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FEATURE ARTICLE

Jellyfish modify the response of planktonic assemblages to nutrient pulses

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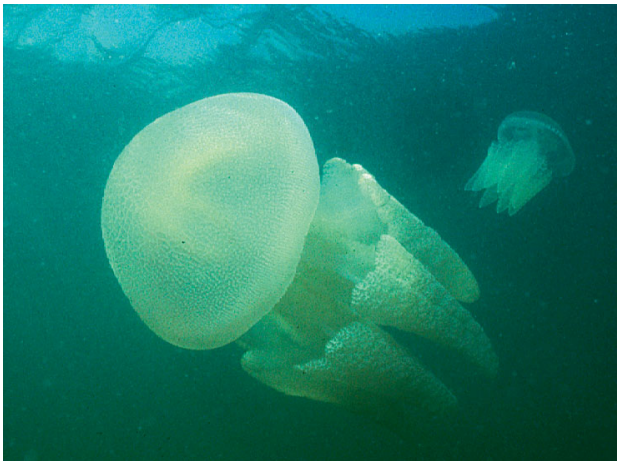
ABSTRACT: The short-term effects of pulses of nutrients and jellyfish *Catostylus mosaicus* on planktonic assemblages were investigated in field-based experiments using 3 m^3 mesocosms. Experiments ran for 5 d and were repeated in autumn and spring at Lake Illawarra, a coastal lagoon in New South Wales, Australia. Experiments consisted of 2 orthogonal treatments, addition/non-addition of nutrients and presence/absence of jellyfish, and were designed to determine how bottom-up (i.e. addition of nutrients) and top-down (i.e. predation by jellyfish) processes influence planktonic assemblages, both independently and in combination. During both experiments, nutrients stimulated primary production and caused changes in phytoplankton assemblages. Nutrients also stimulated production of large tintinnids, suggesting that bottom-up processes may influence 2 trophic levels. Mesozooplankton were consistently depleted in mesocosms containing jellyfish. Jellyfish also caused changes in microzooplankton assemblages, indicating that top-down processes also cascade to at least 2 trophic levels. In mesocosms to which both nutrients and jellyfish were added during spring, concentrations of the red-tide forming, heterotrophic dinoflagellate *Noctiluca scintillans* were 20 times greater than in mesocosms to which nutrients were added alone. We hypothesize that addition of nutrients stimulated production of centric diatoms, the main prey of *N. scintillans*, but that a bloom of *N. scintillans* only formed when jellyfish were also present because jellyfish grazed on populations of herbivorous mesozooplankton (particularly the calanoid copepod *Gladioferens*), which generally out-competed *N. scintillans* for diatom prey. These data provide the first empirical evidence linking jellyfish to the formation of red tides.

KEY WORDS: Red tides · Trophic cascades · *Catostylus mosaicus* · *Noctiluca scintillans*



Jellyfish blooms that occur in eutrophic waters may increase the prevalence of red tides.

Photo: M. J. Kingsford

INTRODUCTION

Pulses of nutrients cause great changes in coastal planktonic assemblages. Nutrient enrichment generally stimulates primary production, increasing the biomass of phytoplankton (so called 'bottom-up' control). In turn, feeding rates of grazers increase, stimulating secondary and, potentially, higher-order production (Ware & Thomson 2005, Olsen et al. 2006). Experimental research in enclosed water masses, particularly lacustrine systems, has also consistently demonstrated that abundances of phytoplankton increase when zooplanktivores are abundant (reviewed by Brett & Goldman 1996). This process may occur because grazing by planktivores reduces abundances of her-

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bivorous zooplankton, which, in turn, reduces grazing pressure on phytoplankton (i.e. top-down control) and because zooplanktivores recycle nutrients directly to phytoplankton (Vanni & Findlay 1990). If periods of nutrient enrichment coincide with periods when planktivores are abundant (i.e. if top-down and bottom-up processes coincide), responses of planktonic assemblages may differ from those observed when either top-down or bottom-up processes occur independently.

Gelatinous zooplankton are the dominant planktivores in many coastal systems and are renowned for forming episodic and spectacular population blooms. There is now compelling evidence that the biomass of jellyfish has increased in many parts of the world (Mills 2001, Purcell 2005, Link & Ford 2006, Lynam et al. 2006). Gelatinous zooplankton typically prey on mesozooplankton and can initiate changes in planktonic assemblages that cascade to lower trophic levels (Olsson et al. 1992, Granéli & Turner 2002, Stibor et al. 2004). Coastal regions are also susceptible to episodic inputs of nutrients, which are often delivered from the surrounding catchments in large pulses following periods of heavy rain. Changes in planktonic assemblages associated with nutrient enrichment are likely to be very different if pulses of nutrients are delivered at times when predatory jellyfish are abundant.

The large scyphozoan jellyfish *Catostylus mosaicus* regularly forms blooms in the estuaries and coastal lagoons of eastern and northern Australia. Average abundances during blooms may exceed 2 medusae m^{-3} (Pitt & Kingsford 2000), but in localised patches, concentrations of small medusae may exceed 100s medusae m^{-3} (K. A. Pitt pers. obs). Many of the estuaries where *C. mosaicus* occurs are also under increasing anthropogenic pressure from urbanization and agricultural development and often receive pulses of nutrients following periods of heavy rain (Gillanders & Kingsford 2002). The objective of our experiments was to determine how pulses of nutrients and the presence of *C. mosaicus* influence planktonic assemblages in a coastal lagoon. Manipulative experiments, using mesocosms, were done over 4 to 5 d to emulate pulse events of nutrients and to measure short-term responses of the planktonic assemblage. Although mesocosm experiments can suffer from artefacts (e.g. Chen et al. 1997), they provide a useful tool for undertaking manipulative experiments in pelagic systems. Experiments were repeated twice, once in autumn and once in spring, to account for temporal changes in planktonic assemblages. Specifically we wanted to determine (1) the independent influences of nutrient pulses and *C. mosaicus* on planktonic assemblages and (2) the influence of the combined effects of nutrient enrichment and medusae.

MATERIALS AND METHODS

The experiments were done at Lake Illawarra, a shallow (average depth 1.9 m), eutrophic, intermittently open/closed coastal lagoon on the south coast of New South Wales, Australia (150° 50′ S, 34° 30′ E). The average rainfall in the catchment is approximately 1100 to 1600 mm yr^{-1} and significant rainfall events (>50 mm) occur 3 to 4 times yr^{-1} (O'Donnell et al. 2004). Winter is typically the driest period. The experiments ran from 11 to 15 May and 12 to 16 September 2001. Longer experiments were not feasible as *Catostylus mosaicus* is a large medusa (>150 mm bell diameter [BD]) and would deplete stocks of zooplankton in the mesocosms over periods exceeding a few days. Experiments were done using 12 mesocosms that were suspended from individual floating platforms placed 10 to 15 m apart and secured using an anchor. Mesocosms consisted of white sailcloth bags that had been lined with transparent plastic bags. The bags extended 2 m below the water line, were approximately 1.2 m^2 and contained approximately 3 m^3 of water. The tops of the bags extended 1 m above the water's surface to prevent any exchange of water between the mesocosms and lagoon. Water that contained natural assemblages of phytoplankton and zooplankton was pumped into the bags from the surrounding lagoon from a depth of 1 m and at a rate of 250 l min^{-1}. There was little tidal movement in Lake Illawarra, so assemblages remained consistent during the preparation of the experiment.

