

## A hierarchy of conceptual models of red-tide generation: Nutrition, behavior, and biological interactions

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### ABSTRACT

Red tides – discolorations of the sea surface due to dense plankton blooms – occur regularly in coastal and offshore waters along much of the world's coastline. Red tides often cause large-scale mortalities of fish and shellfish and significant losses to the aquaculture and tourist industries of many countries. Therefore, understanding and predicting the mechanisms controlling the outbreak, persistence, spread, and decline of red tides are important concerns to scientists, officials, industry, and the public. With increasing knowledge of red-tide species and red-tide events, new mechanisms have been discovered. Based on the nutrition and behaviors of red-tide organisms and biological interactions among them, red-tide outbreaks can be categorized into a hierarchy of four generation mechanisms (GM1–GM4). In the simplest, GM1, all phototrophic red-tide species were treated as exclusively autotrophic organisms without the ability to swim. However, this GM cannot explain red-tide outbreaks in oligotrophic surface waters offshore. Vertical migration (considered in GM2) and mixotrophy (GM3) enable red-tide flagellates to acquire growth factors from nutrient-rich deep waters or co-occurring prey, respectively. In natural environments, all red tides occur by those species outgrowing co-occurring organisms; red-tide species dominate communities by eliminating other species or reducing their abundances. Thus, GM4 contains the direct biological interactions (i.e., inhibition by physical contact or chemical effects) and indirect biological interactions (i.e., acquiring resources faster than others) that can affect the dominance of red-tide species under given conditions. Correctly choosing one of these four GMs for red tides dominated by one causative species is important because the accuracy of predictions may be outweighed by the costs and time required to acquire the relevant information. In this study, mechanisms describing the outbreak, persistence, and decline of red tides were reviewed, the advantages and limitations of each mechanism were evaluated, and insights about the evolution of the mechanisms were developed.

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### 1. Introduction

Red tides – discolorations of the sea surface due to dense plankton blooms – occur along much of the world's coastline and in offshore waters (Holmes et al., 1967; Eppley and Harrison, 1975; ECOHAB, 1995; Jeong, 1995; Horner et al., 1997; Imai et al., 2001;

Sordo et al., 2001; Anderson et al., 2002; Jeong et al., 2003, 2008, 2013b; Alonso-Rodriguez and Ochoa, 2004; Seong et al., 2006; Johnson et al., 2013; Kang et al., 2013; Lee et al., 2013c; Park et al., 2013a). Red tides frequently cause large-scale mortalities of fish and shellfish and significant losses to the aquaculture and tourist industries of many countries (Shumway, 1990; Smayda, 1990; Shumway and Cembella, 1993; Glibert et al., 2005; Anderson et al., 2012; Fu et al., 2012; Park et al., 2013d). Minimizing the economic losses caused by red tides requires some predictive ability, which must be based on an understanding of the processes associated with their formation, persistence, and decline. Funding from governments and private industries of many countries has improved our understanding of red-tide organisms, the dynamics

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of red-tide events, and the prediction, monitoring, and control of red tides, including such fundamental processes as the kinetics of nutrient uptake, vertical migration, and mixotrophy of red-tide organisms (e.g., Margalef et al., 1979; Hallegraeff, 1993; Smayda, 1997; Turner and Tester, 1997; Anderson et al., 2008; Burkholder et al., 2008; Heisler et al., 2008; Jeong et al., 2010c; Menden-Deuer and Fredrickson, 2010; Lewitus et al., 2012; Jeong and Kang, 2013).

All red-tide organisms are either cyanobacteria or protists and thus increase their populations by binary division (e.g., Jeong et al., 2013a,b; Yih et al., 2013). To form a red tide, a species must increase its population density more rapidly than co-occurring species by growing faster, dying slower, and/or aggregating through behavior. These advantages are often obtained through biological interactions with other species, including direct biological interactions such as predator–prey relationships and inhibition by physical contact or chemical effects, and indirect biological interactions, such as acquiring limiting nutrients faster than other species.

Many studies have been conducted on red-tide outbreaks, providing a diverse array of conceptual and mathematical models (e.g., Franks, 1997a; Smayda and Reynold, 2001; Smayda, 2002a). Here we categorize red-tide outbreak dynamics into four generation mechanisms (GMs), based on the red-tide species nutrient-acquisition strategy (i.e., inorganic nutrient uptake, mixotrophy), behavior (e.g., vertical migration), and biological interactions with their communities. For the purposes of this study we will ignore the physical dynamics such as internal waves, turbulence, fronts, upwellings and downwellings, and wind-driven flows that can aggregate or disperse cells and thus accelerate or prevent the formation of red tides (e.g., Franks, 1997b; Smayda, 1997, 2010; Lim et al., 2015). Rather, we review and synthesize the mechanisms governing the outbreak, persistence, and decline of red tides; four GMs are put forward, the strengths and limitations of each mechanism evaluated, and insights drawn concerning the evolution of each of the mechanisms.

## 2. Overall equation of the population dynamics of a red-tide species

Ignoring spatial dependence and physical effects, an overall equation for the change in cell density of a red-tide species  $C$  can be written as:

$$\frac{dC}{dt} = C(k_i - m_c)$$

where  $k_i$  is the specific growth rate of  $C$  for model  $i$ , and  $m_c$  the specific mortality of  $C$ . For each GM we explore the dependence of  $k_i$  and  $m_c$  on the red-tide organism's environment, physiology, behavior, and community interactions. In the final GM models, we add interactions with a second variable that can affect the red-tide organism's population growth.

## 3. GM1 – nutrients and light

Since the 1960s, coastal eutrophication due to heavy nutrient loads in freshwater inputs has led to a simultaneous increase in the number of red-tide events (Harding and Perry, 1997; Cloern, 2001). To understand the outbreak, persistence, and decline of red tides in eutrophic waters, we formulate GM1 under the assumption that all phototrophic red-tide organisms are phytoplankton with no ability to migrate vertically (Table 1; Fig. 1). In this case, nutrient concentrations  $N$  and light intensity  $I$  for photosynthesis are the most important factors affecting the growth rate of the red-tide organism  $C$  (Eppley and Coatsworth, 1968; Eppley et al., 1969; Eppley and Renger, 1974; Carpenter and Guillard, 1971; Harrison, 1976; MacIsaac et al., 1979; Tomas, 1979; Nakamura, 1985a,b; Cloern, 1999, 2001):

$$\frac{dC}{dt} = C[k_1(N, I) - m_c]$$

The specific growth rate for the red-tide organism in GM1,  $k_1$ , is a (potentially unknown) function of nutrient concentration  $N$  and irradiance intensity,  $I$ .

Several studies have directly measured growth rates of red-tide organisms as a function of nutrient concentration or light intensity (Tables 2 and 3). However, the difficulties in making such measurements typically force researchers to measure the uptake rates of nutrients by red-tide species; growth rates are subsequently estimated from uptake rates using relevant conversions (Eppley et al., 1969; Lipschultz, 1995; Zhang et al., 2006; Baek et al., 2008a).

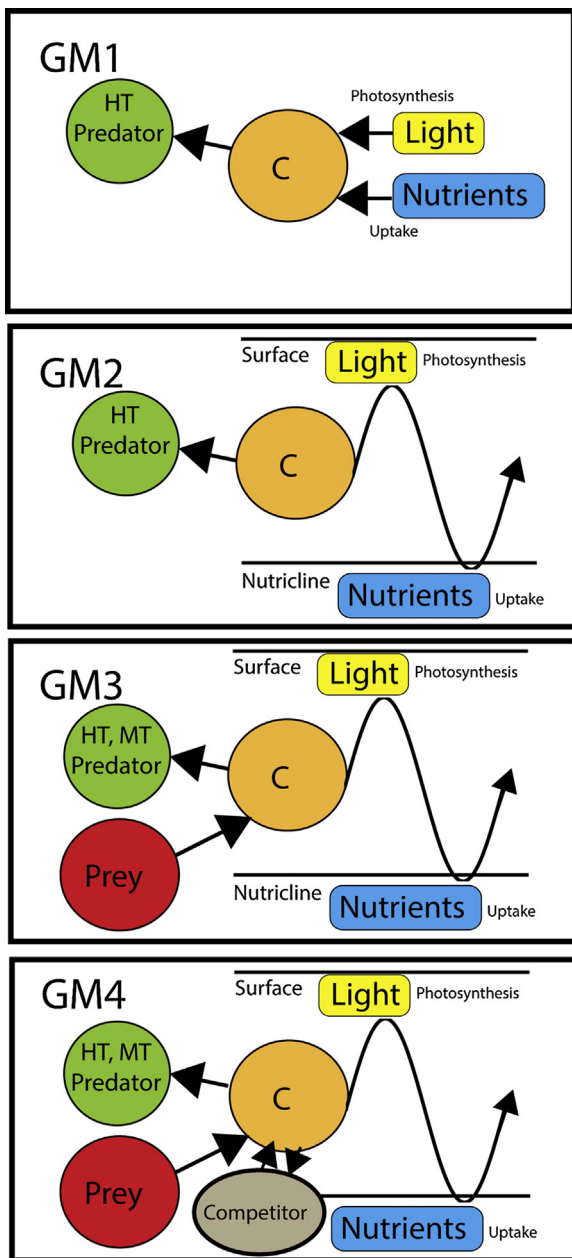
In general, the uptake rate  $U$  of a nutrient by a given red-tide species increases rapidly with increasing nutrient concentration until a threshold concentration is reached; uptake then increases only marginally, or becomes saturated at higher nutrient concentrations (e.g., Eppley and Thomas, 1969). These uptake data are generally fit to a Michaelis-Menten equation:

$$U = \frac{U_{\max}N}{K_u + N}$$

**Table 1**  
The four generation mechanisms (GM1–GM4) of red-tide outbreaks based on the nutrition and behaviors of phototrophic red-tide organisms (PRTO) and their biological interactions. PD: Predator type. HT: Heterotrophic. MT: Mixotrophic. VM: Vertical migration. MA: Mixotrophic ability. BI: Biological inhibition.

GM	Mainly appeared	PRTO	PD	VM	MA	BI <sup>a</sup>	Can explain	Can't fully explain
1	1960s	All	HT	No	No	No	Red tides in eutrophic surface waters nearshore	Red tides in oligotrophic surface waters offshore
2	1970s	Diatoms Flagellates	HT	No Yes	No No	No	Red tides in oligotrophic surface waters offshore	Red tides in oceanic waters, red tides in coastal waters at times when nutrients are depleted
3	1990s	Diatoms Flagellates	HT, MT	No Yes	No Yes	No	Red tides in oceanic waters, red tides in coastal waters at times when nutrients are depleted, rapid succession of dominant species in serial red tides (absolute growth)	Red tides by a few species under conditions favorable for most phototrophs
4	2000s	Diatoms Flagellates	HT, MT	No Yes	No Yes	Yes Yes	Red tides by a few species under conditions favorable for most phototrophs (relative growth)	Need to explore later

<sup>a</sup> Biological inhibition: Direct BI – allelopathy. Indirect BI – outgrow and occupy space under different nutrient levels, thermocline depths, etc.



**Fig. 1.** Diagram showing the evolution of mechanisms of red-tide outbreaks categorized by nutrition, behaviors, and biological interactions of red-tide organisms and their community. GM1: nutrient uptake and photosynthesis. GM2: includes vertical migration. GM3: includes mixotrophy. GM4: includes biological inhibition of and by competitors. Mortality due to predation by heterotrophic predators is in GM1 and GM2, while mortality due to predation by both heterotrophic (HT) and mixotrophic (MT) predators is in GM3 and GM4.

where  $U_{max}$  is the maximum specific uptake rate ( $d^{-1}$ ) and  $K_u$  the nutrient concentration at which  $U = \frac{1}{2}U_{max}$ . When the ambient nutrient concentration  $N < K_u$ , the organisms will be nutrient limited; organisms with lower  $K_u$  will take up nutrients more efficiently at low concentrations than organisms with higher  $K_u$ .

