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Stream inflow and predation risk affect littoral habitat selection by benthic fish

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SUMMARY

1. We examined small, fishless headwater streams to determine whether transport of macroinvertebrates into the littoral zone of an oligotrophic lake augmented food availability for *Cottus asper*, an abundant predatory fish in our study system. We sampled fish and macroinvertebrates during the recruitment and growth season of 2 years, either monthly (2004) or bi-monthly (2005), to observe whether stream inputs increased prey availability and whether variation in total macroinvertebrate biomass was tracked by fish.

2. Observations from eight headwater streams indicated that streams did not increase the total macroinvertebrate biomass in the shallow littoral zone at stream inflows, relative to adjacent plots without stream inputs (controls). The taxonomic composition of stream macroinvertebrates drifting toward the lake differed from that in the littoral lake benthos itself, although there was no evidence of any species change in the composition of the littoral benthos brought about by stream inputs.

3. Although streams made no measurable contribution to the biomass or taxonomic composition of the littoral macroinvertebrate benthos, there was substantial temporal variation in biomass among the eight sites for each of the (n = 7) sample periods during which observations were made. Variation in total biomass was primarily a function of bottom slope and benthic substrata in the lake habitats. Dominant taxonomic groups were Baetidae, Ephemerellidae (two genera), Leptophlebiidae, Chironomidae (three subfamilies) and Perlodidae, although we did not determine the specific substratum affinities of each taxon.

4. Mixed effects linear models identified a significant interaction between macroinvertebrate biomass and plot type (stream inflow vs. control) associated with fish abundance. Across the observed range of macroinvertebrate biomass, fish showed a significant preference for stream inflows, but more closely tracked food availability in the controls. For young-of-the-year (YOY), a negative effect of temperature was also included in the model, and we observed lower temperatures at stream inflows. However, abundance of predatory adults affected habitat selection for YOY. Lake-bottom slope also accounted for variation in abundance in both fish models.

5. Our results suggest that the effect of fishless headwater streams on downstream fish may not always be through direct delivery of food. In this study system, fish preferred stream inflow plots, but this preference interacted with macroinvertebrate biomass in a manner that was difficult to explain. For YOY, predation risk was related to the preference for stream inflows, although the specific factor that mitigates predation risk remains poorly understood.

Keywords: benthic, cottids, habitat selection, lakes, resource matching

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Introduction

Spatial heterogeneity in aquatic productivity can be influenced by nutrients or organisms being exchanged across the terrestrial–aquatic interface (Polis, Anderson & Holt, 1997; Nakano, Miyasaka & Kuhara, 1999; Sabo & Power, 2002; Power *et al.*, 2004; Baxter, Fausch & Saunders, 2005). Resources transported downstream can thus be derived from terrestrial or in-stream production, and organic matter of terrestrial origin and can influence fish habitat downstream (Nakano *et al.*, 1999; Baxter *et al.*, 2004; Wipfli, Richardson & Naiman, 2007; Binckley *et al.*, 2010). The confluence of low-order streams can potentially result in productivity 'hot-spots' downstream (e.g. Grenouillet, Pont & Seip, 2002; Kiffney *et al.*, 2006). Assuming no other habitat limitations, inflowing streams might increase resource availability compared to habitats without inflows. If so, consumers (i.e. fish) could select habitats accordingly, change their behaviour, or grow faster at the individual or population level (Morris, 1994).

The effects of prey transported from small streams on downstream fish populations are often estimated indirectly from measurement, in the case of terrestrial–aquatic fluxes, of the transport of terrestrial insects and the proportion of terrestrial insects in the diet (e.g. Wipfli & Gregovich, 2002). Relatively few studies have conclusively demonstrated a direct response by fish (but see Kawaguchi, Taniguchi & Nakano, 2003; Baxter *et al.*, 2007), and the key difficulty is in demonstrating that food subsidies from upstream increase fish fitness (i.e. growth and condition) relative to that in habitats that lack such input. At the very least, it should be demonstrated empirically that resources transported from streams augment food availability and that there is some response of fish to the extra resources. This is feasible where streams flow into the littoral zone of oligotrophic lakes. In such lakes, the species richness of the benthivorous fish assemblage is sometimes a function of productivity (Mehner *et al.*, 2005; Tolonen *et al.*, 2005), and habitat selection by fish might be a response to the delivery of macroinvertebrate prey by streams.

