Top-down and bottom-up influences of jellyfish on primary productivity and planktonic assemblages

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Abstract

A manipulative mesocosm experiment was done in a saline coastal lake in Australia to compare the top-down and bottom-up influences of jellyfish on primary production and planktonic assemblages. We hypothesized that non-zooxanthellate jellyfish (Catostylus mosaicus) would exert both ‘top-down’ (grazing) and ‘bottom-up’ (nutrient excretion) effects, whereas zooxanthellate jellyfish (Phyllorhiza punctata) would only exert top-down influences, as their dissolved excretory products are internally recycled to their zooxanthellae rather than released into the water column. Experimental treatments consisted of triplicate mesocosms that contained two C. mosaicus, two P. punctata, a combination of C. mosaicus and P. punctata, no jellyfish, and an open-water control (sampling outside mesocosms). Both species of jellyfish preyed heavily on mesozooplankton, initiating a top-down trophic cascade that resulted in increased production of the heterotrophic dinoflagellate Protoperidinium sp. However, no increase in primary production or phytoplankton biomass was observed in the treatments containing P. punctata, indicating that top-down processes did not extend to primary producers. Bottom-up excretion of nutrients, however, caused phytoplankton biomass to more than double in the C. mosaicus treatment compared to all other treatments. Increased primary production was due largely to a 10-fold increase in the diatom Chaetoceros sp. and was predominantly driven by C. mosaicus excreting phosphate (PO43−), which was the limiting nutrient in the lake. Blooms of both zooxanthellate and non-zooxanthellate jellyfish will deplete mesozooplankton and alter the composition of microzooplankton assemblages via top-down processes. Excretion of nutrients by blooms of non-zooxanthellate jellyfish, however, can also greatly increase phytoplankton production and could favor algal blooms.

Jellyfish are renowned for their spectacular and episodic population blooms. Although blooms are a common characteristic of jellyfish populations, recently in some regions they appear to have increased in magnitude and frequency (Mills 2001; Link and Ford 2006; Lynam et al. 2006). There is a need, therefore, to understand the ecological effects of increasing jellyfish populations.

Jellyfish can influence planktonic assemblages through both ‘top-down’ and ‘bottom-up’ processes. Top-down influences result from the jellyfish grazing on mesozooplankton, which in turn reduces grazing of mesozooplankton on lower trophic levels (Granéli and Turner 2002; Stibor et al. 2004). Bottom-up influences result from excretion of dissolved nutrients by jellyfish, which stimulates phytoplankton production, which in turn stimulates secondary and higher order production. For example, excretion of ammonium (NH4+) by populations of jellyfish could theoretically support 8% of the nitrogen requirements for phytoplankton in Lake Illawarra, Australia (Pitt et al. 2005). 11% of the requirements in the Kiel Bight, Western Baltic (Schneider 1989), and 10% of the requirements in the Inland Sea of Japan (Shimauchi and Uye 2007).

Unlike non-zooxanthellate jellyfish, those that harbor symbiotic zooxanthellae are unlikely to exert any bottom-up influence, since their inorganic and organic excreta are sequestered by the zooxanthellae instead of being released into the water column (Kremer 2005; Pitt et al. 2009). Zooxanthellate jellyfish, however, still exert a top-down influence, because while the carbon (C) supplied by the zooxanthellae during photosynthesis can exceed the host’s C requirements (Kremer et al. 1990; McCloskey et al. 1994), they still ingest zooplankton (Kremer 2005; Peach and Pitt 2005). Comparison of the influences of zooxanthellate and non-zooxanthellate jellyfish, therefore, provides a useful means of comparing top-down and bottom-up influences of jellyfish on pelagic primary production and planktonic assemblages.

Phyllorhiza punctata and Catostylus mosaicus (Scyphozoa, Rhizostomeae) commonly co-occur in coastal lagoons and estuaries of eastern Australia. Although morphologically similar, the physiologies of these species differ as a result of the presence of symbiotic zooxanthellae in P. punctata. Both species periodically form population blooms that are likely to affect planktonic communities. For example, the biomass of C. mosaicus in coastal lagoons in New South Wales can attain an average 5 × 105 kg km−2 (Pitt and Kingsford 2003). C. mosaicus and P. punctata both capture mesozooplankton, but the number and relative proportions of taxa captured differ slightly (Peach and Pitt 2005). However, only C. mosaicus excretes dissolved nutrients to the water column (Pitt et al. 2005; West 2008). The aim of this study was to compare the top-down and bottom-up influences of jellyfish by studying how zooxanthellate (P. punctata), non-zooxanthellate (C. mosaicus), and a combination of zooxanthellate and non-
zooxanthellate \((P. \ punctata \text{ and } C. \ mosai cus)\) jellyfish influence primary productivity and planktonic assemblages in a coastal lagoon.

**Methods**

The experiment was performed at Smiths Lake, a largely unmodified, intermittently open and closed coastal lagoon in New South Wales, Australia \((152^o52'E, \ 32^o39'S)\). The lake has an area of \(10.5 \text{ km}^2\), a maximum depth of \(5 \text{ m}\), and was closed to the sea during the study. Twelve mesocosms were suspended from anchored floating platforms that were placed haphazardly \(10-15 \text{ m}\) apart in approximately \(3 \text{ m}\) water depth. Mesocosms consisted of a white sailcloth bag lined with a transparent plastic bag; mesocosms were \(2 \text{ m}\) deep and contained \(3 \text{ m}^3\) of water. The bags extended \(1 \text{ m}\) above the water line to prevent waves overtopping the mesocosms.

