

Chapter 26

At the Frontier of the Integration of Food Web Ecology and Landscape Ecology

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The dynamics of populations, communities, and ecosystems are strongly influenced by the flow of nutrients, food, and consumers across habitats. Trophic linkage across habitats is a common feature even when habitats differ moderately or greatly in structure and productivity. Because of asymmetries in transport processes (e.g., prevailing winds, ocean currents), the net flux of resources is typically in one direction. The mechanisms that transport resources across habitat boundaries and their penetration of the recipient habitat can vary. For example, leaves that fall into a headwater stream can affect the stream over its entire course (as acknowledged in the river continuum concept; Vannote et al. 1980). By contrast, forest-edge birds that forage in neighboring grasslands may move those resources only a few hundred meters into a forest. Because the permeability of habitats to different organisms can diverge significantly, the rate of movement of resources across boundaries will vary with those biotic and abiotic variables that influence permeability.

Resources can be moved by either physical or biotic vectors (see Polis et al. 1996 and references therein). Physical vectors include gravity, wind, and water; biotic vectors include mobile predators and prey. Wind-dispersed resources include nutrients and particulate material (either organic or inorganic—see Witman et al., chap. 22 in this volume). Water movement

can transport large amounts of nutrients across small or great distances (Witman et al., chap. 9, Winemiller and Jepsen, chap. 8, Riley et al., chap. 16, and Menge, chap. 5 in this volume). Deposition of atmospheric nutrients can play a major role in maintaining high levels of productivity in humid regions. Chadwick et al. (1999) argue that humid environments can reach a state of severe nutrient depletion due to weathering and leaching of minerals in soil. However, nutrients derived from the atmosphere can sustain high levels of productivity in downwind terrestrial ecosystems. For example, Hawaiian forests are able to maintain high levels of productivity because of the phosphorous they receive from Asian dust (Chadwick et al. 1999). Ocean water masses can differ greatly in the amounts of biomass and nutrients they transport. Transport occurs both vertically, via upwelling, downwelling, and detrital fallout to the benthos, and horizontally, via currents, tidal movement, and eddy diffusion. These transport mechanisms are important determinants of local marine productivity and food webs (Angel 1984; Barnes and Hughes 1988; Barry and Dayton 1991; Menge, chap. 5, and Witman, chap. 9 in this volume).

Large-scale migrations of birds, fish, and mammals can move nutrients and biomass across continents and oceans (McNaughton 1985; Willson and Halupka 1995; Jefferies 1988a; Willson et al., chap. 19, and Jefferies et al., chap. 18 in this volume). However, the effects of resource transport by mobile consumers can be significant even on relatively small scales (Kitchell et al. 1979). For example, Vanni and colleagues (1996; Vanni and Layne 1997; Vanni et al. 1997; Vanni and Headworth, chap. 4 in this volume) have demonstrated that gizzard shad maintain increased levels of nitrogen in the pelagic zone of lakes and reservoirs via excretion of nitrogen from consumed benthic prey.

Large-scale movements of resources also arise from anthropogenic processes and mechanisms (Bandy and Burel, chap. 21 in this volume). For example, in 1996 Europe imported 13 million tons of soybeans, while Brazil exported almost 4 million tons (Food and Agriculture Organization 1998). Increasing anthropogenic carbon, nitrogen, phosphorous, and sulfur emissions into the atmosphere contribute millions of tons to downwind habitats each year. Similarly, fertilizers applied to agricultural and other lands are a major factor in the eutrophication of streams, lakes, reservoirs, and coastal waters (Carpenter, Caraco et al. 1998; Carpenter, Ludwig, and Brock 1999). Thus, while allochthonous resources may play an important role in the determination of food web structure and dynamics across natural landscapes, large-scale anthropogenic inputs may play a role in the degradation of terrestrial, aquatic, and marine ecosystems.

