Terrestrial support of zebra mussels and the Hudson River food web: A multi-isotope, Bayesian analysis

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Abstract

　　The Hudson River is a strongly heterotrophic system in which the invasive zebra mussel (*Dreissena polymorpha*) comprises >90% of total metazoan biomass. Using a Bayesian mixing model, with isotope ratios of C, N, and H, and four basal resources (phytoplankton, benthic algae, submersed aquatic vegetation [SAV], and terrestrial inputs), we estimated the reliance of 10 consumers on each resource. Copepods, *Bosmina*, and herring (*Alosa aestivalis*) relied 40–60% on phytoplankton primary production; amphipods and young-of-year white perch (*Morone* spp.) relied heavily on benthic algae (50–60%). Terrestrial detritus was an important resource for oligochaetes, zebra mussels, chironomids, and *Bosmina* sp., for which median estimates of reliance were between 40% and 60%. The dual reliance of zebra mussels on terrestrial detritus and phytoplankton production, combined with their high biomass, along with the significant terrestrial support of several other consumers, indicates that terrestrial detritus supports a significant portion of the Hudson River food web. Nonetheless, given that particulate and dissolved organic matter pools are heavily dominated (60–80%) by terrestrial detritus, it is clear that selectivity by consumers for autochthonous organic matter is generally high. Despite its large biomass and productivity, we did not find strong evidence for support of the food web by SAV.

The flow of materials and energy between different ecosystems in a landscape connect these systems in interesting ways (Polis et al. 1997). Aquatic ecosystems typically receive significant inputs of terrestrial organic matter at levels that are often coequal to and sometimes much larger than autochthonous primary production (Caraco and Cole 2004). Large, deep rivers can be extreme in this regard. In turbid, well-mixed waters, phytoplankton can be severely light limited, and macrophytes and benthic algae are restricted to the shallowest, light-exposed portions (Frenette et al. 2006). At the same time, the flow of water from the watershed brings with it a great deal of dissolved and particulate organic matter of terrestrial origin that can dwarf autochthonous primary production (Vannote et al. 1980). The gas and metabolic balances of large rivers demonstrates that terrestrial organic matter is being respired. That is, these rivers are generally undersaturated in dissolved oxygen and supersaturated in CO_2, a result that is consistent with ecosystem respiration (R) being in excess of gross primary production (GPP; Cole and Caraco 2001; Battin et al. 2008). R can exceed GPP only if there is an exogenous source of organic matter. Clearly, respiration (which is often largely microbial) is supported in part by terrestrial inputs. It is not yet clear whether the metazoan food web of large rivers is also subsidized by these terrestrial inputs.

Thorp and Delong (2002), on the basis of the data available at the time, suggested there is a "heterotrophy paradox" in rivers and proposed the Revised River Production Model (RRPM). That is, although the metabolic balance in rivers is decidedly net heterotrophic, metazoan consumers are supported mostly by autochthonous sources

of organic matter. The studies in their review used stable isotopes, mostly δ^{13}C and some additionally with δ^{15}N, and largely visual or strictly algebraic mixing models to evaluate the results. These approaches make it difficult to deal quantitatively with the common problem of having more potential food sources than isotopes, causing authors to resort to qualitative solutions or to lump disparate sources. Since that time, there has been a revolution in isotope mixing models that deal with the problem of mathematically underdetermined mixing models (number of sources is more than number of isotopes +1; Phillips and Gregg 2003) as well as with uncertainty in the isotopic composition of the sources (Moore and Semmens 2008; Boecklen et al. 2011). There have been several studies of large food webs since the Thorp and Delong (2002) review that have used formal isotope mixing models (Martineau et al. 2004; Hoffman et al. 2008), but none yet have made use of isotopes of H, which have been proving useful in studies in both streams (Doucett et al. 2007; Finlay et al. 2010) and lakes (Babler et al. 2011; Cole et al. 2011; Solomon et al. 2011). The contrast in the deuterium-to-hydrogen ratio (δ^2H) between material produced on land by terrestrial photosynthesis and that produced by phytoplankton or benthic algae is very large, typically more than 100 parts per thousand and much larger than small contrasts in δ^{13}C or δ^{15}N of a few parts per thousand. This large contrast in (δ^2H), which is passed up the food web (Doucett et al. 2007), makes δ^2H particularly helpful in determining the importance of terrestrial versus algal resources to a given consumer.

In this study, we examine the allochthonous and autochthonous support of key consumers in the Hudson River as a further test of the RRPM of Thorp and Delong (2002). By using stable isotope ratios of three elements (C, N, and H) and a Bayesian mixing model, we examine the quantitative importance of multiple, potential basal food

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resources to a suite of 10 consumers, including benthic invertebrates, zooplankton, and fish, and to dissolved and particulate organic matter.

Site description

The Hudson River estuary begins at the confluence of the Mohawk and Upper Hudson Rivers near Troy, New York (river kilometer 240), where a dam exists at the natural fall line of the river. From there, the Hudson River flows south, where it merges with New York Harbor at the southern tip of Manhattan Island (river kilometer 0). This 240-km estuary is at sea level and is tidal over its length. The upper $\sim$ 200 km is tidal, freshwater to oligohaline, depending on discharge, and vertically well mixed with respect to temperature and dissolved oxygen (Cooper et al. 1988; Raymond et al. 1997).

The tidal-freshwater Hudson is a strongly net-heterotrophic ecosystem and is dominated by watershed inputs of organic matter (Howarth et al. 1996). This freshwater section of river does not receive either salt or nutrients or organic matter from New York City, which is in the saline part of the estuary. The Hudson is both turbid and well mixed; therefore, the phytoplankton are strongly light limited and primary production is low (Cole and Caraco 2006). Since the invasion of the zebra mussel in 1992, phytoplankton consist mainly of large diatoms with sporadic blooms of *Microcystis* and other cyanobacteria in late summer (Fernald et al. 2007). Mean annual chlorophyll *a* values are below 5 μg L^{-1} and peak values rarely exceed 10 μg L^{-1} (Pace et al. 2010). The major input of organic C to the Hudson is from the watershed at 650 g C m^{-2} yr^{-1}, which is more than six times larger than estimates of net primary production (NPP) of the sum phytoplankton, macrophytes and periphyton (Fig. 1). The dominant macrophytes in the Hudson are the submergent *Vallisneria americana* and the floating leafed *Trapa natans*. Total macrophyte NPP is estimated at 42 g C m^{-2} yr^{-1}. Traditional estimates of NPP of phytoplankton using ^{14}C incubations give about 70 g C m^{-2} yr^{-1}. These values do not include the respiration of phytoplankton in the dark, which can be quite large in this well-mixed and poorly lit system. Thus, the true NPP of phytoplankton may be even lower (Cole and Caraco 2006). The production of benthic algae is poorly known but is probably < 2 g C m^{-2} yr^{-1} (Cole and Caraco 2006). Heterotrophic respiration, dominated by pelagic bacteria (116 g C m^{-2} yr^{-1}) and zebra mussels (83 g C m^{-2} yr^{-1}), are together larger than autochthonous primary production. Thus, the system is strongly net heterotrophic, and the excess in R over GPP results in generally undersaturated dissolved oxygen and supersaturated CO_2 concentrations (Raymond et al. 1997; Caraco et al. 2000; Cole and Caraco 2001). Because the respiration of these known consumers is larger than total autochthonous inputs, the C balance suggests that these consumers (and possibly others) must be subsidized by terrestrial inputs.

