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Population growth and transport of the red tide dinoflagellate, *Noctiluca scintillans,* in the coastal waters off Sydney Australia, using cell diameter as a tracer

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Abstract

Spatial abundance patterns of the heterotrophic dinoflagellate, *Noctiluca scintillans,* were investigated along the southeast coast of Australia to address the hypothesis that population growth of *Noctiluca* is driven by anthropogenic eutrophication. Abundance patterns were related to the immediate physical flow field and not the conditions conducive to growth. *Noctiluca* cells were advected southward with the East Australian Current, which was the dominant transport vector for the cells in this region. Areas of population growth of *Noctiluca* were identified by variations in cell-size distributions. Small cells (<525 μm) were considered to be capable of population growth, in contrast to red tide cells, which are known to be large (>600 μm), senescent, and the end result of a long series of biological and physical processes occurring in temporally and spatially distant water masses. Small cells were therefore considered to be located closer to the region in which growth was stimulated. The proportion of small cells in the samples was significantly correlated with relatively high concentrations of chlorophyll *a.* Consequently, this relationship was used to show that population growth of *Noctiluca* may be stimulated by an increase in chlorophyll *a* due to sewage discharge, although the prevailing hydrological conditions determine the likelihood of such impacts. High chlorophyll *a* concentrations within estuaries were also found to sustain a stable but low standing stock of *Noctiluca,* which may seed oceanic stocks. Thus, by examining cell size rather than abundance distributions, we identified and interpreted the variance in the spatial abundance patterns of *Noctiluca* within a dynamic hydrological environment.

Many red tide forming organisms are prone to advection by prevailing winds and currents (Anderson 1995). These advective processes are often strong enough to transport the organisms over large distances, as observed in the study by Tester et al. (1991). Tester et al. found that an outbreak of the toxic dinoflagellate, *Gymnodinium breve,* in North Carolina was transported by several major current systems from the southwestern coast of Florida, nearly 1,000 km away. The recognition of such transport not only provided an explanation for the anomalously high numbers of red tide algae in areas that are unable to support such prolific growth, but also highlighted the difficulty in determining the controlling factors or initial conditions conducive to population growth of these organisms. Thus, as now commonly recognized, many field studies are often challenged by the necessity to distinguish the transport processes surrounding the study area and the ability to distinguish whether the organism has indeed been advected (Franks and Anderson 1992; Tester and Steidinger 1997; Fraga et al. 1998).

Noctiluca scintillans is a large heterotrophic dinoflagellate that forms conspicuous red tides along many coastal systems around the world (Elbrachter and Qi 1998). *Noctiluca* cells may be considered to behave as passive particles, since unlike most dinoflagellates, *Noctiluca* lacks the ability to swim and actively migrate vertically in the water column. In addition, *Noctiluca* cells are normally positively buoyant due to their large cell vacuole, filled with ammonium ions (Elbrachter and Qi 1998). The buoyancy and the size of the cells may vary depending on their nutritional status (Uhlig and Sahling 1990; Buskey 1995). When the cells are well fed, they tend to sink until digestion and defecation have taken place (Omori and Hamner 1982; Uhlig and Sahling 1990; Kiørboe and Titelman 1998). The fed cells frequently

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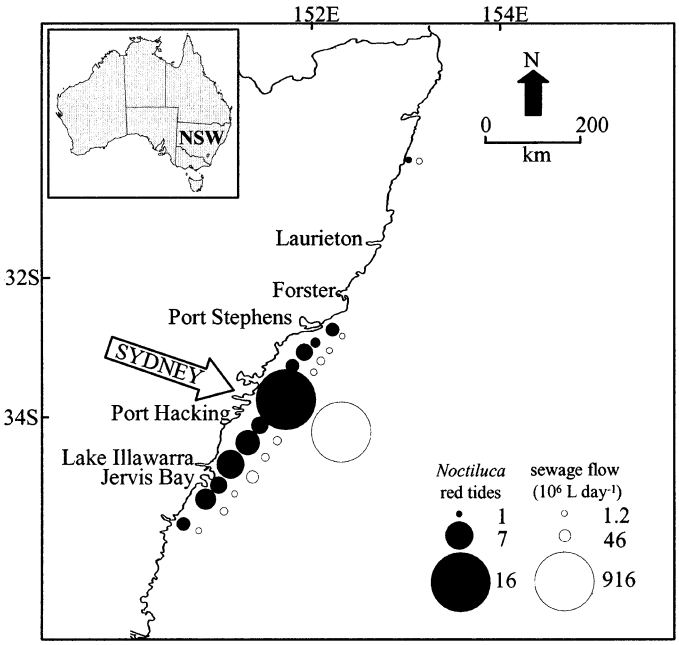


Fig. 1. Map of the New South Wales coast showing the location of the six regions sampled in this study and the number of reports of *Noctiluca* red tides (solid circles) since the 1970s, compared to the average dry weather flow of sewage (open circles) discharged along the coast.

undergo cell division (reproduce) and are consequently smaller in size than starved cells (Buskey 1995), which are irreversibly damaged and no longer divide (Uhlig and Sahling 1990). *Noctiluca* cells that constitute a red tide are starved and are therefore considered to mark the end of population growth. The red tides have been described to be the end result of a long series of biological and physical processes that occurred in temporally or spatially distant water masses (Uhlig and Sahling 1990). They are often characterized by sharp fronts (Franks 1997), indicating that physical processes directly affect the spatial and temporal distribution of the cells (Le Fevre and Grall 1970; Schaumann et al. 1988; Huang and Qi 1997).

The New South Wales (NSW) coast, located in the southeast of Australia, has recently been subject to unprecedented red tides of *Noctiluca* (Ajani et al. 2001*a*). Most of the *Noctiluca* red tides have been reported to occur in coastal waters rather than within estuaries, which suggests that these red tides are most likely a coastal phenomenon (Murray and Suthers 1999; Ajani et al. 2001*a*). Similar to other areas around the world (e.g., Porumb 1992; Hodgkiss and Ho 1997), the incidence and intensity of *Noctiluca* red tides along the NSW coast have apparently increased over the past two decades in conjunction with an increase in human activities along the coast (Nolch 1993; Hallegraeff 1995). Anecdotal reports of *Noctiluca* red tide events occurring along the NSW coast since the 1970s suggest that most of these red tides occur off Sydney, where a relatively high load of sewage is discharged into adjacent coastal waters (Ajani et al. 2001*a;* Fig. 1). The relationship between anthropogenic eutrophication and the occurrence of *Noctiluca* red tides along the southeast coast of Australia may be confounded by increased public and scientific awareness due to the lack of systematic reporting of red tide events and the lack of suitable long-term data sets (Hallegraeff 1993). Given the physical flow field along the coast, the spatial distribution patterns of *Noctiluca* red tides could alternatively result from large-scale advective processes. The current flow patterns along the coast are dominated by the poleward flowing East Australian Current (EAC), which originates in the tropics and flows southward approximately parallel to the coast (Middleton et al. 1997). Hence, the source of *Noctiluca* cells in the coastal waters off Sydney may simply result from longshore advection of cells rather than local growth.

The aim of the present study is to determine whether the abundance of *Noctiluca* is greatest in areas where relatively high amounts of sewage are discharged. Owing to the EAC flow patterns along the NSW coast, an approach for determining the time–space history dispersion patterns of *Noctiluca* cells is also proposed. The approach is based on the relationship between cell size and nutritional state (Buskey 1995). In the present study, we use this relationship to suggest that the proportion of small-sized *Noctiluca* cells found within plankton samples may provide a relative measure of population growth. We also suggest that by using the cell-size approach, the region in which population growth is initiated can be identified, along with the underlying nutrient source(s) for the prey of *Noctiluca.* To an extent, the path of a dispersed population of *Noctiluca* cells is also traced.

Materials and methods

Spatial sampling design and study regions—Plankton samples and hydrographic data were collected from six regions where *Noctiluca* red tides have been reported along a 470-km stretch of the New South Wales (NSW) coast (Figs. 1, 2). In each region, four stations were positioned along an oceanic to estuarine gradient. The oceanic station (O) was within the path of the prevailing oceanic current at the 40–50-m isobath. The coastal station (C) was at the 20-m isobath and was affected by both the estuarine plume and oceanic currents. The two estuarine stations (E1, E2) within each region were located on the basis of the salinity gradient between estuarine and oceanic waters (S_E/S_O), so that each estuarine station was standardized by the extent of tidal influence (Table 1). Estuarine Sta. E2 was least affected by the tides. At each station there were two replicate sampling sites separated by a distance of 0.5–1 km. The overall spatial sampling design consisted of six regions, four stations, and two sites nested within the stations in each region.

Three regions north of Sydney, Laurieton (L, Fig. 2a), Forster (F, Fig. 2b), and Port Stephens (PS, Fig. 2c), were chosen due to their predisposition to coastal upwelling (Rochford 1975; Hallegraeff and Jeffrey 1993; Oke and Middleton 2001), which is the dominant natural nutrient-enrichment process along the coast of NSW. There are no sewage outfalls within the immediate vicinity of the entrance of the estuaries in these regions. The estuary at Laurieton, Forster, and Port Stephens has a catchment area of 720 km^2, 1,420 km^2, and 4,950 km^2, respectively.

