

Beaver invasion alters terrestrial subsidies to subantarctic stream food webs

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Abstract North American beavers (*Castor canadensis*) were introduced to Tierra del Fuego Island in 1946 for their fur, and have since spread across the archipelago and onto the South American mainland. We assessed the impact of invasive beavers on streams of these forested watersheds by quantifying the trophic basis of production (TBP) and consumptive organic matter flows of benthic macroinvertebrate assemblages. TBP was determined in two streams: clear- and black-water. Stable isotopes were used across four streams to further elucidate food web structure and dominant pathways. TBP and stable

isotopes showed that terrestrially derived organic matter (amorphous detritus, leaves, and wood) supported a majority of secondary production in the benthic food webs at all sites (forested reaches, beaver ponds, and sections downstream of ponds with foraged riparian zones). The magnitude of these flows was enhanced in beaver-modified sites compared with forested habitats (4.0–5.3× increase g AFDM m⁻² year⁻¹ in pond habitats, 1.1–2.1× increase in downstream habitats). Diatoms were the only autochthonous resource identified in macroinvertebrate guts, but their contribution to secondary production was small. Consumptive flows mirrored trends in TBP (i.e., dominance of terrestrial sources and greater magnitude in beaver ponds). Collector–gatherer consumption of amorphous detrital material dominated food web flows in all habitats, but was higher in beaver ponds relative to other habitats. Food web structure was simplified in beaver ponds; only two of the five possible functional groups contributed >1% of total organic matter flow in ponds (collector–gatherers and predators). Consumptive flows to predators increased in ponds, and stable isotopes of nitrogen and carbon ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) corroborated a relatively greater importance of predators (greater trophic distance), as well as less diversity of basal resources (less variation in $\delta^{13}\text{C}$) in ponds. Our findings indicate that invasive beaver’s engineering activities resulted in greater flows of terrestrial organic matter subsidies to in-stream food webs, which had a relatively greater change in the clear-water than in the

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black-water stream. Owing to the fact that these streams were naturally dependent on allochthonous resources for a majority of production and material flows, changes wrought by beavers to streams in forested environments are probably less than in watersheds with inherently greater dependence on autochthonous production such as the adjacent steppe biome.

Keywords Cape Horn · *Castor canadensis* · Ecosystem engineer · Ecosystem function · Macroinvertebrate · Trophic basis of production

Introduction

Aquatic ecosystems are subject to a host of human-mediated aspects of global ecological change such as urbanization, riparian habitat degradation, and nutrient enrichment (Naiman & Décamps, 1997). The introduction of non-native species by humans further affects river and stream ecosystems by altering nutrient cycles (Simon et al., 2004), organic matter flow (Strayer et al., 1999), and subsidies to adjacent riparian zones (Baxter et al., 2004). Therefore, in addition to concerns regarding the effects of invasion on aquatic biodiversity (Rahel, 2002), it is necessary to consider the role of the introduced species as drivers of change in ecosystem function.

Non-native species' invasions are not confined to areas dominated by human settlement; even otherwise, remote areas experience this global phenomenon. The Magellanic Sub-Antarctic Forest Biome of southern South America, for instance, is considered as one of the world's most pristine wilderness areas, due to its low human population density, highly intact native vegetation cover and extensive size (Mittermeier et al., 2002; Rozzi et al., 2006). However, portions of this ecoregion include some islands replete with introduced species (Anderson et al., 2006a). Among the exotic assemblage found in the subantarctic archipelago of Chile and Argentina, the North American beaver (*Castor canadensis* Kuhl) has merited particular attention for its ability to modify extensive areas of both terrestrial and aquatic ecosystems (Anderson et al., 2006a, b; Martínez Pastur et al., 2006; Wallem et al., 2007). Since its introduction by the Argentine government in 1946, this invasive species has constituted one of the largest

landscape level alterations in this area since the retreat of the last ice age (Anderson et al., 2009).

The role of beavers as quintessential ecosystem engineers (Jones et al., 1994) is well described in their native habitat, where they down riparian trees to create dams that in turn modify stream biota, hydrology, geomorphology, and biogeochemistry (Naiman et al., 1988, 1994). It is known that these habitat modifications also lead to increased standing stocks of terrestrial organic material in streams (Naiman et al., 1986), but the effects on stream food webs is less studied (Hodkinson, 1975). It is well understood, however, that allochthonous resource linkages are crucial for explaining stream food web dynamics (Fisher & Likens, 1973; Wallace et al., 1999; Baxter et al., 2005) and should be particularly important in cases where strong effects on terrestrial–aquatic linkages are predicted, as is the case with beaver engineering. In this way, studying the effects of beaver invasion on subantarctic streams serves a dual purpose by simultaneously allowing us to understand the consequences of this invasion per se, as well as providing new information on subantarctic stream ecosystems, which are all but unstudied in the high latitudes of South America.

We predicted that beaver invasion would modify resource type and availability to stream consumers in subantarctic streams. We quantified the effects of beaver modifications on resource subsidies and in-stream food web dynamics by assessing the type and magnitude of energy flow to stream macroinvertebrates. The Cape Horn Biosphere Reserve's two dominant stream types (black- and clear-water) were studied in three distinct habitats: forested, beaver ponds, and stream sections immediately downstream of ponds. In order to detect impacts, we quantified: (i) carbon flow dynamics (origin, magnitude, and pathway), using the trophic basis of production (TBP); and (ii) variation in food web structure (trophic length and basal resource diversity) in these three habitats, using stable isotopic signatures of carbon and nitrogen. We anticipated that invasive beaver activity would enhance food web dependence on terrestrial subsidies in ponds (due to organic matter retention), but promote autotrophy in downstream reaches (due to deforestation of riparian vegetation). Based on work that showed reduced macroinvertebrate taxa richness in pond habitats (Anderson & Rosemond, 2007), we expected beaver

impoundments to display simplified trophic structure, but downstream sites were expected to exhibit a broader range of basal resources, due to the addition of autochthonous energy sources. Overall, we anticipated that the effects of beaver invasion would be attenuated in black-water, compared to clear-water streams, because of light limitation of autochthonous resources in the former.

