PERSPECTIVE / PERSPECTIVE

Blowin' in the wind: reciprocal airborne carbon fluxes between lakes and land [1]

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Abstract: Ecologists are increasingly interested in how disjunct habitats are connected through the cross-habitat movement of matter, prey, nutrients, and detritus and the implications for recipient systems. The study of lake ecosystems has been dominated by the study of pelagic (open-water) production and processes, though there is growing awareness of the role of terrestrial inputs and benthic trophic pathways. Here, we review the phenomena of airborne fluxes to and from lakes. We assemble published data on terrestrial particulate organic carbon (TPOC) deposition to lakes, insect production, and insect emergence and use these data to simulate how airborne lake-to-land and land-to-lake carbon flux is expected to scale with ecosystem size, while taking into account among-lake variability in emergence and TPOC deposition. Emergent insect flux to land increases as a function of lake size, while TPOC deposition to lakes decreases as a function of lake size. TPOC deposition exceeds insect emergence in small lakes, while in large lakes, insect emergence exceeds TPOC deposition. We present a general framework for considering directional fluxes across habitat boundaries. Furthermore, our results highlight the overarching role of ecosystem geometry in determining insect emergence, airborne carbon deposition, and net carbon flux between adjacent ecosystems.

Résumé : Les écologistes sont de plus en plus intéressés à savoir comment les habitats séparés sont reliés par des mouvements croisés de la matière, des proies, des nutriments et du détritus entre les habitats et aussi à en connaître les conséquences sur les systèmes récipiendaires. L'étude des écosystèmes lacustres a été dominée par la détermination de la production et des processus pélagiques (en eau libre), bien qu'il y ait une perception croissante du rôle des apports terrestres et des voies trophiques benthiques. Nous faisons une rétrospective du phénomène des flux atmosphériques provenant des lacs et y aboutissant. Nous rassemblons les données publiées sur les précipitations de carbone organique particulaire terrestre (TPOC) dans les lacs, sur la production des insectes et sur l'émergence des insectes et nous utilisons ces données pour simuler comment les flux atmosphériques de carbone du lac vers le milieu terrestre et du milieu terrestre vers le lac sont fonction de la taille de l'écosystème, tout en tenant compte de la variabilité de l'émergence et des précipitations de TPOC entre les lacs. Le flux d'insectes émergés vers le milieu terrestre augmente en fonction de la taille du lac, alors que les précipitations de TPOC dans les lacs diminuent en fonction de la taille du lac. Les précipitations de TPOC sont supérieures à l'émergence des insectes dans les petits lacs, alors que, dans les grands lacs, l'émergence des insectes dépasse les précipitations de TPOC. Nous présentons un cadre général pour l'étude des flux directionnels à travers les frontières des habitats. De plus, nos résultats soulignent le rôle prédominant de la géométrie de l'écosystème dans la détermination de l'émergence des insectes, des précipitations atmosphériques de carbone et du flux net de carbone entre les écosystèmes adjacents.

[Traduit par la Rédaction]

Introduction

> A paradigm forged on the belief that what matters happens in the open-water pelagic just had to change.

The above quote from Reynolds (2008, p. 527) adds to a growing chorus of challenges to the long-standing "pelagiocentric" paradigm of lake ecosystem function (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002; Cole et al. 2006). This expanding view parallels the more general acknowledgement that disjunct habitats can be coupled via food web linkages and that these cross-habitat couplings can have important implications for recipient food webs (Polis et al. 1997, 2004). Habitats can be linked through the movement of predators, prey, detritus, or nutrients — such linkages many be ultimately driven by migration, gravity,

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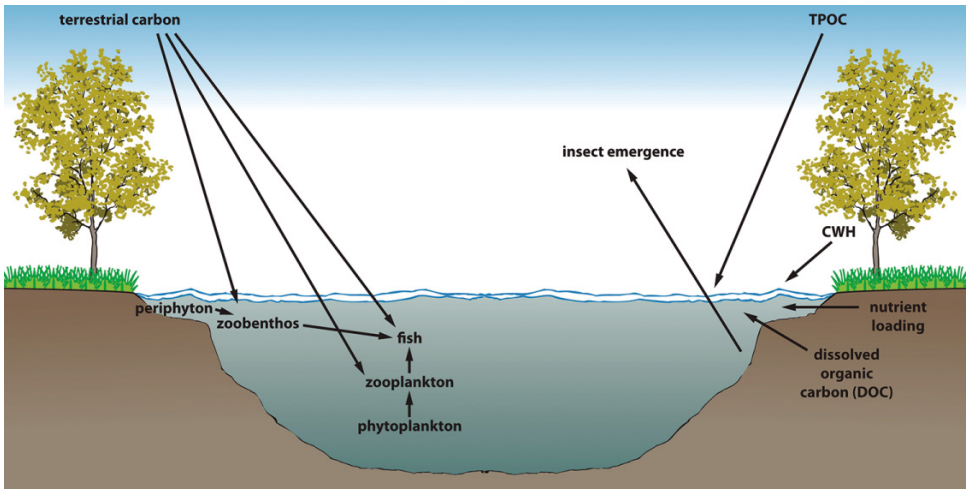
Fig. 1. A generalized north-temperate lake. Left side: some of the major carbon flow pathways. Right side: cross-habitat linkages considered in this paper. TPOC, terrestrial particulate organic carbon; CWH, coarse woody habitat.



currents of water and air, or human activities. These cross-habitat linkages can have important implications for the dynamics of recipient systems. Notable examples include marine inputs subsidizing desert island food webs off the coast of Baja California, Mexico (Polis and Hurd 1995, 1996) and the reciprocal cross-habitat food web linkages involving small streams and their surrounding riparian habitat (Nakano et al. 1999; Nakano and Murakami 2001).

In contrast with many terrestrial continental ecosystems, lakes have often been envisioned as habitat islands in a sea of land (Forbes 1887). Conveniently, they have discrete borders, and for the purpose of investigations, can be viewed as "closed" ecosystems. This feature makes them appealing systems for ecological and biogeochemical study, and several important ideas in the history of ecology derive from the study of lakes as habitat islands (Lindeman 1942; Hutchinson 1959; Carpenter et al. 1985). At the organismal level, it is true that many of the dominant and well-studied lake inhabitants such as fish are confined to lakes for the entirety of their lives. On the other hand, it is widely recognized that lakes are subject to a directional flux of sediments and nutrients from land (Sharpley et al. 1994; Carpenter et al. 1998; Smith and Schindler 2009). Human activities such as agriculture and urbanization greatly exacerbate nutrient inputs to lakes, with major environmental and economic consequences (Sharpley et al. 1994; Carpenter et al. 1998). In addition, many lakes are net heterotrophic systems, necessitating carbon inputs from outside the system (del Georgio and Peters 1994; del Giorgio et al. 1997; Hanson et al. 2003).

The unidirectional nature of the paradigm of lake–land linkages contrasts with the situation for stream ecosystems. Early research and conceptual models in stream ecology highlighted the dominant role of allochthonous inputs as a driver of stream ecosystem carbon and energy budgets (Fisher and Likens 1973; Hynes 1975; Vannote et al. 1980). Upstream–downstream as well as lateral (i.e., main channel – floodplain) habitat linkages have been challenging to study, but are well-integrated into stream ecologists' worldview (Vannote et al. 1980; Junk et al. 1989; Malmqvist 2002), such that streams are generally viewed as a tightly integrated part of the broader watershed ecosystem (Hynes 1975; Allan 1995; Malmqvist 2002). One contributing factor is that lotic systems tend to be more compact in spatial extent relative to lentic systems: the land–water ecotone for streams is visually obvious, and the fact that terrestrial vegetation often overhangs streams is a further reminder of the potential for connectivity between streams and the surrounding terrestrial landscape. In the last decade, a body of experimental research has elucidated the interconnectivity and interdependence of stream and terrestrial food webs (Nakano et al. 1999; Nakano and Murakami 2001; Baxter et al. 2005).

Perhaps it is not surprising that our understanding of the relevant processes linking aquatic and terrestrial habitats (i.e., secondary production, aquatic insect emergence) derives primarily from research on stream ecosystems. In this paper we address airborne cross-habitat linkages involving lake ecosystems, with emphasis on integrating our current understanding of land-to-lake and lake-to-land linkages. We use carbon as a currency for the ecosystem because it is the most commonly used unit for studies of ecosystem production and energy flow, though ecosystem fluxes could also be represented using mass, energy, phosphorus, or nitrogen.

