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Mixotrophic dinoflagellate red tides in Korean waters: Distribution and ecophysiology

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ABSTRACT

We investigated the outbreaks of red tides dominated by dinoflagellates in the coastal waters of Korea from 1981 to 2009. During the study period, 693 mixotrophic dinoflagellate red-tide events occurred. Of these, 36.8% were *Cochlodinium polykrikoides* red tides, with *Akashiwo sanguinea*, *Ceratium furca*, and *Prorocentrum minimum* also frequently forming red tides. Eighty-five percent of mixotrophic dinoflagellate red tides in Korean waters occurred from June to September, in the high water-temperature season. The monthly frequency of outbreaks of mixotrophic dinoflagellate red tides increased from twice in January–March to 228 times in August, but it decreased to 2–9 times in November and December. Eighty-six percent of the outbreak events were recorded in southern coastal waters, 12% in eastern coastal waters, and only 2% in western coastal waters of Korea. There were wide temperature and salinity ranges during red tides associated with *A. sanguinea*, *C. furca*, and *P. minimum*, whereas for *C. polykrikoides* and *Gonyaulax polygramma* the temperature and salinity ranges were narrow. The concentrations of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphate (DIP) in 1996–2000 were higher than the reported values for the half-saturation concentrations of uptake of nitrate and phosphate for most of the causative mixotrophic dinoflagellates. However, the concentrations of DIN and DIP have decreased gradually since 2000 and the frequency of mixotrophic dinoflagellate red tides has also decreased. Thus, DIN and DIP are likely to be the primary factors influencing the frequency of mixotrophic dinoflagellate red tides in Korean waters. Five novel dinoflagellate species have been discovered in Korean coastal waters since 2005 and their morphological and molecular characteristics have been described as new genera and species. It is thus necessary to monitor their dynamics to investigate whether they can form red tides.

1. Introduction

Red tides have occurred in the coastal waters of many countries (Hallegraeff, 1993; Anderson, 1997). Approximately 300 of the estimated 3400–4100 phytoplankton species belonging to diatoms, dinoflagellates, silicoflagellates, prymnesiophytes, euglenophytes, raphidophytes, and cryptophytes (i.e., 7–9%) have been reported to cause red tides (Sournia, 1995; Arrigo et al., 1998; Jeong et al., 2013b; Kang et al., 2013). Of these, only 60–80 species are known to be actually harmful or toxic as a result of biotoxicity, physical damage, anoxia, or irradiance reduction. Furthermore, 75% of all harmful algal bloom species are dinoflagellates (Smayda, 1997). Dinoflagellate red tides are known to have had detrimental effects on fisheries and mariculture (Shumway, 1990; Chang et al., 1995; Burkholder, 1998; Matsuyama, 1999), and they have also had negative impacts on public health and the coastal environment (Shumway, 1990; Van Dolah, 2000).

In the last two decades, many phototrophic dinoflagellates, which were previously thought to have been exclusively autotrophic dinoflagellates, have been shown to be mixotrophic dinoflagellates (i.e., capable of both photosynthesis and ingesting prey) (Bockstahler and Coats, 1993a; Jacobson and Anderson, 1996; Stoecker, 1999; Seong et al., 2006; Burkholder et al., 2008; Glibert et al., 2009; Jeong et al., 2010a,b, 2012; Hansen, 2011). Thus, prey availability can be a critical factor affecting the dynamics of these mixotrophic dinoflagellates.