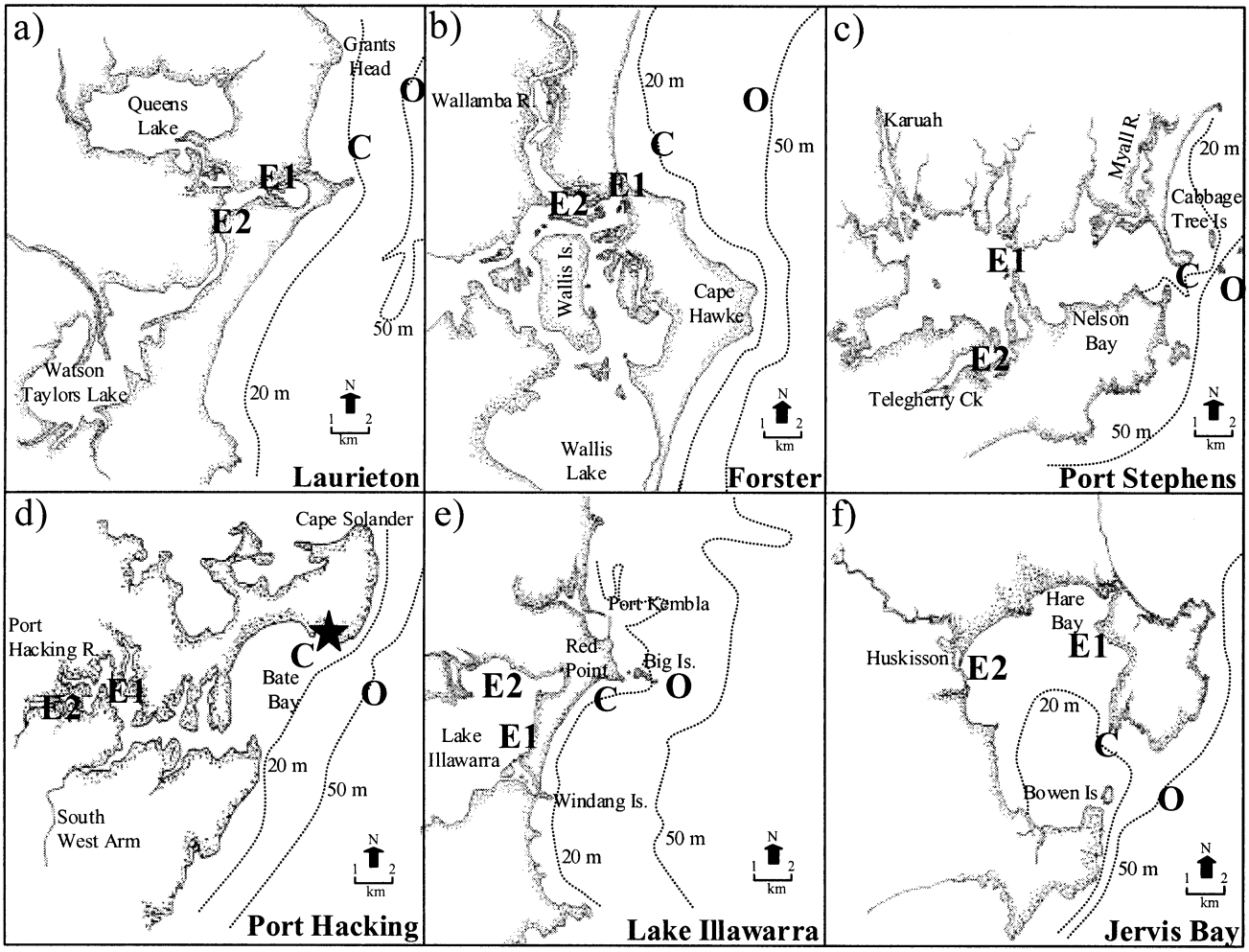


Fig. 2. Maps of the six regions, (a) Laurieton, (b) Forster, (c) Port Stephens, (d) Port Hacking, (e) Lake Illawarra, and (f) Jervis Bay. Each map shows the location of the oceanic (O), coastal (C), and estuarine (E1, E2) stations. Lines denote the position of the 20-m and 50-m isobath. The star in map 2d denotes the location of the shoreline sewage outfall at Port Hacking.

In Sydney, samples were collected from Port Hacking (PH, Figs. 1, 2d), south of Sydney's three main deep-water ocean sewage outfalls. These offshore outfalls collectively discharge primary treated sewage at a rate of 9.2×10^8 liters d^{-1}, equivalent to approximately 80% of Sydney's domestic wastes (Pritchard et al. 2000). Additionally, a shoreline sewage outfall at Potter Point, on the north side of the entrance of Bate Bay, discharges primary treated sewage to the sea surface at a rate of 4.6×10^7 liters d^{-1}. One of the sites at the coastal station at Port Hacking was positioned within the immediate vicinity of the Potter Point sewage outfall (Fig. 2d). South of Sydney, samples were collected from Lake Illawarra (LI, Fig. 2e) and Jervis Bay (JB, Fig. 2f). The coastal station at Lake Illawarra was positioned close to the shoreline sewage outfall at Red Point (1.6×10^7 liters d^{-1}). The two estuarine stations were positioned in Lake Illawarra, south of Red Point. Jervis Bay differs from the other regions since it is a coastal embayment where coastal and oceanic waters inundate the bay continually due to the wide entrance. Tidal currents are relatively weak except in the entrance proper. A tertiary treated shoreline sewage outfall on the western side of the bay (5.8×10^6 liters d^{-1}) has no detectable biological impact (Smith 1994).

Collection of samples—Samples were collected in the austral spring during September 1998 and November 1998 and in the austral summer during February 1999 and March 1999 when the abundance of *Noctiluca* is known to be relatively high (Murray and Suthers 1999; Dela-Cruz et al. 2002). Sampling commenced at Laurieton and continued down the coast to Jervis Bay, taking 7–10 consecutive days to complete each sampling run (one region per day, weather permitting). Samples were collected between 0630 h and 1400 h, coinciding with the timing of the high and/or flood tide on most occasions. Plankton samples were collected using a 0.2-m diameter, 100-μm mesh plankton net towed horizontally on the sea surface for 5 min at a speed of 0.1 m s^{-1} from an inflatable boat, identical to the collection methods of Murray and Suthers (1999). The rate of water flow through the net was determined by the boat engine's tachometer and the rate of drift of debris past the boat. The mesh size of the net was almost half the size of the smallest *Noc-*

Table 1. Bathymetry, sampling interval, and the salinity gradient ($S_{C,E1,E2}/S_O$) between oceanic (O), coastal (C) and estuarine waters (E1, E2) in each region during September, November, February, and March.

Region	Station	Bottom depth (m)	Sampling interval (m)	$S_{C,E1,E2}/S_O$ (Sep, Nov, Feb, Mar)
Laurieton	O	34–36	0, 15, 30	—
(S31°37′, E152°54′)	C	22–28	0, 20	0.99, 0.97, 1.00, 1.00
	E1	5–7	0	0.96, 0.99, 1.00, nd
	E2	3–5	0	0.65, 0.99, 1.00, nd
Forster	O	33–35	0, 15, 30	—
(S32°09′, E152°33′)	C	25–27	0, 20	1.00, 0.99, 0.98, 0.99
	E1	3–5	0	0.78, 1.00, 1.00, 1.00
	E2	3–5	0	0.65, 0.89, 0.80, 0.84
Port Stephens	O	31–38	0, 15, 30	—
(S32°43′, E152°14′)	C	16–17	0, 20	0.99, 1.00, 0.95, 1.00
	E1	8.8–10	0	0.86, 0.84, 0.86, 0.96
	E2	2.4–3.3	0	0.74, 0.97, 0.86, 0.84
Port Hacking	O	48–50	0, 20, 40	—
(S34°03′, E151°13′)	C	15–20	0, 20	nd,* 1.00, 1.00, 1.00
	E1	10–11	0	0.87, 0.98, 0.91, 0.76
	E2	4–5	0	0.77, 0.97, 0.81, 0.68
Lake Illawarra	O	33–37	0, 15, 30	—
(S34°29′, E150°56′)	C	15–20	0, 15	0.95, 1.00, 1.00, 1.00
	E1	2–3	0	0.53, 1.00, 0.96, 0.97
	E2	2–3	0	nd, 0.89, 0.97, 0.97
Jervis Bay	O	48–50	0, 20, 40	—
(S35°07′, E150°47′)	C	20–30	0, 20	1.00, 1.00, 1.00, 1.00
	E1	7–10	0	0.98, 1.00, 1.00, 1.00
	E2	5–6	0	0.98, 1.00, 1.00, 1.00

* nd, no data

tiluca cell reported in previous studies (Polishchuk et al. 1981; Buskey 1995; Murray and Suthers 1999), and the tow speed was low enough to avoid cell damage. Three replicate plankton samples from each site were collected and immediately preserved in 5% formalin (final concentration).

Water samples used for analyses of chlorophyll *a* (Chl *a*) and nutrients (oxidized nitrogen, i.e., nitrate + nitrite, $NO_2^- + NO_3^-$; ammonium, NH_4^+; filterable reactive phosphorus, FRP; and dissolved reactive silicate, $Si(OH)_4$) were collected using 8-liter Niskin bottles. Water samples were collected in the surface, middle, and bottom layers of the water column at the oceanic station and in surface and bottom water layers at the coastal station (Table 1). Water samples were only collected from the surface water layer at the estuarine stations since the water column was <10-m deep and well mixed. Two water samples were collected at each depth, accounting for a total of 56 water samples collected from each region during each sampling time. Water temperature (T), salinity (S), and dissolved oxygen (DO) were measured at 5-m depth intervals at the oceanic and coastal stations and at the surface water layer at the estuarine stations using a MiniSonde® 4 (Hydrolab) interfaced with a data logger (Surveyor® 4, Hydrolab). Wind speed, wind direction, and rainfall for each region were obtained from the Bureau of Meteorology (BOM). Satellite images of sea surface temperature (SST) and sea surface Chl *a* (SeaWiFS) were obtained from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) marine laboratories in Hobart. The general direction of flow of the East Australian Current was inferred from the SST images (Parslow et al. 2000; Oke and Middleton 2001). However, current speed and direction along the coast were also measured 4 d after the November sampling run aboard the CSIRO research vessel, *Franklin.* The speed and direction of surface currents were determined at hourly intervals using an acoustic Doppler current profiler (ADCP). The ADCP data were earth-referenced with either the bottom track velocity or global positioning system (GPS) derived velocity to provide absolute current speeds (m s^{-1}). During the February sampling run, surface current speed and direction were acquired from the ocean reference station (ORS) situated at 33°54′S, 151°18′E on the 65-m isobath, approximately 25 km north of Port Hacking. The ORS is a permanently moored facility maintained by Manly Hydraulics Laboratory for Australian Water Technology, who kindly supplied the data.

Analyses of samples—Preserved plankton samples were gently sieved and rinsed with seawater through a 90-μm mesh sieve and concentrated to 0.1 liter. The abundance of *Noctiluca* and abundance of zooplankton were determined from two replicate 1-ml subsamples of the 0.1-liter concentrate using a dissecting microscope. Cell diameters from the first 60 cells of *Noctiluca* encountered in the plankton samples were calculated from the area of the cells, measured using the public domain image program developed at the U.S. National Institutes of Health (NIH, at http://

rsb.info.nih.gov/nih-image/). Cell diameters were only measured from samples collected in November and February due to the low abundance of *Noctiluca* in the other two months.

Seawater (2 liters) collected for Chl *a* analyses was filtered through a 47-mm diameter, 1.2-μm glass fiber filter (GC-50, Advantec) under low vacuum within 3 h of collection. The filter paper was folded, blotted dry, wrapped in aluminum foil, and stored at -20°C until analysis. The Chl *a* content of the samples was determined using the methods outlined in Lorenzen (1967) and Jeffrey and Humphrey (1975), with a method detection limit of 0.3 mg m^{-3}. Water collected for analysis of nutrients was filtered through a 0.45-μm disposable syringe filter (CA membrane with GF prefilter, Sartorius) within 3 h of collection and frozen at -20°C for $NO_2^- + NO_3^-$, NH_4^+, and FRP analyses, or stored at room temperature in the dark for $Si(OH)_4$ analyses. The nutrient content of the samples was determined using the American Public Health Association Method 4500 modified for $NO_2^- + NO_3^-$, NH_4^+, FRP, and $Si(OH)_4$. The method detection limits were 0.02, 0.14, 0.02, and 0.03 μmol L^{-1}, respectively.

Analyses of data—Hydrographic variability over time, among regions, and among stations was analyzed by principal component analysis (PCA). The physical (T, S, DO), chemical ($NO_2^- + NO_3^-$, FRP, SiO_2, NH_4^+), and biological (Chl *a*) data used in these analyses were measured only from the near surface water layers at each site to allow a comparison between the offshore and estuarine stations. The nutrient structure of each estuary was further examined by calculating the molecular ratios of silicon : nitrogen, silicon : phosphorus, and nitrogen : phosphorus in the water samples and comparing these ratios to the Redfield ratio (silicon : nitrogen : phosphorus = 16 : 16 : 1), which is commonly used as a criterion for stoichiometric nutrient balance (Smayda 1990; Justic et al. 1995). Deviations from the Redfield ratio distinguish whether the estuarine systems are deficient or sufficient in phosphorus, nitrogen, and/or silicon.

Vertical profiles of temperature were constructed from the static point temperature measurements taken at various depths at the oceanic station in each region to define the oceanographic events that took place at the time of sampling. The data were contoured using a distance weighted least squares smoothing option. This smoothing option fits a line through a set of points by least squares, although the surface is allowed to flex locally to fit the data better. The amount of flex was controlled by the tension parameter, which was set at 0.5.

