

Effects of partitioning allochthonous and autochthonous resources on food web stability

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The flux of energetic and nutrient resources across habitat boundaries can exert major impacts on the dynamics of the recipient food web. Competition for these resources can be a key factor structuring many ecological communities. Competition theory suggests that competing species should exhibit some partitioning to minimize competitive interactions. Species should partition both *in situ* (autochthonous) resources and (allochthonous) resources that enter the food web from outside sources. Allochthonous resources are important sources of energy and nutrients in many low productivity systems and can significantly influence community structure. The focus of this paper is on: (i) the influence of resource partitioning on food web stability, but concurrently we examine the compound effects of; (ii) the trophic level(s) that has access to allochthonous resources; (iii) the amount of allochthonous resource input; and (iv) the strength of the consumer–resource interactions. We start with a three trophic level food chain model (resource–consumer–predator) and separate the higher two trophic levels into two trophospecies. In the model, allochthonous resources are either one type available to both consumers and predators or two distinct types, one for consumers and one for predators. The feeding preferences of the consumer and predator trophospecies were varied so that they could either be generalists or specialists on allochthonous and/or autochthonous resources. The degree of specialization influenced system persistence by altering the structure and, therefore, the indirect effects of the food web. With regard to the trophic level(s) that has access to allochthonous resources, we found that a single allochthonous resource available to both consumers and predators is more unstable than two allochthonous resources. The results demonstrate that species populating food webs that experience low to moderate allochthonous resources are more persistent. The results also support the notion that strong links destabilize food web dynamics, but that weak to moderate strength links stabilize food web dynamics. These results are consistent with the idea that the particular structure, resource availability, and relative strength of links of food webs (such as degree of specialization) can influence the stability of communities. Given that allochthonous resources are important resources in many ecosystems, we argue that the influence of such resources on species' and community persistence needs to be examined more thoroughly to provide a clearer understanding of food web dynamics.

Key words: allochthonous resources; compartmentalization; energetics; food webs; intraguild predation; persistence; resource partitioning; spatial subsidies; trophic specialization.

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INTRODUCTION

Energetic resources that enter into a habitat from a more productive habitat (allochthonous resources) frequently increase local productivity and, thus, influence community structure and stability (Vannote *et al.* 1980; Polis & Hurd 1995, 1996; Polis *et al.* 1996; Huxel & McCann 1998; Nakano *et al.* 1999). The input of allochthonous

resources takes diverse forms. Inputs include the movement of leaf litter into headwater streams or soil systems, organic compounds fixed in one habitat and flowing to another, marine pelagic productivity entering benthic zones, dry deposition into terrestrial systems, and the movement of prey species into habitats occupied by a predator or vice versa (Polis *et al.* 1996). In this paper, we focus on energetic resources entering food webs that may arise from the movement of detrital inputs or because of large scale predator/prey movements.

In coastal and marine island systems, allochthonous marine resources can greatly subsidize terrestrial food webs in areas of low productivity (Polis & Hurd 1995, 1996). In general, the movement of resources is in the direction of high to low productivity systems (Polis *et al.* 1996). We previously examined whether energetic allochthonous resources influenced food web stability (Huxel & McCann 1998). We found that low to moderate levels of allochthonous resources could stabilize food web dynamics, but that larger amounts destabilized these dynamics. Low to moderate input values allowed the system to maintain longer food chains; but, as the input increased, the system became unstable through the paradox of enrichment such that greater productivity resulted in higher consumer populations that then drove their prey to extinction (or deleted local resources) (Rosenzweig 1971; Abrams & Roth 1994). We also found that the impact of the inputs is largely determined by the trophic level that received the energy, a result that agreed with predictions made by Polis *et al.* (1996). Studies by Polis and Hurd (1995, 1996) showed that most of the energetic allochthonous resources into their system were at the detritivore level. However, mobile predators and/or prey can also result in large energetic fluxes across boundaries (Polis *et al.* 1996). Polis *et al.* (1996) hypothesized that bottom-up effects would dominate if the basal level received the input; whereas top-down effects would dominate if the top consumer level was the recipient. Huxel and McCann (1998) found that the level of the allochthonous resources influenced whether the system produced top-down or bottom-up control.

Thus, the major food web effects from allochthonous resources are indirect, resulting from an increase in the density of the recipient trophic level (see Polis *et al.* 1996; McCann *et al.* 1998).

The potential influence of the partitioning of autochthonous and allochthonous resources on these indirect effects has not been explored. Resource partitioning may allow a trophic level to persist by compartmentalizing the food web in a similar way to the way that pathways of omnivory create energetic shunts (compartments) in food webs (Polis & Strong 1996). These shunts funnel energetic resources from various resource compartments along pathways (links) in the food webs and have the potential to greatly influence the stability of food webs.

