Measuring Biogenic Carbon Flux in the Ocean

Richard B. Rivkin *et al.* (*1*) propose that neither food-web structure nor new production can be used to predict the magnitude or patterns of downward export of biogenic organic carbon (BC) from the euphotic zone, at least for the duration of their study. These conclusions depend critically on the observations that while both food-web structure and new production estimates were different during and after the spring phytoplankton bloom, the BC flux—as estimated using shallow surface-tethered sediment traps—was similar for the two periods. We argue that the uncertainties associated with the trap-derived BC flux estimates are too large to support these conclusions, and we offer an alternative explanation for the apparent similarity of bloom and post-bloom export fluxes.

An extensive body of literature (*2*) indicates that surface-tethered sediment traps deployed in the upper ocean are subject to collection biases that can lead to order-of-magnitude (or more) errors in the measured particle fluxes. Rivkin *et al.* (*1*) explicitly assume that BC export can be estimated from their traps deployed just below the surface mixed layer. Although they do acknowledge that sampling artifacts can provide flux estimates that differ from those derived by the ^{234}Th method by up to a factor of 3, the studies they cite do not suggest this to be a maximum estimate of the overall uncertainty.

The main collection biases exhibited by sediment traps are a result of the effects of zooplankton ("swimmers") actively entering the trap and water flow around and within the trap, which may alter the collection efficiencies of different particle types ("hydrodynamic effects"). These potential sources of error are generally maximized when zooplankton are abundant and water currents (or current shear) are high. Such conditions are most likely to prevail in and just below the surface mixed layer and will probably be quite different in bloom and post-bloom conditions, thus potentially giving rise to different collection biases during the two periods. But even if swimmer and hydrodynamic conditions were similar both during and after the bloom, different collection biases for the two periods are possible; recent field (*2*) and flume (*3*) studies suggest that different particle types can experience different collection biases. That is, the hydrodynamic effects on phytoplankton aggregates may be very different from those on morphologically different dense particles such as fecal pellets. Such artifacts would be expected to depress the apparent BC flux into a trap during the aggregate-dominated phytoplankton bloom, while elevating the flux in post-bloom conditions when zooplankton (and thus fecal pellets) are more abundant. The egestion of fecal pellets by swimmers while in the traps may further influence collection biases because it is difficult to discriminate between pellets produced by swimmers and those intercepted by the trap. The overall effects would be to smooth out the seasonal cycle of BC flux; other studies using surface-tethered traps beneath the mixed layer show evidence of an artifactual smoothing as a result of traps overcollecting during periods of low productivity and undercollecting during periods of high productivity (*4*).

Moreover, it is widely acknowledged that the direct sinking of phytoplankton aggregates provides the most efficient transfer of BC out of surface waters (*5*). So we are puzzled that the post-bloom BC fluxes described in the report (*1*), which must issue from several trophic transfers within the food web, appear to indicate a higher transfer efficiency of column-integrated primary production (on the basis of primary production × euphotic zone depth) out of surface waters than during the bloom period. An artifactual seasonal smoothing of the BC export fluxes may well have occurred. Finally, the observations of invariant bloom and post-bloom BC fluxes (*1*) are at odds with a wealth of studies, based on a wide range of different marine environments (*6*), that reveal a strong seasonal signal in deep-water BC fluxes that corresponds to bloom–non-bloom seasonality in surface waters (*7*). The dataset in this report (*1*) does not provide evidence of the lack of influence of food-web structure or new production on BC export flux, but rather serves as a reminder of the problems of interpreting the signal from surface-tethered shallow-water sediment traps.

Philip Boyd
National Institute of Water
and Atmospheric Research,
Centre for Chemical and Physical
Oceanography,
Department of Chemistry,
University of Otago,
Dunedin, New Zealand
Philip Newton
Centre des Faibles Radioactivités,
Centre National de la Recherche Scientifique–
Commissariat à l'Energie Atomique,
91198 Gif-sur-Yvette, France