A distribution that matches resources, such as the 'ideal-free' distribution (Fretwell & Lucas, 1970; Fretwell, 1972), and observed departures from ideal matching (e.g. Kennedy & Gray, 1993; Valone, 1993) indicate that violation of assumptions (e.g. Tyler & Clapp, 1995; Tyler & Hargrove, 1997), competition (Grand, 1997; Polivka, 2005; Petty & Grossman, 2010) and/or predation risk (Grand & Dill, 1997; Giannico & Healey, 1999; Alofs & Polivka, 2004; Polivka, 2007) limit the ability of foragers to match production. Behavioural responses to predation risk (reviewed in Oksanen & Lundberg, 1995; Brown & Kotler, 2004) include optimising the trade-off between foraging opportunities and risks (e.g. Alofs & Polivka, 2004; Klaassen, Nolet & Bankert, 2006; Polivka, 2007), sometimes resulting in shifts in the mean condition (or other traits correlated with fitness) of individuals in a population (e.g. Sinclair & Arcese, 1995; Polivka, 2011). The study of factors that affect resource matching is tractable where fish habitat selection is easily quantified. Even when behavioural mechanisms are difficult to associate with forager distribution patterns, identification of predation risk as a limit to resource matching may be possible. Where predation risk influences habitat selection, it can affect our ability to detect a downstream response of fish to the prey delivered by streams.

Fish such as cottids forage on the benthos, whose abundance is relatively easy to quantify (e.g. Polivka, 2005; Petty & Grossman, 2010), and show evidence that individuals respond to the trade-off between food availability and predation risk in a way likely to maximise fitness (Alofs & Polivka, 2004; Polivka, 2007, 2011). We expected that habitat selection patterns that are influenced by this trade-off in the littoral benthos of lakes should be detectable in cottids that occupy such habitats. We asked whether (i) transport of drifting invertebrates by small first-order streams increased the biomass or taxonomic composition of potential prey near the shore of an oligotrophic lake, relative to plots further from stream input and (ii) habitat selection in *Cottus asper* was influenced by spatial and temporal variation in food availability or by predation risk, or both.

Methods

Study system and site selection

Lake Wenatchee is a mid-altitude (*c.* 575 m; surface area *c.* 1000 ha) lake on the eastern slope of the Cascade Range, Washington, U.S.A. (N 47.81151, W 120.72787). It has major inflows from the White and Little Wenatchee Rivers and an outlet to the Wenatchee River. On the south shore of the lake, several small, high-gradient streams drain in from the immediate hillslope, which is located in the Okanogan-Wenatchee National Forest (OWNF). There is little development along the shoreline; land use near our study streams consists of a campground and small seasonal dwellings. Fish near the shore at dawn and dusk include aggregations of pelagic juvenile salmonids (*Onchorhynchus tschawytscha*, *O. nerka*; K. Polivka, unpubl. data) and an abundant population of *Cottus asper* (Polivka,

2011), the most numerous fish consumer of littoral benthic macroinvertebrates in this system. Individuals move near the shore at dusk to forage and potentially to escape predation from larger fishes off-shore, such as bull trout (*Salvelinus confluentus*; unpubl. data). During the day, individuals move off-shore. Larger individuals (>65 mm SL) have been observed to cannibalise young-of-the-year and life-history traits such as growth, survival and body condition are affected by the foraging and predation risk trade-off in this species (Pfister, 2003; Polivka, 2011). For eight streams that flow into the southern shore, we established plots (25 m^2) at the stream inflow to the lake (designated 'inflow') and at an otherwise similar littoral site 20–40 m away from each inflow ('control'). We confirmed that control plots had the same physical features (size, substratum, bottom slope, aspect etc.) as inflow plots.

