COMPLEMENTARY FORAGING BEHAVIORS ALLOW COEXISTENCE OF TWO CONSUMERS

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Abstract. We developed a mathematical model based on the microalgal–gastropod system studied by Schmitt, in which two coexisting consumers (*Tegula eisini* and *T. aureotincta*) feed on a common resource. The two consumers differ in their foraging behavior and their ability to remove microalgae from rock surfaces. *T. eisini* is a digger, moving slowly and grazing the algae down to almost bare substrate, whereas *T. aureotincta* is a grazer, moving more quickly and leaving behind a larger fraction of the algal layer. These complementary foraging strategies result in a size-structured algal resource, with each size class differentially accessible to each of the consumers. Our model recognized three accessibility states for an algal patch: a refuge (recently grazed by the digger and currently inaccessible to either consumer), a low level (exploitable only by the digger), and a high level (exploitable by both consumers). We assumed that all interactions between consumers and resources were linear and examined the relatively short time-scale dynamics of feeding, algal renewal, and individual consumer growth at fixed densities of consumers. Thus, our model complemented related models that have focused on population dynamics rather than foraging behavior. The model revealed that coexistence of two consumers feeding on a single algal resource can be mediated by differences in the consumers' foraging modes and the resource structure that these behaviors create.

We then estimated model parameters using data from Schmitt's experimental studies of *Tegula.* The fits to the experimental data were all very good, and the resulting parameter values placed the system very close to a narrow coexistence region, demonstrating that foraging complementarity in this system facilitates coexistence. The foraging trade-offs observed here are likely to be common in many consumer–resource systems. Indeed, mechanisms similar to those we discuss have been suggested in many other systems in which similar consumers also coexist. This model not only demonstrates that such an argument is theoretically plausible, but also provides the first application of the model, showing that the observed conditions for the *Tegula* system fall very close to the appropriate parameter space. Such quantitative tests are critical if we are to rigorously test the models developed to explain patterns of coexistence.

Key words: exploitation competition; foraging behavior; foraging model; gastropods; herbivore coexistence; marine snails; microalgae; resource structure; Tegula *spp.*

INTRODUCTION

Models of competition, and of the mechanisms that allow coexistence of similar species, remain a cornerstone of community ecology. Considerable theoretical work has focused on the general result that the number of coexisting consumers cannot exceed the number of limiting resources (MacArthur and Levins 1964); many of these papers have led to reevaluation of the meaning of resources. For example, a single resource species might be subdivided into different functional components such as roots and shoots of a plant (Haigh and Maynard Smith 1972), or different developmental

stages (Briggs 1993, Briggs et al. 1993). In such cases, the single resource species can represent two (or more) limiting resources and can permit coexistence of more than one competitor species (Vance 1985). The foraging activities of consumers can also create heterogeneities or patchiness in space and/or time that would otherwise not exist. If consumers differ in their ability to exploit the different patches, then under some conditions, this patchy distribution of a single resource in a homogeneous environment can lead to coexistence of two (or more) consumers.

Two general features of these models appear to be important in producing coexistence: (1) structuring of the resource into distinct subunits (development stages, or patches of different quality distributed in space or time), and (2) differential ability of the consumers to

exploit these subunits (Haigh and Maynard Smith 1972, Briggs 1993). Although the mechanisms suggested by these theoretical studies have been posited to operate in a variety of ecological systems (e.g., McNaughton 1976, Brown 1986, 1989, Kohler 1992, Schmitt 1996, Thrall et al. 1998) and thus promote coexistence, there have been no quantitative tests of these models to determine if the specific features of any real system are appropriate to produce coexistence.

Tilman (1994) has recently extended the competitor–refuge models developed in the 1970s (e.g., Levins and Culver 1971, Horn and MacArthur 1972, Hastings 1980) to demonstrate that an infinite number of plant species (or other sessile consumers) can theoretically coexist on a single limiting resource within a physically homogenous environment. In Tilman's model, coexistence requires a trade-off between, for example, a plant's dispersal ability (i.e., its ability to colonize unoccupied patches, which have high nutrient availability) and its competitive ability (i.e., its ability to deplete nutrients within a patch). Research in the Cedar Creek, Minnesota prairie system provides evidence for this interspecific trade-off (Gleeson and Tilman 1990, Tilman 1990). Tilman (1994) suggested that similar interspecific trade-offs might also have relevance to the coexistence of mobile consumers, foragers that visit many patches during a single foraging bout. An "inferior" competitor could invade a system saturated with a "superior" competitor species if it could find and exploit renewed patches (those of high resource quality, not recently visited) before they are revisited (and hence depleted) by the superior competitor.

In this paper, we present a simple mathematical model for an exploitation competition system consisting of a single resource species and two mobile consumer species with complementary foraging behaviors: "diggers," which can extract resources at low levels, and "grazers," which are poorer within-patch exploiters, but can potentially find good patches more quickly. The model assumes a homogeneous environment within which patchiness arises due to the foraging activities of the consumers. We assume that the consumers utilize no other resource and have no direct interactions other than the exploitation competition mediated through the resource. Our model includes parameters that describe the consumers' foraging behaviors and metabolic costs, as well as the renewal characteristics of the algae.

The model describes consumer growth and seeks conditions under which individuals of both consumer species can exhibit non-negative growth. Thus, it isolates potential mechanisms of consumer coexistence operating on shorter time scales than classical models focusing on population dynamics. One feature of the system allowing this level of focus is that the time scale for resource reproduction is much shorter than the consumers' generational time scales. Because most experiments designed to investigate competitive interactions and coexistence typically focus on individual

responses, rather than long-term population growth, this individual-level approach is particularly powerful and applicable to empirical studies. As a result, we are able to use the experimental data collected by Schmitt (1996) on the marine snails, *Tegula aureotincta* and *T. eiseni,* to parameterize the model and provide an empirical test of the model's predictions. Analysis of data taken for each species in isolation fixes all but one of the model's parameters and shows that the mixed system of *T. aureotincta* and *T. eiseni* sits close to a small region of coexistence in the model's parameter space, in agreement with observed coexistence in the field. Reexamination of several studies on coexisting invertebrate grazers provides additional confirmation of the model formulation and the assumed trade-off between extraction ability and patch-finding ability. However, these studies do not provide adequate information to quantitatively test our model's predictions about the relationship between foraging traits and coexistence. Quantification of these parameters for additional pairs of grazers that coexist, and more importantly, for pairs that do not coexist, will provide a critical next step in evaluating the utility of this model and the importance of complementary foraging behaviors.

Digger–Grazer Model

Our model addresses competitors utilizing a single resource, and was developed with reference to the marine snails *Tegula eiseni* and *T. aureotincta,* which exhibit complementary foraging patterns. *T. eiseni* acts as a digger, moving slowly and removing layers of microalgae down to almost bare rock, whereas *T. aureotincta* acts as a grazer, moving faster and removing a smaller fraction of the algal layer. These two species compete exploitatively and coexist in subtidal rocky environments where predator densities are low (Schmitt 1985, 1996).

Most of the available data in this and other systems have arisen from short-term experiments measuring the interrelations among consumer density, consumer growth, and algal availability (Schmitt 1985, 1996). This experimental focus on individual responses (principally growth), and not long-term population dynamics, means that existing theory addressing population dynamics cannot be used to interpret experimental results. Instead, models focusing on short-term dynamics must be formulated and tied to the available experimental data. Our consumer–resource model, formulated at behavioral time scales, is one such attempt and, as a result, does not address long-term coexistence directly. Rather, as in the experiments, the model focuses on short-term dynamics and uses short-term positive individual growth as a proxy for long-term persistence (i.e., long-term population growth).

