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Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system

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Abstract Ecosystem-wide effects of introduced brown trout (*Salmo trutta* L.) and native river galaxias (*Galaxias eldoni* McDowall) were studied by analysing ecosystem production budgets for two adjacent tributaries of a grassland stream-system in the South Island of New Zealand. One tributary was inhabited by brown trout, the other by river galaxias. No other fish species were present in either stream. The budget for the river galaxias stream indicated little top-down control of invertebrates by fish predation (river galaxias consumed ~18% of available prey production). A large proportion of annual net primary production was required to support production by invertebrates (invertebrates consumed an average of ~75% of available primary production), and mean surplus primary production (i.e. not consumed) was not significantly different from zero. Primary and secondary production were presumably mutually limiting in this system (i.e. controlled by simultaneous top-down and bottom-up mechanisms). In contrast, the budget for the brown trout stream indicated extreme top-down control of invertebrate populations by fish predation; essentially all invertebrate production (~100%) was required to support trout production. Invertebrate production required only a minor portion of annual net primary production (~21%) and primary production was presumably controlled by mechanisms other than grazing (e.g. sloughing, nutrient limitation). Predatory invertebrates had little quantitative effect on prey populations in either stream. Recent experimental studies of invertebrate behaviour, fish behaviour, and food-web structure in New Zealand streams with physically stable channels indicate that a trophic cascade should be observed in streams inhabited by brown trout, in contrast to those inhabited by native fish. The results reported here provide ecosystem-level evidence supporting this prediction.

Key words Predation · Food webs · Trophic cascades · Invertebrates · Fish

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Introduction

Trophic cascades occur when feeding activities by populations at one trophic level have quantitative effects on material and energy flow through non-adjacent trophic levels (Carpenter et al. 1985; Power 1992). Probably the clearest examples of trophic cascades are results of experimental manipulations of aquatic communities that have simple food-chains, rather than complex food-webs (Strong 1992; Polis 1994). There are now a number of examples of trophic cascades from streams. All of these, however, are based on observations among isolated pools or experiments performed using replicated enclosures within single streams (Power et al. 1985; Power 1990; McCormick 1990; Bechara et al. 1992; Wootton and Power 1993; Flecker and Townsend 1994). Trophic cascades have not been documented by studies that explicitly focus on ecosystem-level processes (e.g. energy flow and production) occurring in natural stream systems.

Lack of ecosystem-level evidence for trophic cascades in natural streams may be attributed to the scarcity of systems with the appropriate contrasts needed to demonstrate different feedback regimes among trophic levels (i.e. "natural experiments," *sensu* Diamond 1986). That is, streams with contrasts in trophic structure required to study cascading effects that also occur within geographically uniform regions are rare. The large effort and expense required for such studies are also not trivial impediments. Nevertheless, the lack of evidence at the ecosystem scale may obscure the general importance of trophic cascades in determining differences in basal productivity among stream ecosystems. Although an experimental design incorporating controlled manipulations of ecosystems would clearly be most robust, it seems logical to assume that trophic cascades should also be detectable by comparisons of consumer production and demand within food webs among natural streams offering appropriate contrasts in trophic structure.

The trophic structure of New Zealand stream communities is relatively simple because feeding preferences of primary consumers and predators are extraordinarily generalized and are organized functionally as a strongly hierarchical, three-tiered food chain (Flecker and Townsend 1994; Winterbourn 1995). Such trophic structure is ideally suited for the development of trophic cascades (Power 1992; Polis 1994), as was shown by Flecker and Townsend (1994) in a study of the community-wide effects of the introduction of brown trout (*Salmo trutta* L.) to New Zealand. In their study, which was conducted in replicated enclosures, Flecker and Townsend (1994) experimentally induced a trophic cascade in the presence of brown trout but not in the presence of the native river galaxias (*Galaxias* cf. *vulgaris*). The mechanism in the former case was apparently a consequence of both losses of invertebrates to trout predation, and a reduction in diurnal grazing by primary consumers caused by the presence of trout (Flecker and Townsend 1994; McIntosh and Townsend 1995b, 1996).

The present study uses an observational production-demand approach to investigate the ecosystem-level effects of differences in predation regime, brown trout versus river galaxias, under natural conditions in adjacent tributaries of the Taieri River in the South Island of New Zealand. Flecker and Townsend (1994) and McIntosh and Townsend (1996) have shown experimentally that: (1) brown trout should exert strong top-down control on primary consumers which will result in a cascading effect by enhancing production and biomass accrual of primary producers, and (2) predation by river galaxias and predatory invertebrates should have weak effects on primary consumers, which in turn will exert strong top-down control on primary producers. This prior work has provided a firm base for "ground-truthing" conclusions from the production-demand approach used in the present study. In this paper I assess the ecosystem implications of the experimental results of Flecker and Townsend (1994) and McIntosh and Townsend (1996) by comparing comprehensive production budgets constructed for natural streams with contrasting predation regimes that have been established for at least a century (see Study sites, below). The production budget for the brown trout stream, Sutton Stream, has been previously published (Huryn 1996a). This paper compares results of Huryn (1996a) with a budget prepared for Stony Creek, a river galaxias stream adjacent to Sutton Stream.

Materials and methods

Study sites

Sutton Stream (45°36′S 169°54′E) and Stony Creek (45°35′S 169°54′E) are tributaries of the Taieri River. Both streams are within the greater Sutton Stream catchment which lies between the Lammerlaw and Rock and Pillar mountain ranges in the southeast of the South Island (Fig. 1). The river valleys are incised and rugged with schist bedrock. Vegetation is largely exotic pasture grasses and native tussock grasses that are extensively grazed by livestock. The 400-m study reaches selected at each site have no canopy, although there are native shrubs along the stream margins. The altitude ranges from 600 m above sea level at Sutton Stream to 820 m at Stony Creek. During 1991–1993, mean discharge was 568 ± 26 $l\ s^{-1}$ ($\bar{x} \pm SE$) in Sutton Stream and 461 ± 22 $l\ s^{-1}$ in Stony Creek. Mean concentrations of soluble reactive-phosphorous during this period were essentially equivalent between streams (6 ± 1 and 5 ± 1 $\mu g\ l^{-1}$). Nitrate-nitrogen was also similar (7 ± 1 $\mu g\ l^{-1}$ in Sutton Stream, 8 ± 2 $\mu g\ l^{-1}$ in Stony Creek). Higher nitrate-nitrogen in Stony Creek is attributable to a measurement made on a single date (45 $\mu g\ l^{-1}$, 4 February 1993) and if this is excluded, the mean concentration is reduced to 6 ± 1 $\mu g\ l^{-1}$. Mean daily water temperature ranged from 0.0 to 17.4°C (annual mean = 5.6) in Sutton Stream, and from 0.0 to 16.4°C (annual mean = 6.0) in Stony Creek. Diel fluctuations of water temperature in both streams were as great as 10°C during summer. Stable substrata in Stony Creek and Sutton Stream (bedrock and boulder) cover equivalent areas of channel (62–69% of channel area). Bedrock, however, forms a larger proportion of channel area in Stony Creek (60% vs. 22% in Sutton), whereas boulder covers a larger portion of the channel in Sutton (40% vs. 9% in Stony Creek). Cobble and pebble cover an equivalent area in both streams (31–35%).