Previously, half saturation constants of nutrient uptake ( $K_u$ ) of red-tide diatoms were thought to be lower than those of red-tide flagellates (Smayda, 1997), though this is apparently not generally true. The range of  $K_u$  for nitrate or phosphate uptake by red-tide dinoflagellates (0.3–43.6  $\mu M$  and 0.01–3.6  $\mu M$  for nitrate and phosphate, respectively) is wider than that for diatoms

(0.1–5.1  $\mu M$  and 0.1–1.7  $\mu M$ ) or raphidophytes (0.3–9.0  $\mu M$  and 0.1–2.0  $\mu M$ ) (Table 2). This wider range of  $K_u$  for nitrate and phosphate uptake for dinoflagellates may enable them to form red tides under diverse nutrient conditions. Unfortunately, however, we still have no data on the nutrient uptake rates or growth rates of many major red-tide organisms, including species such as *Prorocentrum micans*, *Scrippsiella trochoidea*, and *Gymnodinium aureolum*.

Similarly to nutrients, the growth rate of a given red-tide organism increases rapidly with increasing irradiance, until it saturates at higher light intensities. Red-tide dinoflagellates tend to grow at lower light intensities than those favoring red-tide diatoms or raphidophytes (Table 3). This ability of red-tide dinoflagellates may facilitate their ability to vertically migrate to deep, dark waters (see GM2, below).

The  $m_c$  in the equation of GM 1 includes the specific mortality of a red-tide organism due to heterotrophic predators (Table 1). Heterotrophs which are known to kill red-tide organisms are heterotrophic protists, metazoans, parasites, and heterotrophic bacteria (Jeong, 1999; Turner, 2006; Jeong et al., 2007, 2014; Park et al., 2013c; Seong and Jeong, 2011, 2013; Yoo et al., 2013c). There is a considerable amount of data on mortality rates of red-tide organisms due to predation by heterotrophic protists or heterotrophic bacteria are rare. In Korean coastal waters, the estimated maximum mortality rates of red-tide organisms due to predation by some large naked ciliates or heterotrophic dinoflagellates are greater than the maximum specific growth rate of most red-tide organisms and thus these heterotrophic protistan predators may sometimes control populations of the red-tide organisms (Table 4). The maximum specific mortality rates of red-tide organisms due to predation by polychaeta larvae and the copepods *Acartia* spp. are usually lower than the maximum specific growth rates of most red-tide organisms, but these metazoan predators may have a considerable grazing impact on populations of some red tide species if the mortality rates by these two metazooplankton predators are combined (Table 4).

GM1 may be useful for understanding the dynamics of red tides dominated by fast-growing organisms (e.g., diatoms) in some eutrophic waters, such as the Kattegat, Scandanavia, and Chesapeake Bay, USA (Harding, 1994; Richardson and Heilmann, 1995; Cloern, 1999, 2001). However, GM1 cannot explain the occurrence of red tides in oligotrophic surface waters where nutrients are always limiting (Table 1). One additional dynamic that may enhance our explanatory power is the inclusion of vertical migration (GM2).

#### 4. GM2 – including swimming

Red tides often occur in oligotrophic offshore waters where surface nutrient concentrations are low, but deep-water concentrations may be high enough to exceed the  $K_u$  for nitrate or phosphate uptake by red-tide organisms (Pearl, 1988; McAndrew et al., 2007). GM1, with  $dC/dt = C[k_1(N,I) - m_c]$ , cannot explain these red tides:  $k_1$  would be too low in surface waters due to the low nutrient concentrations caused by the more-competitive (i.e., lower  $K_u$ ) ambient phytoplankton community. However, some red-tide flagellates show a diel vertical migration, which may give them a competitive advantage. This advantage could be realized through two mechanisms: (1) enhanced ability to take up nutrients from deeper waters, and (2) avoiding predation by predators that migrate out of phase with them.

Hasle (1950) reported phototactic vertical migration of red-tide dinoflagellates in Oslo fjord, and Eppley et al. (1968) reported vertical migration of red-tide dinoflagellates in Californian waters.

**Table 2**  
Maximum growth rate (MG, d<sup>-1</sup>) of red-tide species and half saturation concentration (Ku, μM) for uptake of nitrate (NO<sub>3</sub>) and phosphate (PO<sub>4</sub>).

Species	ESD (μm)	NO <sub>3</sub>		PO <sub>4</sub>		Reference
		Ku	MG	Ku	MG	
<b>Dinoflagellate</b>						
<i>Amphidinium carterae</i>	9.7	2		0.01		Hersey and Swift (1976), Deane and O'Brien (1981)
<i>Prorocentrum minimum</i>	12.7	1.4–7.1		2.0		Cembella et al. (1984), Lomas and Glibert (2000), Fan et al. (2003)
<i>Heterocapsa triquetra</i>	15.0			3.1		Doremus (1982)
<i>Alexandrium minutum</i>	18.1	0.3–1.2	0.2	0.1–3.6	0.3	Frangópulos et al. (2004), Ignatiades et al. (2007), Maguer et al. (2007), Lim et al. (2010)
<i>Karenia mikimotoi</i>	21.3	43.6				Li et al. (2010)
<i>Karenia brevis</i> (= <i>Gymnodinium breve</i> )	23.0	0.1–0.3		0.2		Vargo and Howard-Shamblott (1990), Bronk et al. (2004)
<i>Cochlodinium polykrikoides</i>	25.9	2.1–2.2	0.3	0.6–1.4		Gobler et al. (2012), Kim et al. (2001)
<i>Gyrodinium instriatum</i>	31.2	14.2	0.4	1.8	0.45	Nagasoe et al. (2010)
<i>Alexandrium catenella</i>	30.0	0.6–28.1		0.6–1.3		Collos et al. (2004), Ou et al. (2008), Seeyave et al. (2009), Jauzein et al. (2010)
<i>Akashiwo sanguinea</i>	30.8	1.0–6.6	0.8			Eppley et al. (1969), Thomas and Dodson (1974), Kudela et al. (2008)
<i>Dinophysis acuminata</i>	32.4	0.8				Seeyave et al. (2009)
<i>Alexandrium tamarense</i>	32.6	1.5–2.8	0.3	0.4–2.6	0.3	MacIsaac et al. (1979), Cembella et al. (1984), Yamamoto and Tarutani (1996, 1999), Frangópulos et al. (2004), Leong and Taguchi (2004)
<i>Gymnodinium catenatum</i>	34.1	7.6				Yamamoto et al. (2004)
<i>Lingulodinium polyedrum</i> (= <i>Gonyaulax polyedra</i> )	38.2	0.5–10.3				Eppley et al. (1969), Harrison (1976), Kudela and Cochlan (2000)
<i>Ceratium furca</i>	45.1	0.4–0.5	1.3	0.05–0.2	1.0	Qasim et al. (1973), Baek et al. (2008a)
<i>Ceratium fusus</i>	50.0	0.3		0.03		Baek et al. (2008a)
<b>Diatoms</b>						
<i>Flagellaria pinnate</i>	3.6	0.6–1.7				Carpenter and Guillard (1971)
<i>Thalassiosira pseudonana</i>	4.0	0.3–1.9		0.6–0.7		Eppley et al. (1969), Carpenter and Guillard (1971), Fuhs et al. (1972), Perry (1976)
<i>Chaetoceros gracilis</i>	5.0	0.1–0.3		0.12		Eppley et al. (1969), Thomas and Dodson (1974)
<i>Skeletonema costatum</i>	5.9	0.4–2.1				Eppley et al. (1969), Romeo and Fisher (1982), Tarutani and Yamamoto (1994), Lomas and Glibert (2000)
<i>Thalassiosira oceanica</i>	6.0	0.3–1.0		0.6–0.7		Eppley et al. (1969), Eppley and Renger (1974), Perry (1976)
<i>Pseudo-nitzschia</i> spp.	7.0	1.2				Seeyave et al. (2009)
<i>Thalassiosira weissflogii</i>	14.0	2.8	2.5	1.72		Fuhs et al. (1972), Lomas and Glibert (2000)
<i>Leptocylindrus danicus</i>	17.0	1.2–1.3				Eppley et al. (1969)
<i>Rhizosolenia stolterfothii</i>	20.0	1.7				Eppley et al. (1969)
<i>Asterionellopsis glacialis</i>	20.0	0.7–1.3				Eppley et al. (1969), Romeo and Fisher (1982)
<i>Coscinodiscus lineatus</i>	50.0	2.4–2.8				Eppley et al. (1969)
<i>Ditylum brightwellii</i>	85.0	0.6–2.0				Eppley and Coatsworth (1968), Eppley et al. (1969)
<i>Coscinodiscus wailesii</i>	300.0	2.1–5.1				Eppley et al. (1969)
<i>Chaetoceros</i> sp.		3.1				Lomas and Glibert (2000)
<b>Raphidophyte</b>						
<i>Heterosigma akashiwo</i>	11.5	0.3–2.5	0.5	0.2–2.0	0.5	Tomas (1979), Zhang et al. (2006)
<i>Chattonella antiqua</i>	35.3	0.7–3.0	0.4–0.5	0.1–2.0	0.4–0.6	Nakamura and Watanabe (1983), Nakamura (1985a, b), Nakamura et al. (1988)
<i>Chattonella subsalsa</i>	35.3	9	0.4	0.84	0.4	Zhang et al. (2006)

Such behavior has subsequently been reported by many studies from around the world (Blasco, 1978; Passow, 1991; Koizumi et al., 1996; Park et al., 2001; Baek et al., 2009). Our second GM (GM2) improves on GM1 by adding the ability of flagellates to vertically migrate (Table 1; Fig. 1).

In GM2, we still assume that all phototrophic red-tide species can grow through only photosynthesis (i.e., cannot feed on prey), but now migratory red-tide flagellates can photosynthesize in oligotrophic surface waters during the daytime and take up nutrients from eutrophic deep waters at night. In regions where the nutrient concentration is very low at the surface but increases markedly in deeper waters, migrating between these two layers could increase  $k$  relative to non-migrating

species. In GM2, the rate of change of cell density of a red-tide species  $C$  is

$$dC/dt = C[k_2(N, I, w_s) - m_C(w_s)],$$

where  $k_2$  is the specific growth of a vertically migrating autotrophic red-tide organism. Note that like  $k_1$ ,  $k_2$  depends on nutrients and light. As in GM 1,  $m_C$  in GM 2 includes the specific mortality of a red tide species due to heterotrophic predators (Tables 1 and 4). In GM2, however, both  $k_2$  and  $m_C$  depend on the red-tide organism's swimming speed and behavior given by  $w_s$ . Metabolic losses due to swimming are included implicitly in  $k_2$ .

**Table 3**Maximum growth rate (MG) of red-tide species, threshold light intensity ( $I_0$ ,  $\mu\text{E m}^{-2} \text{s}^{-1}$ ), and half saturation light intensity ( $K_I$ ,  $\mu\text{E m}^{-2} \text{s}^{-1}$ ).