Materials and methods

Study site

Four streams were studied on the north coast of Navarino Island (56°S) in the Cape Horn Biosphere Reserve at elevations below 100 m in mixed forest-bog watersheds. This archipelago (Fig. 1) is the world's southernmost forested ecosystem, found at the extreme tip of the South American temperate forest ecoregion (35–56°S) (Armesto et al., 1995). Twenty-five mating pairs of *C. canadensis* were introduced to Tierra del Fuego Island in 1946 to initiate a fur trade (Lizarralde, 1993). Yet, fur was never commercially harvested, and beavers now inhabit most of the archipelago as well as the

Brunswick Peninsula on the Chilean mainland (Anderson et al., 2006a; Wallem et al., 2007; Anderson et al., 2009).

Study reaches were in the forested portion of catchments with only two dominant tree species: the broadleaf evergreen *Nothofagus betuloides* (Mirbel) Oersted and its deciduous congener *N. pumilio* (Poepp. et Endl.) Krasser (Rozzi et al., 2006). The study watersheds included: Róbalo (Omora Park), Mejillones, Estrella and Faraónes. Unimpacted stream reaches were well shaded in summer (>50% canopy cover, Table 1), and all streams displayed similar physical–chemical characteristics with the exception of dissolved organic carbon (DOC), which was higher in two streams that drained *Sphagnum* bogs and, therefore, were enriched in tannins, i.e., “black-water” streams (Table 1).

All the four catchments were used for stable isotope analyses, but only two streams (one clear-water and one black-water) were used to calculate the TBP. Estimates of macroinvertebrate secondary production had been made in both of these streams concurrent with this study (Anderson & Rosemond, 2007). Each stream had three sampling locations that corresponded to (1) a natural, forested reach never impacted by beavers (forested), (2) an active beaver

Fig. 1 Map of southern South America, including the subantarctic archipelago shared between Chile and Argentina (dotted box in inset map). Study sites were located on the north coast of Navarino Island, Chile in the Cape Horn Biosphere Reserve (shaded area)

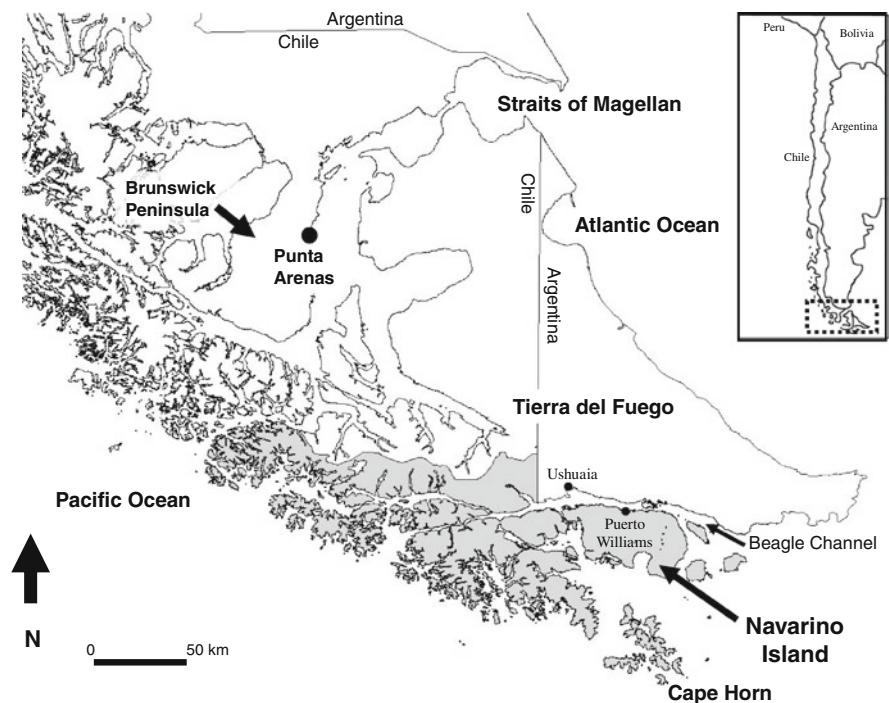


Table 1 Habitat variables from the forested stream study reaches on Navarino Island in the Cape Horn Biosphere Reserve, Chile

Characteristic	Róbalo	Estrella	Mejillones	Faraónes
Water clarity	Clear-water	Clear-water	Black-water	Black-water
Latitude (°S)	54°57′15.0′	54°55′34.8′	54°54′33.7′	54°54′20.0′
Longitude (°W)	67°38′70.5′	67°45′18.2′	67°59′97.8′	68°04′96.7′
Canopy cover (%)	56.3 (9.3)	80.5 (2.6)	68.2 (7.2)	72.8 (11.3)
Width (m)	8.3 (1.1)	3.7 (1.1)	5.6 (0.5)	5.8 (0.6)
Slope (m m ⁻¹)	0.02	0.04	0.02	0.05
Temperature (°C)	4.4 (2)	–	4.8 (2.2)	4.5 (2.2)
Conductivity (µS cm ⁻¹)	68.7	–	130.0	156.0
pH	7.71	–	7.48	7.03
DO (mg l ⁻¹)	10.3	–	10.1	8.3
N–NO ₃ (ppm)	0.06 (0.02)	0.03 (0.01)	0.04 (0.01)	0.06 (0.02)
DOC (ppm)	5.0 (1.5)	3.9 (1.1)	24.2 (8.1)	23.9 (6.9)

