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# On the relative constancy of iodate and total-iodine concentrations accompanying phytoplankton blooms initiated in mesocosm experiments in Antarctica

*Victor W. Truesdale*
School of Biological and Molecular Sciences, Oxford Brookes University, Headington, Oxford, OX3 0BP, UK

*Hilary Kennedy*
School of Ocean Sciences, University of Wales, Bangor, Menai Bridge, Anglesey, LL59 5EY, UK

*Susana Agustí*
IMEDEA (CSIC-UiB), C/ Miquel Marques 21, 07190 Esporles, Mallorca, Spain

*Tim J. Waite*
School of Biological and Molecular Sciences, Oxford Brookes University, Headington, Oxford, OX3 0BP, UK

*Abstract*

The integrated iodate and total-iodine concentrations accompanying accelerated growth of natural phytoplankton in eight 14-m deep mesocosm experiments did not vary significantly. Growth was induced by the addition of nutrients, while light irradiance was controlled by neutral density screens. These measures resulted in a range of particulate organic carbon concentrations of between 13 and 220 $\mu$mol $L^{-1}$, that is, covering some that are well in excess of blooms generally found in the natural environment. This, together with most earlier results obtained from phytoplankton culturing and much hydrographic survey, is used as an opportunity to question whether phytoplankton growth can be the cause of iodate reduction in seawater.

In oxic seawater, iodine exists in dissolved and particulate forms (Wong 1991) at $\mu$mol $L^{-1}$ and pmol $L^{-1}$ concentrations, respectively. It is a biointermediate element incorporated into phytoplankton biomass in near-surface waters and regenerated diagenetically. Despite a slight assimilation by phytoplankton, the major change observed in seawater is the interconversion between iodate and iodide (chemical reduction) in near-surface waters (*see* Truesdale et al. 2000). Iodate is predominant in deep waters (Tsunogai 1971) where the low iodide concentrations are similar to those predicted by the decomposition of organic material sinking from the near-surface waters (Truesdale 1994). Attempts to explain iodate reduction in oxic seawater have linked it to phytoplankton growth, microbial respiration (Truesdale and Bailey 2002), photochemistry (Spokes and Liss 1996), and sediment–water interaction. In the case of phytoplankton the reduction has largely been assumed to be dissimilatory.

The most popular explanation for iodate reduction, that involving phytoplankton, received early support from good correlations between iodate and nutrient concentrations in the permanently stratified water column of the tropical and subtropical oceans (Truesdale et al. 2000). However, a sustained reduction of about the same amount of 0.2 mol $L^{-1}$ iodate is also evident across the temperate shelf, and this remains essentially unchanged during periods of phytoplankton growth (Truesdale 1978*a;* Truesdale and Jones 2000). A straightforward universal coupling between iodate reduction and nutrient cycling may therefore not be justified, and the correlations in tropical waters might exist for complex reasons (Truesdale et al. 2000).

The apparent difference in the link between iodine and nutrients in temperate and tropical regions can be reconciled by any one of three strategies; first, by invoking suppression of iodate reduction in temperate waters; second, by finding separate explanations for the reduction in the two regions; and, finally, by entirely abandoning the idea that phytoplankton are responsible for iodate reduction in one or both regions. Each of these strategies has provided its own subset of ideas. For example, the suppression strategy led to the idea that high nitrate concentrations in temperate waters militate against iodate reduction. In turn, this has led to the notion that iodate reduction is linked to regenerated production rather than new production. Similarly, the idea that a sediment–water interaction in shallow, temperate shelf waters might account for the sustained iodate reduction in temperate coastal waters represents an attempt to avoid a link with phytoplankton growth.