Species	Region	ESD ( $\mu\text{m}$ )	MG	$I_0$	$K_I$	Reference
<b>Dinoflagellate</b>						
<i>Prorocentrum donghaiense</i>	East China Sea	13.3	0.67	0	3	Xu et al. (2010)
<i>Karenia mikimotoi</i>	Hiroshima Bay, Japan	21.3	0.82	1	54	Yamaguchi and Honjo (1989)
<i>Alexandrium fundyense</i>	Monhegan Island	23.0	0.68	15		Etheridge and Roesler (2005)
<i>Cochlodinium polykrikoides</i>	Inokushi Bay, Japan	25.9	0.34	10	32	Oh et al. (2006)
<i>Cochlodinium polykrikoides</i>	Furure Bay, Japan	25.9	0.35	10	45	Kim et al. (2004)
<i>Cochlodinium polykrikoides</i>	Usaka Bay, Japan	25.9	0.54	5	29	Yamatogi et al. (2005)
<i>Alexandrium catenella</i>	Thau, Mediterranean	30.0	0.5	8	23	Laabir et al. (2011)
<i>Akashiwo sanguinea</i>	Hakata Bay, Japan	30.8	0.82	14	92	Matsubara et al. (2007)
<i>Gymnodinium instriatum</i>	Hakata Bay, Japan	31.2	0.44	11	47	Nagasoe et al. (2006a)
<i>Alexandrium tamarensis</i>	Jinhae Bay, Korea	31.2	0.31	21	45	Kwon et al. (2013)
<i>Alexandrium tamarensis</i>	Mikawa Bay, Japan	32.6	0.16	45	62	Yamamoto et al. (1995)
<i>Gymnodinium catenatum</i>	Yeosu, Korea	34.1	0.16	10	43	Oh and Yoon (2004)
<i>Gymnodinium catenatum</i>	Hiroshima Bay, Japan	34.1	0.13	10	17	Yamamoto et al. (2002)
<i>Ceratium furca</i>	Sagami Bay, Japan	45.1	0.52		72 <sup>a</sup>	Baek et al. (2008b)
<i>Ceratium fusus</i>	Sagami Bay, Japan	50.0	0.44		89 <sup>a</sup>	Baek et al. (2008b)
<b>Raphidophyte</b>						
<i>Heterosigma akashiwo</i>	Delaware Inland Bays, USA	11.5	0.99		56	Zhang et al. (2006)
<i>Heterosigma akashiwo</i>	Hakata Bay, Japan	11.5	1.33	34	153	Shikata et al. (2008)
<i>Chattonella antiqua</i>	Osaka Bay	35.3	0.93	10	42	Yamaguchi et al. (1991)
<i>Chattonella marina</i>	Osaka Bay	35.3	0.96	11	63	Yamaguchi et al. (1991)
<i>Chattonella ovata</i> (CO2)	Hiroshima Bay, Japan	35.3	1.45	20	178	Yamaguchi et al. (2010)
<i>Chattonella ovata</i> (CO8)	Hiroshima Bay, Japan	35.3	1.03	16	88	Yamaguchi et al. (2010)
<i>Chattonella subsalsa</i>	Delaware Inland Bays, USA	35.3	0.87		69	Zhang et al. (2006)
<b>Diatom</b>						
<i>Skeletonema costatum</i>	Jinhae Bay, Korea	5.9	1.17	5	92	Oh et al. (2008)
<i>Skeletonema costatum</i>	Hakata Bay, Japan	5.9	1.9	9	139	Shikata et al. (2008)
<i>Eucampia zodiacus</i>	Harima-Nada, Japan	30	3.08	8	63	Nishikawa (2002)

<sup>a</sup> Saturation light intensity.

#### 4.1. Effects of swimming on growth rate

The maximum  $k_2$  will depend on the nutrient concentrations at the depth to which the red-tide species can descend at night, and the light intensity of the depth to which the species can ascend in daytime. The energy gain from nutrient uptake at depth must exceed the energy loss due to vertical migration to allow the flagellates to grow. This metabolic loss due to swimming is difficult to quantify, though some studies have suggested that it may be low (Raven and Richardson, 1984); further study is needed.

The swimming speeds of red-tide flagellates vary a great deal (Table 5). The harmful dinoflagellate *Cochlodinium polykrikoides*, whose maximum swimming speed is  $\sim 1450 \mu\text{m s}^{-1}$ , is the fastest phototrophic dinoflagellate (Jeong et al., 1999a), whereas the dinoflagellate *Ceratium fusus*, whose maximum swimming speed is  $\sim 100 \mu\text{m s}^{-1}$ , is the slowest phototrophic dinoflagellates reported thus far (Baek et al., 2009). The maximum swimming speeds of the cryptophyte *Teleaulax* sp. and *Rhodomonas salina*,  $\sim 20\text{--}60 \mu\text{m s}^{-1}$ , are much lower than those of phototrophic dinoflagellates, whereas those of the raphidophytes *Heterosigma akashiwo* ( $361 \mu\text{m s}^{-1}$ ) and *Chattonella antiqua* ( $222 \mu\text{m s}^{-1}$ ) and the euglenophyte *Eutreptiella gymnastica* ( $275 \mu\text{m s}^{-1}$ ) are comparable to those of dinoflagellates of similar size (Table 5).

The maximum swimming speeds of phototrophic flagellates are not significantly correlated with their size (Fig. 2), and other factors (e.g., shape, flagellate force) presumably determine their maximum swimming speeds. Chains of cells swim faster than solitary cells, for example, and swimming speed increases with the number of cells in the chain (e.g., Fraga et al., 1989).

To gain an advantage in nutrient uptake, red-tide organisms must be able to migrate down to the deeper, colder, nutrient-rich waters near the base of the euphotic zone. Assuming the organism makes this transit twice a day (down at night, up during the day), and assuming that the transit takes only a fraction of a day, we can

calculate the depths to which a given organism might reasonably migrate from the surface. Organisms swimming between 24 and  $1450 \mu\text{m s}^{-1}$  would travel 0.09–5.2 m in an hour. With a migration duration of 10 h, for example, the displacement would be between 0.9–52 m (Table 5). We would thus expect swimming to only be advantageous to nutrient uptake if the nutricline (the region of strong nutrient gradient separating the surface nutrient-poor region from the deeper nutrient-rich region) were closer than this distance, or if the migration took place over a longer time than a few hours (Fig. 3).

Based on the swimming speeds in Table 5, any dinoflagellate or raphidophyte species is likely to outgrow a cryptophyte when the nutricline is  $>2$  m away. Given that the nutricline deepens with distance offshore, we theoretically expect to find a sequence of red-tide-forming species with diatoms closest to shore, and cryptophytes, raphidophytes, slow-swimming dinoflagellates, and fast-swimming dinoflagellates with increasing distance offshore. It is worthwhile to explore this pattern in natural environments.

#### 4.2. Effects of swimming on mortality

The rate of change of a population,  $dC/dt$ , depends not only on its intrinsic growth rate  $k$ , but on its mortality rate  $m_C$ . Indeed, it is the balance of these two dynamics that determines whether a population will experience net growth or net loss. A red-tide organism could form a red tide by increasing its growth rate (as discussed above), or by decreasing its mortality rate  $m_C$ , leading to an increased net population growth rate  $dC/dt$ .

Copepods and other important predators on protists in the ocean often undertake a diel vertical migration (DVM) in which they ascend toward the surface waters at night to feed, and descend to darker waters during the day to avoid visual predators (Holliland et al., 2012; Brierley, 2014). One of the earliest

**Table 4**  
Heterotrophic protistan and metazoan predators on red-tide species, their abundances (AB, cells ml<sup>-1</sup> for prey, HTD, and CL or ind. l<sup>-1</sup> for MZ), and grazing impact (g) by the predator on prey populations in the waters of Masan (MA), Shihwa (SH), Kwangyang (KW), Saemankeum (SAE), Tongyoung (TO), Yeosu (YE), Kohung (KO), and Busan (BU), Korea. MTD: Mixotrophic dinoflagellate. HTD: Heterotrophic dinoflagellate. CL: Ciliate. MZ: Metazoa.

Prey		Predator			g		Location	Reference
Species	AB	Type	Species	AB	(d <sup>-1</sup> )	(h <sup>-1</sup> )		
<b>MTD</b>								
<i>Alexandrium</i> spp.	1–503	HTD	<i>Gyrodinium</i> spp.	1–477		1.18–5.04	SAE, TO, MA	Yoo et al. (2013b)
<i>Amphidinium</i> spp.	6–21	HTD	<i>Gyrodiniellum shihwaense</i>	1–38		0.08–2.6	SH	Jeong et al. (2011b)
	1–16,000	HTD	<i>Pfiesteria piscicida</i>	4–2560		0.01–1.07	MA, KW, YE	Jeong et al. (2006)
<i>Azadinium</i> cf. <i>poporum</i>	0.2–3	CL	<i>Strobilidium</i> sp.	0.1–10		0.052–0.446	SH	Potvin et al. (2013)
<i>Ceratium furca</i>	0.3–53	HTD	<i>Polykrikos kofoidii</i>	1–6		0.01–0.05	MA	Yoo et al. (2013a)
<i>Cochlodinium polykrikoides</i>	6–210	HTD	<i>Polykrikos kofoidii</i>	1–6		0.003–0.11	MA	Yoo et al. (2013a)
	2–207	MZ	<i>Acartia</i> spp.	0.004–0.2		0.00003–0.002	MA	Kim et al. (2013)
<i>Gymnodinium aureolum</i>	13–4033	HTD	<i>Gyrodinium</i> spp. (25–35 μm)	2–78		0.002–0.40	SAE	Yoo et al. (2010a)
	10–4425	CL	<i>Strombidium</i> spp. (>70 μm)	0.1–4		0.007–0.25	SAE	Yoo et al. (2010a)
<i>Heterocapsa triquetra</i>	1–10,243	HTD	<i>Gyrodinium dominans</i> / <i>G. moestrupii</i>	1–748		0.001–0.76	MA	Yoo et al. (2013a)
	2–556	HTD	<i>Gyrodinium spirale</i>	0.2–25		0.001–0.02	MA	Yoo et al. (2013a)
	1–5845	CL	<i>Tiarina fusus</i>	1–22		0.00001–0.001	MS	Yoo et al. (2013a)
	1–10,243	MZ	<i>Acartia</i> spp.	0.001–45.7		0.000003–0.034	MS	Kim et al. (2013)
<i>Prorocentrum minimum</i>	1–16,068	HTD	<i>Gyrodinium dominans</i> / <i>G. moestrupii</i>	1–748		0.00001–1.43	MS	Yoo et al. (2013a)
	60–10,600	HTD	<i>Gyrodinium dominans</i>	0–80		0–0.07	MA, KW	Kim and Jeong (2004)
	8–3993	HTD	<i>Gyrodinium dominans</i> / <i>G. moestrupii</i>	128–2256		0.05–0.66	SH	Kang et al. (2013)
	2–16,070	HTD	<i>Gyrodinium spirale</i>	0.8–25		0.0002–0.13	MS	Yoo et al. (2013a)
	9–10,600	HTD	<i>Gyrodinium spirale</i>	0–60		0–0.231	MA, KW	Kim and Jeong (2004)
	1–27,157	CL	Naked ciliates (>50 μm)	1–57		0.002–6.77	MS	Yoo et al. (2013a)
	294	CL	<i>Strombidinopsis</i> sp.	1		0.21	SH	Kang et al. (2013)
	9–10,600	MZ	<i>Acartia</i> spp.	0.0054–0.4013		0–0.02	MA, KW	Kim and Jeong (2004)
	1–27,157	MZ	<i>Acartia</i> spp.	0.001–45.7		0.00001–0.083	MA	Kim et al. (2013)
	1–16,068	MZ	<i>Polydora</i> sp. (polychaeta larva)	0.001–3.4		0.000002–0.212	MA	Kim et al. (2013)
<i>Scrippsiella trochoidea</i>	1.3–110	HTD	<i>Polykrikos kofoidii</i>	1–6		0.0002–0.003	MA	Yoo et al. (2013a)
	1–50	CL	<i>Tiarina fusus</i>	1–14		0.0001–0.001	MA	Yoo et al. (2013a)
	1–243	MZ	<i>Acartia</i> spp.	0.003–18.1		0.00004–0.030	MA	Kim et al. (2013)
<b>Raphidophyte</b>								
<i>Heterosigma akashiwo</i>	20–87,680	HTD	<i>Pfiesteria piscicida</i>	40–10,200		0.01–0.45	MA	Jeong et al. (2006)
	1–87,677	HTD	<i>Pfiesteria piscicida</i>	2–10,200		0.00002–0.45	MA	Yoo et al. (2013a)
	17–99,200	HTD	<i>Stoeckeria algicida</i>	69–17,400		0.006–8.5	MA	Jeong et al. (2005d)
	1–87,677	HTD	<i>Stoeckeria algicida</i>	2–10,200		0.00003–2.45	MA	Yoo et al. (2013a)
	1–749	CL	<i>Tiarina fusus</i>	1–14		0.0001–0.002	MA	Yoo et al. (2013a)
	1–90,000	MZ	<i>Acartia</i> spp.	0.002–12		0.000002–0.033	MA	Kim et al. (2013)
	1–90,000	MZ	<i>Polydora</i> sp.	0.001–3.6		0.000001–0.011	MA	Kim et al. (2013)

