FOOD WEBS

Integration of Patterns & Dynamics

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Time, Space, and Life History: Influences on Food Webs

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Introduction

Virtually all natural systems are open with great spatial heterogeneity at scales from millimeters to kilometers, and temporal heterogeneity, both periodic and stochastic, on scales from minutes to decades. One of the biggest challenges in ecology today is to ascertain how changes through time and space influence population and community dynamics. Many ecologists now recognize that ecological dynamics are rarely bounded by the area or time typically selected for study and that factors outside a focal system may substantially affect patterns and dynamics. Often between-habitat influences can exceed internal, within-habitat factors. For example, the dynamics of local populations may be linked closely to those of neighboring populations through such spatially mediated interactions as source-sink (e.g., Holt (1985) and Pulliam (1988)) and metapopulation dynamics (e.g., Gilpin and Hanski (1991)), supply-side ecology (e.g., Gaines and Roughgarden (1985) and Roughgarden et al. (1987)), source pool dispersal effects (e.g., Holt (1993)), and the dynamics of discrete populations coupled by dispersal (Hastings, 1993). The identification of landscape ecology as a specific discipline is a testimony to the growing appreciation of multihabitat dynamics.

In the context of food webs, organisms live in a spatial mosaic of different patches and habitats that vary in productivity and in the composition and abundance of resources and consumers. The production and availability of resources change through time on diel, seasonal, and multiannual scales. Consumer-resource interactions and web dynamics are influenced by spatial and temporal variability in resource production and consumption. Yet food webs are usually depicted as static representations of communities, either snapshots at particular times and places or composite portraits aggregating trophic relationships over broader scales of time or space. Static representations fail to capture the dynamic nature of communities; trophic relations change temporally and are influenced by spatial complexity. Moreover, organisms have evolved an array of life history strategies to cope with temporal and spatial changes in resource availability and environmental harshness (Wilbur, 1980; Werner and Gilliam, 1984; Winemiller and Rose, 1992).

A goal of this chapter is to integrate space, time, and life history into food web biology. We suggest ways in which consumer-resource interactions are influenced by spatial heterogeneity, temporal variability, and life history strategy leading to a framework that integrates these factors into food web theory.

Space, Time, Food Webs and Community Ecology

As is obvious to even casual observers, community structure (e.g., species distribution, abundance, diversity) varies in space and time at multiple scales. But the causes of variation are not so obvious. Although succession provided an early defining concept, a truly holistic, multiscale, food web focus

on community structure is yet developing. Notable landmarks leading to our current concepts in community ecology include Elton's (1927) prescient views on food webs (cycles), Lindeman's (1942) trophic dynamic/ecosystem view of communities, Hutchinson's (1959) synthesis of species diversity hypotheses, and the hypothesis of Hairston et al. (1960) for how communities are regulated. These works provide the cornerstones for much of modern community ecology.

A major impetus to many recent advances has been the gradual adoption (after much urging by pioneers such as Connell (1961a, 1961b) and Paine (1966)) of controlled field experimentation as a tool to evaluate causal explanations. Despite their power, however, experiments are limited to relatively small spatial scales and short temporal periods by resources, ethics, and similar constraints (Diamond, 1986). For instance, testing the effects of waves or nutrients in limiting kelp beds or the influence of lions on community structure will probably never be done using controlled experiments. Solutions to these constraints, such as the comparative-experimental approach (e.g., Menge (1991b); see Dayton (1971) for an early example), are a compromise. To gain insight into variation in biotic processes such as predation and competition, experiments (necessarily at small or short spatial or temporal scales) are performed simultaneously at two or more sites (to address larger spatial scales) and repeatedly (to assess larger temporal scales) along physical or biological gradients. Combined with careful, thorough sampling at relevant spatial and temporal scales, such an approach offers much more insight than do simple comparisons.

Despite its potential power, examples of this approach are still rare. Probably because of favorable spatial and temporal scales, most cases are aquatic. Several studies in rocky intertidal habitats show how the importance of disturbance, competition, recruitment, grazing, and predation vary along gradients of environmental stress (wave forces, heat, desiccation) (Dayton, 1971, 1975; Menge, 1976; Lubchenco and Menge, 1978; Lubchenco, 1986). Similar examples are available from marine subtidal habitats (e.g., Dayton et al. (1984), Estes and Duggins (1995),

Barkai and McQuaid (1988) and lakes (Arnott and Vanni, 1993). In terrestrial habitats, several excellent experimental community studies exist (e.g., McNaughton (1985), Brown et al. (1986), and Spiller and Schoener (1990)), but incorporation of variation along environmental gradients is still rare (e.g., Louda (1982)).

Studies of community dynamics along environmental gradients point toward an integrated understanding of the roles of biotic and physical forces in structuring communities. Previously, opposing camps regarded either physical (e.g., Andrewartha and Birch (1954)) or biological (e.g., Lack (1954)) forces as dominant in nature. In a pioneering study in rocky intertidal habitats in Washington State, Dayton (1971) provided the first explicit experimental proof that ecological processes varied in strength along an environmental gradient. Dayton showed that the impact of biotic forces varied with wave exposure (horizontal gradient) and desiccation (vertical tidal gradient), with important consequences for variation in community structure. Importantly, the variable effects of predators, grazers, and competition were associated with variation in food web complexity along the environmental gradients.

In New England, the intensity of competition, predation, and grazing also varied along wave force and desiccation gradients, so that physical disturbance and competition structured wave-exposed communities, and consumer-prey interactions structured wave-sheltered communities (Menge, 1976; Lubchenco and Menge, 1978). An important mechanism was that predation and grazing varied in strength inversely with wave force and heat and desiccation (Menge, 1978, 1983; Lubchenco, 1986). Here too, food web complexity varied over space, increasing with decreasing wave force or heat/desiccation stress (Menge and Farrell, 1989).

A third example indicates that such physical/biotic interdependencies are not confined to marine environments. Louda (1982) used a similar comparative-experimental approach to investigate the cause of the increase in abundance of the shrub *Haplopappus squarrosus* along a coast-to-mountain gradient of increasing environmental stress. Field experiments along this gradient demonstrated that plant abundance varied inversely with the in-

tensity of flower and seed predation by insects, which in turn varied inversely with stress. These examples suggest that within-habitat spatial variation in community structure can reflect the interdependencies of physical and biotic processes.

Community structure and dynamics can also vary temporally. Pimm and Kitching (1987) found that trophic complexity increased during succession of the aquatic community in artificial tree holes. Power (1990) observed food chain length and trophic complexity to increase after winter flooding in a California river, with a concomitant increase in the importance of top-down community regulation. Similar patterns occur in many habitats, where the importance of biotic interactions and food web complexity fluctuates seasonally as consumers either become inactive or leave during periods of high stress (e.g., Dayton (1971), Menge (1976), Lubchenco and Menge (1978), and Winemiller (1990)).

Another potentially important influence on variable community dynamics is recruitment. For instance, the impact of the sea star *Acanthaster planci* on its prey community (corals) may often be weak because this sea star is generally scarce. However, unusually high sea star densities do at times devastate corals, leading to their replacement by algae (Birkeland (1982, 1989); a review in Menge (1982)). The postulated cause of these outbreaks is a relatively unusual conjunction of meteorological and oceanographic conditions during sea star reproduction, leading to exceptionally high recruitment (Birkeland (1982, 1989); but see Olson (1987)). For unknown reasons, these outbreaks collapse quickly, but at least a decade is required for recovery by the coral community.

Although the impact of recruitment fluctuations on communities is relatively unstudied, several examples from marine habitats indicate high prey recruitment can have an important influence on community structure. For instance, population stability of barnacles was high with low recruitment, and low with high recruitment (Gaines and Roughgarden, 1985; Connell, 1985). In a comparison of rocky intertidal communities in Panama and New England, at low average recruitment levels, variation in community structure was explained by variation in recruitment density;

by contrast, when recruitment was high, other processes (e.g., competition) determine community structure (Menge, 1991a). Along the Oregon coast, high recruitment densities of mussels appeared to underlie spatial variation in predation intensity (Menge, 1992; Menge et al., 1994).

