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Stream flow, salmon and beaver dams: roles in the structuring of stream fish communities within an anadromous salmon dominated stream

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Summary

1. The current paradigm of fish community distribution is one of a downstream increase in species richness by addition, but this concept is based on a small number of streams from the mid-west and southern United States, which are dominated by cyprinids. Further, the measure of species richness traditionally used, without including evenness, may not be providing an accurate reflection of the fish community. We hypothesize that in streams dominated by anadromous salmonids, fish community diversity will be affected by the presence of the anadromous species, and therefore be influenced by those factors affecting the salmonid population.
2. Catamaran Brook, New Brunswick, Canada, provides a long-term data set to evaluate fish community diversity upstream and downstream of an obstruction (North American beaver *Castor canadensis* dam complex), which affects distribution of Atlantic salmon *Salmo salar*.
3. The Shannon Weiner diversity index and community evenness were calculated for sample sites distributed throughout the brook and over 15 years. Fish community diversity was greatest upstream of the beaver dams and in the absence of Atlantic salmon. The salmon appear to depress the evenness of the community but do not affect species richness. The community upstream of the beaver dams changes due to replacement of slimy sculpin *Cottus cognatus* by salmon, rather than addition, when access is provided.
4. Within Catamaran Brook, location of beaver dams and autumn streamflow interact to govern adult Atlantic salmon spawner distribution, which then dictates juvenile production and effects on fish community. These communities in an anadromous Atlantic salmon dominated stream do not follow the species richness gradient pattern shown in cyprinid-dominated streams and an alternative model for stream fish community distribution in streams dominated by anadromous salmonids is presented. This alternative model suggests that community distribution may be a function of semipermeable obstructions, streamflow and the distribution of the anadromous species affecting resident stream fish species richness, evenness, biomass and production.

Key-words: Atlantic salmon, *Castor*, fish community diversity model, fish production, semipermeable obstruction.

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Introduction

Stream fish communities frequently show a downstream gradient of increasing species richness (e.g. Kuehne 1962; Horwitz 1978; Schlosser 1987). This gradient is thought to be due to a downstream increase in hydrologic stability of a stream and presence of greater habitat volume, and is effected by the addition of new species rather than replacement of existing species (Harrel, Davis & Doris 1967; Horwitz 1978; Schlosser 1982). This richness gradient model also suggests that there is a change in trophic guilds moving downstream, from generalist to more specialized species; in particular from insectivores to piscivores (Schlosser 1982; Poff & Allan 1995). Disturbance may be expected to influence this distribution pattern if such disturbance interferes with species addition downstream.

A common disturbance in temperate North American streams is the dam-building and impoundment activities of the North American beaver *Castor canadensis*, locally altering the lotic environment to a lentic one. Beavers have profound and far-reaching influences on stream environments, affecting geomorphology (Naiman, Johnston & Kelley 1988), nutrients (Naiman, Melillo & Hobbie 1986), and communities of invertebrates (McDowell & Naiman 1986), and fish (Snodgrass & Meffe 1998; Rosell *et al*. 2005). The dam-building and impoundment activities of beavers may affect fish communities and age structure of species present (Schlosser 1995, 1998) and influence fish movement and distribution (Collen & Gibson 2001). Much of the existing research on the effects of beaver dams on fish communities has examined the direct and proximal effects of beaver dams and impoundments. That is, how the community changes as the stream environment is altered to standing water, and the succession of that pond ecology over time to beaver abandonment (Stock & Schlosser 1991; Schlosser 1995; Schlosser & Kallemeyn 2000). A second focus of beaver ecology and fish has been on the response of rearing salmonids to beaver ponds (e.g. Winkle, Hubert & Rahel 1990; Sigourney, Letcher & Cunjak 2006; see also Collen & Gibson 2001). However, examining larger scale effects of dams on fish communities; that is, on those communities upstream and downstream of the dams, and the influence of these dams on the fish diversity along the stream, has been largely neglected.

Anadromous species may form the majority of fish production in streams along both coasts of North America (primarily *Oncorhynchus* sp. on the west coast, *Salmo* and *Salvelinus* sp. in the east) (e.g. Chapman 1965; Randall *et al*. 1989a; Randall, O'Connell & Chadwick 1989b). Beaver dams are known to potentially act as significant barriers to anadromous fish migration (Collen & Gibson 2001), though this will be dependent upon streamflow, with high discharge facilitating passage past the dams for those species adept at swimming in high flows and leaping obstructions (e.g. adult salmon) (Collen & Gibson 2001; Rosell *et al*. 2005). Beavers will commonly build a series of dams (accessory dams) with the downstream ones backing up water to provide hydraulic support for those upstream (Dugmore 1914; Banfield 1974); this creates a series of potential obstructions to upstream migrating fish The life-history strategy of autumn-spawning anadromy may be expected to be particularly responsive to beaver dams as the beaver tend to construct and maintain their dams in late summer through autumn (Dugmore 1914; Müller-Schwarze & Sun 2003), and so are most active during the periods of autumn-spawner adult migrations. Given the dominance of anadromous species in those fish communities in which they are present, and that their spawning migrations may be susceptible to obstruction by beaver dams, the indirect effects of beaver activities on more spatially removed (e.g. upstream and downstream) communities are of considerable interest.

Much of the work on stream fish diversity has been done in southern or mid-west American streams (e.g. Kuehne 1962; Harrel *et al*. 1967; Lotrich 1973; Horwitz 1978; Schlosser 1987, 1991), not those dominated by anadromous salmonids, and nearly all have examined only species richness. This measure does not include the community attribute of evenness, which is recognized as an important component of a measure of diversity (Pielou 1974). Thus, models of the distribution of community diversity in these latter systems, and the mechanism of that structuring, are presently lacking. We hypothesize here that the fish community in streams dominated by anadromous salmonids is largely structured by the presence of those species, and that the distribution of spawners and subsequent juvenile production is governed by the spatial distribution of beaver dams. In essence, fish community structure is determined by an interaction of beavers and salmon. Specifically, we predict: (1) comparable habitat types upstream of beaver dams, to which access is restricted to salmon in most years, will show increased fish diversity relative to those below the dams, in contrast to the richness gradient concept; (2) over a relatively short stream the change in diversity will be effected through species evenness (i.e. salmon dominance) within the community and not species richness (little addition of species); and (3) species diversity and evenness will be negatively correlated with salmon density as salmon increasingly dominate the community.

Study areas and methods

CATAMARAN BROOK

Catamaran Brook is a third order catchment (52 km^2 drainage area) tributary to the Little Southwest Miramichi River (confluence at 46°53′ N, 66°06′ W) in the Miramichi River system of central New Brunswick,

