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## IDEAL FREE HABITAT SELECTION AND CONSUMER-RESOURCE DYNAMICS

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*Abstract.*—In landscapes in which habitat patches are larger than the home ranges of consumers, ideal free habitat selection is incompatible with pseudointerference. Source-sink dynamics and spillover consumption can be generated only by nonequilibrium situations. At equilibrium, patterns in consumer and resource standing crops and resource mortality are identical to those generated by local dynamics. Predictions of laissez-faire models are relatively robust to feeding interference. Habitat selection of armored catfishes and their interactions with attached algae in a Neotropical stream are consistent with predictions derived by assuming laissez-faire consumer-resource dynamics and ideal free habitat selection, in spite of the limited mobility of consumers and the occurrence of substantial feeding interference. We propose that the simple null model of ideal free habitat selection plus laissez-faire consumption applies to the majority of herbivore-plant systems, because of the even distribution of resources and the lack of efficient weapons in consumers.

Interactions in food webs often occur over spatially heterogeneous landscapes. Heterogeneity may change the outcomes of trophic dynamics from those predicted by assuming homogeneous environments with self-contained dynamics (see, e.g., Rosenzweig 1971; Oksanen et al. 1981; Persson et al. 1988). One possible consequence of spatial heterogeneity is spillover consumption (Holt 1984), in which the energy obtained from high-quality habitats subsidizes exploitation of resources of low-quality patches, which by themselves could not support any consumers. In landscapes with small-scale spatial heterogeneity within the home ranges of individual consumers, spillover consumption can be created because of the lack of searching costs for haphazardly encountered food items (Oksanen et al. 1992a). In landscapes that are heterogeneous on a larger spatial scale, despotic habitat selection (Fretwell 1972) generates source-sink dynamics for consumers (Pulliam 1988), reflected as spillover consumption for resources residing in sink habitats and relatively weak consumption pressure for resources of source habitats (Oksanen 1990). Similar consequences can also be created by costly habitat selection (Morris 1988, 1992). Even with ideal free habitat selection, the applicability of spatially unstructured models to heterogeneous landscapes is unclear.

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According to the analysis of Kacelnik et al. (1992), patterns in standing crops and resource mortalities generated in heterogeneous landscapes by ideal free consumers differ substantially from those predicted by other researchers (Rosenzweig 1971; Oksanen et al. 1981). The difference may, however, be a consequence of a different approach to within-habitat dynamics by Kacelnik et al.

Another potential consequence of spatial heterogeneity is pseudointerference, in which an increase in consumer numbers influences consumer-resource encounter rates more strongly than could be explained on the basis of their impact on resource density, averaged over habitat patches (Hassell and May 1973, 1974, 1985; Free et al. 1977; Comins et al. 1992). One mechanism for pseudointerference is the failure of consumers to redistribute themselves in accordance with changes in resource distribution (Murdoch and Stewart-Oaten 1989). However, pseudointerference can also emerge as a consequence of optimal habitat selection in seemingly ideal free systems (Comins and Hassell 1979).

In spite of their apparent simplicity, the behavior of ideal free consumer-resource systems in heterogeneous landscapes thus appears to provide problems, which we will tackle in the present article. Our analysis is performed in the spirit of the original model of Fretwell and Lucas (1970; see also Fretwell 1972), in which habitat patches are assumed to be larger than the home ranges of individual consumers, although we will also discuss the impact on heterogeneity on a smaller spatial scale.

#### LAISSEZ-FAIRE SYSTEMS

In their model of ideal free habitat selection, Fretwell and Lucas (1970; Fretwell 1972) defined *habitat* as an area that is essentially homogeneous with respect to the physical and biological features relevant to the behavior and survival of the species and *suitability* as the average fitness of residents. (For the sake of consistency with current literature, suitability will be called *quality*.) The maximum value of the suitability of each habitat was defined as its *basic suitability*, to be called *intrinsic quality* in the present article. The ideal free model was then derived from the following assumptions: all individuals have perfect knowledge of the actual quality of each habitat, all individuals are free to settle in the habitat with the highest possible quality, all individuals within a habitat have the identical expected success rate, and the quality of the habitat decreases with increasing population density. As a consequence, the model predicts that individuals in different habitats will have similar fitness. The adverse impact of crowding in intrinsically superior habitats is assumed to balance differences in intrinsic quality. For resource-limited consumers, involved in laissez-faire interactions with their resources, the negative impact of increasing consumer density on habitat quality must be caused by the depletion of shared resources (exploitation competition sensu MacArthur 1972 and Tilman 1982, 1988).

Laissez-faire consumer-resource interactions can be modeled by the following pair of differential equations:

$$dR/dt = rg(R)R - af(R)RC \quad (1)$$

and

$$dC/dt = kaf(R)RC - mC, \quad (2)$$

where  $R$  and  $C$  are population densities of the resource and consumer, respectively,  $r$  is the intrinsic growth rate of the resource population,  $g(R)$  represents the density dependence of resource population growth,  $a$  is the searching efficiency of consumers, and  $f(R)$  stands for the relationship between the consumer's attack rate and resource density (i.e., the functional response, as defined by Holling [1959], is  $af[R]R$ ). The parameter  $m$  is the per capita rate of decline of consumers in the absence of resources, and  $k$  is a parameter related to the efficiency with which consumers use resources (see Rosenzweig 1969, 1971, 1977; Oksanen et al. 1981; L. Oksanen 1990; T. Oksanen 1990).

