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Harmful Effect of Dinoflagellate *Heterocapsa circularisquama* on Shellfish Aquaculture in Japan

Yukihiko MATSUYAMA

Harmful Algal Bloom Division, National Research Institute of Fisheries and Environment of Inland Sea (Maruishi, Ohno, Saeki, Hiroshima, 739-0452 Japan)

Abstract

The marine dinoflagellate *Heterocapsa circularisquama* Horiguchi is the causal agent of red tide on the Japanese coast. In the last decade, *H. circularisquama* red tides have destroyed the shellfish aquaculture industries around the western part of Japan because this dinoflagellate shows a detrimental effect on shellfishes particularly on bivalve molluscs. The current proliferation of *H. circularisquama* throughout western Japan is a cause for concern due to economic loss. The outbreaks of *H. circularisquama* are closely related to the environmental conditions: water exchange rate, water temperature, local and global climate changes. Administrative measures such as algal monitoring systems can be successfully utilized for the distribution and short-term prediction of red tide due to *H. circularisquama* in several locations. However, secondary damage, i.e. decline of demand due to misinformation and cost of measures to prevent the damage, adversely affects the development of shellfish aquaculture even if direct killing of the products can be avoided.

Discipline: Animal pest / Aquaculture / Fisheries
Additional key words: red tide, bivalve, toxicity, secondary damage

Introduction

Worldwide development of harmful algal blooms causes serious problems for public health and fisheries industries[1,4,5,21,23,24]. On the Japanese coast, new marine dinoflagellate *Heterocapsa circularisquama* Horiguchi[9], appeared in 1988 and then rapidly expanded over the western area. The red tide due to *H. circularisquama* has damaged shellfish aquaculture in most of the region[3,12,14,34,37]. Although *H. circularisquama* blooms mainly affect bivalve aquaculture, no harmful effects on wild and cultured fish, other marine vertebrates, and public health hazard were recorded. Therefore, this phenomenon is referred to as "novel red tide". Incidence of this species has increased recently, and the economic losses in aquaculture have been a cause for concern for the industry and society[14].

In the present paper, environmental conditions conducive to the red tide occurrence, review of damage caused to aquaculture, toxicity of the organism, and recent monitoring programs based on scientific data are outlined.

Environmental conditions causing *Heterocapsa circularisquama* bloom

1) Coastal currents and water exchange rate

Fig. 1 shows the distribution of red tide events due to *H. circularisquama* ($>10^6$ cells L^{-1}) on the Japanese coast. *H. circularisquama* is distributed over the western part of Japan, especially on the southern coast of Mie, western coast of Seto Inland Sea, and western coast of Kyushu Island. The most frequent area for red tide is Ago Bay, where *H. circularisquama* has been observed every year since 1992. The areas where *H. circularisquama* blooms were recorded are embayments affected by the warm currents: Kuroshio and Tsushima currents (Fig. 1).

The red tide caused by *H. circularisquama* is commonly observed in semi-closed bays, such as Ago Bay, Uranouchi Bay, and Hiroshima Bay. Dense assemblages of *H. circularisquama* cells have been found in the innermost part of the inlets, but not offshore and in the channels. The distribution pattern of *H. circularisquama* seems