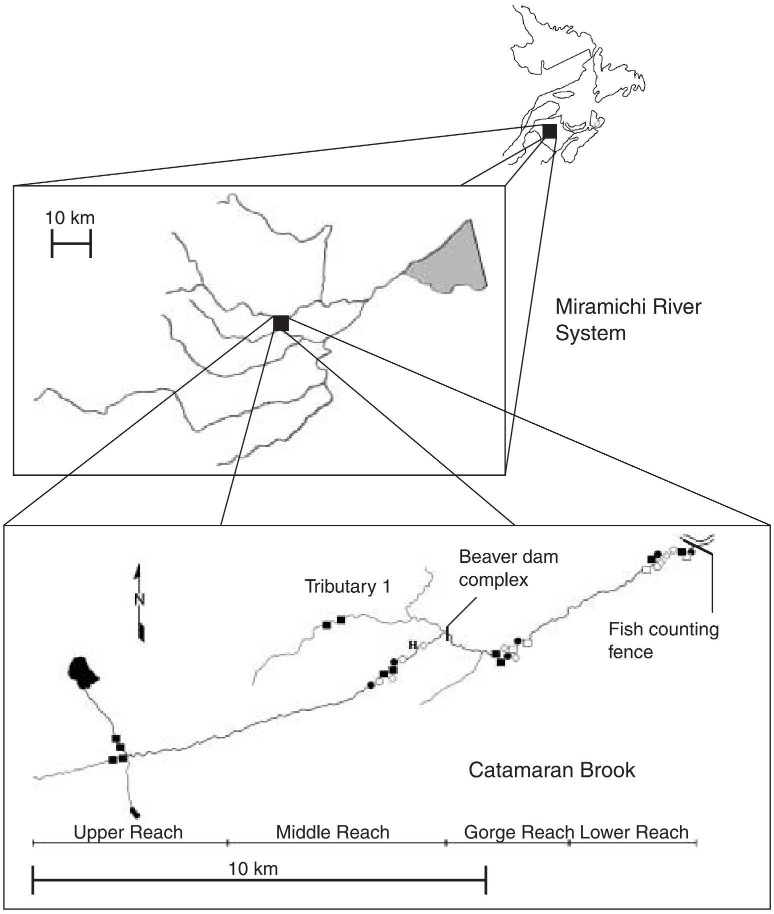

Fig. 1. Catamaran Brook study area illustrating geographical locations mentioned in text and locations of fish sampling sites (closed circles = riffles, open circle = flats, closed squares = runs, open squares = bedrock runs, open diamonds = pools), hydrometric station (H) and fish-counting fence.

Canada (Fig. 1). The stream has a mainstem length of 18·4 km, over which it drains moderate relief topography. The surrounding forest is mature second growth composed of softwood (65%) and hardwood (35%), principally of balsam fir *Abies balsamea*, black spruce *Picea mariana*, red spruce *P. rubens*, eastern white cedar *Thuja occidentalis*, white birch *Betula papyrifera*, yellow birch *B. lutea*, sugar maple *Acer saccharum* and red maple *A. rubrum* (Cunjak, Caissie & El-Jabi 1990; Caissie *et al*. 2002; Cunjak *et al*. 2004). The drainage density of the catchment is relatively low (0·60 km km^{-2}) reflecting the small number of tributaries feeding the stream. There is only a single relatively large tributary (Tributary 1; Fig. 1) downstream of the headwaters, with this branch draining 4·5 km^2 (8·6% of the total basin). The climate of the area is continental with cold winters, including deep snow accumulations, and hot summers.

Catamaran Brook displays a typical snow-dominated hydrological regime with a peak spring freshet. Stream discharge is generally low in August–September, then increasing in late October and November due to autumn rains. Mean annual flow (1990–2004), as measured at the hydrometric station, is 0·58 m^3 s^{-1} with mean summer (August) flows of 0·24 m^3 s^{-1}. Giberson & Caissie (1998) calculated bankfull flows of 5·0 m^3 s^{-1} (at the hydrometric station) and 10·0 m^3 s^{-1} (at the mouth). Two historic hydrological events are of relevance to the results presented here. First, on 24 January 1996 a mid-winter ice break-up following a rain-on-snow event and thaw occurred. This resulted in a flood flow of 6·1 m^3 s^{-1} during a period when maximum flows (during January) are more typically 0·56 m^3 s^{-1}. The physical effects of the ice movement within the channel (scouring and sediment movement) altered the physical characteristics of the channel in the lower part of the stream and impacted the fish populations (St Hilaire *et al*. 1997; Cunjak, Prowse & Parrish 1998). Second, on 30 October 2003 a large magnitude flood of 7·42 m^3 s^{-1} occurred, which is the highest recorded outside of the spring freshet period and fifth highest daily flow recorded from the 16 years of record. This flood was unusual, occurring late in the year, and it breached or destroyed all of the beaver dams in the lower 12 km of the brook during a period of adult salmon spawning movement.

Catamaran Brook differs physiographically and physically in the upper half from the lower. From approximately river km 2·5–5·0 the channel grades into a relatively high-gradient character (> 2%) and becomes bedrock confined for a short distance at the upstream end of this progression. This area is termed the Gorge and physiographically separates the lower and upper parts of the stream. Contributing to the differentiation of the upper and lower halves of the brook near this point is the introduction of flow from Tributary 1, which adds volume to the channel in the lower half of the stream. In the upper half the channel width is reduced and there are an abundance of groundwater contributions (seeps and springs). These groundwater introductions ameliorate the water temperature relative to downstream. Between late April and mid-November the upper half of the brook may be as much as 3 °C cooler than the lower reach (most extreme difference during mid-August), whereas between mid-November and late April water temperature in the upper section is 0·5–1·0 °C warmer than lower reach (R.A. Cunjak unpublished data).

Catamaran Brook was divided into four reaches based on gradient, stream order and channel morphology for purposes of fish sampling and habitat surveys (Fig. 1). In brief, the Lower Reach represents a low gradient section within an unconfined channel flowing through a broad floodplain. There are occasional bedrock exposures. The Gorge Reach is a high gradient area of largely bedrock exposure. The Middle Reach is again a low gradient unconfined channel, similar to the Lower Reach but of lesser width as there is reduced discharge. The Upper Reach and Tributary 1 represent low-order headwater streams of low gradient.

Beavers are active in the basin, and their activities have included the long-term occurrence of a beaver dam complex, present before 1990 when this programme began, in the vicinity of the Tributary 1 confluence

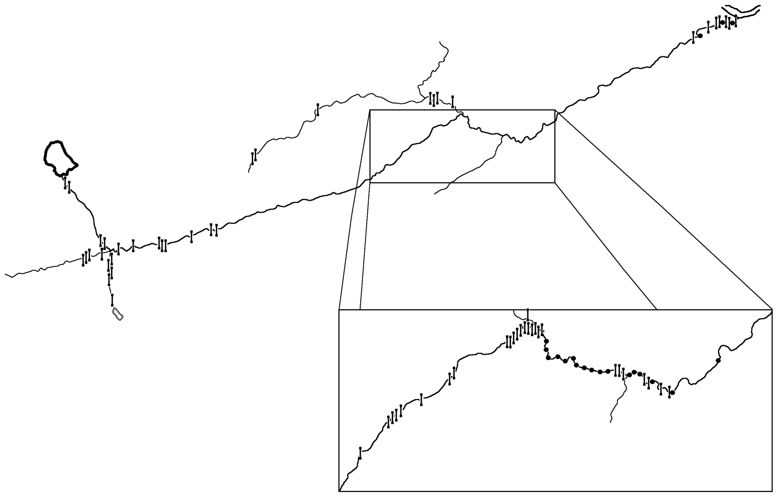

Fig. 2. Catamaran Brook illustrating locations of beaver dams (vertical lines) and spawning areas by salmon (closed circles). Beaver dam locations compiled from various sources 1970–2004; spawning areas from 1990 to 2004.

(Fig. 2). This complex is composed of six to 12 dams ranging in age, height and integrity, but in any year (except 1990 and 2003) at least some of the dams in this complex were considered obstructive to movement of adult salmon upstream. Beaver dam complexes have been documented throughout the area upstream of the Gorge since 1970. Prior to 2001 beaver dam locations were based on air photo interpretation, data from the New Brunswick Department of Natural Resources, and *ad-hoc* stream walks in the summer and autumn. Between 2001 and 2004 a dedicated stream walk to identify and describe beaver dams was conducted in September of each year. Adult salmon migrate into Catamaran Brook to spawn during October and November of the year, with spawning in most years confined below the large complex of dams near the mouth of Tributary 1 and near the mouth of the brook.

