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The energetic consequences of habitat structure for forest stream salmonids

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Summary

1. Increasing habitat availability (i.e. habitat suitable for occupancy) is often assumed to elevate the abundance or production of mobile consumers; however, this relationship is often nonlinear (threshold or unimodal). Identifying the mechanisms underlying these nonlinearities is essential for predicting the ecological impacts of habitat change, yet the functional forms and ultimate causation of consumer-habitat relationships are often poorly understood.
2. Nonlinear effects of habitat on animal abundance may manifest through physical constraints on foraging that restrict consumers from accessing their resources. Subsequent spatial incongruence between consumers and resources should lead to unimodal or saturating effects of habitat availability on consumer production if increasing the area of habitat suitable for consumer occupancy comes at the expense of habitats that generate resources. However, the shape of this relationship could be sensitive to cross-

ecosystem prey subsidies, which may be unrelated to recipient habitat structure and result in more linear habitat effects on consumer production.

3. We investigated habitat-productivity relationships for juveniles of stream-rearing Pacific salmon and trout (*Oncorhynchus* spp.), which typically forage in low-velocity pool habitats, while their prey (drifting benthic invertebrates) are produced upstream in high-velocity riffles. However, juvenile salmonids also consume subsidies of terrestrial invertebrates that may be independent of pool-riffle structure.
4. We measured salmonid biomass production in 13 experimental enclosures each containing a downstream pool and upstream riffle, spanning a gradient of relative pool area (14-80% pool). Increasing pool relative to riffle habitat area decreased prey abundance, leading to a nonlinear saturating effect on fish production. We then used bioenergetics model simulations to examine how the relationship between pool area and salmonid biomass is affected by varying levels of terrestrial subsidy. Simulations indicated that increasing terrestrial prey inputs linearized the effect of habitat availability on salmonid biomass, while decreasing terrestrial inputs exaggerated a 'hump-shaped' effect.
5. Our results imply that nonlinear effects of habitat availability on consumer production can arise from trade-offs between habitat suitable for consumer occupancy and habitat that generates prey. However, cross-ecosystem prey subsidies can effectively decouple this trade-off and modify consumer-habitat relationships in recipient systems.

Introduction

The abundance and productivity of mobile consumers are often strongly linked to the availability of habitat suitable for growth, survival, or reproduction. Consequently, there is often an expectation that increasing habitat availability (e.g., abundance and connectivity of habitat suitable for consumer occupancy) will lead to greater population size or secondary production (Palmer, Ambrose & Poff 1997). While this assumption usually underpins habitat restoration efforts, it has been complicated by numerous studies documenting nonlinear (unimodal and threshold) effects of habitat availability on consumer performance (Venier & Fahrig 1996; Allouche *et al.* 2012; Shideler *et al.* 2017).

Identifying these nonlinearities and their underlying mechanisms is paramount for understanding population limitation in physically heterogeneous environments and for mitigating negative impacts of habitat alteration (Kovalenko, Thomaz & Warfe 2011; Keller *et al.* 2017). One pathway through which nonlinearities can arise relates to habitat complementation (Dunning, Danielson & Pulliam 1992), where different habitat types provide distinct non-substitutable resources for a population. Increasing the abundance of habitat patches suitable for occupancy across a landscape may then have limiting returns or even negative effects on consumer populations if it comes at the expense of indirect functions provided by other habitat patches that are not directly occupied (Schlosser 1995).

A particularly notable example of this phenomena occurs when physical heterogeneity restricts predators from accessing areas of high prey production (Persson *et al.* 1996; Kauffman *et al.* 2007); for instance, if prey originate in refuges with harsh abiotic conditions that exclude predators (Menge & Lubchenco 1981; Tunney *et al.* 2012). If total prey abundance is positively related to the area of refugia, then increasing the availability of habitat suitable for predators should also decrease the abundance of their food. Predator production may therefore exhibit thresholds or optima at intermediate levels of habitat availability when energy intake is maximized relative to spatial requirements (e.g., territory size; Grant & Kramer 1990). In essence, this nonlinearity reflects a trade-off between two key factors regulating populations: food abundance and space suitable for occupancy.

Despite broad support for foraging constraints as a mechanism generating nonlinear habitat effects (Heck & Crowder 1991), few studies have explicitly quantified how different configurations of contrasting habitats influences the biomass production of mobile consumers. Thus, the functional form of consumer-habitat relationships in heterogeneous environments are often unknown and the factors that modify the shape of this relationship are poorly understood. In particular, consumers may respond to habitat availability differently in systems dominated by allochthony, where prey originate outside the system of interest (Polis, Anderson & Holt 1997)). For instance, if renewal rates of cross-ecosystem prey subsidies are unrelated to recipient habitat structure (Richardson, Zhang & Marczak 2010), increasing consumer habitat availability should have less influence on total resource abundance and we may expect more linear effects of habitat availability on consumer production in highly subsidized systems.

We experimentally quantified the relationship between habitat availability and production of juvenile Pacific salmon and trout (Salmonidae) in a temperate forest stream and used simulation modelling to explore how this relationship may be influenced by cross-ecosystem prey subsidies. Stream-rearing salmonids are well-suited to address these questions because their growth and survival are strongly linked to geomorphic channel structure, which regulates both *in situ* prey production and habitat suitable for fish occupancy (Rosenfeld & Boss 2001; Kennedy, Nislow & Folt 2008). Salmonids typically forage in dominance hierarchies where they defend fixed, central-place territories to intercept suspended invertebrates in downstream transport (invertebrate drift; Chapman 1966; Naman, Rosenfeld & Richardson 2016). Drift originates primarily in shallow high-velocity riffles where benthic invertebrates enter drift behaviourally or are dislodged by flow (Leung, Rosenfeld & Bernhardt 2009; Naman *et al.* 2017); however, many salmonids preferentially use deeper low velocity pools where higher capture success and reduced swimming costs make drift-foraging more energetically profitable (Fausch 1984; Hill & Grossman 1993). This incongruence leads to the prediction that salmonid production should peak at intermediate ratios of pool-riffle habitat patches (Poff & Huryn 1998; Rosenfeld & Raeburn 2009).

However, cross-ecosystem inputs of terrestrial invertebrates are also a key property of small forest streams, often dominating annual energy budgets for salmonids (Kawaguchi & Nakano 2001; Sato *et al.* 2011). Terrestrial inputs originate from the riparian zone (Richardson & Sato 2015) and while they are linked to geomorphology over larger scales (Bellmore & Baxter 2014), they do not vary systematically with pool-riffle channel structure (Gowan & Fausch 2002; Naman *et al.* 2017). Consequently, terrestrial inputs could modify the influence of pool-riffle patch configuration on fish production, effectively decoupling the dependence of pool-rearing salmonids from riffle-produced drift.

