HARMFUL ALGAL BLOOMS IN THE FACE OF CLIMATE CHANGE

MASTER ESSAY

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ABSTRACT

Climate change poses risks to humans and natural systems. There are unquestionable alterations of environmental abiotic factors, namely temperature, stratification, nutrient dynamics, irradiance and ocean acidification. Microalgae are essential for the survival of life on Earth and usually have a positive impact on their habitats. They are at the base of the marine food web which means they are primary producers that synthesize inorganic compounds into organic matter through photosynthesis. Phytoplankton blooms are events of rapid biomass accumulation. When blooms cause negative effects in the environment such as toxin production, oxygen depletion or outcompeting of other species, they are called Harmful Algal Blooms (HAB). Blooms are governed by a combination of biotic and abiotic environmental conditions and by the individual species' life history. It is plausible that with climate change there will also be changes in the frequency and duration of HABs. The aim of this essay is to analyze the link between climate change and HABs by connecting changes in environmental abiotic factors with alterations in blooms. Literature research showed that changes in abiotic factors affect phytoplankton species in different ways, given their genotype and phenotype variation. The expansion of HAB frequency is clear, and algae now have more windows of opportunity for developing into blooms. The interactions of these environmental factors with each other and with living organisms are many and create a complex and intricate web of feedback loops that could eventually be detrimental for the marine environment.

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INTRODUCTION

Phytoplankton performs two major roles in the ocean: first it is the base of the marine food chain and second it is responsible for the biological pump. For its first role, microalgae multiply by converting inorganic carbon and nutrients into organic material through the process of photosynthesis Phytoplankton biomass supports herbivorous zooplankton, followed by carnivorous zooplankton and larger animals such as fish and marine mammals (whales, sharks). The second essential role, the biological pump, occurs when particulate organic carbon from phytoplankton is transported to the deep sea. Both these essential processes are tightly linked to abiotic factors controlling the growth of phytoplankton. This implies that when climate changes, thereby affecting temperature, nutrient availability and irradiance there is the probability that one or both of these processes are affected (Winder & Sommer, 2012).

An algal bloom happens when there is rapid production and accumulation of phytoplankton biomass. It usually occurs when abiotic factors (temperature, irradiance, nutrient availability) open a window of opportunity for the phytoplankton to grow swiftly. Blooms can be an episodic event, a seasonal phenomenon or a rare event often caused by uncommon meteorological conditions (Cloern, 1996). Blooms are considered to be harmful when they have detrimental effects on the environment. Consequences of Harmful Algal Blooms can range from oxygen depletion and strong sunlight attenuation in the water column, to the production of toxins able to kill fish, mammals, birds and even people.

In recent years an increase in Harmful Algal Bloom incidence has been observed. Despite the many reasons that could be provoking this intensification there appears to be a link with climate change (Anderson, 2009). Solar irradiance, altered salinity, ocean acidification, eutrophication, and changes in temperature are factors that have the potential to affect algal growth and toxicity (Fu et al., 2012).

Anthropogenic activity is believed to have caused at least two-thirds of the changes in atmospheric and ocean temperature (Hansen & Stone, 2016). Pressure put on ecosystems when physical conditions are altered can have a strong influence on ecological processes. During the past century global temperature rose 0.85° C and it is estimated that 90% of the Earth's energy gets stored in the ocean (IPCC, 2014). Changes in local climate can impact phytoplankton dynamics which have been proven to be sensitive to alterations in the environment.

The purpose of this essay is to determine what exactly are the mechanisms through which climate change affects harmful algal bloom dynamics. The impacts that the before mentioned abiotic factors have on phytoplankton species will be presented along with specific examples. Finally, consequences of HABs and management possibilities will also be discussed.

PHYTOPLANKTON

Phytoplankton are microscopic plants that live in the ocean and are at the base of the aquatic food web. The word phytoplankton breaks up into "*phyto"* (Greek) meaning plant and "*plankton*" meaning drifter or wanderer which refers to those "organisms that are adapted to spend part or all of their lives in apparent suspension in the open water of the sea" (Reynolds, 2006). The term *apparent suspension* is specified since some species have indeed flagellae that allow them to move around and choose where to settle. Nevertheless, phytoplankton's power of motility does not exceed that of turbulent flows therefore their ability to control their habitat depends on currents (Kersey, 2009; Winder & Sommer, 2012).

Phytoplankton, also known as microalgae or marine algae, can be defined as photosynthetic microorganisms. This means they have the capacity to use the energy of the sun to combine carbon dioxide and inorganic nutrients and turn them into organic matter. Organisms that perform photosynthesis are called photoautotrophs and are therefore primary producers.

Unlike on land where organisms that perform photosynthesis tend to be large (trees, grass, bushes, etc.) in water they are microscopic. Microalgae play a major role on Earth by being the major primary producers despite accounting for less than 1% of the global photosynthetic biomass (Winder & Sommer, 2012).

The physiology of these single-celled organisms, having a large area/volume ratio, causes them to sink at quite low rates which allows them to stay near the water surface. This is important because it is where phytoplankton can receive the necessary irradiance levels to sustain their growth (Kersey, 2009).