The flux of allochthonous resources is governed by land use patterns and water movement within and across landscapes and bioregions (Baudry and Burel, chap. 21 in this volume). Watercourses may be constrained by dams, levees, ripraping, ditches, canals, channelization, loss of wetlands, and other human activities. The constraining of riverine systems worldwide has greatly altered the rate of movement of resources from terrestrial systems to aquatic to marine systems. For example, over 98% of the riparian habitat has been lost in the Sacramento River Valley of central California, significantly altering terrestrial inputs into rivers and finally the Pacific Ocean (Malanson 1993). Habitat connectivity has also been significantly reduced, limiting the movement of resources. It has been argued that this loss of connectivity is an important factor in the local extinctions of some species; however, the role of movement corridors remains controversial (Simberloff and Cox 1987; Simberloff et al. 1992). Changes in land cover from native vegetation to exotic pastures or agricultural fields can significantly change the rate of movement of allochthonous resources into adjacent habitats (Baudry and Burel, chap. 21, and Riley et al., chap. 16 in this volume). Exotic vegetation may support lower invertebrate biomass and thus reduce the rate of terrestrial invertebrate movement into adjacent streams (Riley et al., chap. 16 in this volume). Agricultural activities may increase the rate of nutrient inputs into adjacent aquatic systems, causing eutrophication and subsequent changes in plant communities and in the strength of trophic cascades (Carpenter, Brock, and Hanson 1999).

Allochthonous resources can greatly influence the energy, carbon, and nutrient budgets of recipient habitats. While demographic responses mediated by dispersal can be important in local food webs (Holt, chap. 7 in this volume), here we will focus mainly on the effects of resource inputs on local populations and communities. Allochthonous resources can contribute up to nearly 100% of organic matter in many types of habitats—including headwater streams, caves, mountaintops, snowfields, marine aphotic zones and central oceanic gyres, deep oceanic benthic zones, phytoplankton, deserts, and islands (see Polis et al. 1996 and references therein). The allochthonous resources that drive these specialized habitats are often detrital—either of plant or animal origin. Allochthonous resources can be relatively easily differentiated from in situ resources in these specialized habitats. However, mobile organisms moving between similar habitats (grassland to savanna or littoral to sublittoral) can also contribute significant amounts of resources.

Allochthonous resources vary greatly in kind and quality, limiting which species benefit from them. For example, soil microbes and plants can

directly exploit nutrient inputs that are deposited in guano (Hutchinson 1950). Anderson and Polis (1999) showed that soils on islands with seabird colonies had 6 times more N than soils on non-bird islands. Plants on bird islands had 1.6–2.4 times greater N and P concentrations than did plants on non-bird islands. Allochthonous resources in the form of organic matter can range from particulate matter to whale carcasses. For example, particulate matter from oceanic upwelling or headwater streams can subsidize filter-feeding organisms (Whitman, chap. 9, and Menge, chap. 5 in this volume). Species assemblages differ in their use of detritus depending on whether the material is plant or animal matter (G. R. Huxel, unpublished data). In model ecosystems, Huxel and McCann (1998; see also McCann et al. 1998) found that the trophic status of the recipient consumer(s) greatly influenced the stability of the food web.

Thus, allochthonous resources influence individual fitness, population dynamics, the outcome of interspecies interactions (Holt, chap. 7 in this volume), community structure and ecosystem function, and landscape patterns and processes. The effects of allochthonous resources on recipient species may be direct, indirect, or both. Theoretical and empirical studies often show that indirect effects may be greater than direct effects (Huxel and McCann 1998; Abrams et al. 1996; Menge, chap. 5 in this volume). In the rest of this chapter, we will address how allochthonous resources influence single species populations, pairs of interacting populations, communities, and ecosystems/landscapes. We hope to demonstrate that traditional lines of investigation by habitat—freshwater, marine, benthic, pelagic, terrestrial, wetland, and so forth—result in missing key processes and mechanisms that influence local community structure and dynamics.

EFFECTS ON SINGLE SPECIES

The benefits of allochthonous resources are realized through the capture of these resources (as with any resource) and resultant increases in individual survivorship, fecundity, body size, and condition. These resources have direct and indirect implications for populations. Their direct effects include numerical response by the recipient species via increased reproduction with addition of a limiting resource (e.g., C, proteins, fatty acids, N, or P) or via higher survivorship due to increased nutrient levels in tissues. Their indirect effects include enhanced density dependence as a result of numerical response: source-sink dynamics, in which members of the recipient population emigrate due to density-dependent factors

(e.g., increased competition); and decreased competition for particular limiting resources (i.e., ecological release).

