Commentary

Prey exchange between a stream and its forested watershed elevates predator densities in both habitats

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On the 27th of March, 2000, ecology lost two leaders who leave important legacies to the study of food webs. Shigeru Nakano, whose paper with Masashi Murakami appears in this issue of PNAS (1), was visiting Gary Polis at his field site in Baja California. Polis, Nakano, and three other colleagues perished when their boat capsized in a violent, unexpected storm offshore from Bahia de Los Angeles in the Sea of Cortez.

Shigeru Nakano was an extraordinary field biologist, as well as a community ecologist of uncommonly broad vision. Like other great ecologists, his insights were anchored in his deep intuition and knowledge of the natural history of an array of interacting species, in his case, stream fishes, aquatic insects, and birds. Such insight can come only from intensive and prolonged observation in the field. Nakano started his career as a fish biologist, doing detailed work on life histories, diets, and behavior, primarily of Japanese salmonids. In addition to collecting superbly detailed data on fish in their natural environments, he perfected several unique techniques for stream research, including underwater angling which allowed him to remove, measure, mark, and replace individuals in streams at will (2). Nakano's techniques for studying stream fishes expanded as a result of his collaborations with Prof. Kurt Fausch of Colorado State University, who introduced him to the idea of experimental field manipulations. Their collaborations included habitat scale manipulations of insect drift consumed by various salmonid species, with documentation of switches from water column to benthic feeding at different flux thresholds for morphologically generalized vs. specialized salmonid species (3). Nakano's interest in responses of fish and stream food webs to food availability motivated a large scale manipulation of terrestrial insect inputs to the Horonai Stream running through his study site in the Tomakomai Experimental Forest of Hokkaido University, in Hokkaido, the northernmost island of the Japanese archipelago (4). Nakano's achievement in carrying off this massive field experiment is a testimony to his inspirational leadership. He had come to the Tomakomai Experimental Forest as an Associate Professor and Director only several years earlier. Working with students and a few scientific colleagues, Nakano retrained the forestry staff there to perform very different tasks as ecological technicians, carrying out large scale experimental manipulations, and taking data on a wide range of organisms with only remote relationships to timber production. Nakano led by example, spending long hours underwater and traversing the watershed. In so doing, he obtained some of the first large scale manipulative data that showed the strong influence of "resource subsidies" from one habitat to another on the food web and species composition of the recipient community.

The Nakano–Murakami study sets new standards for holism and rigor in food web ecology by quantitatively addressing questions relevant to landscape scales. . .

The idea that flows of energy, materials, or organisms from one habitat to another could strongly influence the structure and dynamics of food webs had been vigorously championed during the 1990s by Gary Polis (e.g., ref. 5). Similar insights had occurred long ago to the great field ecologist Charles Elton (6), but in years that followed, food web studies took two different tracks, both away from landscape scales. Experimentalists, interested in the impacts of species interactions or physical factors on community dynamics and structure, tended to work within one habitat, and usually manipulated conditions or densities of organisms within small (<1–100 m^2) areas, for obvious logistical reasons. As river, lake, terrestrial, or intertidal, open ocean, or subtidal marine ecologists, we were not focusing on processes affecting communties that operated across landscape boundaries (but see ref. 7). The theory that dominated food web ecology in the 1970s and 1980s (e.g., refs. 8 and 9) made no attempt to portray any physical or temporal context. Interest in habitat boundaries and fluxes across them was maintained in ecosystem (10) and landscape ecology (11), but among scientists working at large scales without resolving population dynamics or interactions of species in food webs. Gary Polis had been struck by the importance of landscape scale processes for food webs on the desert islands he studied in the Gulf of Mexico. Like Nakano, Polis was deeply grounded and inspired by natural history, in his case of deserts and the arachnids that lived in them. As an arachnid expert, he had noticed that densities of spiders on these desert islands, particularly small islands, were off the charts (12). Field observations revealed that although spiders preyed on phytophagous insects eating the meager terrestrial vegetation of these islands, their populations were supported primarily by the amphipods and flies that consumed beach wrack derived from the vastly larger and more productive marine environment. It was because of these marine 'subsidies' that predators were able to suppress terrestrial herbivores, and indirectly defend terrestrial plants (13). Polis and colleagues wrote highly influential reviews (e.g., ref. 5) pointing out that subsidies (fluxes of organisms, energy, or materials from productive to less productive habitats) strongly influenced the structure and dynamics of recipient food webs in a wide range of ecosystems.