This paper describes an attempt to detect iodate reduction by growing phytoplankton rapidly on nutrient added to a mesocosm of the type described by Agawin et al. (2002). Following the suggestion of Truesdale and Bailey (2002) that it would be reassuring to find the conditions under which a substantial proportion of the iodate in oxic seawater could be reduced at will, we have been seeking 50% reduction

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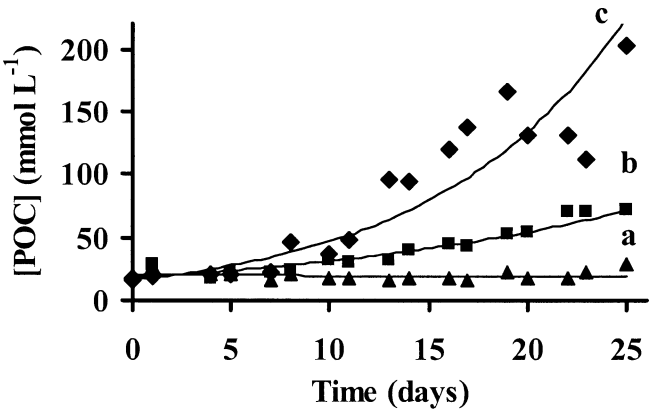


Fig. 1. The variation of particulate organic carbon concentration exemplified by three of the mesocosms. The lines fitted to the experimental points are generated by the exponential model, $[POC]_t = [POC]_o e^{kt}$; the parameters are listed in Table 1. The curves correspond with superscripts a–c in the right-hand column of Table 1.

(chemical reduction), or reduction of about 0.2 mol $L^{-1}$ of iodate. Of course, while mesocosms lack the specificity offered by axenic algal culturing, they offer heterogeneity much more representative of the open sea. No major change in iodine speciation was observed despite heavy growth, and the implications of this are discussed.

## Materials and methods

Samples were collected as an ancillary part of a large-scale in situ mesocosm experiment designed to determine the role of irradiance and ammonium on phytoplankton dynamics in Antarctica (Agawin et al. 2002). The mesocosms were located in a sheltered bay (Johnson's Dock, 62°39.576′S, 60°22.408′W) of Livingston Island, at the north of the Gerlache Strait. Eight mesocosms (14-m deep, 2.3-m diameter, and closed at the base) made of polyethylene were supported in a floating platform moored in about 25 m of water. The perimeter and top of four pairs of mesocosms were covered with neutral density screens to create a variety of irradiances of approximately 100%, 50%, 25%, and 10% of the ambient light field.

The mesocosms were filled with ambient, unscreened surface water in late January 2001. On the first day, and every three days thereafter, an integrated water sample (0–13 m) was taken from each mesocosm and subsampled for dissolved inorganic iodine and particulate organic carbon. Sampling was performed using a flexible plastic hose of about 5-cm internal diameter, weighted at one end. The hose was rinsed in ambient water and then slowly lowered to reach 12 m into the mesocosm. With the top well above the sea level, the weighted end was carefully retrieved by a lanyard attached to the weight. The hose's contents, approximately 20 liters, were collected in a plastic carboy. The retrieved volume corresponded closely to the nominal sampler volume.

Four of the eight mesocosms were augmented with daily additions of ammonium, silicate, and phosphate, with the ammonium concentration being kept below 10 $\mu$mol $L^{-1}$.

Table 1. The [POC] data fitted to the model $[POC] = [POC]_o e^{kt}$. The fittings reflect the actual initial $[POC]_o$ of 22.4 ± 5.5 $\mu$mol $L^{-1}$ in the mesocosms. The uncertainties for parameters $[POC]_o$ and $k$ are standard errors from the fittings, while that for the mean is the standard deviation of the eight estimates. Any pair for a given light intensity are not duplicates, since different amounts of ammonium were added. Superscripts a–c identify the mesocosms exemplified in Fig. 1.

| Light intensity (% ambient) | $[POC]_o$ ($\mu$mol $L^{-1}$) ±1.1 | $k$ ($d^{-1}$) ±0.008 | $r^2$ | ΔPOC over 25 d ($\mu$mol $L^{-1}$) |
|---|---|---|---|---|
| 10 | 13.2 | 0.008 | 0.047 | 0 |
| | 20.6 | −0.004 | 0.023 | 0[a] |
| 25 | 21.1 | 0.011 | 0.133 | 3 |
| | 14.0 | 0.027 | 0.343 | 3 |
| 50 | 19.2 | 0.009 | 0.062 | 3 |
| | 17.4 | 0.047 | 0.960 | 32 |
| 100 | 18.0 | 0.055 | 0.863 | 53[b] |
| | 16.4 | 0.105 | 0.915 | 203[c] |
| | Mean = 17.5±2.9 | | | |

The large, chain-forming diatom *Thalassiosira antarctica* dominated every mesocosm bloom, although other *Thalassiosira* species were also present. During the experiment nitrate concentrations decreased from ~30 $\mu$mol $L^{-1}$ to between 16 and 25 $\mu$mol $L^{-1}$.

