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Spatial and temporal patterns of near-surface chlorophyll *a* in the Great Barrier Reef lagoon

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Abstract. Surface chlorophyll *a* concentrations in the Great Barrier Reef (GBR) lagoon were monitored at individual stations for periods of 6 to 12 years. The monitoring program was established to detect spatial and temporal changes in water quality resulting from increased loads of nutrients exported from the catchments adjoining the GBR. Sampling occurred monthly at up to 86 sites that were located in transects across the width of the continental shelf. In the central and southern GBR (16–21°S), there was a persistent cross-shelf chlorophyll *a* gradient, with higher concentrations near the coast. No cross-shelf gradient was observed in the far northern GBR (12–15°S). Mean chlorophyll *a* concentrations in the far northern GBR ($0.23\ \mu g\ L^{-1}$) were less than half those in the south and central GBR ($0.54\ \mu g\ L^{-1}$). Chlorophyll *a* varied seasonally within regions, with mean summer-wet season (December–April) concentrations ~50% greater than those in the winter-dry season (May–November). Sub-annual, inter-annual and event-related variations in chlorophyll *a* concentrations were observed in several zones. Multi-year patterns in concentrations suggest that relatively short (5–8 years) time series may give spurious estimates of secular trends. Higher chlorophyll *a* concentrations in inshore waters south of 16°S were most likely related to the levels of river nutrient delivery associated with agricultural development on adjacent catchments.

Additional keywords: monitoring, phytoplankton.

Introduction

The Great Barrier Reef (GBR) system is situated on the north-east Australian coast on a shallow continental shelf between 9 and 24°S (Fig. 1). The GBR system is contained within a shallow (<50 m) lagoon (the GBR lagoon), and important components of the system include ~3000 coral reefs, 4300 km^2 of seagrass meadows and 3900 km^2 of mangrove forest along the coast (Brodie 2003). Currents on the inner shelf are primarily south to north, driven by the predominant south-east wind regime; in contrast, on the outer shelf, the East Australian Current flows to the south (south of 16°S), whereas the Hiri current flows to the north (north of 16°S) (Brinkman *et al.* 2002). Net cross-shelf flows are weaker, and inner-shelf waters are thus somewhat isolated from the outer shelf.

Nutrient inputs to the GBR system come from river discharge on the western side, Coral Sea nutrient-rich deep water upwelling on the eastern side, nitrogen fixation by benthic and pelagic cyanobacteria, and rainfall and advection of Coral Sea surface water (Furnas *et al.* 1997). Of these inputs, the river discharge component has increased greatly owing to catchment agricultural development, particularly on those rivers south of Cooktown (Fig. 1) where development has been most intense (Furnas 2003; McKergow *et al.* 2005). Studies using a combination of river monitoring and catchment modelling for the rivers south of Cooktown estimated that nitrogen loads have increased three- to four-fold, phosphorus loads five- to ten-fold and dissolved inorganic nitrogen loads four- to twenty-fold compared with the pre-catchment development period (generally before 1840) (Furnas 2003; McKergow *et al.* 2005). Increases in loads in rivers north of Cooktown, where catchment agricultural development has been minimal, are small.

The increased nutrient loadings from rivers to the GBR lagoon have raised concerns over eutrophication effects on GBR ecosystems (Bell and Elmetri 1995; Brodie *et al.* 2001), and recent studies of reefs along riverine pollution gradients confirmed these fears to be warranted (van Woesik *et al.* 1999; Fabricius and De'ath 2004; Brodie *et al.* 2005; Fabricius 2005; Fabricius *et al.* 2005). In general, reefs in the inshore region south of Cooktown, and thus exposed to nutrient enriched runoff, are in poorer condition than those inshore reefs north of Cooktown.

In many worldwide studies of marine nutrient pollution, chlorophyll *a* has been used as a robust indicator of increased nutrification (Spencer 1985). Chlorophyll *a* as an indicator has been valuable in detecting both spatial and temporal trends

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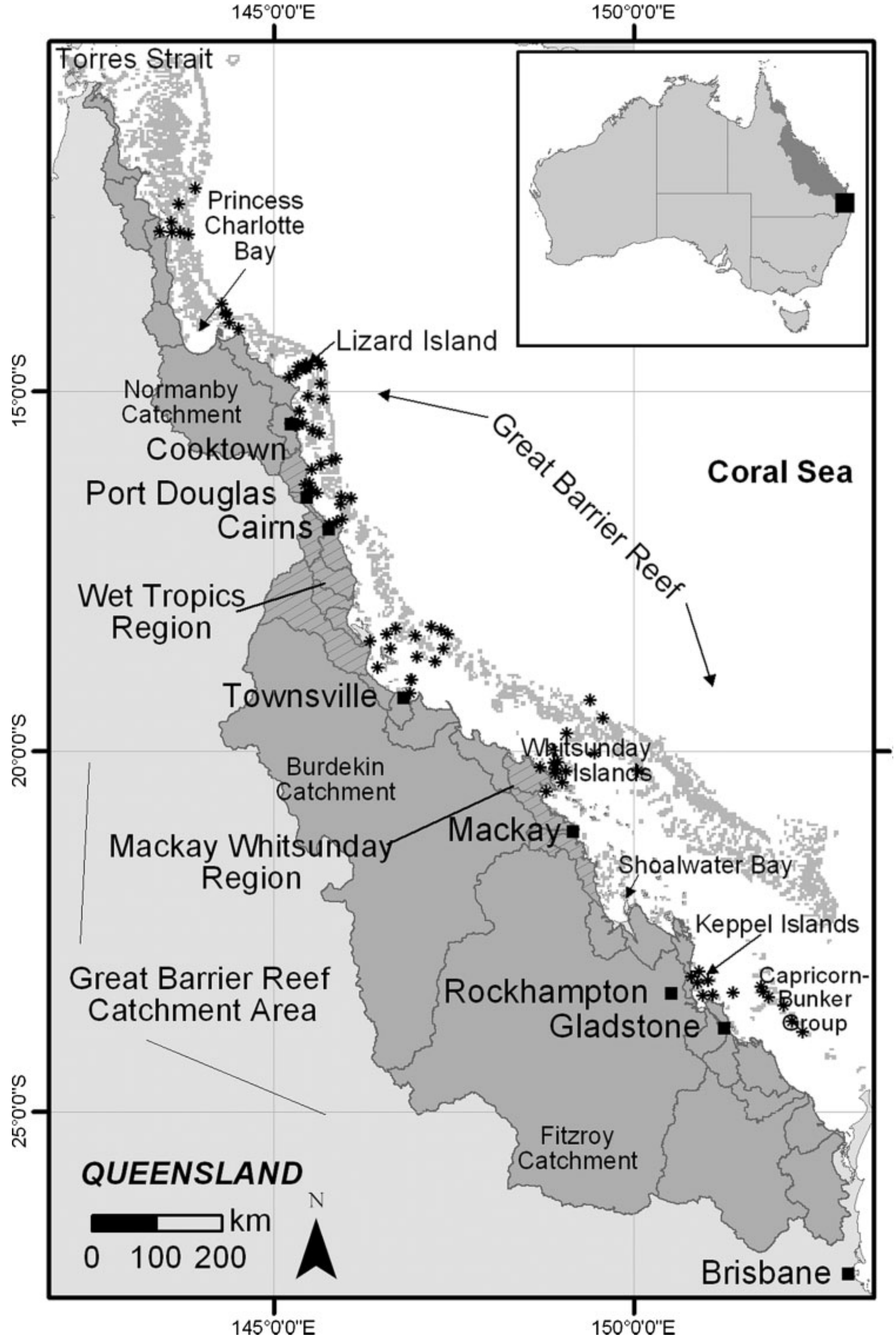