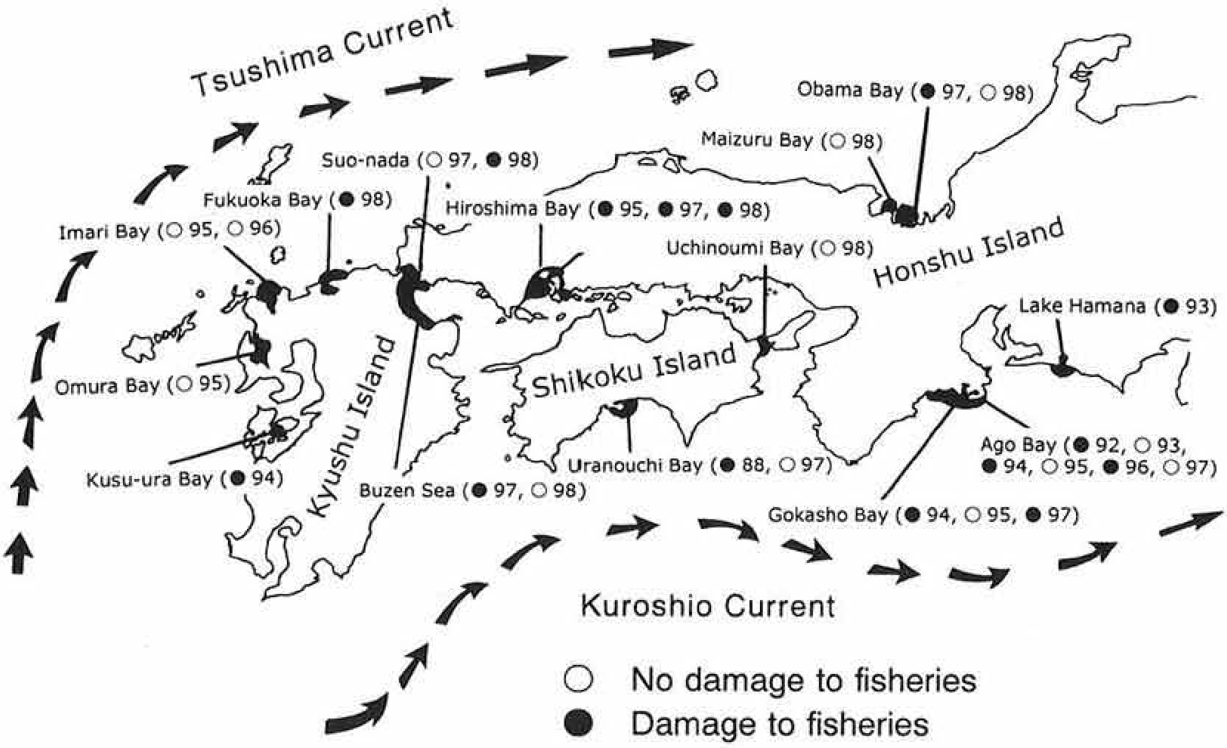

Fig. 1. Records of red tide (>10^6 cells L^{-1}) due to *Heterocapsa circularisquama* in western Japan

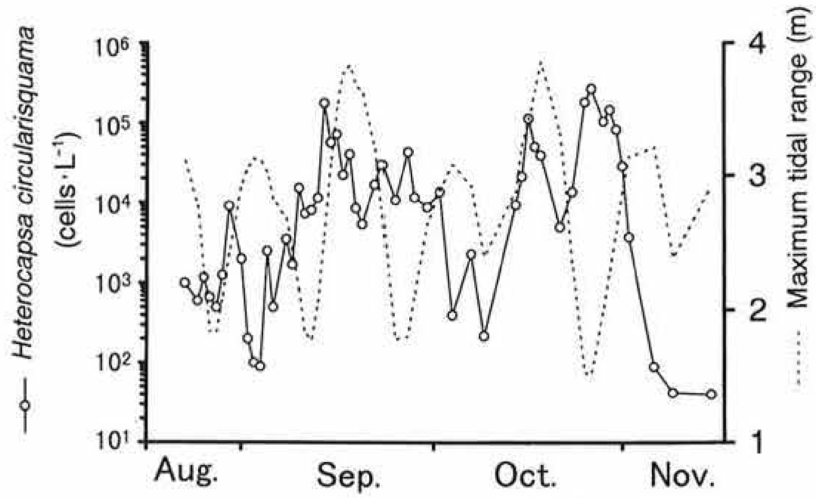

Fig. 2. Relationship between cell densities of *Heterocapsa circularisquama* and maximum tidal range in Ohno strait, Hiroshima Bay in 1997

Maximum tidal range correspond to the daily height ranges between high and low sea level. *H. circularisquama* population increases during the neap tide period and decreases during the spring tide period.

to be strongly affected by the water exchange rate. Natural populations of *H. circularisquama* cells significantly increase during the neap tide and decrease during the spring tide (Fig. 2). This observation clearly indicates that *H. circularisquama* populations are released from semi-closed bays into the offshore zone responsible for spring tidal current. Similar findings have been reported in *Alexandrium tamarense* blooms on the Maine coast[2] and *Gymnodinium mikimotoi* in Gokasyo Bay[27]. Therefore, water exchange mainly influences the horizontal distribution and the periodic changes of red tide due to *H. circularisquama* and other harmful algal species.

2) Water temperature and salinity

Red tide associated with *H. circularisquama* occurs between July and November in the embayments of western Japan. In Ago Bay, the water temperature and salinity level during the *H. circularisquama* bloom ranged from 15 to 31°C and from 24 to 34 psu, respectively[14]. Generally, *H. circularisquama* blooms appear mainly under high water temperature (>23°C) and salinity (>30 psu) conditions. The results of field surveys show that *H. circularisquama* grows well under high water and salinity conditions.

Based on laboratory culture experiments, optimal growth of *H. circularisquama* occurred in a combination of water temperature of 30°C and salinity of 30 psu. However, the growth of *H. circularisquama* decreased significantly below 15°C[31]. These growth responses to temperature and salinity obtained in laboratory culture correspond to those recorded in field surveys. On the other hand, the optimal growth of representative harmful algae (*Alexandrium tamarense, Chattonella antiqua, Gymnodinium mikimotoi, Heterosigma akashiwo*, etc.) which often cause red tide on the Japanese coast occurred in a combination of water temperature from 15 to 25°C and salinity ranging from 20 to 25 psu, respectively[32,33,35,36].

On the coast of western Japan, since the maximum water temperature seldom exceeds 30°C, the growth pattern of *H. circularisquama* in relation to the water temperature is different from that of other harmful algae appearing on the Japanese coast. Based on these physiological characters, *H. circularisquama* seems to be a species of tropical or subtropical origin.