The effects of resource partitioning on competition among species at a particular trophic level (or across trophic levels in systems with omnivory) also need to be addressed (Cody 1968; Schoener 1974). McGehee and Armstrong (1977; Armstrong & McGehee 1980) found that competitors could persist on a single resource given non-linear dynamics, but only when the populations of the competitors are cyclic. Huxel and McCann (1998) found that the persistence of competitors depends on weak links between the competitors and their resource. This agrees with the findings of Armstrong and McGehee (1980) who suggest that coexistence of competitors can only occur when the growth rates of the competitors are below a particular threshold, thereby having a weak link between the prey and their growth rate. In this paper, we examine the impact of partitioning autochthonous and allochthonous resources on food web persistence in a model ecosystem. We are primarily concerned with the persistence of systems with different degrees of specialization under different scenarios of allochthonous input.

Allochthonous resources

Resources and organisms that move across habitat boundaries can be utilized by different trophic levels; the organisms that move across boundaries may also be of different trophic levels (e.g. predators and prey). Polis and Hurd (1996) demonstrated that most allochthonous resources are used by detritivores in their island system. Other systems influenced by allochthonous resources into the consumer level include: marine filter feeding communities in unidirectional currents or advective areas (Menge *et al.* 1996); soil communities (Moore & Hunt 1988; Strong *et al.* 1996); head-