All mesocosms were filled with water containing natural assemblages of plankton on 22 February 2005. Water was pumped into the mesocosms from a depth of \(1 \text{ m}\) and at a rate of \(250 \text{ L min}^{-1}\). Three replicate mesocosms were randomly assigned to each of the following treatments: (1) \(P. \ punctata\) \(2 \text{ P. punctata}\) were added to each mesocosm; (2) \(C. \ mosai cus\) \(2 \text{ C. mosai cus}\) were added to each mesocosm; (3) combined species \(1 \text{ P. punctata and } 1 \text{ C. mosai cus}\) were added to each mesocosm; and (4) mesocosm control (filled with lake water only). A fifth mesocosm control (filled with lake water only). A fifth mesocosm control (filled with lake water only). A fifth mesocosm control (filled with lake water only). A fifth mesocosm control (filled with lake water only).

Individual jellyfish were collected from Smiths Lake with a small hand net and placed in the appropriate mesocosms. The average \((\pm \text{ standard error [SE]})\) wet weights \((\text{wet wts})\) of \(C. \ mosai cus\) and \(P. \ punctata\) were \(590 \pm 15 \text{ g}\) and \(603 \pm 14 \text{ g}\), respectively. The experiment commenced on the afternoon of the 22 February 2005 \(\text{day 1 and ran for 6 d. Physical parameters, nutrient concentrations, primary production, chlorophyll } a\ (\text{Chl } a)\), and plankton concentrations were measured in each mesocosm over the 6-d experiment.

**Physico-chemical parameters**—Light intensity was measured using a light meter \((\text{Licor})\) in one randomly selected mesocosm and in the lake 15 times during the experiment. Light intensity was measured at \(0.5-\text{m}\) and \(2.0-\text{m}\) water depths, with the sensor facing upward to measure incoming light and with the sensor facing downward to measure reflecting light. Water temperature, salinity, and dissolved oxygen \((\text{DO})\) were measured twice daily \((\text{morning and afternoon})\) at depths of \(0.5 \text{ m}\) and \(2.0 \text{ m}\) using a water quality probe \((\text{TPS})\). Samples for analysis of nutrient concentrations were collected twice daily \((\text{morning and afternoon})\) in each treatment. Water samples \(2 \text{ liters each}\) were collected from each of the treatments using a \(2-\text{m}\) long integrated pole sampler with a diameter of \(50 \text{ mm}\). Two subsamples \(25 \text{ mL}\) of the \(2 \text{ liter water sample}\) were filtered through \(0.45-\mu \text{m}\) pore size membrane filters and frozen \((-20^\circC)\). Nutrient concentrations were determined by flow injection analysis at the Department of Environment and Climate Change, New South Wales. Ammonium \((\text{NH}_4^+)\) was analyzed by the automated phenate method, phosphate \((\text{PO}_4^{3-})\) by the automated ascorbic acid reduction method, nitrate and nitrite \((\text{NOx})\) by the automated cadmium reduction method, and silica \((\text{Si})\) by the colorimetric method \((\text{APHA 1999})\). Dissolved inorganic nitrogen \((\text{DIN})\) concentrations were calculated from the sum of \(\text{NH}_4^+\) and NOx concentrations, and dissolved inorganic phosphorus \((\text{DIP})\) was the concentration of \(\text{PO}_4^{3-}\). The ratios \((\text{atom : atom})\) of \(\text{DIN : DIP, Si : DIN, and Si : DIP}\) were calculated for each sample. Concentrations of \(\text{PO}_4^{3-}\), however, were below the detection limits of the autoanalyzer \((0.03 \mu \text{mol L}^{-1})\) throughout the experiment, which prevented \(\text{DIN : DIP and Si : DIP}\) ratios from being reliably calculated. Therefore, the smallest possible \(\text{DIN : DIP and Si : DIP}\) ratios were estimated using the detection limit of the autoanalyzer for the concentration of \(\text{DIP}\).

**Primary production**—The light and dark bottle method was used to measure primary production within each treatment on days 2–6. Three 1-liter glass bottles from each mesocosm were filled with water. DO was measured immediately in one bottle using a biochemical oxygen demand probe \((\text{YSI})\) that was calibrated daily. The other two bottles were sealed, and one was wrapped in aluminum foil to keep the water dark (respiration only) and the other was exposed to natural light (net photosynthesis). One pair of bottles was suspended in each mesocosm at \(20-\text{cm}\) water depth, and another three pairs were suspended in the lake \((\text{lake control})\) at the same depth and incubated for \(4-9 \text{ h}\), after which \(\text{DO}\) was measured. Gross production rates \((\mu \text{mol } \text{O}_2 \text{ L}^{-1} \text{ h}^{-1})\) were calculated as the sum of the net photosynthesis and respiration rates.

**Chlorophyll a**—\(\text{Chl } a\) concentrations were used as an index of the abundance of primary producers. Samples for analysis of \(\text{Chl } a\) were collected after the mesocosms were filled with water, \(3\), and \(6\). Duplicate 1-liter samples of \(\text{water}\) were collected from each treatment using the pole sampler and were vacuum-filtered through \(0.2-\mu \text{m}\) polycarbonate membrane filters \((\text{Whatman})\). A drop of \(\text{MgCO}_3\) was placed on each filter to prevent acidification of the samples. Filters were frozen and stored in darkness. \(\text{Chl } a\) was extracted from the filters using \(90\%\) acetone, and concentrations were determined spectrophotometrically according to the method of \(\text{Lorenzen (1967)}\).

