Detecting Marine Nutrient and Organic Matter Inputs into Multiple Trophic Levels in Streams of Atlantic Canada and France

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Abstract.—We used stable isotope analysis in an attempt to detect marine subsidies from anadromous fish to freshwater benthos in four river systems draining to the Atlantic Ocean. Benthic invertebrates in the West River, Nova Scotia, Canada, had elevated $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values in a downstream reach that suggested consumption of marine-derived organic matter from spawning blueback herring *Alosa aestivalis*. In Doctor's Brook, Nova Scotia, the arrival of rainbow smelt *Osmerus mordax* to spawn led to rapid increases in the $\delta^{13}C$ and $\delta^{15}N$ of a predatory stonefly (Perlidae), but lower trophic levels (mayflies and biofilm) showed inconsistent responses. Sculpin *Cottus* sp. showed no evidence of predation on Atlantic salmon *Salmo salar* eggs in Catamaran Brook, New Brunswick, Canada or the Scorff River, Brittany, France. These analyses suggest that marine organic matter subsidies, in the form of direct consumption of eggs and/or carcasses, are important in streams with concentrated spawning activity such as by alosid and osmerid species, whereas carbon and nitrogen contributions from more sparse spawning species such as by Atlantic salmon may be minimal.

Introduction

The long-term stability of food webs in systems with limited primary productivity may be dependent on inputs of nutrients and organic matter from adjacent or connected productive systems (Polis et al. 1997). One such pairing in temperate regions is oligotrophic streams and rivers with the ocean (Gross et al. 1988). Many rivers have a limited supply of phosphorus, nitrogen, or both (Dodds et al. 2002; Tank and Dodds 2003), and autotrophs and heterotrophs residing within these watercourses may therefore be reliant on seasonal inputs of nutrients and organic matter from beyond the stream boundaries. For example, on the west coast of North America, spawning Pacific salmon *Oncorhynchus* sp. annually deliver more than 10,000 metric tons (mt) of biomass, more than 40 mt of phosphorus, and 400 mt of nitrogen to oligotrophic streams, rivers, and lakes (Gresh et al. 2000). While these num-

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bers are small relative to historic levels (Gresh et al. 2000), they likely contribute to sustaining productivity levels higher than those in nearby systems lacking salmon (Wipfli et al. 1999; Chaloner et al. 2004; Naiman et al. 2009, this volume).

While perhaps not as dramatic as the effects observed in Pacific coast systems (Naiman et al. 2009), previous studies have suggested that the spawning run of anadromous fishes may contribute to the energy budget of rivers draining to the Atlantic Ocean (Durbin et al. 1979; Jonsson and Jonsson 2003; Nislow et al. 2004). Anadromous species such as Atlantic salmon *Salmo salar*, anadromous brown trout *S. trutta*, rainbow smelt *Osmerus mordax*, and several members of the family Alosidae, including American shad *Alosa sapidissima*, allis shad *A. alosa*, twaid shad *A. fallax*, blueback herring *A. aestivalis*, and alewife *A. pseudoharengus* occur in sufficient numbers to suggest that despite their generally iteroparous life histories, they provide considerable quantities of nutrients and organic matter to coastal rivers and streams through excretion and release of gametes and partial die-off.

Many studies have used stable isotope analysis (SIA) to estimate the relative importance of marine nutrient and organic matter subsidies carried by salmon and other anadromous fishes into freshwater (e.g., Bilby et al. 1996; MacAvoy et al. 2000). Due to predictable patterns in isotope fractionation by primary producers between freshwater and the sea (Fry and Sherr 1984; France 1995a), enriched ^{13}C, ^{15}N, and ^{34}S values are often deemed as evidence of marine subsidies to a variety of trophic levels (Kline et al. 1990; Harding et al. 2004). The recent explosion in popularity of SIA as a research tool (Kelly 2000) coupled with modeling efforts that suggest marine nutrients can be important in Atlantic coast streams (Durbin et al. 1979; Jonsson and Jonsson 2003; Nislow et al. 2004) together beg the question, why have we not seen stable isotope evidence for such subsidies in the benthos of Atlantic coast streams (Garman and Macko 1998)?

We initiated a program designed to determine if marine subsidies were present in four systems from both sides of the Atlantic Ocean, two studies related to Atlantic salmon, one related to blueback herring, and one related to rainbow smelt. We attempted to distinguish between nutrient subsidies and organic matter subsidies, discriminating the former as dissolved carbon and nitrogen that would be incorpo-

rated by growing algae and the latter as a direct food resource for consumers in the form of eggs and/or carcasses. Any evidence of marine isotope ratios in the benthos of these catchments would provide future studies with baseline data on the significance of such subsidies in Atlantic drainage streams and would allow for an assessment of the importance of anadromous fishes to their overall energy budgets.

In the Miramichi River drainage, New Brunswick, Canada, Atlantic salmon spawn in several tributaries, including Catamaran Brook (Cunjak et al. 1993). Similarly, in the Scorff River, Brittany, France, Atlantic salmon populations spawn in certain tributaries, including the Scave River and Kerlégan Brook (Baglinière and Champigneulle 1986). Also present in many salmon spawning tributaries are fishes of the family Cottidae (e.g., slimy sculpin *Cottus cognatus* and bullhead *C. gobio*) hereafter collectively referred to as sculpin) that have long been suspected of eating the eggs of salmonid fishes (Moyle 1977; Foote and Brown 1998). Sculpin are spring spawners and females invest large amounts of energy into gonad development during the winter and early spring (Petrosky and Waters 1975; Gray and Munkittrick 2005), with likely high rates of food consumption (Jardine et al. 2005). We therefore sampled both sexes but expected a greater isotopic response in females with the prediction that if salmon eggs were indeed being consumed by sculpin, marine isotope ratios would most likely be measured in muscle and gonad tissue.

In the West River, Nova Scotia, Canada, we sampled both long-lived (dragonflies and stoneflies) and short-lived (mayflies) aquatic macroinvertebrates to assess patterns in stable isotope ratios at a location where blueback herring spawn and at an upstream location above the limit of spawning. We predicted that scavenging of eggs and carcasses by invertebrates in the downstream reach would result in marine isotopic ratios (Chaloner et al. 2002) that were highest in summer following the spawning run and low or absent in the spring prior to the run. We expected that long-lived invertebrates would show limited seasonal variation in response to marine inputs because of their larger body size and lower turnover, while short-lived invertebrates would show rapid and dramatic responses.

In Doctor's Brook, Nova Scotia, Canada, rainbow smelt typically enter the stream in May and deposit eggs and sperm on the stream substrate. We

sampled biofilm and invertebrate grazers and predators in the spawning reach and in an upstream reach not accessible to smelt. These sites were sampled several times over the course of one growing season to determine the timing and extent of marine inputs and to differentiate between direct consumption of marine organic matter (e.g., eggs) and the use of dissolved marine-derived nutrients by primary producers.

Methods

Study Sites and Sample Collection

West River, Nova Scotia, Canada.—The West River (Figure 1) drains an area of approximately 350 km², flowing directly into the Gulf of St. Lawrence (N 45°37′W 61°58′). The landscape of the drainage basin has been greatly modified from natural hardwood forest. Now, the lower West River, where this study was conducted, is largely under agricultural and rural development with the consequent loss of forest associated with these activities. However, riparian buffer strips in these areas remain intact. Bank-full river discharge is estimated at between 30 and 40 m³/s (MacLaren Plansearch 1983). There are 13 lakes within the drainage, ranging in size between less than 5 ha and 65 ha. Gaspereau Lake, the largest, lies off of the main-stem West River and is connected to the main stem by a short (<2.0 km) tributary.