We conducted a field experiment to test the influence of habitat availability (i.e., the proportion of habitat area composed of pool relative to riffle) on consumption, production, and behaviour of an assemblage of drift-feeding salmonids consisting of juvenile coho salmon *Oncorhynchus kisutch* and cutthroat trout *O. clarki*. We tested two alternative hypotheses of how pool-riffle composition may influence productivity based on intrinsic vs. extrinsic resource origin (i.e. drift vs. terrestrial drop). We hypothesized that if drift was the primary mode of resource delivery, increasing pool proportion should impose a food-space trade-off such that (*i*) usable habitat should increase but prey encounter rates should decline with increasing pool habitat, and (*ii*) consumption and production by fish should therefore peak at an intermediate pool proportion. Alternatively, we hypothesized that if terrestrial inputs were the primary mode of resource delivery to fish, pool-riffle composition would limit only the area of suitable habitat for occupancy, such that increasing pool proportion would lead to (*iii*) no changes in energy availability and (*iv*) a linear increase in consumption and production (Fig. 1). Given that drift-feeding fish often exhibit plasticity in foraging behaviour (Fausch, Nakano & Khano 1991), we also made the general prediction that with increasing terrestrial prey inputs (*v*) there should be a shift from territorial central place foraging on drift to search foraging on terrestrial drop. We link these two hypotheses using bioenergetic model simulations to explore the effects of pool-riffle composition on production across a full gradient of drift vs. terrestrial resource inputs. Thus, the experiment and simulations provide a unique test of the mechanisms underlying the form of habitat-productivity relationships, and the potential influence of cross-ecosystem resource subsidies.

Materials and Methods

Study system and logistics - We conducted our study in Webster Creek, a tributary of the Cedar River, a protected watershed on the west slope of the Cascade Mountains in Washington State, USA (see Kiffney *et al.* 2006). Webster Creek is a low gradient, rocky-bottomed pool-riffle stream draining a conifer-dominated, second-growth catchment with riparian vegetation typical of streams in the region. Wetted channel width at the study site averaged 2 m and summer low flow discharge ranged from 0.01-0.03 $m^3 \cdot s^{-1}$. Fish species in Webster Creek include coho, cutthroat trout, brook lamprey *Lampetra richardsoni*, and several species of sculpin *Cottus* spp. (P. Kiffney unpublished).

We selected 13 riffle-pool sequences (Frissell *et al.* 1986) as experimental units within a 2 km stream reach with the goal of maximizing variation in the relative area of pools and riffles (14-80% pool area). The proportion of total area composed of pool relative to riffle (hereafter “pool proportion”) was the independent variable in this study. Relative pool area was not related to longitudinal position of enclosures in the study reach, and enclosures were spaced at least 10 m apart such that invertebrates were unlikely to drift between them (Elliott 2002). Pool-riffle sequences were selected to minimize variation in other physical features, including wood density, canopy cover, pool depth, and riffle velocity (Table 1). To quantify differences in hydraulic conditions between riffles and pools, we measured depth and velocity at 20 cm intervals along 3-5 transects perpendicular to flow in each pool or riffle using a Marsh McBirney flow meter (Hach Company, California). Water temperature was continuously recorded with ibutton® data loggers. Other physical features including residual pool depth, wood abundance, and canopy cover were measured following methods described in Pess *et al.* (2011) and Kiffney & Roni (2007).

To construct enclosures, we anchored 5 mm grid wire-mesh fences at the upstream and downstream end of each pool-riffle sequence using rebar stakes and sealed fences by burying the lower edge 10 cm under the substrate. Fences allowed free passage of drifting invertebrates while preventing movement of fish larger than 30 mm fork length and were cleaned daily during the experiment to prevent clogging. Enclosure fences that are permeable to invertebrates were essential to avoid blocking flow and altering hydraulics within enclosures. However, high permeability could reduce power to detect treatment effects if prey abundance inside enclosures was significantly influenced by drift of invertebrates from outside of enclosures (Cooper, Walde & Peckarsky 1990; Englund & Hamback 2004). While this is an inherent challenge to experiments in flowing water, two lines of evidence suggest prey abundance was primarily produced locally within our enclosures: first, all enclosures were directly downstream of low velocity pools or glides, where drift concentrations were reduced by settlement and predation; and second, the absolute lengths of riffles were sufficient for the majority of upstream drift to settle before being available to fish in pools (Supporting Information 1). In addition, drift from outside enclosures was unrelated to pool-riffle habitat structure (Supporting Information 1; Fig. S2) thus, it would likely generate noise and reduce overall power to detect habitat effects on total prey abundance, rather than cause a directional bias.

Quantifying prey availability - Invertebrate drift was measured three times (day 5, 15, and 25) during the experiment. Drift sampling involved setting 2-3 nets (306.5 cm^2 opening) across the downstream end of each enclosed riffle for 2-4 hours between 1000 and 1400. Terrestrial invertebrate inputs were measured with 1-2 floating pan traps (400 cm^2) containing 10 mm of water and ~5 ml of soap to reduce surface tension, placed haphazardly within each enclosed pool. Pan traps were left for 6-8 h during daylight and were aggregated across three sampling events to calculate a mean value for each pool. All invertebrates were stored in 75% ethanol and then sorted and identified (typically to family or genus) in the laboratory. We measured the body length of each individual with a ocular micrometer and used allometric equations to convert length to mass (Hodar 1996, Benke *et al.* 1999, Kiffney & Naman unpublished data). Drift and terrestrial inputs were computed as a total energy flux per area of total enclosure (kilojoules m^{-2} day^{-1}), with drift flux calculated as the product of drift concentration and stream discharge. Energy density was used as opposed to biomass as it more explicitly integrates variation in prey quality (Beauchamp 2009). Mass conversion factors from Cummins & Wuycheck (1971) and McCarthy *et al.* (2009) were used to convert biomass to energy density.

Fish growth, production, and habitat use - We collected juvenile coho salmon and cutthroat trout using minnow traps and seine nets. Coho ranged from 48-95 mm in length while cutthroat ranged from 50-100 mm. While these species interact and differ slightly in microhabitat use (e.g., Glova 1986), previous work in the system suggests they are not strong competitors (Buehrens *et al.* 2014), and they are treated here as a single drift-foraging assemblage. Fish were held overnight to allow gut clearance, then measured to the nearest mm, weighed to the nearest 0.1 g, and individually marked with elastomer tags (Northwest Marine Technologies, Shaw Island, WA). Equal numbers of coho and cutthroat of a similar size range were stocked at a density of 0.5 fish m^{-2} per area of enclosure (i.e., area of pool and riffle combined). Before stocking, we snorkelled through each enclosure to ensure all salmonids had been removed. We recaptured fish 30 days later and re-measured lengths and weights as described above. We computed growth rates (g day^{-1}) for individuals as [(mass final) - (mass initial)]/duration and total production as the summed mass change of all fish in each enclosure. Because enclosures differed in size, production values were standardized by enclosure area (g m^{-2}). 92% of fish were recaptured across all enclosures suggesting that terrestrial predation was minimal.