Spatial and temporal variation in the plankton data were analyzed using an analysis of variance (ANOVA). Month of sampling, region, and station were treated as fixed factors. Site was treated as a random factor nested in month, region, and station. Homogeneity of variances within each data set was initially tested using Cochran's test. Log-transformed abundance data remained heterogeneous due to the large number of zero values (Cochran's = 0.08, $p < 0.01$). The heterogeneous data were still analyzed, although the probability for the ANOVA was set at 0.01 to reduce the risk of type I errors (Underwood 1981). ANOVAs showing significant effects were further analyzed using a Student–Newman–Keuls (SNK) test.

The condition (e.g., undergoing cell division or senescent) of the *Noctiluca* population(s) was characterized by the variation in the diameter of the cells. The cell diameter data were categorized into 25-μm size class intervals. The resulting size frequency distributions were ordinated by PCA. The size frequency was expressed as a percentage of the total number of cells used for the cell diameter measurements in any given sample. The physical, chemical, and biological data collected from the surface water layers were subsequently correlated with the factor scores generated by the PCA to examine the potential relationships between the cell-size frequency distributions and the environmental data. Since we were specifically interested in examining the proportions of small and large diameter cells in the samples, the size frequency distributions were used in these analyses rather than the average cell sizes, which were biased toward the larger diameter cells. Redundancy analysis (RDA) was also used to quantify the extent to which the environmental variables explained the variability in the cell-size frequency distributions (Van den Brink and ter Braak 1997; ter Braak and Smilauer 1998). The RDA constrains the PCA ordination axis to a linear combination of the environmental variables. Thus the resulting biplot of the RDA only displays the variability in the cell-size frequency distributions that can be explained by the environmental variables measured in the study. The length of the arrows on the biplots is indicative of the amount of variance in the cell-size frequency distributions that can be explained by a specific environmental variable. Environmental and biological variables positioned in the same quadrant on the biplot are significantly positively correlated with each other. The statistical significance of the relationship between the cell-size frequency distributions and the environmental variables was evaluated using Monte Carlo permutation tests.

Results

Hydrographic data—Persistent hydrographic differences were observed between the coastal and estuarine stations in all regions except Jervis Bay (Fig. 3). These differences were not due to a specific combination of physical, chemical, and biological variables but were dependent on the oceanographic and meteorological conditions that prevailed before and during each of the four sampling runs (Table 2). Another feature revealed by the PCA was the general longshore hydrographic homogeneity (with the exception of Forster in November and February) of the surface waters at the oceanic and coastal stations during most of the months sampled (Fig. 3). This trend was not observed at the estuarine stations in which there were clear regional differences in the hydrographic properties of the surface waters.

Hydrographic processes at the coastal and oceanic stations in each region varied among the months of sampling. During September, a zone of uplifting of cold (16°C–17°C) nutrient rich ($NO_2^- + NO_3^-$, 3–7.2 μmol L^{-1}) water was observed between Port Stephens and Jervis Bay (Fig. 4a). The concentrations of Chl *a* in the upper 20 m of the water column

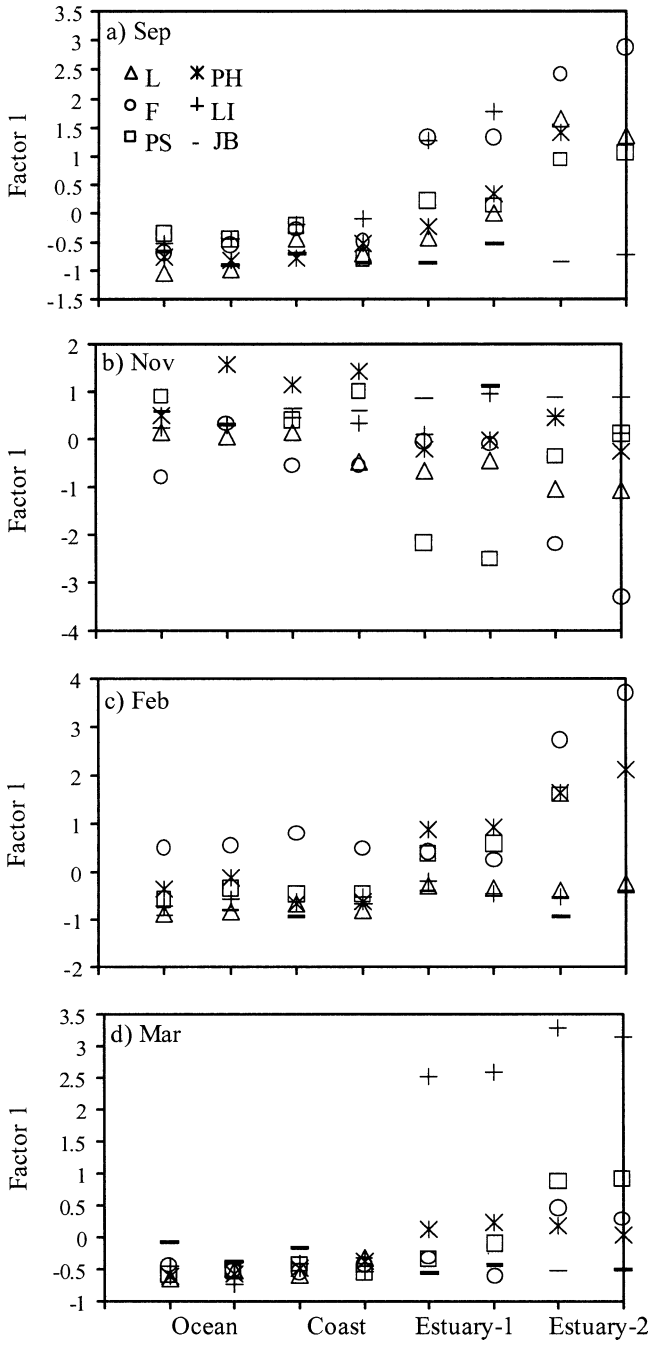


Fig. 3. Factor scores for the first principal component factor generated from a PCA of physical (T, S, DO), chemical (NO_2^- + NO_3^-, FRP, SiO_2, NH_4^+), and biological (Chl *a*) data collected at the oceanic, coastal, and estuarine stations in each region (L, Laurieton; F, Forster; PS, Port Stephens; PH, Port Hacking; LI, Lake Illawarra; JB, Jervis Bay) during (a) September 1998, (b) November 1998, (c) February 1999, and (d) March 1999. The first principal component factor explained 30–40% of total variance.

at Port Stephens, Lake Illawarra, and Jervis Bay were relatively high (>3 mg m^{-3}; Fig. 4e). In contrast, the November sampling run was preceded by strong downwelling favorable southeast winds in each region (15–30 kt, data not shown). The effects of the downwelling event were still evident during the sampling run since the water column between Laurieton and Jervis Bay was relatively well mixed and nutrient poor. During the summer months (February and March), the water column was up to 5°C warmer than during the two previous surveys in spring (Fig. 4c,d,g,h). There was also a surface depletion of nutrients (Fig. 4c,d) and low phytoplankton biomass in the surface waters of most regions (Fig. 4g,h). However, there were localized uplifting events at Laurieton and Port Stephens in February, and again in Port Stephens during March, as indicated by the doming isotherms and high nutrient concentrations (NO_2^- + NO_3^-, >7 μmol L^{-1}) in the bottom water layers (Fig. 4c,d). The February sampling run coincided with the early stages of the uplifting event as shown by the low phytoplankton biomass in the upper mixed layer (1–2 mg m^{-3}), which was relatively nutrient rich (NO_2^- + NO_3^-, 5–7 μmol L^{-1}) at the time of sampling. In contrast, the uplifted cold nutrient rich waters at Port Stephens were observed below 30-m depth in March.

Table 2. Rotated (varimax) component loadings for the first principal component factor generated from a PCA of physical, chemical, and Chl *a* data collected in the surface water layers of the oceanic, coastal, and estuarine stations at Laurieton, Forster, Port Stephens, Port Hacking, Lake Illawarra, and Jervis Bay. Data were collected in September 1998, November 1998, November 1999, and March 1999.

Variable	Sep 98	Nov 98	Feb 99	Mar 99
Temperature	0.45	−0.82	0.89	0.21
Salinity	−0.93	0.74	−0.95	−0.23
Dissolved oxygen	−0.14	0.84	−0.54	0.01
Chlorophyll *a*	0.15	−0.16	0.16	0.96
Ammonium	0.61	0.25	0.43	−0.08
Filterable reactive phosphorus	−0.44	0.12	−0.06	0.93
Oxidized nitrogen	0.11	0.08	−0.15	−0.19
Silicate	0.93	−0.45	0.65	0.94
Percentage of total variance explained	31.8	28	33	34.9

Within the estuaries there were a number of consistent regional differences in the physical, chemical, and biological variables. Surface waters were generally 1°C–2°C warmer in Laurieton, Forster, and Port Stephens than in the southern regions. The surface waters in Jervis Bay consistently had the highest salinity of all the regions sampled (35.1 ± 0.2). In the other estuaries, the salinity of the surface waters varied over time, independent of rainfall. For instance, the lowest (0.3 mm) and highest rainfall (5.4 mm) was recorded at Port Stephens 10 d prior to and during the September and February sampling runs, respectively, but these periods did not correspond with relatively high and low surface water salinities, respectively. The surface waters in Lake Illawarra consistently had the highest concentration of Chl *a* (2.9 ± 1.7 mg m^{-3}). With the exception of the September sampling run, the surface waters in Lake Illawarra also had the highest concentration of FRP (1.8 ± 1.1 μmol L^{-1}). The concentrations of NH_4^+, NO_2^- + NO_3^-, and $Si(OH)_4$ were variable over time, showing no consistent regional patterns among the estuaries.

The molecular ratios of silicon : nitrogen (Si : N), silicon : phosphorus (Si : P), and nitrogen : phosphorus (N : P), cal-

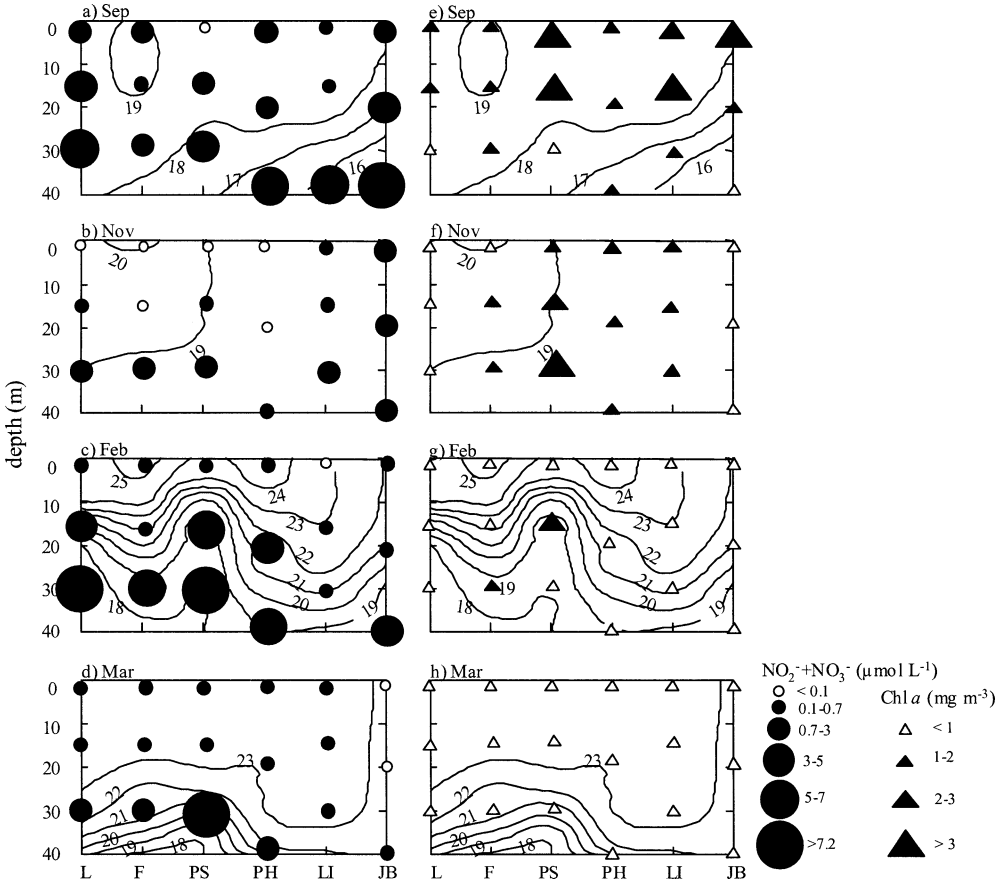


Fig. 4. Contoured profiles of average vertical temperature (°C) at each region's oceanic station during September 1998, November 1998, February 1999, and March 1999. The temperature was contoured every 1°C, and average dissolved inorganic nitrogen (solid circles; $NO_2^- + NO_3^-$ μmol L^{-1}) and chlorophyll *a* (solid triangles; Chl *a* mg m^{-3}) plots are superposed on the temperature data.