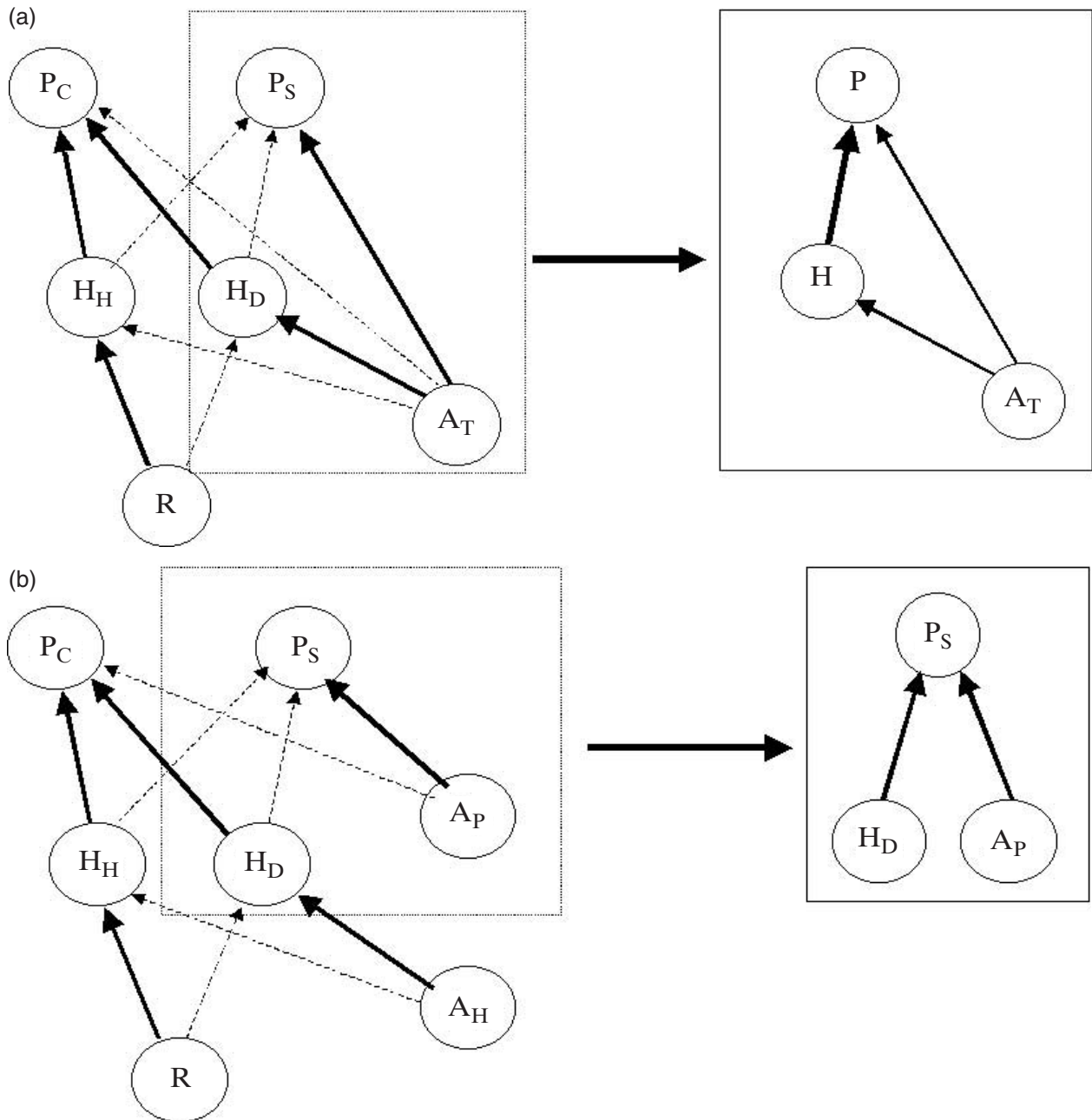


Fig. 1. Food web structures for two alternate scenarios of allochthonous resources: (a) a single allochthonous resource potentially available for both the consumer and predator trophic levels; and (b) separate allochthonous resources available for each consumer and predator. The dashed lines denote those links that are lost when the consumer or predator is a specialist. In the single allochthonous case (a), note that an intraguild predation interaction exists between predators and consumers that compete for the single resource (Polis *et al.* 1989; Morin 1999). These interactions are lost when the predators are strict specialists; however, a strong apparent competition interaction between the consumers then arises. In model system 2 (b), it is important to note that as both the consumers and predators become specialists, the food web develops into two separated compartments, with the allochthonous specialist predator (P_S) and its allochthonous resource (A_P) comprising one compartment. A_H , allochthonous resource available to the herbivore; A_T , total allochthonous resource; H , generalist herbivore; H_D , detritivorous consumer; H_H , herbivorous consumer; P , generalist predator; P_C , predaceous predator; R , basal species.

water streams that receive leaf litter and riparian insects (Nakano *et al.* 1999; Kawaguchi & Nakano 2001); and large order rivers that receive organic carbon from upstream sources (Vannote *et al.* 1980; Rosemond *et al.* 1993).

Allochthonous resource inputs into the top level include carrion or carcasses, the movement of prey species into the habitat and the movement of predators across habitats (Holt 1985; Thornton *et al.* 1990; Polis & Hurd 1995, 1996; Polis *et al.* 1996, 1997a; Vanni 1996; Nakano & Murakami 2001). For example, the Allen paradox (Allen 1951) describes cases in which secondary production within streams is insufficient to support the observed levels of fish production (Berg & Helenthal 1992). Similarly, Rose and Polis (1998) show that coyote populations along the coast in Baja California are highly subsidized by inputs from the ocean (47.8% of their diet) and maintain a higher density at the coast than in adjacent inland areas. These authors provided scores of cases of carnivorous mammals using aquatic foods. In general, predators moving along the interface between ecosystems (i.e. shorelines, river banks, benthic and pelagic systems) can utilize resources across habitats (Carpenter & Kitchell 1993; Polis & Hurd 1995, 1996; Rose & Polis 1998).

Allochthonous resources may enter at multiple trophic levels. The River Continuum Concept (Vannote *et al.* 1980) argues that headwaters provide allochthonous resources for systems at, and downstream from, the input. These inputs include prey, dissolved and particulate organic matter and litter fall. This type of pattern is also seen where rivers carry allochthonous resources into estuaries. Similarly, run-off from terrestrial to aquatic systems (and vice versa, marine to terrestrial) provides litter, dissolved and particulate organic matter and prey.

Flow of the allochthonous energetic resources through the food web may spread evenly throughout the community or may become compartmentalized (Fig. 1), depending on the amount of specialization in the food web. Systems dominated by generalists will distribute resources more evenly, while those dominated by specialists will exhibit more compartmentalization. This degree of specialization can have a strong influence on food web dynamics. McCann *et al.* (1998) demonstrated that systems with a more diffuse flow of

resources tend to be more stable. Thus, one would expect that generalist-dominated systems are more persistent than specialist-dominated systems. In this paper, we vary the feeding preference of species for, and availability of, allochthonous resources to assess if generalist webs are more stable than those of specialists. We defined stability as the persistence of the entire food web.

METHODS

Food web models

To examine the impact of resource partitioning of autochthonous and allochthonous resources on food web persistence, we start with the Yodzis and Innes (1992) parameterization of the Hastings and Powell (1991) tri-trophic food chain model. This model parameterization allows one to focus on consumer–resource systems that are biologically plausible. We used a parameter set (the chaotic parameter set from McCann & Yodzis 1995) that represents potential model outcomes due to differences in empirically observed body size relations (Yodzis & Innes 1992; McCann & Yodzis 1994b). We extend the work of Huxel and McCann (1998) by separating the consumer and top predator trophic levels into two ‘trophospecies’ that allows one to investigate the differences in community persistence in generalist- and specialist-dominated systems.

Allochthonous resources and food chain resources are different and may be separated in space. The movement of consumers and predators across habitat boundaries to feed can contribute substantially to productivity within a food web (Carpenter & Kitchell 1993; Polis & Hurd 1995, 1996; Persson *et al.* 1996; Polis & Strong 1996; Polis *et al.* 1996, 1997a). The preference for the two resources are varied such that the trophospecies of the recipient trophic levels range from generalists with equal preference for the two resources to specialists that feed entirely on one resource. In all cases, each trophospecies feeds on a different resource. Thus, we examined the two extreme and the two intermediate cases in which specialization is not complete, but where there is a strong preference for one type of resource.

Our model systems also differ from the system of Huxel and McCann (1998) in another important

way. Whereas Huxel and McCann (1998) assumed that the rate of allochthonous resource input occurred on a timescale faster than population growth so that the amount of allochthonous resource remained constant, here we assume that these two processes occur on a similar time frame so that allochthonous resources are utilized each time step.

