

Research Article

An energy budget for the Kootenai River, Idaho (USA), with application for management of the Kootenai white sturgeon, *Acipenser transmontanus*

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Abstract. An energy budget provides a useful tool for examining the exchange of energy between trophic levels. In this study we examined the potential for autotrophic productivity and organic material to support higher trophic levels in three distinct geomorphic segments of the Kootenai River, USA. This approach is particularly important given that several species of fish, including the endangered Kootenai white sturgeon (*Acipenser transmontanus*), have been in decline since the installation of a large hydropower and flood control dam on the river. Previous research indicated that (i) the reservoir formed by Libby Dam was retaining significant quantities of nutrients and organic material and (ii) phosphorus was limiting periphyton accrual downstream from the reservoir. Thus food limitation was a likely mechanism contributing to the decline in fish populations. Net daily metabolism (NDM) was positive during only 30% of the

growing seasons from 1993 to 1995 indicating that autochthonous production was rarely sufficient to support higher trophic levels. All reaches were generally exporting transported organic matter (TOM). Results of an energy budget indicated that macroinvertebrate standing crop was generally lower than that which could be sustained by the relatively short bursts of positive NDM. Estimated fish biomass was higher than that sustained by positive NDM or stored TOM at energetic conversion efficiencies (C.E.) of 10% at average and maximum estimated active metabolic rate. Autotrophic and detrital sources were generally insufficient to support the estimated fish biomass. This study combines detailed analyses of both the autotrophic and detrital energy pathways and thereby suggests a mechanistic explanation for the decline in fish abundance ultimately caused by impoundment.

Key words. Energy budget; autochthonous production; organic matter; autotrophy; lotic ecosystem management.

Introduction

Complete understanding of energy flow through an ecosystem can only be made by determining productivity at all trophic levels, starting with the primary producers (Benke, 1993). In aquatic systems this can be done by

measuring primary productivity and community respiration as change in dissolved oxygen, pH, or ¹⁴C uptake (Lindeman, 1942; Odum, 1957; Teal, 1957; Odum, 1983). However, rarely are both primary and secondary productivity quantified for multiple trophic levels because these measurements are time- and labor-intensive (Benke et al., 1988).

Benke et al. (1988) noted that there are two techniques by which stream energetics (flow of energy and the cycling of carbon) can be measured; (1) the energy

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budget approach which uses measurement of in-stream primary productivity (including organic matter cycling) (*sensu* Cummins et al., 1983), and (2) the population-level approach whereby standing stock and specific growth rate are used to calculate production (Benke et al., 1988; Benke, 1993). In this study, the first approach was used extensively, while literature values were used to estimate macroinvertebrate and fish metabolic demands.

Just as the diversity, density, and behavior of aquatic organisms are influenced by the abiotic environment (i. e. the habitat templet), so too is energy flow (Southwood, 1977; Benke, 1988). For example, the availability of energy is influenced by solar input, geology, climate, geomorphology and hydrology (Benke, 1988), as are the suite of organisms present (Hall et al., 1992). Cummins et al. (1989) summarized the importance of allochthonous inputs, in the form of leaf litter, that serve as a major pathway by which energy enters streams, particularly in regions dominated by a deciduous riparian zone. Minshall (1978) noted that autochthonous productivity can provide the major pathway by which energy enters a stream, particularly in more arid climates where deciduous riparian zones are relatively small. In both instances, the abiotic environment established the templet largely responsible for regulating both the form and quantity of energy available to the aquatic system.

Anthropogenic alteration of river systems can significantly impact the abiotic system and result in significant disruption of aquatic ecosystem integrity and the sustainable supply of goods and services thereby provided (Stanford et al., 1996; Poff et al., 1997, 2003; Baron et al., 2002). For example, the Kootenai River ecosystem experienced significant alteration by levy construction and floodplain disconnection (Constable, 1957; Redwing, 1996) and the completion of a large hydropower and flood control dam in 1972. Both of these factors, particularly the latter, have been linked to the initial decline of the Kootenai white sturgeon (*Acipenser transmontanus*) population (Daley et al., 1981; Ennis et al., 1983; Hamilton et al., 1990; Apperson and Anders, 1991; Paragamian and Kruse, 2001; Paragamian et al., 2001). In addition, Woods (1982) found that significant amounts of nutrients and organic matter were being retained by the reservoir formed by completion of the dam. The reservoir was subsequently linked to significant phosphorus limitation of periphyton in river reaches below the dam and the potential for autotrophic food limitation (Snyder et al., 2002). Beginning in 1991, water release through the dam simulated the historic flow regime, although discharge typically only reaches 60% of the historic average spring value of $1840\text{ m}^3\text{ s}^{-1}$ and velocities are less than 1 m s^{-1} (Coutant, 2004). Monitoring of *A. transmontanus* spawning since 1995 suggests that these efforts have led to movement of gravid females upstream to spawning reaches with the documented release of eggs

(Paragamian and Kruse, 2001). However, intensive sampling since 1991 has documented only 17 wild juvenile sturgeon (Paragamian et al., 2001). Because population size is estimated at approximately 1500 adults and 87 juveniles (Paragamian et al., 1996) and there is continued low recruitment, *A. transmontanus* was listed for protection under the Endangered Species Act in September 1994 (USFWS, 1994).

Application of this research for management is particularly important given the dramatic decline of several species of endemic fish including the white sturgeon. The ultimate success of these populations and of associated communities is determined by the ability of the organisms to successfully survive and to reproduce, which is only possible if these organisms maintain a positive energy balance (Waters, 1977; Hall et al., 1992).

Objectives of this study were to (1) assess the influence of the changing habitat on energy flow and carbon cycling, and (2) construct a simple energy budget examining the potential that energy resources could be limiting to macroinvertebrates and fish. Specifically, three reaches were contrasted that varied structurally and functionally from up- to down-stream, shifting from canyon to braid to meander (Snyder, 2001). Synoptic measurements of macroinvertebrate standing stocks were conducted and ecosystem metabolism and carbon spiraling were measured, thereby quantifying the two energetic pathways (autochthonous and allochthonous) by which carbon enters aquatic food chains (Odum, 1957).