Fig. 1. Location of all chlorophyll sampling stations within the GBR lagoon, Australia. Major river catchments and significant cities and towns are also shown.

in nutrification in Chesapeake Bay (Harding and Perry 1997), the Baltic Sea (Wasmund and Uhlig 2003) and the Adriatic Sea (Degobbis *et al*. 2000). Several studies, beginning with the British Museum expedition (1928–29: Marshall 1933) have examined regional phytoplankton distributions and local dynamics in GBR lagoon water, incorporating measurements of chlorophyll *a* concentrations (e.g. Walker 1981; Revelante and Gilmartin 1982; Furnas and Mitchell 1986, 1997; Liston *et al*. 1992; Brodie *et al*. 1997; Furnas *et al*. 2005). With one exception (Brodie *et al*. 1997), published time-series measurements of phytoplankton biomass (chlorophyll *a*) are of relatively short duration (1 to several years). Broad-scale estimates of regional

Table 1. Transects, latitudinal extent of the regional sampling programs, sampling organisations, cross-shelf extent and duration of sampling

Only data from stations on the continental shelf are included. UE, Underseas Explorer; LIRS, Lizard Island Research Station; Q, Quicksilver Pty Ltd; UQ, Queensland University; QPWS, Queensland Parks and Wildlife Service; HIRS, Heron Island Research Station

Cross-shelf transect	Sampling institution	Latitude (°S)	Shelf position	No. of stations	Start date	End date
Far Northern	UE	12–15	All	13	Dec 1996	Nov 2003
Cooktown-Osprey	UE	13–15	All	10	Dec 1997	Jan 2004
Lizard Island	LIRS	14.7	All	8	Jan 1993	Feb 1999
Port Douglas	Q, UQ, UE	15–16	All	7	Jan 1993	Jan 2004
Cairns	QPWS	16.5	All	7	Dec 1992	Jan 2004
Townsville	QPWS	17.5–19	All	8	Oct 1995	Mar 2004
Whitsundays	QPWS	19–20	All	9	Dec 1996	Dec 2003
Keppel Bay	QPWS	23	Inner	6	Mar 1993	Mar 2004
Capricorn-Bunker	HIRS, QPWS	23	Outer	5	Dec 1992	Mar 2004

and seasonal variations in phytoplankton standing crop are given by Furnas and Mitchell (1997) and Furnas *et al.* (2005). Phytoplankton studies undertaken prior to the mid-1980s were carried out before the importance of picoplankton (largely phototrophic cyanobacteria $<2\,\mu$m) was fully recognised. We now know that prokaryotic picoplankton (chiefly *Synechococcus* spp. and *Prochlorococcus* spp.) dominate phytoplankton biomass under normal conditions in the GBR lagoon (i.e. at times of no disturbance or major nutrient input). Larger phytoplankton (chiefly diatoms $>10\,\mu$m) are relatively more important after disturbance events that introduce additional nutrients into the water column (Marshall 1933; Revelante and Gilmartin 1982; Furnas 1989). The colonial N-fixing cyanobacterium *Trichodesmium* is a common constituent of GBR phytoplankton communities, episodically forming conspicuous surface patches and blooms (Revelante *et al.* 1982; Furnas 1992; Bell *et al.* 1999). Chlorophyll *a* concentrations in surface samples from these patches can vary between 10 and $250\,\mu\mathrm{g\,L^{-1}}$ (Revelante *et al.* 1982; Glibert *et al.* 2000).

Compared with coastal regions in other parts of the world, chlorophyll *a* concentrations in the GBR lagoon are generally low ($<1\,\mu\mathrm{g\,L^{-1}}$: Brodie *et al.* 1997; Furnas and Mitchell 1997). In the central GBR, there is a cross-shelf gradient of chlorophyll *a* concentrations, ranging from $\sim 1\,\mu\mathrm{g\,L^{-1}}$ inshore to $0.25\,\mu\mathrm{g\,L^{-1}}$ offshore (Furnas and Brodie 1996). Average regional chlorophyll concentrations vary seasonally, with higher concentrations in the November to April summer period (Furnas and Mitchell 1997). This seasonal variation is a consequence of the seasonality of large-scale nutrient input processes (upwelling, rainfall, river runoff). Seasonally averaged regional chlorophyll *a* concentrations also vary with latitude, with higher concentrations in the far northern (~10°S) and far southern GBR, but with an overall gradient characterised by higher concentrations in the south (Furnas and Brodie 1996; Furnas and Mitchell 1997; Furnas *et al.* 2005).

In the present study, we summarise the first twelve years of results from a broad-scale chlorophyll *a* monitoring program in coastal and lagoonal waters of the GBR. An important goal in this effort was to resolve the extent of regional differences, if any, in phytoplankton biomass (chlorophyll *a*) and levels of natural temporal variability (monthly, seasonal, inter-annual, decadal) that would affect our ability to detect secular changes in chlorophyll *a*. Because the river runoff to the inner-shelf area north of Port Douglas is relatively unmodified in terms of nutrient flux compared with river runoff south of Port Douglas, our initial working hypothesis was that chlorophyll *a* concentrations would be higher in the southern inner-shelf area than in the northern inner-shelf area. Chlorophyll *a* concentrations in outer-shelf waters are unlikely to be strongly influenced by river nutrient fluxes. A concurrent but separate sampling program targeted periods of river flood events when flood plumes were present in the GBR Lagoon (Devlin *et al.* 2001; Devlin and Brodie 2005). Chlorophyll *a* concentrations during these periods can be an order of magnitude higher then those during the non-flood conditions typically sampled in the present study.