The system with a single allochthonous resource entering into both the consumer and top predator level (model system 1; see Fig. 1a) can be written as:

$$\begin{aligned} \frac{dA_T}{dt} &= I - x_c y_c H_H \left(\frac{(1-\omega_1)A_T}{\omega_1 R + R_0 + (1-\omega_1)A_T} \right) \\ &\quad - x_c y_c H_D \left(\frac{(1-\omega_2)A_T}{\omega_2 R + R_0 + (1-\omega_2)A_T} \right) \\ &\quad - x_p y_p P_C \left(\frac{(1-\omega_3)A_T}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_T} \right) \\ &\quad - x_p y_p P_S \left(\frac{(1-\omega_4)A_T}{\omega_4 H_H + \omega_4 H_D + H_0 + (1-\omega_4)A_T} \right) \\ \frac{dR}{dt} &= R \left(1 - \frac{R}{K} \right) - x_c y_c R \left(\frac{\omega_1 H_H}{\omega_1 R + R_0 + (1-\omega_1)A_T} \right. \\ &\quad \left. + \frac{\omega_2 H_D}{\omega_2 R + R_0 + (1-\omega_2)A_T} \right) \\ \frac{dH_H}{dt} &= -x_c H_H + x_c y_c H_H \left(\frac{\omega_1 R + (1-\omega_1)A_T}{\omega_1 R + R_0 + (1-\omega_1)A_T} \right) \\ &\quad - x_p y_p H_H \left(\frac{\omega_3 P_C}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_T} \right. \\ &\quad \left. + \frac{\omega_4 P_S}{\omega_4 H_H + \omega_4 H_D + H_0 + (1-\omega_4)A_T} \right) \\ \frac{dH_D}{dt} &= -x_c H_D + x_c y_c H_D \left(\frac{\omega_2 R + (1-\omega_2)A_T}{\omega_2 R + R_0 + (1-\omega_2)A_T} \right) \\ &\quad - x_p y_p H_D \left(\frac{\omega_3 P_C}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_T} \right. \\ &\quad \left. + \frac{\omega_4 P_S}{\omega_4 H_H + \omega_4 H_D + H_0 + (1-\omega_4)A_T} \right) \\ \frac{dP_C}{dt} &= -x_p P_C \\ &\quad + x_p y_p P_C \left(\frac{\omega_3 H_H + \omega_3 H_D + (1-\omega_3)A_T}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_T} \right) \end{aligned}$$

$$\begin{aligned} \frac{dP_S}{dt} &= -x_p P_S \\ &\quad + x_p y_p P_S \left(\frac{\omega_4 H_H + \omega_4 H_D + (1-\omega_4)A_T}{\omega_4 H_H + \omega_4 H_D + H_0 + (1-\omega_4)A_T} \right) \end{aligned}$$

The system with separate allochthonous resources entering into each of the consumer and top predator levels (model system 2; see Fig. 1b) can be written as:

$$\begin{aligned} \frac{dA_C}{dt} &= I_C - x_c y_c H_H \left(\frac{(1-\omega_1)A_C}{\omega_1 R + R_0 + (1-\omega_1)A_C} \right) \\ &\quad - x_c y_c H_D \left(\frac{(1-\omega_2)A_C}{\omega_2 R + R_0 + (1-\omega_2)A_C} \right) \\ \frac{dA_P}{dt} &= I_P \\ &\quad - x_p y_p P_C \left(\frac{(1-\omega_3)A_P}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_P} \right) \\ &\quad - x_p y_p P_S \left(\frac{(1-\omega_4)A_P}{\omega_4 H_H + \omega_4 H_D + H_0 + (1-\omega_4)A_P} \right) \\ \frac{dR}{dt} &= R \left(1 - \frac{R}{K} \right) - x_c y_c R \left(\frac{\omega_1 H_H}{\omega_1 R + R_0 + (1-\omega_1)A_C} \right. \\ &\quad \left. + \frac{\omega_2 H_D}{\omega_2 R + R_0 + (1-\omega_2)A_C} \right) \\ \frac{dH_H}{dt} &= -x_c H_H + x_c y_c H_H \left(\frac{\omega_1 R + (1-\omega_1)A_C}{\omega_1 R + R_0 + (1-\omega_1)A_C} \right) \\ &\quad - x_p y_p H_H \left(\frac{\omega_3 P_C}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_P} \right. \\ &\quad \left. + \frac{\omega_4 P_S}{\omega_4 H_H + \omega_4 H_D + H_0 + (1-\omega_4)A_P} \right) \\ \frac{dH_D}{dt} &= -x_c H_D + x_c y_c H_D \left(\frac{\omega_2 R + (1-\omega_2)A_C}{\omega_2 R + R_0 + (1-\omega_2)A_C} \right) \\ &\quad - x_p y_p H_D \left(\frac{\omega_3 P_C}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_P} \right. \\ &\quad \left. + \frac{\omega_4 P_S}{\omega_4 H_H + \omega_4 H_D + H_0 + (1-\omega_4)A_P} \right) \\ \frac{dP_C}{dt} &= -x_p P_C \\ &\quad + x_p y_p P_C \left(\frac{\omega_3 H_H + \omega_3 H_D + (1-\omega_3)A_P}{\omega_3 H_H + \omega_3 H_D + H_0 + (1-\omega_3)A_P} \right) \end{aligned}$$