Yearly means from bimonthly or seasonal samples with ± 1 SE; other values were only sampled in summer. Data are lacking at Estrella Stream for some variables (–)

DO dissolved oxygen, N–NO₃ nitrate, DOC dissolved organic carbon

pond (pond), and (3) a site immediately downstream of the beaver pond where the riparian zone had been foraged (downstream). While pond and downstream sites were immediately adjacent to one another, forested sites were located in the closest appropriate habitat uncolonized by beavers. In all the cases, this was within 1 km. The length of each study reach varied, depending on habitat type: (1) forested reaches were approximately 100 m; (2) beaver pond sites were studied in the portion near the dam; and (3) downstream reaches ranged from 10 to 50 m, depending on the length of the site that included foraged riparian zones. The beaver-impacted sites were known to be previously forested before beaver colonization, as evidenced by the geomorphology of the site and the presence of standing dead tree trunks to the edge of the river.

Organic matter origin and flow

TBP

We used the TBP method (Benke & Wallace, 1980, 1997) to quantify the resource base of production and organic matter flows in the food webs of clear-water (Róbalo) and black-water (Mejillones) streams. In each stream and during each season (summer—January, fall—May, spring—October), we collected and preserved in Kahle's solution (Winterbourn et al.,

2000) the dominant benthic taxa that comprised the majority (>75%) of secondary production and categorized them according to their reported functional feeding group (FFG) (Miserendino & Pizzolón, 2000; Anderson & Rosemond, 2007), personal observation of feeding apparatus morphology and new gut content analyses. The major taxa for each FFG included (1) collector–gatherer: *Hyalella araucana* Grosso & Peralta (Amphipoda: Hyalellidae), Gripopterygidae (Plecoptera) and Orthoclaadiinae (Diptera: Chironomidae); (2) scraper: *Meridialaris* spp. (Ephemeroptera: Leptophlebeiidae); (3) filterer: *Gigantodax* spp. (Diptera: Simuliidae); and (4) shredder: *Monocosmoecus hyadesi* Mabilie (Trichoptera: Limnephilidae). Predators included *Lancetes* sp. (Coleoptera: Dytiscidae); Tanypodinae (Diptera: Chironomidae); Empididae, Ceratopogonidae (Diptera); and *Rheochorema magellanicum* Flint (Trichoptera: Hydrobiosidae).

We quantified gut contents from approximately 300 unique samples, based on 2–4 individuals of the 4–5 taxa at each of the three habitat types for two streams and three seasons. Seasonal data then were grouped, making an *n* of 12 per taxon for each stream and location. In the laboratory, gut contents from individual taxa were removed under a dissecting microscope. The contents were sonicated, filtered onto 0.45-µm membrane filters (Gelman Sciences, Ann Arbor, MI, USA), cleared, and fixed onto microscope slides. Fifty food items for each

slide were digitized by area and categorized under 400× magnification, using a phase contrast microscope and ImagePro® 5.1.1 image analysis software, as: (i) amorphous detritus (i.e., without cellular structure), (ii) leaf, (iii) wood, (iv) diatom, (v) fungi, or (vi) animal material. Filamentous algae were never found in guts, and fungi were only recorded once.

Quantified diet data and secondary production values, obtained from Anderson & Rosemond (2007), were used in the TBP method to determine two types of energy pathways: (1) the amount of secondary production attributable to each food type, and (2) the total amount of each food type consumed per year to support the observed values of production. While the TBP determines the relative importance of different food resources in supporting consumers, consumptive flows quantify the mass of materials moving through the food web. The fraction of invertebrate secondary production derived from a specific food type was calculated as its proportional area in the gut multiplied by its assimilation efficiency and again multiplied by the net production efficiency: $F_i = (G_i \times AE_i \times NPE)$, where F_i = fraction of production from food type i , G_i = percent of food type i in gut contents (mean annual percent), AE_i = assimilation efficiency for food type i , and NPE = net production efficiency. We used commonly adopted estimates for AE : 10% for leaves, wood, and amorphous detritus, 30% for diatoms, and 80% for animal material (Hall et al., 2000; Cross et al., 2007), which are based on empirical data (e.g., Slansky & Scriber, 1982; Wotton, 1994, and see references in Benke & Wallace, 1980). Likewise, we used an estimate of 0.4 for NPE based on previous common usage (Wallace et al., 1987; Benke & Wallace, 1997) based on values from the literature (e.g., Edington & Hildrew, 1973; Otto, 1974). F_i was then converted to a relative proportion compared to all food types (PF_i) by dividing the fraction of production of food type i by the sum of all food types ($PF_i = F_i / \sum F_{(i...n)}$). Total flows of organic matter consumed were then expressed as the amount of each food type required to support calculated values of production: $C_i = (PF_i \times P) / (AE_i \times NPE)$, where C_i = the amount consumed of food type i , and P = secondary production of the consumer. All the organic matter flows were reported as g ash-free dry mass (AFDM) $m^{-2} year^{-1}$.

