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Plankton dynamics due to rainfall, eutrophication, dilution, grazing and assimilation in an urbanized coastal lagoon

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ABSTRACT

After a prolonged summer dry period, the effects of a distinctive and continuing rainfall on the nutrients and plankton of an urban coastal lagoon were investigated over 2 months. The lagoon filled up over 5 weeks from <10% of its maximum volume until it broke open to the sea. Nutrients (ammonia and oxidised nitrogen) significantly increased the day after initial rainfall, before returning to pre-rainfall conditions within 5 days. Phytoplankton biomass grew 10 fold within a week after initial rainfall in the 25–30 °C water and declined to near initial levels 2 weeks later. The assemblage of phytoplankton and zooplankton changed dramatically after 1 day and again by 6 days later, gradually returning to the original community by 2 weeks after the initial rainfall. Zooplankton responded within a day with a two fold increase in the adult stages of the calanoid copepod *Oithona* sp., followed a week later by nauplii and adult *Acartia bispinosa*. The influx of adult *Oithona* indicates resting populations that were previously under sampled by our plankton net. The plankton community returned to the initial state by 2 weeks, to being dominated by a centric diatom and *A. bispinosa* after 5 weeks. Dilution of the lagoon reached a maximum of 0.25 d^{-1}, while growth rates of the phytoplankton population reached a maximum of 1 d^{-1}, and *A. bispinosa* nauplii growth of 2.5 d^{-1}. Declines in chlorophyll biomass from the maximum 10 $\mu g\, l^{-1}$, at a rate of approximately 10% d^{-1} are consistent with the modelled uptake by zooplankton. The nutrients from runoff, growth and the influx of new zooplankton into the water column, resulted in a depleted $\delta^{13}C$ and $\delta^{15}N$ stable isotope signature of *A. bispinosa* by 2–4 ppt within 1–2 weeks, consistent with diatom growth and the terrestrial supply of depleted nutrients. $\delta^{34}S$ of *A. bispinosa* was enriched by 2 ppt for 1–2 weeks after rainfall, but unlike C and N, returned to pre-rainfall levels by the end of the study period. We suggest that plankton studies in coastal lakes with variable water levels that are not tidally driven, should account for the influence of changes in water levels to help explain data variability.

1. Introduction

Coastal lagoons receive varying nutrient loads and when closed, have irregular salinities, temperature regimes and water levels as a result of catchment runoff. Long residence times make coastal lagoons susceptible to eutrophication, as nutrients are available for long periods for uptake by biota. Terrestrial organic nutrients and the organic matter produced within the system may be decomposed by bacteria, which can further release bioavailable nutrients (Livingstone, 2001) – particularly under stratified and anoxic conditions (Eyre and Ferguson, 2002). The biomass of standing crops of any primary producers will depend on their rates of production and loss due to dilution and consumption by grazers. It is important therefore to understand the responses of primary producers to changes in nutrients as well as the responses of grazers.

The responses of plankton communities and biomass to eutrophication in coastal lagoons are not well documented. Phytoplankton and zooplankton biomass were reported to be low in a number of estuaries during times of little freshwater influx and therefore small nutrient loads (Allanson and Reid, 1995; Grange and Allanson, 1995; Grange et al., 2000; Froneman, 2000). Zooplankton biomass was higher in estuaries following freshwater pulses and their accompanying nutrient loads (Wooldridge, 1999).

Lagoons which are closed off from the ocean for long periods may have fluctuating water levels as a result of variable freshwater inflow and evaporation. Given the relatively wide and shallow nature of these systems, small changes in water levels may have

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substantial effects on resultant water volumes and surface areas. Changes to lagoon volumes can dilute or concentrate pelagic organisms and influence results of temporal studies if they are not accounted for, and are a major focus of this study.

Changes in the source of nutrients becoming available to consumers can be identified through the use of stable isotope analysis. Carbon and nitrogen stable isotope signatures of animals change in accordance with that of their food source. For example depleted ^{13}C is indicative of greater terrestrial sources relative to marine sources (Fry and Sherr, 1984), or of C3:C4 photosynthesis (Vogel, 1978). Enrichment of the rarer, heavier isotope can occur at each trophic level, at a rate of about 1‰ per trophic level for $\delta^{13}C$ (Rau et al., 1983; Fry and Sherr, 1984) and 2–4‰ for $\delta^{15}N$ (DeNiro and Epstein, 1978, 1981). There is little isotope fractionation of sulphur from prey to predator (Peterson et al., 1985), but the difference of $\delta^{34}S$ content between terrestrial and marine organic matter is much larger than it is for carbon and nitrogen. The $\delta^{34}S$ values for terrestrial vegetation range from +2 to +6‰, whereas marine plant material ranges from +17 to +21‰ (Peterson and Fry, 1987). Presumably the isotopic signatures of nutrient sources during rainfall should be very different to those nutrients available during dry periods (such as from sediment recycling).

Our aims were to document changes in nutrients, phytoplankton and zooplankton before, during and after a period of rainfall in the catchment of an urban coastal lagoon. We paid particular attention to the changes in volume of the lagoon and the influence that dilution may have on our interpretation of plankton concentrations. Secondly, we wished to determine if zooplankton grazing could successfully assimilate phytoplankton blooms. We examined the changes in the C, N, and S stable isotope ratios of *Acartia bispinosa* to assess the influence of storm water derived nutrients, to suggest possible sources.

2. Materials and methods

2.1. Study area and sampling

Dee Why Lagoon is an intermittently closed and open lagoon (ICOLL) situated on the northern beaches of Sydney, Australia (33°45″ S, 151°18″ E, Fig. 1). The lagoon has a maximum depth of 1.4 m, a surface area of 0.3 km^2 and a catchment area of 6.2 km^2. Approximately 80% of the catchment is residential, 5% industrial and the remainder recreational and reserve. Runoff from the catchment enters the lagoon by two main drains, which discharge at the western shoreline of the lagoon. Two sites at the western (inland) and eastern (ocean) ends of the lagoon (Fig. 1) were sampled on nine occasions between January and March 1999, in the austral summer. Sampling was conducted at night to prevent net avoidance by the zooplankton and was constrained by favourable weather. For convenience the sampling dates are with reference to the initial rainfall event on 21 Jan (=Day 0). The initial three sampling dates in January were during a period of no rainfall in the catchment (Day-16, -14 and -10), and the remaining six were during and after substantial and continuing rainfall (Day +1, +6, +7, +12, +14, +34), leading up to the lagoon breaking open to the sea on 26 February. Rainfall data for the catchment were obtained from the NSW Bureau of Meteorology Frenchs Forest monitoring station (3 km west of the lagoon) for the study period.