We assume that the resource located within a very small spatial region (a "patch") can be categorized into one of three levels (see Fig. 1, Table 1). The lowest level is unusable by either the digger or the grazer, and
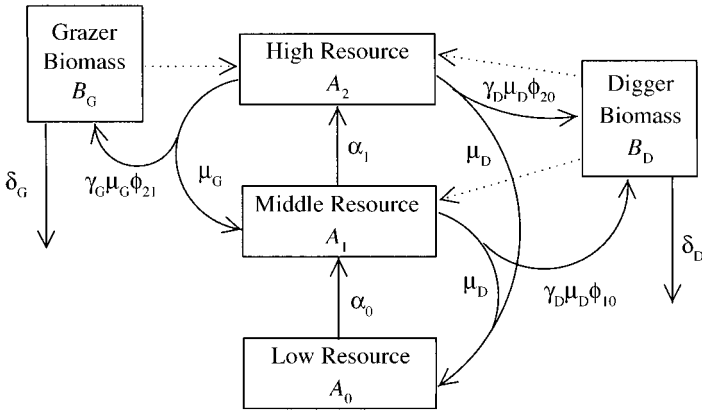
FIG. 1. Representation of the *Tegula* model. The low, middle, and high levels of density make up the size-structuring in the benthic algal mat imposed by the differential foraging strategies taken by the grazers and the diggers. Dotted lines indicate foraging: grazers consume the highest level, and diggers consume the middle and highest levels. Solid lines represent interaction rates with variables and parameters defined in Table 1.

represents a resource refuge. A patch of resource at the lowest level enters the middle level with transition rate α_0. This middle-resource level represents patches of low algal cover that are exploitable by the digger but not the grazer. Middle-level patches enter the highest resource level (i.e., dense cover, or a thick mat) with transition rate α_1, and become exploitable by both the digger and the grazer. Thus, the digger can extract nutrition from both the middle- and high-resource states (and converts these patches into the low algal state), whereas the grazer benefits only from the high-resource state (converting it to the middle state). In the absence of consumers, all patches exist in the high level, or ungrazed state. Thus, by assumption, the environment is homogeneous, and spatial heterogeneity is generated only by the local foraging activities of consumer, with the degree of local depletion of algae depending on the identity of the consumer (grazer or digger).

A unit area of resource habitat can be classified into the fractions of the area at each level: A_0, A_1, and A_2, for the lowest, middle, and highest levels, respectively, with $A_0 + A_1 + A_2 = 1$. Resource consumption rates at each level depend linearly on the consumer population's biomass density (a Type I functional response) and consumer-specific resource clearance rates. We assume that diggers have no complex foraging behaviors; hence, their foraging rates are independent of resource habitat fractions. These assumptions lead to the model equations:

$$\frac{dA_0}{dt} = -\alpha_0 A_0 + \mu_D B_D (A_1 + A_2) \quad (1a)$$

$$\frac{dA_1}{dt} = \alpha_0 A_0 - \alpha_1 A_1 - \mu_D B_D A_1 + \mu_G B_G A_2 \quad (1b)$$

$$\frac{dA_2}{dt} = \alpha_1 A_1 - \mu_D B_D A_2 - \mu_G B_G A_2 \quad (1c)$$

where $B_D = N_D M_D$ and $B_G = N_G M_G$ represent the digger

TABLE 1. Variables and parameters of the digger–grazer model.

Terms	Description	Units
A) Model variables		
A_0	fraction of habitat at low level	none
A_1	fraction of habitat at middle level	none
A_2	fraction of habitat at high level	none
M_D	mass of individual digger	consumer biomass/consumer
M_G	mass of individual grazer	consumer biomass/consumer
N_D	number density of diggers	consumers/area
N_G	number density of grazer	consumers/area
B_D	digger biomass density ($N_D M_D$)	consumer biomass/area
B_G	grazer biomass density ($N_G M_G$)	consumer biomass/area
B) Model parameters		
ϕ_0	resource biomass density of low level	resource biomass/area
ϕ_1	resource biomass density of middle level	resource biomass/area
ϕ_2	resource biomass density of high level	resource biomass/area
α_0	transition rate from low to middle level	time^{-1}
α_1	transition rate from middle to high level	time^{-1}
μ_D	digger's resource clearance rate	area/consumer biomass/time
μ_G	grazer's resource clearance rate	area/consumer biomass/time
γ_D	digger's resource conversion efficiency	consumer biomass/resource biomass
γ_G	grazer's resource conversion efficiency	consumer biomass/resource biomass
δ_D	digger's metabolic rate	time^{-1}
δ_G	grazer's metabolic rate	time^{-1}

and grazer populations' biomass densities (biomass per area) resulting from a product of the respective number densities N_D or N_G (number of consumers per area) and individual consumer mass M_D or M_G (biomass per consumer). Parameters α_0 and α_1 (per unit time) are the transition rates of the lowest and middle resource levels to the next highest level, and μ_D and μ_G (area cleared per consumer biomass per time) denote the individual digger and grazer clearance rates, i.e., the rates at which diggers and grazers, respectively, clear substrate of the algal resource. Note that only two of the three eqs. (1a–c) are independent because the three algal fractions sum to one.

These expressions yield algal habitat fraction dynamics on an areal basis (fraction of the habitat made up of each of the three algal types: low, medium, and high). These fractions are converted to resource biomass using the resource density parameters ϕ_0, ϕ_1, and ϕ_2 (resource biomass per area), giving the total biomass of algae, A_T:

$$A_T = \phi_0 A_0 + \phi_1 A_1 + \phi_2 A_2. \qquad (2)$$

Individual consumer dynamics depend on two processes, consumption and respiration. Consumption represents a two-step process of converting resource biomass into consumer mass. Our model first converts patch-specific clearance rates into resource biomass consumption rates by multiplying by the density of algae removed by the consumer. For example, a grazer of mass M_G feeding on high-level resource patches with a clearance rate $\mu_G M_G A_2$, reduces them to the medium level and changes the algal biomass density from ϕ_2 to ϕ_1. The consumed resource biomass is then $(\phi_2 - \phi_1) \mu_G M_G A_2$. Our model then converts resource biomass into consumer mass with efficiencies γ_D and γ_G (consumer biomass per resource biomass). Net respiration is assumed to be directly proportional to consumer mass, with species-specific respiration rates δ_D and δ_G (per time). These two processes lead to expressions for *individual* digger and grazer masses, M_D and M_G,

$$\frac{dM_D}{dt} = \gamma_D \mu_D M_D (\phi_{10} A_1 + \phi_{20} A_2) - \delta_D M_D \quad (3a)$$

$$\frac{dM_G}{dt} = \gamma_G \mu_G M_G \phi_{21} A_2 - \delta_G M_G. \qquad (3b)$$

Parameters $\phi_{ij} = \phi_i - \phi_j$ represent the reduction in algal biomass density caused by consumers; for example, in the previous example, grazers reduce high-level resource patches by $\phi_{21} = \phi_2 - \phi_1$. Using these ϕ_{ij} parameters, we can clarify the differential utilization of the resource by the consumers. For example, the net resource biomass contained in a unit area of high-level resource patches, ϕ_2, can be represented as three components, $\phi_2 = \phi_{21} + \phi_{10} + \phi_0$, or upon expanding, $\phi_2 = (\phi_2 - \phi_1) + (\phi_1 - \phi_0) + \phi_0 = \phi_2$. The first component, ϕ_{21}, represents the resource biomass that grazers extract from high-level patches, whereas the diggers

extract the first two resource biomass components, $\phi_{21} + \phi_{10} = \phi_{20}$. The last component, ϕ_0, is inaccessible to either consumer. Note that multiplying Eqs. 3a and b on both sides by their respective number densities yields equivalent expressions for digger and grazer population biomasses.

We reemphasize that this model is strictly a behavioral time-scale model for consumer growth, not population dynamics. This distinction is made clear by incorporating N_D and N_G as constants, rather than dynamical variables as in most competition models (e.g., Tilman 1982, Briggs et al. 1993). As a result, equilibration arises as individuals adjust their size to the point at which respiration balances consumption, rather than through changes in N_D and N_G (and the balancing of birth and death rates), as in a population dynamics model.

Invasion criteria

We can recast our consumer–resource model into a model depending only on consumer biomasses by assuming that algal dynamics occur on a fast time scale. This assumption means that algal fractions are always in equilibrium with the slowly changing consumer biomasses. The Appendix details this quasi-steady-state assumption and derives the digger–grazer competition equations involving only the consumer biomass densities:

$$\frac{1}{M_D} \frac{dM_D}{dt} = \gamma_D \mu_D \frac{\phi_{10} \alpha_0 (\mu_G B_G + \mu_D B_D) + \phi_{20} \alpha_0 \alpha_1}{(\alpha_1 + \mu_G B_G + \mu_D B_D)(\alpha_0 + \mu_D B_D)} - \delta_D$$

$$(4a)$$

$$\frac{1}{M_G} \frac{dM_G}{dt} = \frac{\gamma_G \mu_G \phi_{21} \alpha_0 \alpha_1}{(\alpha_1 + \mu_G B_G + \mu_D B_D)(\alpha_0 + \mu_D B_D)} - \delta_G.$$

$$(4b)$$

We define coexistence to occur if the two equilibrium single-consumer systems are invasible by the other consumer (e.g., Holt et al. 1994). Evaluating this criterion is a two-step analysis. We first examine how individual growth varies as a function of conspecific biomass density. Generally, individual growth will be positive at low biomass densities, declining to negative values as biomass increases. Single-consumer equilibria K_D and K_G define the consumer biomasses at which individual growth is zero (Fig. 2A). We next examine individual growth as a function of the biomass density of the other species. If each species has positive individual growth at the other species' equilibrium (see Fig. 2B), then each single-species equilibrium is invasible and we conclude that the species can coexist.