culated from the nutrient data collected from the estuarine stations, indicate that the stoichiometric nutrient balance within the estuaries varied each sampling time (Fig. 5). In September, the surface water layers of all the estuaries had greater concentrations of Si relative to P and/or N. The N : P in the surface water layers of most of the estuaries was similar to the Redfield ratio, with the exception of Port Stephens and Jervis Bay, which had lower concentrations of N relative to P. In November, the surface water layers of all the estuaries had low concentrations of N relative to P and relative to the Redfield ratio (Fig. 5b). Si was in stoichiometric excess over N and P, especially in the surface water layers of Forster and Laurieton. During the summer months, the surface water layers of Laurieton, Port Stephens, and Jervis Bay had a nutrient structure close to the Redfield ratio, whereas the surface water layers of Forster, Port Hacking, and Lake Illawarra had greater concentrations of Si relative to N and/or P (Fig. 5c,d).

Variability in the abundance of Noctiluca—Abundance of *Noctiluca* varied significantly among months, regions, and stations and between sites ($F_{96,575} = 13.26$, $p < 0.001$, ANOVA). The greatest source of variability found in this data set was attributed to the month of sampling, which accounted for 47% of the variability as deduced from the sums of squares generated by the ANOVA (SS for month = 301.14, total SS = 647.89, $F_{3,575} = 410.37$, $p < 0.001$, ANOVA). Generally, abundance of *Noctiluca* was relatively high in November and February irrespective of the region and station sampled (Fig. 6; $p < 0.01$, SNK), while lowest abundance was observed in September (Fig. 6; $p < 0.01$, SNK).

The variability in the abundance of *Noctiluca* among stations was dependent on the region sampled as well as the month sampled ($F_{45,575} = 7.42$, $p < 0.001$, ANOVA). However, for most of the regions and for the majority of the time, a gradient from high abundance of *Noctiluca* at the oceanic station to low abundance at the estuarine station was observed (Fig. 6). This cross-shore trend was of particular interest since the variability in the abundance of *Noctiluca* among the stations of a particular region ($F_{3,575} = 14.12$, $p < 0.001$, ANOVA) was greater than that observed among regions ($F_{5,575} = 2.53$, $p = 0.034$, ANOVA). Additionally, unlike this cross-shore trend, there were no distinct longshore trends in abundance of *Noctiluca* between Laurieton and Jervis Bay within any given month. Abundance of *Noctiluca* was also not persistently high or low within any given region over time (Fig. 6).

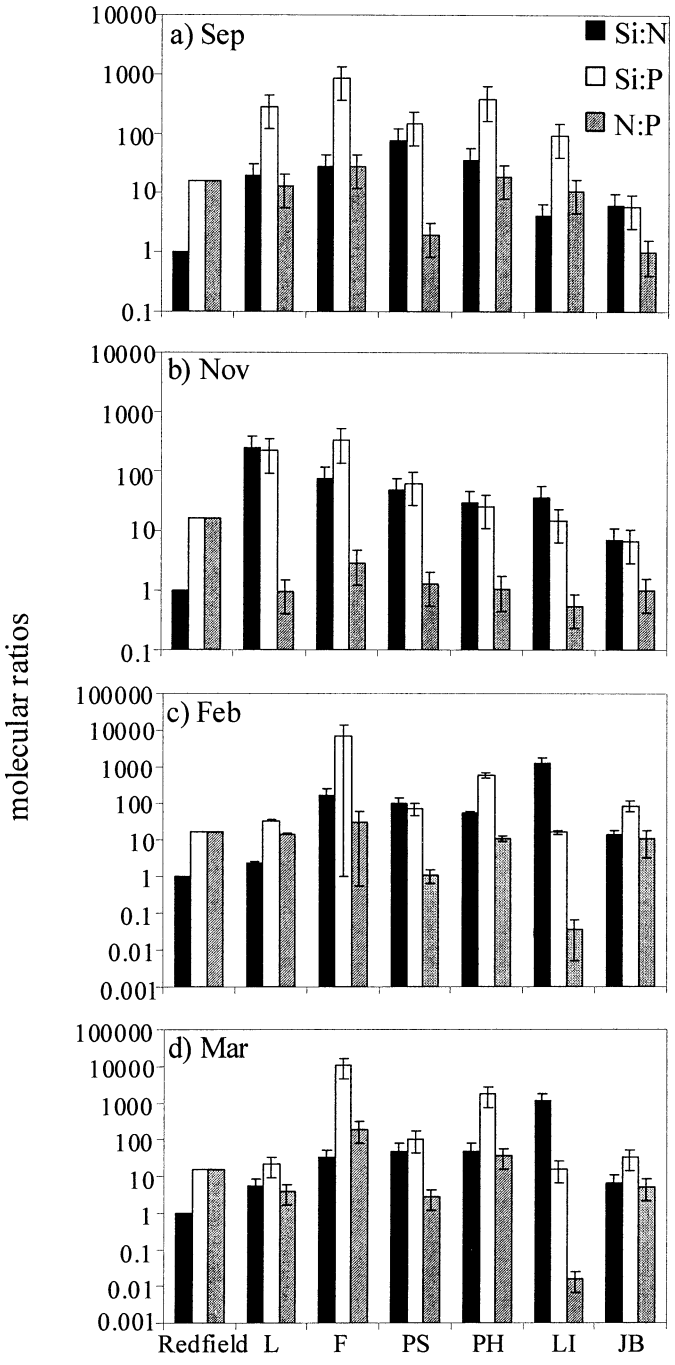


Fig. 5. Molecular ratios of silicon : nitrogen (Si : N), silicon : phosphorus (Si : P), and nitrogen : phosphorus (N : P) determined from the nutrient data collected at the estuarine stations in each region (L, Laurieton; F, Forster; PS, Port Stephens; PH, Port Hacking; LI, Lake Illawarra; JB, Jervis Bay) during (a) September, (b) November, (c) February, and (d) March. The molecular ratios were compared to the Redfield ratio (silicon : nitrogen : phosphorus = 16 : 16 : 1). Each value represents the means (±SE) of molecular ratios calculated from samples collected at the two estuarine stations ($n = 8$).

Condition of Noctiluca *populations as determined from cell diameters*—Similar to the abundance data, cell diameters were highly variable between months, among regions and stations, and between sites ($F_{48,287} = 3.41$, $p < 0.001$, ANOVA), but there were also discernible cross-shore trends in cell diameter (Fig. 7). Cells sampled from the estuarine stations had relatively smaller cell diameters (<525 μm) than those sampled from the oceanic and coastal stations (Fig. 7; $p < 0.01$, SNK). The small cells, with diameters less than 525 μm, were considered in this study to be capable of population growth (*see also* Uhlig and Sahling 1990; Buskey 1995). Those with diameters greater than or equal to 525 μm were considered to be close to the end of population growth. This cutoff size was based on the modal cell-size class determined from the total number of cells measured in the study (Fig. 8). This size was close to the smallest cell diameter of red tides cells (600 μm) previously measured in these regions (Dela-Cruz et al. 2002). Based on this cutoff size, our results generally suggest that oceanic populations of *Noctiluca* were close to the end of population growth, whereas estuarine populations were capable of population growth. Samples collected at the coastal stations were comprised of a mix of small and large diameter *Noctiluca* cells (Fig. 7).

A PCA of the size frequency distribution of the *Noctiluca* cells within the estuaries indicated that the Lake Illawarra samples consistently had the highest proportion of small-sized cells (Fig. 9). In November, groupings were not well defined, but a gradient from small to large cells was evident (Fig. 9a, Table 3). Greater than 90% of the total number of cells sampled at Sta. E2 in Lake Illawarra were <525 μm, but only 1 km upstream at Sta. E1 this proportion decreased to 10%. In February, there were three distinct groups consisting of sites with <5% of cells being smaller than 525 μm (Forster), sites with ~30% of cells being smaller than 525 μm (Laurieton), and sites with as high as 85% of cells being smaller than 525 μm. The Lake Illawarra estuarine sites had the highest proportion of small cells (Fig. 9c). Of all the environmental variables measured, ambient concentrations of Chl *a* and FRP were positively correlated with a high proportion of small cells in November (Chl *a*, $R = 0.59$, $p = 0.004$; FRP, $R = 0.74$, $p < 0.001$) and February (Chl *a*, $R = 0.54$, $p = 0.04$; FRP, $R = 0.59$, $p = 0.02$; Fig. 9a,c). The RDA indicated that 49% and 84% of the variability in the cell-size frequency distribution of the *Noctiluca* cells for the November and February sampling runs, respectively, was significantly explained by all the environmental variables measured during the study ($p = 0.005$). Of this variance, 54.1% and 55% was attributed to the concentration of Chl *a* in the surface water layers at the estuarine stations during the November and February sampling runs, respectively. Two main patterns were evident from the RDA biplots (Fig. 9b,d), the first being the separation of the small and large cells, and the second being the persistent correlation of the small cells with Chl *a* (among other variables), which contributed to a large proportion of the variation in the first axis as indicated by the length of the arrow on the biplot.