The number of sampled habitat types (riffle, run, bedrock run, flat, pool; see Cunjak *et al*. 1993 for classification) varied among reaches. Two replicates of each habitat type within a reach were targeted, with pools being least represented in the sampling compared with the other habitat types (i.e. not sampled every year). Fish sampling was conducted in a consistent manner at between 24 (in 1990, 1991, 1992) and 32 (1996) sites of Catamaran Brook in the early summer of each year of 1990–2004 (Fig. 1).

Fish sampling consisted of backpack electrofishing with the site bounded upstream and downstream by barrier nets (2 mm mesh). In all years after the 1990 sampling season a Pollet lip-seine (Elson 1962) (also 2 mm mesh) was utilized to increase capture efficiency. At least three electrofishing passes were made in a downstream direction at each site to ensure sufficient captures for determination of density of target species [Atlantic salmon *Salmo salar* (Linnaeus), brook charr *Salvelinus fontinalis* (Mitchill) and slimy sculpin *Cottus cognatus* (Richardson)]. Captured fish were measured (to nearest 1·0 mm; fork length for salmonids and cyprinids, total length for others), weighed (±0·01 g), and released back into the site after all passes were completed. The site was measured after electrofishing using three to five transects of wetted width and one to three measures of length from which the sampled area was calculated as the product of mean length and mean width.

Water level (m) was monitored continuously at an automated hydrometric station located 9·25 km upstream of the stream mouth, representing approximately one-half of the catchment, and these data converted to stream discharge ($m^3 s^{-1}$) by Water Survey of Canada (WSC).

Atlantic salmon redd surveys were conducted on an *ad-hoc* basis between 1990 and 2001 with greater effort in documenting positions of redds in 2002–04. A large beaver dam (approximately 30 m long and 2 m high) located at approximately river km 11·5 formed the upstream-most extent of these latter surveys in 2002 and 2004 as this was perceived to limit the upstream passage of adult salmon. Stream discharge immediately below this dam was very low and diffuse and salmon were not expected to surmount this obstruction. However, redds were discovered upstream of this dam following the extreme 2003 flood (L. Weir, Dalhousie University, pers. comm.) indicating it was not a complete barrier at very high flows. Redd location was documented using Global Positioning System equipment in 2002–04.

CALCULATION OF COMMUNITY AND POPULATION VARIABLES

The abundance of species *i* for site *k* sampled in year *t* was calculated from the electrofishing data using the method of Zippin (1958). Community diversity for each site and year was calculated using the Shannon–Weiner diversity index (H'), species richness (R) and evenness of representation by species in the community (J'), where these functions are (from Pielou 1974, 1977):

$$H'_{kt} = -\sum_{R_{kt}} p_{i,kt} \log p_{i,kt} \quad \text{eqn 1}$$

$$J'_{kt} = \frac{H'_{kt}}{\log s_k} \quad \text{eqn 2}$$

R_{kt} = Number of species in sample site k and year t, $p_{i,kt}$ is the proportion of total fish abundance represented by species i at site k and time t, and s_k = total number of species for that given habitat type and reach across all records of sampling (i.e. maximum potential number of species in that habitat type at a given time).

In addition to estimating species diversity, fish production was calculated for the four principal species in Catamaran Brook to correlate patterns of production with diversity. Production was calculated using the

Table 1. List of fish species collected in Catamaran Brook, New Brunswick, over a 15-year period between 1990 and 2004, ranked in order of relative occurrence. Relative occurrence calculated as percentage of 436 individual samples* that contained the species

Rank	Species	Relative occurrence (%)
1	Brook charr (*Salvelinus fontinalis*, Mitchill)	86·2
2	Atlantic salmon (*Salmo salar*, Linnaeus)	82·1
3	Blacknose dace (*Rhinichthys atratulus*, Hermann)	79·8
4	Slimy sculpin (*Cottus cognatus*, Richardson)	70·9
5	Lake chub (*Couesius plumbeus*, Agassiz)	39·9
6	White sucker (*Catostomus commersoni*, Lacepède)	16·3
7	Sea lamprey (*Petromyzon marinus*, Linnaeus)	14·9 (ammocoetes); 3·7 (adult)
8	Creek chub (*Semotilus atromaculatus*, Mitchill)	7·6
9	American eel (*Anguilla rostrata*, Leseur)	5·7
10	Northern redbelly dace (*Chrosomos eos*, Cope)	3·9
11	Threespine stickleback (*Gasterosteus aculeatus*, Linnaeus)	2·3
12	Finescale dace (*Chrosomus neogaeus*, Cope)	1·4
13	Common shiner (*Notropis cornutus*, Mitchill)	1·8
14	Golden shiner (*Notemigonus crysoleucas*, Mitchill)	0·9
Species captured infrequently ($N < 5$) or at fence only		
	Brown trout (*Salmo trutta*, Linnaeus)	
	Gaspereau (*Alosa pseudoharengus*, Wilson)	
	Brown bullhead (*Ameiurus nebulosus*, Leseur)	
	Yellow perch (*Perca flavescens*, Mitchill)	

*436 individual samples based on sampling 24–32 sites annually in summer months between 1990 and 2004; each site and year represent a single sample.

formulation for Incremental Production of Newman & Martin (1983) for each of Atlantic salmon, brook charr, slimy sculpin and blacknose dace *Rhinichthys atratulus* (Hermann). For the purpose of this analysis age-specific production was summed over all ages within a species to provide species production, and then summed over the four dominant species to represent 'Total' fish production. This underestimates total production as those species caught only infrequently (i.e. not captured in successive time intervals) are not included.

ANALYSIS

Species diversity, richness, evenness and production for each habitat type (riffles, runs, bedrock runs, flats, pools) were compared among reaches using Student's *t*-test when only two reaches were compared (bedrock runs and flats), and single factor analysis of variance (ANOVA) when comparing more than two. ANOVA was followed up *post hoc* with Tukey's Honestly Significant Difference test. All testing was conducted at $\alpha = 0{\cdot}10$. Parametric tests were deemed appropriate as: (1) normal probability plots indicated approximate normality of the data; (2) the Central Limit Theorem suggests that at larger sample sizes the estimated mean of a distribution approximates that of a normal distribution, with $N > 30$ being a useful 'rule of thumb' that the sample size is sufficient to meet the requirements of a normal distribution (DeVore 1987); and (3) the *t*-test and ANOVA are known to be robust to departures from assumptions (Zar 1999). Regression analysis involved simple linear and also nonlinear regression. Comparison of slopes and elevations follow Zar (1999). All statistical testing and regressions were conducted using Microsoft Excel XP and Statistical Package for Social Sciences (SPSS ver. 13·0). The uncertainty associated with estimates of the mean are presented as standard error unless indicated otherwise.