The experiment consisted of 2 orthogonal factors (addition/non-addition of nutrients and presence/absence of jellyfish). Thus, there were 4 treatments: (1) a control, (2) jellyfish, (3) nutrients and (4) nutrients + jellyfish. Three mesocosms were randomly assigned to each treatment. Control mesocosms, to which neither jellyfish nor nutrients were added, contained only lagoon water with natural assemblages of phytoplankton and zooplankton. Two *Catostylus mosaicus* (May: 142 ± 3 mm BD; September: 136 ± 3 mm BD) were gently hand-dipped from the lake and added to each mesocosm in the jellyfish treatment. In the nutrient treatment, ammonia (NH_3), nitrate and nitrite (NO_x) and phosphate (PO_4) were added to elevate the concentrations of nutrients in the mesocosms from background concentrations (NH_3 and NO_x 2 to 5 µg l^{-1}; PO_4 70 µg l^{-1}) to levels similar to the upper limits of the nutrient concentrations observed in the lagoon (NH_3: 70.6 ± 2.7 µg l^{-1}; NO_x 71.0 ± 30 µg l^{-1}; PO_4 117.3 ± 8.6 µg l^{-1}; New South Wales Department of Environment and Climate Change unpubl. data). Both nutrients and jellyfish were added in the nutrients + jellyfish treatment. All jellyfish actively swam about the mesocosms throughout the experiments.

Physical variables. Water quality parameters were sampled twice daily using a Yeo-kal 611 water quality probe at a depth of 1 m inside the mesocosms, and additional samples were periodically taken at the same depth from the surrounding lagoon. Nutrient concentrations were determined from 20 ml subsamples of water that were extracted from each mesocosm using a sampling tube. The tube had a diameter of 50 mm and held a volume of approximately 2 l. The tube was slowly inserted to just above the bottom of the mesocosm, the end of the tube was sealed and an integrated sample of the water column was extracted. Samples were filtered through 0.45 µm filters and frozen. Nutrient concentrations were determined using the American Public Health Association (APHA) Method 4500 modified for NO_x, NH_3 and PO_4. The Practical Quantitation Limits were 0.07, 0.14 and 0.03 respectively.

Chlorophyll *a*. Chlorophyll *a* (chl *a*) samples were collected each afternoon (5 d in the May experiment and 4 d in the September experiment). Duplicate 2 l samples of water were collected using the sampling tube and vacuum-filtered through acetate filters. Then the filter papers were frozen and stored in darkness. Chl *a* concentrations were determined fluorometrically following the methods of Strickland & Parsons (1972).

Microplankton. Microplankton was sampled 3 times from each mesocosm during each experiment (0, 24 and 96 h after the May experiment commenced and 6, 36 and 96 h after the September experiment commenced). Duplicate samples of microplankton were collected from each mesocosm on each occasion using the sampling tube. Two litres of water were filtered through a 35 µm nylon mesh sieve and the plankton was fixed in 4% buffered formalin. In the laboratory, phytoplankton were enumerated using a Lund Cell (Lund et al. 1958) and microzooplankton using a Sedgewick-Rafter cell. We used 1 ml for microzooplankton and 0.5 ml for phytoplankton, and multiple fields of view were observed until between 50 and 100 organisms had been identified and counted. Two subsamples were enumerated for each phytoplankton and microzooplankton sample (minimal additional precision was gained for additional subsamples). Concentrations were expressed as numbers l^{-1} and the averages of the 2 subsamples were used for analyses.

Mesozooplankton. Mesozooplankton were sampled at the end of each experiment using a 50 cm diameter plankton net. A 250 µm mesh net was used during May and a 100 µm mesh net during September. The nets were lowered to the bottom of each mesocosm and hauled vertically. It was not possible to take additional samples during the experiment without causing serial depletion of the experimental populations. A smaller mesh size was used in September to increase the size range of mesozooplankton sampled. Due to differences in mesh sizes, direct comparisons in mesozooplankton assemblages between May and September were not attempted. Zooplankton were preserved in 4% buffered formalin. In the laboratory, zooplankton were enumerated in 2 subsamples (2 to 3 ml) in a Bogorov tray. Averages of the 2 subsamples were used in analyses.

Data analyses. Differences in assemblages of phytoplankton, microzooplankton and mesozooplankton were displayed graphically using multidimensional scaling (MDS) plots based on Bray-Curtis similarity measures (Bray & Curtis 1957), and hypotheses about differences among treatments were tested using analyses of similarities (ANOSIMs) (Clarke & Greene 1988). For phytoplankton and microzooplankton assemblages, separate 1-way ANOSIMs were used to assess possible differences in assemblages among jellyfish and nutrient treatments for each time sampled. Where differences in assemblages were detected between treatments, or if there was a strong trend for assemblages to differ, even if not significant at $\alpha = 0.05$, similarity of percentages (SIMPER) tests were used to determine which species contributed the most to the dissimilarity between treatments.

Differences in [chl *a*] and selected phytoplankton and microzooplankton taxa were analysed using repeated measures analyses of variance (ANOVA). The treatments were addition/non-addition of nutrients, presence/absence of jellyfish (both fixed, orthogonal factors) and mesocosms (a random factor, nested within nutrients and jellyfish). Time was the repeated measure. Dependency among times was tested and found to be non-significant. Homogeneity of variances was tested prior to doing ANOVAs using a Cochran's test. Attempts were made to stabilise heterogeneous variances using $\ln(x+1)$ transformations, but if variances could not be stabilised, untransformed data were analysed and α was reduced to 0.01 to reduce the risk of Type I error (Underwood 1997). When significant differences were detected, post-hoc planned contrasts were used to identify where the differences occurred. Differences in concentrations of mesozooplankton (which were sampled at the end of the experiments only) between nutrient and jellyfish treatments were analysed using 2-way ANOVAs, and if significant interactions were observed, post-hoc Student-Newman-Keuls (SNK) tests were used to determine which treatments differed.

RESULTS

Physical variables

The water temperature and salinity in the mesocosms varied from 15.9 to 16.9°C and 29.6 to 30.5 psu during May and 15.6 to 17.3°C and 28.4 to 28.8 psu

during September. Temperatures and salinities did not vary among treatments and remained similar to the surrounding lagoon. During both experiments, concentrations of NH_3 and NO_x in mesocosms enriched with nutrients decreased from 70.6 ± 2.7 and 71.0 ± 3.0 µg l^{-1}, respectively, to control levels (2 to 5 µg l^{-1} for both nutrients) within 20 to 48 h after the experiments commenced. In contrast, concentrations of PO_4 decreased slowly from 117.3 ± 8.6 to 80.1 ± 5.3 µg l^{-1}, and at the end of the experiments these were still elevated relative to control mesocosms (40.3 ± 5.5 µg l^{-1}). Nutrient concentrations in control mesocosms remained stable throughout the experiments.

Chlorophyll *a*

Nutrients and jellyfish had significant effects on [chl *a*] during both the May and September experiments (Table 1). Post-hoc contrasts showed that during May, [chl *a*] was elevated in mesocosms containing nutrients and those containing jellyfish at all times except for the first time sampled (Fig. 1). A similar pattern was observed during September, although [chl *a*] was already more concentrated in mesocosms containing nutrients at the first time sampled (6 h after the experiment commenced; Fig. 1).