The number of algal including phytoplankton species on Earth is actually unknown. Several researchers have tried to find it with estimations varying from a few thousands to several millions. Around 4000 to 5000 species of marine phytoplankton have been described, 300 of which form algal blooms (Silva, 2015; Sournia, 1991). Yet, the amount that is still left to be found is a mystery. The latest estimations calculate that between 20,000 to 100,000 species of phytoplankton exist (Guiry, 2012; Mann & Vanormelingen, 2013). In addition, the definition of "species" creates conflicts and varies greatly when it comes to algae where both morphological or molecular concepts are used.

Microalgae are classified into many different taxonomic groups. Some phytoplankton are organisms without a nuclear membrane, called prokaryotes, as is the case of cyanobacteria. More advanced organisms can be classified under the Eukaryote domain, some examples are diatoms under the phylum Bacillariophyta and dinoflagellates under the phylum Dinophyta.

PHYTOPLANKTON BLOOMS

Phytoplankton blooms are a source of energy for higher trophic levels. They are onset by a combination of factors that include both those related to the individual species' life history and the biotic and abiotic conditions of its environment. A bloom occurs when there is rapid accumulation of phytoplankton in the water column. Weak tides, reduced grazing pressure and sufficient nutrients and light create windows of opportunity for the phytoplankton populations to grow. For blooms to start it is necessary that their growth rate is larger than the loss rate caused by top-down control processes (pelagic and benthic grazing) (Cloern, 1996).

How big a bloom is and how long it will last is controlled by resource dynamics, predator-prey interactions and population feedbacks (Winder & Sommer, 2012). Phytoplankton blooms change every year in terms of size, species composition and time of appearance (Anderson, 2009).

Despite being considerably more common in coastal marine waters, blooms can also occur in the open ocean or freshwater systems. The reason for the coastal prevalence is that nutrient loads are higher nearshore (Anderson, 2012). Blooms have happened for millions of years, fossil sediments from the island of Bornholm (east of Denmark) showed bivalves that had most likely died due to a toxic dinoflagellate bloom (Richardson, 1997).

Historically, blooms have been caused by seasonal related temperature changes. Seasonal algal blooms tend to start with diatom blooms during the transition between winter and spring when there are changes in water temperature and light supply (Winder & Sommer, 2012). Nowadays, important contributors for bloom occurrence are: climate change, eutrophication and alien species transported in ballast waters (Silva, 2015).

In a paper by Reul et al. (2014) the effects that climate change-associated abiotic factors have on the composition and size structure of coastal phytoplankton communities was investigated. In terms of species composition they found that despite the general perception of blooms being explained by bottom-up control, the survival of individuals also depends on the top-down control exerted on them by microzooplankton (direct grazers) and even on the control that mesozooplankton (microzooplankton grazers) have on phytoplankton regardless of not being direct consumers of primary producers. This adds another level of complexity to the understanding of phytoplankton blooms, since changes in climate have their own consequences on these species that are at higher trophic levels.

Blooms are complex since they can be composed of different species or only one. Furthermore they are classified as benign or harmful depending on the consequences they have on the ecosystem, economy or public health (Silva, 2015) .

HARMFUL ALGAL BLOOMS (HAB)

As mentioned in the last section, blooms of phytoplankton species that have negative effects on their environment and on humans are known as Harmful Algal Blooms (HABs). HABs can be formed by species that produce toxins or also by species that despite not being toxic, can deplete the oxygen from the environment, block light or clog fish gills.

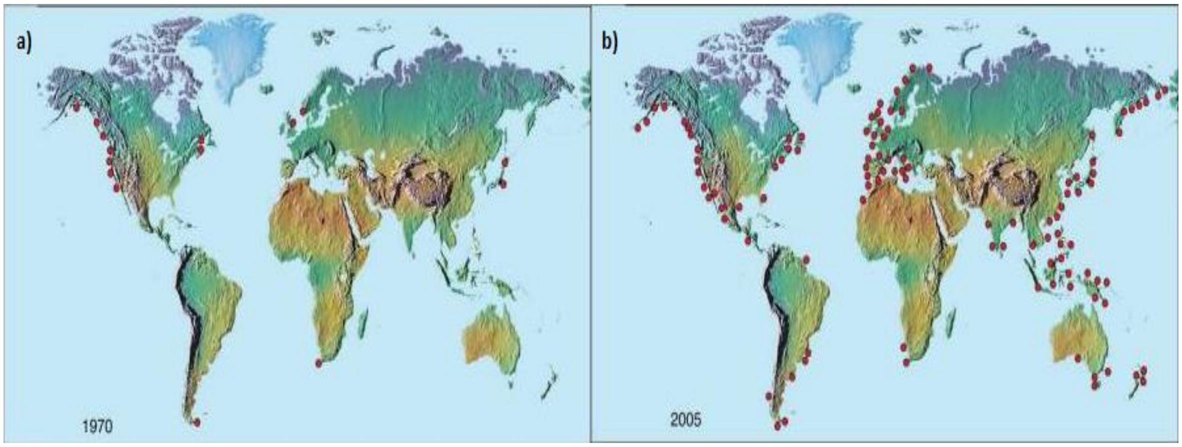

Figure 1 Global expansion of the distribution of paralytic shellfish poisoning (PSP) toxins detected in shellfish and fish. Left: 1970. Right: 2009 From Anderson, 2009.