A second important class of environmental gradients varying over large spatial and temporal scales are controls on productivity. Freshwater and terrestrial studies far outpace marine studies, probably due to differences in both the openness of these habitats and the lability of nutrients or plant production. Lakes are relatively closed and natural gradients in nutrients seem common (e.g., Schindler (1990), Persson et al. (1992)). On land, nutrients can vary markedly over very small distances (e.g., Tilman (1982)), do not move laterally at the high rates possible in water, and are easy to manipulate in controlled experiments. In contrast, marine habitats are open, often have strong currents that cause rapid transport of nutrients, phytoplankton, and other biotic and abiotic components, and nutrients/pelagic productivity vary over very large spatial scales. It is not surprising that efforts to evaluate the influence of nutrients/productivity in combination with other physical and biotic agents in marine field experiments are only very recent (e.g., Bosman and Hockey (1986), Witman et al. (1993), and Menge et al. (this volume)). Assessment of causes of community variation over larger spatial and longer temporal scales has lagged severely relative to intense local studies, and should be the focus of more intensive research in all habitats.

Spatial and Temporal Scaling Effects on Web Structure

A large body of literature indicates that conditions in most habitats vary through time, and that some populations (perhaps most) rarely or intermittently experience strong density dependence or equilibrium dynamics (Wiens, 1977, 1984; Schoener, 1982; Strong, 1986; Dunson and Travis, 1991). Furthermore, few predators forage on prey species in constant ratios over their entire life cycles but instead exhibit marked ontogenetic, size-dependent patterns in predation (Brooks and Dodson,

1965; Werner and Gilliam, 1984; Polis, 1984; Winemiller, 1989a). Diet composition frequently shifts in response to seasonal changes in preferred food availability. For example, loricariid catfishes in the Venezuelan llanos, consume aquatic primary production mostly in the form of living algae during the wet season and as dead macrophyte tissue (detritus) during the dry season (Winemiller, 1990, this volume). Such seasonal dietary variation is more the norm than the exception (Werner and Gilliam, 1984; Polis, 1991a). Shifts in resources often drive changes throughout the web. For example, small variability in plant resources greatly influences the structure of plant-herbivore-parasitoid webs (Price, 1992).

Despite widespread recognition of the dynamic nature of habitats, communities, and trophic interactions (Thompson, 1988), relatively little attention has been given to variation in the time intervals involved in describing food web structure. A web based on large amounts of data collected over an annual cycle (a cumulative web) is more complex than a web using data collected over a host interval, say a week to months (Kitching, 1987; Warren, 1989, 1990; Winemiller, 1990; Schoenly and Cohen, 1991). Because trophic interactions always exhibit some degree of temporal variation, webs estimated over shorter time intervals can gauge more realistically within-system temporal changes in web properties (Winemiller, 1990; Schoenly and Cohen, 1991).

Tropical aquatic webs exhibited significant seasonal differences in several attributes and sink webs differed from their corresponding community webs (Winemiller, 1990). Foraging behavior and population dynamics often can be interpreted in terms of the seasonal influence of specific environmental factors, both abiotic and biotic. In the Venezuelan llanos, dry season contraction of aquatic habitats increases fish densities, leading to more frequent predator-prey encounters. Thus, the mean number of prey per predator node increases during the period of gradual drying (transition season) when prey densities are high. This is followed by a decline during the peak dry season, when densities of small species vulnerable to piscivores are at their lowest levels. The mean number of predators per node is about the same during the wet and transition seasons, because even though fish densities are very low in the expanded wet season environment, more species are present in the local ecosystem due to immigration. This example illustrates that food web structure cannot be interpreted without a reasonable knowledge of spatiotemporal context.

Allochthonous Input and Food Web Dynamics

Population and food web dynamics often depend on the flow of nutrients, food, and consumers among habitats. Trophic linkage across habitats is common when habitats differ in structure and species composition either moderately (e.g., grassland-forest; littoral-sublittoral or pelagic) or greatly (land-water; photic-aphotic zones). For all practical purposes, different habitats or patches always show variation in productivity. Thus, some habitats or patches may be more productive relative to less productive ones nearby. Several types of movement or exchange among habitats exist: organic nutrients (e.g., from runoff, upwelling, guano), detritus (e.g., leaf fall into water, shore drift), prey (e.g., emerging aquatic insects), or consumers (foraging across habitats, migrations).

Such movement is often key to community trophic dynamics, but its exact effects depend upon several factors. First, the direction (e.g., to or from the more productive habitat) matters: in general, the dynamics of species and food webs in less productive habitats are influenced more by their proximity to more productive habitats, than vice versa. Second, the trophic identity of the recipient species (e.g., basal species, top predators) determines possible dynamics. Allochthonous resources tend to produce a numerical response in recipients. If prey or more basal species are recipients, bottom-up effects (increased primary or secondary productivity) can occur. If consumers are recipients, top-down effects (consumer depression of in situ resources) can occur, especially in the less productive habitat; in some cases, spatially subsidized consumers can initiate an apparent trophic cascade.

There can be significant effects of allochthonous flows expressed within trophic

levels. Schoener (1974, 1976) developed a family of models which explicitly considered external inputs of resources for one or more species of consumers competing exploitatively for resources. These models lead to strongly nonlinear competitive interactions both within and between species. Purely exploitative competition on a homogeneous resource flow typically leads to competitive exclusion. Species coexistence is permitted if there is an appropriate mixture of interference and exploitative competition, or if each species has a component of the resource flow which it can exclusively exploit. Spatial fluxes across habitats thus can have profound consequences for the horizontal structure of food webs. In this paper, however, we largely concentrate on the impact of spatial fluxes on the vertical component of food web dynamics.

These dynamics depend on the degree of trophic connectivity among habitats. Connectivity lies between two extremes: totally isolated habitats with no exchange whatsoever versus totally interconnected with no barriers to flow. Several factors influence the degree of trophic connectivity as measured by the rate of exchange across habitat boundaries. Because these aspects of connectivity are well considered in landscape ecology (e.g., Turner (1989), and Dunning et al. (1992)), we do not dwell on them. Briefly, flow rate among compartments integrates several components of both the environment and organism (e.g., patch geometry, boundary permeability, similarity of adjacent patches, and mobility across boundaries). We attempt to integrate landscape ecology with food web dynamics by focusing on trophic connections among habitats that influence community structure through web dynamics. We ask: What happens when habitats that vary in productivity couple with one another trophically?

Case Examples

Movement of nutrients, detritus, prey, and consumers among habitats is ubiquitous. Allochthonous input sustains populations of species at all levels in the web: autotrophs, detritivores, and predators. Populations receiving spatial subsidies often respond numerically via reproduction or immigration.

Later, we demonstrate that such subsidy influences consumer-resource interactions and food web dynamics.

Flow among habitats varies greatly. In some cases, ~100% of organic materials, nutrients and prey are imported, e.g., caves (Culver, 1982; Howarth, 1983), mountaintops (Edwards, 1987), snowfields and other terrestrial areas devoid of vegetation (aeolian communities) (Swan, 1963) such as polar and new volcanic areas (Edwards, 1987; Thornton et al., 1990), marine aphotic zones and central oceanic gyres (Barnes and Hughes, 1988), phytotelmata (Kitching, 1987; Pimm and Kitching, 1987) and some barren deserts (e.g., Seely (1991)) and islands (Heatwole, 1971; Thornton et al. (1990); Polis and Hurd (this volume)).

Physical Transport of Nutrients and Detritus: Water and Wind

The energy, carbon, and nutrient budget of many habitats are greatly influenced by allochthonous input. In general, allochthonous nutrients (N, P, trace elements) allow plant populations to grow and detrital input produces a numerical response in detritivores. Transport can occur via physical (wind, water) or biotic vectors.

Water masses often differ substantially in productivity and organic biomass. Transport, both vertical (upwelling, pelagic detrital fallout to benthos) and horizontal (currents, tidal movement, eddy diffusion), is generally a key determinant of local marine productivity and consequent food webs (Angel, 1984; Barnes and Hughes, 1988; Barry and Dayton, 1991). Pelagic-benthos coupling is a major route for energy and nutrient flow to benthic areas where in situ primary productivity may be relatively low (most areas) or absent (aphotic zones). Worldwide, benthic faunal biomass reflects the productivity of overlying waters, and detritivory on allochthonous food forms the base of the benthic web. Conversely, infusion of bottom nutrients into euphotic surface waters via mixing and upwelling controls phytoplankton productivity and its consequent bottom-up effects and numerical response of consumers throughout the web (Barnes and Hughes, 1988; Barry and Dayton, 1991).

The exchange of productivity between the

pelagic/littoral zones and the intertidal can exert profound consequences in both areas. Nutrient enhancement from coastal upwelling and detrital input can allow both algae and organisms at high trophic levels in the intertidal to increase productivity and standing stock (Bally, 1987; Bosman et al., 1987; Duggins et al., 1989). Menge (1992) argues that nutrient input from oceanic waters to the intertidal may be a key bottom-up determinant of intertidal community structure.

