



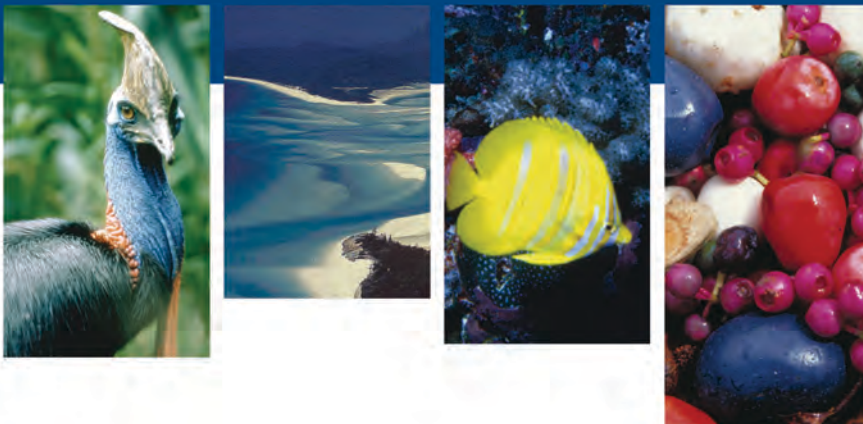
# Commonwealth Environment Research Facilities

## Marine and Tropical Sciences Research Facility



## The influence of nutrients and temperature on the global distribution of algal blooms

Compiled by Leanne Sparrow and Kirsten Heimann



Australian Government  
Department of the Environment,  
Water, Heritage and the Arts



# **The influence of nutrients and temperature on the global distribution of algal blooms**

## **Literature Review**

Compiled by Leanne Sparrow and Kirsten Heimann

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James Cook University



**Australian Government**

**Department of the Environment,  
Water, Heritage and the Arts**

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## Abstract

Algal blooms are defined as increased abundance, biomass or population growth. This review reveals knowledge gaps regarding bloom initiation and nutrient preferences and is divided into four parts.

Part one investigates nutrient effects and challenges the paradigm of macroalgal growth limitation by nitrogen in temperate – but phosphate in tropical regions. Macroalgal nutrient preferences are phyla-specific; diatoms are iron and nitrate co-limited; preferences for other phytoplankton remain to be determined.

Parts two and three investigate global distributions of algal blooms. Macroalgal blooms are restricted to tropical regions and associated with reduced herbivory and disturbances, i.e. cyclones. Macroalgal succession patterns indicate a potential role in reef recovery.

Since phytoplankton blooms occur in all climatic zones, seasonality was included in part three. Diatoms bloom in summer in the tropics but in spring and autumn in all other regions. In contrast, dinoflagellates and other harmful algae bloom in spring in the tropics and any season in other regions, showing strong temperature dependence.

Part four shows that the colonial bloom-forming microalga, *Chrysochysis fragilis* – a new record for the Great Barrier Reef – exhibits some macroalgal traits; blooms occur at high temperatures in oligotrophic conditions, if coral cover is compromised by the crown-of-thorns starfish or bleaching.

## 1.0 Introduction

Algal blooms are broadly defined as a significant increase in abundance (Lapointe 1999), biomass (Legendre 1990), or population size (Smayda 1997). This review will refine this definition as an increase in abundance, which cannot be regulated by grazers for any period of time. Traditionally, nutrient influx by either natural events, i.e. riverine plumes, storms and upwelling (Fujita *et al.* 1989, Longhurst 1993, Grimes and Kingsford 1996, Oke and Middleton 2001, Fitzwater *et al.* 2003, Moisander *et al.* 2003, Wieters *et al.* 2003, Yin 2003, Carstensen *et al.* 2004, Hodgkiss and Lu 2004, Yin *et al.* 2004, Beman *et al.* 2005, Furnas *et al.* 2005), or anthropogenic activities, i.e. coastal urban runoff and sewage (Smith *et al.* 1981, Hodgkiss and Lu 2004, Lapointe *et al.* 2004, Carruthers *et al.* 2005) has been viewed as the primary cause of algal blooms.

Macroalgae are photosynthetic plants found in many environments worldwide. In temperate regions, macroalgae are an important and natural component of the benthic ecosystem, such as the giant kelp (*Macrocystis pyrifera*) beds in California (Edwards and Estes 2006) and the Falkland Islands (Van Tussenbroek 1989). In tropical regions, however, macroalgae are viewed as competitors that threaten the dominance of corals in reef ecosystems. Coral dominance may be challenged by frequent large-scale disturbances, i.e. storms and cyclones (Bythell *et al.* 1993, Dollar and Tribble 1993, Connell *et al.* 1997), which are thought to deliver terrestrial-derived nutrients in concentrations sufficient to trigger and sustain macroalgal blooms (Cooper 1966, Walsh 1983, McCook 1999). In Kaneohe Bay (Hawaii), nutrient influx from sewage – a practice that lasted for approximately fifty years – is thought to have caused a phase shift from reefs dominated by corals to reefs dominated by the green macroalga *Dictyosphaeria cavernosa* (Smith *et al.* 1981, Stimson *et al.* 2001).

Microalgae occur as benthic, epithelic, symbiotic and pelagic forms. Pelagic microalgae are also referred to as phytoplankton, which will be the focus of this review. The phytoplankton community mostly consists of picoplankton (bacteria and cyanobacteria), diatoms and dinoflagellates. Most diatom and cyanobacteria species depend on photosynthesis as their source of energy. In contrast, motile dinoflagellates, chrysophytes and raphidophytes have different feeding strategies. For example, *Pfiesteria piscicida* is a heterotrophic dinoflagellate that feeds on bacteria and cryptophytes (Fan *et al.* 2003b), while others such as *Prorocentrum minimum* are mixotrophic and graze on cryptophytes but photosynthesise as well (Glibert *et al.* 2005).