Setting  $dR/dt = 0$  and  $dC/dt = 0$ , we can solve the density combinations that give a zero rate of population growth for resource and consumers, respectively, as follows:

$$C^* = rg(R)/[af(R)] \quad (3)$$

and

$$R^* = m/[kaf(R^*)], \quad (4)$$

where  $C^*$  is the consumer density at which consumption exactly offsets population growth of the resource,  $R^*$  is the resource density that just maintains consumers at zero population growth, and  $f(R^*)$  is  $f(R)$  evaluated at  $R = R^*$ . Equations (3) and (4) thus generate zero isoclines for the resource and consumer, respectively (Rosenzweig 1977). Increasing productivity of the habitat increases the parameter  $r$  and/or influences the parameters of  $g(R)$  function. These parameters do not appear in equations (2) and (4) and thus do not influence the position of the consumer's (zero) isocline. Consequently, the same consumer isocline applies to all habitats, whereas resource isoclines will be different, depending on the productivity of the habitat.

With respect to the details of population dynamics, there is a big difference between a set of habitats with self-contained dynamics and ideal free systems, in which consumers freely move between habitats in response to changes in resource density. However, the prediction of equal fitness in all habitats implies that immigration and emigration rates cancel. This enables us to use equations (1) and (2) also when modeling dynamics in a heterogeneous landscape with ideal free consumers. The simplest case can be obtained by assuming that the growth of the resource population is logistic,  $g(R) = 1 - R/K$ , and the consumers have linear functional response, in which  $f(R) \equiv 1$ . Substituting this into equation (3), we see that the resource isocline of each habitat becomes a straight line with a negative slope, originating at  $C = r/a$  and meeting the resource axis at  $R = K$ . A set of isoclines for three habitats with different primary productivity (reflected in  $r$  and  $K$ ) is depicted in figure 1A.

The per capita rate of population growth can be regarded as a measure of fitness (model 3 in Brown 1992). Using this index for fitness, we find that the relation between mean consumer fitness and resource density is

$$w = kaR - m. \quad (5)$$

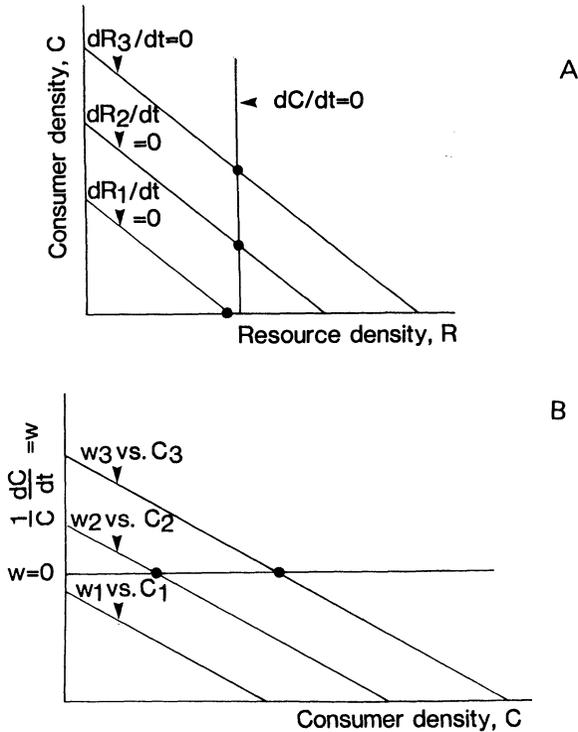


FIG. 1.—A consumer-resource model for three habitats differing in productivity (A) and a model of ideal free habitat selection in consumers in the same set of habitats (B), with assumed laissez-faire dynamics, linear functional response, and strictly resource-limited consumers. Equilibrium for each habitat is denoted by a dot; subindexes refer to habitats (1, least productive; 2, intermediate; 3, most productive). Primary productivity is assumed to have an equally strong impact on  $r$  and  $K$ , as proposed elsewhere (Oksanen et al. 1981) for herbivore-plant systems. In systems with animals as prey, productivity is likely to have a stronger impact on  $K$  than on  $r$ , because of the limited capacity of most animals to convert superabundant resources to offspring.

Provided that the dynamics of resources are rapid, as compared with those of consumers ( $r$  and  $a$  are large relative to  $m$  and  $k$ ), resources will quickly equilibrate at the point of the resource isocline that corresponds to the prevailing consumer density (MacArthur 1972; Holt 1984). Consequently, densities of resources can be converted to consumer densities. We can thus solve equation (3) for  $R$  and substitute into equation (5), which yields the equation determining the relation between the fitness and population density of consumers:

$$w = (ka/r)(rK - aKC) - m. \quad (6)$$

With appropriate scaling of parameters, equation (6) is the inverse of equation (3) for the resource isocline. Thus, given linear functional response and laissez-faire consumption, the graph for ideal free habitat selection of consumers under equi-

librium conditions (fig. 1B) can be obtained from the multihabitat consumer-resource model (fig. 1A) by rotating the axes.

With more complicated functional responses (Type II, Type III, or their modifications), the resource isocline becomes curved (see Rosenzweig 1969, 1971, 1977), and the mapping between models of consumer resource dynamics and habitat choice becomes more complicated. Nevertheless, predictions on the relationship between productivity and equilibrium dynamics do not change, because in all *laissez-faire* systems, consumer fitness depends on resource density only. Consequently, earlier predictions (Rosenzweig 1971; Oksanen et al. 1981) on standing crops and rates of resource mortality at equilibrium apply to heterogeneous landscapes with *laissez-faire* dynamics and ideal free habitat selection. Each habitat with any consumers at all will have the same resource density at equilibrium. More productive habitats will be characterized by higher consumer densities and higher resource mortality rates (or rates of tissue loss).

The equivalence between ideal free systems and systems with self-contained dynamics implies that ideal free habitat selection is incompatible with pseudointerference. The seemingly opposite results derived by Comins and Hassell (1979; see also Murdoch 1977) depend on their assumption of profound spatial heterogeneity in the scale of patch use (i.e., within home ranges of consumers). In such systems, optimal patch use (Charnov 1976) implies that increasing consumer density decreases the degree of patchiness, which thus lowers the tangent of the gain curve. The slope of this tangent (the average gain rate of consumers) represents functional response (T. Oksanen et al. 1992a), which thus becomes dependent on consumer density. Spatial heterogeneity in the scale of habitat selection does not have comparable consequences.