In recent decades the global concern regarding HABs has increased. In figure 1 we can see the clear and dramatic expansion that there has been of phytoplankton blooms that produce PSP toxins. In the 1970s only a few countries show records of blooms whereas nowadays most coastal countries are affected by them. It is possible the lack of prior concern and quantification of phytoplankton blooms results in the dramatic changes in distribution pattern. Nonetheless, at the present time it is generally accepted that phytoplankton blooms have indeed dramatically increased (Anderson, 2009). What scientists still question is what are the mechanisms that have caused blooms to increase and if they are directly related to human activity.

Most research seems to point at anthropogenic activity as the principal cause for HAB explosion. Humans cause blooms through activities that results in terrestrial discharges to the ocean. This discharges contain a high concentration of nutrients (g.e. agricultural fertilizers) and may result in eutrophication which is in part responsible for the excessive growth of some phytoplankton species (Anderson, Glibert & Burkholder, 2002). In other cases toxic algae are transported through ship ballast water and end up settling as invasive species (Hallegraeff & Bloch, 1992) .

CONSEQUENCES OF HARMFUL ALGAL BLOOMS

HABs can be called toxic, those that produce toxins, or non-toxic but they all have negative effects on either ecosystems, human health or regional economy. In terms of human health, toxic blooms' consequences depend on the type of released toxin. Some toxins can cause conditions and symptoms such as: ciguatera, paralysis (paralytic shellfish poisoning- PSP), amnesia (amnesic shellfish poisoning- ASP), diarrhea (diarrheic shellfish poisoning- DSP), skin irritation, nausea, vomiting or difficulty in breathing. Other species release neurotoxins that can be lethal when entering the body, it is actually estimated that 300 people die every year after consuming contaminated shellfish (Anderson, 2009). It is also believed that the byproducts of HABs can, in some cases, be carcinogenic (Richardson, 1997).

HABs can also be toxic to the environment, most notably when the toxins produced by phytoplankton cause the death of marine organisms. In most cases mortality occurs in fish or shrimp but organisms at higher trophic levels can still be affected. Records exist of whales, dolphins and seabirds dying as a consequence of HABs (Hallegraeff, 1993). It can also be the case that shellfish or fish don't die after ingesting certain toxins, but what can be harmless to them can still be lethal to humans or other species higher in the trophic web (Anderson, 2009).

Other environmental effects of HABs are the death of marine plants and animals due to oxygen depletion or obstruction of light, the death of fish caused by phytoplankton clogging up their gills or the displacement of indigenous species (Anderson, 2009).

HABs can also result in high economic losses, specifically in activities linked to tourism. Even in the cases in which the blooming species do not represent a risk for human health they may still produce foams, repellent odors or change the color of the water that scare tourists away (Silva, 2015). Only the United States of America loses over 100 million dollars every year as a consequences of phytoplankton blooms (Anderson, 2000). Seafood stocks can be affected and sales can drop, fishermen can be out of a job, and contaminated people may need treatment and rest. Countries like China have reported loses of millions of dollars as a results of a single phytoplankton bloom (Qiu, 2012).

Some of the most studied groups of HAB forming phytoplankton are: cyanobacteria, diatoms and dinoflagellates. At least a quarter of the Earth's oxygen comes from diatoms, these pelagic organisms have a frustule (cell wall) conformed by two valves. They are mostly solitary but can also form colonies in the form of chains and are known to form blooms in the spring that usually end when they have depleted silica, which they need for their exoskeleton, from their environment (Battarbee et al., 2002). Diatoms of the genus *Pseudo-nitzschia* cause some of the most toxic HABs; they synthesize a neurotoxin called domoic acid that causes short-term memory loss, vomiting and sometimes even death; symptoms can be acute or become chronic (Gaydos, 2012).

Dinoflagellates, as we can infer from their name, have two flagellae which make them motile, instead of silica they may use cellulose for protection and do not produce large quantities of oxygen. When there is a dinoflagellate bloom water is discolored red or brown, hence the name *red tides* that its blooms receive, some species are bioluminescent giving the ocean a glow at night. Unfortunately this group of plankton often releases toxins that harm humans, for example organisms of the genus *Alexandrium* produce paralytic shellfish poisoning toxins (Reynolds, 2006; Fu, 2012).

Cyanobacteria, also known as blue-green algae, are particularly important to the ocean for doing nitrogen fixation. This taxa can have detrimental effects on the environment when their growth rates are high enough for bloom formation, since their toxins can kill fish and make humans ill (Pearl & Otten, 2013).

CLIMATE CHANGE AND HARMFUL ALGAL BLOOMS

Climate change is probably the most complex feature in phytoplankton bloom development. A most important subject for understanding the underlying mechanisms of HAB dynamics and incidence are changes in abiotic factors and their direct effect on phytoplankton growth and survival. The rates of growth of phytoplankton are ruled by temperature, acidification, nutrient availability, water column stratification and light availability, factors which vary naturally every year (Winder & Sommer, 2012).

In recent years we have seen these factors vary more widely: temperature has spiked, the oceans have acidified and glaciers have started to melt at a rapid pace which could change the salinity of water (Fu et al., 2012). If climate drivers can be natural or human, why has the scientific and public discussion attributed climate change to anthropogenic activity? In a titanic labor, Hansen & Stone (2016) systematically assessed anthropogenic climate change with the use of a complex algorithm and found that "two-thirds of the impacts related to atmospheric and ocean temperature can be confidently attributed to anthropogenic forcing".