We start by providing a thumbnail sketch of carbon flows in a generalized north-temperate lake ecosystem (Fig. 1, left side). At the base of the food web, in-lake (autochthonous) primary production occurs in both pelagic (phytoplankton) and benthic (periphyton) habitats. Lakes also receive allochthonous carbon (in various forms) from the watershed, providing an additional potential carbon source to the base of the food web. Dominant primary consumer groups are zooplankton and zoobenthos — these groups rely on a variable mix of terrestrial, benthic, and pelagic carbon sources. There may be additional invertebrate trophic levels (invertebrate predators) within both zooplankton and zoobenthos. These groups provide food for invertivorous fishes, which in turn may be fed upon by piscivorous fishes. The central foci of this paper are nonmicrobial food web linkages that support higher trophic levels such as fishes. Lake-wide carbon cycling and microbial processes are beyond the scope of this paper and have been addressed elsewhere (del Georgio and Peters 1994; del Giorgio et al. 1997; Hanson et al. 2003).

Land-to-lake linkages

Lakes, by definition, tend to occupy low spots or depressions on the landscape. As a result, they are subject to the downhill, gravity-driven delivery of terrestrial-derived materials: organic and inorganic matter, organisms, and nutrients (Likens et al. 1970). Pathways for this land-to-lake transport include stream inflows, groundwater, and wet or dry airborne deposition (Fig. 1, right side). We review these land-to-lake linkages below, emphasizing the role of airborne pathways.

Nutrient loading to lakes

By far the most well-documented linkage between lakes and land is the input of terrestrial-derived nutrients into lakes (Hasler 1975; Sharpley et al. 1994; Carpenter et al. 1998). A large body of research has since linked excess loading of phosphorus from agricultural, municipal, and industrial sources to degradation of water quality and excess algal blooms (Schindler 1974, 1977), prompting efforts to reduce point sources and nonpoint source nutrient runoff to aquatic ecosystems. Nitrogen and phosphorus also enter lakes via atmospheric pathways. In agricultural or urban watersheds, the atmosphere is likely to be secondary in importance to that of nutrient runoff. Most atmospheric nitrogen is anthropogenic in origin and derives from fossil fuel combustion and volatilization from agricultural lands (Carpenter et al. 1998). Atmospheric deposition is the main source of nitrogen as well as an important source of phosphorus to Lake Tahoe and other alpine lakes (Goldman 1961; Jassby et al. 1994). Cole et al. (1990) found that atmospheric fallout was a significant source of phosphorus to Mirror Lake, greatly exceeding stream-derived phosphorus loading. Atmospheric nitrogen deposition is closely linked to watershed export of nitrogen and the resulting coastal zone eutrophication (Howarth et al. 1996; Jaworski et al. 1997). These examples highlight the fact that atmospheric nutrient pathways can have important implications for aquatic systems and water quality.

Terrestrial dissolved organic carbon (TDOC) inputs to lakes

Terrestrial organic carbon enters lakes in either particulate or dissolved form. Dissolved organic carbon (DOC) is a component of rainwater (Willey et al. 2000), though most DOC loading to lakes is received directly from the catchment and is not atmospheric in origin. Catchment-derived DOC flux to lakes is driven by factor such as water residence time and the occurrence and position of wetlands in the watersheds relative to lakes (Dillon and Molot 1997*a*, 1997*b*; O'Connor et al. 2009).

DOC plays a remarkably important role in structuring lake ecosystems (Wetzel 2001). It strongly influences lake transparency and mixing depth (Fee et al. 1996), bioaccumulation of methylmercury (Watras et al. 1998), attenuation of UV radiation (Morris et al. 1995), and is a key substrate for microbial production. Though terrestrial DOC fuels pelagic bacterial respiration in lakes, it is generally not efficiently passed to higher trophic levels (Cole et al. 2002, 2006).

Terrestrial particulate organic carbon (TPOC) inputs to lakes

TPOC in lakes can be operationally defined as material larger than 0.45 μm in diameter. TPOC inputs to lakes can be of diverse origins and include leaves, twigs, insects and insect parts, pollen, and airborne dust. Studies of TPOC inputs to lakes have focused primarily on litterfall and atmospheric deposition, though streams and direct surface runoff are also potential sources of TPOC to lakes.

The relatively few empirical studies of TPOC deposition have been limited with regards to particle size or season. Studies have either quantified leaf (coarse TPOC) inputs during the fall season (Gasith and Hasler 1976; France and Peters 1995) or measured fine organic matter inputs during summer (Cole et al. 1990; Preston et al. 2008). TPOC loading rates are highly variable among lakes. Overall rates of litterfall inputs to lakes are very much influenced by terrestrial vegetation type and forest cover (Rau 1976; France and Peters 1995). Furthermore, within lakes the magnitude and nature of TPOC inputs are highly variable in space and time, depending on factors such as local vegetation type, location relative to the dominant wind direction, and major weather events (Preston 2009). For leaf litterfall inputs, there is generally a rapid decline as a function of distance from shore, with most leaf litter inputs to lakes occurring within 10 m of shore (Gasith and Hasler 1976; France and Peters 1995). Inputs of fine POC to lakes are also elevated adjacent to shore, though there is notable deposition extending substantial distances out into the lake (Preston et al. 2008; Preston 2009).

Insects and coarse woody habitat as TPOC

A notable fraction of airborne organic matter inputs to lakes consists of terrestrial arthropods and arthropod fragments. Though terrestrial insects are rarely dominant in lentic fish diets, they are commonly present (Hunt 1975; Weidel et al. 2008). Mehner et al. (2005) reported that the diet of bleak (*Alburnus alburnus*) was dominated by terrestrial insects (~84%), with potential impacts on the phosphorus budget of the lake. Rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) from Castle Lake, California, consumed >30% terrestrial prey (Vander Zanden et al. 2006). Even siscowets, the deepwater form of lake trout (*Salvelinus namaycush*) from Lake Superior, were found to consume terrestrial insects (Sitar et al. 2008). Francis and Schindler (2009) found that fish consumption of terrestrial arthropod prey declined with increasing lakeshore development. They also found a positive effect of terrestrial prey on salmonid consumption rates, indicating the functional importance of this poorly appreciated cross-habitat link.

Terrestrial arthropods can affect lake ecosystems, aside from their role as fish food. In the summer of 1979, millions of ants were blown into Castle Lake, California, on two occasions, causing notable pulses in water column ammonium concentrations (Carlton and Goldman 1984). In several areas of eastern North America, emergences of 17-year cicada broods produced large inputs of organic matter in the form of cicada carcasses to small aquatic ecosystems (Nowlin et al. 2007; Pray et al. 2009). Although these are dramatic examples, they highlight the potential role of terrestrial arthropods in linking terrestrial and aquatic systems.

Finally, trees and branches from riparian vegetation fall into lakes and can be viewed as particularly large packages of TPOC. Because wood decomposition rates are slow,

fallen trees provide course woody habitat (CWH) to aquatic systems (Schindler and Scheuerell 2002; Francis and Schindler 2006). Recent work has demonstrated a strong negative relationship between CWH and housing density, stemming from the fact that humans tend to remove trees and CWH from lake shorelines (Christensen et al. 1996). CWH is an important refuge habitat for invertebrates and fish and plays an important role in stabilizing predator–prey dynamics (Sass et al. 2006). Schindler et al. (2000) reported a positive relationship between CWH density and fish growth rates.

Implications of terrestrial carbon inputs to lakes

Recent studies have assessed the role of terrestrial-derived organic carbon to lake metabolism and the production of higher trophic levels. Dystrophic and unproductive lakes are well-documented to be net heterotrophic, meaning that bacterial respiration is greater than phytoplankton production (del Georgio and Peters 1994; del Giorgio et al. 1997; Hanson et al. 2003). This net heterotrophy requires an external carbon source, and the role of allochthonous DOC inputs in fueling bacterial respiration is widely accepted (Hanson et al. 2003).

