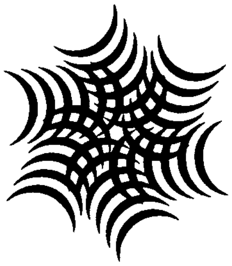
Food Webs at the Landscape Level



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that concentrate high densities of humans along the coast undoubtedly contribute to the degradation of coastal regions worldwide.

Humans and marine subsidies are interwoven in other ways. In many places, marine subsidies have exacerbated the harmful effects of introduced species. Humans have introduced a variety of "beneficial" domestic animals to islands worldwide (Atkinson 1994), including grazers (sheep, goats, rabbits, cattle), omnivores (pigs and boars), and some predators (domestic cats, mongooses, foxes). Other species have accompanied humans by accident, most notably many species of rats. The results of all these introductions have been almost uniformly catastrophic to the native biota. In many cases, the harmful effects of invasive species are highly subsidized by marine resources (see Power et al., chap. 24 in this volume). Typically, an introduced animal increases its population by using marine resources, either shore material or marine birds. These subsidized exotics then depress populations of local endemic species, sometimes to the point of extinction.

OVERVIEW AND CONCLUSIONS

In this chapter, we have shown that flow between the sea and the land occurs in both directions. Islands and coastal areas worldwide are deeply influenced by their juxtaposition to the ocean. Marine nutrients from birds and sea foam fertilize plants and increase productivity. Marine prey and detritus power dense populations of diverse coastal consumers. Marine vertebrates, particularly seabirds, provide a rich source of food that alters the communities of entire islands. Allochthonous marine inputs not only affect recipient species, but percolate and ramify through the food web to govern the dynamics of most species on islands and in coastal areas.

We conclude by stressing that it is not possible to understand either the demography of coastal and island species or the structure and dynamics of coastal communities and ecosystems without the inclusion of the great energetic and nutrient effects of the ocean. Land and water, although existing separately and easily recognized as distinct biological communities, are very real extensions of each other. This insight must govern our research, and our conservation and management efforts, in the coastal ecotone.

Chapter 15

River-to-Watershed Subsidies in an Old-Growth Conifer Forest

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Ecologists have often assumed that material exchange between rivers and terrestrial watersheds is highly asymmetric, with watersheds typically feeding their rivers. There are three reasons to expect this asymmetry. First, watershed land area is considerably greater than that inundated by streams and rivers. Second, terrestrial plant biomass typically dwarfs that of aquatic primary producers. Third, gravity pulls material down slopes. Despite these factors, the amount of energy supplied to food webs by aquatic primary producers can be surprisingly large because of the high biomass-specific productivity and the excellent nutritional quality of common aquatic producers such as diatoms (Boyd 1973; Hanson et al. 1985; Fuller and Mackay 1981). It is therefore interesting to investigate, for various types of ecosystems, how much algae and other aquatic producers support secondary production in rivers, and whether export of river production has any measurable effect on watershed consumers and ecosystem processes.

Ecologists working in desert streams first pointed out that higher trophic levels in rivers could depend primarily on algal rather than terrestrial plant production (Minshall 1978) and that exports from desert rivers could also fuel watershed consumers (Jackson and Fisher 1986). In Sycamore Creek in the Sonoran Desert of Arizona, Jackson and Fisher

(1986) estimated that 97% of the aquatic insect emergence (22.4 grams carbon m^{-2} yr^{-1}) was exported to the watershed, where it fed consumers including ants, birds, and bats. In a prairie stream with higher adjacent terrestrial plant biomass, Gray (1989a, 1996b) documented consumption of aquatic insects by a variety of birds and mammals. Mayer and Likens (1987) studied a heavily shaded New Hampshire stream, Bear Brook. The beech and maple trees surrounding the brook have soft leaves and produce relatively edible litter. Mayer and Likens found that algae, while less than 1% of the standing stock of organic manner in the stream, made up more than 50% of the ingested material in the guts of a common caddisfly species, *Neophylax aniqua*. From published assimilation data, they estimated that at least 75% of this caddisfly's growth was fueled by algae rather than by the more refractory terrestrial detritus. Their results suggested that even in streams that are darkly shaded by deciduous trees with relatively high-quality litter, common aquatic insects may be largely built of algal carbon. More recently, a survey of stable carbon isotope data from studies of seventy temperate rivers suggested that in drainages of greater than 5–10 km^2, algae contributed significantly to the carbon of all lotic consumers except for shredders (Finlay 2001). Members of one guild, scrapers (which includes caddisflies), retained their algal signal even upstream in smaller, darker headwater streams (Finlay 2001).

Do emerging aquatic insects transport significant amounts of algal carbon into terrestrial food webs? Clearly, the degree to which aquatic consumers are fueled by algal versus terrestrial plant production, as well as the predominant direction of trophic exchange between rivers and watersheds, varies among species and sites. We have very little quantitative information as yet about these exchanges (but see Nakano and Murakami 2001). The increasing availability to ecologists of stable isotope and other tracer analyses will greatly facilitate the study of resource fluxes among habitats, once local sources of variation in tracer signatures are sufficiently understood (Finlay et al. 1999, 2002; Cabana and Rasmussen 1996; Ben-David, Hanley, and Schell 1998).