Can we say that by affecting the global climate humans are also indirectly responsible for harmful algal blooms? For answering this it is important to understand how each abiotic factor relates to phytoplankton ecology (size structure and species composition) and if they can ignite a bloom.

ACIDIFICATION

Ocean acidification is a major concern for the survival of marine biodiversity. The additional carbon dioxide that has been produced by mankind in the past century has had detrimental effects on the ocean due to the perturbation of the global carbon cycle (Fu, 2012) It is estimated that one-third of the world's carbon dioxide (CO_2) ends up in the ocean and most of it lingers in the epipelagic zone (Sabine et al. 2004). As carbon dioxide dissolves in water it lowers pH which makes the ocean more acidic. Calderia & Wickett (2003) estimated that the pH of the ocean could decrease by 0.77 units by the year 2300 if we keep on burning fossil fuel resources. So far, records show that the ocean's pH is 0.1 units lower than before the industrial era (IPCC, 2014).

Among the consequences that ocean acidification could have for algal species we find: altered growth, altered carbon fixation rates, alterations in nutrient uptake and increased sensitivity to ultraviolet radiation. (Fu, 2012) Phytoplankton play an important role in the uptake of carbon dioxide (from the atmosphere and therefore in helping set back global warming). Phytoplankton use CO_2 for photosynthesis and biomass production, when cells die and decay to the bottom of the ocean they help sediment part of that CO_2 in a process called the biological pump. Once at the ocean's bottom, CO_2 is stored for thousands of years (Rajeshwar et al., 2014).

Results reported by Tortell et al. (2002) demonstrated a shift in taxonomic composition of different Equatorial pacific phytoplankton assemblages when exposed to a range of CO_2 levels, nonetheless all samples were dominated by diatoms and *Phaeocystis sp.* More recent research shows that some species of dinoflagellates have adaptations that may allow them to benefit from a higher concentrations of CO_2, for instance species with carbon concentrating mechanisms and a low-affinity for fixing CO_2 (Fu et al., 2012). Two specific examples are the toxic *Amphidinium carterae* and *Heterocapsa oceanica* which have effective CO_2 transport systems and can therefore considerably reduce ambient CO_2 concentrations. Since their photosynthesis depends only on pure CO_2, their growth rates could be stimulated in the coming years as more of it becomes available in the ocean (Dason et al., 2004a). On the other hand, there are also those species of marine dinoflagellates, such as the red tide forming *Prorocentrum minimum*, *Heterocaps triquetra*, and *Ceratium lineatum* that are limited by HCO_3 and do not respond to elevated concentrations of CO_2 (Fu et al., 2008; Rost et al., 2006).

ACIDIFICATION & TOXICITY

Because toxins are a secondary metabolite they are linked to photosynthesis, the essential process in primary metabolism (Fu et al., 2012). The toxicity of the diatom *Pseudo-nitzschia* has been widely studied since it represents one of the most damaging HAB species in North America (Lange, 1994). *Pseudo-nitzschia* produces domoic acid (DA) a neurotoxin that causes amnesic shellfish poisoning. To test if an increase in environmental CO_2 could lead to higher toxicity in *Pseudo-nitzschia*, Sun et al. (2011) investigated the effects of modifying concentrations of CO_2 when cultivating it. The study proved that DA levels increased 4 times when increasing CO_2 from 7.4 to 23.9 µmol/L and limiting phosphorous. In a similar study, Tatters et al. (2012), found that the toxicity of *Pseudo-nitzschia* blooms could be greatly exacerbated in the coming years. Their laboratory cultures showed increased DA production on silicate-limited media with CO_2 levels similar to those projected for 2100.

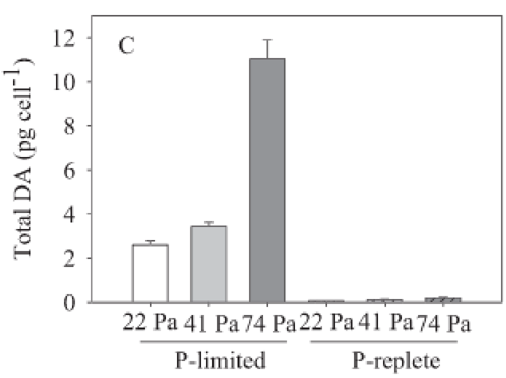

Figure 2. Cellular domoic acid (DA) production by Pseudo-nitzschia in six phosphorous and CO2 treatments. Increasing grey shades represent increasing concentration of CO2 levels. (From Sun et al. 2011)