Studies have assessed the influence of terrestrial-derived carbon on the classical (nonmicrobial) food web. Graham et al. (2006) found that addition of conifer pollen to experimental mesocosms subsidized nutrient levels, producing increased phytoplankton, periphyton, and zooplankton biomass. Terrestrial leaf litter partially supports benthic macroinvertebrate production in lakes (Rau 1976; Solomon et al. 2008). Stable isotope studies suggest that zooplankton rely on a mix of autochthonous and allochthonous carbon (Karlsson et al. 2003). Differentiating autochthonous and allochthonous carbon pathways using stable carbon isotopes can be confounded when sources have overlapping $\delta^{13}C$ values. This problem has been overcome through whole-lake ^{13}C addition experiments. These experiments indicate that in-lake POC and zooplankton in small north-temperate lakes were up to 50% terrestrial in origin (Pace et al. 2004). Terrestrial carbon inputs to aquatic food webs may ultimately be derived from one of several pathways: TDOC, TPOC, or terrestrial prey, defined as terrestrial insects or vertebrates that intentionally or accidentally enter lakes and can be consumed by fish. Cole et al. (2006) reported that TDOC dominated bacterial respiration, but was a minor contributor to higher trophic levels of either benthic or pelagic food webs. In contrast, TPOC inputs were readily incorporated into pelagic and benthic invertebrates, while terrestrial prey items were a major carbon source for certain fish species.

Terrestrial carbon inputs can also affect lentic food webs in reservoir ecosystems containing gizzard shad (*Dorosoma cepedianum*) in the southeastern United States. Gizzard shad exert dramatic direct and indirect food web impacts on phytoplankton, zooplankton, and planktivorous and piscivorous fishes. They can be very abundant and have such impacts because they are omnivorous and consume large amounts of terrestrial detritus (Stein et al. 1995; Vanni et al. 2005). Detritus is abundant in many reservoir systems and subsidizes gizzard shad populations, thereby effectively decoupling them from in situ prey such as zooplankton (Stein et al. 1995; Vanni et al. 2005). The consumption of terrestrial resources allows gizzard shad to play a keystone role in structuring many reservoir ecosystems.

In summary, there are diverse pathways by which organic matter and nutrients of terrestrial origin can be transported to lake ecosystems. These inputs can have important implications for the structure and function of these ecosystems. Inputs of terrestrial-derived nutrients are the major driver of lake eutrophication, an environmental problem of global concern. In addition, terrestrial-derived carbon affects a wide range of lake ecosystem functions: water transparency, UV penetration, water chemistry, and ecosystem metabolism, in addition to partially supporting the production of higher trophic levels.

Lake-to-land linkages

Our understanding of the linkages between lakes and the surrounding landscape has been primarily focused on land-to-lake linkages (Schindler and Scheuerell 2002). Yet a wide range of taxa, including birds, mammals, reptiles, amphibians, fish, and insects, have behaviors and life histories that can couple aquatic and terrestrial habitats, often in complex and reciprocal ways. Perhaps the most potent vector for lake-to-land linkages is aquatic insects. Aquatic insects have complex life histories — typically there is a larval aquatic stage lasting anywhere from several weeks to several years, followed by metamorphosis into a terrestrial adult stage. Only recently have studies examined the role of aquatic insects in linking lakes and surrounding terrestrial habitats and the resultant implications for terrestrial food webs (Finlay and Vredenburg 2007; Gratton et al. 2008; Pope et al. 2009). In a study of 16 lakes from the Trinity Alps Wilderness, California, Pope et al. (2009) found that aquatic insect emergence increased in response to removal of non-native trout and that trout density determined insect emergence from alpine lakes. Along these same lines, Finlay and Vredenburg (2007) found that lakes in the Sierra Nevada mountains of California with introduced trout populations had dramatically reduced (~20×) levels of aquatic insect emergence. These aquatic insects were important prey for terrestrial consumers, particularly mountain yellow-legged frog (*Rana muscosa*), which were ten times more abundant in the absence of non-native trout. This study demonstrated how the introduction of trout severed the food web link between lakes and the surrounding "terrestrial" consumers (adult frogs), leading to declines in native amphibians and potentially their terrestrial predators as well.

Gratton et al. (2008) quantified aquatic insect (midge) infall into terrestrial habitats adjacent to Icelandic lakes. Rates of midge infall to the terrestrial ecosystem were highly variable among lakes, declined with distance from the lakeshore, and at some lakes, were likely sufficient to produce an important fertilizing effect on terrestrial vegetation. Carbon isotope ratios also revealed that near lakes with large midge populations, many terrestrial consumers were highly dependent upon midge-derived trophic pathways (Gratton et al. 2008). A broad literature review of aquatic insect dispersal from aquatic systems revealed that insect deposition to terrestrial ecosystems shows a negative exponential decline as a function of distance from shore (Gratton and Vander Zanden 2009), indicating that this linkage is spatially constrained.

Knight et al. (2005) found that the presence of predatory fish in Florida ponds reduced local abundance of larval and adult dragonflies. Dragonflies themselves prey on other insects as larvae and adults. The reduction in adult dragonflies in the presence of fish resulted in nearby terrestrial plants receiving more visits from pollinators, thereby increasing plant reproductive output. Amphibians can also couple aquatic and terrestrial systems. When salamander larvae metamorphose into terrestrial adults, they transfer substantial amounts of pond-derived production to terrestrial habitats, while oviposition by females transfers terrestrial-derived production back to aquatic systems, highlighting the potential for lentic and terrestrial habitats to be coupled in a reciprocal manner (Regester et al. 2006, 2008).

Carbon flux across the lake–land ecotone

In the above two sections, we surveyed the literature on cross-habitat linkages between lakes and the surrounding terrestrial landscape, highlighting examples of linkages occurring in both directions (i.e., lake-to-land and land-to-lake). Though individual studies have assessed fluxes across this ecotone, an important remaining task is to identify and quantify the factors that modulate the individual and net fluxes in both directions. To do so, we build upon the model of Gratton and Vander Zanden (2009), which considered aquatic productivity and ecosystem geometry as controlling variables modulating the export of aquatic production to land. Here, we extend this model to also include TPOC deposition to lakes and how lake-to-land, land-to-lake, and net airborne carbon flux scale with lake size (variables and symbols used in our calculations are indicated in Table 1). First, we provide a brief overview of three key factors that affect airborne carbon fluxes to and from lakes: aquatic productivity, TPOC deposition, and ecosystem geometry. Following this, we develop the two components of the model (lake-to-land and land-to-lake) and use numeric simulations and the limited existing empirical data to attempt to quantitatively compare the cross-habitat fluxes.

Aquatic production

The magnitude of aquatic insect flux from lakes is constrained by several factors, the most fundamental being aquatic secondary production. Production is an important and potentially unifying concept in ecology (Odum 1968) and represents the rate of generation of new biomass over a given time period. It can be estimated at multiple ecological levels, ranging from populations to whole ecosystems, and provides a common currency for characterizing the flow of carbon through food webs and ecosystems (Lindeman 1942; Odum 1968; Waters 1977).

The basic method for estimating secondary production for a benthic invertebrate population dates to Boysen-Jensen (1919). Since then there have been methodological advances, though the basic idea remains the same and involves tracking the growth and mortality of a cohort of individuals through time — production is calculated as the area under the curve of a plot of number of individuals versus mean mass (the method is also referred to as the Allen curve, increment summation, instantaneous growth, or the cohort methods; Waters 1977). In reality, many populations do not show clear cohorts because of overlapping generations. In such cases, one can assume that the size-frequency distribution of individuals collected throughout the year reflects that of the "average" cohort, thereby allowing production to be approximated (called the size-frequency method; Waters 1977). Investigators have found that production per unit biomass (P/B, turnover rate) does not vary widely for a given taxon. Thus investigators sometimes estimate production as the product of mean annual biomass (estimated from field sampling) and literature-derived P/B values. Studies have also found that P/B varies as a function of body size and temperature, thus allowing for allometric-based empirical methods for estimating production from field biomass data (Banse and Mosher 1980; Plante and Downing 1989). This is particularly useful when scaling production estimates up to the community or ecosystem scale.

Aquatic secondary production is the most widely available indicator of potential insect emergence in lakes. Of course, only a fraction of invertebrate secondary production consists of aquatic insects, which are the taxonomic group that emerges from lakes. Furthermore, only a fraction of the aquatic insect production from a lake emerges and thus potentially links aquatic and terrestrial systems. Finally, some fraction of emergent insects ultimately return to the lake in the form of insect carcasses and either sink, decompose, wash to shore, or are consumed. Though we view aquatic secondary production as an important factor regulating aquatic insect flux from lakes to land, the combination of factors noted above ultimately determine insect emergence and the potential flux to land.