Table 4 (Continued)

Prey		Predator			g		Location	Reference
Species	AB	Type	Species	AB	(d <sup>-1</sup> )	(h <sup>-1</sup> )		
<b>Diatom</b>								
<i>Skeletonema costatum</i>	417–9290	HTD	<i>Protoperidinium bipes</i>	21–137		0.001–0.03	KW	Jeong et al. (2004a)
	4–59,143	HTD	<i>Protoperidinium bipes</i>	1–1018		0.0001–0.52	MA	Yoo et al. (2013a)
	64–1756	HTD	<i>Protoperidinium bipes</i>	7–188		0.00–0.14	SH	Kang et al. (2013)
	417–9290	MZ	<i>Acartia</i> spp.	0.0002–2.01		0–0.0021	KW	Jeong et al. (2004a)
	4–59,143	MZ	<i>Acartia</i> spp.	0.001–28.1		0.00001–0.042	MS	Kim et al. (2013)
<b>Euglenophyte</b>								
<i>Eutreptiella gymnastica</i>	1–17,029	HTD	<i>Gyrodinium dominans</i> /G. <i>moestrupii</i>	0.7–748		0.0001–0.48	MS	Yoo et al. (2013a)
	8–1171	HTD	<i>Gyrodinium dominans</i> /G. <i>moestrupii</i>	7–150		0.01–0.51	SH	Kang et al. (2013)
	21–7575	HTD	<i>Gyrodinium</i> spp. (25–35 μm)	1–50		0.001–0.61	MS	Jeong et al. (2011a)
	1–840	HTD	<i>Polykrikos kofoidii</i>	1–332		0.00003–0.004	MS	Yoo et al. (2013a)
		HTD	<i>Polykrikos kofoidii</i>			0.00–0.07	MS	Jeong et al. (2011a)
	1–11,714	HTD	<i>Protoperidinium bipes</i>	1–1018		0.0001–1.1	MS	Yoo et al. (2013a)
	8–1171	HTD	<i>Protoperidinium bipes</i>	11–233		0.04–0.54	SH	Kang et al. (2013)
		HTD	<i>Protoperidinium bipes</i>			0.001–0.6	MS	Jeong et al. (2011a)
	1–17,029	CL	naked ciliates (≤50 μm)	1–1113		0.00002–0.28	MS	Yoo et al. (2013a)
	1–7857	CL	naked ciliates (>50 μm)	1–57		0.0001–0.06	MS	Yoo et al. (2013a)
	50–1171	CL	naked ciliates (≤50 μm)	1–87		0.000–0.003	SH	Kang et al. (2013)
		CL	naked ciliates (≤50 μm)			0.000–0.22	MS	Jeong et al. (2011a)
		CL	naked ciliates (>50 μm)			0.00–0.13	MS	Jeong et al. (2011a)
<b>Cryptophytes</b>								
Cryptophytes	129–2500	HTD	<i>Gyrodiniellum shiwhaense</i>	0.3–2929		0.00–0.74	SH	Kang et al. (2013)
	13–1600	HTD	<i>Gyrodiniellum shiwhaense</i>	1–157		0.01–1.87	SH	Jeong et al. (2011b)
	40–392,440	HTD	<i>Pfiesteria piscicida</i>	10–10,200		0.00–0.22	MS, KW, YE, BU	Jeong et al. (2006)
	213–2463	HTD	<i>Pfiesteria piscicida</i>	0.2–488		0.00–0.77	SH	Kang et al. (2013)
	300–26,674	CL	<i>Mesodinium rubrum</i>	14–421		0.00–0.01	SH	Kang et al. (2013)
<b>Mixotrophic ciliates</b>								
<i>Mesodinium rubrum</i>	1–1014	HTD	<i>Gyrodinium</i> spp. (25–35 μm)	1–1356		0.236 <sup>a</sup>	MA, SH	Lee et al. (2014b)

<sup>a</sup> Highest value.

explanations for the formation of red tides was due to Wyatt and Horwood (1973), who suggested that dinoflagellates that migrate upward during the day and downward at night (the opposite phase of the copepods) would experience decreased mortality through predation. Thus vertical migration by the red-tide organisms would decrease  $m_C(w_s)$ , potentially leading to a red-tide outbreak.

A second means by which red-tide organisms could decrease their predation mortality through swimming is through the formation of thin layers of extremely high cell concentrations. Such layers often form at the surface of the ocean during red tides, and are the most visible manifestation of such outbreaks. However, thin (<1 m thick) layers of enhanced cell concentrations have also

been observed subsurface, prior to the red tide being visible at the surface (e.g., Omand et al., 2011).

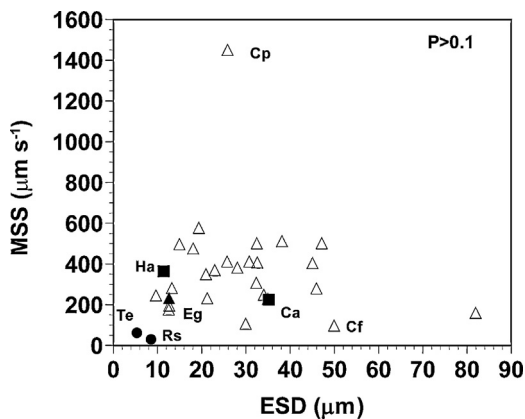
The formation of dense layers of red-tide organisms through swimming (and the interaction of swimming with the underlying physical flows, e.g., Franks, 1997b) can also decrease predation by creating a local environment saturated with chemical exudates from the organisms that may deter grazing or affect the swimming of potential predators. These chemicals could include polysaccharides that change the viscosity and chemical quality of the water, and toxins that affect the behavior of the predators (see Section 6.1).

The literature concerning daily vertical migrations of flagellates is controversial, with some studies showing a daily periodicity

**Table 5**Maximum swimming speed (MSS,  $\mu\text{m s}^{-1}$ ) of red-tide species and calculated depth which the red-tide species can reach after descending for 10 h (CD, m).

Species	ESD	MSS	CD	Reference
<b>Dinoflagellate</b>				
<i>Amphidinium carterae</i>	9.7	244	8.8	Kamykowski and McCollum (1986)
<i>Prorocentrum triestinum</i>	12.6	175	6.3	Berdalet et al. (2007)
<i>Prorocentrum minimum</i>	12.7	194	7.0	Jeong et al. (1999a)
<i>Prorocentrum donghaiense</i>	13.3	280	10.1	Our unpublished data
<i>Heterocapsa triquetra</i>	15.0	496	17.9	Jeong et al. (2002)
<i>Alexandrium minutum</i>	18.1	474	17.1	Lewis et al. (2006)
<i>Gymnodinium aureolum</i>	19.4	576	20.7	Jeong et al. (2010a)
<i>Scrippsiella trochoidea</i>	21.0	348	12.5	Jeong et al. (1999a)
<i>Karenia mikimotoi</i>	21.3	230	8.3	Thronsdon (1973), Smayda (2002b)
<i>Karenia brevis</i>	23.0	417	15.0	McKay et al. (2006)
<i>Alexandrium affine</i>	25.8	410	14.8	Fraga et al. (1989), Smayda (2010)
<i>Cochlodinium polykrikoides</i>	25.9	1449	52.2	Jeong et al. (1999a), Park et al. (2001)
<i>Prorocentrum micans</i>	28.1	380	13.7	Jeong et al. (1999a)
<i>Alexandrium catenella</i>	30.0	175	6.3	Karp-Boss et al. (2000)
<i>Dinophysis acuminata</i>	32.4	306	11.0	Smayda (2010), Lassus et al. (1990)
<i>Gonyaulax polygramma</i>	32.5	500	18.0	Levandowsky and Kaneta (1987)
<i>Alexandrium tamarense</i>	32.6	406	14.6	Lewis et al. (2006)
<i>Gymnodinium catenatum</i>	34.1	247	8.9	Fraga et al. (1989)
<i>Alexandrium ostenfeldii</i>	35.0	227	8.2	Lewis et al. (2006)
<i>Lingulodinium polyedrum</i>	38.2	510	18.4	Jeong (1994)
<i>Akashiwo sanguinea</i>	42.2	300	10.8	Cullen and Horrigan (1981)
<i>Ceratium furca</i>	45.1	403	14.5	Baek et al. (2009)
<i>Dinophysis acuta</i>	47.2	500	18.0	Levandowsky and Kaneta (1987)
<i>Ceratium fusus</i>	50.0	96	3.5	Baek et al. (2009)
<i>Ceratium tripos</i>	82.0	158	5.7	Bauerfeind et al. (1986)
<b>Raphidophyte</b>				
<i>Heterosigma akashiwo</i>	11.5	361	13.0	Yamochi and Abe (1984)
<i>Chattonella antiqua</i>	35.3	222	8.0	Watanabe et al. (1995)
<b>Euglenophyte</b>				
<i>Eutreptiella gymnastica</i>	11.0	275	9.9	Thronsdon (1973), Sommer (1988)
<b>Cryptophyte</b>				
<i>Rhodomonas salina</i>	8.8	24	1.0	Meunier et al. (2013)
<i>Teleaulax sp.</i>	5.6	56	2.0	Meunier et al. (2013)

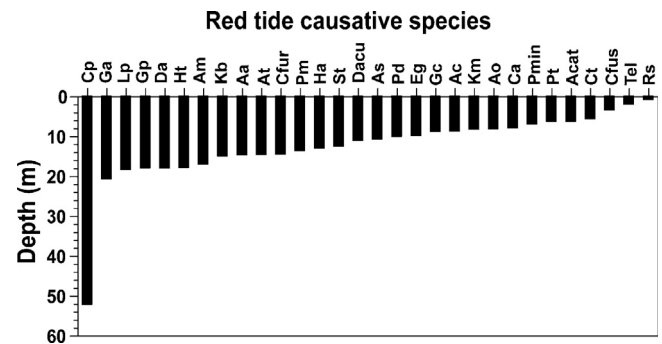
(e.g., Kamykowski and Zentara, 1977; Cullen and Horrigan, 1981; Katano et al., 2011), and others showing vertical movement, but not on a diel time scale. More recently modeling studies (e.g., Ji and Franks, 2007; Ralston et al., 2007) have suggested that the emergence of vertical migration depends on both the water column structure (light, nutrients, temperature and turbulence), and the internal biochemical stores – largely carbon and nitrogen – of the individual organism.



**Fig. 2.** The maximum swimming speed (MSS,  $\mu\text{m s}^{-1}$ ) of phototrophic red-tide dinoflagellates (open triangles), raphidophytes (closed squares), cryptophytes (closed circles), and an euglenophyte (closed triangle) as a function of size (equivalent spherical diameters, ESD,  $\mu\text{m}$ ) shown in Table 5. Cp: *Cochlodinium polykrikoides*, the fastest dinoflagellate. Cf: *Ceratium fusus*, the slowest dinoflagellate. Ha: *Heterosigma akashiwo*. Ca: *Chattonella antiqua*. Te: *Teleaulax sp.* Rs: *Rhodomonas salina*. Eg: *Eutreptiella gymnastica*.