Environmental correlates of fish abundance and macroinvertebrate biomass

We deployed TidBit™ loggers in each stream and in corresponding inflow and control plots to record temperature every 1 h throughout the study. On days when macroinvertebrate and fish sampling took place, we also measured dissolved oxygen and temperature using a YSI 80 probe meter in both the stream and in the middle of each 25 m^2 plot. An estimate of stream discharge was made when invertebrates were sampled. At each littoral site, we measured the slope of the lake bed with a clinometer and estimated visually the relative coverage of mud, sand, gravel, cobble and rock in the substratum. Gravel was defined as mineral material *c.* 0.5–1.5 cm in diameter, cobbles were defined as particles 3–20 cm diameter, whereas rocks were >20 cm diameter. Substratum coverage estimates and bottom slope measurements were taken at the beginning of the study only because they were unlikely to change during the relatively short period (2004–2005) of sampling.

Invertebrate sampling

To determine whether stream drift affected the biomass of the littoral benthos, we sampled benthic macroinvertebrates at inflow and control plots, and drift in the water column of the streams. We sampled all sites monthly between July and September 2004 and bi-monthly (March, May, July and September) in 2005. Thus, in the second year, we lengthened the study season, but did not greatly increase the time spent processing samples in the laboratory.

We sampled the littoral macroinvertebrate benthos with a 250-μm-kick net, taking three independent samples of 1 m^2 benthic area within each 25 m^2 plot type at each site. The substratum was kicked for 30 s to 1 min, to thoroughly agitate the entire 1 m^2 area and suspend macroinvertebrates, where they were collected by sweeping with the net. We preserved each sample in 70% ethanol and sorted the invertebrates from debris in the laboratory under a dissecting microscope. After sorting, we air-dried (for at least 24 h or until constant mass was obtained) and measured the mass of the entire individual sample to the nearest 0.0001 g with an analytical balance. We estimated mean (n = 3) macroinvertebrate biomass (g m^{-2}) in each plot at each site.

We sampled macroinvertebrates in stream drift by diverting as much of the flow as possible through a 10 × 10 cm (opening area) rectangular pipe, placed 10–15 m upstream of the inflow to the lake, and into a 250-μm-mesh drift net. Flow through the pipe (m^3 s^{-1}) was measured at the beginning and at the end of a 24 h sample period. We used an average of current velocity measurements and the height of the water at the opening of the pipe to estimate the total volume of water that passed through the drift net in 24 h. From the percentage of stream flow captured (usually 100%), we estimated the total discharge of the streams using the method described in Wipfli & Gregovich (2002).

It is possible that invertebrates drifting into the lake changed the species composition of the littoral benthos, even if there was not an effect on total biomass. We randomly selected a subsample of the 16 plots (i.e. eight inflows, eight controls) for an analysis of taxonomic composition prior to drying them. From three of the original eight sites, each consisting of inflow, control and drift samples, we identified and recorded the number of individuals in each taxonomic group (usually to family, but genus when possible) in samples from August and September 2004, and May and July 2005. In each of those 4 months, different groups of three sites were selected at random. This procedure was evaluated to determine whether we had sufficient sample size and statistical power to make inferences about changes to the composition of the benthos (see 'Data Analysis' below). After identification of the macroinvertebrates in these samples, we followed the protocol of drying and weighing described earlier.

Fish sampling

At dusk on the same day that macroinvertebrate kick samples were taken, we sampled the abundance of *Cottus asper*. We conducted two passes with a 3-mm-mesh seine