Benthic and pelagic lake habitats are connected via turnover, a process similar to upwelling whereby bottom nutrients, infused into photic waters, stimulate annual pulses of productivity. Lakes also receive many nutrients from nonlake sources (streams, subsurface springs, precipitation, soil erosion, shore vegetation, and litter fall) (Pieczynska, 1975). A major tenet of the River Continuum Concept (Vannote et al. (1980), also see Naiman et al. (1987) and Ward (1989)) is that small streams serve as the primary sites of C input (from precipitation, throughfall, primary production, and allochthonous materials), whereas most C is metabolized by communities of larger-order streams.

Food webs in habitats (rivers, lakes, estuaries) adjacent to land receive three major sources of terriginous input (Ward, 1989): detrital matter from leaf and litter fall, dissolved and particulate organic matter (DOM, POM) from soil during runoff (Meyer and Tate, 1983; Naiman et al., 1987; Turner, 1989), and POM and DOM from floods (Ward, 1989). In many cases, allochthonous input greatly exceeds in situ productivity (Fisher and Likens, 1973; Naiman et al., 1986, 1987) and both plants (Fisher and Likens, 1972; Meyer and Tate, 1983) and consumers (Fisher and Likens, 1972; Covich, 1988; Ward, 1989; Rosemond et al., 1993) benefit greatly.

Great amounts of detritus, nutrients, and sediments rich in organics are exchanged between the channel and adjacent riparian areas via flooding (Ward, 1989), especially in flood river ecosystems (Welcomme, 1979; Edwards and Meyer, 1987). Such input increases productivity of aquatic and land plants and supplies rich food resources for large populations of detritivores (Goulding, 1980; Junk et al., 1989; Winemiller, 1990). This is well known to humans living along the fertile bottomlands of major rivers (e.g., Nile, Mississippi). In general, aquatic input to land produces an edge effect, with greater diversity and densities in riparian habitats compared with surrounding areas (Pieczynska, 1975; Charnov et al., 1976; Jackson and Fisher, 1986).

Coastal areas fringing oceans worldwide receive much energy and material from the sea via shore wrack (algae and carrion) (see Polis and Hurd (this volume 1995, in press)). Polis and Hurd calculated that allochthonous biomass from marine detrital input exceeds total terrestrial primary productivity on 42 of 68 islands in the Gulf of California. Marine material is converted into a diverse assemblage of terrestrial invertebrates and vertebrates at densities many times that of inland populations.

The movement of windborne detritus and nutrients is ubiquitous among terrestrial habitats (Swan, 1963; Likens and Bormann, 1975; Edwards, 1987; Thornton et al., 1990). In systems with little or no autochthonous primary productivity, such material supports surprisingly diverse food webs: examples include caves, mountaintops, snowfields, polar regions, new volcanic areas, phytotelmata, and some barren deserts. Worldwide, nutrient budgets of many ecosystems appear to depend on elements transported from one terrestrial habitat to another via precipitation (Likens and Bormann, 1975). In parts of the Amazon basin with nutrient-poor soils and limited river input, airborne dust apparently is integral to the nutrient budget. Although some material arrives from adjacent habitats, dust from Africa doubles the standing stock of P over 4700–22,000 years (Swap et al., 1992)! Swap et al. (1992) concluded that Amazonian rain forest productivity depends on critical input from another large ecosystem separated by an ocean yet coupled by the atmosphere.

Biogenic Transport of Nutrients and Detritus

The movement of biomass and translocation of nutrients by mobile consumers is an important ecosystem-level process producing substantial and rapid redistribution across habitat boundaries (Kitchell et al., 1979). Large animals are particularly important, be-

cause they typically graze (and remove nutrients) from high-quality patches and transport this material via defecation to lower-quality patches (McNaughton, 1985; Senft et al., 1987; Johnson and Naiman, 1987; Kitchell et al., 1979).

Fish are conduits of biomass and nutrients among aquatic habitats. Anadromous fish (e.g., salmon, alewife) play a vital role in the dynamics of many coastal streams and lakes with major inputs of energy, P, and N of marine origin via reproductive products, excretion, and death (see Durbin et al. (1979)). Daily movement by fish and zooplankton translocates nutrients across boundaries in freshwater (Kitchell et al., 1979; Goulding, 1980; Carpenter et al., 1992; Vanni, this volume; Schindler et al., this volume) and marine systems (Ogden and Gladfelter, 1983; Angel, 1984; Meyer and Schultz, 1985). Great quantities of fecal organic matter rich in fertilizing nutrients are transported within the water column (the diel ladder), between the benthic and pelagic zones (nutrient pump mechanism) (Vanni, this volume), onshore and offshore areas, and to refuge areas (Ogden and Gladfelter, 1983; Meyer and Schultz, 1985). In lakes, the input of P via fish excretion can exceed all other inputs, greatly increases primary productivity, alters the outcome of phytoplankton competition, and stimulates trophic cascades (Carpenter et al., 1992; Vanni, this volume).

Seabirds and pinnipeds feeding on marine fish and invertebrates transport great quantities of nutrients and organic material via guano, food scraps, eggs, feathers, and the bodies of dead young and adults (e.g., 10^4–10^5 tons of marine P is deposited on land annually worldwide (Hutchinson, 1950)) (Polis and Hurd, this volume, in press). Guano, a fertilizer rich in P and N, enhances plant production on land (Hutchinson, 1950; McColl and Burger, 1976; Burger et al., 1978; Ryan and Watkins, 1989) and in intertidal, estuarine, and nearshore waters (Hutchinson, 1950; Bosman and Hockey, 1986). The effects of avian-based materials continue up the food web: consumers grow faster, to larger sizes, and increase in density. Entire food webs on many island and coastal areas depend on allochthonous input from birds (Hutchinson, 1950; Heatwole, 1971; Burger et al., 1978; Williams et al., 1978; Siegfried, 1982; Burger, 1985; Branch et al., 1987; Daugherty et al., 1990; Towns et al., 1990; Duffy, 1991; Polis and Hurd, in press).

Aquatic vertebrates that forage on land transport great quantities of detritus and nutrients to water via guano and feces, e.g., hippos and geese. Beavers bring substantial quantities of organic matter and nutrients to water (Johnson and Naiman, 1987) and establish an entire food chain based on wood decomposition (Naiman et al., 1986). Many fish import large amounts of nutrients and biomass from terrestrial habitats (riparian areas, flood forest, and floodplains) to rivers (Goulding, 1980). Consumers also redistribute large quantities of biomass on land, e.g., grazers in the Serengeti (McNaughton, 1985) and roosting species (Hutchinson, 1950; Culver, 1982).

Movement of Prey

A diversity of species produced in a variety of habitats end up as food for consumers in a second habitat. Movement may be accidental, a product of life history, via migration, or overflow from one habitat to a second. Movement may be among adjacent or distant habitats and is most often unidirectional from more to less productive habitats. Moving prey often form a rich food source for many consumers; such subsidized consumers usually exhibit a numerical response.

Winds frequently transport terrestrial prey great distances. Airborne prey sustain predators (e.g., spiders, insects, lizards, birds, and small mammals) in systems nearly devoid of in situ primary productivity: e.g., volcanic fields and islands, snowfields, and mountain tops (Swan, 1963; Edwards, 1987; Thornton et al., 1990). At a smaller scale, ground, litter, and soil insects frequently occur in canopies of trees (reviewed by Dial (1992)). Large quantities of terrestrial insects and spiders blown onto water are eaten by fish or aquatic insects; this amount may surpass consumption of in situ aquatic insects (Mason and MacDonald, 1982). Many fish use an astonishing diversity of terrestrial invertebrates as an important source of food, at least seasonally (Goulding, 1980; Winemiller, 1990).

Aquatic prey also move passively. The ubiquitous horizontal and vertical movement

of water (see earlier) transports prey. For example, sessile filter feeders eat transported prey, be they produced locally or at a considerable distances. Downstream movement of often great numbers of prey is a frequent and important phenomenon in streams, rivers, and lakes (Ward, 1989; Cooper et al., 1990). Generally most productivity is fixed in riffles and streams and most consumption occurs in ponds (Naiman et al., 1986, 1987).

Active movement of prey also links habitats. Migratory animals transport prey biomass great distances and connect trophically distinct habitats, e.g., songbirds, mammalian grazers, diadromous fish, monarch butterflies, and plague locust. In the Serengeti, migratory prey (e.g., wildebeest) appear to allow resident lions to increase to the point that they depress resident species (e.g., warthogs, impala) (Schaller, 1972). Migration by diadromonous fish transport biomass between marine and freshwater habitats, e.g., bear or eagles eating salmon. Large numbers of diel marine migrants in the deep scattering layer carry a great amount of primary productivity to depth where they form the prey of large populations of bathypelagic and benthic fish and invertebrates (Angel, 1984).