There is evidence of a significant terrestrial subsidy to zooplankton in the Hudson. Caraco et al. (2010) showed that the cladoceran, *Bosmina*, and mixed copepods were
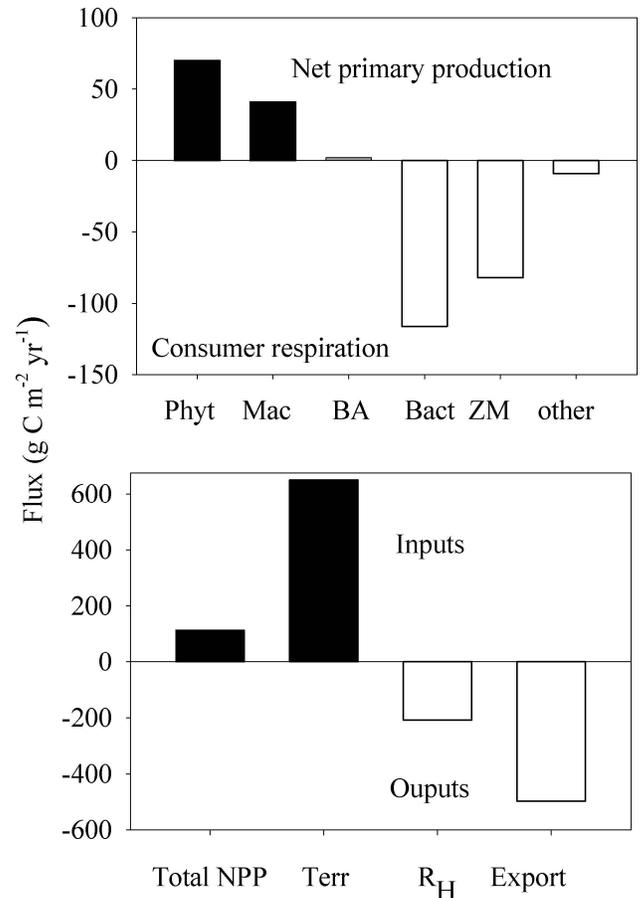
Fig. 1. Organic carbon balance of the tidal-freshwater part of the Hudson River. The upper panel shows net daytime photic zone primary production from phytoplankton (Phyt), net production of macrophytes (Mac; the sum of SAV and *Trapa natans*), and benthic algae (BA) along with the respiration from pelagic bacteria (Bact), zebra mussels (ZM), and other benthic organisms. Data from Cole and Caraco (2006) and sources therein. Note: Actual NPP for phytoplankton may be lower if 24-h algal respiration in the dark is considered (Cole and Caraco 2006). The lower panel shows total net inputs from autochthonous primary production (total NPP, i.e., the sum of the net production of phytoplankton, periphyton, and macrophytes) in comparison to loading from the watershed (Terr), total heterotrophic respiration (R_H, the sum of the respiration of bacteria, zebra mussels, and "other" in the upper panel), and export downstream.

highly depleted in ^{14}C compared to any autochthonous component of primary production. Only suspended particles (particulate organic matter [POM]) of terrestrial origin in the river had δ^{14}C signatures depleted enough to support the zooplankton results. Caraco et al. (2010) estimated that the terrestrial subsidy to zooplankton was about 30–50%, depending on the assumptions made for the age (postglacial soils vs. Devonian shale) of the depleted ^{14}C organic matter. In this article, we examine the terrestrial subsidy to a suite of the major of pelagic and benthic consumers, including the zebra mussel (*Dreissena polymorpha*), in the Hudson River using stable isotopes of C, N, and H and a Bayesian isotope mixing model. The zebra mussel is of particular interest because it is the consumer with by far the

Table 1. Locations and physical characteristics of the Hudson River where the samples were taken. Samples were taken at various locations within each reach. The location of each reach is given as a range of kilometers north of the southern tip of Manhattan Island (river kilometer 0). Shown are the mean depth of the main river channel, the bank to bank width of the river, and the number of consumer (or DOM and POM) samples we obtained and used in this study from each reach (river kilometer).

Reach (river km)	Mean channel depth (m)	Width (km)	No. of consumer or pool samples
60–71	7.3	3.5	21
72–140	11.9	1.2	24
141–173	8.9	1.4	43
173–228	6	0.4	42

largest biomass in the river and has the highest secondary production of any metazoan consumer in the system (Strayer and Smith 2001).

Methods

Stable isotope samples for this study were taken from April through November from river kilometer 45 to 240 over a 3-yr period (2006–2009). Four reaches were visited repeatedly (three to eight times) to produce replicate samples in space and time of each of 10 consumer taxa as well as pools of dissolved organic matter (DOM) and POM. Our goal was to obtain samples from a large area of the river; we are not attempting in this article to examine spatial variability in these consumers. The locations of the reaches along with width and depth are shown in Table 1, as are the number of samples taken and samples in each category (Table 2). Zooplankton, phytoplankton net tows, POM, DOM, and samples of the soft bottom benthos were taken at mid-channel. Among the stations, the mid-channel depths vary from 6 to 11.9 m (Table 1). Zebra mussels were taken at depths where zebra mussels occur (about 0.5–4 m; *see* below). Benthic algae and littoral, rocky-bottom fauna (notably amphipods) were taken from rocks at water depths of about 0.2–0.5 m. The fish were captured in

shallow water (< 1.5 m) using beach seines in the same reaches described above. For individual consumers or pools, sample size varied from 5 (spottail shiners) to 21 (POM) and averaged 11 samples per pool. We evaluated four ultimate sources of organic matter as potentially fueling the food web: phytoplankton, submersed aquatic vegetation (SAV), terrestrial vegetation, and benthic algae. These sources are the major known allochthonous and autochthonous inputs to the river (Cole and Caraco 2006; Fig. 1) and were also possible to sample. We characterized the mean and variance of the stable isotope ratios of these sources using 5–12 samples per source.

Consumers

Zooplankton were sampled using net tows from a boat at the center of the river at each site. Samples were sorted in filtered river water to allow gut clearance and then under a dissecting scope to either species (*Bosmina freyi*) or for the copepods to class (dominated by *Diacyclops bicuspidatus thomasi*, with presence of *Halicyclops* sp., and *Eurytemora affinis*). Each zooplankton sample consisted of about 300–600 individuals for *Bosmina* and > 300 for the copepods. These zooplankton are the numerical dominants in the river (Pace et al. 2010). Zooplankton samples, as well as all consumers and source samples (below), were rinsed in slightly acidic (pH ~ 4) water to remove inorganic C.

Benthos from the soft sediments (oligochaetes, polychaetes, and chironomids) were sampled using a PONAR sampler, also at mid-river. Excluding the zebra mussel, oligochaetes are the numerical dominant, followed by chironomids. Polychaetes are much less abundant (Strayer and Smith 2001). Samples were sieved in the lab to remove small particles and sorted under a dissecting scope as above. About 10–15 individuals were used to create each sample. The oligochaetes are dominated by tubificids and by the genus *Limnodrilus* (Strayer and Smith 2001), but no attempt was made to sort these beyond the subclass. The polychaetes contain two genera (*Scolecolepides* and *Manayunkia*). The chironomids are diverse but dominated by three genera (*Coelotanypus*, *Tanytarsus*, and *Polypedilum*)

Table 2. The number of samples (consumers and DOM and POM) used in this study. Shown are major categories, the taxon level we used in each sample, and the number of samples for which we obtained data for the three isotopes.

		No. of isotope samples		
Major category	Consumer or pool	$\delta^{13}C$	$\delta^{15}N$	δ^2H
Dissolved or suspended organic matter	POM	20	20	21
	DOM	14	NA	14
Zooplankton	*Bosmina*	7	7	7
	Copepods	11	11	11
Soft-bottom benthos	Chironomids	9	8	9
	Oligochaetes	9	9	8
	Polychaetes	4	4	4
Shallow-water benthos	Zebra mussels	20	20	15
	Amphipods	13	13	15
Fishes	Blue-back herring	7	7	
	Morone spp.	8	8	8
	Spottail shiner	5	4	5

that we did not attempt to separate. In all cases, the whole animal was used.

Bivalves (*D. polymorpha*) were taken from rocks collected by scuba diver at the sites as part of an ongoing study (Strayer et al. 2011). After slicing the byssal threads, the bivalves were placed in filtered river water to allow the guts to clear and then dissected. The entire soft part of the animal was used.

Amphipods (*Gammarus fasciatus*) were sampled from shallow water littoral habitats (< 1 m) by collecting rocks in the field. They were sorted in filtered river water after removal from rocks.

Fishes were captured by beach seines in shallow-water habitats. While a large diversity of fishes were encountered, we restricted this analysis to young-of-year blueback herring (*Alosa aestivalis*), spottail shiners (*Notropis hudsonius*), and moronids (dominated by *Morone americana* white perch but could contain *Morone saxatilis* [striped bass], which is difficult to distinguish when small). These species were selected because they are common, ubiquitous, and easily captured. Fishes were stored frozen until dissection. For these small fish (2–5 cm in all cases), scales were removed, but the rest of the animal was used in the sample.

