Chapter 14

Food webs and resource sheds: towards spatially delimiting trophic interactions

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Introduction

Ecologists are bringing more spatial realism to theoretical and data-based studies of food webs, but we are still impeded by our ignorance of movements of consumers and their resources in the real world (e.g. Okubo 1980). These movements determine the fate of populations and the nature of their interactions. They also bear upon applied concerns, such as species habitat requirements (Schell *et al.* 1988; Wennergren *et al.* 1995), or their roles in contaminant transport (Rau *et al.* 1981; Jackson and Schindler 1996; Jackson 1997).

In the course of grappling with spatial dynamics of consumers and resources in the real world, it would be useful to know more about consumer 'resource sheds': source areas for resources consumed by individuals during their lifetimes. (Autotrophs are included here as consumers in the sense that they consume photons and molecules.) In this paper, we will develop this idea, which borrows from concepts developed by Cousins (1990, 1996) and Polis *et al.* (1997). Resource sheds can be spatially bounded, sometimes by abrupt thresholds, other times by diffusive gradients, which are often but not always related to physical heterogeneity in the environment. Using case histories of organisms we have studied in river and watershed food webs of Northern California, as well as published studies from other ecosystems, we will explore how resource sheds may be determined both by physical features of a landscape and by attributes of consumers or resources. We then present a simple model to describe and interpret landscape variation in fluxes of emerging river insects consumed by spiders, lizards, frogs, birds, and bats in the surrounding old growth conifer forest.

The watershed—resource shed analogy

Promoting the notion of a 'resource shed' (such as photon sheds, or nitrogen sheds) might violate Paine's (1996) dictum: 'Thou shalt not commit jargon.' However, there are several reasons for doing so. First, the term efficiently communicates, and focuses attention on a useful concept. This concept is similar but not equivalent to Cousins' 'Ecosystem Trophic Module' (also known as ecotrophic

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decomposer biomass that is eventually transferred along food chains to the consumer in question. For some purposes, however, it might be useful to look further back in time, and upstream along biogeochemical flow paths conveying resources, particularly to sites where isotopic fractionation processes have occurred that can fingerprint sources. For example, if volatilized NH_3 from pig sewage triggers *Pfisteria piscicida* blooms in coastal lagoons off the south-eastern United States (Burkholder *et al.* 1992), it would be of considerable interest to delineate the nitrogen shed feeding this dinoflagellate population.

The time dimension

Watersheds have storage elements (off river lakes, landslide deposits) that retain water or sediment for various lengths of time. Consumers also store resources for various lengths of time in tissues with different turnover rates. For example, vertebrate ear bones may retain for a lifetime atoms acquired during an animal's first days, while atoms in epithelial tissue may be completely exchanged within a few weeks. A consumer's conserved tissues therefore derive from its entire lifetime resource shed (and possibly part of its mother's resource shed, if maternal endowments were substantial). More labile tissues derive from those portions of the resource sheds used by the organism in its more recent past (Fry and Arnold 1982; Fig. 14.2). In resource sheds, as in watersheds (Dietrich *et al.* 1982), the source area expands with the time interval over which elements are acquired.

In addition, the consumer may pick up resources of different ages as it forages. A wood-boring beetle consumes contemporary tissues as it enters through the bark and attacks the cambium. Then it may work its way inward to ingest wood laid down during decades or centuries past. The tree itself may have absorbed young, surficial water while a seedling, then taken up deeper, older groundwater as it grew longer roots (Dawson and Ehleringer 1991). (The water's age is referenced with respect to when it first entered the biosphere as precipitation.)

Limits of the analogy

Considering mobile consumers may push the watershed–resource shed analogy to its breaking point. Unlike recipient channel cross sections or catchment areas, mobile consumers go and get resources, or pick them up over the course of other movements. Tracers have proven invaluable to researchers attempting to keep track of movements of consumers and fluxes of resources, in situations (which are more the rule than the exception) in which direct observations of foraging and fluxes are rare or impossible.

Using tracers to delimit resource sheds

Stable and radioactive isotopes, along with distinctive, persistent molecules like organochlorines or stable lipid residues, are proving increasingly useful in revealing spatial and temporal dimensions of resource sheds. Radioactive ^{14}C, used

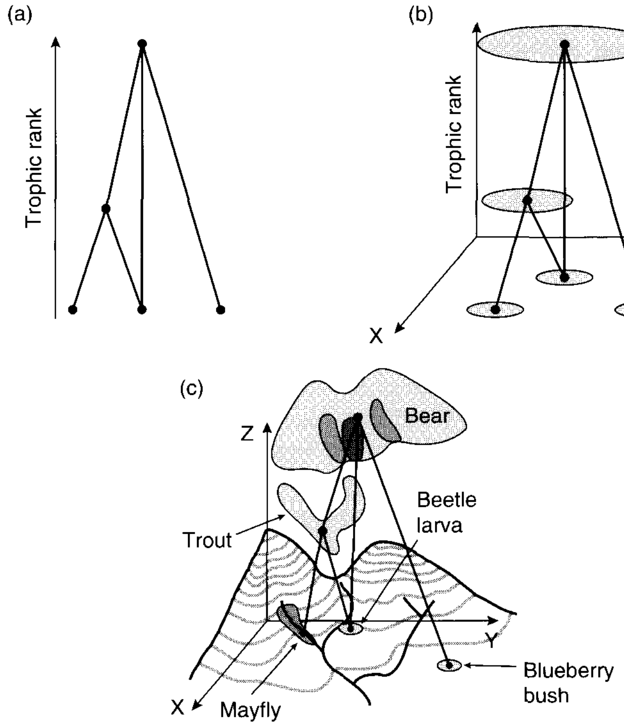

Figure 14.1 Resource sheds of organisms at different trophic levels in a food web, modified from Holt (1996). (a) Food web with no spatial or temporal context (b) and (c) Food web showing source areas for various trophic positions. In all figures, the *z* axis designates trophic rank with producer or decomposer species at the bottom level, intermediate consumers above them, and top predators in the uppermost positions. In (b), Holt uses the *x* and *y* axes to designate the spatial coordinates of landscape patches (the ovals) 'pertinent to the population dynamics' (Holt 1996, p. 314) of the web members. In (c), we have modified his diagram to project the landscape of a hypothetical western North American forest food web. Topographic elevation as well as trophic rank increases up the *z* axis. Shading indicates source areas for trophic resources for organisms, with more darkly shaded areas designating areas from which most fluxes to particular consumers derive.

redwoods (*Sequoia sempervirens*) in California derive much of their nitrogen from marine fog (T. Dawson, unpublished data) as do nitrogen-limited forests in southern Chile (Weathers and Likens 1997). When lateral fluxes of resources are extensive, delineating shed boundaries may require arbitrary cutoffs along the tails of two probability densities: (i) the probability that a given resource unit (e.g. a nitrogen atom) in the body of a consumer entered the ecosystem within radius *x* from that consumer (or the most frequently occupied site in its home range); and (ii) the (much lower) probability that a resource unit within radius *x* of the consumer (or the site) will eventually become incorporated into its body. Again, we might define 'entry' of the resource unit as its assimilation into producer or