**Microplankton**—Microplankton \((35-100-\mu \text{m} \text{ fraction})\) was sampled on days 1 \((\text{i.e., immediately after mesocosms were filled with water})\), \(3\), and \(6\). Duplicate 2-liter water samples were extracted from each mesocosm using the pole sampler and filtered through a \(35-\mu \text{m}\) nylon mesh sieve, and the plankton retained on the sieve was preserved in \(4\%\) buffered formalin in seawater. Phytoplankton assemblages were enumerated microscopically using a Lund cell. Randomly selected fields of view were counted until the count for the dominant taxa and the sum of all other taxa was between \(50\) and \(100\). Individual cells of diatom chains...
were counted and classified to genus and to species level, where possible. Microzooplankton were enumerated using two methods. Ciliates and dinoflagellates were enumerated using a glass Sedgewick–Rafter chamber. Sufficient traverses (≥30) of the chamber were counted until the count for the dominant taxa and the sum of all other taxa was between 50 and 100. Ciliates were identified to the level of order, and dinoflagellates were identified to the genus or species level. Other microzooplankton were measured using a Bogorov tray. Counts were made for the entire sample and organisms were identified to the genus or species level. Abundances of microplankton were expressed as individuals (ind) L⁻¹, and since there were only minor differences between duplicate subsamples, the averages were used for analyses.

**Mesozooplankton**—Mesozooplankton assemblages were sampled on the last day of the experiment using a plankton net (50-cm diameter and 100-μm mesh size) that was lowered to the bottom of each mesocosm and hauled vertically. For the lake-water treatment, the plankton net was hauled vertically from a depth of 2 m. The net only sampled zooplankton as it ascended. It was not possible to sample mesozooplankton in the mesocosms throughout the experiment without causing serial depletion of the mesozooplankton populations. Samples were preserved in 4% formalin in seawater. Mesozooplankton were enumerated using a Bogorov tray. Copepods were identified to the genus or species level where possible. Other crustaceans, polychaetes, and mollusc larvae were identified to the class level.

**Statistical analyses**—Multivariate analyses were undertaken using PRIMER v5 statistical software. Multidimensional scaling (MDS) plots based on Bray–Curtis similarity measures (Bray and Curtis 1957) were used to graphically display differences in phytoplankton, microzooplankton, and mesozooplankton assemblages separately for each time period. One-way analyses of similarities (ANOSIMs; Clarke and Green 1988) were used to test for differences in assemblages of phytoplankton, microzooplankton, and mesozooplankton among experimental treatments. Separate ANOSIMs were done for each sample. When differences were detected, similarity of percentages (Clarke 1993) tests were used to identify the species that contributed the most to the dissimilarity between treatments. For all multivariate analyses, the averages of the two replicate samples were used.

Differences in nutrient concentrations, Si : DIN ratios, gross productivity, Chl a, and selected plankton groups were analyzed using repeated-measures ANOVA using the NCSS 2000 statistical software. Factors were Treatment (C. mosaicus, P. punctata, combined species, control, and lake control), which was fixed and orthogonal; Mesocosm, which was random and nested in Treatment; and Time, which was the repeated measure. Dependency among times was tested with Mauchly’s test of Sphericity, which showed that all variables were independent through time. Where repeated-measures ANOVAs showed significant differences, post-hoc contrasts were done to identify where differences occurred. Ratios of Si : DIP and DIN : DIP were analyzed graphically. For mesozooplankton, which were only sampled on day 6, differences between the abundances of selected plankton groups among treatments were tested with one-way ANOVAs. When ANOVAs detected significant differences, post-hoc Student–Newman–Keuls tests were used to test for differences among means. Prior to all analyses, the assumption of homosce-
dasticity was tested with Levene’s test. When variances were heterogeneous, data were appropriately transformed. When significant heterogeneity still remained even after transformations, analyses were still done on transformed data and $\pi$ was reduced to 0.01 to minimize the risk of Type I error (Underwood 1997).

Results

Physico-chemical parameters—On days 1–3 the incoming light intensity at 0.5-m depth reached a maximum of 1600 $\mu$mol quanta m$^{-2}$ s$^{-1}$, and during days 4–6 it reached 500 $\mu$mol quanta m$^{-2}$ s$^{-1}$. Incoming light intensity was similar in the mesocosms and lake control at 0.5-m water depth; however, at 2-m water depth, incoming light intensity in the mesocosms was approximately half as bright as in the lake. Reflecting light intensity in the mesocosms was $\sim$60% brighter than the lake at both water depths, which was most likely caused by the mesocosms reflecting more incoming light than the lake floor. Water temperature, salinity, and DO ranged from 26.1°C to 29.5°C, 22.0 to 22.4 g kg$^{-1}$, and 87.8% to 113.6% saturation, respectively. All three parameters were remarkably similar between depths (0.5 and 2 m), indicating that mesocosms remained well mixed. Differences among treatments were very minor.