Recent studies have demonstrated that the flow of resources from marine ecosystems to terrestrial ecosystems can be important for coastal populations. For example, Rose and Polis (1998) analyzed how the distribution and abundance of the coyote (*Canis latrans*) in Baja California was affected by resources from the Gulf of California. Coyote populations were 2.4 to 13.7 times denser along the coast than at nearby inland sites. Scat analyses found that scat mass was more than doubled in coastal areas compared with inland areas, indicating greater resource availability in coastal regions. Furthermore, 47.8% of all items found in coastal scats came directly from the marine environment. Similar studies (see table 3 in Rose and Polis 1998 and references therein) revealed that allochthonous resources from the marine environment heavily subsidize many omnivorous terrestrial mammals in coastal areas.

Semelparous vertebrates such as salmonids or squid can strongly subsidize carrion-feeding species. For example, in watersheds where salmonids have disappeared, bald eagle (*Haliaeetus leucorhaphus*) populations have declined dramatically. In Glacier National Park (Montana, U.S.A.), McClelland et al. (1994) observed that kokanee salmon (*Oncorhynchus nerka*) dropped from more than 100,000 spawners before 1987 to zero spawners in 1991. Bald eagle numbers in this region declined precipitously from a peak of 639 in 1981 to 25 in 1989. Similar declines probably have gone unnoticed as salmonid populations elsewhere in western North America have approached or reached extinction.

The effects of allochthonous resources can be particularly dramatic in ecosystems with low intrinsic productivity. Desert systems are typified by low, highly variable precipitation and therefore low productivity—usually one to three orders of magnitude below that of other habitats (Louw and Seely 1982; Ludwig 1986, 1987; Polis 1991; Anderson and Polis 1999). However, since most desert soils have low levels of available nutrients, this factor may also limit primary productivity (Peterson and Schlesinger 1990, 1991; Charley and Cowling 1968; Eftershank et al. 1978; West and Skujins 1978; Hadley and Szarek 1981; Schlesinger and Peterson 1991).

On islands in the Gulf of California, Sánchez-Piñero and Polis (2000) found that tenelionid beetle abundance tracks inputs of either carcasses on islands used by seabirds for nesting or increased plant litter following El Niño events on islands used by seabirds for roosting. Tenelionids are 5 times denser on roosting and nesting islands than on non-bird islands, and they are 6 times denser within than outside seabird nesting colonies.

These effects arise directly through feeding on bird carcasses or fish scraps, or indirectly through increased plant litter due to fertilization by bird guano (see also Anderson and Polis 1999).

Populations may also have a net negative response to increased allochthonous resources. For example, a numerical response to allochthonous resources could theoretically result in overconsumption of all resources and a subsequent crash in population density (as in the "paradox of enrichment"; Rosenzweig 1971). May (1974) showed that increasing the growth rate could cause a population to move from stable to chaotic dynamics. DeAngelis and others (DeAngelis 1992; Huston and DeAngelis 1994; Andersen 1997) have shown that increased nutrient supply rates also can destabilize population dynamics. Various mechanisms could be involved, including self-shading and overconsumption of resources (see Liebold 1997; DeAngelis and Mulholland, chap. 2 in this volume). If allochthonous resource input is seasonally pulsed (R. D. Holt, unpublished data; Sears et al., chap. 23 in this volume), there can be increased population densities and overconsumption of autochthonous resources in other seasons, resulting in severe population crashes.

EFFECTS ON PAIRS OF SPECIES

Predator-Prey Interactions

The quality of the resources available to a consumer can govern the consumer's growth rates. Urabe and Sterner (1996) demonstrated that under low light to nutrient ratios, algae and their herbivores are limited by energetic resources, whereas under high light to nutrient ratios, they are nutrient-limited. This finding may explain why experimental additions of nutrients to test trophic cascade hypotheses have had equivocal results (Brett and Goldman 1996, 1997; Strong 1992; Polis and Strong 1996; Polis et al. 2000).

The subsidization of prey, either directly (e.g., guano to plant) or indirectly through a resources species (e.g., guano to plant to herbivore), can result in an increase in the prey with or without a concomitant increase in predation. If predator numbers are limited by factors other than prey (e.g., nest sites, interference competition, intraguild predation), increased production makes it more likely that prey can escape predator regulation (Sinclair and Arrese 1995). With a sufficient increase in predation pressure, however, the prey species can become extinct. If the flow of allochthonous resources is great enough, then the prey can increase even if predation pressure increases.

However, the ability of the predator to respond numerically to increased prey density or quality (in terms of higher nutrient content) may allow for overcompensation by the predator, driving the prey to low numbers or even extinction (Huxel and McCann 1998; Huxel 1999).