The study reach selected for Sutton Stream is inhabited by brown trout. Stony Creek is inhabited by river galaxias (*Galaxias eldoni* McDowall). No other fish species occur in the study reaches. Both species are members of the suborder Salmonoidei (Moyle and Cech 1988) and are predators, feeding primarily upon benthic and terrestrial invertebrates (Huryn 1996a; Edwards and Huryn 1996). Brown trout were probably introduced to the lower reaches of Sutton Stream during the late 19th century (Thomson 1922). Consequently, populations of invertebrate prey and the ecological processes that these populations mediate in the two streams have

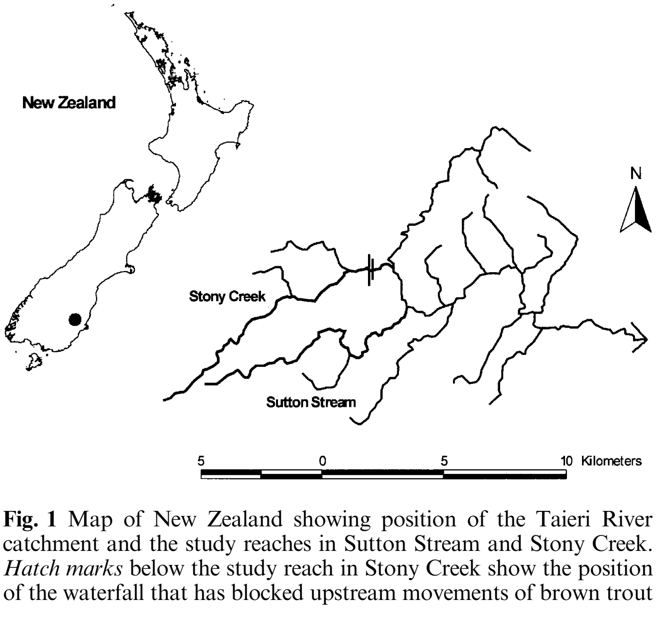

Fig. 1 Map of New Zealand showing position of the Taieri River catchment and the study reaches in Sutton Stream and Stony Creek. *Hatch marks* below the study reach in Stony Creek show the position of the waterfall that has blocked upstream movements of brown trout

been subject to contrasting predation regimes for many decades. A series of cascades and minor waterfalls above the confluence of Stony Creek and the main stem of Sutton Stream apparently block passage of trout into Stony Creek (Fig. 1, cf. Townsend and Crowl 1991).

Methods

Data composing individual compartments for production budgets for each stream were collected simultaneously during November 1991 through December 1993. Compartments include net annual production by primary producers, primary, secondary and top consumers. Ecological efficiencies from the literature were used to estimate food demands for each category of consumers (cf. Benke and Wallace 1980). The significance of differences between compartment statistics was assessed by comparing 95% confidence limits estimated by bootstrapping (Effron and Tibshirani 1993). Compartments for hyporheic invertebrates and inputs by terrestrial invertebrates were included in the comprehensive budget previously constructed for Sutton Stream (Huryn 1996a). The budget constructed for Stony Creek does not include hyporheic and terrestrial compartments. As will be seen below, however, differences between the budgets for the two streams are of such magnitude that inclusion of compartments for hyporheic and terrestrial invertebrates does not affect conclusions.

Primary production

Primary production was measured as ^{14}C uptake by substrata placed in submersed 17-l recirculating chambers. Samples, sized to ~9 cm^2 with a mallet and chisel, were taken from 12 random locations on eight dates between December 1992–December 1993. Incubation commenced around 01300 hours with the injection of 7 ml ^{14}C-NaHCO$_3$ (185 MBq ml^{-1}) into each of three chambers (4 samples chamber^{-1}). After ~2 h, samples were removed, rinsed with acidified stream water (Mulholland et al. 1986), and placed in 50 ml dimethyl sulfoxide to extract ^{14}C-labeled photosynthate (Filbin and Hough 1984). Following extraction, two 1-ml subsamples were taken from each extract, added to 10 ml Phase Combining System (American Chemicals) in 20-ml scintillation vials and assayed with a liquid scintillation analyser. Chlorophyll *a* was measured for subsamples of the remaining extract following Shoaf and Lium (1976). The ratio of total available inorganic carbon to available ^{14}C was used to convert dpm cm^{-2} h^{-1} to mg C fixed cm^{-2} h^{-1} (Wetzel and Likens 1979). During each incubation, concentration of ambient ^{14}C was monitored following Iverson et al. (1976). Sample areas were estimated by covering surfaces with aluminum foil and determining foil area from its density. Annual net production (mg C m^{-2}) was estimated as the product of the average production between sampling intervals, the number of hours of available daylight (excluding twilight hours), and a correction of −10% for night-time respiration (Mitchell 1989).

Benthic macroinvertebrates

Sixteen benthic samples were taken on each of 11 dates between November 1991 and December 1992 using a 900-cm^2 Surber sampler fitted with a 230-μm net. Sample locations were assigned by randomly selecting coordinates that corresponded with locations on the stream channel. In areas of unconsolidated substrata, the stream bed was sampled to a depth of ~10 cm. Over bedrock substrata, a roll of terry cloth was attached to the Surber sampler frame to seal the sampler against the stream bottom. Samples were preserved in 6–8% formalin and stained with phloxine B. Animals were removed from the samples by hand under 15 × magnification, identified to the lowest practical taxonomic level (cf. Winterbourn and Gregson 1989) and their lengths measured (± 0.5 mm).

Annual production was calculated using the size-frequency method (Benke 1984, 1993), and corrected for the cohort production interval (CPI) following Benke (1979). A number of empirical studies have shown that the size-frequency method yields estimates of production that are similar to other methods providing that raw results are corrected by the CPI. For example, an analysis of 101 studies where results of the size-frequency method were compared with other methods (Benke 1993) indicated that in 43 cases the differences between methods was < 10% and in 80 cases they were < 30%. On basis of this comparison, Benke (1993) concluded that differences in production estimates derived by different methods are usually minor. In the present study, CPIs for most taxa were determined from length-frequency histograms constructed for each sample date. *Deleatidium* (Ephemeroptera: Leptophlebiidae), *Olinga* (Trichoptera: Conoesucidae), and *Potamopyrgus* (Prosobranchia: Hydrobiidae), however, were expected to be characterized by numerous overlapping cohorts (e.g. Collier and Winterbourn 1990; Huryn 1996b; personal observation). For these taxa, CPIs were modeled using temperature, density, and size-specific growth data derived from experimental growth chambers following Huryn (1996b). The CPI for oligochaetes was assumed to range from 365 to 730 days (Brinkhurst and Cook 1979). CPIs were also used as an index for comparing life-history traits of invertebrates between streams. Abundances were corrected for unequal sampling intervals following Krueger and Martin (1980). Ash free dry mass (AFDM) was estimated using regressions ($P < 0.05$) of ln-transformed AFDM on ln-transformed body-length. Additional detail is provided by Huryn (1996a,b).