Concentrations of NH$_4^+$ gradually decreased in all mesocosm treatments, but the same trend was not evident in the lake (Fig. 1A; Table 1). Specifically, concentrations of NH$_4^+$ were greater in the lake control than in other treatments on days 4–6 and in the mornings of days 2 and 3. Concentrations of Si decreased in all mesocosms through time but were relatively stable in the surrounding lake (Fig. 1B; Table 1). From days 2 to 6 the lake had significantly higher concentrations of Si than it did in all other treatments. On days 4–6 there were significantly higher concentrations of Si in the control mesocosms than in mesocosms containing jellyfish, and Si concentrations in the $P$. punctata treatment were greater than those in the treatments containing C. mosaicus. Concentrations of NOx did not differ between treatments but did differ between times. Specifically, NOx was significantly higher on days 3, 4, and 6 and in the afternoon of day 5 than during all other sampling times (Fig. 1C; Table 1). Concentrations of NH$_4^+$, NOx, and Si varied among mesocosms within treatments (Table 1). In all treatments, concentrations of PO$_4^{3-}$ remained below the detection limits of the autoanalyzer ($\sim$0.03 $\mu$mol L$^{-1}$) throughout the experiment.

The ratio of Si:DIN decreased through time in all mesocosm treatments compared to the lake control (Fig. 2; Table 1). Specifically, Si:DIN ratios were higher in the lake control from the afternoon of day 3 onward. If concentrations of DIP were conservatively estimated to be 0.03 $\mu$mol L$^{-1}$, then the Si:DIP ratios remained above 120 in the lake control but may have fallen below 30 in the C. mosaicus and combined species treatments after day 4. The minimum possible DIN:DIP ratio of the lake control throughout the experiment was...
Minimum possible DIN : DIP ratios varied among the mesocosm treatments but remained above the Redfield ratio of 16 throughout the experiment in all treatments.

**Primary production**—On days 2 and 3, there were no differences in gross production among treatments (Fig. 3A; Table 2). On day 4, however, the *C. mosaicus* treatment had a higher gross production than did other mesocosm treatments, all of which had higher gross production than the lake. On day 5, *C. mosaicus* still had a significantly higher gross production than the mesocosm control, which had a higher gross production than the lake. Moreover, on day 6, *C. mosaicus* mesocosms had significantly higher concentrations of Chl *a* than did all other treatments.

**Chlorophyll a**—Concentrations of Chl *a* did not vary among treatments during the first 2 d of the experiment (Fig. 3B; Table 2). On day 3, mesocosms containing *C. mosaicus* had significantly higher Chl *a* concentrations than did all other mesocosms. Chl *a* increased in all treatments between days 3 and 5, but it increased more in mesocosms containing *C. mosaicus*. On day 4, all mesocosms containing jellyfish had a significantly higher Chl *a* concentration than did control mesocosms, which were also significantly higher than the lake control. Moreover, on day 5, Chl *a* concentrations in the *C. mosaicus* treatment were significantly higher than in the combined species treatment, which were significantly greater than the *P. punctata*, control, and lake control treatments. Finally, on day 6, *C. mosaicus* mesocosms had significantly higher concentrations of Chl *a* than did all other treatments.

**Phytoplankton**—Assemblages of phytoplankton showed no significant differences among treatments on days 1 and 3 (Fig. 4A,B; Table 3), but on day 6, assemblages in the treatments containing *C. mosaicus* differed compared to the *P. punctata* and control treatments (Fig. 4C). Phytoplankton assemblages were dominated by the diatoms *Chaetoceros* sp. and *Thalassiosira* sp., which contributed 23.2–56.2% and 19.1–55.1%, respectively, of the dissimilarity between treatments on day 6. Concentrations of *Chaetoceros* sp. increased in the *C. mosaicus* treatment but did not change in the other treatments during the experiment (Fig. 5A; Table 4). There was a trend for *Thalassiosira* sp. to increase in all treatments containing jellyfish, with concentrations of *Thalassiosira* sp. being more than four times greater than the mesocosm control and lake control on day 6, but this finding was not significant (*p* = 0.06) (Fig. 5B; Table 4). Concentrations of both *Chaetoceros* sp.
C. mosaicus sp. and 5 treatments were 5 sp. and 5 treatments were 5 sp. and 5 treatments were 5 sp. % P. punctata sp. contributed 10.4–37.1 % Oithona both caused significant, yet 5 sp. contrib-
treatment (Fig. 7A; Table 4). Furthermore, P. punctata 2.6 C. mosaicus Protoperidinium and combined species treatments than in 5 sp. (a sp. were 31.4, 5 sp. than the control 5 sp. and 5 treatments were 5 sp. (% 0.05 Gladioferens a concentrations among treatments and mesocosms during the 6-d experiment 5 sp. stimulated 5 sp. 7.6, 0.01; Fig. 9D). There were no 5 sp. (a sp. were significantly more concentrated 5 sp. 0.01; Fig. 9F) and 5 sp. and 5 treatments were 5 sp. (% 0.001) were less concentrated in the jellyfish treatments 5 sp. (a sp. than 5 sp., 0.001; Fig. 9G).

Results of repeated-measures ANOVAs to test for differences in gross production and Chl a concentrations among treatments and mesocosms during the 6-d experiment. * p = 0.05 for both tests.*

<table>
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<td>df</td>
<td>MS</td>
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<td>1.3</td>
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* ns, not significant; df, degrees of freedom; MS, mean square. Underlining indicates abbreviations.

and Thalassiosira sp. varied between mesocosms within some treatments, but patterns of variation were not consistent among times (Table 4).