Prey movement among habitats is a common by-product of life cycles. Brown and Gange (1990) give many examples of the generalized life cycle of many insects: oviposition in the soil, larvae feed underground on roots or detritus, pupate and adults emerge to mate aboveground. Such a life cycle characterizes some of the most abundant insects on the planet: most termites, ants, cicadas, and many beetles, lepidoptera, and diptera transport belowground organic material to aboveground consumers. In the case of periodic cicadas (the animal with the greatest biomass/area), many bird and insect consumers feed to satiation on emerging adults (Brown and Gange, 1990). There are many examples of subterranean insects eaten by a variety of aboveground predators (e.g., Polis (1991a) and Dial (1992)). Great numbers of emerging aquatic insects are eaten by terrestrial insects, arachnids, amphibians, reptiles, and birds; such consumers often occur in large populations at the water margin (Charnov et al., 1976; Jackson and Fisher, 1986; Polis and Hurd, this volume; Polis and Hurd, 1995, in press). Finally, seabirds are particularly important conduits of biomass from the aquatic to land food webs. As prey, seabirds and their abundant parasites are eaten by a variety of terrestrial predators (Burger, 1985; Daugherty et al., 1990; Towns et al., 1990; Duffy, 1991; Polis and Hurd, this volume, in press).

Movement of Predators/Consumers

Consumers move among habitats or patches on a scale from local foraging paths to long-distance migrations. Factors that influence movement include passive dispersal, foraging decisions, avoidance of enemies, forced movement of subordinates out of high-quality habitats by intraspecific interactions, diel or seasonal migrations, and ontogenetic shifts by life history stages. Many mobile consumers, migrants, and age classes choose habitats based on relative profitability and forage intake (Charnov et al., 1976; Werner and Gilliam, 1984; Senft et al., 1987; see below). Conversely, when consumers move to avoid interference or predation, they often end up in habitats with relatively low productivity (Holt, 1985; T. Oksanen, 1990).

Movement may be facultative (e.g., patch selection by a predator) or obligatory (e.g., life history habitat shifts, migration). Survival may reflect an arithmetic averaging over habitats (any of which in principle could be sufficient), versus a multiplication of survivals over habitats encountered sequentially, each required to complete a life cycle. (The dynamics of species that change feeding habitats during their life history are discussed in a later section.)

A taxonomically diverse group of terrestrial consumers migrate on many temporal and spatial scales (patches to continents) to exploit seasonally distinct habitats. Changes in resource abundance drive seasonal movement of birds across all geographic scales: trees, altitude, intratropical, continental, intercontinental, all on a continuum (Levey and Stiles, 1992). In the Serengeti, nomadic herds opportunistically follow rainfall-related production pulses to concentrate foraging in the relatively most productive habitats (Senft et al., 1987). Aquatic organisms exhibit a continuum of horizontal and vertical, short and long migrations. Many whales, some pinnipeds, and many fish migrate long

distances. The food availability hypothesis for the evolution of diadromy in fish (Gross et al., 1988) posits that the relative productivity of marine and riverine habitats at a given latitude determines if fish predominately feed and grow in the ocean and move to freshwater to reproduce (anadromy) or vice versa (catadromy). These fish feed in the less productive habitats and can exert great effects on prey in these places, e.g., anadromous steelhead in California rivers (Power, 1990).

Predators often forage across several distinct habitats. For example, many consumers move 200–500 m from adjacent habitats (e.g., fields) to exploit forest birds (see references in Andren and Angelstam (1988)). Predators entering habitat islands are an important factor in bird community composition, abundance, and dynamics. Many land and sea birds are important predators on both intertidal and land prey (e.g., Siegfried (1982) and Burger (1985)). Predators worldwide forage along lake and ocean shores to eat aquatic-based resources; these same predators move inland to eat more typical terrestrial prey). Marine mammal and seabird carrion form the food of relatively dense populations of many species (e.g., coyotes and roadrunners in Baja California; lions, jackals, and crows along southwestern Africa) (Polis and Hurd, this volume); foxes in boreal coastal areas (Zabel and Taggart, 1989; Oksanen et al., this volume)).

Fish forage across habitats that vary in prey availability. For example, Caribbean fish eat rapidly renewing algae on reefs, allochthonous (sea grass and *Sargassum*) detritus and forage on adjacent sea grass beds so intensively to exclude grasses for a halo of 10 m around the reef (Randall, 1965; Ogden and Gladfelter, 1983). Many freshwater fish move between habitats to feed, e.g., pelagic and littoral zones or river and floodplain (Welcomme, 1979; Goulding, 1980; Mittelbach and Osenberg, 1992; Schindler et al., this volume). In general, marine zooplankton, fish, birds, and mammals aggregate near regions of high productivity (e.g., upwelling and frontal regions) in response to available food (Barry and Dayton, 1991; Smetacek et al., 1990).

Some consumer movement is passive. For example, movement by pathogenic consumers is a key feature in pathogen-resource dynamics (Walker, 1969; Roberts and Boothroyd, 1972). Plants become diseased from spores blown over short and long distances from con- and heterospecific populations. Further, stages of some rust fungi must move among different host species to develop, e.g., cedar-apple rust alternates between apples and eastern red cedar.

Trophic Dynamics of Movement and Flow Across Habitats

Recipient species almost always benefit from the gain of nutrients or energy from the movement by molecules, detritus, and prey among habitats. Benefit is usually expressed as a numerical response. Food web effects, either from the bottom up or the top down, are a function of where spatial subsidies arrive (basal species, intermediate, or top consumers) and the configuration of the web.

The Flow of Allochthonous Nutrients, Detritus and Prey

If allochthonous nutrients are used by plants, primary productivity is increased, often dramatically. Increased secondary productivity leading to elevated densities of both herbivores and higher-level consumers usually accompanies augmented plant productivity. As documented earlier, such effects are ubiquitous on land (Hutchinson, 1950; McColl and Burger, 1976; Burger et al., 1978; Culver, 1982; Siegfried, 1982; Burger, 1985; Ryan and Watkins, 1989; Daugherty et al., 1990), in the ocean (Meyer and Schultz, 1985; Branch et al., 1987; Barnes and Hughes, 1988; Barry and Dayton, 1991) and in freshwater (Goulding, 1980; Vannote et al., 1980; Kitching, 1987; Naiman et al., 1987; Ward, 1989; Winemiller, 1990; Sterner, this volume). Analogous bottom-up effects occur when detritivores are subsidized by input (Heatwole, 1971; Durbin et al., 1979; Welcomme, 1979; Goulding, 1980; Culver, 1982; Naiman et al., 1986; Bally, 1987; Duggins et al., 1989; Duffy, 1991; Seely, 1991; Menge, 1992; Rosemond et al., 1993; Polis and Hurd, this volume; Rosemond, this volume; Vanni, this volume).

Consumers that use resources originating out of the focal habitat benefit indirectly via

bottom-up effects (see above) and directly via eating allochthonous prey. Prey dispersal from productive to less productive habitats allows predators to increase in the less productive habitat as observed for a diversity of consumers in a variety of habitats (see above) (Heatwole, 1971; Welcomme, 1979; Goulding, 1980; Siegfried, 1982; Holt, 1985; Daugherty et al., 1990; Duffy, 1991; Dial, 1992; Polis and Hurd, this volume). Movement by foraging consumers among habitats produces generally similar effects as prey movement (but see below): consumers persist at densities higher than could be achieved if isolated.

In most cases, the interactions between consumers and their allochthonous resources are donor controlled, i.e., consumers do not affect the renewal rate of these resources (Persson et al., this volume). Thus, consumers benefit but do not affect the renewal dynamics of resources flowing among habitats (i.e., no recipient control). Donor control occurs whenever a resource population is spatially partitioned into subpopulations that occupy different compartments, one of which is available to consumer whereas the other is not (Charnov et al., 1976; Polis and Strong, in press). In the case of consumer movement, some feedback between habitats is likely, i.e., recipient control of resources by consumers may occur in either habitat.