Fish

Fish were sampled by electric fishing on two dates during both November 1991 and November 1992. Study reaches were divided into subsections (~30 m) using stop nets to facilitate sampling. On the first date of each November sampling period, fish captured during a single pass were anaesthetized, measured for length (mm) and wet weight (to 0.1 g), and marked by either removing the adipose fin (brown trout) or by injecting an aqueous solution of alcian blue subcutaneously (brown trout and river galaxias; Kelly 1967). Fish were resampled ~2 weeks later. Abundance and biomass estimates were made using the mark-recapture module provided by Pop/Pro (Kwak 1992). The assumptions and algorithms used by Pop/Pro to estimate abundance, production and the variance of these parameters are based on standard methods and explicit formulae that are available in the literature (Ricker 1975; Bagenal 1978; Newman and Martin 1983; Kwak 1992). On each date, ages of fish from representative length classes were determined using sectioned otoliths (Hall 1991). The credibility of age estimates was assessed by observing marked fish and from changes in annual length-frequency plots over a 4-year period (1991–1995). Biomass of individual fish was estimated using regressions of AFDM against length. On each date, a subsample of specimens representing the available size range were dried to constant mass at 60°C, and ashed at 500°C for a minimum of 4 h to yield AFDM as the difference between dry mass and ash mass. Fish abundance, biomass, and annual production (mg AFDM m^{-2} + 95% CI) were estimated using the instantaneous growth module provided by Pop/Pro (Kwak 1992).

Budget

Food demand by consumers was estimated as the reciprocal of gross production efficiency (GPE) times production, where GPE is the product of assimilation efficiency (AE) and net production efficiency (NPE). Food demand was estimated for each of three trophic categories: primary consumers (macroinvertebrates that browse biofilms), secondary consumers (predatory macroinvertebrates), and top consumers (fish).Ecological efficiencies were obtained from the literature. A summary of the sources and values of ecological efficiencies can be found in Huryn (1996a). Ecological efficiencies reported for brown trout were also used for the river galaxias because such information is not available for the latter species. Differences in the budgets for the two streams, however, were of such magnitude that large departures in efficiencies between fish species would be required to affect conclusions.

Approximate 95% confidence intervals were calculated for budget statistics by bootstrapping, a nonparametric resampling technique (Effron and Tibshirani 1993). Bootstrapping is used to estimate the uncertainty of variables with unknown or complex frequency distributions and where logistical constraints do not allow sufficient replication (e.g. production studies, Morin et al. 1987). Every data set was bootstrapped by randomly resampling with replacement, until 1000 data sets were produced. These recombined data sets were used to produce vectors of 1000 estimates for each parameter (production, P, biomass, B, P/B, abundance, consumer food demand). In other words, the entire study was reproduced 1000 times, using randomized data, to produce vectors containing 1000 estimates of each production parameter. For each vector a mean and approximate 95% confidence interval (CI_b) was calculated using the bias-corrected percentile method (Meyer et al. 1986).At minimum this procedure provides an estimate of the uncertainty inherent in a particular data set and the methods used to describe a given parameter. However, if the data are unbiased and the sampling design provides sufficient coverage, bootstrapping will provide an accurate estimate of the true probability distribution underlying that parameter (Effron and Tibshirani 1993). Additional details about bootstrapping in general, and specific procedures used in the present study are given in Huryn (1996a).

Results

Net primary production

Net primary production in Stony Creek ranged from 1.3 ± 0.3 mg C m^{-2} h^{-1} ($\bar{x} \pm 95\%\ CI_b$) measured in July (austral winter) to 12.2 ± 2.7 mg C m^{-2} h^{-1} measured in February (austral summer, Fig. 2). Annual primary production was 25.1 ± 3.5 g C m^{-2}. Mass as carbon was converted to AFDM using a factor of 2 × (= 50.1 g AFDM m^{-2} $year^{-1}$, Fig. 2 and 3) following McCullough et al. (1979). During the same period, net primary-production in Sutton Stream was approximately 6-fold higher (310 ± 74 g m^{-2} $year^{-1}$, Fig. 3; Huryn 1996a). Seasonal patterns of production in both streams, however, were similar (Fig. 2). Average mass of chlorophyll *a* was approximately 5-fold higher in Sutton Stream (25.4 ± 3.8 mg m^{-2}; $\bar{x} \pm SE$) than in Stony Creek (5.6 + 0.5 mg m^{-2}; Fig. 2).

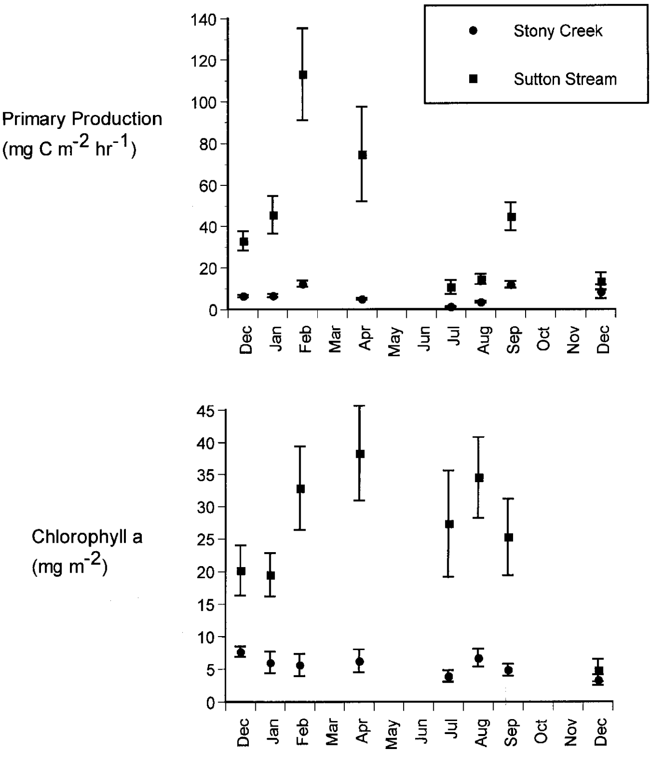

Fig. 2 *Upper panel*: mean net-primary production measured semi-monthly in Stony Creek and Sutton Stream. *Lower panel*: Mean chlorophyll *a*. Note that January and February represent the austral summer, whereas July and August represent the winter. *Error bars* are ± 1 SE