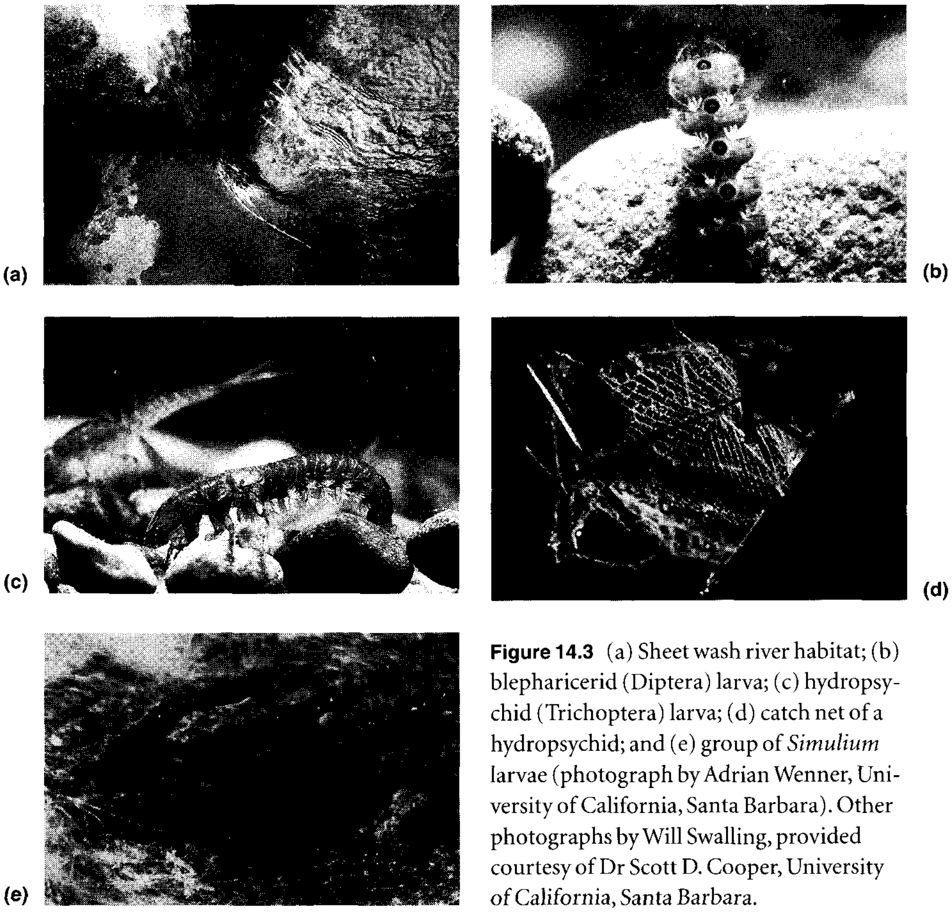

Figure 14.3 (a) Sheet wash river habitat; (b) blephariceridid (Diptera) larva; (c) hydropsychid (Trichoptera) larva; (d) catch net of a hydropsychid; and (e) group of *Simulium* larvae (photograph by Adrian Wenner, University of California, Santa Barbara). Other photographs by Will Swalling, provided courtesy of Dr Scott D. Cooper, University of California, Santa Barbara.

Case histories

Four case histories illustrate the use of isotopic tracers and the roles of consumers, resources and environments in delineating resource sheds for stream-dwelling insects (Finlay *et al.* 1999), forest trees (Simard *et al.* 1997), migratory Bowhead whales (Schell *et al.* 1988) and riparian plants (Ben-David *et al.* 1997a).

Carbon sheds of co-occurring stream insects

Defining resource sheds is somewhat simpler if consumers are sessile, or nearly so. Small (1–10 mm long) larval stream-dwelling insects (Blephariceridae, Simuliidae, Hydropsychidae) live in close proximity in fast-flowing habitats, such as sheet wash over boulders (Fig. 14.3). Blephariceridid larvae (Diptera) use ventral sucker disks to cling to rock surfaces, which they graze. Hydropsychid caddisflies (Trichoptera) capture drifting food particles in funnel-shaped webs attached to substrates. Simuliid (blackfly) larvae (Diptera) affix their posteriors to substrates with glue and silk, and filter particles with their cephalic crown appendages. These larvae are

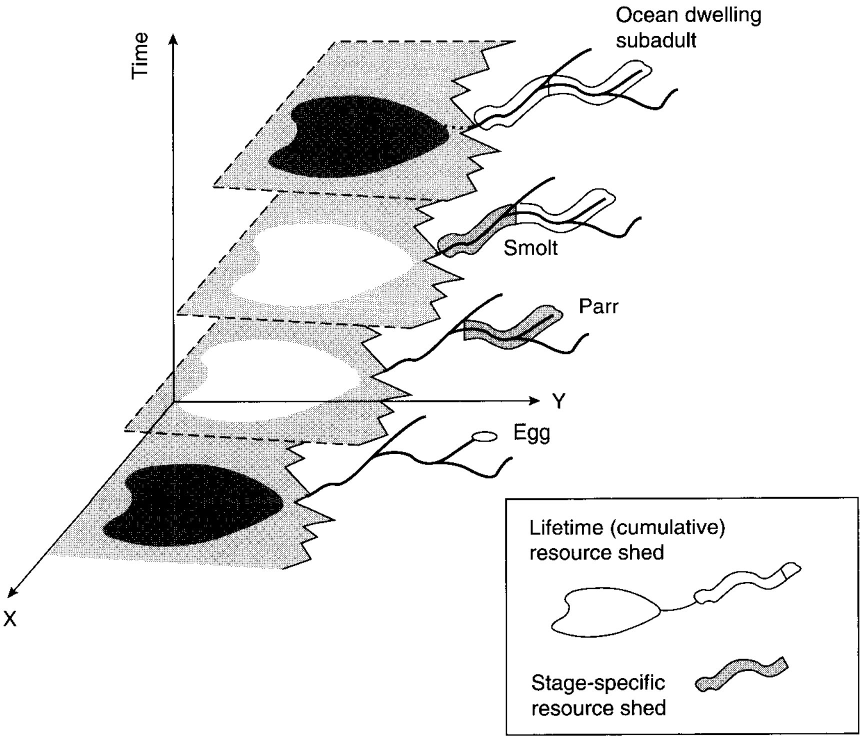

Figure 14.2 Ontogenetic changes in the nitrogen shed of a salmon. Here, the *x* and *y* axes indicate plan-view map coordinates (e.g. of the western coast of North America and a coastal river drainage). The darkened patches designate areas from which the organism derives resources over short time-scales (days or weeks). Tissues with short turnover times (e.g. epithelium) would be built of these resources. The light patches designate source areas for resources accumulated over longer time scales. Tissues with long turnover times (e.g. ear bones) would conserve resources from these areas. The nitrogen shed for a salmon egg corresponds to its mother's habitat, rather than its own habitat.

widely as a dating tool (Aitken 1990), can also serve as a source marker for food web studies. For migrating animals, ^{14}C has been used to determine when, and therefore where, certain resources were acquired (Schell and Ziemann 1988; Schell *et al.* 1988). Applications of stable isotopes have been well-reviewed elsewhere (Rundel *et al.* 1988). There are many sources of variation for stable isotope composition of biological tissues (multiple potential sources and various physical and physiological fractionation processes), and consequently many opportunities for misinterpreting them. Nevertheless, technical innovations, diligence and clever detective work by ecologists are gradually turning more of this noise into signal, as sources of spatial and temporal variation in isotopes are identified (e.g. Schell *et al.* 1988; Finlay *et al.* 1999).

carbon transfer via soil were not used.) These pioneering double label studies showed a substantial net transfer of carbon from birch to fir through fungal hyphae. Two-year-old Douglas fir acquired 3–10% of the total carbon transferred, a net carbon gain of 6% over what trees acquired by photosynthesis alone. Hence, the carbon shed of a tree can be expanded by underground mycorrhizal networks. The flow of carbon down source-sink gradients suggests that shaded individuals can be subsidized by sunlit trees, offsetting site-related growth advantages of the latter. This finding has implications for forest management and interpretation of species interactions over the course of succession.