Total iodine and iodate iodine were determined automatically on GF/F filtered sample by the Ce(IV)–As(III) catalytic method (Truesdale and Smith 1975) and the iodometric method (Truesdale 1978*b*), respectively. The standard deviation (SD) for analytical control standards carried through the entire process at five intervals was 0.002 for both methods and therefore well within the long-term expectation of the methods. Samples for particulate organic carbon (POC) were prefiltered through 200-$\mu$ mesh to remove zooplankton and subsequently filtered onto precombusted GF/F filters. The filters were fumed with concentrated HCl to remove any carbonate, dried (40°C), and stored. POC was determined on a Europa Roboprep C/N Analyzer, with precision better than 5%.

## Results

*The changes in particulate carbon*—Here we have chosen particulate organic carbon (POC) measurements to characterize the extent of growth in the mesocosms. Given our overall findings, it is only necessary to describe the range of growths experienced, and for further detail the reader is referred to Agawin et al. (2002).

The average initial concentration of POC in all enclosures was 22.4 ± 5.5 $\mu$mol $L^{-1}$. By addition of the nutrients and control of the irradiance, blooms of various intensities, equivalent to increases in [POC] of between 0 and 203 $\mu$mol $L^{-1}$, developed. (In the mesocosm generating most biomass a maximum chlorophyll *a* concentration of 93 mg $m^{-3}$ was observed, S. Agusti pers. comm.) The increases in [POC] with time in the mesocosms were found to fit an exponential model well, as exemplified in Fig. 1, and allowed the growth

rate to be characterized easily (Table 1). Although a slightly better fitting could sometimes be obtained by allowing for a slight initial lag phase, for our purposes this did not yield a tangible benefit and was not pursued.

The POC concentrations are minimum estimates and should only be taken as indicative of algal growth. Thus, prefiltration through 200-$\mu$ mesh was effective in excluding zooplankton but would also have retained some of the larger chains of *Thalassiosira antartica.* Size fractionated POC measurements, undertaken during the same mesocosm experiments (H. Kennedy pers. comm.), suggest that the larger than 200-$\mu$ fraction was between 4% and 28% of the total POC, with a mean percentage ($\pm$SD) of 8.6% $\pm$ 5.1% ($n$ = 34). Its greatest contributions were consistently at the bloom maximum when it constituted about 17% of the POC. In addition, no measurements of sinking POC were made, and so the data of Fig. 1 and Table 1 should only be taken to be indicative of algal growth. Any underestimation of POC actually enhances the conclusions drawn from the study.

*Bacterial growth*—Although bacterial numbers differed between mesocosms there was a common pattern. An initial small decrease from about $1 \times 10^6$ to about $2 \times 10^5$ cells ml$^{-1}$ over the first 10 d of the experiment was followed by a rapid increase over the following 15 d to between, at most, 3.5 and $20 \times 10^6$ cells ml$^{-1}$ (D. Vaqué pers. comm.). The increase in bacterial numbers therefore lagged behind POC. As with POC in the upper curve of Fig. 1, bacterial numbers did not always increase smoothly. Nevertheless, for the sake of convenience the same exponential function ($N = N_0e^{at}$) as used in Table 1 for POC was applied to the bacterial growth. The increase from day 7 onward in all but the last three mesocosms of Table 1 was approximated when $N_0$ and $a$ were $5 \times 10^5$ and 0.25 d$^{-1}$, respectively. Taken in the same order, the approximations for the last three mesocosms in Table 1, with the same $N_0$, demanded an $a$ of 0.35, 0.25, and 0.41 d$^{-1}$, respectively. The strong similarity between the variation in bacterial counts and POC, but with the rise in bacterial count lagging slightly behind POC, seems to be consistent with the bacteria growing upon DOC exuded by the phytoplankton.

