

of three phyla is compatible with the view that the establishment of phyla continued into the Cambrian¹⁹, and it provides a more complete framework of character evolution in the assembly of their bodyplans for which developmental explanations must now be sought. The placement of fossil-based developmental data in this context facilitates a thorough integration of palaeontology into evolutionary developmental biology in understanding the evolution of development.

Superphylum Introverta Nielsen 1995 (ref. 20)

Genus *Markuelia* Val'kov 1983 (ref. 21)

Markuelia hunanensis Dong & Donoghue sp. nov.

Etymology. Named for its provenance in the Chinese Province of Hunan.

Holotype. Geological Museum of Peking University, Beijing, China: GMPKU2010.

Stratigraphy and locality. Middle Upper Cambrian Bitiao Formation in Wangcun, Hunan, south China.

Diagnosis. A species of *Markuelia* with six terminal, posterior spines arranged radially and away from a central depression or opening, lacking trunk spines, and showing at least three overlapping rows of posteriorly directed circum-oral scalds.

Remarks. *Markuelia* cannot be allocated to existing rank taxa below Introverta without rendering such taxa paraphyletic. The establishment of many hierarchies of new rank taxa, solely to encompass *Markuelia*, will not serve scientific communication. □

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Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs

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Ecosystems are supported by organic carbon from two distinct sources. Endogenous carbon is produced by photosynthesis within an ecosystem by autotrophic organisms. Exogenous carbon is produced elsewhere and transported into ecosystems. Consumers may use exogenous carbon with consequent influences on population dynamics, predator–prey relationships and ecosystem processes¹. For example, exogenous inputs provide resources that may enhance consumer abundance beyond levels supported by within-system primary production². Exogenous fluxes of organic carbon to ecosystems are often large, but this material is recalcitrant and difficult to assimilate, in contrast to endogenously produced organic matter, which is used more easily^{3,4}. Here we show, by the experimental manipulation of dissolved inorganic ¹³C in two lakes, that internal primary production is insufficient to support the food webs of these ecosystems. Additions of NaH¹³CO₃ enriched the ¹³C content of dissolved inorganic carbon, particulate organic carbon, zooplankton and fish. Dynamics of ¹³C indicate that 40–55% of particulate organic carbon and 22–50% of zooplankton carbon are derived from terrestrial sources, showing that there is significant subsidy of these ecosystems by organic carbon produced outside their boundaries.

In lakes, grazing and microbial–detrital trophic pathways support higher consumers^{5,6}. The importance of dissolved and particulate organic matter not derived from primary producers has been recognized^{4,7}, but not widely considered in studies of food webs¹. System respiration exceeds gross primary production in many lakes, implying the metabolism of exogenous organic carbon⁸. Aquatic bacteria use exogenous dissolved organic carbon (DOC), and subsequent consumption of bacteria by predators provides a pathway for transfer into food webs^{9,10}. However, efficiencies of bacterial growth and trophic transfer of exogenous carbon are often low, and the importance of this pathway is uncertain^{6,11}. Direct use of exogenous carbon by animal consumers is also possible^{12,13}, but poorly understood.

Large-scale tests of the importance of exogenous carbon to food

webs are few; however, the elimination of forest litter inputs in small streams was found to reduce the biomass and production of consumers¹⁴. In larger systems, stable isotopes of elements such as carbon, nitrogen and sulphur can help to distinguish organic matter sources¹⁵, but often isotopic differences between endogenous and exogenous materials are not distinct. An alternative approach is to label endogenous primary production with a tracer and to investigate whether fluxes are sufficient to support consumers¹⁶.

We made daily additions of NaH¹³CO₃ to the mixed layers of Paul Lake and Peter Lake over 42 d, enriching ¹³C in DIC (Fig. 1). Phytoplankton rapidly fixed carbon from enriched DI¹³C, as indicated by increases in the δ¹³C of POC (δ¹³C_{POC}; Fig. 1). POC is a mixture of phytoplankton, small heterotrophic organisms (mainly bacteria) and non-living organic matter. When the NaH¹³CO₃ addition ended, δ¹³C of DIC (δ¹³C_{DIC}) and δ¹³C_{POC} decreased towards background levels. The δ¹³C dynamics of *Daphnia* spp., a consumer of phytoplankton and important prey of invertebrates and fish¹⁷, was very similar to δ¹³C_{POC} in both lakes (Fig. 1).