3) Vertical mixing of seawater

Field surveys revealed that temporary seawater mixing and concomitant upwelling of bottom water enhanced the proliferation of *H. circularisquama* blooms. In Ago Bay, strong disturbances of water stratification by typhoons preceded the red tide outbreaks of *H. circularisquama* in summer (Fig. 3). In the 1988 red tide at Uranouchi Bay, a large-scale intrusion of oceanic water into the bay and resultant seawater mixing were observed before the occurrence of red tide due to *H. circularisquama*[18]. In the western part of Seto Inland Sea, where water columns are very stable due to stratification, *H. circularisquama* bloom hardly occurs in early to mid-summer. However, in autumn when the stratification begins to break down due to the decrease of the surface water temperature, *H. circularisquama* frequently causes red tide in embayments[15]. Temporary or sustained water mixing throughout the water column may provide nutrients and growth-promoting substances from the bottom to the euphotic layer, resulting in increased salinity. Thus, the proliferation of *H. circularisquama* in coastal areas is considered to be triggered by vertical mixing of seawater.

4) Competition with other phytoplankton species

The competition between *H. circularisquama* and other microalgae is also noteworthy. According to field observations carried out over a 3-year

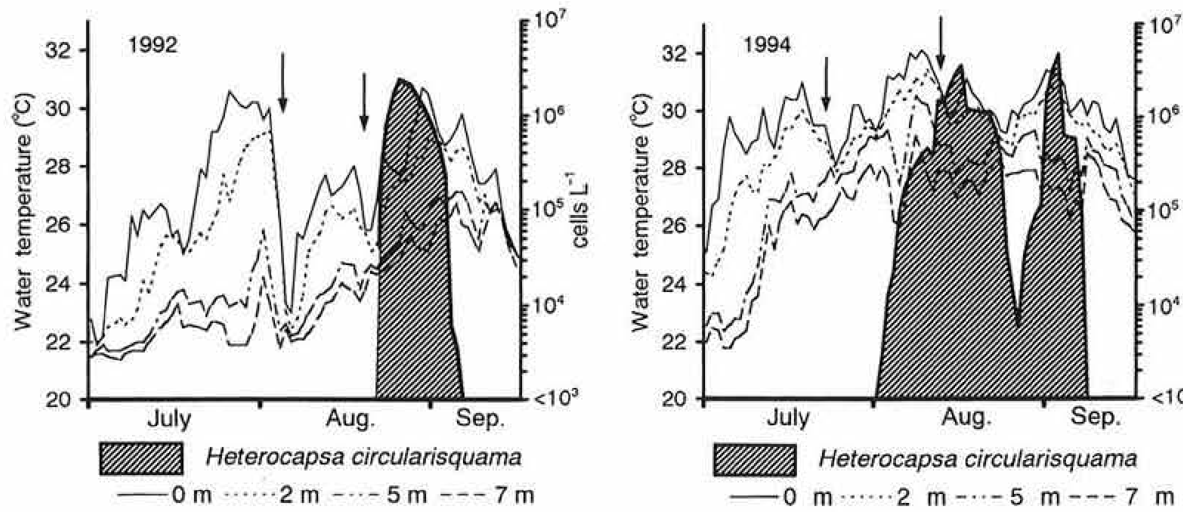

Fig. 3. Changes in water temperature at 4 different depths and mean cell density of *Heterocapsa circularisquama* in Ago Bay

Arrows denote the typhoon events (Matsuyama et al., 1996).

period in Ago Bay, the growth of *H. circularisquama* occurs when the populations of dominant diatoms *Chaetoceros* spp. begin to decrease (Fig. 4). Maximum yield and duration of *H. circularisquama* bloom seem to be strongly affected by the *Chaetoceros* spp. populations. It is considered that the decrease of the dominant diatom population is conducive to *H. circularisquama* growth. Uchida et al.[29] reported that the growth of *H. cicularisquama* was suppressed under bialgal cultures with diatom species including *Chaetoceros didymum, Stephanopyxis palmeriana* and *Licmophore* sp. Under the effect of diatoms, the cells of *H. circularisquama* became round to elliptical and were considered to be temporary cysts. It is assumed that diatom populations regulate the development and decline of red tide due to *H. circularisquama*.