Samples for particulate organic matter were filtered through 1.2-μm-pore-size, 47-mm-diameter Micron-Sep membrane filters (Thomas Scientific). The filtrate (after discarding a rinse) was saved for DOM (below). The material retained by the filter was gently scraped and rinsed into a Petri dish, acidified to pH $\sim$ 4 to volatilize inorganic C, and then dried. To obtain samples for dissolved organic matter, we took 1 liter of filtrate from the Micron-Sep filters (above). The filtrate was acidified to pH $\sim$ 4 to volatilize inorganic C and evaporated to dryness (40°C). This procedure removes inorganic carbon and water, so the remaining C and H isotopes are samples of the organic fraction. This procedure does not remove inorganic N, which in the Hudson can be significant (Caraco et al. 1998). Thus, the DOM samples cannot reliably be used for N isotopes in this system.

Samples for water were filtered (GF/F) and stored in gas tight vials at 4°C for analysis for δ^2H and δ^{18}O in H_2O.

Sources

Terrestrial vegetation—We used freshly fallen leaves or needles of the dominant tree species (oak, maple, beach, pine, and hemlock) in the Hudson's watershed as the basis for the terrestrial end member. We took eight samples for δ^{13}C, δ^{15}N, and δ^2H and pooled these to get the mean and variance of the terrestrial end member.

Phytoplankton—In many systems, it is difficult to physically separate phytoplankton from seston. In the Hudson, by using either 63- or 100-μm-mesh-size plankton nets, we were able to obtain 12 net tow samples that contained almost entirely phytoplankton. Using a dissecting scope, we removed contaminating particles (mostly zooplankton). These net tows contained either large centric diatoms (*Aulacoseira* is a dominant), colonial diatoms (*Fragilaria, Tabellaria*, or *Chaetoceros*), or, on two occasions, colonial cyanophytes (*Microcystis* and *Anabaena*). These taxa are common and often dominant forms in the phytoplankton of the Hudson (Fernald et al. 2007).

SAV—We sampled the dominant macrophyte in the Hudson, *V. americana*, from eight sites at which the plant is fully submersed at low tide. The plant was washed free of particles and adherent organisms and dried (40°C).

Benthic algae—We sampled benthic algae from shallow-water habitats where we were able to get seven samples that visually appeared to be free of obvious nonalgal material. These samples were then inspected under a dissecting microscope, and contaminating particles were removed. Samples consisted of either *Cladophora* or a mixture of cyanophytes and diatoms.

Isotope analyses

Samples for δ^{13}C, δ^{15}N, and δ^2H were sent to the Colorado Plateau Stable Isotopes Laboratory (CPSIL) at Northern Arizona University. To obtain the isotopic signature of the nonexchangeable H fraction, the samples were treated as described in Doucett et al. (2007). Following a benchtop equilibration to correct for exchange of H atoms between samples and ambient water vapor samples for δ^2H were pyrolyzed to H_2 gas following the procedures of Doucett et al. (2007) and Finlay et al. (2010). Water samples were analyzed for δ^2H via cavity ring-down laser spectroscopy. Samples for δ^{13}C and δ^{15}N followed standard procedures for the CPSIL. The analytical precision for replicate samples at CPSIL are 0.1‰ for δ^{13}C, 0.2‰ for δ^{15}N, and 2‰ for δ^2H (M. Caron pers. comm). As percent uncertainties for the data reported here, these are about 0.4% for C, 2.5% for N, and 1.5% for H and are much smaller than the variability among actual samples from the environment.

Bayesian mixing model

To estimate the contribution of each source to each consumer or pool, we used the Bayesian isotope mixing model (BIMM) of Solomon et al. (2011), with slight modifications to incorporate macrophytes as a fourth source. We chose to use this BIMM rather than one of several other published options because of our personal experience with it and for several other reasons: (1) it is the only published model setup to simultaneously use isotopes of C, H, and N in a food web context; (2) it incorporates uncertainty in source isotopes into posterior estimates of resource use; (3) it provides posterior estimates of two poorly known parameters: the total contribution of dietary water to δ^2H and the total trophic fractionation of N (a product of both trophic level and the N fractionation for each trophic level); and (4) it has been extensively tested using synthetic data and added variance (Solomon et al. 2011).

In brief, for each consumer or pool, the model estimates posterior probability distributions for the source proportions (ϕ_T, fraction terrestrial; ϕ_P, fraction phytoplankton;

ϕ_{SAV}, fraction SAV; ϕ_{BA}, fraction benthic algae; $\phi_T + \phi_P + \phi_{\text{SAV}} + \phi_{\text{BA}} = 1$) based on the observed consumer stable isotope ratio data, uninformative priors on the $\varnothing$ parameters, literature-derived informative priors on two physiological parameters (ω_{tot} and δ_{tot}; *see* below), and data-derived informative priors on the residual variance. The uninformative priors on the source proportions ϕ are constrained to add to 1 using the centered log-ratio transform and have a mean of 0.25 and a median of 0.09. The physiological parameter ω_{tot} describes the proportion of the H in the biomass of the consumer that comes from environmental water instead of from diet (Solomon et al. 2009), and the parameter δ_{tot} describes the total fractionation of N isotopes between a consumer and its basal resources. Both of these parameters are a function of trophic level and a per-trophic-level effect. We constructed priors for these parameters following Solomon et al. (2011), with prior estimates of trophic level for each consumer based on feeding mode. The model was fit in WinBUGS as described in Solomon et al. (2011).

As a further way to compare our results, we ran the mean values for each consumer group (and DOM and POM) using IsoSource, a widely used, non-Bayesian isotope mixing model (Phillips and Gregg 2003). For IsoSource, we had to assign fixed values to δ_{tot} and ω_{tot} and used 3‰ for δ (the fractionation of ^{15}N per trophic level) and 15% and 20%, respectively, for ω_{tot} for primary consumers and higher consumers (Babler et al. 2011; Cole et al. 2011). While the isotope mixing equations in IsoSource and the Bayesian model are nearly identical, IsoSource deals with uncertainty differently than in the Bayesian model. IsoSource uses a tolerance parameter, which is the number of isotope delta units within which a fit is considered acceptable (Phillips and Gregg 2003). We used a tolerance value of 2‰ as the starting point but were able to reduce it to 1‰ in 10 of the 12 cases and still get resolvable solutions. In all cases, we stepped through the mixtures at 1% increments.

Results

Basal resources—The four ultimate food sources we considered (terrestrial organic matter, phytoplankton, benthic algae, and SAV) were well separated by their isotopic signatures using all three isotopes (Fig. 2). For example, while phytoplankton and terrestrial organic material had similar values of δ^{13}C, they differed very significantly in both δ^{15}N and δ^2H (Fig. 2). The variance over time and space in the source isotopes was smallest for terrestrial and SAV and largest for phytoplankton (Fig. 2). As in many aquatic habitats, benthic algae and SAV were more enriched in ^{13}C than phytoplankton. As expected, both benthic algae and phytoplankton were strongly depleted in ^{2}H compared to terrestrial organic matter. The SAVs, while more depleted in ^{2}H than terrestrial photosynthesis, were not nearly as depleted as phytoplankton. This intermediate ^{2}H depletion for aquatic macrophytes has been observed in other habitats but does not yet have a good physiological explanation (K. Hondula pers. comm.).

