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## Population ecology of *Noctiluca scintillans* Macartney, a red-tide-forming dinoflagellate

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**Abstract.** The population ecology of the large heterotrophic dinoflagellate *Noctiluca scintillans* Macartney was examined in the coastal ocean and two estuaries in south-eastern Australia from July 1996 to June 1997. High concentrations ( $>100$  cells  $L^{-1}$ ) occurred in spring and again in late summer, and low concentrations ( $<5$  cells  $L^{-1}$ ) in mid summer and mid winter. Abundances were greater in coastal waters than in the estuaries during all months in which concentration exceeded 1 cell  $L^{-1}$ . During the spring bloom, *Noctiluca* cells from coastal stations had small diameters (340–450  $\mu m$ ), a high nutritional status and a high proportion of division stages, indicative of good condition. During the late summer blooms, poor-condition cells were found in coastal waters and especially in the near-surface concentrations of red tides ( $>10^4$  cells  $L^{-1}$ ), and were characterized by large diameters (400–1200  $\mu m$ ), cell lysis and uniformly low nutritional status; at this time, *Noctiluca* cells from estuaries were generally fewer, smaller and in better condition. Overall, cell concentrations were higher in coastal waters than in the estuaries, and red tides of *Noctiluca* probably developed along the local coast (in spring) or were advected into the area from northern regions (in late summer).

*Extra keywords:* heterotrophic dinoflagellate, blooms, seasonality, cell condition

### Introduction

*Noctiluca scintillans* Macartney is an unarmoured heterotrophic dinoflagellate with a global distribution, encompassing temperate, tropical and polar waters. *Noctiluca* can be a conspicuous member of the plankton community, because it may numerically dominate the plankton (Lee and Hirayama 1992) and because it has unusual features such as its relatively large cell size, passive buoyancy and bioluminescence (Uhlir and Sahling 1990). Rapid reproduction and polyphagous feeding behaviours can allow it to increase quickly in abundance (Shanks and Walters 1996).

Conflicting theories have been proposed as to which environmental variables are the most important to *Noctiluca* growth. Rapid population growth has been recorded following phytoplankton blooms (Devassy and Sreekumaran and Nair 1987; Sreekumaran Nair *et al.* 1992; Painting *et al.* 1993; Hayward *et al.* 1995). An increase in *Noctiluca* abundance has also been linked to increasing eutrophication, possibly caused indirectly by an increase in prey abundance (Porumb 1992). These observations are consistent with growth experiments in which high food concentrations were necessary to promote population growth, suggesting that *Noctiluca* in nature may be limited by food availability (Lee and Hirayama 1992). In the German Bight, however, seasonal patterns of temperature and light were found to be critical in causing increased growth, and phytoplankton abundance was unrelated; in addition, salinity was found to be an important influence on the reproductive rate of a popu-

lation, with the summer build-up of *Noctiluca* populations originating in estuaries (Uhlir and Sahling 1995). Lower salinity, higher temperatures and day/night evenness have all been demonstrated to induce higher growth rates of *Noctiluca* in culture (Lee and Hirayama 1992; Uhlir and Sahling 1995).

In Australia, interest in *Noctiluca* has focused on the 'tomato soup'-coloured red tides that form when cells accumulate in dense, senescent patches (Hallegraeff 1981, 1991). *Noctiluca* was probably first reported in Sydney Harbour as early as 1860 (Dakin and Colefax 1940), and since then red tides of *Noctiluca* have been reported only sporadically. In recent years, *Noctiluca* red tides seem to have been occurring around Sydney in increasing frequency (Hallegraeff 1995), although this may be due to increased public awareness and reporting.

The aim of the present study was to obtain baseline data on the abundance of *Noctiluca* along an estuarine-to-oceanic gradient near Sydney, over a period of 12 months. Populations were compared by cell indices such as diameter, nutritional status and proportion of reproductive stages, which change according to conditions in culture (Uhlir and Sahling 1990). The senescent cells from red tides were used as a comparison to infer the relative condition of a population. We wished to determine whether abundance was greater within estuarine waters, as observed in European waters, and whether cell size and condition varied spatially and temporally leading up to a red tide. In the light of findings else-

where, we compared the monthly abundance of *Noctiluca* with environmental data collected at a standard oceanographic station off Sydney.

### Materials and methods

#### Study sites and sampling design

The coastal region is dominated by the warm, poleward East Australian Current (EAC) flowing at 1–2 knots near the 200 m isobath (Nilsson and Cresswell 1981). Around 32°S the main EAC stream departs the coast, heading eastward into the Tasman Sea, leaving a southward-moving eddy field over the shelf. Within 5 km of the coast, local winds and coastally trapped waves also influence or even reverse the southward flow, and together with the EAC may generate sporadic upwelling (Griffin and Middleton 1992; Gibbs *et al.* 1998).

