

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

Literature Review

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

### **Abstract** (194 words):

Algal blooms are defined as increased abundance, biomass, or population growth. This review reveals knowledge gaps regarding bloom initiation, 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 into 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, *Chrysocystis fragilis* – a new record for the GBR, exhibits some macroalgal traits; blooms occur at high temperatures in oligotrophic conditions, if coral cover is compromised by COTS 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 & Kingsford 1996, Oke & Middleton 2001, Fitzwater et al. 2003, Moisander et al. 2003, Wieters et al. 2003, Yin 2003, Carstensen et al. 2004, Hodgkiss & 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 & 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 world-wide. 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 & 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 & 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 50 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 consist 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 2-4 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 & 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**

My 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 & 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 & 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 13% 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 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 GBR 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 Chrysophyceae</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					9
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	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 cavemosa</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

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 & Klumpp 1998); 11. (Lapointe 1989); 12. (Moisander et al. 2003); 13. (Flynn & Wright 1986); 14. (Coale et al. 1996); 15. (Peckol et al. 1994); 16. (Rivers & Peckol 1995); 17. (Hanisak 1979); 18. (Taylor et al. 1995); 19. (Lapointe & O'Connell 1989); 20. (Larned & Stimson 1996); 21. (Lapointe 1987); 22. (Lapointe 1985); 23. (Dy & Yap 2001); 24. (Bjork et al. 1995).

Classification is based on Lee (1999).

## 2.2 Nutrient limitation of diatom blooms

My 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 et al. (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 et al. (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 24 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 & 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.

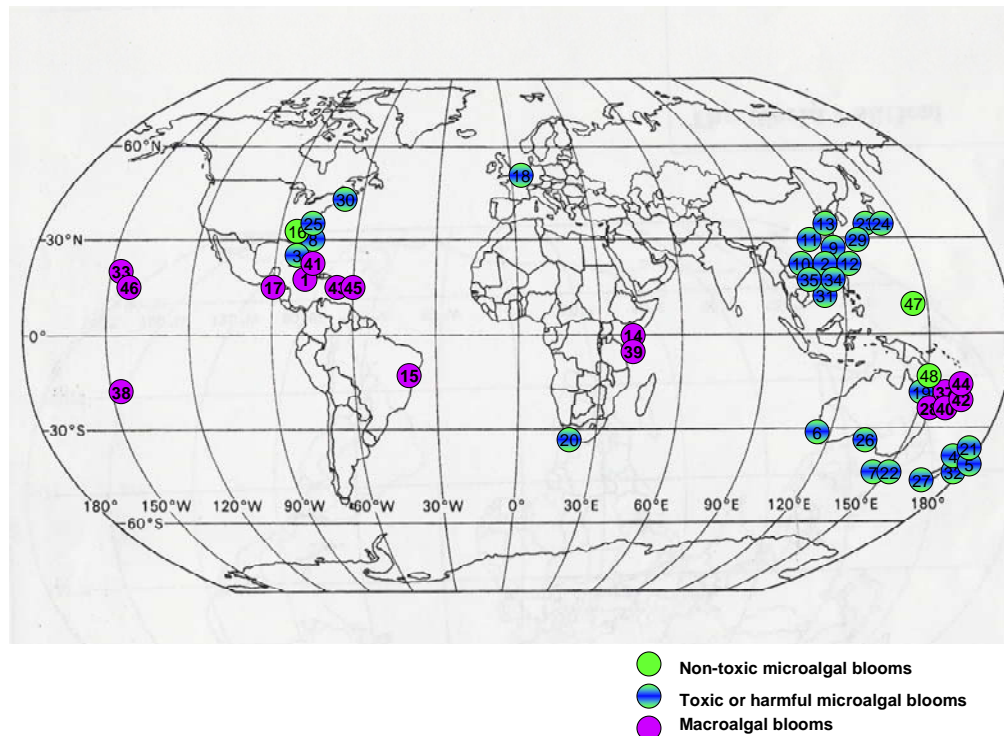
### **2.3 Nutrient limitation of dinoflagellate and other harmful algal blooms**

Dinoflagellate blooms often follow diatom blooms (Riegman et al. 1992, Sanders & 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 & Butler 1986). Nutrient experiments conducted by Fan et al. (2003b) on *Prorocentrum minimum* revealed a high affinity for ammonium and amino acids over nitrate but 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 & Ryan 2004, Clementson et al. 2004). However, HABs have been documented from eutrophic (Yallop 2001, Yamamoto & 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 & Ryan 2004, Kröger et al. 2006) and South Africa (Botes et al. 2003). A combination of factors are 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 – and phytoplankton blooms in polar, temperate and sub-tropical regions (Fig. 1). Therefore this part of the review is divided into two sections, macroalgal – and phytoplankton blooms.



