



Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes

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Despite growing recognition of the energetic connections between aquatic and riparian habitats of streams and lakes, there have been few efforts to quantify the importance of terrestrial insect subsidies to fish in lakes. Further, it is unclear whether lakeshore urbanization alters the magnitude of these fluxes. Because lakeshore development has been found to be negatively correlated with riparian vegetation that serves as habitat for terrestrial invertebrates, we expected that shoreline urbanization would reduce the prevalence of terrestrial invertebrates in fish diets. We quantified the effects of lakeshore urbanization on terrestrial insect subsidies to fish at three scales: a focused comparison of annual patterns in four lakes in the Pacific Northwest, a one-time field survey of 28 Pacific Northwest lakes, and a literature survey of 24 North American lakes. At all geographical scales, terrestrial invertebrate subsidies to fish were negatively correlated with shoreline development. Terrestrial insects comprised up to 100% of fish diet mass in undeveloped lakes, versus an average of 2% of fish diet mass in developed lakes. Trout, *Oncorhynchus* spp., in undeveloped lakes had an average of 50% greater daily energy intake, up to 50% of which was represented by terrestrial prey. Temporal variability of the terrestrial subsidy suggests that these inputs are distinctly pulsed, and this subsidy is absent or temporally rare in undeveloped lakes.

Improving our understanding of the dominant energy sources and pathways supporting upper trophic levels in aquatic ecosystems has been a focus of ecology for decades (Lindeman 1942, Odum 1968). Traditional models of lake food webs focus on energy flow through pelagic pathways (Carpenter et al. 1987, Brett and Goldman 1997), describing carbon fixed by phytoplankton, and transferred to zooplankton and eventually top consumers such as fish. Observations of omnivory by fishes, including opportunistic and ontogenetic prey switching (Werner and Gilliam 1984, Hodgson and Kitchell 1987), expanded traditional views of strictly pelagic lake food webs to include benthic organisms (Diehl 1992). Lake food web studies are now more commonly informed by conceptual models of energy transfers linking pelagic consumers, benthic prey, benthic primary producers and detrital energy pathways (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). Substantial reliance on zoobenthos, both directly and indirectly, is currently recognized as widespread and common to most fish in temperate lakes (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002).

Energy flux between terrestrial and aquatic ecosystems is increasingly recognized as an important component of food webs across a diverse range of biomes (Polis et al. 2004). In lotic ecosystems, tight associations between aquatic and riparian habitats result in prey exchanges across stream-riparian boundaries that subsidize both aquatic and riparian

food webs (Power 2001, Sabo and Power 2002), In particular, terrestrial insects using riparian vegetation as habitat can be an important food source for fish in streams (Nakano and Murakami 2001), representing up to half the total energy budget for some fish (Baxter et al. 2005).

Lakes also receive substantial inputs of terrestrial organic matter from their catchments and this carbon pool is fundamental to lake ecosystem function (Jansson et al. 2007). Most evidence of the transfer of terrestrial carbon through limnetic food webs is via the microbial loop (Jansson et al. 2007); examples of the importance of particulate organic matter (POM) from terrestrial habitats are rarer (but see Richey and Wissmar 1979, France and Peters 1995). Though terrestrial organisms are commonly found in fish diets (Hodgson and Hansen 2005), there has been limited systematic quantification of the degree to which fishes in north temperate lakes rely on terrestrial prey sources (but see Mehner et al. 2005).

The human urban population is increasing across North America and the earth in general (United Nations 2007), and human development is concentrated around freshwaters (Walsh et al. 2003). Development of shorelines is associated with a suite of changes to lake habitat structure and ecosystem function, including riparian deforestation (Christensen et al. 1996, Francis and Schindler 2006), loss of coarse wood (Christensen et al. 1996, Francis and Schindler 2006, Marburg et al. 2006) and emergent

vegetation (Jennings et al. 2003) from littoral zones, and eutrophication (Schindler 2006). These human perturbations are associated with various changes in fish ecology, including reduced growth and abundance (Schindler et al. 2000, Sass et al. 2006), and modified foraging behavior (Sass et al. 2006) and spatial distributions (Scheuerell and Schindler 2004). Despite the widespread loss of riparian vegetation associated with shoreline urbanization, there have been no comprehensive studies of how these changes to lake riparian habitats affect the magnitude of terrestrial insect subsidies to aquatic food webs.

We quantified the effects of lakeshore development on terrestrial insect subsidies to fish in north temperate lakes by comparing fish diets in lakes along a gradient of shoreline development. We expected that terrestrial prey would represent a substantial portion of fish diets on lakes with intact shorelines, owing to riparian vegetation fringing lakeshores that serves as habitat for terrestrial organisms. Because human development of shorelines is associated with reduction in the density of riparian vegetation (Francis and Schindler 2006), we further predicted that inputs of terrestrial insects would be reduced on urban lakes as reflected in fish diets. We consider the relative importance of terrestrial insects through a focused sampling of four lakes, then broaden the scale of our investigation with a survey of 28 Pacific Northwest lakes, and a literature survey of an additional 24 North American lakes.