Size frequency histograms of cell diameters measured from *Noctiluca* cells collected at the oceanic and coastal stations (data pooled) were used to determine the proportion of

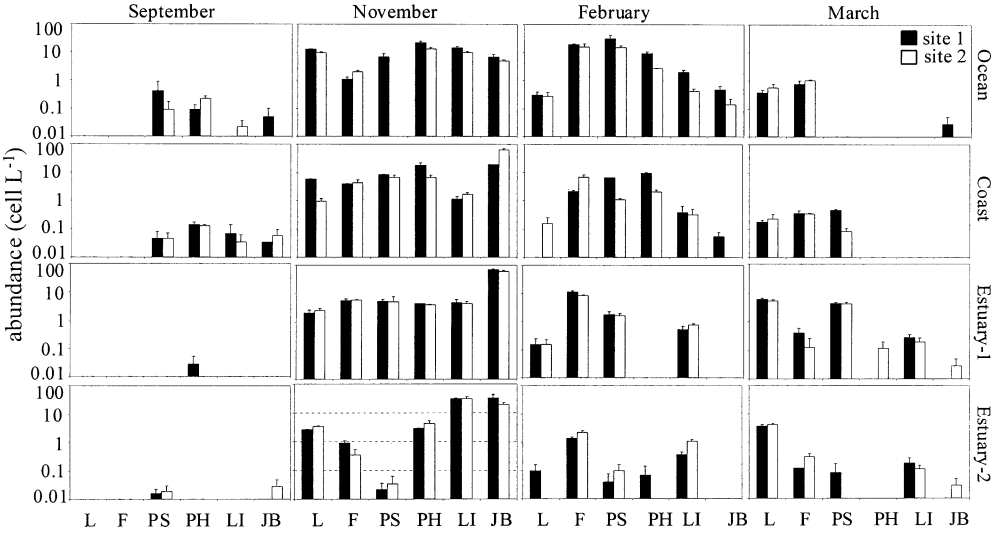


Fig. 6. Abundance of *Noctiluca* (cell L^{-1}) at the oceanic, coastal, and estuarine stations in each region (L, Laurieton; F, Forster; PS, Port Stephens; PH, Port Hacking; LI, Lake Illawarra; JB, Jervis Bay) during September 1998, November 1998, February 1999, and March 1999. Solid and open bars denote the abundance of *Noctiluca* at the two replicate sampling sites in each station. Each value represents the mean (±SE) abundance of *Noctiluca* determined from the three replicate plankton tows at each site.

cells capable of population growth along the NSW coast (Fig. 10). In November, the *Noctiluca* population at Laurieton was close to the end of population growth since greater than 90% of the cells had diameters >525 μm. In Forster, almost 70% of the *Noctiluca* population had cell diameters <525 μm. South of Forster, the proportion of small cells decreased progressively to the extent that almost 100% of the population was close to the end of population growth at Port Hacking (Fig. 10). South of Port Hacking, small cells were found in Lake Illawarra and Jervis Bay, but a relatively high proportion of the cells had diameters >525 μm.

The hydrographic structure of the oceanic and coastal waters in November provided a potential pathway or vector for the transport of *Noctiluca* cells from one region to another. The SST image in November indicated that while the core of the EAC diverged from the coast in an area just north of Forster, a large EAC meander drifted toward coastal regions at Forster and south of Forster as far as Port Hacking (Fig. 10). Southward of Port Hacking, the waters were mostly dominated by the Tasman Front. Long-shore surface current data acquired during the Franklin cruise conducted 4 d after the November sampling showed that the currents between Forster and Port Hacking traveled at speeds ranging between 0.2 to 1.6 m s^{-1}, with average speeds of 0.5 m s^{-1} (Fig. 10). A thermohaline plot constructed from the temperature and salinity data measured at the offshore stations (Stas. O and C) identifies three different water masses within the study regions (Fig. 11a). The dominant water mass (EAC), defined by temperature and salinity ranges of 18.5°C–19.5°C and 35.1–35.5, respectively, was detected in Laurieton, Forster, Port Stephens, and Port Hacking and was associated with the larger sized *Noctiluca* population (Figs. 10, 11). In Forster, where the greatest proportion of small cells was found, the surface water layers at offshore stations were characterized by relatively higher temperatures (>20°C), relatively lower salinities (<35), and relatively higher concentrations of $Si(OH)_4$ (>2.2–3.6 μmol L^{-1}), similar to the thermohaline signature of the estuarine stations. This thermohaline signature was also detected in the surface water layers at the coastal stations in Laurieton. The last water mass, the Tasman Front, was characterized by the lowest temperature (<18.5°C) and highest salinity (35.4–35.5) measured during this time and was found at Lake Illawarra and Jervis Bay.

In February, the *Noctiluca* populations off Laurieton, Forster, and Port Stephens were in a similar state, with the majority of cells having diameters >525 μm (Fig. 10). The *Noctiluca* population at Port Hacking was bimodally distributed, showing a distinct group of small-sized cells (<525 μm) and a group of larger cells (>525 μm). Downstream, at Lake Illawarra and Jervis Bay, the majority of cells sampled had diameters >525 μm. The ordination generated from a PCA of this data revealed that the greatest proportion of small-sized cells was found in samples collected at the coastal station near the sewage outfall at Port Hacking (Fig. 12a, Table 3). Similar to the estuarine data, the small cell diameters were positively correlated with ambient concentrations of Chl *a* in the surface water layers ($R = 0.76$, $p < 0.001$; Fig. 12a). The RDA indicated that 64% of the variability in the cell-size frequency distribution of the *Noctiluca* cells was significantly explained by all the environmental variables measured during the study ($p = 0.005$). Of this variance, 53.2% was attributed to the concentration of Chl *a* in the surface water layers at the coastal and ocean stations. The RDA biplot showed a separation of the small and large cells. The small cells were again positively correlated with Chl *a*, which contributed to most of the variation in the first axis, as indicated by the length of the arrow on the biplot (Fig. 12b).

During this February sampling run, the SST images in-

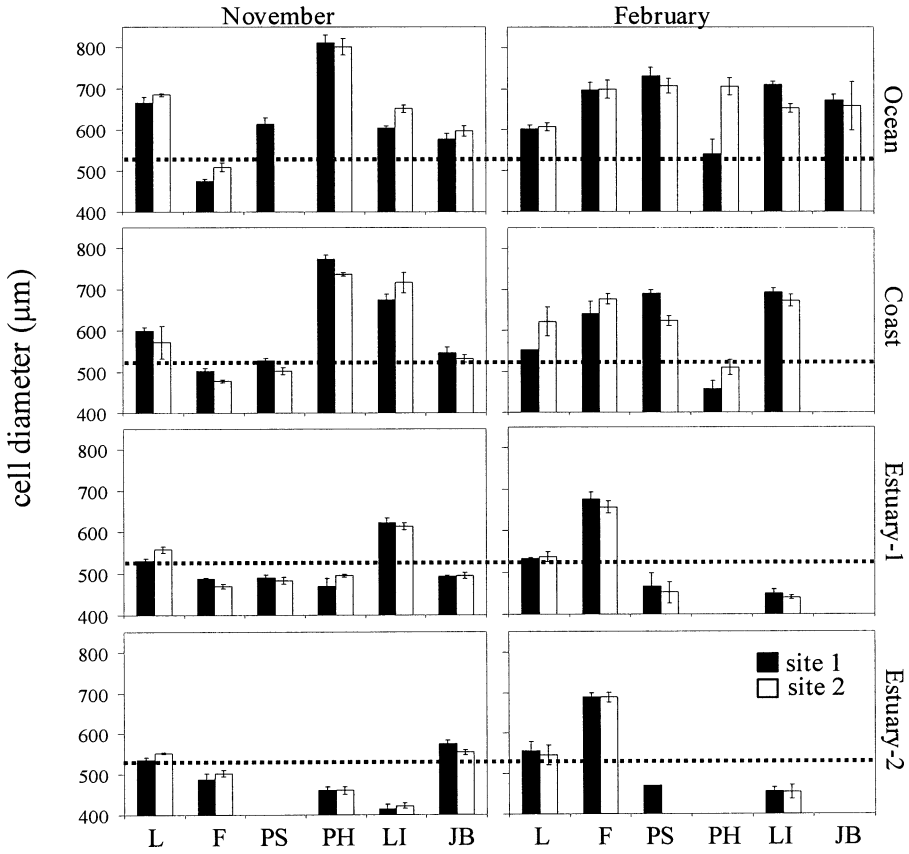


Fig. 7. Cell diameter of *Noctiluca* (μm) at the oceanic, coastal, and estuarine stations in each region (L, Laurieton; F, Forster; PS, Port Stephens; PH, Port Hacking; LI, Lake Illawarra; JB, Jervis Bay) during November 1998 and February 1999. Dotted lines mark the modal cell-size class (525 μm) determined from the total number of cells measured in this study (*see Fig. 8*). Solid and open bars denote the cell diameter of *Noctiluca* at the two replicate sampling sites in each station. Each value represents the mean ($\pm$SE) cell diameter of *Noctiluca* determined from the three replicate plankton tows at each site.

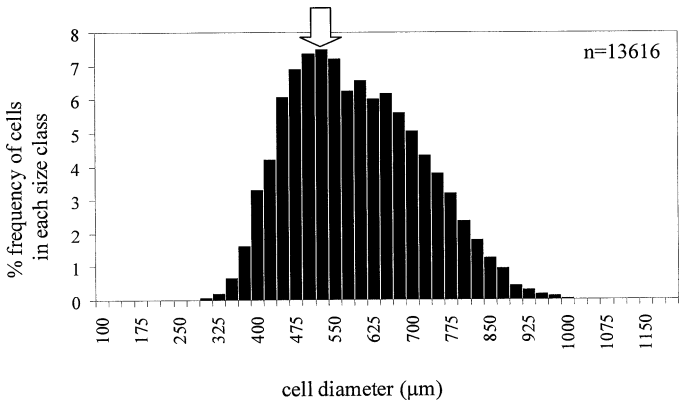
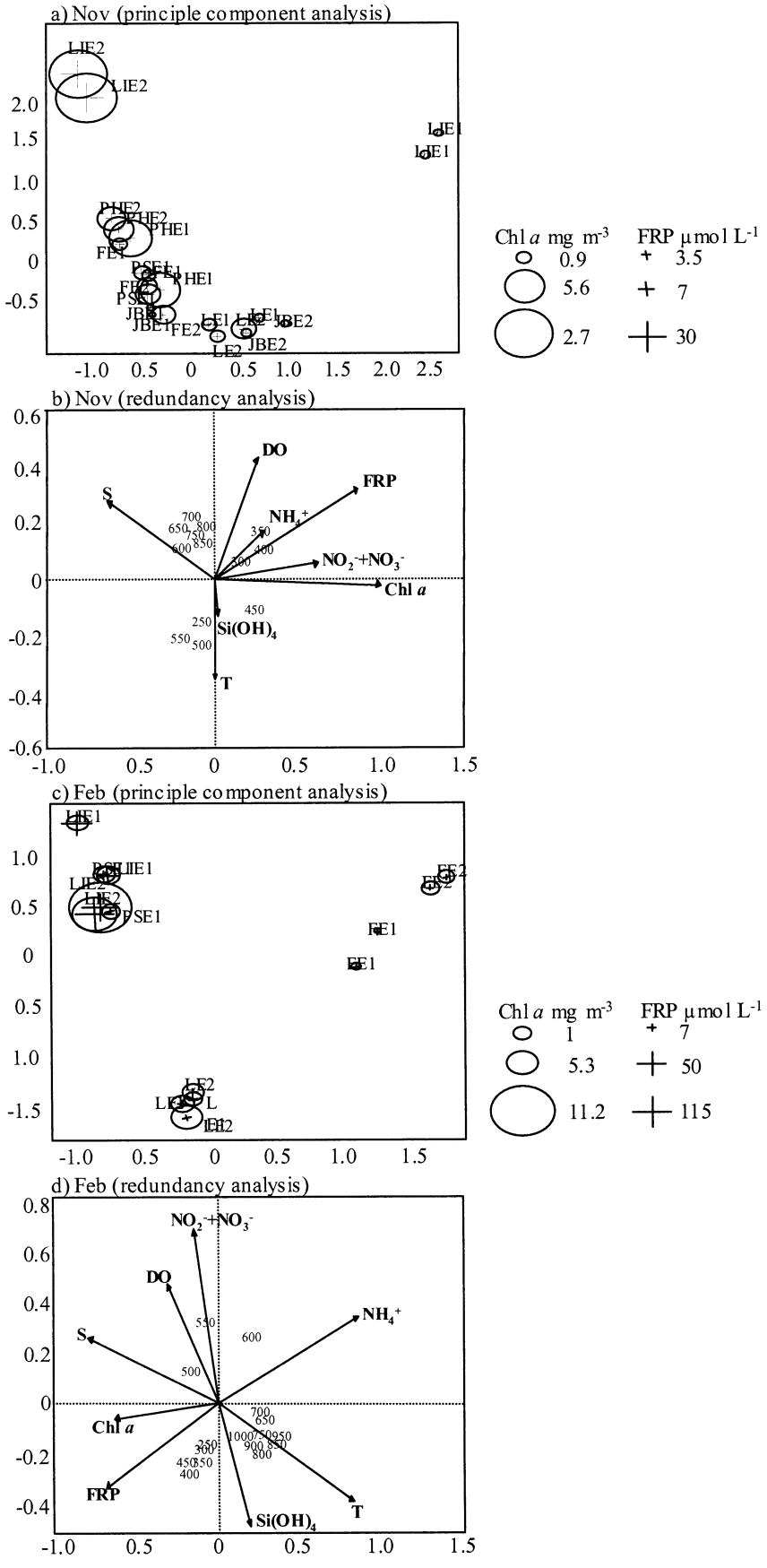


