^5 CFU/g			
Osaka Bay, Seto Inland Sea	2006	Seawater	*H. akashiwo*	2.4×10^3 CFU/mL	Bacterial isolation and co-culture	*Zostera marina* bed	Imai et al. (2016)
			C. antiqua	4.8×10^3 CFU/mL			
			K. mikimotoi	2.4×10^3 CFU/mL			
			H. circularisquama	1.8×10^3 CFU/mL			
			Margalefidinium polykrikoides	2.3×10^3 CFU/mL			
		Zostera marina	*H. akashiwo*	1.2×10^7 CFU/g	Bacterial isolation and co-culture	Seagrass	
			C. antiqua	1.8×10^7 CFU/g			
			K. mikimotoi	6.4×10^7 CFU/g			
			H. circularisquama	9.2×10^6 CFU/g			
			M. polykrikoides	2.8×10^7 CFU/g			

Table 5 (continued)

Sampling site	Year	Source	Target HAB species	Maximum density of AB and GIB	Method	Remark	Ref.
Puget Sound, USA	2012–2013	Seawater	*H. akashiwo*	1.8×10^3 CFU/mL	Bacterial isolation and co-culture	Dumas Bay	Inaba et al. (2017)
			Alexandrium catenella (Group I)	4.1×10^3 CFU/mL		Holmes Harbor	
		Zostera marina	*H. akashiwo*	1.6×10^8 CFU/g		Pier at Friday Harbor Laboratory	
			A. catenella (Group I)	7.5×10^7 CFU/g		Central Padilla Bay	
		Zostera japonica	*H. akashiwo*	2.8×10^8 CFU/g		Central Padilla Bay	
			A. catenella (group I)	1.8×10^8 CFU/g		Central Padilla Bay	
		Ulva lactuca	*H. akashiwo*	1.3×10^8 CFU/g		Shallow Bay, Sucia	
			A. catenella (group I)	6.9×10^5 CFU/g		Cattle Point	
Shinori Coast, Hokkaido	2011	Seawater	*A. catenella* (group I)	2.5×10^3 CFU/mL	Bacterial isolation and co-culture	Seaweed bed	Imai et al. (2020)
		Laminaria japonica	*A. catenella* (group I)	3.7×10^5 CFU/g		Brown alga	
		Sargassum thunbergii	*A. catenella* (group I)	3.7×10^5 CFU/g		Brown alga	
		Corallina pilulifera	*A. catenella* (group I)	1.1×10^6 CFU/g		Red alga	
		Ulva pertusa	*A. catenella* (group I)	3.7×10^5 CFU/g		Green alga	
Akkeshi-ko, Akkeshi Bay, Hokkaido	2011	Seawater	*A. catenella* (group I)	1.1×10^3 CFU/mL	Bacterial isolation and co-culture	Akkeshi Bay	Onishi et al. (2021)
		Zostera marina	*A. catenella* (group I)	4.7×10^6 CFU/g		*Zostera marina* bed	

HAB harmful algal bloom, *AB* algicidal bacteria, *GIB* growth-inhibiting bacteria, *MPN* most probable number, *CFU* colony forming unit

harmful flagellates. In fact, Takahashi et al. (1977) reported that, after a vertical mixing event in coastal areas due to strong winds, nutrients and the seed stock of phytoplankton in bottom sediments primarily composed of diatoms were lifted to the euphotic layer; consequently, diatom blooms occurred and lasted for several days to weeks from spring to summer. Bottom sediment perturbation can thus be utilized as a practical method to artificially induce such a phenomenon (Fig. 7; Imai 2010b). The disturbance of the sea, which is usually caused by natural processes such as typhoons, can be artificially induced by bottom sediment perturbation under calm weather conditions. Bottom sediment perturbation is performed by submarine tillage, originally a common technique in Japan for improving deteriorated bottom sediment environments in the coastal seas (Nakanishi 2002).

There is a lack of knowledge about the effects of bottom sediment perturbation by artificial submarine tillage on phytoplankton communities in seawater; and to the best of the authors' knowledge, Imai et al. (2017a) is the only study to date to have examined such effects. Since the diatom resting stage cells are suspended in the water column, the resulting diatoms that germinate from the resting stage cells in the euphotic layer would join the phytoplankton community. Thus, it can be presumed that the quality (i.e., composition) and quantity (i.e., density) of the phytoplankton community