in the 25 m^2 sample areas at both inflows and controls for each of the eight sites. Use of a seine has been effective in other studies of cottids (Alofs & Polivka, 2004; Polivka, 2005, 2007), though, in some cases, the littoral substratum might have allowed some fish to avoid capture. To prevent this, one crew member kicked the substratum in an effort to dislodge fish from larger cobbles. Most fish were captured on the first pass, but we consistently used two passes at each plot each time for a standardised effort across the study area. Although this may underestimate total fish abundance, we were most interested in comparing relative abundance in each plot type. Because inflow and control plots had similar substrata, we assumed that capture avoidance did not proportionally bias fish abundance estimates in either plot type. All fish were placed into buckets where they were immediately identified, measured (standard length in mm), weighed and released. We also noted the presence of any other species captured (usually juvenile salmonids and cyprinids) and collected the same basic size data. For *C. asper* only, we calculated total abundance, total biomass and young-of-the-year (YOY) abundance (<45 mm SL) for inflows and controls at each site and for each of the seven sampling intervals. For analysis of habitat selection that might be mediated by predation risk, we calculated the ratio of predatory-sized individuals (>65 mm; Pfister, 2003; Polivka, 2011) to YOY at each site/sampling event, and the proportion of the total fish abundance that consisted of individuals large enough to be predators. Because we sampled over the same fixed area each time, we represent fish abundance by the raw numbers sampled, rather than as density. Total fish biomass was highly correlated with abundance ($P < 0.0001$, $r^2 = 0.50$); thus, we analysed fish response using abundance only.

Data analysis

To establish first the potential of our study streams to affect either the environment (temperature and dissolved oxygen) or invertebrate biomass at stream inflows, we calculated the difference in these variables (ΔT, ΔDO, ΔBiomass) between the inflow and control plots at each site during each sampling occasion. For each site, we calculated the average difference between plots across all sampling months and used a one-sample *t*-test to determine whether the average differences among the eight sites and seven sampling periods differed significantly from zero. We then regressed each of those differences against each estimate of stream discharge to determine whether the magnitude of the difference in each variable, between stream inflows and controls, was a function of total stream input. We concurrently analysed both temperature and dissolved oxygen with a three-way ANOVA to determine whether sites or plots (inflows, controls) were consistently associated with variation in these two parameters.

Our sampling design in the lake benthos was a randomised complete block design with repeated measurements. Because the replicate data consisted of 'inflow' and 'control' plots nested among the eight sites, we used a hierarchical mixed effects linear model (with a random intercept) for analysis, with site as the random effect. There was also evidence that the repeated measurements were positively auto-correlated, so a first-order autoregressive correlation structure was applied. Tests of model assumptions revealed that benthic invertebrate biomass data were negatively skewed and required logarithmic transformation. We applied arcsin square-root transformation to the (proportional) data describing the composition of the substratum. ANOVA was used to confirm that the sites did not differ from one another in substratum composition. Our initial model contained all explanatory variables in the fixed component, along with the two-way interaction between habitat and time. Non-significant variables were removed one at a time, and models were compared to each other using ANOVA (likelihood ratio test) to determine whether removing the variable had a significant effect on the model. The Akaike information criterion (AIC) value was used to determine the best model. We excluded dissolved oxygen from this analysis because there were several missing measurements due to a malfunction in the YSI meter and missing values prevent mixed effects modelling.

We used the percent similarity index (PSI) to determine whether the input of taxa via the drift changed the macroinvertebrate community composition at inflow or control plots. The null prediction was that similarity between stream drift and either inflow or control plots would be lower than the similarity between inflow and control plots. We calculated the similarity index for each pair of macroinvertebrate samples (inflow versus control, stream drift versus inflow, stream drift versus control; $n = 3$ sites) from all time periods (August, September 2004; March, May 2005) at each site. Thus, each comparison class consisted of the pooled ($n = 12$) PSI values from all months. The means of the three comparisons classes were compared using a one-way ANOVA. Data were arcsin square-root transformed prior to analysis, and pairwise comparisons among mean similarities were made with Tukey's HSD test. We conducted a power analysis to determine whether the number of subsamples (three sites per month) was sufficient to determine significant differences in mean PSI.