In oligotrophic conditions, phytoplankton communities are dominated by picoplankton (Behrenfeld *et al.* 1996, Coale *et al.* 1996, Frost 1996, Örnólfsson *et al.* 2004, Furnas *et al.* 2005). Picoplankton has been observed to increase in biomass after iron fertilisation experiments in the equatorial Pacific Ocean (Coale *et al.* 1996, Frost 1996) and after nutrient influx in the Great Barrier Reef (Furnas *et al.* 2005). Picoplankton blooms, however, are rarely observed as their growth rates are equalled by their main predators, ciliates and flagellates (Coale *et al.* 1996, Frost 1996, Furnas *et al.* 2005).

Shifts from picoplankton to diatom dominated phytoplankton communities are characteristic events that follow an influx of nutrients and are caused by diatoms capable of two to four doublings a day (Furnas *et al.* 2005). Copepods are the main grazers of diatoms and it has been suggested that the predator's doubling time of one week enable diatoms to bloom before grazing pressures can regulate their growth (Coale *et al.* 1996, Furnas *et al.* 2005).

## 2.0 Nutrients

Algae can assimilate nitrogen from a range of sources, including nitrate, nitrite, ammonium, urea, atmospheric nitrogen (cyanobacteria), recycled organic matter and amino acids (Libes 1992). Nitrate and ammonium are the most common forms of nitrogen occurring naturally; elevated levels however, are typically associated with anthropogenic activities (Lapointe 1987, 1989, Lapointe *et al.* 1992, Libes 1992, Peckol *et al.* 1994, Fong *et al.* 2003, Kasih and Kitada 2004, Lapointe *et al.* 2004). Nutrient experiments can identify nutrients that limit growth of different algal species. Table 1 shows data collated from extensive literature searches on nutrient limitation experiments for various algal species in tropical and temperate regions.

### 2.1 Nutrient limitation of macroalgal blooms

Our analysis of published nutrient experiments (Table 1) casts doubt on the paradigm that growth of macroalgae is nitrogen limited in temperate regions and phosphate limited in tropical regions (Littler *et al.* 1991, Smith and Johnson 1995, Larned 1998, Fong *et al.* 2001). The phosphate binding capacity of carbonate-rich sediments in tropical waters is thought to limit phosphate availability; an assumption that contributed much to the development of this part of the above paradigm (Done *et al.* 1991, Rogers and Miller 2006). However, the limiting nutrient in tropical regions appears to vary between phyla (Table 1) with phosphate limitation only suggested for the heterokont class Phaeophyceae. Ammonium appears to limit growth for chlorophytes, while a combination of nitrogen and phosphate appears to limit growth of rhodophytes and diatoms (class Bacillariophyceae) (Table 1). Although the paradigm that nitrogen is the limiting nutrient in temperate regions appears to still hold, not all studies included phosphate in addition to nitrogen in their experimental design. Only thirteen percent of experiments conducted used all common nutrient sources (nitrate, ammonium and phosphate, Table 1). Therefore the generalising statement of nitrogen limitation in temperate regions versus phosphate limitation in tropical regions becomes questionable.

Analysis of nutrient experiments indicates that elevated nutrient concentrations stimulate macroalgal growth (Table 1). All experiments, however, were conducted with high nutrient concentrations. This does not provide data on the minimal nutrient levels required to sustain growth. Recent studies on the Moorea (French Polynesia) and St. John (Virgin Islands, USA) reefs documented the continued dominance of macroalgae in low nutrient to oligotrophic environments (Smith *et al.* 1981). This contrasts observations in Kaneohe Bay (Hawaii), where macroalgal dominance is thought to be a result of long term elevated nutrient levels (Koop *et al.* 2001). Recent ENCORE experiments on nutrient enrichment on coral reefs in the Great Barrier Reef were conducted over a two-year period. The intention was to unequivocally demonstrate the link between increased nutrient levels and phase shifts from coral to macroalgal dominance (Koop *et al.* 2001). Macroalgae showed a varied response to elevated nutrients and no phase shifts to macroalgal dominance were observed (Koop *et al.* 2001). This indicates that elevated nutrient levels are not the only factor needed for the development of macroalgal blooms in tropical regions.