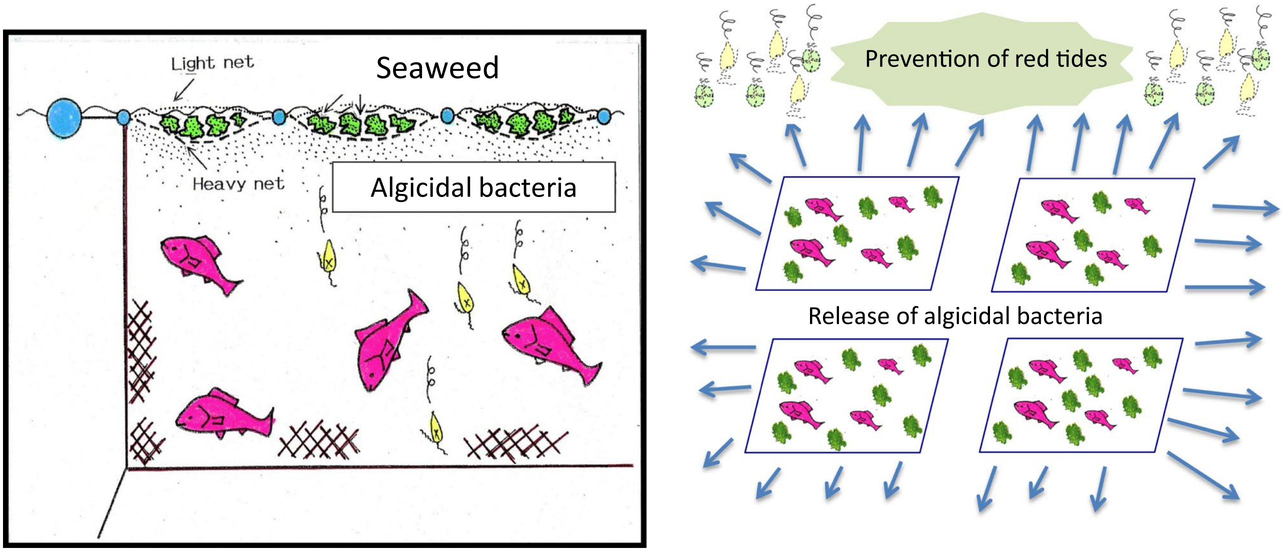

Fig. 6 Schematic representation of polycultured fish with seaweed, and prevention of harmful red tides by the release of algicidal bacteria from the seaweed. Algicidal bacteria derived from seaweeds are widely supplied to surrounding waters and expected to suppress phytoplankton growth and thereby the occurrence of red tides. Data modified from Imai et al. (2002)

are greatly affected and induced to diatom-predominant communities.

The following is a description of the first case report of successful suppression of *Chattonella* populations by bottom sediment perturbation in the Seto Inland Sea (Imai et al. 2017a). Bottom sediment perturbation by submarine tillage was carried out on 7 and 8 July 2016 in the Tomono-Ura area of the Seto Inland Sea, Fukuyama City, Hiroshima Prefecture, where *Chattonella* red tides frequently occur. Two sites, Stn. A in the nontillage area and Stn. B in the sediment perturbation area, were set up to monitor changes in environmental factors and phytoplankton communities. Diatom resting stage cells were present in the bottom sediments at densities of 1.2×10^5 and 1.7×10^5/g (wet sediment) for Stn. A and B, respectively. During the investigation period, the water temperature and salinity tended to show the same pattern at both sites, and the effects of perturbations were negligible. The dynamics of phytoplankton are shown in Fig. 8. In the perturbation area of Stn. B, diatoms increased from 48 to 1383 cells/mL, and *Chattonella* spp. varied between 0 and 34 cells/mL. Diatoms increased significantly on day 0 (immediately following sediment perturbation, 8 July) at Stn. B compared with day -1 (i.e., the day immediately prior to perturbation, 7 July). By day 7, diatoms in the surface layer increased to ~ 30 times the density levels of day -1. Additionally, *Chattonella* spp. first existed in the mid- and bottom depths at a density of 34 cells/mL on day -1 and, following perturbation, declined without proliferating as a whole after 7 days. Overall, perturbation by submarine tillage resulted in the predominance of diatoms and substantially suppressed the growth of *Chattonella* spp. At Stn. A (nonperturbation area), diatoms showed cell densities of 61–376 cells/mL, and *Chattonella* spp. cell densities of 0–30 cells/mL. Since Stn. A was relatively near Stn. B (i.e., the sediment perturbation area), the water mass of the perturbation area probably influenced Stn. A as well. The bottom sediment perturbation was performed again in August 2016, and twice in the summer of 2017, and in both years, the increase in *Chattonella* cells was prevented after each of the sediment perturbation trials similarly as shown in Fig. 8.

Chattonella spp. are repelled by copepods (Uye and Takamatsu, 1990). When diatoms are predominant, zooplankton such as copepods actively graze upon diatoms, and furthermore, the food webs would be driven smoothly, and the situation would be favorable for production of planktivorous fishes such as anchovy, sardine, and horse mackerel. In general, diatoms are less abundant during the period from the time after spring bloom until autumn in the coastal seas of temperate to Arctic areas, leading to frequent occurrences of harmful flagellate blooms in the summer. Sediment perturbation could potentially prevent HABs after the spring bloom, activating food webs, and increasing the total stock and production of fish and other marine life at higher trophic levels.

Competitions of *Chattonella* spp. and diatoms produced by germination and rejuvenation of resting stage cells suspended in seawater were studied using bottle incubation experiments (Imai et al. 2017a). Seawater samples containing suspended sediments were collected from the middle layer (2 m depth) at Stn. B in the bottom sediment perturbation area immediately following the implementation. Then, four experimental plot bottles (a–d) were set by combining