Snorkel surveys were conducted on four occasions to determine pool-riffle habitat preferences and the effective density experienced by individuals foraging in pools. Starting from upstream, we counted all fish through the length of each pool to compare with the known number of fish stocked into the enclosure. We assumed any unaccounted fish were using riffles, which were too shallow for snorkelling (< 20 cm). The effective fish density in pools was then computed as the quotient of the number of fish observed and pool area (number m^{-2}).

Behaviour observations - We conducted observations of territoriality and foraging behaviour on two occasions during the experiment. This involved a snorkelling observer lying motionless at the midsection of each pool for 15 minutes to minimize disturbance artefacts, then recording the number of fish present and the foraging behaviour of each individual over 5 minutes. Snorkeling was superior to other methods (e.g., video recording or streambank observations) in that we could observe the foraging behaviour of all individuals for a set time period. We classified fish as territorial if they maintained consistent foraging positions or non-territorial if they did not hold territories and fed on terrestrial or benthic invertebrates (Nielsen 1992).

Consumption and exploitation efficiency - To estimate fish consumption, we used a modified version of a Wisconsin bioenergetics model parameterized for each species (parameters from: Deslauriers *et al.* 2017), which we fit to observed growth (Supporting Information 2). There was strong correspondence between fitted and observed growth values (Supporting Information 2; Fig. S3), suggesting the model approximated true consumption. We report two metrics of consumption in relation to pool proportion: first, we describe bulk prey consumption by the entire fish assemblage as the *total consumption* of all individuals per area of enclosure (g m^{-2}), and second, we express *exploitation efficiency* as consumption relative to the energy available from the estimated prey flux. Exploitation efficiency was standardized to fall between 0 and 1, where 1 would indicate that 100% of the prey flux through an enclosure was consumed. Estimated consumption exceeded prey availability for two of 13 enclosures but the range of variation in exploitation efficiency overlapped 100%.

Statistical Analysis – We used R version 3.3.2 (R Core Development Team) for all statistical analysis. The effect of pool proportion on total fish production, consumption, and mean individual growth was determined using ordinary least squares (OLS) regression with three a priori model structures (linear, threshold, and quadratic). To further explore potential unimodal responses to increasing pool proportion, we also fit a Monod-Haldane function that provides more flexibility in that it allows slopes to differ on the ascending and descending arms of the curve (Bolker 2007). The model was fit with nonlinear least squares (nls) and was constructed as:

$$p(x) = \frac{mx}{a + bx + x^2}$$

where x is relative pool area and m, a, and b are fitted constants. These four model structures (along with an intercept only model) were compared with Akiake's Information Criteria corrected for small sample sizes (AIC_c) using the MuMin package (Bartón 2009), which selects the most parsimonious model to explain the data (Burnham & Anderson 2002). For top ranked models (ΔAIC_c within 2 of best model; Burnham and Anderson 2002) we computed 95% confidence intervals around coefficients and evaluated overall fits with R^2. In the nonlinear case, we evaluated model fits with root mean square error (RSME).

OLS was also used to evaluate the effect of pool proportion on total energy flux (drift plus terrestrial) and fish density in pools. For proportional responses including terrestrial drop proportion, exploitation efficiency, and foraging mode we used generalized linear models (GLM) with a quasi-binomial distribution to account for over-dispersion. Underlying model assumptions for GLMs were analyzed graphically with diagnostic plots using the R package modEVA (Márcia Barbosa *et al.* 2013). AIC_c model selection ($QAIC_c$ for over-dispersed models) was used to compare each response to a null model (intercept only), then likelihood confidence intervals were computed around the coefficients and overall fits were evaluated with Pearson r^2 using the *RsqGLM* function in modEvA.

Bioenergetic simulations of terrestrial prey additions - To explore the sensitivity of our results to terrestrial subsidies, we used the bioenergetics model to simulate growth at different levels of consumption corresponding to a wide range of terrestrial input rates. Production was computed in each simulation as the sum of growth (mass change) for all individuals in each enclosure. Simulations ranged from no terrestrial inputs (i.e., consumption equivalent to ambient terrestrial drop removed), up to input rates such that all fish were consuming prey at their physiological limit (i.e., satiation). While simulations encompassed a range of 0-1000 times the average ambient input rates (0.005 g m^{-2} day^{-1}), they were still within the documented range of variability in terrestrial inputs across time and space (e.g.Wipfli 1997; Nakano & Murakami 2001). For each simulation, AIC_c was used as described above to determine the most parsimonious OLS regression model form (linear, threshold, or quadratic) relating production to relative pool area (further described in Supporting Information 2).

Unlike more computationally intensive drift-foraging models, our simulations did not explicitly incorporate consumer functional responses and constraints on prey capture success, i.e., simulations assume all added prey would be captured. This assumption is probably unrealistic given prior empirical work (Piccolo, Hughes & Bryant 2008; Neuswanger *et al.* 2014) and given that our exploitation efficiency estimates indicated a significant reduction in the proportion of prey flux consumed at low pool proportions (see *Results*). To address this issue, we modelled three potential scenarios: first, where no additional prey capture was allowed in enclosures where less than 95% of the observed prey was consumed (i.e., assuming strong constraints on capture success in riffle-dominated enclosures); second, where additional prey was allowed to be consumed at the observed efficiency; and third, where all additional prey was consumed.

Results

Prey availability – Consistent with our first hypothesis, combined energy flux from drift and terrestrial inputs declined with pool proportion (Fig. 2a, OLS, W_i = 0.99, R^2 = 0.60; full results for all models are in Supporting Information 3; Table S2). This reduction was driven by variation in drift, which was the dominant mode of prey delivery (Table 1) and declined by an order of magnitude over the gradient of relative pool area (OLS, W_i = 0.98, R^2 = 0.64). As expected, terrestrial invertebrate inputs were not related to pool proportion (OLS, W_i = 0.99 for intercept only model); however, because of the steep decline in drift, the proportion of terrestrial inputs relative to drift increased by ~30% across the gradient of increasing pool proportion (Fig. 2b, GLM, W_i = 0.98 r^2 = 0.23). Similar to other studies, drift was composed primarily of immature stages of Ephemeroptera, Diptera, and Trichoptera and terrestrial drop was composed of adult Diptera, Hymenoptera, and Homoptera (Wipfli 1997).