The δ^2H of Hudson water averaged -59.7‰ (SD = 5.6‰, $n = 21$). There was a tendency for the water to be
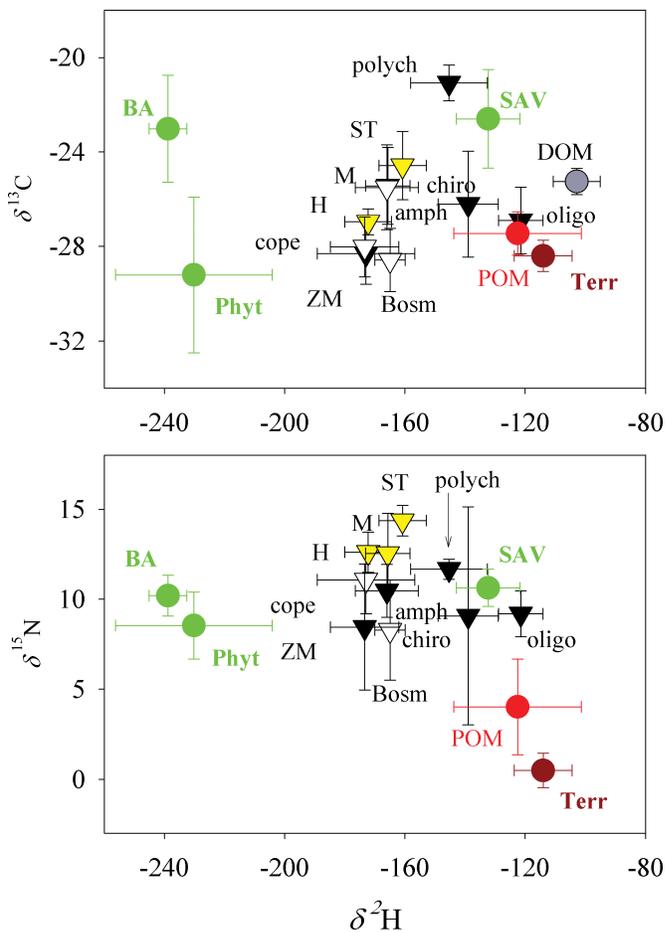
Fig. 2. Stable isotope ratios of key components of the Hudson River food web. The autochthonous sources are solid green circles and include benthic algae or periphyton (BA), phytoplankton (Phyt), and SAV. Terrestrial organic matter is the solid brown circle (Terr), and POM and DOM are shown as red and dark gray solid circles, respectively. Note that DOM is not shown on the lower panel because we do not have data for the δ^{15}N of DOM. Open inverted triangles indicate zooplankton, including *Bosmina* (Bosm) and copepods (cope). Black-filled inverted triangles indicate benthic invertebrates, including amphipods (amph), polychaetes (polych), oligochaetes (oligo), chironomids (chiro), and zebra mussels (ZM). Yellow-filled inverted triangles indicate fishes, including *Morone* spp. (M), herring (H), and spottail shiners (ST). The δ^2H of Hudson River water is ~ -60‰ (*see* text).

slightly more enriched in the downstream portion of the river. A linear regression of δ^2H against river km is significant ($p < 0.001$) but has a very shallow slope (-0.087‰ per river kilometer). Thus, over 100 km of river, the expected change in δ^2H is only about 8‰.

Consumers and organic matter—The isotopic signatures for the consumers (and DOM and POM) were contained within the polygons described by the four sources for δ^{13}C and δ^2H (Fig. 2a), but many of the consumers had higher δ^{15}N, as expected, than the ultimate source terms (Fig. 2b). The plotted values of δ^{15}N are not corrected for trophic fractionation. Making a rough estimate of a 3‰ enrich-
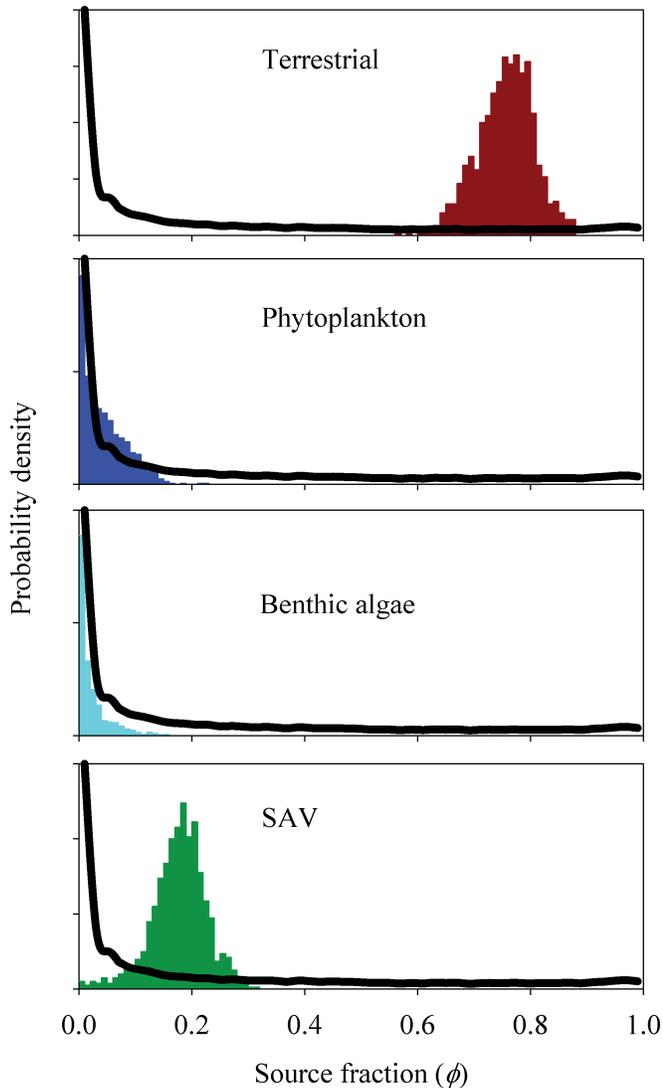
Fig. 3. Estimates of the fractional contribution (ϕ) of each source (terrestrial, phytoplankton, benthic algae, and SAV) to the POM pool in the Hudson River. The histograms show the posterior probability estimates for the contribution of each source to the POM pool. For example, the data indicate that the most likely contribution of SAV to the POM pool is ~ 0.19 and that it is very unlikely that the SAV contribution to the POM pool exceeds 0.30. Black lines show the uninformative prior distributions. In all cases, the area under the curve or histogram equals 1.

ment for primary consumers and 6–12‰ for the fishes, it is clear that the consumers are within the boundaries of the sources.

It is difficult to derive strong inference from the biplots alone, but a few points are obvious. (1) Both POM and DOM plot much closer to the terrestrial source than to other sources. (2) For most of the consumers, mixing lines would have to involve multiple sources. That is, few source combinations are ruled out entirely by the biplots alone. (3) Some of the consumers (e.g., oligochaetes) plot much closer to the terrestrial end member, and others (e.g., copepods) imply a mixing line that includes at least phytoplankton and terrestrial material. (4) The different locations of the

consumers on the biplots suggest that they are not all using the basal resources in the same proportions. (5) The $\delta^{15}N$ data further suggest that most consumers could not rely entirely on the autochthonous sources. Considering trophic level and trophic fractionation, the autochthonous sources are too enriched in ^{15}N to be the sole base of the food web. For example, the $\delta^{15}N$ of *Vallisneria* averaged 10.6‰ (± 1 SD). No primary consumer except the polychaete has a $\delta^{15}N$ that is ~ 3‰ or more higher than this (Fig. 2), suggesting that SAV is not readily assimilated as a major diet item by most consumers. On the other hand, the $\delta^{15}N$ data imply that terrestrial sources are likely involved for many of the consumers (particularly oligocheates, zebra mussels, and both *Bosmina* and the copepod zooplankton; Fig. 2b).

*Modeled sources for consumers and organic matter—*Using the Bayesian mixing model, we estimated posterior distributions for ϕ for each source and consumer. In most cases, the posterior distributions differed substantially from the priors, indicating that the data were informative about the contributions of the sources to the consumers. Examination of the mixing model output enhances the conclusions drawn from visual inspection of the isotope biplots (Fig. 2). In Fig. 3, we show the mixing model results for POM, which is a simplified case, as POM has neither trophic fractionation for N nor dietary water for H (i.e., both δ_{tot} and ω_{tot} are 0). These results show that POM is highly dominated by terrestrial sources and that SAV may make a minor contribution (Fig. 3). The posterior for ϕ_T for POM is unlike that for the prior; its probability mass is shifted strongly toward higher values (Fig. 3). Similarly, the posteriors for ϕ_P and ϕ_{BA} are shifted toward lower values, indicating that it is extremely unlikely that more than 20% of POM comes from phytoplankton or that more than 15% of POM comes from benthic algae. Thus, POM appears to consist of about 80% terrestrial material at the median estimate, with relatively narrow uncertainty (Fig. 3).