Site description

The Kootenai River drains $45,584\text{ km}^2$ (Knudson, 1993) in British Columbia, Montana, and Idaho (Fig. 1) and is the second largest tributary of the Columbia River after the Snake River. The drainage basin is principally underlain by folded, faulted, and metamorphosed Precambrian sedimentary rocks (Ferreira et al., 1992). The catchment is heavily forested and mountainous, and precipitation throughout the basin ranges from 500 to 3000 mm annually (Knudson, 1993). The river drops from 3618 m elevation at the headwaters to 532 m at the confluence with Kootenay Lake. High channel gradients are present throughout much of the system, particularly in the headwaters and in various tributaries.

Three physically different reaches of the Kootenai River between Libby Dam and Kootenay Lake were identified as part of this study (Table 1). These reaches reflect differences in channel morphology, hydraulic slope and floodplain connectivity and were expected to differ in ecosystem structure and function (Vannote et al., 1980; Ward, 1989; Ward and Stanford, 1995). The first reach (canyon) extends from Libby Dam to the Moyie River and flows through a canyon in places, and, otherwise, has a limited flood plain. Substrate consists of large cobble and gravel. In this reach the river flows

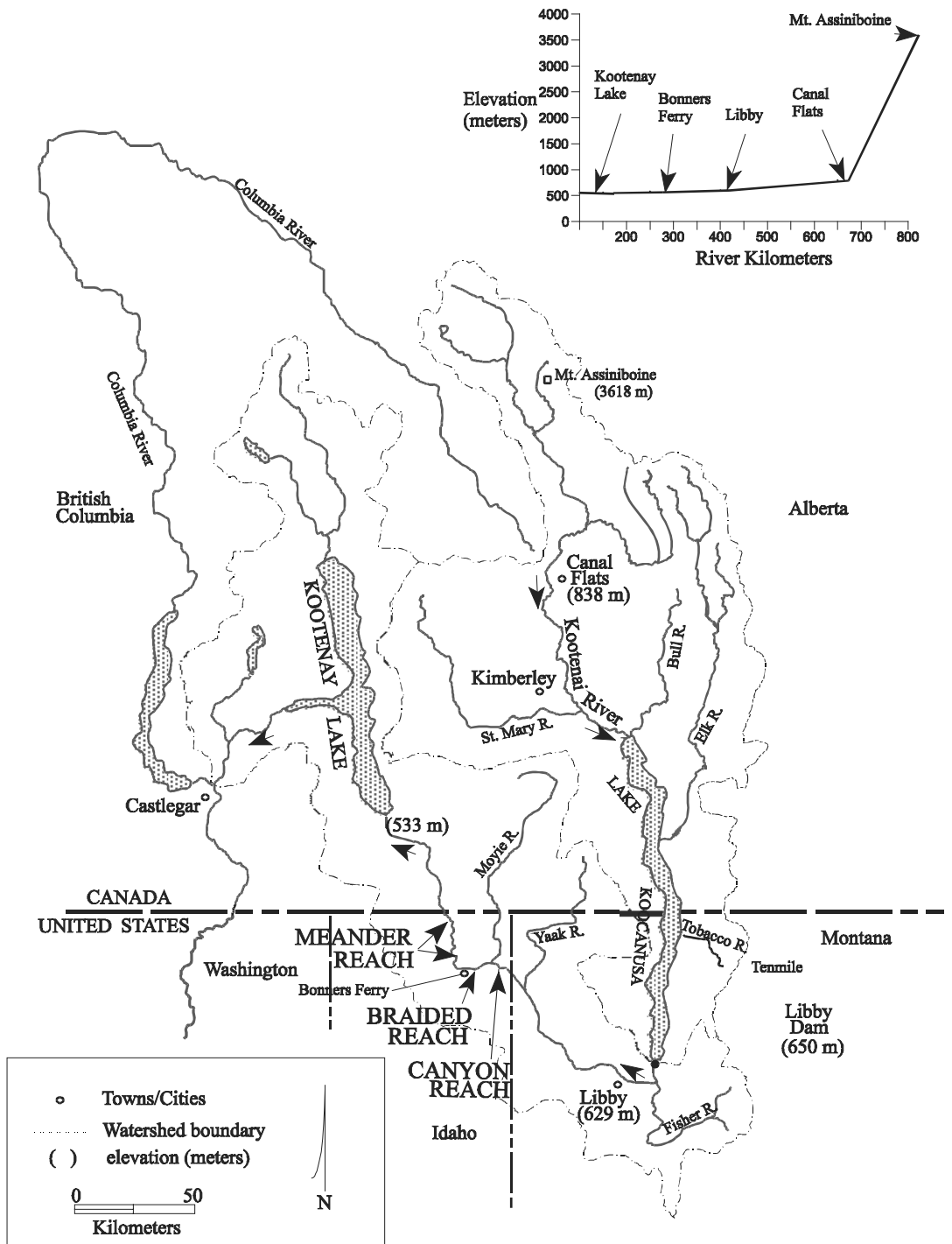


Figure 1. Site map of study reaches and features of the Kootenai River watershed.

in a north-west direction (Fig. 1) and in places is incised 50 to 300m into the local stratigraphy. The second reach (braided) extends from the Moyie River to the town of Bonner's Ferry, Idaho. This reach is extensively braided and gravel is the dominant substrate. The third reach (meander) extends from just downstream of Bonners Ferry

to the confluence of Kootenay Lake and was divided into two study segments (meander 1 and 2). Throughout this reach, the river channel meanders over beds of compacted clay and fine sediments.

Table 1. Physical and chemical characteristics of study sites (+ 1 SD). “Zero” values for median substrate size indicate sand. TIN = total inorganic nitrogen ($\text{NO}_2 + \text{NO}_3, \text{NH}_4$); TP = total phosphorus (unfiltered & digested); PAR = photosynthetically active radiation. For all nutrient samples $n = 5$.