Microzooplankton—Microzooplankton assemblages were similar among treatments on days 1 and 3 of the experiment (Fig. 6A,B; Table 3) but differed on day 6 (Fig. 6C; Table 3). Microzooplankton assemblages were dominated by the dinoflagellates Ceratium furca and Protoperidinium sp., which contributed 20.6–46.6% and 9.6–25.4%, respectively, of the dissimilarity among treatments on day 6. Concentrations of Protoperidinium sp. were similar among treatments on days 1 and 3; however, on day 6 Protoperidinium sp. were significantly more concentrated in the P. punctata and combined species treatments than in the C. mosaicus treatment (Fig. 7A; Table 4). Furthermore, all mesocosms that contained jellyfish had a greater concentration of Protoperidinium sp. than the control mesocosms, which had a greater concentration than the surrounding lake water. Concentrations of C. furca decreased in all treatments throughout the experiment but did not differ among treatments at any time (Table 4). Tintinnids were the most abundant ciliates, and their concentrations decreased in the mesocosm treatments after day 1, and on days 3 and 6 concentrations were lower in all mesocosm treatments compared to the surrounding lake water (Fig. 7B; Table 4). Copepod nauplii were also abundant, and concentrations decreased in all jellyfish treatments through time, while they increased in both the control and lake-water treatments (Fig. 7C; Table 4).

Mesozooplankton—Assemblages of mesozooplankton differed between the end of the experiment (Fig. 8; Table 3). The MDS plot demonstrated clear separation between the jellyfish treatments and the mesocosm control and lake control treatments. Furthermore, the C. mosaicus and P. punctata treatments were separated, and the combined species treatment was interspersed between the C. mosaicus and P. punctata treatments. Mesozooplankton assemblages were dominated by copepods. The cyclopoid copepod Oithona sp. contributed 13.2–28.4% of the dissimilarity between treatments, and the calanoid copepods Gladioferens sp. and Paracala-
nus sp. contributed 10.4–37.1% and 5.6–21.6%, respectively, to the dissimilarity between treatments. Other species that contributed to the dissimilarity between treatments were Lucifer sp. (0.0–25.8%), polychaetes (0.0–8.6%), gastropod veligers (3.1–31.7%), and bivalve veligers (0.0–12.6%).

Gladioferens sp. (F4,10 = 84.7, p < 0.001), Paracalanus sp. (F4,10 = 31.4, p < 0.001), and Oithona sp. (F4,10 = 37.4, p < 0.001) were less concentrated in the jellyfish treatments than in the control treatments (Fig. 9A–C). The lake control had higher concentrations of Gladioferens sp. than the mesocosm control treatment, but there were similar concentrations of Paracalanus sp. and Oithona sp. in the lake control and mesocosm control treatments. The mesocosm control treatment had significantly higher concentrations of Lucifer sp. than did all jellyfish treatments and the lake control (F4,10 = 7.6, p < 0.01; Fig. 9D).

Polychaetes were more concentrated in the lake control than in the mesocosm control treatment, both of which had greater concentrations of polychaetes than all jellyfish treatments (F4,10 = 5.7, p < 0.05; Fig. 9E). The lake control also had higher concentrations of gastropod veligers than did all other treatments, and there were more gastropods in the P. punctata treatment than in all other mesocosm treatments (F4,10 = 6.5, p < 0.01; Fig. 9F). There were no significant differences in concentrations of bivalve veligers between treatments (F4,10 = 1.6, p > 0.05; Fig. 9G).

Discussion

C. mosaicus and P. punctata both caused significant, yet different, changes in primary production and planktonic assemblages, changes that were consistent with the similar top-down but differing bottom-up influences they exert. As predicted, excretion of nutrients by C. mosaicus stimulated primary production, but no bottom-up influence was exerted by P. punctata. Predation by both species, however, exerted a top-down influence on mesozooplankton communities.

Primary production, nutrients, and stoichiometry—Changes in gross production and phytoplankton biomass (as indicated by Chl a) were consistent with our hypothesis.
Gross production and phytoplankton biomass increased in the *C. mosaicus* treatment from day 3 onward, and phytoplankton biomass was nearly seven times greater than in control treatments on day 6. This was driven largely by a 10-fold increase in concentrations of the diatom *Chaetoceros* sp. in the *C. mosaicus* treatment. In contrast, phytoplankton biomass in the *P. punctata* treatment was similar to that of the control treatments on all days except day 4, at which time it was elevated by approximately 25%. Gross production also decreased in the *P. punctata* treatment throughout the experiment. This indicates that *P. punctata* had little influence on primary production, most likely because the nutrients regenerated by *P. punctata* were being sequestered by the zooxanthellae rather than released into the water column. In general, the combined species treatment behaved more like the *P. punctata* treatment than the *C. mosaicus* treatment, indicating that the zooxanthellae in *P. punctata*, which can take up dissolved nutrients from the water column (West 2008), may have competed successfully with phytoplankton for the nutrients excreted by *C. mosaicus*. Previous studies have indicated that non-zooxanthellate jellyfish would have a significant bottom-up effect on primary production, in contrast to zooxanthellate species, which would have little influence (Cates and McLaughlin 1976; Pitt et al. 2005). This is the first study, however, to provide empirical evidence of this effect.

The almost negligible influence of *P. punctata* on production and phytoplankton biomass indicates that top-down influences alone were unable to substantially stimulate primary production in this nutrient-limited system. In contrast, the strong response of phytoplankton observed in the *C. mosaicus* treatment indicates that non-zooxanthellate jellyfish exert a substantial bottom-up influence. Although, as observed for *P. punctata*, the top-down contribution to primary production in the *C. mosaicus* treatment was considered minimal, we could not strictly quantify the exact contributions made by bottom-up and top-down processes. To do so would have required the inclusion of another control in which nutrients were added to natural zooplankton assemblages at the same rate at which they are excreted by *C. mosaicus*, but in the absence of jellyfish predation. All jellyfish, however, are voracious predators of zooplankton, and, indeed, nutrient excretion is driven by the ingestion and digestion of zooplankton prey. Since predation and excretion are tightly coupled in non-zooxanthellate jellyfish it was not feasible to try to separate these processes in the *C. mosaicus* treatment, as bottom-up control cannot occur in the absence of top-down predation on zooplankton.