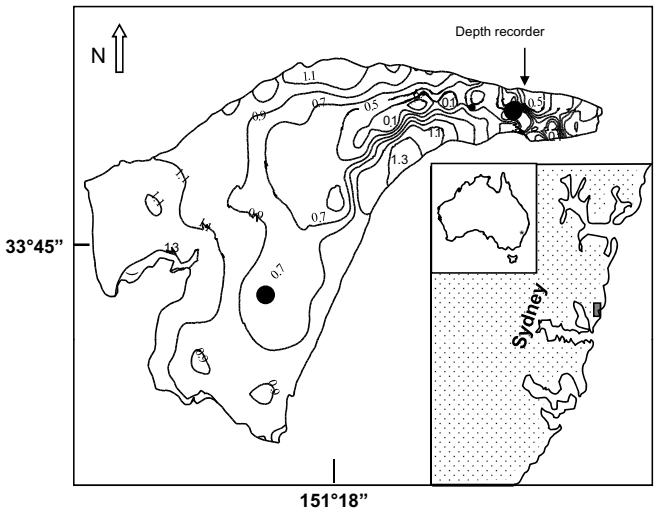

Fig. 1. Location of Dee Why Lagoon and its bathymetry (m) with respect to the ADH. Positions of permanent water level recorder and sampling sites (●) are shown.

A calibrated Seabird 25 Conductivity Temperature and Depth recorder was used to collect temperature, salinity, depth and dissolved oxygen data at 30 cm depth at each site (Fig. 1). No vertical stratification was evident during the study period. The instrument was also fitted with a Seatech Fluorometer to determine chlorophyll *a* biomass. Fluorometer calibration samples (1 l) were collected from 50 cm below the surface at random intervals throughout each sampling occasion and assessed for chlorophyll *a* concentration in the laboratory (Strickland and Parsons, 1972). A regression analysis was conducted for fluorometer values at the time and depth at which calibration samples were collected and the actual chlorophyll *a* concentrations. The regression function was used to calibrate other fluorometer values. Water samples, were collected at 50 cm depth in 1 l bottles for analysis of ammonia and oxidised nitrogen ($NO_2^- + NO_3^-$, NO_x). Water collected for analysis of nutrients was filtered through a 0.45 μm disposable syringe filter within 3 h of collection and frozen at −20 °C for NH_3 and NO_x analyses. The nutrient content of the samples was determined using the American Public Health Association Method 4500 modified for $NO_2^- + NO_3^-$ and NH_3. The Practical Quantification Limits were <0.07, 0.14 and 0.03 μM respectively. Analysis was carried out by a NATA (National Association of Testing Authorities Australia) registered commercial laboratory.

Triplicate phytoplankton samples were collected using 1 l bottles, at 50 cm depth, at each site and each sampling occasion. Samples were preserved using a solution of 3% gluteraldehyde and 97% estuarine water. In the laboratory, samples were concentrated to 10 ml by sedimentation. Phytoplankton were identified and counted using a calibrated Lund Cell (Lund et al., 1958) under a compound microscope.

Replicate zooplankton samples were collected at the surface at each site on each sampling occasion using a 20 cm diameter, 100 μm mesh net. The net was towed in an arc behind the boat for 5 min at 1–2 m s^{-1}. A General Oceanics flow meter was used to calculate the volume of water filtered during each tow (approximately 9.4 m^3). Samples were preserved in a solution of 5% formalin in estuarine water.

Samples were standardised to 500 ml and species composition and abundance were determined by counting two replicate 1 ml sub-samples (0.4%) under a dissecting microscope. Abundances were standardised to the number of organisms per litre. Plankton were identified to the lowest possible taxa (Dakin and Colefax, 1940).

2.2. Stable isotope analyses

Two replicates of 200 adult *Acartia bispinosa* were taken from each sample for carbon, and nitrogen stable isotope analysis. The ^{34}S and ^{13}C isotopes are primarily used to distinguish marine from

terrestrial sources (e.g. Piola et al., 2006). The copepods were not able to empty their stomachs before being sent for analysis as they had been preserved in the field. Copepod samples were not defatted. All material was rinsed in deionised water, freeze dried, weighed and 1.2–2.4 mg was packaged into aluminium foil capsules. The C and N stable isotope analysis on each capsule was conducted using Dumas combustion mass spectrometry, by combusting the capsules and the reaction products were separated by GC (Gas Chromatography) to give pulses of pure CO_2 and N_2 for analysis of total C and N, and ^{13}C:^{12}C and ^{15}N:^{14}N. Isotope values are expressed in delta (δ) notation, $\delta^{13}C$ and $\delta^{15}N$, relative to international standards (Pee Dee Belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$).

Additionally two replicates of 600 individuals (4 mg dry weight) were removed including both sexes, and occasionally with egg sacs for sulphur stable isotope analysis, conducted in a single batch by the Isotope Science Laboratory, University of Calgary, Canada. Sulphur isotope ratios were determined using a Carlo Erba NA 1500 elemental analyser interfaced with Continuous Flow-Isotope Ratio Mass Spectrometry (CF-IRMS). Capsules were combusted at 1020 °C and the reaction products separated by GC to give a pulse of pure SO_2 for analysis of total S and ^{34}S:^{32}S, relative to an international standard (SMOW – Standard Mean Ocean Water). Delta values were determined as follows:

$$\delta X(‰) = \left[\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1\right] \times 1000$$

where $X = {}^{13}C$, ^{15}N or ^{34}S and $R = {}^{13}C$:^{12}C, ^{15}N:^{14}N or ^{34}S:^{32}S, respectively. Error bars are expressed as the standard error of the three replicates, or the machine precision of analyses (whichever was greater), which were $\pm 0.2‰$ for $\delta^{13}C$ and $\delta^{15}N$, and $\pm 0.7‰$ for $\delta^{34}S$.

2.3. Calculation of dilution rates

Bathymetric data of the lagoon were obtained using a *Ratheon* depth sounder integrated with a differential GPS unit. Data were standardised to the Australian Height Datum (AHD). These data were used to determine the volume of the lagoon at depths below 1.0 m AHD. Aerial photographs of the lagoon collected when the lagoon was filled to depths of 1.5 and 2 m AHD respectively (determined with a *Datasonde* water level recorder deployed near the entrance of the estuary (Fig. 1)), were used to determine the increases in volume at these depths.

2.4. Analysis

A 2 factor orthogonal Analysis of Variance (ANOVA) was used to compare phytoplankton cell counts, nauplii, *Acartia* and *Oithona* concentrations, and stable isotope ratios amongst Days (9) and Sites (2). Prior to analyses, data were tested for homoscedasticity using Levene's Test. Where variances were heterogenous, data were appropriately transformed. Following transformation, all data were heterogenous and there was no need to change α to minimise the risk of Type-I error (Underwood, 1997). Post hoc tests were conducted using Student–Newman–Keuls (SNK) multiple comparison tests (Winer et al., 1991). Multidimensional Scaling (MDS) was used to assess changes over time of the phytoplankton and zooplankton communities of the lagoon, using 4th root transformed data. MDS is an ordination technique which reduces a swarm of multivariate data (species concentrations × date matrix) to two or three dimensions to identify patterns in the data structure. The stress value indicates the degree to which the data are distorted in order to fit the required dimensions. A stress value above 0.2 is unacceptable, and a value below 0.15 indicates minimal distortion (Clarke, 1993). There are no values on the axes, so an MDS scatter can be arbitrarily rotated.