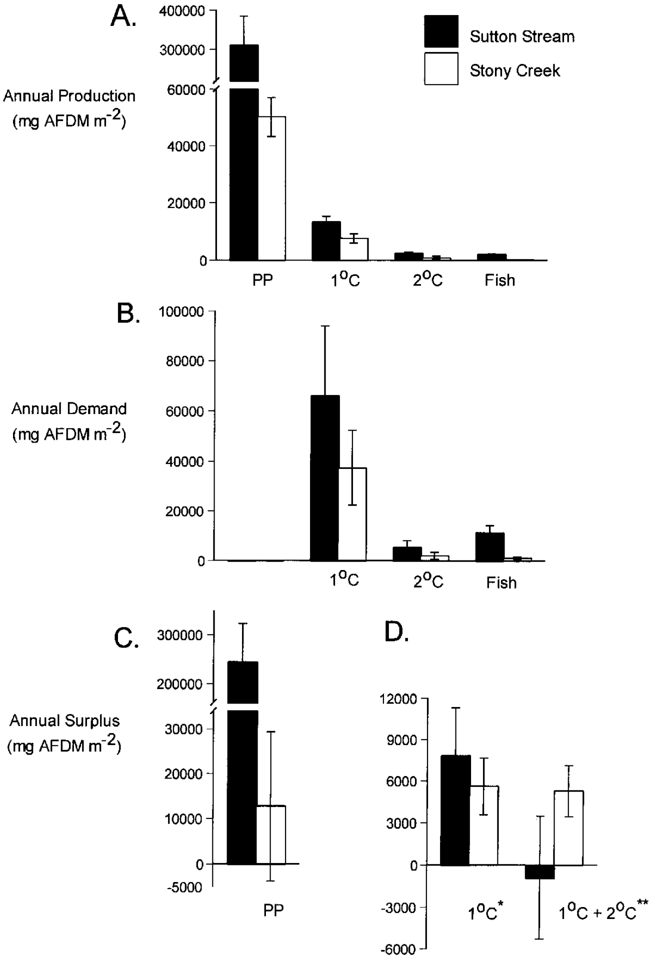

Fig. 3 **A** Annual production measured for primary producers (*PP*), primary consumers (1°C, invertebrates), secondary consumers (2°C, invertebrates) and fish (top consumers) in Sutton Stream and Stony Creek. Note the break in the y-axis. **B** Annual food demand estimated for primary and secondary consumers, and fish. **C** Expected annual surplus of net primary production. Note break in *y*-axis. **D** Expected annual surplus of primary consumer production (1°C) following predation by secondary consumers (predatory invertebrates), and annual surplus of total invertebrate production (1°C + 2°C) following predation by fish. All units are mg AFDM m^{-2} $year^{-1}$; error bars are 95% bootstrap confidence intervals. *Surplus 1°C production after satisfying consumption demands from predacious invertebrates. **Surplus production by all invertebrates after satisfying consumption demands from predacious invertebrates and fish (includes production by predacious invertebrates)

Table 1. Summary of production data for primary consumers from substrata < 10 cm below the bed of Stony Creek and Sutton Stream. Data for all taxa are given for Stony Creek. Data only for the 10 taxa with highest production and total production are given for Sutton Stream (following Huryn 1996a) [*N* abundance (ind. m^{-2}), *B* biomass (AFDM, mg m^{-2}), *P* production (AFDM, mg m^{-2} $year^{-1}$). N, B, P given + 95% CI_b CPI_{min} and CPI_{max} apparent minimum (maximum) cohort production intervals (d). *D* Diptera; *E* Ephemeroptera; *T* Trichoptera; *PL* Plecoptera; *g* prosobranch gastropod, *C* Coleoptera]. Taxa arranged in order of decreasing production

Stony Creek	N	B	P	CPI_{min}	CPI_{max}
Potamopyrgus (G)	5974 (2433)	1126 (752)	2699 (1350)	365	730
Deleatidium myzobranchia-grp (E)	119 (34)	60 (45)	732 (419)	91	211
Oligochaeta	1908 (455)	60 (45)	684 (320)	365	730
Deleatidium lillii-grp (E)	785 (175)	52 (42)	546 (544)	90	330
Coloburiscus (E)	356 (112)	160 (91)	418 (156)	667	700
Pycnocentrodes (T)	461 (112)	62 (47)	400 (150)	274	459
Austrosimulium (D)	269 (67)	28 (18)	307 (268)	64	211
Aphrophila (D)	116 (30)	38 (21)	238 (98)	238	329
Zelandoperla (PL)	92 (27)	76 (50)	224 (75)	636	639
Helicopsyche (T)	295 (69)	40 (30)	194 (53)	335	395
Orthocladiinae "a" (D)	695 (161)	11 (9)	164 (119)	30	208
Neocupurira (D)	38 (14)	22 (13)	147 (62)	208	329
Elmidae (C)	132 (55)	62 (31)	146 (91)	365	759
Olinga (T)	101 (36)	28 (18)	120 (67)	332	697
Pycnocentria (T)	84 (26)	29 (19)	117 (46)	302	428
Hudsonema (T)[a]	208 (92)	19 (12)	87 (53)	329	730
Aoteapsyche (T)[a]	18 (6)	12 (7)	67 (27)	335	365
Zelandobius (PL)	26 (12)	13 (7)	61 (37)	144	293
Maoridiamesa (D)	43 (24)	5 (3)	55 (23)	152	182
Scirtidae (C)	23 (13)	8 (1)	54 (39)	213	302
Miscellaneous	404 (156)	8 (6)	40 (12)	365	365
Nesamaletus (E)	16 (6)	9 (6)	39 (13)	304	395
cf. *Cricotopus* (D)	93 (40)	4 (2)	36 (21)	91	304
Austroperla (PL)	12 (6)	12 (5)	30 (19)	547	678
Eukiefferiella (D)	85 (28)	2 (2)	16 (10)	91	232
Austroclima (E)	8 (5)	2 (1)	11 (9)	185	431
Tanytarsini (D)	31 (16)	1 (< 1)	10 (5)	89	91
Orthocladiinae (D)	27 (12)	< 1 (< 1)	5 (3)	93	182
Chironomini (D)	15 (9)	1 (< 1)	2 (1)	304	365
Total	12434 (2466)	1951 (383)	7647 (1603)	P:B = 3.90 (0.77)	
Sutton Stream	**N**	**B**	**P**	**CPI_{min}**	**CPI_{max}**
Maoridiamesa (D)	1387 (247)	282 (47)	2811 (807)	74	214
Deleatidium lillii-grp (E)	1197 (310)	109 (27)	1855 (1514)	107	273
Olinga (T)	782 (192)	318 (63)	1002 (215)	638	758
Austrosimulium (D)	564 (117)	67 (14)	1082 (694)	51	273
Zelandoperla (PL)	343 (147)	105 (46)	943 (881)	90	289
Helicopsyche (T)	658 (132)	135 (27)	833 (378)	214	424
Aoteapsyche (T)[a]	198 (89)	106 (56)	742 (490)	214	427
Orthocladiinae "a" (D)	2337 (265)	41 (4)	582 (306)	66	182
Potamopyrgus (G)	1528 (381)	182 (43)	537 (250)	365	730
Aphrophila (D)	422 (90)	77 (16)	418 (171)	166	334
Total[b]	15199 (1770)	1629 (146)	11209 (2294)	P:B = 6.88 (1.27)	

