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Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems

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Abstract. Recently, food web studies have started exploring how resources from one habitat or ecosystem influence trophic interactions in a recipient ecosystem. Benthic production in lakes and streams can be exported to terrestrial habitats via emerging aquatic insects and can therefore link aquatic and terrestrial ecosystems. In this study, we develop a general conceptual model that highlights zoobenthic production, insect emergence, and ecosystem geometry (driven principally by area-to-edge ratio) as important factors modulating the flux of aquatic production across the ecosystem boundary. Emerging insect flux, defined as total insect production emerging per meter of shoreline ($\text{g C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$) is then distributed inland using decay functions and is used to estimate insect deposition rate to terrestrial habitats ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$).

Using empirical data from the literature, we simulate insect fluxes across the water–land ecosystem boundary to estimate the distribution of fluxes and insect deposition inland for lakes and streams. In general, zoobenthos in streams are more productive than in lakes (6.67 vs. 1.46 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) but have lower insect emergence to aquatic production ratios (0.19 vs. 0.30). However, as stream width is on average smaller than lake radius, this results in flux (F) estimates 2½ times greater for lakes than for streams. Ultimately, insect deposition onto land (within 100 m of shore) adjacent to average-sized lakes (10-ha lakes, 0.021 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) is greater than for average-sized streams (4 m width, 0.002 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) used in our comparisons. For the average lake (both in size and productivity), insect deposition rate approaches estimates of terrestrial secondary production in low-productivity ecosystems (e.g., deserts and tundra, $\approx 0.07 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). However, larger lakes (1300 ha) and streams (16 m) can have average insect deposition rates ($\approx 0.01\text{--}2.4 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) comparable to estimates of secondary production of more productive ecosystems such as grasslands. Because of the potentially large inputs of emerging aquatic insects into terrestrial habitats, ecosystem processes and terrestrial consumers can be influenced by insect inputs. The relative contribution of lakes and streams to this flux will vary among landscapes depending on the number and size of these ecosystem types on the landscape.

Key words: *allochthonous resources; emerging aquatic insects; food webs; insect dispersal; lake–land linkages; landscape ecology; spatial subsidies.*

INTRODUCTION

No habitat or ecosystem exists in isolation, and there is broad recognition of the importance of cross-habitat linkages in a wide range of settings (Polis et al. 2004). Nutrients, matter, and energy freely cross habitat

boundaries, often with important implications for recipient species and ecosystems (Polis et al. 1997). Yet, the traditional perspective on terrestrial–aquatic linkages has been unidirectional, with a predominant focus on the movement of nutrients, matter, and energy of terrestrial origin (downhill) into aquatic systems (Cole et al. 2006). For example, terrestrial carbon can play a central role in supporting lake food webs (Pace et al. 2004), while the problem of aquatic ecosystem eutrophication is driven by urban and agricultural land use that contributes nutrients to downstream aquatic systems (Carpenter et al. 1998).

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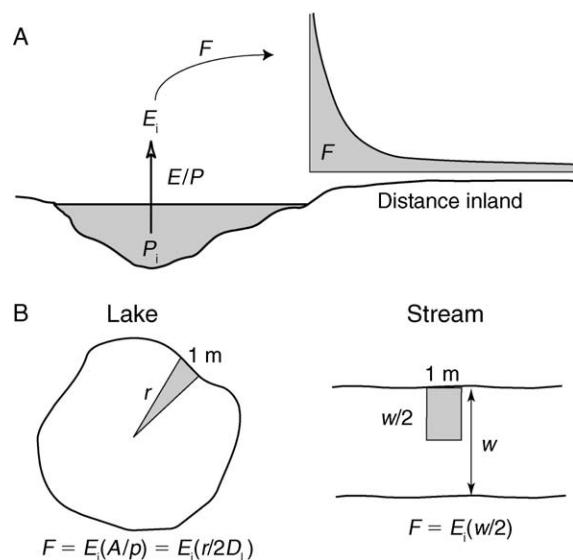


FIG. 1. Diagram of the conceptual model that links aquatic production to land via the emergence and movement of insects inland. (A) Aquatic insect benthic production (P_i , in $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) emerges from lakes and streams as an emergence of aquatic insects (E_i , in $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), which is calculated from estimates of P_i and E_i/P_i ratios (see Table 1). For lakes, P_i is estimated as the product of P_b (benthic macroinvertebrate production, $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) and f_i , the fraction of benthic production that is insects. Emergent aquatic insects move to land and represent a flux (F , in $\text{g C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$) across the water–land boundary, which is distributed over land as insects disperse inland. (B) Total insect production (flux) that emerges from a body of water per length of shoreline (F) is calculated by estimating the area of aquatic habitat that occurs between the center of the water body extending to 1 m of shoreline and multiplying it by E_i , the emergence of benthic insects per m^2 . For lakes, this is the area of a sector of radius r with a perimeter of 1 m (for a perfectly circular lake); for streams, it is the half-width of the stream ($w/2$) across from 1 m of shoreline. A is lake area (m^2), p is the perimeter of the lake (m), and D_L is the shoreline development factor.