Freshwater fish species known to be present in the West River drainage include yellow perch *Perca fluviatilis*, blueback herring, alewife, white sucker *Catostomus commersonii*, northern redbelly dace *Phoxinus eos* (also known as *Chrosomus eos*), American eel *Anguilla rostrata*, creek chub *Semotilus atromaculatus*, and sticklebacks (threespine stickleback *Gasterosteus aculeatus* and ninespine stickleback *Pungitius pungitius*) (S. C. Mitchell, unpublished data; C. MacInnis, Fisheries and Oceans Canada, Antigonish, Nova Scotia, personal communication). The river also contains species with known or suspected sea-run life histories (Atlantic salmon, brown trout, and brook trout *Salvelinus fontinalis*), but these occur in low abundance and spawn in late fall; thus they are unlikely to affect isotope ratios of benthic invertebrates in our study. Jamieson et al. (1982) report the alewife run in the West River occurring generally between May 15 and June 15,

with spawning primarily in lakes for this species and the blueback herring between June 15 and July 15. On June 30, 2003 the lower 5 km of the West River was surveyed during the time of the *Alosa* spawning run to determine distribution and sites of abundance for subsequent sampling. The first sign of *Alosa* (scales on the bank from predation) was found approximately 3 km upstream of the mouth, suggesting that most were remaining downstream near the mouth. An earlier study on osprey *Pandion haliaetus* (Jamieson et al. 1982) found that the birds were feeding heavily on alewife in Gaspereau Lake, indicating that this lake is a significant area for spawning. Therefore, we assume that the principal spawning areas are Gaspereau Lake for alewife and the lower West River for blueback herring. The downstream sample site was selected as it was reasonably certain to include the spawning fish and the location was one of few riffles in the lower reach of the stream. An upstream site (N 45°34′W 62°06′) was selected to act as reference as we were reasonably certain that this site was not used for *Alosa* spawning. We base our decision of the lack of *Alosa* spawning at this site on the following: this tributary is (1) upstream of the confluence of Gaspereau Lake (presumably where much of the alewife spawning in the system occurs) and West River, (2) has no lakes and so would not be attractive to lake-spawning alewife, and (3) undergoes a significant increase in gradient within 1.5 km of its confluence, making it less attractive to these fish.

Invertebrates were collected using D-frame kick nets and identified to family (Merritt and Cummins 1996) at the two sites on several occasions (May 12, 2005, July 16–18 in 2003, 2004, 2005; September 3, 2003; September 22, 2004; November 13, 2004;). We also returned to the two sites in May and July of 2006 to collect water samples that were analyzed for nutrients (nitrate nitrogen, total nitrogen, and total phosphorus). Given that the first run of *Alosa* occurs between June 15 and July 15, our water and biotic samples collected in May (aka spring samples) represent samples that are not directly impacted by marine-derived nutrients. Whenever possible, invertebrates were analyzed individually, but in some instances (e.g., S analysis), pooled samples of 2–10 individuals were used. Additional C and N isotope data were obtained for muscle tissue of blueback herring from the southern Gulf of St. Lawrence (Pastershank 2001). *Alosa* that
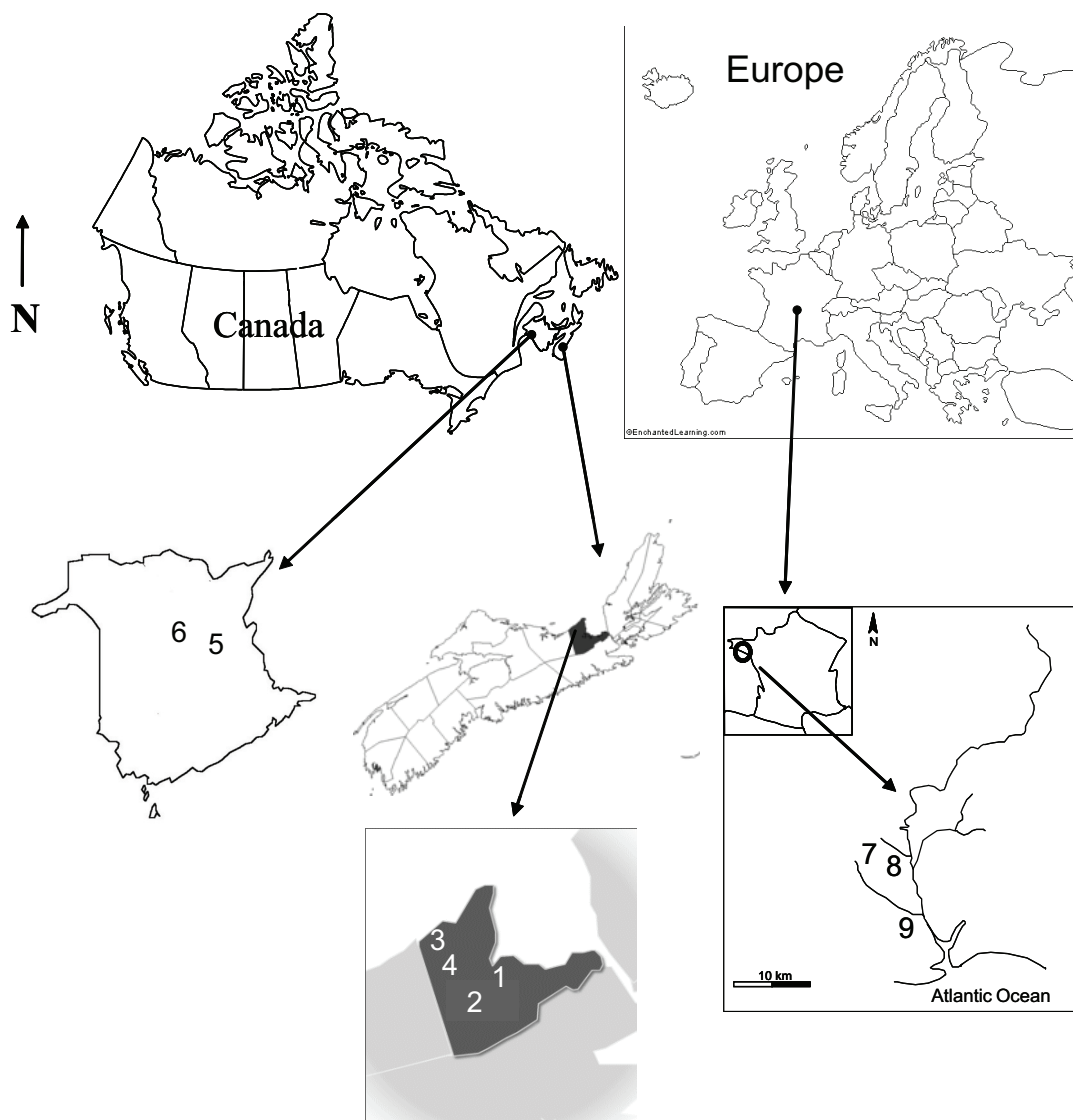
Figure 1.—Sampling locations in this study: West River (1—downstream and 2—upstream) and Doctor's Brook (3—downstream and 4—upstream) in Nova Scotia, Canada; Stewart Brook (5) and Catamaran Brook (6) in New Brunswick, Canada; and Kerlegan Brook (7—upstream and 8—downstream) and Scave Brook (9) in Brittany, France.

spawn in the West River would have similar marine isotope ratios as those fish and were considered as representative of the marine isotope signal for this system (Pastershank 2001).

Doctor's Brook, Nova Scotia, Canada.—Doctor's Brook (Figure 1) is a third-order coastal stream draining an area of 25.3 km² and flowing 10 km to meet the Northumberland Strait of the Gulf of St.

Lawrence in northeastern Nova Scotia (N 45°47′W 62°07′). The lower 6 km is relatively low gradient (<0.05%) but, above this point, drains rugged, high-gradient (~2%) terrain. Forest cover of the catchment is largely intact with some roading, rural development, and small-scale forest harvesting. Riparian vegetation is a mix of softwoods and hardwoods. The hydrologic regime of this small brook is

unknown. Fish species present include brook char, Atlantic salmon, and rainbow smelt (MacInnis, personal communication). Sea-run char and salmon are both rare in the system. Two sites were sampled in this brook, a downstream site approximately 600 m upstream of the brook mouth and an upstream (reference) site about 5 km upstream of the mouth and above known smelt spawning areas.

All samples in Doctor's Brook were collected in 2006. Our first sample occurred at the beginning of the spawning period for smelt (May 8), as evidenced by adults in the river (observed visually and captured in kick nets). Both the downstream reach with spawners and the upstream reach that is inaccessible to spawners were sampled that same day. We targeted three groups for our analysis: predatory stoneflies (Perlidae), herbivorous mayflies (Heptageniidae), and biofilm (rock scrapings). Invertebrates were sampled with D-frame kick nets, and biofilm was removed from the surfaces of stones with a toothbrush (n = 3 samples per site consisting of a minimum of three stones each). The downstream reach was sampled more frequently over the course of the growing season (May 8, 15, 22, 29, June 4, 18, July 7, August 7, September 10) than the upstream reach (May 8, 29, June 18, July 7, August 7, September 10). Smelt eggs were also picked from stones at the downstream reach on May 8 and 15 to obtain stable isotope ratios for this marine food source.