[a] Omnivores, N, B, P weighted by 60% (see text)

[b] Hyporheic production in Sutton Stream contributed an additional 2144 mg m^{-2} $year^{-1}$ (Huryn 1996a)

Primary consumers

Production by primary consumers in Stony Creek was 7648 ± 1603 mg AFDM m^{-2} $year^{-1}$ $(\bar{x} \pm CI_b)$ and the P/B was 3.9 ± 0.8. The major contributor was the prosobranch snail *Potamopyrgus* (2699 ± 1350 mg AFDM m^{-2} $year^{-1}$). The mayflies *Deleatidium* and *Coloburiscus*, and the oligochaetes collectively contributed a further 31%. With the exception of *Deleatidium*, which has generation times as short as 90 days at the study sites (Huryn 1996b), all these taxa either have (*Coloburiscus*, *Potamopyrgus*), or were assumed to have (Oligochaeta, Brinkhurst and Cook 1979), slow growth rates and long life cycles (~1–2 years) compared to other community members (see CPIs given in Table 1). This resulted in a relatively low community P/B. Production by primary consumers in Sutton Stream (exclusive of the hyporheic zone) was 11209 ± 2294 mg AFDM m^{-2} $year^{-1}$ and the P/B was 6.9 ± 1.3 (Huryn 1996a). The major contributors, the chironomids (35% of total;

Table 1), had multi-voltine life cycles and rapid turnover rates compared to other primary consumers. This life cycle attribute resulted in rapid turnover rates and a relatively high P/B in Sutton Stream (6.9) compared to Stony Creek (3.9). Although average production by primary consumers was higher in Sutton Stream compared to Stony Creek, confidence intervals overlap, indicating that the difference is not significant.

Secondary consumers

Total production by secondary consumers in Stony Creek was 856 ± 551 mg AFDM m^{-2} $year^{-1}$ ($\bar{x} \pm CI_b$) and the P/B was 3.8 ± 0.9 (Table 2). The major contributor was *Archechauliodes* (65%). *Hudsonema*, *Aoteapsyche* and the Hydrobiosidae contributed an additional 31% (Table 2). Because they are omnivorous, production by *Aoteapsyche* and *Hudsonema* was divided between primary consumers (40%) and secondary consumers (60%; Hopkins 1976; Benke and Wallace 1980; Huryn 1996a). The low collective P/B is attributable to the long life cycle and low growth rate of *Archechauliodes*. Production by secondary consumers in Sutton Stream (exclusive of the hyporheic zone) was 2144 ± 774 mg AFDM m^{-2} $year^{-1}$ and the P/B was 4.1 ± 1.1 (Huryn 1996a). Major contributors were *Aoteapsyche* (52%) and *Archechauliodes* (33%, Table 2). Although average production by secondary consumers was higher in Sutton Stream compared to Stony Creek, confidence intervals overlap indicating that the difference is not significant.

Top consumers

During November 1991 to November 1992, production by river galaxias was 240 ± 96 mg AFDM m^{-2} $year^{-1}$ ($\bar{x} \pm 95\%$ CI) with a P/B of 0.8 ± 0.4. Mean biomass of river galaxias was 311 ± 121 mg m^{-2} with an abundance of 1.2 ± 0.4 fish m^{-2}. Production by brown trout in Sutton Stream during the same period was 2069 ± 114 mg m^{-2} $year^{-1}$ with a P/B of 1.0 ± 0.2 (Huryn 1996a). Mean biomass of brown trout was 2161 ± 248 mg m^{-2} with an abundance of 0.7 ± 0.1 fish m^{-2} (Huryn 1996a). A comparison of approximate 95% confidence intervals indicates that fish production and biomass was significantly greater in Sutton Stream compared to Stony Creek. P/B ratios, however, were not significantly different and were close to 1.0 showing that fish biomass was generally equivalent to annual production in both streams.

Budget

Mean values of assimilation and net production efficiencies used to estimate food demand by primary consumers were 42 ± 9 and 46 ± 10% ($\bar{x} \pm 95\%\ CI_b$; see Table 1 in Huryn 1996a). Based on these efficiencies, food demand by primary consumers in Stony Creek was 37.3 ± 15.0 g AFDM m^{-2} $year^{-1}$ (Fig. 3), and surplus primary production was 12.8 ± 16.5 g AFDM m^{-2} $year^{-1}$ (~25% of total). Surplus primary production in Sutton Stream was 244 ± 79 g AFDM m^{-2} $year^{-1}$ (~79% of total; Huryn 1996a). Note that the 95% CI_b show that surplus primary production in Sutton Stream was significantly greater than zero, whereas the 95% CI_b calculated for Stony Creek includes zero. Surplus primary production in Stony Creek was also not significantly higher than consumer demands (Fig. 3). In summary, essentially all annual primary production was required to support primary consumer production in Stony Creek, whereas only ~21% of annual primary production was required to support primary consumer production in Sutton Stream.

Total consumer production estimated for the Sutton Stream budget also included the hyporheic zone (~16% of total primary consumer production, Huryn 1996a). The contrast in surplus primary production observed between the two streams would therefore be even greater if hyporheic production had been included in the Stony Creek budget. Although secondary production of invertebrates was measured during November 1991–December 1992 and primary production was measured during December 1992–December 1993, conclusions based on the budget are assumed to be valid because: (1) throughout both 1991–1992 and 1992–1993 native and introduced substrata in Sutton Stream were rapidly overgrown by periphyton, whereas surfaces of substrata in Stony Creek remained clear (Huryn 1996b), and (2) fish production measured in Sutton Stream [2069 ± 114 versus 2187 ± 213 mg AFDM m^{-2} ($\bar{x} \pm 95\%$ CI) during 1992 and 1993, respectively; Edwards and Huryn 1995; Huryn 1996a] and Stony Creek (240 ± 96 versus 181 ± 60 mg AFDM m^{-2} during 1992 and 1993, respectively; A.D. Huryn, unpublished work) was similar during both years which indicates that minimum levels of prey production were also similar.