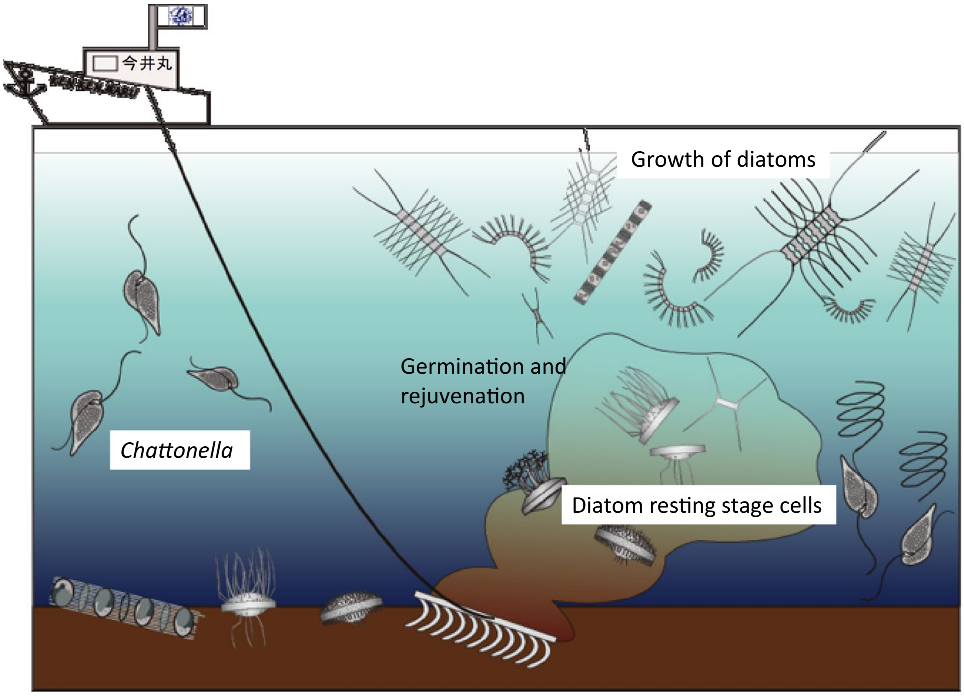

Fig. 7 Schematic representation of sediment perturbation as a control strategy for *Chattonella* red tides in coastal seas. Bottom sediments containing numerous diatom resting stage cells are lifted to euphotic layers by bottom sediment tillage with a submarine tractor or trawling fishing gears. Germinated and/or rejuvenated diatom vegetative cells multiply vigorously and become dominant in the water column, resulting in the decay of *Chattonella* populations by virtue of nutrient exhaustion. Data partly modified from Imai et al. (2017a)

additional concentrations of *C. antiqua* and modified SWM-3 medium with 1/100 strength (Table 6). Experimental conditions were temperature of 25 °C, light intensity of 50 µmol photons/m^2/sec, and photoperiod of 14 h light:10 h dark. Nutrient concentrations in the bottles decreased sharply from days 2 to 4. Fluctuations in phytoplankton for each experimental bottle are shown in Fig. 9. *Chattonella* spp. began to decrease shortly after the start of the experiment, and disappeared by the 14th day. In particular, *Chattonella* spp. disappeared fastest in experimental bottles (a) and (b), containing only the cells of *Chattonella* spp. in the original seawater, at a lower density. Additionally, diatoms grew and reached a density of approximately 10^4 cells/mL, overwhelming *Chattonella* spp. Another bottle experiment was carried out with the addition of HAB species (*C. antiqua* and *K. mikimotoi*), and the bottom sediments obtained at Okimatsuura Fishing Port in Saiki City, Oita Prefecture, at concentrations of 1 g/L and 0.1 g/L. Bottles were suspended at three depths (0, 5, and 9 m) at the coastal point of the Fisheries Research Division of Oita Prefecture (Imai et al. 2017c). Diatoms originating from resting stage cells in sediments proliferated and suppressed *C antiqua* and *K. mikimotoi*, as evidenced by the diatoms becoming predominant in the phytoplankton community in seawater after the addition of sediments to the bottles. This result explains the phenomenon of the changes in phytoplankton assemblages (predominance of diatoms) observed in the water column following the bottom sediment perturbation by submarine tillage in the field.

Large-scale bottom sediment perturbation by submarine tillage trials were conducted in 5 km^2 areas in the northern areas off Sakai City and off Kishiwada City in the middle of Osaka Bay twice in late January and once on 10 February 2020. As mentioned above, outbreaks of the toxic dinoflagellate *A. catenella* (group I) have expanded in Osaka Bay since 1994, and the maximum density has commonly been above 10^3 cells/mL in recent years (Fig. 2). The bottom sediment perturbation aims to suppress the growth of *A. catenella* (group I) in Osaka Bay. As a result of the perturbation, diatoms mainly consisting of the genera *Skeletonema*, *Chaetoceros*, and *Leptocylindrus* were continuously observed at high densities > 10^3 cells/mL. In contrast, *A. catenella* (group I) did not reach warning threshold levels of 5 cells/mL, as defined by the Osaka Prefecture, during the month of February. An alarming density (10 cells/mL) was, however, exceeded in early March, more than 20 days after the perturbation; and a highest value of 31 cells/mL was recorded near the entrance of Sakai Dejima Port on March 23. Compared with the occurrences of higher densities of *A. catenella* (group I) on the order of 10^3 and 10^4 cells/mL over the past several years, this value (31 cells/mL) can be considered as successfully low, with the maximum cell density being 1/100 or less compared with previous years. These results indicate that diatoms were successfully increased after the bottom sediment perturbation, suppressing *A. catenella* (group I) populations and maintaining low toxin levels in bivalves in Osaka Bay in 2020, as no regulated threshold levels of Manila clams or oysters were exceeded. Moreover, this low

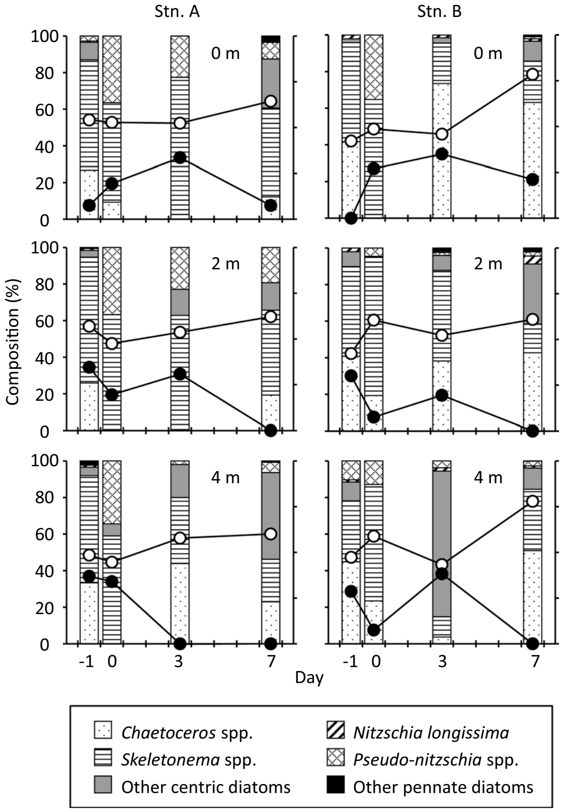

Fig. 8 Changes in cell densities of *Chattonella* (●), diatoms (○), and taxa composition histograms of diatoms at three depths (0, 2, and 4 m) at Stn. A (point outside bottom sediment tillage area) and B (point inside bottom sediment tillage area) in the coastal sea of Tomono-Ura of the Seto Inland Sea, from 7 July (day -1) to 15 July (day 7) 2016. Figure from Imai et al. (2017a)