Catamaran Brook, New Brunswick, Canada.—Catamaran Brook (Figure 1) is the location of a long-term biological research program (Cunjak et al. 1993). It is a third-order, 20.5-km-long brook with a drainage area of 52 km^2 that flows to the Little Southwest Miramichi River in central New Brunswick (N 46°52′W 66°06′). Sampling was conducted in the middle reach (km 5–7), which has a low gradient and a mean annual discharge of 0.69 m^3/s (Cunjak et al. 1993). A fish trap located 500 m from the mouth of the brook has been operated since 1990 (Cunjak et al. 1993). Adult Atlantic salmon enter Catamaran Brook in late September; spawning occurs in late October and early November, with young-of-the-year emergence typically in April and May of the following year. The brook also supports several other coolwater fish species, the most common being brook trout, eastern blacknose dace *Rhinichthys atratulus*, lake chub *Couesius plumbeus*, and slimy sculpin (Mitchell et al. 2004). Some sea-run char enter the brook, but their abundance is low

(R. A. Cunjak, unpublished data). Samples of slimy sculpin muscle tissue were collected by electrofishing in May 2004 within the same reach where approximately 20 salmon redds were identified the preceding autumn (L. Weir, Concordia University, Montreal, Canada, personal communication). The reference site for this study was a tributary of the Northwest Miramichi River, Stewart Brook (N 46°58′W 65°39′), which has an impassable barrier to fish migration. Sculpin samples were collected from Stewart Brook on the same day to compare isotope ratios with those from Catamaran Brook. We also used data from a previous study (Gray et al. 2004) as reference values for sculpin collected above an impassable waterfall in the St. John River, New Brunswick.

Scorff River, Brittany, France.—The Scorff River (Figure 1) is a 62-km-long stream located in Brittany, France (N 47°50′W 3°23′) that flows into the Atlantic Ocean. It rises at low altitude (spring source at 230 m) and drains an area of 480 km^2. Urban areas, woods, and farming (both arable lands and pasture) represent 10%, 31%, and 59% of the drainage area, respectively. The mean annual discharge is 5.01 m^3/s, and dissolved nitrogen levels are generally high (from 20 to 30 mg/L of nitrate, Giovanni 1996). A fish trap located 1 km upstream from the estuary has been operated since 1994 to monitor Atlantic salmon population abundance and movements in the Scorff River. Adult salmon spawn in December; young-of-the-year start to emerge from redds in March of the following year, and smolts (mostly age 1) migrate to sea in March and April of the year following emergence. The Scorff River and tributaries also support other freshwater fish species, including brown trout, European eel *Anguilla anguilla*, European brook lamprey *Lampetra planeri* and European river lamprey *L. fluviatilis*, sea lamprey *Petromyzon marinus*, stone loach *Barbatula barbatula*, European minnow *Phoxinus phoxinus*, and sculpin. Seatrout are rare in the system and sea lamprey spawn in the lower reaches far from our study sites.

The study was carried out in two streams of the lower third of the Scorff River drainage: Kerlégan Brook, a 6.7-km-long tributary and Scave Brook, a 13-km-long stream that flows into the Scorff River estuary. Kerlégan Brook is disrupted by an impassable dam, and only the lower kilometer is accessible to Atlantic salmon. Sculpin were electrofished in November 2003 and January 2004 (i.e., before and

after salmon spawning, at three different sites in Scave Brook (about 1 km upstream from the estuary), Kerlégan Brook downstream of the dam, and Kerlégan Brook upstream of the dam (reference site). Benthic invertebrates representing various foraging strategies were sampled using kick nets at each site in February 2005, together with additional sculpin samples collected in Kerlégan Brook (downstream site). Atlantic salmon ova (~10–15) were taken by manual stripping of three mature females caught in the Scorff River to establish reference marine isotope ratios. In the laboratory, sculpin were killed in a solution of phenoxyethanol (0.1%) as per regulations for ethical treatment of wild animals. White muscle and gonadal tissues from fish, and pooled invertebrate samples (~2–10 individuals), were hermetically stored in vials and frozen until analysis. The abundance (or absence) of Atlantic salmon redds at each site was visually assessed in December 2003 and 2004 (N. Jeannot, INRA Rennes, personal communication) and confirmed by an electrofishing census of young-of-the-year salmon performed in 2004 and 2005.

Stable Isotope Analysis

All fish and invertebrate tissue samples were oven-dried (50–60°C for 24–48 h) and ground to a homogenous powder. For C & N isotope analysis at the Stable Isotopes in Nature Laboratory, Fredericton, New Brunswick, samples were weighed into tin cups and combusted in a Carlo Erba NC2500 elemental analyzer at high temperature. Resultant gases were delivered via continuous flow to a Finnigan Mat Delta XP isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). Isotope ratios are reported in delta notation relative to international standards Peedee Belemnite Carbonate (C) and atmospheric nitrogen (N). Data were corrected using working standards (bass muscle, bovine liver, nicotinamide) that were previously calibrated against International Atomic Energy Agency (IAEA) standards CH6, CH7, N1, and N2. A commercially available standard (acetanilide, Elemental Microanalysis, Ltd.) yielded mean $\delta^{13}C$ and $\delta^{15}N$ of $-33.60 \pm 0.13‰$ SD and $-3.13 \pm 0.19‰$ SD, respectively ($n = 62$). Standard deviations of samples analyzed in duplicate averaged 0.11‰ and 0.10‰ for carbon and nitrogen, respectively.

A subset of *Drunella* sp. samples from West River was analyzed for sulfur isotope ratios at the Colorado Plateau Analytical Laboratory, Flagstaff, Arizona using a Thermo Finnigan Delta Advantage Mass Spectrometer. Isotope ratios are reported in delta notation relative to the international standard Canyon Diablo Troilite. Data were corrected using IAEA standards S1, S2, and S3. A commercially available standard (bovine liver, National Institute of Standards) yielded $\delta^{34}S = 7.61 \pm 0.25‰$ SD ($n = 6$).

Statistical Analysis

For West River invertebrates, differences in stable isotope ratios between sites at different sampling times were tested for those taxa collected at both sites, using a single factor analysis of variance (ANOVA). These included dragonfly larvae (Gomphidae and Corduliidae), stonefly nymphs (Perlidae and Perlodidae), and mayflies *Drunella* sp. For Doctor's Brook, differences in stable isotope ratios over time were tested among groups (Perlidae, Heptageniidae, biofilm) separately for both isotopes and at the upstream and downstream sites, using ANOVA.

For all sculpin, we grouped isotope values for male and female muscle tissues together based on a high degree of similarity within sites that was consistent with previous work (Jardine et al. 2005). For sculpin samples in Catamaran Brook, we tested for differences in isotope ratios between our spawning site and the reference site. For sculpin in the Scorff River, we tested for differences in stable isotope ratios over time in relation to the availability of salmon eggs. For sculpin gonad samples, we compared differences between muscle and gonad $\delta^{13}C$ and $\delta^{15}N$ with previously measured values for sculpin in the absence of potential marine inputs (Jardine et al. 2005). Due to heteroscedasticity of variance, all statistical testing was done using a Kruskal-Wallis one-way ANOVA on ranks, with tests considered significant at $\alpha < 0.05$.

Given that we sampled sites repeatedly over time, we recognize the lack of independence of data within each system. However, we were primarily interested in patterns within systems that served as our level of inference (e.g., within the West River, do sites differ in isotope ratios and are differences dependent on season?). We viewed this as the first step in assessing the importance of marine nutrients and organic matter to Atlantic coast streams. Inferring general patterns across the landscape will

be dependent on observing similar trends in several different systems.

Results

Benthic Invertebrates in the West River, Nova Scotia

Consistent with the delivery of marine derived organic matter, invertebrates sampled in the summer following the spawning of blueback herring at the downstream site in the West River were enriched in ^{13}C and ^{15}N relative to those from the upstream site at the same time (Figure 2). However, given that land-use can significantly affect baseline isotope ratios, to account for these differences between sites and to ensure that these observations of enriched ^{13}C and ^{15}N were not artiacts of other factors, we used two strategies: temporal sampling and stable sulfur isotope analysis.