To assess the relative contributions of endogenous and exogenous carbon to POC, we compared three models of the observed ¹³C

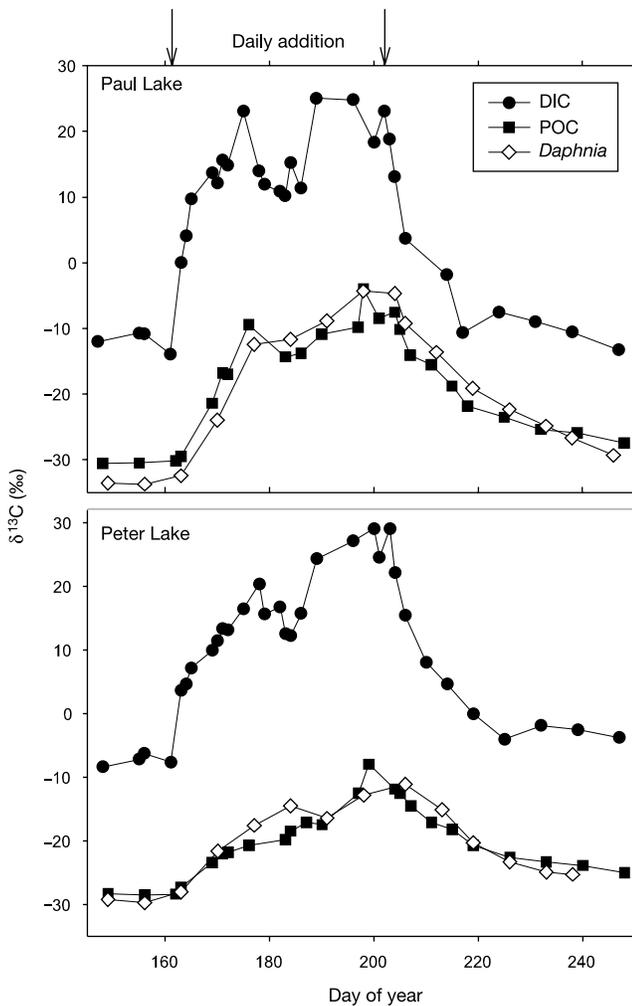


Figure 1 Dynamics of ¹³C before, during, and after the addition of NaH¹³CO₃ to Paul Lake and Peter Lake. Additions were made daily from day 162 to day 203 of the year. The carbon pools are dissolved inorganic carbon (DIC), particulate organic carbon (POC) and *Daphnia* spp. The ¹³C content of samples is expressed as δ¹³C = 1,000 × [(R/0.011237) - 1], where R is the ratio of ¹³C to ¹²C in the sample and 0.011237 is the ratio in a standard.

dynamics. The simplest model assumes that POC is derived solely from within-lake primary production. δ¹³C_{POC} on day *t* is predictable from δ¹³CO_{2(aq)} and photosynthetic fractionation (ε_p).

$$\delta^{13}\text{C}_{\text{POC}t} = (\delta^{13}\text{CO}_{2(\text{aq})} - \epsilon_p)_t \quad (1)$$

δ¹³CO_{2(aq)} is the ¹³C content of aqueous CO₂, the form of DI¹³C that is taken up most readily by phytoplankton¹⁸. Chemical fractionation of ¹³C between CO_{2(aq)} and HCO₃ was calculated from DIC, DI¹³C, pH and temperature¹⁹. The unknown parameter is ε_p, the biological fractionation of ¹³C during photosynthesis. Fractionation is negative in relation to δ¹³CO_{2(aq)} typically ranges from 21 to 28‰ (ref. 20).

The second model assumes that POC is a mixture of phytoplankton carbon derived from photosynthesis and carbon with a terrestrial isotopic signature.

$$\delta^{13}\text{C}_{\text{POC}t} = (1 - w)(\delta^{13}\text{CO}_{2(\text{aq})} - \epsilon_p)_t + w(-28) \quad (2)$$

Terrestrial plants dominant in the lake watersheds use C₃ photosynthesis and have a δ¹³C value close to -28‰. The unknown parameters in equation (2) are ε_p and *w*, the proportion of POC of terrestrial origin.