In order to obtain source-sink dynamics in systems with *laissez-faire* interactions and ideal free habitat selection, it is essential to have nonequilibrium dynamics, due to external factors or the instability of the consumer-resource equilibrium. Optimally behaving resource-limited consumers still distribute themselves along lines of equal resource density, and resource standing crops will tend to become equalized in all habitats populated by consumers. During low phases in consumer numbers, however, only the best habitats are settled, and average consumer fitness is high. During periods of high consumer numbers, the quality of all habitats is depressed, and habitats with low intrinsic quality will be colonized, too, and consumer fitness will be uniformly low.

#### INTERFERENCE SYSTEMS

In many systems, an increase in consumer density decreases the average searching efficiency of consumers, because time is lost in direct encounters between consumers or when passing through an area where prey are hiding, because of the recent presence of another predator (see Abrams 1984a, 1992). The impacts of interference can be accentuated by behavioral changes in dense consumer populations, in which dominating individuals may start to rob food from other consumers. Consequently, the aggregated harvesting may decline with increasing consumer density, as an increasing number of individuals parasitize on others

and, in addition, reduce their feeding efficiency by forcing them to be vigilant (Goss-Custard 1980; Sutherland 1982, 1983).

Two approaches are widely used when modeling interference. One is based on the model of Hassell and Varley (1969), the other on the model of Beddington (1975). There are several reasons to prefer the latter. The Hassell-Varley model is phenomenological, differs structurally from laissez-faire models, and has pathological properties at low consumer densities (Royama 1971). Beddington's model contains some debatable assumptions but appears to be robust to deviations from these (Ruxton et al. 1992). In its original form, however, the model is limited to consumers with Type II functional response. We have thus repeated Beddington's analysis with the generalized functional response of equations (1) and (2). Another unnecessary limitation of Beddington's original model is the tacit assumption of stereotypical behavior during encounters between consumers. This can be remedied by multiplying consumer density by function  $u(C)$ , representing the impact of density-dependent changes in interference behavior. For the sake of simplicity, let  $u(C) = (1 + C)^z$ ; that is, let interference behavior change as some power function of consumer density. (The constant 1 is needed to create a monotonic relationship between  $z$  and the intensity of interference behavior.) The relationship between searching efficiency and consumer density can then be derived from

$$\alpha(C) = a/[1 + iC(1 + C)^z], \quad (7)$$

where  $\alpha(C)$  is the actual searching efficiency of consumers,  $a$  is searching efficiency in the absence of competitors,  $i$  stands for the tendency of consumers to interfere with each other at low population densities, and  $z$  represents the impact of increasing population density on interference behavior. With  $z = 0$ , consumer behavior is stereotypical, and equation (7) can be reduced to Beddington's model by combining it with a Type II functional response. Higher  $z$  values imply that the tendency of consumers to interfere with each other increases with increasing consumer density, as proposed by Goss-Custard (1980) and Sutherland (1982, 1983).

Substituting equation (7) into equation (1), we obtain the resource population dynamic equation for systems with feeding interference as

$$dR/dt = rg(R)R - \alpha(C)f(R)RC. \quad (8)$$

To see how this influences the resource and consumer isoclines, we again make the system as tractable as possible by assuming Beddington-type interference ( $z = 0$ ), logistic resource dynamics ( $g[R] = 1 - R/K$ ), and linear functional response ( $f[R] = 1$ ). For the resource isocline, setting  $dR/dt = 0$ , we obtain

$$C^* = (rK - rR)/(aK - irR), \quad (9)$$

which is downward convex for all  $R > 0$  (fig. 2A).

The consumer isocline can be solved by substituting equation (7) into equation (2). The general case is analytically intractable, but cases in which  $z$  has integer values can be readily studied. We start with the simplest one by assuming  $z = 0$  and  $f(R) = 1$ . Setting  $dC/dt = 0$ , we then obtain

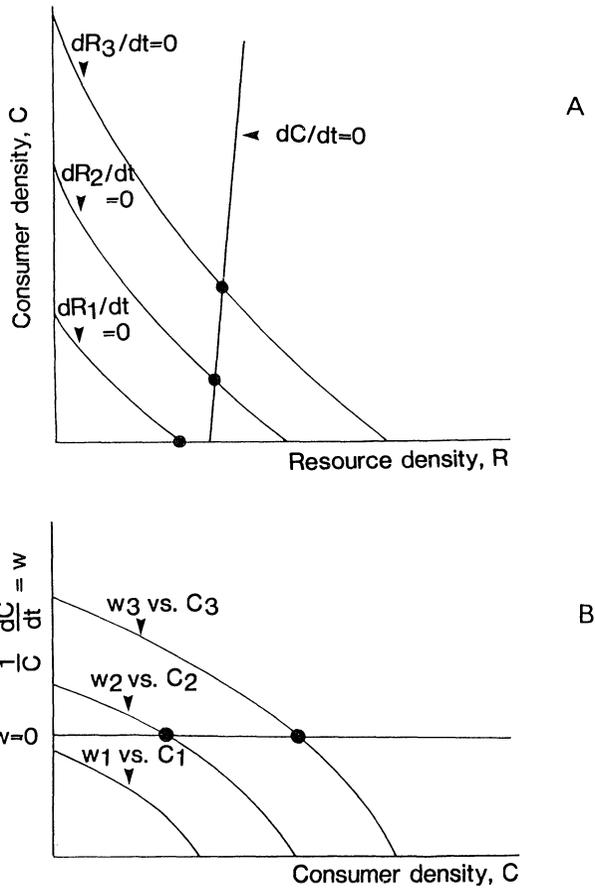


FIG. 2.—A three-habitat model for consumer-resource interaction (A) and ideal free habitat selection (B) corresponding to fig. 1, except that consumers are assumed to have direct feeding interference, which results in an approximately 25% loss of potential foraging time in the upper part of the phase plane.

$$R^* = m(1 + iC)/(ak). \tag{10}$$

Equation (10) generates a consumer isocline with a positive slope, but it is difficult to deduce strongly “slanted” consumer isoclines with this approach. In figure 2A, in which parameter values are chosen so that about 25% of potential foraging time is lost because of consumer-consumer interactions in the upper part of the phase plane, the “slantedness” of the consumer isocline is barely detectable. Again, the same consumer isocline applies to isolated habitats and to landscapes with ideal free habitat selection, in which immigrations and emigrations cancel. This gives us a multihabitat model, in which only resource isoclines are habitat specific (fig. 2A).