Phytoplankton

In May no differences were detected in the assemblages of phytoplankton present among jellyfish treatments at any time, but phytoplankton assemblages did vary between nutrient treatments at 96 h (Fig. 2A, Table 2). The phytoplankton that contributed the most

Table 1. Results of repeated measure ANOVAs of [chl *a*] during the May and September 2001 experiments. N: nutrients, J: jellyfish, M: mesocosm, T: time, NS: not significant, MS: mean square

Variable	df	May		September	
		MS	p	MS	p
N	1	6143.93	<0.01	32235.95	<0.01
J	1	476.84	<0.01	1196.68	0.05
N × J	1	6.53	0.60	96.98	0.53
M (N, J)	8	21.94	<0.01	229.82	<0.01
T	2	271.31	<0.01	2430.22	<0.01
T × N	2	386.92	<0.01	1669.01	<0.01
T × J	2	37.92	<0.01	183.73	0.02
T × N × J	2	4.063	0.15	7.92	0.91
T × M (N, J)	16	2.144	0.01	43.18	<0.01
Error	24	0.947		16.44	
Transformation		Nil		Nil	
Cochran's *C*		0.13, NS		0.63, p < 0.01	
α		0.05		0.01	

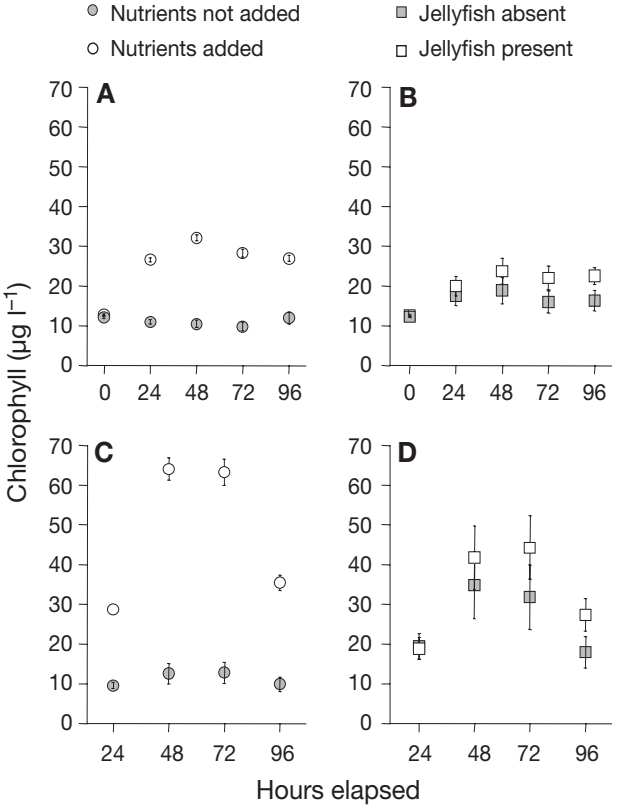

Fig. 1. Temporal variation in mean (±SE) concentrations of chl *a* between (A) nutrient and (B) jellyfish treatments during May and (C) nutrient and (D) jellyfish treatments during September

Table 2. Results of analyses of similarity (ANOSIM) among treatments for phytoplankton, microzooplankton and netplankton assemblages for the May and September 2001 experiments. N: nutrients, J: jellyfish. For phytoplankton and microzooplankton assemblages separate analyses were done for each run. 462 permutations used in all cases

		Phyto-plankton		Microzoo-plankton		Mesozoo-plankton	
		Global R	p	Global R	p	Global R	p
May							
0 h	J	−0.002	0.36	−0.119	0.91		
	N	−0.074	0.77	−0.072	0.68		
24 h	J	0.054	0.25	0.146	0.10		
	N	−0.065	0.64	−0.107	0.88		
96 h	J	−0.109	0.84	0.528	0.01	0.211	0.022
	N	0.628	0.02	0.08	0.23	−0.109	0.929
September							
6 h	J	−0.141	0.96	−0.059	0.71		
	N	0.102	0.14	−0.041	0.29		
36 h	J	−0.039	0.51	0.013	0.36		
	N	0.204	0.08	−0.007	0.37		
96 h	J	0.061	0.23	0.211	0.05	0.617	0.004
	N	0.122	0.12	0.424	<0.01	−0.017	0.45

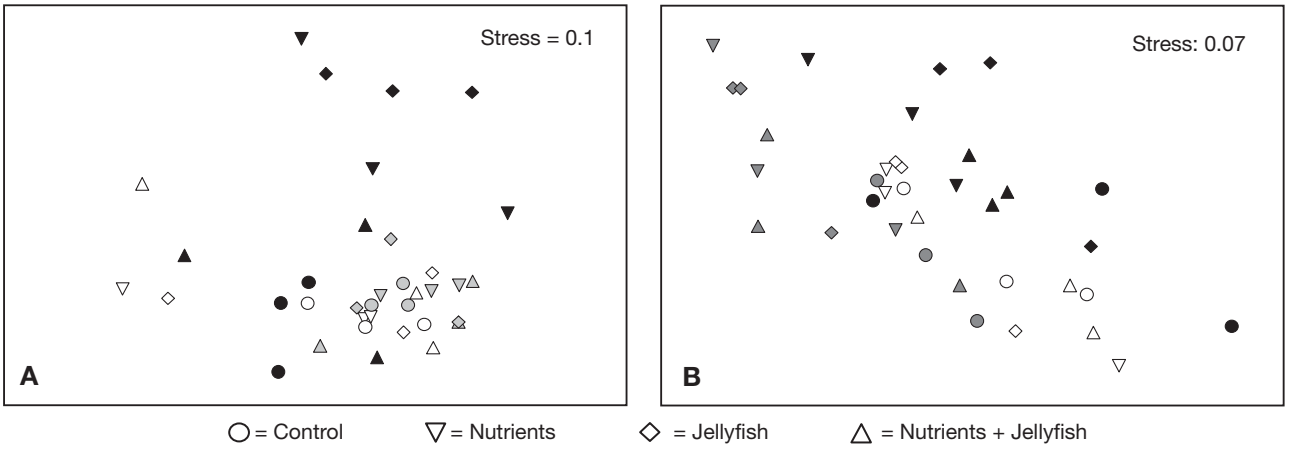

Fig. 2. MDS plots of variation in assemblages of phytoplankton among treatments and runs during (A) May and (B) September. Symbols for May: white = 0 h, grey = 24 h, black = 96 h; for September: white = 6 h, grey = 36 h, black = 96 h

to the dissimilarity between nutrient treatments at the end of the experiment were the centric diatoms of the order Biddulphiales, including *Chaetoceros* sp. (suborder Biddulphiineae; 30.1%), members of the suborder Coscinodiscineae (25.4%, dominated by *Skeletonema costatum* and *Thalassiosira rotula*), and *Ceratulina* sp. (suborder Biddulphiineae; 8.2%). The pennate diatom *Nitzschia closterium* (order Bacillariales) contributed 7.0% to the dissimilarity between nutrient treatments.