In Korean waters, there have been many red tides dominated by mixotrophic dinoflagellates (National Fisheries Research and Development Institute, 2012). Most causative species of red tides in Korean waters before 1980 were diatoms, but this subsequently changed to dinoflagellates (Lee et al., 2013). In particular, the mixotrophic dinoflagellate *Cochlodinium polykrikoides* has been the major red-tide species in the coastal waters of Korea since 1995. This

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dinoflagellate has caused massive mortalities of caged fish (Kim, 1998). In addition, the mixotrophic dinoflagellates *Akashiwo sanguinea*, *Ceratium furca*, and *Prorocentrum minimum* have frequently formed red tides in Korean waters (Cho, 1979; Lee and Lee, 1999; Jeong et al., 2013a). Furthermore, toxic dinoflagellates such as *Alexandrium tamarense*, *Gymnodinium catenatum*, and *Karenia mikimotoi* have also caused red tides in Korean waters. Koreans enjoy eating raw fish, resulting in the rapid expansion of the aquaculture industry (Kim et al., 2005). However, red tides dominated by dinoflagellates have caused great losses in the aquaculture industry (Cho, 1979, 1991; Kim, 1997; Park et al., 2013). Therefore, the outbreaks of dinoflagellate red tides are of critical concern to scientists, government officials, and the aquaculture industry. To better understand dinoflagellate red tides in Korean waters, it is worth analyzing the pattern of outbreaks of red tides.

We have reviewed the causative species of mixotrophic dinoflagellate red tides, the frequency, magnitude, and distribution of those red tides, and environmental factors affecting the population dynamics of the mixotrophic dinoflagellate species in Korean waters from 1980 to 2009. In this review paper, we have used data on red-tide events and their causative species obtained from the annual reports of the National Fisheries Research and Development Institute (NFRDI) and its website (www.nfrdi.re.kr), and data on environmental factors such as water temperature, salinity, inorganic nutrients, and chlorophyll-a obtained from the annual monitoring reports of the Korean Marine Environment (KOEM, 2012) and its website (www.meis.go.kr).

2. Frequency and distribution of dinoflagellate red tides in Korean waters

We defined red tide as the appearance of red, yellow, green, or brown water patch on the sea surface. In Korea, red-tide monitoring started in 1972 and nationwide red-tide monitoring network was established in 1995 when massive *C. polykrikoides* blooms occurred in Korean waters.

2.1. Frequency of mixotrophic dinoflagellate red tides

From 1981 to 2009, 898 events (67.5%) of all red tides in Korean waters were caused by dinoflagellates. Among these, 693 red-tide events were predominantly caused by mixotrophic dinoflagellates, 101 events by heterotrophic dinoflagellates, and 104 events by a mixture of mixotrophic dinoflagellates, diatoms, and raphidophytes.

When we measured the frequency of the outbreaks of mixotrophic dinoflagellate red tides in 5-year intervals, the frequency increased from 41 times in 1981–1985 to 238 times in 1996–2000, but it decreased to 93 times in 2006–2009 (Fig. 1).

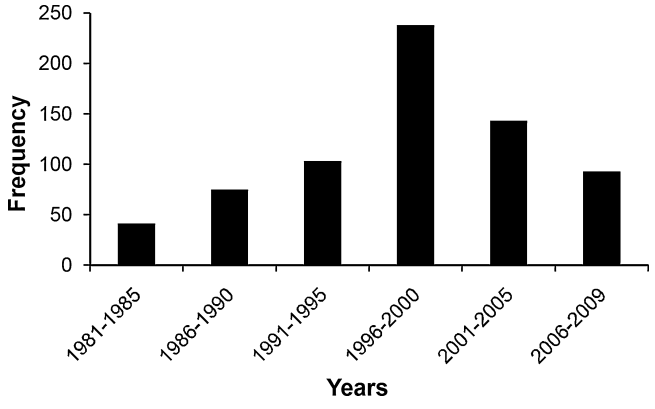

Fig. 1. Frequency of annual mixotrophic dinoflagellate red-tide events occurring in the coastal waters of Korea from 1981 to 2009 in 5-year intervals.

Table 1
Frequency of red-tides outbreaks listed by the dominant mixotrophic dinoflagellate in the coastal waters of Korea from 1981 to 2009, as well as the maximum abundance (MA) and water temperature range during the associated red tides. All data were obtained from the National Fisheries Research and Development Institute (2012).