## 5. GM3 – including mixotrophy

In the 1990s, the mixotrophic feeding ability of some red-tide flagellates was revealed (Bockstahler and Coats, 1993a, 1993b; Nygaard and Tobiesen, 1993; Jacobson and Anderson, 1996;



**Fig. 3.** Depth (m) which a phototrophic dinoflagellate can reach when it descends for 10 h. This depth was calculated by multiplying the maximum swimming speed ( $\mu\text{m s}^{-1}$ ) of a dinoflagellate by 36,000 s. Cp: *Cochlodinium polykrikoides*, Ga: *Gymnodinium aureolum*, Lp: *Lingulodinium polyedrum*, Gp: *Gonyaulax polygramma*, Da: *Dinophysis acuta*, Ht: *Heterocapsa triquetra*, Am: *Alexandrium minutum*, Aa: *Alexandrium affine*, At: *Alexandrium tamarense*, Cfur: *Ceratium furca*, Pm: *Prorocentrum micans*, Kb: *Karenia brevis*, Ha: *Heterosigma akashiwo*, St: *Scrippsiella trochoidea*, Dacu: *Dinophysis acuminata*, As: *Akashiwo sanguinea*, Pd: *Prorocentrum donghaiense*, Gc: *Gymnodinium catenatum*, Ac: *Amphidinium carterae*, Eg: *Eutreptiella gymnastica*, Km: *Karenia mikimotoi*, Ao: *Alexandrium ostenfeldii*, Ca: *Chattonella antiqua*, Pmin: *Prorocentrum minimum*, Pt: *Prorocentrum triestinum*, Acat: *Alexandrium catenella*, Ct: *Ceratium tripos*, Cfus: *Ceratium fusus*, Tel: *Teleaulax sp.*, Rs: *Rhodomonas salina*.



Skovgaard, 1996; Jeong et al., 1997; Stoecker, 1999), and in GM3 we add mixotrophy of red-tide flagellates to GM2 (Table 1; Fig. 1).

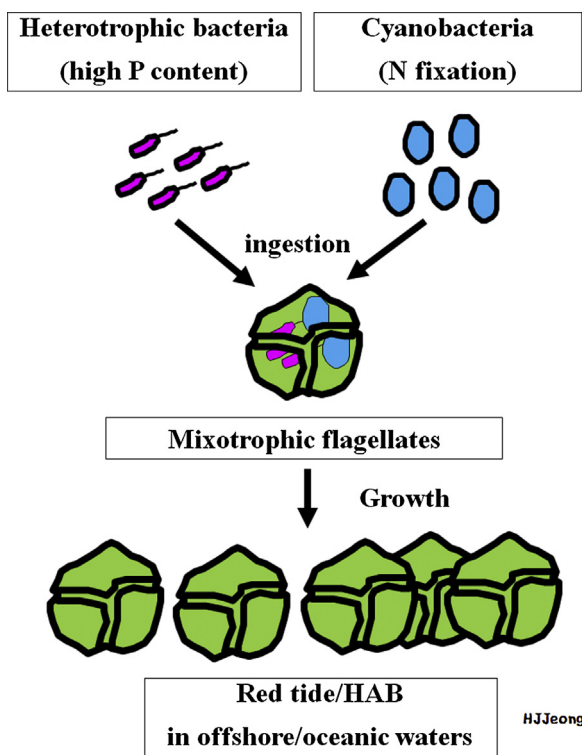
In GM3, the change of cell density of a red-tide species is

$$\frac{dC}{dt} = C[k_3(N, I, w_s, P) - m_c(w_s)]$$

where  $k_3$  is the net mixotrophic growth rate including increases due to the red-tide organism's predation on prey of concentration  $P$ . In this GM, the growth rate  $k_3$  depends critically on the kinds of prey that a given red-tide flagellate is able to feed on, the prey concentration, and the growth and ingestion rates of the flagellate with (i.e., mixotrophic) and without (i.e., autotrophic) prey.

In the last two decades, several dinoflagellates that were thought to be obligate phototrophs have been shown to be mixotrophic (Stoecker, 1999; Jeong et al., 2005a, 2010a, 2012; Burkholder et al., 2008; Kang et al., 2011), feeding on diverse prey including heterotrophic bacteria, cyanobacteria, small flagellates, other mixotrophic dinoflagellates, heterotrophic dinoflagellates, and ciliates (Nygaard and Tobiesen, 1993; Stoecker et al., 1997; Jeong et al., 1997, 1999a,b, 2005b, 2005c, 2012; Li et al., 2000; Park et al., 2006; Seong et al., 2006; Berge et al., 2008b; Glibert et al., 2009; Yoo et al., 2009; Kang et al., 2011). In addition, red-tide raphidophytes such as *Heterosigma* spp. and *Chattonella* spp. have been shown to be able to feed on heterotrophic bacteria and cyanobacteria (Nygaard and Tobiesen, 1993; Seong et al., 2006; Jeong et al., 2010b; Jeong, 2011).

In waters in which the surface nutrient concentrations are too low for red-tide flagellates to grow, and the nutricline is too deep for them to swim to, phototrophic flagellates may obtain the nitrogen and phosphorus for their growth through mixotrophy



**Fig. 4.** Diagram of a possible mechanism for the outbreak and/or persistence of red tides dominated by mixotrophic flagellates in offshore and/or oceanic waters in which inorganic nutrient concentrations are low. Mixotrophic flagellates grow and form a red-tide patch by feeding on cyanobacteria that can conduct nitrogen fixation and on heterotrophic bacteria which usually have high phosphorus contents.

This figure was redrawn from Jeong et al. (2010c) and was published in Ocean Science Journal.

(Fig. 4; Jeong et al., 2010c). Many mixotrophic dinoflagellates such as *Karenia brevis* and *Prorocentrum donghaiense* that form red tides in oceanic waters are able to feed on photosynthetic cyanobacteria and heterotrophic bacteria (Jeong et al., 2005b, 2010c; Glibert et al., 2009), which are found in high abundance in oceanic waters (Cho and Azam, 1990; Partensky et al., 1999; Uysal, 2001; Zubkov et al., 2003). Some cyanobacteria can fix nitrogen (e.g., Mitsui et al., 1986), and heterotrophic bacteria usually have high P:N ratios (e.g., Tezuka, 1990) that are favorable to protist growth. Glibert et al. (2009) reported that grazing by *K. brevis* on the cyanobacterium *Synechococcus* may play a substantial role in sustaining natural populations in N-poor waters, with ingestion rates of 1–84 *Synechococcus* cells *K. brevis*<sup>-1</sup> h<sup>-1</sup>.

The hypothesis that bacteria support positive growth of red-tide forming algae may also be relevant to coastal environments. Seong et al. (2006) reported that the small red-tide dinoflagellate *Heterocapsa rotundata* was able to acquire 76% of its body carbon from bacteria in a day. With a growth efficiency of 30 to 40% for *H. rotundata* feeding exclusively on bacteria, this alga could divide once per 3–4 d. The mixotrophic dinoflagellate *Prorocentrum minimum* and *Heterosigma akashiwo* were able to form 27% and 13%, respectively, of their body carbon from bacteria in a day, and Jeong et al. (2012) reported that the mixotrophic dinoflagellate *Symbiodinium voratum* was able to acquire 30% of its body nitrogen in a day feeding on *Synechococcus* spp. In Masan Bay, Korea, some species have formed red tides when inorganic nutrient concentrations were lower than the reported values of  $K_{ii}$ ; their abundance was significantly correlated with bacteria and other algae (Jeong et al., 2013a). Jeong et al. (2013a) suggested that the mixotrophic nature of these species may enable the species to grow and form red tides under nutrient-limiting conditions.

The extent of mixotrophy of phototrophic dinoflagellates varies considerably (Table 6, Fig. 5). Feeding enhances the growth rates of some phototrophic dinoflagellates, such as *Gymnodinium smaydae*, *Paragymnodinium shiwhaense*, *Amylax triacantha*, and *Fragilidium* cf. *mexicanum*, which grow well mixotrophically, but poorly autotrophically (photosynthetically) (Jeong et al., 1999a; Yoo et al., 2010b; Park et al., 2013b; Lee et al., 2014a). The growth rates of *G. smaydae* and *P. shiwhaense* increased by 2.2 and 1.3 d<sup>-1</sup>, respectively, when allowed to grow mixotrophically, though this is not the case for all dinoflagellates (Table 6).

The sequence of growth rates of the fastest-growing dinoflagellates without mixotrophy is *Ansanella granifera* > *Karlodinium veneficum* and *Prorocentrum donghaiense* > *Symbiodinium voratum*, but with mixotrophy is *Gymnodinium smaydae* > *A. granifera* > *Paragymnodinium shiwhaense* > *K. veneficum* (Fig. 5). Thus, mixotrophy may affect the dominance of one red-tide-causing species over another (see Section 6.1).

The growth rates of phototrophic dinoflagellates were previously thought to be inversely correlated with cell size (Banse, 1982; Smayda, 1997). However, the inclusion of mixotrophic growth rates of dinoflagellates has changed this allometric relationship (Jeong et al., 2010c; Lee et al., 2014a). Thus, in models of the dynamics of red tides dominated by these dinoflagellates, mixotrophic growth rates rather than autotrophic growth rates should be used.

Among ca. 1200 reported species of phototrophic dinoflagellates, only ca. 50 have been shown to be mixotrophic (i.e., 4–5%) (Jeong et al., 2010c; Gómez, 2012; Lee et al., 2014a, 2014c); growth and ingestion rates have been quantified for fewer than 30. Indeed, the prey species of marine red-tide cryptophytes and euglenophytes have not yet been discovered. Understanding the dynamics of a given mixotrophic dinoflagellate requires knowledge of the kinds of prey that the dinoflagellate is able to feed on, optimal prey species, growth and ingestion rates, and grazing impact. Such information is critical to formulating more accurate models of red-tide dynamics.

**Table 6**

Optimal prey, growth rate, and ingestion rate of each mixotrophic dinoflagellate predator species.