We used linear hierarchical mixed effects models to determine whether fish abundance was predicted by plot type (nested within sites), invertebrate biomass or any of the physical environmental characteristics, again using site as the random variable and an autoregressive correlation structure to account for repeated samples at the same sites over time. Model analyses were performed independently for both total fish and young-of-the-year abundances. Initially, we included all explanatory variables (plot type, log-transformed invertebrate biomass, lake bed slope, temperature and five substratum compositions, as well as the interaction between habitat and invertebrate biomass) in the fixed component. For young-of-the-year <45 mm SL, we also included the fraction of predators (>65 mm) in the total number of fish sampled at each site as a fixed effect. Non-significant variables were removed from the models until the best model was achieved, as measured by the AIC values. Because predation risk was likely to be an important predictor, we examined the fraction of predators across plot types (stream junction versus control) with a three-factor (plot, site, time) ANOVA as we did previously for temperature and dissolved oxygen. To test for a correlation between fish abundance and food availability, we performed hierarchical mixed-model regressions of total fish abundance and young-of-the-year abundance independently for inflow and control plots to determine whether the relationship between food resources and fish abundance was different in the two.

Results

Physical variables in streams and the lake littoral zone

Streams varied considerably in size, with total estimated discharge during typical summer flows ranging from 0.002 to 0.115 $m^3 s^{-1}$; mean temperature in each stream across each of the sampling months ranged from 7.16 to 10.26 °C, with seven of the streams ranging between 7.16 and 8.38 °C (Table 1). Winter (November–February) mean temperature in the littoral zone ranged, at the different sites, from 1.0 to 8.9 °C (mean = 3.78 °C), and in summer (July–September) from 13.6 to 19.8 °C (mean = 15.97 °C). As a result of the input of substantially cooler water from the streams, inflow plots averaged *c.* 2 °C cooler than control plots across all summer sampling periods (three-way ANOVA $F_{1,116} = 5.45$, $P = 0.021$; Fig. 1). The difference in temperature observed between a stream inflow and its associated control was partially explained by variation in the total discharge of the stream ($F_{1,6} = 6.45$, $P = 0.045$, $r^2 = 0.433$). Stream 4 was consistently warmer than the other seven and had the lowest discharge (Table 1); thus, thermal effects of stream input were least discernible at that site. Dissolved oxygen was relatively homogeneous among streams; it ranged from 10.31 to 11.56 mg L^{-1} with the warmest stream predictably having the lowest concentration (Table 1). Stream inflow plots averaged slightly higher concentration than control plots (9.91 versus 9.71 mg L^{-1}) across the study period, but neither plot ($F_{1,88} = 0.815$, $P = 0.369$) nor site ($F_{1,88} = 2.10$, $P = 0.151$) nor temporal ($F_{1,88} = 2.66$, $P = 0.107$) differences were evident. Furthermore, the relationship between stream discharge and the difference in dissolved oxygen between inflow and control plots in the lake was not statistically significant ($F_{1,6} = 2.99$, $P = 0.133$, $r^2 = 0.33$).

Table 1 Mean (SE) physical data (temperature, dissolved oxygen, discharge) for eight headwater streams flowing into Lake Wenatchee measured on seven sampling occasions (monthly, July–September 2004; bimonthly, March–September 2005)

Stream	Temperature °C	Dissolved Oxygen (mg L^{-1})	Discharge ($m^3 s^{-1}$)
1	8.06 (0.476)	10.81 (0.333)	0.0037 (0.001)
2	8.38 (0.720)	10.59 (0.453)	0.0310 (0.015)
3	7.16 (0.149)	11.07 (0.376)	0.1383 (0.056)
4	10.29 (1.28)	10.31 (0.479)	0.00005 (0.00003)
5	7.23 (0.412)	11.55 (0.278)	0.043 (0.011)
6	7.54 (0.427)	11.11 (0.319)	0.0092 (0.012)
7	7.70 (0.893)	11.16 (0.443)	0.003 (0.0006)
8	7.67 (0.899)	11.56 (0.237)	0.0139 (0.012)

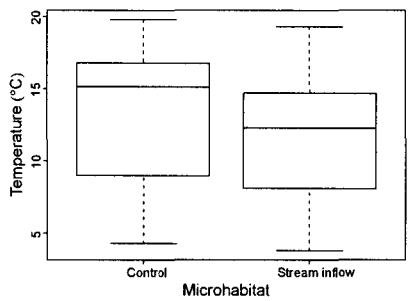

Fig. 1 Temperature at littoral sites with input from streams (Inflows; $N = 8$) and at sites lacking stream input (Control; $N = 8$) corresponding to each macroinvertebrate and fish sampling event. Box-and-whisker plots represent the distribution of temperatures at all sampling events (July–September 2004, March–September 2005) from each of the eight sites. Differences among inflows/controls were significant by three-factor ANOVA (with plot type, site and sampling location as factors; see text).

