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Tropical phytoplankton species and pigments of continental shelf waters of North and North-West Australia

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ABSTRACT: The phytoplankton of the shelf waters of the Gulf of Carpentaria, Arafura Sea, Timor Sea and North-West Australia is basically a diatom flora, distinctly different from the oceanic, predominantly dinoflagellate flora of the Coral Sea and Indian Ocean. Large morphologically elaborate tropical diatoms and dinoflagellates of this shelf region show great species diversity (more than 200 spp. identified) and a variety of symbiotic associations (28 species-pairs recognised). In contrast, the tropical nanoplankton (2 to 20 µm; mainly small diatoms, prymnesiophytes and dinoflagellates; 70 spp.) are remarkably similar in species composition to those of subtropical and temperate Australian waters. Water-column chlorophyll values in both North-West Shelf and Gulf waters ranged from 10 to 55 mg m^{-2}. Nanoplankton accounts for 70 to 97 % of total phytoplankton chlorophyll, except in local diatom or *Trichodesmium* blooms (30 to 60 %).

INTRODUCTION

The continental shelf waters of North and North-West Australia are areas of high biological productivity. The shallow (30 to 60 m) Gulf of Carpentaria is the site of a multispecies prawn fishery and the shallow (40 to 200 m) and wide (200 km) North-West Shelf has a large demersal trawl fishery (Sainsbury, 1979; Bain, 1982). Both Gulf and North-West Shelf waters sustain a high zooplankton biomass (up to 1900 mg dry weight m^{-2}; Tranter and Kerr, 1977; Rothlisberg and Jackson, 1982), but the phytoplankton organisms that support the food chains in these areas are largely unknown. Previous surveys in northern Australian waters and the Java Sea have been restricted to examination of net-phytoplankton (> 35 µm) and spectrophotometric chlorophyll analyses (Allen and Cupp, 1935; Desrosières, 1965; Humphrey, 1966; Humphrey and Kerr, 1969; Markina, 1972; Newell, 1973; Motoda et al., 1978).

An opportunity to study the phytoplankton populations of the North-West Shelf in more detail occurred in June 1980 and 1983 (early winter) and December 1982 (summer), and of the Gulf of Carpentaria and Arafura Sea in March 1982 (autumn). The methodology used (Jeffrey and Hallegraeff, 1980a, b; Jeffrey, 1981; Hallegraeff, 1983) allowed characterisation of the complete phytoplankton flora, including many of the delicate flagellates, and the full range of photosynthetic pigments (chlorophylls, carotenoids and chlorophyll degradation products). Tropical inshore communities of the Gulf of Carpentaria and North-West Shelf were clearly distinguished from tropical oceanic phytoplankton communities of the Coral Sea and Indian Ocean.

MATERIALS AND METHODS

Sampling locations. Fig. 1 shows the location of the stations from which phytoplankton samples were taken, and Table 1 summarises cruise numbers, dates and number of stations occupied. Samples from the North-West Shelf were collected along transects from inshore waters (17 to 40 m depth) to the edge of the continental shelf (euphotic zone depth 150 m). The cruise in the Gulf of Carpentaria and Arafura Sea covered water column depths of 26 to 68 m.

Collection and preparation of samples. Sea water samples for pigment analysis and species identification were collected throughout the upper 150 m of the water column using 8 l Niskin bottles. To determine the proportion of nanoplankton (< 15 µm fraction; Hallegraeff, 1981), subsamples were fractionated through 10 µm-mesh plankton gauze and prepared for

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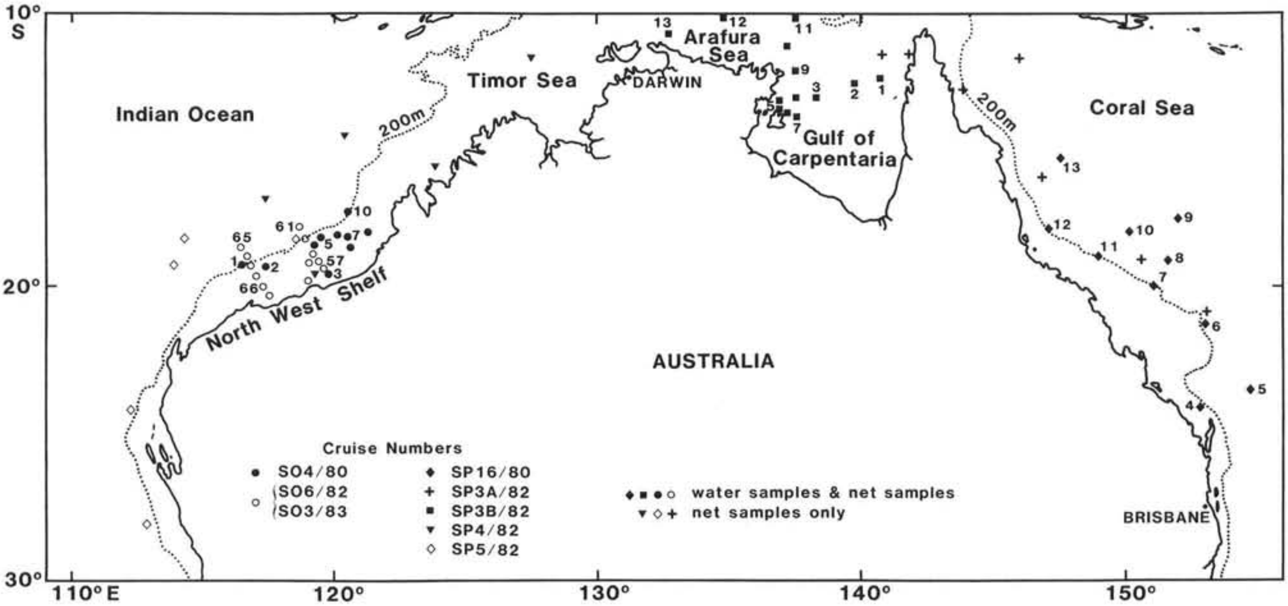

Fig. 1. Map of northern Australia with sampling stations

pigment analysis. Additional collections of the larger phytoplankton species were made with a 37 µm-mesh free-fall plankton net (Heron, 1982).

Pigment analysis. Chlorophyll *a* was determined spectrophotometrically from stored and frozen samples (Jeffrey and Humphrey, 1975), followed by separation of all pigment fractions by thin-layer chromatography (Jeffrey, 1981). This method, which uses washed cellulose as adsorbant, separates the major chlorophylls, carotenoids and chlorophyll degradation products in a two-dimensional system that takes only 10 min per sample.

Species identification. Phytoplankton species were examined microscopically on board ship in the living state. Fluorescence microscopy (using a Zeiss epifluorescence microscope with G436 exciter filter and LP520 barrier filter) was used to distinguish photosynthetic (red or orange fluorescent chloroplasts) from non-photosynthetic algal cells (no fluorescence or golden-green fluorescent cytoplasm). Species abundances were estimated by the inverted microscope technique (Utermöhl, 1958) from water samples concentrated with a continuous-flow plankton centrifuge and preserved with 3 % glutaraldehyde (Jeffrey and Hallegraeff, 1980a). Cell counts were converted to volume estimates by approximating cell shape to the closest solid geometric configuration (Smayda, 1978). Net samples, preserved with 2 % formaldehyde neutralised with hexamine, were used to supplement identification of the larger diatoms and dinoflagellates. Species identifications were achieved by a combination of light microscopy (LM), scanning electron microscopy (SEM) for coccolithophorids, diatoms and armoured dinoflagellates and transmission electron microscopy (TEM) for acid-cleaned diatoms and shadow-cast whole mounts of scale-bearing flagellates. Identification sources were Allen and Cupp (1935); Subrahmanyan (1946) and Simonsen (1974) for diatoms and Taylor (1976) for dinoflagellates. A wide range of individual papers was consulted for nanoplankton (see Hallegraeff, 1983; 1984).

Hydrological measurements. Temperature, salinity and nitrate were measured from water bottle samples using standard methods (Major et al., 1972).