Methods

Focused diet comparison

To assess the effects of shoreline development on terrestrial subsidies to fish, we compared fish diets in two undeveloped lakes (Eunice, Gwendoline) to two developed lakes (Shady, Star) in the Pacific Northwest region of the United States. Eunice and Gwendoline lakes are located in the Univ. of British Columbia's Malcolm Knapp Research Forest near Maple Ridge, British Columbia (19°49'N, 34°122'W) and have fully intact riparian forests. Shady and Star lakes are located in suburban areas of King County, Washington (Shady: 25°47'N, 6°122'W; Star: 21°47'N, 17°122'W), and each has 95% of its shoreline developed by residential dwellings. The four lakes have an average surface area of 13.5 ha (± 2.0 SE) and an average depth of 10.8 m (± 2.3 SE). The lakes are all located below 500 m elevation in the western hemlock *Tsuga heterophylla* zone of the Cascade Range and Puget Trough regions. Cutthroat trout *Oncorhynchus clarkia* were introduced to Eunice Lake in a transplant experiment in 1974 (Hume and Northcote 1985), and subsequently colonized Gwendoline Lake through tributaries. Both Shady and Star lakes are stocked with rainbow trout *Oncorhynchus mykiss*, and also have resident populations of largemouth bass *Micropterus salmoides*, bluegill sunfish *Lepomis macrochirus* and yellow perch *Perca flavescens*.

We sampled each lake 7–8 times between May 2005 and May 2006. During each sampling event, fish were collected by angling or variable mesh gill nets. Live fish were sedated on undeveloped lakes or euthanized on urban lakes using MS-222 (99.5% tricaine methanesulfonate), their gut

contents were evacuated by gastric lavage, and the contents were preserved in 95% ethanol. If fish expired while in the gill nets, entire stomachs were removed in the field and preserved in 95% ethanol. Prior to gut evacuation or stomach removal, all fish were weighed to the nearest 0.1 g.

Fish diet items were identified using a dissecting microscope to a taxonomic level that allowed categorization of prey taxa into habitat of origin. Whole stomachs were dissected and the contents removed and identified using a dissecting microscope. All individual prey items in each diet were counted, and prey taxa were categorized as pelagic, benthic or terrestrial in origin. A subset of individuals ($n = 36$, mean) of each prey taxa from each lake was used to generate lake-specific length–dry mass regressions.

Prey dry mass values for calculating diet proportions were determined either by directly measuring the dry mass of prey items or, more frequently, using prey lengths in combination with length–mass regressions. A per-taxa average length was calculated for each individual diet. Mean dry mass for each prey taxa was then determined for each diet using length–mass regressions, and multiplied by the number of individuals in the diet to give the total dry mass per diet for each taxa. When developing length–mass regressions was impossible owing to a dearth of intact samples, length–mass regressions from the literature were used (Sample et al. 1993, Benke et al. 1999, Sabo et al. 2002, Chimney et al. 2007). Based on total dry mass per taxa, proportions of the diet comprised of prey from benthic, pelagic and terrestrial habitats were calculated for each fish. Whole-lake means of diet proportions were calculated across all individual fish, assuming that the relative representation of different species in gillnets reflected their relative abundance in the lake.

To estimate the relative importance of terrestrial prey items to fish, we compared consumption, daily ration, gut fullness and energy intake of trout, the fish taxa that was common to all lakes. For each fish, maximum consumption C_{\max} was calculated according to the bioenergetics model for *Oncorhynchus mykiss* described by Rand et al. (1993) as

$$C_{\max} = 0.628 \times W^{-0.30} \quad (1)$$

where W is fish wet mass (g). C_{\max} has units of g wet prey mass per g wet fish mass per day. This value for C_{\max} represents maximum consumption at 20°C (Rand et al. 1993) and is therefore a liberal estimate of maximum consumption.

Daily ration (D) was calculated according to a modified Eggers model (Elliott and Persson 1978, Eggers 1979, Principe et al. 2007) as

$$D = F \times R_e \times 24 \quad (2)$$

where F is gut fullness, and R_e is evacuation rate (h^{-1}). Daily ration has units of g prey wet mass per g fish wet mass per day. Gut fullness (F) was calculated according to Principe et al. (2007) as

$$F = \frac{G}{W} \times 100 \quad (3)$$

where G is gut content wet mass (g) and W is individual fish wet mass (g). Gut fullness is assumed to be the average gut fullness over a 24-h period. Gastric evacuation rate (R_e) was calculated following He and Wurtsbaugh (1993) as

$$R_c = 0.049e^{0.072 \times T - 0.060 \log_e(PS)} \quad (4)$$

where T is temperature (°C) and PS is the mean prey wet weight (g).

We compared the allometrically-corrected feeding rate for fish in each lake according to:

$$p = \frac{D}{C_{\max}}$$

where p refers to the proportion of maximum possible consumption rate (based on physiology) observed in each fish (Eby et al. 1995).

Daily energy ration (DE) was also calculated for each fish, as

$$DE = D \times J$$

where J is joules per g of prey wet weight. Prey energy densities and dry weight: wet weight conversions were collected from the literature (Cummins and Wuycheck 1971, Yako et al. 2000, Gray 2005, Koehler et al. 2006) or personal communications (Beauchamp pers. comm.).

Survey of fish diets along urbanization gradient

Between June and August 1998, 28 Pacific Northwest lakes, including the above four lakes, were sampled one time. The lakes have been described in more detail in Moore et al. (2003) and were selected to fall along a gradient of shoreline development ranging from wholly undeveloped to lakes with 100% of the shoreline developed. Development intensity was calculated as the percent of shoreline containing human residential or recreational development within 10 meters of shore. The lakes were monomictic, between 34–522 m above sea level, and had a mean depth of 5.2 m (± 1.0 SE), an average surface area of 18.8 ha (± 3.6 SE) and an average watershed area of 285 ha (± 54 SE) (Bortleson et al. 1976). Fish were collected with gill nets and processed as above, except that on each lake, the gut contents of all similarly-sized individuals of each fish taxa were combined, and per-lake, per-fish species averages were calculated for fish mass, prey taxa frequency (i.e. number of individuals per taxa for each diet), and prey taxa length. Prey habitat of origin, dry weights, and individual and whole-lake means of diet proportions were determined as above.