A major source of nutrients for ecosystems is atmospheric deposition (Erelli et al. 1998; Chadwick et al. 1999; Remmerberg and Gessler 1999; Erelli et al. 1998) found that higher elevations receive greater atmospheric nitrogen inputs, and that birch (*Betula papyrifera*) at these elevations had a foliar N content 13% higher than at lower elevations. However, the growth of insect larvae can be either increased or decreased by changes in foliar N and phytochemistry. Erelli et al. (1998) found that growth of *Oryza leucostigma* larvae decreased with decreasing leaf nitrogen, even though feeding increased. Yet larvae of *Lymantiria dispar* maintained their growth rates by compensating for low N by increasing consumption. This difference may be due to the greater sensitivity of the first instar of *O. leucostigma* to tannins, which are negatively correlated with nitrogen levels. Similarly, Redak et al. (1997) found that simulated atmospheric nitrogen deposits produced chrysomelid beetles on treated plants that were 36% larger and had growth rates 31% greater than those on control plants.

Plant response to herbivory is a key factor in whether (and how) an increased nutrient supply rate influences herbivory. The ability of a plant to resist herbivory may be either constitutive (always present) or inducible (turned on by specific interactions). Plants with induced chemical defense pathways may use increased allochthonous nutrients either for increased growth and reproduction or for increased chemical defenses. Recent studies have suggested that induced defensive responses by plants may allow plants to respond in ecological time to increased herbivory, decreasing the need for constitutive defenses (Karban and Baldwin 1997). Plants need to somehow judge the potential for future herbivory in order to be able to partition resources between growth and reproduction and defense, and increased nutrient levels may influence their response. One major difficulty for researchers is in determining whether the benefits of increased defense outweigh the costs of the production of chemical defenses.

Menge and his colleagues (Menge et al. 1996; Menge, chap. 5 in this volume) observed differences between two wave-exposed sites along the Oregon coast. At one site—Strawberry Hill—Menge found that the abundance of macroalgae was low, while densities of filter feeders and invertebrate predators were high. In contrast, another site—Boiler Bay—exhibited a high abundance of macroalgae and low densities of filter feeders and invertebrate predators. Menge et al. (1996) experimentally demonstrated that at

the Strawberry Hill site, rates of predation by the invertebrate predators and recruitment and growth rates of the filter feeders were higher than at Boiler Bay. Menge (2000b; Menge, chap. 5 in this volume) has argued that the stronger top-down effects at the Strawberry Hill site are due to higher levels of food input for the filter feeders there. The higher levels of allochthonous food resources result from greater entrainment of oceanic currents off the coast of Strawberry Hill than at Boiler Bay. Thus, the landscape contexts of these two biotically similar communities drive their food web dynamics (Menge, chap. 5 in this volume), highlighting the significant influence of the flux of resources across landscapes or seascapes in driving local community dynamics. The similarity between these sites in community composition, in contrast to their different dynamic properties, suggests that the processes that influence the structure of local communities may not be the same as those that drive their dynamics.

The direct subsidization of a predator can lead to one of two outcomes: either the predator will increase its predation pressure on in situ prey (in a process similar to apparent competition, sensu Holt 1977, 1984; Holt, chap. 7 in this volume), or it will feed mainly on the allochthonous resource, relaxing predation pressure on in situ prey (ecological release; Holt 1997; Huxel and McCann 1998). Abrams (1999) has shown that prey switching by predators can stabilize food webs. Similarly, Huxel and McCann (1998; Huxel et al. 2002) found that low to moderate levels of allochthonous input could stabilize food webs, while high levels would result in strong indirect interactions in which the predator would reach high densities and increase predation pressure, causing the in situ prey to become extinct.

The movement of consumers can greatly influence consumer-resource interactions. For example, since the 1930s, lesser snow geese have switched from traditional coastal winter foraging areas to inland agricultural areas (Robertson and Slack 1995; Stutzmanbaker and Butler 1974). Across the Mississippi and Central Flyways, the geese have responded to additional resources provided by crop residue and changes in agricultural practices (Boyd et al. 1982), greatly increasing in numbers from 600,000–800,000 during 1950–1965 to about 2 million birds by 1990 (Jeffries et al., chap. 18 in this volume). In some river valleys the increase has been up to twentyfold (Burgess 1980). The geese migrate to arctic tundra for the summer breeding season, where their birgeoning numbers have resulted in great stresses on the local tundra habitat. Jeffries et al. (2000; Jeffries et al., chap. 18 in this volume) has shown that the tundra vegetation has been stripped from large areas due to foraging by the geese.