Nutrients had a large influence on concentrations of the diatoms *Nitzschia closterium*, *Thalassiosira rotula* and *Ceratulina* sp. (T × N interaction, Table 3) and, in

Table 3. Results of repeated measures ANOVAs for selected phytoplankton taxa sampled during May and September 2001. N: nutrients, J: jellyfish, M: mesocosm, T: time, NS: not significant, MS: mean square

May	df	*Nitzschia closterium*		*Thalassiosira rotula*		*Ceratulina* sp.		*Chaetoceros* sp.		*Skeletonema costatum*	
Variable		MS × 10^8	p	MS × 10^8	p	MS	p	MS × 10^{10}	p	MS	p
N	1	78.21	<0.01	109.15	0.12	0.42	0.90	6.65	0.57	1.05	0.48
J	1	1.22	0.61	42.06	0.32	1.07	0.84	4.54	0.64	0.25	0.72
N × J	1	0.06	0.91	3.71	0.76	0.01	0.98	2.49	0.73	0.10	0.82
M (N, J)	8	4.34	0.12	36.78	<0.01	24.39	0.04	19.23	0.03	1.79	0.01
T	2	42.58	<0.01	93.61	<0.01	3.33	0.55	47.49	0.01	5.08	<0.01
T × N	2	49.63	<0.01	63.54	<0.01	37.11	<0.01	3.42	0.60	0.57	0.29
T × J	2	3.09	0.43	0.43	0.94	4.49	0.45	7.71	0.34	0.06	0.86
T × N × J	2	0.02	0.99	1.42	0.82	2.61	0.63	1.57	0.79	0.40	0.41
T × M (N, J)	16	3.43	0.11	7.44	<0.01	5.39	0.75	6.57	0.34	0.42	0.08
Error	24	1.97		2.52		7.47		5.47		0.22	
Transformation		Nil		Nil		Ln		Nil		Ln	
Cochran's *C*		0.16, NS		0.50, p < 0.01		0.21, NS		0.28 NS		0.19 NS	
α		0.05		0.01		0.05		0.05		0.05	

September	df	*Nitzschia closterium*		*Skeletonema costatum*		*Pseudo-nitzschia seriata*		*Chaetoceros* sp.	
Variable		MS × 10^8	p	MS × 10^{11}	p	MS × 10^9	p	MS	p
N	1	17.81	0.01	21.14	0.10	279.80	0.05	5.55	0.02
J	1	0.34	0.62	1.16	0.67	7.36	0.72	0.10	0.70
N × J	1	0.79	0.45	3.28	0.48	0.08	0.97	0.34	0.48
M (N, J)	8	12.45	<0.01	5.98	<0.01	52.62	<0.01	0.61	0.01
T	2	77.60	<0.01	52.16	<0.01	80.03	0.02	3.65	<0.01
T × N	2	5.35	<0.01	9.84	0.11	26.20	0.23	0.74	0.23
T × J	2	0.87	0.77	5.24	0.29	1.86	0.89	0.44	0.41
T × N × J	2	0.33	0.63	1.27	0.73	2.33	0.87	1.06	0.14
T × M (N, J)	16	0.69	<0.01	3.92	<0.01	16.43	<0.01	0.46	0.14
Error	24	0.14		0.54		1.46		0.29	
Transformation		Nil		Nil		Nil		ln	
Cochran's *C*		0.19, NS		0.27, NS		0.14, NS		0.23, NS	
α		0.05		0.05		0.05		0.05	

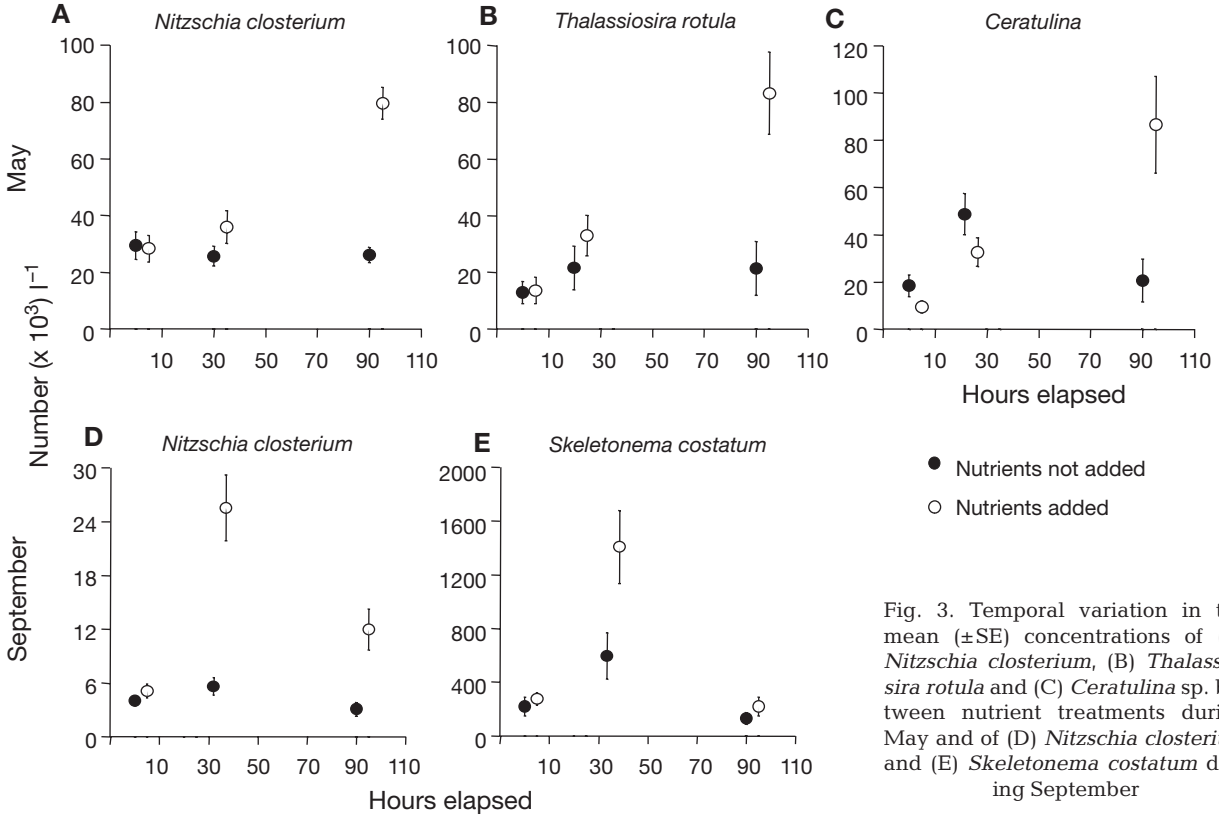

Fig. 3. Temporal variation in the mean (±SE) concentrations of (A) *Nitzschia closterium*, (B) *Thalassiosira rotula* and (C) *Ceratulina* sp. between nutrient treatments during May and of (D) *Nitzschia closterium* and (E) *Skeletonema costatum* during September

all cases, by 96 h these diatoms were 2 to 4 times more abundant in the mesocosms with nutrients than those without (Fig. 3). Other species of diatoms (*Chaetoceros* sp. and *Skeletonema costatum*) did not respond to either jellyfish or nutrients, but concentrations had decreased in all treatments by 96 h. Concentrations of *Ceratulina* sp., *Chaetoceros* sp. and *S. costatum* varied among mesocosms within each treatment, while *T. rotula* also varied among mesocosms, but the pattern of variation among mesocosms varied among times (Table 3).

In September, assemblages of phytoplankton did not vary between jellyfish treatments at any time (Fig. 2B, Table 2). There was a strong indication that nutrients may have caused changes in phytoplankton assemblages by 36 and 96 h ($p = 0.08$ and 0.12 respectively), but this result was not statistically significant (Table 2). SIMPER indicated that the species that may have contributed towards the dissimilarity between nutrient treatments were the pennate diatom *Pseudo-nitzschia seriata* (30.8%), centric diatoms of the order Coscinodiscineae (27.9%, dominated by *Skeletonema costatum*), *Chaetoceros* sp. (9.1%) and *Nitzschia closterium* (6.3%).

Nitzschia closterium also responded to nutrients during September, with elevated concentrations in nutrient treatments at both 36 and 96 h (Table 3, Fig. 3D). Although non-significant, *Skeletonema costatum* showed a strong trend to be more concentrated in the mesocosms containing nutrients at 36 h, but by the end of the experiment, concentrations had decreased and were similar to those in mesocosms without nutrients (Fig. 3E). In contrast, *Chaetoceros* sp. and *Pseudo-nitzschia seriata* also responded to nutrients and were more concentrated in nutrient treatments throughout the experiment. Concentrations of *N. closterium, S. costatum* and *P. seriata* varied among mesocosms, but patterns of variation were not consistent through time (Table 3). Concentrations of *Chaetoceros* sp. varied among mesocosms within treatments (Table 3).