Materials and methods

The monitoring program was designed to monitor water quality status at regional spatial scales (10^2–$10^3\,\mathrm{km^2}$) (Brodie and Furnas 1994), and to detect chlorophyll changes arising from changing inputs of terrestrial nutrients (e.g. Furnas 2003). Partial analyses of early portions of the data set were reported previously (Brodie *et al.* 1994, 1997; Steven *et al.* 1998).

Sampling for the monitoring program described herein was initiated in December 1992 and was carried out at stations in nine regional zones termed ‘transects’ herein (Fig. 1, Table 1). This analysis considers data collected between December 1992 and March 2004. Sampling at individual stations or groups of stations began or ended at different times within the 12-year period and, in some cases, there were extended gaps in the sampling for logistic or organisational reasons. Each transect included sites at both inshore and offshore locations (inshore was defined as <25 km from the coast). These transects and their location are: Far Northern (13°S); Cooktown-Osprey (14°S); Lizard Island (14°S); Port Douglas (15°S); Cairns (16°S); Townsville (18°S); Whitsunday (21°S) and Keppel Bay and Capricorn Bunker (23°S). Within each transect, between 5 and 16 fixed sampling positions were sampled at approximately monthly intervals in order to quantify seasonal changes in phytoplankton biomass. The choice of sampling stations was primarily determined by the availability of local personnel who could be contracted to undertake routine, long-term sampling in a reliable, cost-effective manner. The actual date for sampling within a calendar month was determined by the individual collecting institution and depended on factors such as prevailing weather conditions. In some instances, logistical constraints resulted in periods of no data for some cross-shelf regional transects. Sampling stations were situated some distance (>1 km) from the edge of nearby reefs to avoid confounding influences from biological activity on the reef itself.

Sample and data collection

At each sampling station, two surface water samples were collected by bucket. Duplicate sub-samples (100 mL) were then drawn from each sample and filtered for subsequent chlorophyll *a* analysis. A suite of site variables (water depth, presence of *Trichodesmium* and weather conditions) was measured to aid interpretation of the chlorophyll *a* data. The filtered chlorophyll samples were immediately frozen in a shipboard or laboratory-based freezer. After each sampling cruise, the samples were kept frozen (-10°C) ashore and finally transported frozen for analysis. Chlorophyll and phaeophytin concentrations were determined fluorometrically after grinding in 90% acetone (Parsons *et al*. 1984). The fluorometer was standardised periodically against dilutions of commercially prepared chlorophyll *a* (Sigma) or fresh extracts from log-phase phytoplankton cultures (*Isochrysis galbana*, *Chaetoceros simplex*).

Statistical analyses

For each station, monthly average chlorophyll *a* and phaeopigment concentrations were calculated ($n = 3751$ samples) from the sampling and sub-sampling replicates. Thirty extreme outliers were excluded. These samples contained significant amounts of *Trichodesmium* spp., which skews results because it cannot be easily and representatively sampled. Further statistical analysis was then carried out using generalised additive models (GAMs; Hastie and Tibshirani 1990). Chlorophyll and phaeophytin were analysed as separate response variables. The GAMs used a log-link function (McCullagh and Nelder 1983), which assumes the response variance to be proportional to the mean. This assumption was checked using residual plots. All tests were based on F-ratios (Table 3). The R statistical software was used for all analyses and graphics. Packages nlme, mgcv, and lattice were extensively used (R Development Core Team 2004).

The GAMs accounted for both spatial and temporal effects. For preliminary exploratory analyses, stations were grouped into ‘inshore’ (<25 km from the coast, likely to be influenced by terrestrial runoff and located in less than 20-m water depth) and ‘offshore’ (>25 km from the coast, unlikely to be strongly influenced and located in depths of 20 to 50 m) classes. For regional analysis, some transects were pooled as follows to reduce the nine transects to five regions: Far Northern/Cooktown/Lizard (FN–CL), Port Douglas/Cairns (PD–C), Townsville (TV), Whitsundays (WS) and Capricorn Bunker/Keppel Bay (CB–K). Three far-northern transects (Far Northern, Cooktown and Lizard Island) were relatively close, and Far Northern had fewer data because sampling was carried out on a semi-annual basis; Cairns and Port Douglas transects were adjacent; and Capricorn Bunker and Keppel Bay jointly approximate a cross-shelf transect. For the statistical modelling of spatial and temporal change, the relative distance across the shelf ($0 =$ coastline and $1 =$ end of outer shelf) was used because this better reveals gradual changes, unlike a division of the data into two simple groups of inshore and offshore stations. The following explanatory variables were included in the models: (1) regions comprising Capricorn Bunker/Keppel Bay (CB–K), Whitsunday (WS), Townsville (TV), Port Douglas and Cairns (PD–C), Far North, Cooktown & Lizard Island (FN–CL), (2) smooth trends of relative distance across the shelf within each region, (3) sites with regions, (4) an annual cyclical trend across months, (5) smoothed terms in decimal years (e.g. 1999.5 for 1 July 1999, as opposed to 1999, 2000 etc.) for each region. Purely spatial terms were tested against sites, and all other effects were tested against the residual deviance (McCullagh and Nelder 1983). Models were simplified using backward elimination with highest-order effects removed first. There was no evidence of temporal or spatial correlation of residuals from the fitted models. Partial effects plots were used to interpret the models. These plots show the effects of a particular variable(s) when controlling for all other explanatory variables (i.e. by holding them constant), and compensates for imbalance in the sampling design in the estimation of effects (Table 3).

Results

Monthly averages at each station were calculated, resulting in 3751 cases. The chlorophyll and phaeophytin data were summarised for each combination of the five regions and distances from shore (far [>25 km] and near to the shore [<25 km]) (Table 2*a*). The varying sampling times and frequencies of sampling are evident, as are differences among transects and near/far. The data suggest strong declines in mean chlorophyll concentrations from both south to north, and across the shelf from inshore to offshore; the spatial patterns are similar for both chlorophyll and phaeophytin, with the former having values typically twice those of the latter.

In Fig. 2, results are presented as raw mean station concentrations over time to give an impression of the wide variation in the values for the different transects, the differences from inner stations to outer stations in some regions, and some indication of the variation in values over time. An overall summary of mean chlorophyll *a* concentrations and variability for the grouped inshore and offshore stations in the five latitudinal regions is presented in Fig. 3. A clear increase from north to south is evident, with mean values of chlorophyll and phaeophytin being approximately twice as high in the south. The ratio of chlorophyll to phaeophytin is typically 2:1.