Carbon sheds for migratory whales

Schell and colleagues (Schell *et al.* 1988) have used stable and radioactive isotope analysis to glean information on feeding grounds of Bowhead whales that would have been impossible to learn from field observations. Bowhead whales winter on the ice edge of the Western Bering Sea, then migrate north through the Bering Straight and the Chukchi Sea to spend summers in the Eastern Beaufort Sea. They feed throughout the course of this migration, filtering zooplankton on plates of keratinous baleen attached to their upper jaw. Zooplankton from the Bering Sea are depleted in ^{13}C, because of upwellings from deep ocean water, the import of terrestrial carbon from the Mackenzie River, or both. As the whales move east, they encounter zooplankton that are more enriched in heavy carbon. By looking at changes in stable isotopes along the length of baleen from five whales, Schell and colleagues were able to detect regular cycles of ^{13}C peaks and troughs, which reflected annual movements of the whales from summer feeding grounds in the Beaufort Sea to wintering grounds in the Bering Sea. The time period of cycles in ^{13}C content was deduced by analysis of ^{14}C along the baleen plate. The authors traced ^{14}C content from the young growing edge of the baleen plate of a whale killed in 1971 back towards the distal, older end of the plate, fitting the baleen ^{14}C to the radiocarbon content predicted in marine biota after atmospheric weapons tests in the early 1960s. The good fit of the ^{14}C baleen data to year-by-year predictions confirmed that the ^{13}C cycles were annual, and also supported the hypothesis that Bowhead baleen grew continuously. Their analysis sheds light on the relative importance to whales of foraging grounds in the Bering and Beaufort Seas. Before their study, the conventional wisdom was that Bowhead whales made most of their growth during summer feeding in the Beaufort Sea, and lived off stored fat while wintering in the Western Bering Sea. Cycles of ^{13}C, however, showed wider valleys than peaks, indicating that most bowhead growth occurred during winter feeding in the Western Bering Sea, where ^{13}C was depleted. This finding is of critical conservation importance for the much reduced whale population, given plans for renewed indigenous hunting and potential oil drilling off the coast of Alaska. Schell *et al.* (1988) point out that other keratinous structures like horns, claws, or antlers could be used to reconstruct regional feeding histories in other vertebrates.

all considered primary consumers, feeding on algae and detrital organic matter. Their primary food sources are not obvious, however, from either gut contents or behavioural observations.

Carbon isotope analysis revealed surprising differentiation in the diets of these co-occurring insects (Finlay *et al.* 1999). Jacques Finlay discovered that in sunlit, productive rivers, velocity strongly influences the ^{13}C composition of primary producers, and of the primary consumers that feed on them. CO_2 diffuses much more slowly in water than air. Algae preferentially take up lighter ^{12}C isotopes when supply is not limiting (Keeley and Sandquist 1992). When CO_2 supply is low relative to demand, however, algae take up more ^{13}C. Finlay found a strong relationship between flow velocity and the ^{13}C composition of benthic algae in three productive rivers of northern California, with more ^{13}C enrichment ($\delta\ ^{13}C$ of −22 to −13) in slow-flow (pool) habitats. In fast flowing riffles where delivery of CO_2 to algae is rapid, algal $\delta\ ^{13}C$ ranged from −24 to −32, with some samples even more depleted than the average for terrestrial vegetation ($\delta\ ^{13}C$ of −27). Blephariceridids had similarly depleted ^{13}C signatures ($\delta\ ^{13}C$ of −26), indicating that they were largely built of local sheet flow algae. Hydropsychids and simuliids, in contrast, had the ^{13}C-enriched signals characterizing pool-derived algae. Despite the fact that these insects occur within millimeters of each other, their carbon signatures differ markedly, indicating that the surface-scraping blephariceridids are deriving their carbon from local riffle algae, and the filtering insects are deriving most of their carbon from algal production in pools upstream. Knowledge of these differences in resource sheds could lead to predictions about the relative dominance of these taxa in rivers where geomorphology, water management, or land management (e.g. timber harvest) changed the amount and local productivity of pool vs. riffle habitats. In regions where simuliids are pests of livestock or vectors of human disease (e.g. onchocerciasis, or river blindness (Desowitz 1981)), such information could be of practical use.

Carbon sheds of forest trees

Many terrestrial plants are linked underground by networks of mycorrhizae, or 'fungus-root' symbioses, which spatially expand the underground foraging volumes of individual plants. Simard *et al.* (1997) showed that different species of forest trees that share fungal symbionts are trophically connected by ectomycorrhizae. These investigators labelled birch (*Betula papyrifera*) and Douglas fir (*Pseudotsuga menzies*) with ^{14}C or ^{13}C, respectively. They switched the isotopes given to each species to check for differential isotope mobility, and found none. They also checked for indirect transfer of the label through soil fluxes of gaseous CO_2, sloughed root or fungal cells, or root exudates, by measuring uptake of the label by adjacent cedar, *Thuja plicata*, which are colonized by endomycorrhizae, and do not share in the ectomycorrhizal networks of birch and fir. Uptake of label by cedar was relatively small, showing that the carbon was moving primarily through ectomycorrhizal hyphae. (Robinson and Fitter (1999) and Fitter *et al.* (1999), however, have pointed out that appropriate controls for the possibility of carbon supplements to forest trees (Simard *et al.* 1997). Both resources flow down chemical source-sink gradients (e.g. from sunlit birch to shaded Douglas fir), so that the 'poor get richer' due to the flux. Simard *et al.* suggest that by evening out site-related competitive advantages of trees, this flux may stabilize forests against species loss. Increasing dominance of Douglas fir throughout coastal forests of the Pacific North-west as a result of fire suppression, however, suggests that acting as a resource sink is a successful physiological adaptation for this species rather than the consequence of being a poor competitor.

While the diffusion flow path seems consistent with chemical thermodynamics, the advection-concentration path often occurs in nature due to gravity. Fluids and particles move downslope and concentrate in low points on landscapes. Lowland rivers, lakes, estuaries and coastal lagoons become enriched as they receive and store nutrients from watersheds upslope. This process can be dramatically accelerated by timber harvest, agriculture, and concentrated livestock, resulting in eutrophication and serious harm to local economies, ecosystems, and human health (Carpenter *et al.* 1998 and references therein).