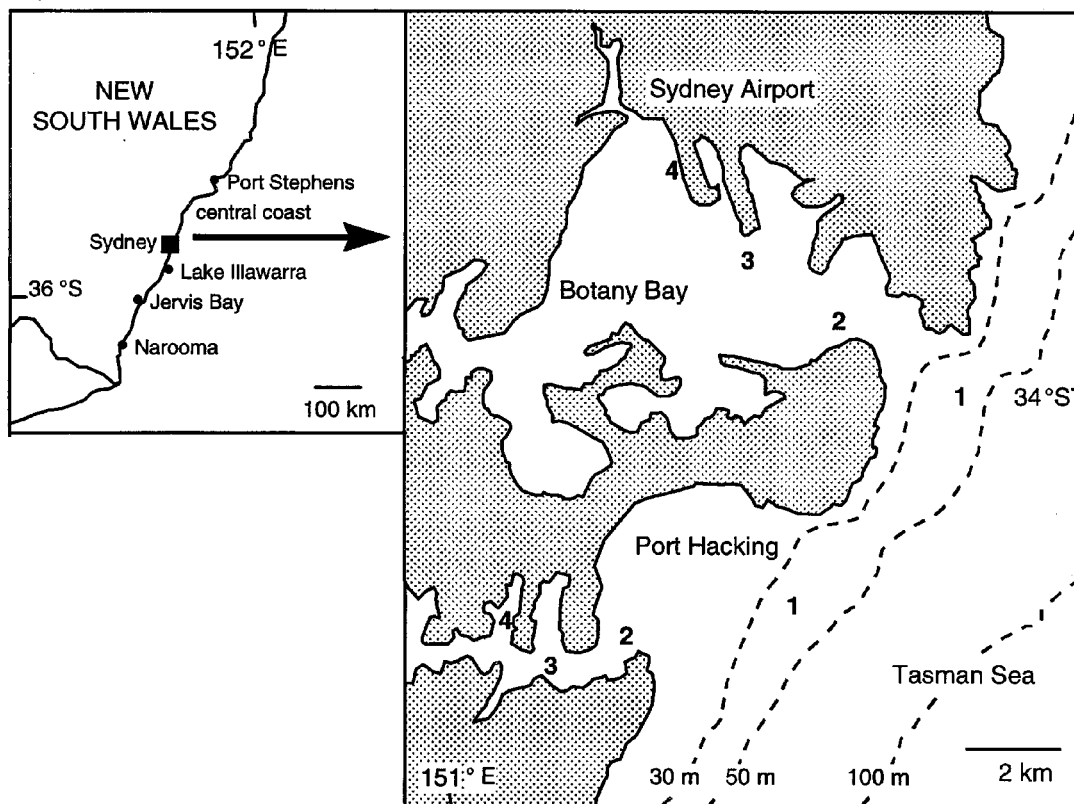
Botany Bay and Port Hacking are two estuaries within the Sydney basin in New South Wales, Australia (Fig. 1). Botany Bay is a large, relatively shallow estuary (area 49.1 km<sup>2</sup>, <8 m outside the shipping channel), surrounded by substantial industrial and residential developments, with a mean annual runoff of  $5.2 \times 10^8$  m<sup>3</sup> (West *et al.* 1985). Port Hacking is a smaller but deeper estuary (area 11.3 km<sup>2</sup>, <23 m depth), surrounded by national park and low-density housing, with a lower mean annual runoff of  $6.9 \times 10^7$  m<sup>3</sup> (West *et al.* 1985). Four stations were sampled in each estuary (Fig. 1); Station 1 (near the 40 m isobath, 2 km offshore), Station 2 (10 m isobath), Station 3 (5 m isobath) and Station 4 (5 m isobath and near a freshwater source).

Sampling was conducted once per month from July 1996 to June 1997. Day-to-day variability in the abundance of *Noctiluca* within the sampling month was assumed to be less than the trends among stations. This assumption was assessed by repeat sampling three days after the March sampling date, and found to be valid for that month (analysis of variance, ANOVA,  $MS(\text{Station}) = 2.75$ ,  $MS(\text{Day}) = 0.23$ ).

Samples were collected between 1000 and 1600 hours, independently of the tide, although Station 1 was well beyond the influence of estuarine plumes (Kingsford and Suthers 1996). A plankton net (20 cm diameter, 100 µm mesh) was towed at approximately 0.5 m s<sup>-1</sup> for 3 min, filtering approximately 2.8 m<sup>3</sup>. Two depth intervals were sampled: at the surface, and at 3–4 m depth. The net had no flowmeter, because of the small diameter of the net and concerns that the flowmeter would obstruct the passage of zooplankton into the net. Velocity, and subsequently flow, were determined by the engine's tachometer and the rate of drift of debris past the boat. Replicate tows were taken within 500 m of the first. Net samples were preserved in 2% formaldehyde in seawater.

#### Measures of physical variables and chlorophyll *a*

Salinity, temperature, turbidity, dissolved oxygen and pH were measured with a Yeo-Kal 611 meter at the surface and at depths of 3, 5 and 10 m. Samples for chlorophyll *a* analysis were taken at the Port Hacking offshore station (Fig. 1) at approximately two-weekly intervals by the NSW Environment Protection Authority. Samples were taken from the surface and 10 m depth in Niskin bottles, then filtered on return to the laboratory. Filter papers were frozen at -20°C until determination of chlorophyll by the



**Fig. 1.** (a) Map of the New South Wales coastline showing the locations of the red tides reported to the NSW Environment Protection Authority. (b) The four sampling stations in Botany Bay and Port Hacking: Station 1 near the 40 m isobath (~2 km offshore); Station 2 at the 10 m isobath (estuary entrance); Station 3 at the 5 m isobath (~2 km upstream); Station 4 at the 5 m isobath and near a freshwater source (3–5 km upstream).

APHA Method 10200 H, which has a practical quantification limit of  $1 \mu\text{g L}^{-1}$ . The concentration of chlorophyll *a* was independent of *Noctiluca* abundance, since *Noctiluca* does not contain chlorophyll *a* except through ingested food (Balch and Haxo 1984).