Production, growth, and habitat use by salmonids – Salmonid production (g m^{-2}) exhibited a nonlinear relationship with pool proportion (Fig. 3a). A threshold model had the most empirical support (W_i =0.38, R^2 = 0.71) but there was also strong support for a quadratic model indicative of a unimodal relationship (ΔAIC_c = 0.24, W_i = 0.34, R^2 = 0.70) and some support for a linear model (ΔAIC_c = 0.99, W_i = 0.22, R^2 = 0.53). Mean individual growth was also non-linearly related to pool proportion with support for both a quadratic (Fig. 3b; W_i = 0.48, R^2 = 0.61) and a threshold relationship (ΔAIC_c = 0.67, W_i = 0.34, R^2 = 0.49). Snorkel observations indicated that fish consistently used pools throughout the experiment. Consequently, as the proportion of pool area declined across enclosures, effective fish density in pools increased by nearly six-fold (Fig. 3c, GLM, W_i = 0.99, r^2 = 0.98).

Foraging behaviour – Fish fed on drift and terrestrial invertebrates during foraging observations with only one benthic foraging attempt observed. The extent to which fish exhibited territorial central place foraging vs. non-territorial surface foraging was influenced by pool-riffle composition. The proportion of fish holding territories declined by ~60% across the gradient of increasing pool habitat (Fig. 3d: GLM W_i=0.98, r^2 = 0.57), with more fish search foraging at the downstream ends of pools.

Consumption and exploitation efficiency – Total estimated consumption showed a unimodal relationship with pool proportion, steeply increasing at low values then slowly declining after a maximum at intermediate pool proportion (Fig. 4a). The Monod-Haldane function had the most support to explain this result (NLS, W_i = 0.92, RMSE = 1.96). Exploitation efficiency also exhibited a strong trend (Fig. 4c) where less than 10% of available prey were consumed at the lowest pool proportion, which sharply increased to 100% of available prey consumed at intermediate and higher pool proportions (GLM, W_i = 0.99, r^2 = 0.97).

Bioenergetic simulations of terrestrial prey additions – Increasing terrestrial inputs across the gradient of increasing pool proportion generally linearized the relationship with fish production (Fig. 5) but the specific shape of the curve, and the input required to change it, differed among prey capture scenarios. In the most restrictive scenario, where no additional prey capture was allowed in enclosures with less than 95% exploitation efficiency, it took a 100-fold increase in input rate to alter the curve, and a 1000-fold increase to linearize the relationship (Fig. 5a). By contrast, in the second scenario where additional prey was consumed at observed efficiencies, the pool proportion-production relationship became linear at double the input rate, with subsequent additions increasing the slope (Fig. 5b). It is important to note that model fits were weaker at 2x and 10x input rates, and that there was also support for threshold models (Supporting Information S3, Table S4), which would have resembled the first scenario. Finally, in the third scenario, where all additional inputs were consumed in all habitats, it required a similar 100-fold increase to linearize the curve; however, the slope of the line gradually diminished and ultimately flattened at the production level expected if all fish were fully satiated, i.e., consuming at their physiological maximum (Fig. 5c). In all three scenarios, simulating reduced terrestrial inputs caused the relationship to be increasingly unimodal and to decline at the highest relative pool areas.

Discussion

Habitat availability (i.e., the proportion of pool relative to the upstream riffle) strongly mediated both space and food abundance for salmonids. Because fish overwhelmingly preferred pools and were stocked at a constant density over total habitat area (pools and riffle combined), the effective fish density strongly declined with increasing relative pool area. However, prey availability correspondingly declined with a decrease in relative riffle area that accompanied increased pool habitat. These responses are consistent with previous work demonstrating strong preference of coho and cutthroat trout for pools (e.g., Lonzarich & Quinn 1995; Roni 2002) and a positive relationship between drift flux and riffle length (Hansen & Closs 2007; Naman *et al.* 2017). The resulting trade-off between suitable foraging habitat and resource availability imposed by these contrasting habitat patch types caused a nonlinear response of salmonid consumption and production, whereby increasing pool proportion had diminishing returns beyond a threshold of ~45% pool. This ratio of habitat types that maximized salmonid production is similar to those predicted by Poff & Huryn (1998) and Rosenfeld (2014) and is also comparable to relationships between pool-riffle composition and salmonid biomass observed in field surveys by Bowlby & Roff (1986)

Our exploitation efficiency estimates corroborate the inference of a trade-off between space (preferred foraging habitat in pools) and food (prey production in riffles). Fish production per m^2 of total enclosure area was lower at reduced pool proportions despite high prey abundance, while production was elevated at higher pool proportions despite lower prey abundance. In the smallest pools, fish had reduced growth, consumption, and production, yet collectively consumed only ~15% of the total prey flux. This unconsumed prey surplus could in principle be available to fish in adjacent habitats downstream of enclosures; however, the extent of this non-local prey source depends on drift distances, which may be short in small streams (Downes & Reich 2008)

Constraints on prey capture in smaller pools likely related to reduced foraging area and greater competition at higher effective fish densities. For instance, more individuals may have occupied poorer quality foraging territories (Imre, Grant & Keeley 2004), agonistic interactions may have increased energy expenditure and decreased foraging time (Wood, Grant & Belanger 2012), or a higher proportion of prey may have been able to drift through shorter pools without detection. Increasing pool area appeared to partially relax these constraints as exploitation efficiency reached an estimated 100% at an intermediate pool proportion (45-50% of total area) that corresponded to an asymptote in total fish production.

Beyond an intermediate pool proportion, fish appeared to become increasingly food limited as the slope of total production diminished. However, despite a clear decline in prey abundance and consumption by fish with increasing pool proportion, it was unclear whether associated fish production also declined or simply levelled off. This ambiguity may be associated with increasing production efficiency, i.e., a larger proportion of food converted into biomass, with pool area. The mechanism potentially causing higher efficiency is unclear, but could relate to the reduced territoriality and increased search foraging we observed as pool area increased. Territoriality becomes increasingly costly as prey availability becomes less predictable (Grant 1993; Sloat & Reeves 2014); therefore, one interpretation of these results is that fish increased their growth efficiency in larger pools by shifting from defending central place territories to search foraging to exploit the greater proportion of terrestrial drop, which may be less spatially predictable than drift at pool-riffle scales (Gowan & Fausch 2002; Naman *et al.* 2017). However, since we did not measure the energetic consequences of foraging behaviour on individual fish, this interpretation is speculative and other factors related to reduced density (e.g. lower activity costs) could also have increased growth efficiency in larger pools (Li & Brocksen 1977).

