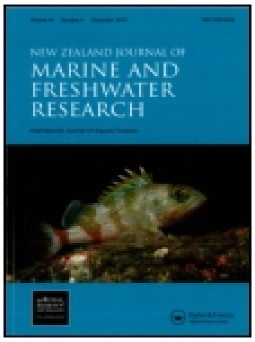

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Algal blooms and climate anomalies in north-east New Zealand, August –December 1992

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Abstract A raphidophyte-dominated phytoplankton bloom extended discontinuously along the north-eastern coastline of New Zealand, from Bream Tail, north of Leigh, to the western coast of the Coromandel Peninsula from late August until December 1992. The bloom was associated with an "El-Niño" phase of the Southern Oscillation, resulting in unusually cold sea temperatures. The dominant bloom species in the north was *Fibrocapsa japonica* and in the south *Heterosigma akashiwo*. Associated species included the coccolithophorid *Gephyrocapsa oceanica* and the naked form of the silicoflagellate *Dictyocha speculum.* By December, numbers of the armoured form of *D. speculum* had increased, as those of raphidophytes and coccolithophorids declined. Bioassays to test for shellfish biotoxins were negative and *Artemia salina* bioassays, indicators of ichthyotoxicity, were negative except for *Heterosigma akashiwo* cultures, isolated from Coromandel water samples.

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Keywords *Fibrocapsa japonica*; *Heterosigma akashiwo;* raphidophyte; *Dictyocha speculum*; silicoflagellate; *Gephyrocapsa oceanica;* climate; coccolithophorid; phytoplankton bloom

INTRODUCTION

Nuisance microalgal blooms are a major concern worldwide and have caused economic losses through the deaths of shellfish and fin-fish and through the poisoning of consumers of contaminated seafoods (Taylor 1990). The toxic species of algae are comparatively few in number, although previously benign species have proved recently to be toxic (Skjoldal & Dundas 1989).

Microalgal blooms have occurred in New Zealand waters both as large-scale seasonal events, as occur regularly off the open coastline along the west coast of the South Island (Bradford & Chang 1987; Chang 1988), and as localised, unexpected events. The non-toxic photosynthetic ciliate *Mesodinium rubrum* has regularly caused red blooms in north-eastern coastal waters and in the Marlborough Sounds (Challis 1990). Blooms of surf diatoms, such as the brown "foamy" *Gonioceros armatum (=Chaetoceros armatum)* and *Aulacodiscus* cf. *kittonii* bloom which formed along the south-west coast of the North Island in March 1992 (pers. comm. C. O'Kelly, Massey University, Palmerston North, New Zealand), form a vital and nutritious food supply for tuatua (*Paphies subtriangulata*) and toheroa (*Paphies ventricosa*) (Cassie & Cassie 1960).

Toxic blooms have also occurred in New Zealand coastal waters. In the summer of 1983, fish and shellfish died at Bream Bay, north of Leigh, during a bloom dominated by the non-toxic diatom *Cerataulina pelagica.* The fish deaths were attributed to anoxia (Taylor et al. 1985), although the toxin-producing prymnesiophyte *Prymnesium calathiferum*, a sub-dominant during the bloom, was also implicated (Chang & Ryan 1985). A small number of sea-caged quinnat salmon died in Akaroa in March 1987 during a dark-brown bloom of the dinoflagellate *Gyrodinium* *aureolum* (Boustead et al. 1987). Another unexpected bloom event occurred in Big Glory Bay, Stewart Island in January 1989. Caged salmon, worth an estimated $17 million to the aquaculture industry, died (Boustead et al. 1989). The causative species was the raphidophyte *Heterosigma akashiwo* (Chang et al. 1990; MacKenzie 1991).

In spring 1992 a bloom occurred which extended more than 200 km along the north-east coast of the North Island, from Leigh down to the Hauraki Gulf (Fig. 1). No fish kills were reported at that time, despite the fact that four of the species in the bloom had elsewhere been implicated in fish kills. The dominant species were the raphidophytes *Fibrocapsa japonica* (Toriumi & Takano 1973) and *Heterosigma akashiwo* (Chang et al. 1990; MacKenzie 1991), the silicoflagellate *Dictyocha speculum* (Bruno et al. 1989) and a *Gyrodinium aureolum*-like species (Jones et al. 1982).

Prediction of the identity of the dominant species in an algal bloom is difficult, as bloom composition depends on many complex, interactive factors. Bloom occurrence itself is easier to predict. Intense rainfall can lead to run-off, with a resultant increase in nutrients in the adjacent coastal waters, and the formation of salinity gradients. A strong common feature between the north-east coast bloom of 1992 and previous persistent blooms along both coasts was the presence of abnormally cold water, due to either large-scale climatic fluctuations (Southern Oscillation Index, the anomaly of air temperature difference between Darwin and Tahiti: Heath 1985; Ballantine 1992) or localised upwelling. Along the north-east coast in 1992, in a negative Southern Oscillation Index, the sea temperatures were lowered overall, the weather was calmer than usual, and high rainfall occurred in short-duration bursts. These conditions were widespread and long-lasting, and might be useful as bloom indicators in the future.

The composition of the austral spring bloom of 1992, the hydrographic conditions occurring during the bloom, and the results of toxicity bioassays of the bloom organisms are presented in this study.