Table 6 Conditions of experimental bottles (Fig. 9) with combinations of inoculation of red tide raphidophyte *Chattonella antiqua* and addition of nutrient source of SWM-3 medium. Data derived from Imai et al. (2017a)

Bottle	*Chattonella antiqua*	Nutrient addition
a	No addition	No addition
b	No addition	SWM-3, 1/100 strength
c	200 cells/mL	No addition
d	200 cells/mL	SWM-3, 1/100 strength

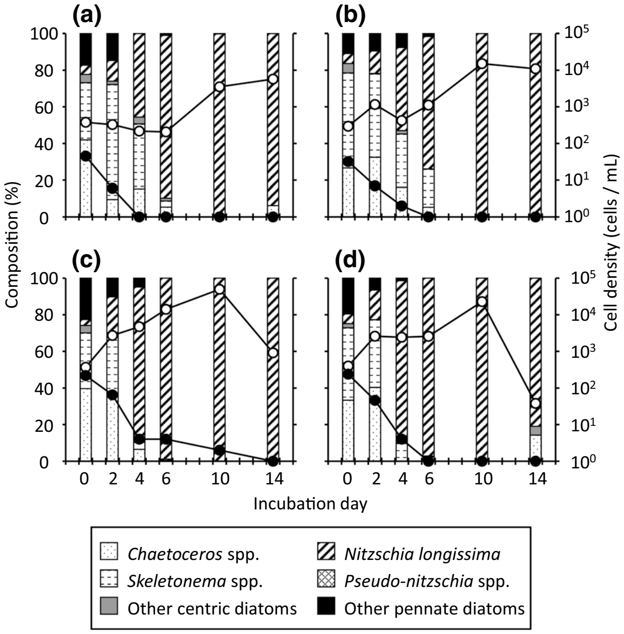

Fig. 9 Changes in cell densities of *Chattonella* (●), and diatoms (○), and taxa composition histograms of diatoms in the incubation bottle experiment. Sediment-suspended samples were collected at a depth of 2 m at Stn. B immediately following the bottom sediment tillage, and prepared bottles were incubated under the following conditions: temperature 25 °C, light intensity 50 μmol photons·m^{-2} s^{-1}, and photocycle 14 h light:10 h dark. See Table 6 for further explanation of bottles (a)–(d). Figure from Imai et al. (2017a)

level of bivalve toxicity is thought to increase the survival rate of higher trophic levels, such as octopuses, that prey on bivalves. The toxins of *A. catenella* (group I) were reported to be transferred and accumulated in zooplankton, leading to the death of animals at higher trophic levels (White 1981; White et al. 1989; Teegarden and Cembella 1996; Turner and Tester 1997). If nontoxic diatoms are predominant, the food webs in the corresponding waters will remain intact.

Details of the above results will be published in the near future (Yamamoto et al., in preparation). It is necessary to continue the bottom sediment perturbation, together with devising the timing and scale of its implementation, to confirm the reproducibility of the results (diatom predominance with suppressed *A. catenella* (group I)), and to refine the technologies used. As a result, an effective, environmentally friendly method can be established to prevent outbreaks of toxic blooms, helping to ensure the safety of marine life and resources into the future.

Theories and criteria for HAB controlling strategies

In the field of agriculture, pest control is crucial for maintaining and improving production, and a great deal of research effort has been devoted to it. When farmed marine organisms are regarded as crops, the pests are equivalent to harmful algae. There are many similarities between HAB control in fisheries and pest control in agriculture, and applying the lessons from increasing crop productivity to marine resources can provide a number of useful perspectives.

In the past, Japanese agriculture adopted a defense-oriented strategy with a focus on plant protection from pests. A variety of organisms inhabited paddy and upland fields, passively preserving the biodiversity; however, novel synthetic pesticides developed after World War II changed the approach to pest control from "defensive" to "offensive." With the exception of agricultural crops, pest control was carried out based on a "disinfection policy," which does not permit the existence of pests and useful organisms, even beneficial insects and animals. As a result, serious issues have arisen, such as the appearance of drug-resistant organisms, dangers of residual pesticides in crops and the environment, and induction of abnormal pest occurrences. These problems have caused major destruction of the natural biota and ecosystem (Kiritani 1979; Naba 2001).

Assessing the direct methods of eliminating HABs, both physical and chemical methods can be regarded as measures exactly based on a "disinfection policy." There is no careful consideration of organisms other than the directly farmed marine life, and all marine organisms (the main target being harmful algae) are indiscriminately exterminated. In agriculture, paddy and upland fields are primarily two-dimensional fields; thus, pesticides accumulate after application and diffuse slowly to the external environment. On the other hand, the sea is a three-dimensional system with depth, being a fluid diffusion system with continuous water flow. Therefore, it can be concluded that control strategies based on spraying substances are implausible in the sea in terms of scale, economy, and environmental security.

Such pest control based on the "disinfection policy" was reconsidered in agriculture. Efforts have been made to combine various measures to minimize the use of pesticides in an approach named "integrated pest management" (IPM) (Kiritani 1997; Naba 2001). The official definition of IPM is "the pest population management systems for reducing pest densities below economic injury level (EIL) and maintaining pest densities lower level by using all appropriate control measures in a reasonable manner." The concept of EIL is drawing a line under the conventional "disinfection policy." Pests damage crops only when they reach a certain density, and even when surpassing this level, if the damage is less than the cost of pest control, it will be meaningless. The strict criteria for EIL will be the pest density at which the benefits of control are maximized. From this point of view, EIL varies depending on the crop, pest type, and control method. It should be acknowledged, however, that pests are not always controlled because of their occurrence but when economic damage is predicted. Therefore, pest control is both a technological and economic issue.