The input of resources from terrestrial habitats into headwater streams has been shown to drive secondary productivity in downstream waters (Vannote et al. 1980; Rosemond et al. 1993). The effects of this increase in productivity on trophic interactions in stream food webs have been greatly understudied until recently. Nakano et al. (1999) recognized that terrestrial inputs into streams represented an important energy source for secondary production, but few studies had examined the role of non-plant terrestrial resources. Allen (1951) suggested that secondary production within streams may be insufficient to support the observed levels of fish production. Nakano et al. (1999) showed that terrestrial arthropods constitute a high-energy and high-nutrient resource in stream food webs that can exceed in situ productivity (Garman 1991; Cloe and Garman 1996). They covered sections of a stream to reduce terrestrial arthropod inputs and excluded or included a predatory fish (Dolly Varden) in some sections as well. Fish in the uncovered sections fed mainly on terrestrial arthropods, while those in the covered sections relied mainly on chironomids (aquatic herbivores). In the covered sections, the biomass of aquatic herbivores decreased and periphyton increased. The duration of the experiment precluded strong numerical responses by the predator; however, over short time scales, buffering of fish effects on in situ stream invertebrates by terrestrial arthropods was observed.

Changes in land cover can significantly alter the amount of invertebrate biomass moving into streams (Edwards and Huryn 1996; Kawaguchi and Nakano 2001; see also Riley et al., chap. 16 in this volume). Edwards and Huryn found that the biomass of terrestrial invertebrates entering adjacent streams in New Zealand was correlated with land use patterns, and that the highest rates of movement into the streams was from native vegetation, suggesting that native vegetation supports more invertebrate biomass. Huryn (1998) found that only the introduced brown trout was able to fully utilize these allochthonous resources, and that it actually required all of the invertebrate production to support its populations, whereas the native galaxiid consumed only 18% of the invertebrate production. Also, the subsidized brown trout caused a top-down cascade resulting in decreased aquatic herbivore and increased algal biomass. Increased nutrient loading from exotic grasses in pastoral habitats further complicates New Zealand stream food webs. High levels of nitrogen cause a shift in algal dominance to filamentous green algae, which are less preferred by aquatic herbivores. This shift in algal community composition acts together with increased predation by the exotic brown trout to decrease grazer densities (Riley et al., chap. 16 in this volume). These studies suggest that the connectivity

of adjacent terrestrial and aquatic habitats plays an important role in maintaining fish populations, and that changes in land cover from native vegetation to managed systems will influence the conservation of fish and other aquatic organisms.

Biological control specialists have long argued that generalist predators may be effective in maintaining low densities of pest species if they are provided with additional resources (prey). Karban et al. (1994) demonstrated that subsidizing the predatory mite *Metaseiulus occidentalis* by releasing an alternative prey, the Williamsite mite, results in greater control of the Pacific spider mite on grapevines. While competition alone between the two herbivorous mites results in lower abundances of the Pacific spider mite, the predator further suppresses the pest. With only the pest species present, the predator becomes extinct on some grapevines; after driving the pest to low densities, and the pest recovers to higher densities after extinction of the predator.

Competitive Interactions

Allochthonous resources may allow competitive species to coexist in either of two ways. First, if the combination of allochthonous and allochthonous resources is great enough, and the competitors are both generalists and can utilize both resources, then competition is reduced. Second, if both resources are low, then specialization on the two different resource types allows for coexistence (Huxel et al. 2002). Competitive interactions may also be important in driving habitat selection whether resources are adequate or not (Brown 1990, 1996; Holt 1985, 1996a, 1997b). Specialization on allochthonous resources is seen in many communities. Some aquatic insects in headwater streams specialize on leaf matter; these "shredders" process the leaf material into finer particles that can be utilized by other aquatic insects. Kelp flies and carrion flies utilize different marine inputs onto desert islands (G. R. Huxel et al., unpublished data). Similarly, tenebrionids can specialize on plant detritus or carrion, or feed more generally on both. Competition among tenebrionid species changes with different levels of inputs of these resources (F. Sánchez-Piñero, unpublished data).