Top-down effects occur when consumers, subsidized by allochthonous resources, increase to high densities and depress in situ resources. Such interactions are almost always asymmetric: prey in the less productive habitat are affected more adversely than are prey in more productive habitats. First, consumers do not depress the renewal rate of imported prey populations; thus consumers are assured of a food supply that it is impossible to overexploit. Second, so subsidized, consumer success is decoupled at least initially from in situ primary productivity and the constraints of local prey dynamics. Third, subsidized consumers can depress local resource abundance below levels possible from isolated in situ consumer-resource dynamics in an interaction similar to apparent competition (Holt, 1984). However, in the place of an alternative productive prey, an alternative productive habitat either furnishes resources to consumers in the less productive habitat or provides food for a consumer that is a generalist among habitats. Thus, the availability of imported food whose rate of renewal is largely independent of consumption can allow a consumer to overexploit resident prey, even to the point of extinction, without the predator itself being endangered.

We illustrate the dynamics of subsidized consumers to show that the availability of imported food determines the effects of consumption on resident populations. For example, two spotted mites move from grass to relatively less productive grapevines; this steady influx allows higher populations of predaceous mites to suppress an in situ pest prey, the Willamette mite, to lower densities then without spatial subsidy (Flaherty, 1969). Intertidal limpets and urchins can occur at very high densities if they receive food from detrital kelp originating sublittorally (Duggins et al., 1989; Bustamante, 1994). These dense intertidal herbivores graze noncoralline algae to low cover. Leaf fall into streams is the major energy source producing extraordinary numbers of herbivorous snails; these snails, so subsidized, depress in situ algae (Rosemond et al., 1993).

Subsidized consumers can influence the structure of entire communities if they suppress key species. Communities should be more stable in those cases where subsidies allow consumers to suppress species capable of explosive reproduction (see below). Alternately, large numbers of subsidized predators can increase to the point that they depress herbivores and plants become more successful—an apparent trophic cascade—apparent because the energy sustaining large consumer densities does not flow up from in situ primary productivity (as in most relevant models) but arises outside the focal habitat (Polis and Hurd, this volume). For example, large populations of coastal terrestrial and semiterrestrial arthropods eat beached algae and carrion; these detritivores provide >90% of the energy intake for spiders, scorpions, and lizards that reach densities one to two orders of magnitude greater than areas without allochthonous import. On the coast of Namibia, abundant spiders, subsidized by a diet of large numbers of marine diptera, suppress insect herbivores of *Atriplex,* and plant dam-

age is significantly less than on plants unprotected by spiders (Polis and Hurd, this volume).

Insects from gap areas in tropical forests often supply the major food source to canopy anoles (Dial, 1992). Spatially subsidized anoles depress resident herbivores, and plant quality increases significantly (e.g., less defoliation and damage to tabonuco trees). These anoles also depress spiders, thus indirectly allowing small (≤ 2 mm) arboreal insects to increase in abundance. Here, as in the spider example above, the import of prey is donor controlled; subsidized consumers exert recipient control on local prey; and such prey depression indirectly allows resources of these prey to be more successful.

Duffy (1991) suggests that such spatially subsidized dynamics often occur around seabird colonies. Large concentrations of avian parasites frequent colonies of densely nesting birds (also see Polis and Hurd (this volume)). Dense populations of spiders, scorpions, ants, and lizards feed on these parasites. Duffy (1991) hypothesizes that ants, when present, limit tick populations; this cascades to produce more successful breeding by birds and less nest abandonment due to parasites.

The Movement of Consumers

Consumers, by moving among habitats, can directly affect their own resources and indirectly affect community structure via food web effects. If consumers feed in two or more areas (e.g., songbirds, ungulates, diadromonous fish, metamorphic insects, or amphibians), movement generally facilitates a numerical response by consumers with consequent effects possible on resources. As delineated above, movement allows higher densities of consumers in less productive habitats than would be normally sustained (e.g., summer breeding versus winter feeding grounds). In some cases, movement may even maintain a population within a habitat too small or unproductive to sustain the population solely on in situ resources.

Enhanced consumer populations often influence resident resources in similar ways as discussed above; in general, movement from productive to less productive habitats depresses resources in the less productive habi-

tats (Holt, 1985). Effects are a function of the specifics of energy gain in the more productive habitat, the proportion of different habitat types, the numerical response of the consumer, and such traits as consumer mobility, voracity, and tracking ability. For example, using consumer-victim models with dispersal of consumers between habitats differing in primary productivity, T. Oksanen (1990) shows that in habitat complexes where a relatively productive habitat abounds, exploitation tends to spill over to the barren habitat, whose trophic dynamics thus become largely driven by the dynamics of the productive habitat. If more barren habitats prevail, spillover exploitation becomes strongly diluted and dynamics approximate those based on in situ productivity.

We expect that cross-habitat foraging by consumers greatly affects resource dynamics at several spatial scales: long distance—migratory birds, marine and terrestrial mammals, and (diadromous) fish; medium distance—two habitats, differing in productivity, are juxtaposed (e.g., coastal and riparian systems; forest edges, estuaries); short distance—predator foraging among patches (e.g., different plant species, riffles and pools; pelagic and littoral). Although such effects are undoubtedly widespread and common, few examples document how such consumer movement facilitates resource depression. More surprisingly, little research has delineated how consumers actually benefit by feeding in different habitats or patches. This lack of information exists because the process is difficult to study and the question previously has not been well focused theoretically.

Earlier, we presented examples of how movement by consumers can facilitate resource depression: pathogen movement among plant hosts (Walker, 1969; Robert and Boothroyd, 1972), halos of intense herbivory in sea grass beds surrounding productive reefs (Randall, 1965), birds foraging on the coast and sea and eating large numbers of land invertebrates (Siegfried, 1982; Burger, 1985). Kerbes et al. (1990) suggest that agricultural changes in southern wintering grounds favorable to lesser snow geese have caused destruction of littoral vegetation on the shores of Hudson Bay; geese, subsidized

to very high densities by crops, have overgrazed lawns of reeds and grass to near zero cover in a period of five to 15 years.

Consumer movement also influences the stability and structure of entire communities when subsidized consumers suppress key species. For example, movement by krill to feed on ice algae maintains sufficiently abundant populations of krill to suppress cyclic blooms of Antarctic phytoplankton, thus stabilizing the pelagic community (Smetacek et al., 1990). We expect that consumer movement and spatial subsidies frequently allow consumers to suppress prey locally and alter the stability properties of many communities.

In some cases, consumer movement facilitates trophic cascades. In the two best studied freshwater cascades, fish predators are subsidized by allochthonous prey at levels capable of suppressing autochthonous prey. Adult and juvenile bass derive much of their food from littoral prey; bass predation on planktivorous fish tops the cascade in the pelagic zone of Wisconsin lakes (Carpenter and Kitchell, 1993; Schindler et al., this volume). Steelhead grow most in the ocean and migrate into California rivers where they initiate strong cascades if conditions are suitable (Power, 1990).

In general, food web effects from consumer movement are similar to those facilitated by prey movement: in both cases, consumers increase in abundance and prey from more productive habitats can depress the abundance of alternative prey in less productive habitats. Prey in low-productivity habitats will be depressed by increased predation; in contrast, predation on prey in high-productivity habitats is relaxed (Holt, 1985). These effects increase with the rate of predator dispersal. T. Oksanen (1990) extended Holt's models to three trophic levels and reached broadly similar conclusions.

However, differences exist between consumer and prey movement. Moving consumers may also affect resource dynamics in the more productive habitat upon their return, whereas the flow of detritus and prey typically does not involve feedback to the productive compartment. In fact, Holt's (1985) general model of a food-limited predator in two habitats produces a broad tendency for predator dispersal in heterogeneous environments to stabilize otherwise unstable predator-prey dynamics in both habitats. Thus a key difference is the presence or absence of feedback and recipient control in the more productive habitat.

Here we have largely emphasized the asymmetrical effects of high- on low-productivity habitats. Unproductive patches can also have reciprocal but subtler effects on the stability of more productive patches. If resources or prey can disperse from low- to high-productivity patches or habitats, such sites can act in effect as spatial refuges. A general feature of predator-prey and host-parasitoid models is that unproductive refuges can exert strong stabilizing effects on productive habitats where predator-prey interactions tend to be unstable, as in the paradox of enrichment (Rosenzweig, 1971; see Holt 1993, Holt and Hassell 1993).

Overview: Subsidized Consumers that Depress in situ Resources

Food web effects from consumer movement generally parallel those from prey movement. In both (1) Consumers increase to higher abundances than if they were supported solely by resources in one habitat; (2) subsidized consumers can depress local resources more than if they were isolated; (3) resources from more productive habitats indirectly depress resource abundance in less productive habitats; and (4) if key prey were suppressed, subsidized consumers can initiate trophic cascades, prevent prey eruptions, and dampen cycles. The strength of each effect increases with rates of both resource flow and consumer dispersal. Spatial effects are generally asymmetric: resources in low-productivity habitats suffer a disproportionate increase in consumption and are often suppressed substantially, whereas resources in more productive habitats are less affected.