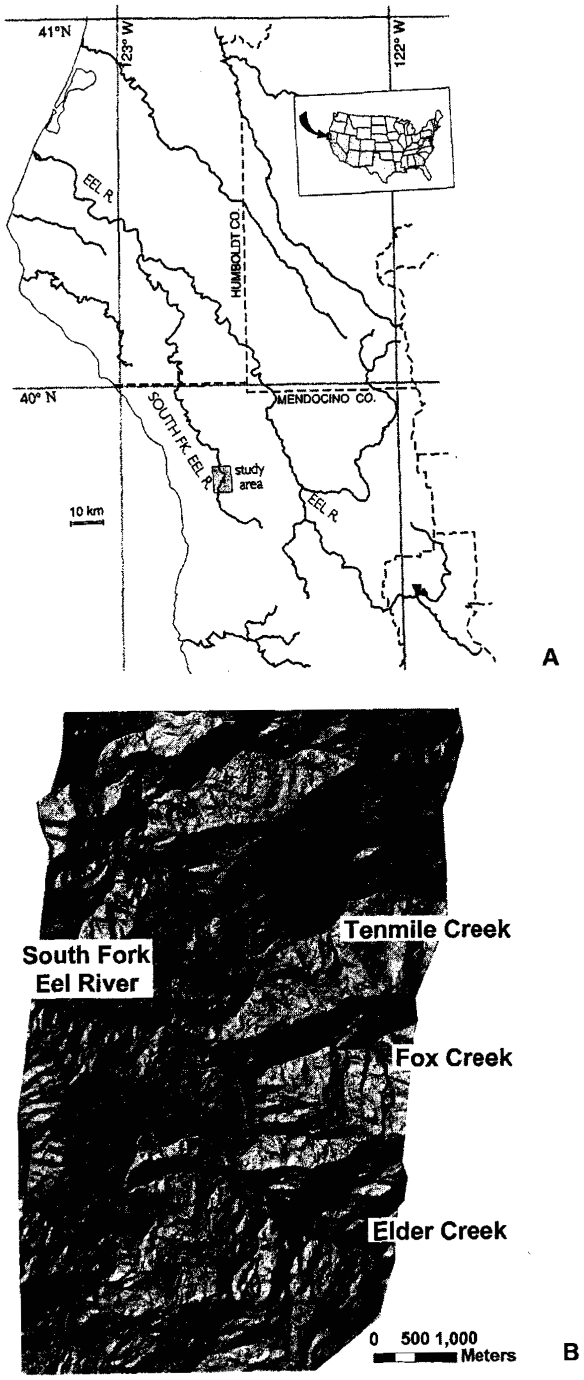
We have begun to study the river-to-forest exchange at the South Fork Eel River of northern California. The watershed supports a mixed old-growth conifer and deciduous forest with some chaparral along ridgetops. This vegetation is not particularly edible (Harris 1984). During the biologically active low-flow summer season, sunny reaches of the South Fork Eel support rapid algal growth, including that of nutritious epilithic algae on rocks and epiphytic algae coating seasonally lush blooms of the filamentous green macroalga *Cladophora glomerata* (Power 1990a, 1990b). Algal standing crops vary dramatically from year to year, depending on whether bed-scouring winter floods have occurred (Power 1992a, 1995; Wootton et al. 1996; and see discussion below). Because insect production and emergence rates are strongly influenced by algae, we wanted to examine whether year-to-year variations in algae and insect emergence affected watershed consumers. This question can be expanded into five, following Polis, Anderson, and Holt (1997):

1. What are the patterns of spatial and temporal variation in aquatic insect emergence?
2. Do watershed consumers track this variation? If not, what constrains them?
3. Does this subsidy influence consumer performance (feeding rates, somatic growth, reproduction, survival, recruitment)?
4. Do subsidies to particular consumers alter their effects on watershed communities or ecosystem properties?
5. How do subsidies and their effects change across landscape gradients or thresholds?

Here, we discuss the application of these questions to the South Fork Eel. First, we describe sources of spatial and temporal variation in insect emergence from the river and its lateral penetration into the watershed. Then we present preliminary observations on how different consumers, which forage over a range of spatial scales, respond to this resource subsidy. Finally, we discuss hypotheses, as yet largely untested in our system, about how subsidies to these consumers might indirectly affect watershed food webs, and about how such effects and interactions may vary across the landscape.

THE STUDY SITE

Our primary study site encompasses about 10 km of the South Fork Eel River and its tributaries (fig. 15.1) within or adjacent to the 3,200 ha Angelo Coast Range Reserve of the University of California Natural Reserve System in Mendocino County, California (39°44′N, 123°39′W). Though timber extraction and cattle grazing are ongoing in the South Fork drainage basin upstream from our site, the reserve and several entire tributary watersheds have been protected from logging since its purchase by Heath and Marjorie Angelo in the 1930s. Where it enters the reserve, the South Fork Eel drains a watershed of 130 km^2. The river flows north, parallel to the Pacific coast, for another 160 km before reaching the sea just south of Arcata, California. Tectonic uplift at the mouth of the river (5 mm per year) is more rapid than



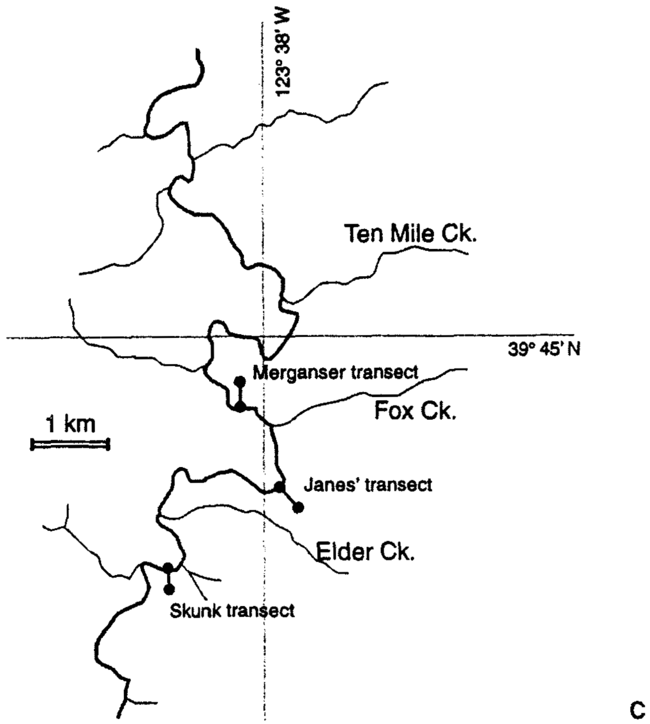


Figure 15.1 (A) Location map of the Angelo Coast Range Reserve study site. (B) Digital elevation data from airborne laser altimetry, showing the topography of the South Fork Eel watershed. (C) Locations of sampling transects and experimental studies.

uplift at our study site (1 mm per year). As a consequence, episodic waves of incision have propagated upstream over several thousand years, causing the river to cut deeply into its bedrock channel. The South Fork Eel is therefore canyon-bound, and is flanked by a series of terraces (abandoned river floodplains) of different ages (Seidl and Dietrich 1992), visible as white areas along the mainstem and tributary channels in figure 15.1B. The river is gravel-bedded, with areas of coarse boulders and intermittently protruding bedrock. The mean gradient of the South Fork Eel is 0.005, with discharge ranging from about 0.5 $m^3\ s^{-1}$ during summer base flow to up to 56 $m^3\ s^{-1}$ during recorded flood peaks (Power 1990b; USGS monitoring data, 1960–1970). Winter floods scour an active channel much wider than the wetted channel during the biologically active summer season. Therefore, despite the incision of the river and the steep surrounding terrain, most reaches of the mainstem receive direct sunlight for 6 to 8 hours a day

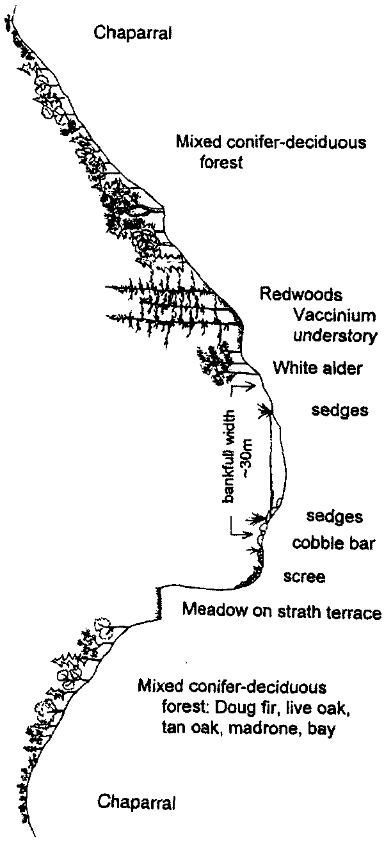


Figure 15.2 Vegetational zonation and characterization of canopy profile from the South Fork Eel River to the ridge.

during the spring and summer season through September. Several small tributaries draining into the South Fork Eel are steeper (gradient 0.01), more extensively shaded by forest, and therefore lower in primary productivity and temperature. One tributary, however, has a drainage area slightly larger than that of the South Fork Eel at the point of confluence. Ten Mile Creek, which flows through what are now open, cattle-grazed grasslands, has a higher primary productivity and temperature than the South Fork Eel (Finlay et al. 1999).