Mean values of assimilation and net production efficiencies used to estimate food demand by secondary consumers were 85 ± 3 and 52 ± 9% ($\bar{x} \pm 95\%\ CI_b$; see Table 1 in Huryn 1996a). Food demand by secondary consumers in Stony Creek was estimated to be 2049 ± 1414 mg AFDM m^{-2} $year^{-1}$ and surplus production by primary consumers was 5598 ± 2057 mg AFDM m^{-2} $year^{-1}$ (Fig. 3). Surplus production by primary consumers in Sutton Stream was 7816 ± 3484 mg AFDM m^{-2} $year^{-1}$. The 95% CI_b show that surplus primary consumer production is significantly higher than secondary consumer demands in both Stony Creek and Sutton Stream (Fig. 3).

Using a gross production efficiency of 18 ± 4%, as reported in the literature for brown trout ($\bar{x} \pm 95\%\ CI_b$; see Table 1 in Huryn 1996a), food demand by river galaxias was estimated to be 1192 ± 473 mg AFDM

Table 2 Summary of production data for secondary consumers from substrata < 10 cm below the bed of Stony Creek and Sutton Stream. Data for all taxa are given for Stony Creek. Data for only the 5 taxa with highest production and total production are given for Sutton Stream (following Huryn 1996a) [*N* abundance (ind. m^{-2}), *B* biomass (AFDM, mg m^{-2}), *P* production (AFDM, mg m^{-2} year^{-1}) N, B, P given + 95% CI$_{bi}$. *CPI*$_{\text{min}}$ and *CPI*$_{\text{max}}$ apparent minimum (maximum) cohort production intervals (days). *D* Diptera, *M* Megaloptera, *T* Trichoptera, *PL* Plecoptera]. Taxa arranged in order of decreasing production

Stony Creek	N	B	P	CPI$_{\text{min}}$	CPI$_{\text{max}}$
Archechauliodes (M)	9 (5)	148 (126)	148 (126)	672	1038
Hudsonema (T)[a]	312 (138)	28 (10)	28 (10)	329	730
Aoteapsyche (T)[a]	27 (9)	19 (9)	19 (9)	335	365
Hydrobiosis (T)	27 (13)	12 (6)	12 (6)	428	824
Psilochorema (T)	88 (22)	11 (2)	11 (2)	301	484
Limnophora (D)	4 (3)	4 (3)	4 (3)	304	431
Tiphobiosis (T)	7 (6)	1 (1)	1 (1)	133	265
Polyplectropus (T)	5 (4)	1 (1)	1 (1)	365	428
Turbellaria	23 (9)	1 (< 1)	1 (< 1)	330	365
Ceratopogonidae (D)	4 (3)	1 (1)	1 (1)	330	365
Megaleptoperla (PL)	2 (1)	1 (< 1)	1 (< 1)	180	238
Empididae (D)	9 (5)	1 (< 1)	1 (< 1)	94	365
Tanypodinae (D)	4 (3)	< 1 (< 1)	< 1 (< 1)	330	365
Total	523 (142)	228 (128)	856 (551)	P:B = 3.77 (0.86)	
Sutton Stream	N	B	P	CPI$_{\text{min}}$	CPI$_{\text{max}}$
Aoteapsyche (T)[a]	296 (135)	158 (87)	1113 (736)	214	427
Archechauliodes (M)	86 (21)	281 (57)	698 (204)	668	1034
Hydrobiosis (T)	97 (22)	24 (7)	73 (22)	608	806
Tanypodinae (D)	99 (46)	19 (14)	60 (38)	244	393
Psilochorema (T)	50 (15)	7 (2)	55 (33)	138	320
Total[b]	409 (59)	532 (105)	2144 (774)	P:B = 4.12 (0.93)	

[a] Omnivores, N, B, P weighted by 60% (see text)

[b] Hyporheic production in Sutton Stream contributed an additional 392 mg m^{-2} year^{-1} (Huryn 1996a)

m^{-2} year^{-1} ($\bar{x} \pm 95\%$ CI$_{\text{b}}$, Fig. 3). Assuming that river galaxias feed entirely on benthic macroinvertebrates (= primary consumer production remaining following predation by secondary consumers + secondary consumer production), surplus benthic macroinvertebrate production was estimated to be 5263 ± 1851 mg AFDM m^{-2} year^{-1}, with an ecotrophic coefficient of 18% (ecotrophic coefficient = proportion of total benthic macroinvertebrate production consumed). Since hyporheic invertebrates were not included in the budget, and river galaxias in Stony Creek feed on terrestrial as well as benthic invertebrates (Edwards and Huryn 1996), this ecotrophic coefficient should be considered conservative. Assuming that the brown trout in Sutton Stream feed entirely upon benthic macroinvertebrates, surplus benthic prey production (surficial + hyporheic) was −930 ± 4370 mg AFDM m^{-2} year^{-1} (Huryn 1996a), with an ecotrophic coefficient of > 100%. If all other prey sources were considered (e.g. terrestrial invertebrates, cannibalism) a deficit was still apparent (−37 ± 4367 mg AFDM m^{-2} year^{-1}, Huryn 1996a). Inspection of confidence intervals shows that surplus invertebrate production in Stony Creek is significantly greater than zero, whereas surplus invertebrate production in Sutton Stream is not significantly different from zero (Fig. 3). In summary, only 18% of available benthic macroinvertebrate production in Stony Creek was required to support river galaxias production in Stony Creek, whereas essentially all available prey production (including hyporheic and terrestrial invertebrates) was required to support trout production in Sutton Stream.

Discussion

Essentially all invertebrate production was consumed by trout in Sutton Stream (Huryn 1996a). This strong control of grazing invertebrates by predation apparently resulted in a trophic cascade that was manifested by the accrual of periphyton in Sutton Stream compared to Stony Creek. Presumably periphyton biomass and production in Sutton Stream was ultimately controlled by non-consumptive processes (e.g. nutrient limitation, sloughing). In striking contrast to Sutton Stream, predation by river galaxias in Stony Creek removed a relatively small proportion of invertebrate production, and grazing intensity by invertebrates in Stony Creek was clearly sufficient to have a strong quantitative effect on their food. Compared to Sutton Stream, where only ~21% of net primary production was consumed by invertebrates, essentially all primary production in Stony Creek was consumed.