$$\frac{dP_S}{dt} = -x_p P_S + x_p y_p P_S \left(\frac{\omega_4 H_H + \omega_4 H_D + (1 - \omega_4) A_p}{\omega_4 H_H + \omega_4 H_D + H_0 + (1 - \omega_4) A_p} \right)$$

where consumer–resource interactions use type II functional responses, R is the basal species; H_H and H_D are the herbivorous and detritivorous species, respectively; of the consumer trophic level, P_C and P_S are the predaceous and scavenger species, respectively; of the top predator trophic level, A_T is the single resource for both the consumer and predator and A_C and A_p are the allochthonous resources into the resource and consumer trophic levels, respectively; R_0 and H_0 are the half saturation points for the functional response between the resource and consumer levels and the functional response between the consumer and predator levels, respectively; x_i is the mass-specific metabolic rate of trophic level i , measured relative to the production-to-biomass ratio of the resource density; y_C is a measure of the ingestion rate per unit metabolic rate of the basal trophic level by consumer trophospecies; and y_p is a measure of the ingestion rate per unit metabolic rate of the predaceous trophospecies. The reason for parameterizing the equations in this manner is so that the x_i parameters scale allometrically with individual body size, while the metabolic types of animals constrain the plausible ranges of parameter y_i (Yodzis & Innes 1992). Specifically, y_i lies within the interval $(1, y_{imax})$, where the value of y_{imax} depends on the metabolic type of species i (see Yodzis & Innes 1992). The values given by Yodzis and Innes (1992) for x_i are derived from the ratio of predator to prey biomass dependent on a coefficient for metabolic rate appropriate to the metabolic type of the species i . Hence, the parameters are biologically plausible, representing realistic predator/prey ratios in body size found in data surveys (Peters 1983; Cohen *et al.* 1993). The ω_i 's are the feeding preference parameters; A_C and A_p are the allochthonous resource parameters to the consumer and predator trophic levels, respectively.

Numerical analyses

We performed numerical analyses over a range of allochthonous resources and over several levels of specialization for the two allochthonous resource

scenarios (one resource for both consumer and predator; separate resources for consumer and predator). We present results from two parameter sets that represent a wide range of consumer–resource dynamics from chaos ($x_C = 0.4$, $y_C = 2.009$, $R_0 = 0.16129$, $x_p = 0.08$, $y_p = 5$, $H_0 = 0.5$) to stable equilibria ($x_C = 0.4$, $y_C = 2.009$, $R_0 = 0.5$, $x_p = 0.01$, $y_p = 5$, $H_0 = 1.5$) (McCann & Yodzis 1994a; McCann & Hastings 1997; Huxel & McCann 1998). Qualitatively similar results were found using an intermediate parameter set that exhibits limit cycles; these are not presented for brevity. Additionally, because we wanted to examine only the influence of the degree of specialization, we held the appropriate parameter values constant for both trophospecies on each of the two higher trophic levels.

The analyses for each case were run for 250 integration steps and then the density means, variations and coefficients of variation were calculated over another 100 integration steps (for a total of 350 integration steps). The analyses were performed only on the final 100 time steps because the model systems produce transients. Similar transients are found in other coupled models (McGehee & Armstrong 1977; Armstrong & McGehee 1980; Engbert & Drepper 1994; Hastings & Higgins 1994; McCann & Yodzis 1994b; Hastings 1995; McCann & Hastings 1997; Hastings 1998; Huxel & McCann 1998; McCann *et al.* 1998). We set a minimum population density of 10^{-5} . For each allochthonous input scenario, analyses were performed over a range of H_H and P_C feeding preference values from $\omega_i = 0.50$ (generalist case) to $\omega_i = 1.00$ (strict specialist case) for each species on the recipient trophic level, where $i = 1$ for H_H and $i = 3$ for P_C . The feeding preference of the detritivore (H_D) and the scavenger (P_S) were equal to $(1 - \omega_i)$ and $(1 - \omega_3)$, respectively. We performed numerical simulations of model systems 1 and 2 for several pairs of feeding preference values and at two values of allochthonous resources for model system 1 (high and low) and four values for model system 2 (high, high; high, low; low, high; and low, low) (see Tables 1–4 for values of feeding preference and allochthonous resources used). For the stable parameter set numerical simulations, we used 0.01 for the low values of allochthonous resources and 0.20 for the high levels. Because the chaos parameter set simulations always resulted in

Table 1 Model results for the single allochthonous resource model (model system 1) using the chaos parameter set. The table lists the species that persist in the model system after 350 time steps: 1=the basal species; 2=the herbivorous consumer; 3=detritivorous consumer; 4=the predaceous predator; and 5=the scavenger predator