Two criteria result from the test for coexistence (see Appendix). The first criterion specifies when grazers can invade a system of diggers. Following the previous two-step analysis, we first solve the digger equilibrium values from Eqs. 1b, 1c, and 3a, using the relation $A_0 = 1 - A_1 - A_2$ and $B_G = 0$. The resulting condition
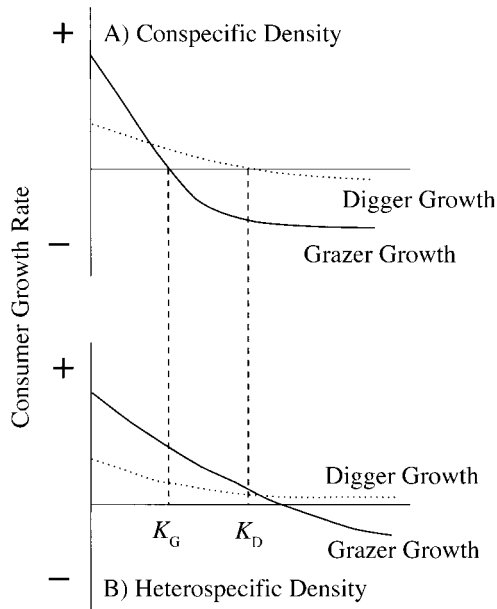
Fig. 2. Schematic relationships between consumer growth rates as functions of (A) conspecific and (B) heterospecific consumer biomass densities necessary for digger–grazer coexistence. Equilibrium biomass densities K_D and K_G are the conspecific biomass densities (in the absence of heterospecifics) at which consumer growth rates are zero. If, as pictured, both consumer species have positive growth rates at these heterospecific biomass densities, then the single-consumer systems are mutually invasible.

for positive individual grazer growth, $dM_G/dt > 0$, yields

$$\frac{\delta_G}{\gamma_G \mu_G} < \phi_{21} A_2^*(K_D, 0) \qquad (5)$$

where $A_2^*(K_D, 0)$ is the equilibrium high-level resource fraction of the digger-only system (see Eq. A.17). Multiplication of $A_2^*(K_D, 0)$ by ϕ_{21} yields the total amount of resource accessible to the grazer.

We can relate Eq. 5 to R^* concepts (Tilman 1982). The R^* rule, usually applied to competition for a common resource pool, is that the competitor with the smallest R^* outcompetes the others. In our model, the R^* rule must be slightly modified because the resource is structured into components that are differentially accessible by the two species. In this case, a species' R^* only includes the resource accessible to it, excluding resource components that it cannot utilize. Hence, from Eq. 5, we define the ratio $R_G^* = \delta_G/\gamma_G \mu_G$ to represent the amount of accessible resource biomass needed for an individual grazer to balance intake and metabolism; if a grazer's available resource falls below this level, it experiences negative growth. Hence, if diggers deplete the amount of resource biomass accessible to the grazers below R_G^*, then the grazers cannot invade. Conversely, grazers can invade if their accessible resource biomass in the digger-only system is greater than R_G^*.

The second invasibility criterion specifies when diggers are able to invade a grazer-only system. The Appendix shows that diggers will invade if

$$\frac{\delta_D}{\gamma_D \mu_D} < \phi_{10} + \frac{\delta_G}{\gamma_G \mu_G}. \qquad (6)$$

If we define the digger's $R_D^* = \delta_D/\gamma_D \mu_D$, then we can relate Inequality (6) to the more general R^* rules: diggers will invade if their R_D^* is less than the resource accessible to them in the grazer-only system. This accessible resource is composed of two parts, the middle-level resource unavailable to the grazer, and the equilibrium high-level resource at which the grazer persists, equivalent to the grazer's R_G^*.

As we will examine in detail, coexistence occurs when the grazer, a superior competitor on the best resource (i.e., $A_2^*(0, K_G) < A_2^*(K_D, 0)$), leaves behind the middle-level resource that the digger exploits in compensation for its inferior competitiveness on the high-level resource. Thus, coexistence arises because of a trade-off at the individual scale between area-intensive and area-extensive foraging. The complementary foraging behaviors produce a structured resource with an overlap in consumer utilization, and thereby permit coexistence.

APPLICATION TO *TEGULA*

Parameter estimation using laboratory data

In this section, we obtain parameter estimates for the *Tegula* system from the experiments reported by Schmitt (1996) and test whether the predictions of our model are consistent with the observations. In those experiments, snails of uniform size were collected from the field and were used to create two replicates of 10 different densities (0–42 snails/0.1 m²) in flow-through laboratory tanks lined with terra-cota tiles that had been previously colonized by algae. A subset of the collected snails was dried for 48 h at 60°C and weighed to obtain initial dry tissue masses (excluding shell and operculum). After 73 d, the experiment was terminated, snails were removed from their tanks, dried, and weighed, and algal density was estimated by scraping tiles and determining the amount of chlorophyll *a* (see Schmitt (1996) for details). Changes in snail mass across the treatments ranged from mass gains of up to 60% in the low-density snail treatments to losses of up to 25% in the high-density snail treatments. Variation between replicates was up to 20% for both snail mass gains and final algal densities.

Results of the experiment provide the final algal densities at the end of the experiment and the change in snail mass during the experiment as a function of the number of snails per tank. To relate the data to our model, we assume that the final algal densities represent algal densities that have equilibrated to the grazing activities imposed by the snail treatment; the transient times to reach equilibrium were short so that we could

use the observed change in snail mass to approximate the instantaneous rates of change in snail mass. All of the experimental treatments used to parameterize the model dealt with grazers and diggers isolated from heterospecifics.

Algal abundance

We estimated the first set of parameters by fitting the model's predicted dependence of algal biomass on snail biomass to data for algal biomass. Our model provides algal fractions as a function of fixed consumer densities by setting the time derivatives in Eqs. 1b, c to zero and using the condition $A_0 + A_1 + A_2 = 1$. These equilibria depend on snail biomass; thus, we assume that the algal equilibrium densities respond quickly to the slowly changing snail biomass. Schmitt's experimental studies of *Tegula* did not provide direct estimates of the three algal fractions. Instead, his studies estimated the total resource density, which we relate to the model by multiplying each algal fraction by the appropriate resource biomass density parameter:

$$A_T(B_D, B_G) = \phi_0 A_0(B_D) + \phi_1 A_1(B_D, B_G)$$
$$+ \phi_2 A_2(B_D, B_G) \qquad (7)$$

(see Eq. A.4 for explicit dependencies).

In the absence of both diggers and grazers ($B_D = 0$, $B_G = 0$), $A_0 = 0$, $A_1 = 0$, and $A_2 = 1$, thus, from Eq. 7, the total resource density is $A_T(0, 0) = \phi_2$. Schmitt's experiments yielded $\phi_2 = 1.81$ μg Chl a/cm^2 for the algal density in the absence of snails at the end of the experiment.

To estimate additional parameters from algal density data, we used results obtained when each species was established at a gradient of densities. These results yielded relationships between total algal biomass and consumer biomass. We simplified the model predictions by using a Taylor series expansion of Eq. 7 giving, to first-order approximation, linear functions relating total algal biomass density to digger (or grazer) biomass:

$$A_T(B_D, 0) \cong \phi_0 + \frac{\alpha_0}{\mu_D}(\phi_1 - \phi_0)\frac{1}{B_D} \qquad (8a)$$

$$A_T(0, B_G) \cong \phi_1 + \frac{\alpha_1}{\mu_G}(\phi_2 - \phi_1)\frac{1}{B_G} \qquad (8b)$$

(see derivations of Eqs. A.11 and A.8). Parameters were estimated by linear regressions of final algal density on the inverse of final snail biomass density (Fig. 3A). The intercepts of Eqs. 8a and b provide estimates for ϕ_0 and ϕ_1, respectively. Using the ϕ_i's, the slopes provide estimates for α_0/μ_D and α_1/μ_G.