Results

COMMUNITY DIVERSITY, RICHNESS, EVENESS, SPECIES COMPOSITION AND PRODUCTION

There have been 18 fish species recorded within Catamaran Brook (Table 1), 14 from the electrofishing sampling and four very infrequent species captured at the fish-counting fence. Fish community diversity (H') is greater in the Middle Reach than other reaches for riffles and runs, and equivalent to the Lower Reach for flats and pools (Fig. 3, Table 2). The Gorge Reach is consistently of less diversity for a given habitat type than the Lower and Middle reaches. Diversity of the lower order streams (Tributary 1 and Upper Reach) is less than the mainstem sites in the pools and intermediate between the Lower and Gorge reaches in the runs. Thus, H' immediately upstream of the beaver dams (Middle Reach) is significantly greater than that immediately downstream (Gorge Reach) in comparable habitats. There is a clear distinction of species evenness relative to richness between sites upstream and downstream of the beaver dams (Fig. 4), with downstream sites showing depressed evenness for a given species richness relative to above the dams. The sole exception

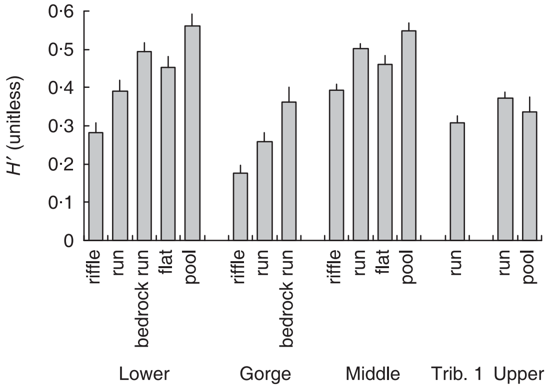

Fig. 3. Mean Shannon–Weiner diversity (H') index for each habitat type and reach in Catamaran Brook, 1990–2004. Error bars are standard errors.

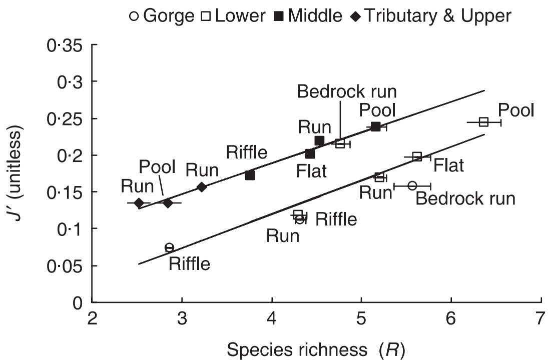

Fig. 4. Relationship of mean species evenness to richness for sites upstream of beaver dams (Middle and Upper reaches, Tributary 1), and downstream of dams (Lower and Gorge reaches) in Catamaran Brook, 1990–2004. Error bars are 90% confidence intervals. Regression equations are: Below Dams $J' = 0{\cdot}046 \pm 0{\cdot}011 \times R' - 0{\cdot}064 \pm 0{\cdot}054$, $r^2 = 0{\cdot}705$, $N = 8$, $F = 17{\cdot}67$, $P = 0{\cdot}005$. Above Dams $J' = 0{\cdot}042 \pm 0{\cdot}003 \times R' + 0{\cdot}021 \pm 0{\cdot}001$, $r^2 = 0{\cdot}971$, $N = 7$, $F = 199{\cdot}05$, $P < 0{\cdot}0001$.

is the Lower bedrock runs that clearly group with those sites upstream of the beaver dams indicating the evenness of this site is more similar to those upstream. Slopes of the regression lines for upstream and downstream sites are equivalent ($P > 0{\cdot}25$) but the elevations differ ($P < 0{\cdot}001$), indicating that while evenness increases with richness in similar manner in both areas of the stream, the evenness for a given richness is significantly lower downstream of the dams. The Gorge Reach includes the lowest evenness of all reaches in Catamaran Brook. Mean species richness in the Middle Reach ($3{\cdot}77 \pm 0{\cdot}01$ for riffles, $4{\cdot}53 \pm 0{\cdot}02$ for runs) is intermediate to that of the Gorge ($2{\cdot}86 \pm 0{\cdot}02$ and $4{\cdot}32 \pm 0{\cdot}04$, respectively) and Lower Reach ($4{\cdot}30 \pm 0{\cdot}05$ and $5{\cdot}20 \pm 0{\cdot}04$, respectively) and so increased diversity in the Middle Reach is not obviously attributable to increased richness.

Species composition differs for comparable habitat types upstream and downstream of the beaver dams (Fig. 5). Below the dams salmon are the most frequently captured species in all habitat types with the exception of pools. This frequency of capture is much greater

Table 2. Results of statistical testing of Shannon-Weiner diversity, species richness, species evenness, and total fish production within comparable habitat types among reaches. Statistically equivalent sites indicated by underscore

	Flats	Bedrock runs	Pools	Riffles	Runs
Ho:	Lower = Middle	Lower = Gorge	Lower = Gorge = Middle	Lower = Gorge = Middle	Lower = Gorge = Middle = Tributary = Upper
Test	t-test	t-test	ANOVA; Tukey HSD	ANOVA; Tukey HSD	ANOVA; Tukey HSD
Diversity (H')	$P = 0{\cdot}409$; d.f. = 52	$P = 0{\cdot}002$; d.f. = 46	$F = 16{\cdot}49$, d.f. = 46, $P < 0{\cdot}0001$	$F = 23{\cdot}68$, d.f. = 86, $P < 0{\cdot}0001$	$F = 16{\cdot}58$, d.f. = 167, $P < 0{\cdot}0001$
	Lower Middle	Lower > Gorge	Lower Middle > Upper	Middle > Lower > Gorge	Middle > Lower Upper Tributary Gorge
Richness (R)	$P = 0{\cdot}0004$; d.f. = 42	$P = 0{\cdot}035$; d.f. = 53	$F = 28{\cdot}22$, d.f. = 47, $P < 0{\cdot}0001$	$F = 17{\cdot}80$, d.f. = 88, $P < 0{\cdot}0001$	$F = 32{\cdot}08$, d.f. = 169, $P < 0{\cdot}0001$
	Lower > Middle	Gorge > Lower	Lower Middle > Upper	Lower Middle > Gorge	Tributary Upper Gorge Middle Lower
Evenness (J')	$P = 0{\cdot}409$; d.f. = 52	$P = 0{\cdot}002$; d.f. = 46	$F = 18{\cdot}91$, d.f. = 47, $P < 0{\cdot}0001$	$F = 24{\cdot}04$, d.f. = 88, $P < 0{\cdot}0001$	$F = 15{\cdot}18$, d.f. = 169, $P < 0{\cdot}0001$
	Lower Middle	Lower > Gorge	Lower Middle > Upper	Middle > Lower > Gorge	Middle Lower Upper Tributary Gorge
Production	$P = 0{\cdot}127$; d.f. = 36	$P = 0{\cdot}002$; d.f. = 48	$F = 4{\cdot}02$, d.f. = 41, $P = 0{\cdot}026$	$F = 8{\cdot}40$, d.f. = 82, $P = 0{\cdot}0005$	$F = 11{\cdot}54$, d.f. = 155, $P < 0{\cdot}0001$
(g m^{-2} $year^{-1}$)	Lower Middle	Gorge > Lower	Middle Upper > Lower	Gorge > Lower Middle	Tributary Gorge Middle Lower Upper