Stable isotopes

Within-stream sub-samples ($n = 3$) of basal resources and major invertebrate taxa were collected at each habitat type in all the four streams under this study during spring, summer, and fall to analyze their stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$). The number of invertebrate taxa sampled was limited by the ability to obtain sufficient quantities of material, but in each case, samples from populations representing all the FFGs were obtained. Basal resources collected included leaves, wood, coarse benthic organic matter (CBOM >1 mm), fine benthic organic matter ($250 \mu m < FBOM < 1 mm$), very fine benthic organic matter ($0.7 \mu m < VFBOM < 250 \mu m$), seston, biofilm, and DOC. The guts of invertebrates were removed before freezing, and all the samples, except DOC which was frozen, were then dried at 70°C before transporting them to the Analytical Chemistry Laboratory at the Odum School of Ecology, University of Georgia. Athens, GA, US. In the laboratory, basal resources and macroinvertebrate samples were homogenized with a ball mill, weighed on a micro-balance (Sartorius M2P) and analyzed using an isotope ratio mass-spectrometer (Finnigan Delta Plus, ± 0.10 ppm) (for more information on sample collection and processing of basal resources see Anderson & Rosemond, 2007).

Mixing models were not used to determine the amount of production supported by particular food sources because basal resources could not be significantly distinguished (see “Results”). Annual means for $\delta^{13}C$ and $\delta^{15}N$ (± 1 SE) were calculated and graphed in a scatter plot. Ranges shown in bi-plots indicate variability among streams.

Results

Organic matter sources

Amorphous detritus (assumed to be largely derived from FBOM resources in the stream and from terrestrial sources) supported the majority of benthic macroinvertebrate secondary production, accounting for 52–75% of the TBP in all stream types and habitats (Table 2; All FFGs). Although amorphous detritus was the dominant energy source for macroinvertebrate production in all the habitats, it was

relatively more important to beaver pond food webs, compared to forested and downstream sites. The amount of secondary production supported by leaves and wood also increased in ponds versus forested sites, but less total production was attributable to these basal resources (Table 2). The sum of all terrestrially-derived allochthonous food resources supported 94% of secondary production in ponds versus 83 and 77% in forested and downstream sites for the clear-water stream. There was essentially no increase in relative support from allochthonous sources in ponds in the black-water stream with 91% in ponds compared to 91 and 87% in forested and downstream sites, respectively (Table 2). However, in absolute terms, the amount of secondary production supported by allochthonous sources increased greatly in ponds compared to forested habitats. These absolute increases were relatively similar in both black-water (5.3×) and clear-water (4.0×) streams (Table 2). An increase in allochthonous support of secondary production also was observed in downstream habitats (1.1–2.1× compared to forested sites in black- and clear-water streams), but this effect was small compared to that observed in ponds.

In addition, there was some evidence for greater relative importance of autochthonous (diatoms) food sources to secondary production at the downstream sites in both streams and overall more production was based on diatoms in the clear-water stream, compared to the black-water stream (Fig. 2; Table 2). The amount of secondary production supported by autochthonous resources was greater in absolute value in downstream sections compared to forested habitats (3.2–1.8× in the clear- and black-water streams, respectively) and also in beaver ponds, compared to forested habitats (1.3–5.7× in the clear- and black-water streams, respectively). However, these increases were generally small in magnitude (Table 2).

As expected, the secondary production of different FFGs was supported by different food resources, and the importance of particular FFGs to total secondary production reflected resource availability in particular habitats. Amorphous detritus supported the majority of collector–gatherer production in all the habitats (53–81%), but the magnitude and percentages of support were the highest in beaver ponds. The production of filterers, scrapers, and shredders was also largely supported by amorphous detritus.

However, these FFGs were for the most part missing from pond food webs (except for shredders in the black-water pond). Filterers and scrapers had the overall greatest proportions of production based on diatoms (ranging from 8 to 51%), but there were no consistent changes in the degree to which diatoms supported production of these groups based on habitat (e.g., forested versus downstream) (Table 2). In addition, the contribution of animal material to macroinvertebrate predators increased 11.6–18.0× in beaver ponds (black- and clear-water streams, respectively) compared to forested habitats (Table 2).

Organic matter flow magnitude and pathways

Organic matter flow food webs, based on consumptive flows of resources to consumers, showed that the total mass of organic matter, particularly amorphous detritus, increased as a result of beaver invasion (Fig. 3). The relative contribution of terrestrially derived material ranged from 90 to 93% in the clear-water downstream and natural sites, respectively, to 97% in the clear-water beaver pond, while all the three sites in the dark-water stream were 95–96% based on terrestrial material flows (Fig. 3). The pathway that dominated material flow in all the sites was amorphous detritus to collector–gatherers, which alone accounted for 49–71% of material flow in the forested and downstream ecosystems and 80–87% in the beaver ponds. Consumptive flows to predators were comparatively small, but were higher in ponds than in other habitats (0.8–0.18 g AFDM m⁻² year⁻¹ in clear- and black-water ponds, respectively, compared to 0.01–0.07 g AFDM m⁻² year⁻¹ in other habitats). In all the sites, Tanyptodinae chironomids were the most productive predators, but increased in beaver ponds.