Following the framework established by the Convention on Biological Diversity (CBD), biodiversity should be maintained not only in natural environments but also in agricultural fields. It is necessary to maintain and/or improve the densities of endangered and rare species above the extinction threshold. However, in addition to the original pests, other insect species become pests at certain densities. Therefore, it is necessary to manage their densities as well so as not to exceed the EIL. This form of management is referred to as integrated biodiversity management (IBM). Since coexistence with various organisms is pursued without excluding other potential pest species, primary control policies are moving from IPM to IBM (Kiritani 2000).

The following are the comprehensive considerations on the relationships between countermeasures and the stage of red tide occurrences. Figure 10 shows a conceptual diagram for preventing and/or controlling the occurrences of red tides. The "damage causing level" corresponds to the aforementioned EIL. Preventive countermeasures must be implemented before the density of causative red tide organisms reaches the critical level, a point defined as the "control threshold" (CT), derived from the concept used in agricultural pest control. The CT can be set between the "background" and "damage-causing" levels. To best prevent and/or control the occurrence of red tides, the dynamics of the targeted red tide organisms must be properly monitored, enabling prediction of the outbreaks themselves.

In the case of bottom sediment perturbation, if these actions are performed at the point of the CT of HAB species according to monitoring information, nutrient salts are expected to be consumed by the subsequent growth of diatoms, and the occurrence of red tides by harmful flagellates is likely to be prevented. With regards to red tide species that are susceptible to viruses, spraying of marine bottom sediments containing effective viruses has been reported to control harmful species populations, such as the bivalve-killing dinoflagellate *H. circularisquama*, through infection (Nakayama et al. 2020). In the early stages of dinoflagellate *K. mikimotoi*-induced red tides, a thin layer with high cell density is usually formed at the mid-depths of specific water areas (Uchida et al. 1998; Yamaguchi 1994; Miyamura 2016; Aoki et al. 2017). The initial destructive methods applied to this thin layer, such as clay spraying (Murata 2017), the movement of thin-layer populations to the surface (i.e., unsuitable depths for their growth and survival; Miyamura 2017), and the application of bottom sediment perturbation using dragnets (Imai et al. 2017a) with air bubbling when possible, are effective for suppressing *K. mikimotoi* populations. As for red tides exceeding the CT level and reaching the EIL when preventive or immediate control measures are unsuccessful, clay spraying is commonly applied as a last resort (particularly in aquaculture fisheries) to reduce the damage inflicted (Kagoshima Prefecture 1982, 2018; Kim 2006; Imai 2017b).

It is fundamentally important to prevent the occurrences of HABs over long timescales by the creation of water environments that naturally suppress the growth of HAB-causative organisms. The restoration and creation of seagrass and seaweed beds have been proposed as environmentally friendly strategies to prevent the occurrence of HABs (Imai et al. 2006a, 2017b; Imai 2015). Furthermore, the effects of

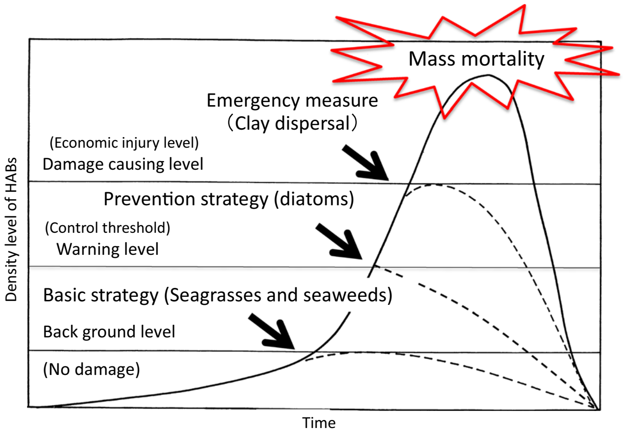

Fig. 10 Conceptual diagram for prevention and/or control of harmful algal blooms at each level of bloom development. Bold line shows the change in harmful algae with no strategy implemented, arrow shows the timing for the implementation of countermeasure technology, and dotted line shows the change in harmful algae concentrations after treatment. Data partly modified from Imai (2017b)

combined aquaculture of fish and seaweeds may be promising (Imai et al. 2002, 2012, 2020; Imai 2019; Inaba et al. 2020). These effects take advantage of the natural function of seaweeds and seagrasses, providing inhabitable substrates to algicidal and growth-inhibiting bacteria, which are then supplied to the surrounding waters. It is expected that the coastal marine ecosystem itself will self-maintain in a healthy state, with relatively higher densities of bacteria limiting algal growth, and in which phytoplankton communities containing HAB species do not proliferate into overscale and destructive blooms (Imai and Yamaguchi 2012; Imai 2015; Imai et al. 2017b).

As the ocean is home to a vast array of species and organisms, the minimum criterion that must be met for successful countermeasures to red tides is “When the implemented red tide control measures are successful or fail, they should not have significant adverse effects on the marine lives in the ecosystem” (Imai 2017a). Ultimately, simple technologies supported by profound ecological research could meet such criteria, thus preventing and controlling harmful algal blooms in feasible and environmentally friendly ways.

Harmful cyanobacterial blooms and control strategies

Cyanobacterial blooms have frequently occurred in lakes and reservoirs across the globe (except in polar regions), primarily due to eutrophication and climate change (O’Neil et al. 2012; Paerl and Otten 2013; Harke et al. 2016). Toxic and nuisance cyanobacterial blooms pose serious problems to water resource uses, such as drinking and agriculture. There is a long history of deaths due to toxic cyanobacterial blooms in grazing livestock and wild animals (Stewart et al. 2008). For example, the recent deaths of 300 African elephants in Botswana in 2020 attracted international attention, and the cause is suspected to be toxic cyanobacterial blooms in drinking water ponds (https://www.bbc.com/news/world-africa-54234196). Additionally, water toxified by the cyanobacterium *Microcystis aeruginosa* posed a great danger to US residents reliant upon water from Lake Erie, forcing drinking water to be imported by tanker trucks from distant areas (Steffen et al. 2017). In Japan, harmful and toxic cyanobacterial blooms have also posed critical environmental problems, such as interrupting the supply of drinking water, and spoiling landscapes that are important for tourism (Takamura 1988; Shimizu et al. 2016; Imai et al. 2019).

