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Review of the main ecological features affecting benthic dinoflagellate blooms

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Abstract – Both benthic and planktic dinoflagellates can produce harmful algal blooms. However most of the studies conducted so far emphasized on planktic species. In the present review, we assessed the main ecological factors affecting the population dynamics of bloom-forming benthic dinoflagellates, with particular emphasis on *Ostreopsis* and *Gambierdiscus*. Based on the basic equation of population dynamics, we mainly focused on growth, predation, mortality, immigration and dispersion. Factors determining the dynamics of benthic dinoflagellate populations are very different from the well-studied case of planktic dinoflagellates. The relative movement of cells and water is the main difference as benthic dinoflagellates depend on a fixed substratum while planktic dinoflagellates depend on a water body. Any alteration in the substratum will affect benthic dinoflagellate populations, as for example the changes in seaweeds concentrations due to predation by sea urchins. We also evaluated the impact of global changes on dinoflagellates bloom occurrence.

Benthic dinoflagellates / *Ostreopsis* / *Gambierdiscus* / ciguatera

INTRODUCTION

Most authors working on harmful algal blooms (HAB) have their main experience in plankton rather than benthos ecology. Recently, the importance of benthic HABs is gaining increasing interest, mainly based on the impact of ciguatera, a syndrome caused by dinoflagellates of genus *Gambierdiscus*, which is the most important food borne disease of non-bacterial origin on the world (Parsons *et al.*, 2012), and on the likely relationship between *Ostreopsis* blooms and respiratory problems in the Mediterranean Sea shores (Mangialajo *et al.*, 2008). These harmful benthic dinoflagellate genera that cause HABs are mainly epiphitic on macroalgae growing on shallow rocky habitats.

The basic equation of population dynamics is:

dN/dt = (Growth + Immigration) – (Predation + Mortality + Dispersion)

Thus, algal blooms dynamics depend on the balance between gains and losses of cells. If gains, due to replication or advection of cells are higher than losses from grazing, mortality and dispersion, a bloom will occur. While these terms have been well studied for phytoplankton, this is not the case for benthic

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dinoflagellates, which usually grow in a shallow and well-illuminated environment where nutrients are usually scarce or depleted (Tindall & Morton, 1998, Shears & Ross, 2009, Pistocchi *et al.*, 2011). Here we review the singularities of the main factors of this equation for benthic HABs in comparison to planktic HABs.

GROWTH

Growth of photoautotrophs depends on the fixation of inorganic carbon and the uptake of nutrients. Carbon fixation depends on light energy through photosynthesis while nutrient uptake is limited by their availability in the seawater, physical constraints and both processes are temperature-dependent. Phytoplankton communities are associated with a particular water body, but benthic dinoflagellates are associated with a substrate. At a mesoscale, while planktic species play an important role in the water body history where they grow, for example, depleting its nutrients in the photic zone, this is not the case of benthic dinoflagellates which, being linked to a substrate, are affected by water with characteristics defined elsewhere. In addition, benthic species play a minimal role in defining the chemical properties of water bodies, since at a mesoscale their biomass is very small compared to that of phytoplankton for a big water volume.

Light provides energy for carbon fixation through photosynthesis. Benthic dinoflagellates are common in surface pristine waters where light is intense and photoinhibition can be expected unless they use strategies to avoid high irradiances. For example, Ballantine *et al.* (1988) suggested that *Ostreopsis lenticularis* can migrate to shaded areas of the macroalgae. Using PAM fluorometry, P-E curves (Rapid Light Curves (RLC), of relative Electron Transport Rate (rETR) *vs* irradiance) (Schreiber, 2004) can be obtained within a few minutes in a non invasive way. High-light adapted organisms have higher maximal photosynthetic rates and their photosynthetic apparatus saturates at higher irradiances compared with low-light adapted cells. P-E curves obtained by PAM fluorometry on some benthic dinoflagellates include characteristics more typical of shade-adapted rather than high-light adapted organisms. This is the case of *Gambierdiscus*, which may exploit the three-dimensional structure of the algal host thallus to minimize light exposure (Villareal & Morton, 2002). During a virtually monospecific bloom of *Ostreopsis* cf. *ovata* studied in Llavaneres, NW Mediterranean Sea (unpublished results), P-E curves were obtained at different depths (2, 4 and 7m) with a cuvette version of Walz Water-PAM fluorometer. The photosynthetic parameters in RLC's showed that dinoflagellates from surface and deep samples were light-adapted and shade-adapted, respectively, at a given time during the day. But these RLC's were also variable during a 24h cycle. As a general trend, higher rETR values were observed in the morning reaching a mid-day maximum, and decreasing rETR values from mid-day till a mid-night minimum (Fig. 1).