MATERIALS AND METHODS

Phytoplankton monitoring

Sea water samples were obtained 2–3 times per week from May 1992, from surface waters near Pumphouse Reef in the Leigh Marine Reserve (Fig. 1). During storm periods, samples were obtained from the Leigh laboratory's sea water pump. Subsamples (10 ml) were preserved in buffered formalin (~2% final concentration), with some comparative samples in Lugol's iodine, and settled for 4 h in Utermöhl counting chambers. Organisms were identified and total counts of the dominant species carried out using an Olympus IMT–2 inverted microscope. Additional treated (Lugol's) and untreated samples were examined at the height of the bloom. Samples were also examined from the greater Hauraki Gulf region on two occasions during the bloom. These were collected with a water sampler lowered from a helicopter.

Biomass volumes were estimated on the basis of simple geometric formulae (the silicoflagellates and the coccolithophorids were treated as spheres and the raphidophytes as ellipsoids of revolution).

Samples to be identified by scanning electron microscope (Philips 505) were filtered (0.45 µm cellulose nitrate/acetate (HA) millipore) and salt crystals removed by washing with distilled water.

Chlorophyll measurements

Chlorophyll *a* absorbances were determined with a Hewlett Packard 8452A Diode Array Spectrophotometer. Measured amounts of sea water were passed through a millipore (HA, 47 mm) cellulose nitrate/acetate filter under vacuum. As filtration slowed, the vacuum was released and the filters rinsed with distilled de-ionised water to remove salts. Filters were frozen (–20°C) for 24 h before extraction in 90% acetone : dimethylsulphoxide 3 : 1 (v/v). Samples were kept in dim light during this time, to prevent bleaching of pigments, until centrifuged (Sorvall RC3B) for 10 min (Larson 1992). Pigment absorbances were read against a solvent blank at 655 nm. Pigment concentration was calculated as $\mu g\ l^{-1}$ (Parsons et al. 1984).

Isolation and culture of bloom microalgae

Cells were isolated by picking them out individually under the light microscope with a micropipette or by serial dilution in general-purpose media, using Multiwell tissue culture plates (Becton Dickinson). Media included CHRY (Andersen et al. 1991), GP (Loeblich & Smith 1968) and GP with urea instead of potassium nitrate as nitrogen source.

Cultures were maintained in 50 ml plastic containers (Labserv, NZ) at 18°C at a light intensity of 100 $\mu mol\ m^{-2}\ s^{-1}$ and under a 14 : 10 h light : dark regime. Cultures were subcultured weekly until established, and then monthly.

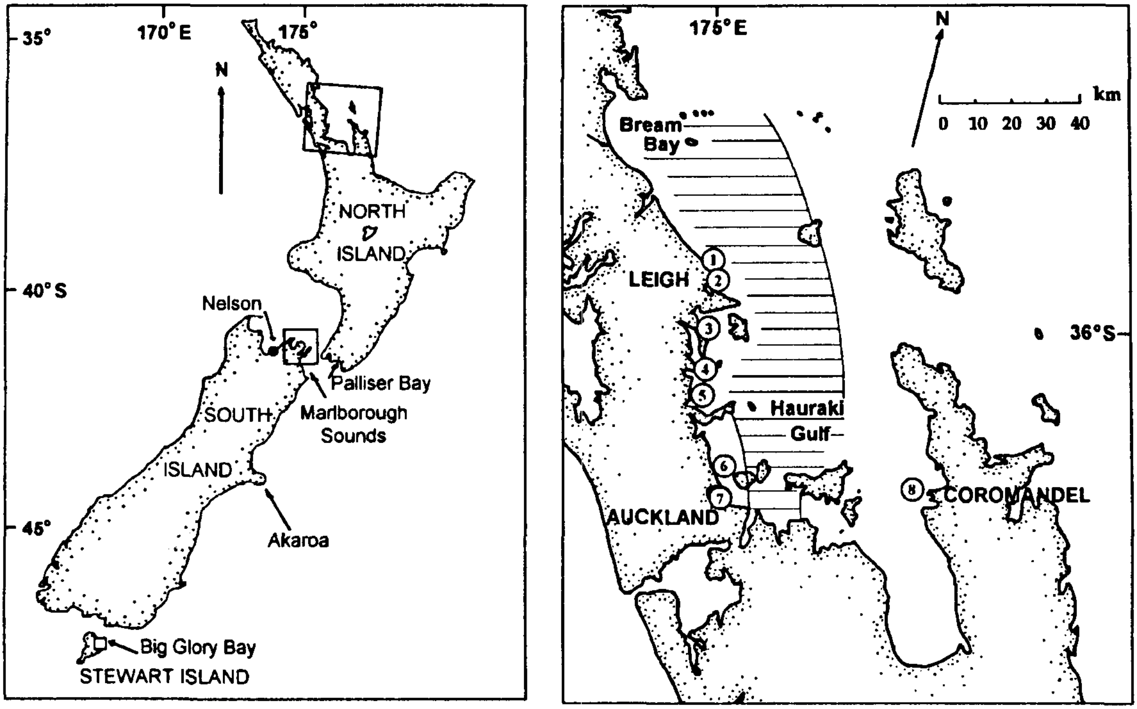

Fig. 1 Location map showing Leigh Marine Reserve on the north-eastern New Zealand coast. The key sampling sites during the 1992 raphidophyte bloom were in the vicinity of, from north to south: 1, Goat Island; 2, Ti Point; 3, Snells Beach; 4, Mahurangi Harbour; 5, Orewa Beach; 6, Browns Bay; 7, Waitemata Harbour; and 8, Coromandel. Cross-hatching represents the discolouration, caused by the bloom, that was observed during an aerial survey on 13 September 1992.