For the mayflies *Drunella* sp., individuals at the downstream site were enriched in ^{15}N at all times (spring 2005 and summer 2004 and 2005, Figure 3A) and enriched in ^{13}C in both summer samples (2004 and 2005, $p < 0.01$) but not the spring ($p = 0.873$, Figure 3A). For dragonfly larvae (Odonata: Corduliidae) sampled from the two sites at different times, individuals from the downstream (spawning)

site were enriched in ^{15}N at all times compared with the upstream site (spring, summer, and fall, $p < 0.01$, Figure 3B). For δ^{13}C, individuals at the downstream site were enriched in ^{13}C compared to the upstream site in the summer and fall ($p < 0.01$) but not in the spring ($p = 0.109$, Figure 3B). Similarly, for stonefly larvae (Plecoptera), individuals at the downstream site were enriched in ^{15}N at all times (Figure 3C) and enriched in ^{13}C in the summer and fall ($p < 0.01$) but not the spring ($p = 0.071$, Figure 3C).

For the subset of *Drunella* sp. samples analyzed for δ^{34}S (Table 1), individuals from the upstream site in the spring had the lowest δ^{34}S while values at the upstream site in the summer were similar to those at the downstream site in the spring. Samples from the downstream site in consecutive summers had the highest δ^{34}S values.

In streamwater samples, nitrogen and phosphorus concentrations were slightly higher at the downstream site compared to the upstream site (upstream May: nitrate < 0.05 mg/L, total nitrogen (TN) < 0.3 mg/L, total phosphorus (TP) < 0.005 mg/L; July: nitrate = 0.07 mg/L, TN = 0.18 mg/L, TP = 0.007 mg/L; downstream May: nitrate <0.05 mg/L, TN < 0.3 mg/L, TP = 0.006 mg/L; July: nitrate = 0.11 mg/L, TN = 0.32 mg/L, TP = 0.012 mg/L). Both sites, however, had concen-
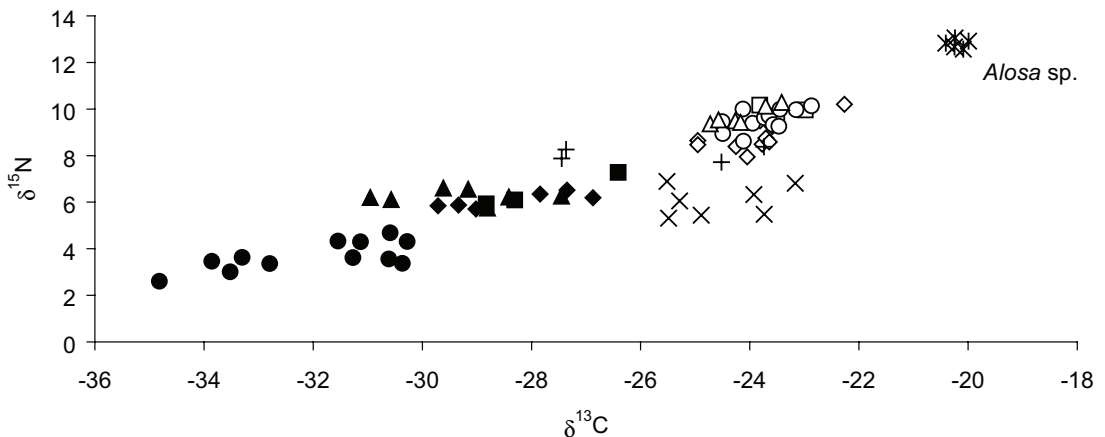

Figure 2.—Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios of all invertebrates sampled during the summer in the West River, Nova Scotia, Canada. Samples from the upstream site (no blueback herring spawning) are indicated by solid symbols; from the downstream site (blueback herring spawning), by open symbols. Taxa include *Drunella* sp. (circles), Perlidae (triangles), Corduliidae (diamonds), Megaloptera (squares), Psephenidae (X's, only present at the downstream site), and Pteronarcyidae (+'s, only present at the downstream site). Isotope ratios for *Alosa* sp. in the upper right are shown for reference (data from Pastershank 2001).
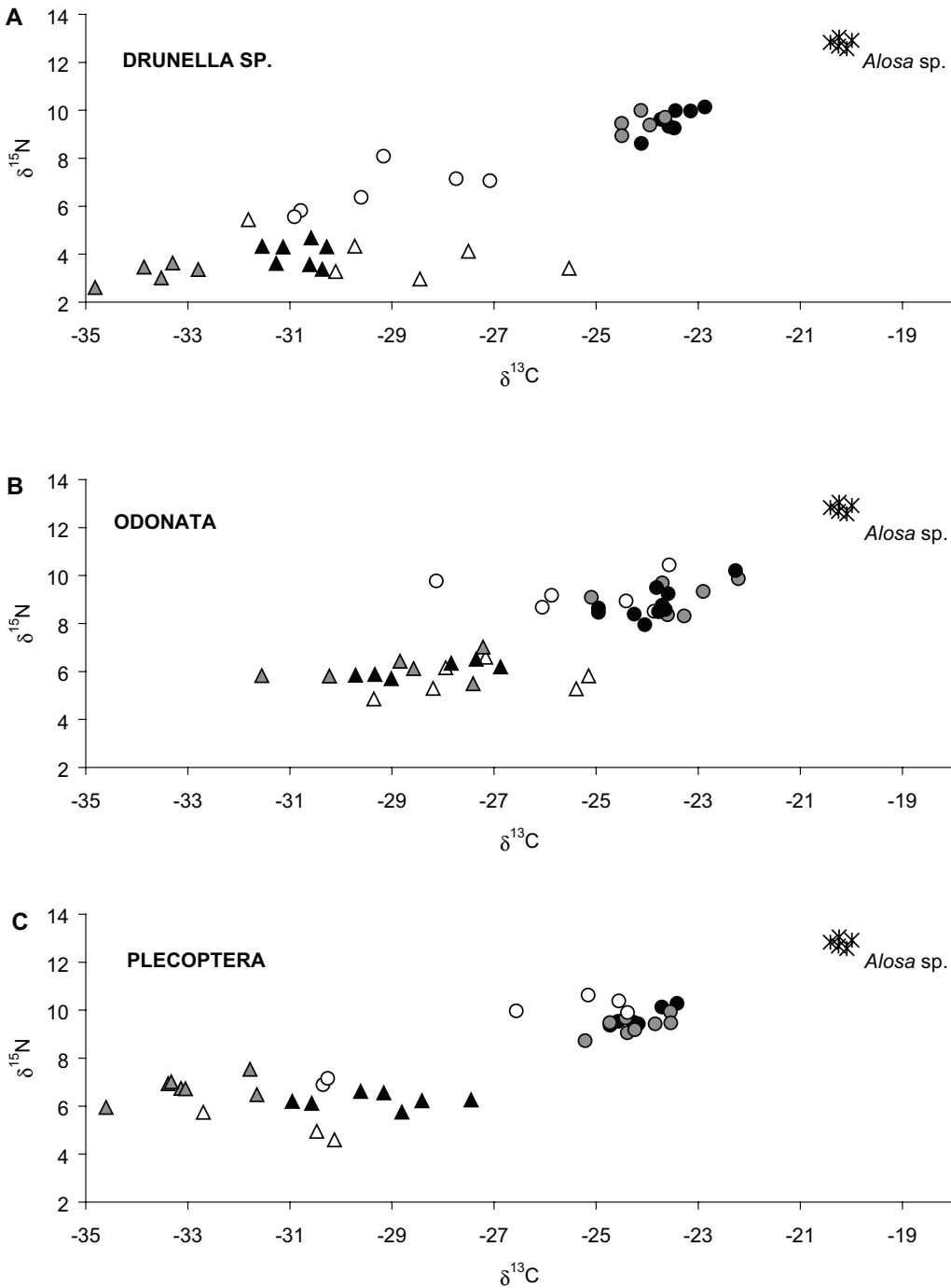
Figure 3.—Scatterplot of *Drunella* sp. (A), Odonata (B), and Plecoptera (C) stable carbon and nitrogen isotope ratios from the upstream (reference—triangles) and downstream (spawning—circles) sites in the West River, Nova Scotia, Canada in spring prior to blueback herring spawning (open symbols) and following blueback herring spawning (shaded and solid symbols). Isotope ratios for *Alosa* sp. in the upper right are shown for reference (data from Pastershank 2001).

Table 1.—Stable sulfur isotope ratios ($\delta^{34}S \pm SD$, $n = 2$–3 pooled samples per site and time) of *Drunella* sp. at the upstream and downstream sites in the West River, Nova Scotia, Canada prior to blueback herring spawning (spring) and for each of 2 years following spawning (summer). Note: summer 2005 data from the upstream site were unavailable because of limited remaining sample material.