Bustamante et al. (1995a) found exceptionally high biomasses of two intertidal limpets in the mid- to low intertidal communities of rocky shores in South Africa. Previously these limpets had been regarded as generalist consumers; however, Bustamante and colleagues found that the two limpets had highly specialized feeding mechanisms. *Patella argenvillei* is found in low regions of semi-exposed shores in association with adjacent

kelp beds, and *P. granatina* is found in sheltered boulder bays. *P. granatina* feeds on kelp and seaweed debris, and *P. argenteiflora* feeds on kelp plants. Thus, the subtidal production of kelp fronds subsidizes both species; however, their coexistence is maintained by habitat selection and timing of feeding.

While allochthonous nutrients may have large effects on some systems, we do not suggest that all plant communities will exhibit strong responses to these additional resources, because many different resources may influence plant community structure. Competition among plants is often governed by the availability of nutrients, light, or space (Hutchinson 1967; Harper 1977). Recent theory on resource competition has been based on the importance of hypothesized trade-offs between minimum requirements for nutrient resources (Tilman 1982). This theory predicts that there should be negative correlations between the supply rate of major limiting nutrients and the availability of at least some secondary nutrients or among the availabilities of different limiting nutrients. However, Liebold's (1997) analysis of four data sets from large-scale surveys of lakes shows mostly positive correlations among the availabilities and supplies of nutrients. In contrast, he found that a fifth data set, obtained in an area of high acidification, did show several important negative correlations that are consistent with the resource competition models. Liebold suggested that negative correlations between nutrient levels and light levels indicate that an important trade-off among species may involve low light requirements versus low nutrient requirements. As mentioned above, Urabe and Sterner (1996) showed that algae populations were energy-limited at low light to nutrient ratios, while at high light to nutrient ratios they were nutrient-limited. Similarly, Goldberg and Milner (1990) found that nutrient additions had little effect on plant productivity in a dry year, and that changes in diversity in experimental plots depended upon which nutrients were added to the plot. They also found that plots with nitrogen additions had greater mortality due to increased light limitation. These findings suggest that systems with high rates of allochthonous nutrient input may not respond strongly to additional resources. Thus the role of allochthonous nutrients in light-limited systems needs to be more fully addressed.

EFFECTS ON MULTIPLE SPECIES INTERACTIONS

Allochthonous resources allow for the examination of one of the major areas of debate in community ecology: the relative importance of top-down versus bottom-up effects. Since Lindeman's (1942) study of food web

dynamics in lake ecosystems, the debate over whether food webs are controlled by top-down or bottom-up effects has been ongoing. Lindeman suggested that the species and processes in communities formed cycles, with resources moving from detritus to plants (or directly to detritivores) to primary consumers to secondary consumers, and whatever resources are not utilized by these trophic levels back to detritus (fig. 26.1). Hairston et al. (1960) argued that control of food webs is top-down in terrestrial ecosystems, such that carnivores limit populations of herbivores, allowing plants to grow mostly unimpeded by herbivory and making the world green. This green world hypothesis was expanded into the exploitative ecosystem hypothesis (fig. 26.2) for most types of habitats by various food web ecologists (Fretwell 1977, 1987; Oksanen et al. 1981; Carpenter and Kitchell 1993). They suggested that the dynamics of food webs in general are dominated by top-down processes, such that in food chains with odd numbers of trophic levels, the odd-numbered trophic levels increase in biomass, while in even-numbered food chains, the even-numbered trophic levels increase. Other researchers, however, argued that bottom-up processes exert strong control on food web structure and dynamics (e.g., donor control, sensu DeAngelis 1980), in that food web dynamics are controlled by the rate of resource input (White 1978; McQueen et al. 1986; DeAngelis 1980, 1992; Strong 1992; Polis and Strong 1996; Huxel and McCann 1998). Here we argue that both top-down and bottom-up processes can influence food web structure and dynamics (Polis and Strong 1996; Persson et al. 1996; Rosemond et al. 1993; Vanni 1987; Lynch and Shapiro 1981). Thus, allochthonous resources can influence food web dynamics via two general pathways: as resources for predators, which then have cascading effects on prey, and as resources for primary producers or primary consumers, resulting in more resources for predators.