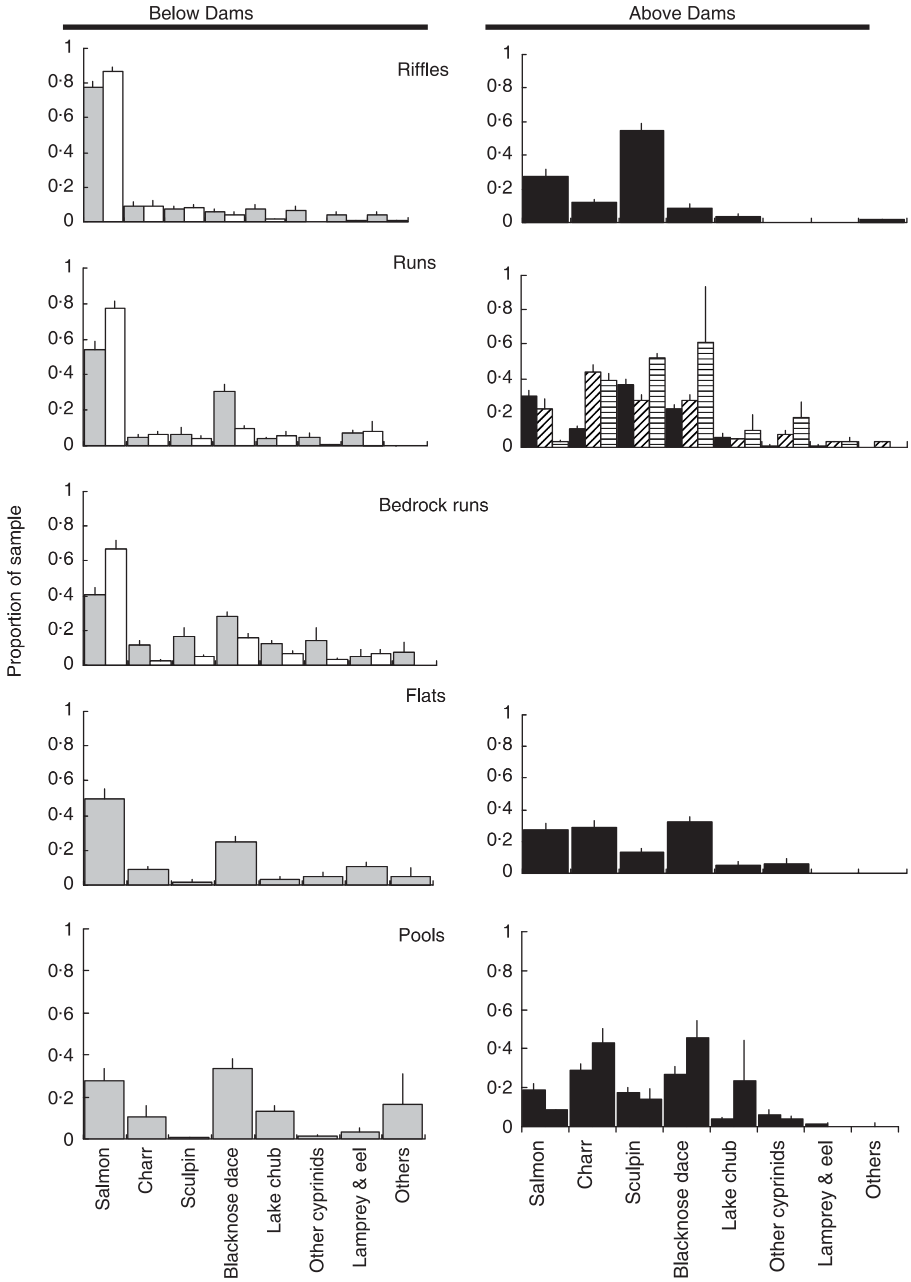

Fig. 5. Mean proportion of samples (error bars are SE) in which species were captured during summer electrofishing in Catamaran Brook, 1990–2004, by habitat type and reach below and above beaver dams. Lower Reach = shaded columns, Gorge Reach = white columns, Middle Reach = black columns, Upper Reach = diagonal pattern, Tributary 1 = horizontal pattern. Other cyprinids include creek chub *Semotilus atromaculatus* (Mitchill), golden shiner *Notemigonus crysoleucas* (Mitchill), common shiner *Notropis cornutus* (Mitchill), northern redbelly dace *Chrosomos eos* (Cope) and finescale dace. Others include white sucker *Catostomus commersoni* (Lacepède) and three spine stickleback.

than all other species in riffles of the Lower and Gorge reaches, and the runs and bedrock runs of the Gorge (i.e. salmon > 65% of captured fish on average). In runs and bedrock runs of the Lower Reach there is greater representation by other species, notably the blacknose dace (approximately 25–30% of fish captured). With the exception of the Lower bedrock runs, charr and sculpin are present at only low frequency (< 10% of captures) below the beaver dams. Upstream of these dams, the species composition changes, with increases in the frequency of sculpin and decreases in salmon frequency (riffles, runs, flats, pools), and increases in charr (runs, flats, pools).

Total fish production is not distributed equally among reaches or species within a reach (Table 2, Fig. 6). In the Lower and Gorge reaches production is greatest within riffles and runs; upstream of the dams, pools show the greatest production within a reach. The Gorge Reach shows higher production than the other reaches in the riffles and bedrock runs. In the Lower and Gorge reaches production is dominated by salmon (accounting for > 80% of total production) while

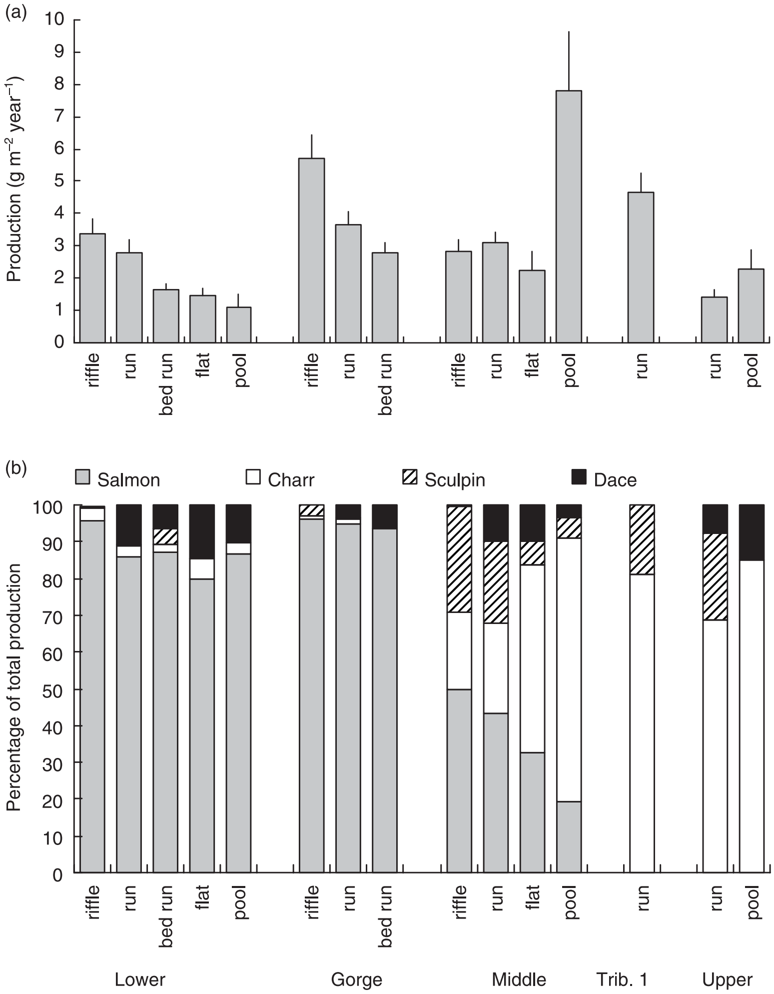

Fig. 6. Mean total fish production of four dominant species combined (a) and percentage of total production by species (b) by habitat type and reach in Catamaran Brook, 1990–2004. Error bars are standard error.