Fig. 8. Frequency distribution of cell diameters measured from the *Noctiluca* cells collected in samples in November 1998 and February 1999 (n = 13,616). Cell diameters were categorized into 25-μm size class intervals, ranging from 100 to 1,200 μm. The arrow indicates the modal cell size (525 μm) of the total number of cells measured in this study.

dicated that the EAC flowed close to the coastline of regions south of Laurieton until just north of Lake Illawarra, where the Tasman Front intruded (Fig. 10). Surface currents at the ORS just north of Port Hacking were flowing southward at an average speed of 0.5 m s^{-1} (Fig. 10). The thermohaline plot showed that the coastal and oceanic waters in most of the regions had similar temperature and salinity properties (Fig. 11b). However, the more southern sampling regions had slightly cooler water temperatures, while the surface water layers at Forster had slightly higher temperature and lower salinity, again similar to the thermohaline signature of the estuarine stations (Figs. 10, 11). The salinity–ammonium and salinity–Chl *a* property plots showed that the concentration of ammonium in the surface water layers of the sewage outfall site at Port Hacking was within the range observed in the other sites and regions, whereas concentrations of Chl *a* in the surface water layers at the sewage outfall site were up to four times greater (Fig. 11).

Discussion

Identifying regions of population growth of Noctiluca—Hydrographic processes along the NSW coast influence the


a) Nov (principle component analysis)
b) Nov (redundancy analysis)
c) Feb (principle component analysis)
d) Feb (redundancy analysis)
Chl a mg m-3
FRP µmol L-1
0.9
3.5
5.6
7
2.7
30
1
7
5.3
50
11.2
115
DO
FRP
S
NH4+
NO2-+NO3-
Chl a
Si(OH)4
T

spatial distribution patterns of *Noctiluca*. The main hydrographic feature along the NSW coast is the EAC, which may cause localized and/or mesoscale upwelling of nutrient-enriched slope water along various regions of the coast (e.g., Laurieton, Forster, and Port Stephens, Fig. 4; Rochford 1975; Tranter et al. 1986; Oke and Middleton 2001). These upwelling events trigger blooms of phytoplankton (Hallegraeff and Jeffrey 1993), which have been shown to be the principal diet of *Noctiluca* off the Sydney coast (Dela-Cruz et al. 2002). The present study also shows that the EAC may transport *Noctiluca* cells over hundreds of kilometers, meaning that the spatial variability in the abundance of *Noctiluca* must also be partly attributed to advective processes rather than to local growth alone. Consequently, the historical time–space dispersion patterns of *Noctiluca* must be determined before the underlying nutrient source(s) for the phytoplankton prey of *Noctiluca* can be identified.

Remote sensing has been effectively used to trace the origins of dispersed red tide algae and subsequently identify the mechanisms controlling bloom dynamics (Anderson 1995; Tester and Steidinger 1997). The present study also used remotely sensed sea surface temperatures and static point measures of water mass characteristics to distinguish whether the *Noctiluca* cells were advected (Fig. 10). These measures were related with the cell-size distributions of *Noctiluca*, not only to trace the path of the advected cells, but also to identify the region of population growth. The cell-size approach is based on results from the culturing studies of Buskey (1995), which show that *Noctiluca* cells that are rapidly dividing (i.e., reproducing) are small as a result of sufficient prey supply. Culturing studies using local *Noctiluca* populations in various geographic regions such as the German Bight (Hanslik 1987), west coast of Sweden (Kiorboe and Titelman 1998), and the South China Sea (Qi and Li 1994) show similar results to those of Buskey (1995). The small well-conditioned populations are known to differ from senescent red tide cells, which are starved, have ceased dividing, and become buoyant and large (Uhlig and Sahling 1990). When applied to field data, these culturing results imply that small *Noctiluca* cells will be found in regions where growth is stimulated, that is, closer to the nutrient source that stimulates growth of their phytoplankton prey. Accordingly, larger cells will be found further away from the region of growth and hence further away from the underlying nutrient source. The results in the present study imply that *Noctiluca* populations along the NSW coast are usually those that have been advected away from the region where growth is stimulated, since most of the cells sampled in the study were large (Figs. 6, 7).

During the November sampling run, the greatest proportion of small-sized *Noctiluca* cells was found at Forster. South of Forster, the results showed increasing abundance and cell size of the *Noctiluca* population, corresponding with the changing temperature and salinity properties of the EAC as it traveled southward to Port Hacking (Figs. 10, 11). The SST image taken on 7 November 1998 showed a consistent current of warmer waters traveling parallel to the coast between Forster and Port Hacking. Long-shore surface current data showed that the currents between Forster and Port Hacking traveled at an average speed of 0.5 m s^{-1} (Fig. 10). At these speeds, a cell originating in Forster would travel ~40 km d^{-1} and therefore take approximately 6 d to reach Port Hacking. With a doubling of abundance once every 2 d, which is the average to optimum growth rate for *Noctiluca* populations (Elbrachter and Qi 1998), the abundance of *Noctiluca* could increase eightfold during a 6-d transit (assuming no losses due to mortality). These estimates are consistent with the sampling data obtained during the November sampling run where we observed average abundances of *Noctiluca* of 2.8 cells L^{-1} at Forster and 14.8 cells L^{-1} at Port Hacking, equivalent to a fivefold increase in abundance (Fig. 6). Thus the average longshore current speeds indicated a transit time that was consistent with the observed increase in abundance of *Noctiluca* as the population traveled southward. The southward advection of *Noctiluca* cells introduces the possibility that some of the *Noctiluca* populations observed off Sydney's coastal waters are a downstream consequence of nutrient-enrichment processes further north. Certainly, the earlier studies of Hallegraeff and Reid (1986) show that some phytoplankton species that originate in the Coral Sea are frequently transported southward with the EAC. Recent modeling studies based on long-term data also indicate that the EAC ordinarily flows southward and parallel to the coast during the austral spring and summer at speeds varying between 0.3 and 0.6 m s^{-1} (Marchesiello and Middleton 2000; Oke and Middleton 2001).

Identifying the nutrient sources for the phytoplankton prey of Noctiluca—The results in this study show a strong correlation between the cell size of *Noctiluca* and the concentration of Chl *a* in surface water layers (Figs. 9, 13). Specifically, the RDA indicates that the concentration of Chl *a* in the surface water layers accounts for at least 50% of the total variability observed in the cell-size frequency distri-

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Fig. 9. Ordination plots constructed from a PCA or RDA of *Noctiluca* cell-size frequency distributions determined from samples collected at the estuarine stations (E1, E2) in each region (L, Laurieton; F, Forster; PS, Port Stephens; PH, Port Hacking; LI, Lake Illawarra; JB, Jervis Bay) during the (a, b) November, and (c, d) February sampling runs. The cell sizes were categorized into 25-μm size classes ranging between 100 and 1,200 μm. The first two axes generated in the PCA or RDA are shown since they account for >60% of total variance. There were no *Noctiluca* cells present in the estuarine stations at Jervis Bay and Port Hacking in February. Filterable reactive phosphorus (crosses; FRP μmol L^{-1}) and chlorophyll *a* (open circles; Chl *a* mg m^{-3}) concentrations in the surface water layers at the estuarine stations are superposed on the PCA ordinations to show the relationships between these environmental variables and the proportion of small *Noctiluca* cells. The length of the arrows on the RDA ordinations is indicative of the amount of variance in the cell-size frequency distributions that can be explained by a specific environmental variable. For clarity, every alternate cell size is shown on the RDA plots.

Table 3. Component loadings for the first two principal component factors generated from a PCA of the cell size frequency distribution data acquired from samples collected in the surface water layers of the estuarine or coastal and oceanic stations at Laurieton, Forster, Port Stephens, Port Hacking, Lake Illawarra, and Jervis Bay during November 1998 and February 1999.

	Nov 98, estuary		Feb 99, estuary		Feb 99, ocean/coast	
Size class	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
250	−0.06	−0.11	−0.29	0.38	−0.45	0.15
275	−0.18	0.12	−0.22	0.13	nd	nd
300	−0.34	0.38	−0.36	0.40	−0.18	−0.36
325	−0.48	0.63	−0.56	0.56	−0.25	0.10
350	−0.35	0.73	−0.52	0.59	−0.73	0.65
375	−0.48	0.78	−0.72	0.53	−0.55	0.55
400	−0.63	0.72	−0.75	0.62	−0.71	0.67
425	−0.70	0.62	−0.75	0.60	−0.75	0.64
450	−0.84	0.31	−0.84	0.46	−0.73	0.62
475	−0.76	−0.06	−0.87	0.06	−0.86	0.38
500	−0.65	−0.61	−0.72	−0.37	−0.81	−0.05
525	−0.25	−0.88	−0.41	−0.83	−0.69	−0.60
550	0.25	−0.86	−0.21	−0.86	−0.58	−0.64
575	0.64	−0.63	−0.02	−0.87	−0.60	−0.66
600	0.87	−0.25	0.54	−0.62	−0.37	−0.81
625	0.89	−0.21	0.74	−0.59	−0.17	−0.86
650	0.90	0.04	0.98	0.05	0.40	−0.71
675	0.93	0.07	0.84	0.02	0.43	−0.60
700	0.92	0.25	0.87	0.02	0.88	−0.19
725	0.87	0.35	0.95	0.21	0.86	−0.01
750	0.84	0.38	0.92	0.26	0.91	0.13
775	0.80	0.45	0.94	0.27	0.82	0.18
800	0.81	0.48	0.93	0.26	0.82	0.25
825	0.71	0.40	0.96	0.29	0.81	0.43
850	0.58	0.36	0.95	0.28	0.77	0.30
875	0.82	0.47	0.74	0.33	0.78	0.22
900	nd*	nd	0.73	0.30	0.54	0.24
925	nd	nd	0.81	0.24	0.58	0.20
950	nd	nd	0.73	0.30	0.34	0.26
975	nd	nd	nd	nd	0.24	−0.04
1000	nd	nd	0.51	0.22	0.29	0.14
Percentage of total variance	45.2	23.6	52.6	19.9	39.6	20.7

* nd, no data.

bution data. This correlation is important since it was consistent through time and space, unlike the correlations between abundance and Chl *a,* and thus may perhaps be used universally to identify the underlying nutrient sources for the phytoplankton prey of *Noctiluca.* Further culturing and field research is needed in other comparative ecosystems to test whether this relationship is indeed robust. Apart from cell size, other cell condition indices of *Noctiluca,* such as reproductive and nutritional status, may perhaps be used effectively to trace the origins of the cells, since these condition indices are the main determinants for cell size. However, obtaining absolute counts of reproductive cells or cells that contain food particles is difficult since *Noctiluca* feeds and reproduces during the evening (Uhlig and Sahling 1982).