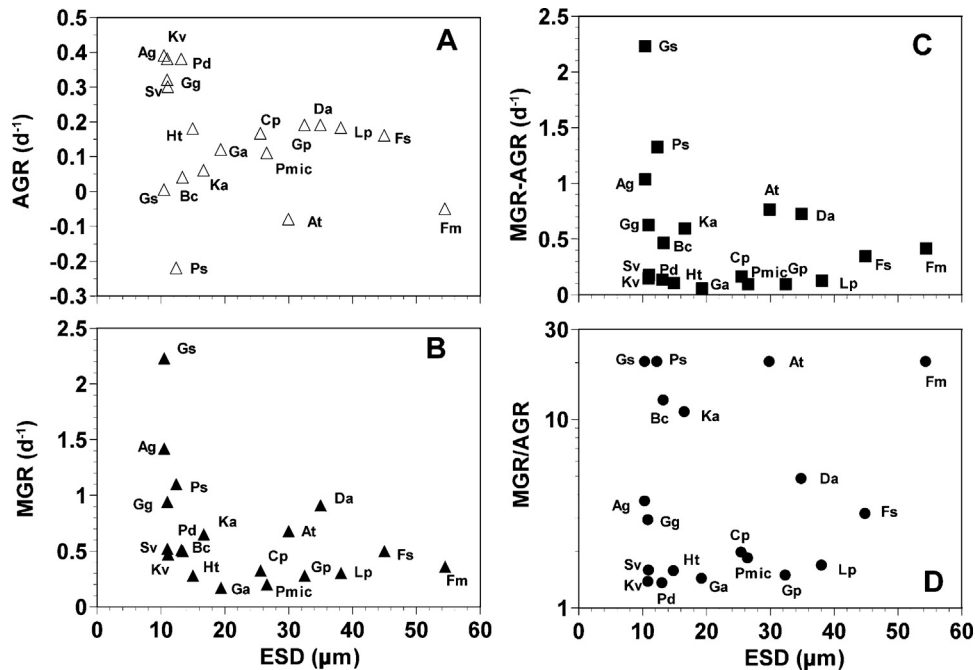
Predator	ESD	Optimal prey	ESD	T	LI	MMGR	AGR	RMAG	(M-A)	MIR	Reference
<b>Engulfment feeding</b>											
<i>Ansanella granifera</i>	10.5	<i>Pyramimonas</i> sp.	5.6	20	20	1.43	0.39	3.7	1.04	0.97	Lee et al. (2014c)
<i>Prorocentrum donghaiense</i>	13.3	<i>Teleaulax</i> sp.	5.6	20	20	0.51	0.38	1.4	0.14	0.03	Jeong et al. (2005a)
<i>Heterocapsa triquetra</i>	15.0	<i>Teleaulax</i> sp.	5.6	20	20	0.28	0.18	1.5	0.10	0.04	Jeong et al. (2005a)
<i>Karlodinium armiger</i> <sup>a</sup>	16.7	<i>Rhodomonas baltica</i>	10.7	15	180	0.65	0.06	10.8	0.59	0.97	Berge et al. (2008b)
<i>Cochlodinium polykrikoides</i>	25.8	<i>Teleaulax</i> sp.	5.6	20	50	0.32	0.17	2.0	0.16	0.16	Jeong et al. (2004b)
<i>Prorocentrum micans</i>	26.6	<i>Teleaulax</i> sp.	5.6	20	20	0.20	0.11	1.9	0.09	0.04	Jeong et al. (2005a)
<i>Amylax triacantha</i>	30.0	<i>Mesodinium rubrum</i>	22.0	15	20	0.68	-0.08	-8.5	0.76	2.54	Park et al. (2013b)
<i>Gonyaulax polygramma</i>	32.5	<i>Teleaulax</i> sp.	5.6	20	50	0.28	0.19	1.5	0.09	0.18	Jeong et al. (2005c)
<i>Lingulodinium polyedrum</i>	38.2	<i>Scrippsiella trochoidea</i>	25.1	20	50	0.30	0.18	1.7	0.12	0.36	Jeong et al. (2005a)
<i>Fragilidium subglobosum</i>	45.0	<i>Ceratium tripos</i>	59.5	15	45	0.50	0.16	3.1	0.34		Hansen and Nielsen (1997)
<i>Fragilidium cf. mexicanum</i>	54.5	<i>Lingulodinium polyedrum</i>	37.9	22	20	0.36	-0.05	-7.2	0.41	9.75	Jeong et al. (1999a)
<b>Peduncle feeding</b>											
<i>Gymnodinium smaydae</i>	10.5	<i>Heterocapsa rotundata</i>	9.5	20	20	2.23	0.01	>10	2.22	1.60	Lee et al. (2014a)
<i>Karlodinium veneficum</i>	11.0	<i>Storeatula major</i>	6.6	20	250	0.52	0.38	1.4	0.14	0.13	Adolf et al. (2006)
<i>Gyrodinium galatheanum</i> (currently <i>K. veneficum</i> )	11.0	<i>Storeatula major</i>	6.6	20	372–384	0.94	0.32	2.9	0.62	0.12	Li et al. (1999)
<i>Symbiodinium voratum</i>	11.1	<i>Heterosigma akashiwo</i>	11.5	20	20	0.47	0.30	1.6	0.17	0.13	Jeong et al. (2012)
<i>Paragymnodinium shiwhaense</i>	12.4	<i>Amphidinium carterae</i>	9.7	20	20	1.10	-0.22	-4.9	1.32	0.38	Yoo et al. (2010b)
<i>Biecheleria cincta</i>	13.4	<i>Heterosigma akashiwo</i>	11.5	20	20	0.50	0.04	12.5	0.46	0.49	Kang et al. (2011)
<i>Gymnodinium aureolum</i>	19.4	<i>Teleaulax</i> sp.	5.6	20	20	0.17	0.12	1.4	0.05	0.06	Jeong et al. (2010a)
<i>Dinophysis acuminata</i>	35.0	<i>Mesodinium rubrum</i>	22.0	20	60	0.91	0.19	4.8	0.72	1.30	Kim et al. (2008)

ESD, equivalent spherical diameter ( $\mu\text{m}$ ); T, temperature ( $^{\circ}\text{C}$ ); LI, light intensity ( $\mu\text{E m}^{-2}\text{s}^{-1}$ ); MMGR, maximum mixotrophic growth rate ( $\text{d}^{-1}$ ); AGR, autotrophic growth rate ( $\text{d}^{-1}$ ); RMAG, ratio of mixotrophic to autotrophic growth rate; (M-A), (MMGR-AGR); MIR, maximum ingestion rate ( $\text{ngC predator}^{-1}\text{d}^{-1}$ ).

<sup>a</sup> Indicates the capability of feeding by both peduncle and engulfment. Berge et al. (2008a) suggested that *Karlodinium armiger* feeds on *Rhodomonas baltica* mainly by engulfment.

The  $m_C$  in the equation of GM 3 includes the specific mortality rate of a red-tide species due to both heterotrophic and mixotrophic predators (Tables 1, 4 and 7). The maximum specific mortality rates of red-tide species due to mixotrophic predators can be greater than the maximum growth rates of the red-tide species in the coastal waters of Korea; thus these mixotrophic

predators may sometimes control the populations of the red-tide species. In particular, the grazing impacts of some large red-tide species on the co-occurring small red-tide species are sometimes considerable (Table 7). This mortality could cause the decline of red tides dominated by the prey, and lead to a subsequent red tide of the predatory species (e.g., Jeong et al., 2005a). For example, in



**Fig. 5.** The maximum growth rate ( $\text{d}^{-1}$ ) of phototrophic dinoflagellates growing exclusively photosynthetically (AGR, A) and growing mixotrophically (MGR, B), MGR-AGR (C), and MGR/AGR (D) as a function of the cell size (equivalent spherical diameters, ESD,  $\mu\text{m}$ ) of the predator when each predator fed on the optimal prey species (see Table 6). The temperature effect was not considered because the optimal temperature for each dinoflagellate species is different from that of the others. Ag: *Ansanella granifera*. At: *Amylax triacantha*. Bc: *Biecheleria cincta*. Cp: *Cochlodinium polykrikoides*. Da: *Dinophysis acuminata*. Fs: *Fragilidium subglobosum*. Fm: *Fragilidium cf. mexicanum*. Ga: *Gymnodinium aureolum*. Gg: *Gyrodinium galatheanum*. Gp: *Gonyaulax polygramma*. Gs: *Gymnodinium smaydae*. Ht: *Heterocapsa triquetra*. Ka: *Karlodinium armiger*. Kv: *Karlodinium veneficum*. Lp: *Lingulodinium polyedrum*. Pd: *Prorocentrum donghaiense*. Pmic: *Prorocentrum micans*. Ps: *Paragymnodinium shiwhaense*. Sv: *Symbiodinium voratum*.

**Table 7**

Red tide species as prey and predator, their abundances (AB, cells ml<sup>-1</sup>), and grazing impact by the predator on prey populations in the waters of Masan (MA), Shihwa (SH), Kwangyang (KW), Saemankeum (SAE), Tongyoung (TO), and Kohung (KO), Korea, Krka Estuary (KE), Croatia, and Los Angeles-Long Beach harbor (LALB), USA. MTD: Mixotrophic dinoflagellates.

Prey		Predator		g		Location	Reference
Species	AB	Species	AB	(d <sup>-1</sup> )	(h <sup>-1</sup> )		
<b>Cyanobacteria</b>		<b>Raphidophytes</b>					
<i>Synechococcus</i> spp.	51–194,460	<i>Heterosigma akashiwo</i>	22–228,000	0.001–1.238		MA, SH	Jeong et al. (2010b)
<b>Cryptophytes</b>		<b>MTDs</b>					
Cryptophytes	10–1615	<i>Cochlodinium polykrikoides</i>	23–2065		0.001–0.745	KO, SAE	Jeong et al. (2004b)
	75–3550	<i>Gonyaulax polygramma</i>	123–20,000		0.002–0.479	KW, SAE, TO	Jeong et al. (2005c)
	1–4270	<i>Gymnodinium aureolum</i>	14–4425	0.001–0.498		SAE	Jeong et al. (2010a)
	211–28,118	<i>Heterocapsa triquetra</i>	11–18,000		0.091 <sup>a</sup>	MA	Jeong et al. (2005a)
	5–2523	<i>Prorocentrum donghaiense</i>	0–102,000		2.67 <sup>a</sup>	KO, KW, TO, MA	Jeong et al. (2005a)
	1–28,118	<i>Prorocentrum micans</i>	1–6944		0.043 <sup>a</sup>	KO, TO, MA	Jeong et al. (2005a)
<b>Diatoms</b>		<b>MTDs</b>					
<i>Skeletonema costatum</i>	16–4533	<i>Gonyaulax polygramma</i>	1–1810		0.001–0.222	SAE, KW, TO	Yoo et al. (2009)
	20–13,200	<i>Prorocentrum micans</i>	58–6944		0.001–0.1	MA, TO	Yoo et al. (2009)
<b>MTDs</b>		<b>MTDs</b>					
<i>Amphidinium</i> spp.	6–2094	<i>Paragymnodinium shiwhaense</i>	3–1375		0.001–0.067	SH	Yoo et al. (2010b)
<i>Heterocapsa rotundata</i>	117–717	<i>Gymnodinium smaydae</i>	1–26		0.08–0.23	SH	Lee et al. (2014a)
<i>Heterocapsa triquetra</i>	3–1271	<i>Gymnodinium smaydae</i>	1–26		0.002–0.019	SH	Lee et al. (2014a)
<i>Prorocentrum</i> spp. ( <i>P. minimum</i> + <i>P. triestinum</i> )	4–486	<i>Lingulodinium polyedrum</i>	7–605		0.026 <sup>a</sup>	KO, SAE, KE	Jeong et al. (2005a)
<i>Scrippsiella trochoidea</i>	1–59	<i>Lingulodinium polyedrum</i>	13–547		0.011 <sup>a</sup>	LALB, KO, SAE	Jeong et al. (2005a)
<b>Prasinophytes</b>		<b>MTDs</b>					
<i>Pyramimonas</i> sp.	3–53,243	<i>Ansanella granifera</i>	1–403	0.003–2.78		SH	Lee et al. (2014c)
<b>Raphidophytes</b>		<b>MTDs</b>					
<i>Heterosigma akashiwo</i>	6–2138	<i>Biecheleria cincta</i> (= <i>Woloszynskia cincta</i> )	0.1–113	0.001–1.102		SH	Kang et al. (2011)

<sup>a</sup> Highest value.

Masan Bay, Korea, in 2004, a bloom dominated by a mixture of *Amphidinium* sp. and *Heterosigma akashiwo* was followed by one dominated by a mixture of *Prorocentrum minimum* and *P. triestinum*. This bloom was followed by one of *Cochlodinium polykrikoides*, and finally by one of *P. micans*. Interestingly, *P. minimum* and *P. triestinum*, which are able to feed on *A. carterae* and *H. akashiwo*, were ingested in turn by *C. polykrikoides* and *P. micans* (Jeong et al., 2004b, 2005a). Under these circumstances, dissolved nutrients may not play as important a role in the succession of dominant red-tide species as the direct trophic transfer of one red-tide species into the next. This may cause an uncoupling between nutrient concentrations and mixotrophic red-tide dinoflagellate abundances in natural environments (Jeong et al., 2005a).

GM3 may have predictive power for red tides in oligotrophic oceanic waters or nutrient-depleted coastal waters, or serial red tides in eutrophic coastal waters in which the red-tide-causing species grows much more quickly than expected from the growth rates  $k_1$ ,  $k_2$  or  $k_3$  (Table 1). This GM focuses mainly on absolute growth of a given red-tide flagellate species at the population level, rather than relative growth (i.e., competition) at the community level. Modifications to GM3 will be required to understand the formation of red tides by a few species under conditions favorable for most phototrophs.

## 6. GM4 – including biological interaction

In temperate Masan Bay, Korea, red tide events occurred 36 times in one year from June 2004 to May 2005, caused by a diverse array of coexisting red-tide species (Jeong et al., 2013a). *Heterocapsa triquetra* formed red tides in winter, while *Cochlodinium polykrikoides* and *Akashiwo sanguinea* formed red tides during summer; *Prorocentrum minimum* formed red tides in both summer and winter. To understand outbreaks of single-species red tides from a diverse community, we must consider biological interactions among coexisting red-tide species. GM4 builds on GM3 by

incorporating the biological interactions and relative growth rates of diverse red-tide species (Table 1; Fig. 1).

Two types of biological interaction can regulate the relative dominance of red-tide species: direct and indirect. In direct biological interaction, a red-tide species may kill other species, or inhibit the growth or swimming ability of other species by physical contact or chemical effects (i.e., allelopathy, physical inhibition, etc.). In indirect biological interactions a red-tide species could outgrow other species, for example, thereby reducing the resources available to other species. These two biological interactions are not mutually exclusive, and may interact.