Variable	Canyon	Braid	Meander
Reach length (km)	92	7.5	82.5
Mean velocity (m s^{-1})	0.63 (0.23)	0.65 (0.63)	0.17 (0.06)
Mean depth (m)	2.08 (0.26)	2.25 (0.73)	6.43 (1.55)
Mean max. summer surface PAR ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	680 (344)	839 (295)	1083 (227)
Gradient (m km^{-1})	0.6	0.5	0.02
Channel Sinuosity	1.0	1.1	1.9
Median Substrate Size (cm)*	12	12	0
Substrate Embeddedness (%)*	35	15	0
Macrophyte Cover (%)*	2	3	37
Alkalinity (mg L^{-1} as CaCO_3)*	60	42	49
Hardness (mg L^{-1} as CaCO_3)*	93	75	83
Conductivity ($\mu\text{S cm}^{-1}$)	213.3 (45.9)	198.8 (51.7)	198.5 (58.3)
$\text{NO}_3 + \text{NO}_2$ (mg L^{-1} as N)	0.085 (0.027)	0.081 (0.023)	0.074 (0.039)
NH_4 (mg L^{-1} as N)	0.012 (0.005)	0.008 (0.004)	0.013 (0.007)
TP (mg L^{-1} as P)	0.009 (0.000)	0.007 (0.001)	0.012 (0.003)
molar TIN:TP	42 (18)	38 (13)	17 (10)

*Measured one time only Aug 1994

Methods

Previous research indicated that phosphorus was limiting periphyton accrual (Snyder, 2001; Snyder et al., 2002). Because of this, particular attention was devoted to two potential sources of food: transported organic matter (TOM) and autotrophic productivity. In the current analysis, detailed measurements of primary productivity and TOM were combined with measures of benthic invertebrate standing stock and literature values for fish standing stock to identify the potential for autotrophic productivity and/or TOM to sustain the food web through at least three trophic links. This energetic budget has several limitations. For example, fish biomass was not directly measured and was based on published reports. In addition, it was beyond the scope of this project to construct a bioenergetic model for the major species of fish present in the river (sensu Winberg, 1956; Calow, 1985; Adams and Breck, 1990). Thus, we used published values of oxygen consumption as a measure of metabolic rate.

Metabolism often is measured by placing the fish (typically unfed) into a respirometer and measuring oxygen consumption. This value is represented as standard metabolic rate and assumes that the organism is at rest. By changing current velocity inside the respirometer, active metabolic rate can be estimated (Facey and Grossman, 1990). Soofiani et al. (1985) note that in natural settings, metabolic rate is likely located somewhere between standard and active metabolism and that brief bursts of swimming can consist of a large portion of available energy.

Energy budget

Positive net daily metabolism (NDM) values measured using single station open system techniques (sensu Owens, 1974) were used to determine the energy available to higher trophic levels produced by within-reach autotrophic production (Snyder, 2001). NDM ($\text{g O}_2 \text{m}^{-2} \text{day}^{-1}$) is an integrative measure of metabolism and describes the total amount of O_2 produced in excess of 24-hour community respiration ($\text{CR}_{24\text{hr}}$). As such, it provides a measure of the amount of energy fixed in excess of respiration during a 24-hour period that can be either stored as biomass or exported. NDM is useful in describing the magnitude of autotrophy or heterotrophy in a river system. A river system that has a positive NDM value can be considered autotrophic (e.g. production in excess of respiration), whereas a system with negative NDM can be considered heterotrophic (e.g. respiration in excess of production).

Dissolved oxygen (O_2) was monitored in the water column using anchored-buoy systems equipped with Campbell Scientific data loggers (model BDR 320) connected to Royce oxygen probes (model 900 with stirrers) suspended in the water column. Data loggers recorded O_2 concentration every 10 min by averaging values measured every 10 seconds. Meter accuracy was checked against Winkler titrations. Oxygen diffusion coefficients were calculated using standard equations (Odum, 1956; Janzer, 1977; Bennett and Rathbun, 1972).

The rate of O_2 change in a 24-hour period was plotted and corrected for diffusion. CR_{24} was estimated by determining average O_2 rate of change at night and using

this average nighttime respiration rate to plot daytime respiration rate. Gross primary productivity (GPP) and CR could then be estimated by determining the area under the rate of change plots (Odum, 1956; Hall and Moll, 1975; Janzer et al., 1977; Meyer and Edwards, 1990).

The carbon (C) content of TOM and benthic organic matter (BOM) was calculated assuming 1 g ash-free dry mass (AFDM) = 0.526 g C (Winberg 1971). Carbon (derived from oxygen values) was converted to kilocalories (kcal) using 1 g carbon = 10.96 kcal (Winberg, 1971; Salonen et al., 1976). Three gross energy conversion efficiencies (C.E.) were calculated for NDM (10%, 30%, and 50%). Typically, C.E. is estimated to be approximately 10% (Lindeman, 1942; Slobodkin, 1962; Strayer, 1991), but we used the higher values to conservatively bracket maximum potential biomass. The conversion efficiency for TOM was estimated to be 2% (Araujo-Lima et al., 1986; Allan, 1995). Energy requirements of macroinvertebrates and fish were calculated as standard metabolic rate (MR_s) for insects and both standard and active metabolic rate (MR_a) for fish. For macroinvertebrates, MR_s was calculated based on the seasonal mean temperatures that were observed in the Kootenai River in 1995 and assuming $Q_{10} = 2.5$ (Gilbert and Raworth, 1996). The following formula was used to estimate seasonal metabolism (Schmidt-Nielsen 1990):

$$R_2 = R_1 \times Q_{10}^{(T_2 - T_1)/10} \quad (1)$$

where,

R = respiration (rates at two different temperatures)

$Q_{10} = 2.5$

T = temperature

For macroinvertebrates, the five most abundant taxa from each sampling period were included in the energy budget and specific metabolic rates were obtained from literature values (Spector, 1956; Odum, 1957; Teal, 1957; Prosser, 1973). If metabolic rates for a particular taxon were not available, rates from a closely related species were used. Data on the resident fish populations were less detailed making seasonal comparisons difficult. In addition, a comprehensive set of standard and active metabolic rates for fish species present in the Kootenai was limited. Thus, we sought to bracket potential fish production by using (i) three conversion efficiencies (10, 30 and 50%) and (ii) the minimum standard and maximum active metabolic rates of those taxa for which literature values were available.