*Iodine chemistry*—There was an absence of the substantive iodate reduction (>0.2 $\mu$mol L$^{-1}$) sought. Indeed, no significant reduction of iodate was observed. The distributions of the 71 results for both iodate and total iodine (Fig. 2) are narrow, with the span of that for iodate amounting to about one-half that for total iodine. The means ($\pm$SD) for iodate and total-iodine concentrations were 0.397 $\pm$ 0.007 and 0.404 $\pm$ 0.017 $\mu$mol L$^{-1}$, respectively. Since replicate analysis of an analytical quality control standard itself yielded a mean $\pm$ SD of 0.331 $\pm$ 0.002 $\mu$mol L$^{-1}$ and 0.440 $\pm$ 0.002 $\mu$mol L$^{-1}$ for iodate and total iodine, respectively, the variation within the sample population can be seen to be only slightly greater than that generated by analytical uncertainty.

The results have also been examined by linear regression of iodine concentrations on time. Correlation was poor, with correlation coefficients typically less than 0.4. All gradients except one were slightly positive, indicating apparent gains

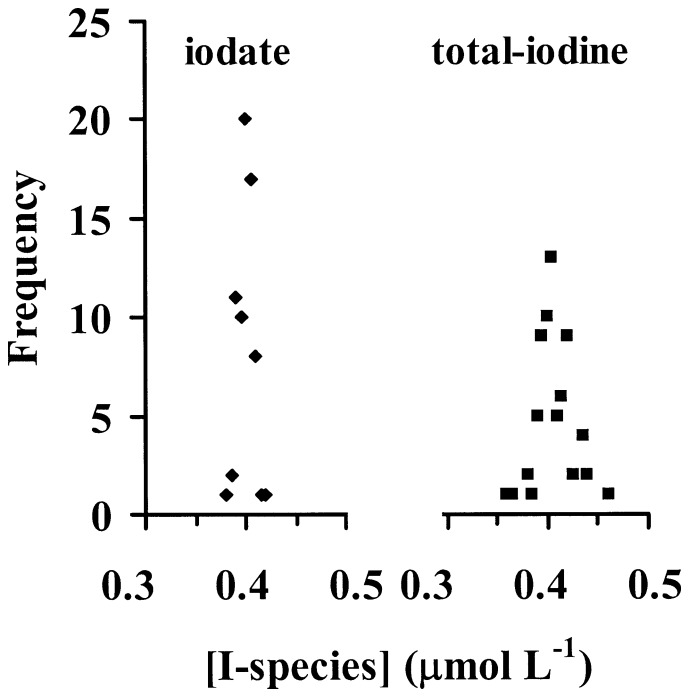


Fig. 2. The frequency distributions of the 71 iodate and total-iodine concentration measurements.

in iodate and total-iodine concentration (with SD) over the 25 d of growth amounted to 0.007 $\pm$ 0.006 and 0.015 $\pm$ 0.016 $\mu$mol L$^{-1}$, respectively. In both cases these are not significantly different from zero. Exceptionally, in the mesocosm generating most biomass, the results suggested a decrease of total-iodine concentration of 0.023 $\mu$mol L$^{-1}$ over the growth period. No pattern corresponding to the growth conditions could be discerned in these gradients.

## Discussion

When considering interconversion of iodine species it is intrinsically simpler if uptake of iodine from solution is minimal. Moreover, this is the condition generally observed in the oceans. The results for total-iodine concentration demonstrate that this was the case in the mesocosm experiments, and the maximum uptake was less than one-tenth of the iodate reduction that we were hoping to find. Therefore, any effect from either iodine assimilation by the phytoplankton or iodine contamination from the added nutrients and associated equipment was minimal. Extending the Redfield ratio model (Redfield et al. 1963) to include iodine using a $\Delta I/\Delta C$ ratio of $\sim 1 \times 10^{-4}$ (Elderfield and Truesdale 1980) means that the $\Delta$[POC] measurements of Table 1 predict changes in total iodine due to assimilation over the full growth period, of about $-0.005$ $\mu$mol L$^{-1}$ in all but one mesocosm. Exceptionally, in the mesocosm generating most biomass it is predicted to be $-0.02$ $\mu$mol L$^{-1}$, which is generally in accord with the observed change ($\pm$SD) of $-0.023$ $\pm$ 0.016 $\mu$mol L$^{-1}$.