We stress that these phenomena (flow, consumer movement, subsidized consumers, suppression of resources in low-productivity habitats) can occur over all spatial scales. Although most of our examples used distant areas or distinct habitats to illustrate these effects, such dynamics can occur sympatrically among microhabitat patches (e.g., Dial, 1992) or even intermingled plant species (e.g., Flaherty, 1969) that differ in productivity.

Such suppression is decoupled from in situ productivity (Holt, 1985; T. Oksanen, 1990). Consequently, consumer subsidy is inconsistent with most dynamics and ratio- and prey-dependent consumer-resource models developed to explain the patterns of abundance based solely on in situ productivity (e.g., Oksanen et al., 1981, Oksanen, 1988, Arditi and Ginzburg, 1989, Holt, 1985, and T. Oksanen, 1990).

Food Web Dynamics in Time

A community can vary over ecological time in three basic ways: externally imposed variation (e.g., due to weather, disturbance), endogenous variation (e.g., as in succession, predator-prey dynamics), and in species composition via colonization and extinction. We focus on how such variation influences the dynamics of consumers, their resources, and food webs.

Food Web Consequences of Changes in Productivity through Time

Productivity is a function of rainfall, temperature, light, nutrients, and species composition; all vary through time. Temporal patterns in productivity vary from relative constancy (e.g., in the equatorial tropics) to sharp pulses with all production in bursts separated by intervals with little or no net primary productivity (e.g., deserts and other extreme environments). Productivity varies temporally at scales from hours (e.g., diel cycles of photosynthesis) to months (e.g., spring blooms, summer growing seasons) to years (e.g., wet and dry years, El Niño periods).

Here we concentrate on how temporal variation in productivity influences consumer-resource dynamics. We feel a useful analogy can be drawn between temporal variation in productivity and spatial variation among habitats and find it useful to dichotomize time (as we did space) into more or less productive periods or habitats. Noy-Meir (1973, 1974) proposed the pulse-reserve hypothesis to explain the responses of populations to the extreme variation in productivity that characterizes deserts. We contend that similar processes occur to various degrees in all communities and suggest that this conceptualization is a robust, general way to incorporate temporal variability in productivity into community and food web theory.

Noy-Meir argues that plants and animals grow and establish reserves (e.g., seeds, tubers, tissue, fat, eggs) during good (wet) times; these reserves maintain the population or individual during interim lean (dry) periods. Large quantities of detritus are also produced during good periods. Thus, great stores of living tissue and detritus from productivity pulses form a reserve that is slowly released during long intervals of low productivity. The consensus is that such temporal translocation of organic matter and energy from good to bad times is central to the dynamics of desert communities (Noy-Meir, 1973, 1974; Polis, 1991b). Autecologically, it allows primary producers and consumers to persist during periods of little or no water availability and net primary productivity: perennial plants stay alive on their own reserves and annual plants remain dormant seeds in the soil; primary consumers survive on stored living plant tissue, dormant seeds, and/or detritus; and predators metabolize fat reserves and derive much of their energy from detritivores and granivores.

Such pulsed production and storage of reserves permitting persistence from good times to bad occurs to some degree in all (seasonal) habitats from boreal forests to temperate grasslands and tropical savannas to temperate streams and lakes to marine pelagic and benthic systems. For example, in eutrophic marine systems, episodic blooms of phytoplankton fuel great reproduction and growth by consumers; in some cases, primary productivity exceeds consumer requirements and a great proportion flows directly into the decomposer system. Here it is eventually eaten by abundant benthic detritivores or stored and gradually released to consumers via consumption or upwelling (Barnes and Hughes, 1988).

This process can significantly influence the dynamics and structure of communities and food webs. First, the entire community is stabilized in the sense that temporally supplemented species are not lost during unfavorable periods. Second, during less productive periods, the use of reserves maintains higher populations of consumers than possible from current levels of productivity (analogous to

the input of allochthonous resources subsidizing consumer populations at higher levels than maintained by in situ productivity). Third, most primary productivity is stored as detritus when it is converted into large populations of detritivores and eventually released into the plant-herbivore-consumer food web as nutrients to plants and prey for consumers (Polis and Strong, in press). This gradual reinfusion of detrital material should dampen the destabilizing effects of pulsed productivity. Fourth, temporal supplementation can alter consumer-resource dynamics.

Higher consumer numbers should depress resource populations below levels expected if the consumer did not use reserves (as with a spatial subsidy). In some cases, temporally supplemented consumers can suppress eruptions in resource populations and dampen cycles and the destabilizing effects of pulses of productivity (as expected from classic time lags when prey and predator growth are out of phase; see krill and copepod examples below). These proposed dynamics are functions jointly of the sequence of favorable to unfavorable periods, and the storage capacity and life history strategies of resources and consumers (see below). Large numbers of healthy consumers emerging from a good period will tend to exert a much greater effect on their resources as compared to those few consumers surviving a poor period. Conversely, consumer numbers may decrease during poor periods, sometimes to the point where low consumer populations cannot regulate their resources, especially at the onset of productive conditions (potentially initiating destabilizing time lags).

Storage capacity describes the manufacture, use, and release of reserves produced during favorable periods. Chesson and Huntley (1988, 1989) analyzed storage effects in the context of competitive coexistence. Their models highlighted the idea that long-lived life history stages (adults of many species, dormant seeds, cysts, or other resting stages) or tissue (fat, roots, and rhizomes of long-lived perennial plants) buffer population decline during unfavorable conditions, including competitive interactions. Here, we take the same insight—that energy and material is stored from good times—and focus on how storage influences web and consumer-resource interactions. Large age classes of long-lived species can exert persistent and large effects on their resources and consumers for many years.

The dynamic effects of storage reflect three factors. The trophic position of storage matters. Storage by predators generally should depress resources because it allows predator persistence when prey are rare. Storage by resources (detritus, seeds, prey) with gradual release to consumers should generally stabilize consumer-resource relationships. Second, the length of the interval between pulses of productivity influences the proportion of reserves depleted. Long periods between pulses of high productivity will reduce consumer abundance, consequently impeding resource suppression at the next productive period. This process underlies the evolution of masting by plants (e.g., bamboos) and synchronous reproduction in periodic insects (e.g., cicadas) (Janzen, 1976). Third, the rate of release of reserves influences dynamics. Reserves used slowly and regularly (e.g., detritus and seeds) will likely stabilize consumer populations and consumer-resource dynamics, compared to reserves released rapidly (e.g., leaves or fruit). This speculation may explain the observation that populations of desert detritivores and granivores are often much more stable than populations of desert herbivores (Louw and Seely, 1982; Seely, 1991).

Life history response to variable productivity is particularly important. Life histories are generally such that predators usually take much longer to recover from low populations compared to prey. Thus, frequent disturbance or highly variable productivity should benefit prey because low predator populations cannot increase as rapidly as prey. Within a trophic level, species vary in their response to productivity pulses; some closely track changes, whereas others are relatively insensitive (Louw and Seely, 1982; Howarth, 1983; Polis, 1991b; Polis and Yamashita, 1991). Thus populations of opportunistic (fugitive or r-selected) consumers should fluctuate widely within and between years in response to food; they grow exponentially during benign periods and decrease precipitously during unfavorable conditions. Conversely, populations of equilibrial (K-selected) species

are less tightly linked to short-term changes in resources and are relatively stable regardless of great changes in productivity. Equilibrial species possess a suite of adaptations to variable productivity that allow them to maintain relatively stable and often large populations throughout long periods of unfavorable conditions. Opportunistic and equilibrium species exhibit different but complementary predator-prey dynamics. Opportunistic species provide a rapid numerical response to prey, whereas long-lived equilibrium species provide a constant source of consumption, even during prolonged periods of low food availability and at the onset of productivity pulses. Thus traits of both opportunistic and equilibrial species each tend to stabilize prey populations especially during periods of increase.

Chesson and Huntley (1988, 1989) discuss how life history traits affect storage. They suggest that storage is particularly important in species with high temporal variability in abundance and recruitment. Citing fish, they give evidence that adults from a particularly successful recruitment class can dominate the population for many reproductive periods and give rise to a strong year class during favorable conditions (also see Persson and Johansson (1992)). Such populations exhibit a storage effect; adult densities often remain high for many years, despite large variations in resources for early life stages. As argued above, storage effects at the individual level permit survival during unproductive periods. For example, a diversity of predators ranging from scorpions to vipers respond to variable productivity by gorging during good times and starving, often for long periods, during poor periods (Louw and Seely, 1982; Polis, 1991b).