#### Counts of *Noctiluca* and measures of other population indices

Net samples were gently rinsed on a sieve ( $90 \mu\text{m}$  mesh) and thence into a 100 mL volumetric cylinder. After thorough mixing, two replicate 1 mL subsamples were removed and examined in an S-tray under an Olympus SZ60 dissecting microscope. In samples displaying dense concentrations, subsample size was reduced to 0.1 mL. Only whole, undamaged cells were counted, but damaged cells were rarely observed. Counts were made of the number of *Noctiluca* cells present and of the total number of plankton individuals in the  $>100 \mu\text{m}$  size fraction sampled.

To determine reproductive condition, the first 500 *Noctiluca* cells in each sample (using additional subsamples if necessary) were examined for the presence of swarmer-forming cells and for cells in the process of asexual division. Swarmer-forming cells are cells that have undergone multiple nuclear divisions, and in a bud-like process tiny flagellate cells have formed on their surface. These cells may be important in sexual reproduction (Schnepf and Drebes 1993; Hoehfeld and Melkonian 1995; Uhlig and Sahling 1995).

Cell diameters of *Noctiluca* were measured from each sample under the dissecting microscope, after cells had been stained for at least 24 h with lactophenyl cotton blue. Images were recorded with a Phillips CCD camera linked to an Apple Quadra computer equipped with NIH Image software. The area was measured of the first 30 whole cells in each subsample, and cell diameter was calculated. To ascertain that the preservation and staining techniques were not affecting the size of individual cells, 60 cells were measured from a sample of live cells on the day of collection, and these were compared with a sample preserved in 2% formaldehyde, sieved and stained with lactophenyl cotton blue. There was no significant difference (*t*-test,  $\mu_1 = 537.04$ ,  $SD_1 = 140.78$ ,  $\mu_2 = 514.02$ ,  $SD_2 = 93.97$ ,  $P = 0.30$ ).

Nutritional status was determined from two random subsamples of a stained sample, by examining the first 30 *Noctiluca* cells. Each cell was ranked from 0 to 3 on its nutritional status (Uhlig and Sahling 1995): 0, empty cells containing no food vacuoles; 1, fed cells with a small food vacuole; 2, well fed cells with prominent food vacuole/s; and 3, very well fed cells (usually only observed in laboratory cultures under optimum food conditions).

#### Sampling of red tides of *Noctiluca*

Samples were taken from six of the red tides reported to the NSW Environment Protection Authority throughout the course of this study (Table 1). Two of these samples were collected from the centre of the discoloured water in 1 L sample jars, from the surface layer and from 50 cm below the surface layer. All other samples collected were from an arbitrary volume, and only condition indices were measured. Samples were preserved immediately in 2% formaldehyde.

#### Data analysis

The abundances and cell diameters of *Noctiluca* were compared across estuaries, stations, months and depths by ANOVA. The results of the first (July) sampling were not included in this analysis, because replicate tows were not taken. Abundance was transformed to  $\log_{10}(x + 1)$  to normalize the variance. Homogeneity of variance of the transformed data was tested for each ANOVA by using Cochran's C test (Winer 1971). Means were compared *post hoc* by using Bonferroni probabilities. When data on condition indices were normally distributed, they were examined by using Pearson (product-moment) correlations or linear regression, where appropriate.

Samples of *Noctiluca* from different months, stations and estuaries, as well as the red-tide samples, were compared by condition indices with non-metric multi-dimensional scaling (MDS, Kruskal and Wish 1978) with

**Table 1. Red tides of *Noctiluca* reported to the NSW Environment Protection Authority during the study period (EPA, unpublished), and those that were sampled (\*)**

Symbols RTa–RTd are included for reference to Fig. 7; †red tides that were not measured for condition indices because of a high proportion of lysed cells

Date	Locality	Sample collected
9 Oct. 1996	Sydney (Manly)	* (RTa)
3 Jan. 1997	Sydney beaches (Warriewood–Manly)	–
9 Jan. 1997	Jervis Bay (St Georges Basin)	–
29 Jan. 1997	Port Stephens	* †
4 Feb. 1997	central coast	–
5–7 Feb. 1997	Sydney beaches (Collaroy–Coogee, Sydney Harbour beaches)	*Coogee *Nielsen Park (RTb)
5 Feb. 1997	Jervis Bay	* (RTc)
18 Feb. 1997	Sydney (Manly)	–
18 Feb. 1997	Sydney (Warriewood)	–
24 Feb. 1997	Narooma (Forsters Bay)	–
15 Mar. 1997	Sydney (Long Reef)	–
9 Apr. 1997	Lake Illawarra	* (RTd)