The third model was similar to model 2 but included an additional term for carbon derived from recent photosynthesis, denoted by the parameter *m*.

$$\delta^{13}\text{C}_{\text{POC}t} = (1 - w)[(1 - m)(\delta^{13}\text{CO}_{2(\text{aq})} - \epsilon_p)_t + m(\delta^{13}\text{CO}_{2(\text{aq})} - \epsilon_p)_{t-u}] + w(-28) \quad (3)$$

Carbon turnover is not instantaneous, and this model accounts for carbon from primary production residing over time in POC. The unknown parameters in equation (3) are ε_p, *w*, *m* and *u*, where *m* is the proportion of POC formed by photosynthesis *u* days before *t* (see Methods and Supplementary Information).

Assuming that POC is completely phytoplankton carbon (model 1) provides a poor fit to the data (Table 1). This model predicts more negative values of δ¹³C_{POC} in Paul Lake than were observed at the beginning and end of the experiment, and more positive values than were observed during the middle of the experiment (Fig. 2a). Adding a second pool of carbon (that is, terrestrial carbon) not labelled by the ¹³C addition substantially improves the model fit (Fig. 2b, Table 1). Model 3 provides the best fit to the data (Fig. 2c), and this improvement is highly significant (Table 1). Similar results were obtained when models 1, 2 and 3 were applied to data from Peter Lake (Table 1).

The best estimates of ε_p (±1 s.d.) are 11.4 ± 0.7‰ and 11.5 ± 1.1‰ in Paul Lake and Peter Lake, respectively. For all

Table 1 Parameter values* for models of POC and *Daphnia* ¹³C dynamics in Paul Lake and Peter Lake

POC	Model	ε _p	w	m	u	RSD	AIC
Paul Lake	1	17.8 ± 1.42				7.07	83.0
Paul Lake	2	9.5 ± 2.00	0.46 ± 0.047			3.21	66.1
Paul Lake	3	11.5 ± 0.90	0.40 ± 0.027	0.44 ± 0.071	8 ± 0.87	1.58	53.0
Peter Lake	1	21.6 ± 1.55				7.53	84.5
Peter Lake	2	10.2 ± 2.44	0.59 ± 0.042			2.49	59.9
Peter Lake	3	11.4 ± 1.25	0.55 ± 0.028	0.51 ± 0.116	9 ± 1.75	1.49	51.7
<i>Daphnia</i>							
Paul Lake	1	16.6 ± 1.94				7.45	56.8
Paul Lake	2	11.3 ± 3.21	0.38 ± 0.096			5.26	53.3
Paul Lake	3	14.5 ± 0.95	0.22 ± 0.045	0.56 ± 0.077	13 ± 1.07	2.22	43.5
Peter Lake	1	19.7 ± 1.89				7.03	49.2
Peter Lake	2	10.8 ± 3.06	0.55 ± 0.067			2.86	38.6
Peter Lake	3	12.5 ± 0.72	0.50 ± 0.020	0.92 ± 0.076	6 ± 0.48	0.83	25.2
Peter Lake	3	12.8 ± 1.08	0.48 ± 0.031	0.54 ± 0.073	10†	1.33	30.7

*Shown are the parameter values (ε_p, *w*, *m* and *u*) with bootstrapped estimates of s.d., mean residual s.d. (RSD) and Akaike information criteria (AIC) for models of POC and *Daphnia* ¹³C dynamics in Paul Lake and Peter Lake. Number of observations: *n* = 24, POC models; *n* = 16, Paul *Daphnia* models; *n* = 14, Peter *Daphnia* models. †*u* was fixed in this analysis.

three models, ϵ_p is less than 20‰ (Table 1), which contrasts with the fractionation observed in cultures and marine systems^{18,20} but is consistent with a previous whole-lake ¹³C addition¹⁶.

We considered three analogous models for the ¹³C dynamics of *Daphnia* spp. (hereafter *Daphnia*) by replacing the left-hand term of equations (1) to (3) with $\delta^{13}C_{Daphnia}$. Model 3 also provided the best fit to the $\delta^{13}C_{Daphnia}$ data (Table 1). For Paul Lake, the model captures the overall dynamics but predicts higher values before the addition and overestimates the decline in ¹³C after the addition (Fig. 3, top). Measured losses of ¹³C from both *Daphnia* and POC (Fig. 2) were slower than the model estimates, probably owing to a low turnover of structural carbon.