Table 1. Summary of cruises, stations and areas sampled

Cruise no	Date	Number of stations	Area
SO 4/80	8–18 Jun 1980	10	North-West Shelf
SO 6/82	3–16 Dec 1982	19	North-West Shelf
SO 3/83	14 Jun–1 Jul 1983	17	North-West Shelf
SP 3B/82	18–30 Mar 1982	13	Gulf of Carpentaria, Arafura Sea
SP 16/80	5–19 Nov 1980	13	Coral Sea
SP 3A/82	4–18 Mar 1982	5	Coral Sea
SP 4/82	22 Apr–5 May 1982	5	Timor Sea, West Coast of Australia
SP 5/82	6–19 May 1982	5	West Coast of Australia

RESULTS

Phytoplankton chlorophyll biomass

Table 2 summarizes the chlorophyll concentrations of all samples taken on the North-West Shelf and the Gulf of Carpentaria and Arafura Sea. Chlorophyll maxima reached 1.07 µg l^{-1} on the North-West Shelf, 2.34 µg l^{-1} in the Gulf of Carpentaria and 1.26 µg l^{-1} in the Arafura Sea. Total water column values in these areas ranged from 10 to 55 mg m^{-2}. The nanoplankton (< 15 µm fraction) formed a major component of the phytoplankton (70 to 97 % of total chlorophyll) in 23 out of 30 stations, whereas the other 7 stations showed values of 30 to 60 % (Table 3). Chlorophyll profiles showed deep (40 to 80 m) maxima in autumn in the central part of the Gulf (Fig. 2a) and in summer on the North-West Shelf when the water column was stratified (Fig. 2b).

Table 2. Concentration of phytoplankton chlorophyll *a* in continental shelf waters of North and North-West Australia as determined by spectrophotometry

Area	Month	Chlorophyll *a* concentration (mean ± SD) Water column total (mg m^{-2})	Water column maximum (µgl^{-1})	Number of observations
North-West Shelf	Jun 1980	36.3 ± 12.0 (range 21.9–54.7)	0.49 ± 0.18 (range 0.22–0.69)	10
	Dec 1982	27.4 ± 6.8 (range 10.0–38.1)	0.60 ± 0.21 (range 0.27–1.07)	19
	Jun 1983	22.2 ± 13.3 (range 7.0–49.7)	0.43 ± 0.16 (range 0.25–0.85)	17
Gulf of Carpentaria	Mar 1982	36.1 ± 8.2 (range 25.8–48.4)	1.42 ± 0.56 (range 0.78–2.34)	10
Arafura Sea	Mar 1982	37.5 ± 3.4 (range 34.1–40.9)	1.02 ± 0.29 (range 0.70–1.26)	3

Table 3. Nanoplankton (<15 µm) chlorophyll at selected stations

Area	Month	% of total water column chlorophyll (mean ± SD)	Number of observations
North-West Shelf	Jun 1980	84 ± 9 (range 67–97)	10
	Dec 1982	64 ± 4 (range 60–68)	3
	Jun 1983	73 ± 16 (range 53–88)	6
Gulf of Carpentaria	Mar 1982	72 ± 21 (range 30–96)	9
Arafura Sea	Mar 1982	68 ± 18 (range 55–88)	2

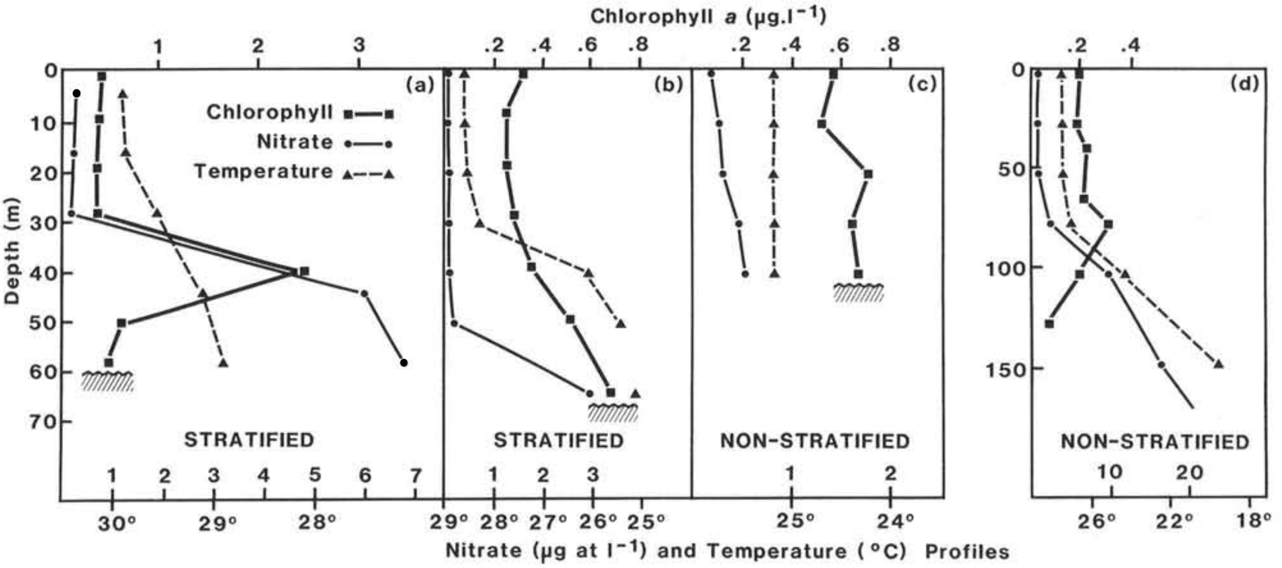

Fig. 2. Typical chlorophyll depth profiles in the Gulf of Carpentaria (a) and on the North-West Shelf (b, c, d) under stratified (a, b) and non-stratified (c, d) conditions, compared with nutrient and temperature structure of the water column. (a) SP 3B/82 cruise, Stn. 2; (b) SO 6/82, Stn. 57; (c) SO 4/80, Stn. 3; (d) SO 4/80, Stn. 10

Chlorophyll profiles showed an uniform distribution with depth when the water column was well-mixed (Fig. 2c), both in autumn in the Arafura Sea and inshore waters of the Gulf of Carpentaria (Stns. 4, 5, 6) and in winter on the North-West Shelf. Nutrient-rich water ($NO_3 - N > 3$ µgat l^{-1}) was always present at the shelf edge at depths below 100 m (Fig. 2d), but under certain stratified conditions this nutrient layer penetrated into shallower waters, both in the Gulf of Carpentaria (Fig. 2a) and on the North-West Shelf (Fig. 2b).

Phytoplankton pigment composition

Sixty thin-layer pigment chromatograms were examined from North-West Shelf phytoplankton. Selected examples are shown in Fig. 3a, b, c. Dominant pigments were chlorophyll *a* and carotene (present in all algal types), fucoxanthin, chlorophyll *c* (from diatoms and golden brown flagellates), chlorophyll *b* (green flagellates) and 2 unidentified yellow and 1 pink xanthophyll (Fractions 13, 14 and 15). Trace amounts of peridinin (from photosynthetic dinoflagellates) were present on 20 % of the chromatograms. Small amounts of chlorophyll degradation products were also detected (17 to 19 % of total chlorophyll *a*; Table 4) and these were more clearly identified in pooled samples where ample pigment was available for analysis (Fig. 3b, c). Chlorophyll *a* degradation products detected included pheophytin *a* (Fraction 5), 1 or 2 unidentified blue-green derivatives (Fractions 6, 7), 1 to 3 chlorophyllide-like zones (Fractions 8, 9, 10), unidentified brown origin material (Fraction 11) and a pheophorbide-like pigment (Fraction 12). White fluorescent material at the solvent front and sometimes also at the origin of the chromatogram was identified as lipid by staining with iodine vapour. Pigment ratios were estimated by quantitative elution of fractions from three selected chromatograms (Table 4).