In a similar mesocosm study by Pitt et al. (2007), performed in Lake Illawarra, Australia, the presence of *C. mosaicus* caused a significant increase in phytoplankton biomass after 24–36 h. Pitt et al. (2007) suggested that excretion of NH$_4^+$ by *C. mosaicus* was likely to have caused the increase in primary production. However, in Smiths Lake PO$_4^{3-}$ is likely to be the main nutrient limiting primary production (Smith and Heggie 2003; Everett et al. 2007). Phytoplankton growth can depend on the stoichiometric ratio of nitrogen (N) and phosphorus (P) in the water column, where the Redfield ratio of 16:1 (N:P) is required for balanced growth (Redfield 1958; Sterner and Elser 2002). In the current experiment concentrations of PO$_4^{3-}$ were lower than the detection limit of the

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**Fig. 4.** MDS plots showing differences in assemblages of phytoplankton sampled on (A) day 1, (B) day 3, and (C) day 6. Each symbol represents the phytoplankton assemblage in an individual mesocosm, and the proximity of the symbols indicates the degree of similarity between assemblages (i.e., symbols closer together indicate assemblages are more similar than those further apart).

Gross production and phytoplankton biomass increased in the *C. mosaicus* treatment from day 3 onward, and phytoplankton biomass was nearly seven times greater than in control treatments on day 6. This was driven largely...
autoanalyzer (<0.03 μmol L−1) and this prevented accurate measurements of PO₄³⁻ and, therefore, DIN:DIP and Si:DIP ratios. To determine the smallest possible DIN:DIP and Si:DIP ratios, calculations were done using 0.03 μmol L−1 PO₄³⁻, as this represented the maximum possible PO₄³⁻ concentration. Actual ratios, however, were likely to be much larger than those estimated using this approach, since actual PO₄³⁻ concentrations were probably less than 0.03 μmol L⁻¹. Despite this, DIN:DIP ratios were estimated to have remained above the Redfield ratio of 16 in all treatments throughout the experiment. The high DIN:DIP ratio and the very low PO₄³⁻ concentrations measured in all treatments during the experiment indicate that growth of primary producers was severely limited by the availability of P. P-limitation in Smiths Lake is thought to result from the high nitrogen loads recycled from decomposition of organic matter and the trapping of P in the sediments (Smith and Heggie 2003).

In Smiths Lake individual C. mosaicus excrete PO₄³⁻ at a rate of 5.4 μmol kg wet wt⁻¹ h⁻¹, whereas P. punctata exhibit no net excretion of PO₄³⁻ (Pitt et al. 2005). Using these data, the C. mosaicus in the current experiment would have excreted PO₄³⁻ at a rate of 5.9 μmol h⁻¹, and the P would have been rapidly assimilated by phytoplankton and would have stimulated primary production. Furthermore, C. mosaicus excretes DIN and DIP at a ratio (atom:atom) of ~22:1 (Pitt et al. 2005), which is lower than the estimated minimum DIN:DIP ratio of the water column during this experiment (i.e., <54) but higher than the Redfield ratio of 16. Hence, although the excreta of C.

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Table 3. Results of analyses of similarity (ANOSIM) among treatments (Catostylus mosaicus; Phyllorhiza punctata; combined species; no jellyfish control; and lake-water control) to detect differences between assemblages of phytoplankton, microzooplankton, and mesozooplankton. Analyses were done separately for each sampling time, and 999 permutations were done for each analysis.

<table>
<thead>
<tr>
<th>Time</th>
<th>Phytoplankton Global R</th>
<th>Phytoplankton p</th>
<th>Microzooplankton Global R</th>
<th>Microzooplankton p</th>
<th>Mesozooplankton Global R</th>
<th>Mesozooplankton p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day 1</td>
<td>0.159</td>
<td>0.112</td>
<td>−0.169</td>
<td>0.900</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 3</td>
<td>0.108</td>
<td>0.173</td>
<td>0.256</td>
<td>0.055</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 6</td>
<td>0.311</td>
<td>0.017</td>
<td>0.403</td>
<td>0.007</td>
<td>0.683</td>
<td>0.001</td>
</tr>
</tbody>
</table>
mosaicus would have provided a valuable source of P for primary producers, the mesocosms containing C. mosaicus would have remained P-limited throughout the experiment. Chaetoceros sp., the diatom that responded most dramatically in the C. mosaicus treatment, has been found to dominate in high-DIN : DIP conditions (Lagus et al. 2004). Chaetoceros spp. require less NH$_4^+$, PO$_4^{3-}$, and Si (very

![MDS plot showing differences in assemblages of microzooplankton sampled (A) day 1, (B) day 3, and (C) day 6. Details as per Fig. 4.](image)

> Table 4. Results of repeated-measures ANOVAs testing for differences in selected microplankton among treatments and mesocosms, sampled over 6 d. *z = 0.05 for all tests.