Does macroinvertebrate drift from headwater streams affect prey availability in the littoral?

Neither the drifting biomass ($F_{1,33} = 1.20$, $P = 0.281$), nor the invertebrate biomass difference ($F_{1,39} = 0.020$, $P = 0.889$) between plots (inflows versus controls) was

correlated with discharge from the streams. On average, the biomass of transported by the stream (mg m^{-3}) was 3% of the average density of the standing crop (mg m^{-2}) at the inflow plots. Hierarchical mixed effects models indicated no significant difference in macroinvertebrate biomass between inflow and control plots, nor was there an interaction between plot type and any of the other variables (Table 2). Although there was considerable spatial and temporal variation in macroinvertebrate biomass, the difference in biomass between inflows and controls was statistically zero (t_7 = 1.40, P = 0.203) over the entire study. Of the potential explanatory variables, bed slope and four substratum variables (cobble, gravel, sand and mud) were significant (Table 2) and represented the best-fit model to describe macroinvertebrate biomass within the study.

Macroinvertebrate community composition in the littoral benthos was not measurably affected by drift. Samples analysed showed the highest similarity of macroinvertebrate taxa in the comparison between inflow and control plots and lowest similarity when stream drift was compared with either inflow or control plots ($F_{2,33}$ = 9.25, P = 0.0006; Fig. 2). Power analysis indicated that we would require an inordinate number of samples ($N = 2.4 \times 10^4$) for the observed similarity between inflow and drift samples (0.471) to be significantly different from the observed similarity between control and drift samples (0.466), at a power of 1-β = 0.80, indicating that the subsampling procedure was adequate to determine whether stream drift changed the composition of the littoral benthos.

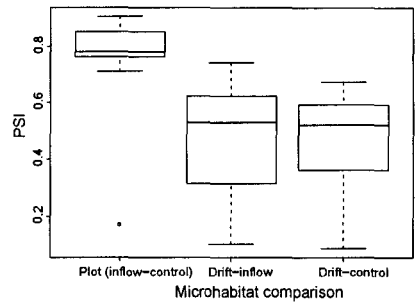

Fig. 2 Box-and-whisker representation of the proportional similarity index (PSI) comparing macroinvertebrate taxonomic composition on a randomly selected subset of three stream and near-shore lake site groups (see text) analysed for sample periods (August–September 2004, May–July 2005). PSI values are grouped by comparison type, i.e. stream inflow and control samples in the lake ('Lake Microhabitats'), and stream drift with either stream inflows or controls. PSI comparing lake microhabitats was significantly higher ($F_{2,33}$ = 9.25, P = 0.0006) than PSI comparing either lake microhabitat type to the drift.

Do fish track total resource availability?

In the mixed effects model for total fish abundance, none of the substratum variables were significant; thus, they were removed from the initial model. After applying the autoregressive correlation structure to the model to account for repeated measurements, the best model identified significantly higher total fish abundance at stream inflows. There was also a significant positive association between total fish abundance and invertebrate biomass and bed slope (Table 3). Despite there being no detectable difference in invertebrate biomass between the different inflows and controls (Table 2), the interaction term of habitat type × invertebrate biomass was significant in explaining variability in fish abundance in the best-fit model (Table 3).

Young-of-the-year fish abundance was described by the same variables affecting total fish (habitat, invertebrate

Table 2 Coefficients and statistical output for the best-fit mixed effects linear model for log-transformed macroinvertebrate biomass fit to environmental predictors by restricted maximum likelihood (REML), with site as the random intercept and an AR(1) correlation structure (d.f. = 99)

Fixed effects	Slope	Standard error	*P*-value
Bed slope	0.07	0.03	0.006
Cobble substratum*	1.63	0.73	0.028
Gravel substratum*	1.34	0.55	0.017
Sand substratum*	1.56	0.53	0.004
Mud substratum*	2.01	0.70	0.005

*Substratum proportions were arcsin square-root transformed for analyses.