For Peter Lake, two lags (u) fit the data (Table 1). A 6-d lag provides the best fit (Fig. 3, bottom) but a high estimate of m . This model implies that nearly all of the phytoplankton carbon consumed by *Daphnia* is recent as opposed to produced on the same day as measurements of *Daphnia* ¹³C. A time lag of 10 d results in a slightly worse fit but an estimate of m that is consistent with other models. In either case, model 3 provides an excellent fit (predicted versus observed: $u = 6$, coefficient of correlation squared (r^2) = 0.98; $u = 10$, $r^2 = 0.95$). The strong relationship between $\delta^{13}C_{POC}$ and $\delta^{13}C_{Daphnia}$ (Fig. 1) also suggests that *Daphnia* fed primarily in the surface layer and not on sources from deeper layers

including methanotrophic bacteria (refs 21, 22, and see Supplementary Information).

Carbon assimilated by *Daphnia* is transferred up the food web. *Daphnia* is a key prey for insects that are, in turn, principal dietary items of fish¹⁸. In addition, *Daphnia* accounts for nearly 100% of the initial diet of young-of-the-year (YOY) largemouth bass (*Micropterus salmoides*) in Paul Lake²³. During the ¹³C addition, $\delta^{13}C$ of YOY bass increased from -28.4 to -9.7, indicating that exogenous and endogenous carbon moves from POC to *Daphnia* to fish.

On the basis of the models, POC consisted of 40% and 55% organic matter with a $\delta^{13}C$ value close to -28‰ in Paul Lake and Peter Lake, respectively (model 3; 'w' in Table 1). The balance derived from primary production. POC turns over within 1–10 d through respiration, conversion to DOC, consumption or sinking¹⁶. Thus, new inputs must replace the continuous losses of POC. The ¹³C additions indicate that a large fraction of this carbon comes from sources other than within-lake primary production.

There are several possible pathways for exogenous carbon to enter lakes and subsequently be transformed into POC available to consumers such as *Daphnia*. DOC of terrestrial origin can be converted to POC through chemical and biological mechanisms including aggregation, coagulation, flocculation and bacterial uptake. But bacterial production seems insufficient to account for much of the carbon required by consumers¹⁶. On the basis of atmospheric inputs of terrestrial material to lakes²⁴, we estimate that POC deposition could be 50–100 mg C m⁻² d⁻¹, an input sufficient to account for the PO¹³C dynamics observed in the addition experiments. Physical conversion of DOC to POC could constitute a large flux, because DOC is over ten times the concentration of POC. DOC in river water rapidly aggregates into submicrometer particles that contain DNA, lipids and sugars¹³.

Similar aggregations in lakes might constitute food for organisms such as *Daphnia* that feed on small particles. Resuspended sediments might also contribute to POC with a $\delta^{13}C$ value similar to that of terrestrial carbon. Paul Lake and Peter Lake are small and