Macroinvertebrate standing crop and benthic and transported organic matter

Macroinvertebrates were sampled concurrently with BOM in 1994–95. In the canyon and braided reaches, collection

was accomplished via SCUBA using a dome sampler equipped with a battery powered suction pump. Approximately 10 stratified (right, mid, left channel) random samples were collected at 3 equidistant transects along a 1-km segment of each study reach ($n = 29$ and 31 for canyon and braid, respectively). Diver and dredge worked from a boat attached to a kevlar cable strung perpendicularly across the river. In the meander reaches, samples were collected using a petit Ponar dredge ($n = 27$ and 38 for the meander 1 and 2 reaches, respectively). All samples were preserved in 5% formalin solution and transported to Idaho State University for identification and enumeration.

BOM, collected in conjunction with the macroinvertebrate samples, was portioned into size fractions, dried, and organic matter content (AFDM) measured by combustion at 550 °C for 24 h. TOM was measured using nested 1000- μ m and 53- μ m nets suspended at 0.6x depth at three locations across the river channel. Samples were collected three times daily for approximately 30 min during each sampling period. This resulted in a total of 27 measurements per reach during the three years of study. Discharge through the nets was measured with General Oceanics standard velocity meters mounted immediately upstream of the nets. Samples were frozen and AFDM determined. Dissolved organic carbon was measured only once during the study due to budget limitations.

Macroinvertebrate dry mass (g m^{-2}) was converted to wet mass (conversion factor = 12.5; (Wetzel, 1983)), from which secondary productivity could be calculated based on previous research conducted in the river ($\text{g wet weight m}^{-2} \text{ year}^{-1}$; production/biomass = 4.5 sensu Perry and Huston, 1983). Electrofishing and hook and line surveys reported total fish biomass at 5.87, 3.23, 8.09, and 3.71 g (wet weight) m^{-2} for the canyon, braid, meander 1 and 2, respectively (Partridge, 1983; Apperson and Anders, 1991; Paragamian, 1994).

Results

Macroinvertebrates

Results of macroinvertebrate sampling in all three geomorphic segments indicated that density (m^{-2}), biomass (g m^{-2}) and taxa richness were variable and low (Table 2). Contribution of energy from TOM, NDM, and BOM for the four study reaches ranged from 0.21 to 29.42, 0.75 to 276.56, and 26 to 2203 kcal $\text{m}^{-2} \text{ day}^{-1}$, respectively (Table 3). Positive NDM and/or stored TOM was sporadic and occurred in approximately 30% of the measurements (Table 3). The organic matter budget indicated that each of the four study reaches were generally losing carbon (Table 4), with only 8 of 29 sampling events indicating positive carbon accrual.

The five most abundant macroinvertebrate taxa in each sampling period were used to calculate oxygen

Table 2. Macroinvertebrate metrics in the Kootenai River, 1994–95. SD = standard deviation. Samples collected via dome suction sampler using SCUBA in the canyon and braid; meander samples collected with petite ponar dredge.

Location	Date	n-size	DENSITY		BIOMASS		RICHNESS	
			(# m ⁻²)	(SD)	as dry wt. (mg m ⁻²)	(SD)	(#)	(SD)
Canyon	May 1994	18	453	(477)	120	(163)	5	(2)
	Aug. 1994	4	913	(234)	26	(4)	8	(1)
	Sept. 1995	7	358	(354)	25	(30)	31	(22)
Braid	May 1994	7	758	(939)	44	(41)	4	(2)
	Aug. 1994	10	402	(382)	40	(70)	5	(2)
	Sept. 1995	14	2506	(2894)	135	(316)	12	(6)
Meander 1	Aug. 1994	12	479	(606)	27	(24)	2	(1)
	Aug. 1995	15	604	(1372)	1062	(4001)	2	(1)
Meander 2	May 1994	11	700	(1237)	124	(181)	2	(2)
	July 1995	12	1250	(2406)	164	(456)	3	(2)
	Aug. 1995	15	498	(345)	28	(22)	3	(1)

Table 3. Contribution (kcal m⁻² day⁻¹) of the primary producers and the transported and benthic organic matter to higher trophic levels. All four reaches sampled 9 times (3 times per year during the growing season in 1993–95). In this table, missing data indicate either negative net daily metabolism (NDM) or lack of stored transported organic matter (TOM). Benthic organic matter (BOM) was only assessed one time and was assumed to be relatively stable compared to NDM and TOM.

Site	Date	NDM kcal m ⁻² day ⁻¹	TOM kcal m ⁻² day ⁻¹	BOM kcal m ⁻² day ⁻¹
Canyon	Aug 93		10.06	
	Jul 94	3.28		
	Aug 94		10.38	93
Braid	Jun 93	0.44		
	Jul 93	1.20		
	Aug 93	0.44	6.59	
	Jul 94	5.58		
	Aug 94			26
	Oct 94		13.5	
	Jun 95		55.91	
Jul 95		0.75		
Meander 1	Jun 93	4.70		
	Jul 93		3.13	
	Jul 94		12.93	
	Aug 94	2.08		2144
	Oct 94		19.81	
	Apr 95	4.92		
Jul 95		34.21		
Meander 2	Jul 93	2.41	10.33	
	Jul 94		40.62	
	Aug 94		1.48	2203
	Jun 95		276.56	