TPOC deposition

The second factor in our generalized model of airborne carbon fluxes to and from lakes is TPOC deposition. As noted above, we define TPOC as terrestrial-derived particles that are deposited upon lake surfaces. For the sake of simplicity, our model ignores airborne DOC in rainwater and non-airborne or non-atmospheric TPOC sources (river inflows and overland deposition). TPOC is diverse in origin and includes pollen, leaf litterfall, insects, and airborne dust. As such, it is difficult to generalize with regard to chemical composition, lability, and food quality. Furthermore, rates of TPOC deposition onto lake surfaces are highly variable among lakes, and for individual lakes, TPOC inputs can vary widely in space and through time (Preston et al. 2008; Preston 2009). Terrestrial particle deposition is typically measured using floating collectors distributed on the lake surface, from which total deposition can be approximated. Studies often separate large and small fractions (for example, Preston et al. 2008 considered large to be >153 μm and small as 0.7–153 μm).

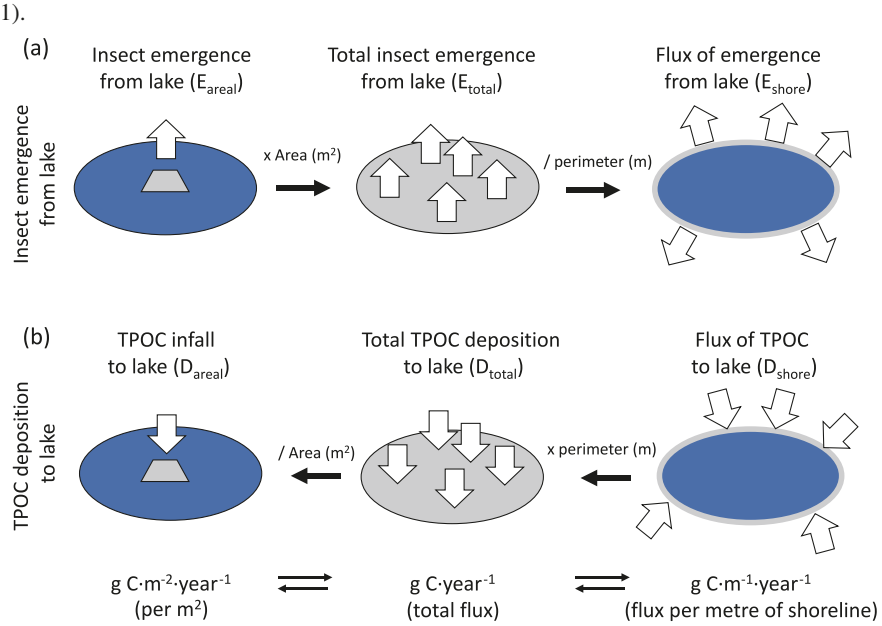
Ecosystem geometry

The third factor mediating airborne aquatic–terrestrial linkages is ecosystem geometry, which refers to both ecosystem size and shape. Lakes can be simplified by reducing their complex geometries into two easily quantifiable attributes: lake perimeter (p) and area (A). Ecosystem geometry is fundamental in mediating the strength of land–lake linkages, primarily because it determines the perimeter to area ratio (p/A) (Polis and Hurd 1996). Small lakes are dominated by

Table 1. Variables used in this study.

Variable	Symbol	Unit	Equation
Shoreline development factor	D_L	—	$p/[2(\pi A)^{1/2}]$
Lake perimeter	p	m	—
Lake area	A	m^2	—
Lake radius	r	m	$(A/\pi)^{1/2}$
Benthic secondary production	P_b	g C·m^{-2}·year^{-1}	—
Fraction of benthic secondary production consisting of insects	f_i	(Fraction)	—
Benthic insect production	P_i	g C·m^{-2}·year^{-1}	$P_b \times f_i$
Emergence			
Fraction of benthic insect production that emerges from the lake	f_e	(Fraction)	—
Insect emergence	E_{areal}	g C·m^{-2}·year^{-1}	$P_i \times f_e$
Total flux, aquatic to terrestrial	E_{total}	g C·year^{-1}	$E_{areal} \times A$
Emergent insect flux: per metre of shore	E_{shore}	g C·m^{-1}·year^{-1}	E_{total}/p
Deposition			
Shoreline deposition: terrestrial deposition per metre of shoreline	D_{shore}	g C·m^{-1}·year^{-1}	—
Total flux, terrestrial to aquatic	D_{total}	g C·year^{-1}	$D_{shore} \times p$
Terrestrial deposition: per square metre of lake	D_{areal}	g C·m^{-2}·year^{-1}	D_{total}/A

Fig. 2. Illustration of our approach for estimating lake-to-land and land-to-lake carbon fluxes. (*a*) Aquatic insect emergence from lakes. Calculations in this study moved from left to right. (*b*) TPOC deposition to lakes. Calculations in this study moved from right to left (see variables listed in Table 1).

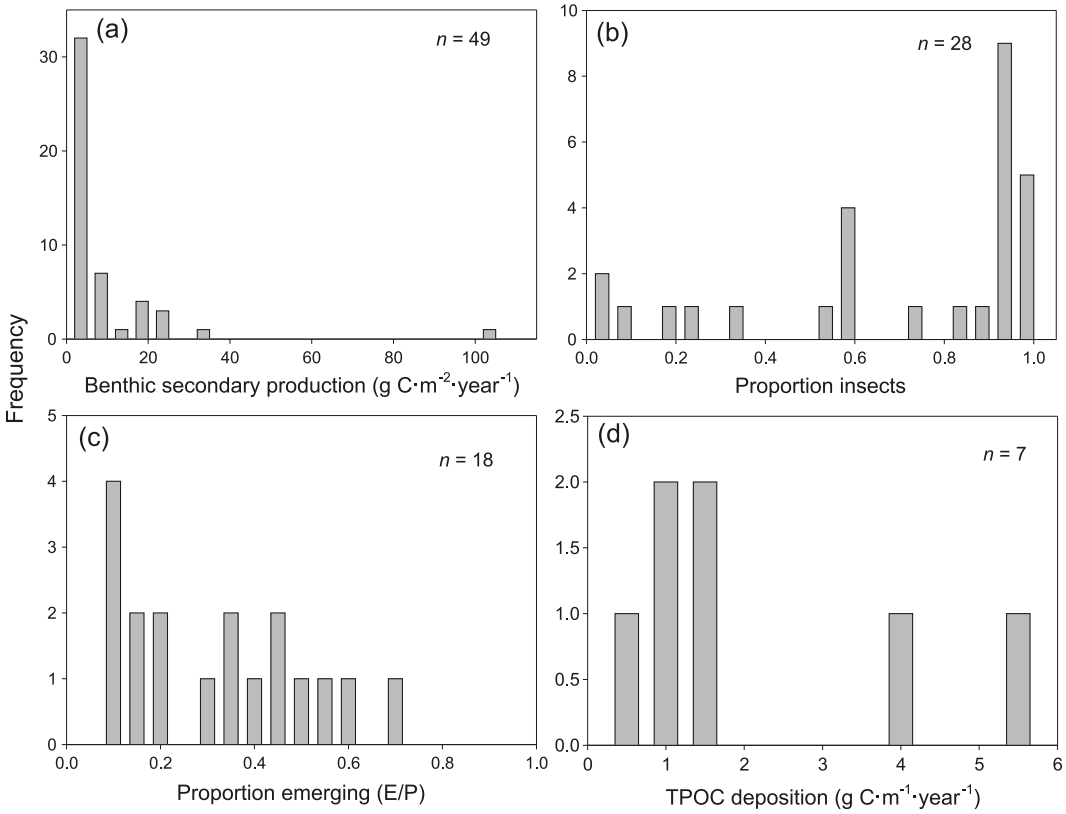


"edge" or shoreline effects (i.e., p/A is relatively large) because the entire lake can be in close proximity to the shoreline, similar to the situation for streams. In contrast, large lakes have less shoreline relative to their surface area (p/A is smaller). In addition, lake shape determines the overall shoreline length for a given lake size. The shoreline development factor ($D_L = p/[2(\pi A)^{1/2}]$, where p is perimeter (m) and A is area (m^2)) is a widely used measure of shoreline complexity in which lake perimeters (p) are compared with the perimeter of an idealized circular lake of similar area. D_L ranges from 1.0 for a perfectly circular lake to >15 for some highly reticulate reservoir systems (Kalff 2002).