Literature survey

The published literature was searched for reports of the diet composition of trout *Oncorhynchus* spp., bass and yellow perch. Only studies that assigned prey items into benthic, pelagic, and terrestrial categories were considered (Appendix 1). Many papers could not be included because benthic and terrestrial insects were lumped into a single group. Shoreline development intensity information was collected either from the published studies, from personal communications with the study authors, or estimated using Google Earth (Mountain View, California, USA). Whole-lake means of diet proportions were determined as above.

Statistical analyses

All statistical analyses were conducted using Systat 11.0. Proportional data were arcsine-square root transformed to improve normality. We tested for seasonal and development effects on the proportion of terrestrial insects in fish diets using ANOVA and Tukey's LSD post-hoc tests ($\alpha = 0.05$) with date, development and date \times development as main effects. We tested for the effect of development on gut fullness, daily ration and daily energy ration using Student's t-tests ($\alpha = 0.05$).

Results

Focused comparison

Shoreline development was associated with reduced quantities of terrestrial insects in fish diets on annual and seasonal scales. Across all sampling events, 40% of fish sampled in the undeveloped lakes consumed terrestrial insects, and $>25\%$ of fish in undeveloped lakes consumed at least 10% terrestrial insects (Fig. 1). In contrast, a very small minority (2.4%) of fish sampled in developed lakes had terrestrial insects in their diets, and only in very small proportions of total diet mass (Fig. 1).

Seasonally, the proportion by mass of terrestrial insects in fish diets varied greatly on four Pacific Northwest lakes, from 0–100% (Fig. 2). The terrestrial diet proportion was significantly higher in undeveloped lakes as compared to developed lakes across all seasons ($F_{1,269} = 13.68$, $p < 0.001$), with the diets of fishes in the undeveloped lakes composed of up to 100% terrestrial insects, as compared to a maximum of 2% in the two developed lakes. These results were similar whether we included all fish taxa in the developed lake data, or whether we considered only the diets of trout. There was a significant effect of date on the proportion of terrestrial prey in diets of fish from

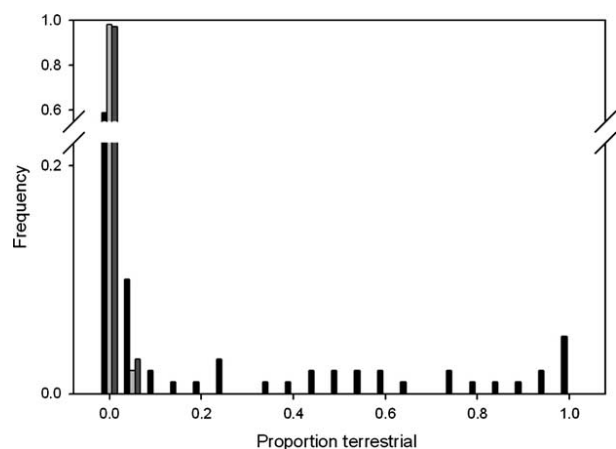


Figure 1. Frequency distribution of the proportion of individual fish diets, by dry mass, comprised of terrestrial prey in four lakes in the Pacific Northwest. Shown are diets of cutthroat trout from two undeveloped lakes (dark bars, $n = 182$), and rainbow trout (dark grey bars, $n = 77$) and all fish taxa (light grey bars, $n = 125$) from two developed lakes. Note break in scale on y-axis from 0.25 to 0.55.

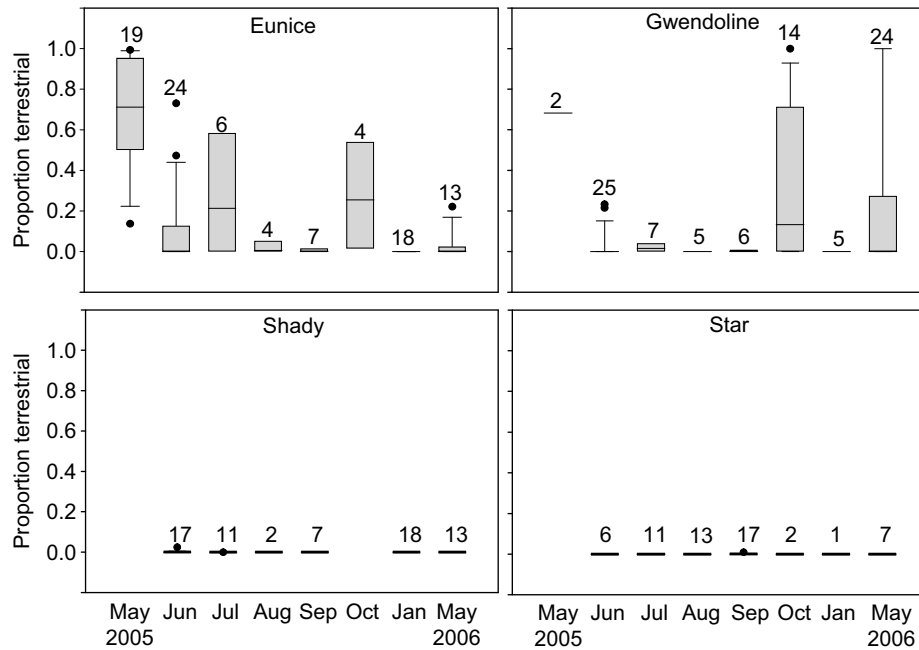


Figure 2. Seasonal patterns of proportion, by mass, of fish diets comprised of terrestrial insects from four Pacific Northwest lakes. Boxes represent medians (vertical line) plus the central 50% of all values. Symbols represent outliers, numbers above bars are sample sizes. Eunice (n = 95) and Gwendoline (n = 88) lakes are undeveloped, Shady (n = 68) and Star (n = 57) lakes are developed. Urban lakes were not sampled in May 2005.