Feeding Preference	Allochthonous Resource	
	High	Low
$\omega_1 = 1.00, \omega_3 = 1.00$	None	None
$\omega_1 = 1.00, \omega_3 = 0.90$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.75$	None	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 1.00$	None	None
$\omega_1 = 0.90, \omega_3 = 0.90$	None	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.75$	None	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 1.00$	None	None
$\omega_1 = 0.75, \omega_3 = 0.90$	None	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.75$	None	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 1.00$	None	None
$\omega_1 = 0.50, \omega_3 = 0.90$	None	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.75$	None	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5

Table 2 Model results for the single allochthonous resource model (model system 1) using the stable parameter set. The table lists the species that persist in the model system after 350 time steps: 1=the basal species; 2=the herbivorous consumer; 3=detritivorous consumer; 4=the predaceous predator; and 5=the scavenger predator

Feeding Preference	Allochthonous Resource	
	High	Low
$\omega_1 = 1.00, \omega_3 = 1.00$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.90$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.75$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 1.00$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.90$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.75$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.50$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 1.00$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.90$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.75$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.50$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 1.00$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.90$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.75$	2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.50$	2, 3, 4, 5	1, 2, 3, 4, 5

Table 3 Model results for the two allochthonous resource model (model system 2) using the chaos parameter set. The table lists the species that persist in the model system after 350 time steps: 1=the basal species; 2=the herbivorous consumer; 3=the detritivorous consumer; 4=the predaceous predator; and 5=the scavenger predator

Feeding Preference	Allochthonous Resource			
	High, High	High, Low	Low, High	Low, Low
$\omega_1 = 1.00, \omega_3 = 1.00$	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.90$	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.75$	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.50$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 1.00$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.90$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.75$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.50$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 1.00$	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.90$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.75$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.50$	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 1.00$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.90$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.75$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5

Table 4 Model results for the two allochthonous resource model (model system 2) using the stable parameter set. The table lists the species that persist in the model system after 350 time steps: 1=the basal species; 2=the herbivorous consumer; 3=the detritivorous consumer; 4=the predaceous predator; and 5=the scavenger predator

Feeding Preference	Allochthonous Resource			
	High, High	High, Low	Low, High	Low, Low
$\omega_1 = 1.00, \omega_3 = 1.00$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.90$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.75$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 1.00, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 1.00$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.90$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.75$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.90, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 1.00$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.90$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.75$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.75, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 1.00$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.90$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.75$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5
$\omega_1 = 0.50, \omega_3 = 0.50$	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5	1, 2, 3, 4, 5

all species becoming extinct at 0.20 for the high level, we used 0.10 instead. These values were chosen because we wanted to examine the influence of resource partitioning among different parameter sets at varying levels of specialization and allochthonous resources. This required that the systems be relatively stable. Based on the results from Huxel and McCann (1998), we hypothesized that these systems would be relatively stable at low levels of allochthonous resources.

RESULTS

Single allochthonous resource (model system 1)

The simulations with one resource for both consumers and predators (model system 1) were generally less persistent than the simulations with separate resources (model system 2) (Fig. 1). This was particularly true for simulations with the chaos parameter set that experienced extinction of all species for many simulation conditions. At a high level of allochthonous resources, species only persisted in simulations in which the predators

were generalists ($\omega_3 = \omega_4 = 0.50$), with one exception (Table 1). At low allochthonous resources all species persisted in the simulations in which there was some overlap in the diet of specialists ($\omega_3 < 1.00$). In the stable parameter simulations, although in no simulations did all species become extinct, at high allochthonous resources species *R* persisted only where the consumers were specialists ($\omega_1 = 1.00$, Table 2). The two consumer trophospecies showed a decrease in density with increasing generalization of the two predator trophospecies, but did not become extinct. The allochthonous specialist predator (*P_S*) increased in density as it became less specialized.

Separate allochthonous resources for consumers and predators (model system 2)

In simulations with the chaos parameter set with high allochthonous resources for the consumers, only when the consumers were generalists did all trophospecies persist (Table 3). Otherwise, the autochthonous specialist (*H_H*) became extinct. At low allochthonous resource for the consumers, *H_H* persisted at $\omega_1 = 1.00$ and $\omega_3 > 0.50$ (some preference for the allochthonous resources) and also

persisted at $\omega_i = 0.75$ (especially when the allochthonous resource for the predators was low).

In all of the simulations for the stable parameter set, all species persisted (Table 4). As with the chaos parameter set simulations with model system 2, R was maintained at its carrying capacity and showed little population fluctuation.

DISCUSSION

The results demonstrate that the following factors all influenced species' persistence and population level variance: (i) the trophic level(s) into which the allochthonous resource entered the community (model system 1 compared to model system 2); (ii) partitioning of allochthonous and autochthonous resources on food web stability; (iii) the amount of allochthonous resource input; and (iv) the strength of consumer–resource interactions. The results from these model systems also suggest that the effect of apparent competition on food web persistence as a result of resource partitioning may be stronger than the resultant decrease in indirect competition in high productivity systems. The last three factors (ii–iv) are discussed below within the context of the two model systems.