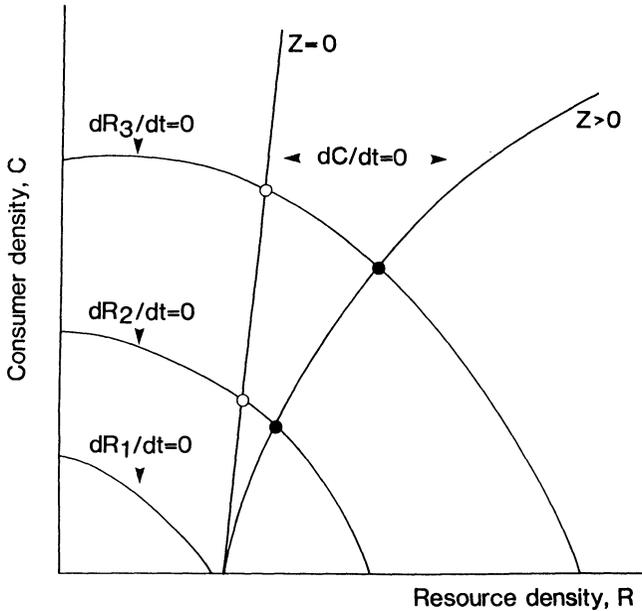


FIG. 3.—A three-habitat model for consumer-resource interaction with linear ( $z = 0$ ) and nonlinear ( $z > 0$ ) feeding interference. The  $z = 0$  alternative corresponds to fig. 2A. The  $z > 0$  alternative presupposes density-dependent behavioral changes, in which the tendency of consumers to interfere with each other increases with increasing consumer density, as proposed by Sutherland (1982, 1983).

We can again make corresponding substitutions as in the previous section to obtain the relationship between the population density and mean absolute fitness of consumers with Beddington-type interference. We assume, thus,  $z = 0$ ,  $f(R) = 1$ , and  $g(R) = 1 - R/K$ . After some rearrangements, we obtain

$$w = [karK + (riakK - a^2kK)C]/(r + 2riC + i^2rC^2) - m. \quad (11)$$

The mapping between models of habitat selection and consumer-resource dynamics (fig. 2B) now becomes relatively complicated, especially if the assumptions  $z = 0$  and  $f(R) = 1$  are relaxed. Nevertheless, some general results can be derived directly from equations (2) and (7). Parameters related to resource dynamics do not appear in either equation. Consequently, the same zero consumer isocline applies for all habitats. Moreover, the consumer isocline can still be interpreted as a line of equal fitness. With ideal free habitat selection, equilibrium densities of consumers will thus settle at the intersections between the consumer isocline and the habitat-specific resource isoclines. Consequently, abundance and mortality patterns generated by ideal free habitat selection are identical to those generated by numerical dynamics in similar habitats with self-contained dynamics (fig. 3). As in the case of laissez-faire models, source-sink dynamics and spillover consumption can only be generated by nonequilibrium dynamics. Moreover, dramatic forms of interference behavior, reflected as large values of  $i$  or  $z$ , are

required to generate patterns substantially different from those predicted by laissez-faire models.

STUDIES ON HABITAT SELECTION AND INSIGHTS IN CONSUMER-RESOURCE DYNAMICS IN  
HETEROGENEOUS LANDSCAPES

Models of habitat selection have been frequently tested by constant input rate experiments (see, e.g., Harper 1982; Parker and Sutherland 1986; Milinski 1988). In these experiments, consumers are starved for a while. Thereafter they are introduced to the experimental system, in which resources are supplied at point sources. Consumers are normally observed to distribute themselves in a numerical ratio that corresponds to the ratio of supply rates. This input matching is consistent with ideal free habitat selection. Possibilities for making inferences on consumer-resource interactions from these experiments are limited (Kacelnik et al. 1992; Lessells 1995). If input rates are interpreted as equivalent to the net growth rate of resources in the absence of consumption, input matching is consistent with the combination laissez-faire consumer-resource dynamics and ideal free habitat selection. (Proof can be obtained by solving equations [3] and [4]; the  $C^*$  thus obtained is directly proportional to  $rg[R^*]$ .) Unfortunately, the critical measurables distinguishing between interference and laissez-faire models are standing crops of resources. These cannot be easily measured in experimental systems, in which all supplied resources are immediately consumed (i.e., which have zero standing crops and 100% resource mortalities).

Observational and experimental field studies provide a more relevant approach to resource-based habitat selection and consumer-resource dynamics. Wintering shorebirds consuming invertebrates of intertidal mudflats constitute popular objects for studies on habitat selection and consumer-resource dynamics (Goss-Custard 1980, 1985; Sutherland 1982, 1983; Sutherland and Koene 1982; Goss-Custard et al. 1984, 1992; Goss-Custard and dit Durell 1988). The data are, by and large, compatible with the assumption of ideal free habitat selection. Interference behavior is frequent, especially in high-density populations of visually foraging species. However, even in mudflats with the highest observed oystercatcher density ( $> 200$  individuals per hectare), interference reduced individual feeding rates only by 7%–25%, as compared with interference-free situations (Goss-Custard and dit Durell 1988). The observed level of interference thus appears to be comparable to figure 3, with  $z$  slightly greater than zero.