Given that changes in total iodine were tiny, the results show that minimal systematic change in iodate reduction ac-

companied a range of algal bloom intensities equivalent to an increase in [POC] of between 0 and at least 203 $\mu$mol $L^{-1}$. These biomasses are high compared to those normally encountered in open waters ($<10$ $\mu$mol $L^{-1}$), and even higher than those (30 to 90 $\mu$mol $L^{-1}$) observed in Antarctica during coastal or ice-edge blooms (Smith and Nelson 1985). For reasons given above, the actual bloom intensities were probably even higher. Therefore, the results do not support the belief generally permeating the marine iodine literature that change in iodine speciation is due directly to phytoplankton growth. It is noted, incidentally, that the waters studied, being from Antarctica, contained close to the maximum possible iodate concentration. Hence, any potential for iodide oxidation would have been minimal.

We want the reader to appreciate that our mesocosm experiments rested upon the extremely simple (coarse) hypothesis that if phytoplankton are indeed responsible for the good correlations obtained between nutrient and iodate concentrations at tropical stations, an abundance of growth should enhance iodate reduction. The appropriateness of this is perhaps best appreciated by considering the analogous experiment that might well have been conducted a century ago to prove that phytoplankton growth affects nutrient concentrations. In this case the consistency of the loss of phosphate and nitrogen from solution during growth of the algae would have been very important. The fact that nutrient concentrations will decrease during algal growth is such a part of routine daily activity and knowledge that it is now unremarkable. In the case of iodate reduction the situation is much more complex precisely because such consistency does not exist. The mesocosm result adds to this uncertainty.

The absence of substantive iodate reduction from even the combined effects of phytoplankton and marine bacteria means that there is nothing to differentiate into effects due to phytoplankton and bacteria. Both may well have affected iodate, but not substantially enough. Similarly, for the sake of brevity we have not detailed the mesocosm experiments as we would have done if substantive iodate reduction had been observed. Instead, they are grouped as a range of environments of differing production.

The limitations of our experiments do not escape us. They relate both to water from a specific region and to a phytoplankton assemblage generated therein. We should very much like to have repeated them in many different hydrographic locations, including tropical locations. In the meantime, this experiment with iodine is unique and its results need to be accommodated into any general theory of iodate reduction.

*Wider discussion*—It is difficult to place our mesocosm results within the context of other results concerned with iodate reduction by marine phytoplankton because, when examined critically, the literature is ambiguous. Had there been general agreement that phytoplankton reduce iodate we would have suspected that our mesocosm experiments were reflecting some deficiency in iodate-reducing ability related to the locality or to the experimental design. The former might well have stemmed from a variety of causes including an inability of the Antarctic species represented to assimilate or reduce iodate, the environmental conditions characteristic of polar environments, or the presence of additional organisms in the mesocosm as compared with an axenic culture, interfering with the reduction process. If, instead, the literature had shown clearly that phytoplankton do not reduce iodate substantially, then the mesocosm results would have added one extra piece of evidence to the general conclusion. Given these uncertainties, here we feel it appropriate to identify the previous studies with which our results are consistent and those with which they are not. Additionally, we search for ways in which the inconsistencies might be resolved. So far, much of the work on iodine has been of a pioneering nature and there is room for reinterpretation of the results.

Our finding of no significant change in iodine speciation in the mesocosms is consistent with the similar lack of any major change in the iodine speciation at natural iodate concentrations in the various laboratory cultures of Truesdale (1978*a*) and Butler et al. (1981). These experiments relied upon iodate and total-iodine analysis. Our mesocosm result also conforms with a similar lack of iodide production at natural concentrations of iodate recently observed in separate cultures of *Isochrysis galbana*, *Cyclotella cryptica*, *Skelotenema cosatatum*, and *Synechococcus* (Waite and Truesdale 2003).

The mesocosm result is also consistent with Waite and Truesdale (2003) only witnessing iodide production by the alga *Isochrysis galbana* when the prevailing iodate concentration was at least an order of magnitude greater than found naturally. Over the range 0 to 250 $\mu$mol $L^{-1}$ iodate, the iodide generated followed a Michaelis–Menten behavior, so that below 5 $\mu$mol $L^{-1}$, iodide production rate decreased markedly. At 0.45 $\mu$mol $L^{-1}$ the rate was judged to be too low to explain the changes found in the natural environment.