Microzooplankton

In May, nutrients had no detectable influence on assemblages of microzooplankton, but microzooplankton communities differed between jellyfish treatments at the end of the experiment (Fig. 4A, Table 2). Smooth large (80 to 120 µm) tintinnids (24.1%), small (<80 µm) armoured dinoflagellates (20.5%), rough small (<80 µm) tintinnids (13.6%) and large (80 to 130 µm) armoured dinoflagellates (12.8%) contributed the most to the dissimilarity between jellyfish treatments.

Concentrations of calanoid copepod nauplii had decreased in mesocosms containing jellyfish at the end of the experiment (Table 4, Fig. 5A). There was also a

Table 4. Repeated measure ANOVAs for selected microzooplankton taxa sampled during May and September 2001. N: nutrients, J: jellyfish, M: mesocosm, T: time, NS: not significant, MS: mean square

May	df	Small armoured dinoflagellates		Copepod nauplii		Large armoured dinoflagellates		Large smooth tintinnids		Small rough tintinnids	
Variable		MS × 10^6	p	MS	p	MS × 10^5	p	MS × 10^6	p	MS × 10^6	p
N	1	0.69	0.82	7.35	0.54	72.34	0.42	1.51	0.30	0.84	0.75
J	1	27.46	0.18	406.13	<0.01	408.99	0.08	22.80	<0.01	0.63	0.78
N × J	1	3.31	0.62	10.89	0.46	0.96	0.93	1.27	0.34	0.08	0.92
M (N, J)	8	12.38	<0.01	17.82	0.13	100.06	<0.01	1.22	<0.01	7.47	<0.01
T	2	6.66	0.47	184.34	<0.01	41.63	0.08	19.71	<0.01	51.17	<0.01
T × N	2	2.52	0.74	18.69	0.19	22.06	0.24	1.51	<0.01	1.68	0.65
T × J	2	15.70	0.19	54.76	0.02	48.15	0.06	23.25	<0.01	0.53	0.87
T × N × J	2	0.004	0.99	18.25	0.19	7.02	0.62	1.34	0.01	0.18	0.95
T × M (N, J)	16	8.36	0.02	9.97	0.63	14.08	0.06	0.23	0.13	3.83	0.01
Error	24	3.39		11.81		7.09		0.14		1.41	
Transformation		Nil		Nil		Nil		Nil		Nil	
Cochran's *C*		0.18, NS		0.22, NS		0.23, NS		0.40, p < 0.01		0.21, NS	
α		0.05		0.05		0.05		0.01		0.05	
September	df	Small armoured dinoflagellates		Small naked dinoflagellates		Copepod nauplii		Rough large tintinnids		Large ciliates	
Variable		MS × 10^6	p	MS	p	MS × 10^5	p	MS × 10^6	p	MS × 10^6	p
N	1	19.82	0.08	127.41	0.03	0.05	0.90	6.72	0.36	0.002	0.98
J	1	0.63	0.71	0.158	0.93	20.87	0.03	2.98	0.54	0.16	0.84
N × J	1	1.19	0.61	15.99	0.37	0.44	0.71	13.63	0.21	0.76	0.65
M (N, J)	8	4.14	<0.01	17.49	<0.01	2.97	<0.01	7.17	<0.01	3.48	<0.01
T	2	78.21	<0.01	225.38	<0.01	6.94	<0.01	14.80	<0.01	4.61	0.04
T × N	2	1.65	<0.01	125.24	<0.01	0.31	0.46	4.76	0.06	2.33	0.17
T × J	2	0.97	0.56	8.32	0.26	2.42	0.01	1.51	0.37	0.92	0.48
T × N × J	2	0.002	0.99	8.54	0.26	0.20	0.61	7.62	0.02	1.18	0.39
T × M (N, J)	16	0.16	<0.01	5.68	<0.01	0.38	0.14	1.42	0.06	1.18	<0.01
Error	24	0.04		1.92		0.24		0.71		0.12	
Transformation		Nil		Nil		Ln		Ln		Ln	
Cochran's *C*		0.31, p < 0.05		0.24, NS		0.13, NS		0.21, NS		0.25, NS	
α		0.01		0.05		0.05		0.05		0.05	

strong, but non-significant trend for large armoured dinoflagellates to be more abundant in treatments containing jellyfish (Table 4, Fig. 5B). After 96 h, smooth large tintinnids were most abundant in mesocosms containing only nutrients and were also abundant in control mesocosms but remained in small concentrations in mesocosms containing jellyfish (Table 4, Fig. 5C). Jellyfish had no influence on concentrations of small armoured dinoflagellates or small rough tintinnids (Table 4). With the exception of calanoid copepod nauplii, all microzooplankton varied among mesocosms, but patterns of variation of small armoured dinoflagellates and small rough tintinnids among mesocosms varied through time (Table 4).

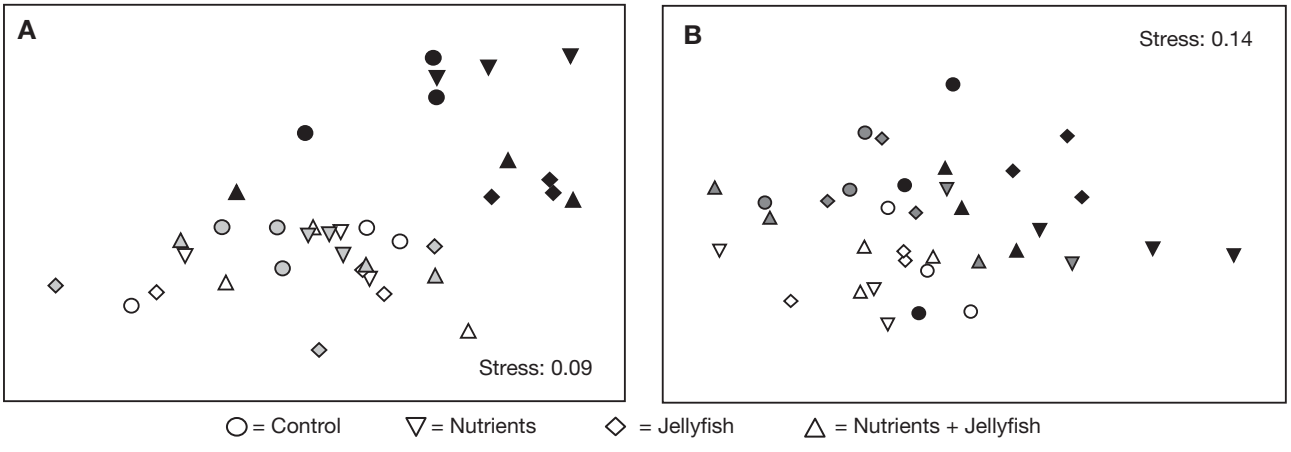

Fig. 4. MDS plots of variation in assemblages of microzooplankton among treatments and runs during (A) May and (B) September. Symbols for May: white = 0 h, grey = 24 h, black = 96 h; for September: white = 6 h, grey = 36 h, black = 96 h

