



OMNIVOROUS FOOD WEB, PREY PREFERENCE AND ALLOCHTHONOUS NUTRIENT INPUT

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INTRODUCTION

Empirical and theoretical studies have pointed out the importance to consider not only the autochthonous materials along the food webs, but also to include allochthonous inputs and its influence on food web dynamics. In food chain models, theoretical results demonstrated that the effects of nutrient input on stability are well established, suggesting that low nutrient levels lead to stabilization when consumer species feed on autochthonous resources. On the other hand, if these inputs are increased or consumer preference turns to external resources, the dynamics become decoupled and species may be lost (Huxel and McCann, 1998). However, some empirical evidence suggests that allochthonous inputs (e.g. water to land and land to land) can sustain a major abundance of individuals resulting in longer food chains and webs (Polis et al. 1997).

In food web theory, omnivory - found to be widespread in nature - has an important role in stabilization of trophic systems due to its multichannel weak interactions among trophic levels (McCann et al. 1998). Notwithstanding its ubiquitousness and its influence on food web dynamics, few studies have focused on the influence of allochthonous nutrient input into omnivorous systems (Huxel and McCann, 1998; Huxel et al. 2002).

Given the importance of trophic interaction strength in omnivorous systems, this study purports to analyze the influence of allochthonous nutrient input into consumer level in the ultimate dynamics of an omnivory food web, where consumption is dictated by switching behavior to

the predators (i.e. based upon the relative prey densities, within the frame of predator switching).

OMNIVORY MODEL AND ALLOCHTHONOUS INPUT

A model for a three species omnivory food web with allochthonous input into the consumer trophic level (C) with all consumption rates described by a switching term can take the following form:

$$dR/dt = R(1-R/K) - \tilde{x}_2 x_c y_c RC / (R_0 + R) - \tilde{x}_1 x_p y_{pr} RP / (R_{02} + R)$$

$$dC/dt = \tilde{x}_2 x_c y_c RC / (R_0 + R) + \tilde{x}_1 x_c y_c A / (A_0 + A) - \tilde{x}_2 x_p y_{pc} CP / (C_0 + C) - x_c C$$

$$dP/dt = \tilde{x}_1 x_p y_{pr} RP / (R_{02} + R) + \tilde{x}_2 x_p y_{pc} CP / (C_0 + C) - x_p P$$

where R , C and P are resource, consumer and predator densities, respectively; K is the resource carrying capacity; R_0 , R_{02} are the half-saturation densities of the resource (R) and C_0 the half-saturation density of the consumer (C); x_c , x_p are the mass-specific metabolic rates; y_c , y_{pr} and y_{pc} are measures of ingestion rate of consumer species and predator. A_0 stands for the half saturation constant of the allochthonous input (A). The parameters set were held constantly (e.g. producing chaotic dynamics when a simple food chain took place).

Consumer prey preference between resource and allochthonous input (\tilde{x}_i) and predator prey preference between resource and consumer (\tilde{x}_i) were incorporated into the model as follows:

$$\tilde{x}_1 = w_1 A / (w_1 A + (1-w_1)R); \tilde{x}_2 = 1 - \tilde{x}_1$$

$$\tilde{x}_1 = w_2 R / (w_2 R + (1-w_2)C); \tilde{x}_2 = 1 - \tilde{x}_1$$

The parameter w_i (0 - 1) represents the preference degree of consumption of allochthonous input over

resource (R) consumption by consumer (C). Similarly, w_2 ($0 - 1$) describes the preference degree of consumption of resource (R) over consumption of consumer (C) by predator (P). The food web dynamics will be analyzed, by means of bifurcation analysis, with respect to preference term (w_1), basal productivity (K) and allochthonous input (A). In the case of preference, for $w_1 = w_2 = 0$ the omnivory model becomes a tritrophic food chain, while for $w_1 = w_2 = 1$, it becomes a decoupled food web with consumer consuming solely the allochthonous input and predator preying only upon the resource.

RESULTS AND DISCUSSION

Prey preference

A stable state is observed for $0 < w_1 < 1.0$, suggesting the lack of influence of this preference term on the system stability. Indeed, no extinction occurs whatsoever. Nonetheless, it is interesting to notice that resource level declines with increase of w_1 . In fact, when w_1 increases, C prefers A over R , which in turn, releases C from the competition on R with P . As a result C increases and since P significantly preys upon C ($1 - w_2 = 0.89$), its density also increases leading to a decrease of R despite its low preference for the basal resource ($w_2 = 0.11$).

Allochthonous input

The stability of the model remains unaltered irrespective of the allochthonous input values ($0 < A < 1.0$). Resource population declined with increases in A . It is important to remark that now C is strictly omnivorous (i.e., $w_1 = 0.5$), and hence, increases in A can significantly augment C density and its resource consumption rate. In turn, this increase in C makes P feed on C with a higher rate by virtue of its strong preference for consumer ($1 - w_2 = 0.89$). Consequently, P would also respond with increases in its density, strengthening its predation on R despite its low preference ($w_2 = 0.11$) for the basal species.

Gradient of productivity (enrichment)

The simulations suggest a steady state for C and P throughout the nutrient enrichment values (K), and consumer and predator can invade and persist irrespective of carrying capacity levels. The resource dynamic grows linearly, reaches a saturation level. It is interesting to observe that low values of K have a negative effect on the predator density. This may occur due to the fact that the predator is outcompeted by the consumer in the consumption of R . On the other hand, since

C consumes the allochthonous input and the resource, it experiences an increase in its density. Beyond a certain value of K , P is not outcompeted any longer by C , and the result of this competition yields an increase in P and a decrease in C .

Several empirical studies have analyzed the influence of allochthonous input on consumer trophic level (Polis et al. 1997) suggesting important changes in food web structure, interaction strength and abundance of the recipient trophic level. In this study, a constant allochthonous input was incorporated into the consumer level of an omnivory food web. Consequently, two coupled omnivorous food webs give rise: (1) predator - consumer - resource; (2) consumer - resource - allochthonous input.

As general outcomes, the prey preference simulation keeps the food web dynamics in a stable state in the long term throughout the parameters values of w_1 . Also, it is interesting to observe that the higher allochthonous nutrient input (A) the higher consumer and predator densities. This increase in consumer population was also observed by Rose and Polis (1998) studying coyotes population from the arid deserts of Baja California - densities of coyotes from coastal sites sustained by the allochthonous nutrient input from the Pacific Ocean were higher than those pertaining to coyotes from inland sites.

The effect of nutrient enrichment suggested both predators and consumers are able to invade and persist irrespective of the considered K levels. Many authors have suggested that allochthonous inputs can greatly subsidize terrestrial food webs in areas of low productivity increasing the population abundance of trophic levels or even sustaining a complex food web (Polis et al. 1997).

CONCLUSION

In conclusion, allochthonous input can alter food web dynamics influencing the interaction strength among populations, increasing "strong links" or "weak links" according to food web configuration and population densities of each trophic level. These effects that depend on factors such as amount and kind of allochthonous input, recipient trophic levels and consumption preference structure, can play an important role in the determination of food web dynamical outcomes.

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