2.5. Determining rates of changes of populations

In order to take account of dilution in the observed plankton dynamics, a simple model of individual populations is constructed. The local rate of change of the population of a plankton species, or tendency, is given by:

$$\frac{\partial P}{\partial t} = (\mu - \phi)P - \frac{dV/dt}{V}P$$

where P is the concentration of plankton species, ϕ is the mortality rate, μ is the growth rate, V is the volume of the lagoon, and t is time. The first term on the right hand side is growth minus grazing, and the second term is dilution. If the above equation is divided by P, the equation becomes:

$$\frac{dP/dt}{P} = (\mu - \phi) - \frac{dV/dt}{V}$$

and terms have the units of d^{-1}. Measurements of P and V through time allow determination of the tendency and dilution terms, and the subsequent calculation of the growth minus grazing term.

3. Results

3.1. Rainfall, water level and volume

A distinct dry period between 22 December and 20 January occurred when only 11 mm of rainfall was recorded, followed by a wet period between 21 January and 24 February, when 270 mm of rain was recorded (Fig. 2a). During the dry period, the depth of the lagoon remained around 1.15 m, and increased to between 1.75 and

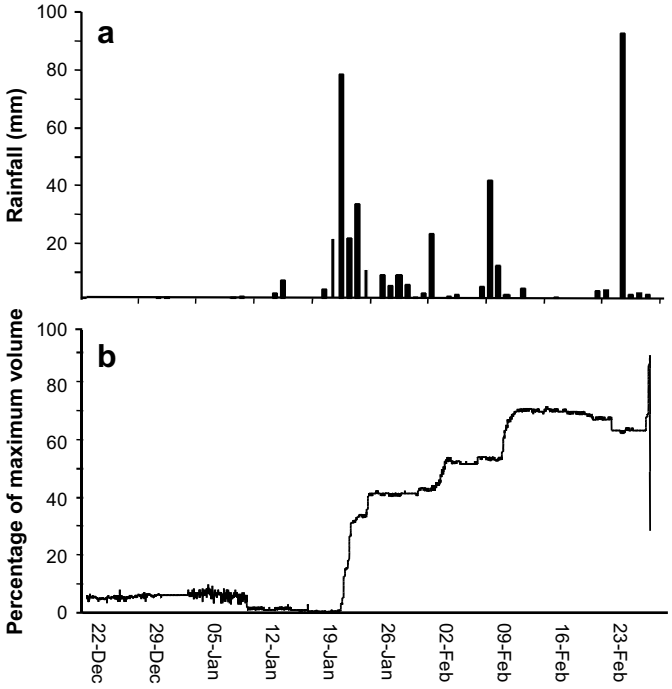

Fig. 2. a) Daily rainfall (mm) in catchment of Dee Why Lagoon over study period, b) changes in the percentage of the maximum volume of Dee Why Lagoon over the study period.

2.2 m during the wet period after 21 January, increasing the volume of the lagoon by up to 100% (Fig. 2b).

At both sites, water temperature declined by approximately 5 °C (from 30 °C) by Day +6, while salinity declined by more than half, from around 20 to <10 in the subsequent 2 weeks (Fig. 3).

3.2. Nutrients

Prior to the rainfall event, ammonia and oxidised nitrogen concentrations at both sampling sites were generally low (<0.05 μg l^{-1} and <0.02 mg l^{-1} respectively). After one day of heavy rainfall however (i.e. Day +1), both nitrogenous nutrients had rapidly increased to 0.13 μg l^{-1} and 4.7 mg l^{-1} respectively, and then declined to initial levels by the next sampling date on Day +6 (Fig. 4a, b). Ammonia had returned to the high values (0.15 μg l^{-1}) on Day +34.

3.3. Plankton

There were no significant differences between the algae counts at the two sites in Dee Why Lagoon (Table 1a, Fig. 5a). Phytoplankton counts were low (<1 × 10^3 cell ml^{-1}), on Days-16, -14, -10 and +1. Following this, counts increased significantly (Table 1a, Fig. 5a) from <1 × 10^3 cell ml^{-1} to >30 × 10^3 cell ml^{-1} on Day +6 and +7. Counts declined significantly over Day +12 and +14 back to initial levels, but increased to approximately 10 × 10^3 cell ml^{-1} on Day +34. Chlorophyll *a* data (depth averaged) showed a similar pattern with a nearly 10 fold increase in biomass on Day +6 and +7, a similar subsequent decline over the following 8 days to <4 μg l^{-1}, near initial levels by Day +14 (and including Day +34, Fig. 5b).

Over the study period, the phytoplankton community was dominated by centric diatoms (67%), chrysophytes (7%) and *Leptocylindrus* spp. (7%; Table 2). The community changed considerably over the time of the study, with each of the three dominant taxa being found at bloom proportions (>50% of that community) at a particular sampling occasion.

Multidimensional scaling analysis of the phytoplankton community showed a dramatic change after the rainfall event. The first three (dry weather) sampling events had a similar group of species, determined at the 80% Bray–Curtis dissimilarity index, while Day +1, and Day +6 the community had changed substantially. Over Day +7, +12, +14 the community returned to a similar pre-rainfall state, but had changed to a new community nearly 3 weeks later before the lagoon opened (Day +34, Fig. 6). Before the rainfall event phytoplankton samples were dominated by an unidentified chrysophyte, a pennate diatom and a species of *Navicula*. Immediately following the initial rainfall, samples were dominated by a *Chilamonas* sp. (D +1). After a few days (D +6, D +7, D +12), samples were dominated by centric diatoms, and then over time became increasingly dominated by a species of *Leptocylindrus* (Table 3, Simper Analysis, Clarke and Warwick, 1994). Zooplankton taxa were dominated by calanoid copepods (copepodite and adult stages of *Acartia bispinosa*, 60%), copepod nauplii and by cyclopoid copepods (*Oithona* spp., Table 4).