Season (year)	Site	$\delta^{34}S$
Summer (2004)	Upstream	12.5 ± 0.1
	Downstream	14.1 ± 0.3
Spring (2005)	Upstream	9.8 ± 0.2
	Downstream	12.2 ± 0.1
Summer (2005)	Downstream	14.1 ± 0.7

trations below levels expected to be found at sites impacted by agriculture (e.g., nitrate > 0.15 mg/L, Harrington et al. 1998) and are in the range of values considered to have ideal or acceptable water quality (TN = 0.47 mg/L, TP = 0.06 mg/L, Dodds and Welch 2000).

Benthic Invertebrates in Doctor's Brook, Nova Scotia

Smelt eggs were enriched in ^{13}C and ^{15}N relative to available food sources for consumers in Doctor's Brook (Figure 4). Consumers at the downstream (spawning) site had elevated $\delta^{15}N$ but similar or lower $\delta^{13}C$ compared to the upstream (reference) site. Both time and group significantly affected both isotopes at both sites, with some interaction between terms ($p < 0.05$, Figures 5 and 6). At the downstream site, all three groups (Perlidae, Heptageniidae, biofilm) showed a distinct increase in $\delta^{13}C$ coincident with smelt spawning (Figure 5A). Perlidae showed the most pronounced increase, rising ~4‰ between the first sample and its peak on Julian day 142. Peaks in $\delta^{13}C$ of biofilm (Julian day 155) and Heptageniidae (Julian day 169) occurred later than those observed in Perlidae and were not accompanied by peaks in $\delta^{15}N$. The upstream site also had variable $\delta^{13}C$ in the three groups, but changes over time were not consistent in any direction (Figure 5B). Also, the range of mean $\delta^{13}C$ values observed at the downstream site was far greater compared with the upstream site for all three groups (Perlidae downstream range = 5.5‰, upstream = 2.3‰; biofilm downstream range = 3.1‰, upstream = 1.8‰; Heptageniidae downstream range = 5.3‰, upstream = 4.3‰). Perlidae at the downstream site had $\delta^{15}N$ values that changed over time suggestive of a contribution of marine organic matter to their diet from smelt (Figure 6A). The peak in Perlidae $\delta^{15}N$ oc-

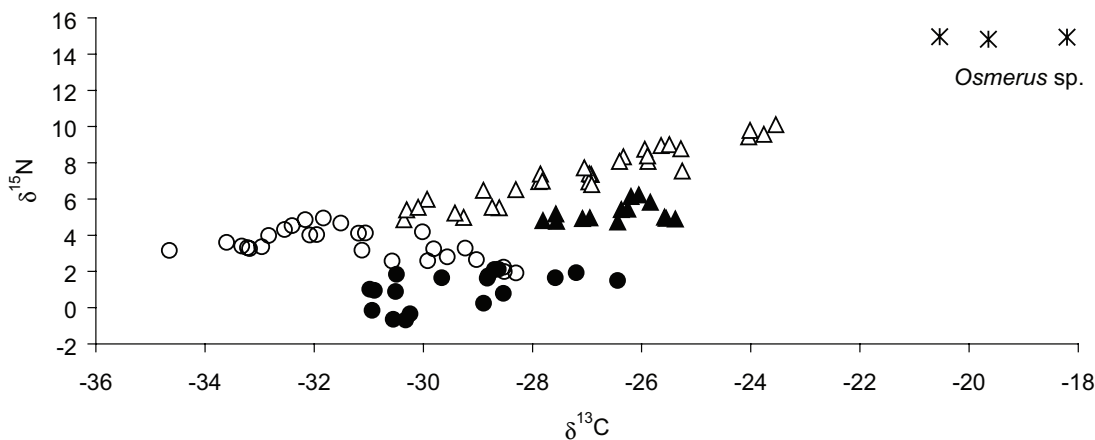*Figure 4.*—Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of all invertebrates sampled in Doctor's Brook, Nova Scotia, Canada. Samples from the upstream site (no smelt spawning) are indicated by solid symbols for Perlidae (triangles) and Heptageniidae (circles). Samples from the downstream site (smelt spawning) are indicated by open symbols for Perlidae (triangles) and Heptageniidae (circles). Isotope ratios for smelt eggs in the upper right are shown for reference.
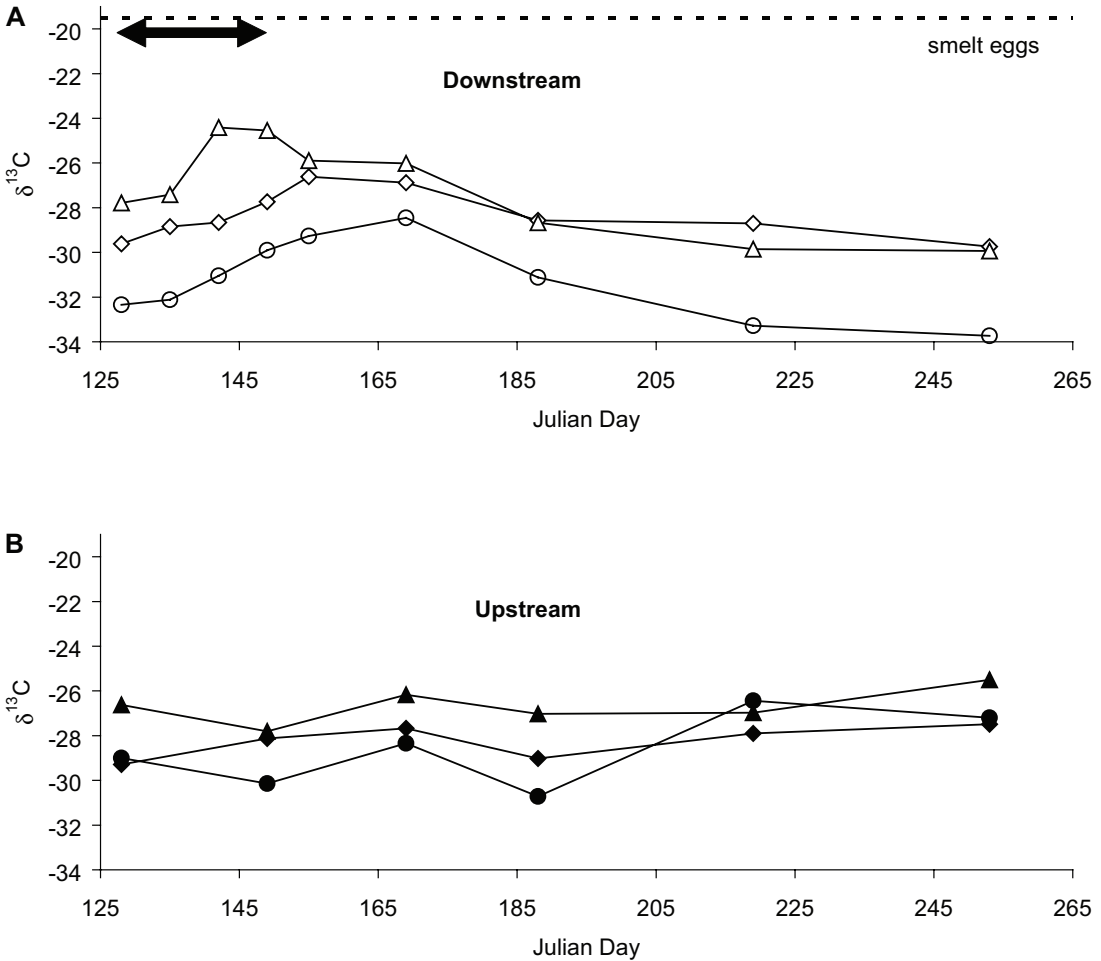
Figure 5.—Stable carbon isotope ratios in Doctor's Brook, Nova Scotia, Canada over time in a downstream reach with smelt spawning (A) and an upstream reach that is inaccessible to smelt (B). The hatched line indicates $\delta^{13}C$ of smelt eggs, and the arrow indicates the duration when eggs were deposited on the stream bottom and available as an organic matter and nutrient source to Perlidae (triangles), Heptageniidae (circles) and biofilm (diamonds).

curred on the same day (Julian Day = 142) as the peak in Perlidae $\delta^{13}C$, and overall Perlidae $\delta^{13}C$ was strongly correlated with Perlidae $\delta^{15}N$ at the downstream site (Figure 4). Biofilm and Heptageniidae $\delta^{15}N$ values did not show a consistent response to smelt spawning, but were enriched in ^{15}N relative to the upstream site (Figure 6B). The range of values in $\delta^{15}N$ was greater in Perlidae at the downstream site (4.2‰ versus 1.1‰), but ranges in biofilm (3.2‰, 3.9‰) and Heptageniidae (2.5‰, 1.9‰) $\delta^{15}N$ were similar between the two sites.