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Response: To address the issue of seasonal smoothing of BC flux, we examined the effects of swimmers and water motion on our sediment trap samples in the Gulf of St. Lawrence specifically and the magnitude of collection bias for surface-tethered sediment traps in general. With regard to swimmers, neither zooplankton abundance (*1*) nor production rates of fecal pellets were significantly different during and after the bloom that we studied (*2*). It follows that the effects of swimmers and their products on estimated C fluxes should have been similar during bloom and non-bloom periods. Concerning possible hydrodynamic bias, the movement of the surface floats tethered to the traps (*3*) indicate that water velocities were 7.9 to 13.8 cm s^{-1} in April and 12.5 to 33.3 cm s^{-1} in June. However, because our traps were free-drifting, relative water motion over the trap opening was significantly lower (*4*, *5*). Based upon these findings (*4*, *6*), we estimate that relative water velocities over our traps were less than 10 cm s^{-1} and trap Reynolds numbers (R*t*) were less than 8000 (*6*). These values are below the threshold water velocities (12 to 15 cm s^{-1}) and R*t* (about 10^4), above which significant hydrodynamic effects on trap collections are observed (*5*, *7*). Moreover, the low and uniform (<0.5 to 3.5×10^{-4} s^{-1}) Brunt-Väisälä frequencies below 40 m during the two observation periods indicate little hydrodynamic activity near trap depths.

Collection bias has been inferred from differences in vertical flux predicted from disequilibrium between ^{234}Th and ^{238}U in the upper water column and from the flux estimated from ^{234}Th collected in sediment traps (*4*, *8*, *9*). From limited observations (*4*), it was hypothesized that traps will overcollect during periods of low particle flux and undercollect during periods of high particle flux, and that this will cause seasonal smoothing of vertical fluxes. Boyd and Newton contend that this seasonal smoothing was responsible for the similarity in BC fluxes during the bloom and post- bloom periods in the Gulf of St. Lawrence. However, seasonal smoothing of BC flux

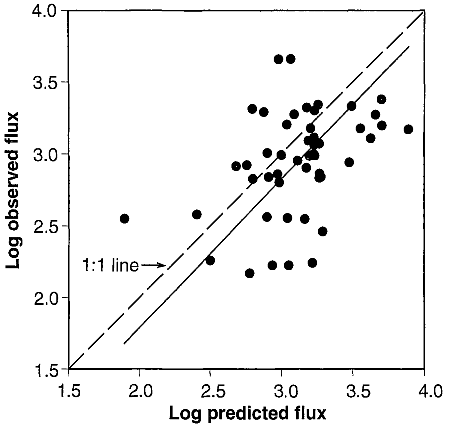

Fig. 1. Relation between Log 10 predicted and Log 10 measured ^{234}Th fluxes (dpm m^{-2} day^{-1}). Data are from table 1 of (*8*); data point 42 was excluded (*12*). Model II regression equation is Log Observed Flux = −0.284 (±0.860) + 1.037 (±0.275) Log Predicted Flux, $r^2 = 0.17$, $n = 50$. Values in parentheses are the 95% confidence intervals. Dashed 1:1 line is given for visual reference.

assumes that the collection bias depends on the magnitude of the flux. Collection bias, defined as the ratio of observed ^{234}Th flux: predicted ^{234}Th flux (O-^{234}Th:P-^{234}Th), typically varies by a factor of 2 to 3 (*10*). We reanalyzed the data set in the paper by Buesseler (8) and found that about 90% of the reported observations fell within a factor of 3 of the median O-^{234}Th:P-^{234}Th value of 0.66. The slope and intercept of the Model II regression of Log O-^{234}Th flux on Log P-^{234}Th flux (*11*) are not significantly different from 1 and zero, respectively (Fig. 1), when a single extreme value is omitted [O-^{234}Th:P-^{234}Th = 83; (*12*)]. The relation, although significant, explains only 17% (r^2) of the variance. These results do not support the premise of a flux-dependent collection bias and seasonal smoothing of fluxes and instead suggest a weak but systematic undercollection over the entire range of reported fluxes. Thus, the magnitude of the bias is generally small (two- to threefold) and not greater than or equal to tenfold as stated by Boyd and Newton.