The concentration of Copepod nauplii varied significantly among dates and sites (Table 1b, Fig. 7a), mainly due to the large increase on Day +34, particularly at the lower site. Naupliar

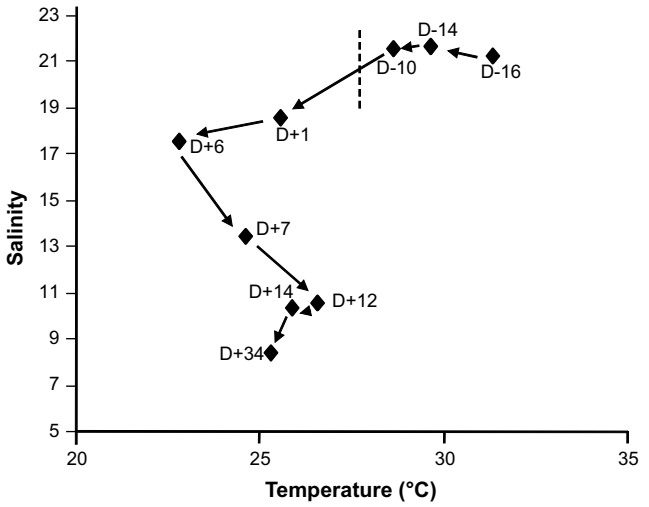

Fig. 3. Average salinity–temperature plot of data recorded on each sampling date in Dee Why Lagoon over the study period. Sampling days are indicated by the letter D. Dashed vertical line indicates initial rainfall event.

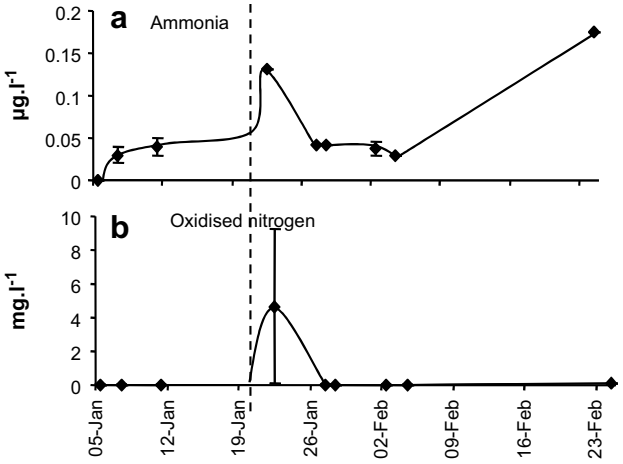

Fig. 4. Average concentrations of a) ammonia, and b) oxidised nitrogen at the two sites in Dee Why Lagoon over study period. Error bars are standard error. Dashed vertical line indicates initial rainfall event.

Table 1
Results of ANOVA comparisons of concentrations of various taxa over the study period. ns, not significant; $^{*}0.05 < p < 0.01$; $^{**}p < 0.01$.

	Source	SS	df	MS	F	P
a) Phyto	Days (D)	4.1 × 10^6	8	6.8 × 10^6	441.4	**
	Sites (S)	5.9 × 10^6	1	5.9 × 10^6	0.4	ns
	D × S	9.3 × 10^6	8	3.7 × 10^6	1.9	ns
b) Nauplii	Days (D)	5.7 × 10^6	8	7.1 × 10^6	36.1	**
	Sites (S)	2.2 × 10^6	1	9.6 × 10^6	7.6	*
	D × S	6.0 × 10^6	8	4.5 × 10^6	4.2	**
c) *Acartia*	Days (D)	7.3 × 10^6	8	9.6 × 10^6	13.1	**
	Sites (S)	7.5 × 10^6	1	7.4 × 10^6	8.0	*
	D × S	7.5 × 10^5	8	3.8 × 10^6	1.8	ns
d) *Oithona*	Days (D)	2.6 × 10^5	8	5.0 × 10^6	17.9	**
	Sites (S)	1.8 × 10^6	1	1.8 × 10^6	6.4	*
	D × S	3.3 × 10^6	8	4.1 × 10^6	1.5	ns
e) δ^{13}S	Days (D)	123.5	8	15.4	231.1	**
	Sites (S)	0.5	1	0.5	1.88	ns
	D × S	2.1	8	0.3	3.93	**
f) δ^{15}N	Days (D)	17.3	8	2.2	171.6	**
	Sites (S)	0.01	1	0.02	1.5	ns
	D × S	0.07	8	0.01	0.7	ns
g) δ^{34}S	Days (D)	44.5	8	5.6	29.9	**
	Sites (S)	1.5	1	1.5	8.0	**
	D × S	20.3	8	2.5	13.7	**

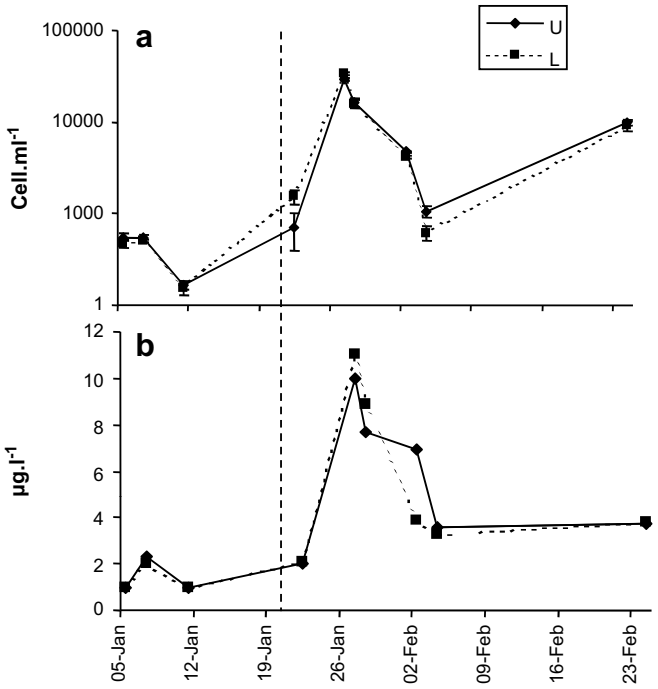

Fig. 5. a) Changes to average phytoplankton concentrations (cells ml^{-1}) and b) phytoplankton biomass (µg chl $a\,l^{-1}$) at two sites within Dee Why Lagoon over the study period. Error bars are standard error; U, upper, western site (solid line); L, lower, eastern site (dashed line). Vertical dashed line indicates initial rainfall event.

concentrations were low (<500 l^{-1}) during Day-16, -14, -10 and Day +1, then increased significantly on Day +6 and Day +7, before declining to pre-rainfall concentrations by Day +12, +14 until the last sampling date, 5 weeks after the initial rainfall (Fig. 7a). The concentration of *Acartia bispinosa* varied significantly over time and between sites (Fig. 7b, Table 1c). 56% of the variability amongst *A. bispinosa* was due to time and 34% due to site, with the lower site having had significantly greater concentrations. Like the nauplii, *A. bispinosa* concentrations were generally similar over the first four sampling events, including the day after rainfall and then increased significantly on Day +6, +7 and +12, before returning to pre-rainfall values at both sites on Day +14. Similar to the nauplii, the concentrations increased by Day +34, nearly 5 weeks after the initial rainfall (Fig. 7b).