Sculpin in Catamaran Brook and the Scorff River

Salmon eggs were highly enriched in ^{13}C (–21.1 ± 0.5‰ SD) compared with values for invertebrates from all Scorff River sites measured in the current study (–29.5 ± 2.2‰ SD, Table 2) and those from Catamaran Brook's Middle Reach (reported by Doucett 1999; Table 2). For $\delta^{15}N$, salmon eggs (12.7 ± 0.3‰ SD) were indistinguishable from invertebrates from the Scave River and the upstream site in Kerlégan Brook (Table 2), enriched in ^{15}N
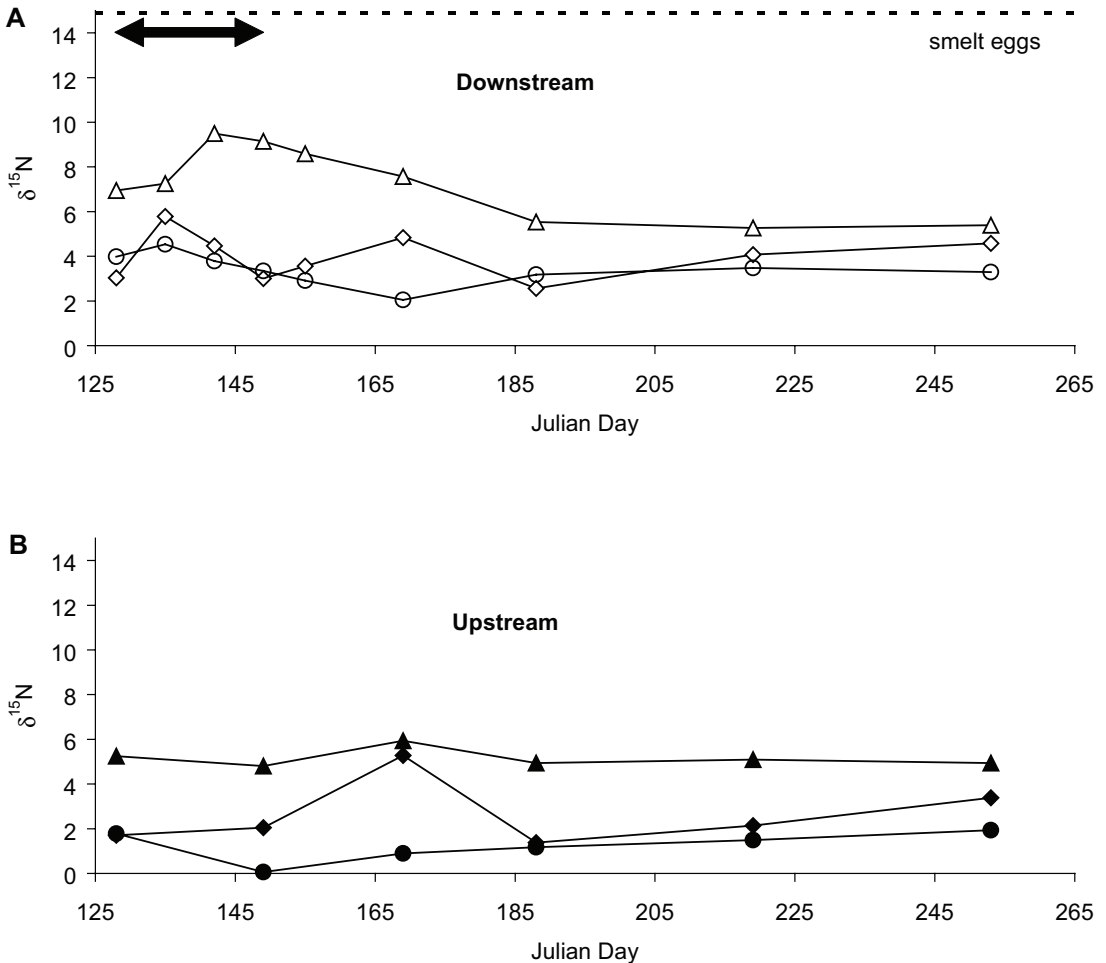
Figure 6.—Stable nitrogen isotope ratios in Doctor's Brook, Nova Scotia, Canada over time in a downstream reach with smelt spawning (A) and an upstream reach that is inaccessible to smelt (B). The hatched line indicates $\delta^{15}N$ of smelt eggs, and the arrow indicates the duration when eggs were deposited on the stream bottom and available as an organic matter and nutrient source to Perlidae (triangles), Heptageniidae (circles) and biofilm (diamonds).

relative to invertebrates from the downstream site in Kerlégan Brook (Table 2), and enriched in ^{15}N compared with invertebrates from Catamaran's Middle Reach (Doucett 1999; Table 2).

Contrary to our expectations, there was very little within-site variation in sculpin muscle $\delta^{13}C$ (Catamaran Brook SD = 0.6‰, Stewart Brook SD = 0.6‰, Kerlégan Brook downstream SD = 0.7‰, Kerlégan Brook upstream SD = 0.6‰, Scave River SD = 0.6‰, Table 2) and $\delta^{15}N$ (Catamaran Brook SD = 0.3‰, Stewart Brook SD = 0.4‰, Kerlégan Brook downstream SD = 0.4‰,

Kerlégan Brook upstream SD = 0.5‰, Scave River SD = 0.8‰, Table 2) at all sites on both sides of the Atlantic Ocean. No individuals had isotope ratios suggestive of a marine contribution to the diet, and at most sites, sculpin were strongly linked to local aquatic invertebrates with diet-tissue differences consistent with previous studies (Catamaran sculpin $\delta^{13}C$ – invertebrate $\delta^{13}C$ = –0.1‰, sculpin $\delta^{15}N$ – invertebrate $\delta^{15}N$ = 5.9‰; Kerlégan downstream sculpin $\delta^{13}C$ – invertebrate $\delta^{13}C$ = 0.6‰, sculpin $\delta^{15}N$ – invertebrate $\delta^{15}N$ = 2.0‰; Scave sculpin $\delta^{13}C$ – invertebrate $\delta^{13}C$ = 1.5‰, sculpin

Table 2.—Stable carbon ($\delta^{13}C$ ± SD) and nitrogen ($\delta^{15}N$ ± S.D.) isotope ratios of invertebrates (inverts) and *Cottus* sp. muscle and gonad tissues relative to availability of Atlantic salmon eggs ($\delta^{13}C$ = −21.1 ± 0.5‰, $\delta^{15}N$ = 12.7 ± 0.3‰) in Canadian and French rivers. Note: invert data for Catamaran Brook are from Doucett (1999); no invert data were available for Stewart Brook.

Site	Egg availability	Date	Sex	Tissue (n)	$\delta^{13}C$	$\delta^{15}N$
Catamaran Brook	High	May 2004	M + F	muscle (11)	−28.2 ± 0.6	8.9 ± 0.3
		June 1998		inverts (14)	−28.1 ± 2.1	4.0 ± 1.4
Stewart Brook	Absent	May 2004	M + F	muscle (15)	−27.4 ± 0.6	11.1 ± 0.4
Kerlegan Brook (downstream)	Absent	November 2003	M + F	muscle (5)	−26.6 ± 0.6	10.8 ± 0.4
			F	gonad (4)	−27.7 ± 0.6	10.7 ± 0.5
	Low	January 2004	M + F	muscle (6)	−26.5 ± 0.4	10.5 ± 0.4
			F	gonad (3)	−27.9 ± 0.4	11.8 ± 0.6
	Low	May 2004	M + F	muscle (6)	−26.9 ± 1.1	10.5 ± 0.5
			F	gonad (2)	−29.6 ± 4.0	9.4 ± 0.1
	High	February 2005	M + F	muscle (14)	−27.0 ± 0.5	10.3 ± 0.2
			F	gonad (10)	−28.1 ± 0.4	11.3 ± 0.3
		February 2005		inverts (5)	−27.4 ± 1.0	8.5 ± 2.0
Kerlegan Brook (upstream)	Absent	November 2003	M + F	muscle (6)	−27.7 ± 0.6	10.9 ± 0.4
			F	gonad (4)	−28.1 ± 0.6	9.7 ± 0.5
	Absent	January 2004	M + F	muscle (6)	−27.4 ± 0.3	10.7 ± 0.3
			F	gonad (3)	−28.4 ± 0.3	10.9 ± 0.9
	Absent	May 2004	M + F	muscle (6)	−27.5 ± 0.8	10.3 ± 0.5
			F	gonad (5)	−27.7 ± 0.6	9.6 ± 0.4
		February 2005		inverts (4)	−31.4 ± 2.0	12.9 ± 2.7
Scave River	Absent	November 2003	M + F	muscle (7)	−28.5 ± 0.5	17.5 ± 0.6
			F	gonad (2)	−29.0 ± 0.3	18.8 ± 0.2
	High	January 2004	M + F	muscle (6)	−28.6 ± 0.5	17.4 ± 0.3
			F	gonad (3)	−28.5 ± 0.0	17.7 ± 0.2
	High	May 2004	M + F	muscle (6)	−29.2 ± 0.5	17.4 ± 1.3
			F	gonad (3)	−29.0 ± 0.6	17.1 ± 0.4
		February 2005		inverts (5)	−30.2 ± 1.2	11.8 ± 4.1