Recently, the importance of stream productivity to surrounding terrestrial habitats has been examined (Nakano et al. 1999, Baxter et al. 2005). Such work has demonstrated that rivers and streams can be significant exporters of nutrients, matter, and energy to the surrounding terrestrial landscape via migrations of anadromous fishes (Moore et al. 2007) and aquatic insect emergence (Henschel et al. 2001, Sabo and Power 2002b). Many insect species have aquatic larval stages, but switch to terrestrial habitats when they emerge from their aquatic habitat as adults. Emerging aquatic insects can therefore create cross-habitat linkages between aquatic and surrounding terrestrial ecosystems, with locally important implications for terrestrial food webs and ecosystems (Power et al. 2004; see Plate 1).

In contrast to streams, there has been a dearth of studies examining fluxes from lakes to the surrounding landscape (Gratton et al. 2008). Lake and stream ecosystems differ in profound ways, including secondary productivity, invertebrate community composition, and

ecosystem geometry. Yet we lack a general conceptual framework for understanding fluxes of aquatic productivity (lotic and lentic) to terrestrial ecosystems. How might we expect aquatic–terrestrial fluxes to differ for lotic (lakes and ponds) and lentic (stream and river) ecosystems? How variable do we expect these fluxes to be, and what are the drivers of the observed variability?

In this study we develop a conceptual model for understanding the linkages between aquatic habitats and the surrounding terrestrial landscape, building on ideas presented by Polis and Hurd (1996) and Gasith and Hasler (1976) who examined spatial linkages between islands and the surrounding sea and terrestrial organic inputs into lakes, respectively. We then compile data from the literature on lotic and lentic systems for key variables in the model and use those data sets to estimate aquatic–terrestrial fluxes, highlighting the interactive roles of ecosystem productivity and ecosystem size/geometry as the key drivers of variability in aquatic–terrestrial linkages, and allowing for a contrast of cross-habitat fluxes for lake and stream ecosystems.

METHODS

Conceptual model

Benthic production and emerging aquatic insects.—The amount of material potentially moving from water to land is set ultimately by the benthic secondary production (P_b , $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) of the aquatic system. This is calculated on a per area basis in aquatic habitats from studies of benthic consumers. Some fraction (f_i) of P_b consists of insects (P_i , $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), taxa for which the adult life stages generally leave the aquatic system and are of interest for studying water–land linkages. Of insect secondary production, P_i , some fraction emerges from the aquatic ecosystem. We refer to this as insect emergence (E_i , $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), which is sometimes measured directly using emergence traps. Alternatively, where insect production data are available, E_i for a particular body of water can be estimated from published values of E_i/P_i from the literature as

$$E_i = P_i(E_i/P_i). \quad (1)$$

Flux to land and ecosystem geometry.—As emerging aquatic insects move to land, the geometry of the body of water and the water–land interface will influence the flux of materials between the two ecosystems. We define the flux (F) of emerging aquatic insects to land as the amount of insect production annually leaving the body of water per meter of aquatic shoreline ($\text{g C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$; Fig. 1A). For lakes and ponds, it is straightforward to delineate the boundaries of the ecosystem (i.e., the area of lake), calculate total ecosystem production, and by dividing by the length of shoreline we can compute F (Fig. 1B). For streams and rivers, it is less clear how to delineate the ecosystem. Nevertheless, for this model the most important consideration is the amount of emergent material produced, which then moves across a given



PLATE 1. A swarm of midges (Chironomidae) on the shores of Lake Myvatn in Northern Iceland. Aquatic insects emerge out of the body of water where they develop as larvae and move over land to mate. Here they often die and are consumed by terrestrial predators or decomposers, thus creating a linkage between aquatic and terrestrial ecosystems. Photo credit: David Hoekman.

length of shoreline. For streams this is equivalent to simplifying a stream or river to a segment for which we can calculate the area and edge (Fig. 1B).

For lakes, we can calculate flux by multiplying insect emergence (E_i) by the total surface area of the ecosystem (A , m^2) and dividing by the total length of lake shoreline (p , m), or $F = E_i A / p$. For perfectly circular lakes $A = \pi r^2$ and $p = 2\pi r$, where r is the radius of the lake, or $F = E_i r / 2$. This is equivalent to calculating the area of the sector of a circle of radius r given a shoreline of length 1 m and multiplying it by insect production per square meter, yielding total insect emergence per meter of shoreline. Natural lakes are rarely circular and the relationship can be adjusted for lakes of irregular shapes by including a shoreline development factor (Kalf 2002), $D_L = p / [2(\pi A)^{1/2}]$. Perfectly circular lakes have $D_L = 1$, while a lake of the same area with twice the perimeter has $D_L = 2$. We can estimate the amount of insect emergence per meter of lake shoreline (lake flux, $g\ C\ m^{-1}\cdot yr^{-1}$) as:

$$F = E_i r / (2D_L). \quad (2)$$

For streams, we estimate F by multiplying aquatic insect production (E_i) by the mean perpendicular distance from the center of the stream to shore ($w/2$, w = stream width; Fig. 1B) or

$$F = E_i w / 2. \quad (3)$$

Thus, for both streams and lakes, F scales linearly with ecosystem size, as defined by its radius or half width of the body of water.

Distributing aquatic flux inland.—Insect emergence reaching the shore is subsequently distributed inland, such that aquatic production flux to land can be expressed on a per unit area (m^{-2}) basis. Dispersal of aquatic insects away from shore has been typically modeled as either negative exponential ($y = ae^{-bx}$) or inverse power functions ($y = ax^{-b}$), where y = abundance of aquatic insects, and x is distance from water's edge. Distributing the aquatic insect flux (F) to inland habitats corresponds to setting the indefinite integral of the dispersal function equal to F and solving for the intercept (a), given a shape of the dispersal function set by the slope, b . By solving the integral at different distances

TABLE 1. Variables used in conceptual model.