Phytoplankton species abundance and diversity

In terms of cell number, the most abundant species were found in the nanoplankton, the large diatoms and the blue-green alga *Trichodesmium* were moderately abundant, with the large dinoflagellates less important. Maximum cell concentrations of the nanoplankton ranged from 10^3 to 10^6 cells l^{-1}. Small (1 to 3 µm) flagellates (e.g. *Micromonas pusilla*) occurred at maximum concentrations of 10^5 to 10^6 cells l^{-1}, small diatoms (*Nitzschia bicapitata, Nitzschia closterium, Thalassiosira* spp.) at 10^4 to 10^5 l^{-1}, small dinoflagellates (*Gymnodinium* spp.) at 10^4 to 10^5 l^{-1} and coc-

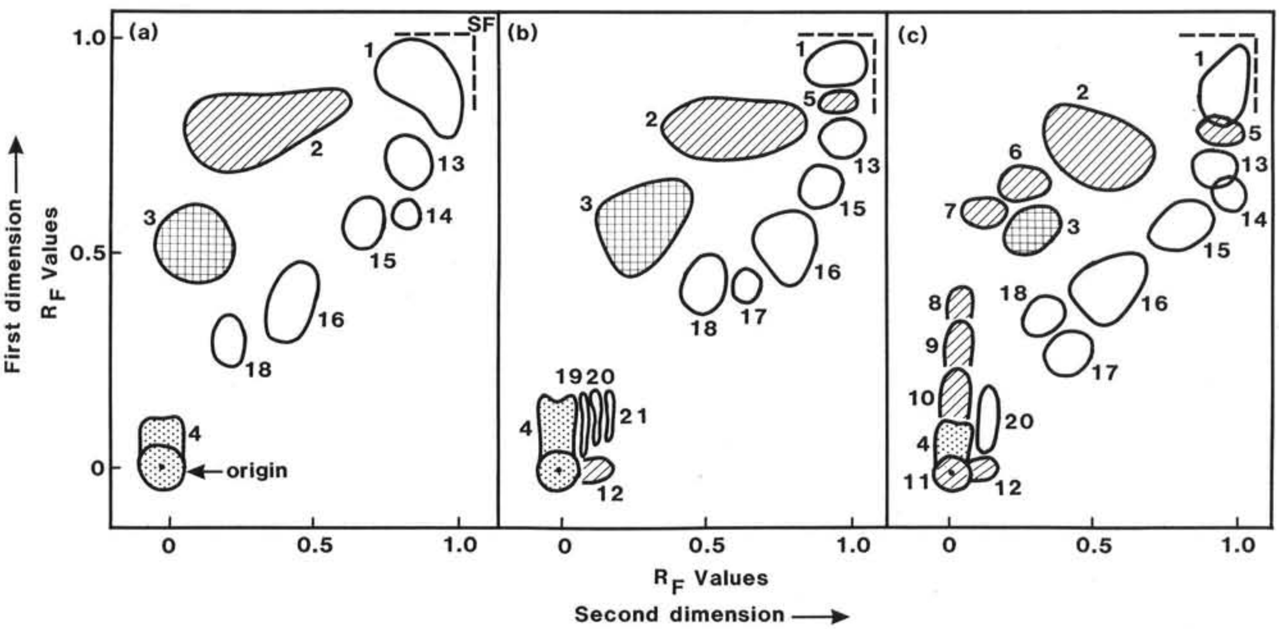

Fig. 3. Cellulose thin-layer chromatograms of photosynthetic pigments from North-West Shelf samples. (A) SO 3/83 cruise, hydrology Stations 10, 11, combined water samples; (B) SO 6/82 cruise, Stns. 62, 63, 64, 67, combined water column samples; (C) SO 4/80 cruise Stns. 4, 9, combined water column samples. Solvent systems, first dimension; n-propanol in light petroleum (60 to 80 °C), 1.5:98.5 (v/v); second dimension; chloroform, light petroleum, acetone, 20:80:0.5 (v/v/v). Pigment fractions: 1: carotenes (yellow); 2: chlorophyll *a* (blue-green); 3: chlorophyll *b* (olive-green); 4: chlorophyll *c* (light-green); 5: pheophytin *a* (grey); 6, 7: unidentified chlorophyll *a* derivatives (blue-green); 8, 9, 10: chlorophyllide *a*-like derivatives (blue-green); 11: unidentified chlorophyll *a* derivative (brown origin material); 12: pheophorbide *a*-like derivative (grey); 13, 15: unidentified xanthophylls (yellow); 14: unidentified xanthophyll (pink); 16: fucoxanthin (orange); 17: peridinin (red); 18: neofucoxanthin (orange); 19: unidentified xanthophyll (blue); 20: unidentified xanthophyll (orange); 21: unidentified xanthophyll (yellow); SF = solvent front

Table 4. Relative proportions of photosynthetic pigments in North-West Shelf samples, determined by quantitative elution of pigment fractions from selected chromatograms. (1) SO 4/80 cruise, Stns. 4, 9, combined water column samples; (2) SO 4/80 cruise, Stns. 1, 8, 10, subsurface samples combined; (3) SO 6/82, Stns. 62, 64, 67, combined water column samples

Pigments	Total pigment fraction per chromatogram (μg)			Chlorophyll *a* derivatives as % of total 'chlorophyll *a*'			Pigment ratios		
	1	2	3	1	2	3	1	2	3
Chlorophyll *a*	3.22	1.03	7.29	83	81	82			
Chlorophyll *b*	0.43	0.14	2.36						
Chlorophyll *c*	0.53	0.15	1.10						
Pheophytin *a*	0.17	–	0.45	5	–	5			
* Unidentified chlorophyll *a* derivatives (brown origin)	0.38	0.13	1.19	12	10	13			
** Unidentified chlorophyll *a* derivatives (blue-green)	–	0.12	–	–	9	–			
Fucoxanthin	0.98	0.35	2.63						
Peridinin	trace	trace	0.17						
Chlorophyll *a*:*b*							7.49	7.36	3.09
Chlorophyll *a*:*c*							6.08	6.87	6.63
Chl *a*:fuxoxanthin							3.29	2.94	2.77
Chl *a*:peridinin							–	–	43

* Fraction 11 (Fig. 3) ** Fraction 5 + 6 + 7 + 8 + 9 (Fig. 3)

colithophorids *(Gephyrocapsa oceanica)* and other golden brown flagellates at 10^3 to 10^4 l^{-1}. The larger diatoms were present with 10^3 to 10^4 cells l^{-1} for *Nitzschia* species (e.g. *N. fraudulenta, N. lineola*), 10^3 l^{-1} for *Chaetoceros* and *Rhizosolenia* species, and 10^2 l^{-1} for *Thalassionema* and *Thalassiothrix* species. Local blooms of the blue-green alga *Trichodesmium* spp. (up to 10^3 trichomes l^{-1}) were observed in large windrows which extended at times for several kilometres. Large dinoflagellates were less important numerically and occurred with < 10 cells l^{-1}.

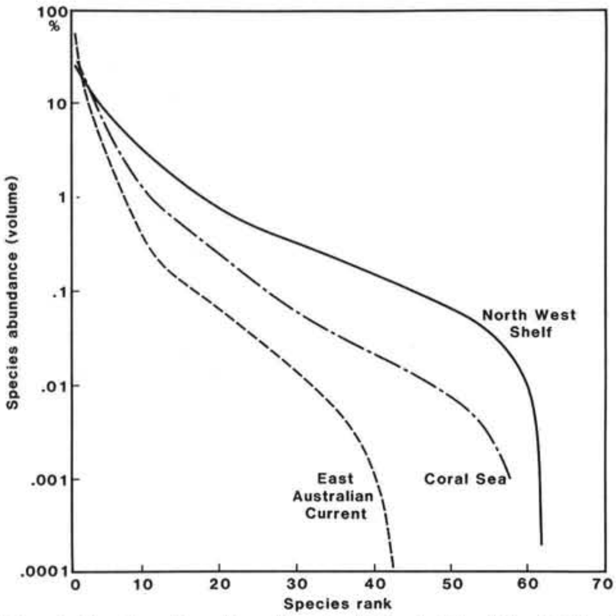

Fig. 4. Species diversity of tropical (North-West Shelf, Coral Sea) and subtropical phytoplankton (East Australian Current), as characterised by dominance-diversity curves. Relative species abundance (by cell volume) plotted on log-scale on ordinate; species ranked from most (rank no. 1) to least abundant (rank no. 63) on abscissa. For each region, water-column-integrated cell counts of all species were combined from 7 to 10 different sampling stations. Individual data points have been omitted from graphs for clarity

Species diversity was characterised by dominance-diversity curves (Hallegraeff and Ringelberg, 1978; Jeffrey and Hallegraeff, 1980a). Fig. 4 compares a typical curve of North-West Shelf phytoplankton with curves for Coral Sea and less diverse East Australian Current phytoplankton. Cell numbers were integrated over the water column and relative species abundance (by cell volume) plotted on a log scale on the ordinate, with species ranked from most (rank no. 1) to least abundant (rank no. 63) on a linear abscissa. The North-West Shelf samples showed flat sigmoid curves with long intermediate segments, indicative of a great species diversity with both an even distribution of species abundances as well as a large number of species present. A total of 43 to 63 phytoplankton species were recognised per station from water samples, and net samples added a further 5 to 17 species.

Phytoplankton species composition

The complete phytoplankton species list of all stations in the Gulf of Carpentaria and on the North-West Shelf is given in Table 5.

A wide variety of nanoplankton (70 species) from 8 algal classes was identified from water bottle samples. These included prymnesiophytes (36 spp.), small

Table 5. Phytoplankton species list of the Gulf of Carpentaria and North-West Shelf samples: Diatoms (DIAT, 151 spp.), dinoflagellates (DIN, 112 spp.), prymnesiophytes (PRYM, 36 spp.), chrysophytes (CHRYS, 3 spp.), prasinophytes (PRAS, 4 spp.), cryptomonads (CRYP, 3 spp.), cyanobacteria (CYAN, 2 spp.) and euglenoids (EUGL, 1 spp.)