The vectoring of river or marine resources upslope by migrating fish or foraging bats, eagles, bears, or other mobile top predators is notable because it counters, at least locally, the otherwise dominant tendency for nutrients to be shed down hill. For example, certain California bats feed almost exclusively over quiet, lowland water, but roost in large, thermally stable structures (massive trees or rock formations) that tend to occur high in landscapes (Rainey *et al.* 1992). As these bats migrate between nocturnal feeding areas and their day roosts, they convey nutrients from agriculturally enriched lowland rivers upslope, sometimes tens of kilometres, to nutrient-poor chaparral or forest ridge habitats (Rainey *et al.* 1992; Power *et al.*, in press). These localized nutrient 'resets' (translocations of nutrients lost from watersheds back upslope) occur on even larger scales with anadromous salmon supplying marine nitrogen to blueberries growing along Alaska streams (Ben-David *et al.* 1998).

On a more modest scale, river-derived nitrogen and carbon can move back upslope by biological diffusion (*sensu* Okubo 1980). After aquatic insects emerge from productive rivers in northern California, they diffuse laterally into less productive forested watersheds, their flux decreasing exponentially with distance from the river (Fig. 14.4, Power *et al.*, in press). What factors influence the magnitude of this flux, and its lateral decay rate?

Controls on fluxes of aquatic insects available to watershed consumers

We have been studying the importance of emerged aquatic insects to terrestrial consumers (various spiders, lizards, birds and bats) in the watershed of the South Fork Eel River, in north-western California (39°44′N; 123°39′W). We sample emergence with floating traps set on the water surface (Fig. 14.5). We sample lateral penetration of insects into the surrounding old-growth conifer forest by harvesting insects from sticky and pitfall traps deployed from the river to the ridge (typically only 200–300 m away from the river, as the terrain is steep in this canyon-bound

Nitrogen sheds for riparian plants

A growing number of studies are documenting that salmonid migrations import marine carbon and nitrogen (which are enriched in ^{13}C and ^{15}N relative to terrestrial C and N) to freshwater macroinvertebrates and fish (Cederholm *et al.* 1989; Kline *et al.* 1993; Bilby *et al.* 1996), terrestrial mammals (Ben-David *et al.* 1997a,b), and even riparian plants (Ben-David *et al.* 1998) high in coastal watersheds. Ben-David and colleagues sampled ^{15}N content in vegetation growing in areas with contrasting flood regimes and predator activity along six streams with salmon runs in the Tongass National Forest in South-west Alaska. They hypothesized that three possible pathways could convey marine nitrogen to riparian vegetation: deposition of salmon carcasses on floodplains during receding floods, dissolved nitrogen in stream water, and transport of salmon carcasses by predators that carry and cache them well upslope from the river. In four of five plant species sampled, ^{15}N was enriched where predators were active in conveying and caching salmon carcasses. Three of the five plant species (blueberry (*Vaccinium* spp.); Devil's club (*Oplopanax horridus*); and spruce (*Picea sitchensis*)), all showed nitrogen enrichment near the river, which declined sharply with distance from the channel and elevation. This trend was absent in skunk cabbage (*Lysichitum americanum*), which grew in moist swales filled with decaying leaves. The authors conjectured that plants in these microhabitats might not be nitrogen-limited. Small mammals (deer mice, shrews, voles, and squirrels) sampled along these elevational gradients showed the same ^{15}N enrichment patterns as the plants. If these small mammals had been eating salmon carcasses, their ^{13}C would also be enriched. That this was not the case indicated that the marine derived ^{15}N entered these small mammals through herbivory on the plants that drew their CO_2 from the air.

Shapes, sizes, and boundaries of resource

Some resource sheds are simple discrete patches (e.g. photon sheds for intertidal limpets or sessile scraping stream insects). In some cases, their boundaries are sharpened by predator-induced resource avoidance (Sih 1982; Power 1984; Power *et al.* 1989; Lima and Dill 1990), intra- or interspecific territoriality (Ben-David *et al.* 1997b; Carpenter and MacMillen 1976; Berry and Playford 1992), or physical constraints on the consumer (e.g. the 60 m limit on diving depth by sea otters (VanBlaricom and Estes 1988)). Many resource sheds, however, involve complex networks of structures or flow paths that convey or expose resources to consumers from dispersed or distant sources. The tracer studies reviewed above illustrate how movements of consumers (e.g. Bowhead whales), physical advection of resources (e.g. pool-produced algae for riffle-dwelling filter feeders), or vectoring of resources by other organisms (e.g. mycorrhizal networks or migrating salmon) can shape and expand resource sheds of organisms to a counter-intuitive extent. Resources can either move 'down diffusion gradients' (from areas of high to low concentration), or 'up gradient', to become collected and concentrated. The diffusion case occurs in the mycorrhizal hyphal network supplying nutrients and

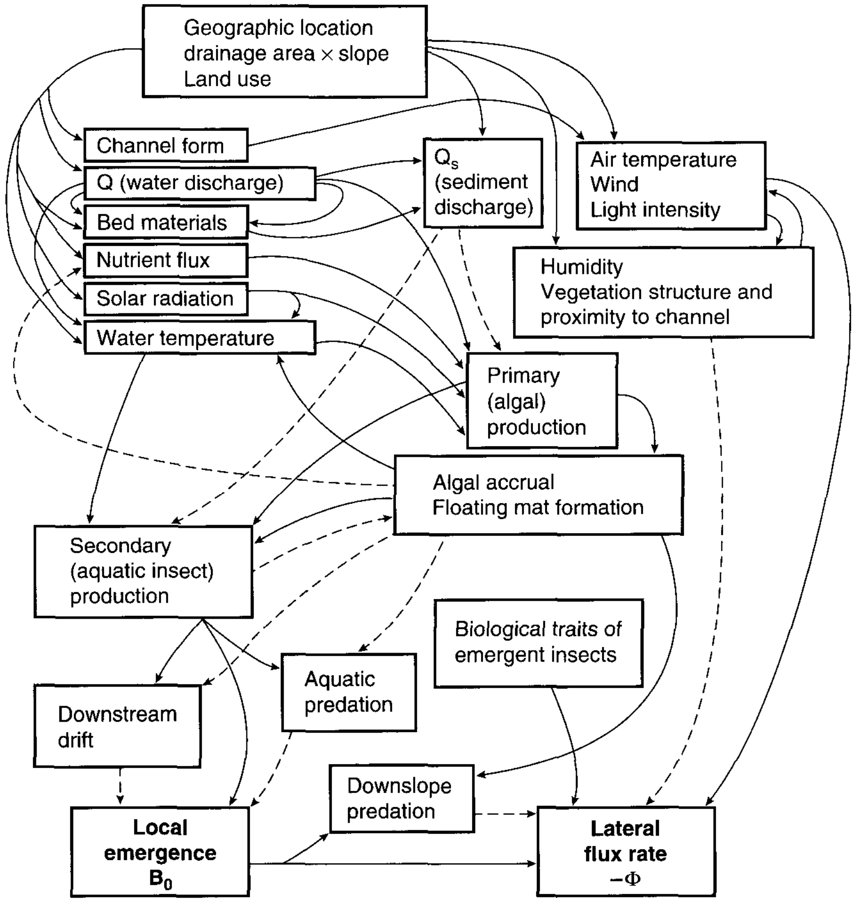

Figure 14.6 Causality flow chart linking landscape position, environment and biology to emergence rates (B_0) and lateral insect flux into the forest ($-\phi$). Dashed arrows indicate reduction of downstream by upstream entities.

moves laterally through the watershed. If ϕ = infinity, the emerged insects concentrate directly over the water, and do not move laterally away from the river. Fitting equation (14.1) with representative data from our summer 1998 emergence and river-to-ridge watershed sticky trap transects gives preliminary estimates of $\phi = 0.010\ \mathrm{m}^{-1}$ in early June, and $\phi = 0.016\ \mathrm{m}^{-1}$ in mid-July, when emergence from the river is greater and, in the watershed, soil moisture and insect densities are both lower (Fig. 14.4).