**Table 1:** Summary of limiting nutrients on growth of different algal species sourced from nutrient experiments.

Region	Algal species	Algal group	Location	Growth limited by nutrients							Reference
				NO <sub>3</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>	PO <sub>4</sub> <sup>3-</sup>	N+P	Fe	Inhibited	DON	
<b>Haptophyta</b>											
temperate	<i>Phaeocystis</i> sp.	micro	North Sea	x	x	x					2
<b>Heterokontophyta Class Bacillariophyceae</b>											
temperate	<i>Monoraphidium</i> sp.	micro	Baltic Sea	x		x		Fe + P			12
temperate	<i>Nitzschia</i> spp.	micro	Baltic Sea	x	x	x		Fe + P			12
temperate	<i>Phaeodactylum tricornutum</i>	micro	U.K.						NO <sub>3</sub> by NH <sub>4</sub>	x	13
tropics	Unidentified	micro	equatorial Pacific					x			14
<b>Heterokontophyta Class Chrysochyceae</b>											
temperate	<i>Aureococcus anophagefferens</i>	micro	Long Is., USA	x	x				DIN	x	3; 4
<b>Heterokontophyta Class Phaeophyceae</b>											
temperate	<i>Pelvetiopsis limitata</i>	macro	Oregon, USA	x	x						1
tropics	<i>Chnoospora implexa</i>	macro	GBR		x		x				5
tropics	<i>Dictyota cervicornis</i>	macro	Puerto Rico	x			x				6
tropics	<i>Dictyota divaricata</i>	macro	Belize		x	x	x				7
tropics	<i>Dictyota</i> spp.	macro	Jamaica	x			x				8
tropics	<i>Hydroclathrus clathratus</i>	macro	GBR		x		x				5
tropics	<i>Lobophora variegata</i>	macro	Jamaica	x			x				8
tropics	<i>Padina japonica</i>	macro	Hawaii		x		x				9
tropics	<i>Padina tenuis</i>	macro	GBR		x		x				5
tropics	<i>Sargassum baccularia</i>	macro	GBR		x		x				5; 10
tropics	<i>Sargassum baccularia</i>	macro	GBR		x		x		high		10
tropics	<i>Sargassum echinocarpum</i>	macro	Hawaii		x		x				9
tropics	<i>Sargassum polyceratum</i>	macro	Jamaica	x			x				8
tropics	<i>Sargassum polyceratum</i>	macro	Florida	x	x		x				11
tropics	<i>Sargassum pteropleuron</i>	macro	Florida	x	x		x				11
<b>Chlorophyta</b>											
temperate	<i>Cladophora vagabunda</i>	macro	Waquoit Bay USA		x		x				15; 16
temperate	<i>Codium fragile</i>	macro	Rhode Is. USA	x							17
temperate	<i>Nannochloropsis</i> spp.	micro	Waquoit Bay USA	x			x			x	18
tropics	<i>Caulerpa racemosa</i>	macro	Hawaii		x		x				9
tropics	<i>Caulerpa sertularioides</i>	macro	Hawaii		x		x				9
tropics	<i>Chaetomorpha linum</i>	macro	Jamaica	x			x				8
tropics	<i>Cladophora prolifera</i>	macro	Bermuda	x			x			x	19
tropics	<i>Codium edule</i>	macro	Hawaii		x		x				9
tropics	<i>Codium isthmocladum</i>	macro	Jamaica	x			x				8
tropics	<i>Codium isthmocladum</i>	macro	Florida		x		x				8
tropics	<i>Dictyosphaeria cavernosa</i>	macro	Hawaii	x	x						20
tropics	<i>Dictyosphaeria vershuysii</i>	macro	Hawaii		x		x				9
tropics	<i>Halimeda opuntia</i>	macro	Belize		x		x				7
tropics	<i>Ulva fasciata</i>	macro	Hawaii		x		x				9
<b>Rhodophyta</b>											
temperate	<i>Gracilaria tikvahiae</i>	macro	Waquoit Bay USA		x		x				15; 16
tropics	<i>Acanthophora spicifera</i>	macro	Puerto Rico	x			x				6
tropics	<i>Acanthophora spicifera</i>	macro	Belize		x		x			x	7
tropics	<i>Gracilaria salicornia</i>	macro	Hawaii		x		x				9
tropics	<i>Gracilaria tikvahiae</i>	macro	Florida	x	x		x				11; 21; 22
tropics	<i>Hypnea musciformis</i>	macro	Puerto Rico	x			x				6
tropics	<i>Kappaphycus alvarezii</i>	macro	Hawaii		x		x				9
tropics	<i>Kappaphycus alvarezii</i>	macro	Philippine		x						23
tropics	<i>Laurencia poitei</i>	macro	Florida	x	x		x				11
tropics	<i>Lithophyllum kotschyannum</i>	micro	Zanzibar	x	x		x		phosphate		24

**Legend:**

x - denotes the nutrient sources used  
 coloured areas - denotes the nutrient source that limited growth

NO<sub>3</sub><sup>-</sup> :NitrateNH<sub>4</sub><sup>+</sup> :AmmoniumPO<sub>4</sub><sup>3-</sup> :Phosphate

N+P :Nitrogen &amp; Phosphate

Fe :Iron

DON :Dissolved Organic Nitrogen

**References:** 1. (Fujita *et al.* 1989); 2. (Riegman *et al.* 1992); 3. (Berg *et al.* 1997); 4. (Laroche *et al.* 1997); 5. (Schaffelke 1999); 6. (Fong *et al.* 2003); 7. (Lapointe *et al.* 1987); 8. (Lapointe 1997); 9. (Larned 1998); 10. (Schaffelke and Klumpp 1998); 11. (Lapointe 1989); 12. (Moisander *et al.* 2003); 13. (Flynn and Wright 1986); 14. (Coale *et al.* 1996); 15. (Peckol *et al.* 1994); 16. (Rivers and Peckol 1995); 17. (Hanisak 1979); 18. (Taylor *et al.* 1995); 19. (Lapointe and O'Connell 1989); 20. (Larned and Stimson 1996); 21. (Lapointe 1987); 22. (Lapointe 1985); 23. (Dy and Yap 2001); 24. (Bjork *et al.* 1995).

Classification is based on Lee (1999).

## 2.2 Nutrient limitation of diatom blooms

Our analysis of nutrient experiments (Table 1) suggests that diatom growth may be limited by iron in temperate and tropical regions. There are three major oceanic regions of high nitrate and low chlorophyll (HNLC). Iron fertilisation experiments were conducted in two of these regions, the tropical equatorial Pacific Ocean (Behrenfeld *et al.* 1996, Coale *et al.* 1996, Frost 1996) and in the polar Southern Ocean (de Baar *et al.* 1995, Reay *et al.* 2001). HNLC areas also exist in coastal regions. Fitzwater and others (2003) suggested that iron was required in association with nitrate to initiate phytoplankton blooms in discrete coastal HNLC 'pockets' of California, which are not supplied with nutrients via upwelling. Using this unique coastal system, Fitzwater and others (2003) demonstrated this interdependence with iron fertilisation experiments. Iron addition increased phytoplankton growth in the HNLC 'pockets' but not in upwelled areas. A further experiment was conducted using upwelled waters. Iron was added to one sample followed by the addition of nitrate to both samples after a decline in chlorophyll *a* – and nitrate concentrations. The sample with additional iron redeveloped maximum chlorophyll *a* levels in less than twenty-four hours, while the other did not. The iron requirement for the initiation of diatom blooms is associated with the chemical pathway of nitrate assimilation, because the enzyme nitrate reductase requires iron as a co-factor (Frost 1996, Paerl *et al.* 1999).