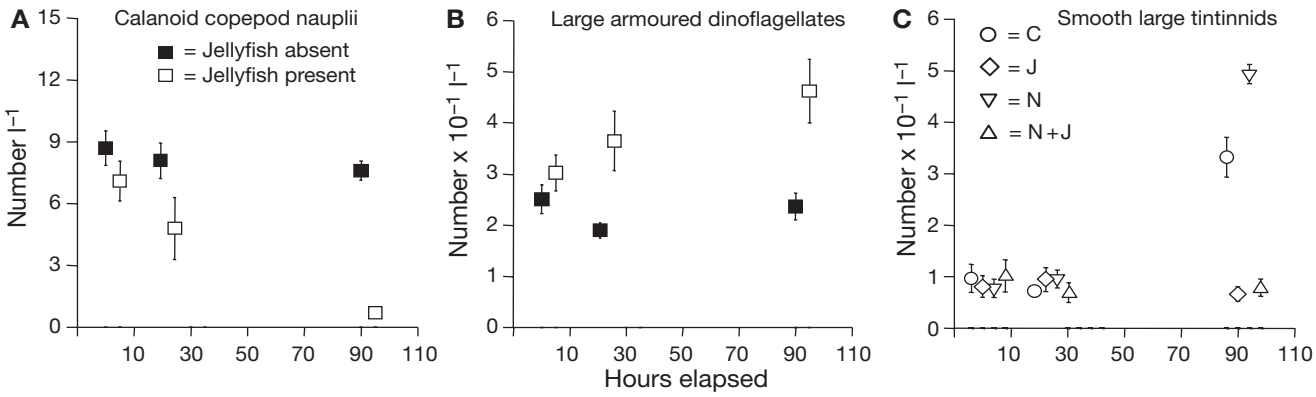

Fig. 5. Temporal variation in the mean (±SE) concentrations of (A) calanoid copepod nauplii and (B) large armoured dinoflagellates between jellyfish treatments and of (C) smooth large tintinnids among all treatments during May. C = control, N = nutrients added, J = jellyfish added

In September, differences in microzooplankton assemblages between jellyfish and nutrient treatments were detected after 96 h (Table 2, Fig. 4B). The species that contributed most to the dissimilarity between the nutrient and jellyfish treatments, respectively, were small armoured dinoflagellates (19.4% and 16.1%), small naked dinoflagellates (15.0% and 12.3%), rough large tintinnids (12.3% and 12.6%) and large ciliates (11.2 and 12.7%).

Small armoured and small naked dinoflagellates were 2 to 3 times more concentrated in treatments containing nutrients after 96 h (Table 4, Fig. 6A,B). As in May, concentrations of calanoid copepod nauplii were greatly reduced in mesocosms that contained jellyfish (Fig. 6C). At the end of the experiment, large rough tintinnids were more than 20 times more concentrated in mesocosms to which nutrients had been added, but the response was inhibited in the mesocosms that contained both nutrients and jellyfish (Table 4, Fig. 7). Ciliates did not respond to either nutrients or jellyfish. Concentrations of copepod nauplii, rough large tintinnids and large ciliates varied among mesocosms, while variation among mesocosms for small armoured and small naked dinoflagellates and large ciliates varied among times (Table 4).

Mesozooplankton

In May, assemblages of mesozooplankton varied among jellyfish treatments (Fig. 8A). Polychaetes were the only abundant taxon sampled and contributed 39.9% to the dissimilarity between jellyfish treatments. Polychaetes were half as concentrated in mesocosms containing jellyfish (261 ± 41 cf. 583 ± 37 m^{-1}).

On an MDS plot in September, replicates from jellyfish (J and NJ) and non-jellyfish (C and N) treatments showed clear separation, indicating that assemblages of netplankton differed in the presence of jellyfish (Fig. 8B). Differences among treatments were confirmed using ANOSIM (Table 2), and SIMPER indicated that the zooplankton responsible for the dissimilarity between jellyfish treatments were *Noctiluca scintillans* (34.6%), the calanoid copepod *Gladioferens* (14.0%), *Gladioferens* nauplii (13.9%) and bivalve veligers (9.4%). *Gladioferens* copepods and nauplii were less

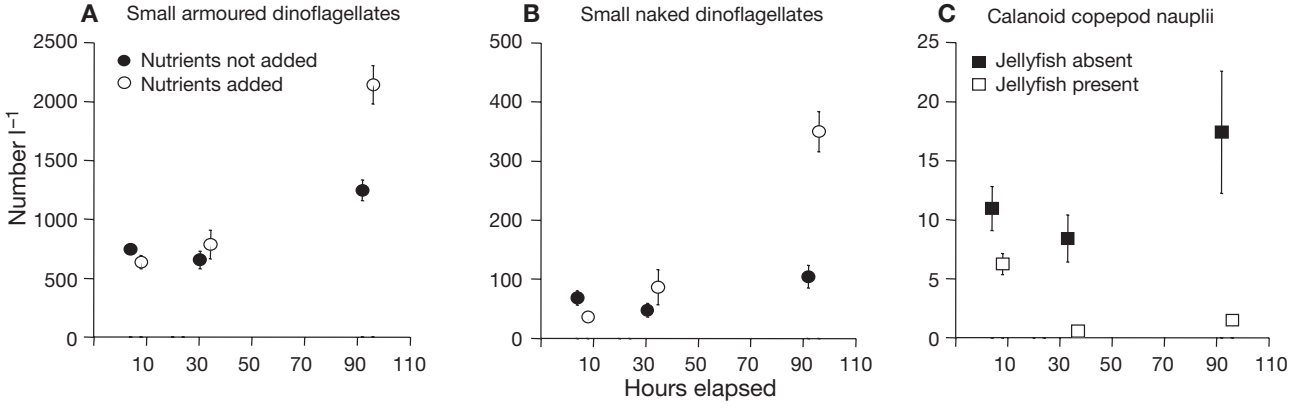

Fig. 6. Temporal variation in the mean (±SE) concentrations of (A) small armoured dinoflagellates and (B) small naked dinoflagellates between nutrient treatments and of (C) calanoid copepod nauplii between jellyfish treatments during September

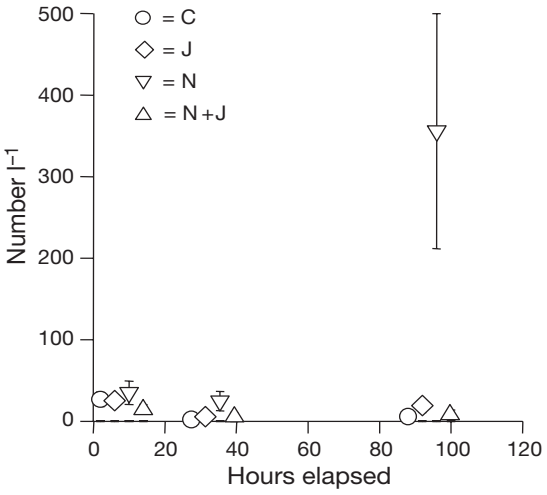

Fig. 7. Temporal variation in the mean (±SE) concentrations of rough large tintinnids (number l^{-1}) among treatments during September. C = control, N = nutrients added, J = jellyfish added

abundant in treatments containing jellyfish and, although non-significant, a similar trend was observed for bivalve veligers (Table 5, Fig. 9). There was a significant interaction between jellyfish and nutrients for *N. scintillans* (Table 5), and post-hoc SNK tests revealed that concentrations were substantially elevated in the mesocosms that contained both nutrients and jellyfish compared to those that contained nutrients alone (Fig. 10). There was also a strong, but non-significant, trend for concentrations to be elevated in treatments containing nutrients and jellyfish compared to those that only contained jellyfish.