Vegetation is elevationally zoned across the valley from the river to the ridge (fig. 15.2). Algae and aquatic mosses grow in the wetted summer channel. Sedge tussocks (*Carex nudata*) and associated plants grow on rock bars that are dry during summer and inundated during winter (see Levine 2000 for description of this vegetation). Riparian trees line the channel, dominated by white alder (*Alnus rhombifolia*), along with Oregon ash (*Fraxinus latifolia*), big-leaf maple (*Acer macrophyllum*), and willow (*Salix* sp.). Farther upslope in moist swales, large Coast redwood (*Sequoia sempervirens*) and understories of California huckleberry (*Vaccinium ovatum*) occur. Drier, steeper, well-drained slopes support mixed conifer and deciduous forests, including large Douglas fir (*Pseudotsuga menziesii*), live oaks (*Quercus chrysolepis* and *Q. wislizenii*, canyon and interior live oak, are both common), and tanbark oak (*Lithocarpus densiflora*), with patchy local stands of madrone (*Arbutus menziesii*), bay (*Umbellularia californica*), and black oak (*Quercus kelloggii*). In understories of upland forests, poison oak (*Toxicodendron diversilobum*) is common. Meadows occur within the Angelo Reserve on higher river terraces. Chaparral grows along the ridgetops (generally only several hundred meters from the channel margins), dominated by manzanita (*Arctostaphylos* spp.), ceanothus (*Ceanothus* spp.), and chamise (*Adenostoma fasciculatum*). Canopy height is taxon-, slope-, and soil-dependent and so is irregular, with numerous gaps, but exceeds 50 m in redwood stands near the channel and decreases upslope in drier oak stands or chaparral to only a few meters near the ridge (fig. 15.2).

VARIATION IN SUBSIDIES

Emerging aquatic insects vary in their availability to consumers over space and time. Factors driving this variation act on both the rate of emergence of insects from the river and the lateral penetration of these insects into the watershed.

Variation in Emergence

Rates of emergence of insects are higher from channels with higher algal primary productivity. Channel productivity varies among tributaries and longitudinally with insolation, sediment texture, and nutrient availability, which in turn are determined by geology, climate, and land use in the watershed. A smaller-scale, but particularly intense, source of spatial variation in our system is the distribution of floating mats of algae (primarily *Cladophora glomerata*, with associated epiphytes). Floating algal mats accumulate in slack-water areas or lodge on emergent rocks in riffles (fig. 15.3). The rate of insect emergence is 3 to 6 times greater from floating mats

Figure 15.3 Floating algal mats are hotspots of insect emergence in the South Fork Eel River.

than from submerged algae and many times greater than from bare gravel substrates (Power 1990b).

Floating mats could increase insect emergence for at least four reasons. First, they are convenient oviposition sites that minimize the exposure of female insects to aquatic predators. Second, they are rich feeding arenas, with copious growths of epiphytic diatoms and organic seston filtered from the river. Third, the mats trap sun-warmed water and, on a daily basis, become up to 8°C warmer than the surrounding water column (M. E. Power, unpublished data). For larvae of insect taxa that can tolerate the diel fluctuations of temperature and oxygen in these habitats, floating mats are food-rich incubators that accelerate their growth and development.

A fourth reason that floating mats may increase insect emergence is that they serve as partial refuges from aquatic predators. Larger fish in our system rarely forage from algal mats at the water surface (Power 1990b). Therefore, floating algal mats not only increase the secondary production of certain aquatic insects, but also route more of this production away from aquatic consumers, into the watershed.

Variation in insect emergence caused by the presence or absence of floating algal mats, the smallest spatial scale we are currently studying, is driven by the longest temporal scale of variation that we investigate: year-to-year variation in algal accrual that occurs because of hydrologically mediated trophic interactions. When northern California experiences its "normal" Mediterranean climate regime, scouring winter floods eliminate most algal and benthic biomass from the riverbed. During the following spring (April–June), the river subsides, clears, and warms. During this window of time, before animals become dense, the river food web can be thought of as having only one functional trophic level (sensu Fretwell 1977). By late spring or early summer, *Cladophora* blooms. As the summer drought progresses, consumer density increases as fish and invertebrates recruit, grow, and concentrate in the seasonally contracting river habitat. During this period, interactions mediated through three or four trophic levels influence the persistence of the algal standing crops that develop in the spring.

Food chains are shorter in northern California rivers when channels do not experience flood scour, following drought years or in artificially regulated channels (Power 1992a). Under prolonged stable flow conditions, benthic insect assemblages become dominated by slow-growing, heavily armored or sessile grazers: late successional taxa that, while slow to recover from physical scour disturbance, are relatively invulnerable to fish and other predators once they do. When they dominate the food web, food chains with only two functional trophic levels develop, and algae are suppressed (Power 1992a, 1995; Power et al. 1996; Wootton et al. 1996).

Year-to-year variation in nutrient flushing into the channel with variable rainfall could also contribute to annual variation in algal blooms, as it does in desert streams (Grimm et al. 1981; Grimm 1987). Experiments, however, suggest that top-down control by herbivores plays a dominant role in driving annual variation in Eel River algae. For example, removing a caddisfly, *Dicosmoecus gilvipes*, from experimental enclosures during drought years released algal standing crops that had been previously suppressed by this important predator-resistant but flood-vulnerable grazer (Wootton et al. 1996).

In addition to variation in insect emergence between high-algae years and low-algae years, we have observed strong within-year seasonal variation. Peak insect emergences follow algal mat formation in July, and emergences decline after algae senesce and disappear in August (Power 1990b). In addition, striking diel and day-to-day variation occurs because of the pulsed, often synchronized emergence patterns of common mayfly, caddisfly, stonefly, aquatic lepidopteran, and megalopteran taxa in our systems. Various degrees of synchrony have been documented for aquatic insect emergences in other fresh waters (Butler 1984; Sweeney 1984; Flecker et al. 1988). The post-emergence activity of aquatic insects may vary as well; for example, with temperature (Waringer 1991; Ward et al. 1996). Such variation would affect the lateral spread of these insects into the watershed and their availability to consumers.