**Figure 1. World-wide distribution of algal blooms**

1. (Hughes 1994); 2. (Hodgkiss & 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 & 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 & Riedel 1993); 17. (Williams et al. 2001); 18. (Riegman et al. 1992); 19. (Muslim & Jones 2003); 20. (Botes et al. 2003); 21. (Chang & Ryan 2004); 22. (De Salas et al. 2004a); 23. (Matsuyama et al. 2001); 24. (Okaichi 1985); 25. (Noga 1998); 26. (Munday & 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 & 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 & Miller 2006). Increase in macroalgal coverage is well documented and has been referred to as phase shifts, which after disturbance events degrade, threaten or delay the recovery of coral reefs (Done 1992, McCook 1999, Stimson et al. 2001, Thacker et al. 2001, Jompa & McCook 2002, Diaz-Pulido & 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). I 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 & McCook 2002, Tuya & 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 & 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 & 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 & Koslow 1978, Walsh 1983, Diaz-Pulido & 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.

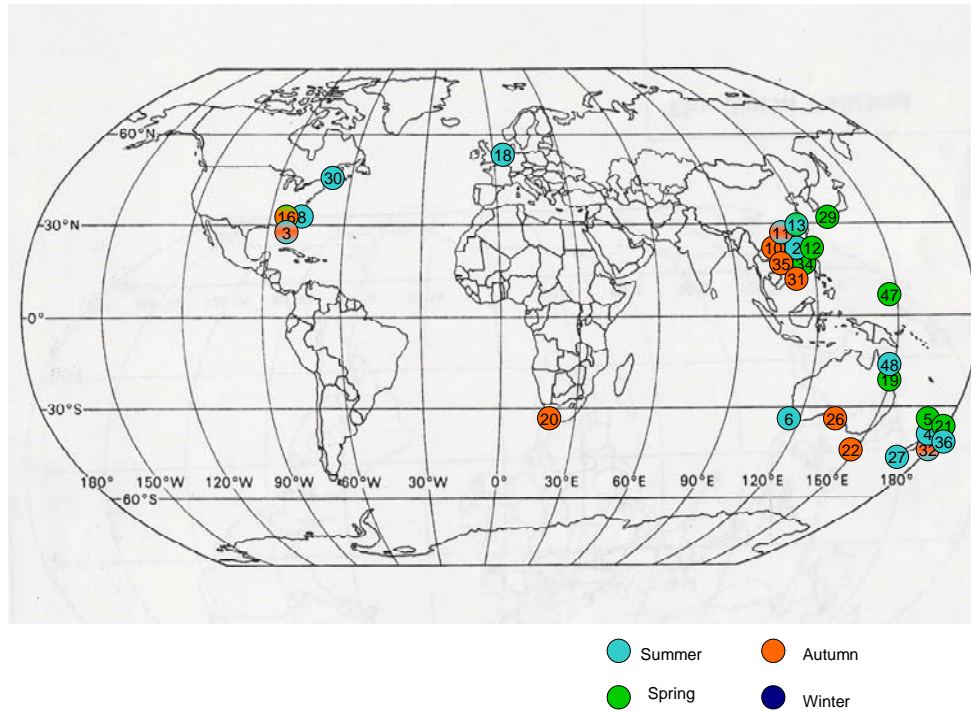
Jamaica (Hughes 1994); Caribbean (Done et al. 1991); Moorea (French Polynesia) (Rogers et al. 1991, Rogers & Miller 2006); and St. John (US Virgin Islands) (Rogers et al. 1991, Connell et al. 1997, Halford et al. 2004, Rogers & Miller 2006)), I conclude, that the presence of *Dictyota* sp. and *Halimeda* sp. maybe 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 i.e. *Diadema* sp..

Based on the observed macroalgal successional patterns on reefs, I propose that macroalgal cover increase after a major disturbance is a natural and important part of coral reef recovery and not a threat of degradation. I believe that the current definition is too limited with focus being restricted to the impact on corals. I 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 world-wide and research focuses on nutrient resource use and limitation. Picoplankton (bacteria and cyanobacteria) communities are naturally dominant in oligotrophic waters but 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 (Fig. 1) and seasonal occurrence of diatom and dinoflagellate blooms (Fig. 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 (Fig. 2). Analysis of seasonal patterns is limited by a lack of data on sea surface temperatures during and preceding blooms.