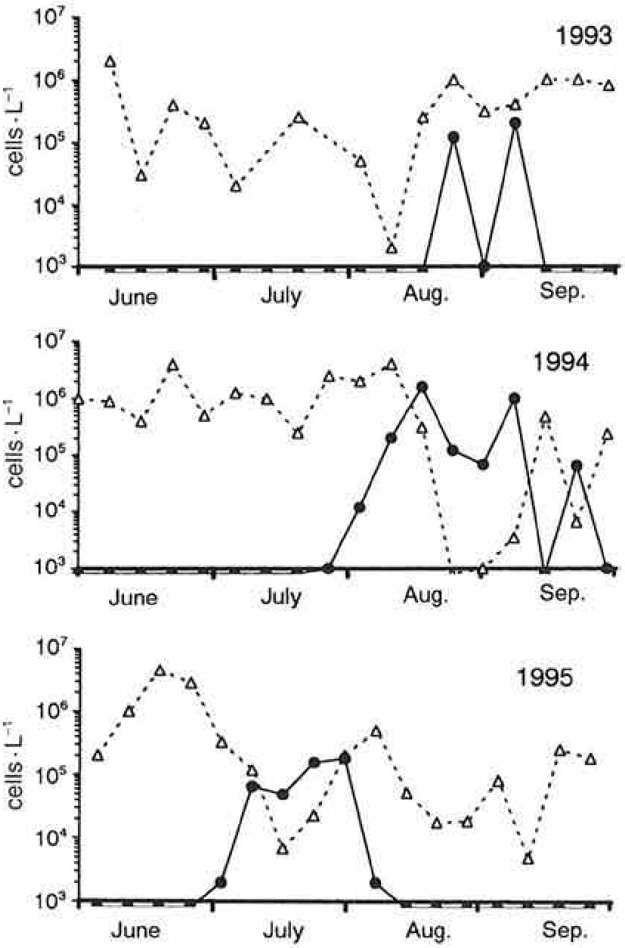

Fig. 4. Changes in cell densities of *Heterocapsa circularisquama* (P) and predominant diatom *Chaetoceros* spp. (g) in Tategami Inlet, Ago Bay (1993–1995)
H. circularisquama frequently appears when the population of *Chaetoceros* spp. is low (niche) which is probably due to the high water temperature and strong stratification. Massive bloom ($>10^6$ cells L^{-1}) and concomitant death of pearl oyster were observed during the 1994 bloom period. The data sets were provided in part by T. Kobayashi, Mie Prefectural Fisheries Technical Center.

Furthermore, *H. circularisquama* was found to kill a mixotrophic dinoflagellate *Gyrodinium instriatum* and tintinnid ciliate *Favella taraikaensis*[10,28]. The results show that *H. circularisquama* is toxic to active predators and competitors. From the ecological point of view, this characteristic might be advantageous for bloom formation in natural environments[10,16].

5) *Long-term trend of* Heterocapsa circularisquama *blooms*

The records of red tide due to *H. circularisquama* are shown in Fig. 5. The red tide incidence associated with *H. circularisquama* has rapidly increased since the early 1990s. Why can *H. circularisquama* appear and colonize the Japanese coast? Laboratory experiments reveal that *H. circularisquama* can not grow at 10°C or less[31], and does not form typical resting cysts that can survive below 10°C (Uchida & Matsuyama, unpub. data). Hence, the overwintering vegetative cells are the likely seed population for bloom initiation of this species. This growth strategy is considered to be disadvantageous for the occurrence of this species in temperate and cold seas.

On the Japanese coast, however, the water temperature in winter has significantly increased since the late 1980s[11], probably due to global climate change (green house effect and El Nĩno phenomenon). Recently, the tropical and subtropical dinoflagellate P*rorocentrum sigmoides* Böhm has frequently appeared in western Japan[30]. In the Seto Inland Sea, the water temperature in winter considerably increased in the last decade, except for the period 1995–1996 (Fig. 5). Accordingly, tropical marine animals, e.g. green shell mussel *Perna viridis*, have frequently appeared in the Seto Inland Sea since the early 1990s. This hydrographic change may be conducive to the overwintering of *H. circularisquama* on the Japanese coast. The relationship between the water temperature in winter and initial occurrence of red tide due to the dinoflagellate *G. mikimotoi* was also observed in the previous study[7]. Hydrographic change in terms of water temperature is likely to bring about changes of the phytoplankton communities in the Japanese coastal waters.