Thus, while beaver ponds were characterized by greater organic matter flows, particularly from terrestrially derived material, they had a reduced number of trophic pathways. Collector–gatherers and predators were the only FFGs in which energy flow pathways accounted for more than 1% of the total flow in beaver ponds. Downstream sites were similar to forested reaches, both having a complete FFG assemblage and more balanced resource flows compared to ponds. All habitats, however, were dominated by linkages between amorphous detritus support of collector–gatherers (Fig. 3).

Table 2 TBP per FFG, expressed as g AFDM m⁻² year⁻¹ and percentage of total flow (%), for stream benthic food webs

FFG	Food type	TBP g AFDM m ⁻² year ⁻¹ (%) of FFG production per habitat					
		Clear-water			Black-water		
		Forest	Pond	Downstream	Forest	Pond	Downstream
Collector-gatherer	Amorphous	0.89 (55)	5.49 (77)	2.23 (53)	1.47 (74)	9.48 (81)	1.45 (73)
	Diatom	0.19 (12)	0.45 (6)	0.86 (20)	0.11 (6)	1.08 (9)	0.16 (8)
	Leaf	0.46 (28)	1 (14)	0.94 (22)	0.31 (16)	0.84 (7)	0.36 (18)
	Wood	0.09 (5)	0.22 (3)	0.18 (4)	0.05 (2)	0.12 (1)	0.02 (1)
	Animal	0	0	0	0.05 (3)	0.24 (2)	0.01 (0.3)
	Total	1.63	7.16	4.21	1.99	11.76	2
Filterer	Amorphous	0.05 (43)	0	0.02 (92)	0.09 (52)	0	0.15 (44)
	Diatom	0.06 (51)	0	0.002 (8)	0.07 (45)	0	0.16 (46)
	Leaf	0.01 (6)	0	0	0.004 (3)	0	0.03 (9)
	Wood	0	0	0	0.0005 (<1)	0	0
	Animal	0	0	0	0	0	0
	Total	0.12	0	0.02	0.17	0	0.34
Predator	Amorphous	0	0	0	0	0	0
	Diatom	0	0	0	0	0	0
	Leaf	0	0	0	0	0	0
	Wood	0	0	0	0	0	0
	Animal	0.01 (100)	0.18 (100)	0.02 (100)	0.04 (100)	0.8 (100)	0.07 (100)
	Total	0.01	0.18	0.02	0.04	0.8	0.07
Scraper	Amorphous	0.18 (65)	0	0.22 (50)	0.06 (80)	0	0.2 (92)
	Diatom	0.09 (32)	0	0.22 (48)	0.01 (19)	0	0.02 (8)
	Leaf	0.001 (3)	0	0.002 (<1)	0.001 (1)	0	0.001 (<1)
	Wood	0	0	0	0	0	0
	Animal	0	0	0.007 (2)	0	0	0
	Total	0.28	0	0.46	0.07	0	0.20
Shredder	Amorphous	0.001 (9)	0	0.01 (31)	0.004 (55)	0.01 (25)	0.0001 (26)
	Diatom	0	0	0.01 (36)	0.001 (9)	0.001 (3)	0.0002 (49)
	Leaf	0.01 (77)	0	0.005 (27)	0.003 (36)	0.008 (33)	0.0001 (26)
	Wood	0.002 (14)	0	0.001 (6)	0	0.01 (39)	0
	Animal	0	0	0	0	0	0
	Total	0.01	0	0.02	0.01	0.03	0.0005
All FFGs	Amorphous	1.12 (55)	5.49 (75)	2.48 (52)	1.62 (71)	9.49 (75)	1.8 (69)
	Diatom	0.34 (17)	0.45 (6)	1.09 (23)	0.19 (8)	1.08 (9)	0.34 (13)
	Leaf	0.48 (23)	1 (14)	0.95 (20)	0.32 (14)	0.85 (7)	0.39 (15)
	Wood	0.09 (4)	0.22 (3)	0.18 (4)	0.05 (2)	0.13 (1)	0.02 (1)
	Animal	0.01 (<1)	0.18 (2)	0.03 (1)	0.09 (4)	1.04 (8)	0.08 (3)
	Total	2.05	7.34	4.73	2.27	12.59	2.61
	<i>Allochthonous</i>	1.69 (83)	6.71 (94)	3.61 (77)	1.99 (91)	10.47 (91)	2.21 (87)
	<i>Autochthonous</i>	0.34 (17)	0.45 (6)	1.09 (23)	0.19 (9)	1.08 (9)	0.34 (13)

Final allochthonous and autochthonous percentages exclude animal material from the calculation

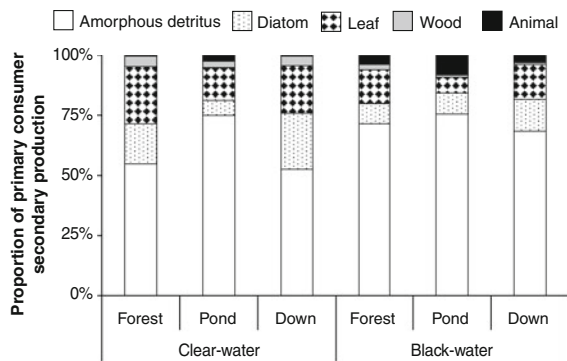


Fig. 2 The proportion of primary consumer production derived from basal resource food categories in forested, beaver pond, and downstream sites in clear-water (Róbaló) and black-water (Mejillones) streams

Food web structure

Stable carbon isotopic signatures of basal resources varied little among habitat types (Fig. 4). However, in forest and downstream sites, biofilm was consistently more negative, and seston was slightly more enriched in ^{13}C than FBOM (biofilm was not available at pond sites). All the fractions of benthic organic matter and seston also were slightly more enriched in ^{13}C than riparian leaves (mean *Nothofagus* leaf $\delta^{13}\text{C} = -30.4 \pm 0.4$, $n = 9$) and wood (mean $\delta^{13}\text{C} = -29.47 \pm 0.4$, $n = 9$). DOC was more enriched in ^{13}C than all other carbon sources sampled (mean $\delta^{13}\text{C}$ per habitat = Forest: -26.3 ± 0.3 , Pond: -26.3 ± 0.04 , Downstream: -26.8 ± 0.1 , $n = 4$ per habitat).