Variable	Abbreviation	Units	Lakes	Streams
Benthic macroinvertebrate production	P_b	$\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$	L	
Fraction of production that is insect	f_i		L	
Benthic insect production	P_i	$\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$	$P_b f_i$	L
Ratio of aquatic insect emergence to benthic production	E_i/P_i		L	L
Insect emergence	E_i	$\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$	[Eq. 1] $P_i(E_i/P_i)$	$P_i(E_i/P_i)$
Lake area	A	m^2	a	
Lake radius	r	m	$(A/\pi)^{1/2}$	
Stream width	w	m		b
Shoreline development factor	D_L		1.32†	
Emergent insect flux to shore	F	$\text{g C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$	[Eq. 2] $E_i r/(2D_L)$	[Eq. 3] $E_i w/2$

Note: L, estimated from literature; a, range from 10 to 100 000 m²; b, range from 1 to 6400 m.

† Median value for UK lakes (Hughes et al. 2004).

from shore (x) one can calculate the total insect flux ($\text{g C}/\text{yr}$) arriving at a $1 \text{ m} \times x \text{ m}$ strip of land, or the average aquatic insect input ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) distributed to terrestrial habitats a given distance from shore.

In summary, our conceptual model identifies two general factors that affect aquatic insect flux to shore (F , $\text{g C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$): (1) aquatic insect production (P_i) and subsequent emergence (E_i), and (2) ecosystem "size" (width) and geometry.

Estimation of aquatic fluxes to land

To evaluate the input of aquatic insect emergence to land predicted from this general model (Fig. 1) we collected literature data for key variables, P_i and E_i (Table 1), and estimated flux to land (F) through numerical simulations. Our approach brings together our conceptual model with empirical data sets, and enables us not only to compare aquatic–terrestrial fluxes for lakes and streams, but also to examine the role of ecosystem size and productivity as sources of variability in this cross-habitat linkage.

Lakes.—We conducted an exhaustive literature search for studies estimating whole-lake macrozoobenthos production, insect production, and emergence (Appendices A and C). Estimates represent the average annual production for the entire lake (as opposed to a specific habitat or depth), and comprise all or at a minimum the dominant group of zoobenthic species. All production-related data (for lakes and streams) were converted to g C (dry mass) using published and widely accepted conversion factors (Cummins and Wuycheck 1971). Macrozoobenthos production (P_b) estimates were found for 49 lakes and for 28 of those lakes there was sufficient information to estimate the proportion composed of insect production (f_i). Insect emergence as a proportion of insect production (E_i/P_i) could be estimated for only 11 of these 51 lakes (Appendix C). Data were supplemented by additional E_i/P_i and P_i values presented by Jackson and Fisher (1986) and Strayer and Likens (1986). From the empirical data sets for P_b ($n = 49$), f_i ($n = 28$), and E_i/P_i ($n = 18$), we calculated $E_i = P_b f_i (E_i/P_i)$ for all possible combinations of the variables ($n = 24\,698$ combinations) and thus generated a frequency distribu-

tion for E_i . Aquatic insect flux to shore (F) is a function of insect emergence (E_i), as well as lake area (A , or more simply lake radius, r) and shoreline development factor (D_L ; Eq. 2). Although for real lakes, A and D_L can be measured directly, we estimated the distribution of F across a range of idealized lake sizes ($r = 10$ – $120\,000$ m) to bracket the smallest ponds and largest lakes (e.g., Great Laurentian Lakes), assuming lakes were circular, and using $D_L = 1.32$ as an average shoreline development factor (Hughes et al. 2004).

Streams.—We collected published estimates of P_i , E_i , and E_i/P_i for streams. The stream production literature typically reports insect production (P_i), and therefore insect emergence (E_i) can be estimated as $P_i(E_i/P_i)$. Stream insect production estimates ($n = 61$) were taken primarily from the review by Benke (1993), supplemented with additional estimates (Appendix B). Stream E_i/P_i values (generally taxa-specific, $n = 19$) were collected from the literature (Appendix C). From the empirical data, we calculated the distribution of E_i from all possible combinations ($n = 1159$) of $P_i(E_i/P_i)$. We also identified 16 direct estimates of insect emergence (E_i) (Appendix D), which allowed us to validate our emergence estimates based on Eq. 1. As with lakes, we calculated F (Eq. 3) across a range of stream widths to bracket the smallest first-order streams (1 m) to the largest 10th-order rivers (6400 m).

Flux to land.—Finally, insect flux to shore was distributed inland to estimate the amount of insect input ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) to adjoining terrestrial habitats. We performed an exhaustive search of the primary literature and obtained estimates of aquatic insect dispersal inland as a function of distance from shore. We either used author's fit of decay functions, or we recalculated best fit functions from available graphs to describe insect abundance as a function of distance inland from shore. We standardized fits to either inverse power or negative exponential functions and calculated the average of the slope (b) for those function types separately.