In Fig. 4, we illustrate three examples for consumers that span the range of results. The amphipod shows a clear reliance on benthic algae with some indication of minor reliance on terrestrial material. Estimates of reliance on phytoplankton and SAV are low, highly variable, and not different from the prior distribution (Fig. 4a). For both *Bosmina* and the zebra mussel, we see about an even split in terrestrial and phytoplankton as likely sources and no evidence that either benthic algae or SAV are significant (Fig. 4b). The mixing model also provides posterior estimates of the physiological parameters, δ_{tot} and ω_{tot} (Fig. 4, lower two rows). For all three of these primary consumers, the trophic fractionation for $\delta^{15}N$ agrees closely with the prior distribution, with the most likely values near 3‰. The posterior distribution for the amount of H coming from "dietary water" (ω_{tot}) is shifted lower than our priors, particularly in the case of the zebra mussel. For these three primary consumers, ω_{tot} had means near 16%, similar to but slightly lower than prior literature (Solomon et al. 2009; Wang et al. 2009).

To facilitate comparisons among all the consumers, Fig. 5 shows box-and-whisker plots of the posterior
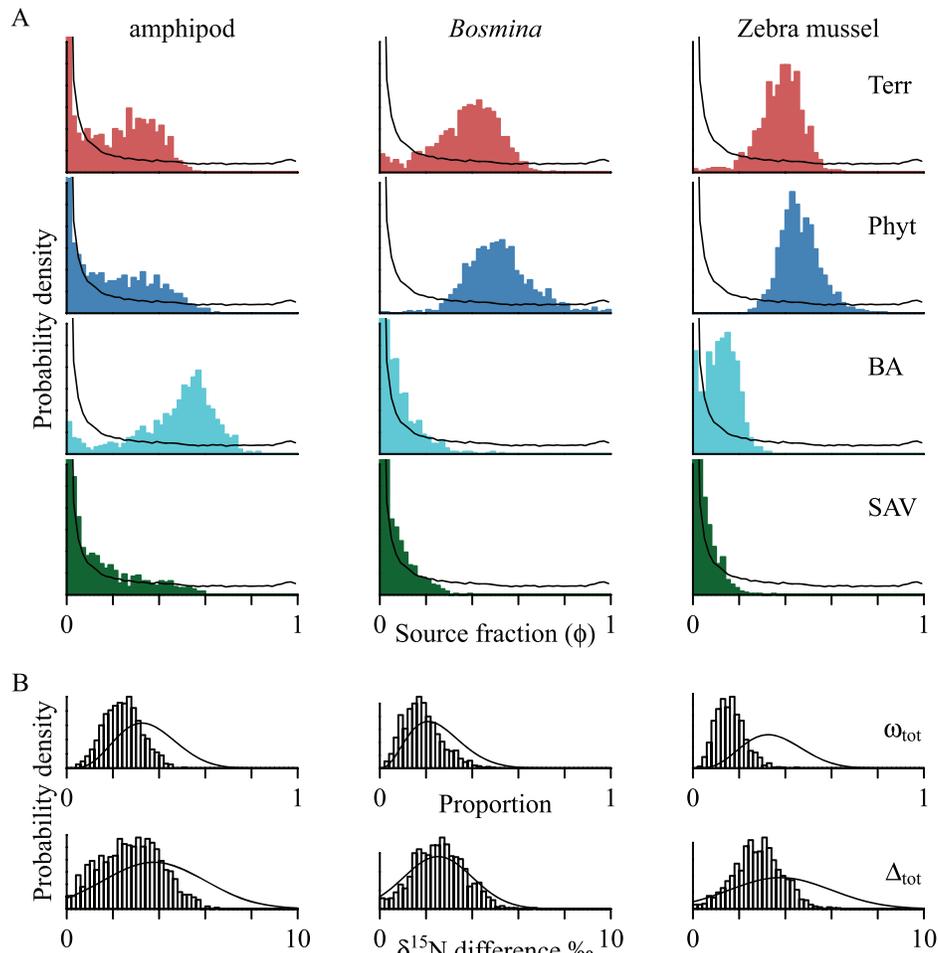
Fig. 4. (A) Estimates of the fractional contribution (ϕ) of each source (terrestrial, Terr; phytoplankton, Phyt; benthic algae, BA; and SAV) to the biomass of three consumers (amphipods, *Bosmina*, and zebra mussels) in the Hudson River. Histograms show the posterior probability estimates for the contribution of each source to each consumer. (B) Estimates of the total contribution of dietary water to tissue H (ω_{tot}) and the total trophic fractionation of N (δ_{tot}) for each consumer. Histograms show the posterior probability estimates for these two parameters. In all panels, gray lines indicate prior distributions, which were uninformative for the source contributions but informed by literature data for ω_{tot} and δ_{tot}.

distributions of ϕ for each source and consumer (as well as DOM and POM), along with the prior distributions. Terrestrial support is obviously high for POM, DOM, and several consumers (*Bosmina*, zebra mussel, and oligochaetes; Fig. 5a). In these cases, the median for ϕ_T is 30% or higher. As the median for ϕ_T drops for other consumers, the variance also increases. Thus, for several of the consumers (*Morone* spp., spottail shiner, and polychaetes), the 95% credible interval includes or approaches zero. For these consumers, while we cannot rule out some terrestrial subsidy, we also do not have strong positive evidence for it. There are several consumers (herring, copepods) where the posterior distribution is variable but suggests that an important terrestrial subsidy is highly likely.

The consumers show a similar response to terrestrial and phytoplankton resources (Fig. 5b). That is, several of the consumers for which terrestrial was significant also show a

significant proportion of phytoplankton (*Bosmina*, zebra mussel, herring, and copepod). Phytoplankton is clearly an unimportant source for DOM, POM, polychaetes, and both *Morone* spp. and spottail shiners (Fig. 5b).

Benthic algae (Fig. 5c) are important for amphipods, *Morone* spp., spottail shiners, and possibly polychaetes but unimportant for either of the zooplankters or the zebra mussel. Finally, SAV shows up as likely important in only two cases: DOM, where it may be as much as 35% of the total, and polychaetes, where the median is high although with high variance.