<table>
<thead>
<tr>
<th>Variable: Transformation: Levene's test:</th>
<th>df</th>
<th>MS</th>
<th>p</th>
<th>Levene's test:</th>
<th>df</th>
<th>MS</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaetoceros sp. ln(X+1)</td>
<td>4</td>
<td>2.3</td>
<td>0.456</td>
<td></td>
<td>20</td>
<td>2.5</td>
<td>0.504</td>
</tr>
<tr>
<td>Thalassiosira sp. ln(X+1)</td>
<td>10</td>
<td>2.0</td>
<td>0.028</td>
<td></td>
<td>45</td>
<td>0.1</td>
<td>0.056</td>
</tr>
<tr>
<td>Ceratium furca ln(X+1)</td>
<td>20</td>
<td>7.1</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protoperidinium sp. ln(X+1)</td>
<td>20</td>
<td>2.5</td>
<td>0.024</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tintinnids Sup(X+1)</td>
<td>20</td>
<td>3.6</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepod nauplii Sup(X+1)</td>
<td>20</td>
<td>5.3</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Transformation: Levene's test: df</th>
<th>MS</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>4</td>
<td>2.3</td>
</tr>
<tr>
<td>Time</td>
<td>20</td>
<td>0.5</td>
</tr>
<tr>
<td>M(T)</td>
<td>45</td>
<td>0.1</td>
</tr>
</tbody>
</table>

* ns, not significant; df, degrees of freedom; MS, mean square. Underlining indicates abbreviations.

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mosaicus would have provided a valuable source of P for primary producers, the mesocosms containing C. mosaicus would have remained P-limited throughout the experiment. Chaetoceros sp., the diatom that responded most dramatically in the C. mosaicus treatment, has been found to dominate in high-DIN : DIP conditions (Lagus et al. 2004). Chaetoceros spp. require less NH$_4^+$, PO$_4^{3-}$, and Si (very...
low half-saturation constants) and are very good competitors for P, compared to other species of phytoplankton (Eppley and Thomas 1969; Conway and Harrison 1977; Lagus et al. 2004). Therefore, the increased availability of PO$_4^{3-}$ in mesocosms containing C. mosaicus was likely to favor Chaetoceros sp. more than other phytoplankton species. The overall increase in primary production in mesocosms containing C. mosaicus, therefore, was likely to be predominantly due to bottom-up excretion of recycled nutrients, particularly PO$_4^{3-}$.

Concentrations of Si decreased through time in all mesocosms, and toward the end of the experiment concentrations were lower in the two treatments containing C. mosaicus than in the P. punctata or mesocosm control treatments. Diatoms assimilate dissolved Si for growth, and, therefore, the reduction in Si was likely to reflect increasing diatom biomass in the mesocosms. The growth rate of diatoms was rapid and caused Si to be depleted at a faster rate than N. Diatoms generally dominate when Si concentrations exceed a threshold of ~2 μmol L$^{-1}$ (Egge and Aksnes 1992). Furthermore, there is generally a shift from diatoms to non-siliceous algae at Si : DIN and Si : DIP ratios <2 and 30, respectively (Sommer 1996, 1998; Sommer et al. 2002). In the present experiment, after day 3 concentrations of Si in all mesocosms fell below 2 μmol L$^{-1}$ and Si : DIN ratios were <2. Si : DIP ratios also may have fallen below 30 in the two treatments containing C. mosaicus after day 4. There was no evidence, however, of a shift from diatoms to non-siliceous algae in the current experiment. Given that Si : DIP ratios were probably much higher than those calculated conservatively using the detection limit of 0.03 μmol L$^{-1}$ PO$_4^{3-}$, it is likely

![Graph showing mean (±SE) concentrations of (A) Protoperidinium sp., (B) total tintinnids, and (C) total copepod nauplii among treatments sampled on days 1, 3, and 6 (n = 6). Horizontal lines indicate no statistically significant difference between treatments from post-hoc comparisons.](image-url)
that although the mesocosms were being pushed toward Si limitation, as a result of its very low absolute concentrations, P probably remained the major nutrient limiting primary production in all treatments.

Microzooplankton—The presence of jellyfish also caused changes to the microzooplankton assemblage. This could have been due to bottom-up processes (including nutrient enrichment and/or prey availability, depending on whether the microzooplankton were heterotrophic or mixotrophic), top-down predation pressure, or a combination of both. For example, the heterotrophic dinoflagellate Protoperidinium sp. increased in all jellyfish treatments. Reduced grazing by mesozooplankton in the jellyfish treatments probably exerted a top-down influence. A bottom-up influence was also possible, since species of Protoperidinium selectively feed on species of Thalassiosira over both dinoflagellates and other diatom species (Buskey 1997), and Thalassiosira abundance increased in all jellyfish treatments, including P. punctata. Changes in the relative abundances of species may also influence competitive interactions. For example, ciliates are major grazers of Thalassiosira (Sommer et al. 2005). The reduction of ciliates (i.e., tintinnids) that was observed in all mesocosm treatments may have further contributed to an increase in Protoperidinium sp., as competition between Protoperidinium sp. and ciliates would have decreased.