Dominant and subdominant species (1 to 100 % of phytoplankton biomass)			
NANOPLANKTON (2 to 20 µm)			
Amphidinium sp.	DIN	•*Helladosphaera cornifera*	PRYM
Amphora sp.	DIAT	*Hemiselmis* sp.	CRYP
Anoplosolenia brasiliensis	PRYM	•*Meringosphaera mediterranea*	CHRYS
•*Anthosphaera robusta*	PRYM	•*Minidiscus trioculatus*	DIAT
Calciopappus caudatus	PRYM	•*Michaelsarsia elegans*	PRYM
•*Calciosolenia murrayi*	PRYM	•*Micromonas pusilla*	PRAS
Calyptrolithophora gracillima	PRYM	*Nanoneis hasleae*	DIAT
Calyptrolithophora pirus	PRYM	*Navicula* sp.	DIAT
Calyptrosphaera oblonga	PRYM	*Nephroselmis pyriformis*	PRAS
•*Caneosphaera molischii*	PRYM	•*Nitzschia bicapitata*	DIAT
•*Chilomonas marina*	CRYP	•*Nitzschia constricta*	DIAT
Cochlodinium sp.	DIN	*Nitzschia* cf. *fonticola*	DIAT
Corisphaera wetsteinii	PRYM	•*Oolithotus fragilis* subsp. *cavum*	PRYM
•*Coronosphaera mediterranea*	PRYM	•*Oxytoxum nanum*	DIN
•*Crenalithus sessilis*	PRYM	•*Oxytoxum variabile*	DIN
Cryptomonas spp.	CRYP	•*Phaeocystis pouchetii*	PRYM
•*Calcidiscus leptoporus*	PRYM	•*Pyramimonas obovata*	PRAS
•*Chrysochromulina pringsheimii*	PRYM	*Pyramimonas* sp.	PRAS
Chrysochromulina spp. (3)	PRYM	•*Rhabdosphaera claviger*	PRYM
Deutschlandia anthos	PRYM	*Scrippsiella* sp.	DIN
•*Dictyocha fibula*	CHRYS	•*Scyphosphaera apsteinii*	PRYM
Dictyocha fibula v. *regularis*	CHRYS	•*Syracosphaera lamina*	PRYM
•*Discosphaera tubifer*	PRYM	•*Syracosphaera pirus*	PRYM
•*Distephanus speculum* v. *octonarius*	CHRYS	•*Syracosphaera pulchra*	PRYM
•*Emiliania huxleyi*	PRYM	•*Thalassionema nitzschioides* v. *parva*	DIAT
•*Eutreptiella* sp.	EUGL	•*Thalassiosira allenii*	DIAT
•*Gephyrocapsa ericsonii*	PRYM	•*Thalassiosira diporocyclus*	DIAT
•*Gephyrocapsa oceanica*	PRYM	•*Thalassiosira lineata*	DIAT
•*Grammatophora oceanica*	DIAT	•*Thalassiosira mala*	DIAT
•*Gymnodinium nanum*	DIN	•*Thalassiosira oceanica*	DIAT
•*Gymnodinium punctatum*	DIN	*Thalassiosira oestrupii* v. *venrickae*	DIAT
•*Gymnodinium simplex*	DIN	*Thalassiosira partheneia*	DIAT
Gymnodinium spp.	DIN	*Thalassiosira subtilis*	DIAT
Gyrodinium sp.	DIN	*Umbellosphaera irregularis*	PRYM
•*Halopappus adriaticus*	PRYM	•*Umbilicosphaera hulburtiana*	PRYM
•*Helicosphaera carteri*	PRYM	•*Umbilicosphaera sibogae*	PRYM
		Umbilicosphaera sibogae var. *foliosa*	PRYM
Dominant diatoms and cyanobacteria			
Bacteriastrum comosum	DIAT	•*Chaetoceros radicans*	DIAT
•*Bacteriastrum furcatum*	DIAT	•*Detonula pumila*	DIAT
Bacteriastrum hyalinum	DIAT	*Eucampia cornuta*	DIAT
Bellerochea horologicalis	DIAT	•*Eucampia zodiacus*	DIAT
•*Chaetoceros affine*	DIAT	•*Lauderia annulata*	DIAT
•*Chaetoceros anastomosans*	DIAT	•*Nitzschia fraudulenta*	DIAT
Chaetoceros atlanticus	DIAT	*Nitzschia heimii*	DIAT
Chaetoceros atlanticus v. *neapolitana*	DIAT	*Nitzschia lineola*	DIAT
Chaetoceros coarctatus	DIAT	•*Nitzschia pungens*	DIAT
Chaetoceros compressus	DIAT	•*Rhizosolenia alata*	DIAT
•*Chaetoceros pseudocurvisetus*	DIAT	*Rhizosolenia alata* f. *indica*	DIAT
•*Chaetoceros didymus*	DIAT	*Rhizosolenia bergonii*	DIAT
Chaetoceros diversus	DIAT	*Rhizosolenia calcar-avis*	DIAT
•*Chaetoceros laciniosum*	DIAT	*Rhizosolenia clevei*	DIAT
Chaetoceros laevis	DIAT	*Rhizosolenia cylindrus*	DIAT
•*Chaetoceros lorenzianus*	DIAT	•*Rhizosolenia hebetata*	DIAT
Chaetoceros messanensis	DIAT	*Rhizosolenia hyalina*	DIAT
•*Chaetoceros peruvianus*	DIAT	•*Rhizosolenia imbricata*	DIAT

• Ubiquitous species also known from Sydney coastal waters

Table 5. Continued

Dominant diatoms and cyanobacteria			
Rhizosolenia phuketensis	DIAT	*Thalassiosira sackettii*	DIAT
•*Rhizosolenia robusta*	DIAT	*Thalassiosira spinosa*	DIAT
•*Rhizosolenia setigera*	DIAT	*Thalassionema bacillaris*	DIAT
•*Rhizosolenia stoltherfothii*	DIAT	•*Thalassionema nitzschioides*	DIAT
•*Rhizosolenia styliformis*	DIAT	•*Thalassiothrix delicatula*	DIAT
•*Thalassiosira eccentrica*	DIAT	•*Thalassiothrix frauenfeldii*	DIAT
Thalassiosira leptopus	DIAT	•*Thalassiothrix longissima*	DIAT
Thalassiosira punctifera	DIAT	•*Trichodesmium erythraeum*	CYAN
Thalassiosira simonsenii	DIAT	*Trichodesmium thiebautii*	CYAN
Rare diatoms and dinoflagellates (0.0001 to 1 % of phytoplankton biomass)			
Actinocyclus ehrenbergii	DIAT	•*Ceratium teres*	DIN
•*Actinoptychus undulatus*	DIAT	•*Ceratium trichoceros*	DIN
Actinoptychus splendens	DIAT	•*Ceratium tripos*	DIN
Actinoptychus trilingulatus aff.	DIAT	*Ceratium tripos* v. *indicum*	DIN
Asterolampra marylandica	DIAT	•*Ceratium tripos* v. *pulchellum*	DIN
Asteromphalus arachne	DIAT	•*Ceratium vultur*	DIN
•*Asteromphalus flabellatus*	DIAT	*Ceratocorys armata*	DIN
•*Asteromphalus heptactis*	DIAT	*Ceratocorys horrida*	DIN
•*Asteromphalus sarcophagus*	DIAT	*Citharistes apsteinii*	DIN
Amphisolenia asymmetrica	DIN	•*Climacodium frauenfeldianum*	DIAT
•*Amphisolenia bidentata*	DIN	*Cocconeis* sp.	DIAT
Amphisolenia thrinax	DIN	•*Corethron criophilum*	DIAT
•*Bacillaria paradoxa*	DIAT	•*Corythodinium elegans*	DIN
Biddulphia tuomeyi	DIAT	•*Coscinodiscus concinnus*	DIAT
Blepharocysta splendor-maris	DIN	*Coscinodiscus gigas*	DIAT
Campylodiscus sp.	DIAT	*Coscinodiscus granii*	DIAT
•*Cerataulina pelagica*	DIAT	*Coscinodiscus janischii*	DIAT
Ceratium biceps	DIN	*Coscinodiscus jonesianus*	DIAT
Ceratium breve	DIN	*Coscinodiscus nodulifer*	DIAT
•*Ceratium candelabrum*	DIN	*Coscinodiscus perforatus*	DIAT
•*Ceratium carriense*	DIN	•*Coscinodiscus radiatus*	DIAT
Ceratium cephalotum	DIN	*Coscinodiscus reniformis*	DIAT
Ceratium contortum	DIN	*Coscinodiscus stellaris*	DIAT
Ceratium contrarium	DIN	*Cyclotella striata*	DIAT
Ceratium declinatum	DIN	*Cymatosira lorenziana*	DIAT
Ceratium dens	DIN	•*Dinophysis caudata*	DIN
Ceratium depressum	DIN	*Dinophysis circumsutum*	DIN
Ceratium digitatum	DIN	•*Dinophysis cuneus*	DIN
•*Ceratium furca*	DIN	*Dinophysis doryphorum*	DIN
•*Ceratium fusus*	DIN	•*Dinophysis hastata*	DIN
Ceratium geniculatum	DIN	*Dinophysis miles* v. *indica*	DIN
Ceratium gibberum	DIN	•*Dinophysis ovum*	DIN
Ceratium gravidum	DIN	*Dinophysis rapa*	DIN
•*Ceratium horridum*	DIN	•*Dinophysis rotundatum*	DIN
Ceratium humile	DIN	•*Dinophysis sphaerica*	DIN
Ceratium incisum	DIN	*Diploneis bombus*	DIAT
•*Ceratium kofoidii*	DIN	*Diploneis crabro*	DIAT
Ceratium lunula	DIN	*Diploneis debyii*	DIAT
Ceratium macroceros	DIN	*Diploneis nitiscens*	DIAT
•*Ceratium massiliense*	DIN	*Diploneis weissflogii*	DIAT
Ceratium paradoxides	DIN	•*Dissodium asymmetricum*	DIN
•*Ceratium pentagonum*	DIN	•*Dissodium lunula*	DIN
Ceratium platycorne	DIN	*Ditylum sol*	DIAT
Ceratium praelongum	DIN	*Eunotia sp.*	DIAT
Ceratium ranipes	DIN	*Fragilaria sp.*	DIAT
Ceratium schroeteri	DIN	*Gonyaulax birostris*	DIN
•*Ceratium setaceum*	DIN	*Gonyaulax hyalina*	DIN
Ceratium symmetricum	DIN	*Gonyaulax pacifica*	DIN