Modeling lake-to-land flux

Our approach for examining insect emergence from lakes is based on Gratton and Vander Zanden (2009) (illustrated in Fig. 2*a*). Some fraction (f_i) of lake benthic secondary production (P_b) consists of benthic insects (P_i). Aquatic insects are the sole taxonomic group that emerges from lakes, thus potentially linking aquatic and terrestrial habitats. Some fraction of benthic insect production emerges (f_e) from the lake (E_{areal}). Based on the above, $E_{areal} = P_b \times f_i \times f_e$ (note that P_b, P_i, and E_{areal} are expressed on a per square metre basis; g C·m^{-2}·year^{-1}). Total aquatic insect flux is calculated as the product of insect emergence E_{areal} and lake area A

Fig. 3. Literature-derived data used in our simulations: (*a*) benthic secondary production (P_b), (*b*) proportion of benthic secondary production comprised of insects (f_i), (*c*) fraction of insect production that emerges (f_e), and (*d*) TPOC deposition per unit shoreline (D_{shore}).



(m^2): $E_{total} = E_{areal} \times A$ (g C·year^{-1}). Flux per metre of shoreline (E_{shore}, g C·m^{-1}·year^{-1}) is estimated by dividing total flux by lake perimeter: $E_{shore} = E_{total}/p$. For a circular lake, $A = \pi r^2$ and $p = 2\pi r$, where r is the lake radius. Variation in lake shape can also be accounted for by including the shoreline development factor: $E_{shore} = E_{areal} \times r/(2D_L)$ (Gratton and Vander Zanden 2009).

We give the above conceptual framework an empirical footing using a combination of literature-derived and simulated data for the above parameters (Gratton and Vander Zanden 2009). Benthic secondary production and insect emergence data were available for a broad cross-section of lake types from around the world, though there are surprisingly few estimates available. Of the 49 whole-lake benthic secondary production estimates for lakes, only 14 were published after 1980. The majority of the production estimates dated from the International Biological Programme of the 1960s and 1970s. These data were used to simulate potential fluxes of aquatic insects to land in a previous study (Gratton and Vander Zanden 2009).

Values of benthic secondary production (P_b) were highly right-skewed, with a median value of 2.3 g C·m^{-2}·year^{-1} (Fig. 3*a*). On average, insects comprised about 70% of benthic secondary production (f_i = 0.70 ± 0.33, mean ± 1 standard deviation, SD; Fig. 3*b*), while approximately 30% of insect production leaves lakes in the form of insect emergence (f_e = 0.30 ± 0.04, mean ± 1 SD; Fig. 3*c*). Because insect production and emergence were independent of lake area, we used these data to simulate how production and ecosystem size interact to determine the flux of aquatic insects to land (Gratton and Vander Zanden 2009). We randomly selected a value of P_b, f_i, and f_e from our empirical data (n = 49, 28, and 18, respectively) and calculated the product, which is a pseudo-estimate of insect emergence ($E_{areal} = P_b \times f_i \times f_e$; g C·m^{-2}·year^{-1}). This was repeated 5000 times. We then generated 5000 corresponding values of lake area (A, m^2) from a hypothetical lake size distribution with a constant number of lakes in each $\log_{10}$ size class. For each simulated lake, we calculated total emergence ($E_{total} = E_{areal} \times A$; g C·year^{-1}) and insect flux per metre of shoreline ($E_{shore} = E_{total}/p$; g C·m^{-1}·year^{-1}). For simplicity, all lakes in our model were treated as circular.

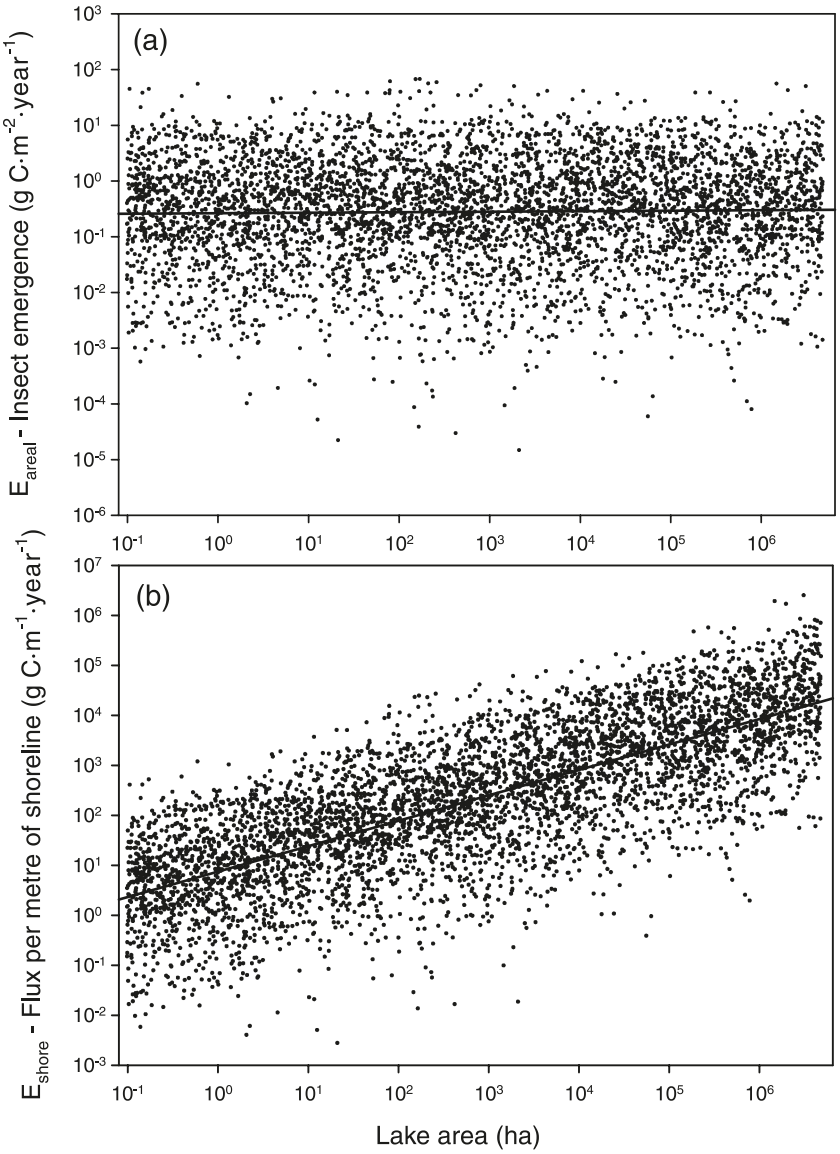
Results: lake-to-land

Our estimates of insect emergence (E_{areal}, g C·m^{-2}·year^{-1}) varied widely among lakes and were independent of lake size (Fig. 4*a*). Expressing emergence as the flux per metre of shoreline (E_{shore}, g C·m^{-1}·year^{-1}) has the effect of incorporating ecosystem geometry, such that E_{shore} increases with lake size (Fig. 4*b*). The residual scatter (Figs. 4*a* and 4*b*) reflects the among-lake variation in secondary production and insect emergence. The positive relationship with lake size is intuitive because the amount of lake surface area per metre of shoreline increases as a linear function of lake radius (and thus area).

Modeling land-to-lake flux

A similar conceptual approach as above was used to estimate terrestrial-derived aerial inputs to lakes, though applied in reverse (Fig. 2*b*, moving right to left). We used empirical

Fig. 4. Scaling of lake-to-land airborne carbon flux with lake size based on 5000 simulated lakes: (*a*) insect emergence on an areal basis: E_{areal}, g C·m^{-2}·year^{-1}; (*b*) emergent insect flux per metre of shoreline: E_{shore}, g C·m^{-1}·year^{-1}.



estimates of airborne carbon deposition, D_{shore}, expressed per metre of shoreline (g C·m^{-1}·year^{-1}, Fig. 2*b*), as presented in Preston et al. (2008). Theoretically, D_{shore} should be independent of the size of the recipient lake, since it is expressed on a per metre of shoreline basis. There were only seven empirical estimates of D_{shore} (Fig. 3*d*), and the data were collected using diverse sampling methods (mesh size, seasonality, and sampling intensity). Because of the small sample size, we fit a negative exponential model to the D_{shore} estimates (σ = 1.88 g C·m^{-1}·year^{-1}; Fig. 3*d*). From the fitted distribution, we generated 5000 D_{shore} values and 5000 corresponding lake areas (again, same number of lakes in each $\log_{10}$ size class). For simplicity, we assumed recipient lakes were circular, with a perimeter p, radius r, and area A. For each simulated lake, we calculated total flux to the lake ($D_{total} = D_{shore} \times p$; g C·year^{-1}) and the flux per square metre of lake ($D_{areal} = D_{total}/A$; g C·m^{-2}·year^{-1}). Since we assume lakes to be circular, this equation simplifies to $D_{areal} = (2D_{shore})/r$.