Stream ecologists had long assumed that consumers in streams, such as fish, depended on terrestrial production, but the influence of this cross-habitat subsidy had not previously been documented with large scale field experimentation. Naka-

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no's roofing experiment in the Horonai stream quantitatively demonstrated several important results. Reduction of terrestrial insect inputs intensified fish predation on aquatic invertebrate herbivores, triggering a trophic cascade (an increase in stream algal biomass caused by release from grazing) when enclosed fish could not emigrate from covered reaches of stream (4). When free to move, however, fish emigrated from channels with reduced inputs of terrestrial insects, but native Japanese salmonids left first, apparently excluded by introduced rainbow trout (S. Nakano, personal communication). This second finding triggered Nakano's interest in the idea that terrestrial subsidies could enhance the persistence of native salmonids where rainbow trout had invaded headwater streams.

As Nakano's interests expanded to larger scales and questions, he turned his attention to the possible influence of stream subsidies on terrestrial consumers in the forest. For a number of reasons, streams traditionally had been considered recipients rather than sources of energy for food webs. Land area exceeds inundated area in watersheds; terrestrial plant biomass typically dwarfs that of aquatic primary producers; and gravity pulls material down slopes. Despite these factors, large amounts of energy are supplied to stream food webs by small standing crops of aquatic primary producers, because producers like diatoms have high biomass-specific productivity and superior nutritional quality (14–16). Could terrestrial consumers be affected by exports of stream derived carbon? Emergent insects from desert rivers were shown to be crucial resources for watershed consumers (17), and evidence from temperate rivers suggested important influences of emerging aquatic insects on spiders, lizards, and bats (18, 19). In a conversation with Masashi Murakami, who had studied birds in the Tomokomai forest, Nakano realized that seasonal shifts in the asymmetry of productivity between the stream and the forest under the eastern continental climate regime of Hokkaido could be a significant factor governing food web exchange between these two habitats (M. Murakami, personal communication).

During the summer months, the largely deciduous forest surrounding the Horonai stream is leafed out and supports large standing crops of folivores like lepidopteran larvae. These in turn are fed on by a suite of migratory and resident birds. The roofing experiment and analyses of fish stomach contents during the summer showed terrestrial insects to be very important to stream fishes as well. During the winter, however, trees lose their leaves. Lack of edible vegetation as well as cold temperatures suppress terrestrial secondary production. The stream during these leafless periods receives more sunlight and is warm relative to the terrestrial environment due to the large groundwater contribution to its flow. Consequently, peak periods of insect production in the forest and the stream are seasonally offset. Nakano and Murakami (1) have documented these resource dynamics and the responses of fish and bird predators with the most intensive long term field campaign ever achieved in the study of cross-habitat fluxes. For two years at monthly or biweekly intervals, they sampled standing crops of insects in the streambed and in the forest, pumped the stomachs of various stream fishes to determine (without harm to the fish) their diets, and made intensive observational surveys of foraging by birds. Remarkably, they amassed over 13,000 feeding observations on birds during this effort, and in 7,200 of these, they were able to establish the habitat origin of the prey. Cross habitat subsidies in both directions were major, contributing an estimated 25% and 44% to the annual energy budgets of birds and fish, respectively. Their results (1) are the best demonstration in any system, terrestrial, freshwater, or marine, of seasonal shifts of cross-habitat resource subsidies. In contrast to previous studies that found, or assumed, fixed asymmetries in the productivity of adjacent habitats, these authors demonstrate that the stream feeds the forest food web during spring and fall, but the forest feeds the stream during the summer. Seasonal complementarity of cross-habitat subsidies maintains higher densities, and possibly diversities, of both birds and fishes than would otherwise be supported.

The Nakano–Murakami study (1) sets new standards for holism and rigor in food web ecology by quantitatively addressing questions relevant to landscape scales, but with close attention to the phenology, diet, and behavior of the species mediating these cross-habitat interactions. It stimulates questions for a number of future investigations. How might reciprocal subsidies influence adjacent food webs where ecosystems have different seasonalilty, for example, in Mediterranean climates where winter stream productivity is reduced by scouring floods and summer terrestrial production is depressed by drought? How might seasonally shifting subsidies influence the abundance or activities of web members other than predators, for example, primary producers, herbivores, detritivores, or decomposers? How do the physiologies and life histories of species affect their responses to seasonal offsets in resource exchanges? What is the role of various storage, tracking, or averaging adaptations of organisms in governing how pulses of productivity disseminate spatially and temporally through food webs (20, 21)? How will adjacent food webs respond when seasonal rhythms of adjacent habitats are altered, as in California rivers, which have seasonally reversed hydrographs modified for conveying water to agriculture, or in ecosystems experiencing different precipitation regimes under greenhouse warming? The challenges of expanding our grasp of the spatial and temporal scales of food web processes, while still resolving species interactions and dynamics, are great. So, however, is the need for this level of information for forecasting ecological change, and so are the insights and inspiration that we can draw from the life work of both Gary Polis and Shigeru Nakano.

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