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

2. (Hodgkiss & 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 & Riedel 1993); 18. (Riegman et al. 1992); 19. (Muslim & Jones 2003); 20. (Botes et al. 2003); 21. (Chang & Ryan 2004); 22. (De Salas et al. 2004a); 26. (Munday & 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).

### 3.2.1 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 & Lu 2004, Yin et al. 2004). Studies have primarily focussed on coastal waters in Hong Kong (Yin 2003, Hodgkiss & Lu 2004, Yin et al. 2004), where nutrient provision during the monsoon season are thought to be involved in bloom formation and perpetuation (Trott & Alongi 1999, Yin 2003, Hodgkiss & 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 – (Fig. 2) have been recorded predominantly during the start of the wet season in Hong Kong (Yin 2003, Hodgkiss & 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 (1844) 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 (Fig. 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.

### **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 & 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) (Fig. 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* followed by *Chaetoceros* sp. Temperatures recorded during these spring and autumn blooms were within a similar temperature range (17 - 25°C) (Sanders & 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 & 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 & Middleton 2001, Fan et al. 2003a, Irwin et al. 2003, Yamamoto & Seike 2003, Yin 2003, Chang & 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 & 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 (Tomas 1980) and in dinoflagellate blooms in Hong Kong (Qi et al. 2004). Blooms have been consistently recorded within a temperature range of 15°C to 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 & 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 subtropical 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 GBR in the 1980s, while records of *C. fragilis* blooms are more recent.

*Chrysocestis fragilis* colonies covered dead coral substrate in the Austral summer 2002/2003 after bleaching or COTS plague events (Schaffelke et al. 2004). Blooms were observed on the outer reefs of the central GBR, 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. My work and recent research by the North Queensland Algal Identification/ Culturing Facility (NQAIF) at JCU suggests that temperature but 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, US Virgin Islands (Rogers & 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 that: Growth of macroalgae is nitrogen limited in temperate regions and phosphate limited in tropical regions (Littler et al. 1991, Smith & 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 et al. (1981) blamed the continuous input of sewage (~50 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 GBR (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 (Fig. 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 (AAs) and vitamins. Elevated levels of AAs 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 *Chrysochloris fragilis* blooms on outer reefs of the GBR in oligotrophic conditions strongly suggests temperature as a driving factor in bloom initiation.

**References:**

- Ahern KS, O'Neil JM, Udy JW, Albert S (2006) Effects of iron additions on filament growth and productivity of the cyanobacterium *Lyngbya majuscula*. *Marine and Freshwater Research* 57:167-176
- Albert S, O'Neil JM, Udy JW, Ahern KS, O'Sullivan CM, Dennison WC (2005) Blooms of the cyanobacterium *Lyngbya majuscula* in coastal Queensland, Australia: disparate sites, common factors. *Marine Pollution Bulletin* 51:428-437
- Behrenfeld MJ, Bale AJ, Kolber ZS, Aiken J, Falkowski PG (1996) Confirmation of iron limitation of phytoplankton photosynthesis in the equatorial Pacific Ocean. *Nature* 383:508-511
- Beman JM, Arrigo KR, Matson PA (2005) Agricultural runoff fuels large phytoplankton blooms in vulnerable areas of the ocean. *Nature* 434:211-214
- Berg GM, Glibert PM, Lomas MW, Burford MA (1997) Organic nitrogen uptake and growth by the chrysophyte *Aureococcus anophagefferens* during a brown tide event. *Marine Biology* 129:377-387
- Bjork M, Mohammed SM, Bjorklund M, Semesi A (1995) Coralline algae, important coral-reef builders threatened by pollution. *Ambio* 24:502-505
- Botes L, Smit AJ, Cook PA (2003) The potential threat of algal blooms to the abalone (*Haliotis midae*) mariculture industry situated around the South African coast. *Harmful Algae* 2:247-259
- Brinkman R, Wolanski E, Deleersnijder E, McAllister F, Skirving W (2001) Oceanic inflow from the Coral Sea into the Great Barrier Reef. *Estuarine Coastal and Shelf Science* 54:655-668
- Bu XW, Xu WY, Zhu DD, Chen GX (2005) Discussion about mechanism of harmful algal blooms breakout. *Acta Oceanologica Sinica* 24:101-106
- Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* 12:143-152
- Carruthers TJB, van Tussenbroek BI, Dennison WC (2005) Influence of submarine springs and wastewater on nutrient dynamics of Caribbean seagrass meadows. *Estuarine Coastal and Shelf Science* 64:191-199
- Carstensen J, Conley DJ, Henriksen P (2004) Frequency, composition, and causes of summer phytoplankton blooms in a shallow coastal ecosystem, the Kattegat. *Limnology and Oceanography* 49:191-201
- Carstensen J, Frohn LM, Hasager CB, Gustafsson BG (2005) Summer algal blooms in a coastal ecosystem: the role of atmospheric deposition versus entrainment fluxes. *Estuarine Coastal and Shelf Science* 62:595-608
- Chang EH, Ryan KG (2004) *Karenia concordia* sp. nov. (Gymnodiniales, Dinophyceae), a new nonthecate dinoflagellate isolated from the New Zealand northeast coast during the 2002 harmful algal bloom events. *Phycologia* 43:552-562
- Chang FH, Anderson C, Boustead NC (1990) First record of a *Heterosigma* (Raphidophyceae) bloom with associated mortality of cage-reared salmon in Big Glory Bay, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24:461-469
- Chang FH, Chiswell SM, Uddstrom MJ (2001) Occurrence and distribution of *Karenia brevisulcata* (Dinophyceae) during the 1998 summer toxic outbreaks on the central east coast of New Zealand. *Phycologia* 40:215-222
- Clementson LA, Parslow JS, Turnbull AR, Bonham PI (2004) Properties of light absorption in a highly coloured estuarine system in south-east Australia which is