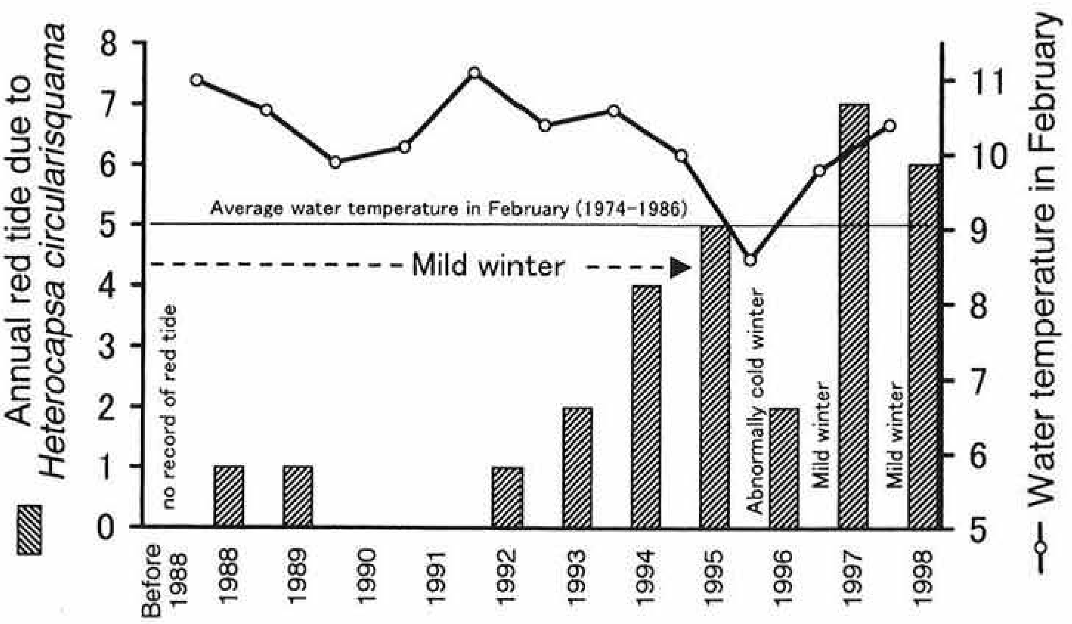

Fig. 5. Long-term trend of red tide events due to *Heterocapsa circularisquama* in Japan and winter water temperature (February) in eastern Seto Inland Sea (Harima-nada)
The data sets of water temperature were provided by Y. Hori, Hyogo Prefectural Fisheries Experimental Station.

6) Possible origin

There have been no records of *H. circularisquama* red tide and related shellfish mortality in Japan before 1988. It remains to be determined whether *H. circularisquama* is a native species of Japan. Considering the growth response to water temperature, it is possible that *H. circularisquama* originates from tropical or subtropical regions, and has recently invaded Japanese coastal areas by warm current and/or artificial transportation. Recently, simulated experiments have revealed that *H. circularisquama* could easily migrate to distant areas in association with shellfish transportation[8]. During the last 2 decades, large shellfish spats, especially pearl oyster and short-necked clam, have been imported to Japan from Southeast Asia for aquaculture. It is therefore possible that *H. circularisquama* invaded Japan from tropical or subtropical seas (T. Honjo, pers. commun.). However, further studies should be carried out to analyze the artificial dispersal of *H. circularisquama*.

Damage to fisheries and toxicity

1) Shellfish damage to aquaculture industries

In September 1988, extensive red tide due to *H. circularisquama* and subsequent death of short-necked clams *Ruditapes philippinarum* occurred in Uranouchi Bay, Kochi Prefecture (Table 1). Red tide due to *H. circularisquama* occurred at Fukuoka Bay in 1989, and at Ago Bay in 1992, resulting in high mortality of shellfish[13,34].

Until 1998, 26 cases of *H. circularisquama* red tide (including 15 incidences leading to fisheries damage) had been recorded in 14 locations of western Japan (Fig. 1). The red tide due to *H. circularisquama* was associated with massive killing of commercially important bivalve species: short-necked clam *R. philippinarum*, pacific oyster *Crassostrea gigas*, pearl oyster *Pinctada fucata*, blue mussel *Mytilus galloprovincialis*, etc.[13,14,34,37]. The current proliferation of *H. circularisquama* throughout western Japan destroyed the local shellfish mariculture. Economic losses of shellfish aquaculture by direct killing of marketable products were estimated to amount to about at least 10 billion-yen in the last decade.

On the other hand, there are no records of death of finfish and crustacean species or public health hazard due to the consumption of shellfish and other seafood products in association with the red tide of *H. circularisquama*[16]. This type of bio-hazard in marine animals is markedly different from previous damage caused by harmful algae responsible for paralytic shellfish poisoning (PSP),

Table 1. Records of damage to shellfish species due to red tide associated with *Heterocapsa circularisquama* in western Japan

Date	Shellfish species affected	Notes	Location	Reference
1988	*Ruditapes philippinarum*	1,560 t losses	Uranouchi Bay	
1989	*Crassostrea gigas* *Mactra chinensis* *Mytilus galloprovincialis* *Ruditapes philippinarum* *Solen strictus*	mass mortality	Fukuoka Bay	34
1992	*Pinctada fucata*	30–90% mortality loss of >18 million individuals	Ago Bay	13
	Crassostrea gigas *Mytilus galloprovincialis* *Chlamys nobilis*	mass mortality		
1993	*Ruditapes philippinarum* *Crassostrea gigas*	50–90% decrease of harvest mass mortality	Lake Hamana	
1994	*Pinctada fucata*	40–90% mortality in areas with extensive assemblages	Ago Bay	14
1994	*Pinctada fucata*	mean 65.4% mortality in 2 years old individuals	Kusu-ura Bay	37
	Ruditapes philippinarum *Crassostrea gigas* *Solen strictus* *Mactra veneriformis* *Musculista senhousia* *Anomalocardia aquamosus* *Dosinorbis japonica* *Glossaulax didyma*	mean 69.5% mortality mass mortality		
1995	*Pinctada fucata*	5–36% mortality	Ago Bay	
	Crassostrea gigas *Ruditapes philippinarum* *Mytilus galloprovincialis*	36–68% mortality, 610 t losses >70% mortality, 210 t losses 10–55% mortality	Hiroshima Bay	15
1996	*Pinctada fucata*	mass mortality losses of 1.5 milion individuals	Ago Bay	
1997	*Pinctada fucata* *Crassostrea gigas* *Mytilus galloprovincialis*	mass mortality	Obama Bay	
	Crassostrea gigas *Mytilus galloprovincialis* *Sulculus diversicolors*	mass mortality in spats and adults 75% mortality in assemblage areas mortality in natural population	Hiroshima Bay	
	Ruditapes philippinarum	210 t losses	Buzen Sea	3
	Ruditapes philippinarum *Crassostrea gigas* *Mactra veneriformis*	50% decrease of spat yield considerable mortality	Suo-nada	
1998	*Crassostrea gigas*	30–98% mortality ca. 5,000 t losses	Hiroshima Bay	
	Ruditapes philippinarum	50–90% mortality		
	Atrina pectinata	considerable mortality	Suo-nada	