Model system 1

With a single allochthonous resource, the system exhibited greater persistence of species at low input relative to high input. This supports previous findings (Huxel & McCann 1998). Competition between consumers and predators for the same allochthonous resources resulted in greater reliance of the consumers (when they were generalists and intraguild predation was a factor) on the resource species (R), driving it to extinction in some cases. It is important to note that predators had access to most of the allochthonous resources either directly or indirectly via the consumers. Therefore, in these simulations with a single allochthonous resource, an intraguild predation situation arises in which the consumers and predators compete for allochthonous resources, yet the predators prey upon the consumers (Fig. 1a). Intraguild predation in model system 1 resulted in decreased stability compared to model system 2 in which no intraguild predation arises (Fig. 1b). This agrees with

the findings of other models that have examined the influence of strong intraguild predation on food web dynamics (Polis *et al.* 1997a; Holt & Polis 1998; McCann *et al.* 1998).

In simulations of model system 1 with high levels of input, generalization resulted in greater persistence with strong interactions (chaos parameter set); while for weaker interactions (stable parameter set), specialization produced greater persistence. This result occurred because specialization on the allochthonous resource in systems with large inputs resulted in increased densities of the specialist (and perhaps for the generalist with less competition). This allowed higher predator levels and a strong trophic cascade, eventually causing extinction of the autochthonous resource. However, in systems dominated by weaker links (the stable parameter set), specialization can lead to reduced pressure on the resource species (the basis of the autochthonous component), allowing it to persist.

These results support those of Raffaelli and Hall (1992) who tested Paine's hypothesis (1980) that strong functional predator–prey links should lead to compartmentalization. They found significant evidence for compartmentalization in published food webs. However, in field experiments involving the food web of the Ythan estuary, Raffaelli and Hall (1992) found no strong links and no compartments in the food web, which agrees with Paine's hypothesis.

Model system 2

Overall, model system 2 was more stable than model system 1. Several factors may account for this. First, in model system 2 specialization of the predators results in a two compartment food web (Fig. 1b), eliminating a strong indirect effect of the allochthonous resources utilized by the predators. Second, allochthonous resources entering both the consumer level and the predator level eliminated competition between the two trophic levels for allochthonous resources. Finally, having separate resources insured that the consumers had enough resources to ensure population growth to offset the losses due to predation.

The only species to become extinct in model system 2 was H_H and then only in simulations using the chaos parameter set (Table 3). When H_H

was a generalist in these simulations, it did not become extinct. This was probably due to its lower growth rate on the autochthonous resource for which it strongly competed against H_D when both were generalists. Lower growth rates of both consumers, then resulted in lower growth rates of the predators and a more stable system.

Role of allochthonous resources and interactions among food chains

Post *et al.* (2000) studied the community dynamics of systems with two food chains linked by a common top predator. This scenario is intermediate to our two model systems. They found that as prey preference values of the top predator moved from no preference (generalist predator feeding equally on both food chains: no compartmentalization) to strong preference for one of the prey (specialist predator feeding mainly on one food chain: compartmentalization), the system became more stable because chaos was eliminated. Their generalist model was developed to study the influence of a mobile predator moving between habitat boundaries (in this case a predatory fish that fed on littoral as well as pelagic prey). Thus, the mobile predator acts to transport allochthonous resources into the pelagic food web (Carpenter & Kitchell 1993; Polis *et al.* 1996; Vanni 1996; Huxel & McCann 1998).

In most cases, intermediate levels of specialization result in the least persistent systems. This is due to two effects. First, at low allochthonous input values and intermediate levels of specialization, the allochthonous specialist cannot persist because of apparent competition in which the higher densities of the autochthonous specialist increase predation pressure on the allochthonous specialist, causing it to become extinct. Thus, apparent competition should be more significant in systems that have high degrees of specialization for allochthonous versus autochthonous resources (but few obligate specialists). Second, at higher input levels, the allochthonous specialist may greatly increase its numbers and suppress the trophic level below it, even though it only derives a small part of its diet from these autochthonous resources. This suggests that food web interactions are stronger in more productive systems (Holt 1977; Polis & Hurd 1996; Spiller & Schoener

1996). However, this top-down effect is broken when the predators are obligate specialists so that the predator feeding only on the allochthonous resources does not influence the rest of the food web. Such specialization produces two separate or compartmentalized chains within the food web and the aforementioned exception to the trend that systems become less persistent as allochthonous input increases. However, for a number of reasons, we doubt that this occurs in nature very often.

Decreasing stability with increasing specialization influences the relative importance of local and regional processes (Ricklefs & Schluter 1993). Frank and Amarasekare (1998) suggested that increased specialization would result in increased extinction rates. This may be especially significant when resources for the specialists are highly variable. Similarly, any strong interaction that tends to destabilize food webs (such as intraguild predation; Polis *et al.* 1997a; Holt & Polis 1998; McCann *et al.* 1998) should result in increased importance of regional processes to maintain the system. Thus island systems that have increased species richness due to increased specialization may experience cycles: colonization by specialists; competition between generalists and specialists leading to extinction of generalists; and then extinction of specialists. Extinction of specialists occurs as their resource becomes limited due to environmental perturbations or overcompensation (because specialists have stronger interactions with their resource).