Regarding the control of these harmful cyanobacterial blooms, nutrient input reduction and breaking down stratification are both effective methods in small-scale reservoirs (Paerl and Otten 2013). Copper sulfate has been sprayed to exterminate cyanobacterial blooms in drinking water reservoirs, and activated charcoal has been used to deodorize water affected by odor-producing cyanobacteria. However, these chemical treatments have a high cost (Shimizu et al. 2016). Therefore, prevention and control of nuisance cyanobacterial blooms have become an urgent and critical issue.

Environmentally friendly biological control measures for cyanobacterial blooms have been extensively investigated (Sigee et al. 1999; Gumbo et al. 2008; Ndlela et al. 2018; Pal et al. 2018; Imai et al. 2019). In limnetic microbial ecology, investigations on useful microbes, such as algicidal bacteria and lytic viruses, have been actively pursued (Yamamoto 1988). Many studies have been conducted on the aquatic distribution of these microorganisms and the algicidal activities of isolates (Mitsutani et al. 1987; Manage et al. 2001; Kim et al. 2008; Shimizu et al. 2017). The biological suppression of harmful cyanobacterial blooms using these microorganisms has also been pursued (Sigee et al. 1999; Gumbo et al. 2008). However, the technology to appropriately utilize these microorganisms for the prevention and control of blooms has not yet reached the levels required for practical use on scales beyond the laboratory (Ndlela et al. 2018).

In Lake Biwa of Shiga Prefecture, and Lake Oshima Onuma of Hokkaido, bacteria showing algicidal and growth-inhibiting activities against the toxic cyanobacterium *Microcystis aeruginosa* have recently been discovered in aquatic plants such as the emerging plant *Phragmites australis*, the floating-leaved plant *Trapa japonica*, and the submerged plants *Myriophyllum verticillatum* and *Utricularia vulgaris*. A new discovery is that effective (algicidal and growth-inhibiting) bacteria are found to inhabit the surface biofilm of water plants at high densities (Imai 2010a; Kojima et al. 2016; Daido et al. 2018; Miyashita et al. 2019). Maximum densities on the order of 10^4 CFU/mL in water, and 10^6 to 10^8 CFU/g (wet weight) were detected for these effective bacteria in aquatic plants (Table 7). For example, from the surface biofilm of reed stems collected in Lake Oshima Onuma, the detected densities of these bacteria effective against *M. aeruginosa* were 5.2×10^5–4.8×10^6 CFU/g (wet weight; Fig. 11), and the densities of these bacteria in waters of reed belt were 4.3×10^1–2.4×10^3 CFU/mL (Kojima et al. 2016). A co-culture experiment was also conducted by adding lake water collected from the reed zone near the campsite on the northeast coast of Lake Oshima Onuma to a sample of *M. aeruginosa* bloom collected at Onuma Port (Imai et al. 2014). As a result, a decrease in 98% of *M. aeruginosa* was recorded at 1/10 addition, 94% at 1/100 addition, and 78% at 1/1000 addition. Comparatively, no decrease in *M. aeruginosa* cells was observed in the control sample bottle without addition of lake water collected in the reed zone. Thus, the presence of certain aquatic plants is thought to supply bacteria that have the ability to suppress the growth of nuisance cyanobacteria to the surrounding water, probably decreasing the frequency and severity of cyanobacterial blooms in lakes and ponds.

An antagonistic relationship between aquatic plants and phytoplankton has long been documented in lake ecosystems (Hogetsu et al. 1960; Nemoto and Fukuhara 2012). One such study reported long-term observations in a Swedish lake, documenting distinct antagonistic relationships between aquatic plants and phytoplankton (Blindow et al. 1998). During the period of limited nutrient loadings, the lake water was transparent, phytoplankton biomass was small, submerged plants proliferated widely, and fish-eating fishes were abundant. Alternatively, as nutrient loading increased and eutrophication progressed, phytoplankton biomass increased sharply, and the lake water became turbid due to the predominance of cyanobacteria, leading to the disappearance of submerged aquatic plants and the dominance of plankton-eating fishes. In this way, there are generally two stable states in lake ecosystems: "transparent" and "turbid" (Scheffer et al. 2001; Scheffer and Jeppesen 2007; Schallenberg and Sorrel 2009). However, in a turbid lake, a "transparent state" was partially observed in some areas where aquatic plants were growing well (Scheffer et al. 1994).

As a mechanism of the antagonistic relationship between aquatic plants and phytoplankton, allelopathy by aquatic plants has been proposed previously (Hogetsu et al. 1960; Nakai et al. 2000). However, as mentioned above, aquatic plants harbor enormous densities of cyanobactericidal and growth-inhibiting bacteria (Table 7). A significant negative correlation was observed between the distribution densities of *M. aeruginosa*, and cyanobactericidal bacteria and growth-inhibiting bacteria in the lakes of Onuma Quasi-National Park, Hokkaido (Miyashita et al. 2019). From

Table 7 Summary of published studies on algicidal or growth-inhibiting bacteria targeting nuisance bloom species in freshwater systems associated with aquatic plants