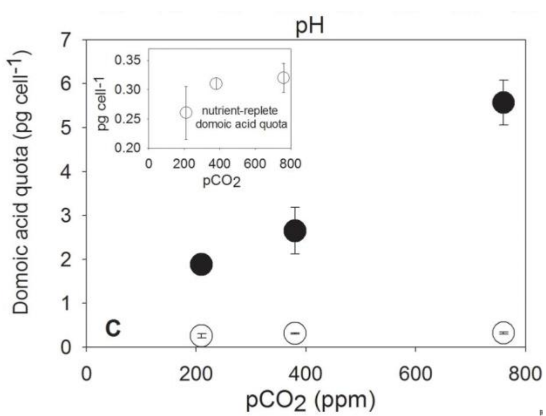

Figure 3. Domoic acid (DA) quota (pg/cell) versus PCO2 in Pseudo nitzschia fraudulenta cultures grown under Si (OH)4 limited and nutrient replete conditions at seawater CO2 concentrations of 200 ppm (preindustrial atmospheric levels, 360 ppm (modern levels) and 765 ppm (projected year 2100 levels). (From Tatters et al. 2012)

WATER COLUMN STRATIFICATION: TEMPERATURE, WIND ACTION AND NUTRIENT AVAILABILITY

In the past years global atmospheric temperature has increased significantly, about 0.8°C since 1880. It is expected to rise 2-4°C in the next 100 years (Hallegraeff, 2010). The magnitude of this temperature changes has happened before but at a much slower pace and starting from cooler initial temperatures (IPCC, 2014). Temperature can influence community structure of HAB species because it could change the timing of initiation of blooms (Fu et al., 2012). With a rising temperature, seasonal patterns would be altered which could change the windows of opportunity for microalgae species to grow (Wells et al., 2015).

The ocean does not warm up evenly, most of the energy from temperature rise is stored in the upper 700 m, particularly the 75 m closest to the surface which according to the IPCC (2014) report warmed 0.11°C from 1971 to 2010. Increases in temperature cause water stratification due to a thermocline, a thin line that separates layers of water masses with different temperatures. Normally, the upper layer is uniform thanks to the mixing done by waves and currents that upwell nutrients to the surface. (Winder & Sommer, 2012).

As the ocean surface warms and stratification is enhanced, nutrient upwelling is reduced. As a consequence the windows of opportunity for HAB development change and so do phytoplankton communities (Fu et al., 2012). Phytoplankton need to be close to the ocean's surface to capture sunlight, but as nutrients in the upper layer are depleted, only certain species will be able to bloom. Moore et al. (2008) hypothesized that dinoflagellates would be favored in future climate scenarios since they have two flagella with which they could swim to lower layers of the water column to uptake nutrients and so ultimately more dinoflagellate HABs would be seen in the future. In a later study, Moore et al. (2009) showed (Fig. 4) that with elevated air and temperatures, more toxic dinoflagellate blooms would be present in Washington, USA.

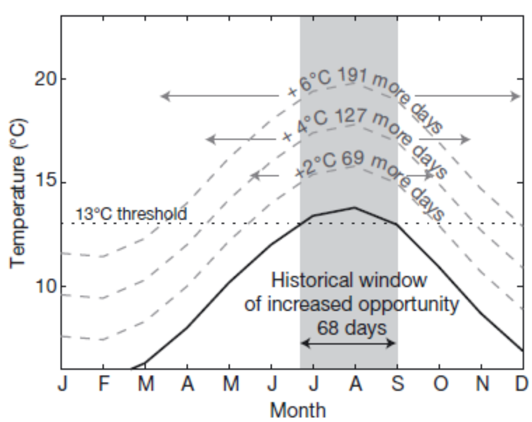

Figure 4. Expansion of the annual temporal window for blooms of saxitoxin-producing dinoflagellates in Puget Sound, Washington, USA at projected sea surface warming levels. The annual bloom window could expand from 68 to 259 days. (From Moore et al. 2009)

Stratification can also be the result of different water densities, salinities or oxygenation and it is actually a cornerstone process for phytoplankton population dynamics (Rajeshwar, Sinha, & Hader, 2014; Winder & Sommer, 2012). Climate change affects not only the ocean's temperature but also its salinity and pH by altering the global water cycle (Moore et al., 2008).

To study the effects that the projected climate change for 2100 would have on the Dutch Wadden Sea, Peperzak (2003) grew 8 species (6 harmful and 2 non-harmful) of phytoplankton under a 4°C rise and increased salinity stratification. As a result he found that the two non-harmful species did not significantly change. For the harmful species, two raphidophytes (the red tide forming *Fibrocapsa japonica* and the brevetoxin producer *Chattonella antiqua*) and two dinoflagellates (*Prorocentrum micans* and *Prorocentrum minimum*) doubled their growth rates, a prymnesiophyte and a diatom died rapidly. The four species that doubled their growth rates are observed regularly in the coastal zone of the Netherlands, so there is a risk that HABs by these species will increase substantially. Nonetheless, drawing conclusions was found to be difficult since temperature and salinity are based on projections.