A single study investigated effects of continuous eutrophication on phytoplankton community structure in Junk Bay (Hong Kong) (Hodgkiss and Lu 2004). This study found that diatoms are common almost all year round but blooms still only occur in summer. However, it remains unclear whether these summer diatom blooms were linked to a higher concentration of iron in addition to elevated nitrate levels.

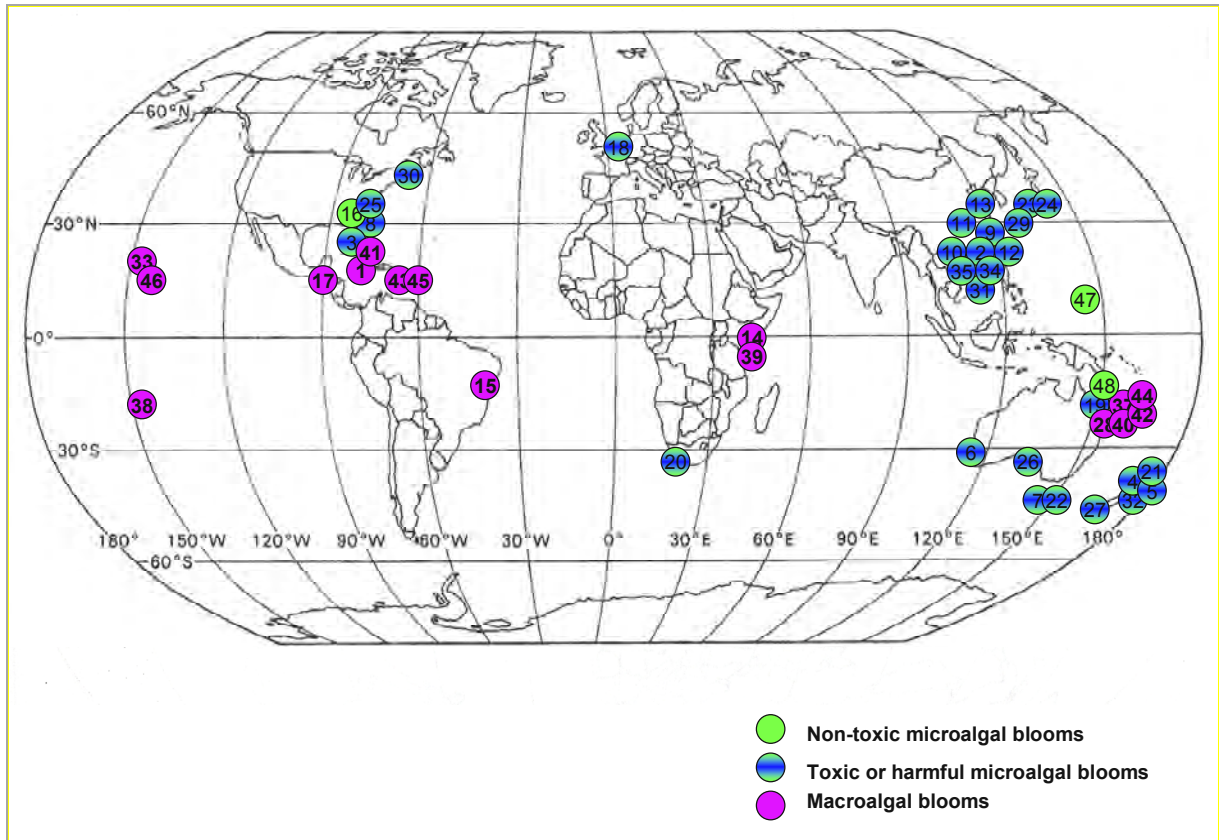
## 2.3 Nutrient limitation of dinoflagellate and other harmful algal blooms

Dinoflagellate blooms often follow diatom blooms (Riegman *et al.* 1992, Sanders and Riedel 1993, Ennet *et al.* 2000, Yallop 2001, Carstensen *et al.* 2005). This suggested that dinoflagellates may obtain nitrogen from other sources, i.e. dissolved free amino acids released from grazed and senescent diatoms or from excretions by zooplankton preying on diatoms (Flynn and Butler 1986). Nutrient experiments conducted by Fan *et al.* (2003b) on *Prorocentrum minimum* revealed a high affinity for ammonium and amino acids over nitrate however no clear conclusion was drawn. Research on blooms of *Olisthodiscus luteus* (chrysophyte) in Narragansett Bay, Rhode Island (USA) also failed to demonstrate that elevated nutrients were the major factor to trigger blooms (Tomas 1980).

Harmful algal blooms (HABs) are predominantly caused by dinoflagellates, but also by chrysophytes and raphidophytes. HABs have been related to eutrophication of coastal waters (Laroche *et al.* 1997, Noga 1998, Fan *et al.* 2003b, Qi *et al.* 2004). HABs appear to have increased since the 1980s and are frequently reported in association with intense mariculture (Yuzao *et al.* 1993, Khan *et al.* 1997, De Salas *et al.* 2004b, De Salas *et al.* 2004a) and shellfish farming (Matsuyama *et al.* 2001, Chang and Ryan 2004, Clementson *et al.* 2004). However, HABs have been documented from eutrophic (Yallop 2001, Yamamoto and Seike 2003, Yin 2003) to oligotrophic waters in Tasmania (Australia) (Clementson *et al.* 2004, De Salas *et al.* 2004b, De Salas *et al.* 2004a), New Zealand (Chang *et al.* 1990, Chang *et al.* 2001, Irwin *et al.* 2003, Chang and Ryan 2004, Kröger *et al.* 2006) and South Africa (Botes *et al.* 2003). A combination of factors is likely responsible for HABs, as indicated by the reported broad nutrient scale at which HABs occur. Further research is needed to pinpoint these factors.