To predict how fluxes of aquatic insect resources may change across sites or under different environmental conditions, we need to unpack and examine some of the ecological variables aggregated into the two parameters of equation (14.1) (Fig. 14.6). Rates of emergence B_0, will depend on local aquatic insect production, and how much of this emerges locally. Secondary production of aquatic insects in

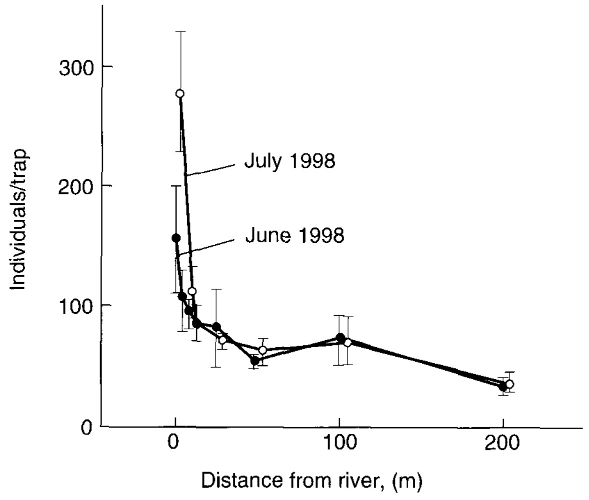

Figure 14.4 Exponentially decreasing insect abundance with distance from the river. June 1998 and July 1998 sticky trap data with Stickum Special *R* on clear acetate sheets rolled into cylinders and deployed ≈ 1 m off the ground. Points are averages of means of three sites (averaged from three transects per site); lines show 2 SE.

Figure 14.5 Traps sampling emergence of insects (B_0) from the South Fork Eel River.

river). Descriptions of the site and the study are given in Power (1990) and Power *et al.* (in press), respectively.

Consistently, we find that the flux of aquatic insects declines exponentially as one moves inland from the river, typically so steeply that within 10 m, the flux is less than half of its value at the river's edge. The flux of these emerged insects past a point at distance x (m) from the river, B_x ($\mathrm{g\,m^{-2}\,d^{-1}}$), depends on the rate of emergence of insects from the river channel reach supplying this flux (B_0 ($\mathrm{g\,m^{-2}\,d^{-1}}$) and the flux decay coefficient, ϕ, ($\mathrm{m^{-1}}$), so that

$$B_x = B_0\, e^{-\phi x} \tag{14.1}$$

If emergence is measured, ϕ is the only free parameter in equation (14.1). If $\phi = 0$, the emergence flux passing up through the water surface does not decay at all as it

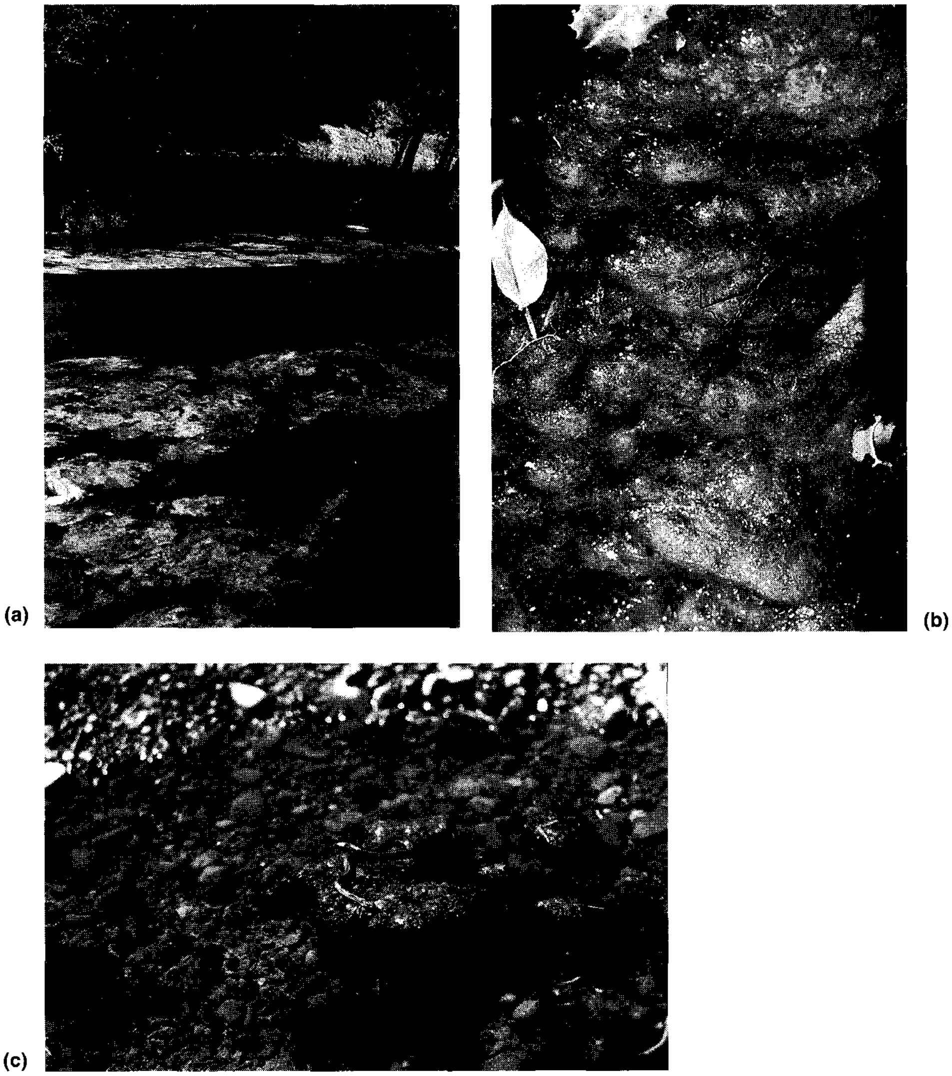

Figure 14.7 Floating algal mats in the South Fork Eel River. (a) Mats accumulate in slack water areas and around emergent rocks in riffles. (b) Close-up of a mat showing ceratopogonid (Diptera) egg masses (black spots) with a predatory water strider (*Gerris remigis*) who will probably consume a very small fraction of the mat's insect emergence. (c) Floating mat shown with a basking aquatic garter snake (*Thamnophis couchi*). Predation risk from these piscivores may deter Eel River fish from foraging in floating algal mats.