Thus the influence of resources on multiple species interactions within a food web or a food web module (sensu Holt 1997a) can either be direct or indirect. Polis and Strong (1996) suggested that most strong trophic cascades occur in systems that are significantly subsidized. In Huxel and McCann's (1998) model food web modules, allochthonous resources initiate strong indirect interactions from either bottom-up or top-down effects. Indirect interactions that are similar to apparent competition (Holt 1977, 1984) occur in these model systems when a consumer increases in density due to allochthonous resources, resulting in a top-down effect on its allochthonous resources. This effect can then cascade down to reduce predation pressure on the next lower trophic level. However, if the consumer is inefficient in converting the allochthonous resource into greater

spawning salmonids boost productivity (1.5–6.8 times; Michael 1998) in freshwater streams and adjacent riparian zones (Lytle and Elliot 1998; Willson et al., chap. 19 in this volume).

The potential for overfertilization of terrestrial ecosystems is great. Form et al. (1998) have suggested that nitrogen deposition is leading to degraded conditions in many North American forests. The excess nitrogen can cause disruptions in plant-soil nutrient relations, increased soil acidification, increased runoff of nitrate into streams, decreasing water quality, and eutrophication of coastal waters. Increased nitrogen may cause a shift from slow N-cycling coniferous forest stands to fast-growing and fast N-cycling deciduous forests (Fenn et al. 1998).

Riverine, lake, estuarine, and coastal marine habitats are also greatly influenced by nutrient and organic matter loading (Sklar and Browder 1998; Carpenter, Caraco et al. 1998; Mallin et al. 1999). In these aquatic ecosystems, nutrient and organic matter input can result in toxic algal blooms, hypoxic and anoxic conditions, fish die-offs, reduced biological diversity, loss of aquatic bed plants and coral reefs, reduced water quality, and increased prevalence of disease. Carpenter, Caraco et al. (1998), in a literature review, found (1) that eutrophication is widespread in rivers, lakes, estuaries, and coastal ecosystems; (2) that agricultural practices and urban areas are the major sources of nonpoint pollution for these systems; (3) that inputs of N and P into agricultural land exceed outputs in produce; (4) that nutrient flows to aquatic systems are directly related to livestock densities and that the manure outputs of these animals exceed the manure needs of crops to which manure is applied; (5) that P inputs to agricultural systems cause a surplus of P in soils, which often results in transport to aquatic systems; and (6) that excess fertilization and manure production on agricultural lands create surplus N and leaching of N into aquatic systems.

Large-scale disturbances can cause greatly increased inputs of nutrients and organic matter into aquatic systems from terrestrial systems. This is especially true in areas with high densities of livestock, as noted by Carpenter, Caraco et al. (1998). The Cape Fear watershed has high densities of humans, chickens, and swine; for example, the North Carolina swine population was 9.8×10^6 animals in 1997 (Mallin 1999). Hurricanes Dennis, Floyd, and Irene all struck this area in 1999, resulting in inputs of aquatic systems of over 265×10^6 l of human waste, and probably similar (if not greater) amounts of waste from chicken and swine operations.

Increased organic matter input into aquatic systems following such large disturbances can result in hypoxic or anoxic conditions, leading to mass die-offs of fish and shellfish. For example, following two hurricanes

that struck the Cape Fear watershed, dissolved oxygen levels decreased to 2 mg l^{-1} in the mainstem Cape Fear River and to zero in the Northeast Cape Fear River for more than 3 weeks (Mallin et al. 1999). The Cape Fear estuary also experienced hypoxia for several weeks. The cause was heavy sediment loads from agricultural systems, including waste from large swine operations. Benthic organisms (both invertebrates and vertebrates) were especially hard hit, with densities of some organisms dropping to near zero or zero at some sampling sites.

Eutrophication in aquatic systems can lead to significant losses of species diversity and alter ecosystem processes. It can also result in turnover to "unfavorable" species such as *Pfiesteria* and noxious invaders such as *Caulerpa*. For example, Burkholder and Glasgow (1997) found that *Pfiesteria*, a causative agent of major fish kills, can be stimulated to produce toxic zoospores by inorganic and organic phosphates, which are major components of agricultural and urban runoff. *Pfiesteria* has become a major health threat in the Chesapeake Bay ecosystem, but is not the only species causing problems in eutrophic coastal waters. Blazer et al. (1999) suggest that *Aphanomyces* may be the cause of lesions of menhaden in the Chesapeake Bay. Outbreaks of nuisance algae cause extensive problems due to their production and release of toxins and result in anoxia as the dead algae are decomposed (Carpenter, Caraco et al. 1998). Seehausen et al. (1997) suggest that eutrophication is a major factor in the loss of fish diversity. In eutrophic freshwater systems, changes in planktonic communities from edible to toxic or inedible species occur frequently (Carpenter, Caraco et al. 1998). Blooms of cyanobacteria are common in many lakes that experience eutrophication. Blooms of these organisms can result in fish die-offs, decreased water quality, and anoxia.