Toxicity bioassays

Artemia salina eggs (Brooklands Aquarium, San Fransisco) were used for standard *Artemia* bioassays in tissue culture plates (Persoone & Wells 1987). Following hatching of the eggs, ten *Artemia* larvae and 1 ml of either exponential or stationary phase microalgal culture were added to each well. All tests were carried out in quadruplicate. Positive controls were provided by *Prymnesium parvum*, obtained from F. H. Chang, NIWA - Oceanographic, Wellington. Strains of *Fibrocapsa japonica* (CS 235) obtained from the CSIRO Culture Collection of Microalgae, Hobart, Tasmania, were also used as controls. They cause a distress reaction in *Artemia* similar to that caused by ichthyotoxic strains of *Heterosigma akashiwo.*

Mouse bioassays for paralytic shellfish toxin were carried out according to the AOAC official methods of analysis (Anon. 1959); for diarrhoeic shellfish toxin according to the methods of analysis established by the Ministry of Health and Welfare, Japan (1981).

Climate data

The Leigh Marine Laboratory has maintained daily marine and atmospheric climate records since 1967 (Evans 1992), including sea surface temperature, sea state, and wave surge. These records enable an assessment of the strength of climatic anomalies preceding and accompanying algal bloom events on the open north-east coast.

Salinity data were provided by Professor Ohwada (Ocean Research Institute, University of Tokyo); these had been obtained by RV *Hakuho Maru* on its approach to Auckland, 7 October 1992.

RESULTS

Identification and abundance of phytoplankton

From 28 August, chlorophyll *a* concentrations in sea water samples taken at Leigh increased (Fig. 2), and filters became rapidly clogged. These events and microscopic examination of the filters indicated an

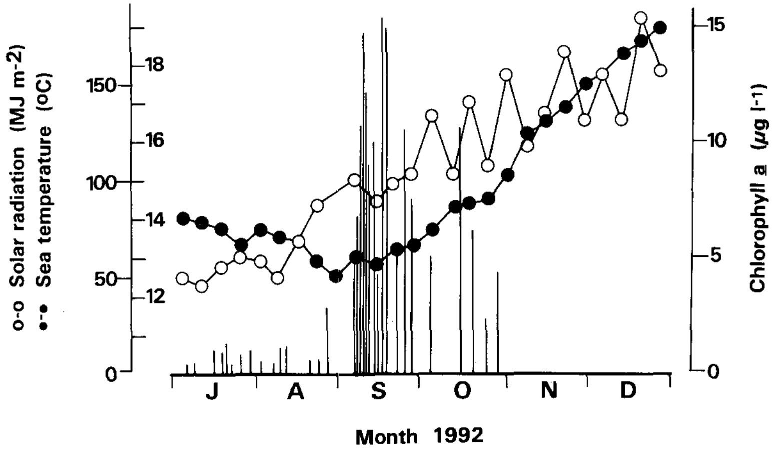

Fig. 2 Relationship between increasing solar radiation, sea temperature, and chlorophyll *a* concentrations at Leigh, July-December, 1992.

increase in phytoplankton biomass. The first visual intimation that a bloom event was occurring was on 8 September when the water became an unusually bright green. A mixed diatom population was recorded, which included *Rhizosolenia* sp. An increase in raphidophyte and coccolithophorid species was first observed on 9 September. Chlorophyll readings dropped 6 days later: at that time large numbers of copepod eggs were present in the plankton. The chlorophyll *a* concentrations increased over several days and the resultant bloom, now olive-green and dominated by the raphidophyte *Fibrocapsa japonica* (Toriumi & Takano 1973), continued for a further 2 months. The doubling rate in this early phase of the bloom, as inferred from chlorophyll concentrations, was 2 days (Haywood 1993).

Highest cell numbers of *F. japonica* at Leigh were 1.1 × 10^5 cells l^{-1} in early October (Fig. 3). *F. japonica* also appeared in samples collected on 12 October off the Noises Islands, 5 nautical miles north-east of Browns Bay, and again on 13 November in samples from Ti Point to as far south as Browns Bay (Table 1).

Fibrocapsa japonica was also noted in samples taken from three sites off the Coromandel coast in mid November, although *Heterosigma akashiwo*, another raphidophyte, was the dominant species there. The dinoflagellates *Scrippsiella trochoidea* and *Gymnodinium sanguineum* also occurred in moderate numbers at that site.

Fibrocapsa japonica was first observed in New Zealand waters on 23 October 1991 in samples from the west Coromandel coast (unpubl. data). Numbers then exceeded 2.0 × 10^5 cells l^{-1} and diminished steadily during the following weeks. This is a new taxonomic record for New Zealand coastal waters.

Other microalgal groups represented in the Leigh samples were Dinophyceae, Bacillariophyceae, Prymnesiophyceae, and Dictyophyceae (Table 2). The coccolithophorids *Gephyrocapsa oceanica* and *Emiliania huxleyi* were present throughout spring and into summer at all the bloom sites, *G. oceanica* occurring in consistently high numbers (Table 1). However the biomass was always far less than for either *F. japonica* or *Dictyocha speculum*.