The data sets were obtained from Fishery Regulation Office, Fisheries Agency of Japan.

diarrheic shellfish poisoning (DSP), amnesic shellfish poisoning (ASP), neurotoxic shellfish poisoning (NSP), ciguatera poisoning, and ichthyotoxicity.

2) General characteristics of shellfish affected by red tide

The effects of *H. circularisquama* on bivalve molluscs were described in previous studies[3,14,15,19]. Matsuyama et al.[14] observed that exposure of pearl oysters to $5\text{–}10 \times 10^6$ *H. circularisquama* cells L^{-1} resulted in death within several days although the level of dissolved oxygen was not critical. The dead individuals were characterized by a marked shrinkage of the mantle, decrease of glycogen lobe attached to the mantle and gut discoloration (Fig. 6). The symptoms clearly reflected the direct cytotoxic effect of *H. circularisquama* on pearl oyster physiology. Similar harmful effects on oyster *C. gigas* and the mussel *M. galloprovincialis* were observed during the red tide which occurred in Hiroshima Bay[15]. Based on detailed field surveys, in most of the bivalve species, the filtration rate is significantly reduced at a density of $5\text{–}20 \times 10^4$ *H. circularisquama* cells L^{-1}. As a result, alterations of bivalve physiology clearly started from a cell density below 1%.

3) Exposure experiment using cultured strain

Nagai et al.[19] showed that the mortality of pearl oyster spats by *H. circularisquama* depends on the cell density of this alga. Pearl oysters exposed to *H. circularisquama* cells at a density above 10^7 cells L^{-1} showed an unusual contraction of the mantle and gills, clapping, sustained valve closure, paralysis, and heartbeat stop within 24 h. Furthermore, the mussel *M. galloprovincialis* significantly reduced its feeding activity when exposed to 10^4 cells L^{-1} of *H. circularisquama*, but not in culture with 10^6 cells L^{-1} of morphologically similar dinoflagellates *Scrippsiella trochoidea* and *Heterocapsa triquetra*[16]. Some harmful algae are known to be toxic to marine shellfish. The blooms associated with the unarmored dinoflagellate *Gyrodinium aureolum* and picoplankton *Aureococcus anophagefferens* referred to as "brown tide" lead