Table 3 Coefficients and statistical output for the best-fit mixed effects linear models for (a) total *C. asper* abundance, and (b) YOY *C. asper* abundance. Models fit by REML, with site as the random intercept and an AR(1) correlation structure (d.f. = 100, total fish abundance; d.f.=98 for YOY abundance)

Fixed effects	Slope	Standard error	*P*-value
(a)			
Plot type (inflow/control)	12.37	5.05	0.016
Invertebrate biomass*	3.92	1.47	0.009
Bed slope	0.79	0.29	0.008
Plot type × Invert. biomass*	−3.66	1.74	0.038
(b)			
Plot type (inflow/control)	7.07	3.22	0.031
Invertebrate biomass†	2.65	0.90	0.004
Bed slope	0.36	0.18	0.055
Plot type × Invert. biomass†	−2.50	1.10	0.025
Fraction of predators†	−5.32	1.53	0.001
Temperature	−0.32	0.14	0.021

*Macroinvertebrate biomass was log-transformed for analyses.
†Invertebrate biomass was log-transformed and fraction of predators was arcsin square-root transformed for data analyses.

biomass, bed slope, and the interaction between habitat and invertebrate biomass), as well as strong negative associations with the fraction of predators present (which was not different between inflow and control plots; three-way ANOVA, $F_{1,106} = 1.45$, $P = 0.231$) and temperature (Table 3). Based on the model, the combined effects of temperature and predation risk on YOY fish abundance indicate that YOY individuals may tolerate a slightly greater predation risk in cooler microhabitats.

When inflows and controls were separated and analysed independently, we found that the overall positive relationship between the numerical abundance of *C. asper* and macroinvertebrate biomass was driven by correlations at control plots for both total ($\beta = 4.449$, $P = 0.005$, Fig. 3a) and YOY ($\beta = 2.618$, $p = 0.002$, Fig. 3b) fish abundance. At stream inflows, regression indicated no significant trend in total fish ($\beta = 0.925$, $P = 0.650$) or YOY ($\beta = 0.303$, $P = 0.803$) abundance that could be explained by invertebrate biomass alone.

Discussion

Delivery of resources by streams can provide a subsidy to downstream habitats (Polis *et al.*, 1997; Wipfli & Baxter, 2010). Although there are several examples of transport rates from headwater streams varying across landscapes (e.g. Nislow & Lowe, 2006; Binckley *et al.*, 2010), and resource accumulation at the downstream confluence with larger streams (Kiffney *et al.*, 2006), demonstration of a positive fish response in habitats that receive such inputs is difficult. The challenge in determining whether this transport is a true 'subsidy' is to show (i) increased availability of specific resources not present in similar habitats and (ii) that consumers (fish in this case) benefit from these otherwise unavailable resources (Kawaguchi *et al.*, 2003; Baxter *et al.*, 2004, 2007). We attempted to detect a fish response to prey input by streams in this study, but were limited by the small size of the streams available.

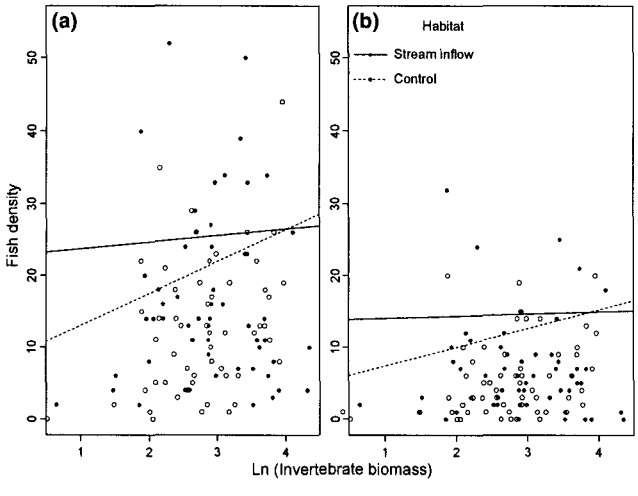

Fig. 3 *Cottus asper* total (a) and young-of-the-year (b) abundance as a function of log-total biomass of macroinvertebrates with hierarchical mixed-model linear regression lines (see text) for each near-shore habitat type. Positive relationships indicating resource tracking are significant only for 'control' sites, but a significant plot type invertebrate biomass interaction was revealed by multivariate hierarchical analysis.

