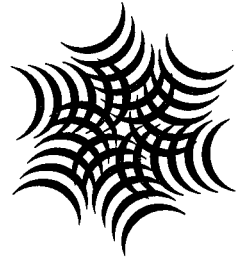


**Food Webs** at the Landscape Level



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## Food Web Subsidies at the Land-Water Ecotone

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Consideration of the connections between seemingly discrete systems has deep roots in ecology. In fact, recognition of the interrelatedness of systems is often perceived as one of the hallmarks of the "ecological" worldview (Oelschaeger 1991). Yet ecological studies traditionally emphasize the dynamics occurring within individual habitats or ecosystems. The linkages among habitats have drawn much less attention. Real-world ecological landscapes are heterogeneous mosaics of disparate habitats that are energetically and dynamically linked at multiple ecological scales (Turner 1989). Understanding these linkages requires a shift in focus from the internal dynamics of a predefined study system to the dynamics of a heterogeneous landscape consisting of interacting habitat elements. The chapters presented in part 2 take such an approach in their studies of food web dynamics across the land-water interface.

Research conducted at the land-water interface has traditionally focused on the unidirectional flow of energy, nutrients, and organisms from terrestrial habitats to adjacent aquatic habitats (Hasler 1975; McClelland and Valiela 1998; Smith 1998). The productivity of headwater streams, for example, can be dominated by terrestrial (allochthonous) organic matter and arthropod inputs (Wallace et al. 1997; Nakano et al. 1999), while higher-order river reaches can be jointly fueled by instream primary production, nutrients

and organic matter from upstream river reaches (Vannote et al. 1980), and land-derived materials from riparian zones and floodplains (Goulding 1980). Streams act as conduits of land-derived nutrients and organic matter, while lakes and estuaries typically serve as sinks for nutrients and contaminants within watersheds (Hasler 1975; McClelland and Valiela 1998). In fact, anthropogenic nutrient and contaminant inputs originating from the land have long been recognized as a primary source of eutrophication and contamination of inland waters (Hasler 1975; Vollenweider 1968).

In contrast to the well-known examples of trophic linkages from land to water, exchanges from water to land are poorly understood, and their consequences for the dynamics of populations and ecosystems are even less well known (but see Jansson 1988; Willson and Halupka 1995; Polis and Hurd 1996b; Polis, Anderson, and Holt 1997; Ben-David, Hanley, and Schell 1998). As the chapters in part 2 illustrate, our unidirectional view of land-water coupling must be revised in light of growing evidence that aquatic productivity can influence the dynamics of terrestrial ecosystems. Since terrestrial inputs also contribute to sustaining aquatic productivity (Peterson, Hobbie, and Corliss 1986), trophic connections across the land-water interface are most accurately represented as a cyclic process rather than a unidirectional flow. With this in mind, the chapters presented here address two main topics: first, the extent to which nutrients, materials, and organisms cross the land-water interface, particularly in the direction from water to land, and second, the consequences of these allochthonous resources for populations and food webs dynamics in the receiving system.

To what extent do allochthonous resources support river productivity, and does the export of this material back to terrestrial consumers affect terrestrial food webs? Power et al. (chap. 15) examine this question in the Eel River watershed by looking at broad-scale patterns in aquatic insect emergence and the consequences of this aquatic subsidy for a range of terrestrial consumers. Emergence is highly variable in space and time, but highest in the presence of floating algal mats. Once insects have emerged, their densities decline rapidly with distance away from the river. Terrestrial consumers (lycosid spiders, lizards, and bats) are more abundant along the stream margin, and their densities are correlated with densities of aquatic insects. Bats play a particularly important role in the transport of aquatic nutrients and materials back to terrestrial systems, providing a clear example of how rivers can influence watershed ecosystems far upslope from regions traditionally classified as riparian zones.