• Ubiquitous species also known from Sydney coastal waters

Table 5. Continued

Rare diatoms and dinoflagellates

(0.0001 to 1 % of phytoplankton biomass)

•*Gonyaulax polygramma*	DIN	*Pleurosigma* sp.	DIAT
Gossleriella tropica	DIAT	*Podolampas bipes*	DIN
•*Guinardia flaccida*	DIAT	*Podolampas elegans*	DIN
Gyrosigma sp.	DIAT	*Podolampas palmipes*	DIN
Hemiaulus sinensis	DIAT	*Podolampas reticulata*	DIN
Hemidiscus cuneiformis	DIAT	*Podolampas spinifera*	DIN
Heterodinium milneri	DIN	*Podosira stelliger*	DIAT
Heterodinium rigdenae	DIN	•*Prorocentrum lima*	DIN
Histioneis dolon	DIN	•*Prorocentrum micans*	DIN
Histioneis mitchellana	DIN	•*Prorocentrum rostratum*	DIN
Histioneis pulchra	DIN	*Prorocentrum triestinum*	DIN
•*Leptocylindrus danicus*	DIAT	*Protoceratium areolatum*	DIN
•*Leptocylindrus mediterraneus*	DIAT	*Protoperidinium depressum*	DIN
•*Licmophora* sp.	DIAT	*Protoperidinium diabolus*	DIN
•*Mastogloia rostrata*	DIAT	*Protoperidinium divaricatum*	DIN
Neostreptotheca subindica	DIAT	•*Protoperidinium divergens*	DIN
Nitzschia americana	DIAT	*Protoperidinium leonis*	DIN
Nitzschia braarudii	DIAT	*Protoperidinium murrayi*	DIN
•*Nitzschia closterium*	DIAT	•*Protoperidinium oceanicum*	DIN
Nitzschia fluminensis	DIAT	•*Protoperidinium pallidum*	DIN
•*Nitzschia longissima*	DIAT	*Protoperidinium sourniai*	DIN
Nitzschia marina	DIAT	*Protoperidinium tubum*	DIN
Nitzschia panduriformis	DIAT	*Pseudoeunotia doliolus*	DIAT
Nitzschia punctata	DIAT	*Pyrocystis fusiformis*	DIN
Nitzschia sicula	DIAT	*Pyrocystis noctiluca*	DIN
•*Nitzschia sigma*	DIAT	•*Pyrocystis robusta*	DIN
•*Odontella mobiliensis*	DIAT	•*Pyrophacus horologicus*	DIN
Odontella sinensis	DIAT	*Raphoneis amphiceros*	DIAT
Ornithocercus francescae	DIN	*Raphoneis surirella*	DIAT
Ornithocercus heteroporus	DIN	•*Roperia tesselata*	DIAT
•*Ornithocercus magnificus*	DIN	•*Skeletonema costatum*	DIAT
Ornithocercus splendidus	DIN	•*Skeletonema menzellii*	DIAT
Ornithocercus quadratus	DIN	•*Stauroneis membranacea*	DIAT
Ornithocercus skogsbergiii	DIN	*Stephanopyxis palmeriana*	DIAT
Ornithocercus steinii	DIN	*Surirella* sp.	DIAT
Ornithocercus thumii	DIN	*Synedra toxoneides*	DIAT
•*Oxytoxum subulatum*	DIN	*Trachyneis aspera*	DIAT
Parahistioneis para	DIN	•*Triadinium polyedricus*	DIN
Palmeria hardmaniana	DIAT	*Triadinium sphaericum*	DIN
•*Paralia sulcata*	DIAT	*Triceratium pentacrinus*	DIAT
Pinnularia spp.	DIAT	*Triceratium broeckii*	DIAT
•*Planktoniella sol*	DIAT	*Triceratium dubium*	DIAT
Pleurosigma directum	DIAT	*Triceratium favus*	DIAT
Pleurosigma diversestriatum	DIAT	*Trigonium alternans*	DIAT
Pleurosigma normanii	DIAT	*Triposolenia bicornis*	DIN

• Ubiquitous species also known from Sydney coastal waters

diatoms (15), small dinoflagellates (10), prasinophytes (4), cryptomonads (3), chrysomonads (3), euglenoids (1) and cyanophytes (2).

The diatom and dinoflagellate floras, taken from net samples, were remarkably similar in the Gulf of Carpentaria, Arafura Sea, Timor Sea and North-West Shelf. The large (30 to 1000 µm) diatom flora included *Bacteriastrum* (3 spp.), *Chaetoceros* (15), *Coscinodiscus* (10), *Nitzschia* (13), *Rhizosolenia* (13) and *Thalassiosira* (6). The large dinoflagellate flora included *Ceratium* (37 spp.), *Dinophysis* (10), *Ornithocercus* (7) and *Protoperidinium* (8). These species exhibit elaborate morphologies. Examples of morphological extremes are the spines of the dinoflagellate *Ceratocorys horrida* (Fig. 5), the wing-like extensions of the dinoflagellates *Ornithocercus steinii* (Fig. 6) and *Ceratium cephalotum* (Fig. 7) and the diatom *Planktoniella sol* (Fig. 8), and the long setae of the diatoms *Bacteriastrum furcatum* (Fig. 9) and *Bacteriastrum hyalinum* (Fig. 10).