The correlation between cell size and Chl *a* was used in this study to show that population growth of *Noctiluca* may be stimulated by phytoplankton grown on sewage discharge. The concentration of Chl *a* in surface waters was relatively high in the area adjacent to the shoreline outfall at Port Hacking during the February sampling run (Fig. 12). Ocean color images of sea surface Chl *a* did not reveal longshore transport of phytoplankton from the north (image not shown), indicating that the high biomass of phytoplankton observed at the coastal station was due to in situ growth. The cell-size data also showed that the *Noctiluca* population at this station was not advected from the north. In fact, the data showed that the proportion of small *Noctiluca* cells observed at the shoreline sewage outfall site was large enough to numerically dominate the *Noctiluca* population(s) at the oceanic sites. Unlike others who have conducted studies in this region (Pritchard et al. 1996, 2000), we were unable to identify a sewage signature from our measurements of nutrient concentrations. While sewage has relatively high concentrations of ammonium (Pritchard et al. 2000), *Noctiluca* may also influence ambient ammonium concentrations (Montani et al. 1998), therefore making it difficult to infer a sewage signature from the ammonium concentrations alone. The other environmental data indicate that the physical and chemical properties of the water column at Port Hacking during the February sampling were not indicative of any other nutrient source arising from either land runoff after recent rains, upwelling events, or from the Port Hack-

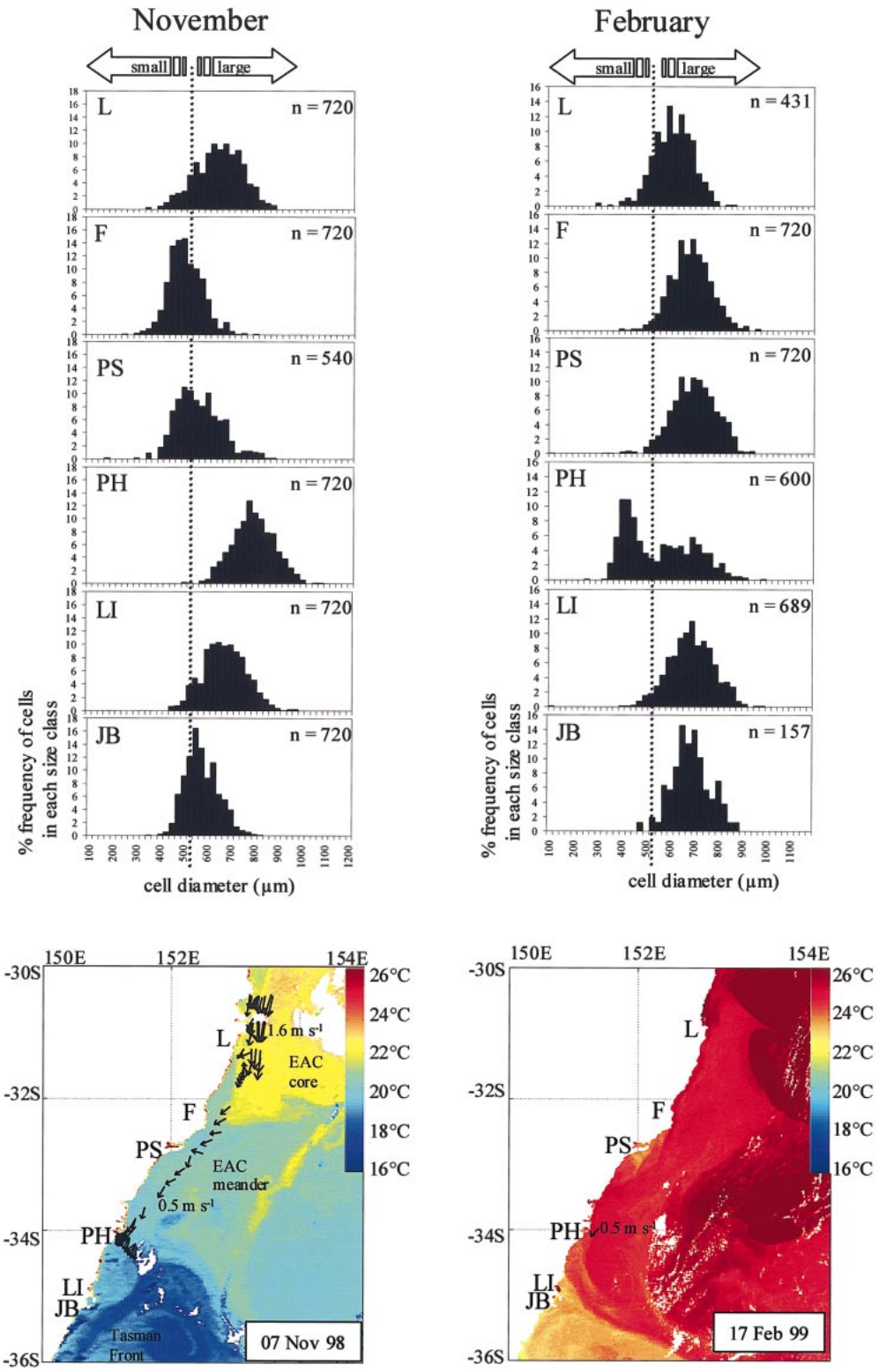

Fig. 10. Frequency histograms generated from the cell diameter measurements of *Noctiluca* cells sampled at the oceanic and coastal stations (data pooled) in Laurieton (L), Forster (F), Port Stephens (PS), Port Hacking (PH), Lake Illawarra (LI), and Jervis Bay (JB) during November and February. Dotted lines mark the modal cell-size class (525 μm) determined from the total number of cells measured in this study (*see Fig. 8*). Sea surface temperature images below the histograms show the nature of the East Australian Current (EAC) at the time of sampling. The black arrows on the SST images denote the ambient speed and direction of surface currents determined from acoustic Doppler current profiles (November) or current meters at Sydney's ocean reference station (February).

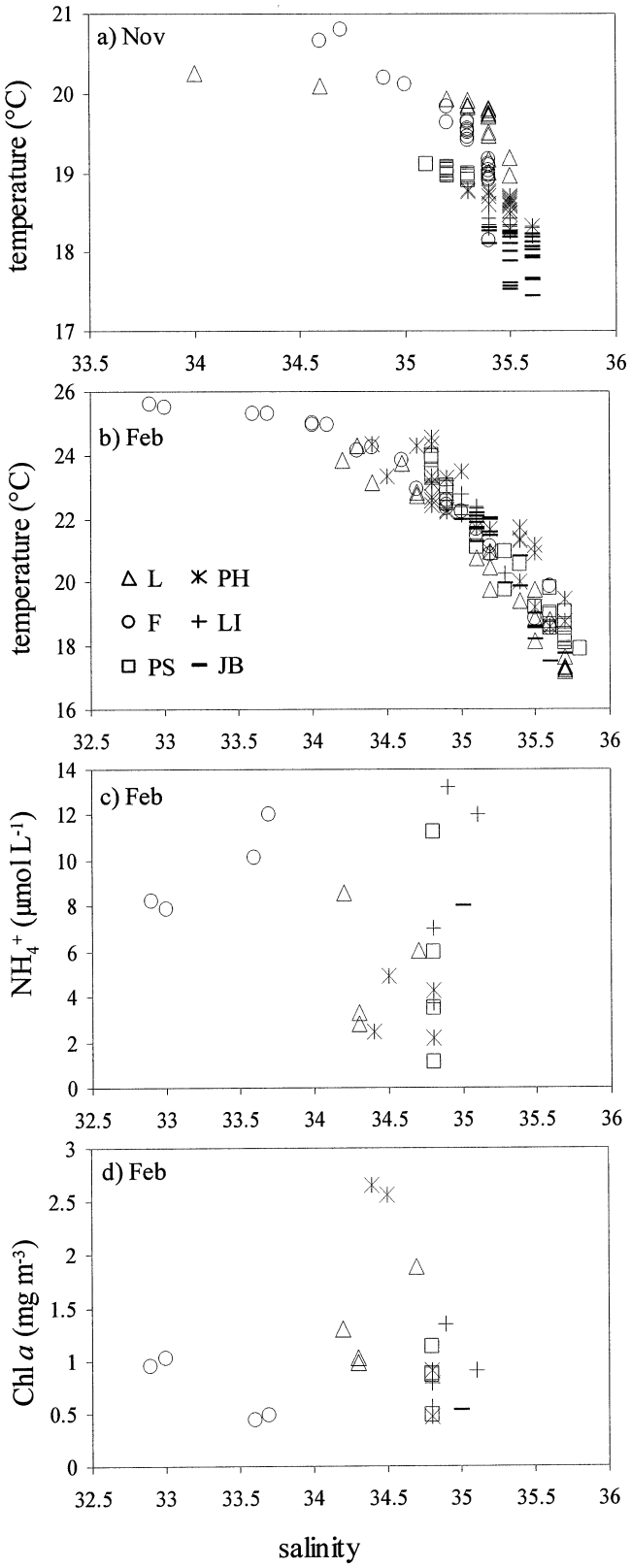

Fig. 11. Property–property plots of (a) temperature (°C) and salinity in November, (b) temperature (°C) and salinity in February, (c) ammonium (NH_4^+ μmol L^{-1}) and salinity in February, and (d) chlorophyll *a* and salinity in February. Temperature and salinity plots are generated from data collected at 5-m depth intervals at the oceanic and coastal stations in each region during November and February. Ammonium/chlorophyll *a* and salinity plots are generated from data collected in the surface water layers at the oceanic and coastal stations in each region during February.

ing estuary (Fig. 11). Therefore it would appear that the sewage discharge from the shoreline outfall at Port Hacking stimulated growth of phytoplankton, which in turn stimulated growth of *Noctiluca.*

In general, it is suggested that sewage influences on the population growth of *Noctiluca* at Port Hacking would only be sporadic, since the sewage effects were not observed during the other sampling runs in this study. It is possible that a recirculation cell accentuated the sewage effects during the February sampling run. The recirculation cell occasionally forms in the lee of the peninsula and can persist over periods (~5 d; Anderson and Gordon 1993) long enough to stimulate growth of the phytoplankton prey of *Noctiluca.* It is also significant to note that the behavior of the sewage plume from the shoreline outfall at Port Hacking differs from the behavior of the sewage plumes from the three deep-water ocean outfalls. Sewage is discharged into surface waters at the shoreline outfall, whereas the sewage from the three deep-water ocean outfalls is discharged near the sea floor (~60-m depth) and is therefore trapped below the thermocline during the austral spring and summer. Numerical model simulations of the sewage plumes from the deep-water outfalls show that the maximum likelihood of sewage impacts in surface waters only occurs during the unstratified conditions of the late austral winter (Pritchard et al. 1996). During these winter months, the biomass of the phytoplankton prey of *Noctiluca* is typically low due to cooler water temperatures and lower light levels (Ajani et al. 2001*b*). Thus, owing to the present hydrological conditions, it appears that the sewage discharges from the three deep-water ocean outfalls rarely influence the biomass of phytoplankton and consequently the abundance of *Noctiluca* off the Sydney coast. It would be of particular interest to continue investigations on the effects of anthropogenic nutrient discharges on the plankton community off Sydney, given that nutrient discharges and hydrological cycles are likely to be variable over time.