Our mesocosm result is also consistent with all of the several iodine hydrographic studies on the European Shelf (e.g., Truesdale 1978*a;* Truesdale and Jones 2000), as well as the investigation of Truesdale and Bailey (2002) in the Southern Benguela system. The former show little or no temporal change in iodate and total iodine despite marked seasonal phytoplankton growth. This lack of a seasonal change in iodine speciation was nonetheless accompanied by a sustained difference in iodate concentration of about 0.2 $\mu$mol $L^{-1}$ between oceanic and inshore, shelf waters. In the Southern Benguela system minimal change in iodate and total iodine was found in highly productive, upwelling waters. We note that the open hydrographic environments, like our mesocosm experiment, involve bacteria and other organisms.

The condition of our mesocosm experiment, like that of most algal culturing conducted with iodine as well as the above mentioned hydrographic regimes, is characterized by high nitrate concentrations. Since various workers have suggested that high nitrate concentrations might suppress iodate reduction (e.g., Truesdale 1978*a;* Wong et al. 2002) this is potentially an important issue for the mesocosms. We note, however, that the only experimental test of this so far (Waite and Truesdale 2003) showed that a shift from nitrate to ammonium nutrition in *I. galbana* had no effect upon iodate reduction at raised iodate concentrations. Moreover, apportioning a total of 20 $\mu$mol $L^{-1}$ nitrogen between nitrate and ammonium, with initial nitrate concentrations of 20, 15, 10, 5, 1, and 0 $\mu$mol $L^{-1}$, did not induce iodate reduction at 0.45

$\mu$mol $L^{-1}$ iodate. Incidentally, in terms of nitrate and ammonium concentrations, these cultures were very much closer to that of the mesocosm experiment's mixed ammonium and nitrate nutrition than any other algal cultures used with iodine. We note also that, using Michaelis–Menten kinetics, Truesdale and Bailey (2002) showed that the effectiveness of the competition between nitrate and iodate would be far less affected by changes in nitrate concentration than might first appear. Finally, Waite and Truesdale (2003) have shown that deactivation of nitrate reductase, the enzyme in phytoplankton hitherto thought to facilitate iodate reduction, left *I. galbana*'s iodate-reducing ability unaffected.

Radiochemically measured iodine uptakes and interconversions in phytoplankton cultures (Sugawara and Terada 1967; Moisan et al. 1994) appear, at first, to conflict radically with the results of our mesocosm experiments. However, further investigation shows that either (1) the evidence for iodate reduction is often implied rather than actually measured or (2) iodate reduction is not the only interpretation that can be made from the results.

In terms of iodine uptake, Sugawara and Terada (1967) found that in cultures of the diatom *Navicula* sp. approximately 50% and 20% of the $^{131}I$ added as iodide or iodate, respectively, was removed over a period of about a month. Changes of this magnitude, even though they are removals and not straightforward reductions, would seem to imply a major change in speciation. Interestingly, taken in relation to the amount of each iodine species originally present, these losses from solution amount to only $0.062 \pm 0.002$ $\mu$mol $L^{-1}$ for both iodide and iodate. That is, irrespective of the original iodate to iodide concentration ratio (0.309 $\mu$mol $L^{-1}$ iodate, 0.130 $\mu$mol $L^{-1}$ iodide; 70% iodate), it is as if equal masses of iodate and iodide had been removed by the cells. In our study, the mesocosm water essentially contained only iodate, and the result of Sugawara and Terada (1967) would be equivalent to a loss of about 0.06 $\mu$mol $L^{-1}$ total iodine. Given that growth in the mesocosms was probably less dense than in the laboratory cultures, the measured loss of 0.023 $\mu$mol $L^{-1}$ total iodine over 25 d in the mesocosm supporting the highest algal biomass agrees well with Sugawara and Terada's result. Unfortunately, further analysis of the data of Sugawara and Terada (1967), to yield invaluable information about the change in the relative proportions of iodate and iodide in the cultures, is not easily conducted. We note incidentally that Sugawara and Terada (1967) used a culture with a very high concentration of nitrate (1 mmol $L^{-1}$). This fact needs to be considered in any argument that invokes nitrate outcompeting iodate to explain a difference in iodate reduction in temperate waters, as compared with those of the tropics. The contribution of Sugawara and Terada (1967) is one of few pieces of evidence supporting iodate reduction by phytoplankton, and it clearly supports this in a high nitrate condition.