undeveloped lakes ($F_{6,151} = 4.49$, $p < 0.001$), and post-hoc tests revealed that terrestrial diet proportions were significantly greater in October than in other months (Fig. 1). There was no significant seasonal variation in terrestrial diet proportions in fish from developed lakes ($F_{6,188} = 0.52$, $p = 0.79$). The most common prey taxa in fish diets were chironomid and other dipteran pupae, *Daphnia* spp., amphipods and isopods (Table 1). Annual whole-lake averages of the terrestrial contribution to fish diets in undeveloped lakes were 17.4% (Eunice) and 13.9% (Gwendoline) of dry mass, versus 0.0% for both developed lakes.

There was considerable seasonal variation in daily energy ration (DE) and the relative contribution of benthic, pelagic, and terrestrial prey to DE in both the undeveloped and developed lakes (Fig. 3), though daily energy ration was on average 35% greater per season in undeveloped lakes (Table 2). Benthic resources contributed the most energy to trout on both developed and undeveloped lakes, across all months. Terrestrial insect contributions to daily energy ration were biggest in undeveloped lakes in May and June 2005. Total energy intake followed predictable seasonal trends associated with water temperature, such that intake was greater in warmer months and reduced in cold, winter months (Fig. 3).

Across all sampling events, mean gut fullness was twice as large in trout from undeveloped lakes (two sample t-test, $p = 0.001$) and daily ration, which combines gut fullness with evacuation rate, was nearly twice as large in trout from undeveloped lakes (two sample t-test, $p = 0.02$) compared to the two developed lakes (Table 2). Daily energy ration was on average 50% greater in trout from undeveloped lakes (two sample t-test, $p = 0.0003$; Table 2). Daily energy

ration owing to benthic prey was significantly greater on undeveloped lakes as compared to developed lakes (two sample t-test, $p = 0.001$). C_{max} was greater on undeveloped lakes (two sample t-test; $p < 0.0001$) because fish were smaller in those lakes, but daily ration as a percent of C_{max} (p) was not significantly different among lakes or between lake development types (Table 2), averaging 37.5% across all fish. Mean prey energy density ($J g^{-1}$ prey wet mass) was greater for terrestrial insects than either benthic or pelagic prey items (Table 3).

Changes in terrestrial insect subsidies along an urbanization gradient

In the survey of 28 Pacific Northwest lakes, consumption of terrestrial prey in undeveloped lakes was often high but variable (from 0–81% of dry mass). In lakes with greater than 10% shoreline development, terrestrial contributions to fish diets were not detected. Data from the literature on North American lakes also showed the loss of terrestrial insects from fish diets on lakes with high levels (i.e. > 50%) of shoreline development (Fig. 4).

Predation on terrestrial insects by trout, bass, and yellow perch declined with shoreline development in 28 Pacific Northwest lakes and 24 North American lakes (Fig. 5). Predation on terrestrial insects varied in low development and undeveloped lakes, and terrestrial prey items were absent from diets at lakeshore development intensity above 50%. Trout consumed higher proportions of terrestrial prey than either bass or perch. In fact, terrestrial prey were not detected at all in perch diets, though only one lake with 0% development was included in the analysis of perch diets.

Table 1. The most common prey items in diets of fishes in four Pacific Northwest lakes. Values for most common taxa represent the proportion of fish diets in which each prey taxon appears. Values for most abundant taxa represent the proportion of diets in which the prey item is the most abundant by dry weight.

	Most common	Most abundant
Eunice	Diptera pupae (0.54)	Daphnia (0.29)
	Daphnia (0.36)	Diptera pupae (0.18)
	Trichoptera larvae (0.26)	
	Spider (0.23)	
Gwendoline	Diptera pupae (0.60)	Diptera pupae (0.18)
	Amphipoda (0.34)	Daphnia (0.17)
	Daphnia (0.31)	
	Ephemeroptera larvae (0.26)	
Shady	Diptera pupae (0.48)	Isopoda (0.30)
	Chironomidae larvae (0.44)	Daphnia (0.19)
	Chaoborus larvae (0.38)	
	Daphnia (0.34)	
Star	Chironomidae larvae (0.69)	Chironomidae larvae (0.39)
	Diptera pupae (0.45)	Daphnia (0.23)
	Daphnia (0.41)	
	Amphipoda (0.32)	

Discussion

Extensive research in stream ecosystems has highlighted the importance of linkages between riparian vegetation and aquatic food webs as terrestrial invertebrates are a substantial source of energy for stream fishes. This study expands this concept to lake ecosystems, demonstrating that lakeshore riparian habitat performs the same function as streamside riparian habitat, namely in supporting the delivery of terrestrial insects to surface waters where they are consumed by fishes. The riparian vegetation density on the urban lakes in the focused comparison was approximately one-tenth that of the undeveloped lakes (Francis and Schindler 2006), and the corresponding decrease in the terrestrial portion of fish diets suggests that this

deforestation has direct effects on fish diets. At a broader geographical scale, a 2002 survey of 20 of the 28 of the Pacific Northwest lakes in the present study demonstrated a decrease in riparian forest density with urban shoreline development (Francis and Schindler 2006). Though not directly measured, understory riparian vegetation also decreased along the same gradient, and the results here indicate that concomitant with this riparian denudation is a decrease in terrestrial insects in fish diets. Furthermore, the intensity of lakeshore urban development appears related to the importance of terrestrial prey for fishes, as terrestrial insects were not detected in diets at urbanization levels above 50% shoreline development.