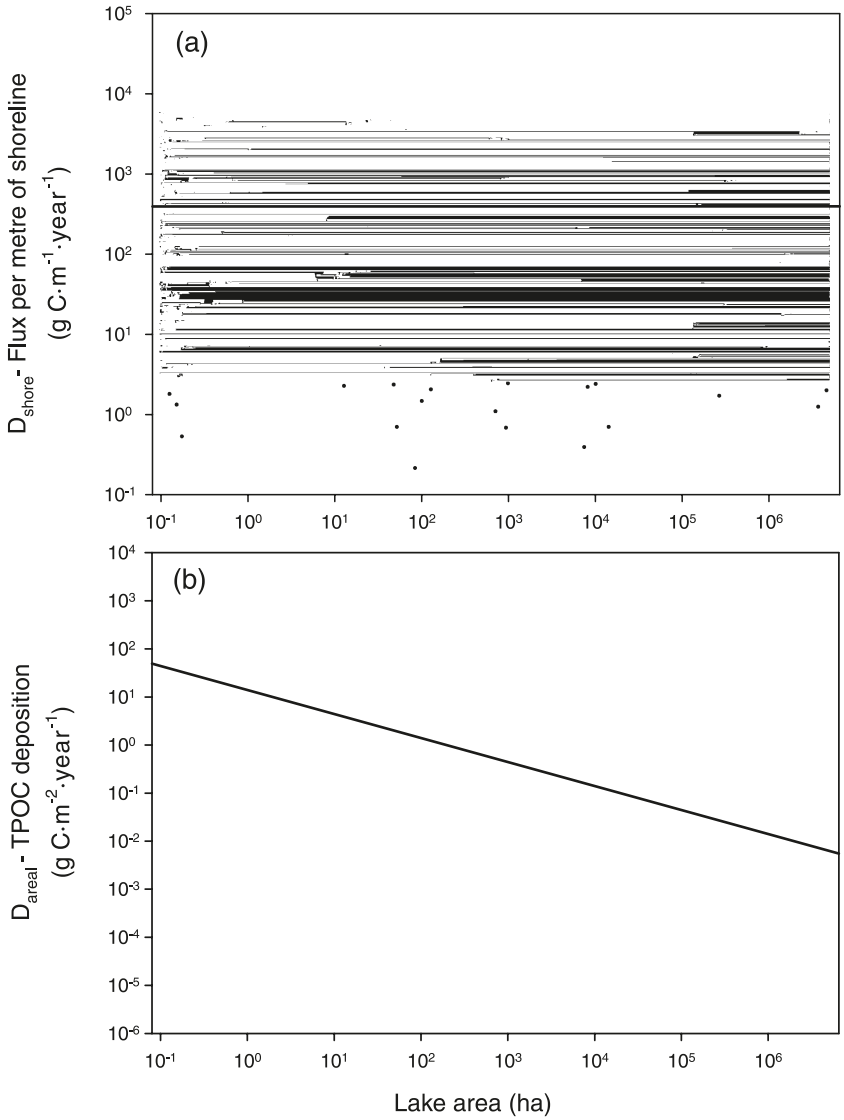
Results: land-to-lake

Airborne carbon deposition D_{shore} varied widely among lakes. In our simulation, D_{shore} was modeled to be independent of lake area (Fig. 5*a*). When expressed as per square metre of lake surface area D_{areal}, average deposition decreases as a function of lake size, as airborne TPOC deposition is diluted over a larger surface area (Fig. 5*b*). These results are intuitive — compared with large lakes, small lakes are dominated by edge and are thus subject to greater airborne inputs, all else being equal. The scatter around the trend lines (Figs. 5*a* and 5*b*) reflects among-lake variation in D_{shore}. Numerous unaccounted-for factors, such as riparian vegetation type and position relative to dominant wind direction, are likely responsible for the variation in the amount of airborne land-to-lake carbon flux.

Results: net airborne carbon flux

The overall patterns of land-to-lake airborne carbon flux

Fig. 5. Scaling of land-to-lake airborne carbon flux with lake size based on 5000 simulated lakes. (*a*) TPOC deposition per metre of shoreline: D_{shore}, g C·m^{-2}·year^{-1}; (*b*) TPOC deposition expressed on an areal basis: D_{areal}, g C·m^{-2}·year^{-1}.



contrast with those for lake-to-land (Figs. 4 and 5). We compared how total carbon flux (E_{total} and D_{total}) scales with lake area in each direction. Both E_{total} and D_{total} increase as a function of lake area (Fig. 6). Assuming "typical" insect emergence and TPOC deposition rates, terrestrial inputs to lakes exceeds insect emergence ($D_{total} > E_{total}$) in lakes smaller than 2000 ha. For larger lakes, insect emergence exceeds aerial TPOC flux to the lake ($D_{total} < E_{total}$). For the vast majority of lakes on the planet, most of which are small (Downing et al. 2006), the airborne flux of terrestrial carbon to lakes is likely to exceed that of insect emergence. It is only in moderate-sized lakes that carbon fluxes are comparable, while in large lakes, emergence is expected to exceed terrestrial airborne inputs. Lake geometry determines the net flux across the lake–land ecotone when examined across the full range of ecosystem sizes, though there is also a high degree of variability (not shown in Fig. 6) that derives from variation in benthic production, insect emergence, and TPOC deposition rates (e.g., the scatter in Figs. 4 and 5).

Discussion

The scope of ecological research has expanded over the past decade to include the movement of nutrients, matter, and energy across habitat boundaries (Polis et al. 1997, 2004). These fluxes often have important consequences for the structure and dynamics of the recipient systems, such that the dynamics of an ecosystem are often driven by processes and fluxes emanating from an adjacent habitat or ecosystem (Polis et al. 1997, 2004). Interestingly, the importance of cross-habitat fluxes and food web linkages are surprisingly poorly known for lakes (Schindler and Scheuerell 2002). In contrast, a great body of research has now accumulated for stream ecosystems. On the one hand this makes sense; the ratio of edge to volume partially determines potential for habitat coupling (Schindler and Scheuerell 2002). Streams are generally small and are thus dominated by edge habitat, which would tend to promote coupling of the two habitats. In contrast, lakes are relatively large and are less dominated by edge habitats. On the other

terrestrial ecosystem are poorly appreciated (Gratton and Vander Zanden 2009). While such fluxes may play a minor role in overall ecosystem carbon budgets, emergent insects are high-quality resources that are aggregated in riparian and nearshore areas. Thus, they are often an important resource for riparian consumers and ecosystems, particularly adjacent to large rivers and lakes (Gratton and Vander Zanden 2009). The broader implications of such lake-to-land fluxes are poorly explored (Finlay and Vredenburg 2007; Gratton et al. 2008; Pope et al. 2009), but the effects may exceed those reported for streams because of fundamental differences in ecosystem geometry between these ecosystems.

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References

Allan, J.D. 1995. Stream ecology. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Banse, K., and Mosher, S. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. **50**(3): 355–379. doi:10.2307/2937256.

Baxter, C.V., Fausch, K.D., and Saunders, W.C. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. **50**(2): 201–220. doi:10.1111/j.1365-2427.2004.01328.x.

Boysen-Jensen, P. 1919. Variation of the Limfjord. 1. Studies on the fish food in the Limfjord 1909–1917, its quantity, variation and annual production. Report of the Danish Biological Station, **26**: 5–44.

Carlton, R.G., and Goldman, C.R. 1984. Effects of a massive swarm of ants on ammonium concentrations in a subalpine lake. Hydrobiologia, **111**(2): 113–117. doi:10.1007/BF00008623.

Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. Bioscience, **35**(10): 634–639. doi:10.2307/1309989.

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. **8**(3): 559–568. doi:10.1890/1051-0761(1998)008[0559:NPOSWW]2.0.CO;2.

Christensen, D.L., Herwig, B.R., Schindler, D.E., and Carpenter, S.R. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. Ecol. Appl. **6**(4): 1143–1149. doi:10.2307/2269598.

Cole, J.J., Caraco, N.F., and Likens, G.E. 1990. Short-range atmospheric transport: a significant source of phosphorus to an oligotrophic lake. Limnol. Oceanogr. **35**(6): 1230–1237. doi:10.4319/lo.1990.35.6.1230.

Cole, J.J., Carpenter, S.R., Kitchell, J.F., and Pace, M.L. 2002. Pathways of organic carbon utilization in small lakes: results from a whole-lake ^{13}C addition and coupled model. Limnol. Oceanogr. **47**(6): 1664–1675. doi:10.4319/lo.2002.47.6.1664.