We excluded results from the lowest snail densities ($N_G = 3$ and $N_D = 3$), due to clear deviations from the linear approximation (which works best when N is large). A further complication arose using Eq. 8a to fit the digger data, because the intercept was negative and
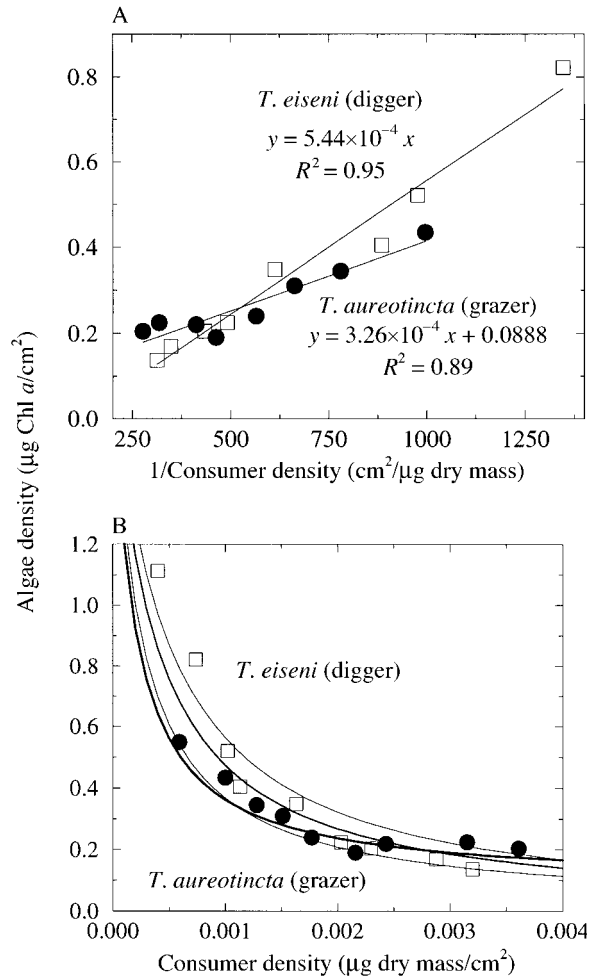

Fig. 3. (A) Algal standing stock density plotted as a function of the inverse consumer biomass density for both the grazer (*T. aureotincta*, ●) and the digger (*T. eiseni*, □). Model analysis predicts linear relationships for high consumer densities, and yields the model parameters ϕ_0, ϕ_1, α_1/μ_G, and α_0/μ_D. (B) Algal density plotted as a function of the untransformed snail densities. The solid lines depict Eqs. A.7 and A.10, using the parameters determined from the linear fits to the data of Fig. 1. Three trial values for the transition rate ratio, $\alpha_1/\alpha_0 = 0.04$ (lower curve), 0.06 (middle curve), and 0.08 (upper curve), generate three curves for the digger.

gave an estimate of $\phi_0 = -0.068$ ($R^2 = 0.97$). This value is biologically implausible; hence, we refitted the curve constraining the intercept to be zero ($\phi_0 = 0$) for all subsequent analyses. Resulting linear fits to the algal–snail biomass data were very good ($R^2 = 0.89$, 0.95). Comparing the fitted functions with Eqs. 8a and 8b yields the parameter values: $\phi_1 = 0.0888$ μg Chl a/cm^2; $\alpha_0/\mu_D = 6.13 \times 10^{-3}$ μg dry mass/cm^2; and $\alpha_1/\mu_G = 1.89 \times 10^{-4}$ μg dry mass/cm^2 (Table 2).

These parameter estimates, however, are based on linear approximations to the exact expressions for $A_T(B_D, 0)$ and $A_T(0, B_G)$. We can test our linearization scheme by substituting the parameter estimates into the

TABLE 2. Experimentally determined values for the parameters appearing in Eqs. 1–3.

Model parameters	*Tegula* values
ϕ_0	0.0 μg Chl a/cm^2
ϕ_1	0.0888 μg Chl a/cm^2
ϕ_2	1.81 μg Chl a/cm^2
α_0/μ_D	6.13×10^{-3} μg dry mass/cm^2
α_1/μ_G	1.89×10^{-4} μg dry mass/cm^2
$\gamma_D\,\alpha_0$	4.12×10^{-5} μg dry mass·(μg Chl a)$^{-1}$·d^{-1}
$\gamma_G\,\alpha_1$	8.37×10^{-6} μg dry mass·(μg Chl a)$^{-1}$·d^{-1}
α_1/α_0	0.06
δ_D	0.00177 d^{-1}
δ_G	0.00907 d^{-1}

Notes: The data of Schmitt (1996) leave only one unconstrained parameter, an absolute measure of the algal transition rate (α_0 or α_1), which has no effect on the coexistence conditions.

full forms of these expressions (see Eq. A.4). However, the full form for $A_T(B_D, 0)$ depends on the transition rate ratio α_1/α_0. Thus, we next compared the observed relationships with theoretical curves for several values, $\alpha_1/\alpha_0 = 0.04$, 0.06, and 0.08 (Fig. 3B). The value $\alpha_1/\alpha_0 = 0.06$ provided a good visual match to the untransformed digger data, but we presume the uncertainty in the transition rate ratio, α_1/α_0, is relatively large.

Consumer growth

We next sought estimates for the remaining parameters of the model by examining the relationship between snail growth and snail density. Thus, as detailed in the Appendix, we obtained the following linear approximations for individual consumer growth dependent on inverse consumer biomass:

$$\frac{1}{M_D}\frac{dM_D}{dt} = \gamma_D\phi_{10}\alpha_0\frac{1}{B_D} - \delta_D \qquad (9a)$$

$$\frac{1}{M_G}\frac{dM_G}{dt} = \gamma_G\phi_{21}\alpha_1\frac{1}{B_G} - \delta_G. \qquad (9b)$$

Intercepts of Eqs. 9a and 9b provide estimates for the metabolic losses δ_D and δ_G, respectively. Using the ϕ_i's determined from the algal fits and the slopes from Eqs. 9a and b, we can estimate the aggregate parameters $\alpha_0\gamma_D$ and $\alpha_1\gamma_G$, respectively.

Snail growth was linearly related to the inverse of snail biomass density (Fig. 4; as in Fig. 3A, data from the lowest snail densities were excluded). Linear regression ($R^2 = 0.92$ and 0.97) yielded estimates for the remaining model parameters: $\delta_D = 0.00177$ d^{-1}; $\delta_G =$

0.00907 d^{-1}; $\gamma_D\alpha_0 = 4.12 \times 10^{-5}$ (μg dry mass·(μg Chl a)$^{-1}$·d^{-1}); and $\gamma_G\alpha_1 = 8.37 \times 10^{-6}$ (μg dry mass·(μg Chl a)$^{-1}$·d^{-1}). These parameters, estimated from linear approximations, were then placed back into the full theoretical expressions and compared with the untransformed experimental data (Fig. 4B). There was a good fit between the fitted theoretical curves and the experimental data for the grazer. The digger relationship again depends on the transition rate ratio, α_1/α_0, and a good fit between the theoretical curves and the experimental data was observed for $\alpha_1/\alpha_0 = 0.06$.

Plausibility of parameter estimates

The parameter estimates (Table 2) obtained using Schmitt's (1996) experimental data can be checked for plausibility by comparisons with independent data. In
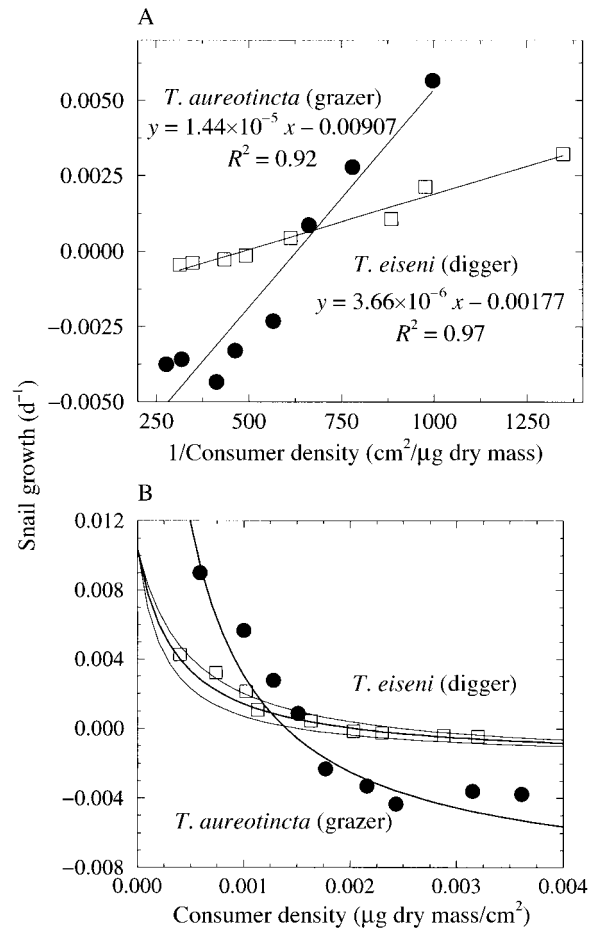