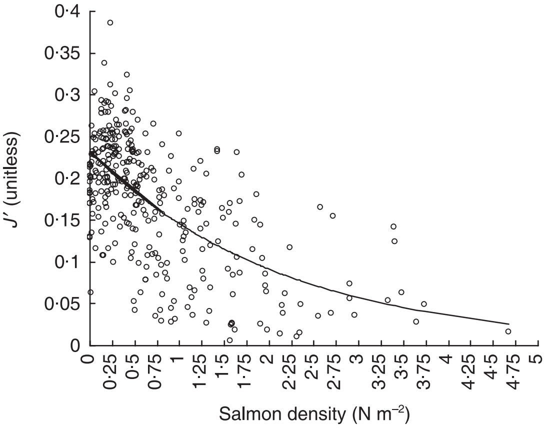

Fig. 7. Community evenness as a function of Atlantic salmon density in Catamaran Brook, 1990–2004. Data are from all habitat types in Lower, Gorge and Middle reaches ($N = 326$). Regression equation is: $J' = 0{\cdot}232 \pm 0{\cdot}006 \times \exp(-0{\cdot}466 \pm 0{\cdot}041 \times \text{density})$, $r^2 = 0{\cdot}392$, $F = 1735$, $P < 0{\cdot}001$. A similar plot of H' against density (not shown) yields the equation $H' = 0{\cdot}534 \pm 0{\cdot}014 \times \exp(-0{\cdot}479 \pm 0{\cdot}042 \times \text{density})$, $r^2 = 0{\cdot}392$, $F = 144{\cdot}7$, $P < 0{\cdot}001$.

upstream of the dams sculpin and charr contribute greater amounts to total production. From these results it is clear that there is a fundamental spatial distinction in fish community diversity, evenness, species composition and production between sites in the upper half and lower half of Catamaran Brook.

ROLE OF ATLANTIC SALMON IN AFFECTING THESE MEASURES

Atlantic salmon within Catamaran Brook appear to play a large part in the structure of the fish community, influencing diversity and evenness, species composition and production. The relationship of diversity and evenness with salmon density each follow a negative exponential function (Fig. 7). This influence of salmon on diversity is further evidenced as diversity in riffles and runs (preferred salmon habitat) of the Middle Reach is greater than that in all other reaches for these habitats. The Middle riffles and runs have lower salmon densities compared with more downstream reaches. The increase in mean diversity of the riffles and runs of the Middle Reach over the other reaches below the beaver dams is 40–100% (relative to riffles in Lower and Gorge, respectively) and 29–94% (runs in respective reaches). Further, habitats not typically dominated by salmon show similar diversity, richness and evenness (pools) and similar diversity and evenness (flats) between Lower and Middle reaches (Table 2). Salmon density has a statistical effect on species richness:

$$\text{Richness} = -0{\cdot}37 \pm 0{\cdot}10 \text{ salmon density } (\text{N m}^{-2}) + 4{\cdot}93 \pm 0{\cdot}11,\ (r^2 = 0{\cdot}036,\ n = 327),\ F = 13{\cdot}37;\ P = 0{\cdot}0003 \qquad \text{eqn 3}$$

but given the extremely low value of r^2 (i.e. little variation accounted for by salmon density) and low value of the slope, requiring an increase of three salmon per square metre to reduce richness by one species, this relationship is not ecologically significant (i.e. requiring an increase in salmon density an order of magnitude greater than that commonly seen in natural systems). Riffles in the Lower Reach show significant decreases in salmon density between the 1990–95 (pre-ice event) and 1996–2004 (post-ice event) periods (Table 3). Coincidentally, fish species diversity, evenness and richness all increased significantly between these two periods for the riffles in this reach. Species additions after 1996 were sea lamprey *Petromyzon marinus* (Linnaeus) ammocoetes, three spine stickleback *Gasterosteus aculeatus* (Linnaeus), American eel *Anguilla rostrata* (Leseur) and finescale dace *Chrosomus neogaeus* (Cope).

Salmon may affect the composition of a community by replacing a species. Within the Middle Reach there is an inverse relationship in density between salmon and sculpin in riffles (Fig. 8), with values of less than approximately 0·4 salmon m^{-2} resulting in higher sculpin densities. Note that this relationship excludes the years 1996 and 1997 for which the winter ice event reduced densities of both species (R.A. Cunjak unpubl.

Table 3. Comparison of Atlantic salmon density, species diversity, evenness and richness (mean ± SE) in riffles of the Lower Reach between 1990 and 1995 (pre-ice event) and 1996–2004 (post-ice event). Testing conducted using Student's *t*-test

	Pre-ice event (1990–95)	Post-ice event (1996–2004)	% change	*P*-value
Atlantic salmon density (N m^{-2})	1·52 (± 0·27)	0·71 (± 0·10)	(–) 46·7	0·007
Diversity (H')	0·18 (± 0·04)	0·34 (± 0·03)	(+) 88	0·0017
Richness	3·63 (± 0·24)	4·89 (± 0·24)	(+) 34	0·006
Evenness (J')	0·08 (± 0·02)	0·15 (± 0·01)	(+) 87	0·0017

data) and so represents a stochastic environmental perturbation that overrides the biotic interactions. That the salmon replace the sculpin, at least in terms of proportion of the community (which is important in calculating H' and J'), is shown in Fig. 8, in which the slope of the regression line is not different from –1·0, indicating a direct linear replacement. The years 1996 and 1997 are included in this regression as the measure of proportion representation is still meaningful under environmental disturbance. The two species may be expected to be affected approximately equally. Regression analysis excluding these two points showed the equation of the line did not differ significantly from that when they were included. Under this condition, the evenness or richness of the community does not change as a single species is replaced by another in direct proportion. The community does change, however, from one that is sculpin-dominated to one dominated by salmon. Figure 8 suggests further, that this replacement may not be a linear function as shown, but perhaps a step function with the change occurring when salmon represent between 0·2 and 0·3 of the total fish community. The available data are not sufficient to resolve the exact nature of the relationship yet, but future sampling may allow the determination of this within that area of Fig. 8.

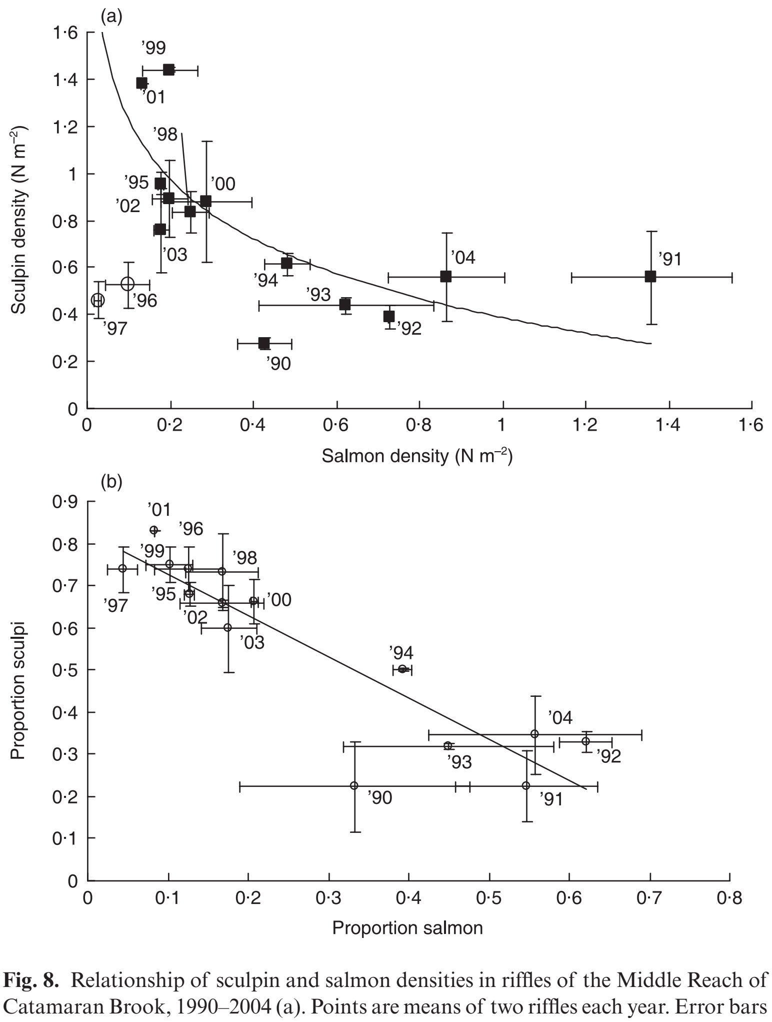

Fig. 8. Relationship of sculpin and salmon densities in riffles of the Middle Reach of Catamaran Brook, 1990–2004 (a). Points are means of two riffles each year. Error bars are standard error. Open symbols excluded from regression as they represent the effect of the 1996 ice event. Regression equation is: Sculpin density = –0·840 ± 0·226 × log (salmon density) + 0·387 ± 0·123, r^2 = 0·558, F = 70·63, P < 0·001. Panel b shows the relationship of proportion of catch comprised by sculpin to the proportion of salmon for riffles in the Middle Reach. Error bars are standard errors. Equation of the line is: proportion sculpin = –0·976 ± 0·136 × proportion salmon + 0·822 ± 0·045, r^2 = 0·782, F = 51·14, P < 0·001.