A CASE STUDY ON ARMORED CATFISH AND ALGAE IN A NEOTROPICAL STREAM

Habitat selection and population dynamics of armored catfishes (Loricaridae; dominating species: *Ancistrus spinosus*) in the Rio Frijoles, Panama, were studied (Power 1981, 1984a, 1984b, 1987; see also Power et al. 1989) for 2.5 yr. The catfishes interact with attached algae on rocky basements of stream pools (Power 1984a). The system is thus relatively similar to terrestrial vertebrate-plant systems in having macroscopic, substrate-bound vegetation consumed by a mobile grazer.

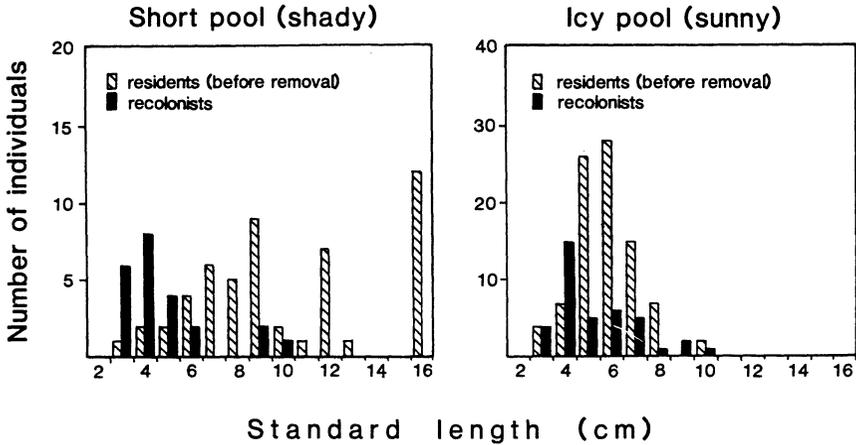


FIG. 4.—Size distributions of *Ancistrus* in a dark and a sunny pool before and 18 d after loricariids were removed from the pools during a dry-season experiment (see Power 1981).

Reproduction of armored catfishes takes place in hollow logs or rock crevices, which are available in some stream pools. Juveniles first settle in shallow riffles, where they shelter under riffle cobbles. At lengths of 3–4 cm, catfishes start to outgrow the cover available in riffles. Simultaneously, their vulnerability to gape-limited predators in pools decreases. Thus individuals of this size class, called settlers, face about equal risks of predation in both habitats and can move extensively without increasing their risk of predation. Settlers were found to rapidly colonize two pools, where larger resident catfishes (modal lengths 9 and 6 cm, respectively) had been experimentally removed (fig. 4).

During the study, 1,308 catfishes were individually marked and periodically recaptured. The majority of these individuals were never observed outside the pool where they were marked, which suggests that catfishes live sedentarily after passing the settler stage, owing to the risk of avian predation in waters less than 20 cm deep (Power 1984b; Power et al. 1989). For the same reason, catfishes avoid shallow parts of pools. The mobility of catfishes increases again, when they reach reproductive size and must often travel over long distances when searching for ponds with appropriate breeding sites (Power 1984a).

The catfishes are strongly food limited for much of the year (Power 1984b). While foraging, catfishes are frequently involved in agonistic interactions. In the two sunny pools under intense surveillance, 24% (66/273) and 17% (27/159) of feeding bouts of *Ancistrus* ended in skirmishes. Corresponding values for two shaded pools with lower catfish densities were 8% (16/191) and 8% (2/24). The somatic growth rates of prereproductive *Ancistrus* living in three dark pools, one half-shaded pool, and one sunny pool were statistically indistinguishable during the dry season, when the fishes lost weight or barely maintained it, and during the rainy season, when they were able to grow (Power 1984b). This similarity in somatic growth rates suggests that average rates of food intake were similar in the five pools. Moreover, estimated survival rates in pools with different canopy

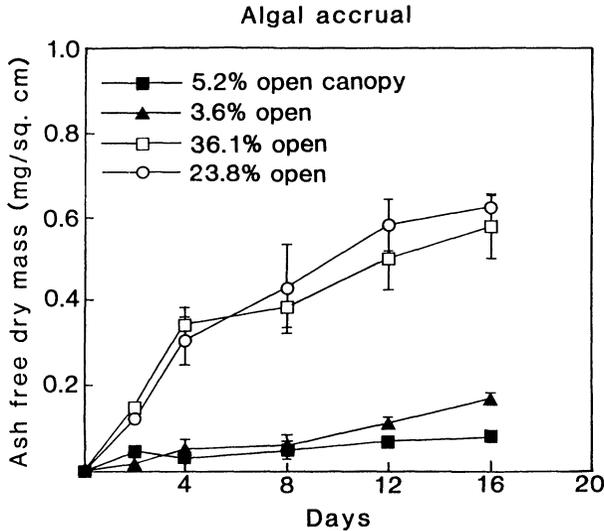


FIG. 5.—The accrual of organic mater (mostly algae) over 16 d on tiles placed in positions inaccessible to grazers in two dark and two moderately sunny pools. Points indicate means from four to eight samples, collected according to a staggered schedule, that separated effects of accrual time from other time-dependent influences. Bars are 2 SE.

cover were statistically indistinguishable (Power 1984a). The habitat selection of armored catfishes thus corresponds to the predictions of the ideal free model.