Another way to study how benthic dinoflagellates are adapted to light is the study of their pigment composition, e.g. the ratio of peridinin to chl c_2 as proposed by Zapata *et al.* (submitted). These authors argue that low-light adapted benthic dinoflagellates like *Prorocentrum levis* exhibit higher peridinin to chl c_2 ratios, while planktic species like *Alexandrium tamarense* that can bloom in well illuminated surface waters display lower ratios. *Ostreopsis* and *Gambierdiscus* showed intermediate values (Zapata *et al.*, submitted).

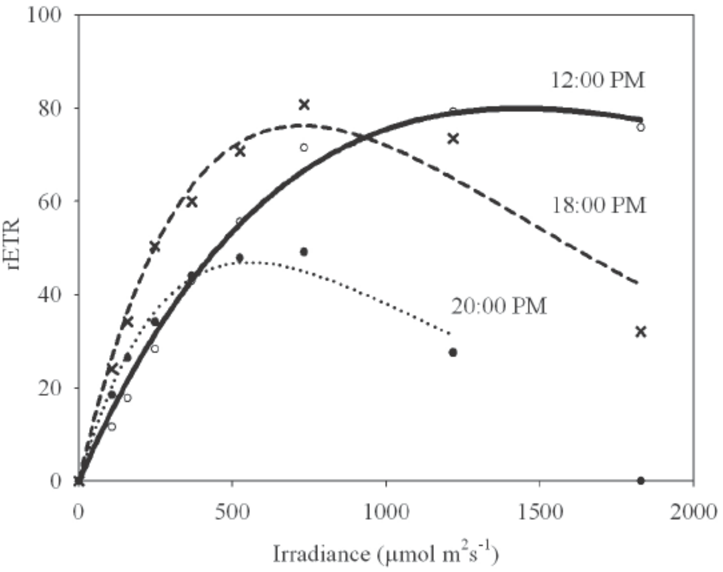

Fig. 1. Fluorescence rapid light curves (RLC) obtained by PAM fluorometry of field samples taken from seaweeds at 0.5 m depth during a bloom of *Ostreopsis* cf. *ovata* in Llavaneres, NW Mediterranean sea during a day.

At very low Reynolds numbers, cells live in an environment where viscosity is more important than inertia (Purcell, 1977, Berg & Purcell, 1977). In very turbulent waters the viscosity in the seawater smoothes out fluctuations smaller than a few millimetres (Lazier & Mann, 1989) so nutrient uptake by small cells, less than 100 µm in diameter, will depend only on diffusion. If nutrient concentration in bulk water is low, when nutrient uptake by the cell is higher than the rate of diffusion, a nutrient-depleted zone develops around the cell. Planktic organisms having the ability to swim can reduce to some extent the thickness of this nutrient-depleted zone, thus increasing diffusion towards the cell surface (Kiørboe, 1993). In the benthic environment, as cells are linked to the substrate, their relative movement to water surrounding them depends more on water motion than on swimming. As water movement due to currents or waves can be about three orders of magnitude higher than dinoflagellates swimming speed, the ability of benthic dinoflagellates to take up nutrients in low nutrient waters is higher than that of phytoplankton. The efficiency of benthic species in nutrient uptake depends not only on their own physiological characteristics like V_{max} or K_s, but also on water velocity according to the mass-transfer theory (Atkinson, 2001). As viscosity decreases when temperature increases, high temperatures will favour nutrients transport.

Nutrient remineralisation in sediments is important and also enhanced by warm temperatures, so release of nutrients by the sediments can provide a continuous nutrient supply that can be instantaneously taken up by all benthic algae and hence, nutrient concentrations remain low. All these factors may explain why benthic dinoflagellates can bloom in warm and nutrient poor waters (Tindall & Morton, 1998; Shears & Ross, 2009; Pistocchi *et al.*, 2011).