throughout the forested watershed around the South Fork Eel River, wherever the vegetation provides sufficiently stiff branches to support its elaborate web in areas with some cover from wind (S. Khandwala and M.E. Power, personal observations). This spider invests so much silk in its web that it moves very infrequently our largely algal-based river food web depends on local primary production (and food quality) of algae, and temperature (see Benke (1984, 1993), and Sweeney (1984) for more general reviews). The proportion of insects that emerge, rather than drift downstream or end up in aquatic predators, is heavily influenced by habitat structures that retain and refuge aquatic insects. In the South Fork Eel River and its more productive tributaries, floating algal mats play a major role in enhancing local aquatic insect production, retaining it locally, and diverting it away from aquatic consumers and out into the watershed (Power 1990). Floating algal mats (Fig. 14.7) provide safe oviposition sites for female aquatic insects, and sun-warmed, food-rich incubators for larvae. The mats (made up largely of the macroalga *Cladophora glomerata* in our system) filter and accumulate organic seston from the river, and become overgrown with nutritious diatom epiphytes. During the afternoon, they commonly become more than 8°C warmer than the surrounding water. They are cooler than the water by night (diel air temperatures fluctuate with 2–3 times the amplitude of river temperatures during the summer), but temperature variation itself can hasten the development of aquatic insects (e.g. Huffaker 1944; Sweeney and Schnack 1977; Gresens 1997). The importance to terrestrial consumers of floating algal mats as hot spots of insect emergence is easily demonstrated by the numerical responses of cursorial wolf spiders (Lycosidae) to river margins where mats occur naturally or have been experimentally introduced (Power *et al.*, in press, Parker and Power 1993).

The rate at which flux declines laterally as emerged insects move into the forest, ϕ, is controlled by many factors. These include (i) the behaviour of the adult insects (densities and positions of swarming aggregations—some mayflies swarm directly over the water, while some chironomids may fly well upslope to swarm over landmark trees (M. Butler, personal communication); (ii) their active and passive responses to environmental conditions (temperature, wind, air humidity, light, and vegetative clutter); and (iii) downslope interception of insects by intervening terrestrial predators. At the South Fork Eel, emerging insects suffer nocturnal depredation by bats (W.E. Rainey, unpublished data) and tetragnathid spiders that line the river channel (A. Smyth, unpublished data), and diurnal losses to birds, lizards (J. Sabo, unpublished data), and adult odonates that also concentrate their hunting along the river channel.

Consumers of river-derived insects

Resource shed estimation for a stationary watershed consumer

Emerging aquatic insects are tracked and consumed by a variety of terrestrial predators (Jackson and Fisher 1986; Gray 1989; Power *et al.*, in press; Henschel *et al.*, in press). At our study sites along the South Fork Eel River and its tributaries, bats, lizards, and most spiders (lycosids, tetragnathids) concentrate their foraging activities around the river channel, particularly during the summer drought when forest, meadow and chaparral habitats upslope become dry and less productive. One common consumer, however, does not numerically track river-derived insect prey. The filmy dome spider, *Neriene radiata* (Linyphiidae) (Fig. 14.8) is common

3 insects from both sources become well-mixed as they move laterally; and
4 they are intercepted in proportion to their local abundance,
we should be able to predict the fraction of pool- *vs.* riffle-fed prey in the diet of a spider as a function of its distance from the river, and its longitudinal position relative to the riffle and pool sources (Fig. 14.9). If prey from other habitats are not important carbon sources for spiders, the fraction of river- vs. pool-derived prey in their diets can be calculated from simple mixing models (Fry and Sherr 1988). These mixing model predictions can be calibrated with field measurements of emergence and lateral flux of insect prey. Deviations of obsenvation isotopic ratios from predictions could reveal flaws in our parameter estimation for the flux-determined resource shed geometry, or in our four assumptions.

Mobile watershed consumers of river-derived insects

In contrast to filmy dome spiders, the more mobile consumers of river-derived insects that we are studying (bats, lizards, lycosid and tetragnathid spiders) numerically track high concentrations of emerging prey (W.E. Rainey, J. Sabo, K. Marsee, and A. Smyth, unpublished data; Power *et al.* in review). We can reformulate equation (14.1) to describe the degree to which collective consumption rates of predators at distance x from the river (C_x ($\mathrm{g\,m^{-2}\,d^{-1}}$)) as

$$C_x = C_0\, e^{-\eta x} \tag{14.2}$$

where C_0 ($\mathrm{g\,m^{-2}\,d^{-1}}$), is the collective consumption rate (predator density × per capita biomass consumption rate) of predators feeding directly over the river, and η ($\mathrm{m^{-1}}$), describes the change in their collective consumption rate with distance from the river. If η is less than ϕ, predators are less aggregated around the river than their prey (Fig. 14.10a). This sets up concentric changes in predator:prey ratios that create spatial 'death halos' discovered in the lupine-western tussock moth-parasitoid system by Maron and Harrison (1997). This situation would favour evolution by emerging insects to swarm and search for mates directly over the river (e.g. mayflies). If η is greater than ϕ, predators are more aggregated around the river than are their prey (Fig. 14.10b). In this case, selection would favour emerging insects that quickly moved laterally into the watershed, away from the danger zone (as some chironomids with 'hill topping' lekking behaviour do). The impact of predators on the behaviour and life history traits of emerging aquatic insects has been discussed by Edmunds and Edmunds (1979), Butler (1984), and Flecker *et al.* (1988).

Fitting acoustic data on bat collective foraging activity in mid-July gives preliminary estimates of $\eta = 0.070$, 0.026, and 0.014 for three different river reaches which differ in channel width and cross-valley profiles. These estimates suggest that bats are over-aggregated in the first two reaches, and well-matched to insect flux densities in the third (recall that $\phi = 0.016$ in mid-July). In general, insect fluxes and predator tracking abilities will change in ways that may be partially predictable from fixed site characteristics as we move downstream from the headwaters of a river system (Figs 14.6; 14.11). Can we predict how thresholds or gradients in

Figure 14.8 Michael S. Parker (Southern Oregon University) contemplating a cluster of filmy dome spiders (*Neriene radiata*) in the South Fork Eel watershed.

(M.S. Parker, personal observations). It therefore serves as a nearly sessile point sampler of prey flux. During a year of high filmy dome spider abundance, Michael Parker found that spiders along the river margin spun smaller webs, and had fatter abdomens and longer times to starvation in experiments. Spiders several hundred meters back from the river spun much larger webs, were thinner, and starved faster (Parker, unpublished data, discussed in Power *et al.*, in press). These findings are consistent with results from stable isotope analysis. The ^{13}C content of filmy dome spiders suggests that they may derive at least half of their carbon from river-derived prey, even when located hundreds of m back from the river (J.C. Finlay, unpublished data).