FACTORS AFFECTING SALMON

Given the apparent role of salmon in affecting stream fish community composition and production, determining the factors affecting salmon distribution and production is important. Beaver dams can lead to uneven distribution of adult spawners and subsequent juvenile production in Catamaran Brook. Two principal areas are utilized by spawning salmon within the stream: (1) from the stream mouth for a distance approximately 2 km upstream, and (2) between 5·0 and 8·0 km upstream of the mouth (Fig. 2; data from R.A. Cunjak unpublished; L. Weir, Dalhousie University, unpublished; redd surveys 2002–04). This latter area is located between the beaver dam complex and the upstream end of the Gorge. The area between 2·0 and 5·0 km is not used by spawners and this is likely due to the large substrate of the area (primarily cobble). The beaver dams in most years appear to be obstructive and produce a clumped distribution of spawning. As further evidence of the effect of beaver dams in this system an obstructive dam in 1994 was located approximately 500 m upstream of the mouth of the brook. Forty redds were counted between this dam and the stream mouth (R.A. Cunjak, unpubl. data). In addition, the fortuitous extreme flood of 2003 indicated that when the opportunity to bypass a beaver dam was available, a large proportion of adult salmon will take advantage of it and spawn in the Middle Reach (20 of 60 redds).

That beaver dams may act as obstructions, and so affect subsequent salmon production upstream, is also

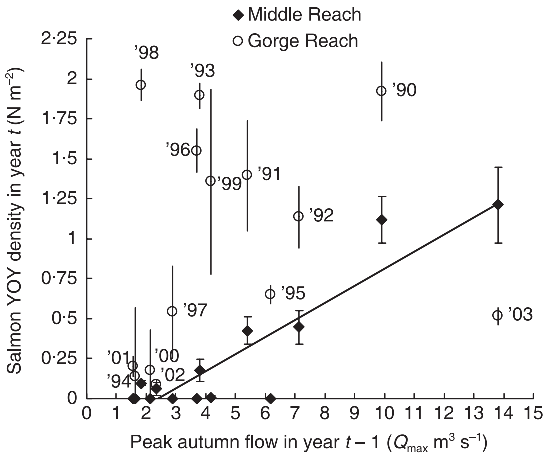

Fig. 9. Relationship of mean salmon YOY density in year t within riffles and runs of the Middle and Gorge reaches with autumn peak flows during adult upstream migration (Q_{max}) in year $t - 1$. Values indicate year of Q_{max}; YOY year is value +1. Error bars are standard errors. Regression equation for line shown is: salmon YOY density = $0{\cdot}198 \pm 0{\cdot}026 \times Q_{max} - 0{\cdot}250 \pm 0{\cdot}081$, $r^2 = 0{\cdot}818$, $F = 59{\cdot}635$, $P < 0{\cdot}001$, $N = 14$.

a function of the magnitude of the autumn streamflow during the period of adult upstream migration; i.e. the dams are 'semipermeable' dependent upon autumn streamflow. Figure 9 illustrates that salmon young-of-the year (YOY) densities of year t in the Middle Reach are a function of maximum autumn streamflow during the period of adult upstream migration (Q_{max}) the previous year ($t - 1$). The years in which $Q_{max} > 7{\cdot}5$ m^3 s^{-1} (1990, 2003) the beaver dams do not appear to be an impediment, while at lower flows they allow only a few adults through to yield low YOY densities (e.g. low flow years 1991–93, 1998, 2002) or no adults resulting in zero YOY recruitment (e.g. flow years 1995–97, 1999–2001). A linear function was fit to these data, but a step function may be more appropriate with the step occurring between 7·5 and 9·5 m^3 s^{-1} (i.e. approximately bankfull flow). Additionally, in several years when flows were low (e.g. 1991–93, 1996, 1998, 1999) and spawners not able to access the Middle Reach, they spawned below the dams, which resulted in elevated YOY densities in the Gorge. Therefore, the dams affect not only the Middle reach (negatively), but also salmon abundance in the Gorge Reach (positively). The YOY years 1995, 1998, 2001–03 in which the Gorge Reach also had low YOY densities reflect very low adult returns in the previous autumn and so even with much of the spawning likely occurring in this area, the recruitment was still low. The high 1991 YOY density reflects the high adult returns (222 adults estimated) in 1990. The effect of the 1996 ice event is apparent on YOY densities in both the Gorge and Middle reaches as greater YOY density was expected given the relatively high streamflow and also the large number of adults returned in 1995 (244 adults). This ice event appears to have been catastrophic on the eggs and subsequent YOY density in the Middle Reach, resulting in zero YOY in 1996.

Discussion

SPATIAL DISTRIBUTION OF COMMUNITIES AND ROLE OF SALMON

Fish communities upstream and downstream of the beaver dam complex differ significantly in terms of species diversity, evenness, composition, total production and species-specific production. Below the dams Atlantic salmon predominate, being particularly dominant in the Gorge Reach, while upstream the brook charr and slimy sculpin are much more prevalent. Inferences regarding this distribution of fish are confounded however, by the differing environments upstream and downstream of the dams. In the Middle Reach the brook is of lower water temperature with a greater abundance of groundwater (Edwards & Cunjak 2006), both of which are preferred environments for the charr and sculpin (Symons, Metcalfe & Harding 1976; Otto & Rice 1977; Edwards & Cunjak 2006). Thus, we do not suggest that these species are being actively excluded from below the dams by salmon (though this may be occurring, particularly for the slimy sculpin) but rather that they are confined to the Middle Reach of Catamaran Brook by their own habitat preferenda.

Even considering these environmental conditions, Atlantic salmon appear to have an effect in structuring the fish community of Catamaran Brook, affecting community diversity by reducing evenness. This is most pronounced in the typical salmon habitats of riffles and runs, and when habitat alteration (e.g. ice event) reduce salmon densities. The mechanism by which this influence is exerted, at least on the slimy sculpin, appears to be competitive exclusion. Straškraba *et al*. (1966) and Moyle (1977) maintained that there is little evidence for competition between salmonids and sculpin, but Reutz, Hurford & Vondracek (2003) found brown trout *Salmo trutta* (Linnaeus) to be a superior competitor to slimy sculpin and Jørgensen *et al*. (1999) reported an inverse relationship in density of bullhead *Cottus gobio* (Linnaeus) and Atlantic salmon similar to that reported here. The numerical dominance of salmon, and so determination of community structure, is likely a function of the great fecundity and subsequent egg deposition of this anadromous species, relative to resident stream species. The anadromous life history of the Atlantic salmon not only maximizes growth of individual fish relative to a stream resident strategy, but also allows the species to numerically dominate in those streams in which they are found.