We now illustrate some of these proposed dynamic effects. Dayton (1989) found that temporal variation in productivity greatly influenced dynamics in an Antarctic benthic community. In the 1960s, extensive anchor ice made most organisms rare including a dominant sponge (*Homaxinella*) and its predators. In the 1970s, anchor ice was reduced and *Homaxinella* covered 50–80% of the substrate; although many predators appeared, they did not limit *Homaxinella*. In the 1980s, much anchor ice formed and *Homaxinella*

was virtually eliminated. However, an order of magnitude more predators were present in the 1980s compared to the 1960s although *Homaxinella* densities were similar.

Differences in life cycle and storage capacity by dominant copepods may be key factors structuring communities in large areas of the ocean (Parsons and Lalli, 1988). In the temperate North Atlantic, *Calanus finmarchicus* overwinters at shallow depths in relatively warm water and thus maintains few energy reserves for the spring. Thus, *Calanus* must feed before it reproduces in the spring and exhibits a poor, delayed numerical response to spring phytoplankton production. Because of this time lag, the phytoplankton bloom is suppressed later in the same year by multiple generations of *Calanus*. In the temperate North Pacific, larger *Neocalanus plumchrus* overwinter at deeper depths in colder water and thus maintain greater energy reserves. In spring, *Neocalanus* does not need to feed to produce eggs and exhibits an efficient numerical response to phytoplankton production. With no time lag, phytoplankton are suppressed by this one generation of *Neocalanus* and do not bloom. Although overall productivity is similar in these two communities, life cycle and storage differences totally alter consumer-resource dynamics. Parsons and Lalli (1988) suggest that such differences extend throughout the entire community. In the North Atlantic, ungrazed spring phytoplankton production enters the benthic food web as detritus where, they speculate, it is eventually expressed in a rich fishery of demersal fish (e.g., cod, haddock, pollock, hake, flatfish). In the North Pacific, phytoplankton biomass remains in the pelagic food web and ultimately supports a productive pelagic fishery (e.g., mackerel, salmonids, jacks).

Earlier, we discussed the dynamics of grazers and their phytoplankton resources. Antarctic krill (Smetacek et al., 1990) maintained high populations by living on stored reserves and eating ice algae during winter periods of low plankton production and thus could suppress blooms during spring and summer periods of high productivity.

The temporal dynamics of sea urchins are a particularly important determinant of kelp bed communities. Under certain conditions (e.g., extirpation of otter predators), urchin

grazing can eliminate most macroalgae and produce a community of encrusting coralline algae and unpalatable species (Elner and Vadas, 1990). Such urchin barrens can be maintained for long periods when urchins remain at high densities by eating alternative foods and metabolizing stored reserves (Duggins, 1980). Thus historically high food levels produced large populations that continue to depress their resource long after the pulse has passed.

Food Web Dynamics: Life History

The life history traits of a species in large measure determine how its dynamics will play out through time and across space. The major life history traits are usually considered to be growth trajectories (size from time of birth through life), age and size at maturity, age- and size-specific mortality patterns, age- and size-specific fecundity patterns (Stearns, 1992). A particularly important set of life history patterns not easily reduced to these traits stems from the response of species to temporal variation in the environment (see below). Superimposed on these basic life history traits, many significant aspects of a species' biology change systematically with age or stage, including diet (see below), the suite of natural enemies, competitive ability, dispersal mode, and habitat choice. Much of the complexity of food web dynamics stems from the fact that communities comprise a mixture of species with radically differing life histories. In effect, the life history of a species defines its role as a conduit that transfers resources from one time period to the next, and often from one place to another. Moreover, life history strategies often match major environmental features (e.g., time since disturbance), with predictable consequences for food web patterns (see below).

The Effects of Age Structure/Ontogenetic Shifts on Consumer-Resource Interactions

Life history omnivory (different stages eat different resources) is common in species that undergo ontogenetic shifts in habitat; diet changes substantially with life stage either discontinuously (e.g., at metamorphosis) or slowly with growth (Wilbur, 1980; Polis,

1984, 1988; Werner and Gilliam, 1984; Mittelbach et al., 1988; Olson and Olson, 1989). Such life histories are exhibited by most metazoan species; Werner (1988) estimates that 80% of all animal species metamorphose. Resources of such species can span a size range of three to four orders of magnitude. Even among nonmetamorphic species, diet often changes greatly among age classes; size differences make age classes of many such species more distinct in their diets than most biological species (Polis, 1984).

Radical changes in habitat and diet are a dramatic illustration of ontogenetic shifts. Most amphibians and many insects feed and grow as larvae in water and feed as adults on land. Either the aquatic or terrestrial environment can be more productive (Werner and Gilliam, 1984; Wilbur, 1988). A tremendous diversity of marine consumers forage in different habitats during ontogeny. Juveniles often, but not always, forage in more productive environments than do adults. For example, benthic species with planktotrophic (feeding) larvae allow littoral and continental shelf macrofauna to eat planktonic production (Barnes and Hughes, 1988). The efficacy of this strategy varies with latitudinal patterns of productivity. Production is continuous over tropical shelves and here some 80–85% of benthic species have planktotrophic larvae; in temperate regions, productivity is seasonal and 60% of larvae are planktotrophic; in polar zones, primary productivity peaks for only a few weeks and planktotrophic larvae do not occur. Similarly, the life history of marine nektonic crustacea, fish, and squid place them in areas most productive for growth of that stage: early development occurs in nursery areas (semienclosed bays, lagoons, and estuaries) rich in juvenile food and adults return to the open ocean to feed (Barnes and Hughes, 1988). In some deep-water species (e.g., angler fish), pelagic eggs move young from aphotic to photic zone where they are able to feed; adults migrate back to aphotic. In tropical rivers that flood, many fish produce pelagic eggs that float into floodplains to hatch. Juveniles feed in these rich areas before returning to the river where primary productivity is low (Welcomme, 1979; Goulding, 1980).

Such life history shifts can either impede consumer control or suppress resources via

dynamics similar to those of spatial subsidy. The strength of coupling between any one consumer stage and its resources is dependent on the relative resource supply of each stage (R_s) of a consumer species (see Wilbur (1980); we use *resource supply* in the sense that the abundance of food resources sets the potential maximum population size of that stage). Stages moving from relatively greater to less productive conditions will tend to saturate the less productive environment at initial abundances (N_s) greater than the maximum that could be supported by the R_s of that environment (i.e., $N_s > R_s$). Thus, relatively high resource levels for one stage will make consumer control of resources by the next stage more likely. Conversely, stages coming from conditions of relatively low to high resource levels will undersaturate the R_s of the more productive conditions (i.e., $N_s < R_s$); this will impede the regulatory abilities of the stage in the more productive conditions and potentially disrupt recipient control.

Many examples show that stage-specific resource levels (R_s) vary greatly with significant effects upon numbers of that stage (N_s). Relative levels of productivity and mortality are hypothesized to be the two selective forces explaining metamorphosis and habitat shifts (Werner and Gilliam, 1984; Wilbur, 1980, 1988). These authors show clearly for a great many species that different stages experience different conditions of resource availability. Migratory diadromous fish grow primarily in the more productive habitat (ocean or freshwater) and move as adults into the less productive habitat to reproduce (Gross et al., 1988); the abundance of adults is always greater than would be supported by their oligotrophic habitat.

Stage-specific resource limitation may be a major source of observed patterns of variation in recruitment success. For example, larval stages of amphibians (Wilbur, 1980), many marine fish and invertebrates (Birkeland, 1982, 1989; Olson and Olson, 1989) and insects (Prout and McChesney, 1985) are often severely food-limited, whereas adult R_s stages are not. This suggests that adult R_s is greater than that of larvae (although the opposite may occur via recruitment limitation (Wilbur, 1980)). In general, widespread ontogenetic bottlenecks (Werner and Gilliam, 1984) occur because stage-specific resources

(R_s) differ. For example, large piscivorous perch are not resource-limited in highly productive lakes, but juvenile recruitment to these stages is resource-limited (Persson and Greenberg 1990; also see dramatic examples in Larkin and Smith (1954), Werner and Gilliam (1984), and Lasenby et al. (1986)). Very high to very low productivity alternate from the wet to dry seasons in Venezuelan swamps (Winemiller 1989a and b, 1990) and rivers in the Amazonian Basin (Welcomme, 1979; Goulding, 1980). In the wet season, early stages of fish grow rapidly in an environment of resource abundance. These large populations experience moderate to severe resource shortages during the dry season (i., $N_s > R_s$) resulting in resource depletion, mass mortality, and an annual population bottleneck.