At the whole-GBR scale, there are persistent regional (latitudinal) differences in mean surface chlorophyll *a* and phaeophytin concentrations (Fig. 3, Table 2*a*). In Table 2, summary statistics for chlorophyll and phaeophytin for each region divided into inshore (<25 km) and offshore (>25 km) stations and are shown. For most of the GBR lagoon, this division corresponds approximately to the bathymetric division at 20 m between the inner-shelf and the middle and outer-shelf areas. Irrespective of season or latitude, mean chlorophyll *a* concentrations were

Table 2. Summary statistics (no. of samplings *N*, mean, median, *P*10 and *P*90) for chlorophyll and phaeophytin concentrations in nearshore (inner) and offshore (outer) waters of (*a*) the five regions and (*b*) north and south of Port Douglas

FN–CL, Far Northern/Cooktown/Lizard; PD–C, Port Douglas/Cairns; TV, Townsville; WS, Whitsundays; CB–K, Capricorn Bunker/Keppel Bay

Region	Inner/ Outer	*N*	Mean	Median	*P*10	*P*90	*N*	Mean	Median	*P*10	*P*90
(*a*)											
FN–CL	Inner	304	0.234	0.212	0.105	0.385	304	0.115	0.101	0.050	0.205
PD–C	Inner	947	0.502	0.353	0.111	1.075	947	0.270	0.163	0.048	0.594
TV	Inner	122	0.591	0.446	0.181	1.167	122	0.279	0.206	0.090	0.555
WS	Inner	173	0.370	0.335	0.095	0.631	173	0.227	0.210	0.061	0.399
CB–K	Inner	712	0.618	0.419	0.160	1.304	712	0.267	0.195	0.065	0.562
FN–CL	Outer	503	0.242	0.212	0.118	0.407	503	0.128	0.108	0.055	0.230
PD–C	Outer	484	0.210	0.173	0.073	0.365	484	0.114	0.095	0.035	0.202
TV	Outer	165	0.165	0.128	0.050	0.316	165	0.082	0.063	0.026	0.154
WS	Outer	9	0.153	0.145	0.058	0.259	9	0.097	0.102	0.027	0.151
CB–K	Outer	332	0.519	0.328	0.165	1.103	332	0.191	0.157	0.068	0.353
(*b*)											
PD–C/TV/WS/CB–K	Inner	1954	0.538	0.375	0.130	1.125	1954	0.265	0.183	0.055	0.565
FN–CL	Inner	304	0.234	0.212	0.105	0.385	304	0.115	0.101	0.050	0.205
PD–C/TV/WS/CB–K	Outer	990	0.306	0.215	0.075	0.543	990	0.135	0.105	0.037	0.245
FN–CL	Outer	503	0.242	0.212	0.118	0.407	503	0.128	0.108	0.055	0.230

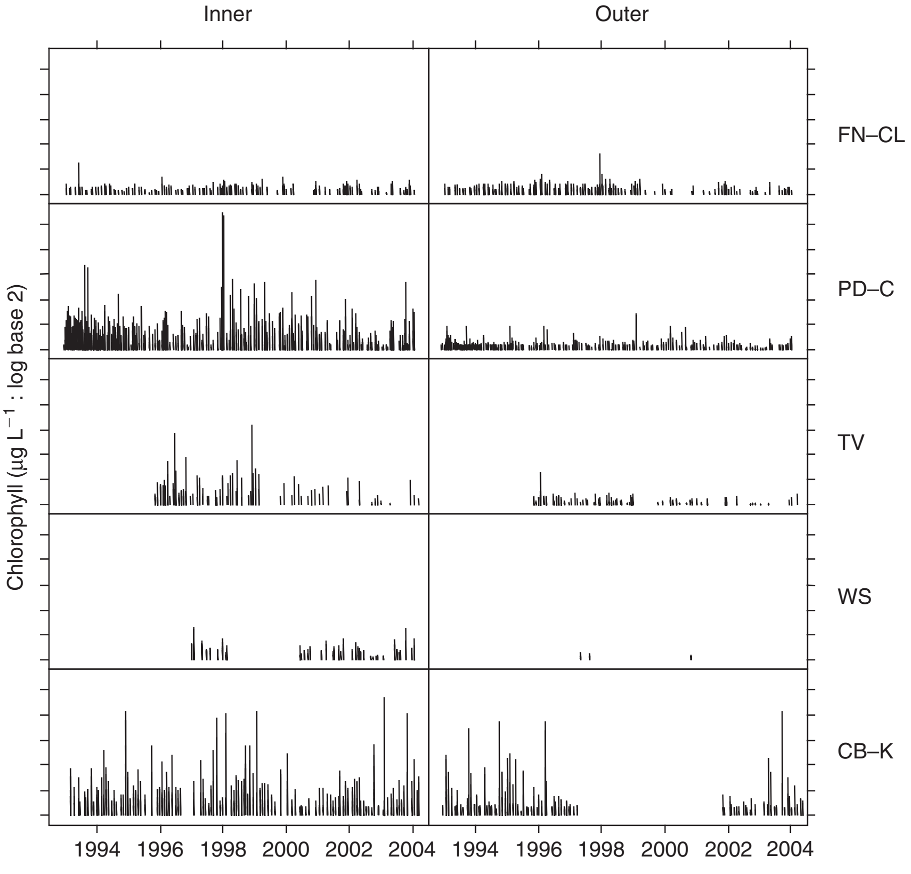

Fig. 2. Monthly mean chlorophyll values within the five pooled regions and segmented into two cross-shelf distance classes: within 25 km (inner) and further than 25 km (outer) from the coast.

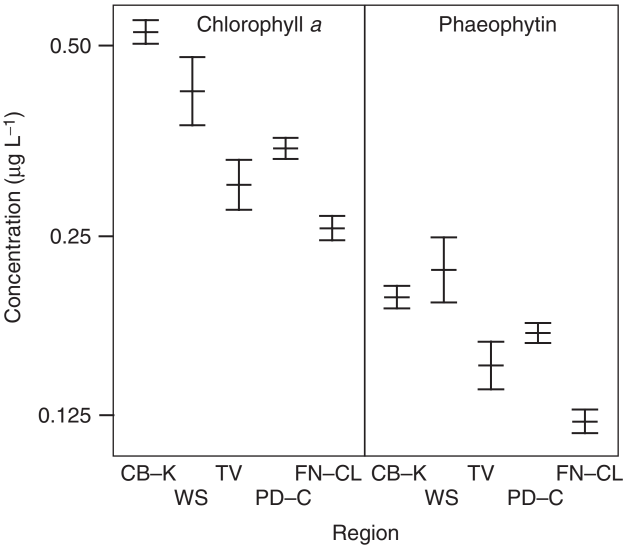

Fig. 3. Partial-effects plots of means (±2 s.e.) of chlorophyll and phaeophytin for the five regions.