- prone to blooms of the toxic dinoflagellate *Gymnodinium catenatum*. Estuarine Coastal and Shelf Science 60:101-112
- Coale KH, Johnson KS, Fitzwater SE, Gordon RM, Tanner S, Chavez FP, Ferioli L, Sakamoto C, Rogers P, Millero F, Steinberg P, Nightingale P, Cooper D, Cochlan WP, Landry MR, Constantinou J, Rollwagen G, Trasvina A, Kudela R (1996) A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. Nature 383:495-501
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67:461-488
- Cooper MJ (1966) Destruction of marine flora and fauna in Fiji caused by the Hurricane of February 1965. Pacific Science 20:137-141
- Costa Jr. OS, Leao ZMAN, Nimmo M, Attrill MJ (2000) Nutrifcation impacts on coral reefs from northern Bahia, Brazil. Hydrobiologia 440:307-315
- de Baar HJW, de Jong JTM, Bakker DCE, Loscher BM, Veth C, Bathmann U, Smetacek V (1995) Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. Nature 373:412-415
- De Salas ME, Bolch CJS, Hallegraeff GM (2004a) *Karenia asterichroma* sp. nov. (Gymnodiniales, Dinophyceae), a new dinoflagellate species associated with finfish aquaculture mortalities in Tasmania, Australia. Phycologia 43:624-631
- De Salas ME, Bolch CJS, Hallegraeff GM (2004b) *Karenia umbella* sp. nov. (Gymnodiniales, Dinophyceae), a new potentially ichthyotoxic dinoflagellate species from Tasmania, Australia. Phycologia 43:166-175
- Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Marine Ecology Progress Series 232:115-128
- Diaz-Pulido G, McCook LJ (2003) Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026-2033
- Dobretsov SV, Qian P-Y, Wahl M (2005) Effect of solar ultraviolet radiation on the formation of shallow, early successional biofouling communities in Hong Kong. Marine Ecology Progress Series 290:55-65
- Dollar SJ, Tribble GW (1993) Recurrent storm disturbance and recovery - a long-term study of coral communities in Hawaii. Coral Reefs 12:223-233
- Done T (1992) Constancy and change in some Great-Barrier-Reef coral communities - 1980-1990. American Zoologist 32:655-662
- Done TJ, Dayton PK, Dayton AE, Steger R (1991) Regional and local variability in recovery of shallow coral communities: Moorea, French Polynesia and central Great Barrier Reef. Coral Reefs 9:183-192
- Dy DT, Yap HT (2001) Surge ammonium uptake of the cultured seaweed, *Kappaphycus alvarezii* (Doty) Doty (Rhodophyta: Gigartinales). Journal of Experimental Marine Biology and Ecology 265:89-100
- Edwards MS, Estes JA (2006) Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective. Marine Ecology Progress Series 320:79-87
- Ennet P, Kuosa H, Tamsalu R (2000) The influence of upwelling and entrainment on the algal bloom in the Baltic Sea. Journal of Marine Systems 25:359-367
- Fabricius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin 51:384-398
- Fan C, Glibert PM, Alexander J, Lomas MW (2003a) Characterization of urease activity in three marine phytoplankton species, *Aureococcus anophagefferens*,