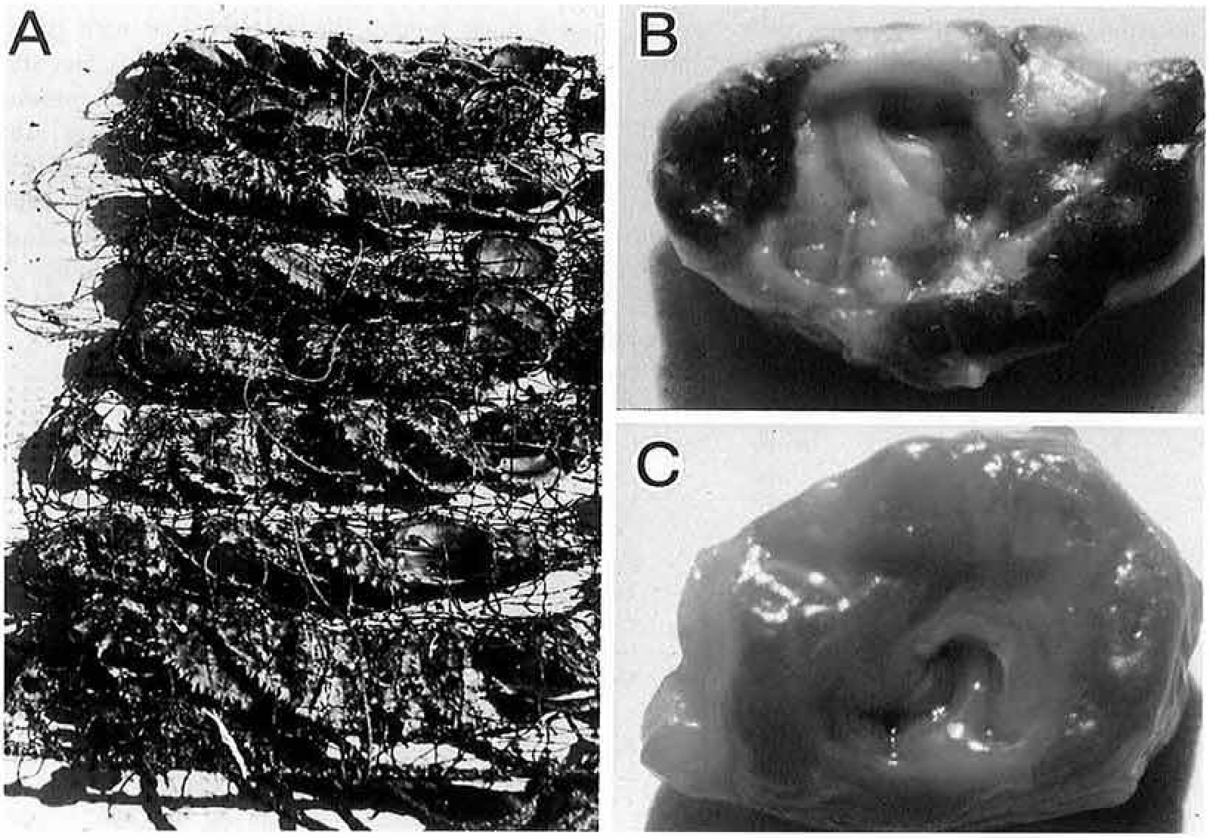

Fig. 6. Photographs of pearl oyster Pinctada fucata affected by Heterocapsa circularisquama in 1992
A: Dead pearl oysters. B: Individual cultured at site without red tide.
C: Individual cultured at site with red tide.

to considerable failure in mussel and scallop farming[23]. Laboratory-rearing experiments using these algae showed considerable detrimental effects on various bivalve species[12,20,25]. However, the effect of these harmful algae on marine animals is not species-specific. Red tide due to *G. aureolum* kills not only shellfish but also finfish and crustacean species[26]. Although *H. circularisquama* frequently kills various bivalve species within a short period of time (<24 h) as described previously[15,19], no death and adverse effects were observed in finfish and crustaceans. These facts suggested that the harmful effect of *H. circularisquama* on bivalves is specific and pronounced compared to other harmful algal species (Table 2).

4) Harmful effects of Heterocapsa circularisquama *on other animals*

Laboratory exposure experiments showed that various marine animals such as bivalves, gastropods[17], solitary acidians, and jellyfish are affected by *H. circularisquama* unlike vertebrates, crustaceans, starfish, and sea urchins (Table 2). On the other hand, although the occurrence of illness associated with the consumption of bivalves that accumulated *H. circularisquama* cells may be a cause for concern in humans, shellfish poisoning has never been observed in samples collected from red tide areas. Direct HPCL analysis failed to detect PSP toxins or DSP toxins in the cells of *H. circularisquama*[16]. No death or symptoms were observed in 5 mice to which a cultured cell pellet of *H. circularisquama* had been injected in intraperitoneally at a rate of 10^6 cells individual^{-1}.

5) Characterization of Heterocapsa circularisquma *toxicity*

Nagai et al.[19] suggested that the toxicity of *H. circularisquama* to bivalves was mediated by a chemical agent. Thereafter, it was shown that the toxic effect of *H. circularisquama* on bivalves was not due to extracellular metabolites, cell exudates, and "naked cells" prepared by sonication and centrifugation. Furthermore, trypsin and SDS (sodium dodecyl sulfate) treatments were found to decrease drastically the toxicity of *H. circularisquama* cells (Fig. 7). Therefore, labile protein-like complex localized on the cell surface pre- sumably exerts a detrimental effect on bivalves[16]. However, purification and characterization of toxic fractions have not been successful because this agent is highly labile under neutral conditions.

6) Secondary damage to fisheries industries

Secondary damage to fisheries may occur during the *H. circularisquama* red tide periods, sometimes causing serious economic losses. As mentioned above, *H. circularisquama* bloom does not cause human illness associated with the consumption of harvested products. This fact should be recognized and fishermen and consumers should be informed that "shellfish killing" during red tide due to *H. circularisquama* is different from "shellfish poisoning" due to toxic dinoflagellate blooms such as those of the genera *Alexandrium*, *Gymnodinium*, and *Dinophysis*. Mis-

Table 2. Effects of *Heterocapsa circularisquama* on various animals

Animals	cells L^{-1}	Symptoms	Reference
Bivalves	10^4–10^5	Feeding inhibition	15, 16
	$>10^6$	Death	3, 15, 19
Gastropods	10^4–10^5	Unusual locomotion	17
	$>10^6$	Death	17
Solitary acidians	$>10^6$	Feeding inhibition	
Jellyfish	$>106^6$	Tentacle shrinkage	
Protozoa[a)]	10^5–106^6	Feeding inhibition	10
	$>10^6$	Death	10
Dinoflagellates	$>10^6$	Death by cell contact	28
Mouse	$>10^9$[b)]	–	16
Finfish	$>106^6$	–	
Crab	$>10^7$	–	
Lobster, shrimp	$>10^7$	–	
Star fish	$>10^7$	–	
Copepods	$>10^7$	–	
Diatoms	$>10^7$	–	29

–: Not affected. a): Species-specific. b): Intraperitoneal injection.