DISCUSSION

Nutrients and jellyfish initiated very different responses in the planktonic assemblages. Combining nutrients and jellyfish, however, initiated some unique changes not apparent when treatments were applied individually. Nutrients caused a rapid increase in [chl *a*] during both May and September, indicating an overall increase in primary production. There was evidence that nutrients influenced trophic levels higher than primary producers in both experiments, but results were limited to smooth large tintinnids in May and rough large tintinnids and small armored and small naked dinoflagellates in September. Tintinnids are predominantly phytophagous (Stoecker et al. 1981, Verity 1985) and the increased concentrations observed in the nutrient treatment are likely to be a direct result of increased phytoplankton availability.

Table 5. Results of 2-way ANOVAs examining variation in concentrations of selected mesozooplankton among Nutrient and Jellyfish treatments during May and September 2001. N: nutrients, J: jellyfish, NS: not significant, MS: mean square

Variable	df	May		September							
		Polychaetes		*Gladioferens*		*Gladioferens* nauplii		Bivalve larvae		*Noctiluca scintillans*	
		MS × 10^3	p	MS × 10^6	p	MS × 10^6	p	MS × 10^3	p	MS	p
N	1	13.96	0.22	2.03	0.26	1.50	0.45	16.16	0.93	0.12	0.82
J	1	315.07	<0.01	3.25	0.01	3.36	0.01	7011.43	0.10	24.14	0.01
N × J	1	0.44	0.82	1.65	0.31	0.61	0.63	0.11	0.99	13.90	0.04
Error	8	7.84		1.38		2.40		2008.16		2.27	
Transformation		Nil		Nil		Nil		Nil		Ln	
Cochran's *C*		0.59, NS		0.75, NS		0.54, NS		0.60, NS		0.48, NS	

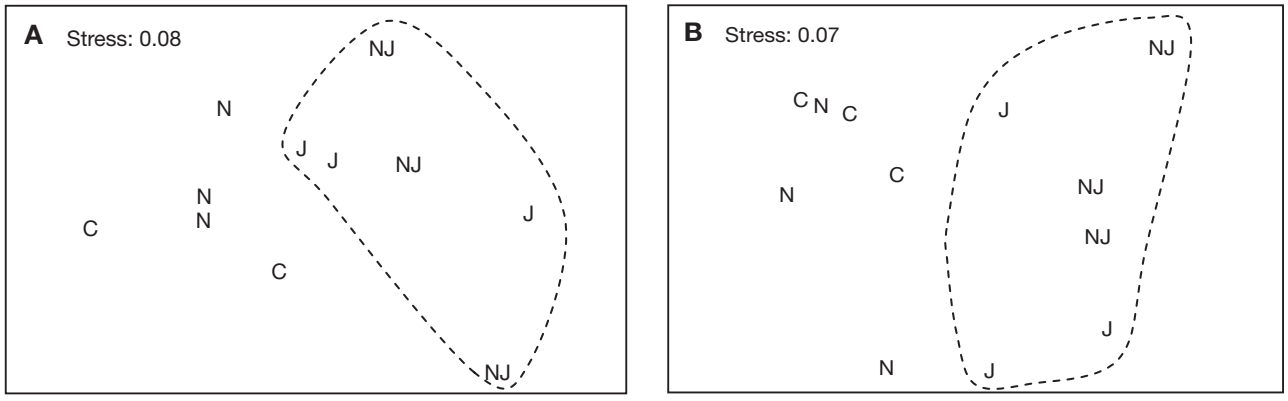

Fig. 8. MDS plots of variation in assemblages of mesozooplankton among treatments at the end of the (A) May and (B) September experiments. C = control, N = nutrients added, J = jellyfish added, NJ = nutrients and jellyfish added

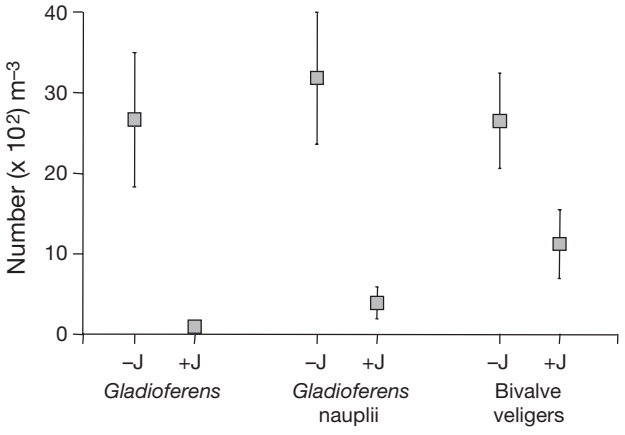

Fig. 9. Mean (±SE) concentrations of *Gladioferens*, *Gladioferens* nauplii and bivalve veligers in the absence (–J) and presence (+J) of jellyfish during September

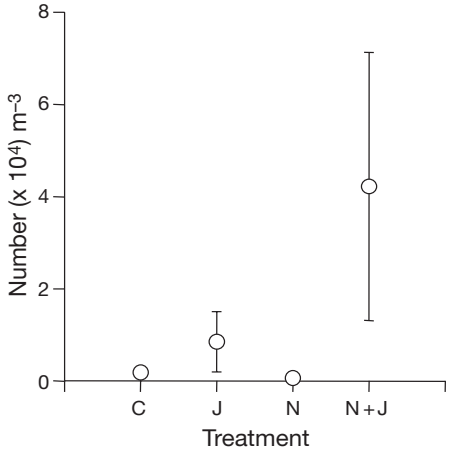

Fig. 10. Mean (±SE) concentrations of *Noctiluca scintillans* (number m^{-3}) among treatments during September. C = controls, N = nutrients added, J = jellyfish added

Dinoflagellates, however, may be autotrophic, mixotrophic or heterotrophic and the functional groups used may have comprised species of varying trophic modes. Their increase in concentration may have been a direct response to nutrient enrichment, a response to increased availability of prey or due to a combination of both processes. Since the response of dinoflagellates was much slower than that of phytoplankton, particularly during September, their increase most likely reflected increased food supply rather than a simple response to nutrient enrichment. Mesozooplankton did not respond to increases in nutrients, which probably reflects their longer turnover times, and longer experiments may be needed to determine if bottom-up responses cascade to higher trophic levels.

Jellyfish had a considerable impact on the mesozooplankton community, with concentrations of all of the most abundant taxa decreasing in mesocosms exposed to jellyfish. *Catostylus mosaicus* captures a range of mesozooplankton, but most notably copepods, mollusc veligers and polychaetes (Browne & Kingsford 2005, Peach & Pitt 2005), and most of these groups decreased substantially in treatments containing jellyfish. Jellyfish also caused changes in the assemblages of microzooplankton during both the May and September experiments. During May, concentrations of large armoured dinoflagellates increased in the presence of jellyfish. Most likely, this represented a top-down process because grazing by *C. mosaicus* on mesozooplankton may have reduced the grazing pressure of mesozooplankton on the dinoflagellates. This result contrasts with that of Sommer et al. (2004), however, who observed that armoured dinoflagellates were not preyed on by mesozooplankton in a mesocosm study. The mesozooplankton in their study was dominated by copepods, and while copepods were also numerically dominant in our study, it is possible that the other abundant mesozooplankton, such as polychaetes or mollusc veligers, may have preyed on the armoured dinoflagellates. Such trophic cascades are consistent with those previously observed in ctenophore–copepod–ciliate food webs (Granéli & Turner 2002).