consumption (Table 5). Respiration rates were obtained from the literature for representative taxa of Diptera, Ephemeroptera, Trichoptera, Collembola, Annelida, Crustacea, Gastropoda, and Nematoda (Table 6). When possible, specific respiration data for taxa listed in Table 5 were used. These data were then combined with maximum NDM and TOM values (from Table 3) to estimate the maximum potential sustained macroinvertebrate biomass (Table 7). Energy requirements of the major macroinvertebrate taxa were then weighted according to relative abundance. For example, in the canyon reach, maximum NDM and stored TOM were 3.28 and 10.38 (kcal m⁻² day⁻¹), respectively (Table 7). At 30% C.E., energy available from NDM was 0.98, while energy available from TOM at 2% C.E. was 0.21 (kcal m⁻² day⁻¹). Summed together, this represents 1.19 kcal m⁻² day⁻¹ of energy that can be partitioned among the primary consumer trophic level. Given that Diptera (mainly Chironomidae) represented 56% of the population in the canyon, 0.67 kcal of energy was available to this group. The Diptera require, on average, 0.367 kcal g⁻¹ day⁻¹ during the summer when temperatures are high and metabolic rates are maximized (Table 6). Thus by dividing the fraction of energy (in this case 0.67 kcal m⁻² day⁻¹) available to the taxonomic group by the energy required by the same group (0.367 kcal g⁻¹ day⁻¹), the potential biomass that can be sustained is calculated and compared with measured macroinvertebrate standing stock (Table 7). Measured macroinvertebrate biomass was higher than modeled biomass with the exception of the first meander reach in the summer (Fig. 2).

Fish

Literature values for MR_s and MR_a were available for a limited number of fish species present in the various

Table 4. Organic matter (OM) budget comparing inputs (gross primary productivity (GPP) + imported transported organic matter (TOM)) with outputs (community respiration (CR_{24hr}) + exported TOM) in each of the four study reaches. Values in bold indicate OM accrual within a given reach. Reach area (m²) as follows: canyon = 444,170; braid = 842,393; meander 1 = 316,159; and meander 2 = 355,293.

Site	Date	INPUTS kcal m ⁻² day ⁻¹			OUTPUTS kcal m ⁻² day ⁻¹			CARBON ACCRUAL (+) or LOSS (-) (kcal m ⁻² day ⁻¹)
		GPP	Import TOM	TOTAL INPUT	CR24hr	Export TOM	TOTAL OUTPUT	
Canyon	Jun-93	3.9	14.5	18.4	9.7	37.0	46.7	-28.3
	Jul-93	10.2	12.6	22.8	35.1	31.1	66.3	-43.5
	Aug-93	0.7	60.4	61.0	1.1	50.3	51.4	9.6
Braid	Jun-93	14.0	8.8	22.8	15.3	11.1	26.4	-3.7
	Jul-93	9.4	4.9	14.3	15.3	14.7	30.0	-15.7
	Aug-93	1.3	43.9	45.2	2.1	37.3	39.4	5.8
Meander 1	Jun-93	4.7	0.0	4.7	2.1	15.4	17.5	-12.8
	Jul-93	26.3	11.0	37.2	50.5	7.8	58.4	-21.2
	Aug-93	6.0	21.0	27.0	16.8	49.0	65.8	-38.8
Meander 2	Jul-93	42.0	18.6	60.6	63.9	8.3	72.2	-11.5
	Aug-93	1.8	35.5	37.2	2.6	53.2	55.8	-18.6
Canyon	Jul-94	34.6	56.2	90.7	31.6	76.7	108.3	-17.6
	Aug-94	21.4	25.0	46.4	80.6	13.6	94.2	-47.8
	Oct-94	5.7	36.2	41.9	61.5	46.5	108.0	-66.1
Braid	Jul-94	29.8	26.4	56.2	24.1	31.3	55.4	0.8
	Aug-94	13.7	8.9	22.5	52.8	11.3	64.1	-41.6
	Oct-94	3.1	30.6	33.6	51.2	17.1	68.3	-34.6
Meander 1	Jul-94	9.1	238.0	247.1	23.7	225.1	248.8	-1.7
	Aug-94	16.6	29.9	46.6	29.0	36.6	65.6	-19.0
	Oct-94	9.5	168.4	177.9	11.6	148.6	160.2	17.7
Meander 2	Aug-94	41.7	23.7	65.3	74.2	22.2	96.4	-31.0
Canyon	Jun-95	52.1	448.9	501.0	129.2	484.3	613.5	-112.5
	Jul-95	31.1	166.2	197.3	75.5	179.5	255.0	-57.7
Braid	Jun-95	39.9	322.9	362.8	93.4	266.9	360.4	2.4
	Jul-95	11.5	70.7	82.2	55.7	69.9	125.6	-43.4
Meander 1	Jun-95	17.9	1468.9	1486.9	36.4	3530.7	3567.2	-2080.3
	Jul-95	27.7	234.6	262.3	45.8	200.4	246.2	16.1
Meander 2	Jun-95	41.4	1471.3	1512.7	68.8	1194.8	1263.6	249.1
	Jul-95	23.2	237.2	260.4	36.6	351.1	387.8	-127.4

Table 5. Combined list of five most abundant taxa collected during each of three sampling periods (Spring & Summer '94; Summer '95). When identical taxa were found on more than one sampling date, the higher relative abundance was used. These taxa were then used in construction of the energy budget. Numbers below indicate % relative abundance.

Canyon	Braid	Meander 1	Meander 2
55.8 Chironomidae	50.0 Chironomidae	47.7 Chironomidae	52.8 Chironomidae
12.0 <i>Ephemera inermis</i>	17.3 <i>Cinygmula sp.</i>	29.2 Oligochaeta	24.2 Oligochaeta
7.2 Oligochaeta	9.0 Oligochaeta	5.3 <i>Glossosoma sp.</i>	8.8 Hydracharina
6.2 <i>Serratella tibialis</i>	6.5 <i>Serratella tibialis</i>	3.3 Chelifera	5.8 Hirudinae
5.7 Ostracoda	6.3 Hydracharina	3.3 Collembola	3.3 <i>Helobdella fusca</i>
5.7 <i>Cinygmula sp.</i>	4.0 Ostracoda	3.3 Fossaria	2.4 Microsporidae
3.1 Hydracharina	3.5 Corixidae	3.3 Notonectidae	1.5 <i>Dicronota sp.</i>
2.6 <i>Rhithrogena robusta</i>	1.8 <i>Hydropsyche sp.</i>	2.7 Hydracharina	1.3 <i>Stenopelmus sp.</i>
1.7 <i>Ephemera nemoura</i>	0.9 Optioservus	1.9 Nematoda	
	0.7 <i>Ephemera inermis</i>		

Table 6. Mean energy (kcal g⁻¹ day⁻¹) used in respiration by macroinvertebrates for given temperatures (T °C). Su = Summer, W = Winter (based on average seasonal *in-situ* temperature).