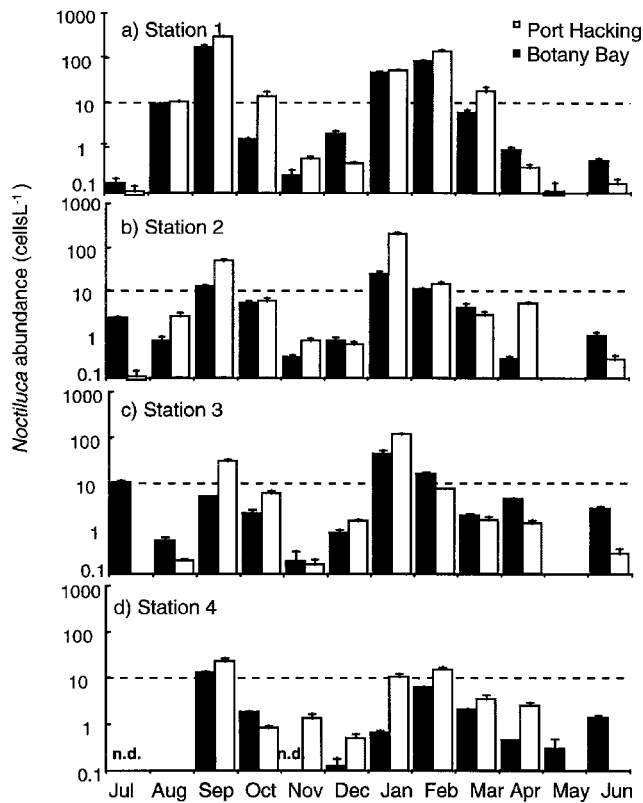
PRIMER software (Carr 1996). Cell diameter, coefficient of variation of diameter, nutritional status, proportion of division stages and proportion of swarmer cells, as well as the percentage dominance of *Noctiluca* in the zooplankton community, were the variables used in the MDS. Values used from the monthly samples were means of subsamples, replicate tows, depths and estuaries across stations ( $n = 16$  for each mean, because most variance was associated with month and station). For the samples from red tides, two subsamples were measured and a mean taken. Unlike a parametric multivariate technique such as principle components analysis, MDS allowed for the inclusion of non-normally distributed data such as the proportions of division stages and of swarmer cells. Each condition index was initially standardized, so that all indices contributed equally to the analysis. Dissimilarity matrices were generated from the Euclidean distances between variables in different samples. An iterative technique was then used to find the best display in two dimensions of the six dimensional dissimilarities. The stress value is a measure of how well the data can be displayed in two dimensions, with low values ( $<0.1$ ) indicating an accurate display of the data. There are no values on the axes because an MDS scatter can be arbitrarily rotated.

## Results

### *Effect of months, stations and depths on abundance of *Noctiluca**

*Noctiluca* was present at most stations at all times of the year, although abundance clearly changed from month to month (Fig. 2). Trends in monthly abundance differed significantly with respect to station, depth and estuary, with month being the single most important cause of variation, accounting for 52% of the total sum of squares (ANOVA,  $MS = 24.862$ ,  $F = 71.123$ ,  $P < 0.001$ ). Two main peaks in abundance occurred, in September and in January–February, when concentrations exceeded  $100 \text{ cells L}^{-1}$ . Abundance at some stations increased by up to two orders of magnitude between sampling months (for example from July to August at Station 1, or December–January at Station 3). There was no consis-

tent difference between the two estuaries ( $MS = 0.075$ ,  $F = 2.318$ ,  $P = 0.129$ ), though during the months of greatest abundance a generally greater concentration was observed in



**Fig. 2.** Abundance (mean  $\pm$  s.e., cells  $L^{-1}$ ) of *Noctiluca* at four stations in Botany Bay and Port Hacking from July 1996 to June 1997. Values are means of subsamples, replicate tows, and depths ( $n = 8$ ). n.d. signifies no data. The line at 10 cells  $L^{-1}$  is included for comparison. September and January–February were periods when red tides were reported. *Post hoc* comparisons of means for station in the two estuaries (Bonferroni probabilities at  $P = 0.05$ ): Botany Bay  $1 \geq 2 \geq 3 > 4$ , Port Hacking  $1 \geq 2 > 4 > 3$ .

Port Hacking than in Botany Bay (month  $\times$  estuary,  $MS = 1.165$ ,  $F = 36.148$ ,  $P < 0.001$ ).

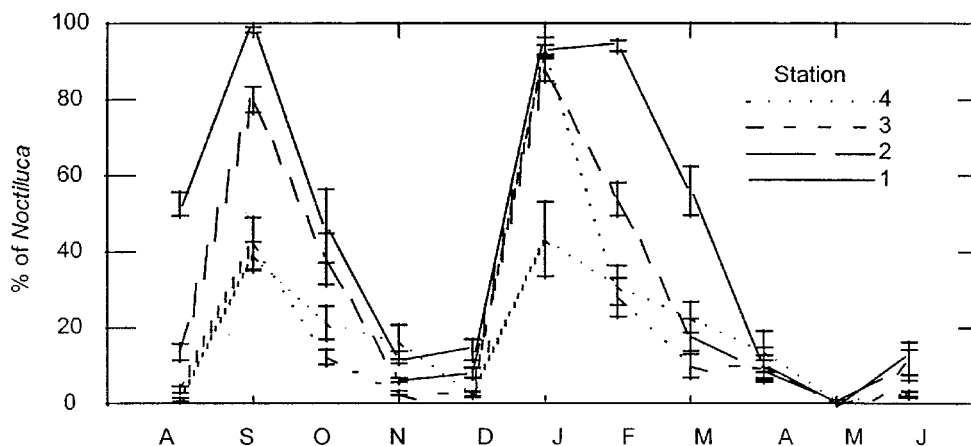
Station 1, the most offshore station, had significantly greater abundances than the more estuarine stations, with a trend towards a constant decline from Station 1 to Station 4 (12.8% of total SS,  $MS = 4.226$ ,  $F = 131.072$ ,  $P < 0.001$ ). At Station 4, a lower but more consistent abundance was observed of generally 1–10 cells  $L^{-1}$  (month  $\times$  station,  $MS = 1.709$ ,  $F = 53.019$ ,  $P < 0.001$ ). Differences in abundance between depths were much smaller than those due to other factors, and were not significant overall ( $MS = 0.052$ ,  $F = 1.623$ ,  $P = 0.203$ ). However, certain stations (e.g. Station 4) and months (e.g. most stations during September and November) showed contrary trends, when abundances at 3–4 m depth either equalled or exceeded those at the surface (depth  $\times$  station  $\times$  month,  $MS = 0.271$ ,  $F = 8.391$ ,  $P < 0.001$ ).