In Fig. 6, we compare estimates of ϕ_T from our Bayesian mixing model to those derived from IsoSource. Because of the way uncertainty is handled in IsoSource, the apparent variance for a given source is much smaller than that for the Bayesian model (Boecklen et al. 2011). The means for ϕ_T among consumers from both approaches tend to agree; a regression between the two is highly significant ($p < 0.01$)
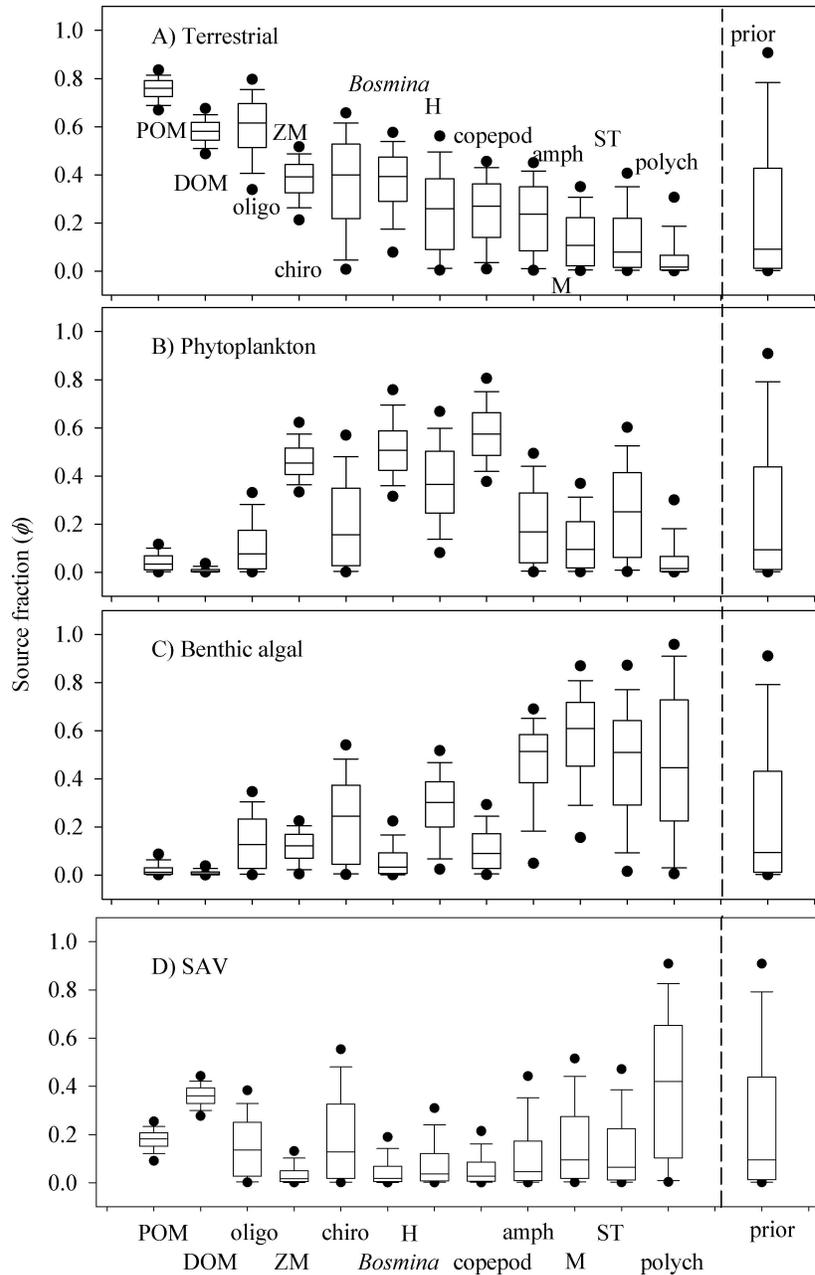
Fig. 5. Posterior estimates of the fractional contribution of each source (ϕ) to each consumer or pool in the Hudson River. Boxplots show the 5th, 25th, 50th, 75th, and 95th percentiles of the posterior distributions. To the right of the dotted line is the distribution of the prior. The abbreviations follow Fig. 2. In all cases except DOM, the analysis is based on three stable isotope ratios (C, H, and N). DOM is based on C and H (*see* text). Abbreviations are the same as in Fig. 2.

and explains a large fraction of the variability ($r^2 = 0.79$). The slope is slightly greater than unity (1.1 ± 0.17), so, compared to the Bayesian model, IsoSource (with the parameters we used here) overestimates the terrestrial fraction by about 10%. Nevertheless, the pools and consumers that were associated with high values of ϕ_T by the Bayesian model were similarly assigned by IsoSource (Fig. 6). On this plot, we can see that for 10 of the 12 cases, IsoSource assigns a value of $> 20\%$ terrestrial for the

means. For the Bayesian model, 9 of the 12 cases have $> 20\%$ terrestrial support. Further, there is good agreement about which pools have significant terrestrial support with few exceptions. For example, the Bayesian model assigns a lower and more variable fraction to terrestrial support for spottail shiners than does the IsoSource model. The Bayesian model assigns a larger fraction of DOM to SAV than does IsoSource, but both models estimate that DOM is dominated by terrestrial inputs. The substantially lower
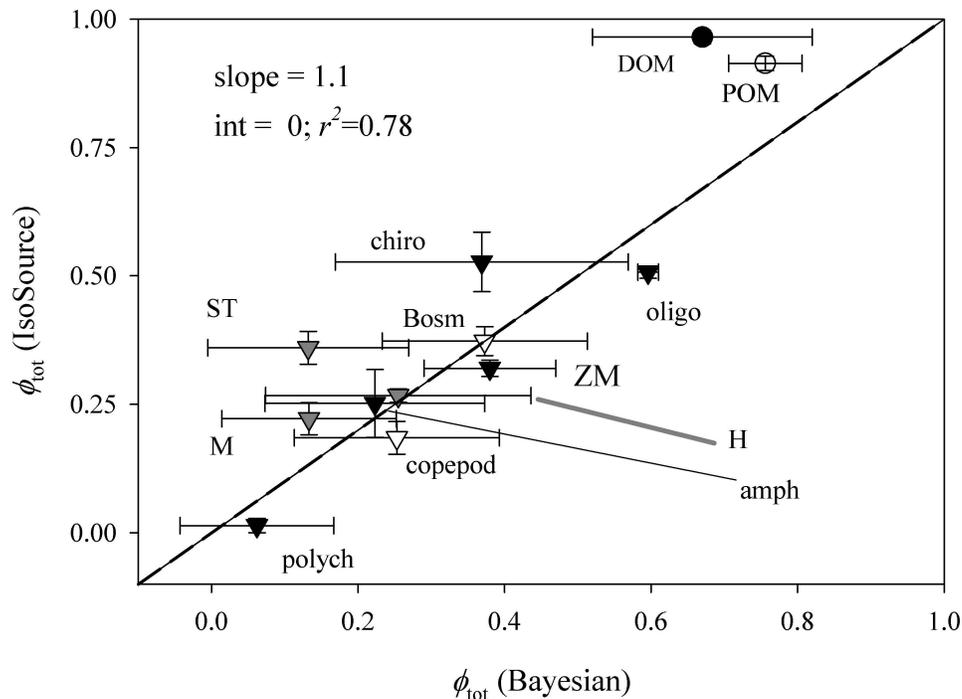
Fig. 6.   Estimates from two different mixing models—IsoSource and the Bayesian mixing model (Solomon et al. 2011)—of the fractional contribution of the terrestrial source (ϕ_1) to each consumer or pool. In both cases, the mean and standard deviation of the distributions are shown. Abbreviations follow those in Fig. 2. Inverted triangles are consumers (zooplankton, white), benthic invertebrates (solid black), and fishes (solid black). DOM and POM are filled and open circles, respectively.

uncertainty in the IsoSource output compared to the Bayesian one is inherent in the designs of these very different models and should not be compared directly since the Bayesian model considers many sources of uncertainty, while IsoSource does not.

Dietary water and nitrogen trophic fractionation—The Solomon et al. (2011) BIMM uses prior information and the data to estimate posterior distributions for two physiological parameters: dietary water (ω_{tot}) and the total trophic fractionation of N (δ_{tot}). Across the consumers, estimated dietary water varied from about 16% of total body H (zebra mussel) to more than 30% (*Morone* spp. and spottail shiner). As expected, ω_{tot} increased with increasing trophic level (Fig. 7). However, the posterior values for mean ω_{tot} are lower than those for our prior distributions. In the prior, we used $\omega = 0.25$ for the mean value of dietary water per trophic level above the basal resource based on the literature (Solomon et al. 2009; Wang et al. 2009), while the data from this study are consistent with a value of $\omega = 0.16$ (Fig. 7). The posterior estimates for trophic fractionation for nitrogen were consistent with prior estimates based on known feeding mode for each taxon and literature values of the enrichment for $\delta^{15}N$ per trophic level. For example, the plot for *Bosmina* (Fig. 3) shows near perfect agreement between the prior and posterior distributions of δ_{tot}; for the zebra mussel and amphipod, the posterior estimate of δ_{tot} is slightly higher at the mean and more variable than our prior distributions.

Discussion

Basal resources for the Hudson River food web—The Hudson River has multiple basal resources that are potentially available to consumers. Our results suggest that different consumers in the Hudson utilize these resources to very different degrees, in agreement with other studies on riverine food webs in both tropical (Hamilton et al. 1992; Hunt et al. 2012) and temperate (Martineau et al. 2004; Hoffman et al. 2008) regions. Further, our results show that these resources are not used in proportion to their abundances or loading rates. For example, benthic algae, which makes up a very small fraction of the organic load to the river, is extremely important to amphipods and some fishes. SAV, which has high biomass and productivity, does not appear to be significant in any of the members of the food web we examined. While many of the consumers utilize both phytoplankton and terrestrial organic matter, the relative proportions are strikingly different for different consumers.