Taxonomic group	Su T = 13.6	W T = 3.2	Annual T = 9.7	Source
Diptera	0.367	0.141	0.221	Walsh 1948, Odum 1957, Prosser 1973, Minshall (unpublished data)
Ephemeroptera	0.779	0.301	0.470	Fox et al. 1935, Minshall (unpublished data)
Trichoptera	0.372	0.144	0.224	Fox and Simmonds 1933, Spector 1956, Odum 1957, Minshall (unpublished data)
Collembola	0.008	0.003	0.005	Prosser 1973
Annelida	0.094	0.036	0.056	Spector 1956, Teal 1957
Crustacea	0.263	0.101	0.159	Fox and Simmonds 1933, Spector 1956, Odum 1957, Teal 1957
Gastropoda	0.021	0.008	0.012	Odum 1957, Minshall (unpublished data)

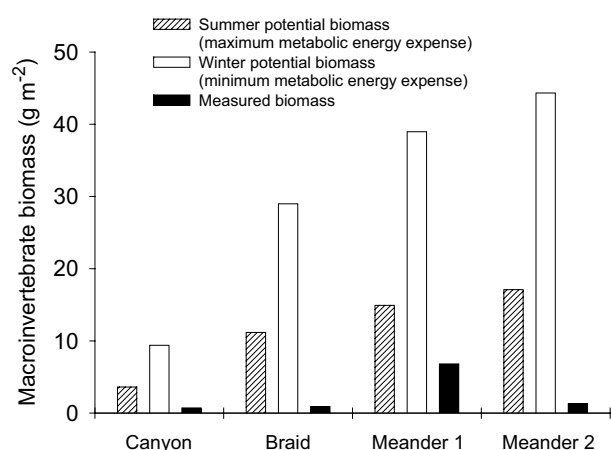


Figure 2. Energy budget for macroinvertebrates in four study reaches of the Kootenai River, Idaho. Budget is based on pooled data from 1993–95. Solid bars represent measured macroinvertebrate biomass; open and hatched bars are biomass estimates based on calculated food availability and metabolic demands. See text for description of budget calculations.

study reaches (Table 8). In all cases, literature values for MR were at temperatures within +/- 5°C of the Kootenai River and fish were assumed to represent the third trophic level. Both standard and active metabolic rates of fish present in the Kootenai River were used to provide minimum (min. MR_s), maximum (max. MR_a), and average (ave. MR_a) fish energetic requirements.

To estimate the energy available at the tertiary trophic level (e.g. secondary consumer), inputs from positive NDM and stored TOM were used, as done for the macroinvertebrates. If the canyon reach is used as an example, positive NDM and stored TOM supplied at most 3.28 and 10.38 kcal m⁻² day⁻¹ to the reach, respectively (Table 9). At the secondary consumer trophic level (e.g. fish), this provided 0.004 kcal m⁻² day⁻¹ from TOM, while NDM provided 0.033 kcal m⁻² day⁻¹ at 10% C.E. Based on the literature review (Table 8), maximum energy use by fish (max. MR_a) was 0.09 kcal g⁻¹ day⁻¹, which, if divided by 0.037 kcal m⁻² day⁻¹ (the sum of energy available from

NDM and TOM) yields an estimated sustainable fish biomass of 0.41 g m⁻². This value can then be compared to the measured fish biomass of 5.87 g m⁻² for the canyon reach. Similar calculations, based on the summary data presented in Table 8, were conducted for minimum standard and average active metabolic rate (Table 9).

Results indicated that measured fish biomass was lower than that sustained by NDM and TOM at 10% C.E. At this C.E., fish were energy-limited at both maximum and average active metabolic rates (Fig. 3). Alternatively, minimum fish metabolic demand yielded much higher biomass values that those recorded (Fig. 3). At a C.E. of 30%, fish were close to reaching their potential biomass in the canyon and first meander reach, or exceeding their potential in the braid and second meander reach (Table 9).

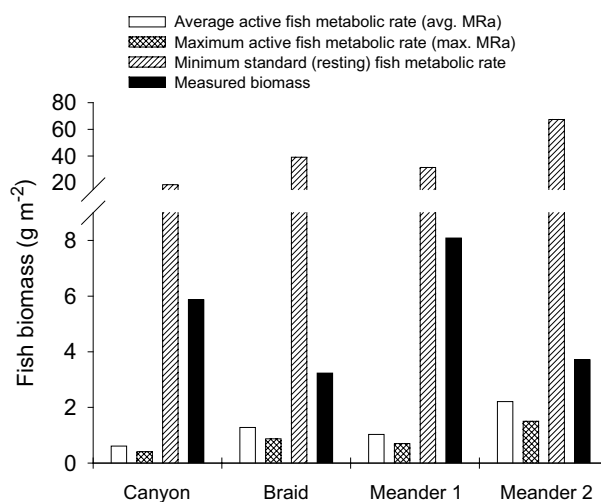


Figure 3. Energy budget for fish in four study reaches of the Kootenai River, Idaho. Budget is based on pooled data from 1993–95. Solid bars represent measured fish biomass; open and hatched bars are biomass estimates based on calculated food availability and resting and active metabolic demands at 10% conversion efficiency. See text for description of budget calculations.

Table 7. Macroinvertebrate biomass and productivity (estimated vs. measured) for the study reaches. Note that only positive, maximum NDM values (open system) are used (see Table 3). TOM had to be stored within a given reach in order to be included in the energy budget. Energy required for macroinvertebrates was estimated from literature values (see Table 6). RA = relative abundance; C.E. = gross conversion efficiency; Su = Summer; W = Winter. Values in bold are used in Figure 2.