Mesozooplankton—At the end of the experiment mesozooplankton were less concentrated in treatments containing jellyfish than in both of the control treatments, presumably because of predation by the jellyfish. Jellyfish also initiated changes in the species composition of mesozooplankton, which may have been a result of selective predation. Selective predation by jellyfish can occur as a result of different numbers and types of nematocysts (Peach and Pitt 2005), postcapture sorting by the jellyfish (Hansson 2006), and/or behavioral avoidance of the jellyfish by the mesozooplankton (Carr and Pitt 2008). In this experiment, jellyfish appeared to selectively prey on the copepods Gladioferens sp., Paracalanus sp., and Oithona sp. as well as on Lucifer sp. and polychaetes. However, other dominant species were not preyed upon. For example, concentrations of bivalve veligers were similar in the controls and jellyfish treatments, indicating that jellyfish did not prey on them. There are conflicting reports about predation by jellyfish on bivalve veligers. Several studies have found bivalve veligers on the oral arms of jellyfish (Peach and Pitt 2005; Carr and Pitt 2008). Moreover, a previous mesocosm study found a substantial yet nonsignificant decrease in concentrations of bivalve veligers in the presence of jellyfish (Pitt et al. 2007). However, Purcell (1992) found that while the scyphozoan Chrysaora quinquecirrha captures bivalve veligers, 98% of those ingested are not digested and can even survive following egestion. In addition, by comparing the carbon isotope signatures ($^{13}$C) of mollusc veligers and C. mosaicus, Pitt et al. (2008) suggested that mollusc veligers contributed only a small proportion (<13%) of carbon assimilated by C. mosaicus. From this mesocosm study, it appears that if C. mosaicus and P. punctata captured bivalve veligers either they did not ingest them or the veligers survived digestion. Gastropod veligers were also more abundant in the P. punctata treatment compared to both the C. mosaicus and combined species treatments. C. mosaicus capture ~10 times more gastropods than P. punctata (Peach and Pitt 2005). Therefore, P. punctata is likely to exert a lower grazing pressure on gastropods, although further feeding experiments are required to confirm this.

Potential mesocosm-induced artifacts—Mesocosms are sometimes criticized because of the potential artifacts they can induce. They remain, however, our only option for undertaking manipulative experiments on pelagic systems. We assessed some of the potential artifacts by including a lake control that, when compared against the mesocosm control, enabled us to determine how mesocosms influenced the different variables. Mesocosms had no influence on concentrations of NOx. Effects on PO$_4^{3-}$ could not be accurately assessed, but in all treatments concentrations remained below detection limits. However, concentrations of Si and, to a lesser extent, NH$_4^+$ did decrease in the control mesocosms relative to the lake, most likely because the mesocosms were isolated from the sediments and freshwater discharges, which are major sources of these nutrients (Fenchel et al. 1998). However, although the mesocosms were being pushed toward Si limitation toward the end of the experiment, P was always the major nutrient limiting primary production in the mesocosms. Mesocosms did appear to inflate gross production rates, but the biomass and community structure of phytoplankton were unaffected by the mesocosms. The difference in gross production, therefore, may have been due to the differing light conditions between the mesocosms and lake. Indeed, the reflected light intensity in the mesocosms was 60% greater than in the lake. The greater availability of reflected light may have increased rates of
photosynthesis inside the mesocosms and led to higher rates of gross production, even though phytoplankton biomass and community structure were unchanged. There was some indication from the MDS plot that mesocosms may have influenced assemblages of microzooplankton. Tintinnids, however, were the only taxon for which there was evidence of potential mesocosm-induced artifacts. The decrease in tintinnids may be partially explained by competition with *Protoperidinium*, which became slightly depleted in the lake but remained constant in the mesocosms throughout the experiment, but artifacts, such as possible adhesion of tintinnids to the walls of the mesocosm, cannot be excluded. Assemblages of mesozooplankton, however, were similar between the mesocosm control and the lake. Overall, the mesocosms seemed to generate relatively minor artifacts and provided a reasonable tool for manipulating planktonic assemblages over periods of several days.

Fig. 9. Mean (±SE) concentrations of (A) *Gladioferens* sp., (B) *Paracalanus* sp., (C) *Oithona* sp., (D) *Lucifer* sp., (E) polychaetes, (F) gastropod veligers, and (G) bivalve veligers among treatments on day 6 (*n* = 3). C = *C. mosaicus*; P = *P. punctata*; CS = combined species; MC = mesocosm control; and LC = lake control. Horizontal lines indicate no difference between treatments from post-hoc comparisons.
Both *P. punctata* and *C. mosaicus* exerted top-down predation pressure on mesozooplankton, causing significant declines in most species of mesozooplankton. The increase in the heterotrophic dinoflagellate *Protoperidinium* sp. in all jellyfish treatments indicated that top-down pressure exerted by jellyfish can initiate changes that cascade to multiple trophic levels. The lack of increase in Chl *a* in the *P. punctata* treatment, however, indicated that the top-down trophic cascade did not extend to primary producers. Instead, increased primary production was only observed in the presence of *C. mosaicus*, most likely because of the excretion of PO$_4^{3-}$, but this effect was possibly enhanced by a concurrent reduction in grazing by mesozooplankton. This study provides the first empirical evidence of how top-down and bottom-up processes exerted by jellyfish influence pelagic primary production and planktonic assemblages.

Acknowledgments

We thank J. Browne, M. Carpenter, E. Carr, G. Coade, E. Czobik, R. Gardiner, S. Jacobs, C. Legett, D. Liu, J. Potts, and P. Scanes for assistance in the field and laboratory and M. Arthur for statistical advice. We also thank the two anonymous reviewers who helped us improve the manuscript. The project was funded by the New South Wales Department of Infrastructure, Planning and Natural Resources and the Hermon Slade Foundation.

References


Associate editor: Peter G. Verity

Received: 09 December 2008
Accepted: 04 June 2009
Amended: 03 July 2009