FIG. 4. (A) Consumer growth curves for both *T. aureotincta* (●) and *T. eiseni* (□) plotted against the inverse consumer biomass density. Model analysis suggests linear relationships, and the regression coefficients determine model parameters δ_D, δ_G, $\gamma_D\alpha_0$, and $\gamma_G\alpha_1$. (B) Consumer growth data plotted against the consumer biomass densities. The solid lines plot the predicted growth rates using model parameters obtained through the fits in Figs. 1 and 3. As in the algal plot, three trial values for the transition rate ratio, $\alpha_1/\alpha_0 = 0.04$, 0.06, and 0.08, are considered for the digger curve.

this section, we examine the plausibility of our estimates of clearance rate, patch transition rate ratio, metabolic rates, and conversion efficiencies to determine if they are consistent with other known biological aspects of the *Tegula* system.

Clearance rates.—Using the previously discussed values, we find the ratio of the grazer-to-digger algal clearance rates, $\mu_G/\mu_D = 1.95$, showing that the grazer encounters high-density algae patches at almost twice the rate of the digger. Schmitt (1996) performed experiments that measured the area cleared per unit time for each grazer. The ratio of those values was ~2.1, in rough agreement with our estimate. Our predicted value depends on our determination of the transition rate ratio, α_1/α_0, which has an uncertainty of $\geq 10\%$; likewise, Schmitt's data have uncertainties of ~10%.

Algal transition rate ratio.—Our estimate of the patch transition rate ratio, $\alpha_1/\alpha_0 = 0.06$, is roughly equal to our ratio of the resource density parameters, $\phi_{10}/\phi_{21} = 0.052$. If the two ratios were identical, then $\alpha_0\phi_{10} = \alpha_1\phi_{21}$; i.e., the algal biomass growth rates (the product of patch transition rate and algal biomass difference) would be the same for the two patch types. Hence, our estimated patch transition rate ratio, α_1/α_0, reflects the longer time required to produce the greater abundance of algae in the high level. The close match between the two estimated ratios suggests consistency within our set of parameter estimates.

Conversion efficiencies.—These data allow us to predict the grazer-to-digger conversion efficiency ratio, γ_G/γ_D. The fits yield 3.4, meaning that for every unit of algae consumed by each consumer species, grazers fix 3.4 times more of the algal biomass into consumer biomass than do diggers. We are unaware of the physiological basis for these underlying conversion efficiency differences.

Metabolic rates.—The estimated ratio of grazer and digger metabolic rates is $\delta_G/\delta_D = 5.1$. Metabolic rates can be compared to relative movement speeds because metabolic rates increase with increasing speed for organisms ranging from terrestrial animals (Schmidt-Nielsen 1995, Calder 1996) to marine gastropods (Newell and Roy 1973, Denny 1980, Houlihan and Innes 1982). Respiration rates for the winkle *Littorina littorea* demonstrated a five- to sevenfold increase between the quiescent and active states (Newell and Roy 1973), and the trochids *Monodonta articulata, M. turbinata, Gibbula richardi,* and *G. rarilineata* demonstrate twofold increases when active in air (Houlihan and Innes 1982). There are at least two potential sources for metabolic costs in the gastropod *Tegula.* First, Denny (1980) vividly demonstrates the important contribution of mucus production to overall locomotion costs in the terrestrial gastropod, *Ariolimax columbianus,* and this per unit distance cost scales directly with speed. Alternatively, Denny (1980) demonstrated for *A. columbianus* that the internal power generated increases linearly with the slug's speed, a relationship
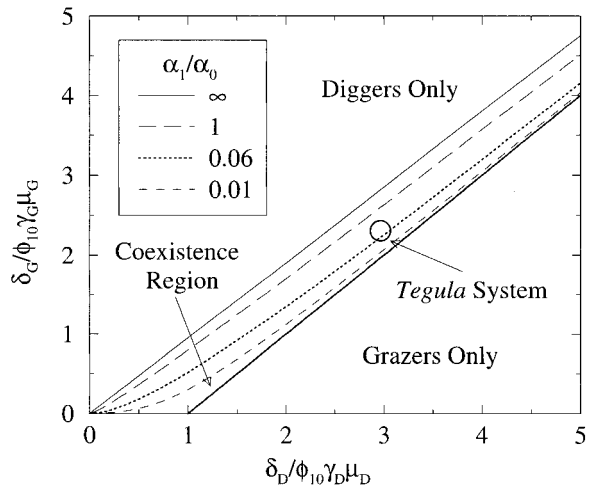

FIG. 5. The coexistence region for the *Tegula* system, with algal parameters fixed to the values determined through the fits in Figs. 1 and 4. The condition separating the coexistence region and digger-only region depends on the transition rate ratio; boundaries are shown for four values of the ratio. The heavy line separates the coexistence region from the grazer-only region. When the transition rate ratio approaches zero, the coexistence region is nonexistent. Estimates for the ratios $\delta_G/(\phi_{10}\gamma_G\mu_G)$ and $\delta_D/(\phi_{10}\gamma_D\mu_D)$ from the *Tegula* data, denoted by the circle, place the system just outside the coexistence region, but within a 5% change in the estimated ratios.

that arises because transporting a mass m over some distance with speed v requires a power output of ϵmv, where ϵ is a proportionality constant. If we assume that the greatest portion of *Tegula*'s metabolic rate arises from these transportation costs, then we would expect equality between the metabolic rate ratio and the power output ratio, $\delta_G/\delta_D = \epsilon_G m_G v_G/\epsilon_D m_D v_D$. Schmitt (1996) reports a measured speed ratio of $v_G/v_D = 7.0$, close to that of the estimated metabolic rates. If we assume that the coefficients ϵ_G and ϵ_D are identical (due to a lack of information), then we expect the ratio of the snail masses (including shells) to be $m_G/m_D = 0.73$. For the snails used in Schmitt's experiments, individual biomasses were 2.75 g for *T. aureotincta* and 3.52 g for *T. eiseni,* giving the ratio of total wet masses as ~0.78, in close agreement with our estimate.

COEXISTENCE

There are four possible competitive outcomes: (1) extinction of both species; (2) persistence of only the grazer; (3) persistence of only the digger; and (4) coexistence of the digger and grazer (Fig. 5). The outcomes depend on the resource parameters and the aggregate digger and grazer parameters, $\delta_D/\gamma_D\mu_D$ and $\delta_G/\gamma_G\mu_G$. Persistence for each species requires a simple balance between consumption and metabolism, i.e., $\delta_D/\gamma_D\mu_D = R_D^* \leq \phi_{20}$ and $\delta_G/\gamma_G\mu_G = R_G^* \leq \phi_{21}$. Within the region where each species can persist in the absence of competition, we have three competitive scenarios:

the digger wins, the grazer wins, or both species coexist.

Coexistence occurs in the narrow region indicated by the overlap of the two invasibility conditions (Eqs. 5 and 6; Fig. 5). The region's size depends on the ratio of the patch transition rates (α_1/α_0). In the limit $\alpha_1/\alpha_0 \rightarrow 0$, the boundaries for the two invasibility conditions are equivalent and there is no overlap: one species or the other always wins. However, as α_1/α_0 increases, the coexistence region expands because the grazer's invasion boundary pushes into the digger's persistence region. This coexistence region attains its maximal area as $\alpha_1/\alpha_0 \rightarrow \infty$.

Substituting the parameter values listed in Table 2 into the invasibility criteria yields the conditions that must be satisfied for coexistence. Numerically, the resultant conditions are $2.43 < 2.33$ (grazer invasion criterion; Eq. 5) and $2.97 < 3.31$ (digger invasion criterion; Eq. 6). Hence, the estimated parameters predict grazer exclusion, but a change of only 5% in the grazer invasion condition's numerical values, well within the error associated with the parameter estimates, would yield coexistence.