$\delta^{15}N$ – invertebrate $\delta^{15}N$ = 5.7‰). The exception was the upstream site in Kerlégan Brook where sculpin were depleted in ^{15}N (10.6 ± 0.4‰ SD) relative to both local invertebrates ($\delta^{15}N$ = 12.9 ± 2.7‰ SD) and salmon eggs, suggesting an alternative ^{15}N-depleted food source or that our $\delta^{15}N$ value for invertebrates was artificially high at the time of sampling due to unpredictable N inputs to the system. Over time, sculpin showed no evidence of an isotopic shift in relation to the availability of

salmon eggs ($p > 0.05$, Table 2), and often sites that were inaccessible to salmon had sculpin with higher $\delta^{13}C$ and $\delta^{15}N$ than those from spawning sites. Female sculpin gonads similarly showed no indication of a shift towards a diet of salmon eggs at sites where salmon spawners were present (Table 2). Sculpin gonads were depleted in ^{13}C compared with muscle, similar to previous estimates for sculpin with no opportunity to forage on salmon eggs (Jardine et al. 2005).

Discussion

We found considerable evidence for the use of marine-derived organic matter by benthic invertebrates in the West River and Doctor's Brook but no evidence of consumption of Atlantic salmon eggs by sculpin in either Catamaran Brook or the Scorff River. These data indicate that the importance of marine carbon and nitrogen carried by anadromous fishes may be more apparent in streams with concentrated spawning activity, such as by *Alosa* sp. and *Osmerus* sp., and less obvious in areas with more scattered spawning activity by reduced populations of Atlantic salmon.

In the West River, we observed considerable differences in isotope ratios between the upstream and downstream sites and between pre- and post-spawning by blueback herring. While $\delta^{15}N$ values were higher in all taxa at the downstream site at all times, $\delta^{13}C$ values were similar between sites in the spring prior to the arrival of blueback herring. This may be related to nutrient limitation, in that benthic algae at the downstream site could be N-limited and hence incorporate marine nitrogen leading to high $\delta^{15}N$ throughout the growing season (Chaloner et al. 2002), while marine carbon is consumed directly by invertebrate scavenging of eggs and carcasses that are only available for a short duration. While we did not measure isotope ratios in benthic algae directly, known herbivores at the downstream site (water pennies Psephenidae, mayflies Heptageniidae) collected after the spawning run all had elevated $\delta^{15}N$. Herbivore isotope ratios have been shown to approximate those of their algal diet (Doucett 1999; Finlay 2001). On the west coast of North America, streams are often nitrogen limited, and hence, the $\delta^{15}N$ signal from spawning Pacific salmon can be more apparent in benthic food webs than $\delta^{13}C$ (Kline et al. 1990). Stream benthic communities are known to efficiently retain nitrogen, especially when it is in particulate form (Dodds et al. 2004), as would be expected under marine subsidy scenarios. Marine carbon, meanwhile, may appear briefly in a variety of taxa through direct egg/carcass consumption, but its relative importance diminishes over the growing season as that food source is consumed (Kline et al. 1990).

Similar to the West River, in Doctor's Brook, the downstream site had consistently higher $\delta^{15}N$ than the upstream site. Kline et al. (1993) also found that salmon-influenced sites had benthic algae with higher $\delta^{15}N$ than control sites regardless of the timing of sampling. In Doctor's Brook, all three of our study groups showed a $\delta^{13}C$ response coincident with smelt spawning, but only the predatory stoneflies (Perlidae) indicated a response in their $\delta^{15}N$. This suggests that direct consumption of eggs is likely the major pathway for marine inputs to enter this system, and the increases in $\delta^{13}C$ observed in biofilm and its direct consumer (Heptageniidae) may have simply reflected seasonal variation (Finlay 2004) in the absence of a marine influence or contamination of biofilm samples by broken and decomposing eggs. Alternatively, the system may be phosphorus-limited, and the addition of P by decomposing smelt eggs stimulated primary production in the downstream reach, leading to reduced dissolved CO_2 availability, less discrimination against ^{13}C by algae, and subsequent elevations in primary producer $\delta^{13}C$ that was tracked by grazing Heptageniidae (Finlay 2004). A third and less likely scenario is that benthic algae, fungi, and bacteria present in biofilm are carbon-limited and the increase in $\delta^{13}C$ in the downstream reach following smelt spawning was a result of the incorporation of marine C that is enriched in ^{13}C. The resolution of these questions will require detailed analyses of stream water nutrient concentrations over time. Temporal analyses of water nutrients (and their isotope ratios) would also aid in unraveling the relative influence of direct (organic matter) and indirect (dissolved nutrients) pathways of entry into stream food webs. Kline et al. (1990) proposed that the latter pathway would be made apparent by increased $\delta^{15}N$ in all trophic levels at spawning sites while the former would be indicated by increased $\delta^{13}C$ in consumers at those sites. Our results from the West River and Doctor's Brook suggest that both of these pathways may be important.

Slimy sculpin in Catamaran Brook where salmon spawners were present had $\delta^{13}C$ and $\delta^{15}N$ values that differed little from sculpin collected above a barrier impassable to anadromous fishes in both the current study and an earlier study (Gray et al. 2004). Similarly, in the Scorff River, sculpin showed no evidence of salmon egg consumption since stable isotope values did not differ between sites or before and after salmon spawning. Contrasting results were obtained on the Pacific coast by Kline et al. (1993) who found a significant contribution of

sockeye salmon *Oncorhynchus nerka* eggs and emergent fry to the diet of the coastrange sculpin *Cottus aleuticus*. Other studies, however, have found egg consumption by sculpin to be extremely rare, with eggs occurring in only 45 of 7,785 stomachs (0.6%, summarized in Moyle 1977). Given the limited movement of sculpin (Cunjak et al. 2005), it was necessary to ensure that salmon spawner density was high enough to increase the probability of observing evidence of egg consumption. We therefore specifically targeted sculpin from river habitats immediately downstream of redds excavated by salmon the previous autumn. Despite this concerted effort, we found no individuals that had isotope ratios suggestive of a marine food source. Isotopic change in response to a shift in diet is strongly related to growth in ectotherms such as fishes (Hesslein et al. 1993) and invertebrates (Fry and Arnold 1982). Since sculpin likely have limited somatic growth through the winter, the lack of evidence for marine food consumption in muscle tissue was not surprising. However, there was also no evidence in the Scorff River for a marine signature when analyzing isotope ratios of female sculpin gonads, which grow during winter and would be expected to have fast turnover rates similar to liver tissue (Perga and Gerdeaux 2005) and rapidly growing invertebrates. If there was preferential shunting of available nutrients to developing tissues, we predicted that female gonads might show evidence of marine food sources. Instead, female gonads had more negative $\delta^{13}C$ and more positive $\delta^{15}N$ than muscle, consistent with earlier work on sculpin with no access to marine food sources (Jardine et al. 2005). Differences in $\delta^{13}C$ between eggs and muscle are due to high lipid loads in the former tissue, while $\delta^{15}N$ differences are likely due to differences in amino acid content (Jardine et al. 2005). The lack of a marine isotopic signal in the tissues of sculpin suggests that while salmon eggs may have been consumed occasionally, they formed a small enough fraction of the diet as to avoid detection using isotope analysis. Invertebrates were not sampled concurrently with sculpin, so it is unknown whether eggs were being consumed by invertebrates at our Scorff River sites at times of high salmon egg deposition.