Boyd and Newton's argument that export efficiency is inversely related to trophic complexity is valid only if the system is in equilibrium. A major point of our report (*1*) was that food web structure, new production, and BC export were not related because the surface layer ecosystem was not in equilibrium. Further, the composition of the BC flux can differ markedly in near-surface (that is, immediately below the euphotic zone) and deep-water (for example, greater than 1000 m) traps. Because coprophagy and coprorhexy recycle most fecal material within the upper water column (*13*), copepod fecal pellets often make up a negligible fraction of the material in deep traps (*14*), where the flux principally consists of phytodetritus, fecal pellets from large microphages, and the soma, exoskeletons, and feeding webs from a variety of planktonic and midwater grazers. Because copepods may feed omnivorously when the abundance of large phytoplankton is low and the microbial food web dominates (*1*), fecal pellet flux from the euphotic zone can be high; however this fecal material may not be recorded in deep-water traps. Although our observations may appear to be at odds with deep-water flux showing seasonal signals (*15*), these two types of flux are not comparable.

Richard B. Rivkin, *Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada;* ***Louis Legendre,*** *Département de Biologie, Université Laval, Québec, QC G1K 7P4, Canada;* ***Don Deibel,*** *Ocean Sciences Centre, Memorial University of Newfoundland;* ***Jean-Éric Tremblay, Bert Klein,*** *Département de Biologie, Université Laval;* ***Kenneth Crocker,*** *Ocean Sciences Centre, Memorial University of Newfoundland;* ***Suzanne Roy,*** *Institut Nationale de la Recherche Scientifique-Océanologie, Rimouski, QC G5L 3A1, Canada;* ***Norman Silverberg,*** *Institut Maurice-Lamontagne, Ministère des Pêches et des Océans, Mont-Joli, G5H 3Z4 QC, Canada;* ***Connie Lovejoy, Fabrice Mesplé,*** *Département de Biologie, Université Laval;* ***Nancy Romero,*** *Institut Maurice-Lamontagne;* ***M. Robin Anderson,*** *Fisheries and Oceans Canada, Newfoundland Region, St. John's, NF A1C 5X1, Canada;* ***Paul Matthews,*** *Ocean Sciences Centre, Memorial University of Newfoundland;* ***Claude Savenkoff, Alain Vézina, Jean-Claude Therriault,*** *Institut Maurice-Lamontagne;* ***Joel Wesson,*** *Department of Atmospheric and Oceanic Sciences, McGill University, Montreal, QC H3A 2K6, Canada;* ***Chantal Bérubé,*** *Institut Maurice-Lamontagne;* ***R. Grant Ingram,*** *Department of Atmospheric and Oceanic Sciences, McGill University*

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2. Fecal pellet production rates (pellets per copepod per hour) of 0.1 to 1.1 in April and 0.05 to 0.7 in June were not significantly different (unpaired t test, P = 0.05).
3. Traps (10:1 aspect ratio and drag area of about 1 m^2) were deployed below the euphotic zone (50 m) for 24 hours.
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6. In the Sargasso Sea, the water velocity over the opening of drifting traps, determined with hydrodynamic sensors on the trap array, was 8 to 25% of the absolute velocities determined from the movement of surface floats (5). With the use of an upper value of 25%, we found the water velocities over our traps, and the *Rt* in the Gulf of St. Lawrence, to be 2.0 to 3.5 cm s^{-1} and 2000 to 3500, respectively in April and 3.0 to 8.1 cm s^{-1} and 3100 to 8100, respectively in June.
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10. In coastal waters, the seasonal mean O-^{234}Th:P-^{234}Th flux ratio is 0.56 (n = 48; range 0.24 to 1.78) [C. L. Wei and J. W. Murray, *Limnol. Oceanogr.* **37**, 296 (1992)]. The range is similar in offshore waters [K. H. Coale and K. W. Bruland, *ibid.* **30**, 189 (1985)].
11. Log 10 transformation of the O-^{234}Th:P-^{234}Th flux ratio normalizes the distribution (Shapiro-Wilk test) and 90% of all observations fall within a factor of 3 of the mean ratio of 0.68.
12. The O-^{234}Th:P-^{234}Th flux ratio was 83 in the Black Sea sub-oxic zone [C. L. Wei and J. W. Murray, *Deep Sea Res.* **38**, S855 (1991)]. This extreme ratio may be a result of Mn oxyhydroxides recycling processes which govern the distribution of dissolved ^{234}Th across the oxic-anoxic interface.
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