### 3.0 Global distribution of algal blooms

Information on locations of algal bloom organisms was collated and distributions plotted on a world map, showing that macroalgae are dominant in tropical regions, and phytoplankton blooms in polar, temperate and sub-tropical regions (Figure 1). Therefore this section of the review is divided into two sections – macroalgal, and phytoplankton blooms.



**Figure 1:** Worldwide distribution of algal blooms.

1. (Hughes 1994); 2. (Hodgkiss and Lu 2004); 3. (Kirkpatrick *et al.* 2004); 4. (Chang *et al.* 2001); 5. (Rhodes *et al.* 2001); 6. (Robb *et al.* 2003); 7. (Clementson *et al.* 2004); 8. (Fan *et al.* 2003b); 9. (Hodgkiss and Ho 1997); 10, 34, 35. (Qi *et al.* 2004); 11. (Iwataki *et al.* 2002); 12. (Yeung *et al.* 2002); 13. (Bu *et al.* 2005); 14. (Costa Jr. *et al.* 2000); 15. (McClanahan *et al.* 2001); 16. (Sanders and Riedel 1993); 17. (Williams *et al.* 2001); 18. (Riegman *et al.* 1992); 19. (Muslim and Jones 2003); 20. (Botes *et al.* 2003); 21. (Chang and Ryan 2004); 22. (De Salas *et al.* 2004a); 23. (Matsuyama *et al.* 2001); 24. (Okaichi 1985); 25. (Noga 1998); 26. (Munday and Hallegraeff 1998); 27. (Chang *et al.* 1990); 28. (Fabricius *et al.* 2005); 29. (Khan *et al.* 1997); 30. (Tomas 1980); 31. (Yuzao *et al.* 1993); 32. (Kröger *et al.* 2006); 33. (Smith *et al.* 1981); 37, 38. (Done *et al.* 1991); 39. (McClanahan *et al.* 2005); 40. (Halford *et al.* 2004); 41, 42, 43. (Rogers and Miller 2006); 44. (Rogers 1996); 45. (Rogers *et al.* 1991); 46. (Walsh 1983); 47. (Lobban *et al.* 1995); 48. (Schaffelke *et al.* 2004).

### 3.1 Potential role of macroalgal blooms in reef recovery processes

Recovery of a coral reef is commonly defined as the return of coral abundance and diversity to its pre-disturbance conditions (Rogers *et al.* 1991, Connell *et al.* 1997, Halford *et al.* 2004, Rogers and Miller 2006). Increase in macroalgal coverage is well documented and has been referred to as phase shifts, after which disturbance events degrade, threaten or delay the recovery of coral reefs (Done 1992, McCook 1999, Stimson *et al.* 2001, Thacker *et al.* 2001, Jompa and McCook 2002, Diaz-Pulido and McCook 2003, Fabricius *et al.* 2005). Successional patterns are known in settlement of biofouling organisms (Dobretsov *et al.* 2005) but little is known on possible successional patterns of macroalgae in the recovery of coral reefs. Walsh (1983) recognised a succession of macroalgae after a severe storm along Kona Coast, Hawaii. A green alga, *Enteromorpha* sp., increased in abundance directly after the storm and was succeeded by several red algal species, including *Liagora papenfussii*, before succession by the weedy brown alga *Rosenvingea orientalis*. The recovery of the reef to pre-storm conditions was observed in conjunction with the decline of *R. orientalis* (Walsh 1983). A similar pattern was noted by Hughes (1994) in Jamaica (Caribbean) after Hurricane *Allen* in 1980. A bloom of the red alga *Liagora* sp. was succeeded by 'weedy' algal types, which were not identified. In contrast to Walsh's study (1983), the 'weedy algae' in Jamaica were succeeded by the brown algae *Sargassum*, *Lobophora* and *Dictyota* as well as the green alga *Halimeda* (Hughes 1994). We suggest that the dominance of the brown algae in Jamaica may be a symptom of an imbalance in the ecosystem due to overfishing or disease, preventing recovery of the reef to coral dominance. There is currently insufficient data on successional recovery patterns to really distinguish between macroalgae directly involved in reef recovery processes and space invaders.

Many studies on macroalgal abundance use non-descript categories such as fleshy, turf, crustose coralline and calcareous (McClanahan 1997, McCook 1999, Diaz-Pulido and McCook 2002, Tuya and Haroun 2006), but few classifications of algal species correlate with their assigned category. For example, the brown alga *Lobophora variegata* was recently referred to as a turf alga (Tuya and Haroun 2006) but included in the fleshy category by others (McClanahan *et al.* 2002). *Halimeda* sp. is the only alga consistently categorised as calcareous (McClanahan 1997, McClanahan *et al.* 2001, McClanahan *et al.* 2002). In contrast, other calcified algae such as the brown alga *Padina* sp. (Huisman 2000) and several red algae including *Liagora* sp. are continually categorised as fleshy (McClanahan 1997, McClanahan *et al.* 2001, Tuya and Haroun 2006). In conclusion, identification at least to genus preferably to species is needed to be able to recognise the important role of macroalgae associated with successional recovery patterns on coral reefs.