To distribute the insect flux to shore, F ($\text{g C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$) inland, we solved for the intercept parameter (a) such that the indefinite integral of the dispersal function from shore (1 m) to a point far from shore (300 m) was equal

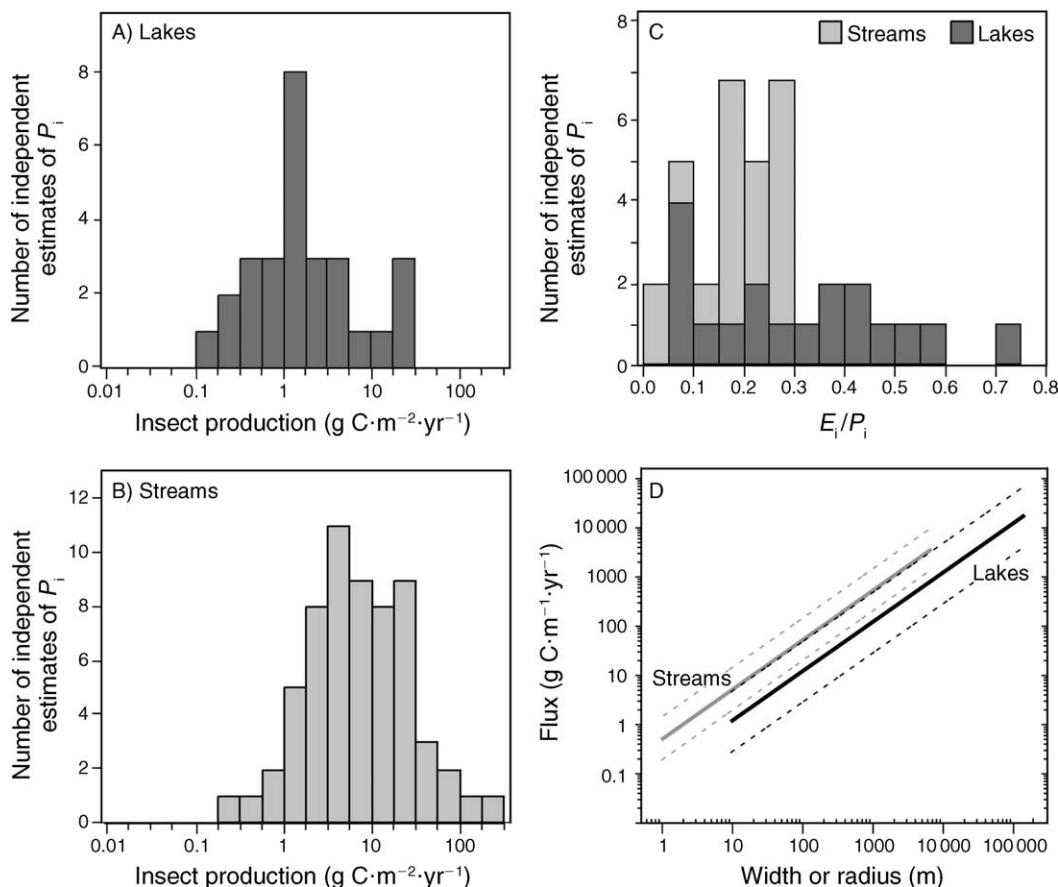


FIG. 2. Distribution of literature-derived estimates of benthic insect production (P_i) from (A) lakes and (B) streams. Raw data are given in Appendices A and B. (C) Frequency distribution of literature-derived estimates of E_i/P_i ratios for lakes (dark gray) and streams (light gray). Raw data are in Appendix C. (D) Flux ($\text{g C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$) of emergent aquatic insects across the water-land boundary as a function of ecosystem size, either stream width (w , gray lines) or lake radius (r , black lines). Solid lines are the median values for all possible permutations of literature data (Eqs. 2 and 3) at each size class, and dotted lines bound the upper 75% and lower 25% quartiles of estimates. Stream size categories range from small first-order streams (1 m) to the largest rivers (e.g., Mississippi River at its widest point, 6400 m). Lake size classes range from small ponds (0.1 ha or 17 m radius) to the largest freshwater lakes (e.g., average of the Great Laurentian Lakes, 48 000 km^2 or $\sim 124\,000$ m radius). Note the log scale of some axes.

to F estimated from the simulations. From those equations we calculated the average amount of aquatic insect emergence ($\text{g C}/\text{yr}$) landing within a 1-m strip at different distances from the shoreline (e.g., 10, 50, 100, 200 m) and also the distance inland at which insect abundance is 50% and 10% of initial abundance at the shore. By dividing total insect deposition rate $\text{g C}/\text{yr}$ by the total area (m^2) over which the deposition rate is measured (e.g., from shore to 100 m), it is possible to estimate an average deposition rate, expressed as $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

Statistical analyses

Differences between streams and lakes in P_i and E_i/P_i , estimated from the literature were tested by ANOVA using log-transformed data in JMP 7 (SAS Institute 2007). Unless otherwise noted, we report either mean \pm

SE, or median (25–75% interquartile range, IQR) of a variable depending on how data are distributed.

RESULTS

Distributions of P_i , E_i/P_i , and E_i for lakes and streams

Benthic insect production in lakes was about four times lower than stream benthic insect production (lakes, $P_i = 1.46$ [0.77–4.28] $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $n = 28$, Fig. 2A; Appendix A; streams, $P_i = 6.67$ [2.71–19.92] $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $n = 61$, Fig. 2B; Appendix B), a difference which is statistically significant ($F_{1,87} = 19.36$, $P < 0.0001$). Estimating a distribution of P_i values using all possible combinations of P_b and f_i from the literature (Appendix A) gives a median P_i for lakes of 1.38 [0.31–4.75] $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, which is similar to reported P_i values that were measured directly for lakes. There was no relationship between insect production and lake area or

TABLE 2. (A) Flux (F , $\text{g}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$) to the shoreline is distributed inland using either inverse power or negative exponential decay functions. (B) Total insect “infall” (gC/yr^{-1}) that occurs in a 1-m strip from shore to a given distance x (m) inland is solved by calculating the area under the dispersal curve.