Table 1 Comparison of cell numbers of dominant species at sites throughout the north-eastern coastal region of New Zealand, 13 November 1992. Sites were in the vicinity of 1, Leigh Marine Reserve; 2, Ti Point; 3, Snells Beach; 4, Mahurangi Harbour; 5, Orewa Beach; 6, Browns Bay; 7, Waitemata Harbour; 8, Coromandel (refer to Fig. 1). Cell numbers are expressed as thousands per litre; P, present.

Site	1	2	3	4	5	6	7	8
Fibrocapsa japonica	10.6	19.0	5.8	1.4	P	2.8	<0.1	1.2
Heterosigma akashiwo	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	10.2
Dictyocha speculum	5.4	2.0	1.6	1.2	0.3	0.4	<0.1	1.4
Gephyrocapsa oceanica	104.9	65.4	45.2	35.8	82.7	10.0	<0.1	P
Gyrodinium/Gymnodinium sp.	6.4	14.6	19.8	14.0	<0.1	0.2	<0.1	0.8

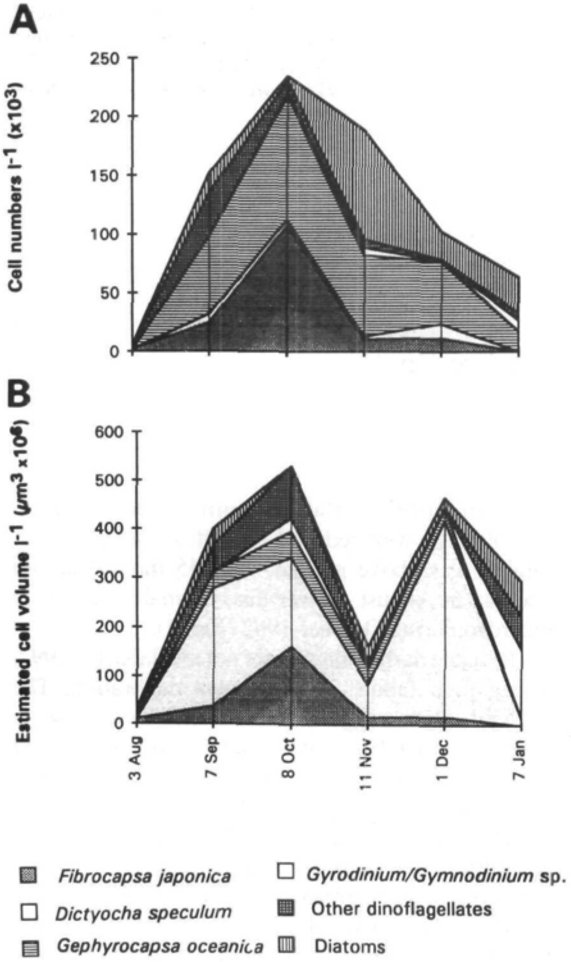

Fig. 3 **A**, Cell numbers of individual bloom species at Leigh, August 1992 to January 1993. **B,** Estimated cell volumes (using standard geometric formulae) of those species.

Dictyocha speculum was monitored throughout the bloom because of its known implication in fish kills. It occurred in its naked form at Leigh until December, when only the armoured form was present. In November, cells at all the sampled sites were of the naked form except at Mahurangi Harbour and at Coromandel. At the latter site twice as many cells were armoured as were naked. The comparatively large size (40 µm diameter) of the silicoflagellate meant that in terms of biomass it was of particular importance in the bloom, even when numbers were relatively low.

The bloom extended for over 200 km at its peak and samples taken from the Hauraki Gulf in mid October contained similar species to the Leigh samples, in particular *F. japonica, D. speculum, G. oceanica,* and *Gyrodinium/Gymnodinium* sp. The latter species was originally identified by light microscopy as *Gyrodinium aureolum,* but the identification was not confirmed at that time by scanning electron microscopy (SEM). A similar-looking organism, isolated from the Auckland region in February, 1993, was identified as *Gymnodinium breve* by SEM (Chang 1993) .

Isolation and culture

Fibrocapsa japonica, H. akashiwo, D. speculum, and *G. oceanica* were isolated and established in culture. *D. speculum* took several days to double in number, whereas *G. oceanica* multiplied rapidly in CHRY medium. *F. japonica* grew well in GP medium, the cells (20 × 12 µm) appearing bean-shaped. In GP medium with urea as nitrogen source the cells were larger (25 x 20 µm) and irregular in shape.

Toxicity bioassay

Fresh sea water samples and exponential and stationary phase cultures of the bloom microalgae were tested for toxicity using the standard *Artemia* bioassay. The bioassay indicated that the New Zealand strains of *F. japonica* were not toxic. The Japanese strain used as a positive control for the bioassay caused immediate acute distress to the *Artemia*. None of the other bloom microalgae from Leigh caused either death or distress.

Fresh sea water samples from Coromandel did cause an immediate distress reaction. The only cultured isolate from those samples which caused a similar reaction was *Heterosigma akashiwo,* which also occurred in relatively high numbers in the fresh samples.

Mouse bioassays, carried out to assess whether paralytic and diarrhoetic shellfish toxins were present in mussels from the Coromandel area in mid November, were negative.