While changes in community composition and subsequent changes in ecosystem processes are clear, the relationship between eutrophication and diversity is more problematic. The relationship between diversity and productivity is thought to be hump-shaped (Huston 1979, 1994; Rosenzweig 1995). Diversity should increase from low to moderate productivity levels, but then decrease from moderate to high levels. Rosenzweig (1971) termed this decrease in diversity with increasing productivity "the paradox of enrichment." It has been debated whether this paradox actually exists, with some suggesting that in systems with multiple limiting resources, the paradox will not hold, or if it does, it will do so only over a limited range of values (Huxel 1999; Liebold 1997). However, many experimental systems have shown that nutrient additions lead to higher productivity and a loss in diversity (Rosenzweig 1995). Anderson and Polis (1999) demonstrated that

guano additions to desert islands in the Gulf of California resulted not only in increased productivity, but also in a change in species composition from perennials to annuals and a decrease in species richness.

Allochthonous resources can greatly benefit ecosystems when resources are added at low to moderate levels. As mentioned above, Chadwick et al. (1999) provided evidence that Hawaii's terrestrial ecosystems would be N-limited if not for the deposition of atmospheric N resources that originate in central Asia. Similarly, Polis and colleagues (Polis and Holt 1995, 1996a, 1996b; Polis, Anderson, and Holt 1997; Polis et al. 1998; Anderson and Polis 1999) have demonstrated that islands in the Gulf of California which have low terrestrial productivity due to low N and limited precipitation, have high levels of consumers due to inputs from the highly productive marine ecosystem of the Gulf.

CONCLUSIONS AND IMPLICATIONS

The flow of resources between habitats and across landscapes is an important factor in local communities. Two major factors are important determinants of the effects of these resources: the permeability of habitat boundaries to the resources; and the potential for utilization of the resources by the species of a local food web. Additionally, the strength of the environmental gradient across the habitats influences the movements of species (individuals) across the boundary. A further question is how species diversity changes across the boundary. One could imagine that diversity might be higher in the ecotonal area; however, this pattern varies among taxa and boundary types. Competitive and predatory interactions may greatly influence species habitat choices and therefore the potential for evolutionary change due to habitat selection (Brown 1990, 1996; Holt 1985, 1996a, 1997b).

Habitats of low productivity are typically net recipients of allochthonous resources. Thus, species that are inhabitants of these systems may rely greatly on the allochthonous resources. Population abundances in low-productivity sites will be dramatically reduced if these resources are missing. For example, Sánchez-Piñero and Polis (2000) found that abundances of tenebrionid beetles are significantly lower on desert islands in the Gulf of California that do not have allochthonous inputs from seabirds (either guano or carcasses and carrion). Thus, the conservation of species within low-productivity sites depends on the conservation of surrounding habitats with higher productivity because land use patterns can regulate the flux of resources and species (Baudry and Burel, chap. 21 in this volume, Carpenter, Caraco et al. 1998; Carpenter, Ludwig, and Brock 1999).

Finally, the linking of food web processes with landscape processes is an important step in understanding the structure and dynamics of communities. As pointed out in this volume by various authors, in order to understand food web interactions, we need to discern the fluxes of resources across landscapes and understand the implications of the contextual location of communities within a landscape. Species interactions can be significantly altered by this ecological context, making predictions and results from simple food web models difficult to interpret. Direct and indirect effects, driven by allochthonous resources may alter the strength of competitive, predatory, and other interactions between and among species. The importance of allochthonous resources underscores the arguments of Polis and Strong (1996), who suggested that resources could enter a food web through many different channels (hence their term "multichannel omnivory"). Increased resources may cause significant changes in the structure and composition of communities and ecosystems. Therefore, in the conservation of sensitive and fragile habitats, the ecological and landscape milieus of these systems have to be taken into account.

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