Superficially, the claim of Moisan et al. (1994) that phytoplankton can take up (and reduce) as much as 3% of the ambient pool of iodate (0.18 to 0.25 $\mu$mol $L^{-1}$) on a daily basis, and the entire pool in about 1 month, conflicts radically with the results reported here. They observed that the amount of radio-iodine absorbed by phytoplankton in consecutive 30-min periods decreased over 4 h. They suggested that the iodate uptake was opposed by an increasingly faster return of radio-iodine to solution, which eventually culminated in a steady state. Indeed, we find their results adhere very closely to a model of two opposing first-order reactions, yielding an exponential increase toward an asymptote. Of course, as they argue, if the counter-process transported iodine as iodide back to solution, overall this system would provide an excellent mechanism for reduction of iodate to iodide. However, other possibilities exist and it is perhaps premature to overlook them. It is possible that they actually investigated the equilibration of radiogenic and nonradiogenic iodate in a system of culture solution and, say, sites on the cell wall. Under such circumstances the observations of Moisan et al. (1994) could be consistent with a very much lower rate of reduction in a third reaction, or even no reduction at all. Their mathematical fittings would still be valid, but the rate constant for generation of iodide would have been subsumed within the rate constant they actually calculated. Finally, there is much potential uncertainty in the calculation of Moisan et al. (1994) of a day or a month's iodate reduction. By fitting a straight line to the first few points of the uptake versus time graph, an initial, not a sustained rate, is measured. The calculated uptake rate grossly inflates the estimate of the monthly reduction. The actual removal of iodate would amount, at most, to the 0.1 to 1 nmol per $\mu$g chlorophyll *a* observed in the first 5 or so hours, and the further 98% of light period for the month could well be irrelevant.

The results obtained here in the mesocosm are not consistent with the iodate concentration changes imposed by the phytoplankta, *Synechococcus* sp., *Dunaliella tertiolecta, Amphidinium carterae,* and *Skeletonema costatum* at ambient iodate concentration (Wong et al. 2002). The magnitude of one of these changes ranks with the 0.20 $\mu$mol $L^{-1}$ target suggested by Truesdale and Bailey (2002) as unequivocal proof of iodate reduction and is therefore important. (Incidentally, the cultures contained nitrate under conditions similar to those used by Truesdale 1978*a,* Butler et al. 1981, and Waite and Truesdale in press, yet the yields of iodide are very much greater.) The losses of iodate were between 0.15 and 0.30 $\mu$mol $L^{-1}$ for all but the cultures of *Tetraselmis* sp. and *Emiliania huxleyi,* which lost about 0.1 and 0.0 $\mu$mol $L^{-1}$, respectively. The iodide productions accompanying iodate loss were generally much smaller, suggesting that uptake was more prevalent than reduction. Taking the iodide produced as a proportion of the iodate originally present provides reductions of 53% in the *Dunaliella* sp. culture, about 15% in the cultures of *Tetraselmis* sp. and *Synechococcus* sp., and less than 5% in the cultures of *E. huxleyi* and *Amphidinium* sp. The experiment with *Synechococcus* sp. was odd in that twice as much iodide appeared as iodate disappeared. Putting aside the latter problem then, out of the six species tested the only major reduction could be seen as having occurred with *Dunaliella* sp.

We conclude that while the ability of phytoplankton to reduce iodate is not now contentious, the issue of whether they can do it quickly enough under natural conditions is. Currently, there is as much evidence against iodate reduction in the seas being mediated by phytoplankton as there is for it. In this context, our mesocosm results are highly pertinent.

Further, suggestions that there should be differences in iodate reduction between temperate and tropical water, involving new and regenerated production, do not appear so far to have translated easily into experimental proof based on ammonium and nitrate uptake. In regard to this it is especially interesting to see that some of the major pieces of evidence in favor of iodate reduction by phytoplankton, including the most serious claim (Wong et al. 2002), relate to cultures containing nitrate. Given these points it is still reasonable to seek a mechanism that can explain iodate reduction both in the tropical water column and across the temperate shelf.

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