#### Percentage dominance of the zooplankton by *Noctiluca*

During the months of highest abundance (September, January–March), *Noctiluca* dominated the  $>100 \mu m$  plankton size fraction at Station 1 (Fig. 3). *Noctiluca* generally constituted a higher proportion of the zooplankton at Station 1 than at Station 4, because the abundance of the  $>100 \mu m$  plankton size fraction was constant, with no significant difference in the total number of plankton individuals (ANOVA, post-hoc pairwise comparison,  $P = 1.0$ ). The majority of other organisms were small copepods of the genera *Oithona* and *Paracalanus*.

#### Red tides of *Noctiluca*

Most red tides which were reported, occurred during late summer (Table 2). Samples of *Noctiluca* from red tides were collected at localities in Sydney, Lake Illawarra, Port Stephens and Jervis Bay. In two of the six red tides sampled, Port Stephens and Coogee, lysis had occurred in 67% and 86% of *Noctiluca* cells, respectively, compared with  $<5\%$



**Fig. 3.** *Noctiluca* as a percentage of the  $>100 \mu m$  plankton size fraction at four stations in both Botany Bay and Port Hacking from August 1996 to June 1997. Values are means ( $\pm$  s.e.) of subsamples, replicate tows and depths ( $n = 8$ ).

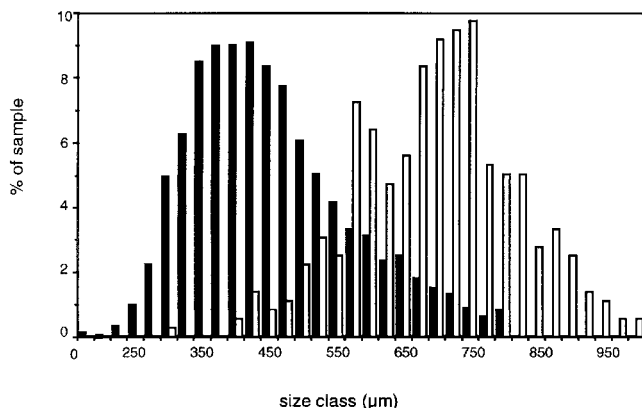


observed in the monthly sampling. The average concentration of *Noctiluca* in the surface waters of the two red tides quantitatively sampled was  $2.2 \times 10^5$  cells  $L^{-1}$  (s.e.  $2.6 \times 10^3$ ), slightly less than the range previously reported ( $0.5 \times 10^6$  to  $3 \times 10^6$  cells  $L^{-1}$ , Le Fevre and Grall 1970; Morton and Twentyman 1971; Fung and Trott 1973; Konovalova 1989). Below the surface layer, the mean concentration of *Noctiluca* was  $6.3 \times 10^3$  cells  $L^{-1}$  (s.e.  $2.2 \times 10^3$ ).

#### Cell diameter, nutritional status and proportion of reproductive stages

The *Noctiluca* cells from red tides were generally larger than the cells from the monthly samples (Fig. 4). In the monthly samples, 50% of the cells had diameters of 350–500  $\mu m$ , with the smallest being 185  $\mu m$  and the largest being 822  $\mu m$ . In the red tide samples, 40% of the cells had diameters of 650–775  $\mu m$ , with the largest being 1183  $\mu m$ . The distribution of the diameters of cells from the red tides appeared to be bimodal, which was related to the different red tides. The mean diameters of the 60 cells measured from red tides at Sydney (Nielsen Park), Jervis Bay and Lake Illawarra were 711, 784 and 741  $\mu m$ , respectively, whereas cells from the red tide at Sydney (Manly) had a mean diameter of 592  $\mu m$ .