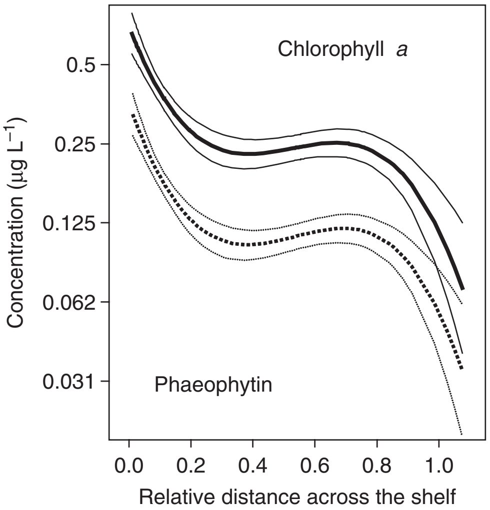

Fig. 4. Partial-effects plots showing change in mean chlorophyll and phaeophytin with relative distance across the shelf (±2 s.e.).

higher inshore than offshore (Fig. 4). Patterns for chlorophyll and phaeophytin are similar, and values of chlorophyll are consistently twice those of phaeophytin. The effect varies among regions (Fig. 5), and the patterns for chlorophyll and phaeophytin are similar. A strong consistent decline in chlorophyll *a* across the shelf in PD–C and TV, a quadratic change in WS with high values close to shore and offshore, and no discernible change in FN–CL and CB–K is shown in Fig. 5. Chlorophyll *a* concentrations at inshore TV are 3.4 times the offshore TV concentration; inshore PD–C is double the offshore value; inshore CB–K and WS is 1.4 times the offshore value; and FN–CL showing little difference across the shelf. The systematic difference between the inshore stations north of Port Douglas (FN–CL) (mean 0.23 μg L^{-1}) and those south of Port Douglas (mean 0.37–0.62 μg L^{-1}) is evident. When the data are further grouped into the whole inshore area either north or south of Port Douglas (Table 2*b*), the difference is about double: mean 0.23 μg L^{-1} in the north *v.* mean 0.54 μg L^{-1} in the south; i.e. in the inshore areas, chlorophyll *a* concentrations are 1.9 times higher in the southern and central regions (CB–K, WS, TV and PD–C) that in the northern region (FN–CL). The situation is similar for phaeophytin in inner-shelf regions: levels were 1.96 times higher when averaged over the four inner-shelf southern and central regions sectors that in FN–CL. There are smaller differences among the regions in the central and southern area for both the inshore and offshore. All offshore results show moderate variability among regions, with highest mean concentrations in the north and south and lowest mean concentrations in the central regions.

Persistent cross-shelf gradients in mean chlorophyll *a* concentration were observed for stations on the four central and southern GBR sampling sectors (PD–C, TV, WS, CB–K), but the gradient was strongest for TV and PD–C (Fig. 5). In contrast, significant cross-shelf differences in mean chlorophyll *a* concentrations were not observed among the Far Northern, Lizard Island and Cooktown-Osprey transect stations. In this area of the GBR, river discharge of nutrients is little elevated above pre-1850 natural levels (Table 4), and nutrients probably limit phytoplankton growth for most of the year. Surface phaeophytin concentrations exhibited a similar latitudinal pattern and the same degree of cross-shelf difference.

When grouped by month, mean chlorophyll *a* concentrations exhibited an annual cycle in all latitudinal zones (Fig. 6), with the highest mean concentrations occurring in the February to May period. Patterns of chlorophyll and phaeophytin are similar. Values of chlorophyll are consistently twice that of phaeophytin. The phaeophytin cycle lags that of chlorophyll by approximately one month throughout the year (Fig. 6). Longer-term variations in mean chlorophyll *a* concentrations were also observed (Fig. 7). The patterns of chlorophyll and phaeophytin are similar, but there are no consistent trends. The timing, duration and magnitude of these changes varied between latitudinal sectors. FN–CL, PD–C and CB–K show non-linear change over years, whereas TV and WS show no discernible change.

Inshore waters of the central and southern GBR between 16° and 23°S had mean chlorophyll *a* concentrations (overall mean 0.54 μg L^{-1}) approximately twice the average concentration measured in the inner-shelf waters adjacent to Cape York Peninsula (13–16°S; mean 0.21 μg L^{-1}). River discharge to the south of 16°S is higher per length of coast than in the north, and for most of the coast, the area of catchments – the nutrient source – is greater. Thus, nutrient loads to inner-shelf waters in the far north may have been less than in the south. This may account for some of the latitudinal difference in chlorophyll concentrations observed in the present study. However, a probably greater effect that accounts for the latitudinal differences is the current loads of river-sourced nutrients to the shelf. Catchments adjacent to the FN–CL region are characterised by minimal agricultural development with low-density cattle grazing, no cropping and low human population numbers. The river catchment areas bordering the Central and Southern GBR that contain the CB–K, WS, TV and PD–C sectors are far more developed, with more intensive beef cattle grazing, large areas of sugarcane cultivation, horticulture, cotton and grain crops and larger human