Herbivory exclusion experiments have the potential to mimic conditions that follow major disturbances and overfishing events. *Enteromorpha* sp. has been identified consistently as an early coloniser after a major disturbance and in herbivory exclusion experiments (Ogg and Koslow 1978, Walsh 1983, Diaz-Pulido and McCook 2002, McClanahan *et al.* 2002, McClanahan *et al.* 2005). Experiments on healthy reefs identified *Dictyota* sp. and *Halimeda* sp. to be dominant in uncaged plots but *Padina* sp. in caged areas (Thacker *et al.* 2001, McClanahan *et al.* 2002). The dominant macroalgal species in uncaged plots are least preferred by herbivorous fish but the preferred food of the sea urchin *Diadema* sp. (Szmant 2001, Tuya *et al.* 2001). In contrast, *Padina* is preferred by herbivorous fish and therefore thrives in the caged plots designed to exclude them. Because *Halimeda* sp. and *Dictyota* sp. were present in uncaged plots on healthy reefs and on reefs in final succession after a major disturbance event, i.e. Jamaica (Hughes 1994); the Caribbean (Done *et al.* 1991); Moorea (French Polynesia) (Rogers *et al.* 1991, Rogers and Miller 2006); and St. John (Virgin Islands, USA) (Rogers *et al.* 1991, Connell *et al.* 1997, Halford *et al.* 2004, Rogers and Miller 2006), we conclude that the presence of *Dictyota* sp. and *Halimeda* sp. may be an indicator

for reef recovery status. However, it would be important to determine biomass of these algae in relation to reef area to draw the line between recovery and reef invasions due to reduced herbivory from, for example, *Diadema* sp..

Based on the observed macroalgal successional patterns on reefs, we propose that the increase of macroalgal cover after a major disturbance is a natural and important part of coral reef recovery and not a threat of degradation. We believe the current definition is too limited, with focus being restricted to the impact on corals and suggest a more inclusive definition relating to the complete ecosystem: “*Recovery of a coral reef is a successional process in which the return and re-growth of all reef organisms is essential to rebuild a dynamic ecosystem, where coral dominance denotes the completion of the recovery process.*”

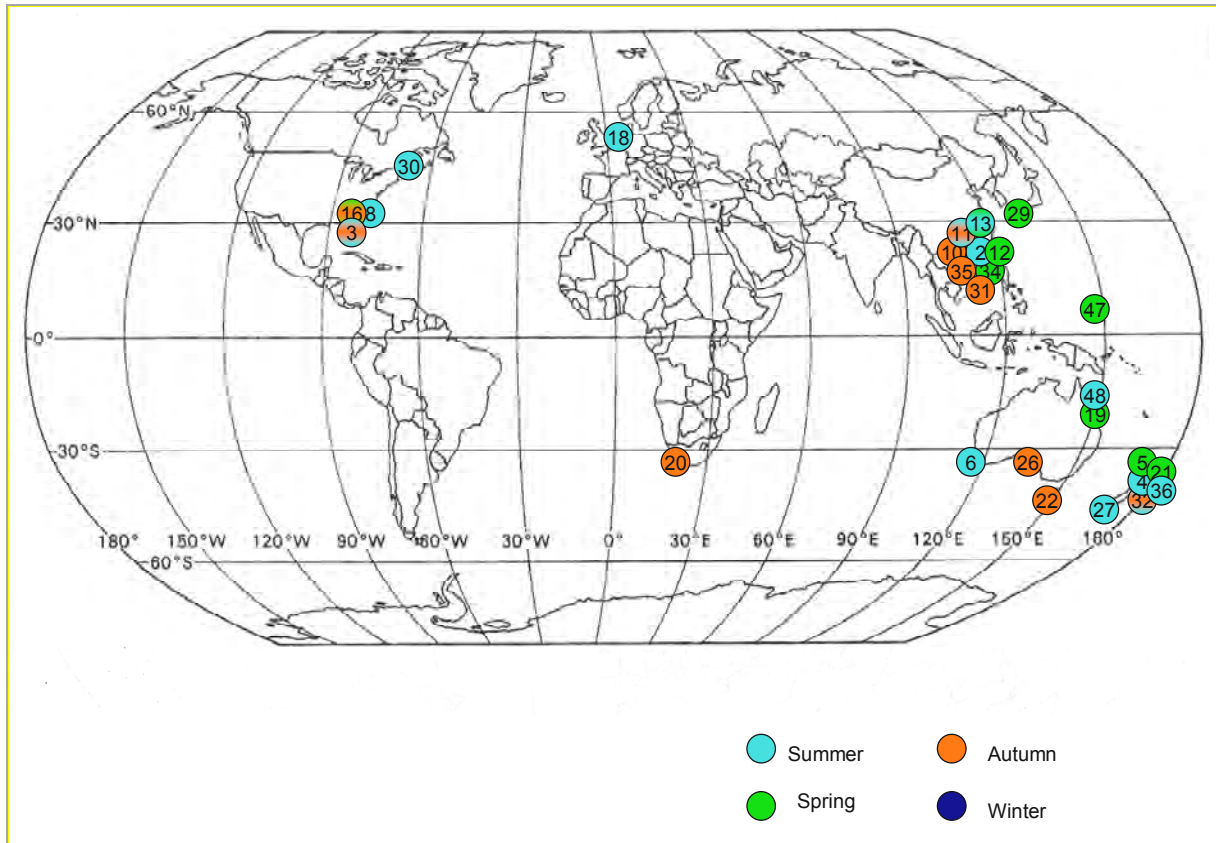
## **3.2 Seasonal distribution of phytoplankton blooms**

Diatom and harmful algal blooms are most intensely studied worldwide and research focuses on nutrient resource use and limitation. Picoplankton (bacteria and cyanobacteria) communities are naturally dominant in oligotrophic waters however blooms are rarely reported as the growth rates of grazers matches those of picoplankton (Coale *et al.* 1996, Frost 1996, Furnas *et al.* 2005). Data were collated and analysed for global (Figure 1) and seasonal occurrence of diatom and dinoflagellate blooms (Figure 2). Picoplankton blooms were omitted due to the paucity of information. Seasonal temperature pattern can be associated with the main global temperature regions – tropical, sub-tropical, temperate and polar (Figure 2). Analysis of seasonal patterns is limited by a lack of data on sea surface temperatures during and preceding blooms.