A)		Insect dispersal inland					Distance (m) at which abundance is $x\%$ of initial		
Type	Flux to shore [†] ($\text{g}\cdot\text{C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$)		Decay curve [‡]	Slope (b) [§]	Intercept (a) [¶]		50%	10%	1%
	Median	[25–75% IQR]			Estimate	[25–75% IQR]			
Streams	2.10	[0.84–6.24]	inv. power	0.614	0.1005	[0.0403–0.2978]	65	238	296
			neg. exp.	0.072	0.1510	[0.0606–0.4478]	9	32	64
Lakes	21.4	[4.72–82.66]	inv. power	0.614	1.0235	[0.2253–3.9458]	65	238	296
			neg. exp.	0.072	1.5392	[0.3389–5.9344]	9	32	64

B)		Total insect infall ($\text{g}\cdot\text{C}/\text{yr}$) from (1, x m) (median [IQR])			
Type	Decay curve	10 m	50 m	100 m	200 m
Streams	inv. power	0.40 [0.16–1.18]	0.93 [0.37–2.75]	1.29 [0.20–3.81]	1.76 [0.70–5.20]
	neg. exp.	1.08 [0.43–3.20]	2.05 [0.44–3.79]	2.10 [0.84–6.23]	2.10 [0.84–6.24]
Lakes	inv. power	4.04 [0.89–15.57]	9.44 [2.08–36.41]	13.09 [2.88–5.48]	17.89 [3.94–68.95]
	neg. exp.	10.98 [2.42–42.34]	20.85 [4.59–80.38]	21.42 [4.72–82.60]	21.44 [4.72–82.66]

[†] Estimated for streams of width = 4 m; lakes of radius = 178 m (10 ha).

[‡] Inverse power (inv. power) or negative exponential (neg. exp.) decay curves are used to distribute insect deposition rate inland.

[§] Average slope parameters derived from literature (Appendix E).

[¶] Estimated by solving indefinite integral of dispersal curve, given F and b .

stream width (log–log-transformed, $r = -0.07$, $P = 0.73$; $r = 0.18$, $P = 0.17$, respectively), supporting the independent treatment of those variables in this model.

Lakes have significantly higher insect emergence to production ratios, E_i/P_i , than do streams (lakes, 0.30 ± 0.04 , $n = 18$; streams, 0.19 ± 0.02 , $n = 19$; $F_{1,35} = 5.11$, $P = 0.03$, Fig. 2C; Appendix C). In addition, our estimates of stream E_i/P_i closely match other published values for streams (0.24 ± 0.06 [95% CI]; Stutzner and Resh 1993).

For lakes, E_i estimated from Eq. 2 was 0.318 [0.070–1.226], while for streams insect emergence rate E_i was over three times greater at 1.052 [0.422–3.119] $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. A survey of the literature found direct estimates of E_i for streams measured using emergence traps (Appendix D), which were comparable (1.730 [1.225–2.460], $n = 16$) to those estimated from Eq. 1.

Estimates of flux

Insect flux to shore (F) increases linearly as a function of lake radius and stream width on a log–log scale (Fig. 2D). The slope of this relationship ($b = 1$) is defined by the structure of the model, while the intercept is determined by the average insect emergence (E_i) of the system, which is dependent on P_i and E_i/P_i . Thus for an equal-sized body of water, F from streams is higher than from lakes (Fig. 2D). For example, a river that is 100 m wide has a median flux of 52.6 $\text{g}\cdot\text{C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$, while a circular lake of radius 100 m has a flux of 12.1 $\text{g}\cdot\text{C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$.

Insect dispersal from water

Twelve studies were found for which there were estimates of aquatic insect dispersal away from water (Appendix E). Abundance patterns of adult aquatic

insects were best described by either inverse power or negative exponential functions of distance from shore (Appendix F). The average slope parameters across the studies that fit inverse power functions to abundance data were $b = 0.614 \pm 0.083$ (mean \pm SE, $n = 7$) and for studies using a negative exponential function were 0.0718 ± 0.049 ($n = 7$). The inverse power function describes an initially steep decay of insects away from shore but quickly decelerates to have a long tail. In contrast, the exponential decay curves initially decline less rapidly with distance from shore, but abundances approach zero in the tail of the distribution more rapidly. Insect abundance is 10% of the initial flux at 32 m from shore for the exponential decay and at 238 m for the inverse power function (Table 2A).