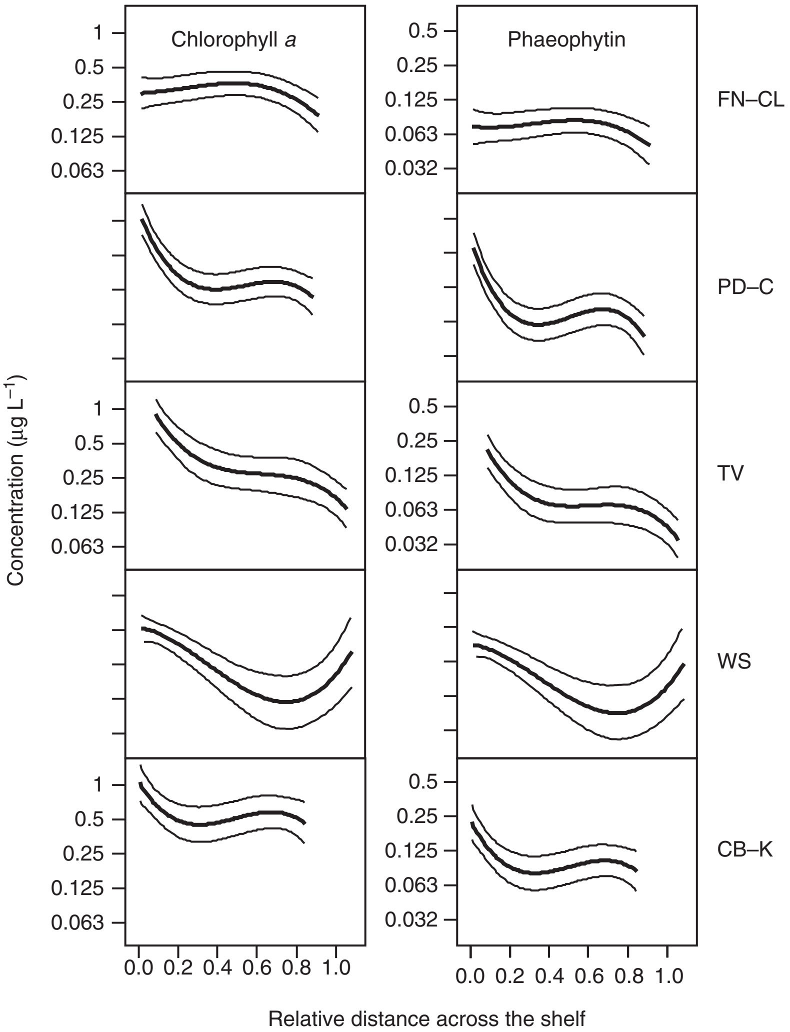

Fig. 5. Partial-effects plots showing trends of chlorophyll and phaeophytin concentrations with relative distance across the shelf (±2 s.e.) for each of the five regions.

populations. The cropping activities, primarily sugarcane cultivation, are supported by high fertiliser application rates. Table 4 summarises the estimated current mean annual loads of nitrogen and phosphorus from rivers with adequate monitoring data north and south of Port Douglas, the estimated natural loads (i.e. before agricultural development) and the estimated increase factor for each river from natural to current states (data from Furnas 2003). The one catchment north of Port Douglas with monitoring data (the Normanby River) shows no significant increase from natural to current condition in terms of nitrogen (TN) and phosphorus (TP) loads. In contrast, south of Port Douglas, two- to six-fold increases in both TN and TP exports from rivers are apparent. River-discharged nutrients are primarily delivered to the inner-shelf part of the GBR lagoon (Devlin *et al.* 2001, 2002), with limited amounts directly reaching the mid- and outer-shelf reefs of the GBR except in the areas adjacent to the Cairns–Cooktown region where the shelf is narrow (Devlin and Brodie 2005). The large increases in nutrient loads, which have occurred over the last 150 years, are likely to be an important part of the explanation for the higher concentrations of chlorophyll on the inner-shelf south of Port Douglas.

In the transects south of Port Douglas (PD–C, TV, WS, CB–K), chlorophyll concentrations exhibit a strong cross-shelf gradient from the coast to the outer reef (Fig. 5). The principal sources of new nutrients for the GBR lagoon were quantified by Furnas *et al.* (1997) as river discharge, Coral Sea upwelling, rainfall and biological nitrogen fixation. However, most nutrient requirements for phytoplankton growth are supplied from recycled stocks (Furnas *et al.* 1997, 2005). River discharge also supplies iron, silica, carbon and micronutrients, as well as nitrogen and phosphorus, and is the principal source of new nutrients adjacent to the coast. It is likely that this input supports the cross-shelf chlorophyll gradients in the southern GBR area. Resuspension of shallow benthic sediments owing to strong winds in depths less than 15 m keeps nutrients in circulation in this area, and is an important factor that influences

Table 3. ANOVA of chlorophyll and phaeophytin

The design and statistical analysis are fully described in 'Statistical analyses'. Variation owing to location across the shelf is partitioned in two ways: first by Across and Region × Across$^{(A)}$, and second by profiles for each regions$^{(B)}$. Variation owing to Year and Region × Year was treated similarly$^{(C,D)}$. FN–CL, Far Northern/Cooktown/Lizard; PD–C, Port Douglas/Cairns; TV, Townsville; WS, Whitsundays; CB–K, Capricorn Bunker/Keppel Bay

Source of variation	d.f.	Chlorophyll			Phaeophytin		
		MS	*F*	*P*	MS	*F*	*P*
Region	4	68.67	19.91	<0.001	37.37	7.48	<0.001
Across^{A}	3	166.67	264.53	<0.001	187.76	284.49	<0.001
Region × Across^{A}	12	14.25	22.63	<0.001	13.85	20.99	<0.001
Across (FN–CL)^{B}	3	4.84	1.40	0.25	2.98	0.60	0.617
Across (PD–C)^{B}	3	135.42	39.27	<0.001	150.75	30.20	<0.001
Across (TV)^{B}	3	53.13	15.40	<0.001	46.13	9.24	<0.001
Across (WS)^{B}	3	6.91	2.00	0.123	5.94	1.19	0.320
Across (CB–K)^{B}	3	23.39	6.78	<0.001	37.39	7.49	<0.001
Sites	63	3.45	5.47		4.99	7.53	
Months	4	12.59	19.97	<0.001	8.59	12.95	<0.001
Year^{C}	3	17.17	27.25	<0.001	22.83	34.60	<0.001
Region × Year^{C}	12	4.71	7.47	<0.001	6.46	9.79	<0.001
Year (FN–CL)^{D}	3	1.80	2.86	0.035	14.55	21.94	<0.001
Year (PD–C)^{D}	3	10.02	15.90	<0.001	12.65	19.08	<0.001
Year (TV)^{D}	3	0.16	0.26	0.857	1.27	1.91	0.125
Year (WS)^{D}	3	0.64	1.01	0.387	0.49	0.73	0.531
Year (CB–K)^{D}	3	23.05	36.57	<0.001	19.71	29.73	<0.001
Error	3620	0.63			0.66		

Table 4. Increases in nutrient loads (tonnes) in selected GBR catchment rivers over the last 150 years

River	Pre-1850		Current		Increase factor	
	TN (t)	TP (t)	TN (t)	TP (t)	TN	TP
Normanby	2500	250	2000	210	0.8	0.8
Division at Port Douglas (~16°S)						
Russell-Mulgrave	300	30	1400	150	4.7	5
Johnstone	400	40	1900	200	4.8	5
Tully	250	30	1300	140	5.2	4.7
Herbert	300	40	1600	170	5.3	4.2
Burdekin	5000	600	9000	1700	1.8	2.8
Fitzroy	3000	300	5300	1000	1.8	3.3

near-shore chlorophyll concentrations (Walker 1981). Upwelling of nutrient-rich deep water principally affects the outer shelf (Andrews and Gentian 1982; Furnas and Mitchell 1986, 1996). The cross-shelf chlorophyll *a* concentration gradients observed in the present study south of Port Douglas are similar to those reported in earlier work, e.g. by Furnas and Brodie (1996) and Furnas and Mitchell (1997), with a sharp initial decline within the first 20 km from the coast and a small decline from the 20-km mark to the shelf edge (Fig. 5). These changes are similar to gradients in chlorophyll and phytoplankton productivity recorded in Morton Bay, just to the south of the GBR lagoon; however, mean chlorophyll *a* concentrations are higher in Morton Bay (O'Donohue *et al.* 2000). Chlorophyll concentration gradients in Morton Bay were attributed to river discharge of nutrients derived from urban and agricultural activities in the river catchments (O'Donohue and Dennison 1997).