- Prorocentrum minimum*, and *Thalassiosira weissflogii*. Marine Biology 142:949-958
- Fan CL, Glibert PM, Burkholder JM (2003b) Characterization of the affinity for nitrogen, uptake kinetics, and environmental relationships for *Prorocentrum minimum* in natural blooms and laboratory cultures. Harmful Algae 2:283-299
- Fitzwater SE, Johnson KS, Elrod VA, Ryan JP, Coletti LJ, Tanner SJ, Gordon RM, Chavez FP (2003) Iron, nutrient and phytoplankton biomass relationships in upwelled waters of the California coastal system. Continental Shelf Research 23:1523-1544
- Flynn KJ, Butler I (1986) Nitrogen sources for the growth of marine microalgae - role of dissolved free amino-acids. Marine Ecology Progress Series 34:281-304
- Flynn KJ, Wright CRN (1986) The simultaneous assimilation of ammonium and L-arginine by the marine diatom *Phaeodactylum tricorutum* Bohlin. Journal of Experimental Marine Biology and Ecology 95:257-269
- Fong P, Boyer KE, Kamer K, Boyle KA (2003) Influence of initial tissue nutrient status of tropical marine algae on response to nitrogen and phosphorus additions. Marine Ecology Progress Series 262:111-123
- Fong P, Kamer K, Boyer KE, Boyle KA (2001) Nutrient content of macroalgae with differing morphologies may indicate sources of nutrients for tropical marine systems. Marine Ecology Progress Series 220:137-152
- Frost BW (1996) Phytoplankton bloom on iron rations. Nature 383:475-476
- Fujiki T, Toda T, Kikuchi T, Aono H, Taguchi S (2004) Phosphorus limitation of primary productivity during the spring-summer blooms in Sagami Bay, Japan. Marine Ecology Progress Series 283:29-38
- Fujita RM, Wheeler PA, Edwards RL (1989) Assessment of macroalgal nitrogen limitation in a seasonal upwelling region. Marine Ecology Progress Series 53:293-303
- Furnas M, Mitchell A, Skuza M, Brodie J (2005) In the other 90%: phytoplankton responses to enhanced nutrient availability in the Great Barrier Reef Lagoon. Marine Pollution Bulletin 51:253-265
- Glibert PM, Trice TM, Michael B, Lane L (2005) Urea in the tributaries of the Chesapeake and coastal bays of Maryland. Water, Air, and Soil Pollution 160:229-243
- Grimes CB, Kingsford MJ (1996) How do riverine plumes of different sizes influence fish larvae: Do they enhance recruitment? Marine and Freshwater Research 47:191-208
- Halford A, Cheal AJ, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology 85:1892-1905
- Hanisak MD (1979) Growth patterns of *Codium fragile* ssp. *tomentosoides* in response to temperature, irradiance, salinity and nitrogen source. Marine Biology 50:319-332
- Hodgkiss IJ, Ho KC (1997) Are changes in N:P ratios in coastal waters the key to increased red tide blooms? Hydrobiologia 352:141-147
- Hodgkiss IJ, Lu S (2004) The effects of nutrients and their ratios on phytoplankton abundance in Junk Bay, Hong Kong. Hydrobiologia 512:215-229
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551
- Huisman JM (2000) Marine plants of Australia. University of Western Australia Press, Nedlands, Western Australia