### **3.2.1 Seasonal distribution of phytoplankton blooms in tropical and sub-tropical regions**

In these regions diatom blooms occur during the summer wet season (Yin 2003, Hodgkiss and Lu 2004, Yin *et al.* 2004). Studies have primarily focussed on coastal waters in Hong Kong (Yin 2003, Hodgkiss and Lu 2004, Yin *et al.* 2004), where nutrient provision during the monsoon season are thought to be involved in bloom formation and perpetuation (Trott and Alongi 1999, Yin 2003, Hodgkiss and Lu 2004, Qi *et al.* 2004, Yin *et al.* 2004). Although uptake of nitrate and iron has been linked to increased temperature (Reay *et al.* 2001), there is insufficient data to determine the temperature maxima for nutrient acquisition and optimal growth.

Dinoflagellate blooms – also known as red tides (Figure 2) – have been recorded predominantly during the start of the wet season in Hong Kong (Yin 2003, Hodgkiss and Lu 2004, Kirkpatrick *et al.* 2004, Qi *et al.* 2004), but in autumn in Florida (Kirkpatrick *et al.* 2004). The oldest record of red tides (1,844) were documented in Florida prior to intensive anthropogenic activities and were caused then and nowadays by *Karenia brevis* (Kirkpatrick *et al.* 2004). Hong Kong and southern China report high numbers of blooms with each dominated by an individual dinoflagellate species (Figure 2). Blooms of *Noctiluca scintillans* in China only occur between 19-22°C (spring) (Yuzao *et al.* 1993), whereas blooms of *Gyrodinium aureolum* in the South China Sea occur at 25°C (Qi *et al.* 2004). Current research, however, continues to pay little attention to temperature as a contributing factor in initiating dinoflagellate blooms.



**Figure 2:** Seasonal distribution of phytoplankton blooms.

2. (Hodgkiss and Lu 2004); 3. (Kirkpatrick *et al.* 2004); 4. (Chang *et al.* 2001); 5. (Rhodes *et al.* 2001); 6. (Robb *et al.* 2003); 8. (Fan *et al.* 2003b); 10, 34, 35. (Qi *et al.* 2004); 11. (Iwataki *et al.* 2002); 12. (Yeung *et al.* 2002); 13. (Bu *et al.* 2005); 16. (Sanders and Riedel 1993); 18. (Riegman *et al.* 1992); 19. (Muslim and Jones 2003); 20. (Botes *et al.* 2003); 21. (Chang and Ryan 2004); 22. (De Salas *et al.* 2004a); 26. (Munday and Hallegraeff 1998); 27. (Chang *et al.* 1990); 29. (Khan *et al.* 1997); 30. (Tomas 1980); 31. (Yuzao *et al.* 1993); 32. (Kroger *et al.* 2006); 36. (Rhodes *et al.* 2001); 47. (Lobban *et al.* 1995); 48. (Schaffelke *et al.* 2004).

### 3.2.2 Seasonal distribution of phytoplankton blooms in temperate regions

With the exception of California (summer) (Fitzwater *et al.* 2003), diatom blooms occur mostly in spring in temperate climates (Riegman *et al.* 1992, Grimes and Kingsford 1996, Ennet *et al.* 2000, Yallop 2001, Fitzwater *et al.* 2003, Carstensen *et al.* 2004, Fujiki *et al.* 2004, Örnólfsson *et al.* 2004, Skaloud *et al.* 2006) (Figure 2). Sanders and Riedel (1993) found that diatoms dominated phytoplankton communities in spring and autumn in Chesapeake Bay (Maryland, USA). Spring blooms were dominated by *Thalassiosira pseudonana*, while autumn blooms were a succession of diatom species initiated by *Thalassiosira*, but succeeded by *Leptocylindrus danicus* and followed by *Chaetoceros* sp. Temperatures recorded during these spring and autumn blooms were within a similar temperature range (17-25°C) (Sanders and Riedel 1993). Extensive studies have focussed on nutrient limitation of diatom blooms but these studies did not investigate the potential temperature link for elevated nutrient acquisition, which is required if we are to understand complex interactions of factors for bloom initiations completely.

In temperate regions dinoflagellate and other harmful algal blooms have been documented within all seasons, although rarely in winter (Sanders and Riedel 1993). The majority of dinoflagellate blooms are recorded during summer (Tomas 1980, Chang *et al.* 1990,

Riegman *et al.* 1992, Yuzao *et al.* 1993, Berg *et al.* 1997, Khan *et al.* 1997, Laroche *et al.* 1997, Chang *et al.* 2001, Oke and Middleton 2001, Fan *et al.* 2003a, Irwin *et al.* 2003, Yamamoto and Seike 2003, Yin 2003, Chang and Ryan 2004, Clementson *et al.* 2004, De Salas *et al.* 2004b, Fujiki *et al.* 2004, Carstensen *et al.* 2005, Kröger *et al.* 2006), less frequently in spring (Yuzao *et al.* 1993, Khan *et al.* 1997, Fan *et al.* 2003a, Irwin *et al.* 2003, Chang and Ryan 2004, Fujiki *et al.* 2004) and autumn (Tomas 1980, Wieters *et al.* 2003, De Salas *et al.* 2004b, De Salas *et al.* 2004a). This suggests that seasonal upwelling may be less important for certain dinoflagellate bloom species.