Cole, J.J., Carpenter, S.R., Pace, M.L., Van de Bogert, M.C., Kitchell, J.L., and Hodgson, J.R. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. Ecol. Lett. **9**(5): 558–568. doi:10.1111/j.1461-0248.2006.00898.x. PMID:16643301.

del Georgio, P.A., and Peters, R.H. 1994. Patterns in planktonic P:R ratios in lakes: influence of lake trophy and dissolved organic carbon. Limnol. Oceanogr. **39**(4): 772–787. doi:10.4319/lo.1994.39.4.0772.

del Giorgio, P.A., Cole, J.J., and Cimbleris, A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature (London), **385**(6612): 148–151. doi:10.1038/385148a0.

Dillon, P.J., and Molot, L.A. 1997*a*. Dissolved organic and inorganic carbon mass balances in central Ontario lakes. Biogeochemistry, **36**(1): 29–42. doi:10.1023/A:1005731828660.

Dillon, P.J., and Molot, L.A. 1997*b*. Effect of landscape form on export of dissolved organic carbon, iron, and phosphorus from forested stream catchments. Water Resour. Res. **33**(11): 2591–2600. doi:10.1029/97WR01921.

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M., and Middelburg, J.J. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol. Oceanogr. **51**(5): 2388–2397. doi:10.4319/lo.2006.51.5.2388.

Fagan, W.F., Siemann, E., Mitter, C., Denno, R.F., Huberty, A.F., Woods, H.A., and Elser, J.J. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. Am. Nat. **160**(6): 784–802. doi:10.1086/343879. PMID:18707465.

Fee, E.J., Hecky, R.E., Kasian, S.E.M., and Cruikshank, D.R. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnol. Oceanogr. **41**(5): 912–920. doi:10.4319/lo.1996.41.5.0912.

Finlay, J.C., and Vredenburg, V.T. 2007. Introduced trout sever trophic connections in watersheds: consequences for a declining amphibian. Ecology, **88**(9): 2187–2198. doi:10.1890/06-0344.1. PMID:17918397.

Fisher, S.G., and Likens, G.E. 1973. Energy flow in Bear Brook, New Hampshire — integrative approach to stream ecosystem metabolism. Ecol. Monogr. **43**(4): 421–439. doi:10.2307/1942301.

Forbes, S.A. 1887. The lake as a microcosm. Bulletin of the Peoria Scientific Association, **1887**: 77–87.

France, R.L., and Peters, R.H. 1995. Predictive model of the effects on lake metabolism of decreased airborne litterfall through riparian deforestation. Conserv. Biol. **9**(6): 1578–1586. doi:10.1046/j.1523-1739.1995.09061578.x.

Francis, T.B., and Schindler, D.E. 2006. Degradation of littoral habitats by residential development: woody debris in lakes of the Pacific Northwest and Midwest, United States. Ambio, **35**(6): 274–280. doi:10.1579/06-R-141R2.1. PMID:17240759.

Francis, T.B., and Schindler, D.E. 2009. Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. Oikos, **118**(12): 1872–1882. doi:10.1111/j.1600-0706.2009.17723.x.

Gasith, A., and Hasler, A.D. 1976. Airborne litterfall as a source of organic-matter in lakes. Limnol. Oceanogr. **21**(2): 253–258. doi:10.4319/lo.1976.21.2.0253.

Goldman, C.R. 1961. The contribution of alder trees (*Alnus tenuifolia*) to the primary productivity of Castle Lake, California. Ecology, **42**(2): 282–288. doi:10.2307/1932080.

Graham, M.D., Vinebrooke, R.D., and Turner, M. 2006. Coupling of boreal forests and lakes: effects of conifer pollen on littoral

communities. Limnol. Oceanogr. **51**(3): 1524–1529. doi:10.4319/lo.2006.51.3.1524.

Gratton, C., and Vander Zanden, M.J. 2009. Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. Ecology, **90**(10): 2689–2699. doi:10.1890/08-1546.1. PMID: 19886479.

Gratton, C., Donaldson, J., and Vander Zanden, M.J. 2008. Ecosystem linkages between lakes and the surrounding terrestrial landscape in northeast Iceland. Ecosystems, **11**(5): 764–774. doi:10.1007/s10021-008-9158-8.

Hanson, P.C., Bade, D.L., Carpenter, S.R., and Kratz, T.K. 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. Limnol. Oceanogr. **48**(3): 1112–1119. doi:10.4319/lo.2003.48.3.1112.

Hasler, A.D. 1975. Coupling of land and water systems. Springer-Verlag, New York.

Hilsenhoff, W.L. 1967. Ecology and population dynamics of *Chironomus plumosus* (Diptera—Chironomidae) in Lake Winnebago, Wisconsin. Ann. Entomol. Soc. Am. **60**: 1183–1194.

Howarth, R.W., Billen, G., Swaney, D., Townsend, A., Jaworski, N., Lajtha, K., Downing, J.A., Elmgren, R., Caraco, N., Jordan, T., Berendse, F., Freney, J., Kudeyarov, V., Murdoch, P., and Zhu, Z.L. 1996. Regional nitrogen budgets and riverine N&P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. Biogeochemistry, **35**(1): 75–139. doi:10.1007/BF02179825.

Hunt, R.L. 1975. Food relations and behavior of salmonid fishes. *In* Coupling of land and water systems. *Edited by* A.D. Hasler. Springer-Verlag, New York.

Hutchinson, G.E. 1959. Homage to Santa Rosalie, or why are there so many kinds of animals? Am. Nat. **93**(870): 145–159. doi:10.1086/282070.

Hynes, H.B.N. 1975. The stream and its valley. Verh. Int. Verein. Limnol. **19**: 1–15.

Irvine, K. 2000. Macrodistribution, swarming behaviour and production estimates of the lakefly *Chaoborus edulis* (Diptera: Chaoboridae) in Lake Malawi. Adv. Ecol. Res, **31**: 431–448. doi:10.1016/S0065-2504(00)31023-6.

Jassby, A.D., Reuter, J.E., Axler, R.P., Goldman, C.R., and Hackley, S.H. 1994. Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California–Nevada). Water Resour. Res. **30**(7): 2207–2216. doi:10.1029/94WR00754.

Jaworski, N.A., Howarth, R.W., and Hetling, L.I. 1997. Atmospheric deposition of nitrogen oxides onto the landscape contributes to coastal eutrophication in the northeast United States. Environ. Sci. Technol. **31**(7): 1995–2004. doi:10.1021/es960803f.

Junk, W.J., Bayle, P.B., and Sparks, R.E. 1989. The Flood Pulse Concept in River–Floodplain Systems. Proceedings of the International Large River Symposium, Can. Spec. Publ. Fish. Aquat. Sci. 106.

Kalff, J. 2002. Limnology. Prentice-Hall, Upper Saddle River, N.J.

Karlsson, J., Jonsson, A., Meili, M., and Jansson, M. 2003. Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. Limnol. Oceanogr. **48**(1): 269–276. doi:10.4319/lo.2003.48.1.0269.

Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A., and Holt, R.D. 2005. Trophic cascades across ecosystems. Nature (London), **437**(7060): 880–883. doi:10.1038/nature03962. PMID:16208370.

Krieger, K.A., Bur, M.T., Ciborowski, J.J.H., Barton, D.R., and Schloesser, D.W. 2007. Distribution and abundance of burrowing mayflies (*Hexagenia* spp.) in Lake Erie, 1997–2005. J. Great Lakes Res. **33**(sp1): 20–33. doi:10.3394/0380-1330(2007)33[20:DAAOBM]2.0.CO;2.

Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W., and Pierce, R.S. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in Hubbard Brook watershed-ecosystem. Ecol. Monogr. **40**(1): 23–47. doi:10.2307/1942440.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. Ecology, **23**(4): 399–418. doi:10.2307/1930126.

Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. Freshw. Biol. **47**(4): 679–694. doi:10.1046/j.1365-2427.2002.00895.x.

Mehner, T., Ihlau, J., Dorner, H., and Holker, F. 2005. Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes? Limnol. Oceanogr. **50**(6): 2022–2031. doi:10.4319/lo.2005.50.6.2022.

Morris, D.P., Zagarese, H., Williamson, C.E., Balseiro, E.G., Hargreaves, B.R., Modenutti, B., Moeller, R., and Queimalinos, C. 1995. The attentuation of solar UV radiation in lakes and the role of dissolved organic carbon. Limnol. Oceanogr. **40**(8): 1381–1391. doi:10.4319/lo.1995.40.8.1381.