Lateral Penetration into the Watershed

Quantifying the flux of emerging insects from rivers into watersheds is a daunting task, not only because of the considerable spatial and temporal variation in the subsidy source (emergence), but also because of the varied three-dimensional movements of insects after emergence. Jackson and Resh (1989) found that taxa caught in their canopy-level sticky traps dispersed a greater distance laterally into the forest than those trapped at stream height. The aggregation and dispersal of aquatic insects above forest canopies is largely unstudied, but in open settings over large African rivers, ground-based radar regularly detected discrete clouds of insects at heights of 30–130 m, which drifted over the shores in response to wind variations (Reynolds and Riley 1979). We have not yet appraised vertical variation in insect fluxes in our watershed, although we hope to initiate canopy-level sampling programs in the near future. The patterns reported here derive only from sampling using pitfall traps at ground level, sticky traps positioned 1.5 m above the ground, and light traps hung about 2 m above the ground. We used these sampling techniques on river-to-ridge transects, which extended 150–250 m upslope (perpendicular from the river) along the mainstem of the South Fork Eel and 10 m away from two less productive tributaries: Elder Creek and Fox Creek (see fig. 15.1C).

The pitfall and sticky trap data show a strong concentration of both aquatic and terrestrial arthropods near the river. Insect fluxes declined exponentially (both in numbers and in biomass) away from the river, with reductions of 50% within 10 m of the river's edge (fig. 15.4). Comparisons of the South Fork Eel with its darker tributaries showed, unsurprisingly, that lateral fluxes of insects at comparable distances from the water margin declined with decreasing watershed productivity. The results of light trapping (fig. 15.5) were similar in midsummer, when massive emergences of caddisflies resulted in peak biomass near the river. During other seasons, however, light trapping revealed a different pattern, in which sampled insect biomass, dominated by noctuid moths, peaked in the forest up to 150 meters away from the river.

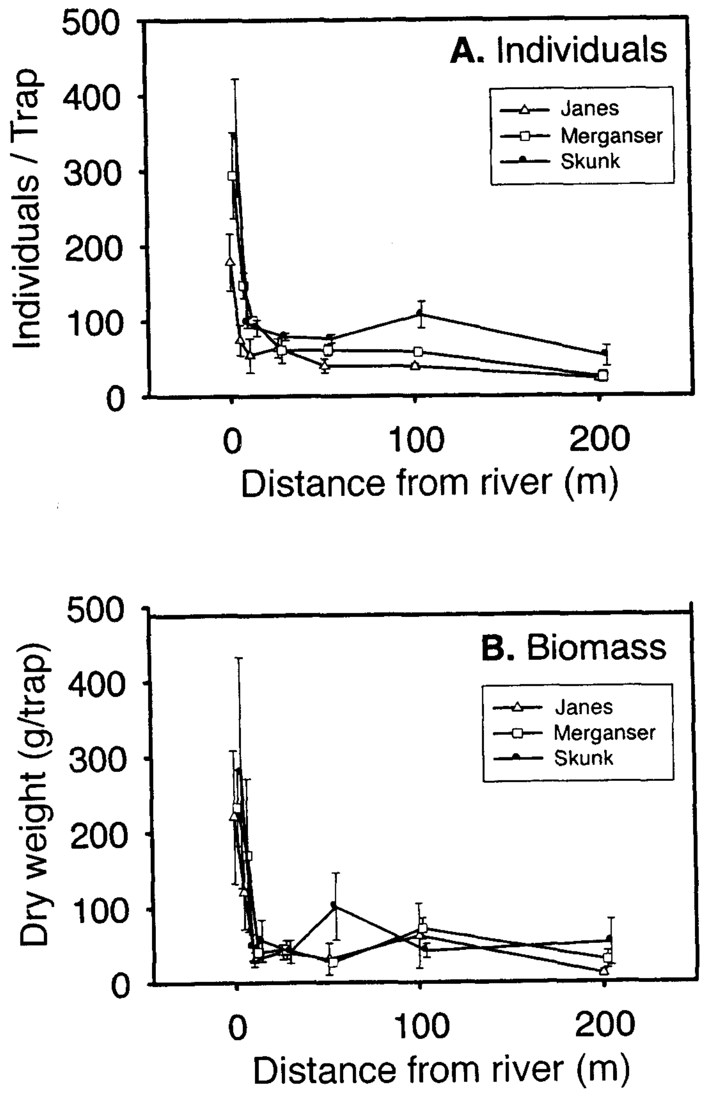


Figure 15.4 Numbers and biomass of invertebrates collected on sticky traps along transects perpendicular to the South Fork Eel River at three sites (averages of three replicate transects spaced 10 m apart per site) distributed over a ca. 5 km reach. Traps were 605 cm^2 acetate sheets, covered in Tanglefoot, rolled into a cylinder, and suspended from iron ("rebar") rods 1.5 m above the ground on 2–7 July 1998, a period of peak emergence. Biomass (dry weight) was estimated from length-weight regression (Rogers et al. 1976).

Figure 15.5 Light trap transect, showing river and riparian habitat along the South Fork Eel River.

RESPONSES OF WATERSHED CONSUMERS TO AQUATIC INSECT SUBSIDIES

The trophic and non-trophic requirements of consumer species determine how they are distributed over landscapes. Their local distributions and abundances, in turn, determine how closely consumers can track aquatic insect subsidies and what effects their subsidized populations may have on ecosystems. We will illustrate these classic ecological arguments with observations of consumers that forage over a range of spatial scales in the South Fork Eel watershed. These consumers include nearly stationary filmy dome spiders (*Neriene* sp., Linyphiidae), web-spinning, but potentially mobile, long-jawed spiders (*Tetragnatha versicolor,* Tetragnathidae), cursorial wolf spiders (Lycosidae), lizards (*Sceloporus* spp.) that defend territories along river rock bars and in upland meadows, and bats that forage by night over the river corridor and commute to roosts several kilometers away.

Filmy Dome Spiders

The least mobile consumers that we study are filmy dome spiders (*Neriene* sp.). Spider eggs overwinter in the forest floor litter. They hatch in the spring, and by late spring, the young spiders have spun distinctive webs with concave-down domes 30–60 cm above the ground in twiggy vegetation. As the spiders grow and mature, their webs become larger and denser. They shift their webs upward to positions 1–5 meters above the forest floor, still favoring sites where stiff, dense structure, such as the leafless, twiggy understory of oaks and tan oaks, is available for web support. Reproduction occurs in midsummer (July), with males moving into the webs of females. Aside from these local movements, filmy dome spiders appear to be relatively site-faithful. As their webs increase in size, they may become too massively invested in silk for the spiders to ingest and reposition them economically (M. S. Parker, personal observation).