LOCATION	Energy prod. by primary producers as NDM (kcal m ⁻² day ⁻¹)	Energy transported into reach as TOM (kcal m ⁻² day ⁻¹)	Energy avail. from NDM (kcal m ⁻² day ⁻¹) 30% C.E.	Energy avail. from TOM (kcal m ⁻² day ⁻¹) 2% C.E.	taxonomic group	summed RA for each major taxonomic group	Fraction of avail. energy weighted by RA of each tax. group (kcal m ⁻² day ⁻¹) 30% C.E.	Max. potential biomass weighted for RA of top 5 most abundant taxa (g m ⁻²)		Measured total macroinverte. biomass-wet weight (g m ⁻²)
								max. energy 30% C.E. Su	min. energy 30% C.E. W	
Canyon	3.28	10.38	0.98	0.21	Diptera	56	0.67	1.82	4.72	0.71
					Ephemeroptera	28	0.33	0.43	1.11	
					Trichoptera	7	0.08	0.22	0.58	
					Annelida	6	0.07	0.76	1.98	
					Crustacea	3	0.04	0.38	0.99	
					sum		1.19	3.62	9.38	
Braid	5.58	55.91	1.67	1.12	Diptera	50	1.55	4.23	10.97	0.91
					Ephemeroptera	24	0.74	0.96	2.48	
					Trichoptera	2	0.06	0.17	0.43	
					Annelida	9	0.28	2.98	7.73	
					Crustacea	4	0.12	1.32	3.43	
					Gastropoda	1	0.03	1.51	3.92	
					sum		2.79	11.17	28.97	
Meander 1	4.92	34.21	1.48	0.68	Diptera	53	1.64	4.49	11.63	6.8
					Trichoptera	6	0.19	0.50	1.30	
					Annelida	30	0.93	9.93	25.76	
					sum		2.76	14.92	38.69	
Meander 2	2.41	276.56	0.72	5.53	Diptera	55	1.71	4.66	12.07	1.32
					Annelida	33	1.02	10.93	28.33	
					Gastropoda	1	0.03	1.51	3.92	
					sum		2.76	17.09	44.33	

Table 8. Minimum, maximum and average metabolic rates or demand ($\text{kcal g}^{-1} \text{day}^{-1}$) for fish taxa commonly found in all study reaches. MR_s = standard metabolic rate for a fish at rest; MR_a = active metabolic rate for a fish in motion. For a complete list of fish taxa and associated metabolic rates, see Snyder (2001). Values in bold are used in the energy budget calculations for fish and are meant to provide a lower minimum, upper maximum, and realistic average of fish energy requirements.

Common name	Scientific name	min. MR_s	max. MR_a	avg. MR_a	Source
Rainbow trout	<i>Salmo gairdneri</i>	0.006	0.090	0.061	Rao 1968, Dickenson & Kramer 1971, Webb 1971, Facey & Grossman 1989, Myrick and Cech 2000
Cutthroat trout	<i>Onchorhynchus clarkii</i>	na	0.013	na	Kindschi & Koby 1994
Largescale sucker	<i>Catostomus macrocheilus</i>	0.012	na	na	Prosser 1973
Northern pikeminnow	<i>Ptychocheilus oregonensis</i>	0.002	na	na	Cech et al. 1994
Sturgeon	<i>Acipenser transmontanus</i>	0.014	0.047*	na	Crocker and Cech 1998, McKenzie et al. 2001*

*Active metabolic rate for Adriatic sturgeon only

Discussion

Results of the energy budget indicated that both within-reach autotrophic production (measured as positive NDM) and stored TOM supplied energy to the system only at a limited time during the growing season, mainly June, July, and August. Assumptions included the following: (1) positive NDM values were used to estimate energy available from autotrophs, (2) TOM had to be stored within a given study reach in order to be used by the biota, (3) fish biomass was estimated from research conducted within the study reaches in Idaho (Partridge, 1983; Paragamian, 1994), and (4) conversion efficiency of NDM ranged from 10 % to 50 %, and 2 % for TOM.

These results should be interpreted in the context of an open system which is linked to both upstream and lateral sources of energy (Minshall, 1978; Junk et al., 1989). Upstream energy sources include input from either autochthonous or allochthonous sources. By including TOM, the contribution of these upstream sources of carbon can be incorporated in the energy budget and the reach can be characterized by carbon accrual, loss, or steady-state. The reaches were mainly characterized as exporting, thus food rarely was available in the form of TOM. Even with a net import of organic matter, the biological conversion efficiency used in these calculations was low (C.E. = 2 %) relative to the C.E. used for autotrophic production (10 %, 30 %, 50 %), although it is representative of other studies (Arujo-Lima et al., 1986; Allan, 1995).

All of the study reaches possessed some BOM, contrary to the predictions of the OM budget in which all reaches generally exporting TOM. Explanations for this include potential error in TOM estimates based on (1) the temporal scale over which measurements were made and natural daily variation in TOM, and (2) sample size (either volume or surface area) and extrapolation of TOM and BOM estimates to the entire river segment. Furthermore, other sources of OM may have entered the study reaches. For example, Newbold et al. (1997) noted

discrepancies in an OM budget that they attributed to unmeasured sources of OM such as from storm transport and overland flow, input from soil-water drainage, lateral inputs of riparian litter, and groundwater inputs. Even so, TOM measurements were collected in the same manner across the four study reaches. Therefore, the comparisons among sites should be robust to potential errors in the estimates of actual TOM concentrations.

Historic organic matter dynamics also are important to consider (Cummins et al., 1983; Minshall et al., 1992; Webster and Meyer, 1997) and it is probable that detrital input in the form of leaf litter and large woody debris would have been substantially higher because of the lateral connectivity and annual inundation of an extensive and complex flood plain in the meander reach. Peak flows which historically occurred on the Kootenai River (1274 to $1841 \text{ m}^3 \text{ s}^{-1}$), would have inundated this flood plain, leading to nutrient exchanges and transformations (Chauvet and Decamps, 1989; Dahm et al., 1998). Such exchange could increase the productivity of both the flood plain and the river system, as well as provide increased refugia and habitat for lotic organisms (Power et al., 1988; Stanford et al., 1996; Baron et al., 2002; Coutant, 2004). This exchange does not occur due to Libby Dam and subsequent flood control, as well as the presence of levees and clearing of the riparian zone downstream from Bonner's Ferry.