- Irwin A, Hallegraef GM, McMinn A, Harrison J, Heijnis H (2003) Cyst and radionuclide evidence demonstrate historic *Gymnodinium catenatum* dinoflagellate populations in Manukau and Hokianga Harbours, New Zealand. *Harmful Algae* 2:61-74
- Iwataki M, Wong MW, Fukuyo Y (2002) New record of *Heterocapsa circularisquama* (Dinophyceae) from Hong Kong. *Fisheries Science* 68:1161-1163
- Jompa J, McCook LJ (2002) Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology* 271:25-39
- Kasih GAA, Kitada T (2004) Numerical simulation of water quality response to nutrient loading and sediment resuspension in Mikawa Bay, central Japan: quantitative evaluation of the effects of nutrient-reduction measures on algal blooms. *Hydrological Processes* 18:3037-3059
- Khan S, Arakawa O, Onoue Y (1997) Neurotoxins in a toxic red tide of *Heterosigma akashiwo* (Raphidophyceae) in Kagoshima Bay, Japan. *Aquaculture Research* 28:9-14
- Kirkpatrick B, Fleming LE, Squicciarini D, Backer LC, Clark R, Abraham W, Benson J, Cheng YS, Johnson D, Pierce R, Zaias J, Bossart GD, Baden DG (2004) Literature review of Florida red tide: implications for human health effects. *Harmful Algae* 3:99-115
- Koop K, Booth D, Broadbent A, Brodie J, Bucher D, Capone D, Coll J, Dennison W, Erdmann M, Harrison P, Hoigh-Guldberg O, Hutchings P, Jones GB, Larkum AWD, O'Neil J, Steven A, Tentori E, Ward S, Williamson J, Yellowlees D (2001) ENCORE: the effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Marine Pollution Bulletin* 42:91-120
- Kröger K, Gardner JPA, Rowden AA, Wear RG (2006) Long-term effects of a toxic algal bloom on subtidal soft-sediment macroinvertebrate communities in Wellington Harbour, New Zealand. *Estuarine Coastal and Shelf Science* 67:589-604
- Lapointe BE (1985) Strategies for pulsed nutrient supply to *Gracilaria* cultures in the Florida Keys: interaction between concentration and frequency of nutrient pulses. *Journal of Experimental Marine Biology and Ecology* 93:211-222
- Lapointe BE (1987) Phosphorus- and nitrogen-limited photosynthesis and growth of *Gracilaria tikvahiae* (Rhodophyceae) in the Florida Keys: an experimental field study. *Marine Biology* 93:561-568
- Lapointe BE (1989) Macroalgal production and nutrient relations in oligotrophic areas of Florida Bay. *Bulletin of Marine Science* 44:312-323
- Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42:1119-1131
- Lapointe BE (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (Reply to the comment by Hughes et al.). *Limnology and Oceanography* 44:1586-1592
- Lapointe BE, Barile PJ, Matzie WR (2004) Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. *Journal of Experimental Marine Biology and Ecology* 308:23-58
- Lapointe BE, Littler MM, Littler DS (1987) A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. *Aquatic Botany* 28:243-255

- Lapointe BE, Littler MM, Littler DS (1992) Nutrient availability to marine macroalgae in siliciclastic versus carbonate-rich coastal waters. *Estuaries* 15:75-82
- Lapointe BE, O'Connell J (1989) Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda: eutrophication of a confined, Phosphorus-limited marine ecosystem. *Estuarine Coastal and Shelf Science* 28:347-360
- Larned ST (1998) Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Marine Biology* 132:409-421
- Larned ST, Stimson J (1996) Nitrogen-limited growth in the coral reef chlorophyte *Dictyosphaeria cavernosa*, and the effect of exposure to sediment-derived nitrogen on growth. *Marine Ecology Progress Series* 145:95-108
- Laroche J, Nuzzi R, Waters R, Wyman K, Falkowski PG, Wallace DWR (1997) Brown tide blooms in Long Island's coastal waters linked to interannual variability in groundwater flow. *Global Change Biology* 3:397-410
- Lee RE (1999) Phycology. Cambridge University Press, Cambridge
- Legendre L (1990) The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in oceans. *Journal of Plankton Research* 12:681-699
- Libes SM (1992) An introduction to marine biogeochemistry. John Wiley & Sons Inc., Canada
- Littler MM, Littler DS, Titlyanov EA (1991) Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. *Coral Reefs* 10:199-209
- Lobban CS, Honda D, Chihara M, Schefter M (1995) *Chrysocystis fragilis* gen. nov., sp. nov. (Chrysophyceae, Sarcinochrysidales), with notes on other macroscopic Chrysophytes (Golden Algae) on Guam reefs. *Micronesica* 28:91-102
- Longhurst A (1993) Seasonal cooling and blooming in tropical oceans. *Deep-Sea Research Part I-Oceanographic Research Papers* 40:2145-2165
- Matsuyama Y, Uchida T, Honjo T, Shumway SE (2001) Impacts of the harmful dinoflagellate, *Heterocapsa circularisquama*, on shellfish aquaculture in Japan. *Journal of Shellfish Research* 20:1269-1272
- McClanahan TR (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* 218:77-102
- McClanahan TR, Cokos BA, Sala E (2002) Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. *Marine Pollution Bulletin* 44:441-451
- McClanahan TR, Maina J, Starger CJ, Herron-Perez P, Dusek E (2005) Detriments to post-bleaching recovery of corals. *Coral Reefs* 24:230-246
- McClanahan TR, Muthiga NA, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19:380-391
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357-367
- Moisander PH, Steppe TF, Hall NS, Kuparinen J, Paerl HW (2003) Variability in nitrogen and phosphorus limitation for Baltic Sea phytoplankton during nitrogen-fixing cyanobacterial blooms. *Marine Ecology Progress Series* 262:81-95