These conclusions follow those of Flecker and Townsend (1994), who conducted an experimental study of trout and river galaxias food-web structure in the nearby Shag River catchment. Flecker and Townsend (1994) used fish abundances based on Sutton Stream (A.S. Flecker, personal communication) and replicated enclosures to show that over a period of 10 days the presence of trout was associated with a $\sim$2-fold reduction in macroinvertebrate biomass and a 2-fold increase in periphyton biomass compared to the presence of river galaxias. Indeed, the experiment by Flecker and Townsend (1994) formed the basis for the hypothesis that differences in ecosystem productivity between Sutton Stream and Stony Creek resulted from differences in predation regime.

Despite dramatic differences in levels of primary production, levels of secondary production of primary consumers in Sutton Stream and Stony Creek were roughly similar [cf. $\mathrm{CI_b}$; Sutton Stream 11209 ± 2294 and Stony Creek 7648 ± 1603 mg AFDM m^{-2} year^{-1} ($\bar{x} \pm \mathrm{CI_b}$)]. Given the similarity of trophic demands by primary consumers in the two streams, it seems remarkable that production by periphyton in Sutton Stream apparently escaped grazer regulation (e.g. Hansson 1992), whereas production by periphyton in Stony Creek was reduced to low levels. The most direct explanation is that invertebrate production and resource demand in Sutton Stream is limited by trout predation. As a result, production by primary producers and grazers has become uncoupled (e.g. Mittelbach et al. 1988). In Stony Creek, however, production by primary producers and their grazers appears to be closely coupled. Production by periphyton approximated the estimate for consumption by grazers in Stony Creek which resulted in low levels of periphyton biomass (as chlorophyll *a*, Fig. 2). Since primary production is largely a function of biomass (providing that light and nutrient levels are sufficient), periphyton production will be low when subject to heavy grazing regimes (Lamberti and Resh 1983). Assuming that primary production in Stony Creek was controlled by grazing, production by periphyton and its grazers may be regulated by a "duality of top-down and bottom-up processes (Power 1992)." In other words, production by primary producers in Stony Creek may be limited by the continuous removal (top-down) of biomass and chlorophyll required for maintaining high rates of primary production, whereas production by primary consumers may be limited by low levels of primary production imposed by their feeding activities (bottom-up) – a relationship that may have become uncoupled under the heavy predation regime caused by the historical introduction of brown trout to Sutton Stream. It should be noted, however, that detritus produced by grazers in Stony Creek probably also contributed to the pool of food available for primary consumers, in which case food limitation may have been more apparent than real (e.g. Strayer 1988).

After considering the results of the production budgets, it became clear that similar conclusions about the trophic dynamics of the two systems would be reached by the analysis of biomass alone. Differences in patterns of biomass among trophic levels at Sutton Stream and Stony Creek most clearly mimicked the 3 trophic-level version of the pure top-down model of Fretwell (1977), as interpreted by Power (1992 – see Power's Fig. 4). Power's interpretation of Fretwell's model (Power 1992) predicts that: (1) predator biomass will increase along a gradient of increasing system productivity [e.g. Stony Creek – low system productivity, low fish biomass (311 mg AFDM m^{-2}), Sutton Stream – high system

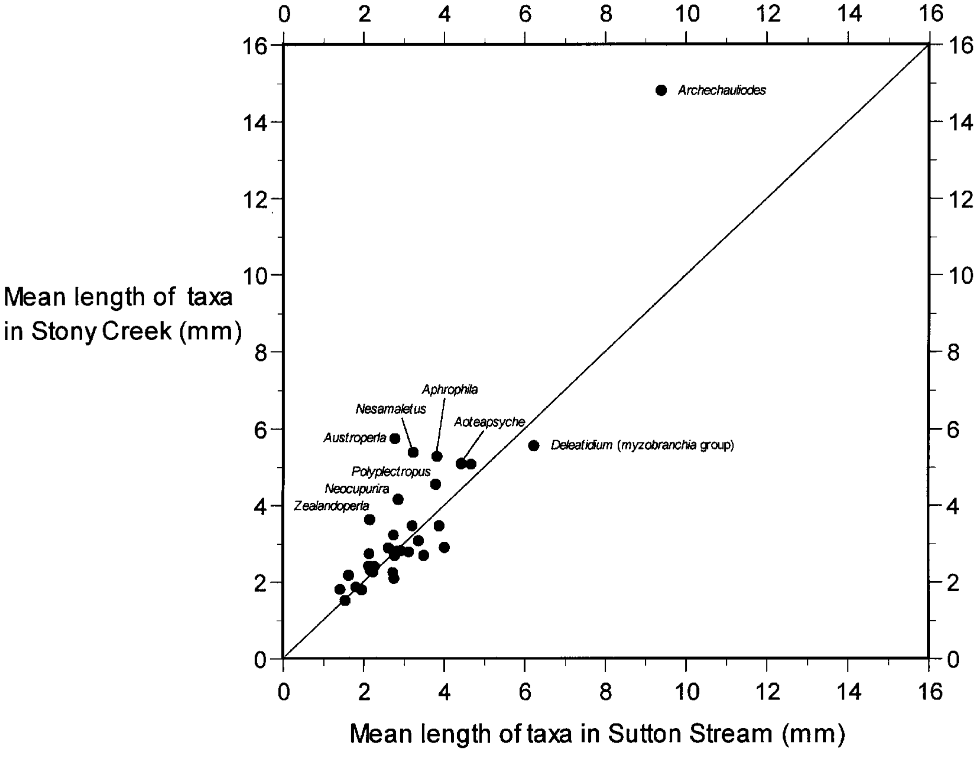

Fig. 4 Comparison of mean length of invertebrate taxa that occur in both Sutton Stream and Stony Creek. The *diagonal line* indicates position of points expected if lengths were identical among streams. Note that departures are almost invariably toward larger sizes in Stony Creek (low predation pressure) compared to Sutton Stream (heavy predation pressure). Taxa that show greatest departures are identified. *Archechauliodes*, *Aphrophila*, and *Zealandoperla* are heavily used by trout in Sutton Stream (Huryn 1996a). Although uncommon in Sutton Stream, trout are expected to be effective predators of *Nesamaletus* and *Polyplectropus* (McIntosh and Townsend 1994; cf. Townsend and Hildrew 1988, and personal observation). The only departure from the general pattern is *Deleatidium* (*myzobranchia* group). Larvae of these mayflies live in torrential habitats (personal observation) which may provide a refuge against heavy predation pressure

productivity, high fish biomass (2161 mg AFDM m^{-2})]; (2) primary consumer biomass will decrease along this productivity gradient because of increasing top-down control by predators [Stony Creek – higher grazer biomass (1951 mg AFDM m^{-2}), Sutton Stream – lower grazer biomass (1629 mg AFDM m^{-2})]; and (3) in highly productive systems, predator biomass will exceed prey biomass (e.g., fish biomass: total benthic prey-biomass in Stony Creek was 0.14; in Sutton Stream this ratio was 1.00). Finally, Fretwell's model predicts that biomass of primary producers will accumulate in highly productive systems as a consequence of strong top-down control of primary consumers by predation, and this is precisely what was observed – biomass of chlorophyll *a* in Sutton Stream was 25 mg m^{-2}, whereas in Stony Creek it was 6 mg m^{-2}.