Model considerations

In model systems 1 and 2, the predators specialize on either allochthonous or autochthonous resources, but not among the consumer trophospecies. This has important consequences in real food webs. For example, in their island systems, Polis and Hurd (1995, 1996) found that >90% of prey for coastal terrestrial predators, such as scorpions, spiders and lizards, are detritivores that feed on marine detrital inputs. These abundant predators can suppress population densities of plant herbivores, thus decreasing plant damage (Polis & Hurd 1996). Similarly, Spiller and Schoener (1996) found that predatory spiders are highly selective, feeding mainly on detritivores and only on a limited set of herbivores, while predatory lizards feed

mainly on herbivores. However, the system presented here does not allow for preference of the predators between the herbivorous consumer and the detritivorous consumer. Preference of the predators on these competing trophospecies could have one of two effects: (i) if the preference is for the more competitive species or the species that achieves the highest population density due to resource availability, then predator-mediated coexistence will occur (Paine 1966; Caswell 1978); and (ii) if the inferior competitor is preferred, then the effect of apparent competition will be increased for the generalist case as compared to the specialist case (Holt 1977).

In our models, the amount of allochthonous resource input into the systems was constant at each time step. However, in natural systems the relative amounts of allochthonous and autochthonous resources can vary significantly over time. Polis *et al.* (1997b) demonstrated that during a wet El Niño year terrestrial plant cover increased 28.8-fold relative to dry non-El-Niño years. In systems that experience temporally varying allochthonous resources (on the same scale as population dynamics), the results should be intermediate to those found here, given that the amounts of allochthonous resources at any point in time do not vary significantly from those used in our model systems. Occasional large inputs (such as a whale washing ashore) may greatly inflate local detritivore/scavenger densities (Polis & Hurd 1995, 1996).

The model also assumes that the mass-specific metabolic rates and the ingestion rates of the consumers and predators are the same for allochthonous resources as for the autochthonous rates for which they were developed (Yodzis & Innes 1992). One could reasonably assume that these rates would differ between trophically similar species, especially given differences in specialists relative to generalists. Similarly, Crooks and Soulé (1999) showed that intermediate carnivore predators were more efficient at capturing birds and other small vertebrates. Also one might expect that differences exist depending on the diet of the species, for example, studies have shown that herbivore assimilation efficiencies/rates are much lower than those of carnivores. Furthermore, Huxel (1999) has shown that low food quality can influence consumer–resource interactions. Quality differences

exist among various allochthonous resources and among allochthonous and autochthonous resources (G. R. Huxel *et al.*, unpubl. data, 2001).

Finally, one can envisage, in a variety of systems, a number of autochthonous resources that mimic the dynamics of allochthonous resources, in that they are not recipient or ‘top-down’ controlled. These can be ephemeral resources, such as summer or winter annuals in desert systems, that experience significant year-to-year variation in biomass (Chesson & Huntley 1997). These resources add to the complexity of food webs, thereby increasing the influence of donor-controlled processes that occur in ‘multichannel omnivory’ systems (Polis & Strong 1996). One would expect that specialists on these ephemeral resources would also exhibit high levels of temporal and spatial variability thereby increasing the risk of extinction. These extinctions would then increase the role of regional processes and the interconnectedness of habitats (Frank & Amarasekare 1998).

The present results suggest that food webs dynamics are strongly influenced by: (i) resource partitioning; (ii) the trophic level(s) that have access to allochthonous resources; (iii) the amount of allochthonous resource input; and (iv) the strength of consumer–resource interactions. Thus, comprehension of the dynamics of a particular community will require understanding of the degree to which allochthonous resources play a role relative to autochthonous resources. This will necessitate examining the amount of allochthonous resources, the utilization of those resources by members of the community (and the trophic level of those members), and the strength of consumer–resource interactions on both allochthonous and autochthonous resources. Finally, our model systems support the intuitive ‘multichannel’ omnivory concept of Polis and Strong (1996) that suggests that real food webs are replete with direct and indirect connections and these multiple links are important forces in food web dynamics and stability. The results from these model systems imply that food webs that experience low to moderate inputs of allochthonous resources can exhibit increased species’ persistence and result in food chains becoming decoupled – weakening trophic cascades to trophic trickles (Huxel & McCann 1998; McCann *et al.* 1998). As research extends beyond the simple tritrophic food chain models to

include various components of multichannel omnivory, such as classical omnivory (Polis & Strong 1996; McCann & Hastings 1997) and allochthonous resources (Polis *et al.* 1997a; Huxel & McCann 1998; McCann *et al.* 1998), it is becoming clear that the dynamics of food webs are both complex and highly dependent on the diversity of trophic connections and connections with other systems.

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