This energy budget indicated that macroinvertebrates in the Kootenai River downstream of Libby Dam generally were not limited by primary production and TOM. In other words, macroinvertebrates were not reaching the maximum potential standing crop that would be possible based on autotrophic productivity and TOM. A possible explanation is that longer-lived macroinvertebrates were unable to utilize the relatively short burst of positive production that occurred during the growing season, whereas shorter-lived species, such as the *Chironomidae*, made more efficient use of this ephemeral energy source. It is also possible that macroinvertebrates were habitat

limited, particularly in the meander reaches that are dominated by a substrate of sand and clay. This rationale seems less likely in the canyon and braid, where substrate consists of gravel and large cobble.

At a conversion efficiency of 10%, fish abundance appeared to be limited in all reaches based on average active (ave. MR_a) and maximum active (max. MR_a) metabolic rates. The average active rate represents the energy required by a fish during normal activity, whereas maximum metabolic rate (MR_a) represents a fish during high energy expenditure (e.g. burst swimming). As expected, at minimum standard metabolic rates fish were not food-limited. A realistic conversion efficiency likely is somewhere between 10 and 30%. For example, rainbow trout fed on hatchery food maintained approximately a 30% C.E. (Myrick and Cech, 2000). It is highly likely that in the wild, conditions would not be as optimal. In addition, as with the macroinvertebrates, the fish energy budget utilized optimum conditions of positive NDM and stored TOM and these autotrophic and detrital food resources were rarely contributing energy to higher trophic levels.

Food limitation appears to provide a mechanism for the decline in fish that has occurred over the last three decades, although the assumptions of the energy budget must be recognized. Also, the potential error inherent in hook-and-line sampling for sturgeon and electroshocking for all other species should be considered. Because electroshocking likely underestimated fish population densities (the more likely scenario vs. overestimation), the severity of limitation would actually increase (Peterson et al., 2004). Thus potential sampling error for both macroinvertebrates and fish likely underestimated actual population densities. In addition, fish could be habitat limited. Considering the lack of connection with a flood plain and riparian zone in the meander reach, habitat limitation seems a likely confounding factor. Finally, it is possible that top-down control by predators such as was occurring, the possibility of which could be examined further (e.g., Power et al., 1988; Power, 1992). Examples of potential predators for larval sturgeon include but are not limited to the largescale sucker (*Catostomus macrocheilus*), peamouth (*Mylocheilus caurinus*), northern pikeminnow (*Ptychocheilus oregonensis*) and larger sturgeon (Parsely et al., 2002).

The energy budget suggests that food limitation may be a contributing factor to sturgeon decline, particularly during early life-history stages. Little is known about juvenile sturgeon habitat and food requirements, although Parsely et al. (2002) noted that copepods, Ceratopogonidae larvae and diptera pupae and larvae represent likely food resources. In addition, research on the lower Fraser River indicated that juvenile sturgeon were utilizing slough and large backwater habitats adjacent to the main channel for rearing (Hildebrand et al., 1999). This type of habitat historically would have been abundant in the

Table 9. Fish estimated vs. measured biomass for the study reaches. Potential sustained fish biomass calculated at three metabolic rates from Table 8; average active (ave. MR_a), maximum active (max. MR_a), and minimum standard (MR_s) metabolic rates; 0.061, 0.090, and 0.002 kcal $g^{-1} day^{-1}$, respectively. Values in bold are used in Figure 3. MR = metabolic rate, s = standard, a = active, C.E. = gross conversion efficiency.

LOCATION	Energy prod. by primary producers as NDM (kcal $m^{-2} day^{-1}$)	Energy transported into reach as TOM (kcal $m^{-2} day^{-1}$)	Energy avail. from TOM at 2ndary consumer level (kcal $m^{-2} day^{-1}$)		Energy avail. from NDM at secondary consumer trophic level (kcal $m^{-2} day^{-1}$)		Fish biomass potentially sustained by available energy (NDM + TOM) assuming minimum, maximum and average fish metabolic demand				Measured total biomass (g m^{-2})	
			2% C.E.	10% C.E.	30% C.E.	50% C.E.	10% C.E.	30% C.E.	50% C.E.	10% C.E.		Maximum MR_a (g m^{-2}) 10% C.E.
Canyon	3.28	10.38	0.004	0.033	0.295	0.820	0.61	4.91	13.51	0.41	18.48	5.87
Braid	5.58	55.91	0.022	0.056	0.502	1.395	1.28	8.60	23.24	0.87	39.08	3.23
Meander 1	4.92	34.21	0.014	0.049	0.443	1.230	1.03	7.48	20.39	0.70	31.44	8.09
Meander 2	2.41	276.56	0.111	0.024	0.217	0.603	2.21	5.37	11.69	1.50	67.36	3.71

meander reach of the Kootenai River. The present day disconnection that occurs as a result of levy construction has almost eliminated this type of habitat, with the exception of wildlife refuges near Deep Creek, Idaho, and Creston, British Columbia. Recently, Coutant (2004) proposed that larval and juvenile sturgeon populations throughout Columbia Basin, including the Kootenai River, experience a significant bottleneck caused by severely constrained river/floodplain connectivity.

In summary, metabolism measurements were combined with measurement of macroinvertebrate standing crop (1994–1995) and fish biomass into a simple energy budget. The energy budget was used to assess the possibility of food-limitation as a reason for the declining population of Kootenai River sturgeon (*Acipenser transmontanus*). Metabolism in the Kootenai River was low, and rarely was NDM positive. This suggests that energy produced upstream or from allochthonous sources was important to the food web. Our results suggest food limitation is a possible contributing factor to recent sturgeon decline. Reconnection of the river and floodplain in the extensive meander segment in conjunction with restoring the historical flow regime would likely enhance river productivity and increase habitat heterogeneity (Stanford et al., 1996), which could aid in restoring the viability of the Kootenai River sturgeon.

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