Table 2
List of the dominant phytoplankton taxa and groups documented during the study, and used in the MDS analysis.

Taxa	Total/Litre	Percent Abundance
Unknown Centric diatom	35520.5	67.5
Unidentified chrysophyte	3646.7	6.9
Leptocylindrus spp.	3578.8	6.8
Pseudonitzschia spp.	2335.2	4.4
Chaetoceros spp.	2224.2	4.2
Chilamonas sp.	1066.9	2.0
Flagellated spp.	999.0	1.9
Non-flagellated spp.	886.9	1.7
Gymnodinium sp.	832.9	1.6
Unknown Pennate	404.9	0.8
Cocconeis sp.	253.8	0.5
Amphora sp.	225.9	0.4
Navicula spp.	225.4	0.4
Heterocapsa sp.	129.0	0.2
Nitzschia closterium	57.0	0.1
Micromonas/Mantoniella	53.9	0.1
Thalassiosira sp.	44.2	0.1

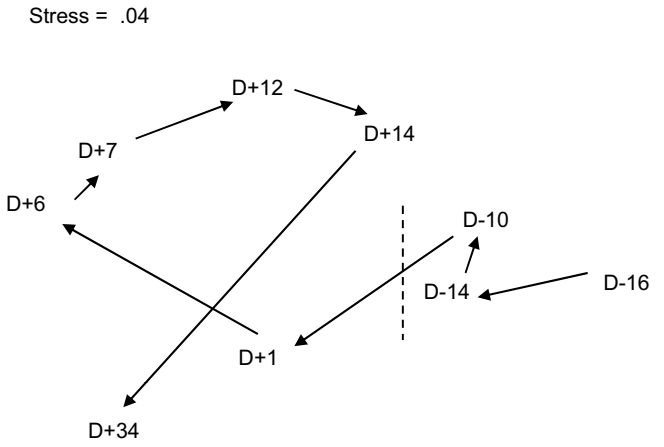

Fig. 6. Multidimensional scaling plot showing changes to phytoplankton community over the study period. Sampling days are indicated by the letter D. Changes between sampling dates are indicated by arrows. Stress = 0.04. Vertical dashed line indicates initial rainfall event.

Table 3
Results of SIMPER Analysis showing the average percent dissimilarity between groups and the taxa contributing to 60% or more of the cumulative dissimilarity.

	% Dissimilarity	Cumulative % Dissimilarity
a) D-16, D-14 & D-10 vs D +1 (46%)		
Chilamonas sp.	14	14
Chaetoceros sp.	14	28
Chrysophyte	11	39
Flagellate (unidentified)	8	48
Pennate diatom (unidentified)	7	55
Non-flagellate (unidentified)	6	61
b) D-16, D-14 & D-10 vs D +6 & D +7 (75%)		
Centric diatom (unidentified)	47	47
Chaetoceros	9	55
Pseudonitzschia	9	64
c) Day D +1 vs D +6 & D +7 (51%)		
Centric diatom (unidentified)	55.17	55.2
Pseudonitzschia	10.6	65.8
d) Day D-16, D-14 & D-10 vs D +12 & D +14 (50%)		
Centric diatom (unidentified)	48.3	48.3
Chrysophyte	9.1	57.4
Chilomonas	8.5	65.9
e) D +1 vs Days D +12 & D +14 (46%)		
Centric diatom (unidentified)	32.7	32.7
Chaetoceros	11.4	44.1
Unidentified taxon	5.7	51.8
Pennate diatom (unidentified)	5.5	57.3
Chilomonas	5.2	62.5
f) Days D +6 & D +7 vs Days D +12 & D +14 (52%)		
Centric diatom (unidentified)	41.8	41.8
Pseudonitzschia	11.2	53.0
Chaetoceros	11.1	64.1
g) Days D-16, D-14 & D-10 vs D +34 (73%)		
Leptocylindrus	30.0	30.0
Chaetoceros	16.6	46.6
Gymnodinium (unidentified)	9.5	55.1
Flagellate (unidentified)	8.4	63.5
Days D +6 & D +7 vs D +34 (73%)		
Centric diatom (unidentified)	35.1	35.1
Leptocylindrus	22.7	57.8
Pseudonitzschia	7.7	64.8
Days D +12 & D +14 vs D +34 (63%)		
Leptocylindrus	0.8	30.8
Chaetoceros	17.0	47.8
Gymnodinium	10.9	58.7
Centric diatom (unidentified)	9.3	68.0

Table 4
List of zooplankton taxa total abundance per unit of volume, and percentage composition during the study, used in the MDS.

Taxa	Total	% Composition
Acartia bispinosa	9981.6	43.2
Barnacle nauplii	46.0	0.2
Bivalves	2228.3	9.6
Calanoid nauplii	5193.0	22.5
Chaetognaths	48.0	0.2
Cladocerans	36.3	0.2
Crab larvae	31.5	0.1
Cyclopoid A	776.2	3.4
Cyclopoid B	17.5	0.1
Cyclopoid C	12.0	0.1
Fish larvae	33.0	0.1
Gladioferans sp.	488.7	2.1
Medusae larvae	87.3	0.4
Oithona spp.	3374.3	14.6
Ostrocods	539.0	2.3
Polychaetes	126.1	0.5
Shrimp larvae	26.0	0.1
Tintinnids	68.8	0.3

Oithona sp. concentrations significantly increased by nearly 50% on Day +1 (Fig. 7c), before returning to pre-rainfall abundance by Day +6 and +7. The majority of variance was explained by Day (70%, Table 1d), and the downstream site had significantly greater concentrations (25% of the total variance, Table 1d).

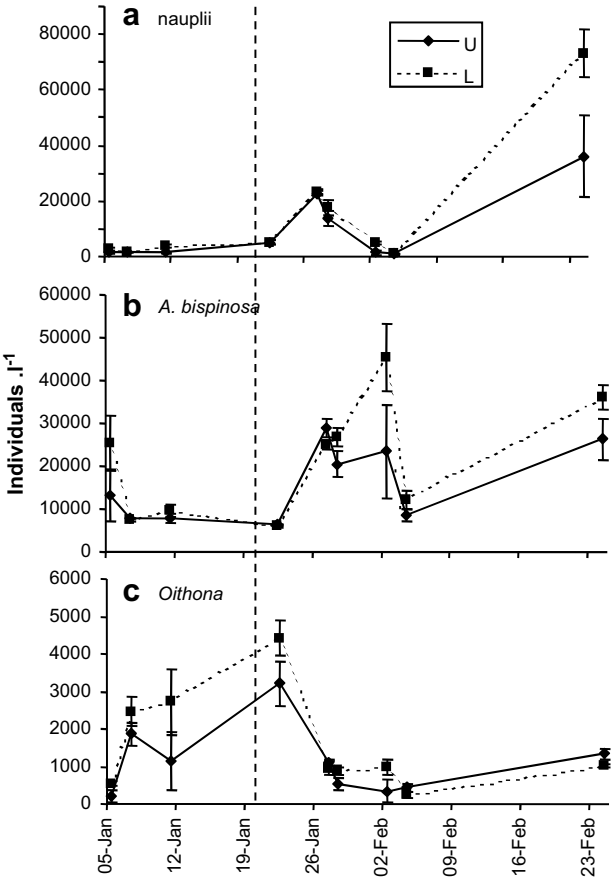

Fig. 7. Temporal changes in the average concentrations of a) copepod nauplii, b) *A. bispinosa* and c) *Oithona spp.* over the study period. Error bars are standard error; U, upper, western site (solid line); L, lower, eastern site (dashed line). Vertical dashed line indicates initial rainfall event.