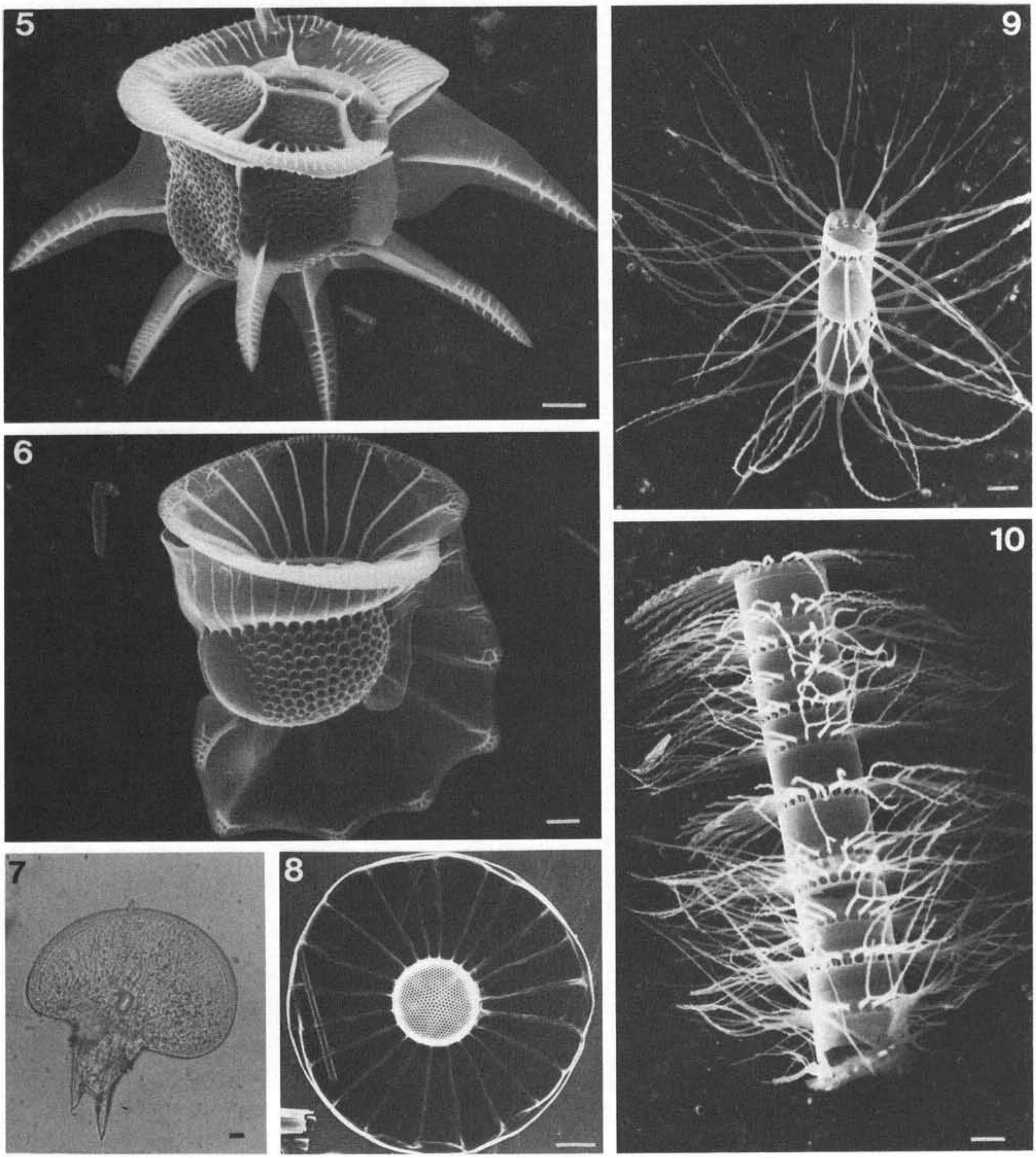

Fig. 5 to 10. Morphological characteristics of tropical dinoflagellates and diatoms (scale bar = 10 µm). 5: Dinoflagellate *Ceratocorys horrida* with spine-like extensions of hypotheca. SEM. 6: Dinoflagellate *Ornithocercus steinii* with wing-like extensions of hypotheca and epitheca. SEM. 7: Dinoflagellate *Ceratium cephalotum* with enlarged, flattened epitheca. LM. 8: Diatom *Planktoniella sol* with marginal wing. SEM. 9 and 10: Chain-forming diatoms *Bacteriastrum furcatum* and *Bacteriastrum hyalinum* with long setae surrounding the cells

Table 6. Symbiotic associations observed in Australian tropical phytoplankton

Host	Symbiont	Area: Coral Sea	Area: NW Shelf	Area: Gulf	Morphological characteristics of the association	Figure
Dinoflagellate	Blue-green alga					–
Amphisolenia bidentata	*Synechococcus carcerarius*	+	+		Endocytic	19 a, b
Amphisolenia thrinax	*Synechococcus carcerarius*	+	+		Endocytic	18
Citharistes apsteinii	*Synechococcus carcerarius* *Synechocystis consortia*	+			In intercingular chamber	–
Dinophysis miles	*Synechococcus carcerarius?*		+		Endocytic	–
Dinophysis rapa	*Synechococcus carcerarius?*		+		Endocytic	–
Histioneis mitchellana	*Synechococcus carcerarius*		+		In intercingular chamber	–
Histioneis pulchra	*Synechococcus carcerarius*	+			In intercingular chamber	–
Ornithocercus francescae	*Synechococcus carcerarius*		+		Loose association with girdle lists	–
Ornithicercus heteroporus	*Synechococcus carcerarius*	+	+	+	Loose association with girdle lists	17
Ornithocercus magnificus	*Synechococcus carcerarius*	+	+	+	Loose association with girdle lists	–
Ornithocercus quadratus	*Synechococcus carcerarius*	+	+	+	Loose association with girdle lists	–
Ornithocercus steinii	*Synechococcus carcerarius*		+	+	Loose association with girdle lists	–
Parahistioneis para	*Synechococcus carcerarius*	+			In intercingular chamber	
Diatom	Blue-green alga					
Chaetoceros compressus	*Richelia intracellularis*		+		Epiphytic	–
Neostreptotheca subindica	*Synechocystis consortia*	+	+		Endocytic	21
Rhizosolenia clevei	*Richelia intracellularis*	+	+	+	Endocytic	20 b
Rhizosolenia cylindrus	*Richelia intracellularis*	+			Endocytic	20 a
Diatom	Coccolithophorid					
Planktoniella sol	unidentified coccolithophorid		+		Casual attachment to marginal wing	–
Thalassiosira punctifera	*Crenalithus sessilis*	+	+	+	Casual attachment to girdle area	11
Diatom	Diatom					
Bellerochea horologicalis	*Licmophora* sp.		+		Casual attachment	13
Odontella sinensis	*Nitzschia* sp.			+	Casual attachment	–
Thalassiosira subtilis	*Licmophora* sp. *Nitzschia bicapitata*		+	+	Casual attachment	12
Diatom	Ciliates					
Chaetoceros coarctatus	*Vorticella oceanica*	+	+	+	Epiphytic	14
Coscinodiscus gigas	unidentified ciliate		+	+	Epiphytic	15
Palmeria hardmaniana	*Amphorella borealis*		+		Epiphytic	16 a, b
Microzooplankton	Dinoflagellate					
Acantharians	*Symbiodinium microadriaticum*	+	+	+	In cytoplasm	–
Foraminiferans	*Symbiodinium microadriaticum?*	+	+	+	In cytoplasm	–
Radiolarians	*Symbiodinium microadriaticum*	+	+	+	In cytoplasm	–