Nakano, S., and Murakami, M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc. Natl. Acad. Sci. U.S.A. **98**(1): 166–170. doi:10.1073/pnas.98.1.166. PMID:11136253.

Nakano, S., Miyasaka, H., and Kuhara, N. 1999. Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology, **80**: 2435–2441.

Nowlin, W.H., González, M.J., Vanni, M.J., Stevens, M.H.H., Fields, M.W., and Valente, J.J. 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. Ecology, **88**(9): 2174–2186. doi:10.1890/06-0570.1. PMID:17918396.

O'Connor, E.M., Dillon, P.J., Molot, L.A., and Creed, I.F. 2009. Modeling dissolved organic carbon mass balances for lakes of the Muskoka River watershed. Hydrol. Res. **40**(2–3): 273–290. doi:10.2166/nh.2009.106.

Odum, E.P. 1968. Energy flow in ecosystems: a historical review. Am. Zool. **8**: 11–18.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Van De Bogert, M.C., Bade, D.L., Kritzberg, E.S., and Bastviken, D. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature (London), **427**(6971): 240–243. doi:10.1038/nature02227. PMID:14724637.

Plante, C., and Downing, J.A. 1989. Production of freshwater invertebrate populations in lakes. Can. J. Fish. Aquat. Sci. **46**(9): 1489–1498. doi:10.1139/f89-191.

Polis, G.A., and Hurd, S.D. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proc. Natl. Acad. Sci. U.S.A. **92**(10): 4382–4386. doi:10.1073/pnas.92.10.4382. PMID: 7753815.

Polis, G.A., and Hurd, S.D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Nat. **147**(3): 396–423. doi:10.1086/285858.

Polis, G.A., Anderson, W.B., and Holt, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food web. Annu. Rev. Ecol. Syst. **28**(1): 289–316. doi:10.1146/annurev.ecolsys.28.1.289.

Polis, G.A., Power, M.E., and Huxel, G.R. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, Ill.

Pope, K.L., Piovia-Scott, J., and Lawler, S.P. 2009. Changes in aquatic insect emergence in response to whole-lake experimental

manipulations of introduced trout. Freshw. Biol. **54**(5): 982–993. doi:10.1111/j.1365-2427.2008.02145.x.

Pray, C.L., Nowlin, W.H., and Vanni, M.J. 2009. Deposition and decomposition of periodical cicadas (Homoptera: Cicadidae: Magicicada) in woodland aquatic ecosystems. J. North Am. Benthol. Soc. **28**(1): 181–195. doi:10.1899/08-038.1.

Preston, N.D. 2009. External drivers of lakes in forested watersheds: aeolian organic carbon inputs and ice phenology. Ph.D. thesis, Center for Limnology, University of Wisconsin – Madison, Wis.

Preston, N.D., Carpenter, S.R., Cole, J.J., and Pace, M.L. 2008. Airborne carbon deposition on a remote forested lake. Aquat. Sci. **70**(3): 213–224. doi:10.1007/s00027-008-8074-5.

Rau, G.H. 1976. Dispersal of terrestrial plant litter into a subalpine lake. Oikos, **27**(1): 153–160. doi:10.2307/3543445.

Regester, K.J., Lips, K.R., and Whiles, M.R. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. Oecologia, **147**(2): 303–314. doi:10.1007/s00442-005-0266-2.

Regester, K.J., Whiles, M.R., and Lips, K.R. 2008. Variation in the trophic basis of production and energy flow associated with emergence of larval salamander assemblages from forest ponds. Freshw. Biol. **53**(9): 1754–1767. doi:10.1111/j.1365-2427.2008.02073.x.

Reynolds, C.S. 2008. A changing paradigm of pelagic food webs. Int. Rev. Hydrobiol. **93**(4–5): 517–531. doi:10.1002/iroh.200711026.

Sass, G.G., Kitchell, J.F., Carpenter, S.R., Hrabik, T.R., Marburg, A.E., and Turner, M.G. 2006. Fish community and food web responses to a whole-lake removal of coarse woody habitat. Fisheries, **31**(7): 321–330. doi:10.1577/1548-8446(2006)31[321:FCAFWR]2.0.CO;2.

Schindler, D.W. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. Science (Washington, D.C.), **184**(4139): 897–899. doi:10.1126/science.184.4139.897. PMID:17782381.

Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. Science (Washington, D.C.), **195**(4275): 260–262. doi:10.1126/science.195.4275.260. PMID:17787798.

Schindler, D.E., and Scheuerell, M.D. 2002. Habitat coupling in lake ecosystems. Oikos, **98**(2): 177–189. doi:10.1034/j.1600-0706.2002.980201.x.

Schindler, D.E., Geib, S.I., and Williams, M.R. 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. Ecosystems, **3**(3): 229–237. doi:10.1007/s100210000022.

Sharpley, A.N., Chapra, S.C., Wedepohl, R., Sims, J.T., Daniel, T.C., and Reddy, K.R. 1994. Managing agricultural phosphorus for protection of surface waters: issues and options. J. Environ. Qual. **23**(3): 437–451. doi:10.2134/jeq1994.00472425002300030006x.

Sitar, S.P., Morales, H.M., Mata, M.T., Bastar, B.B., Dupras, D.M., Kleaver, G.D., and Rathbun, K.D. 2008. Survey of siscowet lake trout at their maximum depth in Lake Superior. J. Great Lakes Res. **34**(2): 276–286. doi:10.3394/0380-1330(2008)34[276:SOSLTA]2.0.CO;2.

Smith, V.H., and Schindler, D.W. 2009. Eutrophication science: where do we go from here? Trends Ecol. Evol., **24**(4): 201–207. doi:10.1016/j.tree.2008.11.009. PMID:19246117.

Solomon, C.T., Carpenter, S.R., Cole, J.J., and Pace, M.L. 2008. Support of benthic invertebrates by detrital resources and current autochthonous primary production: results from a whole-lake C-13 addition. Freshw. Biol. **53**(1): 42–54.

Stein, R.A., De Vries, D.R., and Dettmers, J.M. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. Can. J. Fish. Aquat. Sci. **52**(11): 2518–2526. doi:10.1139/f95-842.

Vadeboncoeur, Y., Vander Zanden, M.J., and Lodge, D.M. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. Bioscience, **52**(1): 44–54. doi:10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2.

Vander Zanden, M.J., and Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology, **83**(8): 2152–2161. doi:10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2.

Vander Zanden, M.J., Chandra, S., Park, S., Vadeboncoeur, Y., and Goldman, C.R. 2006. Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. Can. J. Fish. Aquat. Sci. **63**(12): 2608–2620. doi:10.1139/F06-148.

Vanni, M.J., Arend, K.K., Bremigan, M.T., Bunnell, D.B., Garvey, J.E., Gonzalez, M.J., Renwick, W.H., Soranno, P.A., and Stein, R.A. 2005. Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. Bioscience, **55**(2): 155–167. doi:10.1641/0006-3568(2005)055[0155:LLAFWE]2.0.CO;2.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**(1): 130–137. doi:10.1139/f80-017.

Waters, T.F. 1977. Secondary production in inland waters. Adv. Ecol. Res, **10**: 91–164. doi:10.1016/S0065-2504(08)60235-4.

Watras, C.J., Back, R.C., Halvorsen, S., Hudson, R.J.M., Morrison, K.A., and Wente, S.P. 1998. Bioaccumulation of mercury in pelagic freshwater food webs. Sci. Total Environ. **219**(2–3): 183–208. PMID:9802248.

Weidel, B., Carpenter, S., Cole, J., Hodgson, J., Kitchell, J., Pace, M., and Solomon, C. 2008. Carbon sources supporting fish growth in a north temperate lake. Aquat. Sci. **70**(4): 446–458. doi:10.1007/s00027-008-8113-2.

Wetzel, R.G. 2001. Limnology: lake and river ecosystems. Academic Press, San Diego, Calif.

Willey, J.D., Kieber, R.J., Eyman, M.S., and Avery, G.B., Jr. 2000. Rainwater dissolved organic carbon: concentrations and global flux. Global Biogeochem. Cycles, **14**(1): 139–148. doi:10.1029/1999GB900036.

Woods, H.A., Fagan, W.F., Elser, J.J., and Harrison, J.F. 2004. Allometric and phylogenetic variation in insect phosphorus content. Funct. Ecol. **18**(1): 103–109. doi:10.1111/j.1365-2435.2004.00823.x.