Temperature, however, was identified as a major initiating factor for *Olisthodiscus luteus* (chrysophyte) blooms in Rhode Island (USA) (Tomas 1980) and in dinoflagellate blooms in Hong Kong (Qi *et al.* 2004). Blooms have been consistently recorded within a temperature range of 15-25°C across sub-tropical and temperate regions for blooms of *Noctiluca scintillans* in China (Yuzao *et al.* 1993), *Gyrodinium aureolum* in Hong Kong (Qi *et al.* 2004), *Karenia brevisulcata* in Wellington (New Zealand) (Chang *et al.* 2001) and *Olisthodiscus luteus* in Narragansett Bay (USA) (Tomas 1980). In contrast to the wealth of information regarding nutrient limitations, only few studies have included temperature as a factor and clearly more studies of this type are needed to obtain a full picture.

### **3.2.3 Seasonal distribution of phytoplankton blooms in polar regions**

Polar regions are characterised by diatom blooms during spring with research focussing on nutrient and iron limitation in the Southern Ocean (de Baar *et al.* 1995, Reay *et al.* 2001). This research identified that blooms are associated with nutrient influx from upwelling events and ice melts as well as an increase in temperatures up to about 5°C (Reay *et al.* 2001). Although blooms occurred, complete utilisation of available nutrients was limited by low temperatures (de Baar *et al.* 1995). This was attributed to the temperature and iron dependent assimilation of nitrate (de Baar *et al.* 1995, Reay *et al.* 2001).

No records of dinoflagellate blooms exist for polar regions, possibly due to the much cooler temperatures.

## 4.0 Algae with an identity crisis

There are some microalgae that appear to have an identity crisis. These microalgae prefer to grow as mucilaginous colonies or filaments becoming visible to the naked eye. Filamentous cyanobacteria, i.e. *Trichodesmium* sp. and *Lyngbya majuscula* form long chains that often aggregate to form thick bundles (Muslim and Jones 2003, Ahern *et al.* 2006). The ability of some cyanobacteria to fix atmospheric nitrogen is considered an important factor for bloom initiation in oligotrophic tropical and sub-tropical waters (Albert *et al.* 2005, Ahern *et al.* 2006).

The chrysophytes, *Chrysocystis fragilis* and *Chrysophaeum taylori* are golden brown unicellular algae that exude mucilage in which cells are embedded to form colonies (Schaffelke *et al.* 2004). These chrysophyte colonies attach to hard benthic substrates such as dead coral rubble. *Chrysophaeum taylori* was first identified in the central Great Barrier Reef in the 1980s, while records of *C. fragilis* blooms are more recent. *Chrysocystis fragilis* colonies covered dead coral substrate in the Austral summer of 2002/2003 after bleaching or crown-of-thorns starfish plague events (Schaffelke *et al.* 2004). Blooms were observed on the outer reefs of the central Great Barrier Reef, where waters are typically oligotrophic with infrequent minor upwelling events (Brinkman *et al.* 2001). There are limited studies on growth of *C. fragilis* colonies and a lack of published data on environmental factors triggering blooms. Our work and recent research by the North Queensland Algal Identification / Culturing Facility (NQAIF) at James Cook University suggests that temperature, and not eutrophication, is a major factor for *C. fragilis* blooms (pers. comm.). As described for some phytoplankton (microalgae) blooms, it was expected that nutrients were at least one contributing factor for *C. fragilis* bloom formation. Apparent nutrient independence of *C. fragilis* for bloom initiation appears to be a shared characteristic with macroalgal blooms at Moorea (Done *et al.* 1991) and St. John (Virgin Islands, USA) (Rogers and Miller 2001). This highlights that microalgal growth form should be considered when generalising conditions characteristic for either micro- or macroalgal blooms.

## 5.0 Summary

A general paradigm states: Growth of macroalgae is nitrogen limited in temperate regions and phosphate limited in tropical regions (Littler *et al.* 1991, Smith and Johnson 1995, Larned 1998, Fong *et al.* 2001). Based on available literature, this review concludes that the first part of the paradigm appears to hold true, but the predicted phosphate limitation of macroalgae in tropical regions is questioned, as nutrient limitations appears to be phylum-specific (Table 1). Research by Smith and others (1981) blamed the continuous input of sewage (for roughly fifty years) as the major cause of macroalgal blooms in Kaneohe Bay (Hawaii). This conclusion is challenged by recent studies, such as the ENCORE nutrient enrichment experiment, where nutrient addition did not cause a phase shift to macroalgal dominance on reefs in the Great Barrier Reef (Koop *et al.* 2001). In addition, long-term macroalgal dominance was also documented in oligotrophic environments due to reduced herbivory from overfishing or disease. Successional macroalgal patterns on reefs have been suggested as important in the recovery process; however, more research is needed to ascertain this hypothesis.

Phytoplankton blooms are commonly dominated by diatoms and dinoflagellates. Nutrient limitation and iron fertilisation experiments indicate that diatom growth is limited by iron availability, a metal important for nitrate assimilation. Diatom blooms are seasonal (Figure 2) occurring in summer in the tropics when monsoonal rains supply both nutrients, but occur mainly in spring in temperate and polar regions when upwelling supplies essential nutrients. More research is needed to establish the current iron levels in eutrophied waters and the minimum nutrient levels associated with temperature to trigger diatom blooms.

Current research into limiting factors of HABs continues to focus on nitrogen sources without consideration for the mixed feeding strategies or preferred temperatures of these organisms. Temperature, however, appears to be an important factor for these blooms (no blooms recorded over 25°C).

HABs occur across a range of environments from nutrient-enriched waters of Hong Kong to pristine waters of Tasmania (Australia). Blooms are frequently associated with regions that have intensive maricultural activities, potentially supplying free amino acids and vitamins. Elevated levels of amino acids and vitamins would suit the mixotrophic feeding strategies of many harmful algae, but this has not been explored.

In summary, temperature appears to be an important factor in the initiation of phytoplankton blooms; however, research continues to focus on nutrient limitation. A recent study on *Chrysochromulina fragilis* blooms on outer reefs of the Great Barrier Reef in oligotrophic conditions strongly suggests temperature as a driving factor in bloom initiation.

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