Bioenergetic simulations allowed us to explore the sensitivity of habitat-production relationships to terrestrial subsidies. Our simulation results should be tempered by uncertainty in the functional response by fish to prey subsidies, which would require direct empirical validation; however, our results were qualitatively similar across the three capture efficiency scenarios that we modelled, suggesting that our inferences are likely robust. Generally, adding subsidies linearized the effect of pool proportion on production as predicted, while reducing subsidies accelerated the decline of fish production at high pool proportion. Taken together, these results imply that whether pool-dominated stream habitats are energetic sources vs. sinks depends on the magnitude of terrestrial prey inputs. While our specific predictions are constrained to the range of pool areas measured in this study (~14-70 m^2), terrestrial inputs may be even more important for sustaining fish production in larger pool-like habitats with low drift fluxes; for instance, side-channels, or floodplains (Rosenfeld & Raeburn 2009; Bellmore *et al.* 2013).

Taken together, our results suggest a general model for how hydraulic habitat composition and resource delivery shape reach-scale production for drift-feeding fish in small streams. When invertebrate drift is the primary mode of prey delivery, pool-riffle composition will govern both suitable habitat area and resource renewal rates, but with increasing terrestrial inputs, resource availability (prey flux) will become increasingly decoupled from pool-riffle structure. This model is pertinent to defining rearing habitat capacity and quality for salmonids, a continuing challenge in both basic and applied contexts (e.g., Rosenfeld 2003; Ayllón *et al.* 2012). Food and space have long been recognized as key factors regulating stream salmonid populations, often through population bottlenecks during summer growth periods (Kennedy *et al.* 2008; Piccolo, Frank & Hayes 2014), yet they have been integrated into assessments of habitat quality only relatively recently (Rosenfeld *et al.* 2014). Our study provides a rare quantification of population-level salmonid production across a gradient of habitat configuration and reinforces the notion that maximizing production may involve trade-offs between pools and riffles, which have distinct functional roles (Poff & Huryn 1998; Wipfli & Baxter 2010). They also provide new context for the effects of food and space on territorial species like stream salmonids in that habitat-production relationships are further dependent on the origin and mode of resource delivery (i.e. invertebrate drift vs. terrestrial drop). Note that this model does not consider habitat-related trade-offs occurring at other salmonid life stages (e.g., spawning vs. rearing) that may also play an important role in population dynamics.

The specific predictions from this model apply to pool-foraging salmonids in small streams. In larger rivers flow patterns may be considerably more complex in vertical and transverse dimensions (Lamouroux *et al.* 1999); however, the basic trade-off between higher resource fluxes and increased energetic foraging costs in high velocity habitats still apply. Similarly, the shape of non-linear responses to pool-riffle composition may vary with body size or taxon, both of which strongly affect velocity tolerance (Nislow, Folt & Parrish 1999; Rosenfeld & Boss 2001). For instance, we may expect more rapidly decreasing production with increasing pool area for species that forage at high velocities (e.g., Atlantic salmon). In addition, other abiotic conditions (e.g., temperature, light input) will further modify habitat effects on salmonids (e.g., Harvey, White & Nakamoto 2005); therefore, optimal hydraulic configuration that maximizes energy flux relative to spatial requirements may be dynamic and these conditions should be considered in future investigations.

More generally, our experiment provides a rare demonstration of a key mechanism driving nonlinear effects of habitat availability on consumer production. This has immediate applied implications insofar as it suggests that adding preferred habitat for a focal species may have limiting returns if it comes at the expense of habitat that generates their prey resources. While our study deals with riffles and pools in streams, similar inferences have been made in other systems, e.g. mangroves (e.g., Mumby, Edwards & Arias-Gonzalez 2004), reefs (Paxton *et al.* 2017), and lakes (Tunney *et al.* 2012). In a more basic context, our results highlight the importance of both indirect and direct functions of habitat patches for mobile consumers. Quantifying the contributions of these habitat functions to consumer production may be critical to understand population regulation and energy flow in heterogeneous landscapes.

Our work also highlights several important but underappreciated ways in which cross-ecosystem prey subsidies interact with habitat heterogeneity. First, while many studies have focused on the direct and indirect effects of subsidies on recipient consumer-resource dynamics and food webs (e.g., Marcarelli et al. 2011), fewer have examined how these effects are mediated by recipient habitat structure (but see: Orr *et al.* 2008; Tiegs *et al.* 2008). Our findings indicate that physical habitat heterogeneity may be a key factor mediating prey subsidy effects on recipient consumers. For instance, terrestrial invertebrate additions may have limited effects in riffle-dominated habitats where foraging efficiency is physically constrained, but strong effects in pools, which are more suitable for foraging yet low in food supply. Second, the sensitivity of the habitat-production relationship to simulated variation in terrestrial prey inputs implies that subsidies can decouple not only food web dynamics (Huxel & McCann 1998) but also consumer-habitat relationships in recipient ecosystems. This is an intriguing aspect of cross-ecosystem resource subsidies that warrants further attention.

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Columbia (Permit No. A13-0052) and the Washington Department of Fish and Wildlife (Permit No. 15-245).

Data Accessibility

Raw data are available on figshare http://doi.org/10.6084/m9.figshare.6025823 (Naman, et al 2018a). R code for bioenergetics and drift model are available on Zenodo https://doi.org/10.5281/zenodo.1217156 (Naman et al 2018b).

Supporting Information

Supporting Information 1 Additional analysis of the potential influence of invertebrate drift produced outside enclosures.

Supporting Information 2 Additional description of the Wisconsin bioenergetics model. Model calibrations of fitted to observed growth.

Supporting Information 3 Output from regression models used for the analysis of the experiment and bioenergetics simulations.

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Table 1. Mean abiotic conditions and prey input rates in each experimental enclosure.

