Harmful Algae 47 (2015) 97–115

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

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

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ARTICLE INFO

Article history:
Received 31 March 2015
Received in revised form 10 June 2015
Accepted 10 June 2015
Available online 30 June 2015

Keywords:
Biological interaction
Diatom
Dinoflagellate
Flagellate
HAB
Mixotroph
Vertical migration

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.

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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http://dx.doi.org/10.1016/j.hal.2015.06.004

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[a]	Can explain	Can't fully explain
1	1960s	All	HT	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		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		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

[a] Biological inhibition: Direct BI – allelopathy. Indirect BI – outgrow and occupy space under different nutrient levels, thermocline depths, etc.