Estimates on aquatic insect deposition rate into terrestrial habitats

Calculations of deposition rate to land ($\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) can be made for lakes and streams of different sizes (Fig. 2D) and at different distances from shore (Appendix F). Because deposition rate is a continuous function of distance from shore, we arbitrarily selected a distance and dispersal function in order to compare insect deposition across lakes and streams of different sizes. Using the exponential decay curve to describe insect dispersal shows that by 100 m inland, all of the flux has been deposited (Table 2). Thus, dividing F ($\text{g}\cdot\text{C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$) by 100 m gives an estimate of the average deposition rate ($\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) next to a body of water within 100 m distance. As an example, a 10-ha lake (178 m radius) is estimated to have a median flux to land of 21.4 $\text{g}\cdot\text{C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$ [4.7–82.7 $\text{g}\cdot\text{C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$], while a river 4 m in width exports a median of 2.10 $\text{g}\cdot\text{C}\cdot\text{m}^{-1}\cdot\text{yr}^{-1}$ [0.84–

6.24 g C·m⁻¹·yr⁻¹] (Fig. 2D), resulting in ≈ 0.21 [0.047–0.83] g C·m⁻²·yr⁻¹ and ≈ 0.02 [0.008–0.06] g C·m⁻²·yr⁻¹ average insect deposition rate within the first 100 m of shore, respectively (Table 2B). These ecosystem dimensions are chosen to represent average lake and stream sizes.

DISCUSSION

The simple conceptual model developed in this study (Fig. 1) provides a foundation for characterizing the movement of aquatic productivity from lakes and streams to land via the movement of adult aquatic insects. This model builds on general ideas originally formulated for lakes as recipients of terrestrial inputs (Gasith and Hasler 1976) and for islands surrounded by water (Polis and Hurd 1996). Those models emphasized the role of the geometry of donor and recipient ecosystems, focusing on area-to-perimeter ratios as controlling factors influencing allochthonous inputs into the recipient system. The ratio of ecosystem size (as indexed by stream half-width or lake radius) to shoreline is key because it ultimately determines total insect production exported per unit of shoreline, or the flux (Fig. 2D). Our model predicts that large and/or productive lakes and streams are most likely to be significant exporters of emerging aquatic insects to adjacent terrestrial habitats.

Emergent insect production

The intercept of the relationship between stream width or lake radius and flux is set by benthic production of the aquatic ecosystem (Fig. 2D). Interestingly, our data indicate that streams have about four times higher rates of benthic insect production (P_i) than do lakes. Such a pattern might be expected because benthic habitat is dominant in streams, while lakes are composed of both pelagic and benthic habitats. Though this finding is based on a comparison of the available data, there are several potential sources of bias that should be considered. First, ecosystems for which data are available may not be reflective of lentic and lotic ecosystems in general, and the vast majority of the study sites are from north-temperate latitudes. Second, in some cases the insect production values reported for streams may not be representative of whole stream ecosystems, but rather the specific habitats that were sampled in the original studies. Riffle habitats are easier to sample (relative to pools) and may also have higher rates of insect production. As such, estimates of E_i/P_i may also be biased downward due to elevated estimates of P_i in streams. Despite these issues, comparison of the frequency distributions of insect production for lakes and streams (Fig. 2A, B) suggests real differences in insect production between these two ecosystem types. Still, the reasons and mechanisms for this difference are not well elucidated, and this question invites further investigation.

Flux to land

Given a distribution of potential emergent insect production from a body of water, the width of a body of water determines total F , measured as the amount of emergent insects intersecting a given amount of shoreline. Comparing estimates of F therefore requires establishing a range of sizes over which the comparisons between bodies of water will be made. For example, the model predicts that small streams of ~ 1 m (e.g., first order) will have median F of 0.053 [0.21–1.56] g C·m⁻¹·yr⁻¹, while a large river (100 m, 6th–7th order) will have fluxes of 52.6 [21.1–156.0] g C·m⁻¹·yr⁻¹. In contrast, a small 4-ha lake (113 m radius) is expected to have F of 13.59 [2.99–52.38] g C·m⁻¹·yr⁻¹, while a large 4000-ha lake (e.g., Lake Mendota, Wisconsin, 3500 m radius) is predicted to have fluxes of 430 [95–1657] g C·m⁻¹·yr⁻¹, suggesting that lakes, by virtue of their larger widths, will have significantly greater F to land than even large rivers.

It is possible to calculate a size-weighted F to land using frequency distributions for lakes and streams in the natural landscape. Downing et al. (2006) estimated that most lakes in the world ($\approx 52\%$) are in the smallest size classes (0.1–0.2 ha) and only $\sim 5\%$ of lakes are > 3.2 ha, making median lake radius ~ 21 m (using a circle as an idealized lake). Lake size distributions for lakes > 4 ha calculated from available data sets for Wisconsin (USA; M. J. Vander Zanden, *unpublished data*) and the UK (Hughes et al. 2004) found a median lake area of 13 and 9.3 ha, respectively (169–203 radius; smaller lakes not included in these surveys). For stream size distributions, Leopold et al. (1964) used stream hydraulic theory developed by Horton (1945) and Strahler (1957) to estimate the relative frequency of streams of orders one through 10, their average stream segment length (km), mean drainage area (km²), and therefore their mean discharge (Q). From mean stream discharge (Q , m³/s) it is possible to estimate average stream width ($w = 0.4146Q^{0.454}$; Webster and D'Angelo 1997). These calculations suggest that first-order streams are the most common in the landscape, and average ~ 1.8 m in width. Using the same discharge–width relationship, studies from the literature summarized in Appendix A have median widths of ~ 4 m, while global river discharge data from Vörösmarty et al. (1998) have estimated median widths of 16 m. Irrespective of the data sets used, streams are 1–2 orders of magnitude narrower in width than the average lake/pond. As a result, even though streams have three times more insect emergence than lakes, their smaller sizes result in about 2.5 times less flux to land compared to lakes.