The requirement for stiff web support may prevent the spiders from tracking river-to-ridge gradients in insect flux. Densities of filmy dome spiders censused from June through September in 1998 showed little change from the river to the ridge, 250 m away from the channel (fig. 15.6). Because of their low mobility and their failure to track river-subsidized insect fluxes spatially, individual performances of filmy dome spiders can serve as useful indicators of the importance of prey flux from rivers to the watershed. Michael Parker's observations during a year (1994) of high filmy dome spider abundance indicated that near the end of their growing season in September, spiders near the river had smaller webs, grew to larger sizes, and had longer times to starvation in laboratory tests than spiders of the same age 100–200 meters away from the river. Preliminary stable carbon isotope analysis suggests that filmy dome spiders may derive significant amounts of their carbon from algal-based river production, even when they are located several hundred meters from the river (J. C. Finlay, unpublished data).

Tetragnathid Spiders

Tetragnathid spiders (*Tetragnatha versicolor*), subjects of the dissertation research of Adrianna Smyth, are the second least mobile of the watershed consumers considered here. They spin orb webs, which they can ingest and relocate on a daily basis if foraging at a site proves unrewarding. Tetragnathids are extremely vulnerable to desiccation, and this limits their distributions worldwide to the margins of lakes and rivers. Along the South Fork Eel and its tributaries, tetragnathids are found only within about a meter of the water's edge during the summer drought. They commonly spin webs in riverside sedges (*Carex nudata*). Tetragnathid densities in the sedges that border much of the mainstem are much higher than are densities along a less productive, half-shaded tributary, Elder Creek (A. Smyth, unpublished data). Along the South Fork Eel and Elder Creek,

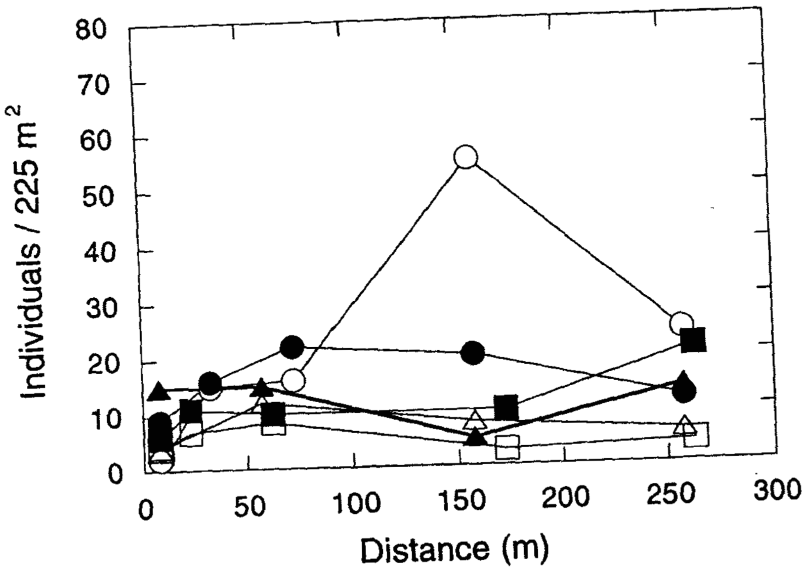


Figure 15.6 Abundances of filmy dome spiders in webs along six river-to-ridge transects at three sites along the South Fork Eel River, 26 June–8 July 1998. (From S. Khandwala, J. C. Finlay, and M. E. Power, unpublished data.)

Smyth experimentally introduced extra structure for web sites and supplemented food by importing floating algal mats. Her experiments have shown that in the mainstem of the South Fork Eel, tetragnathid densities increase only in response to the addition of structure, while in the less productive tributary, tetragnathid densities increase if food, structure, or both are supplemented. Corresponding to the difference in food limitation between the river and tributary spiders, she found a difference in their foraging patterns: tetragnathids along the mainstem foraged only by night, while those along the less productive tributary foraged 24 hours per day (A. Smyth, unpublished data). While release from food limitation is sufficient to explain the curtailed foraging by tetragnathids along the mainstem, the spiders there may also be more constrained by physical factors, such as dryness, heat, or wind, during the day (A. Smyth, personal observation). Whatever the cause of the shorter foraging period of mainstem tetragnathids, the difference has led Smyth to the counterintuitive prediction that in less productive, darker tributaries, these spiders may transfer more aquatic insect production to terrestrial predators than they do along sunny mainstem channels, where they are denser and probably more productive. Smyth's recent discovery of two dipteran egg parasitoids on tetragnathid egg masses along the sunny mainstem may change this interpretation, however.

Lycosid Spiders

Cursorial wolf spiders (Lycosidae) do not spin webs, but stalk prey along the ground. Lycosids occurred in our watershed from the river margin up to the ridgetops, but were most abundant near the river (fig. 15.7A). In addition, lycosid densities were highest along the most productive mainstem habitat, intermediate along half-shaded Elder Creek, and lowest along a heavily shaded, less productive tributary, Fox Creek (K. Marsee, unpublished data; (fig. 15.7B). In addition to tracking differences in aquatic productivity among river channels, lycosids responded rapidly to algal mat manipulations that altered insect emergence over smaller scales. Where floating algal mats were naturally present, or where they were experimentally imported, insect emergence was higher. Within 24 hours, lycosids became more abundant along river shorelines adjacent to areas where mats had been imported or were naturally present than along shorelines where mats had been removed or were naturally absent (Parker and Power 1993). A positive correlation between lycosid spider densities and algal mat abundance was observed in five different river systems in northern California (Parker and Power 1993).

Lizards: *Sceloporus occidentalis* and *S. graciosus*

Sceloporus lizards in our watershed occur in upland meadow habitats and along river margins. Although these lizards have previously been studied only in upland habitats, John Sabo has found that during spring and summer in the South Fork Eel watershed, their densities are 7 times greater along river rock bars than in those habitats. In addition to the higher availability of insect prey in the river corridor, lizards find cover and favorable thermal environments in rock bar habitats. Sabo evaluated the importance of food subsidy relative to these other factors by experimentally reducing aquatic insect flux without influencing cover or thermal regimes. He constructed 2 m high fences of plastic and bird netting that enclosed about 90 m^2 of river margin rock bar habitat. Experimental treatments had a wall bordering the river (a "subsidy shield"). These enclosures reduced fluxes of aquatic insects by about 55% (numbers) and 70% (biomass) and those of terrestrial insects by a smaller amount (20% numbers and