The results in this study show that nutrient sources within estuaries may be important for phytoplankton growth and consequently *Noctiluca* growth along the NSW coast. The small *Noctiluca* cells found off Forster during the November sampling run were constrained within a distinct estuarine water mass at the offshore stations (Figs. 10, 11), thus suggesting that the *Noctiluca* population sampled at these offshore stations originated from the estuary. While *Noctiluca* populations were persistently less abundant within the estuaries, these populations were in better condition (smaller cells) than neighboring offshore populations, with only a few notable exceptions (e.g., populations within the Forster estuary during the February sampling run). Estuarine and oceanic waters have distinct hydrographic properties (Fig. 3), which indicates that conditions supporting growth of estuarine and oceanic *Noctiluca* populations differ. Estuarine wa-

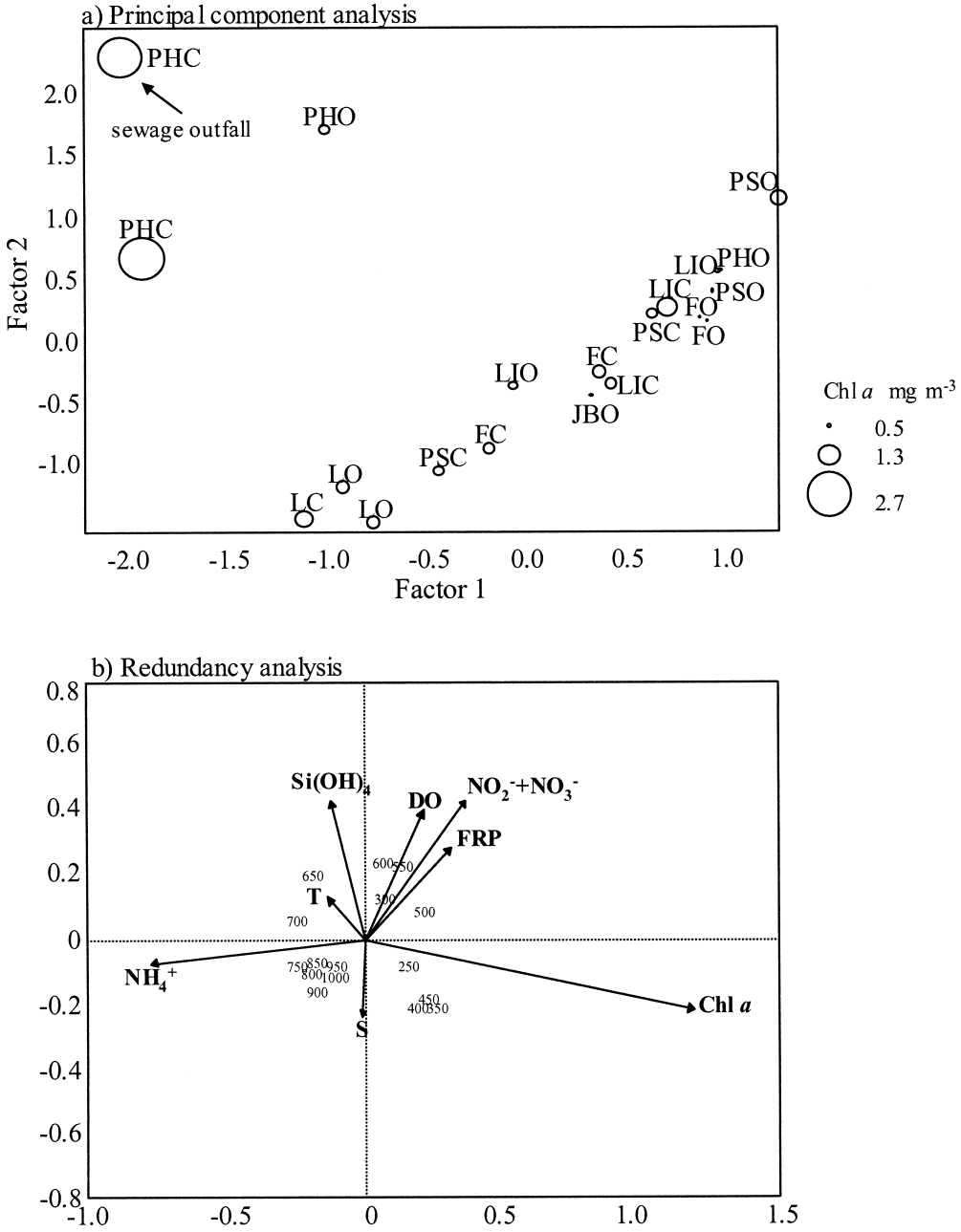

Fig. 12. Ordination plots constructed from a PCA or RDA of *Noctiluca* cell-size frequency distributions determined from samples collected at the oceanic (O) and coastal (C) stations in each region (L, Laurieton; F, Forster; PS, Port Stephens; PH, Port Hacking; LI, Lake Illawarra; JB, Jervis Bay) during February. The cell sizes were categorized into 25-μm size classes ranging between 100 and 1,200 μm. The first two axes generated in the PCA or RDA are shown since they account for >60% of total variance. Chlorophyll *a* (open circles; Chl *a* mg m^{-3}) concentrations in the surface water layers at the oceanic and coastal stations are superposed on the PCA ordination to show the relationship between chlorophyll *a* concentrations in surface waters and the proportion of small *Noctiluca* cells. The length of the arrows on the RDA ordination is indicative of the amount of variance in the cell-size frequency distributions that can be explained by a specific environmental variable. For clarity, every alternate cell size is shown on the RDA plot.

terways along the NSW coast are likely to support a higher standing stock of phytoplankton than offshore waters. In particular, estuaries that support a high proportion of small *Noctiluca* cells, such as Lake Illawarra (Fig. 9), have relatively high concentrations of phosphorus to presumably support a higher standing stock of phytoplankton (Labry et al. 2002). Consequently, these estuaries may support a stable but low standing stock of *Noctiluca* when primary productivity is

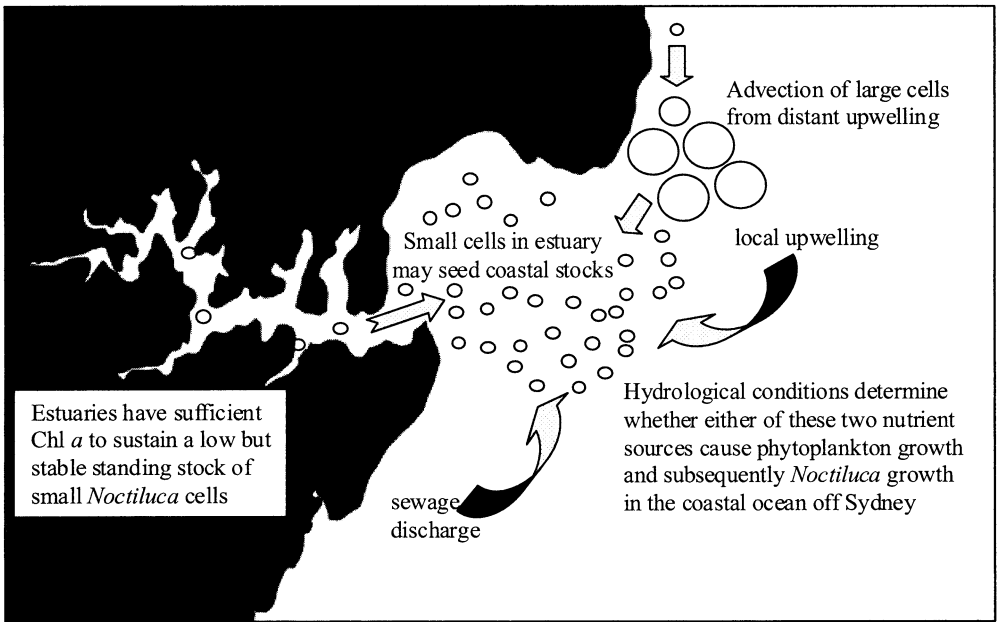

Fig. 13. A conceptual model of the nutrient sources and processes that may stimulate population growth of *Noctiluca* along the New South Wales coast during the austral spring and summer. The model is based on the relationship between cell size and ambient chlorophyll *a* concentrations, which may be used to trace the path of a dispersed *Noctiluca* population (open circles) and identify the underlying nutrient source(s) that stimulate growth of the phytoplankton prey of *Noctiluca.* This model suggests that chlorophyll *a* concentrations within estuaries are able to sustain low but stable standing stocks of *Noctiluca.* The estuarine stocks may seed coastal and oceanic stocks that become depleted during periods of low prey availability. The availability of nutrients that promote growth of the phytoplankton prey of *Noctiluca* in oceanic and coastal waters is episodic, being dependent on the timing and magnitude of coastal upwellings or the hydrological conditions that allow the sewage plume to penetrate above the thermocline.

low in the coastal ocean. As indicated in this study, these estuarine populations may eventually seed coastal and oceanic populations (Fig. 10). Certainly, tidal exchange in the estuaries near Sydney is sufficient to facilitate the transfer of materials to and from the estuaries (Relevante and Gilmartin 1978; Kingsford and Suthers 1996; Middleton 1997).

While conditions within the estuaries are generally conducive for survival of low and stable standing stocks of *Noctiluca,* episodic upwelling events along the NSW coast deliver relatively high amounts of nutrients ($NO_2^- + NO_3^-$, 18.4 μmol L^{-1}), which trigger diatom blooms (Hallegraeff and Jeffrey 1993; Ajani et al. 2001*b;* Dela-Cruz et al. 2002) and subsequently *Noctiluca* blooms (Dela-Cruz et al. 2002). Previous studies imply that *Noctiluca* requires a relatively high amount of its phytoplankton prey to support optimal growth (Lee and Hirayama 1992; Kiorboe and Titelman 1998). The rich supply of nutrients brought in by the upwelling events increases the concentrations of dissolved inorganic nitrogen in the water column to concentrations well above the ambient levels and exceeds the amount of dissolved inorganic nitrogen delivered by sewage discharges (Pritchard et al. 2000). In contrast, while the estuaries sampled in the present study contain sufficient or in some cases excess amounts of phosphorus and silicate, the estuaries appear to be nitrogen limited (Fig. 5). This nutrient imbalance may be the cause for limited phytoplankton growth (to bloom proportions), and hence *Noctiluca* growth, within estuaries. The trend toward increasing eutrophication of coastal estuaries may promote higher standing stocks of phytoplankton in the future and consequently higher standing stocks of *Noctiluca* in the estuaries. Further studies are also needed to investigate the effects of low salinity, predation, or competition between zooplankton on growth of *Noctiluca* within the estuaries (Elbrachter and Qi 1998).

Based on the findings of this study, a conceptual model has been constructed of the process driving population growth of *Noctiluca* along the NSW coast during the austral spring and summer (Fig. 13). This model is based on the concept that *Noctiluca* requires a sufficient supply of phytoplankton prey for optimal growth. Estuarine waterways in NSW have a standing stock of phytoplankton that can sustain low and stable stocks of *Noctiluca* cells. However, phytoplankton abundance, and hence *Noctiluca* abundance, may be limited in the estuaries due to low nitrogen loadings or imbalances compared to the amount and proportion of nutrients derived from oceanic processes and sewage discharge. These estuarine populations are nonetheless important, since they seed oceanic populations, which may become depleted during periods of low prey availability. The availability of nutrients that promote growth of the phytoplankton prey of *Noctiluca* in the oceanic and coastal environment is episodic, being dependent on the timing and magnitude of coastal upwellings or the hydrological conditions that allow the sewage plume to penetrate above the thermocline. The prevail-

ing conditions may also transport the *Noctiluca* cells over various temporal and spatial scales, and hence abundance patterns may not necessarily reflect the immediate conditions conducive to growth. By examining cell size rather than abundance distributions, the variance in the spatial abundance patterns of *Noctiluca* in a dynamic hydrological environment may be identified and interpreted.

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