There is no clear-cut limit to differentiate benthic from planktic dinoflagellates, so a continuum from planktic to benthic behaviour can be found and hence, many of their associated characteristics show also a continuum. Benthic forms are mainly epiphytic and tend to be flatter than those which are more planktic. Being flattened, the surface/volume ratio is higher than in spherical cells, so this shape helps nutrient uptake under oligotrophic conditions. *Ostreopsis* is flatter and more benthic than *Coolia*, and also prefers more stirred waters compared with *Coolia* (Vila *et al.*, 2001).

The f/2 medium is the most commonly used to grow marine microalgae giving excellent results in most cases. However, there are many experiences in which, using full strength medium to grow benthic dinoflagellates, the cells appear distorted and they do not grow well, while those grown on a diluted medium look much healthier (Holmes *et al.*, 1990). This can reflect the fact that they are adapted to grow in low nutrient environments (Tindall & Morton, 1998; Shears & Ross, 2009; Pistocchi *et al.*, 2011).

In addition to being well adapted to oligotrophic conditions, mixotrophy cannot be discarded. The presence of red bodies in many cells of *Coolia* or *Ostreopsis* is frequently reported (Aligizaki & Nikolaidis, 2006, Selina & Orlova, 2010) and could represent an effect of mixotrophy although this has not been proven. These bodies were observed only in field samples, but when the cells with these bodies are isolated and grown in artificial inorganic medium, the bodies disappear (Authors personal observations).

The importance of temperature for the development of benthic HABs is reflected in the fact that these events occur mainly in tropical waters or in temperate areas during summer (Pistocchi *et al.*, 2011; Parsons *et al.*, 2012). *Ostreopsis* is considered a tropical or subtropical species, but records in colder waters are increasing. It has been observed in temperate regions at latitudes higher than 40º such as the Basque coast of Spain (Laza-Martinez *et al.*, 2011), near Vladivostok, Russia (Selina & Orlova, 2010) and Wellington, New Zealand (Rhodes, 2011). In the Mediterranean Sea, *Ostreopsis* blooms in summer (Mangialajo *et al.*, 2011; Vila *et al.*, 2001) when nutrients are relatively low and light and temperature are high. In all cases, it is clear that when *Ostreopsis* blooms the water is warm although in some cases the bloom may occur after the temperature maximum (Selina & Orlova, 2010; Totti *et al.*, 2010). High water temperatures, high irradiance and high remineralisation are factors that converge to create an environment favouring benthic HABs.

PREDATION

Little is known about the predators able to control populations of benthic dinoflagellates, although the role of invertebrates might be important. Nevertheless it is well known that ciguatera is a syndrome caused by toxins produced by epiphytic dinoflagellates of genus *Gambierdiscus* which are accumulated in fish through the food web. Herbivorous fish are the first predators of *Gambierdiscus* when grazing macroalgae eating also the epiphytes. In this case fish not only predate the dinoflagellates but also their substrate (*i.e.* seaweeds) limiting further development of the bloom.

MORTALITY

The role of parasites such as perkinsid (Alveolata) is being increasingly recognized in planktic species (Norén *et al.*, 1999, Figueroa *et al.*, 2008) and they also affect benthic species (Leander & Hoppenrath, 2008). They have a zooid stage that can infect dinoflagellate cells where they multiply to form a spherical sporangium that liberates many new zooids. They have been tested in many cultures and it has been observed that they can infect many different species. Parasite zooids are abundant when there is a bloom of a susceptible species and they can affect the concentration and even cause the end of a bloom, nevertheless it is unlikely that they control the growth dynamics of the host species when the latter is in low abundance.

IMMIGRATION AND DISPERSION

Immigration and dispersion are very important factors in planktic blooms but as benthic dinoflagellates are more or less attached to the substrate, their circumstances are quite different. Benthic dinoflagellates use different mechanisms for being benthic. *Prorocentrum levis* or *Prorocentrum lima* are strongly attached to the substrate so their dispersion is difficult. Other taxa, like *Ostreopsis*, are attached by mucus threads that form a kind of spider web which encloses the cells and whose size increases as the cells multiply (Fraga unpublished observations). The production of mucus by *O. lenticularis* is higher at higher irradiances (Heil *et al.*, 1993) and this species also forms gas bubbles from daylight photosynthesis. Together, these factors allow this species to float and detach from the substrate, drift to the surface and colonize other areas, helped by the usually stronger winds during the day. Exposure to wind and wave action explains differences in distribution due to dispersion (Shears & Ross, 2009).