DISCUSSION

A sizable body of theoretical work has focused on whether a single resource species can be "partitioned" into different limiting components and thereby allow coexistence of more than one species of consumer. Coexistence has been shown to be possible, theoretically, if the limiting resource fluctuates on an appropriate time scale between states that alternatively favor different consumer species. Such fluctuations could arise from external forces (Levins 1979) or from the activities of the consumers themselves (Koch 1974*a*, *b*, Armstrong and McGehee 1980). Coexistence also is possible when different components of a limiting resource simultaneously exist in a single environment. For example, Briggs et al. (1993) showed that more than one parasitoid species could coexist on a single host species by attacking different developmental stages of the host. Tilman (1994) found that coexistence of sessile organisms (plants) competing for a single limiting resource could occur in a physically homogeneous environment in which spatial heterogeneity in the resource arises solely from resource extraction activities and death of the consumers. The essential feature of Tilman's model that allows coexistence is a trade-off in the abilities of species to colonize unoccupied patches and deplete resources within a patch.

We have extended this perspective to mobile consumers capable of visiting many patches during a feeding episode where patchiness in the limiting resource arises from the foraging activities of the consumers. We found that mobile consumers with complementary foraging attributes can coexist in an otherwise homogeneous environment. A key to coexistence is a trade-off in the consumers' ability to locate abundant food and to deplete food within a patch. Coexistence is possible because consumption produces patchiness in the shared resource, such that local resource densities favoring each species exist in the environment. As such, our system can be viewed as a spatial analogue to the temporally heterogeneous one modeled by Armstrong and McGehee (1980).

Our theoretical approach was motivated, in part, by the large empirical literature on exploitation competition between species of mobile herbivores. Numerous examples of competition for microalgae between herbivores in benthic marine and freshwater environments have been reported (Branch 1984, Carpenter 1990, Robertson 1991, Underwood 1992, McClanahan et al. 1996, Schmitt 1996). For example, competitors from one of the more comprehensively studied systems involving two species of marine snails in the genus *Tegula* (Schmitt 1985, 1996) have persisted together with relatively small fluctuations in abundances (<20% of the long-term mean) for at least four population turnovers on a reef with intense competition (Schmitt 1985, 1996).

A near-universal feature of empirical studies of competition for microalgae is the focus on individual performance, e.g., body growth, fecundity, and mortality of the herbivores. The studies of *Tegula* by Schmitt (1985, 1996) were no exception. A specific goal of our study was to test our model using data from the *Tegula* system. Our desire to use available data to test model predictions dictated that we construct a "behavioral" or "within-generation" time-scale model.

Our criterion for "coexistence" and, hence, the absence of competitive exclusion, rests on the ability of a single individual of each consumer to have positive body growth when the population biomass of the other species is at equilibrium with the resource. Parameter values calculated from the equilibrium equations of our model, using growth data for each *Tegula* species in isolation (Schmitt 1996), indicate that this system of competitors lies on the edge of parameter space that allows coexistence. This result suggests that the mechanism that we modeled may provide a sufficient, although perhaps not complete, explanation for their coexistence. As we will discuss, features of the *Tegula* species that promote coexistence may be prevalent among other pairs of benthic herbivores that compete exploitatively for microalgae. Long-term processes might well alter coexistence prospects. For example, reproduction requires a separate allocation of resources that we have not considered. Likewise, fluctuations in resource productivity and consumer mortality and disturbances may play a role in long-term coexistence. These potentially important processes must be considered for any conclusive determination, either empirical or theoretical, of long-term coexistence.

The connection between our criterion for coexistence, based on individual performance, and the more traditional view is relatively straightforward for eco-
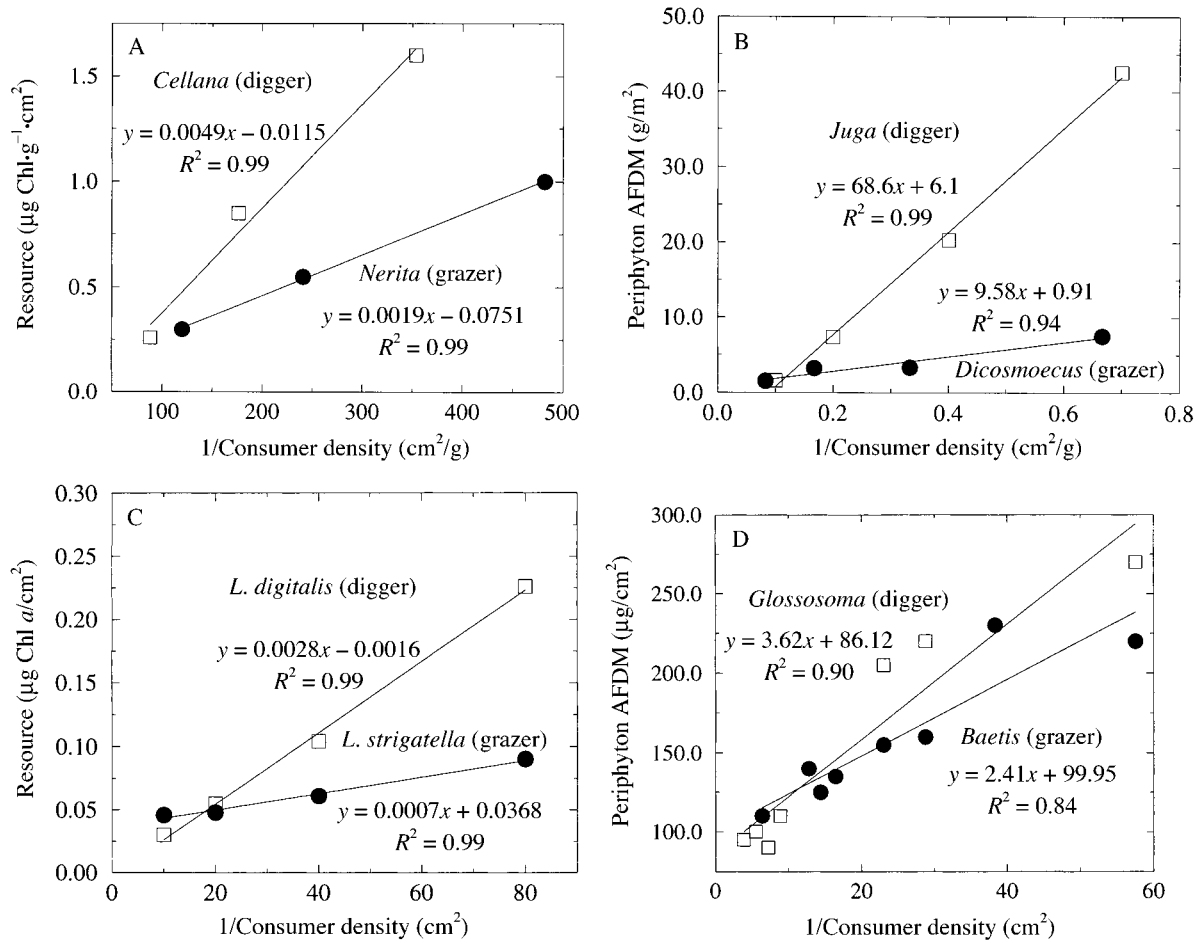
FIG. 6. Microalgal abundance vs. inverse consumer density from a variety of marine and freshwater systems. (A) Data from Underwood (1984) on the *Nerita atramentosa* (snail, grazer)–*Cellana tramoseria* (limpet, digger) system from the marine intertidal shore in eastern Australia. Data are from his Experiment 1, mid- and lower intertidal zones. (B) Data from Steinman et al. (1987) on ash-free dry mass of algae in a freshwater stream system in North America: *Juga silicula* (snail, digger) and *Dicosmoecus gilvipes* (caddisfly larva, grazer). (C) Data from R. J. Schmitt and S. S. Anderson (*unpublished manuscript*) on the marine intertidal shore along the western United States using the limpets *Lottia digitalis* (digger) and *L. strigatella* (grazer). (D) Data from the freshwater system of Kohler (1992), using ash-free dry mass of algae for *Glossosoma nigrior* (caddisfly larva, digger) and *Baetis tricaudatus* (mayfly larva, grazer).

logically closed populations in which population dynamics are determined solely by the demographic rates of local individuals. However, populations of many marine and freshwater species that consume microalgae are open by virtue of bipartite life cycles. For example, most benthic marine organisms have early developmental stages that disperse widely as plankton, and many freshwater herbivores are the larvae of highly mobile, terrestrial-dwelling adults. The traditional concepts of competitive exclusion and coexistence are problematic for species in which colonization of local populations is from external sources; regardless of the outcome of local competition, continued invasion of an inferior competitor can preclude total exclusion (Schmitt 1996).