Algal productivity in the Rio Frijoles was light limited. Variation in primary productivity was due to differences in canopy cover. Algal growth rates were measured in two dark (3.6% and 5.2% open canopy) and two moderately sunny (23.8% and 36.1% open canopy) pools as accrual of organic matter on tiles that were inaccessible to grazers (fig. 5). In the two sunnier pools, rates of photosynthesis and respiration of intact algal assemblages on chips of rock substrate were also measured in stream-incubated light/dark bottles. The two independent measurements of primary production gave congruent results: with the conversion of  $0.375 \text{ mg O}_2 \text{ mg}^{-1} \text{ C}$  (Cox 1976) and  $0.94 \text{ mg C mg}^{-1}$  organic weight (McIntire and Phinney 1965), the rates of net primary production were  $0.097$  and  $0.113 \text{ mg ash-free dry mass (afdm) cm}^{-2} \text{ d}^{-1}$ . These values are approximately double those measured by harvesting organic matter on tiles, which would be expected if primary production were negligible at night (Power 1981, 1984a, 1990). Algal growth rates were correlated with canopy cover in the four pools in which accrual on tiles was measured. In spite of the small number of data points, the regression was statistically significant and had high explanatory power (fig. 6A; algal accrual [ $\text{mg afdm cm}^{-2} \text{ d}^{-1}$ ] =  $0.0025$  [percentage open canopy] -  $0.0008$ ,  $r^2 = 0.958$ ,  $P$  [one-tailed] <  $.025$ ).

Algal standing crops (dominated by adnate diatoms) were also measured in those four pools (Power 1981, 1984a). Algal cells (diatoms) were counted and measured under  $300\times$  magnification after being detached from bedrock chips sampled systematically along grids in each of the four pools, and counts were

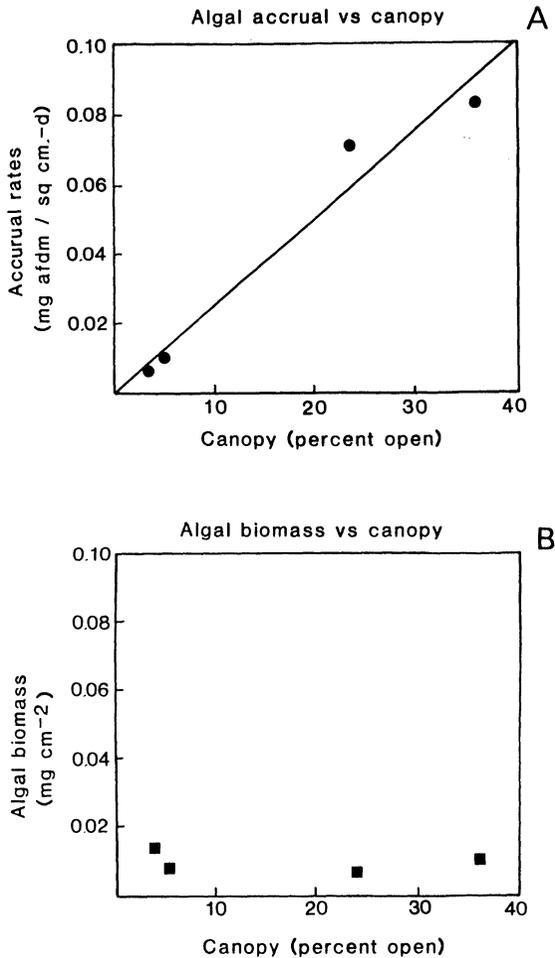


FIG. 6.—The relationships of canopy cover over a pool to the accrual rate of algae (A) over the first 4 d of growth in that pool and to the biomass of algae (B), systematically harvested from 10 sites spaced at 0.5-m intervals along bedrock platforms in pools.

converted to biomass estimates ( $\text{mg afdm cm}^{-2}$ ) using the conversion of Stevenson and Stoermer (1982). In contrast to algal productivity, algal standing crops showed a flat relationship with forest canopy cover (fig. 6B; standing crop [ $\text{mg afdm cm}^{-2}$ ] =  $-0.000052$  canopy [percentage open] +  $0.0102$ ,  $r^2 = 0.068$ , NS).

Maximum algal biomasses in the absence of grazers (carrying capacities) for the two sunny pools were estimated from accrual measurements over 16 d (fig. 5) by fitting a second-order polynomial to the accrual and by choosing the standing crop predicted for day 20. The values thus obtained ( $0.584 \text{ mg cm}^{-2}$  for the relatively homogeneous pool with 36.1% open canopy and  $0.608 \text{ mg cm}^{-2}$  for the pool with 23.8% open canopy but much local variation in shading) compared well with independent measurements made of algal standing crops on cobbles from

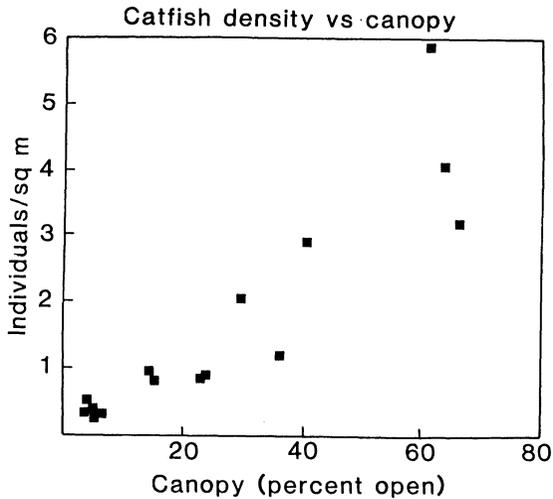


FIG. 7.—The relationship of canopy cover to armored catfish density

the shallow (< 10 cm deep) margins of other sunny pools, where algae escaped catfish grazing and attained a median standing crop of  $0.68 \text{ mg afdm cm}^{-2}$  (range,  $0.27\text{--}1.50$ ;  $n = 17$ ) (Power 1984b, p. 524). Asymptotic standing crops for the two dark pools were estimated by eye from figure 6 to be  $0.2 \text{ mg cm}^{-2}$  and  $0.1 \text{ mg cm}^{-2}$  for the 5.2% open and 3.6% open canopy pools, respectively. These estimates are educated guesses, but the magnitudes of carrying capacities inferred for dark pools are consistent with the relatively scanty algal cover in shallow parts of shaded pools (M. E. Power, personal observation).