Another regional-scale driver of phytoplankton productivity and chlorophyll concentrations in the GBR is tidal mixing (Liston *et al.* 1992). In the areas of the GBR shelf with large tidal ranges and/or strong tidal currents, specifically (1) the lagoon south of Mackay and north of Shoalwater Bay and (2) the Torres Strait, strong tidal currents regularly resuspend benthic sediments, keeping nutrients from the sediments available to the water column. As a consequence, chlorophyll concentrations remain high (Furnas and Brodie 1996).

The chlorophyll and phaeophytin data exhibit a seasonal signal, with the monthly means of pooled chlorophyll data peaking in March and with a minimum in September (Fig. 6). An ~1.5-fold difference between mean values in February and August was observed. The difference results from the variation in nutrient inputs to the GBR owing to variability of shelf-break upwelling, rainfall and wet-season runoff concentrated

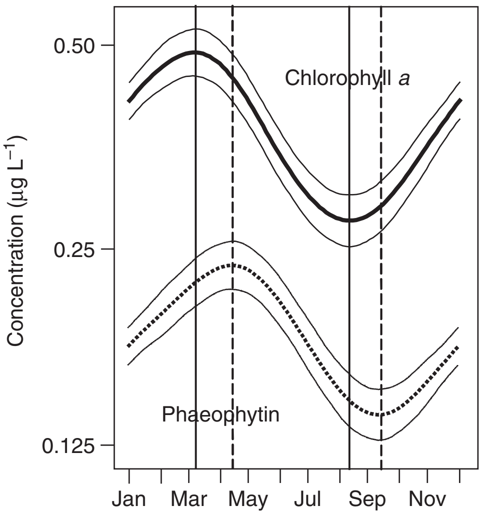

Fig. 6. Partial-effects plots showing cyclical seasonal change within years (±2 s.e.) of chlorophyll and phaeophytin concentrations.

in the December to March period (Furnas and Mitchell 1986, 1996; Furnas 2003). Similar seasonal fluctuations associated with temperature, light availability and nutrient enrichment have been measured in other Australian coastal waters immediately to the south of the GBR (O'Donohue and Dennison 1997). Seasonality in tropical plankton populations is less pronounced than in temperate waters (Sournia 1969; Longhurst 1993), with increases largely a consequence of seasonal variation in disturbance regimes or nutrient inputs that inject nutrients into the euphotic zone. The phaeophytin peak lags the chlorophyll peak by approximately one month (Fig. 6). Because phaeophytin is a degradation product of chlorophyll after cell death, this lag is probably a result of breakdown/degradation kinetics and time.

The longest periods of sustained sampling in the current dataset (>10 years) were conducted in the FN–CL, PD–C and CB–K transects (Fig. 7). In this time period, these regions showed no consistent temporal trends. However, within individual transect data sets, there are indications of both event-based and multi-annual variation. These patterns are partially correlated among regions. Overall, the period of monitoring is not yet sufficient to resolve or interpret these temporal trends.

Discussion

In order to detect and monitor secular changes in chlorophyll concentrations in GBR waters, it is first necessary to resolve the magnitude of spatial and temporal variability in the signals arising from natural causes. Large, hydrodynamically open tropical shelf ecosystems such as the GBR pose significant challenges to monitoring efforts because they are large enough to support persistent regional differences in plankton populations related to water residence times and nutrient availability (Denman and Powell 1984), and yet are responsive to episodic, local- and regional-scale events (wind-forced sediment resuspension, river plumes, cyclonic disturbances, upwelling), which can induce episodic changes in nutrient availability that exceed changes arising from non-episodic seasonal and inter-annual fluctuations in nutrient input. Of particular importance, both the pelagic and benthic biological communities of the GBR are capable of rapidly assimilating and sequestering added nutrients. If nutrients can be regarded as a currency for the production of biomass, measures of biomass using indicators such as chlorophyll provide the best measure of the quantity of nutrients in circulation within regions.

In the present study, chlorophyll was used as a general indicator of nutrient availability. Chlorophyll results suggest that the inner shelf south of Port Douglas is nutrient-enriched relative to offshore waters and the far-northern GBR, and the most parsimonious explanation for this is above-natural nutrient fluxes from land-based sources to this part of the GBR lagoon.

The presence of generally higher concentrations of chlorophyll and hence higher phytoplankton biomass in the southern inshore area compared with the lower and likely natural concentrations in the northern inshore area has important implications for several ecosystem responses of the GBR. The effects of muddy marine snow have been suggested as factors in the degradation of inner-shelf coral reefs in the Wet Tropics region between Townsville and Port Douglas (Wolanski *et al.* 2003). Formation of the muddy marine snow is believed to be accelerated in the presence of elevated phytoplankton and microorganism abundances and, in particular, of the transparent exopolymer particles (TEP) produced by microbes and diatoms (Fabricius *et al.* 2003). Muddy marine snow may smother small coral reef organisms such as coral polyps (especially those in the juvenile stage) and barnacles. Muddy marine snow may be less common in the region north of Port Douglas where chlorophyll concentrations and phytoplankton biomass are lower, and this difference may be one factor responsible for the difference in reef condition between the Wet Tropics and Princess Charlotte Bay reefs. Inner-shelf reefs in Princess Charlotte Bay are in much better condition than those off the Wet Tropics coast (Fabricius and De'ath 2004; Fabricius *et al.* 2005); however, much of the difference is associated with the disturbance history of the two regions. In studies of Whitsundays reefs, van Woesik *et al.* (1999) observed a significant negative relationship between chlorophyll *a* concentrations and the following community characteristics: percentage scleractinian coral cover, species richness and coral abundance.