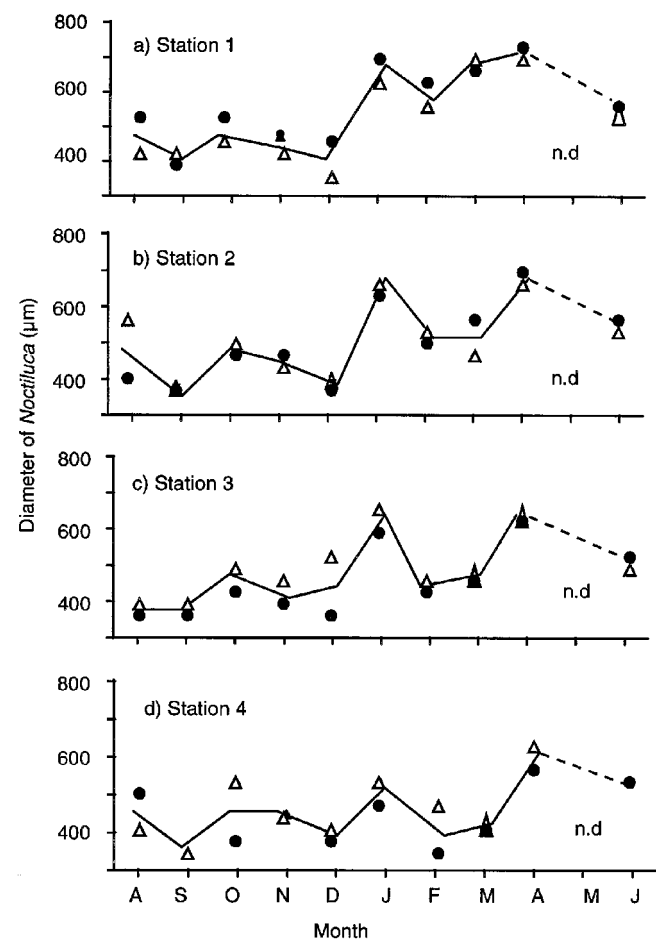
Differences in diameters of *Noctiluca* from the monthly samples taken at Port Hacking and Botany Bay were found to be mostly attributable to the sampling month (29% of the total SS, ANOVA,  $MS = 340427$ ,  $F = 370.36$ ,  $P < 0.001$ , Fig. 5). The smallest cells (<400  $\mu m$ ) were found in September and December, and the largest (>550  $\mu m$ ) occurred in January, April and June (May samples contained too few cells to measure). This pattern varied among stations, with the populations at the most-estuarine station during January, February and March consisting of cells not significantly larger than those present in other months (month  $\times$  station,



**Fig. 4.** Size-frequency histogram of the diameters of *Noctiluca* from (black columns) monthly sampling in Botany Bay and Port Hacking ( $n = 6960$ ) and (white columns) samples of four red tides ( $n = 240$ ). Note that the cells from red tides are generally larger, and that size distribution appears to be bimodal.

$MS = 43606$ ,  $F = 47.440$ ,  $P < 0.001$ ). In general, cells at Stations 3 and 4 were smaller than those at the offshore stations ( $MS = 155920$ ,  $F = 169.63$ ,  $P < 0.001$ ).

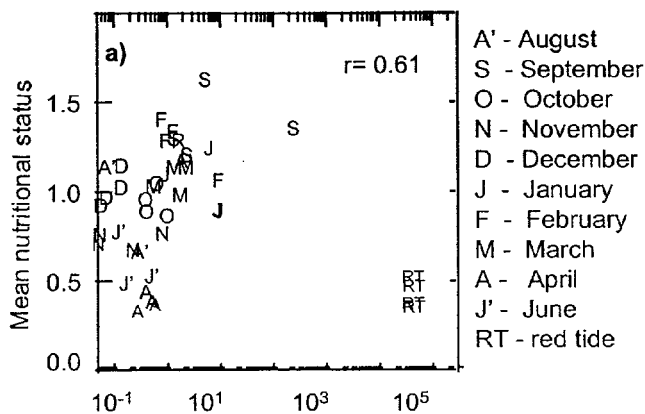
The nutritional status of *Noctiluca* was significantly negatively correlated with cell diameter ( $r = -0.54$ ,  $P < 0.001$ ). The abundance of *Noctiluca* in the monthly samples was positively correlated with nutritional status ( $r = 0.61$ ,  $P < 0.001$ , Fig. 6), whereas the cells from the red tides had a uniformly low nutritional status (0.4–0.6), despite high abundances. The April, June and November samples had the lowest nutritional status of the monthly samples (0.3–0.7), and the September samples had the highest (1.6–2.0). The positive relationship between nutritional status and abundance was not observed during all months. In February, samples



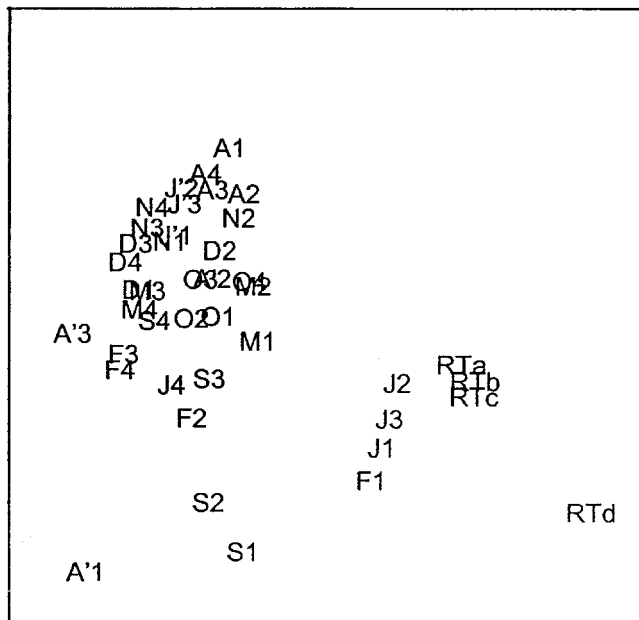
**Fig. 5.** Cell diameter of *Noctiluca* at four stations ( $\Delta$ ) Botany Bay and ( $\bullet$ ) Port Hacking from August 1996 to June 1997: s.e. bars are less than the symbol size. Values are means of cells from replicate tows and depths ( $n = 120$ ) except for August stations ( $n = 40$ , not included in ANOVA). May samples contained too few cells to measure. Line is included for comparison, n.d. signifies no data. September and January–February were periods when red tides were reported. *Post hoc* comparisons of means for station in the two estuaries (Bonferroni probabilities at  $P = 0.05$ ): Botany Bay  $1 > 2 > 3 > 4$ , Port Hacking  $1 > 2 > 4 > 3$ .

showed a negative relationship between nutritional status and cell abundance, such that the *Noctiluca* cells from stations with the highest abundance were also the emptiest.