Mixotrophic dinoflagellate	Frequency	MA (cells ml^{-1})	Temperature (°C)
Akashiwo sanguinea	77	3000	12.0–28.5
Alexandrium affine	1	3000	
Alexandrium fraterculus	2	20,000	24.1
Alexandrium sp.	10	8000	16.0–26.0
Alexandrium tamarense	4	1800	14.8–23.0
Ceratium furca	56	33,000	17.8–29.5
Ceratium fusus	6	6600	18.9–20.2
Ceratium sp.	12	5500	21.3–26.5
Cochlodinium polykrikoides	255	30,000	17.3–31.0
Cochlodinium sp.	2	5140	
Gonyaulax polygramma	18	14,000	21.1–27.4
Gonyaulax sp.	9	10,000	23.9–27.5
Gymnodinium sp.	21	17,550	18.8–27.5
Heterocapsa sp.	2	7700	10.7–11.0
Heterocapsa triquetra	5	56,000	10.2
Karenia mikimotoi	17	62,500	26.0–27.1
Pheopolykrikos hartmannii	2	3500	
Prorocentrum donghaiense	25	45,000	17.7–28.1
Prorocentrum micans	29	45,000	18.9–28.0
Prorocentrum minimum	43	85,000	17.0–26.5
Prorocentrum sp.	74	77,000	15.0–30.5
Prorocentrum triestinum	19	48,400	16.2–28.1
Scrippsiella trochoidea	4	15,000	21.1–26.7

The NFRDI reported 11 genera and 23 species of mixotrophic dinoflagellates that caused red tides in Korean waters between 1981 and 2009 (Table 1). *C. polykrikoides* red tides accounted for 37% of the total mixotrophic dinoflagellate red tides from 1981 to 2009 (Fig. 2), and *Prorocentrum* spp. for 27% including unidentified *Prorocentrum* species. Furthermore, *A. sanguinea*, *C. furca*, and *P. minimum* also formed red tides frequently (11%, 8%, and 6%, respectively) (Fig. 2). However, the predominant red-tide species in the 5-year intervals changed during the study period. For example, *K. mikimotoi* red tides accounted for 27% of all dinoflagellate red tides in 1981–1985, *A. sanguinea* and *C. polykrikoides* red tides for 20% each in 1986–1990, *C. polykrikoides* red tides for 46% in 1991–1995, and *C. polykrikoides* red tides for 30% in 1996–2000 (Fig. 2). In addition, *C. polykrikoides* red tides accounted for 43% of all dinoflagellate red tides in 2001–2005 and 61% in 2006–2009 (Fig. 2).

K. mikimotoi red tides occurred 11 times in 1981–1985, only 1–3 times in 1986–2000, and then, they did not occur after 2001 (Fig. 3A). *Prorocentrum micans* red tides occurred 5–7 times in all intervals except 2006–2009, when there were no occurrences (Fig. 3B). Furthermore, the frequency of red tides dominated by *A. sanguinea* and *P. minimum* increased until 1996–2000, but decreased thereafter (Fig. 3C and D). Furthermore, *C. furca* red tides did not occur before 1991–1995. However, their frequency rapidly increased to 39 times in 1996–2000, but then decreased dramatically to 1–3 times in 2001–2009 (Fig. 3E). In addition, *Prorocentrum triestinum* red tides did not occur or only rarely occurred between 1981 and 1995, but increased to 9 and 6 times in 1996–2000 and 2001–2005, respectively (Fig. 3F). The frequency of *Prorocentrum donghaiense* (previously *P. dentatum*) red tides was 1–2 times in 1981–1995, but this rapidly increased to 14 times in 2001–2005 (Fig. 3G). However, its red tides did not occur in 2006–2009. In addition, *C. polykrikoides* red tides occurred only 3 times in 1981–1985, but the frequency of its red tides rapidly increased to 72 times in 1996–2000, before slightly decreasing to 57 times in 2006–2009 (Fig. 3H). Furthermore, *Gonyaulax polygramma* red tides occurred only twice in 1986–1990 and were not observed in 1991–2000 (Fig. 3I). However, the frequency rapidly increased to