- Munday BL, Hallegraef GM (1998) Mass mortality of captive southern bluefin tuna (*Thunnus maccoyii*) in April/May 1996 in Boston Bay, South Australia: A complex diagnostic problem. *Fish pathology* 33:343-350
- Muslim I, Jones G (2003) The seasonal variation of dissolved nutrients, chlorophyll *a* and suspended sediments at Nelly Bay, Magnetic Island. *Estuarine, Coastal and Shelf Science* 57:445-455
- Noga EJ (1998) Toxic algae, fish kills and fish disease. *Fish pathology* 33:337-342
- Ogg JG, Koslow JA (1978) The impact of Typhoon Pamela (1976) on Guam's coral reefs and beaches. *Pacific Science* 32:105-118
- Okaichi T (1985) Fish kills due to the red tides of *Chattonella*. *Bulletin of Marine Science* 37:772
- Oke PR, Middleton JH (2001) Nutrient enrichment off Port Stephens: The role of the East Australian current. *Continental Shelf Research* 21:587-606
- Örnólfsson EB, Lumsden SE, Pinckney JL (2004) Nutrient pulsing as a regulator of phytoplankton abundance and community composition in Galveston Bay, Texas. *Journal of Experimental Marine Biology and Ecology* 303:197-220
- Paerl HW, Willey JD, Go M, Peierls BL, Pinckney JL, Fogel ML (1999) Rainfall stimulation of primary production in western Atlantic Ocean waters: roles of different nitrogen sources and co-limiting nutrients. *Marine Ecology Progress Series* 176:205-214
- Peckol P, De-Meo-Anderson B, Rivers J, Valiela I, Maldonado M, Yates J (1994) Growth, nutrient uptake capacities and tissue constituents of the macroalgae *Cladophora vagabunda* and *Gracilaria tikvahiae* related to site-specific nitrogen loading rates. *Marine Biology* 121:175-185
- Qi Y, Chen J, Wang Z, Xu N, Wang Y, Shen P, Lu S, Hodgkiss IJ (2004) Some observations on harmful algal bloom (HAB) events along the coast of Guangdong, southern China in 1998. *Hydrobiologia* 512:209-214
- Reay DS, Priddle J, Nedwell DB, Whitehouse MJ, Ellis-Evans CJ, Deubert C, Connelly DP (2001) Regulation by low temperature of phytoplankton growth and nutrient uptake in the Southern Ocean. *Marine Ecology Progress Series* 219:51-64
- Rhodes LL, Mackenzie AL, Kaspar HF, Todd KE (2001) Harmful algae and mariculture in New Zealand. *Journal of Marine Science* 58:398-403
- Riegman R, Noordeloos AAM, Cadee GC (1992) *Phaeocystis* blooms and eutrophication of the continental coastal zones of the North Sea. *Marine Biology* 112:479-484
- Rivers JS, Peckol P (1995) Interactive effects of nitrogen and dissolved inorganic carbon on photosynthesis, growth, and ammonium uptake of the macroalgae *Cladophora vagabunda* and *Gracilaria tikvahiae*. *Marine Biology* 121:747-753
- Robb M, Greenop B, Goss Z, Douglas G, Adeney J (2003) Application of Phoslock<sup>TM</sup>, an innovative phosphorus binding clay, to two Western Australian waterways: Preliminary findings. *Hydrobiologia*:237-243
- Rogers CS, McLain LN, Tobias CR (1991) Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. *Marine Ecology Progress Series* 78:189-199
- Rogers CS, Miller J (2001) Coral bleaching, hurricane damage, and benthic cover on coral reefs in St John, US Virgin Islands: A comparison of surveys with the chain transect method and videography. *Bulletin of Marine Science* 69:459-470
- Rogers CS, Miller J (2006) Permanent 'phase shifts' or reversible declines in coral cover? Lack of recovery of two coral reefs in St. John, US Virgin Islands. *Marine Ecology Progress Series* 306:103-114