With some simplifying assumptions, isotope analysis could be used to test the usefulness of equation (14.1) in delineating the 'aquatic insect shed' for filmy dome spiders at various positions along the river and into its watershed (Fig. 14.8). As reviewed above, the carbon of insects feeding on pool-grown algae is enriched in ^{13}C, while the carbon of insects feeding on riffle algae is considerably depleted (Finlay *et al.* 1999). Jacques Finlay has pointed out that this isotopic distinction should be maintained in consumers that are close to the river, but should blur in more distant consumers that intercept both pool and riffle prey that mix as they diffuse away from the river. If we assume that

1 pools and riffles are point sources of prey;
2 the flux gradient is maintained as a steady state;

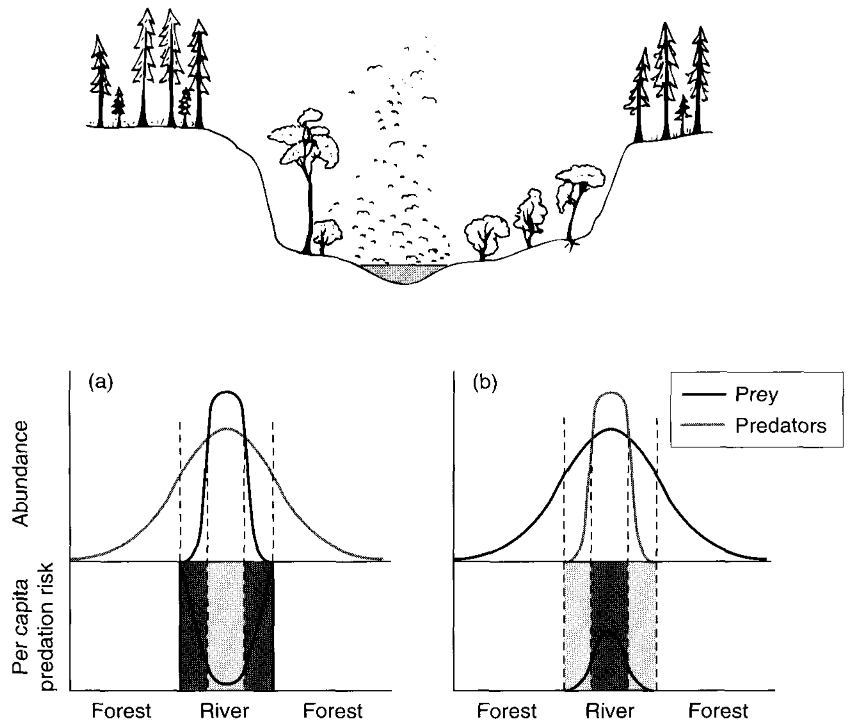

Figure 14.10 Predator tracking (collective consumption) superimposed on emergent insect flux distributions, and resulting spatial patterns of predation risk. (a) Predators are less aggregated than their prey, and potentially generate lateral 'death halos' (Maron and Harrison 1997), selecting for limited lateral prey dispersal. (b) Predators are more aggregated than their prey, potentially selecting for rapid lateral prey dispersal.

environmental conditions along river networks will influence resource fluxes and consequent interactions at different landscape positions?

Longitudinal changes along river networks

Stream drainage networks begin some distance down from the watershed divide, where the downslope flux of water and sediment first cuts a distinct channel head into the hillside. The position of the channel head can move up and downslope with changes in rainfall or sediment discharge (Montgomery and Dietrich 1988). The upstream limit for production of aquatic insects begins downstream from the channel head, where surface water is retained long enough for taxa to complete their larval lives. Clearly, this boundary will also change with precipitation regime, and the permeability of the bed and the surrounding watershed (Hynes 1975). Downstream, channels collect discharge from larger drainage areas and their slopes decrease. They widen, deepen, and flow faster according to empirical rules of hydraulic geometry (Leopold *et al.* 1964) that relate channel width, depth, and

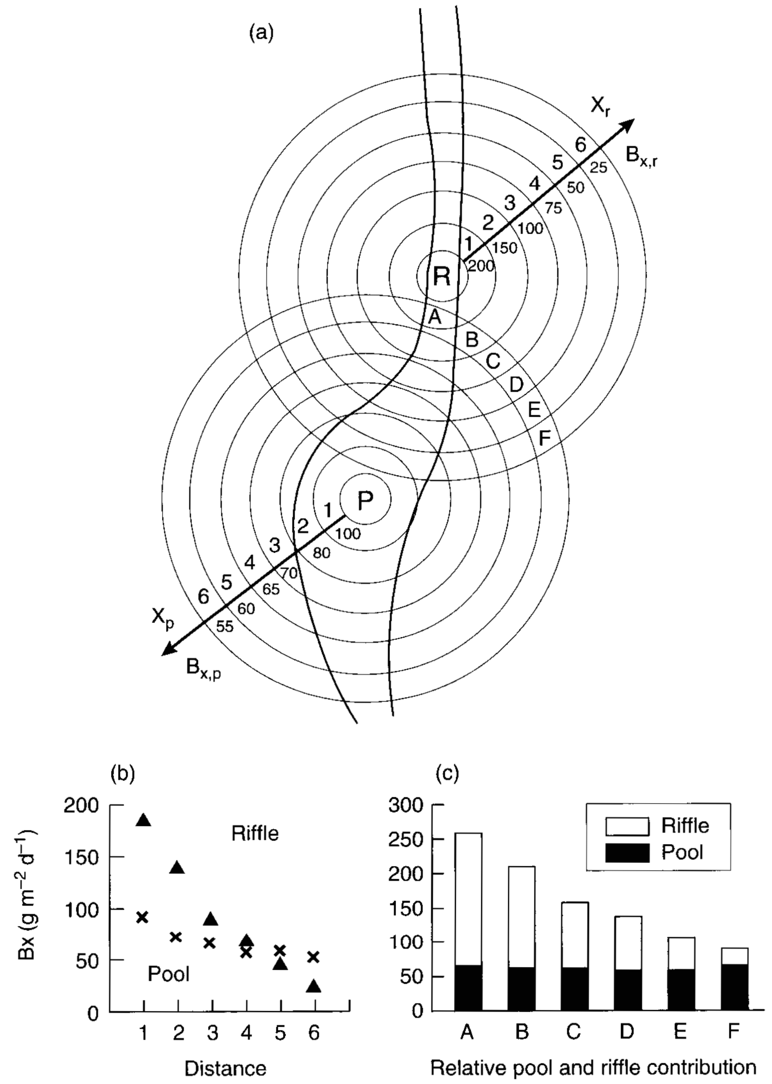

Figure 14.9 Predicted mixing of riffle (R) and pool (P) produced insects as a function of distance from the river. We assume that riffle emergence is higher than pool emergence (as our sampling has indicated, and as predicted by other studies demonstrating higher productivity of riffle areas). Lateral flux of insects is assumed to attenuate more rapidly in riffles, however, because they are often located in narrower, more confined reaches of the river channel. B_x represents the biomass flux of insects at distance x from the emergence source. In (a) emergence sources are depicted as points, which might be a good approximation if most emergence derives from discrete small patches of floating algae. In other cases, emergence sources might better be depicted as stream reaches, and the two-dimensional projection of the flux on to the habitat surface would shift from circular to oval. (b) Shows the decline in Bx with distance from the point source and (c) shows the relative contribution to Bx from riffle and pool insects at points A–F indicated in (a).