The zooplankton community (Table 4), as revealed by MDS showed that the communities were similar on each Day-16, -14 and -10, as defined by the 50% dissimilarity level of the Bray–Curtis dendrogram. The community dramatically changed by Day +1, and again by Day +6. Over the following 8 days the community returned to a similar pre-rainfall state (Day +7, +12, +14), but had changed to a new community nearly 3 weeks later (Day +34, Fig. 8), similar to the phytoplankton community (Fig. 6).

3.4. Analysis of processes affecting plankton

The model constructed above uses observations of plankton tendency and lagoon volume changes to calculate the dilution and growth – grazing terms for each population. The growth – grazing term for phytoplankton peaked at approximately 1.5 mg chl *a* m^{-3} d^{-1} (Fig. 9c), which represents a growth rate of about 1 d^{-1} (Fig. 9b), between 20th and 27th January. The peak of the growth – grazing term occurred during the time of maximum increase in lagoon volume (Fig. 9a). Even so, the growth – grazing term is approximately four times greater than the dilution term. There is a trough immediately afterwards which corresponded to the maximum growth minus mortality term for the *Acartia bispinosa* (Fig. 9d). The *A. bispinosa* most negative values of the growth – grazing term occur on the 3rd February (Fig. 9d), and are associated with a large positive value of the nauplii term (Fig. 9f). In fact, the nauplii reach a maximum growth minus grazing term of 3 d^{-1}, a very fast doubling time. In contrast to the nauplii and *A. bispinosa*, the cyclopoid terms are negative between 20th and 27th January (Fig. 9e), as simply illustrated in the raw counts (Fig. 7c). After this initial negative response to the increase lagoon volume, the cyclopoid population follows a similar trend to the nauplii and *A. bispinosa*.

3.5. Stable isotope analysis

The $\delta^{13}C$ ratio of *Acartia bispinosa* fell significantly from approximately –26.0‰ to –31.1‰ (SE = 0.2) by Day +12, but importantly there was no change by Day +1 (Fig. 10a, Table 1e). A month after rainfall, $\delta^{13}C$ in *A. bispinosa* had risen to –29.4‰ by Day +34. There was a significant interaction in the two factor ANOVA

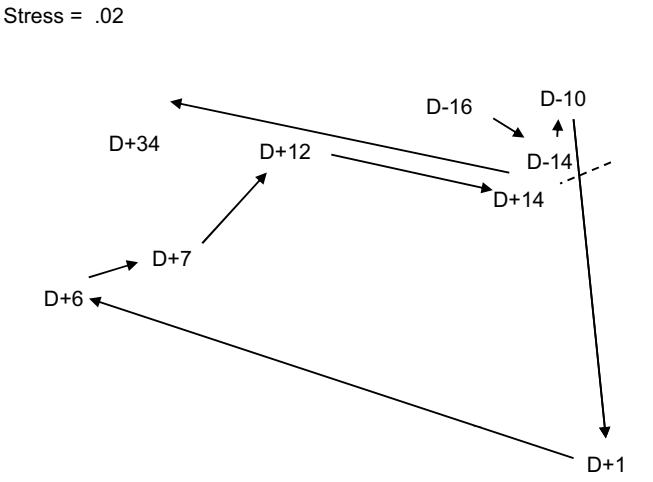

Fig. 8. Multidimensional scaling plot showing changes to zooplankton community over the study period. Sampling days are indicated by the letter D. Changes between sampling dates are indicated by arrows. Stress = 0.02. Vertical dashed line indicates initial rainfall event.