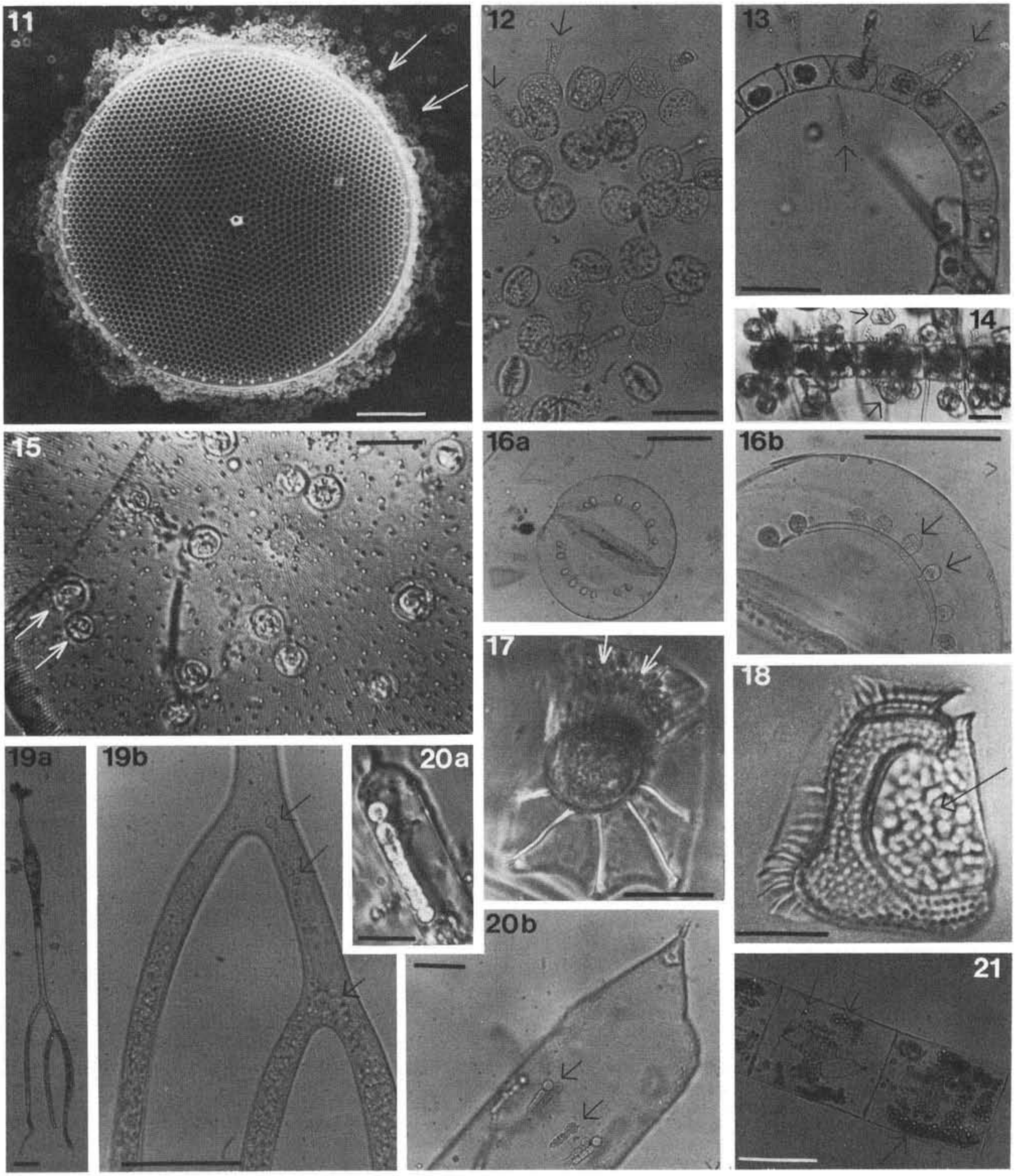

Fig. 11 to 21. Symbiotic associations in Australian tropical phytoplankton. 11: Diatom *Thalassiosira punctifera* with the coccolithophorid *Crenalithus sessilis* (arrows) attached to its girdle area; SEM; scale bar = 20 µm. 12: Gelatinous colony of diatom *Thalassiosira subtilis* with epiphytic diatom *Licmophora* sp. (arrows); LM; scale bar = 50 µm. 13: Chain-forming diatom *Bellerochea horologicalis* with epiphytic diatom *Licmophora* sp. (arrows); LM; scale bar = 50 µm. 14: Chain-forming diatom *Chaetoceros coarctatus* with epiphytic ciliate *Vorticella oceanica* (arrows); LM; scale bar = 20 µm. 15: Partial view of large centric diatom *Coscinodiscus gigas* with epiphytic ciliates (arrows); LM; scale bar = 100 µm. 16: a, b: Diatom *Palmeria hardmaniana* with epiphytic ciliate *Amphorella borealis* located along 2 hemispherical slits (arrows); LM; scale bar = 50 µm. 17: Dinoflagellate *Ornithocercus magnificus* with blue-green alga *Synechococcus carcerarius* (arrows) in loose association with girdle lists; LM; scale bar = 50 µm. 18: Dinoflagellate *Citharistes apsteinii* with intercingular chamber packed with *Synechococcus carcerarius* and *Synechocystis consortia* (arrow); LM; scale bar = 20 µm. 19: a, b: Dinoflagellate *Amphisolenia thrinax* with endocytic blue-green alga *Synechoccus carcerarius* (arrows); LM; scale bar = 100 µm. 20: (a) Small diatom *Rhizosolenia cylindrus* with single cell of endocytic blue-green alga *Richelia intracellularis*; LM; scale bar = 10 µm; (b) Large diatom *Rhizosolenia clevei* with numerous *Richelia intracellularis* (arrows); LM; scale bar = 100 µm. 21: Large diatom *Neostreptotheca subindica* with the endocytic blue-green alga *Syncheocystis consortia* (arrows); LM; scale bar = 50 µm

Table 7. Fluorescence characteristics of tropical Australian dinoflagellates

Species	Photosynthetic (red chloroplast fluorescence)	Partially fluorescent (green fluorescence with red patches)	Non-photosynthetic (diffuse green cytoplasm fluorescence)	Blue-green algal symbionts (orange fluorescence)
Amphisolenia asymmetrica			+	
Amphisolenia bidentata			+	+
Amphisolenia thrinax			+	+
Blepharocysta splendor-maris			+	
Ceratium biceps	+			
Ceratium breve	+			
Ceratium candelabrum	+			
Ceratium carriense	+			
Ceratium cephalotum	+	+		
Ceratium contortum	+			
Ceratium contrarium	+			
Ceratium dens	+			
Ceratium depressum	+			
Ceratium digitatum	+			
Ceratium furca	+	+		
Ceratium fusus	+			
Ceratium geniculatum	+			
Ceratium gibberum	+			
Ceratium horridum	+			
Ceratium incisum	+			
Ceratium kofoidii	+			
Ceratium limulus	+			
Ceratium lunula	+			
Ceratium massiliense	+			
Ceratium paradoxides	+			
Ceratium pentagonum	+			
Ceratium platycorne	+			
Ceratium praelongum	+			
Ceratium schroeteri	+			
Ceratium teres	+		+	
Ceratium trichoceros	+			
Ceratium tripos	+			
Ceratium tripos v. *pulchellum*	+			
Ceratium vultur	+			
Ceratocorys horrida	+	+	+	
Ceratocorys armata			+	
Citharistes apsteinii			+	+
Corythodinium elegans	+			
Corythodinium tesselatum	+			
Dinophysis caudata	+	+		
Dinophysis circumsutum			+	
Dinophysis cuneus			+	
Dinophysis doryphorum			+	
Dinophysis miles v. *indica*	+			+
Dinophysis ovum	+			
Dinophysis rapa			+	
Dissodium asymmetrica			+	
Gonyaulax birostris	+			
Gonyaulax pacifica	+			
Gonyaulax polygramma	+			
Gymnodinium sp.	+			
Gymnodinium sp.			+	
Histioneis mitchellana			+	+
Histioneis pulchra			+	+
Ornithocercus francescae			+	+
Ornithocercus heteroporus			+	+
Ornithocercus magnificus			+	+
Ornithocercus quadratus			+	+
Ornithocercus steinii			+	+

Table 7. Continued

Species	Photosynthetic (red chloroplast fluorescence)	Partially fluorescent (green fluorescence with red patches)	Non-photosynthetic (diffuse green cytoplasm fluorescence)	Blue-green algal symbionts (orange fluorescence)
Oxytoxum scolopax	+			
Oxytoxum subulatum			+	
Parahistioneis para			+	+
Podolampas bipes			+	
Podolampas palmipes			+	
Pronoctiluca pelagica			+	
Prorocentrum lima	+			
Prorocentrum micans	+			
Protoperidinium elegans			+	
Protoperidinium depressum			+	
Protoperidinium divergens			+	
Protoperidinium leonis			+	
Protoperidinium pallidum	?		+	
Pyrocystis fusifomis	+			
Pyrocystis (Dissodinium) lunula	+			
Pyrocystis noctiluca	+			
Pyrophacus horologicum	+			
Scrippsiella trochoidea	+			
Triadinium polyedricus	+			
Triposolenia bicornis			+	

Many symbiotic associations were recognised (Table 6). Twenty-eight associations ranged from casual attachment between diatoms and coccolithophorids (Fig. 11), diatoms and diatoms (Fig. 12 and 13), diatoms and ciliates (Fig. 14, 15 and 16) to more specialised relations (Fig. 17, 18, 19, 20 and 21). The colourless dinophysoid dinoflagellates with wing-like extensions often contained orange fluorescent blue-green algae in a possibly symbiotic relation. In *Ornithocercus* up to 100 symbiotic cells (3 to 8 µm diameter) were found extracellularly in the girdle list region (Fig. 17), but in *Citharistes* and *Histioneis* similar cells were contained in special chambers (Fig. 18). A specialised endocytic relationship was observed for *Amphisolenia* (Fig. 19). These blue-green algal symbionts are all thought to belong to the same 2 species *Synechococcus carcerarius* (spherical cells) and *Synechocystis consortia* (elongated cells; Norris, 1967), but their ultrastructure is unknown. Some symbionts (e.g. dinoflagellate *Symbiodinium microadriaticum*, and blue-green *Synechococcus carcerarius*) occurred with a wide range of host species, but others appeared