Insect deposition into terrestrial habitats

Insect deposition rate into terrestrial habitat is a smooth function of distance from the water–land interface: the majority of insect deposition occurs near shore and declines with distance from shore. The higher the flux, the higher the initial deposition rate (i.e.,

intercept of curves in Appendix F is higher) and therefore the greater the insect deposition rate inland. To simplify comparisons, we can arbitrarily examine average deposition rate within the first 100 m from shore for lakes and streams. Using an average lake of 10 ha (178 m radius), this corresponds to a median insect deposition rate of $0.21 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ within the first 100 m. An average stream of 4 m width (second order) has a median expected insect deposition rate within the first 100 m from shore of $0.021 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, an order of magnitude less than for lakes.

To put those estimates into perspective, terrestrial net primary production in ecosystems with low productivity such as Low Arctic tundra is about $20\text{--}60 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Bliss et al. 1973) and in temperate grasslands is $150\text{--}300 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Chapin et al. 2002). Using McNaughton et al.'s (1989) relationship between net primary productivity and net secondary production, we estimate net secondary production (e.g., herbivorous insects) on land as $0.02\text{--}0.07 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and $0.19\text{--}0.40 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, for tundra and temperate grasslands, respectively. Those values suggest that insect deposition rate around a 10-ha lake ($0.21 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) is comparable to terrestrial secondary production in low productivity ecosystems, while deposition around streams is about one order of magnitude lower than terrestrial secondary production.

Similar comparisons can be made for lakes and streams of different sizes and of differing adjacent terrestrial secondary production. For example, large lakes in the UK and Wisconsin are ~ 1300 ha (2000 m radius, 99.5th percentile of the frequency distribution, distribution truncated at 4 ha). These are expected to have insect deposition rate of $2.4 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the first 100 m near shore. Similarly, fourth order rivers (16 m) are in the 99.5th percentile of the width frequency distribution and are expected to have insect deposition rate of $0.08 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the first 100 m near shore. By comparison, secondary production in tropical savannas, grasslands, and forests, and temperate forests is estimated between 0.5 and $2.0 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (McNaughton et al. 1989). From this comparison it is clear that at the higher end of the frequency distribution of ecosystem sizes, insect flux to land for lakes are much higher than for streams; in this case, there is a $30\times$ difference between the two. Though large bodies of water are rare in the landscape, they are often the focus of human activity and management and can be significant in their linkages to land via the export of insects.

Examining insect deposition rate as average inputs may underestimate the potential impact on terrestrial ecosystems in several ways. First, in temperate regions insect emergences from streams and lakes often occur as pulses during brief periods (MacKenzie and Kaster 2004) and can therefore represent significantly higher than average availability of resources. Second, the relative importance of those allochthonous resources may vary across taxa, with some consumers such as

spiders along shorelines and riparian areas dependent on capturing flying prey such as emerging aquatic insects (Henschel 2004, Kato et al. 2004). Thus, estimating average annual insect deposition rate into terrestrial systems is a prerequisite for understanding effects on terrestrial consumers. Finally, terrestrial communities directly adjacent to shorelines (<10 m) will experience significantly greater inputs than the average distributed across 100 m (Table 2B) and insect deposition rate will likely have a greater impact on nearshore communities (Paetzold et al. 2005). Nevertheless, more detailed studies are needed to determine the effects of emerging aquatic insects on terrestrial food web interactions in real-world situations (Murakami and Nakano 2002, Sabo and Power 2002a).

An additional effect of emergent insect deposition into terrestrial systems is through the delivery of nutrients such as N or P. For example, converting insect deposition rate values to g N (C:N ≈ 5.9 for herbivorous insects; Fagan et al. 2002) shows that insects emerging from large lakes (~ 1300 ha) can deposit significant quantities of N (0.41 [$0.1\text{--}1.6$] $\text{g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) into the adjacent terrestrial systems, values comparable to atmospheric deposition (e.g., central Europe, $0.5\text{--}3.5 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, avg $1.7 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; Stevens et al. 2004). Inputs of N in the range of $1.5\text{--}3.0 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ into nutrient poor terrestrial communities such as tundra can result in rapid changes in biomass and shifts in species composition (Shevtsova et al. 2005). Thus, our general conceptual model and empirical findings suggest that fluxes of emergent aquatic insects to land may be important conduits not only of carbon, but also of N into terrestrial systems, with inputs comparable to terrestrial secondary production and atmospheric deposition of N. Notably, we expect that effects on land should be most pronounced around large and/or productive bodies of water, such as shallow eutrophic lakes and rivers.

Assumptions and refinement of model

Our approach to modeling aquatic–land linkages makes a number of simplifying assumptions. Foremost is that the empirical estimates of benthic insect production ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) data for lakes and streams are broadly representative of these ecosystems. It is notable that our empirical data for lakes did not include phantom midges (*Chaoborus*). *Chaoborus* can comprise an important component of insect production in lakes, but have a partially planktonic life history. As a result, they are not often included in studies of benthic insect production, and were not included in our estimates. Such omissions could underestimate E_i from lakes.