The spatial effects of the salmon on the community is dependent upon the presence of obstructive barriers, such as beaver dams, and the magnitude of streamflow when the adults are ascending the stream determining spawner distribution. Spawning salmon may distributes themselves in a patchy manner due to habitat (Moir,

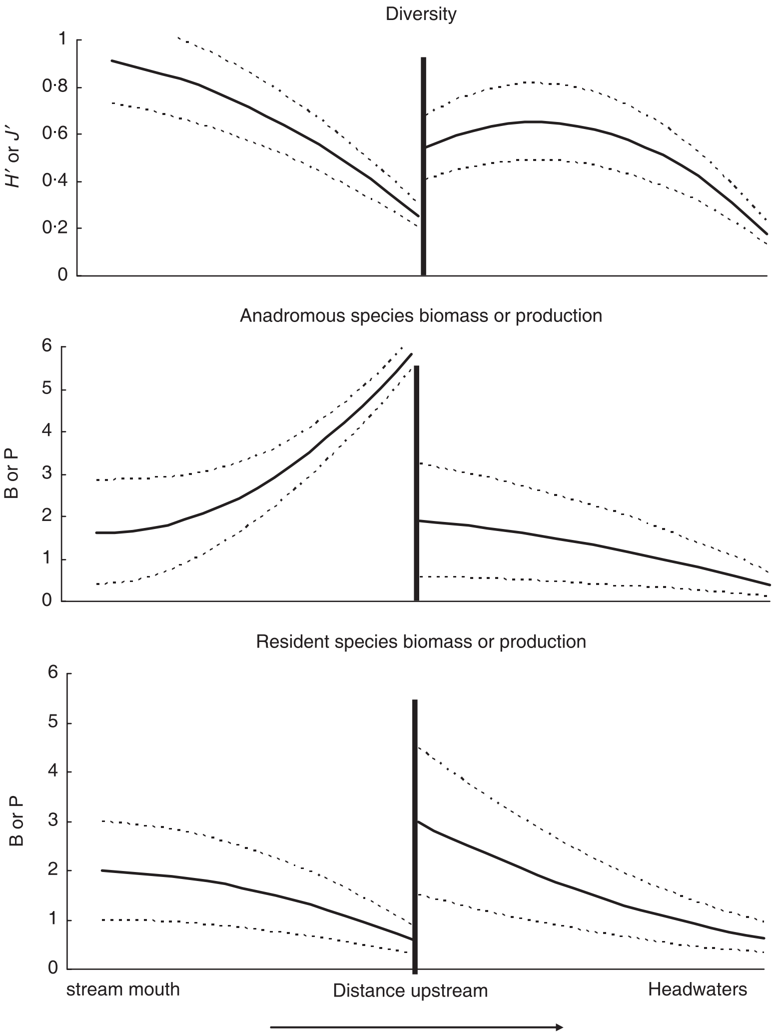

Fig. 10. Conceptual model for fish community diversity (H') or evenness (J') of fish communities and biomass (B) or production (P) of anadromous and resident species in streams interrupted by semipermeable obstruction (black column) such as beaver dams. Dashed lines represent temporal variability about the response.

Soulsby & Youngson 1998; Moir *et al*. 2004) even in the absence of beaver dams. When dams are present, however, they can reduce both density and production of salmon upstream of the dams and inflate these variables immediately downstream. Thus beaver dams can cause a patchy distribution of salmon density and production through the stream, which then affects the community. Autumn streamflow is critical in allowing dispersal of salmon upstream, but also plays a significant part in determining the number of adults entering the brook to spawn (e.g. Huntsman 1948; Banks 1969; Jonsson 1991). Hay (1989) argued that allowing the adult salmon access as far upstream as possible is very important to optimize salmon recruitment in the stream. As salmonids often do not appear to disperse great distances from the redd (Hay 1989; Beard & Carline 1991) the two factors of autumn streamflow and locations of beaver dams are of critical importance in the spatial distribution of salmon and the subsequent fish community structure.

AN ALTERNATIVE CONCEPTUAL MODEL

Within Catamaran Brook, representing a 'typical' anadromous Atlantic salmon dominated stream, we do not see the general patterns described earlier by the species richness gradient concept with increasing species richness and piscivory proceeding downstream. Rather, maximal diversity occurs in the central area of the brook, upstream of the dams. Richness is depressed in the Gorge Reach, and the piscivores (principally larger brook charr in this case) are dominant in the upper half of the brook. The spatial scale examined here (i.e. third order stream) is similar to that used by others (first to fourth order by Kuehne 1962; Sheldon 1968; Whiteside & McNatt 1972; Lotrich 1973; Schlosser 1982, 1985, 1987) in reporting the richness gradient, and so we conclude that differences are not due to scale. Tramer & Rogers (1973) found fish species richness did not increase in a downstream direction in their study stream, but this was attributed to pollution affecting the fish communities. In streams dominated by anadromous salmonids, the richness gradient concept likely does not apply due to the dominance of the single species and influence exerted by it. Instead, based on these results from Catamaran Brook we propose the following conceptual model illustrating changes in diversity, evenness, production (anadromous vs. nonanadromous), and variability of these measures upstream and downstream of a semipermeable obstruction. This model is intended for streams dominated by anadromous species with a stream-rearing juvenile stage.

Community diversity will be highest near the stream mouth and decline proceeding upstream to the obstruction (Fig. 10). This is due to the locations near the stream mouth being more likely to contain representatives from the confluent larger river system, species that may not proceed long distances up the smaller tributaries. This follows the richness gradient concept. Diversity will decrease moving upstream as the biomass or production of the anadromous species increases to a maximum production (minimum diversity) immediately below the obstruction. This increasing anadromous production will cause a reduction in production by resident species. Immediately upstream of the obstruction, community diversity and resident species production both increase relative to below the obstruction. Diversity does not recover to maximal levels at the mouth and we propose increases proceeding upstream from lower values immediately above the dam to a peak before declining due to either reducing stream order or effects of anadromous species from those occasions when they do bypass the first obstruction. Anadromous species biomass or production increases above the dams to either the next obstruction, or where tributaries become too small or gradient too high for use, after which production declines. Resident fish species production is highest above the beaver dams due to frequently lacking salmon presence, but also as beaver ponds are hypothesized as a source of colonization for stream species (Schlosser 1995). Resident fish production declines moving upstream as species and biomass are reduced due to the influence of anadromous species and decreasing stream order/increasing gradient. In terms of temporal variability, we expect the lowest variability in community diversity, biomass or production to be immediately below the obstruction, where anadromous species dominate and are of lower sensitivity to number of returning adult spawners, and in the upper reaches where the influence of anadromous species is less. Near the stream mouth and immediately upstream of the obstruction, variability will be greatest as the community is continually adapting to introduction of new species, in some cases (anadromous species) having profound effects in terms of species composition and abundance.

Naiman *et al*. (1986) noted that beaver dams and ponds should be overlain within the conceptual framework of the River Continuum Concept of Vannote *et al*. (1980) as they effectively interrupt the continuum. The results here support this as we suggest that within anadromous salmonid-dominated streams beaver dams may result in a maximal fish community diversity in mid stream, rather than at lower reaches as predicted by the River Continuum Concept or the gradient concept. The activities of beaver represent an example of Connell's (1978) Intermediate Disturbance Hypothesis in which without their presence a lower diversity throughout the length of the stream would be expected as salmon would dominate the entire length of stream. Beaver dams and ponds are not permanent structures but rather create a temporally varying patchwork mosaic across the landscape (Schlosser & Kallemeyn 2000), which, at least for Atlantic salmon streams, have profound effects on the fish community.

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