Henschel (chap. 13) also examines the magnitude and consequences of the transport of riverine aquatic insects to terrestrial consumers. He

combines observational studies and predator removal experiments to demonstrate that spider populations inhabiting riparian corridors are subsidized by emergent aquatic insects. This subsidy allows the spiders to depress populations of terrestrial herbivores. Such a reduction in terrestrial herbivore populations may translate to reduced levels of herbivory in the system, hence initiating a trophic cascade.

Polis and colleagues (chap. 14) review the energetic and dynamic importance of marine inputs to coastal ecosystems. Marine subsidies are delivered to coastal systems in many forms, including algal wrack, carrion, seabird- and marine mammal-derived detritus, and windblown materials. Wrack and carrion, and the invertebrate communities associated with them, benefit a broad range of terrestrial consumers, such as coyotes, lizards, and rodents. Meanwhile, seabirds supply guano and foraging scraps to the system, which augment plant, arthropod, scavenger, and detritivore production. Resource-driven "bottom-up" effects support elevated populations of consumers at multiple trophic levels. These augmented consumers are more likely to exert top-down control of in situ prey.

Riley and colleagues (chap. 16) draw comparisons between land-water interactions in two very different systems: the Taieri River in New Zealand and the Ythan estuary in Scotland. In the Taieri River, nutrient loading has led to increased productivity, lengthened food chains, and dampened trophic cascades, while transporting surplus algal biomass downstream to subsidize food webs. Meanwhile, in the Ythan estuary, increases in organic material and nutrient loading have resulted in increased biomass of macroalgae and deposit feeders, although decades of increasing nutrient enrichment have had little effect on the overall dynamics of the system.

The movement of energy, nutrients, prey, and consumers across habitat boundaries can be energetically and dynamically important to the receiving ecosystem. The consequences of such movement can range from effects on population dynamics to influences on broader ecosystem processes. Another recurring theme in each of the chapters in part 2 is that allochthonous resource subsidies typically vary in space and time; in fact, the spatial and temporal details of a resource subsidy can dictate whether, and to what extent, that subsidy affects the dynamics of the receiving system. Allochthonous subsidies need not be energetically important in the long term to enhance and concentrate populations of consumers in the receiving system. Minor allochthonous subsidies delivered during critically low food periods can maintain consumer populations at much higher levels than in the absence of the subsidy. In turn, a subsidized consumer may be more likely to exert top-down control of in situ prey (see Henschel, chap. 13).

Where multiple trophic levels are subsidized (as in Power et al., chap. 15, and Polis et al., chap. 14), the dynamic consequences of these inputs become greatly confounded.

Identifying trophic connections across ecotones is particularly important in disturbed or fragmented landscapes, where human interruption of these connections can resonate well beyond the sphere of the perturbed system. The quantity and quality of aquatic and marine resources available at the land-water interface creates an enormous potential to concentrate terrestrial consumers, producing "hotspots"—or, in this case, "hotstrips"—of animal abundance, activity, and species richness along coasts, rivers, estuaries, and lakeshores. Destruction and alteration of these ecotones can interfere with the transport of marine and aquatic resources to terrestrial and coastal consumers, with unknown, but potentially dramatic, consequences for terrestrial communities.

However we decide to delineate the boundaries of our study systems, greater recognition of the trophic connections across them has clear and implicit implications for our understanding of human effects on both natural and managed ecosystems. For example, the movement of persistent contaminants such as methyl mercury, DDT, and PCBs is expected to shadow the movement of energy across such habitat boundaries (Crawford 2001). Another outcome of a better understanding of trophic subsidies across habitat boundaries may be that we are better able to predict interactions between exotic and native species. Exotic species that effectively outcompete and replace native species may achieve success because they possess a heightened ability to utilize allochthonous inputs, or perhaps other introduced species, as a resource (Savidge 1987). Finally, the goal of selecting and protecting natural areas is inherently a landscape-level endeavor. By broadening the arena of food web ecology to consider trophic interactions across ecotones and at the landscape level, our efforts will become increasingly relevant to conservation and resource management decisions.