Sampling site	Year	Source	Target HAB species	Maximum density of AB and GIB	Remark	Ref.
Lake Biwa	2007	Water	*Microcystis aeruginosa*	2.0×10^4 CFU/mL	Reed belt	Imai (2010a)
		Phragmites australis	*M. aeruginosa*	9.8×10^6 CFU/g	Emerging plant	
Onuma Quasi-National Park, Hokkaido	2013	Water	*M. aeruginosa*	2.4×10^3 CFU/mL	Water plant zone	Kojima et al. (2016)
		Phragmites australis	*M. aeruginosa*	4.8×10^6 CFU/g	Emerging plant	
Goryokaku Park Moat, Hakodate	2015	Water	*M. aeruginosa*		Water plant zone	Daido et al. (2018)
		> 3 µm fraction		7.8×10^3 CFU/mL		
		< 3 µm fraction		1.3×10^4 CFU/mL		
		Trapa japonica	*M. aeruginosa*	2.7×10^7 CFU/g	Floating-leaved plant	
Onuma Quasi-National Park, Hokkaido	2012	Water	*M. aeruginosa*		Water plant zone	Miyashita et al. (2019)
		> 3 µm fraction		4.4×10^4 CFU/mL		
		< 3 µm fraction		4.5×10^3 CFU/mL		
		Trapa japonica	*M. aeruginosa*		Floating-leaved plant	
		Leaf		1.2×10^7 CFU/g		
		Water root		1.4×10^8 CFU/g		
		Myriophyllum verticillatum		1.1×10^7 CFU/g	Submerged plant	
		Utricularia vulgaris		9.2×10^6 CFU/g	Submerged plant	

Bacterial densities were determined with the method of bacterial isolation and co-culture experiment

HAB harmful algal bloom, *AB* algicidal bacteria, *GIB* growth-inhibiting bacteria, *CFU* colony forming unit

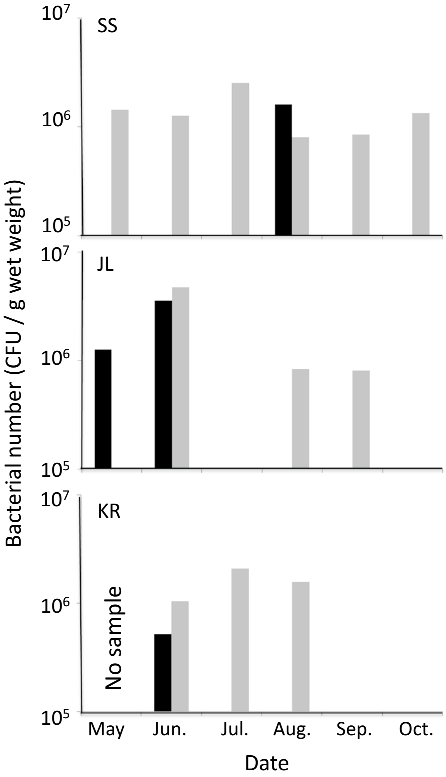

Fig. 11 Number of algicidal bacteria (black column) and growth-inhibiting bacteria (gray column) against toxic cyanobacterium *Microcystis aeruginosa* detected from biofilm of reed stem samples collected at Sansui (SS), Junsainuma Lake (JL), and Karima River (KR) in Onuma Quasi-National Park, Hokkaido. Figure from Kojima et al. (2016)

these results, the activities of abundant cyanobactericidal and growth-inhibiting bacteria inhabiting the biofilm on the surface of aquatic plants can form the basis of a newly proposed mechanism driving the antagonistic relationship between aquatic plants and phytoplankton. Taking these bacterial activities into consideration, the occurrence of cyanobacterial blooms would be suppressed by systematically creating water plant zones and appropriately managing them in lakes with frequent cyanobacterial blooms (Imai et al. 2019; Miyashita et al. 2019). It is worth accumulating further case studies on the application of water plants to examine the prevention of cyanobacterial blooms in the future.

Overview and future challenges

The Seto Inland Sea is a representative, semiclosed water area in Japan. Severe eutrophication was once persistent during an era of rapid economic growth, and the shallow coastal ecosystems, including seaweed and seagrass beds, tidal flats, and shallow sea areas, were lost on a large scale due to intensive reclamation. Considering the massive existence of effective bacteria (algicidal and growth-inhibiting bacteria) inhabiting seagrass and seaweed beds, the disappearance of these habitats means the loss of these effective bacteria on a large scale, which in turn influences the frequency and strength of HABs.

The restoration and creation of coastal seaweed and seagrass beds to prevent the occurrence of HABs should be put forward as part of the Sato-Umi Initiative (Fig. 12). The term "*Sato-Umi*" is defined as "a coastal area where bioproductivity and biodiversity have increased due to human intervention" (Yanagi 2008). In this sense, red tides can be regarded as the extreme state of biodiversity impairment, since a single phytoplankton species dominates the entire aquatic region. It is presumed that effective bacteria derived from seaweeds and seagrasses will be continuously supplied to the surrounding water, spreading to the adjacent water bodies, and preventing the occurrence of harmful algal blooms (Imai and Yamaguchi 2012; Imai 2015). This situation appears to correspond to the "clear state" of a lake system, with little phytoplankton biomass when aquatic plants are abundant. It should be emphasized that targeted planning of seawater passing through seaweed and/or seagrass beds and affecting HAB areas is the key to maximizing their effects.

Shallow coastal ecosystems such as seaweed beds, seagrass beds, and tidal flats support rich biodiversity, biomass, and are extremely important as a system for natural water purification and fostering juvenile marine life (Duffy 2006; Orth et al. 2006; Mukai 2011; Furukawa 2016; Nakaoka et al. 2017; Cullen-Unsworth and Unsworth 2018). Nutrients and organic matter loaded into the shallow waters of coastal areas are quickly taken up by various marine organisms, occupying multiple food webs, such as epiphytic microalgae (mainly pennate diatoms), bacteria, protozoa, sessile and phytal animals, etc. Furthermore, these nutrients and organic matter are retained by animals and plants with relatively long lifetimes. Therefore, it can be understood that the growth of phytoplankton is a flow of nutrients on a much shorter timescale, and prevented mainly through benthic/epiphytic diatoms in tidal flats, seaweed, and seagrass beds. From the viewpoint of material cycling, these habitats have the ability to prevent the occurrence of exceptional phytoplankton blooms (Imai et al. 2017b).