B_0 will increase abruptly downstream after channel and valley walls widen enough for river beds to receive enough sunlight to support macroalgal growth (Vannote *et al.* 1980). Positions of these transitions can be predicted for specific watersheds by the application of solar radiation models to high resolution digital elevation data from laser altimetry (D. Allen, unpublished data). Downstream from middle reaches, attached algal production will decrease as stable bedrock, boulder, and cobble substrates give way to finer gravels and sand or silt, on which attached algae are frequently silted or chronically abraded. Water column turbidity increases, decreasing benthic algal productivity (Vannote *et al.* 1980). If, however, lowland rivers have access to their floodplains (increasingly uncommon in the Northern Hemisphere), aquatic insect production will be supported by periphyton on emergent and floating macrophytes and semiaquatic floodplain vegetation (e.g. Forsberg 1993). The emergence of insects from lowland river reaches will depend on floodplain characteristics (morphology, especially of off-river water bodies; hydrologic cycles; extent and type of vegetation (Junk 1973, 1970; Junk *et al.* 1989; Power 1995; Power *et al.* 1995)), and are likely to be higher over inundated floodplains and off-river water bodies than over the main channel (Fig. 14.11c).

The lateral fluxes of insects into watersheds will also be influenced by longitudinal position in the drainage network (Fig. 14.11), although the net influences are perhaps less clear than for emergence. Near the headwaters, lateral penetration of emergence to the watershed is probably reduced. Because insects will be less active in the cool gorges, they will be physically confined by steep channel walls, and sheltered there from winds that might otherwise advect them away from the channel. Emerged insects (e.g. adult chironomids) near headwaters are commonly seen in swarms within dark, cave-like air pockets under large boulders, hovering over the surface of small pools. In lower, more open river reaches, insects are denser and warmer, both factors which might enhance their lateral diffusion (Okubo 1980). Wider channels will also be windier, so that insects could be advected laterally, or might leave open channel areas to avoid displacement or desiccation. Where, as at the Eel River, flow is seasonal, there would be less vegetative structure next to the stream to interfere with flight and offer resting perches. Lateral fluxes in lower reaches could be diminished, however, if predators aggregating to these more productive feeding grounds can deplete their prey, or if ovipositing females are strongly attracted to algal mats or still water surfaces (Horvath 1995).

Conclusion

Although landscape control on species distributions has been a venerable focus in the literature in ecology (Elton 1927; Shelford 1932; Holridge 1967), there is still considerable scope for research on the degree to which fixed site characteristics allow partial prediction of ecological processes (Brown 1995; Wiley *et al.* 1990, 1997; Wiens *et al.* this volume). River networks exhibit, and impose, partially predictable features and regimes on landscapes, which influence resource sheds, such

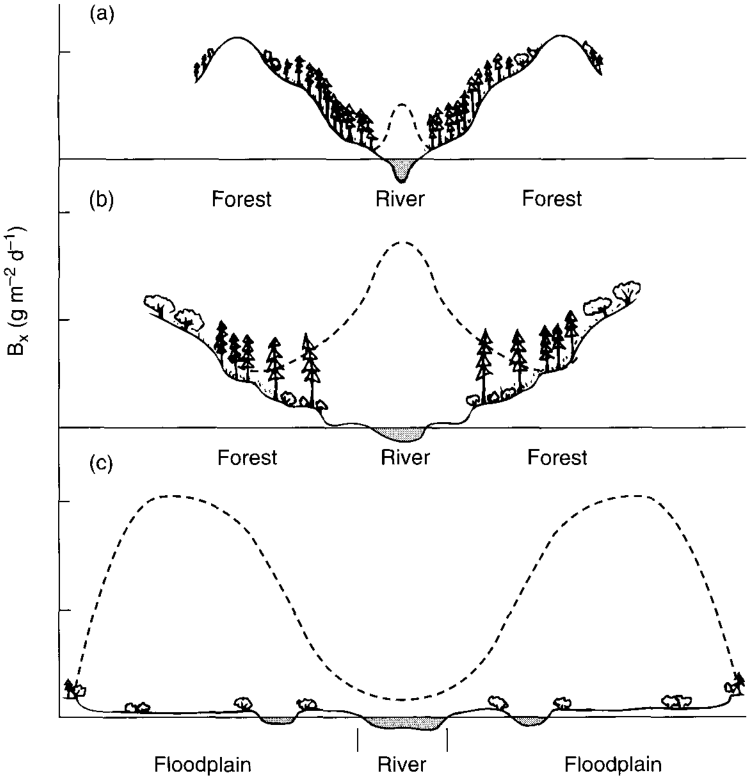

Figure 14.11 Cross sections through a river at its (a) headwaters; (b) middle reaches; and (c) lowland reaches with floodplains, with predicted patterns of emergence and lateral fluxes of aquatic insects from these positions.

velocity to discharge, which scales with drainage area. Width : depth ratios increase and channels change from cascades and stepped pools in narrow gorges, to meandering pools and riffles in middle reaches, to broad floodplains with off-river water bodies in the lowlands. Corresponding to these slope and drainage area-driven changes, bed materials change from boulders and bedrock in headwaters to cobbles and gravel in mid-reaches to fine sand and silt near river mouths (Leopold *et al.* 1964; Montgomery and Buffington 1997; Fig. 14.11). Disturbance regimes related to sediment transport change from rare (few or none per millennium) but catastrophic debris slides in headwaters to bed scouring floods in middle reaches that move cobbles and gravels as frequently as several times per year to chronic sand and silt transport in lowland rivers (Dietrich and Dunne 1978; Benda and Dunne 1990).

Are these geomorphically predictable changes in habitat structure and physical processes useful in predicting resource fluxes and delimiting boundaries of resource (emerged insect) sheds? If algal productivity and standing crops (e.g. floating mats) are major controls on aquatic insect emergence, we can predict that

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as the source areas supplying emergent insects to terrestrial insectivores. Resource supplies and physical conditions in turn constrain the interactions of consumers and their effects on ecosystems and communities.

Environmental heterogeneity is usually viewed as a fact of life that complicates or thwarts our ability to apply predictive models to ecological interactions. It is certainly the case that the uplift of a mountain range or the conversion of warm and cold oceanic circulations are historically determined, idiosyncratic phenomena that interfere with the ability of ecologists to apply general models ubiquitously. In non-theoretical applications, however, reading landscapes has long helped humans predict specific distributions and behaviours of organisms. Spear fishermen knew where and when to wait for migrating salmon to swim up a waterfall. Trappers could predict which foot of which sex of beaver would be caught in traps positioned in marshes around their lodges. As we struggle to merge the general dynamics of theoretical spatial ecology with the static description of landscape ecology, we will probably enjoy at least modest success by tailoring dynamic models of fluxes and interactions to boundary conditions and parameter constraints imposed by a partially ordered physical world.

Acknowledgments

We would like to thank Jacques Finlay and Gilbert Cabana for enlightening us about the use of stable isotopes in ecology, Bob Holt, Libby John and an anonymous reviewer for their helpful ideas and comments, and Terry Chapin for his early unflagging encouragement. This research was funded by the National Science Foundation (DEB–961517) and the Water Resources Center of California (WRC-895). The University of California Natural Reserve System, by providing a site protected for field research at the Angelo Coast Range Reserve, has made much of our work possible.

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