The numbers of armored catfishes were counted once a month for 12 consecutive months, in each of 16 pools, chosen to represent the range of canopy variation over the Rio Frijoles: three sunny (percentage open canopy, > 50); three moderately sunny (percentage open canopy, 25–50); four half-shaded (percentage open canopy, 10–24); and six dark (percentage open canopy, < 10) pools. Fish were counted by snorkeling slowly from the downstream to the upstream end of each pool, covering the entire area and searching under ledges with an underwater flashlight. Lengths of censused catfish were estimated (with an error of < 10%) for computation of biomasses from length-weight regressions (Power 1981). Densities of armored catfish, averaged for given pools over the 12 censuses, were positively correlated with the openness of the canopy (fig. 7). The densities are expressed in numbers; similar relationships hold for catfish biomass, because biomass and numbers of catfish were highly correlated ( $r = 0.883$ ,  $n = 16$ ,  $P < .001$ ). Moreover, catfish numbers matched direct estimates of local grazing pressure (Power 1984a). Thus, feeding activities of catfishes corresponded to numerical densities.

The data on standing crops of catfishes and attached algae in the four pools, in which all relevant variables (catfish density, mean and maximal algal standing crop, and accrual rate) were measured or estimated on the basis of local data, are summarized as a phase diagram (fig. 8), in which we also have plotted the

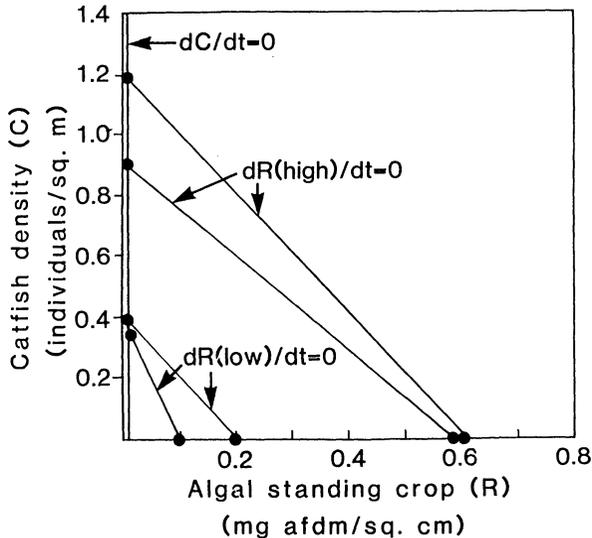


FIG. 8.—Phase diagrams for catfishes and algae in two dark and two sunny pools, in which algal biomass was directly measured. The catfish isocline is derived on the basis of the four observed density combinations of algae and catfishes. Algal carrying capacities (intercepts of algal isoclines with the  $X$ -axis) were estimated from accrual curves (fig. 6), as explained in the text. The straight lines with a negative slope are the simplest algal isoclines consistent with our data.

simplest imaginable consumer and resource isoclines compatible with our data. The resource isoclines are based on two points and on the observation of numerical stability (Power 1984a), which implies that the slope of the resource isocline at equilibrium is likely to be negative (Rosenzweig 1971, 1977; Tanner 1975). The resource isoclines of figure 8 imply a linear functional response, which need not be correct. An alternative interpretation is that catfishes have a Type III functional response, saturating at high algal densities but accelerating when the standing crop of algae is very low, because small algal cells in depressions and interstices of grazed substrates are difficult to get. The latter interpretation implies that the resource isocline is curved (steepest at low and high algal standing crops) and may have a positive slope at intermediate algal standing crops. The consumer isocline of figure 8 is vertical. The least-square method would yield a leftward-slanted consumer isocline, but slightly rightward-slanted isoclines (corresponding to fig. 2A and to the  $z = 0$  alternative of fig. 3) would also be within the limits of confidence.

The behavior of the catfish-algae system thus cannot be distinguished from predictions derived from the models of ideal free habitat selection and laissez-faire consumer-resource dynamics, although the consumers were neither ideal (omniscient) nor free, and clear and substantial feeding interference was observed.

## DISCUSSION

The combination of ideal free habitat selection and laissez-faire consumer-resource dynamics constitutes a biological null model of habitat selection and trophic dynamics in a heterogeneous landscape. This combination includes the basic assumptions of adaptive behavior, dependence of consumer fitness on encounters with resources, and a negative impact of these encounters on the fitness of resources—along with the assumption of “ideal” consumers, perfectly adapted to their environment. When these premises are satisfied, the simple models discussed earlier (Rosenzweig 1971; Oksanen et al. 1981) apply, by and large, to local sets of habitats, connected by frequent consumer dispersal. The main exception is stability. When local systems are tightly interconnected by consumer dispersal, co-occurrence of equilibrium and cyclic dynamics is impossible. If the functional response of consumers is such that enrichment is destabilizing, and the destabilizing forces generated by productive habitats prevail, the whole landscape will be characterized by synchronous, consumer-resource cycles. However, the amplitude of cycles is influenced by spatial heterogeneity in ideal free systems too. In areas in which all habitats have high intrinsic quality, consumer-resource limit cycles can periodically lead to an almost total depletion of resources, followed by a crash of consumers to very low levels (Gilpin 1975). In a heterogeneous landscape, consumption pressure in high-quality habitats is relaxed when these habitats become moderately depleted, which makes low-quality habitats an attractive alternative. In addition to within-habitat behavioral responses of consumers (Abrams 1982; L. Oksanen 1990) and resources (Abrams 1984*a*, 1984*b*, 1992; Oksanen and Lundberg 1995), spatial heterogeneity may thus contribute to keep the amplitude of consumer-resource cycles within reasonable limits even in ideal free laissez-faire systems.