The streams in our study system did not consistently contribute to variation in the biomass of the standing crop of macroinvertebrates in the lake littoral zone. Similarly, taxonomic composition of the macroinvertebrate benthos at stream inflows was not measurably changed by the drift of stream taxa. Drift distances can be short (Danehy *et al.*, 2011) and proportional to stream size (Kiffney *et al.*, 2006); thus, the minimal impact observed on littoral macroinvertebrate biomass and composition might be due to the small size of the streams. Alternatively, if stream taxa were consumed selectively by *C. asper*, the composition of the macroinvertebrate benthos might be similar in both inflow and control plots. To avoid destructive sampling for the temporal component of this study, we did not examine fish gut contents to identify consumption of stream-derived prey at inflow plots.

The low biomass drifting in streams reported above (average 3% of the benthos) suggests the lack of a strong subsidy, although the mixed effects model suggested that both littoral habitat selection and food resource tracking by *C. asper* was influenced by stream input. The significant interaction between plot type and invertebrate biomass resulted from the increasing relationship between fish abundance and benthic invertebrate biomass in control plots and lack thereof at stream inflows. At low standing crop in the benthos, inflow plots had higher fish abundance than control plots (Fig. 3). If this were due to a prey subsidy from streams, we would predict a consistent subsidy across all levels of standing crop in the benthos and parallel lines in Fig. 3. The convergence of inflow and control plot lines in both Fig. 3a,b suggests the lack of a subsidy, unless the habitat become saturated with food from either source such that fish abundance no longer increases. Such an effect would be difficult to detect without a well-controlled experiment and would not be discernible from gut contents alone.

The pattern in YOY abundance was affected by consistent and substantial negative effects of increasing predation risk and temperature (Table 3). During the summer, the relatively cooler inflow plots (Fig. 1) can reduce predation risk by reducing foraging requirements. Meta-

bolic demands generally increase for ectotherms like fish in warmer water, resulting in increased foraging (e.g. Garvey, Ostrand & Wahl, 2004; Byström *et al.*, 2006), which can increase exposure to predation risk. Higher metabolic demands may result in reduced energetic reserves and individuals in this condition are predicted to take more risks to forage (e.g. Clark, 1994; Kotler *et al.*, 2010; Polivka, 2011). Occupancy of the cooler inflow plots (Fig. 1) could reduce risk to YOY individuals, both via lower foraging requirements of the young fish and lower predatory activity from adults. When prey biomass in the benthos is low, it could be advantageous for all size classes to occupy stream inflows because energetic requirements are also lower. Further experimentation is required to address the influence of these bioenergetic mechanisms, but other evidence from this study system shows that condition index in YOY *C. asper* is affected in a manner consistent with a strong foraging/predation risk trade-off (Polivka, 2011).

Downstream transport of macroinvertebrates has been well-studied (e.g. Binckley *et al.*, 2010; Wipfli & Baxter, 2010), although its effects higher in the food web, such as on fish, are highly variable (Rosenfeld & Raeburn, 2009), sometimes only inferred qualitatively (Wipfli & Gregovich, 2002), and usually clearest when terrestrially derived prey are being transported downstream and consumed by fish (Kawaguchi *et al.*, 2003; Baxter *et al.*, 2004, 2007). Habitat selection by *C. asper* in our study system was highly variable and hierarchical linear models enabled us to identify a positive interaction between stream inflow habitats and standing crop of benthic invertebrates. Additional mechanisms and inputs of habitat selection behaviour in this study system remain unexplained because we found no evidence of a direct resource subsidy, probably due to small stream size. Moving beyond observational studies such as this one will require additional research into bioenergetics and trophic dynamics.

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