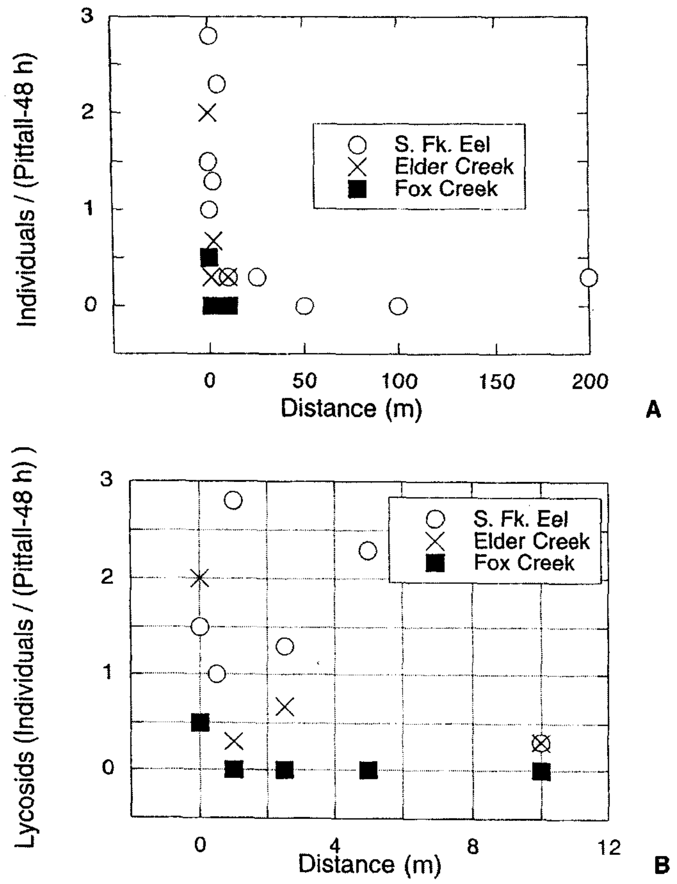


Figure 15.7 (A) Abundances of lycosid wolf spiders in pitfall traps (9.4 cm diameter), set for 24 h at various distances from the sunny, productive mainstem South Fork Eel (circles), a half-shaded tributary, Elder Creek (Xs), and a dark, unproductive tributary, Fox Creek (squares). (From K. Marsee, unpublished data.) (B) Same data truncated at 10 m from the river to show more clearly the abundances of riparian zone wolf spiders in channels of different productivities.

biomass). Control treatments were open to the river. In an experiment designed to examine the effects of subsidy reduction on lizard performance, the growth of lizards in enclosures with subsidy shields was reduced relative to the growth of lizards in control enclosures and free-ranging lizards (Sabo and Power 2002a). In a second experiment examining numerical responses by lizards to subsidies, the fences had open walls facing landward. More lizards emigrated from shielded areas than from unshielded controls (Sabo and Power 2002b).

Bats: Vespertilionidae and Molossidae

Bats are the most mobile of the small insectivores in our watersheds. Abundant species (*Myotis yumanensis, M. californicus, M. lucifugus, Eptesicus fuscus, Lasionycteris noctivagans, Tadarida brasiliensis*) forage commonly or primarily over still or slowly moving water and adjacent riparian vegetation. Most are aerial hunters, but some take insects from the surface of the water or glean them from vegetation.

William Rainey and Elizabeth Pierson have assessed bat foraging activity near ground level at our study site and along other California rivers. Their data, from multiple bat ultrasound detectors, are consistent with results elsewhere in demonstrating intensive foraging directly over the river channel by bats flying up to at least 20 m in height, but relatively little bat activity beneath or in the forest canopy up to similar heights (Thomas 1988; fig. 15.8). The data in figure 15.8 underestimate the steepness of the river-to-ridge gradient in bat foraging activity because this analysis is based on the number of 15-second intervals during which at least one bat was detected acoustically. In the forest, one bat is typically present in an acoustic sample, but we commonly observe groups of bats foraging simultaneously over the South Fork Eel. The steep decline in acoustic foraging activity away from the river indicates that bats, like lizards and lycosids, are tracking the exponential gradient in insect flux as measured by our sticky trap samples, and not the moths with the off-river density peak detected by

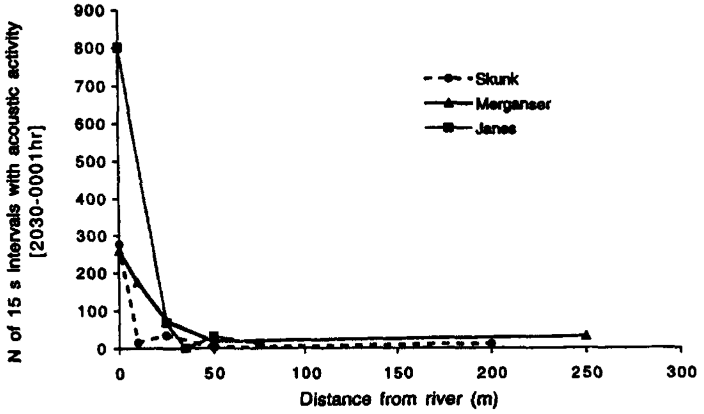


Figure 15.8 Distribution of bat foraging activity from the river to the ridge along three transects (see fig. 15.1C), as indexed by the number of 15-second intervals with at least one bat foraging call recorded by ultrasonic detectors.

our light trap samples (see fig. 15.4). Like our current insect trapping, however, ground-based bat detection does not permit the study of foraging above the canopy (Kalcounis et al. 1996).

CONSTRAINTS ON SUBSIDY TRACKING BY CONSUMERS AND THEIR ECOSYSTEM-LEVEL EFFECTS

Both trophic and non-trophic factors constrain the distributions and abundances of various consumers, determining both how closely they can track resource subsidies and the effects of their subsidized populations on local resources. We do not yet know enough to interpret the ecosystem-level effects of subsidies, but will offer some speculations based on our natural history observations to date.

The consequences of trophic subsidies to consumers in the receiving ecosystems depend on (1) the importance of the subsidy to the consumer, (2) the importance of the consumer in its ecosystem, and (3) the consumer's trophic position (i.e., where the subsidy enters the food web [Polis et al. 1998]). If consumers show strong numerical responses to a resource subsidy, closely tracking fluxes over space and time, we would suspect that the subsidy is important to them. If the resource subsidy determines environmental quality for a consumer species, close (nearly perfect) spatial tracking of the resource flux should result in an ideal free distribution of the consumer population (Fretwell and Lucas 1970), in which individuals in densely populated, heavily subsidized areas have the same fitness as individuals in sparsely populated, poorly subsidized areas.

It is when consumers are prevented from spatially tracking a subsidy that we have the opportunity to evaluate the effect of the subsidy on their individual fitnesses, which should ultimately affect their population dynamics. This is best illustrated in our system by filmy dome spiders, which appeared to be severely constrained by the requirement for stiff, dense structure to support their elaborate webs. These spiders had relatively flat river-to-ridge distributions, which did not match the exponentially declining flux of river-subsidized insects along this gradient. During 1995, a year of high population density for filmy dome spiders, their per capita growth and metabolic reserves decreased markedly with their distance from the river, while their foraging effort, as reflected by web diameter, increased (M. S. Parker, unpublished data). These trends were still evident, but weaker, in 1998, when spider densities declined sharply through the summer (S. Khandwala et al., unpublished data). Predation pressure on the spiders may have been more intense during 1998, as we measured 40–80% declines over the summer in their censused densities, and we observed many webs without spiders that were nearly intact except for small (<2 cm long) tears. This type of damage could be done by wasps, which prey on similar spiders in other ecosystems (G. A. Polis and D. H. Wise, personal communication).