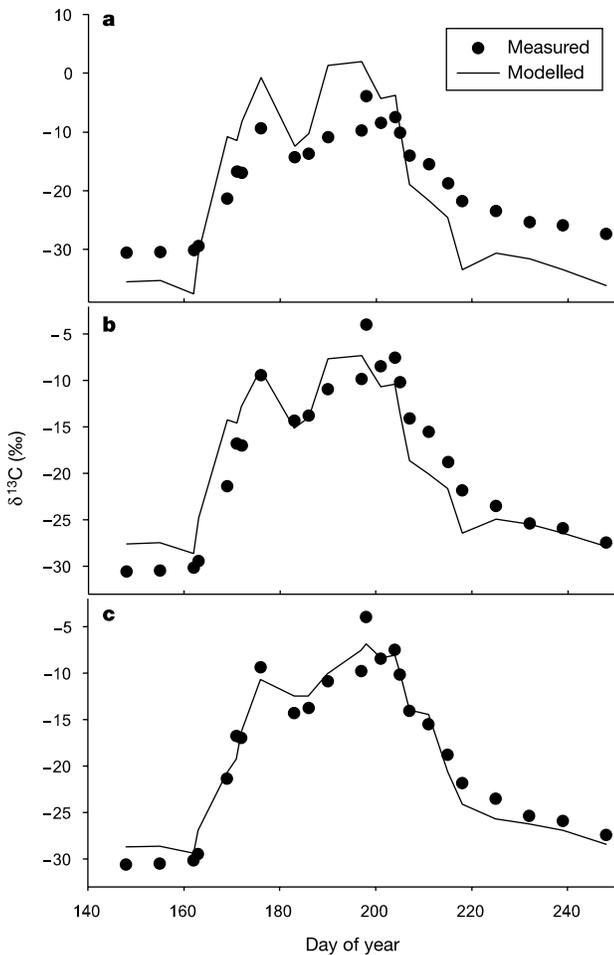


Figure 2 Comparison between measured and modelled $\delta^{13}C_{POC}$ in Paul Lake. **a**, Model 1 assumes that all POC is phytoplankton. **b**, Model 2 assumes that POC is a mixture of phytoplankton and organic carbon with a fixed value of -28, the signature of terrestrial organic matter. **c**, Model 3 is similar to model 2 but contains additional parameters for carbon that is recently derived from primary production in the lake. Equations for each model are given in the text.

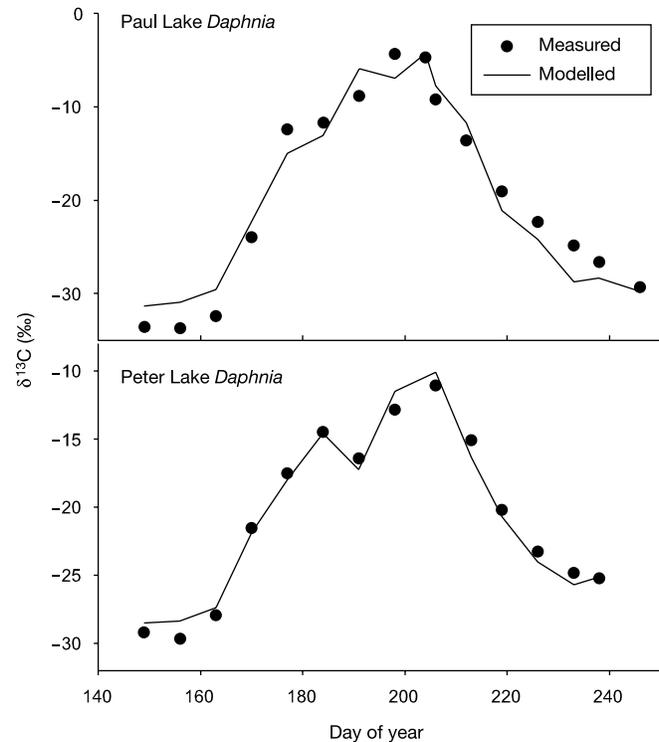


Figure 3 Comparison between measured and modelled $\delta^{13}C$ of *Daphnia* in Paul Lake and Peter Lake based on model 3.

deep, with a limited littoral area as a source of resuspended material, and limited fetch to create wind-driven waves¹⁷. Thus, resuspension is probably a small input in these lakes. A combination of terrestrial carbon inputs from both dissolved and particulate materials probably accounts for the large pool of exogenous carbon in POC. Quantitative measurements of these inputs are needed to determine their significance.

The dynamics of the ¹³C isotope in our whole-lake addition experiments clearly indicates that about half of the POC, first, is not based on current or recent primary production; second, has a δ ¹³C value consistent with that of terrestrial plants; third, is assimilated by animals; and last, is passed up the food web to fish. These results provide evidence that inputs of terrestrial carbon support secondary production in lakes of 17,000–24,000 m². The magnitude of this support is large but may be sensitive to nutrient enrichment. In a previous experiment with additions of nitrogen and phosphorus, less than 10% of zooplankton biomass seemed to be derived from allochthonous carbon⁷. Under the ambient nutrient loading of our experiments, *Daphnia*, which is traditionally considered a herbivore, received 20–50% of its carbon from a source other than primary production. Thus, the food webs are not simply based on internal primary production but are also coupled to watershed inputs of organic carbon. These inputs supplement the production of consumers and seem to be important in many ecosystems¹. For lakes, movements of organic carbon connect terrestrial ecosystems with aquatic food webs and support not only bacteria, but also invertebrates and fish. □