Terrestrial support of components of the food web—The results of two modeling approaches, a Bayesian mixing model and as well as the simpler linear model, IsoSource, suggest that some of the consumers in the Hudson River, as well as DOM and POM, are made of significant proportions of organic matter derived from the watershed. Both models also agree that certain consumers (e.g., polychaetes) appear not to significantly access terrestrial
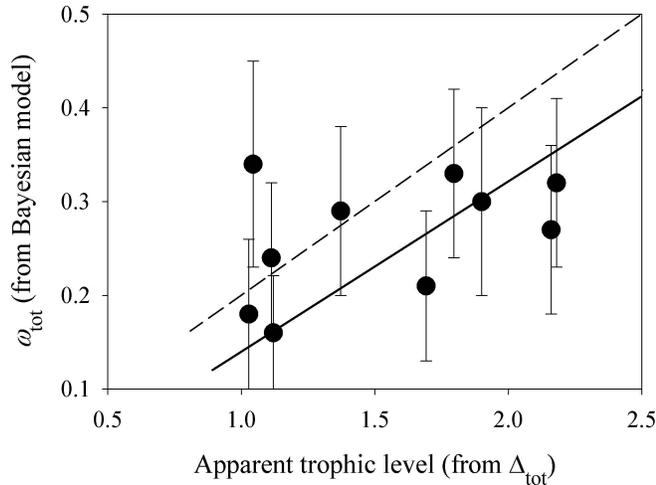
Fig. 7. Dietary water (ω_{tot}) and apparent trophic level from the Bayesian model. Each point represents a different consumer. Apparent trophic level (the mean posterior estimate of δ_{tot} divided by 2.54, the mean value for N fractionation per trophic level) is an approximate estimate of the number of trophic levels above basal resources for a given consumer; it coarsely sorts organisms into different trophic categories. Error bars are ± 1 SD. The dashed line shows the hypothetical relationship between ω_{tot} and trophic level if $\omega = 0.25$, as we assumed in constructing priors for ω_{tot}. The sold line is the regression through the plotted data, which is consistent with $\omega = 0.16$.

organic matter, while others (e.g., *Bosmina*, zebra mussels, and oligochaetes) may be a third or more made of terrestrial organic matter. As the organic matter budget of the Hudson River is dominated by terrestrial inputs, it is not surprising that DOM and POM appear to be isotopically more similar to terrestrial organic matter than to aquatic sources. Filter feeders in particular (e.g., *Bosmina* and *Dreissena*) would have to exhibit very strong selectivity to completely avoid terrestrial particles. Both *Bosmina* and *Dreissena* are about 40% terrestrial (median posterior estimate; Fig. 5), and POM is 80% terrestrial and less than 10% phytoplankton. For these organisms to be formed about 40% from phytoplankton requires that the electivity for autochthonous sources be quite high. That is, both *Bosmina* and *Dreissena* are consuming autochthonous material at about 6-fold that predicted by random feeding (or an electivity index of about 0.7). The present study agrees with the assertion in the literature that autochthonous sources are preferentially used over allochthonous sources (Marcarelli et al. 2011). Even the most terrestrially subsidized consumer in our data set, oligochaetes, is still only 60% terrestrial at the median. Thus, while many of the consumers are significantly supported by terrestrial organic matter, they also show significant and, in most cases, dominant reliance on autochthonous sources. Thus, our study provides some support of the heterotrophic paradox and RRPM of Thorp and Delong (2002). On the other hand, the utilization of terrestrial resources is quite large for several of the Hudson River consumers, a result that is in contrast to some other studies in large rivers (Bunn et al. 2003; Martineau et al. 2004).

The results here for zooplankton are in agreement with those for the York River Estuary of Hoffman et al. (2008), who estimated, based on $\delta^{13}C$ and $\delta^{15}N$, that zooplankton, including *Bosmina*, were made of a mixture of allochthonous and autochthonous sources. Further, these results here bolster the conclusions of Caraco et al. (2010) based on ambient $\delta^{14}C$ in the Hudson River. As in the present study, Caraco et al. (2010) found that both copepods and *Bosmina* had significant terrestrial support and that cladocerans were more dependent on terrestrial organic matter than were copepods. Several authors have suggested that zooplankton in lakes are often significantly subsidized by terrestrial inputs (Jansson et al. 2007; Rautio et al. 2011; Solomon et al. 2011). The work in lakes can be complicated by the possibility of zooplankton feeding in the metalimnion, where the phytoplankton may be isotopically distinct from those in the surface water (Francis et al. 2011). The tidal-freshwater Hudson has no metalimnion. It is non-stratified, well mixed, and isothermal (Cooper et al. 1988; Raymond et al. 1997), so this complication does not affect our results here.

The use of other basal resources—Several consumers relied heavily on benthic algae. The importance of benthic algae to aquatic food webs (or at least to key organisms) is in keeping with studies in streams (Vander Zanden and Vadeboncouer 2002; Finlay et al. 2010) and lakes (Solomon et al. 2008; Rautio et al. 2011). Yet it is a striking result in that benthic algae are an extremely small component of the organic loading to the Hudson River. An organic carbon budget for the Hudson suggests that the primary production of benthic algae is much less than 1% of total organic carbon loading and much smaller than the primary production of either macrophytes or phytoplankton (Cole and Caraco 2006). Nevertheless, median estimates of reliance on benthic algae were above 40% for amphipods, *Morone* spp., and spottail shiners. We collected amphipods from littoral rocks in shallow water, where benthic algae are most abundant. The high values for benthic algae in the two fishes probably reflect their use of amphipods or other nonsampled invertebrates from these shallow benthic habitats.

In contrast, SAV—and *Vallisneria* in particular—is a significant component of the organic matter loading to the river and larger than that from phytoplankton (Cole and Caraco 2006). However, SAV is not a large food source for any of the organisms we sampled, a result similar to that report for a tropical river by Petit et al. (2011). It may be the case that SAV and floating-leafed vegetation (e.g., *Trapa*) is quite significant to the diverse invertebrate communities in those specific habitats. We did not include *Trapa* as a specific resource because of its complex life history. *Trapa* grows from seed each year. Early in its annual development, *Trapa* is entirely submersed and isotopically similar to *Vallisneria*. After the plant reaches the surface, its C and H isotopes start to resemble terrestrial plants, but it is enriched in ^{15}N as much as *Vallisneria* (Caraco et al. 1998, 2010). With $\delta^{15}N$ near 8‰, *Trapa* would be similarly limited in scope in most of the food web according to the models and the biplots.

Issues and broader application—As a tidal, freshwater river, one could argue that the Hudson is not representative of all aquatic systems or all rivers. The food web of the Hudson is similar to that of many lakes and deep rivers with well-developed planktonic and benthic primary producers and consumers. From the point of view of terrestrial subsidies, however, this study demonstrates, independent of the system, the potential for terrestrial organic matter to enter the food web when terrestrial loading is large.

As with any study of food webs based on stable isotopes, the choice of the end members can be problematic. We used fresh material for phytoplankton, benthic algae and macrophytes, and leaves collected from the forest floor for the terrestrial input. If there are large changes in isotope ratios of any of these materials during decomposition, these end members may not be perfectly appropriate. Working in the Hudson, Caraco et al. (1998) found that terrestrial litter incubated in situ for 120 days had significant increases in $\delta^{15}N$ of up to 10‰ and small, nonsignificant decreases in $\delta^{13}C$ of about 2‰. Applying this result to the end members in the present study, the $\delta^{15}N$ results would eliminate decomposed material as a source to the food to most if not all of the food web. That is, once decomposed, the greatly enriched $\delta^{15}N$ of any of the end members would be too high to be a significant source to any of the consumers.

While the three autochthonous end members used in this study are representative of autochthonous inputs to the river, there may be additional terrestrial inputs that we have not considered. For example, the Hudson receives sewage at several locations in the tidal-freshwater region, and we have no direct estimate of its isotopic content. This sewage would be of terrestrial origin and likely be a mixture largely of C-3 and C-4 plants and their consumers. A mixture like this could make sewage similar to our measured $\delta^{13}C$ values for SAV and similar to that seen in wastewater by Ulseth and Hershey (2006). Our mixing models indicate that SAV (or anything with similar isotope ratios) is not an important source to the food web but is a significant source to the DOM. Thus, it is possible that our conclusion that DOM is only 65% terrestrial (and 35% SAV) could be an underestimate of the terrestrial component and an overestimate of the contribution from SAV.