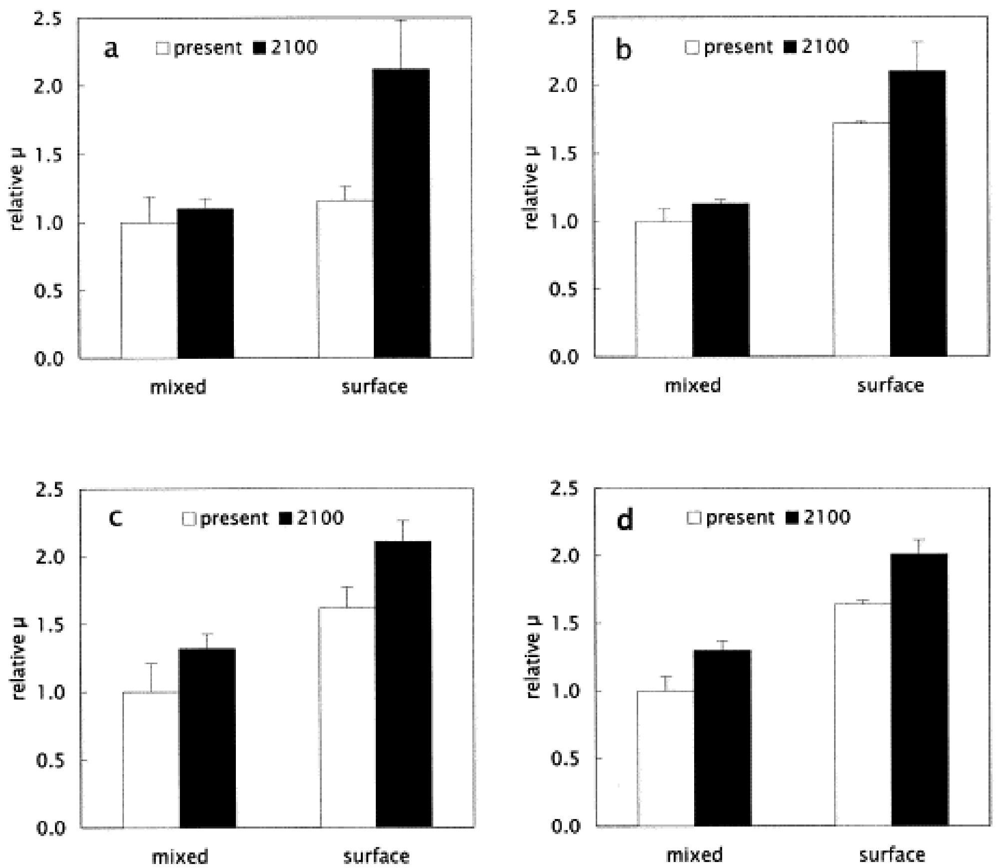

Figure 5. Mean growth rates (± S.D.) of P. micans (a), P. minimum (b), F. japonica (c) and C. antiqua (d) under 2100-mixed, present-surface and 2100-surface conditions relative to the growth rate under present mixed conditions. (From Peperzak 2003)

A more recent study done in the North Sea and the Northeast Atlantic showed a phytoplankton community shifting from dinoflagellates to diatoms (*Pseudo-nitzschia* and *Thalassiosira spp.*) when increasing sea surface temperature (Hinder et al., 2012). The difference between the results of these two studies is probably because the latter focused on the open ocean where physics dynamics and nutrient availability differ widely to what happens in coastal waters.

HABs toxicity is expected to be sensitive to different temperature scenarios (Paerl & Huisman 2008). The relationship between temperature rise and HAB toxicity is not yet very clear (Griffith et al., 2016) Some toxic cyanobacteria have shown to be favored over non-harmful cyanobacteria when exposed to higher temperatures (Paerl & Huisman 2008). When the environmental modulation of karlotoxin produced by the dinoflagellate *Karlodinium veneficum* was investigated, cultures exhibited an increased toxicity at temperatures greater than 25°C (Adolf et al., 2009). Furthermore, based on extensive literature, Fu et al. (2012) argue that the expansion of ciguatera fish poisoning caused by toxins of the dinoflagellate genus *Gambierdiscus* are caused by increasing temperatures in the sea surface that result in a higher growth rate and higher production of ciguatoxins (Bomber et al., 1988).

Rising temperatures do not always mean higher toxicity, such is the case for *Cochlodinium polykrikoides,* a species that shows maximum growth at temperatures of 24 to 27°C but whose toxicity decreases at higher temperatures. This species has positive growth rates from 15 to 30°C, which means it can develop into blooms in temperate regions where it will be more toxic than when occurring at tropical latitudes (Fig. 6, Griffith & Gobler, 2016). Regarding other species, the few studies done on the diatoms of the genus *Pseudo-nitzschia* to link increasing temperature to a higher domoic acid release have observed none to very little correlation (Bates et al., 1998; MacIntyre et al., 2011)