Climate

Climate data have been recorded daily on the open coast at the Leigh Laboratory since 1967 (Evans 1992). The largest deviations from average conditions were the low sea surface temperatures (SST: Fig. 4). At the start of the bloom, late in August, these were the lowest on record (26 years) and were below 13°C on 24 days (Fig. 2). Temperatures had been below

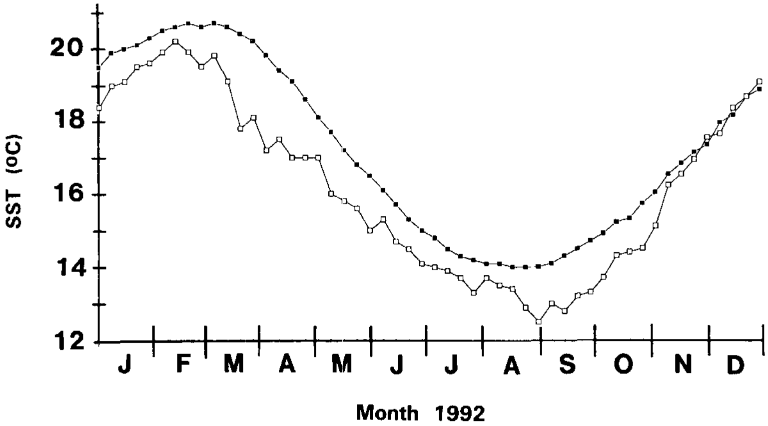

Fig. 4 Sea surface temperatures at Leigh during 1992. Upper line: 25-year weekly averages (1967–91); lower line: weekly averages for 1992.

average for the proceeding 21 months and had become more extreme over that period. In September 1992 the SST was 3.5 standard deviations below the 25-year mean. By mid November the SST had risen to equal the seasonal norm.

Solar radiation was very close to average for July, August, and September with little variation during the remainder of the year. A marked increase in solar radiation (Fig. 2) occurred just 2 weeks before the onset of the bloom.

Wave surge measured at Leigh was generally lower than average (Fig. 5), with fewer strong onshore winds, a condition expected during the "El-Niño" phase of the Southern Oscillation. August was particularly calm and September was calmer than average. Some strong wave action occurred in October and December.

During 1992, rainfall was normal or low up to the end of June, with reduced run-off. From early July rainfall was above normal, with 45 mm falling on one day in August. Lower-than-normal values were recorded during October 1992 (Fig. 5).

Reliable daily salinities are not available for 1992, owing to a failure in instrument calibration. The available data suggests that salinity was close to normal in October, with a salinity boundary near Leigh (> 35.0‰ north of Leigh and < 34.9‰ to the south). It is unlikely that there was any thermal stratification at the start of the bloom. Typically there are very small salinity changes on this coast and variations do not correlate strongly with local rainfall.

The highly anomalous SST recorded at Leigh were not local events, as is shown by satellite-derived data (Fig. 6). The SST anomalies of 1992 continued a

Table 2 Phytoplankton species present, and their abundance, at the height of the raphidophyte dominated bloom at Leigh, 8 October 1992. Abundance scale as follows (cells l^{-1}): 1, ≤ 500; 2, 501–5000; 3, 5001–10 000; 5, >100 000.

	Abundance		Abundance
Dinophyceae		**Bacillariophyceae**	
Ceratium furca	1	*Leptocylindricus danicus*	2
Dinophysis acuminata	1	*Navicula* sp.	2
Gymnodinium sp. (50 m)	1	*Nitzschia* sp.	1
Gymnodinium sp. (10 m)	2	*Pleurosigma* sp.	1
Gyrodinium/Gymnodinium sp.	2		
Gyrodinium glaucum	1	**Dictyophyceae**	
Oxytoxum sp.	2		
Prorocentrum triestinum	2	*Dictyocha speculum*	3
Protoperidinium sp.	1		
Scrippsiella sp.	2	**Cryptophyceae**	
Prymnesiophyceae		*Cryptomonas* sp.	3
Emiliania huxleyi	1	**Raphidophyceae**	
Gephyrocapsa oceanica	5	*Fibrocapsa japonica*	5