The prevalence of terrestrial insects in fish diets clearly declined with shoreline development in the 28 lake, single-sample, survey. In the four lakes, where more intensive sampling accounted for seasonality, patterns were less clear. Annual means of the proportion of terrestrial insects in fish diets from the intensive, semi-regular sampling of four lakes were qualitatively similar to the pattern observed in the survey, despite seasonal cycles that may control inputs of terrestrial insects (Nakano and Murakami 2001) and evidence that insect inputs to aquatic ecosystems are pulsed and stochastic (Carlton and Goldman 1984). Our intensive sampling of four Pacific Northwest lakes likely missed some major insect deposition events, as evidenced by the high variation in terrestrial diet proportions in undeveloped lakes (Fig. 3). Presumably terrestrial insect flux events on urban lakes were missed with roughly equal probability and therefore comparisons between lake types are relevant on both annual and finer time scales. Because of heavy exploitation in the developed lakes, we were unable to catch fish in urban lakes on all sampling dates, most notably in May and October 2005, months with substantial terrestrial insects in fish diets on undeveloped lakes. However, the absence of terrestrial insects on developed lakes was so consistent across all sampling

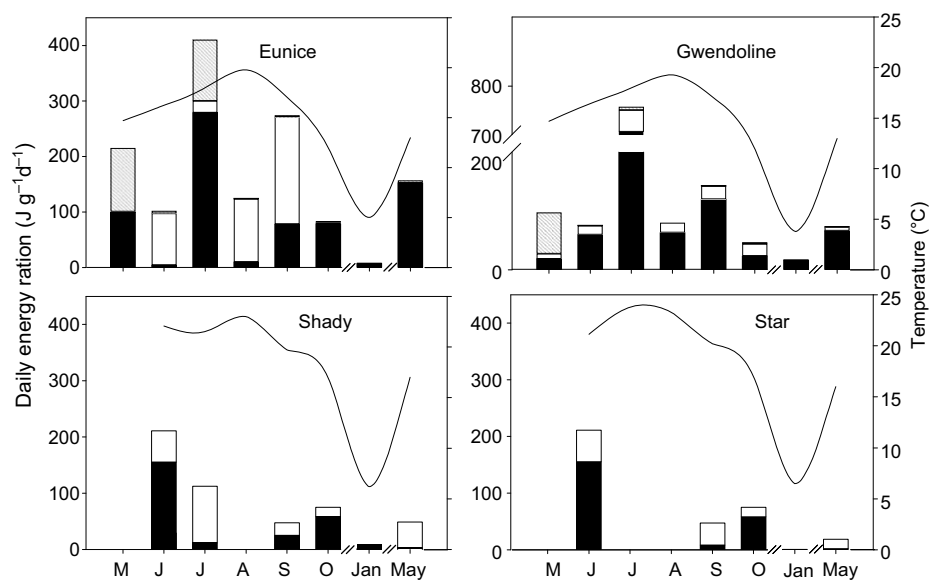


Figure 3. Daily energy rations for four lakes in the focused comparison. Different colors in bars represent different prey habitat type: dark fills are benthic, open fills are pelagic, and hatched fills are terrestrial. Note break in scale on y-axis for Gwendoline Lake. Lines represent surface temperatures for each sample period.

Table 2. Consumption and energy intake rates for trout *Oncorhynchus* spp. in four Pacific Northwest lakes. Eunice and Gwendoline lakes are undeveloped, Shady and Star lakes are developed. All values are annual means. Fish mass is in grams of wet mass; gut fullness is in grams of prey wet mass per gram of fish wet mass; daily ration is in grams of prey wet mass per gram of fish wet mass per day; C_{\max} is in grams of prey wet mass per gram fish wet mass per day; p is the ratio of gut fullness to C_{\max} .

Lake	Fish mass (g)	Gut fullness (g g ⁻¹)	Daily ration (g g ⁻¹)	C_{\max} (g g ⁻¹ d ⁻¹)	p
Eunice	62.1	0.005	0.025	0.154	0.147
Gwendoline	86.2	0.003	0.016	0.154	0.101
Shady	348.2	0.002	0.012	0.088	0.121
Star	292.4	0.002	0.015	0.107	0.136

periods, and in both Shady and Star lakes, it is more than likely that our sampling regime captured the pattern of terrestrial diet proportions in those lakes. Furthermore, the coherence between patterns observed in Pacific Northwest lakes and those from lakes around North America and across multiple fish taxa indicates that our intensive sampling captured the general pattern of terrestrial insects in fish diets, that riparian vegetation serves a similar function among geographic locations, and that terrestrial insects can be an important subsidy, regardless of ecoregion or forest type.