The highest proportions of division stages of the monthly samples were seen in August and September, and few were observed at other times. The proportion of swarmer-forming cells was generally highest in August and was unrelated to the abundance of *Noctiluca*. The red-tide samples contained generally low percentages of division stages and swarmer-forming cells.



**Fig. 6.** Nutritional status plotted against concentration of *Noctiluca*. Values are means of samples from estuaries, depths, replicate tows and sub-samples ( $n = 16$ ) except for red tides ( $n = 2$ ). Correlation excludes red tides. Concentration of red-tide cells was determined from surface samples only.



**Fig. 7.** MDS ordination plot of the dissimilarity matrix of condition indices of *Noctiluca* from monthly sampling ( $n = 16$ ) and from red-tide samples ( $n = 2$ ). Stress = 0.07. Symbols for monthly samples are the same as for Fig. 6; 1–4 refers to the Station number. Symbols for red tides are given in Table 1.

The multivariate analysis of all six condition indices using MDS (Fig. 7; stress value 0.07), grouped together the three red tides from Sydney (Manly), Sydney (Nielsen Park) and Jervis Bay, taken in October 1996 or February 1997, and separated the red-tide sample from Lake Illawarra in April 1997. Of the monthly samples, those from January at Stations 1–3 were most similar in condition to the red-tide samples. The samples from September at Stations 1–2 and August at Station 1 differed in condition from the October–December and March–June samples. Samples from early summer (October–December) and late summer (March–June) clustered together in their cell condition.

*Relationship with temperature, salinity and chlorophyll*

*Noctiluca* was found in water temperatures of 14.2–24.2°C, and salinities of 28.0–36.5 (Table 2). Temperature increased gradually at Station 1 from an initial 16.2°C in August to a maximum of 22.5°C in February, while salinity fluctuated between 34.6 and 36.5. At Station 4, both temperature and salinity showed greater variation, fluctuating between 14.2 and 24.2°C, and between 28.0 and 36.0, respectively. Chlorophyll *a* concentration in the surface waters at the Port Hacking offshore station, measured within 2 days of the sampling for *Noctiluca*, was highest in September, when concentrations reached 2.9 µg L<sup>-1</sup> (Table 2). Apart from this, and small increases in December and June, concentrations remained low (<1 µg L<sup>-1</sup>) throughout the study period.

**Discussion**

*Abundance and dominance of Noctiluca*

Concentrations of *Noctiluca* were 1–2 orders of magnitude greater in coastal waters than in the estuaries during all months in which average *Noctiluca* concentration was >1 cell L<sup>-1</sup>. The spring and late-summer blooms of *Noctiluca* did not first appear in the estuaries, as they do in other regions where *Noctiluca* is abundant, such as the German Bight (Uhlig and Sahling 1995).

Our use of a 100 µm mesh net may have underestimated the abundance of *Noctiluca* (Uhlig and Sahling 1995), compared to bottle samplers, particularly when abundances exceeded 1 per litre (about half our samples). On the other hand, the net was needed to obtain sufficient individuals for the analyses of size and condition at all stations, and the larger sampling volume contributed to the low inter-sample variability. In sum, the trends we report in abundance are probably conservative.

*Interpretation of size and other condition indices of Noctiluca*

Cell diameter was used as an indicator of the condition of *Noctiluca*, because cell size has been shown to be a product of the culture conditions (Hanslik 1987; Qi and Li 1994; Buskey 1995). Cultures of *Noctiluca* from the German Bight



and from Texas coastal waters that were fed an optimal diet were observed to divide often (0.3–0.8 doublings per day, Hanslik 1987; 0.45 doublings per day, Buskey 1995) and to have prominent food vacuoles compared with those held without food, which ceased dividing. The cultures with the greatest rate of division (in the ‘best condition’) also contained the smallest cells (361–389  $\mu\text{m}$  diameter), and the starved cultures contained larger cells (441–512  $\mu\text{m}$ ) with no food vacuoles (Hanslik 1987; Buskey 1995).

The large diameters and low nutritional states of *Noctiluca* from the red tides sampled in this study therefore reflected their poor condition. The high proportion of lysed cells in some of the red tides indicated that the red tide populations were senescent. For this reason, the immediate cause of the red tides was not likely to be growth *in situ*, but rather a physical accumulation of cells from the surrounding waters in the surface layer, due to their increased buoyancy (Schaumann *et al.* 1988; Uhlig and Sahling 1990; Huang and Qi 1997; Elbrächter and Qi 1998).

*Noctiluca* from offshore stations during January–February were only marginally smaller than those from the concurrently occurring red tides, indicated by their proximity to the red tide group in the MDS plot of cell condition indices (Fig. 7). The *Noctiluca* cells collected in September were at a similar concentration but had smaller diameters (340–450  $\mu\text{m}$ ), and those from offshore stations showed the highest ranking of nutritional status and a generally higher proportion of division stages. Cell condition was therefore better during the September bloom than the January–February bloom. Rather than representing growth *in situ*, it is possible that the abundance of *Noctiluca* on sampling dates in January and February may also represent an accumulation from spatially or temporally distant water masses.