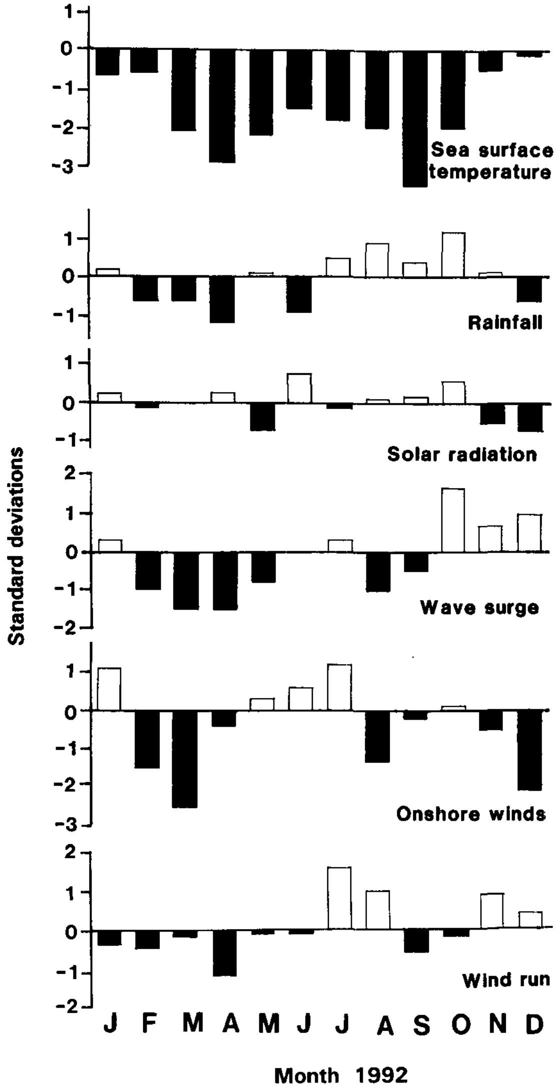

Fig. 5 Monthly anomalies for six climate factors at Leigh during 1992, expressed as standard deviations of the long-term mean (1967–91).

downward trend from the previous years (Fig. 7): 1989 was very warm, 1990 near average and 1991 was very cool. This 4-year trend closely followed a trend in the Southern Oscillation Index (SOI), which signals the El-Niño/La Niña changes of the tropical Pacific.

Water quality

Water quality was studied throughout 1992, and large plumes of sediment from run-off were recorded at Leigh on July 14 and 22, a month before the bloom (Haywood 1993). Suspended solids measured from 4 to 18 g m^{-3} during the bloom as against 1–4.5 g m^{-3} during non-bloom conditions. Throughout the bloom there were reports of discoloured water and low underwater visibility.

DISCUSSION

Bloom composition

The Leigh phytoplankton bloom, spring-summer 1992, was of particular interest because of its composition, persistence and extent—albeit patchy—along more than 200 km of coastline. The bloom was notable for the multiple dominance of species; *Fibrocapsa japonica, Heterosigma akashiwo, Dictyocha speculum,* and *Gephyrocapsa oceanica* were present in substantial numbers from September to December, and were observed in samples as far south as the Coromandel Coast. *F. japonica* was also noted for the first time in the Marlborough Sounds in December 1992, increasing the known range of this microalga.

Fibrocapsa japonica was first noted in New Zealand in October 1991 (unpubl. data). The raphidophyte was then the dominant species (2.2×10^5 cells l^{-1}) in a brown-coloured bloom off the west Coromandel coast, in which *D. speculum* was also present. It succeeded a September bloom of the gonyaulacoid dinoflagellate *Lingulodinium polyedra.* That bloom occurred during a period of fine weather with westerly winds and sea surface temperatures rising from a cool 13°C in September to 14.5°C in October. It dissipated in late October following heavy rains, only to be succeeded by a mixed diatom bloom (*Leptocylindricus danicus, Thalassiosira* sp., and *Thalassionema* sp.) during December.

The germination of cysts of *F. japonica* has been linked to periods of low temperature, with high rates of germination in vitro if cysts are held at 12°C (Yoshimatsu 1987). Cold sea surface temperatures might well have been a key factor in the composition of both the earlier Coromandel bloom and the 1992 Northland bloom.

The dominant microalga present in samples taken from Coromandel in November 1992 was *H. akashiwo*, numbers of which exceeded those of *F. japonica* at this site by a factor of 10. By then SSTs in the Hauraki Gulf had increased from the previous month's low to between 17.4 and 18.1°C. Hydro-logical conditions in the north differed from those present during the ichthyotoxic bloom of *Heterosigma akashiwo* which occurred at Big Glory