Across all sampling events, gut fullness and daily ration were greater on the undeveloped lakes (Table 2). These patterns in consumption and ration are expected based on allometric relationships, which account for the fact that smaller fish have higher mass-corrected ration (Rand et al. 1993). Therefore, the smaller average size of fish in the two undeveloped lakes (Table 2) could explain the greater gut fullness and ration sizes observed in those lakes. A more informative metric of consumption rate, p , daily ration as a percent of C_{\max} , was roughly equal between developed and undeveloped lakes, indicating fish in undeveloped lakes are not consuming at significantly higher rates than their counterparts in developed lakes, despite the addition of terrestrial prey. However, higher daily energy rations (Table 2) and greater mean prey energies (Table 3) indicate important and significant differences in diet quality between the two lake types that may translate into greater growth of the fish from undeveloped lakes. These results suggest that lakes with intact shorelines have greater capacity to grow and sustain fish populations, in part due to the importance of the increased inputs of terrestrial prey.

The four lakes studied varied dramatically in terms of fish exploitation and density, resulting in strong differences in mean size of fish, and especially trout species, with rainbow trout in developed lakes being much larger than the cutthroat trout in the undeveloped lakes. While we did not directly estimate fish population sizes in each lake, we observed that fish relative density was much higher in the

undeveloped lakes. Because of this, we might expect that competition for prey resources among fish in the undeveloped lakes is greater than in the developed lakes. Therefore, one potential alternative explanation for these results is that consumption of terrestrial prey simply reflects prey switching to a less desirable prey source (i.e. terrestrial prey) owing to increased competition for the preferred diet items (i.e. benthic invertebrates). Furthermore, higher productivity of the urban lakes owing to increased nutrient inputs (Moore et al. 2003) might lead to the assumption that the developed lakes have more productive benthic communities and therefore higher availability of benthic prey resources. However, daily energy rations owing to benthic resources were higher in the undeveloped lakes, suggesting that the patterns of terrestrial prey contributions to diets reflect changes in terrestrial prey availability. Further, previous research on these same lakes showed higher densities of benthic invertebrates in the undeveloped lakes as compared to the urban lakes (Francis et al. 2007), suggesting that, if anything, competition for benthic prey is actually greater in the urban lakes.

Variability in the contribution of terrestrial prey to daily energy ration across lakes and across seasons (Fig. 3) suggests several potential co-occurring dynamics. The frequency distribution of the proportion of terrestrial insects in fish diets (Fig. 2) is a continuous, unimodal distribution with a long tail of extreme events that reflects pulsed resources. While inputs of terrestrial insects to streams are relatively constant during the warmer months (Nakano and Murakami 2001), no such pattern has been observed on lakes. Rather, where they have been measured, terrestrial inputs to lakes are highly variable both temporally and spatially (Norlin 1964, 1967, Cole et al. 1990) and characterized by extreme deposition events (Carlton and Goldman 1984). Therefore, terrestrial insects may represent a greater portion of ration and energy per annum than is reflected in the data here, owing to a mismatch between resource pulses and sampling events. Mehner (2005) measured terrestrial insect subsidies to bleak *Alburnus*

Table 3. Energy densities of prey by habitat type, and of diet by lake. Prey energy densities are mean joules per gram wet mass of all prey items from each habitat type found in fish diets in the four Pacific Northwest lakes, based on published energy density values. Daily energy intake is the mean, across all fish, of the diet proportion (by wet mass) represented by each prey item, multiplied by that prey's energy density (J g⁻¹ wet mass).

Habitat	Prey energy density (J g ⁻¹ wet mass)	Lake	$p \times$ daily energy intake (J g ⁻¹)
Benthic	7154	Eunice	854.3
Pelagic	5409	Gwendoline	784.9
Terrestrial	9561	Shady	455.6
		Star	596.0

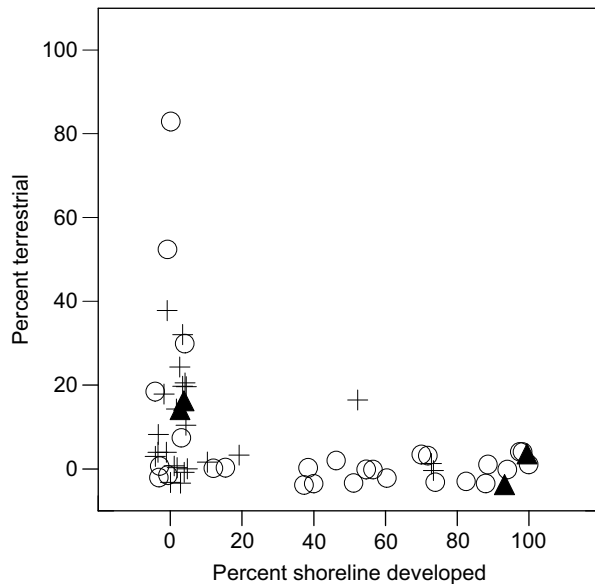


Figure 4. Percent of fish diets, by mass, of terrestrial origin from 52 North American lakes along a shoreline development gradient. Each symbol represents the annual average for a given lake/year combination, for four lakes sampled multiple times from 2005–2006 (▲), 28 Pacific Northwest lakes sampled once in 1998 (○), and 24 North American lakes from a literature review (+). Overlapping symbols are staggered for visibility.

alburnus, sampling monthly between April and October over two years, and found that, averaged over this time frame, terrestrial insects represented 84% of bleak diets by biomass. Here, we found that on the undeveloped lakes, terrestrial insects represented 13–17% of annual trout diets. It is possible that if terrestrial insect fluxes occur in pulses, as is suggested by the high variation observed in undeveloped lakes, repeated and more regular sampling would inflate our estimates of their occurrence in fish diets. Despite the irregular nature of the terrestrial insect subsidy in undeveloped lakes, its importance is highlighted when compared to the total absence of any terrestrial prey use by fish in urban lakes. Furthermore, given the higher energetic densities of terrestrial prey relative to aquatic taxa, the overall contribution of terrestrial subsidies towards annual growth may be greater than the proportional contribution to diets indicates.