Direct biological effects usually involve the contact of one organism with another, through the release of enzymes on the prey's surface, for example. The rates of such contacts are determined by the concentrations of both species: the more individuals of each species, the more often they will encounter each other. The simplest mathematical form of a direct inhibition between a red-tide species of concentration  $C$  and another red-tide species of concentration  $P$  is given in GM4d (GM4-direct) by the coupled equations

$$\frac{dC}{dt} = C[k_4(N, I, w_s, P) - m_C(w_s) - m_{Pd}P]$$

$$\frac{dP}{dt} = P(k_p - m_{Cd}C)$$

Here  $k_p$  is the second species' specific growth rate,  $m_{Cd}$  the direct mortality rate of  $P$  caused by  $C$ , and  $m_{Pd}$  the direct mortality rate of  $C$  caused by  $P$ . Note that the population mortality rates of  $P$  and  $C$  are determined by the products of the concentrations of  $P$  and  $C$ . One mathematical consequence of the formulation of the direct interaction is that the strength of the interaction will decrease as the concentration of either species approaches zero. This will tend to allow the coexistence of both species even though one may be at very low concentrations.

Indirect biological effects occur through one species affecting the environment of the other species, but without the necessity of physical contact. Two obvious examples are the uptake of nutrients or prey by one species, making them unavailable to another species, or the shading caused by dense layers of a red-tide species reducing the photosynthesis of co-occurring autotrophs. These interactions can be generally described by GM4i (GM4-indirect):

$$\frac{dC}{dt} = C[k_4(N, I, w_s, P) - m_C(w_s)] - m_{Pi}P$$

$$\frac{dP}{dt} = P(k_P - m) - m_{Ci}C$$

In this version,  $C$  and  $P$  have a natural mortality rates  $m_C$  and  $m$ , respectively, but they also have an additional mortality rate  $m_{Ci}$  and  $m_{Pi}$  due to the indirect effects of the presence of  $C$  or  $P$ , respectively. Note that these indirect mortality rates depend only on the individual concentrations of  $C$  or  $P$  – not the product of the concentrations as in GM4d – indicating that contact of  $C$  and  $P$  is not necessary to cause mortality. An interesting mathematical consequence of this formulation is that one species can drive the other locally extinct, as the strength of the interaction depends only on the concentration of one species – not the product of the species concentrations as in GM4d.

The goal of the following sections is to describe the types of dynamics that determine the mortality rates  $m_{Cd}$ ,  $m_{Pd}$ ,  $m_{Ci}$ , and  $m_{Pi}$ .

### 6.1. Physical contact or chemical effects (allelopathy) – $m_{Cd}$ and $m_{Pd}$

While some red-tide species ingest potential competitors, others can kill or reduce the abundance of co-occurring red-tide species through physical contact or chemical effects (i.e., allelopathy, Table 8). In GM4d these effects appear in the parameters  $m_{Cd}$  and  $m_{Pd}$ . Note that allelopathy would only be modeled as a direct effect if the chemical was released by one species upon contact with an individual of the other species, or if the concentration of one species stimulated the proportional release of the chemical by the other species. If the allelopathic chemical were released into the water regardless of the presence of the second species, it would appear as an indirect effect (Section 6.2). Lim et al. (2014) showed that the diatoms *Skeletonema costatum*, *Chaetoceros danicus*, and *Thalassiosira decipiens* inhibited the growth rate and reduced the swimming speed of the harmful dinoflagellate *Cochlodinium polykrikoides*. This may reduce the extent of vertical migration of *C. polykrikoides* and, in turn, delay or prevent the outbreak of *C. polykrikoides* red tides (Lim et al., 2014). Interestingly, other studies have shown that *C. polykrikoides* caused co-occurring species to lose flagella and motility, experience other cell morphological modifications (Tang and Gobler, 2010), or have decreased growth rates (Yamasaki et al., 2007), presumably through allelochemicals or cell contact. Such negative effects usually require extremely high cell concentrations, though some toxic species such as *Alexandrium* spp. produce negative effects on other species at relatively low concentrations (Table 8). Including such effects in models is essential; however, parameterizing such interactions requires a great deal more work.

### 6.2. Indirect inhibition – $m_{Ci}$ and $m_{Pi}$

Indirect inhibition among species in a community can occur through a variety of mechanisms, including the sequestration of inorganic nutrients or removal of prey leading to growth limitation of competitors, the formation of dense layers that reduce the irradiance available to competitors, and the production of chemicals that decrease the growth rate of competitors or the

predation rate of predators. In model GM4i these effects are parameterized by  $m_{Ci}$  and  $m_{Pi}$ .

As discussed in Section 3, in model GM1 the species with the lowest  $K_u$  would tend to take up and sequester the available nutrients, thus out-competing coexisting autotrophs (Eppley et al., 1969; Smayda, 1997). This indirect effect depends mainly on the biomass and physiology of the red-tide-forming species, as opposed to the biomass of the species it is affecting (Morel, 1987; Grover, 1989; Edwards et al., 2012). Such inhibition is often included implicitly in models of red tides that include multiple species competing for the same nutrients (Irwin et al., 2006; Litchman et al., 2007; Litchman and Klausmeier, 2008; Fiksen et al., 2013).

The vertical swimming discussed in Section 4 often leads red-tide organisms to form extremely dense layers at the surface of the ocean. Such layers, even if only 1 m thick, can significantly reduce the irradiance available to photoautotrophs deeper in the water column (Agustf, 1991; Gallegos and Jordan, 2002). This reduction in the light available to potential competitors would decrease their net growth rate, thus enhancing the ability of the red-tide organisms to form a red tide (Huisman and Weissing, 1994; Litchman and Klausmeier, 2008).

Many red-tide species produce toxins; these chemicals can reduce their mortality by affecting predation by potential predators. *Alexandrium fundyense* (formerly *Alexandrium tamarense* and *Gonyaulax tamarensis*), for example, produces saxitoxins that can reduce predation by copepods (e.g., Ives, 1987; Turner, 2014) and ciliates (e.g., Hansen, 1989). The formation of dense layers of red-tide organisms will enhance the concentration and efficacy of such toxins released into the surrounding waters, possibly affording enhanced protection from predation. Furthermore, some chemicals such as polysaccharides, polyunsaturated aldehydes, dimethylsulfoniopropionate (DMSP) produced by red-tide organisms can also reduce mortality rate of the red tide organisms by lowering ingestion rates of their predators (Malejl and Harris, 1993; Strom et al., 2003; Sopanen et al., 2006; Poulson et al., 2009; Ianora et al., 2011). Such red-tide species may thus outcompete other species that do not produce such chemicals.

The direct and indirect biological inhibitions included in GM4d and GM4i arise from the fact that the red-tide organism is present in a diverse planktonic community. Simply growing quickly is not a guarantee that an organism can form a red tide: it must grow more quickly than its competitors, and die more slowly while it is growing. Growth and death are two very separate dynamics, and different organisms will interact with their communities in different ways to achieve net growth rates high enough to form a red tide. In GM4d and GM4i the red-tide species can remove competitive species both by killing them through contact (direct), and by affecting their growth rates (indirect). In addition, the red-tide species can decrease their own mortality rates by poisoning potential predators (indirect). Including such interactions in predictive models will require significant improvements in our knowledge and understanding of the community interactions among red-tide species and the planktonic ecosystem in which they reside.

## 7. Biological interaction map, conclusions

As a conceptual synthesis of models GM1–4, we use the dinoflagellate *Cochlodinium polykrikoides* as the red-tide-forming species  $C$ , and diagram its interaction with its environment and planktonic community  $P$  (Fig. 6). This diagram, a so-called biological interaction map (BIM), shows that the red-tide species interacts directly or indirectly with many other species. For example, *C. polykrikoides* can ingest diatoms or cryptophytes. This would appear as a gain  $k_3CP$  or  $k_4CP$  for *C. polykrikoides* in models GM3 and GM4d, respectively. On the other hand, diatoms

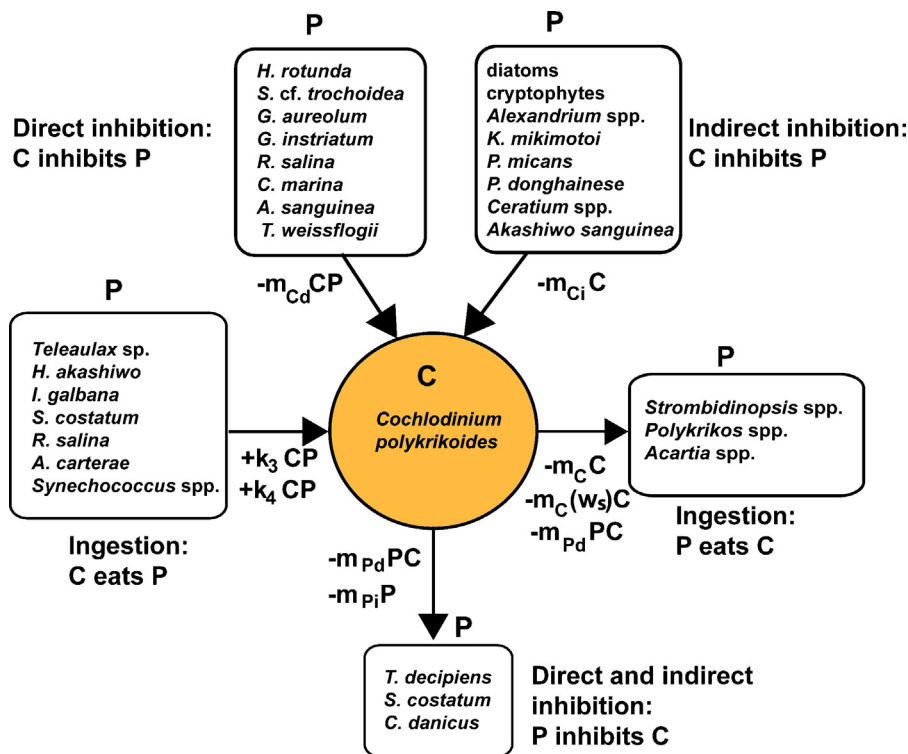
**Table 8**

Allelopathic effects of red-tide species. The numbers in the parentheses are initial concentrations of the target species (cells ml<sup>-1</sup>). GI: growth inhibition, MM: morphological modification, GS: growth stimulation, ISS: inhibition of swimming speed.