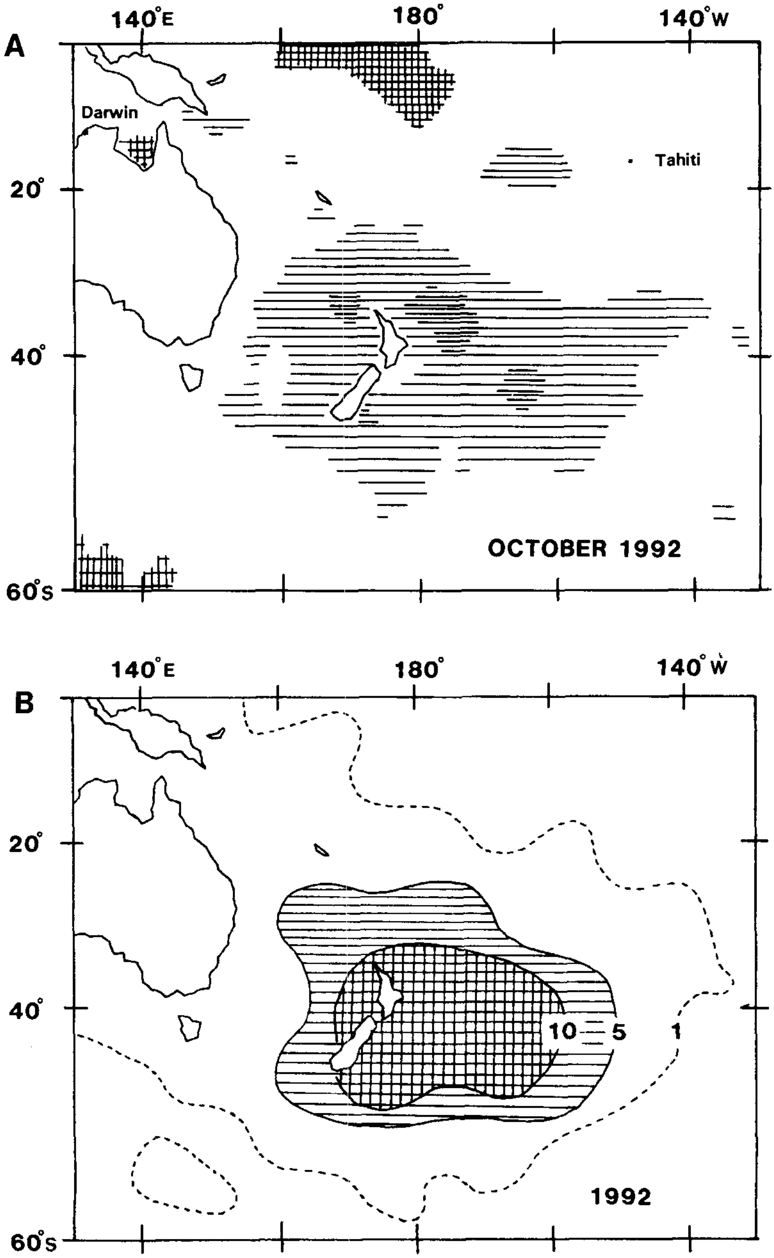

Fig. 6 Satellite-derived sea surface temperature (SST) anomalies in the South Pacific. **A,** October 1992. Blank: areas within 1°C of average; single horizontal hatching: between −1°C and −2°C; double horizontal bars: between −2°C and −3°C; cross-hatching: between +1°C and +2°C. **B,** Contours showing the number of months during 1992 when SST anomalies were more than 1°C below average.

Bay, Stewart Island, in January 1989. At that time, water temperatures remained at a uniform 15–15.5°C, with salinities of between 33.8 and 34.3‰. Then bloom development occurred after a prolonged period of calm weather and was accompanied by several episodes of intense rainfall under conditions of light winds (MacKenzie 1991). *H. akashiwo* has been described as eurythermal and euryhaline for at least some strains, and nutrient factors, rather than temperature and salinity, have been proposed as the prime cause of blooms in Japanese waters (Yamochi 1983). Increased supplies of chelated iron due to river run-off during the rainy season is considered of critical importance in the initiation of *H. akashiwo* blooms (Yamochi 1983). Run-off was considered a contributing factor in the 1989 Big Glory Bay bloom

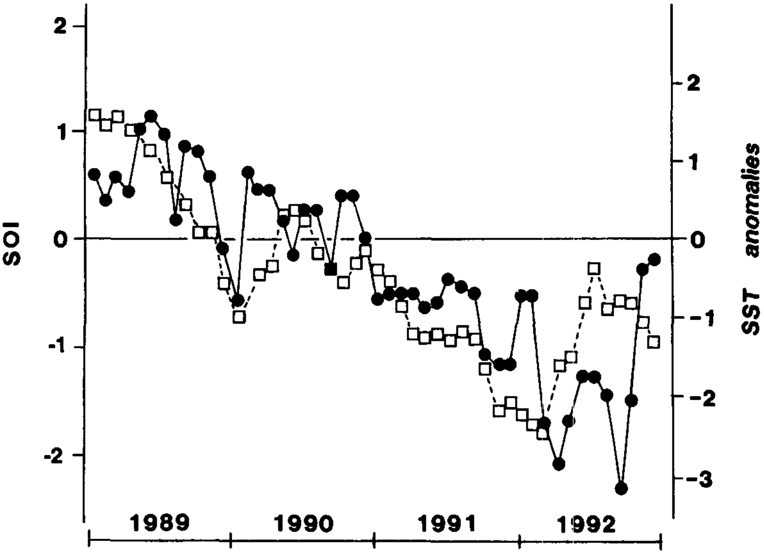

Fig. 7 Monthly sea surface temperature (SST) anomalies during 1989–92 at Leigh are presented as standard deviations from the long-term mean (1967–92) (●). These deviations are plotted with the Southern Oscillation Index (SOI), (the anomaly of air temperature difference between Darwin and Tahiti), as 5-month running averages (□).

(MacKenzie 1991). The reason for the domination of *H. akashiwo* at Coromandel in 1992 is unclear, as there are no data on nutrient conditions at that time, but growth stimulation by warmer sea temperatures or run-off following heavy rainfall are both possible.

The distress reactions of *Artemia* during the bioassay for toxicity in the Coromandel strain of *Heterosigma* indicated that an irritant of some sort was being produced. Before sampling at Coromandel, brown-coloured water had been observed and mussels were reported as having a peppery taste. In tests carried out by laboratory staff, mussels caused a tingling sensation to the tongue lasting several minutes. Skin irritations were also reported by fishers operating in the bloom area. The causative species was not established in either case. Mussels from the area tested negative for diarrhoeic and paralytic shellfish toxins using established regulatory mouse bioassay methods. No fish are farmed in this area (although there are several live crayfish holding facilities) and so the risk of deaths from ichthyotoxins is minimal.