Feeding mechanisms may also play an important role in determining the condition of *Noctiluca*. It is known that in high concentrations *Noctiluca* can form mucoid feeding webs and so feed more efficiently (Omori and Hamner 1982; Uhlig and Sahling 1990; Shanks and Walters 1996). This may then represent a positive feedback, in inducing more rapid population growth in the build-up to blooms. We did not observe mucoid web feeding *in situ*, but the abundance of *Noctiluca* outside red tides was positively correlated to its nutritional status, possibly because of feeding efficiency at high concentrations.

The proportion of reproductive stages was generally low in this study. It is known that most asexual reproduction occurs at night (Uhlig and Sahling 1982). Therefore, the absolute concentration of division stages found during the day cannot directly reflect the population reproductive rate, but can be used to indicate temporal changes in reproduction, which peaked in September off Sydney. Population growth of *Noctiluca* is considered to be primarily by means of asexual reproduction (Uhlig and Sahling 1982).

#### *Environmental factors causing September and January–February blooms*

The peaks in abundance of *Noctiluca* exhibited little typical relationship with temperature (Table 2). Unlike the populations of *Noctiluca* in the German Bight and South China Sea (Dapeng Bay), in which a single period of high abundance occurs every year, correlated to water temperature (Uhlig and Sahling 1995; Huang and Qi 1997), two maxima in *Noctiluca* abundance were observed in 1996–97, at water temperatures among the lowest and highest, respectively, recorded throughout the year at the offshore station (16°C and 21.0–22.5°C). A similar pattern was observed during 1997–1998 (EPA, unpublished). As the water temperature along the New South Wales coast was never prohibitive to growth of *Noctiluca*, other factors may be more important in determining relative growth rates. It is possible that *Noctiluca* population growth was positively influenced by equal day/night length (Table 2). This has been found in laboratory studies to affect the circadian rhythm of asexual reproduction and thus to stimulate population growth (Uhlig and Sahling 1982).

The maximum concentration of chlorophyll *a* observed during the study occurred in early September, and was within the range previously reported for phytoplankton blooms off Port Hacking (Hallegraeff and Jeffrey 1993). During September, diatoms such as *Skeletonema costatum* were observed in the vacuoles of *Noctiluca* cells. Apart from this September peak, and a smaller increase in late November, concentrations of chlorophyll *a* on sampling dates remained low (<1  $\mu\text{g L}^{-1}$ ) from December to June, including the period of high *Noctiluca* abundance in mid summer. A positive relationship between *Noctiluca* abundance and phytoplankton blooms has been found in some studies (Devassy and Sreekumaran Nair 1987; Sreekumaran Nair *et al.* 1992; Painting *et al.* 1993; Hayward *et al.* 1995), but the apparently complex nature of this relationship is shown by one study, in which a negative correlation between *Noctiluca* abundance and chlorophyll *a* concentration was found and interpreted as showing that *Noctiluca* may exert predation pressure on phytoplankton (Huang and Qi 1997). *Noctiluca* in culture can consume between 0.2 and 2  $\mu\text{g}$  phytoplankton  $\text{L}^{-1} \text{day}^{-1}$  during the most rapid phase of growth (0.3–0.8 doublings per day) at an initial concentration of 10 cells  $\text{L}^{-1}$  (Hanslik 1987; Lee and Hirayama 1992). This could lead to a rapid decrease in phytoplankton abundance and eventual food limitation, depending on the rate of growth of the phytoplankton population (Hanslik 1987; Uhlig and Sahling 1990; Shanks and Walters 1996).

The coastal nature of the *Noctiluca* blooms recorded in this study is of relevance when attempting to measure the importance of different nutrient sources to *Noctiluca* growth. Previous studies have found that oceanic nutrient sources, such as from upwelling, are seasonally important along the

New South Wales coastline in inducing rapid growth of diatoms (Hallegraeff and Jeffrey 1993), and growth of *Noctiluca* may be the result of the increased abundance of prey. Estuarine nutrients and local eutrophication may also play a role in maintaining prey and predator populations during times of little upwelling.

#### *Estuarine Noctiluca and interactions with other plankton*

In contrast with the coastal samples, *Noctiluca* at the most estuarine stations were generally smaller (Fig. 5), particularly during January–March, with a medium nutritional status, but their abundance was relatively low, rarely exceeding 10 cells L<sup>-1</sup>. In other New South Wales estuaries, such as Lake Illawarra and Lake Macquarie, *Noctiluca* has been found more abundant, with concentrations exceeding 100 cells L<sup>-1</sup> at times in areas of Lake Macquarie (Bugler 1980; MacIntyre 1993). Thus, predation or competition with other zooplankton could have depressed *Noctiluca* abundance at our estuarine stations. Few studies have attempted to document the instance of predation on *Noctiluca*, because of difficulties in identifying the cells among gut contents of zooplankton or fish, although the large copepod *Calanus helgolandicus* can consume up to 70 *Noctiluca* per day in culture, corresponding to 20% of its body weight (Petipa 1965 in Uhlig and Sahling 1982). Other zooplankters, particularly small copepods such as *Oithona* sp and *Paracalanus* sp, were found to be more abundant at the most estuarine stations, and *Noctiluca* may have been limited here by biological processes (e.g. Kimor 1979).

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