Carbon signatures of the collector–gatherer amphipods (*H. araucana*), which dominated energy flow in all habitats, were near their presumed resource base of FBOM in forests and ponds, and were slightly more negative than FBOM at downstream habitats. Carbon signatures of scraping and filtering taxa (*Meridialaris* spp. and *Gigantodax* spp.) were variable among streams and were more negative than organic matter sources, being particularly negative in sites downstream of beaver ponds. Predator signatures were either close to organic matter sources (e.g., Hirudinidae leeches and diving beetles [*Lancetes* sp.]) or more negative. Consumer signatures were the most negative and exhibited the greatest range in $\delta^{13}\text{C}$ at downstream habitats.

$\delta^{15}\text{N}$ values indicated that CBOM displayed the lowest trophic position in all three habitat types,

while predatory taxa such as leeches, the caddisfly *R. magellanicum* and the diving beetles had the highest trophic status of all benthic macroinvertebrate consumers (Fig. 4). The variation in $\delta^{13}\text{C}$ values was the greatest at downstream sites (due to more negative signatures than at other sites) and was the lowest in ponds (Fig. 4). Sources of carbon to consumers could not be differentiated (biofilm similar to CBOM). We also found that signatures for biofilm and seston had high $\delta^{15}\text{N}$ signatures, often being at the same purported trophic level as the highest macroinvertebrate predator.

Discussion

Energy base and flow

In this study, our focus was on evaluating the effects of introduced North American beavers on basal resources, which in turn influenced energy flow to stream consumers. We predicted that the magnitude of the impacts of this invasive ecosystem engineer would depend on the degree to which it contributed to create or alter unique properties in the system (Crooks, 2002). Results of low benthic organic matter standing crop from the forested reaches showed that these streams are naturally unretentive of organic matter due to their high gradients and flashy flow regime (see also Mao et al., 2008). Therefore, by impounding streams, an important effect of this invasion was related to the magnitude of energy flow from terrestrially derived organic material, which was substantially higher in beaver ponds than in other habitats. This result indicates that beaver enhance cross-boundary resource subsidies. However, the energy base itself was not significantly modified, as the resources contributing to secondary production were the same throughout, and amorphous detritus-dominated organic matter flows in all the food webs.

As predicted, energy flows from autochthonous energy resources increased downstream of beaver ponds, but these changes were slight compared to the major role of terrestrially derived material in supporting secondary production. The removal of canopy cover, particularly in the clear-water stream, was expected to cause a significant increase in epilithic algal production in biofilm, but stream food webs still remained dependent on allochthonous resources.