Indeed, our coexistence criterion, focusing on individual growth, is more appropriate for competing species with ecologically open populations than are the traditional criteria that focus on population dynamics. An exception occurs when food is not the limiting resource and the overall abundance of a consumer is limited by the supply of offspring (which is independent of local fecundity). In this case, the ability of colonists to reach sexual maturity is not a reasonable coexistence criterion. However, food was limiting in the *Tegula* system that we modeled; individual growth of both consumers on a natural reef tripled when the competing species was removed (Schmitt 1985). Furthermore, observations that the individual growth of *Tegula* under ambient conditions was near the "knife-edge" between positive and negative growth provide further evidence that microalgae were limiting (Schmitt 1985, 1996) and that competition was important in determining coexistence in this system.
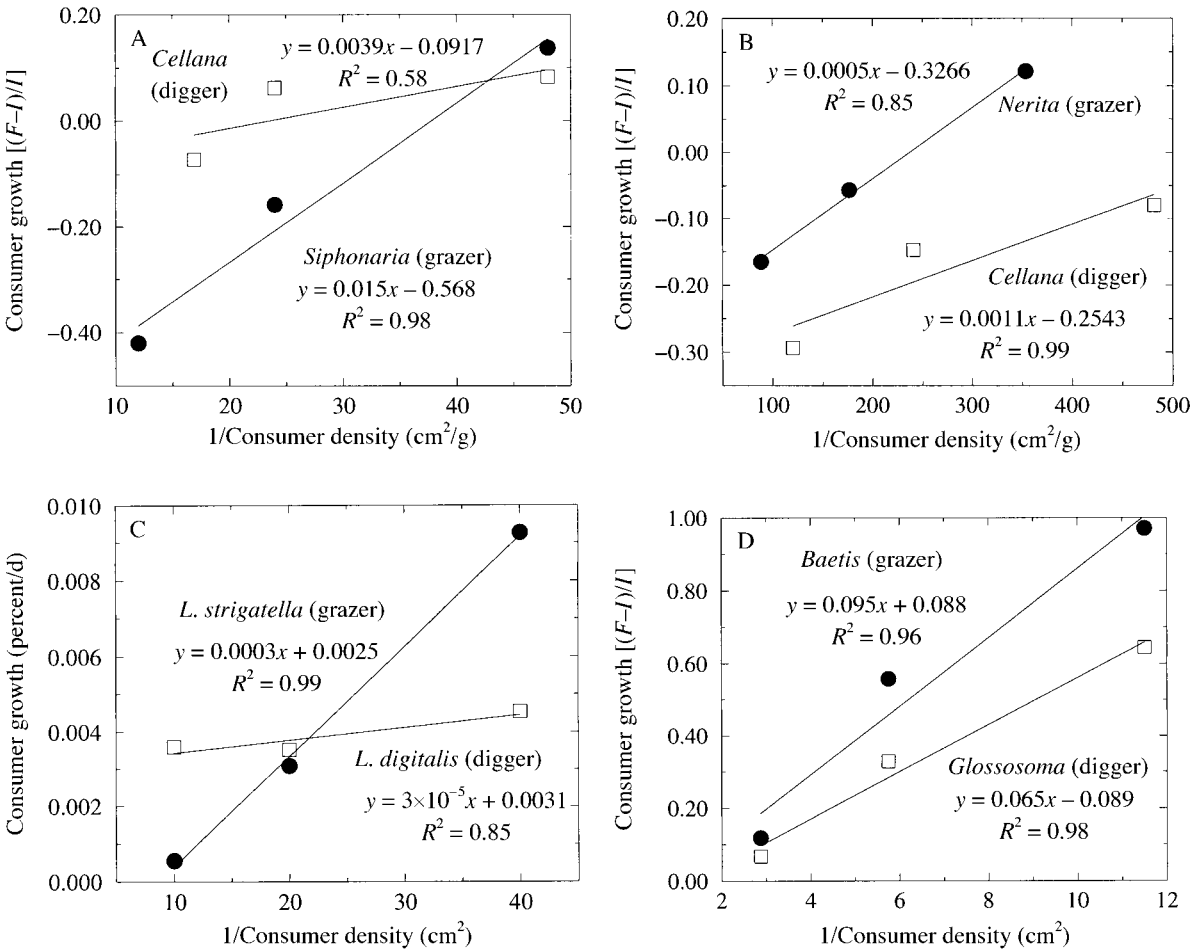
FIG. 7. Consumer growth vs. inverse consumer density from a variety of marine and freshwater systems. (A) Data from Creese and Underwood (1982) on the *Siphonaria denticulata* (snail, grazer)–*Cellana tramoseria* (limpet, digger) system from the marine intertidal shore in eastern Australia. (B) Data from Underwood (1984) on the *Nerita atramentosa* (snail, grazer)–*Cellana tramoseria* (limpet, digger) system from the marine intertidal shore in eastern Australia. (C) Data from R. J. Schmitt and S. S. Anderson (*unpublished manuscript*) on the marine intertidal shore along the western United States using the limpets *Lottia digitalis* (digger) and *L. strigatella* (grazer). (D) Data from the freshwater system of Kohler (1992) for *Glossosoma nigrior* (caddisfly larva, digger) and *Baetis tricaudatus* (mayfly larva, grazer). The data for *Baetis* near 3 cm^2 and 6 cm^2 were confounded by low survivorships (20% and 40%, respectively) through the course of the experiment.

A primary assumption of our model is that the vertically structured nature of the microalgal resource results from the foraging activity of the herbivores. Variation in the effect of one herbivore on the performance of another frequently has been attributed to differences in the degree to which microalgae were cropped close to the substratum (Underwood 1978, 1984, Branch and Branch 1980, Underwood and Jernakoff 1981, Creese and Underwood 1982, McAuliffe 1984, Fletcher and Creese 1985, Hill and Knight 1987, 1988, Steinman et al. 1987, Kohler 1992, Schmitt 1996). Such differences often can be traced to morphological variation in feeding structures (Underwood 1978, Branch and Branch 1980, Underwood and Jernakoff 1981, Creese and Underwood 1982, Steneck and Watling 1982, Black et al. 1988, Hill and Knight 1988, Steneck et al. 1991). For example, Hill and Knight (1987, 1988) compared the

effects of grazing by co-occurring mayfly nymphs (genus *Ameletus*) and caddisfly larvae (*Neophylax*) on freshwater periphyton. Mayfly larvae, which use brush-like labial palps to feed, removed microalgae from the upper layer of the periphyton, but had no discernible effect on the lower adnate layer. By contrast, the caddisfly larvae, which have hard, scraper-edged mandibles, were able to depress periphyton in both the upper and lower layers (Hill and Knight 1988; also see McAuliffe 1984).

Available empirical evidence also suggests that the degree to which a consumer depletes microalgae in a patch varies inversely with the area that it grazes per unit time (e.g., Underwood 1977, 1978, Steinman et al. 1987, Kohler 1992, Schmitt 1996). The apparent prevalence of this covariation among mobile herbivores prompted Schmitt (1996) to suggest that benthic con-

sumers may be constrained in their abilities to both maximally extract food in each patch harvested and maximize the area that they graze per unit time (also see Underwood 1978). These differences may represent a general trade-off for harvesting food under different resource levels (Schmitt 1996); area-intensive grazing (i.e., depressing microalgae to a low level in a patch) should confer a relatively greater intake rate of food when or where food is scarce (a thin layer of microalgae) in the environment, whereas area-extensive foraging (i.e., feeding over a larger area per unit time) should result in a greater intake rate when food is abundant.

If such a trade-off is common, then other pairs of co-occurring benthic consumers should be expected to affect microalgal densities in a pattern similar to that observed for *Tegula*. This contention is supported by four examples taken from the literature (representing two freshwater and two marine systems), in which independent information was presented that allowed us to classify each species in a pair of consumers as an area-intensive forager (digger) or area-extensive forager (grazer). The pattern of effects of intraspecific variation in consumer pressure on microalgal density was qualitatively similar both among the four pairs of herbivores (Fig. 6) and with that seen for *Tegula* (Fig. 3). At low herbivore densities (i.e., high area per consumer), the area-extensive species reduced microalgae to a greater extent than did area-intensive foragers. However, increases in herbivore densities produced comparatively smaller declines in microalgae for area-extensive than for area-intensive foragers (Fig. 6). As a consequence, area-intensive species depressed food to a lower level at some high consumer density.