The zebra mussel and the Hudson carbon budget—At about 10 g C m^{-2}, the biomass of zebra mussels is larger than the biomass of all other consumer organisms in the Hudson River combined, including bacteria and fish (Strayer and Smith 2001). The respiration of zebra mussels, estimated at 84–111 g C m^{-2} yr^{-1}, is nearly as large as that of pelagic bacteria (116 g C m^{-2} yr^{-1}; Cole and Caraco 2006) and much larger than the respiration of all other metazoans combined. The large use of terrestrial organic matter by zebra mussels is therefore a significant part of the energy use by the entire Hudson metazoan food web. If zebra mussels respire organic sources in the same proportions as the makeup of their biomass, we estimate that zebra mussel respiration would consume about 46 g C m^{-2} yr^{-1} (or about 7%) of the terrestrial input of organic matter. Zooplankton and benthic organisms excluding the zebra

mussel each respire about 5.4 g C m^{-2} yr^{-1}. If the zooplankton are 40% terrestrial and we use oligochaetes (the numerical dominant after zebra mussels and at 60% terrestrial) as the model benthic organism, we add an additional 2.2 (zooplankton) plus 3.2 (benthic, non–zebra mussel) g C m^{-2} yr^{-1} of respiration of terrestrial material. Thus, metazoan respiration of terrestrial organic matter in the Hudson could be about 51 g C m^{-2} yr^{-1}, or about 8% of the estimated terrestrial input, and dominated by the zebra mussel. Although terrestrial inputs are significant to the organic matter balance of other pelagic and benthic consumers, these are small absolute subsidies to the food web in comparison to that of the zebra mussel, a recent invader in the Hudson (Caraco et al. 1997). Thus, the overall use of terrestrial organic matter by metazoan consumers was in all likelihood dramatically lower prior to the invasion of the zebra mussel in 1992.

Isotopic composition of phytoplankton—Obtaining an accurate estimate of the stable isotope composition of phytoplankton is often a challenge requiring either difficult physical separation techniques or more indirect approaches (Hamilton et al. 2005). In the present study, we were fortunate in being able to collect a number of plankton net tows that were entirely algal and used these as the bases of our estimates. It is very obvious in the Hudson that phytoplankton has a distinctly different isotopic signature from POM and that POM is dominated by terrestrial material, as it is in the St. Lawrence River (Martineau et al. 2004). It is likely that terrestrial material dominates riverine POM, but we do not know of a quantitative review of this topic.

What does the measured isotopic signature of the Hudson phytoplankton imply? At the mean $\delta^{2}H$ of H_2O, the photosynthetic fractionation for ^{2}H for benthic algae and phytoplankton (ε_H) averaged 171‰ and 179‰, respectively, which is similar to other reports (Doucett et al. 2007) and similar to what we obtained in the Hudson using dilution regrowth approaches (Caraco et al. 2010).

Past data on $\delta^{13}C$ of DIC in the Hudson averaged -10.2 ± 1.06‰ (SD, $n = 106$‰; Caraco et al. 2010). At about 1 mmol L^{-1} with a mean pH of 7.7, this DIC consists mostly of the HCO_3^- ion. Using the equations in Mook et al. (1974), the $\delta^{13}C$ of the CO_2 moiety of the DIC averages about -19‰ to -20‰. At the mean, measured values of phytoplankton isotopes, this implies a photosynthetic fractionation of about 10‰ (ε), which is in keeping with other values from freshwaters but lower than that of marine phytoplankton (Bade et al. 2006). Had we used literature values of -20‰ for photosynthetic fractionation (as for C-3 terrestrial plants) of ^{13}C, the $\delta^{13}C$ of phytoplankton would be about -40‰, far lower than any consumers in the food web. If this were the basis of the phytoplankton end member, we would have estimated a much higher terrestrial support of zooplankton and zebra mussels than we report here.

As we do not have values for the $\delta^{15}N$ of NO_3 and NH_4, we cannot guess about photosynthetic fractionation for N. The relatively heavy values of $\delta^{15}N$ for phytoplankton, macrophytes, and benthic algae are consistent with prior literature in the Hudson (Caraco et al. 1998) and elsewhere

(Vuorio et al. 2009). It is likely that the DIN pool is somewhat heavy because of sewage inputs, of which there are several along the Hudson (Caraco et al. 1998). Nevertheless, for the Hudson, it is clear that phytoplankton have a distinctively different isotopic signature from bulk POM, of which they make up a small part.

Multiple basal resources for the food web of rivers— Different consumers depend on different basal resources and different mixtures of basal resources in the Hudson River as in other aquatic systems. Working in a shallow river in the Ste. Marguerite River in Canada and using $\delta^{13}C$ and a regression approach, Rasmussen (2010) demonstrated that some organisms were largely supported by terrestrial inputs (shredders, including plecopterans, the dipteran, *Tipula* spp., and some limnophilid trichopterans). Others, known algivores such as baetid mayflies, glossosomatid trichopterans, and small amphipods, were nearly entirely supported by benthic algae. The shredders averaged 80% terrestrial support, while the algivores averaged 15%. Filter feeders were intermediate in their use of terrestrial material. In view of the diverse response of different taxa to their available basal food resources, it is difficult to characterize an entire food web as being allochthonous or autochthonous. In deeper rivers with long residence times, like the Hudson, we have the added complexity of phytoplankton and pelagic consumers as well as organisms like oligochaetes that live on the soft sediment in deep water. The isotopic results here suggest a diversity of resource use from nearly entirely benthic algae (amphipods) to about 60% terrestrial (oligochaetes) and some (zebra mussels and *Bosmina*) about 50% phytoplankton. Because zebra mussels dominate the biomass, secondary production, and respiration of metazoan consumers, one could argue that their mixed support on terrestrial and phytoplankton dominates the material flow through the metazoan food web. However, if one were interested in the three fishes for which we have data, these relative flows are apparently less relevant. Herring, for example, may obtain 30% of their organic matter from terrestrial inputs and an additional 30–40% from phytoplankton (both probably through their consumption of zooplankton). The remaining 30–40% comes largely from benthic algae according to the model. This is consistent with observations of the gut contents of Hudson herring, which appear to eat amphipods (K. Limburg pers. comm.). Larval shad (*Alosa sapidissima*) in the Mataponi River, Virginia, also relied heavily on allochthonous resources, especially in years of high discharge (Hoffman et al. 2007). Thus, the very small input to the river in the production of benthic algae is highly significant to herring through an intermediate consumer: amphipods.

One of the intriguing questions left unanswered by this study is how terrestrial organic matter enters the river food web. There are several possibilities. Metazoans could consume bacteria that assimilated DOM of terrestrial or mixed origins, metazoans could directly utilize small particles of terrestrial origin, or metazoans could, perhaps, assimilate some terrestrial-derived DOM directly. There is some evidence that zebra mussels are capable of a small degree of direct assimilation of DOM, but this is not likely to be important in their overall C balance in the Hudson (Baines et al. 2007). Similarly, the few studies that have investigated DOM uptake by zooplankton suggest that it is at best a very minor pathway (Speas and Duffy 1998). Thus, direct consumption of DOM is not likely to explain our results. In the Hudson, the secondary production of bacteria is larger than the primary production of phytoplankton (Findlay et al. 1991). Thus, terrestrial DOM via bacteria could be quite important to either zebra mussels or zooplankton. It is widely known that zooplankton can assimilate bacteria (Jansson et al. 2007), and bacterial consumption by zebra mussels has been observed in the lab (Selegean et al. 2001). That the zooplankton in the Hudson directly consume significant material of terrestrial origin would be consistent with laboratory studies that have shown that *Daphnia* can grow and reproduce on mixtures of terrestrial leaves and phytoplankton or on microbially colonized pollen grains alone (Brett et al. 2009; Masclaux et al. 2011). We do not know of similar laboratory studies for the capabilities of either oligochaetes or zebra mussels (the other organisms in the Hudson that exhibited a high use of terrestrial sources) to consume terrestrial particles directly. Thus, both indirect access of terrestrial organic matter via the microbial loop and direct consumption of particles are viable hypothesis for how metazoans in the Hudson access terrestrial organic matter.

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