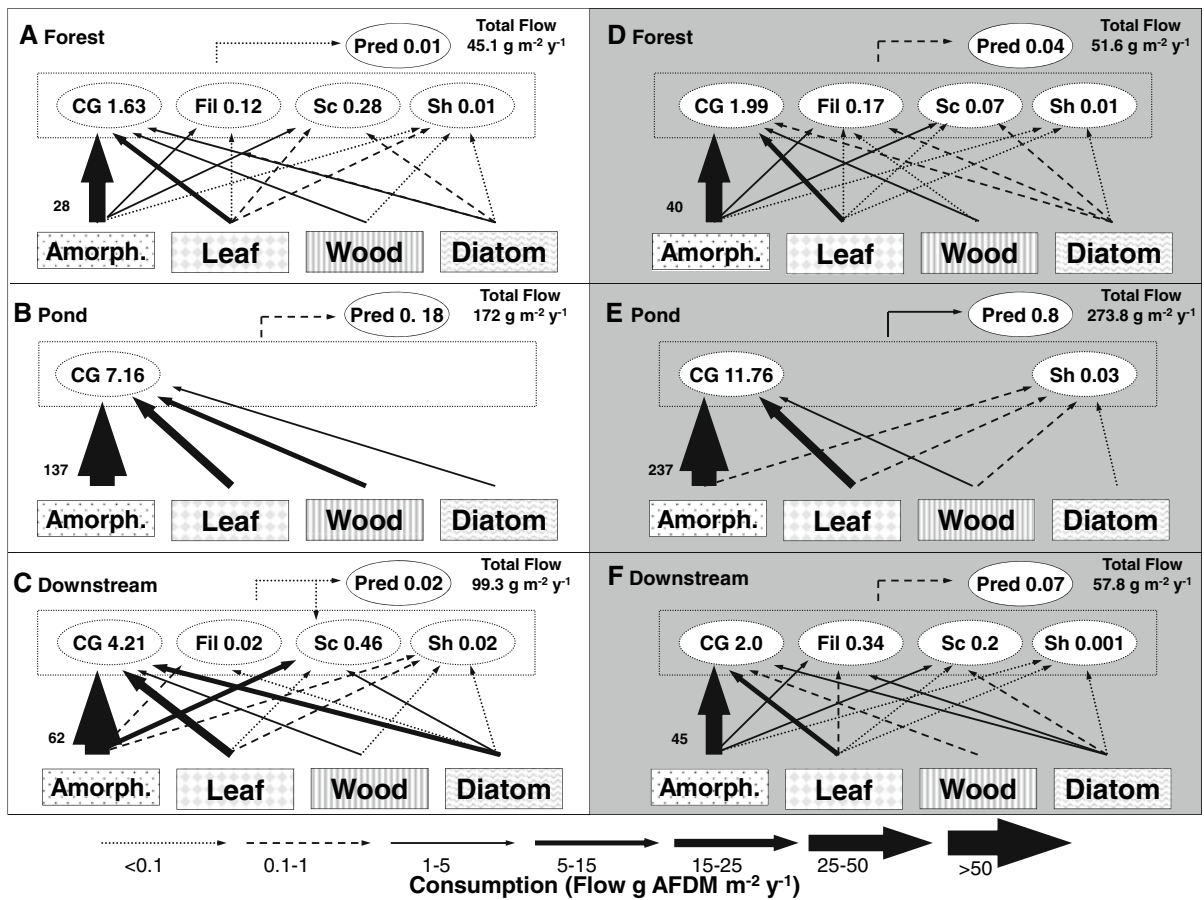


Fig. 3 Total organic matter consumption flows (g AFDM m⁻² year⁻¹) derived from basal resource categories to produce secondary production of FFGs in forest (A, D), beaver pond (B, E), and downstream (C, F) habitats. Black-water stream is denoted by shading, and the size of arrow signifies amount of organic matter flow. Rectangles signify basal resources, and ellipses designate FFGs. Secondary production values are provided for each FFG, which included (site): CG collector-gatherers: *H. araucana* [Hyalellidae] (All), Oligochaeta (Pond),

Non-tanypodinae chironomids [Chironomidae] (All); *Sh* shredders: *M. hyadesi* [Limnephilidae] (Forest and Downstream); *Sc* scraper: *Meridialaris* spp. [Leptophlebeiidae] (Forest and Downstream); *Fil* filterer: *Gigantodax* spp. [Simuliidae] (Forest and Downstream); *Pred* predator: Tanypodinae [Chironomidae] (All), Ceratopogonidae (All), *Lancetes* sp. [Dytiscidae] (Pond), Empididae (All), *R. magellanicum* [Hydrobiosidae] (Forest and Downstream). *Amorph.* Amorphous detritus

Biofilm was apparently dominated by heterotrophic organisms and often included apparent FBOM deposition. Yet, for particular FFGs (e.g., gatherers, filterers, and scrapers), diatoms were a component of both ingestion and secondary production, and overall the impacts of beavers on autochthonous resources in both pond and downstream sites were attenuated in black-water streams.

Such increased support of stream food webs by amorphous detritus (presumably derived from consumption of terrestrially derived fine particulate

organic matter) as observed in this study is also predicted to occur over larger spatial scales in fluvial ecosystems (Vannote et al., 1980). Along some forested catchment gradients, amorphous detritus increases in importance to invertebrate secondary production, shifting dependence from leaf material at low order sites, to diatoms at intermediate sites, and finally to amorphous detritus at larger river segments (Rosi-Marshall & Wallace, 2002). These trends correspond to “river continuum concept” predictions of changes that related energy base and fauna along a

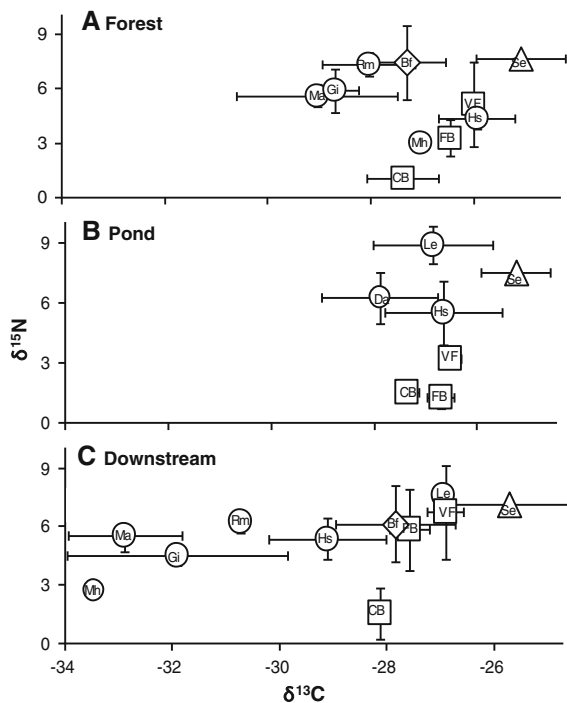


Fig. 4 Scatter plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for natural, pond, and downstream sites (\pm SE). *Square boxes* represent benthic organic matter (CB coarse benthic organic matter, FB fine benthic organic matter, VF very-fine benthic organic matter); *triangles* are seston (Se); *diamonds* are biofilm (Bf); and *circles* indicate dominant taxa for each FFG (Hs: *H. araucana* [gatherer], Le: Hirudinidae leech [invertebrate predator], Gi: *Gigantodax* spp. [filterer], Rm: *R. magellanicum* [predator], Da: Dytiscidae adult, *Lancetes* sp. [predator], Ma: *Meridialis* spp. [scraper], Mh: *M. hyadesi* [shredder])

watershed's longitudinal extension (Vannote et al., 1980). The increase in energy flow along this continuum can be as much as 20 \times from fifth to seventh order streams (Rosi-Marshall & Wallace, 2002). In comparison, beaver engineering enhanced the flow (ingestion) of amorphous detritus by 3.8–5.3 \times in ponds for these high latitude streams in southern South America with no change in stream order.