It is important to remember, however, that patterns of biomass among trophic levels are the consequence of production-demand relationships and that current models of trophic dynamics essentially use the variable "biomass" as a surrogate for "production." With this in mind, it also must be realized that differences in the production dynamics within a given trophic level may underlie fundamental differences in trophic dynamics among streams that are overlooked when biomass alone is considered. Qualitative differences in community structure, for example, had large consequences for the relative production dynamics of invertebrates between Sutton Stream and Stony Creek. Of the ten top primary consumers in Stony Creek, four had life cycles that took ≥ 12 months to complete; two had life cycles lasting ≤ 6 months (Tables 1 and 2). Of the ten top primary consumers in Sutton Stream, only two had life cycles that took ≥ 12 months to complete; four had life cycles lasting ≤ 6 months. Because of such differences, invertebrate biomass in Sutton Stream was more dynamic than biomass in Stony Creek, and provided substantially more prey biomass (as production) to higher trophic levels, even though mean standing-stock biomass was similar between streams.

Along with strong contrasts in production dynamics among invertebrates, there were also differences in size structure. Average individual size was generally larger in Stony Creek. Of taxa common to both streams, for example, seven had average lengths larger than 5 mm in Stony Creek, compared to only two in Sutton Stream (Fig. 4). These community and population characteristics are consistent with those predicted for communities of benthic invertebrates exposed to radically different predation regimes. Size selective predation by trout with a bias toward large prey is well documented (Allan 1978), and a shift in size distribution to smaller individuals under intensive predation regimes has been reported for benthic invertebrates in lotic habitats (Peckarsky 1984; Johnson et al. 1992). Since invertebrate size is positively correlated with life span at the study sites ($r = 0.48$, $P < 0.01$), a selection for smaller taxa as a result of a heavy predation regime should also result in overall higher P/B ratios as observed in Sutton Stream. The relatively small size and short life-cycles of the invertebrates of Sutton Stream allows prey populations to maintain relatively high levels of production even given the extreme predation pressure exerted by brown trout.

Although these community- and population-level differences among streams are consistent with the premise of top-down control in Sutton Stream and bottom-up control in Stony Creek, other factors may be at play. For example, larvae of the Chironomidae collectively contributed ~35% of production in Sutton Stream, compared to ~4% in Stony Creek. High levels of periphyton biomass in Sutton Stream undoubtedly contributed to high numbers of chironomids which burrowed within mats of periphyton that covered the substrata. In this case, top-down control of less cryptic grazers may have mediated the development of a thick algal turf that provided exceptional habitat for chironomids in Sutton Stream compared to Stony Creek. High levels of chironomid production in Sutton Stream may therefore be an indirect consequence of predation by brown trout.

It is important that these strong contrasts in trophic and community structure do not obscure the fact that Stony Creek and Sutton Stream differ most fundamentally on an ecosystem scale. Annual net primary production in Sutton Stream was 6-fold greater than primary production in Stony Creek. It is this profound difference in energy base, and the potential role that community-scale processes may have played in producing such a difference, that is probably of most general significance. Regardless of the factors ultimately controlling biomass accrual, it is apparent that ~79% of the net primary production in Sutton Stream will be transported to downstream reaches as non-consumptive loss. On the other hand, transport of periphyton-derived organic matter from Stony Creek in forms other than fecal pellets is expected to be relatively minor. Non-consumptive loss of periphyton from streams such as Sutton Stream may be important subsidies to heterotrophic reaches of the Taieri River downstream (Young and Huryn 1996). The potential far-reaching ecosystem effects associated with differences in predation regime among tributaries of a given drainage deserve further study.

The introduction of predatory fish to naive ecosystems has elsewhere been shown to enhance ecosystem-level productivity of lakes as a result of cascading trophic interactions (e.g. Kaufman 1992; Goldschmidt et al. 1993). The comparative study of ecosystem characteristics of the streams used in the present study, however, does not provide a definitive statement regarding the effect of the introduction of trout on New Zealand streams. Although the ecosystem-level characteristics of Sutton Stream and Stony Creek support predictions about differences in trophic dynamics between streams with trout or native fish based on experimental studies (Flecker and Townsend 1994; McIntosh and Townsend 1996), firm conclusions are obscured by fundamental differences between the streams.

Sutton Stream and Stony Creek were chosen for study because they both had excellent populations of fish and were located in adjacent and physically similar catchments. Stony Creek has the highest abundance of river galaxias documented for the Taieri River drainage. Sutton Stream has the second highest abundance of brown trout (Taieri and Southern Rivers Programme, Department of Zoology, University of Otago, Dunedin, unpublished work). It was thought that contrasts in trophic dynamics as a consequence of the different fish populations would be greatest among these streams. The large discrepancy in biomass and production between the populations of trout and river galaxias used in the study, however, almost certainly biased results toward a large effect by trout. The presence of uncontrolled physical factors that may have influenced levels of primary production among streams also complicated the interpretation of budget results.

Obvious factors known to limit primary production in streams, such as nutrient and light regime, were similar among sites (see Study sites, above) and were probably not responsible for the observed contrast. There was, however, a larger area of bedrock substrata in Stony Creek compared with Sutton Stream (see Study sites above) which may have influenced periphyton biomass by mediating different regimes of shear-stress on the stream bed which in turn may have mediated different rates of sloughing (Biggs and Thomsen 1995). A continual reduction of biomass to low levels because of sloughing would limit primary production in much the same manner as extreme grazing pressure. Since actual production of periphyton was measured, substantial losses due to sloughing (or other non-consumptive losses) would have been detected as an equally substantial surplus of net primary production in the Stony Creek budget. The budget results, however, indicated that non-consumptive losses were minor and that the potential for a close coupling of grazer and periphyton production is real. The lack of precise control of such site-specific variables often complicates the assessment of results of natural experiments (Diamond 1986). Regardless of the uncertainty inherent in the design of the present study, the potential for ecosystem-level effects resulting from the introduction of brown trout to New Zealand streams cannot be ignored.

The introduction of brown trout to New Zealand has caused the fragmentation of populations of native river galaxias (Townsend and Crowl 1991), and the evolution of novel patterns of diel drifting and feeding behaviour by many benthic invertebrates (McIntosh and Townsend 1994, 1995a,b). Experimental studies have shown that brown trout are also capable of causing trophic cascades and accrual of periphyton compared to native conditions (Flecker and Townsend 1994; McIntosh and Townsend 1996). The present study suggests that the introduction of brown trout has caused increases in the ecosystem productivity of streams as well.

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