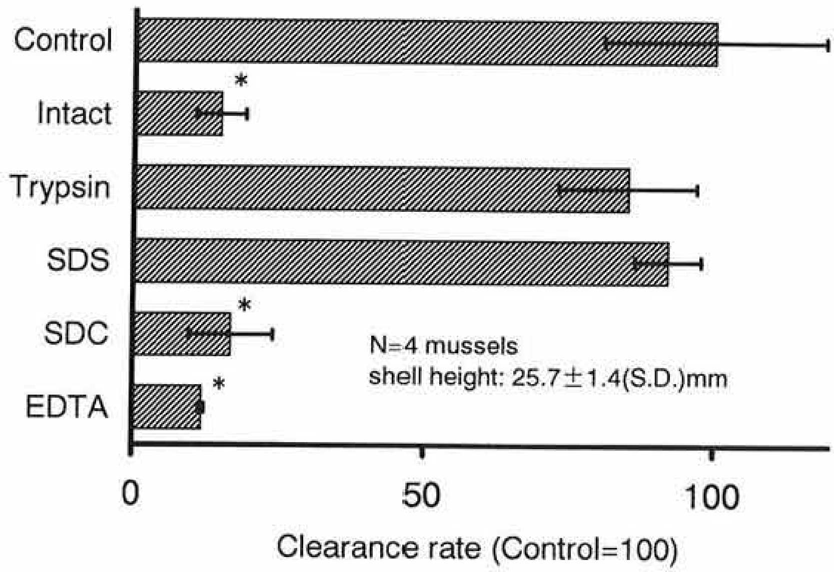

Fig. 7. Relative clearance rates of *Mytilus galloprovincialis* exposed to chemically treated *Heterocapsa circularisquama* cells (Control: *Isochrysis galbana*, 8×10^6 cells^{-1})

Initial cell density of *H. circularisquama* ranged from $2.5 - 2.8 \times 10^5$ cells L^{-1}. SDS: sodium dodecylsulfate. SDC: sodium deoxycholate. Each chemical was used at a concentration lower than that which would inhibit the swimming of *H. circularisquama*. Error bars show ±S.D. *$p<0.005$ (t-test).

information may lead to a considerable decrease in the demand for shellfish and market price[23]. Massive *H. circularisquama* bloom occurred in a restricted area of Hiroshima Bay, in 1997. Although no outbreaks of shellfish poisoning occurred, oyster demand rapidly declined when the occurrence of red tide due to *H. circularisquama* was broadcasted in several TV programs. Market price of oyster decreased by 10–30% due to the decrease of the demand compared with the previous year. In the oyster farming industry of Hiroshima Bay, approximately several hundred persons are employed as oyster shuckers with a low salary. The decrease of the market price directly affects shucker employment.

Monitoring, prediction, and methods of prevention of red tide

1) Monitoring of red tide due to H. circularisquama

In Japan, monitoring systems for harmful algal blooms have been developed by the Fisheries Agency and local government organizations (mainly Prefectural Fisheries Experimental Stations) since the early 1970s. These monitoring systems operate successfully and provide information on the incidence of red tide and shellfish poisoning as mentioned previously[21]. Since 1992, in several locations, regular monitoring systems on *H. circularisquama* blooms have been set up. The local government uses early warning systems based on the data obtained from regular oceanographic surveys. Fishermen are routinely able to obtain the information about harmful algal bloom (cell density, water temperature, and distribution of cell assemblages, etc.).

2) Prevention of fisheries damage due to H. circularisquama

To our knowledge, it is difficult to control or destroy the large natural populations of red tide organisms by applying direct prevention methods. Various prevention techniques (i.e. spraying of active clay, hydrogen peroxide, and coagulants, etc.) were developed previously[6,22]. However, widespread application of these procedures for marine environments may exert a secondary harmful effect on other valuable organisms (i.e. diatoms, zooplankton, fish, benthos, etc.). The simple and most effective method is the transfer of cultured organisms from a red tide area to a non-red tide area. In Ago Bay, pearl oyster aquaculturists began to remove the pearl oysters when the cell density of *H. circularisquama* exceeded about 10^5 cells L^{-1}. No fisheries damage has occurred in this bay recently. However, oyster and clam aquaculturists are still affected by red tide caused by *H. circularisquama* because the removal procedure is costly and labor-intensive. As described above, red tide damage caused by *H. circularisquama* leads to a loss of marketable products and secondary damage such as decrease of demand for the products and loss of competitiveness in the market due to the high cost of the products to compensate for the cost of prevention of the damage.

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