				Depth (m)		Velocity (m s^{-1})		Prey (mg day^{-1})	
Enclosure	Pool proportion	Total Area (m^2)	Canopy %	Riffle	Pool	Riffle	Pool	Drift	Terrestrial
1	0.66	27.57	70	0.08	0.29	0.31	0.05	315.5	16.1
2	0.22	48.40	60	0.11	0.21	0.30	0.03	763.7	13.5
3	0.51	72.11	55	0.11	0.21	0.36	0.05	559.1	60.4
4	0.82	34.38	65	0.06	0.37	0.24	0.13	141.6	37.2
5	0.20	30.96	80	0.10	0.19	0.24	0.04	1473.9	4.7
6	0.70	18.61	80	0.09	0.26	0.29	0.08	141.0	1.7
7	0.39	19.54	15	0.09	0.22	0.25	0.05	402.7	3.7
8	0.22	41.49	70	0.11	0.22	0.32	0.04	5950.7	32.8
9	0.15	40.25	15	0.11	0.21	0.30	0.05	1167.8	32.5
10	0.48	50.56	5	0.11	0.35	0.35	0.03	498.9	40.5
11	0.27	19.36	60	0.10	0.20	0.35	0.04	775.9	10.9
12	0.45	31.89	30	0.11	0.22	0.24	0.04	833.7	9.7
13	0.27	13.20	70	0.08	0.22	0.37	0.07	552.6	9.5

Figures

Figure 1 Conceptual representation of how pool-riffle configuration may affect salmonid productivity across a gradient of prey origin (drift vs. terrestrial drop). For a given density of fish, as the proportion of pools relative to riffles increases along the x-axis, the area of suitable foraging habitat increases (solid line). When drift is the dominant mode of prey delivery, food availability will decrease as the proportion of pool increases (dashed line). However, with an increasing proportion of terrestrial prey, food availability should be gradually decoupled from pool-riffle configuration as shown by the light grey dashed lines up to the dotted line where all prey is terrestrially derived. Maximum production will occur along the bolded red arrow at the intersection of the two lines (hollow points), where food abundance is optimized relative to habitat availability. The two open circles show the optimal pool-riffle configurations at 0% and 100% terrestrial prey.

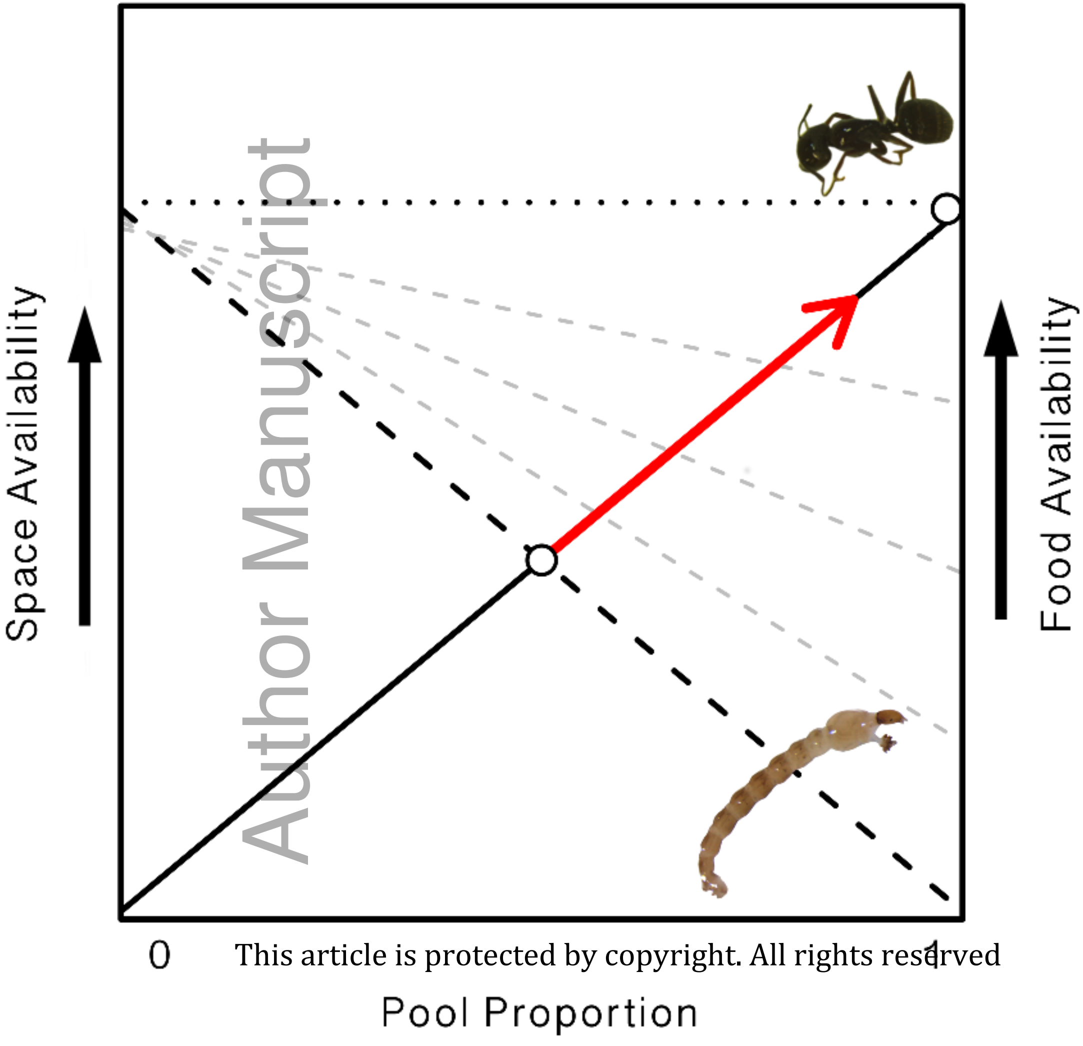
Figure 2 (*a*) Total prey flux (drift and terrestrial combined) in kilojoules m^{-2} day^{-1} and (*b*) the proportion of total prey from terrestrial drop (TD) across the gradient of relative pool area. Solid lines are based on the top ranked regression models; dashed lines are 95% confidence intervals.

Figure 3 The effects of relative pool area on (a) Total fish production (g m^{-2}) of all coho and cutthroat trout in each enclosure; (b) instantaneous growth rates [bold points are the mean value across all fish in each enclosure; light points are individual fish (circles for coho; triangles for cutthroat]; (c) density of all fish in pools based on snorkel observations (n m^{-2}); and (d) the proportion of all fish observed in each pool defending territories. Solid and dashed lines are consistent with Figure 2.

Figure 4 The effect of relative pool area on (a) total consumption (g m^{-2}) of all fish in each enclosure throughout the experiment as estimated with the bioenergetics model. Regression line is from the Monod-Haldane function fit by nonlinear least squares. (b) The exploitation efficiency expressed as the proportion of total prey flux through each enclosure consumed by fish.

Figure 5 Bioenergetic model simulations of total fish production across a gradient of subsidy additions or reductions. The three panels depict three different scenarios of prey capture success:

(a) where additional prey is only consumed in enclosures where observed exploitation efficiency was greater than 95%; (b) where additional prey is consumed at the observed exploitation efficiency; and (c) where all additional prey is consumed. Each line represents the most parsimonious (lowest AIC_c) linear regression model for the relationship between production and pool proportion. pC_{max} = 1 represents the physiological limit for daily consumption.