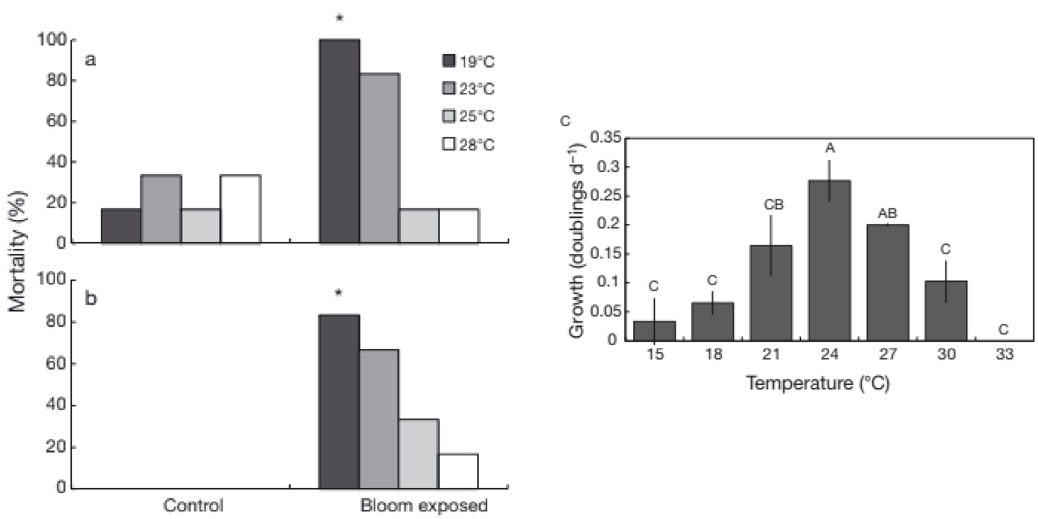

Figure 6. Mortality of Cyprinodon variegatus (a) and Menidia beryllina (b) when exposed to a Cochlodinium polykrikoides bloom at different water temperatures. C) Effect of temperature on growth of Cochlodinium polykrikoides (From Griffith & Gobler, 2016)

Most of the existing literature is based on studying the effect of a single factor in HAB species (reviewed by Fu et al., 2012; reviewed by Hallegraeff, 2010). The future ocean will challenge phytoplankton with simultaneous changing conditions of temperature, acidification, light and nutrient availability. Very seldom studies have been done analyzing combined effects.

Fu et al. (2007) analyzed the effects of changing CO2 and temperature on two species that typically bloom together, the toxic raphidophyte *Heterosigma akashiwo* and the dinoflagellate *Prorocentrum minimum*, producer of the shellfish poisoning venerupin toxin.Each species reacted differently, photosynthetic rates of the raphidophyte increased only when CO2 and temperature increased together, whereas the dinoflagellate's photosynthetic rates responded only to CO2 availability.

Following the same framework, Fu's research group analyzed the growth of the raphidophyte *Chattonella subsalsa*, producer of brevetoxins, and the dinoflagellate *Alexandrium catenella,* producer of the neurotoxin saxotoxin, under CO2 and temperature conditions predicted for the end of the century (Fu et al., 2012). Figure 7a shows how the growth of *C. subsalsa.* could be enhanced with a 4°C increase in temperature and double the amount of available CO2 (750 ppm). *A. catenella* was exposed to four treatments: control, high CO2, high temperature and greenhouse (high temperature and high CO2). Cellular toxin contents did not differ much from the control when temperature was increased but they were around 50% higher at high CO2 (Figure 7b). This results indicate that *Alexandrium catenella* could be more toxic in acidified regimes regardless of temperature shifts.

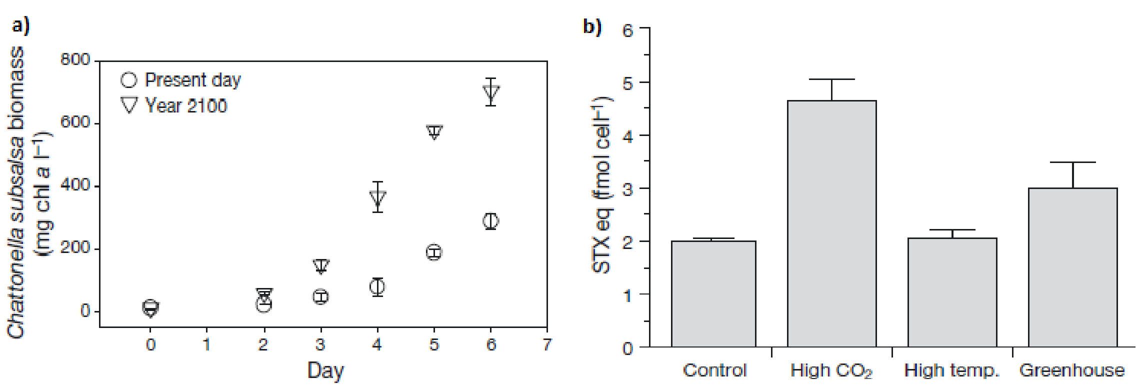

Figure 7. a) Chattonella subsalsa. Growth at present-day temperature and pCO2 (20°C and 375 ppm CO2), and at levels projected for the year 2100 (24°C and 750 ppm CO2)
b) Alexandrium catenella, Paralytic shellfish toxin contents when grown at control (15°C, 380 ppm CO2), high CO2 (15°C, 800 ppm), high temperature (19°C, 380 ppm) and greenhouse (19°C, 800 ppm).
(From Fu et al, 2012)

Phytoplankton being photoautotrophs depend on light for photosynthesis and the future ocean could change light availability for some species (Fu et al., 2012). As surface stratification is enhanced by temperature or salinity shifts, phytoplankton close to the sea surface will be exposed to higher ultraviolet radiation (Gao et al., 2012). The amount of light/irradiance in the water column depends greatly on the transparency of the water and dissolved particles can affect this. If a region is eutrophic or oligotrophic this may also have a great impact on light availability (Rajeshwar et al., 2014).