Free et al. (1977) concluded that the patterns predicted by laissez-faire dynamics are not substantially influenced by realistic levels of feeding interference. The data on the catfish-algae system illustrate this point. The argument of Free et al. can be made more transparent by considering the consequences of serious feeding interference, when 50% of potential foraging time is lost in interactions between consumers at high consumer densities. This loss can be compensated for by doubling up the prey density. A consumer isocline that reaches twice as high a resource density in the upper part of the phase plane as in the neighborhood of the resource axis is still steep and predicts patterns relatively similar to those generated by laissez-faire models.

The dynamics of consumer resource interactions in a heterogeneous landscape appear to be robust to minor deviations from the premises of ideal (omniscient) consumers and free between-habitat movements. It appears to suffice that a fraction of consumers are relatively mobile and have a rough perception of the quality of a fair number of habitat patches. Patches with plenty of resources will then attract recruits, which will lead to a decline in habitat quality. Indeed, our data indicate substantial random variation in standing crops of algae in Rio Frijoles (fig. 6*B*), while the constancy of catfish growth rates tells that these differences must be ephemeral. If, however, the redistribution of consumers is periodically

impossible or if between-patch movements are very difficult or risky, large numbers of consumers can be trapped in relatively depleted patches, and pseudointerference emerges (Murdoch and Stewart-Oaten 1989). An example of pseudointerference due to periodic immobility of the consumers is provided by the interaction between *Cactoblastis* and *Opuntia* (Caughley and Lawton 1981), whereas the mites of Huffaker et al. (1963) illustrate pseudointerference due to difficulties or costs of between-patch movements. The interaction between the vole *Microtus agrestis* and herbaceous vegetation of the Tvärminne archipelago, Finland (Pokki 1981), demonstrates that this mechanism can be effective in field situations too. Vole numbers in the archipelago appear to be relatively stable, although within-island dynamics indicate the potential for violent fluctuations and wholesale depletion of the vegetation. Notice that such consequences of dispersal barriers can be modeled directly, too, by including emigration and immigration terms to equations relating within-patch consumer dynamics to local resource densities (Crowley 1981).

Despotic behavior makes the freedom of habitat selection a privilege of the most dominating individuals, which thus creates source-sink dynamics (Łomnicki 1978, 1987; Pulliam 1988) and spillover consumption (T. Oksanen 1990) in spatially heterogeneous landscapes. The cost-gain balance of despotic behavior depends on the distribution of resources (Davies and Houston 1984) and on the riskiness of trespassing, which influences the optimal response of subordinate individuals to territorial signals. Fretwell (1972) argued that the habitat selection of breeding birds normally follows the ideal despotic model, which seems to be the case (Newton 1979; Mikkola 1982; Andrén 1990; Bernstein et al. 1991; Dhondt et al. 1992; Ens et al. 1992). Intra- and interspecies despotic behavior is common among carnivorous and insectivorous mammals (Mech 1966; Schaller 1972; Erlinge and Sandell 1988; Hanski and Kaikusalo 1989; Oksanen et al. 1992*b*). Despotic behavior of the strongest guild members is often accompanied by intraguild predation (Mikkola 1982; Oksanen et al. 1985; Polis et al. 1989). Herbivores do not normally have comparable weapons. Thus, the defense of feeding areas appears to be uneconomical, unless resources are strongly aggregated in space (Jarman 1974; Owen-Smith 1977). Some herbivores make their resources defendable by hoarding them (Smith 1974; Huntly 1987), but such hoarding behavior is much less frequent in herbivores than in granivores (Vander Wall 1990), in which it can lead to despotism within and between species (Smith 1981).

It thus seems likely that the combination of ideal free habitat selection and laissez-faire dynamics is typical on the bottom of food webs, whereas interference competition and despotic behavior, including intraguild predation, are the rule higher up in the web. Consequently, the response of food chain dynamics to local productivity gradients should conform to the predictions (Oksanen et al. 1981) in relatively barren areas with herbivores as effective top consumers, as suggested by data (Oksanen 1983). Conversely, Wollkind's (1976) model, with direct density dependence among predators, and its multihabitat counterpart (T. Oksanen 1990) should apply to trophic dynamics in landscapes in which at least some habitats are productive enough to support carnivores. The observed positive trend in herbivore biomass in response to increasing primary productivity (McNaughton

et al. 1989; Moen and Oksanen 1991) supports this conjecture. Notice, however, that standing crops of herbivores are strongly influenced by human interference (e.g., hunting policies); the existence of a corresponding positive trend in relatively undisturbed ecosystems is debatable (L. Oksanen et al. 1992; Crête and Manseau 1995). Moreover, a positive trend can also be caused by behavioral or evolutionary responses of prey to predation (Abrams 1984a, 1992, 1994; Oksanen 1992; Oksanen and Lundberg 1995). The population-dynamic importance of despotic behavior in carnivores is thus an open question.

In pelagic ecosystems, the shifting distribution of resources appears unfavorable for resource monopolization. Moreover, only genuine piscivores are well equipped to inflict serious damage on animals of their own size (Gerking 1994). Biomass patterns in temperate, boreal, and polar lakes correspond to the predictions of the holistic theory of lake dynamics (Persson et al. 1988, 1992; Hansson 1992; Diehl et al. 1993), which implies ideal free habitat selection and laissez-faire dynamics. The poorest fit is observed in shallow lakes dominated by territorial pikes (Persson et al. 1992; see also Eklöv 1992; Eklöv and Diehl 1994). The potential for explaining patterns in nature by combining ideal free distribution with laissez-faire consumer resource dynamics thus seems to be maximal in three-dimensional pelagic systems, whereas two-dimensional littoral systems seem to function more like their terrestrial counterparts.

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