Methods

Study sites and field methods

Paul Lake and Peter Lake are located at University of Notre Dame Environmental Research Center, Michigan, USA (46° 13' N, 89° 13' W). These lakes have been studied extensively, and published data¹⁷ on the mixing depth, temperature, pH, carbon concentrations, productivity and trophic structure aided our design of the ¹³C additions. A third lake, Hummingbird, was monitored for ¹³C as a reference for natural variability (Supplementary Information). We dissolved 20 g (Paul) or 30 g (Peter) of NaH¹³CO₃ in lake water and pumped the solution into the upper, mixed layer from a moving boat. Previous studies²⁵ indicate that solute additions mix completely within 24 h. Loadings were 0.24 mol of ¹³C d⁻¹ to Paul Lake and 0.35 mol of ¹³C d⁻¹ to Peter Lake. The cumulative addition over 42 d altered total DIC by less than 1%. The added NaH¹³CO₃ (Isotech) was more than 99% ¹³C. Daily additions maintained an increase in DI¹³C over longer periods of time. In a previous experiment, a single addition of NaH¹³CO₃ to a lake resulted in a rapid loss of ¹³C to the atmosphere and limited movement of ¹³C into the food web, despite the addition of nutrients (N and P) to promote carbon fixation¹⁶.

Measurement of standing stocks and ¹³C

Carbon concentrations and ¹³C contents in various pools were measured at weekly or more frequent intervals. Concentrations of DIC were measured with a gas chromatograph. POC and chlorophyll *a* were measured in samples retained on GF/F filters. POC was determined in concert with analyses of ¹³C (see below). Filters for chlorophyll *a* were extracted in methanol, and concentrations were determined by fluorometry. We estimated zooplankton abundance from vertical net hauls. The ¹³C content of DIC, POC, the cladoceran, *Daphnia* spp. and YOY largemouth bass, *M. salmoides* (Paul Lake only), was measured by mass spectrometry.

We collected samples for DIC and POC daily before each addition. Samples for analysis of DI¹³C were collected in 100-ml serum vials, acidified to pH 2 with H₂SO₄, closed with gas-tight seals, and sent to the University of Waterloo stable isotope facility for analysis. Analysis of POC samples for both total C concentration and ¹³C content were conducted at the University of Alaska stable isotope facility. A subset of the daily collection of DIC and POC samples was analysed to characterize the dynamics of ¹³C before, during and after the addition. Analyses of ¹³C in dried tissue of *Daphnia* spp. and *M. salmoides* were also made at the University of Alaska. *Daphnia* were collected at least weekly by towing a net immediately beneath the surface at night and subsequently isolating animals from live samples under a dissecting scope. YOY bass were collected either from the guts of adult bass or by electroshock sampling. We dried and ground whole fish for tissue analysis.

Statistics and modelling

To derive a time series, δ ¹³CO_{2(aq)} data were interpolated to generate daily values, and the model was evaluated for the dates that δ ¹³C_{POC} or δ ¹³C_{*Daphnia*} were sampled in each lake. The best-fitting parameters for the three models (Table 1) were determined by least squares²⁶, and models were compared by the mean residual s.d. and the Akaike information criterion²⁷. A worked example of model 3 calculations and the method for estimating the parameter *u* are given in the Supplementary Information. We estimated parameter uncertainty by bootstrapping²⁸. Bootstrapped parameter distributions for the models were roughly normally distributed, and parameter bias²⁸ was only a few per cent of

the s.d. Residuals for the models were approximately normally distributed. We chose a value of -28‰ to represent terrestrial organic matter on the basis of measurements of the δ ¹³C of wetland and forest plants (*n* = 10) surrounding Paul Lake and Peter Lake.

For Peter Lake and Paul Lake, model 3 residuals averaged about 1.5‰ (Table 1) and were comparable to error in the data. PO¹³C samples taken over 24 h on 20–21 June 2001 had a mean and s.d. (*n* = 6) of -16.6 ± 2.1‰ and -21.0 ± 0.7‰ for Paul Lake and Peter Lake, respectively. The variation of these samples reflects analytical and sampling error, as well as dynamics in PO¹³C (uptake and loss of ¹³C). Although the diel sampling series probably overestimates variability of the PO¹³C data used in the model (all samples were taken at the same time of day), the comparison indicates that the model residual error was of the same magnitude as the error in the data.

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