Globally, human populations are becoming increasingly urban. The United Nations predicts that in the next 40 years, two-thirds of the world's population will live in urban areas (United Nations 2007). Pressures on ecosystems in and around urban areas are intensifying, and land-use changes associated with urbanization affect climate, biodiversity, biogeochemical cycles and hydrological cycles (Grimm et al. 2008). Because of human reliance on freshwater ecosystem services, urbanization is concentrated near coastlines (Walsh et al. 2003, Grimm et al. 2008) and therefore human effects are magnified in aquatic ecosystems. Human activities have cumulative effects on lakes, from non-point source pollution and eutrophication (Schindler 2006) to habitat alteration (Jennings et al. 2003, Francis and Schindler 2006, Francis et al. 2007). Loss of riparian habitat is an effect that is essentially

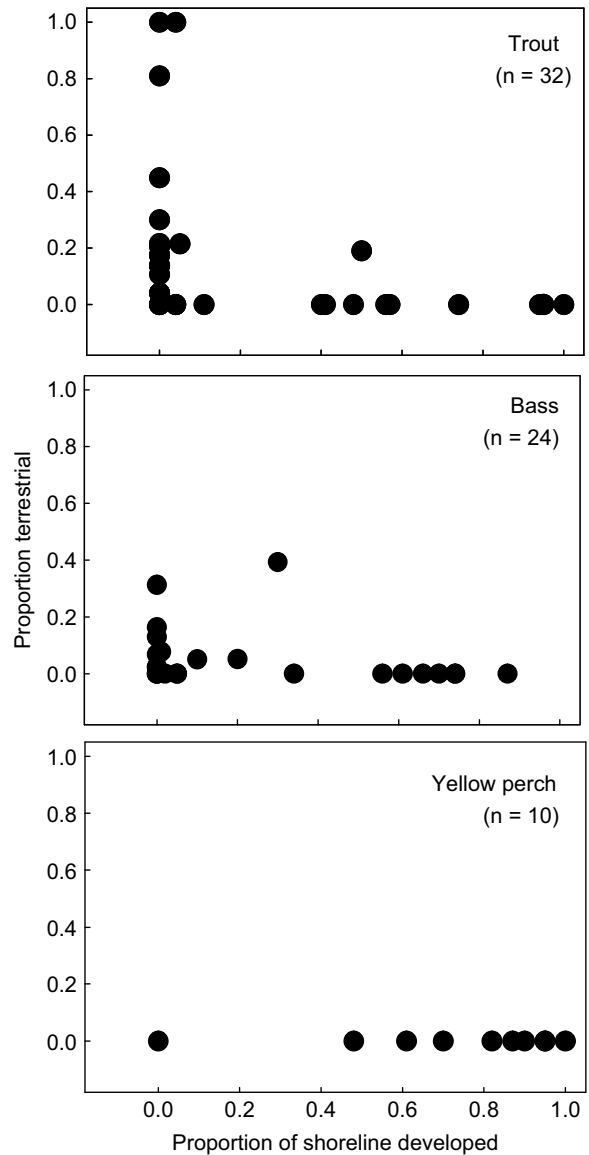


Figure 5. Proportion of diet represented by terrestrial prey in three fish taxa in 52 North American lakes along a gradient of urban development. Symbols represent means for a single lake/year pair.

unexplored, though the results from this study indicate that alteration of riparian forests likely has consequences for lake populations and food webs. Overall, these results highlight the importance of lakeshore riparian habitats as sources of terrestrial insects to surface waters and demonstrate that terrestrial insects are an important, though variable, energy subsidy for fish. How lake communities respond to reductions in these subsidies remains unknown.

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Appendix 1. References from literature search of proportional contributions of terrestrial insects to fish diets.