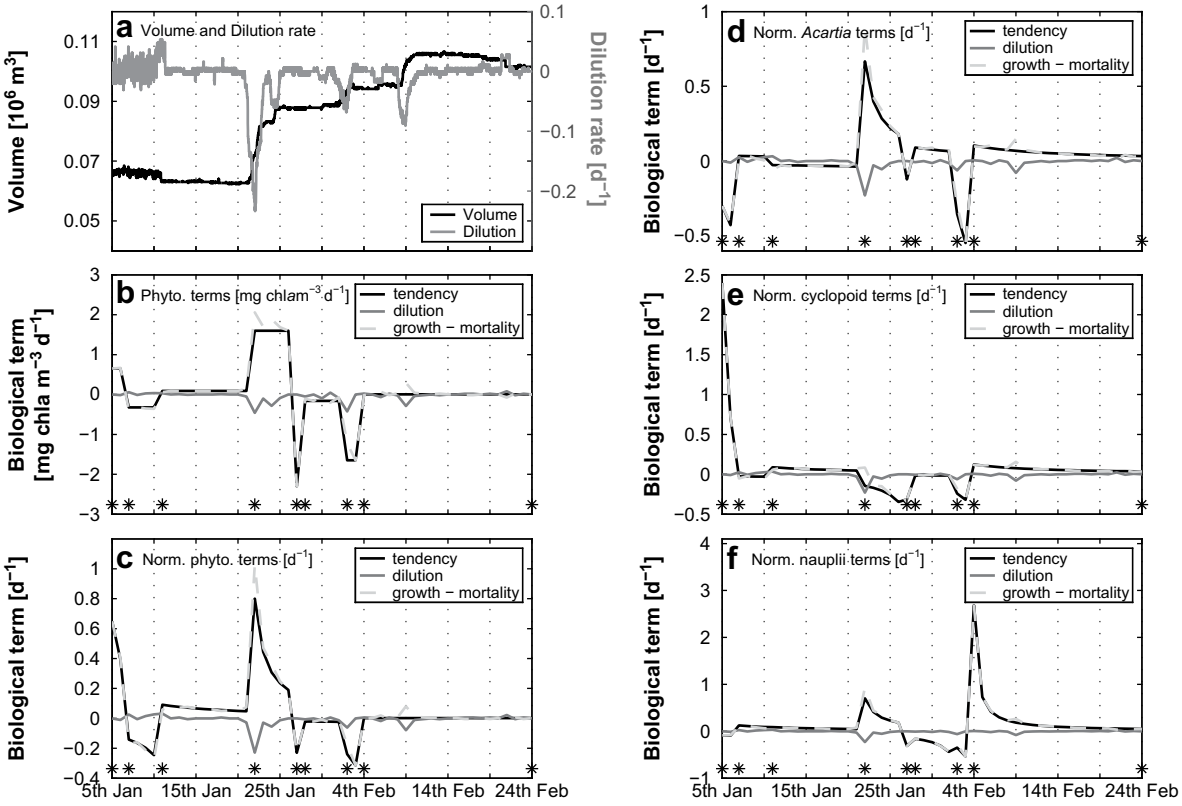

Fig. 9. Properties of Dee Why Lagoon during the sampling period from January 5 until March 6 1999 (a) volume (m^3) and dilution rate (d^{-1}); (b) phytoplankton terms in concentration per unit time (productivity); and (c) phytoplankton terms normalised to biomass (growth rate). Terms for zooplankton are given in units of d^{-1} for (d) *Acartia*, (e) cyclopoid and (f) nauplii. Terms are tendency (the measured local rate of change), dilution (inferred from volume change), and the sum of biological processes (growth minus grazing).

(day × site, $p < 0.01$, Fig. 10a), but except for the initial dry weather period, data from the two sites tracked each other.

The $\delta^{15}N$ values in *Acartia bispinosa* rapidly declined from 11.3‰ to 10.3‰ by Day +1, and continued to decline to 9.3‰ on Day +6 and +7 (Fig. 10b), returning to 10.3‰ by Days +12, +14. $\delta^{15}N$ values gradually increased to 10.6‰, 5 weeks after initial rainfall, which was not significantly different from the initial dry weather values (Table 1f, SNK test).

The $\delta^{34}S$ values in *Acartia bispinosa* exhibited the opposite trend of $\delta^{15}N$ (Fig. 10b, c), with no change on Day +1, and significantly increasing from approximately 10‰ to 12‰ by Day +6 (Table 1g, Fig. 10c). The values were not significantly different to the average pre-rainfall values by 5 weeks after the initial rainfall. Except for the first two dates, the Lower and Upper sites tracked each other. Overall the stable isotope ratios were significantly correlated, particularly carbon and nitrogen ($r = 0.67$).

4. Discussion

Rainfall and the runoff of associated nutrients resulted in a rapid and significant change to phytoplankton biomass and composition. This increased biomass was rapidly assimilated by zooplankton which increased in abundance as a result of being mixed into the pelagic system from the bottom of the estuary and through secondary production. By accounting for dilution in our calculations we were able to document the significance of changes to plankton concentrations. This is rare in studies from temporarily closed coastal systems with highly variable depths and volumes which could influence the ability to detect changes in concentrations of pelagic organisms. Analysis of stable isotopes indicated that copepods were feeding on nutrients derived from the catchment, but had also made use of benthic influenced food sources.

Zooplankton biomass was generally greater at the uppermost site in the lagoon. This may reflect the shallower nature of this site relative to the other which would have allowed a greater number of any bottom associated plankton to be captured during plankton tows.

Phytoplankton and zooplankton communities both changed composition 6 days after rainfall and associated nutrient influx, but then returned to, or near to, the initial state by Day +14. The phytoplankton cell concentration increased 10 fold and chlorophyll *a* 5 fold, 6 days after the initial heavy rain, tracked by a similar pulse in zooplankton abundance – mostly of adults – that collapsed from the water column by Day +12. The potential for zooplankton grazing to remove the phytoplankton growth is explored later.

Rainfall has been linked with high phytoplankton production in two coastal lagoons in North Carolina (Hubertz and Cahoon, 1999). Conflicting results however were reported in two sub-tropical South African estuaries. In the Kariega Estuary, freshwater flow was not related to chlorophyll *a* concentration, while in the Great Fish Estuary, chlorophyll *a* was related to freshwater flow with elevated phytoplankton biomass being found in the middle reaches of the estuary following rainfall events (Grange and Allanson, 1995). Strong links between rainfall, phytoplankton biomass and zooplankton biomass, have been reported in intermittently opened and permanently open Southern African estuaries (Jerling and Wooldridge, 1995; Froneman, 2002). The entrance states of two coastal lakes in South Africa were shown to influence the biomass of phytoplankton, with greatest concentrations occurring after rainfall which did not lead to the entrances being opened (Thomas

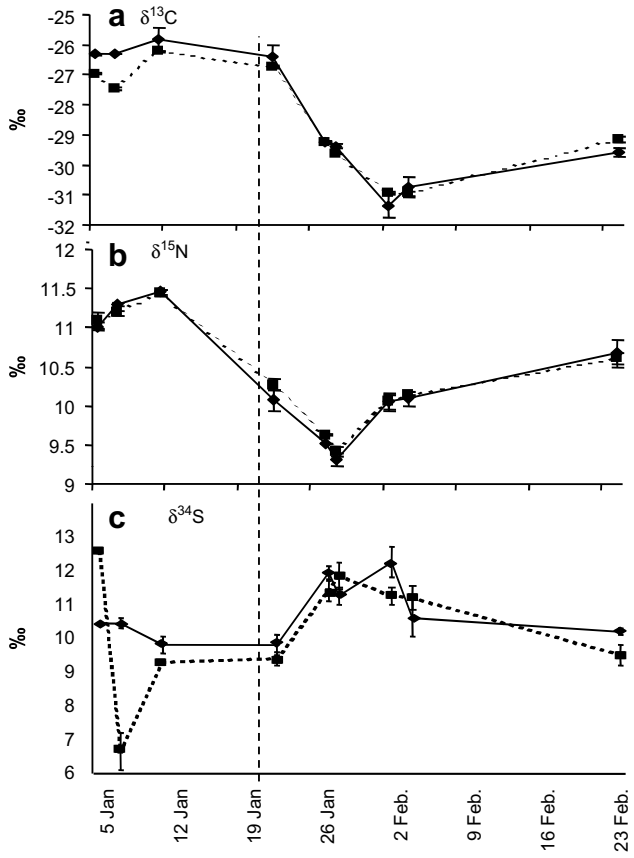

Fig. 10. Temporal changes in the stable isotope ratios (a) δ^{13}C, (b) δ^{15}N and (c) δ^{34}S in *A. bispinosa*. Error bars are standard error, but machine error is 0.2‰ for C and N, and 0.7‰ for S; U, upper, western site (solid line); L, lower, eastern site (dashed line). Vertical dashed line indicates initial rainfall event.

et al., 2005). Papers have discussed the influence of the entrance state of lagoons on plankton (e.g. Perisinotto et al., 2000; Froneman, 2002), however none of these papers accounted for the influence of changes to lagoon volume and associated dilution, which may have influenced the magnitude and therefore significance of their findings.