The stream food webs in the Cape Horn Biosphere Reserve were found to be dependent predominantly on terrestrially derived organic matter as a basal resource, which has also been found for streams in other forested biomes (Fisher & Likens, 1973; Vannote et al., 1980; Wallace et al., 1997, 1999). However, unlike the studies in the forested stream ecosystems cited above, secondary production in

streams studied here relied principally on fine benthic organic matter, rather than coarse material such as leaves. Macroinvertebrates in *Nothofagus* forest streams in New Zealand also have been shown to derive most of their energy from fine particulate organic matter rather than leaves or periphyton, which also have a relative absence of the shredder FFG (Winterbourn & Ryan, 1994). In the case of subantarctic streams, our results for the purported shredders require a re-evaluation of the classification established in previous studies (e.g., Miserendino & Pizzolón, 2000) at least for the extreme southern portion of these taxa's range and also reconfirm that FFG does not always indicate diet.

The range in macroinvertebrate carbon signatures suggested that an undetected source of the more depleted $\delta^{13}\text{C}$ at reaches downstream of beaver ponds and contributed to a greater range in carbon signatures, which may indicate more diverse food resources, in those habitats. This variation is likely due to microbial transformation of carbon resources or utilization of basal resources that we did not collect (e.g., primary producers or microbial exudates). In other catchments with bog habitats, such as those in the subantarctic archipelago, values as low as -54‰ (Kohzu et al., 2004) have been observed for carbon isotopes due to methanotrophic bacteria, but algal isotopes can be highly negative as well (Finlay, 2004). Variation in carbon signatures was not, however, coupled with any evidence of increased trophic diversity with gut analyses or TBP. Stable isotope data were deemed less definitive than gut contents and TBP in identifying food web pathways; however, they raise interesting questions regarding the source of the depleted ^{13}C signatures that we observed downstream of beaver sites.

Trophic structure

We found that taxa diversity and resource variability decreased in beaver ponds (Anderson & Rosemond, 2007), but these engineered habitats also showed enhancement of higher trophic levels by increasing organic matter flows to invertebrate predators. However, as a percentage of total organic matter flow and secondary production, benthic predatory taxa were always a very small fraction of the assemblage, production, and energy flow in these streams. The trend of increased flows to predators that we detected

using TBP was corroborated by our stable isotope results; both showed greater vertical structure in the beaver impacted food webs, which has also been detected in studies from North America (McDowell & Naiman, 1986). The beaver's effects on downstream sites were the opposite of those observed in ponds, where greater trophic diversity and flow dynamics were very similar to natural, forested sites. Overall, beaver invasion is having large impacts in the pond habitats they create, but that the ultimate affect on the resource base of stream food web is in fact attenuated due the natural conditions of these streams (i.e., naturally being dependent on allochthonous material).

The finding that a relatively small amount of invertebrate primary consumer production goes to invertebrate predators contrasts with studies of streams in eastern North America that described invertebrate predators consuming approximately 75–100% of invertebrate production (Wallace et al., 1997; Hall et al., 2000; Cross et al., 2006). While the fate of some invertebrate production undoubtedly goes to vertebrate predators (Huryn, 1998), insect emergence can also be a significant link between aquatic and riparian ecosystems in the form of an aquatic prey subsidy to riparian consumers (Jackson & Fisher, 1986; Sabo & Power, 2002; Sanzone et al., 2003; Baxter et al., 2005), but it is unclear whether beaver modifications would increase insect emergence (Naiman et al., 1984). Vertebrate predators in this system include one common native fish (*Galaxias maculatus*) and two species of introduced trout (brook and rainbow) (Moorman et al., 2009), which consume some portion of invertebrate production not evaluated here. Determining the fate of benthic secondary production will be necessary to further elucidate the potential in-stream and transboundary effects of beaver in subantarctic ecosystems.

Conclusion

Invasive beavers have inhabited the extreme southern tip of Chile and Argentina for 60 years, and during this time, they have colonized most of the archipelago and become a major influence on the biota and ecosystems at these high latitudes. Their impacts have converted extensive areas of riparian forest to

meadows (Anderson et al., 2006b; Martínez Pastur et al., 2006), which is arguably the largest landscape transformation experienced by subantarctic forests since the retreat of the last ice age (Anderson et al., 2009). It is also speculated that this alteration may be creating a new alternative stable state for these ecosystems since riparian forest regeneration has been suppressed (Anderson et al., 2006b; Martínez Pastur et al., 2006).

We have previously shown that subantarctic streams have very low secondary production, as expected for high latitude and nutrient-poor ecosystems, and that beaver invasion increases the production of benthic consumers to levels more typical of a temperate biome (Anderson & Rosemond, 2007). Here, we used two complementary methods (TBP and stable isotopes) to demonstrate that the introduced North American beaver's engineering impacts also ultimately affected terrestrial-aquatic linkages and in-stream food web structure and dynamics. However, due to the fact that these streams were naturally dependent on allochthonous resources (particularly amorphous detritus), changes wrought by beavers to the streams in the forested portion of the archipelago may have less impact on benthic ecosystem processes in this landscape than they would have in other ecosystem types. In contrast to the subantarctic forested ecoregion, beavers are now invading grassland ecosystems farther north, which are likely more dependent on primary production and may be more affected by beaver impacts than the forested sites studied here.

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