In both experiments, [chl *a*] was elevated by approximately 25% in treatments containing jellyfish, suggesting that jellyfish may stimulate primary production. The rapidity of the response, which was apparent within 24 to 36 h, however, indicates that it is unlikely to have resulted from a top-down process because in a trophic cascade changes in primary production should lag behind those in zooplankton assemblages. Jellyfish also had no discernable effects on assemblages of phytoplankton during either experiment, indicating that top-down processes may not cascade to the level of primary producers. *Catostylus mosaicus* excretes ammonium at a rate of 1 to 1.5 mg kg^{-1} (wet weight) h^{-1} (Pitt et al. 2005). During the early stages of the experiments, the ammonium excreted would have resulted from feeding done prior to the jellyfish being added to the mesocosms, rather than a recycling of nitrogen within the mesocosms. Mesocosms containing jellyfish, therefore, also effectively had an addition of nutrients. Based on the size of the medusae used in the study, their weight would have equated to approximately 1 kg each (Pitt & Kingsford 2003). If we conservatively estimate that the first 10 h of excretion represents nitrogen obtained from feeding prior to placement in the mesocosms, then the amount of additional ammonium excreted by the 2 medusae in each mesocosm would be approximately 8.5 µg l^{-1}. This value represents approximately 10% of the ammonia that was added to the nutrient treatments and may account for the rapid increase in [chl *a*] seen in the jellyfish treatments. Because jellyfish had no detectable influence

on phytoplankton assemblages, however, the additional nutrients in the jellyfish treatments had minimal influence on community structure, and were therefore unlikely to have confounded interpretations of our results.

The major objective of this research was to identify interactive effects of jellyfish and nutrients. Interactions were observed for 3 groups—smooth large tintinnids in May, and rough large tintinnids and the heterotrophic dinoflagellate, *Noctiluca scintillans* in September. Although the smooth and rough large tintinnids increased substantially in the mesocosms to which only nutrients were added, their production was inhibited in mesocosms that contained both nutrients and jellyfish. Jellyfish generally appear to capture few tintinnids (Stoecker et al. 1987, Larson 1991). *Catostylus mosaicus* does capture tintinnids, but tintinnids have been observed on the oral arms of less than half the medusae sampled at a given time, suggesting that it does not prey intensively on them (Browne & Kingsford 2005). Towards the end of the experiment, however, food may have been limited and so grazing by *C. mosaicus* may have inhibited the increase in tintinnids seen in the mesocosms treated with nutrients only.

Evidence of synergism between nutrients and jellyfish was found for 1 species only; the red-tide forming, heterotrophic dinoflagellate *Noctiluca scintillans*. *N. scintillans* has a global distribution, and during spring and summer may form blooms in the coastal waters and estuaries of New South Wales (NSW), including Lake Illawarra (Dela-Cruz et al. 2002, 2003). In the coastal waters adjacent to Lake Illawarra, upwelling of nutrient-rich slope water is thought to promote production of diatoms preyed on by *N. scintillans*, stimulating production of the dinoflagellate (Dela-Cruz et al. 2002). In the current study, however, nutrients alone had no effect on concentrations of *N. scintillans*, even though production of diatoms on which *N. scintillans* is known to prey (e.g. *Chaetoceros* sp.) was enhanced by the addition of nutrients. When both nutrients and jellyfish were added to the mesocosms, however, concentrations of *N. scintillans* were, on average, more than 20 times greater than the mesocosms to which nutrients had been added alone.

Noctiluca scintillans grazes on a range of prey, including phytoplankton, protists and the eggs of copepods (reviewed by Elbrächter & Qi 1998). In the coastal waters of NSW, however, the dominant food of *N. scintillans* is centric diatoms (Dela-Cruz et al. 2002). In the current study, the calanoid copepod *Gladioferens* and bivalve veligers were the most abundant mesozooplankton in the mesocosms without jellyfish. In culture, *Gladioferens* feeds efficiently on diatoms such as *Chaetoceros* (Payne & Rippingale 2000). If prey was limiting, therefore, *Gladioferens*, may have competed directly with *N. scintillans* for diatom prey. *N. scintillans,* however, probably competes poorly with other mesozooplankton because it is a largely immobile, interception predator and its clearance rates are less than those of similar sized zooplankton (Hansen et al. 1997, Kiørboe & Titelman 1998). More mobile mesozooplankton, such as copepods, are likely to have much greater encounter rates and rapidly deplete phytoplankton when resources are limiting. Consequently, although the addition of nutrients to mesocosms may have stimulated primary production and increased the availability of food for *N. scintillans*, the competition exerted by co-occurring mesozooplankton (in particular *Gladioferens*) in the absence of jellyfish may have limited production of *N. scintillans.*

Catostylus mosaicus is a voracious predator of mesozooplankton and, with the exception of *Noctiluca scintillans*, it effectively removed most mesozooplankton from the mesocosms, including the copepod and naupliar stages of *Gladioferens*. Jellyfish, however, feed selectively on different types of zooplankton (e.g. Fancett 1988), possibly due to variations in the morphology of their nematocysts (Purcell & Mills 1988). While *N. scintillans* has been recorded on the oral arms of *C. mosaicus* (Browne & Kingsford 2005, Peach & Pitt 2005), it is generally considered to be a poor source of prey due to its low carbon (Kiørboe & Titelman 1998) and high ammonia (Okaichi & Nishio 1976) content. *N. scintillans* may not, therefore, be the preferred source of prey of *C. mosaicus*, and the large concentrations of *N. scintillans* that remained in the mesocosms containing jellyfish at the end of the experiment indicate that *C. mosaicus* did not graze intensively on this species. For *N. scintillans* to achieve growth rates conducive to forming red tides, its prey must be concentrated (Kiørboe & Titelman 1998). The greatest growth of *N. scintillans* occurred, therefore, only when both nutrients and jellyfish were present, since the nutrients stimulated rapid growth of diatoms which *N. scintillans* was able to graze on in the absence of substantial competition from other herbivorous mesozooplankton.

Gelatinous zooplankton have been previously linked to blooms of plankton, but data have been correlative and it is difficult, therefore, to attribute causation (Schneider & Behrends 1998, Fock & Greve 2002, Oguz et al. 2001). For example, modeling of trophic interactions in the Black Sea indicates that phytoplankton blooms are especially pronounced when gelatinous predators are abundant (Oguz et al. 2001). Analysis of the Helgoland Roads time series in the North Sea also indicated an inverse correlation between *Noctiluca scintillans* and the ctenophore *Pleurobrachia pileus*, hydromedusae, chaetognaths and copepods, all of which were thought to prey on *N. scintillans* (Fock & Greve 2002). The food web model generated by Fock &

Greve (2002) indicates that scyphozoan jellyfish and the ctenophore *Beroe* prey on *P. pileus* and copepods, but not on *N. scintillans,* suggesting that if scyphozoans were present, their predation on *P. pileus* and copepods may reduce the predation pressure of the ctenophore and copepods on *N. scintillans*, potentially enabling it to form blooms. Blooms of *N. scintillans* occur predominantly in spring and summer (Elbrächter & Qi 1998), which coincides with the major period of population growth of many medusae (Möller 1980, Brewer 1989). Our study provides the first empirical evidence linking gelatinous zooplankton to the development of red tides.

The biomass of gelatinous zooplankton has increased in many parts of the world (Mills 2001, Purcell 2005). In some cases this has resulted from the introduction of invasive species (Shiganova 1998, Graham et al. 2003), but increases in abundances of native species have also occurred (e.g. Brodeur et al. 1999, Link & Ford 2006, Lynam et al. 2006). Eutrophication of coastal waters has also increased dramatically over the past century (Clarke et al. 2006) and is likely to continue to increase as populations grow and land is cleared for agricultural and urban development. There is an increasing likelihood, therefore, that jellyfish blooms will coincide with periods of nutrient enrichment, potentially leading to the formation of more red tides.

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