Causative species	Affected species	Condition	Effects	Reference
<i>Akashiwo sanguinea</i> (100)	<i>Chattonella antiqua</i> (100)	Cell to cell, cell to filtrate	GI	(1)
<i>Alexandrium catenella</i> (1004)	<i>Rhodomonas salina</i> (9300), <i>Dunaliella salina</i> (7400)	Cell to cell	GI	(2)
<i>Alexandrium fundyense</i> (150)	<i>Thalassiosira cf. gravida</i> (20)	Cell to filtrate	GI, Bleaching	(3)
<i>Alexandrium lusitanicum</i> (1602)	<i>D. salina</i> (7400), <i>Amphidinium crassum</i> (256)	Cell to cell	GI	(2)
<i>Alexandrium minutum</i> (1471/7000)	<i>A. crassum</i> (256), <i>D. salina</i> (7400), <i>R. salina</i> (9300), <i>Prorocentrum donghaiense</i> (20,000)	Cell to cell	GI	(2), (5)
<i>A. minutum</i> (10,500)	<i>Thalassiosira weissflogii</i> (42,000)	Cell to filtrate	GI	(4)
<i>Alexandrium ostenfeldii</i> (1273)	<i>A. crassum</i> (256), <i>T. weissflogii</i> (3600), <i>R. salina</i> (9300), <i>D. salina</i> (7400)	Cell to cell	GI	(2)
<i>Alexandrium tamarense</i> (979)	<i>A. crassum</i> (256), <i>T. weissflogii</i> (3600), <i>D. salina</i> (7400), <i>R. salina</i> (9300)	Cell to cell	GI	(2)
<i>A. tamarense</i> (10,500)	<i>T. weissflogii</i> (42,000)	Cell to filtrate	GI	(4)
<i>A. tamarense</i> (2800/7000)	<i>P. donghaiense</i> (10,000–100,000)	Cell to cell	GI	(5), (6)
<i>Alexandrium taylori</i> (608)	<i>A. crassum</i> (256), <i>D. salina</i> (7400), <i>R. salina</i> (9300)	Cell to cell	GI	(2)
<i>Cochlodinium polykrikoides</i> (2450)	<i>A. sanguinea</i> (340), <i>Gymnodinium instriatum</i> (250), <i>Chattonella marina</i> (787)	Cell to cell, cell to cell with 5 µm mesh barrier	GI, MM	(7)
<i>C. polykrikoides</i> (2450)	<i>Gymnodinium aureolum</i> (1180), <i>Heterocapsa rotundata</i> (1240), <i>Scrippsiella cf. trochoidea</i> (2590), <i>R. salina</i> (29000), <i>T. weissflogii</i> (3660)	Cell to cell	GI and/or MM	(7)
<i>C. polykrikoides</i> (696)	<i>A. sanguinea</i> (313)	Cell to cell	GI, MM	(8)
<i>C. polykrikoides</i> (696)	<i>A. sanguinea</i> (1264)	Cell to filtrate	No effect	(8)
<i>Gymnodinium mikimotoi</i> (2000/44,000 <sup>a</sup> )	<i>H. circularisquama</i> (200)	Cell to cell, cell to filtrate	GI, cyst formation	(9)
<i>Gyrodinium instriatum</i> (100/1000)	<i>Skeletonema costatum</i> (10–1000)	Cell to cell	No effect, MM	(10)
<i>H. circularisquama</i> (50,000 <sup>a</sup> )	<i>Prorocentrum dentatum</i> (50,000 <sup>a</sup> ), <i>S. costatum</i> (50,000 <sup>a</sup> ), <i>Heterosigma akashiwo</i> (50,000 <sup>a</sup> )	Cell to cell	GI	(11)
<i>H. circularisquama</i> (200)	<i>G. mikimotoi</i> (2000 <sup>a</sup> )	Cell to cell	GI, cyst formation	(9)
<i>H. circularisquama</i> (200)	<i>G. mikimotoi</i> (4600 <sup>a</sup> )	Cell to filtrate	No effect	(9)
<i>Karenia brevis</i> (2400)	<i>A. sanguinea</i> (-), <i>Amphora</i> sp. (-), <i>Asterionellopsis glacialis</i> (-), <i>Peridinium</i> sp. (-), <i>Prorocentrum mexicanum</i> (-), <i>Prorocentrum minimum</i> (-), <i>Rhizosolenia cf. setigera</i> (-), <i>Rhodomonas lens</i> (-), <i>S. costatum</i> (-), <i>Thalassiosira</i> sp. (-)	Cell to cell	GI	(12)
<i>K. brevis</i> (2400)	<i>Chlorella capsulata</i> (-), <i>Odontella aurita</i> (-)	Cell to cell	No effect	(12)
<i>K. brevis</i> (2400)	<i>A. sanguinea</i> (-), <i>Peridinium</i> sp. (-), <i>P. minimum</i> (-), <i>R. lens</i> (-), <i>Thalassiosira</i> sp. (-)	Cell to filtrate	No effect	(12)
<i>K. brevis</i> (2400)	<i>Amphora</i> sp. (-), <i>Asterionellopsis glacialis</i> (-), <i>Prorocentrum mexicanum</i> (-), <i>Rhizosolenia cf. setigera</i> (-), <i>Skeletonema costatum</i> (-)	Cell to filtrate	GI	(12)
<i>Prorocentrum donghaiense</i> (10,000)	<i>Phaeodactylum tricornutum</i> (10,000)	Cell to cell, cell to filtrate	GI	(13)
<i>P. donghaiense</i> (19,000–190,000)	<i>Scrippsiella trochoidea</i> (10,000)	Cell to cell, cell to filtrate	Both GI and GS depend on cell density	(14)
<i>P. donghaiense</i> (10,000–100,000)	<i>A. tamarense</i> (2800)	Cell to filtrate	Both GI and GS depend on cell density	(6)
<i>Prorocentrum micans</i> (10,000)	<i>S. costatum</i> (10,000), <i>K. mikimotoi</i> (10,000)	Cell to cell	GI	(15)
<i>P. micans</i> (10,000)	<i>S. costatum</i> (10,000)	Cell to filtrate	GI	(15)
<i>P. micans</i> (45,000)	<i>K. mikimotoi</i> (7500)	Cell to filtrate	GI	(15)
<i>P. minimum</i> (100–10,000)	<i>S. costatum</i> (100–10,000)	Cell to cell, cell to filtrate	Both GI and GS depend on cell density	(16)
<i>Chattonella antiqua</i> (100)	<i>A. sanguinea</i> (100)	Cell to cell, cell to filtrate	GI	(1)
<i>H. akashiwo</i> (100)	<i>A. sanguinea</i> (100)	Cell to cell, cell to filtrate	GI	(19)
<i>S. costatum</i> (100/1000)	<i>G. instriatum</i> (10–1000)	Cell to cell	GI, MM	(10)
<i>S. costatum</i> (2000)	<i>Prorocentrum dentatum</i> (100–10,000), <i>Prorocentrum triestinum</i> (100–10,000)	Cell to filtrate	Both GI and GS depend on cell density	(17)
<i>S. costatum</i> (2000)	<i>P. minimum</i> (10)	Cell to filtrate	GS	(17)
<i>S. costatum</i> (250,000)	<i>C. polykrikoides</i> (107/400)	Cell to cell, cell to filtrate	GI, ISS	(18)
<i>Chaetoceros danicus</i> (50,000)	<i>C. polykrikoides</i> (44/400)	Cell to cell, cell to filtrate	GI, ISS	(18)
<i>Thalassiosira decipiens</i> (1000)	<i>C. polykrikoides</i> (100/400)	Cell to cell, cell to filtrate	ISS	(18)

(1) Qiu et al. (2011), (2) Tillmann et al. (2008), (3) Lyczkowski and Karp-Boss (2014), (4) Fistarol et al. (2004), (5) Yang et al. (2010), (6) Wang et al. (2006), (7) Tang and Gobler (2010), (8) Yamasaki et al. (2007), (9) Uchida et al. (1999), (10) Nagasoe et al. (2006b), (11) Yamasaki et al. (2011), (12) Kubanek et al. (2005), (13) Cai et al. (2014), (14) Wang and Tang (2008), (15) Ji et al. (2011), (16) Tameishi et al. (2009), (17) Yamasaki et al. (2010), (18) Lim et al. (2014), (19) Qiu et al. (2012).

<sup>a</sup> Actual cell concentration when the effects occurred. (-) unknown concentration.



**Fig. 6.** Biological interaction map (BIM) for *Cochlodinium polykrioides*. The diagram describing the biological interactions between the red-tide species and co-occurring species was established based on the literature and our recent findings. Direct predator–prey relationships: *C. polykrioides* is able to feed on diatoms or cryptophytes. In turn, *C. polykrioides* is fed on by ciliates, heterotrophic dinoflagellates, and copepods. Direct inhibitory effects: Diatoms are able to kill *C. polykrioides* by physical contact and/or chemical effect, and *C. polykrioides* is able to kill the red-tide dinoflagellate *Akashiwo sanguinea*. Indirect biological interactions: With increasing nutrient concentration in the surface water, competing diatoms can outgrow *C. polykrioides*. In addition, with increasing thermocline depth, the fast-swimming *C. polykrioides* can descend deeper than co-occurring diatoms, cryptophytes, *Alexandrium* spp., *Karenia mikimotoi*, *Prorocentrum micans*, *Prorocentrum donghainese*, *Ceratium* spp., and *Akashiwo sanguinea* and outgrow these competing red-tide species (see Table 5 and Fig. 3). The direction of the arrows indicates a benefit to (into) or a loss from (out of) *Cochlodinium*. These red-tide species co-occurred in the coastal waters of the South Sea, Korea, from May to October 2014 (Our unpublished data).

are able to kill *C. polykrioides* by physical contact, chemical effects or by out-competing them, leading to the loss terms  $m_{Pd}PC$  (direct) or  $m_{Pi}P$  (indirect) to *C. polykrioides* in models GM4d and GM4i, respectively. In addition, heterotrophic protistan and metazoan predators are able to feed on *C. polykrioides* in models GM1–4 and mixotrophic predators in models GM3–4 (Jeong et al., 1999b; our unpublished data). Because of its strong swimming, *C. polykrioides* can outcompete diatoms when a nutricline forms, and outcompete other dinoflagellates or microflagellates when the nutricline is located at depths  $>20$  m (model GM2). This BIM provides a basis for better understanding the interactions between a target species and other competing species and eventually the red-tide causative species under diverse environmental conditions.

To accurately predict the occurrence of red tides, we need to understand the absolute and relative growth and mortality rates of a red-tide organism. To form red tides such a species may employ vertical migration, mixotrophy, predation, and/or chemical defenses to both enhance their growth rates, and decrease their mortality rates. The diversity of strategies and the disproportionate occurrence of dinoflagellates among red-tide-forming species may be related to the dinoflagellate genome: dinoflagellates have more chromosomes and genes than the other organism groups (Lin, 2011). These genes are more highly expressed than those of other groups (Hou and Lin, 2009), and genetic variation among dinoflagellates is large (Lin, 2011). This wide genetic diversity may enable dinoflagellates to thrive in diverse environments. One potentially fruitful avenue for red-tide research would be to

explore the possibility of predicting red tides by analyzing gene expression in these organisms.

Based on the nutrition and behaviors of red-tide organisms and their biological interactions, we categorized red-tide outbreak mechanisms into conceptual models (GM1–GM4). In GM1, all phototrophic red-tide species were treated as exclusively autotrophic organisms without active swimming ability. Using GM2 (swimming) and GM3 (mixotrophy), we could explain the outbreaks of red tides in nutrient-poor offshore and coastal waters. The potential for swimming-induced reduction in mortality may also allow GM2 and GM3 to explain the occurrence of red tides in the presence of competitors and predators. GM4 reflects biological interactions among red-tide species, such as predator–prey relationships, inhibition by physical contact or chemical effects, and the sequestration of resources (nutrients, light) from other species. This GM can explain red tides by a few species under conditions favorable for most phototrophs, and the succession of dominant species in serial red tides. This hierarchy of GMs may help in establishing new GMs and to contribute to increases in the accuracy of red-tide prediction.

Correctly choosing one of these four GMs for red tides dominated by one causative species is important because the accuracy of predictions may be outweighed by the costs and time required to acquire the relevant information. The parameters that should be measured for GM1 are the specific growth rate of one red-tide species as a function of (1) nutrient concentration and (2) irradiance intensity, (3) the concentrations of nutrients in the surface water, (4) the abundance of the red tide species, (5) the

abundances of its potential heterotrophic predators, and (6) mortality of the red tide species due to predation by heterotrophic predators. However, the additional parameters which should be obtained for using GM4 are (7) the concentrations of nutrients at several depths, (8) the abundance of the red tide species at several depths, (9) prey species, (10) mixotrophic growth and ingestion as a function of prey concentrations, (11) the abundance of its potential prey at several depths, (12) the abundances of its potential heterotrophic predators at several depths, (13) the abundances of its potential mixotrophic predators at several depths, (14) mortality of the red tide species due to predation by heterotrophic predators, (15) mortality of the red tide species due to predation by mixotrophic predators, (16) its swimming speed and vertical migration ability at sea, (17) direct inhibition factors, and (18) indirect inhibition factors. The estimated cost of obtaining data on the parameters for GM4 in Korea is at least 4 times that for GM1. Simultaneously, the time required to obtain the parameters for GM4 will be much greater than that for GM1. Though GM4 is likely to provide more accurate predictions than the other GMs, the cost and time for using GM4 are much greater than those for using GM1. Therefore, GM1 can be used for fast growing red-tide diatoms in eutrophic, shallow coastal waters, while GM4 should be used for slow-growing, but fast-swimming mixotrophic red-tide dinoflagellates like *Cochlodinium polykrikoides* offshore.

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