Almost nothing is known about the life strategies of benthic dinoflagellates. For instance, it is unclear whether these organisms have particular life-cycle features as a consequence of their different ecological positions compared to planktic species. Few cyst descriptions have been published. Only short-term pellicle cysts from sexual reproduction in *Coolia monotis* (Faust, 1992) and pellicle and thecate cysts of *O.* cf *ovata* (Bravo *et al.*, 2012) have been described. In turn, no dormant resting cysts were detected neither in culture nor in nature. The fact that pellicle and thecate cysts of *O.* cf *ovata* from bloom-incubated samples were able to germinate up to 6 months after their formation suggests that those cysts may constitute an overwintering population responsible for bloom recurrence (Bravo *et al.*, 2012).

GLOBAL CHANGE IMPACT

During the last decade, reports of respiratory problems among people who were in some places of the Mediterranean coast have created public concern in the affected areas. Due to circumstantial evidence, these problems have been related to blooms of the dinoflagellate *Ostreopsis* (Rossini, 2011). Although an increasing awareness of these problems is evident, it is possible that the increase in *Ostreopsis* bloom events has been caused by a phase shift in benthic microalgae communities due to anthropogenic or natural environmental change. These reports of intoxications become common in the Mediterranean Sea after mass mortalities of benthic invertebrates were recorded as a consequence of the exceptional 2003 heat wave (Garrabou *et al.*, 2009). The mortalities could also affect non identified potential predators of *Ostreopsis*, and a potential cascade effect leading to an increase in *Ostreopsis* populations.

Long-term phytoplankton population changes have been reported (Edwards *et al.*, 2006; Beaugrand *et al.*, 2008) but they were smooth and no catastrophic phase shifts were observed in phytoplankton over inter-annual scales. Nevertheless, benthic dinoflagellates live in a more complex and fragile system. Abrupt and catastrophic phase shifts from coral to macroalgal domination have been reported in coral reefs (Hughes, 1994; Bellwood *et al.*, 2004; Nyström *et al.*, 2000) where benthic dinoflagellates are common. The impact of these ecosystem shifts on the populations of benthic dinoflagellates have not been studied in depth, but, for example, we could expect that when a system dominated by corals shifts to one dominated by macroalgae (Hughes, 1994), a change in dinoflagellate communities may also occur.

It is known that sea urchin populations play a key role in the ecology of shallow rocky systems (Lawrence, 1975). In temperate kelp forests, an increase in the abundance of sea urchins due to, for example, a grazing reduction, may create barren zones (Shears & Babcock, 2003; Jackson *et al.*, 2001) whereas in tropical coral reefs a reduction in the populations of sea urchins may cause a shift from a coral dominated to macroalgae dominated system (Hughes, 1994). Increases in sea urchin abundance may even favour the colonization of invasive coral species in areas that were previously dominated by macroalgae (Coma *et al.*, 2011). Obviously, changes in the benthic communities, in particular macroalgal abundance, are likely to play a determinant role in the dynamics of epiphytic dinoflagellates success. Therefore, a close relation between *Ostreopsis* and sea urchins population dynamics is likely. While *Ostreopsis* blooms may kill or severely damage sea urchins (Vila *et al.*, 2008; Ferreira, 2006; Shears & Ross, 2009; Sansoni *et al.*, 2003), the latter can destroy the habitat of *Ostreopsis* by removing macroalgae from rocky substrates (Shears & Ross, 2010) so a balance between sea urchins and *Ostreopsis* might be important.

Another common alteration of reefs is coral bleaching caused by high sea surface temperatures (Glynn, 1993), which has already been associated to ciguatera outbreaks caused by overgrowth of *Gambierdiscus* (Hallegraeff, 2010; Bagnis *et al.*, 1992) as an opportunistic species.

CONCLUSIONS

The main ecological difference between benthic and planktic dinoflagellates is that while planktic species depend on a water body, benthic species depend on a substrate. Hence, some of the well studied processes in plankton dynamics of harmful algal blooms are not applicable to the study of benthic algal blooms, and hence different approaches to their study should be carried out. Benthic systems may suffer abrupt alterations due to cascade effects triggered by the action of some benthic organisms and/or environmental changes that affect the substrate and trophic relations among species.

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