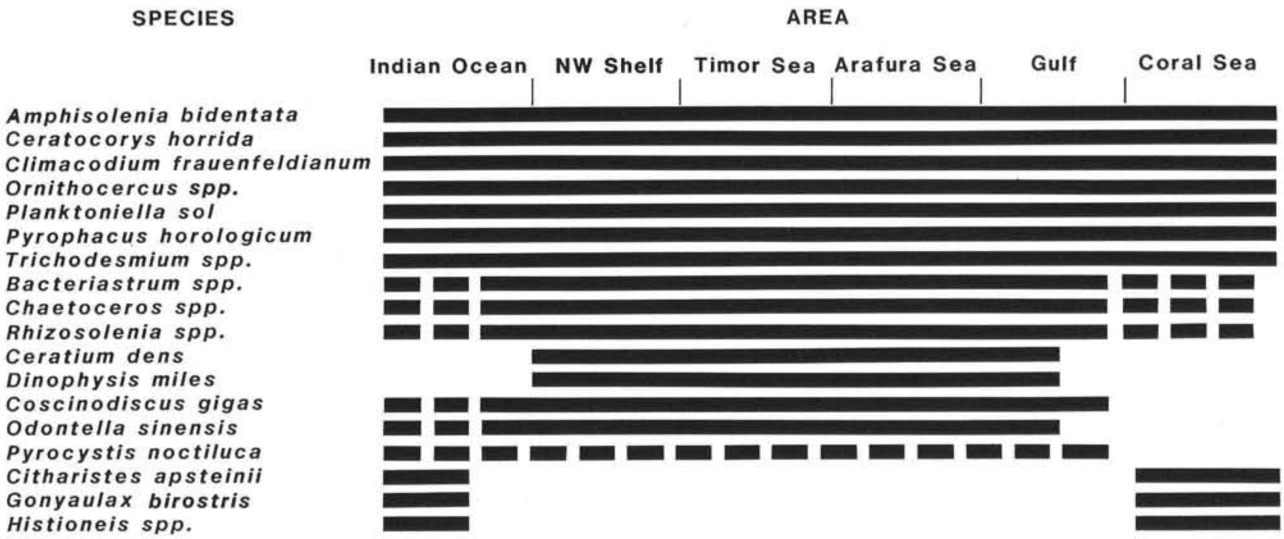

Fig. 22. Distribution of selected tropical phytoplankton species in coastal waters of northern Australia. Solid Bar = common (10^4 to 10^6 cells l^{-1}); broken bar = rare (10 to 10^3 cells l^{-1})

to be remarkably host-specific. The coccolithophorid *Crenalithus sessilis* associated only with the diatom *Thalassiosira punctifera*, and the blue-green alga *Richelia intracellularis* only with the diatoms *Rhizosolenia clevei* and *R. cylindrus*. Symbionts were always present in these species found in tropical waters but the host species were without their symbionts when found in the cooler waters of the Great Australian Bight and Tasman Sea.

Phytoplankton species distribution

Most nanoplankton and also many diatom and dinoflagellate species were found throughout the northern coasts of Australia, from the Coral Sea into the Indian Ocean (Fig. 22). The diatoms *Bacteriastrum*, *Chaetoceros* and *Rhizosolenia* exhibited great abundance and species diversity in continental shelf waters but were less abundant in the offshore Coral Sea and Indian Ocean. A few dinoflagellate species were more restricted in their distribution: *Ceratium dens* and *Dinophysis miles* were found only in shelf waters, and *Citharistes apsteinii*, *Gonyaulax birostris* and *Histioneis* spp. only in open ocean environments.

Non-photosynthetic dinoflagellates

Examination of living phytoplankton samples under the fluorescence microscope showed that many of the dinoflagellates (33 out of 79 species examined) were non-photosynthetic (Table 7). These included some species of *Ceratium*, *Dinophysis* (part *Phalacroma*) and *Oxytoxum* and all species of *Amphisolenia*, *Blepharocysta*, *Citharistes*, *Diplopsalis s. l.*, *Histioneis*, *Ornithocercus*, *Parahistioneis*, *Podolampas*, *Protoperidinium* and *Triposolenia*. Photosynthetic species of *Ceratium* and *Dinophysis* were often very weakly pigmented, and sometimes dinoflagellate fluorescence varied even within a single species. For example, *Ceratocorys horrida* showed intensely pigmented red-fluorescent cells in shelf waters and non-pigmented green fluorescent cells at offshore stations. A few partly fluorescent cells were also seen.

DISCUSSION

Phytoplankton biomass. The phytoplankton chlorophyll concentrations of the continental shelf waters of northern Australia (Table 2) are significantly higher than those of other parts of the Eastern Indian Ocean. Chlorophyll values in the productive Java upwelling area are up to 0.85 μg l^{-1} with a water column total of 30 to 40 mg m^{-2}, but offshore waters of the Indian Ocean generally contain chlorophyll levels < 0.15 μg l^{-1} and water column totals of only 15 to 20 mg m^{-2} (recalculated values from Humphrey, 1966 and Humphrey and Kerr, 1969). Several mechanisms have been proposed for nutrient enrichment of North Australian continental shelf waters. These include inflow from the Banda Sea upwelling area and nutrient regeneration from bottom sediments in the Gulf of Carpentaria (Forbes, in press) and tidally induced internal waves interacting with the bottom slope on the North-West Shelf (Baines, 1981).

Phytoplankton pigment composition. The chromatographic pigment analyses (Fig. 3; Table 4) indicate that diatoms, golden-brown flagellates and green flagellates are the major planktonic primary producers in northern Australian tropical shelf waters. The low concentrations of the dinoflagellate carotenoid peridinin suggest that photosynthesis by dinoflagellates is insignificant. This is confirmed by the absence of fluorescent chloroplasts in most of these cells (Table 7) and the observations of only weakly pigmented photosynthetic species. It would be of considerable interest to establish to what extent some dinoflagellate species can switch from an autotrophic to a heterotrophic mode of nutrition and if this is accompanied by reversible chloroplast resorption and regeneration. Degenerate plastids or protoplastids have been reported in the non-photosynthetic *Crypthecodinium cohnii* (Kubai and Ris, 1969).

Importance of the nanoplankton. Nanoplankton is a major component of tropical phytoplankton, accounting for 70 to 97 % of the total chlorophyll, except in local diatom and *Trichodesmium* blooms in shallow (20 to 70 m) inshore waters where only 30 to 60 % of the chlorophyll biomass is nanoplankton (Table 3). The importance of these small organisms in the tropical Indian Ocean has been suggested previously from fractionated carbon, photosynthesis and chlorophyll measurements (Saijo, 1964; Mullin, 1965; Saijo and Takesue, 1965). In the present work, the quantitative importance of small pennate diatoms, golden-brown flagellates, minute green flagellates and small dinoflagellates was confirmed by light and electron microscopy. Small cyanobacteria in the picoplankton size range (0.2 to 2 μm) have also been recognized and will be described elsewhere. Many nanoplankton species found in the tropical waters (25 to 30 °C) of the North-West Shelf and the Gulf of Carpentaria are also common in subtropical and temperate Australian waters (15 to 20 °C). Species such as *Micromonas pusilla* and *Minidiscus trioculatus*, identified in Australian tropical and subtropical waters, have also been recorded from Arctic West Greenland (0 to 13 °C; Thomsen, 1982). Tolerance of a wide range of temperatures

(Throndsen, 1976), or the ability to form strains adapted to different temperature regimes, may contribute to the success of nanoplankton species in the world's oceans.

Diversity of large diatoms and dinoflagellates. In contrast to the nanoplankton, the large tropical diatoms and dinoflagellates are distinctly different from species in subtropical and temperate waters. The main differences are the possession of large spines, horns, setae and wing-like structures in tropical forms, common symbiotic associations and greater species diversity. More than half of the 200 taxa identified (Table 5) can be regarded as tropical species. On the shallow North-West Shelf and in the Gulf of Carpentaria diatoms show the greatest diversity, while in offshore waters of the Indian Ocean and Coral Sea dinoflagellate species are more numerous (Taylor, 1976; Jeffrey and Hallegraeff, unpubl.). Their bizarre shapes may aid flotation, increase nutrient uptake through enhanced rotational movement and greater cell surface area for absorption, and protect against grazing from small zooplankton. Symbiotic associations may benefit both host and symbiont through mutual exchange of organic and inorganic nutrients, but thus far only the *Rhizosolenia-Richelia* pair has been examined by appropriate microautoradiographic techniques (Taylor, 1982 and references therein). Why tropical phytoplankton exhibit and maintain a high diversity, similar to that of other plants and animals in tropical aquatic and terrestrial habitats, has yet to be answered satisfactorily.

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