Space Availability
Food Availability
0
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Pool Proportion

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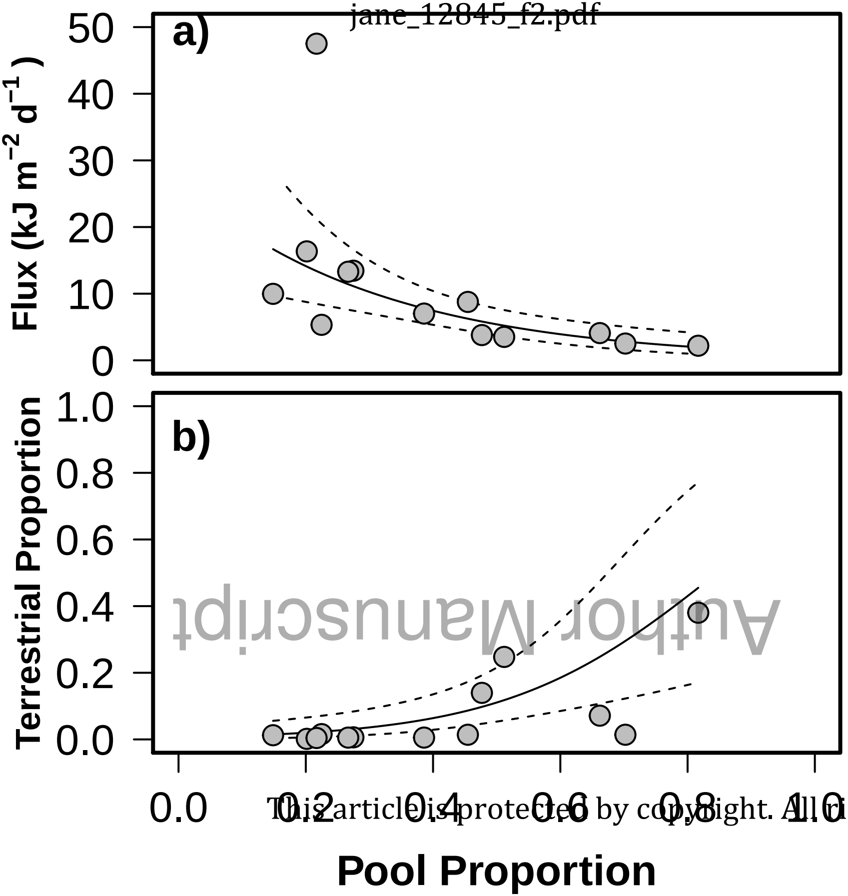