The year-to-year variation in spider densities and disappearance rates may suggest two alternative fates of the river insect subsidy to spider populations. During years of weaker predation, the subsidy may enter the watershed food web as detritus when the spiders die (during September and October) and their bodies and web contents are delivered to the forest litter. In years of higher predation, the subsidy may move up one or several trophic levels through predators (wasps, birds, other spiders) in the terrestrial food web. Because of their small per capita foraging rate and body size, both nutrient and food web transfers mediated through filmy dome spiders are probably not energetically important at the ecosystem level, except in years of extremely high spider abundance.

Tetragnathid spiders are restricted to water margins by their need for moisture. It therefore does not make sense to evaluate their river-to-ridge distributions in light of insect fluxes. Higher densities of tetragnathids along productive than unproductive channel margins (e.g., the South Fork Eel vs. Elder Creek) could reflect numerical resource subsidy tracking by these spiders over the spatial scales of hundreds to thousands of meters separating watersheds. We do not know enough about the mobility of this species over its annual lifetime to ascertain the degree to which individual movements versus demographic differences in population production among watersheds account for this pattern of tetragnathid density at the South Fork Eel. The demographic explanation seems more likely in light of the fact that egg masses are laid locally on sedges (A. Smyth and C. Anderson, personal observations). Spiders along dark tributaries may be both more food-limited and more subject to predation, because food limitation requires them to extend their foraging activity into dangerous daytime hours, when they are vulnerable to diurnal predators such as birds, wasps, and lizards. If Smyth's predictions are correct, the fate of ecosystem subsidies to tetragnathids should differ among streams of different productivity. More of their production should be transferred upward in terrestrial food webs along unproductive streams, while along more productive streams, more should be recycled directly back into the channel when winter floods inundate the spiders' bankside habitats.

Wolf spiders (lycosids) are cursorial hunters that do not use webs. They can be found along the entire river-to-ridge elevational gradient, so their moisture requirements do not appear to be limiting to their spatial distributions, although there may be differences among the species in our system in this regard. Lycosid densities closely correspond to the river-to-ridge exponential gradient in aquatic insect flux, although experimental work is required to establish whether this relationship is causal. Like tetragnathids, lycosids are more abundant along productive than unproductive streams, a pattern that could reflect either prey tracking or a response to some physical condition (wind, temperature, humidity) that also varies among watersheds. Lycosids numerically track aquatic insect fluxes over scales of meters to tens of meters along river channels, as demonstrated by their behavioral recruitment to emergence hotspots associated with floating algal mats (Parker and Power 1993). While we have much to learn about the factors limiting lycosids in the South Fork Eel watershed, their body size, tendency toward nocturnal activity, and life history characteristics suggest that they may be subject to heavy predation, as they are in other systems (Hering and Plachter 1997). Sabo and Smyth have hypothesized that the primarily nocturnal activity patterns of lycosids along the South Fork Eel may be a response to diurnal lizard predation. This hypothesis is supported by the greater diurnal abundances of lycosids observed along a small, but productive, tributary in the system where lizards are absent (J. C. Finlay and J. L. Sabo, personal observations). At present, our best guess for the fate of river subsidies routed through lycosids would be their transfer to higher trophic levels, such as lizards, birds, scorpions, carabid beetles, or other spiders, which abound in riparian corridors.

The sevenfold increase in the densities of western fence and sagebrush lizards, *Sceloporus occidentalis* and *S. graciosus*, from upland meadows to river margins can be attributed, at least in part, to tracking of river-subsidized insect production. Sabo's large-scale subsidy manipulations have shown that river insect subsidies enhance somatic growth and reduce emigration of lizards. In food webs, lizards are positioned at higher trophic levels than spiders (e.g., Spiller and Schoener 1988). Over small (behavioral) time scales, river subsidies lessen the effects of lizard predation on terrestrial arthropods (Sabo and Power 2002a). Over longer (population dynamic) time scales, however, numerical responses of lizards to river insect subsidies suggest the opposite effect (Sabo and Power 2002b), as has been found for aquatic subsidies to predators in other systems (Polis and Hurd 1995; J. Henschel, chap. 13 in this volume).

Flying predators have greater mobility, and hence more subsidy tracking potential, than ground-based spiders and lizards. Aerial vertebrates (birds and bats), with their high per capita feeding rates, have especially high potentials for subsidy-mediated effects. Swallows and black phoebes (*Sayornis nigricans*) forage along the South Fork Eel and its large, productive tributary, Ten Mile Creek. We are just beginning to observe these birds (J. Gutierrez, unpublished data) and can only speculate about how subsidies may influence their populations and ecosystem roles.

Mobility, vigilance, and parental care may restrict the amount of trophic transfer of subsidies up food chains by birds, particularly by colonially roosting bank and cliff swallows (*Riparia riparia* and *Hirundo pyrrhonota*), although trophic transfer to parasites may be important (Loye 1985a, 1985b; Polis, Anderson, and Holt 1997). The effects of birds as subsidized predators should depend on their degree of feeding specialization with respect to diet and habitat; black phoebes are more generalized in this regard, and so have more potential to exert subsidized predator effects on upland insects. Here, we will focus on a third effect, nutrient translocation from rivers to watersheds, as it is instructive to compare the potential effects of birds and bats.

The spatial scale of nutrient translocation by swallows may be limited by nest site selection that ties them to the river channel. Swallows in our system and along many other rivers nest in holes in the river bank (bank swallows) or construct mud nests on vertical rock faces or their anthropogenic equivalent, bridges (cliff swallows). They consume river insect production, sometimes in substantial amounts where colonies are large, but nutrient translocation away from the river is modest, as excretion is concentrated primarily within the winter-active channel. Black phoebes in our watershed forage over both rivers and meadows, and they nest in upland structures as well as along stream banks and under bridges. Therefore, they have slightly more potential than swallows to translocate river nutrients to higher positions in watersheds. In our study area, their numbers, activities, and movement scales are modest, however, compared with those of river-foraging bats.

Constraints on the landscape positions of both their foraging and their roosting sites may cause bats to translocate nutrients from river production to points higher in landscapes that may not receive comparable point inputs of nutrients from other sources (Rainey et al. 1992; Pierson 1998). In western North America, foraging by many bat species is concentrated, at least during the summer and fall, over open, quietly flowing streams, rivers, and ponds (Brigham et al. 1992; Herd and Fenton 1983; Brigham 1990). Bats foraging over water may choose pools and other quiet reaches rather than headwaters in part because turbulent water interferes with ultrasonic prey detection (von Frenckell and Barclay 1987). Foraging in narrow, higher-gradient tributaries is also constrained by the effects of vegetative clutter on prey detection and flight path (Brigham et al. 1997; Mackey and Barclay 1989). Lower insect densities in these typically shaded streams also may influence foraging site selection. Common aerially hunting bats are opportunistic foragers, recruiting rapidly to artificial (e.g., light-attracted) and natural insect aggregations and responding to foraging calls of conspecifics and insect flight sounds (Vaughan 1980; Fenton and Morris 1976; O'Farrell and Miller 1972).