The presence of the naked form of *D. speculum* during the earlier stages of the bloom was notable. As both this microalga and *F. japonica* disintegrated with the addition of Lugol's iodine to samples, it is likely that the presence of both this form of the silicoflagellate and the raphidophyte have often been overlooked in New Zealand waters in the past. Only by monitoring live as well as treated samples, and observing the lysis of live cells under the light microscope following Lugol's treatment, were the identities and numbers of these two species established.

Bursts of rain, with ensuing flows of nutrients into coastal waters, have been implicated in the initiation of *D. speculum* blooms in Scandinavia (Moestrup & Thomsen 1990). Although there were few occasions of substantial run-off at Leigh, the first records of *D. speculum* were in July and coincided with days in which plumes of sediment from run-off were observed in the coastal waters off Leigh (Haywood 1993).

The naked form of the silicoflagellate has been linked to mortalities of caged fish in Danish waters, although bacteria residing in the microalgal cytoplasm might have been implicated (Moestrup & Thomsen 1990). Its growth is thought to be independent of the availability of dissolved silicate and by December all cells appeared to be armoured. *D. speculum* is considered to be synonymous with *D. fibula* (Fanuko 1989). Cold temperatures (10°C) are ideal for the successful culturing of *D. fibula* (Van Valkenburg & Norris 1970); the long generation times of 49 h recorded in the literature correspond with the very slow growth of the Leigh isolate of *D. speculum* in culture. Light/dark ratios appear to have an effect on skeleton development in vitro (Van Valkenburg & Norris 1970). Warmer sea temperatures and increasing daylengths might well have led to the change to the armoured form of this species during the 1992 bloom.

The coccolithophorid *G. oceanica,* accompanied by low numbers of *Emiliania huxleyi,* remained in high numbers throughout the northern bloom.

E. huxleyi dominated in blooms occurring at other sites around the New Zealand coastline, numbering 8×10^6 cells l^{-1} at Big Glory Bay, Stewart Island during November 1992 and up to 2.4×10^5 cells l^{-1} in samples from the Marlborough Sounds in December 1992 (unpubl. data).

Environmental factors

Although the precise triggers for the increase of particular species involved in the blooms and the limiting factors affecting their subsequent abundance are likely to vary specifically and regionally, the widespread nature of the bloom and its duration suggest some general forcing factor. The most obvious candidate is the extremely low, widespread, and long-lasting SST phenomenon, which could have acted to inhibit or reduce the normal phytoplankton community and hence provide an advantage to whatever species were least affected.

The idea of a widespread climatic forcing factor is supported by the total set of biological patterns, especially those related to frequency of occurrence. The SST anomalies of 1992 were rare and extreme events, unique in the 26-year record at Leigh. The algal blooms were also rare and extreme events, both in themselves and in the subsequent biological disruptions. The unusual features of the bloom included its intensity, its duration, its geographic extent, the species involved, their multiple dominance, and their regional differences. The subsequent disruptions included the death of most kelp plants in the deeper half of the beds (R. Babcock, University of Auckland, pers. comm.), widespread and selective death of sponges (C. Battershill, NIWA - Oceanographic, pers. comm.), high penguin mortality (Janice Molloy, Department of Conservation, pers. comm.) and various localised but severe mortalities in grazers and bivalves (S. Hooker, University of Auckland, pers. comm.).

The nearest equivalent climatic event at Leigh was the summer of 1983. The very low sea temperatures then were also accompanied by a major, widespread algal bloom (albeit with different bloom dominants) and severe biological disruptions (Taylor et al. 1985).

In both cases, although the detailed causes and limiting factors are likely to be highly variable, the extremely low SST appear to have acted as a general forcing factor. It is therefore useful to look at the probability of recurrence. If it is assumed that the SST anomalies are a single and randomly distributed set, then the return period of the 1992 cold period is very long, in excess of 100 years for many features. However there is good evidence that SST anomalies are in fact non-random, with a pattern relating to Pacific-wide climate oscillations. The SST anomalies recorded at Leigh and other New Zealand stations show a clear relationship to the Southern Oscillation, with low SST associated with a negative Southern Oscillation Index (SOI), which in turn is associated with El-Niño conditions in the tropical Pacific. If the Leigh SST anomalies are analysed as two separate sets (based on positive or negative SOI) then the expected return period of the 1992 events is in the order of 20–40 years. Considering that SOI is a relatively crude index for the purpose, the return period could be much lower.

The duration of the 1992 Leigh bloom and the wide distribution of the dominant species indicate that the raphidophyte *F. japonica*, like its close relative *H. akashiwo*, is now firmly established in New Zealand waters. Toxicity bioassays suggest that *Fibrocapsa* was non-toxic, but its presence will need to be monitored in the future, particularly throughout the intensive aquaculture regions. It is significant that in January 1993, following the collapse of the 1992 bloom, a further toxic dinoflagellate dominated bloom developed, which included the neurotoxin producer *Gymnodinium* cf. *breve*. In this later episode, shellfish toxins caused the total disruption of the bivalve industry in New Zealand. There is substantial evidence that the chemical conditioning of the water column during blooms is an important factor in species succession (Gauthier & Aubert 1981), and it is conceivable that the earlier bloom played a role in the composition and toxicity of the subsequent bloom.

It is very rare that a bloom is monitored from inception to completion; most blooms are investigated reactively. The substantial data available in this instance should prove valuable in developing predictive models for the future and also in determining the factors that led on to the toxic bloom of 1993.

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