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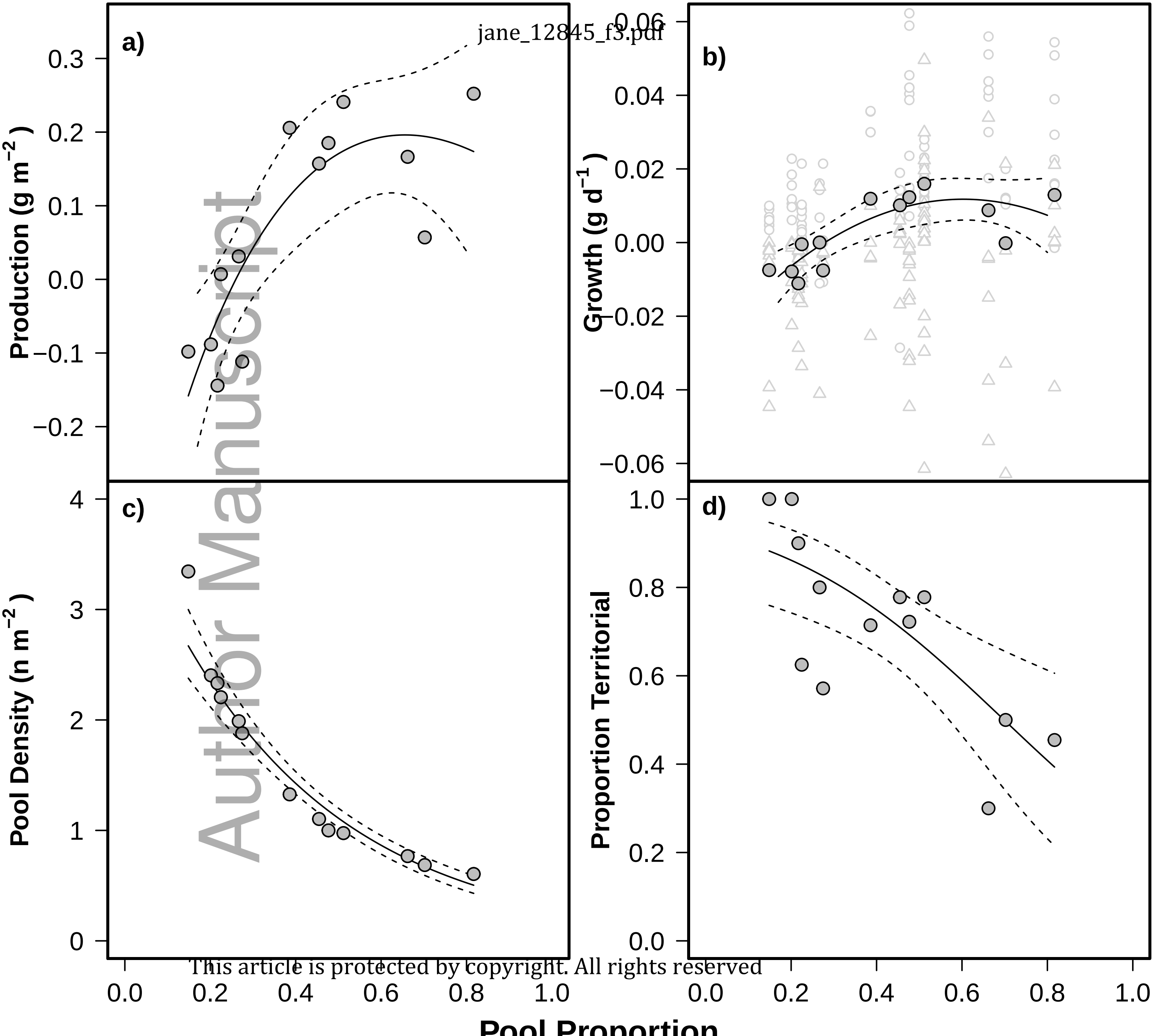
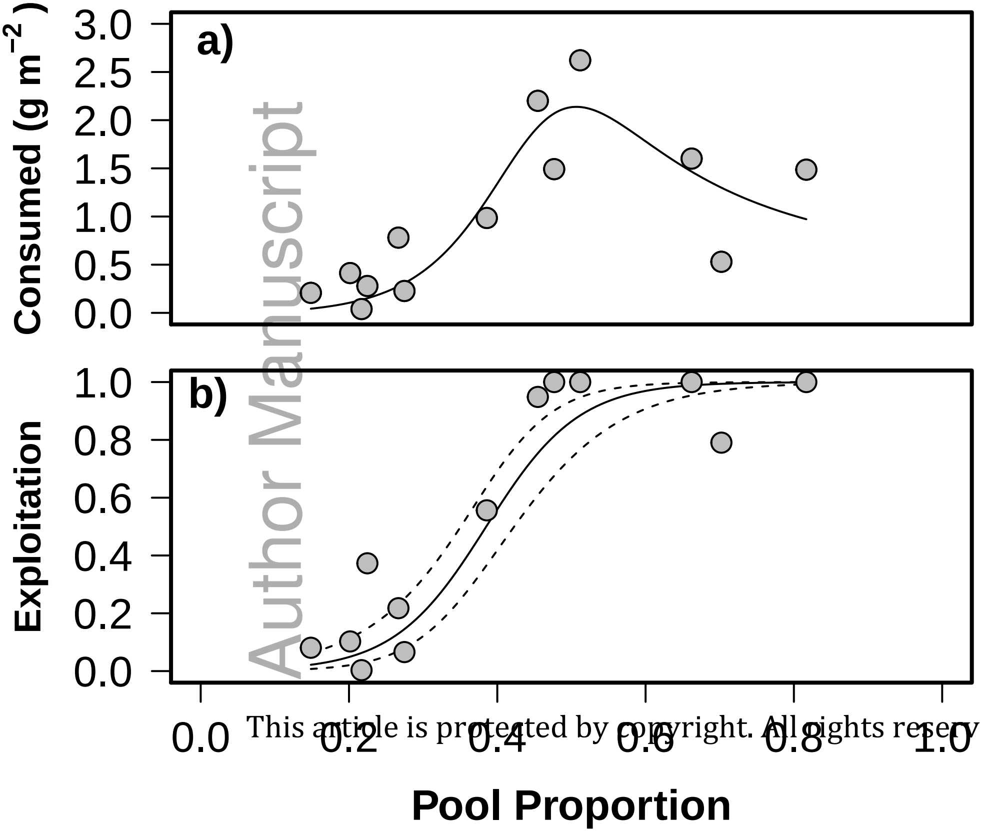
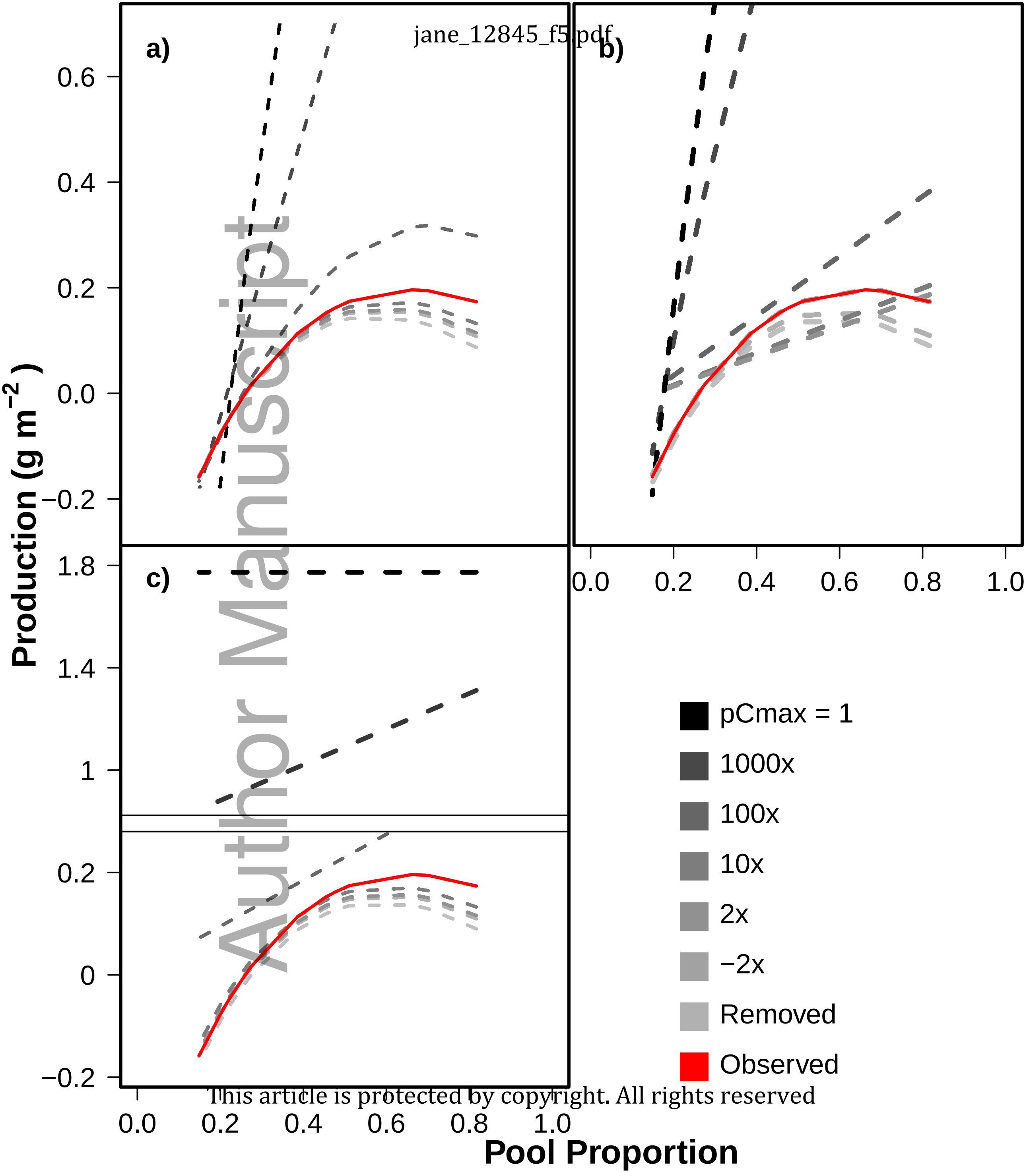



a)
Consumed (g m^{-2})
3.0
2.5
2.0
1.5
1.0
0.5
0.0
b)
Exploitation
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Pool Proportion


a)
b)
c)
Production (g m^{-2})
0.6
0.4
0.2
0.0
−0.2
1.8
1.4
1
0.2
0
−0.2
0.0
0.2
0.4
0.6
0.8
1.0
Pool Proportion
pCmax = 1
1000x
100x
10x
2x
−2x
Removed
Observed