In freshwater ecosystems, many cyanobactericidal bacteria have also been found on the surfaces of reed stems, submerged and floating-leaved plants (Table 7). Although there are abundant differences between the sea and inland waters, there appears to be a shared phenomenon between seaweeds and seagrasses in the sea, and aquatic plants in lakes and ponds providing excellent habitats for effective bacteria that are expected to control phytoplankton dynamics. Therefore, the *Sato-Umi* concept for coastal waters can be adapted to freshwater systems as well (Fig. 13). Moreover, in terms of

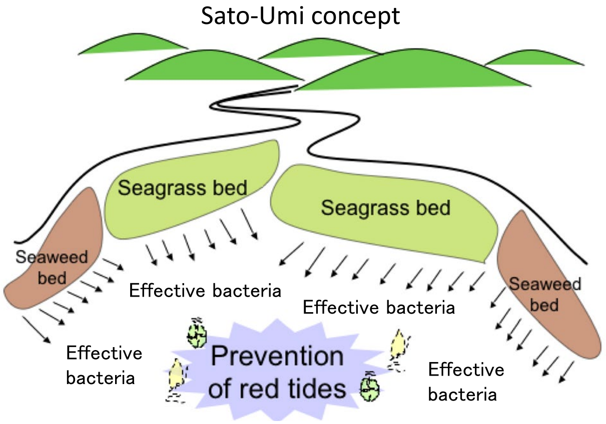

Fig. 12 Schematic representation of preventive strategies for red tide occurrence by restoration and/or development of seaweed and seagrass beds in coastal areas under the concept of "*Sato-Umi*." Effective bacteria (algicidal bacteria + growth-inhibiting bacteria) would be added to seawater, preventing red tide occurrences by suppressing phytoplankton populations to moderate levels. Figure from Imai et al. (2009)

maintaining and acquiring clean water resources, such as drinking water, the aquatic plant zone must be the focus of greater research efforts, as it is expected to mitigate the toxification and odorization of lake water. With these situations in mind, water plant management involving some budgetary measures in lake systems is thought to be reasonable. It is essential to properly interact with lakes and keep them healthy for future generations.

It has been pointed out that the occurrence of HABs is greatly affected by climate change, especially increasing global temperatures (Trainer et al. 2020; Wells et al. 2020). Water temperature is on the rise in the Seto Inland Sea, and representative summer red tides of *Chattonella*, which historically occurred in August until the mid-1990s, have been starting approximately one month earlier in July over the past ~ 25 years (Nishikawa et al. 2014). Since the germination time of cysts would accelerate due to warming, it would follow that the formation of *Chattonella* red tides would also occur earlier. In the summer of 2014, the raphidophyte *Chattonella marina,* and the dinoflagellate *M. polykrikoides* were detected for the first time along the coast of Yoichi, Hokkaido, northern Japan (Shimada et al. 2016a). In addition, red tides by the harmful dinoflagellate *K. mikimotoi* were detected, resulting in mortality of salmon and squid in Hakodate Bay, Hokkaido, for the first time in 2015 (Shimada et al. 2016b; Kakumu et al. 2018). Moreover, the bivalve-killing dinoflagellate *H. circularisquama* has expanded its red tide range northward up to Lake Kamo on Sado Island in the Sea of Japan (Kondo et al. 2012). These trends imply that other red tides that presently occur in southwest Japan will expand to the northeast on the side of the Sea of Japan. Toxifications of useful bivalve mollusks with toxic dinoflagellates have been a great threat to the coastal waters of Tohoku and Hokkaido to date, but the potential of further bivalve mortality driven by harmful red tides may be added in the near future. The problem of harmful algal blooms shows no signs of decreasing, and since the social needs for scientific research on HABs are not decreasing either, further investigations and practical applications of prospective technologies are necessary for controlling HABs.

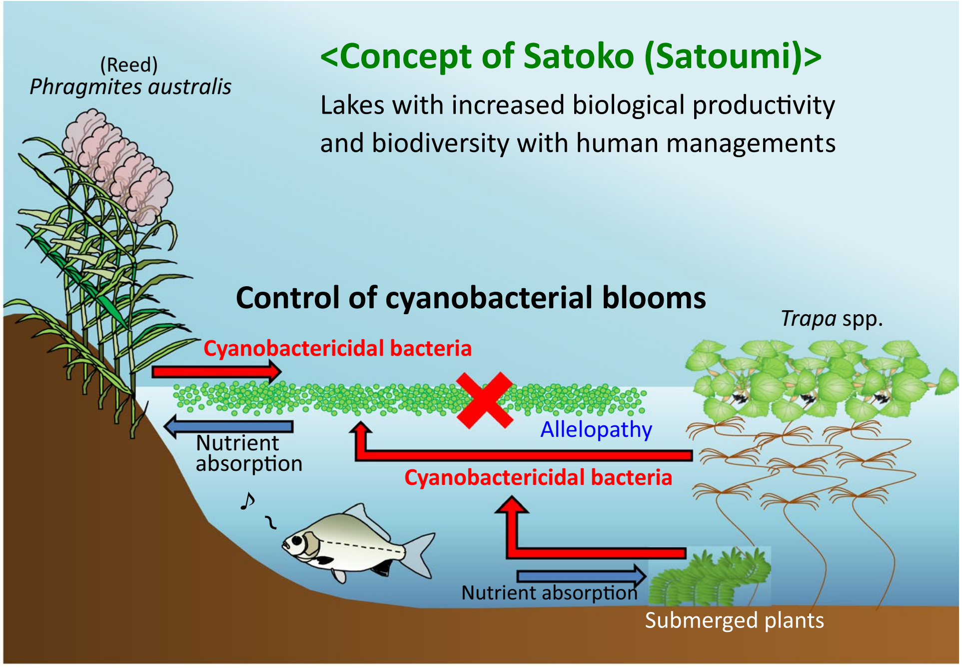

Fig. 13 The concept of "*Sato-Umi*" initiatives in lake systems, such as Lake Onuma, where the management of aquatic plants is proposed to be a key process. Figure from Imai et al. (2019)

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