In contrast, bat day roosts (usually located by radiotelemetry) are often high in forested watersheds. During warmer months, common species usually roost in cavities or crevices on large-diameter, canopy-emergent trees; some of these species also roost in caves, mines, and fractured vertical rock (Brigham and Barclay 1996; Pierson 1998). As small, long-lived heterotherms, bats select roosts offering thermal inertia, flight access, and isolation from diurnal predators. Such sites are often nearer drainage divides than lowland rivers for several reasons. Massive rock outcrops are often made of more resistant material than surrounding rocks, and after millennia of erosion tend to become high points in landscapes. Over historic time, logging may also have a role in the current landscape separation of bat roosting and foraging sites. Residual large trees and open-structured old-growth stands in many western U.S. forests are often on steep slopes far away from rivers. Commuting costs apparently do not play a dominant role in roost site selection, as one-way distances from day roosts to regularly occupied nocturnal foraging sites near and over water are usually several kilometers for 5–15 g bats (Pierson 1998).

Bats capture and ingest a significant fraction of their body weight in insects each night (estimated at 0.5–1 times body weight for the common aquatic forager *Myotis lucifugus* [Barclay et al. 1991]). Less nutritious parts of prey, such as wings of larger prey (e.g., megalopterans), may be culled and discarded in flight or at temporary feeding roosts, but typical soft-bodied aquatic insects are ingested whole. Gut passage times are rapid, so that foragers are redepositing comminuted prey and urine while they are foraging over the water. Ingestion usually exceeds excretion, however, and satiated bats of several species move to aggregated or solitary feeding roosts relatively near the river for intervals during the night. These night roosts may be tree exteriors and cavities or artificial structures with high thermal mass, such as concrete bridges. Both numbers of animals and individual fidelity over years at such sites can be high (Pierson et al. 1996). Annual guano deposition at such locations can range from grams to multiple kilograms dry weight. The temporal and spatial scale of river-to-watershed export of nutrients from bat night roosts depends on their location, which can be over the active channel (no export), in trees on rarely flooded terraces, or tens of meters above the flood zone. Day roosts are more consistent sites of nutrient export, as similar guano deposits accumulate at these sites, typically several kilometers from the river foraging site. The colony size and the persistence and character of the roost feature determine whether a day roost becomes a temporary or persistent hotspot of river-derived nutrients, which might locally affect upland decomposers, producers, or consumers.

We are planning to investigate the influence of translocations by bats of river subsidies at two different scales. Bat guano in tree hollows is consumed by some invertebrate detritivores, and culled insect parts are taken by ants and rodents. Guano in these settings is also frequently searched by vertebrate insectivores, and when exposed to rain or fog, it disappears rapidly. Nutrient translocation through detrital food webs to primary producers or decomposers has unknown but possibly interesting effects in N-limited old-growth conifer forests. Where bats roost in large numbers, input of river-derived nutrients to terrestrial landscapes has potential ecological significance. Several thousand Mexican free-tailed bats (*Tadarida brasiliensis*) roost on a cliff face at Rhyolite Dome, at Sutter Buttes, California. Their guano has elevated ^{15}N, consistent with their foraging over and around the agrochemically polluted Sacramento River, about 10 km away. Turkey mullein plants (*Eremocarpus setigerus*) growing downslope near the colony are ^{15}N enriched relative to conspecifics or other plant taxa growing lateral to or at a greater distance from the colony, offering the opportunity to trace river-derived nitrogen in an oak grassland food web in the upper watershed.

Nutrient translocation is a more likely consequence of river subsidies to bats than transfer up food webs to higher trophic levels. Data on bats in the diets of forest predators are limited, but their long mass-specific life spans and low reproductive rates (many bats have maximum longevity of more than 20 years, and only one offspring per year) suggest that they have not been subject to heavy predation over evolutionary time (Austad and Fischer 1991; Gillette and Kimbrough 1970).

In addition to translocating nutrients, bats may act as subsidized predators because there is a seasonal mismatch between the annual bat activity cycle and the flood and drought-mediated aquatic productivity cycle. Bats accommodate to low insect availability in colder seasons by episodic torpor, hibernation, or migration. When they first return or emerge with depleted energy reserves in the spring (April–May), food availability is low and uncertain. In wet years, river discharge may still be high, resulting in much lower aquatic insect emergence than will occur later. Terrestrial habitats around the Eel, though cool at this time, are also damp and green and are producing more insects than they will during the summer drought. We expect that open, productive terrestrial areas (meadows, forest edges, revegetating burns and landslide scars) experience intensified foraging by bats whose annual energy budgets are largely based on river production. Seasonal patterns of bat foraging habitat selection matched seasonal shifts in insect production among aquatic and terrestrial habitats in central Sweden (de Jong and Ahlen 1991). These seasonal shifts in foraging sites could be considered "subsidies in time," as described for pulse-and-release desert ecosystems and others reviewed by Polis and colleagues (Polis et al. 1996).

CONCLUSION

Investigations of river-to-watershed subsidies such as ours and those reported by Willson (chap. 19 in this volume) and others (e.g., Ben-David, Hanley, and Schell 1998) are beginning to reveal that rivers strongly influence watershed ecosystems far upslope from regions traditionally classified as riparian zones. These findings imply that our management (or mismanagement) of rivers may affect terrestrial ecosystems more extensively than was previously thought.

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Chapter 16

Sources and Effects of Subsidies along the Stream-Estuary Continuum

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Much has been made recently of the potential importance of allochthonous materials (subsidies) to the organization of food webs (Polis et al. 1996; Polis, Anderson, and Holt 1997; Polis and Hurd 1996b). The realization that most ecological systems are open to some degree and that allochthonous materials cross the boundaries between systems is not new; these ideas were a major feature of the findings in the 1970s of the International Biological Programme, which provides much of the backdrop for our current thinking on subsidies. However, new research on subsidies is not simply a reinventing of the ecosystem approach. The focus of research has moved away from mainly descriptive statements about the magnitude of allochthonous inputs to address their effects on food web dynamics, especially indirect effects.

Polis, Anderson, and Holt (1997) suggest that subsidy dynamics have several key features:

- Subsidy-consumer interactions are characterized by donor-controlled dynamics, in which the consumer has no effect on the production or supply rate of the subsidy.
- The subsidy crosses a boundary between two biologically distinct habitats or compartments.
- The interactions among the species in the recipient compartment have different dynamic features than in similar compartments not