The growth rate of some photosynthetic algae has been proven to depend on irradiance, for instance the growth rate of *Alexandrium catenella*, a toxic dinoflagellate producer of the paralytic shellfish poisoning (PSP) toxin. One study (Laabir et al., 2011) tested this dinoflagellate´s specific growth rate starting at a minimum irradiance of 10 µmol photons $m^{-2}s^{-1}$ and found that cell yield increased significantly until 90 µmol photons $m^{-2}s^{-1}$. No photoinhibition occurred at the maximum irradiance levels tested of 260 µmol photons $m^{-2}s^{-1}$. Zhang et al. (2006) compared the growth of the two toxic raphydophytes *Chattonella subsalsa* and *Heterosigma akashiwo*, and found that light intensity affected them in a similar way. Optimum growth for both species was found within the range of 100-600 µmol quanta $m^{-2}s^{-1}$ and no photoinhibition happened at the highest light level used.

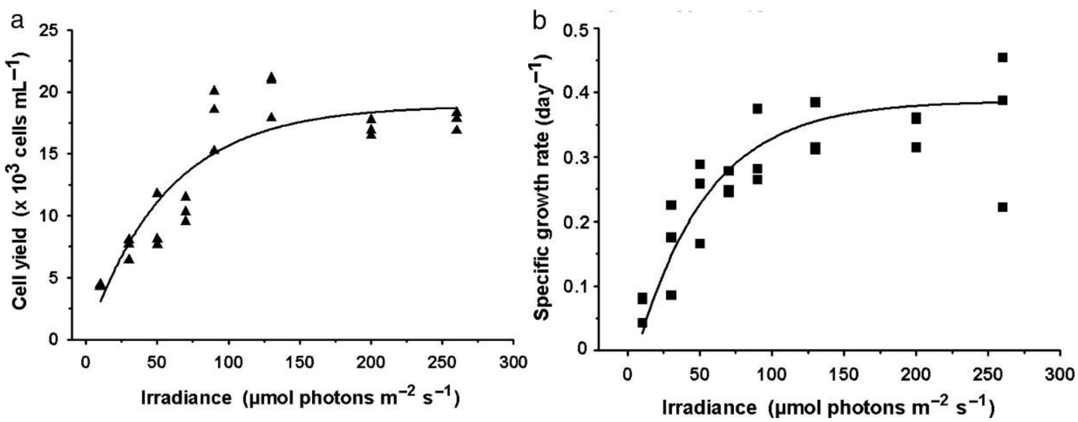

Figure 8. Final cell concentration (a) and specific growth rate (b) for A. catenella strain ACT03 at various irradiance values at temperature 20C and salinity 38 psu. (From Laabir et al., 2016)

SOLAR IRRADIANCE & TOXICITY

Studies on different species have tried to link light intensity with toxin production. One example of toxin production enhanced by light is seen in *Pseudo-nitzschia* spp. where total toxin production increased under a long photoperiod (18 hours of light, 6 hours of dark) as opposed to a short photoperiod (9 hours of light, 15 hours of dark) (Fehling et al., 2015). In contrast, other species' toxin production does not appear to differ between low light and high light conditions, as is the case of the diarrheic shellfish poisoning toxin producer *Dinophysis* spp. (Tong et al. 2011). In the case of the genus *Alexandrium*, Lim et al. (2006) found that if light is positively related to growth rates, it is actually temperature and not light that has a higher impact on toxicity.

CONCLUSION

Anthropogenic activities from the past century have caused climate to change, as a consequence environmental factors such as temperature, light irradiance, salinity, nutrient input, grazing pressure and other physical conditions have been altered (Anderson, 2009; IPCC, 2014). Changes in HABs have been associated with climate change, identifying the exact mechanisms through which the alteration of abiotic factors impacts bloom dynamics is essential for the understanding and future management of the problem (Fu et al., 20012; Hallegraeff, 2010).

We may predict that phytoplankton will now face waters that have higher concentrations of carbon dioxide in the upper 200 m of the column, higher temperatures and higher light irradiance but less nutrient concentration due to the strong stratification caused by temperature rise. This will only happen in the open ocean since coastal areas are expected to receive high concentrations of nutrients due to terrestrial run-off which will result in eutrophication (Gao et al., 2012).

A limitation for this essay was the lack of literature regarding the effects that the combined abiotic factors may have on phytoplankton species. Furthermore, most of the cited studies used only one strain of a phytoplankton species and results can widely vary from and results can be very different among strains of a same species. (Martinez et al., 2010). It would be positive for the understanding of the topic if a new outtake was applied on research and more multifactorial laboratory experiments would be performed to understand the complexity of HAB formation.

So what is left to do if there is a Harmful Algal Bloom? Here, once more, species diversity makes it very challenging to have a “one size fits all” solution. Monitoring HABs is a way in which fisheries can be protected and economic losses reduced, levels of water toxicity can be measured or fishing can be done away from HABs. A very clever method of bloom control has been using clay particles so that they clump together with microalgae and can be easily removed. Chemical control was one of the first methods of bloom control. Another solution is prevention, which is currently being done by controlling waste discharges in industrial areas (Watson, 1997).

The ocean is changing rapidly and unmercifully and only will survive those species of phytoplankton that can adapt thanks to their size structure, light tolerance, ability for nutrient competition and possibility of motility. Phytoplankton’s species diversity is large, combined with large population sizes and fast generation times, it is safe to say they will adapt to the future ocean. What remains a challenge for scientists is to understand how community structure will be affected and how exactly HAB species will react to different scenarios and how can they be controlled.

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