Experiments and models by Mittelbach, Osenberg, and colleagues have delineated particularly well the relationship between R_s and N_s for juvenile and adult stages in sunfish populations (Mittelbach and Chesson, 1987; Mittelbach et al., 1988; Mittelbach and Osenberg, 1993). They showed that resource availability (R_s) at one stage significantly influences resource use and suppression at the other stage. When resource availability is high for juveniles, adults increased to saturation and overexploited their resources (i.e., $N_s > R_s$); when juvenile resources are low, adults do not depress their resources, as $N_s < R_s$. In general, complex life histories accompanied by stage-specific use of resources that differ in type and abundance can either impede top-down control (if $N_s < R_s$) or produce recipient control and resource suppression (if $N_s > R_s$).

Food Webs and Life History Strategies

Recently, Winemiller and Rose (1992) distinguished three end points in a life history continuum describing attributes of North American freshwater and marine fishes. The basic pattern is remarkably similar to that reported for neotropical fishes (Winemiller, 1989b) and can account for patterns of variation in other higher taxa ranging from plants to insects (Winemiller, 1992). Opportunistic species have high reproductive rates (but low absolute fecundities) and mature early at small sizes. Due to their short population turnover rates and large intrinsic rates of in-

crease, these organisms rapidly colonize appropriate habitats following disturbances (i.e., colonizing or weed species) and rapidly respond to changes in resources. Equilibrium species delay maturation, exhibit low reproductive rates and fecundities, but invest more resources in each offspring, resulting in enhanced early survivorship. These species are presumably better equipped to cope with competition and predation in relatively saturated habitats (sensu K-selected species of Pianka (1970)). The third end point consists of periodic life history: these species delay maturation until attainment of body sizes large enough to permit production of extremely large clutches of small offspring. Even though average survivorship of early life stages is exceedingly low, periodic species frequently produce strong recruitment classes under favorable conditions, and adults may persist in the community for many years, even decades. Hence, it is the periodic species with highly variable episodes of recruitment that exhibit the greatest population storage effect, as touched on earlier.

What are the effects of different life histories on population regulation and food web dynamics? We identified at least two: (1) An influence of the intrinsic rate of increase in prey relative to its predator—the direction and magnitude of change is to a degree, system dependent; and (2) the potential uncoupling of predator density from changes in resource density due to ontogenetic niche shifts and the storage effect in long-lived species. The life historical perspective on food webs leads to some interesting contrasts in the dynamics of terrestrial versus aquatic ecosystems.

Most aquatic ecosystems show a gradient of populations with short generation times and high intrinsic rates of increase among primary producers and consumers low in the trophic hierarchy leading to longer generation times and lower intrinsic rates of increase among higher consumers (Carpenter, 1988). Primary production in streams is largely derived from attached diatoms and filamentous algae. The grazer web in streams is joined with the detrital-microbial web, and both sources of production are consumed by a great variety of small aquatic invertebrates (mayflies, stoneflies, dipteran larvae, damselfly larvae, mollusks, etc.). In lakes, phyto-

plankton and microbes support zooplankton, which in turn serve as a resource for small planktivorous fishes. Fishes and other vertebrates that consume larger prey are affiliated mostly with relatively equilibrium- and periodic-type life histories (Winemiller and Rose, 1992). In aquatic systems, prey populations are persistent and resilient in the face of either chronic or periodic predation. Because of the time lag between predator and prey population dynamics, predator populations generally do not entirely deplete prey with short life cycles and high intrinsic rates of increase. However, due to the great storage effect of periodic- and equilibrium-type predators, great potential exists to uncouple the response of predatory fish population dynamics from variation in prey abundances. Periodic dominant year classes among predatory species is probably one factor that accounts for trophic cascades in aquatic communities (see also the earlier discussion of the potential influence of spatial heterogeneity, and Schindler et al. (this volume)).

In contrast to aquatic systems, most terrestrial systems contain a mixture of primary producers, some with short generation times and high rates of increase (e.g., annuals and other colonizing herbaceous plants, including asexually propagating forms) and others with very long generation times and low rates of increase (e.g., trees and many other woody plants). Throughout the life history spectrum, terrestrial plants display a diverse array of antiherbivore tactics, including qualitative (toxic secondary compounds) and quantitative defenses (compounds reducing relative nutritional content, thorns, mutualisms with ants) (Cates and Orians, 1975; Feeny, 1976; Polis and Strong, in press). Terrestrial consumers at all levels display a greater mixture of life history strategies than their aquatic counterparts. Invertebrate herbivores generally have short generations of less than one year and high rates of increase, but vertebrate herbivores may have very high (rodents) or very low (bison, elephants) intrinsic rates of increase. Many dominant herbivores feed on a variety of plants (ranging from herbaceous annuals to woody perennials), resulting in less sweeping communitywide changes. Outbreaks of herbivores do occur in some settings, and these have well-documented effects on target vegetation (e.g., prickly pear

cactus-*Cactoblastis* moth (Monro, 1967); Klamath weed-*Chrysolina* beetle (DeBach, 1974), urchin-kelp (Duggins, 1980), but for the most part, habitats are not denuded of plants. Terrestrial carnivores also show a range of life history strategies: spiders and predatory insects have high rates of increase compared with lions and eagles. Trophic cascades are a rarity in terrestrial habitats (Strong, 1992), and the great mixture of life history strategies at all levels of terrestrial trophic hierarchies may be partly responsible.

Community Assembly

The ideas and examples we have presented are largely concerned with the quantitative impact of spatial flows and temporal pulses, and, particularly, the asymmetric effect of high- on low-productivity places or periods. But there are more qualitative effects as well, effects which may be particularly significant in interpreting patterns at large spatial scales. Viewed over sufficiently long timescales, all local communities are ephemeral assemblages, created in the first place by the spatial process of colonization, and then modified in their composition by local extinction or evolution (Davis, 1986). Species colonization is a qualitative process, determining presence/absence of a given species in a community. Given that a species is present, its local dynamics may be quantitatively influenced by flow rates, as discussed and abundantly documented above. But even those species whose dynamics seem to be largely governed by in situ birth and death processes colonized the community at one time. Differences among sites (e.g., along a gradient) in food web structure may reflect differences in colonization and extinction dynamics.

The dynamics of community assembly (Diamond, 1975) are likely to be important in explaining food web patterns. Food web assembly has received some attention in the theoretical literature (e.g., Post and Pimm (1983) and Drake (1990)), but relatively little attention to date has been given to the spatial aspects of web assembly. A basic attribute of a food web is that it implies sequential dependencies of consumers on resources (including other consumers), a fact with a number of consequences. First, even in the absence of other interactions, spatial dynamics influencing species at low trophic rank (e.g., island area and distance effects in colonization/extinction) can indirectly imply spatial effects for species at higher ranks. Holt (1993, this volume) has developed an island biogeographic theory for food chains of linked specialists supported by basal plant species, and concludes that effects of area and distance may be stronger for species at high trophic rank. He suggests that such effects may be weaker if higher-ranked species have generalized diets (e.g., omnivory). Moreover, spatial flows of basal resources may confound this expectation. For instance, on some islands and in primary succession the earliest colonists may be predators able to subsist on an input of detritus (e.g., insect or bird carcasses (Polis and Hurd, this volume; and see above)). Second, trophic linkages imply a potential for species interactions leading to exclusion via exploitative competition (for shared resource) or apparent competition (for shared predation). Coupled with chance events in colonization, this can imply different pathways in community assembly, leading to noninvasible, alternative community status. Several authors have presented theoretical arguments suggesting that alternative states become quite likely as the number of available interacting species increases (Gilpin and Case, 1976; Pimm, 1982; Drake, 1990). Allee effects can readily generate alternative stable states even in systems with relatively few species, such as two prey sharing a predator (Holt, 1977). Systems with strong intraguild predation may be particularly prone to the existence of alternative states (Polis and Holt, 1992). Substantial spatial heterogeneity in web structure may thus exist, in the absence of any underlying persistent heterogeneity in the environment, because of the chance vicissitudes of colonization history.

Conclusions and Implications

It is useful to stand back for a second and place the above observations into the context of the historical development of food web theory. A substantial literature now exists devoted to food webs conceptualized as nodes connected by links, and emphasizing

statistics such as connectance and ratios of species at different trophic ranks. We could view this body of work as the fruition of the first historical phase in the development of food web ecology. We firmly believe that progress toward the next mature phase of food web studies mandates grappling with the complexities of spatial processes, temporal heterogeneity, and life history strategies. These strands must all be interwoven into a broad conceptual framework to arrive at a deep understanding of food web structure and dynamics.

Acknowledgments

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