An additional assumption made in this model is that all emerging adult aquatic insects do not return to the body of water from which they emerged. Although this is almost certainly not always the case (e.g., females returning to water to lay eggs), there are scant data in the literature to suggest what fraction of emerging

insects permanently leaves the aquatic system. Jackson and Fisher (1986) suggest that for streams on average 82% ($\pm 7\%$, mean \pm SE, $n = 9$) of aquatic production does not return to water and for lakes 71% ($\pm 8\%$, $n = 5$) indicating that likely over three-quarters of emergent benthic insect production enters terrestrial habitats. It would be straightforward to include an additional term in the model to account for the fraction of insects that are expected to permanently leave the aquatic ecosystem to enter the terrestrial one. The net effect would be to lower the flux of aerial insects to land by a constant amount.

This current conceptual model does not attempt to make predictions relevant to particular places or regions. Rather, it is a general and theoretical treatment of the factors affecting flux. More refined models that include additional lake or stream variables (Hakanson and Boulion 2003) or geographic position may enhance the ability of the model to predict which bodies of water will be more likely to have significant exports of emerging aquatic insects to terrestrial habitats. For example, lakes often have areas of high benthic productivity nearshore and relatively unproductive areas in deeper parts of the lake. A more appropriate estimate of the ability of aquatic systems to export material would use an estimate of "effective size," which adjusts average ecosystem production by variables associated with morphology and/or physicochemical characteristics of the bodies of water. For example, lake morphometry interacts with nutrient levels to influence benthic and pelagic primary production rates (Vadeboncoeur et al. 2008), which in turn influences benthic insect production. Although we found no effect of lake size on P_i , this pattern warrants further testing with more extensive data sets. Refinements can also be made for streams, where stream depth and discharge, substrate type, stream order, or other landscape variables may be included as factors affecting stream invertebrates and benthic production (Richards et al. 1996). Finally, this model can be extended to account for other ecosystems linkages where juvenile and mobile adult life stages live in different habitats (e.g., wetlands–terrestrial linkages).

Another simplifying assumption is that all insects behave comparably and disperse evenly inland. Large insects that are strong fliers (e.g., dragonflies) may move further inland than average, while stoneflies may prefer to move along stream corridors with occasional movement inland (Macneale et al. 2005). Although for simplicity we used mean slope estimates for the functions describing insect movement inland, a distribution of slope parameters that reflects the variation in insect dispersal patterns (Appendix E) could be used to account for differences in dispersal capacity. Environmental conditions, prevailing wind directions, obstacles (mountains), or vegetation types (Petersen et al. 1999) could also affect the spread of insects inland and may influence actual fluxes to land.

Scaling to real landscapes

Export of energy and nutrients from aquatic ecosystems occurs via the movement of emerging aquatic insects into terrestrial habitats. The simple model we propose suggests that by understanding variation in benthic production in lakes and streams and how it scales with the amount of aquatic habitat per length of shoreline, it is possible to estimate inputs of aquatic insects to land, measured as a flux across the water–land boundary. To understand the role of aquatic–terrestrial linkages in real landscapes, however, will require an estimate of the total amount of stream and lake habitat in a region. Thus, within any given terrestrial landscape the relative frequency of lakes and streams will determine their relative influence on the surrounding land. For example, using available GIS data layers we calculated the total amount of land within 100 m of lakes and streams as $\sim 13.5\%$ and 8% , respectively, in northern Wisconsin (Vilas County, 46° N, 90° W) and 1.4% and 27.4% , respectively, in southwestern Wisconsin (Iowa County, 43° N, 90° W). As a result, even though the average lake is expected to have a larger influence on land than the average stream, in areas such as southwestern Wisconsin streams may have a cumulatively larger impact on land by virtue of there being more linear kilometers of streams relative to area of lakes. This simple calculation also shows that for those areas of Wisconsin, $\sim 25\%$ of land is within 100 m of any body of water, suggesting that a significant proportion of the terrestrial environment is within range of potential influence of aquatic ecosystems.

Our challenge is to understand the key controlling variables that influence the magnitude of aquatic–terrestrial linkages. Whether streams and lakes are fundamentally different in their productivity of emerging insects requires further examination, though our analysis of data from the literature suggests some potentially significant differences. Moreover, streams are relatively narrow and thus have less surface area per shoreline than do lakes, which tend to be larger. These physical attributes determine the amount of aquatic production that moves across a given length of shoreline. As a result, the average lake has about 2.5 times the flux of emerging insects as does the average stream. Larger lakes and streams have fluxes that can result in insect deposition comparable to in situ net secondary production on land, particularly in low productivity terrestrial ecosystems such as deserts or tundra. Although fluxes from aquatic ecosystems to terrestrial landscapes have been historically deemed too small, insignificant, or rare to be of relevance to terrestrial ecosystem dynamics, this model and the estimates of flux based on empirical data suggest that movement of emergent aquatic insects may form a significant and ubiquitous link between aquatic and terrestrial ecosystems.

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APPENDIX A

Production values for lakes synthesized from the literature (*Ecological Archives* E090-190-A1).

APPENDIX B

Production values for streams synthesized from the literature (*Ecological Archives* E090-190-A2).

APPENDIX C

Summary *E:P* ratios for streams and lakes (*Ecological Archives* E090-190-A3).

APPENDIX D

Estimates of annual emergence of aquatic insects from streams summarized from the literature (*Ecological Archives* E090-190-A4).

APPENDIX E

Summary of insect dispersal studies derived from the literature (*Ecological Archives* E090-190-A5).

APPENDIX F

Illustration of insect deposition rate as a function of distance from shore (*Ecological Archives* E090-190-A6).

APPENDIX G

Reference list for studies cited in Appendices A–E (*Ecological Archives* E090-190-A7).