- Rogers RW (1996) Spatial, seasonal and secular patterns in the cover of green algae on Heron reef flat, Great Barrier Reef, Australia. *Botanica Marina* 39:414-419
- Sanders JG, Riedel GF (1993) Trace-element transformation during the development of an estuarine algal bloom. *Estuaries* 16:521-532
- Schaffelke B (1999) Short-term nutrient pulses as tools to assess responses of coral reef macroalgae to enhanced nutrient availability. *Marine Ecology Progress Series* 182:305-310
- Schaffelke B, Heimann K, Marshall PA, Ayling AM (2004) Blooms of *Chrysoecystis fragilis* on the Great Barrier Reef. *Coral Reefs* 23:514
- Schaffelke B, Klumpp DW (1998) Nutrient-limited growth of the coral reef macroalga *Sargassum baccularia* and experimental growth enhancement by nutrient addition in continuous flow culture. *Marine Ecology Progress Series* 164:199-211
- Skaloud P, Rezácová M, Ellegaard M (2006) Spatial distribution of phytoplankton in spring 2004 along a transect in the eastern part of the North Sea. *Journal of Oceanography* 62:717-729
- Smayda TJ (1997) What is a bloom? A commentary. *Limnology and Oceanography* 42:1132-1136
- Smith JS, Johnson CR (1995) Nutrient inputs from seabirds and humans on a populated coral cay. *Marine Ecology Progress Series* 124:189-200
- Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35:279-380
- Stimson J, Larned ST, Conklin E (2001) Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. *Coral Reefs* 19:343-357
- Szmant AM (2001) Introduction to the special issue of *Coral Reefs* on "Coral Reef Algal Community Dynamics". *Coral Reefs* 19:299-302
- Taylor DI, Nixon SW, Granger SL, Buckley BA, McMahon JP, H.-J. L (1995) Responses of coastal lagoon plant communities to different forms of nutrient enrichment - a mesocosm experiment. *Aquatic Botany* 52:19-34
- Thacker RW, Ginsburg DW, Paul VG (2001) Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs* 19:318-329
- Tomas CR (1980) *Olisthodiscus luteus* (Chrysophyceae). V. its occurrence, abundance and dynamics in Narragansett Bay, Rhode Island. *Journal of Phycology* 16:157-166
- Trott LA, Alongi DM (1999) Variability in surface water chemistry and phytoplankton biomass in two tropical, tidally dominated mangrove creeks. *Marine and Freshwater Research* 50:451-457
- Tuya F, Haroun RJ (2006) Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: a multi-scaled approach. *Marine Ecology Progress Series* 311:15-28
- Tuya F, Martin JA, Reuss GM, Luque A (2001) Food preferences of the sea urchin *Diadema antillarum* in Gran Canaria (Canary Islands, central-east Atlantic Ocean). *Journal of the Marine Biological Association of the United Kingdom* 81:845-849
- Van Tussenbroek BI (1989) Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falklands South Atlantic Ocean. *Marine Biology* 100:419-430

- Walsh WJ (1983) Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs* 2:49-63
- Wieters EA, Kaplan DM, Navarrete SA, Sotomayor A, Largier J, Nielsen KJ, Veliz F (2003) Alongshore and temporal variability in chlorophyll *a* concentration in Chilean nearshore waters. *Marine Ecology Progress Series* 249:93-105
- Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222:187-196
- Yallop ML (2001) Distribution patterns and biomass estimates of diatoms and autotrophic dinoflagellates in the NE Atlantic during June and July 1996. *Deep-Sea Research Part II* 48:825-844
- Yamamoto T, Seike T (2003) Modelling the population dynamics of the toxic dinoflagellate *Alexandrium tamarense* in Hiroshima Bay, Japan. II. Sensitivity to physical and biological parameters. *Journal of Plankton Research* 25:63-81
- Yeung PKK, Wong FTW, Wong JTY (2002) Large subunit rDNA sequences from *Alexandrium catenella* strains isolated during harmful algal blooms in Hong Kong. *Journal of Applied Phycology* 14:147-150
- Yin KD (2003) Influence of monsoons and oceanographic processes on red tides in Hong Kong waters. *Marine Ecology Progress Series* 262:27-41
- Yin KD, Zhang JL, Qian PY, Jian WJ, Huang LM, Chen JF, Wu MCS (2004) Effect of wind events on phytoplankton blooms in the Pearl River estuary during summer. *Continental Shelf Research* 24:1909-1923
- Yuzao Q, Ziaping Z, Ying H, Songhui L, Congju Z, Yaquing L (1993) Occurrence of red tides on the coasts of China. In: Smayda TJ, Shimizu Y (eds) *Toxic Phytoplankton Blooms in the Seas*. Elsevier Science Publishers, p 43-46