Lake	Location	Citation
Amchitka Island	Alaska, USA	Palmisano, J. J. and W. T. Helm. 1971. <i>BioScience</i> 21: 637–641
Bear Lake	Idaho/Utah, USA	Ruzycki, J. R. et al. 2001. <i>Trans. Am. Fish. Soc.</i> 130: 1175–1189
Beaver Creek beaver ponds	Idaho, USA	Hilderbrand, R. H. and J. L. Kershner. 2004. <i>N. Am. J. Fish. Mgmt.</i> 24: 33–40
Big Crooked Lake	Wisconsin, USA	Frey, A. P. and M. A. Bozeck. 2003. <i>J. Fresh. Ecol.</i> 18: 43–54
Buttle Lake	British Columbia, Canada	McMynn, R. G. 1953. <i>Mgmt Publication No. 2 of the BC Game Commission.</i>
Castle Lake	California, USA	Swift, M. C. 1970. <i>Calif. Fish Game</i> 56: 109–120
Castle Lake	California, USA	Wurtsbaugh, W. A. et al. 1975. <i>Trans. Am. Fish. Soc.</i> 1: 88–95
Deer Island Lake	Arizona, USA	Saiki, M. K. and J. C. Tash. 1978. <i>Am. Mid. Nat.</i> 100: 116–125
Jorgens Lake	Minnesota, USA	Soupir, C. A. et al. 2000. <i>Can. J. Zool.</i> 78: 1759–1766
Lake Oahe	South Dakota, USA	Lynott, S. T. et al. 1995. <i>J. Fresh. Ecol.</i> 10: 399–407
Lake Opeongo	Ontario, Canada	Martin, N. V. 1970. <i>J. Fish. Res. Brd. Canada</i> 27: 125–146
Lake Taneycomo	Missouri, USA	Weiland, M. A. and R. S. Hayward. 1997. <i>Trans. Am. Fish. Soc.</i> 126: 758–773
Lake Washington	Washington, USA	M. Mazur, pers. comm.
Lake Washington	Washington, USA	McIntyre, J. K. et al. 2006. <i>Trans. Am. Fish. Soc.</i> 135: 1312–1328
Little Moose Lake	New York, USA	Weidel, B. C. et al. 2000. <i>J. Fresh. Ecol.</i> 15: 411–428
Locator-WarClub Lakes	Minnesota, USA	Soupir, C. A. et al. 2000. <i>Can. J. Zool.</i> 78: 1759–1766
Loiten Lake	Minnesota, USA	Soupir, C. A. et al. 2000. <i>Can. J. Zool.</i> 78: 1759–1766
Long Lake	Michigan, USA	Hodgson, J. R. et al. 1997. <i>Ecol. Fresh. Fish.</i> 6: 144–149
Mactaquac Arm	New Brunswick, Canada	Hanson, S. D. and R. A. Curry. 2005. <i>Trans. Am. Fish. Soc.</i> 134: 356–368
Marion Lake	British Columbia, Canada	Efford, I. E. and K. Tsumura. 1973. <i>Trans. Am. Fish. Soc.</i> 1: 33–47
Oromocto Lake	New Brunswick, Canada	Hanson, S. D. and R. A. Curry. 2005. <i>Trans. Am. Fish. Soc.</i> 134: 356–368
Peter Lake	Michigan, USA	Hodgson, J. R. et al. 1989. <i>Trans. Am. Fish. Soc.</i> 118:11–19
Pomme de Terre Lake	Missouri, USA	Pope, K. L., et al. 2001. <i>Environ. Biol. Fish.</i> 61: 329–339
Quill Lake	Minnesota, USA	Soupir, C. A. et al. 2000. <i>Can. J. Zool.</i> 78: 1759–1766
Skiatook Lake	Oklahoma, USA	Long, J. M. and W. L. Fisher. 2000. <i>J. Fresh. Ecol.</i> 15: 465–481
Spirit Lake	Iowa, USA	Pelham, M. E. et al. 2001. <i>Ecol. Fresh. Fish.</i> 10: 198–211
Stockton Lake	Missouri, USA	Pope, K. L. et al. 2001. <i>Env. Biol. Fish.</i> 61: 329–339

Appendix 2. Prey energy densities used in calculations of daily energy ration.

Prey taxa	Stage	J g ⁻¹ wet weight	Citation
Acari	Adult	21860	Cummins and Wuycheck 1971
Amphibia	Larvae	1700	Yako et al. 2000
Amphipod	Adult	2427	Gray 2005
Annelid	Adult	1981	Gray et al. unpubl.
Anisoptera	Larvae	21320	Cummins and Wuycheck 1971
Aphididae	Adult	11915	Gray et al. unpubl.
Apidae	Adult	12670	Gray et al. unpubl.
Arachnid	Adult	5321	Gray et al. unpubl.
Bivalve	Adult	22708	Cummins and Wuycheck 1971
Bosmina	Adult	3976	Koehler et al. 2006
Chaoboridae	Larvae	3976	Koehler et al. 2006
Chironomidae	Larvae	2475	Gray 2005
Chironomidae	Pupae	3400	Koehler et al. 2006
Coccinellidae	Adult	7968	Gray 2005
Coleoptera	Adult	7968	Gray 2005
Copepoda	Adult	3976	Koehler et al. 2006
Culicidae	Adult	4859	Gray 2005
Daphnia	Adult	3976	Koehler et al. 2006
Diptera	Adult	8923	Gray et al. unpubl.
Diptera	Larvae	2581	Gray et al. unpubl.
Diptera	Pupae	3400	Koehler et al. 2006
Ephemeroptera	Adult	20429	Cummins and Wuycheck 1971
Ephemeroptera	Larvae	22872	Cummins and Wuycheck 1971
Formicidae	Adult	11125	Gray et al. unpubl.
Gastropoda	Adult	6570	Cummins and Wuycheck
Hemiptera	Adult	10927	Gray et al. unpubl.
Holopedium	Adult	3976	Koehler et al. 2006
Hymenoptera	Adult	12230	Gray 2005
Isopoda	Adult	3335	Gray 2005
Isoptera	Adult	12230	Gray et al. unpubl.
Lepidoptera	Larvae	8502	Gray et al. unpubl.
Notonectidae	Adult	20170	Cummins and Wuycheck 1971
Oligochaete	Adult	1981	Gray 2005
Pipunculidae	Adult	8923	Gray et al. unpubl.
Polyphaemus	Adult	3976	Koehler et al. 2006
Sciaridae	Adult	8923	Gray 2005
Sialidae	Larvae	21788	Cummins and Wuycheck 1971
Staphylinidae	Adult	1866	Gray et al. unpubl.
Tenthredinidae	Adult	8923	Gray et al. unpubl.
Trichoptera	Pupae	5814	Gray et al. unpubl.
Trichoptera	Adult	7756	Gray 2005
Trichoptera	Larvae	5814	Gray et al. unpubl.
Zygoptera	Adult	23674	Cummins and Wuycheck 1971
Zygoptera	Larvae	21742	Cummins and Wuycheck 1971