4.1. Rainfall driven influx of plankton into the lagoon

Heavy rainfall in the catchment had the potential to advect planktonic species from freshwater habitats into the lagoon, influencing the plankton composition of the receiving waters. We believe this scenario to be unlikely as the catchment of Dee Why Lagoon is highly urbanized and is dominated by concrete lined drains and storm water infrastructure, with few water bodies where plankton communities could develop. Any ponds and wetlands which are located in the catchment are small and do not hold sufficient plankton to influence the communities in the lagoon.

4.2. Bloom and assimilation by adult copepods

The most surprising observation was the increase in adult zooplankton, sometimes within a day (*Oithona*), suggesting the existence of a resting or aestivating population that was previously un-sampled. Our findings suggest a behavioural response to the flushing by runoff and to the increased food supply in the water column. It is possible that zooplankton may also have switched diets following rainfall in response to the increased food supply in the water column. A similar scenario was suggested for zooplankton in temporarily opening South African lagoon, when the diets of zooplankton may have changed from benthic-micro-algae to pelagic phytoplankton following rainfall (Perisinotto et al., 2000).

The dual response by the zooplankton (growth by phytoplankton assimilation and an influx of new zooplankton) is evident in the stable isotope composition. The overall change in each of the 3 elements indicates that they represent different processes and trophic pathways. δ^{15}N was the most variable, declining significantly within 24 h of the initial rainfall, suggesting that a new population was being sampled from the water column, as the ^{15}N change was too soon to be from assimilation. ^{15}N continued to decline only to Day +6, +7 but rapidly recovered Day +12, +14. The δ^{13}C and δ^{34}S were not significantly different by Day +1, but had changed by Day +6, and δ^{13}C continued to decline by Day +12. The declining δ^{13}C composition is consistent with blooming populations of diatoms, that preferentially fix the lighter isotope (France, 1995). Declining δ^{13}C composition is also associated with terrestrial sources of C rather than marine (Piola et al., 2006). δ^{34}S increased during the initial 12 days, consistent with the assimilation of nutrient derived from the sediment. Fractionation of sulphur isotopes primarily occurs during bacterial reduction of sulphate to hydrogen sulphide by anaerobic bacteria (Hoefs, 1997), thus distinguishing benthic vs pelagic sources (Peterson et al., 1985). Therefore we surmise that rainfall and mixing introduced ^{34}S enriched, benthic food sources into the water column which the copepod population consumed, assimilated and subsequently depurated. Interesting, the carbon and nitrogen stable isotope composition remained depleted, the nitrogen nearly returned to pre-rainfall levels, while the sulphur returned to the pre-rainfall values after 2 weeks. In general, ^{34}S did not provide any further insight than ^{13}C in this study.

Dee Why Lagoon has a small catchment (6.2 km^2) and receives little freshwater input during dry periods. Available nutrients during dry weather are comprised from those recycled within the estuary and those supplied by atmospheric deposition, wave overtopping from the ocean, ground water flow and those discharged into the estuary by any dry weather flow. These nutrients did not support a large pelagic phytoplankton biomass during the dry period of this study. Nutrient fluxes from the sediment in Dee Why Lagoon were reported to have little influence on pelagic algae during dry periods (Eyre and Ferguson, 2002). Approximately 70% of recycled nitrogen was released as inert nitrogen gas. Bioavailable ammonia and oxidised nitrogen released from the sediment were suggested to be sufficient to maintain benthic associated algae, and not to be available to pelagic phytoplankton (Eyre and Ferguson, 2002). It is possible that copepods assimilated significant nutrients from the disturbed benthos of the lagoon, rather than directly from phytoplankton stimulated by runoff and associated detritus.

The role of microzooplankton in the grazing of phytoplankton is very important in Dee Why Lagoon, although data showed that grazing by microzooplankton alone could not control the increase in algal biomass (Redden et al., 2002). This study collected zooplankton using a 100 μm mesh net which would have sampled the larger fraction of zooplankton normally classified as microzooplankton. The data from this present research suggest that plankton larger than 100 μm are also important grazers of algal biomass, and were able to control the rapidly increased phytoplankton biomass. This assimilation may have been delayed by phytoplankton being consumed by microzooplankton which are subsequently consumed by larger zooplankton.

4.3. Grazing rates of zooplankton

Despite no measurements that allowed the separate determination of growth and mortality terms, the calculation of the sum of the two terms allowed the observations to be interpreted in a dynamical sense. In particular, the relative magnitude of dilution can be compared with the biological processes. The similar sized increases of phytoplankton and *Acartia bispinosa* immediately following the first rain event provides evidence that the increases may have come from resting populations, most likely in the sediments. The large losses in phytoplankton, *A. bispinosa* and nauplii between the 2nd and 4th of February (Figs. 5 and 7) may reflect a combination of grazing reducing phytoplankton biomass and then the resultant lower food supply reducing secondary production. The decreased numbers of adult *A. bispinosa* may indicate that they had returned to the bottom of the lagoon to feed on microphytobenthos and therefore been deeper than our sampling depth.

Fig. 9 also shows that the nauplii increased more after the second sampling event than the first. This probably reflects the influence of the increased food supply over rainfall event on the fecundity of the copepods. The third event, on the 8th February was not sufficiently sampled to gauge the planktonic response.

4.4. Incorporating the changing lagoon volume

Accounting for dilution in temporarily open/closed systems is important when dealing with biological variables which inhabit the open water of these systems and which are generally reported as concentrations. The volumes of closed systems are highly variable and change significantly following rainfall. The influence of rainfall derived nutrients can potentially be missed or under emphasised because of the effects of dilution. In many studies the influence of rainfall on closed systems has been reported to be considerable, but the significance of the rainfall is understated (Thomas et al., 2005).

In our study if dilution had not been considered, growth rates of phytoplankton and *Acartia* would have been underestimated by 25% at the peak bloom periods around the 21st January. In contrast, the maximum growth rate of nauplii, which occurred during a period of small lagoon volume changes, could have been well estimated without considering dilution. A key step in our analysis was to incorporate the lagoon volume in the plankton and nutrient concentrations. Although the rapid increase in phytoplankton which followed the initial rainfall event was quickly assimilated by the zooplankton, the closed system remained highly susceptible to becoming eutrophic if nutrients continued to be discharged into the estuary. It is likely that effective zooplankton grazing by the dominant copepod *Acartia bispinosa* together with the high denitrification rates (Eyre and Ferguson, 2002) were instrumental in preventing eutrophic conditions from occurring. Additionally, break out of the lagoon after a sustained period of rainfall, would have resulted in a substantial flux of nutrients and carbon to the ocean which, together with the subsequent tidal flushing (>60% of volume each tidal cycle) until the lagoon closed, would assist in maintaining mesotrophic conditions within the lagoon.

Our study shows the importance of measuring volume changes in small water bodies, and of making intensive sampling when trying to determine the influences of factors such as rainfall on rapidly responding variables such as nutrients, phytoplankton and zooplankton.

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