One of the greatest challenges in using SIA across systems is the confounding influence of varying baseline isotope ratios. Both $\delta^{13}C$ and $\delta^{15}N$ can vary considerably across the landscape due to natural and anthropogenic processes. Stable carbon ratios show a general trend of enrichment in ^{13}C from headwaters to lower reaches of rivers (Finlay 2001), owing to changes in dissolved inorganic carbon isotope ratios and CO_2 supply and demand (Finlay 2004). Human activities such as manure-based agriculture and forestry contribute to elevated baseline $\delta^{15}N$ in rivers and streams (Udy and Bunn 2001; Anderson and Cabana 2005). Taken together, we expected a progressive increase in both $\delta^{13}C$ and $\delta^{15}N$ from small undeveloped streams to more developed stretches of river downstream even in the absence of anadromous fish influence. While this is the case in the West River, Nova Scotia (our upstream reference site was a partially shaded stream with limited forestry and agricultural activity, whereas our downstream site was partially developed with considerable agricultural activity near an urban centre), N and P stream-water concentrations at the downstream site were low and similar to undeveloped systems (Harrington et al. 1998; Dodds and Welch 2000), suggesting that a high $\delta^{15}N$ baseline from agriculture is not a concern in this system. However, most coastal streams in Brittany, France drain intensive agricultural catchments, and dissolved N levels and baseline $\delta^{15}N$ are unusually high compared to most other areas. The lower reaches of the Scorff River have nitrate concentrations that exceed 20 mg/L (Giovanni 1996). As a consequence, the biota in the Scorff River is ^{15}N-enriched compared with the ocean (Charles et al. 2004), and $\delta^{15}N$ is therefore less effective as a tracer of marine inputs. In all of our systems, concerns about baseline $\delta^{15}N$ differences between sites prompted our use of temporal sampling and stable sulfur isotope analysis.

Temporal sampling was conducted by analyzing components of the food web before and after the arrival of blueback herring in the West River in June, sculpin in the Scorff River before and after the arrival of Atlantic salmon in December, and food web components in Doctor's Brook after the arrival of smelt in May. We assumed that if the differences in isotope ratios of short-lived organisms such as mayflies or actively growing tissues like female gonads were due to natural patterns and anthropogenic influences, they would remain apparent throughout the year, while differences caused by spawning anadromous fishes would be pronounced following their arrival but less so prior to their arrival. For sculpin, we found no evidence of temporal

variations in C and N isotopes in relation to salmon egg availability. Conversely, the short-lived mayfly *Drunella* sp. showed a strong increase in stable isotope ratios at the downstream site in the West River that were not related to ontogenetic diet shifts, as individuals collected in the summer at both sites were smaller than those from the spring (T. Jardine, unpublished data). This suggests that a pulse of *Drunella* sp. emergence from the stream occurred prior to blueback herring spawning and the subsequent generation in the summer at the downstream site had access to marine food sources, resulting in elevated $\delta^{13}C$ and $\delta^{15}N$. *Drunella* sp. are also rapid colonizers (Miyake et al. 2003) and hence could drift to concentrated spawning areas to take advantage of available organic matter. In Doctor's Brook, our first sample occurred during the smelt spawning period, so we were unable to assess isotope ratios pre- and postspawning. Predatory stoneflies (Perlidae) in Doctor's Brook showed strong isotopic responses to smelt arrival at the downstream site, indicating direct consumption of eggs. This is not surprising given that eggs, a potential high-quality food resource, are in high abundance during this time period and are small enough in diameter (~1 mm, Scott and Crossman 1998) for consumption by most invertebrates. Blueback herring eggs also have a small diameter (~1 mm, Scott and Crossman 1998), making them an attractive food source for invertebrates, including stoneflies, in the West River; we have also observed elevated $\delta^{13}C$ and $\delta^{15}N$ in predatory stoneflies collected from Atlantic salmon egg incubation baskets in New Brunswick rivers (Cunjak, unpublished data), suggesting that even for patchy spawners such as salmon with larger eggs, a localized influence of marine organic matter inputs may be observed in smaller-bodied predators whose diet may consist entirely of eggs for an extended period of time (e.g., during winter).

Our second approach to assess the influence of marine inputs was to use stable sulfur isotopes. Sulfur isotope ratios differ markedly and consistently between freshwater and marine environments (Mekhtiyeva et al. 1976; Doucett et al. 1999) and seem to be less affected by land-use activities than $\delta^{13}C$ and $\delta^{15}N$. Benthic macroinvertebrates in rivers have known $\delta^{34}S$ values that range from −5‰ to 8‰ (Doucett et al. 1999; Wayland and Hobson 2001), while anadromous alosids have been shown to have $\delta^{34}S$ values that range from 13‰ to 15‰

(MacAvoy et al. 1998). *Drunella* sp. from the West River in the current study had $\delta^{34}S$ values that fell between these two groups, with samples from the downstream (spawning) site having values within the range of those observed previously in alosids (MacAvoy et al. 1998). While this observation and the observed increase in $\delta^{34}S$ from spring to summer in *Drunella* sp. at the downstream site support our hypothesis of marine inputs, the concurrent increase in $\delta^{34}S$ at the upstream site (9.8 ± 0.2‰ SD in spring to 12.5 ± 0.1‰ SD in summer), where no spawning occurs, exceeded the increase observed at the downstream site. This casts uncertainty on the degree of natural variability within a site, as our current knowledge of $\delta^{34}S$ patterns in freshwater biota is limited. Furthermore, sulfur inputs from sea spray and precipitation at coastal sites such as the downstream site in the West River could be entering the food web independently from anadromous fishes, leading to elevated $\delta^{34}S$ values (Novak et al. 2001). Trophic fractionation of sulfur is also highly variable among species, and the average $\delta^{34}S$ difference between an animal and its diet is 0.4 ± 0.5‰ SD (McCutchan et al. 2003). Seasonal changes may be related to changes in diet-tissue fractionation or inherent variation in $\delta^{34}S$ of algae as observed in $\delta^{13}C$ (France 1995b), but more research is required to draw any conclusions regarding sulfur isotope patterns.

Population sizes of anadromous fishes, including salmonids, alosids, and osmerids, are known to fluctuate considerably on an annual basis (Cunjak and Therrien 1998; Gresh et al. 2000; Chaput and Atkinson 2001; Acolas et al. 2006). These fluctuations would presumably influence isotope ratios in the receiving environment such that differences between spawning and reference sites would be more pronounced in years with higher spawner abundance. Consequently, $\delta^{15}N$ levels in sediments and consumers are now being promoted as surrogates for historic and current salmon escapement levels (Bilby et al. 2001; Finney et al. 2002, Gregory-Eaves et al. 2004). While we had reasonable estimates of spawner abundance in our salmon rivers (Catamaran Brook and Scorff River), we are unsure of population sizes of blueback herring in the West River and rainbow smelt in Doctor's Brook. Knowledge of changes in spawner biomass from year to year could assist in modeling the potential contribution of alosids and osmerids to freshwater energy

budgets (Durbin et al. 1979). Similarly, detection of marine inputs using SIA rests largely on the timing of sampling. Inherent variability in primary producer isotope ratios (Finlay 2004; Figures 4 and 5) over time could lead to false conclusions regarding the presence or absence of marine inputs if sampling in time is limited.

Our results suggest that marine subsidies are likely present in Atlantic coast streams, but these pathways differ from Pacific coast systems in that, due to limited semelparity in the species present, they appear to be restricted to direct consumption of eggs by invertebrates and nutrient release from egg decomposition rather than through the incorporation of dissolved nutrients from carcass decay, particularly at the low population densities evident today. While bulk organic matter subsidies appear to be obtained from alosids (Durbin et al. 1979) and osmerids, contributions from Atlantic salmon at current population sizes may be more subtle, perhaps in the form of phosphorus additions as suggested by Nislow et al. (2004). Lyle and Elliott (1998) estimated minimal C, N, and P contributions (0.09–0.24%) by Atlantic salmon and sea trout to the current overall energy budgets of English rivers, which may be tempered further by energy export in the form of seaward migration by smolts. Given the historic range and abundance of anadromous fishes in eastern North America and Western Europe, and consequent declines over the past two centuries, organic matter and nutrient subsidies may be greatly reduced with consequences for the productivity of oligotrophic lakes, streams, and rivers. Future research is necessary to determine if productivity may be restored through management intervention such as fertilization (e.g., Ashley and Stockner 2003) to replace historic subsidies that are now reduced or absent. Stable isotope analysis should continue to assist in this regard by providing evidence that these subsidies are indeed being incorporated into freshwater food webs.

Acknowledgments

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