The higher chlorophyll *a* concentrations and hence phytoplankton biomasses measured in inner-shelf waters south of Port Douglas may have implications for the species composition of phytoplankton in this area. Nutrient-depleted areas of the tropical oceans are largely dominated by prochlorophytes, particularly by *Prochlorococcus* spp. (Campbell *et al.* 1994). In slightly more nutrient-enriched conditions, e.g. coral-reef lagoonal environments (Blanchot and Charpy 1997), other picocyanobacteria such as *Synechococcus* spp. increase in abundance. On the GBR shelf, *Synechococcus* was more abundant and had greater biomass than *Prochlorococcus* at most inshore and mid-shelf sites in the central GBR, whereas significant *Prochlorococcus* populations were confined to mid- and outer-shelf sites with more pronounced oceanic characteristics (Crosbie and Furnas 2001). Diatoms in shelf waters of the GBR are capable of growth rates in the range of two to five doublings per day, compared with rates of less than two doublings per day for microflagellates and picoplankton (Furnas 1991), and may be able to preferentially grow in nutrient-enriched conditions. On the GBR shelf, chlorophyll from species of >10 μm showed the greatest increase

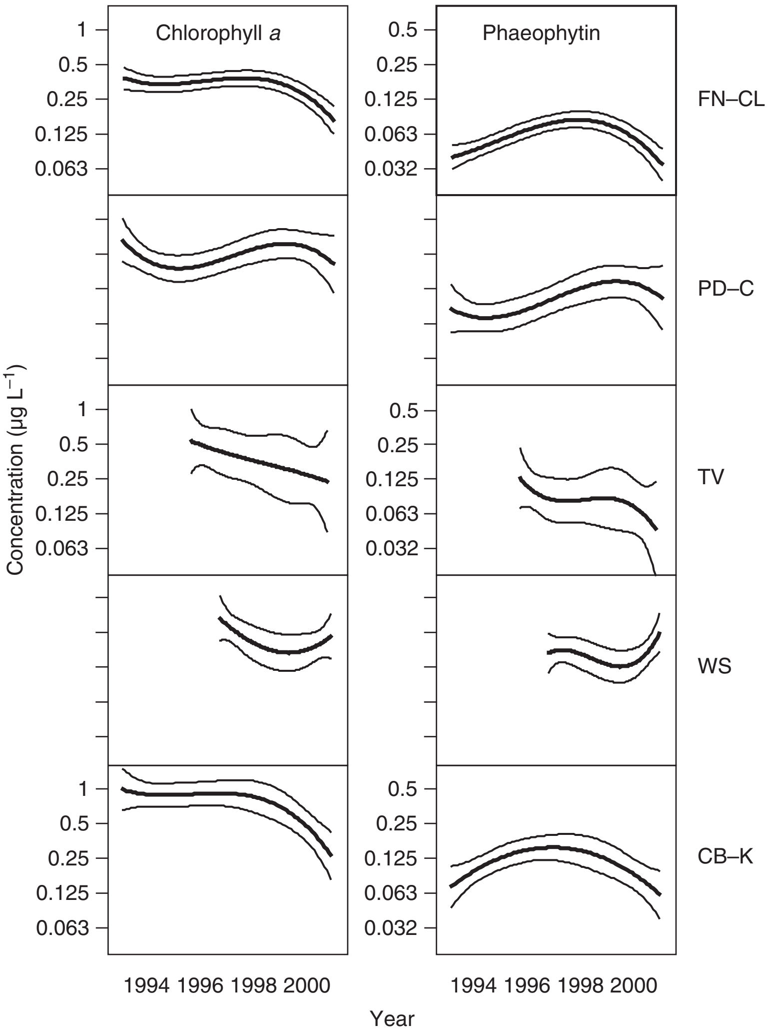

Fig. 7. Partial-effects plots showing long-term trends (±2 s.e.) for chlorophyll and phaeophytin concentrations within each of the five latitudinal regions.

in concentration at the front of a flood plume from the Burdekin River (McKinnon and Thorrold 1993), which would have been associated with a large input of nutrient-rich water (Devlin *et al.* 2001).

The higher phytoplankton biomass in coastal waters south of Port Douglas may thus be also associated with a persistent difference in phytoplankton speciation. Differences in the contributions of different size classes of phytoplankton to the standing crop and primary production in the northern and southern GBR were previously measured (Furnas and Mitchell 1988). In February 1986 and 1988, picoplankton accounted for 59% of phytoplankton standing crop in the northern GBR, compared with only 25% in the central and southern GBR (Furnas and Mitchell 1988). It is also clear that although picoplankton usually dominate biomass and primary production on the GBR shelf (Furnas and Mitchell 1986), episodic bloom conditions driven by river discharge, resuspension events or upwelling are more likely to be dominated by larger phytoplankton, chiefly diatoms (Revelante and Gilmartin 1982; Furnas 1989; Ayukai *et al.* 1997*a*). Bell *et al.* (1999) suggested that changes in delivery of river-borne nutrients such as phosphorus and iron may also promote the growth of *Trichodesmium*, and that ‘new’ nitrogen fixed by *Trichodesmium* spp. may now contribute to eutrophication of the central GBR lagoon. If the differences in phytoplankton biomass and potentially phytoplankton speciation are a result of increased nutrient inputs associated with agricultural development, then this may have considerable implications for trophic relationships within plankton communities in the affected areas. Similar changes in phytoplankton biomass and species’ size composition were reported from Singapore (Gin *et al.* 2000) and Japan (Tada *et al.* 2003).

The crown-of-thorns starfish (COTS) (*Acanthaster planci*) has been a major cause of episodic damage to reefs of the GBR and other regions worldwide over the last 40 years (Birkeland and Lucas 1990). COTS have a planktonic larval stage of a few weeks duration in which they are dependent on phytoplankton as a food source. It has now been shown that survival of COTS larvae requires suitable phytoplankton with chlorophyll concentrations above 0.25 μg L^{-1} (Ayukai *et al.* 1997*b*). The elevated concentrations of chlorophyll in the southern inshore area (particularly in the Wet Tropics area, 16 to 19°S) recorded during the present study are in a range suitable to promote better-than-normal survivorship, especially during the period when COTS larvae are present in the water column (November to January). In contrast, in the inshore northern area (FN–CL) and most offshore areas, mean chlorophyll *a* concentrations are $<$0.25 μg L^{-1} and larval starvation is likely to occur (Brodie *et al.* 2005).

Analysis of the 12-year data set of the present study revealed that persistent regional patterns in chlorophyll concentrations within the GBR lagoon can be resolved, but that 12 years may not be long enough to clearly resolve multi-year temporal patterns. Inshore waters in the south of the GBR adjacent to rivers with catchments developed for agriculture have chlorophyll concentrations that are higher (approximately double) than those in the far northern GBR adjacent to catchments with minimal development. The chlorophyll monitoring program reported in the present study is planned to continue for at least several more years.

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