A remaining issue is whether the area-intensive–area-extensive foraging dichotomy results in predictable and consistent patterns of density-dependent growth responses of co-occurring herbivores. Evidence from the literature on other pairs of consumers suggests that the qualitative patterns of density-dependent growth exhibited by *Tegula* (Fig. 4) may be a general feature of mobile herbivores that compete exploitatively for microalgae (Fig. 7). Although the data are sparse, for all four pairs of competing consumers, the grazer (categorized by independent evidence) grew faster than the digger at low densities of conspecifics (Fig. 7), and its body growth was relatively more sensitive to variation in conspecific density (i.e., had a steeper slope). These two features suggest the area-extensive–area-intensive trade-off, although the available data are insufficient to determine whether coexistence would be predicted within our model framework.

The work presented here emphasizes the central importance of two general features that allow competitors to coexist on a single resource species: the structuring of that resource species into discrete components, and differences in the abilities of the competitors to use those components. Here, we have shown that the foraging activities of mobile consumers can structure the shared resource and lead to fine-scale spatial heterogeneity in an otherwise homogeneous environment. The heterogeneity results from differences in the ability of consumers to extract food within a patch, and in movement rates while foraging. Coexistence is possible when the ability to find patches of abundant food varies inversely with the ability to deplete resources in a patch. To the extent that is known, such a trade-off between resource extraction and patch-finding abilities appears to be common for co-occurring consumers that (at least potentially) compete for microalgae. It remains to be determined whether the mechanism modeled here is a general feature that contributes to coexistence of such species in nature.

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APPENDIX

DIGGER–GRAZER MODEL ANALYSIS

Resource equations

Our model, formulated at behavioral time scales of consumers, assumes three discrete resource levels with habitat fractions A_0, A_1, and A_2 ($A_0 + A_1 + A_2 = 1$). Resource consumption is directly proportional to resource density and consumer biomass density. These assumptions lead to resource equations

$$\frac{dA_0}{dt} = -\alpha_0 A_0 + \mu_D B_D (A_1 + A_2) \tag{A.1a}$$

$$\frac{dA_1}{dt} = \alpha_0 A_0 - \alpha_1 A_1 - \mu_D B_D A_1 + \mu_G B_G A_2 \tag{A.1b}$$

$$\frac{dA_2}{dt} = \alpha_1 A_1 - \mu_D B_D A_2 - \mu_G B_G A_2 \tag{A.1c}$$

where $B_D = N_D M_D$ and $B_G = N_G M_G$ represent the digger and grazer biomass densities (biomass per area) resulting from a product of the respective number densities N_D or N_G (number of consumers per area) and individual consumer mass M_D or M_G (biomass per consumer). Parameters α_0 and α_1 (time^{-1}) are the transition rates of the lowest and middle-resource levels to the next highest level, and μ_D and μ_G (area cleared per consumer biomass per time) denote the individual digger and grazer clearance rates.

Quasi-steady-state resource.—We assume, throughout our analysis, that changes in resource abundance occur quickly relative to the longer time scales associated with the consumers. This assumption enables equilibrium analysis of the resource equations, providing equilibrium resource fractions as a function of consumer biomass. Thus, setting the time derivatives in Eqs. A.1b and c to zero gives

$$0 = \alpha_0(1 - A_1 - A_2) - \alpha_1 A_1 - \mu_D B_D A_1 + \mu_G B_G A_2 \tag{A.2a}$$

$$0 = \alpha_1 A_1 - (\mu_D B_D + \mu_G B_G) A_2 \tag{A.2b}$$

and leads to

$$A_0(B_D) = \frac{\mu_D B_D}{\alpha_0 + \mu_D B_D} \tag{A.3a}$$

$$A_1(B_D, B_G) = \frac{\alpha_0(\mu_G B_G + \mu_D B_D)}{(\alpha_1 + \mu_G B_G + \mu_D B_D)(\alpha_0 + \mu_D B_D)} \tag{A.3b}$$

$$A_2(B_D, B_G) = \frac{\alpha_0 \alpha_1}{(\alpha_1 + \mu_G B_G + \mu_D B_D)(\alpha_0 + \mu_D B_D)} \tag{A.3c}$$

for the three resource fractions, given consumer biomass densities B_D and B_G. These equations provide the total resource density after multiplying each fraction by the appropriate resource biomass density parameters, ϕ_0, ϕ_1, and ϕ_2 (resource biomass per area), representing the amount of resource biomass contained in a unit area if the habitat fraction $A_i = 1$. Total resource density is then

$$A_T(B_D, B_G) = \phi_0 A_0(B_D) + \phi_1 A_1(B_D, B_G) + \phi_2 A_2(B_D, B_G)$$

$$= [\phi_0 \mu_D B_D(\alpha_1 + \mu_G B_G + \mu_D B_D)$$

$$+ \phi_1 \alpha_0(\mu_G B_G + \mu_D B_D) + \phi_2 \alpha_0 \alpha_1]$$

$$\div [(\alpha_1 + \mu_G B_G + \mu_D B_D)(\alpha_0 + \mu_D B_D)]. \tag{A.4}$$

Consumer equations

Consumed resource biomass is converted into individual consumer mass with efficiencies γ_D and γ_G (consumer biomass per resource biomass), and diggers and grazers have respi-

ration rates δ_D and δ_G (time^{-1}). These assumptions yield

$$\frac{dM_D}{dt} = \gamma_D \mu_D M_D(\phi_{10} A_1 + \phi_{20} A_2) - \delta_D M_D \tag{A.5a}$$

$$\frac{dM_G}{dt} = \gamma_G \mu_G M_G \phi_{21} A_2 - \delta_G M_G \tag{A.5b}$$

where $\phi_{ij} = \phi_i - \phi_j$ represent the resource biomass differences between levels i and j. Substituting the quasi-steady-state resource fractions from Eq. A.3 into Eq. A.5, we obtain

$$\frac{1}{M_D}\frac{dM_D}{dt} = \gamma_D \mu_D \frac{\phi_{10}\alpha_0(\mu_G B_G + \mu_D B_D) + \phi_{20}\alpha_0\alpha_1}{(\alpha_1 + \mu_G B_G + \mu_D B_D)(\alpha_0 + \mu_D B_D)} - \delta_D$$

$$= f(B_D, B_G) \tag{A.6a}$$

$$\frac{1}{M_G}\frac{dM_G}{dt} = \gamma_G \mu_G \phi_{21}\frac{\alpha_0\alpha_1}{(\alpha_1 + \mu_G B_G + \mu_D B_D)(\alpha_0 + \mu_D B_D)} - \delta_G$$

$$= g(B_D, B_G). \tag{A.6b}$$

Single-consumer systems

We are interested in two experimental treatments, grazers only ($B_D = 0$) and diggers only ($B_G = 0$), considered in turn. In both treatments, we linearize the resource density and consumer growth functions to simplify data analysis.

Grazers-only system.—1. *Algal response.*—When only grazers inhabit the system ($B_D = 0$), the total resource density (Eq. A.4) simplifies to

$$A_T(0, B_G) = \frac{\dfrac{\alpha_1 \phi_2}{\mu_G} + \phi_1 B_G}{\dfrac{\alpha_1}{\mu_G} + B_G}. \tag{A.7}$$

Linearization proceeds by assuming that the consumer density is a large quantity, allowing a series expansion,

$$A_T(0, B_G) = \frac{\left(\dfrac{\alpha_1 \phi_2}{\mu_G} + \phi_1 B_G\right)\dfrac{1}{B_G}}{\left(\dfrac{\alpha_1}{\mu_G} + B_G\right)\dfrac{1}{B_G}} = \frac{\phi_1 + \dfrac{\alpha_1 \phi_2}{\mu_G B_G}}{1 + \dfrac{\alpha_1}{\mu_G B_G}}$$

$$\cong \left(\phi_1 + \frac{\alpha_1 \phi_2}{\mu_G B_G}\right)\left(1 - \frac{\alpha_1}{\mu_G B_G}\right)$$

$$\cong \phi_1 + \frac{\alpha_1}{\mu_G}(\phi_2 - \phi_1)\frac{1}{B_G}, \tag{A.8}$$

keeping terms up to first-order in $1/B_G$. In the expansion, we make use of the standard Taylor series expansion, $1/(1 + x) \cong 1 - x + x^2 - x^3 + \ldots$, for $|x| < 1$.

2. *Grazer growth.*—When in isolation from diggers ($B_D = 0$), the grazer's biomass dynamics (Eq. A.6b) can be expressed as

$$\frac{1}{M_G}\frac{dM_G}{dt} = \frac{\phi_{21}\alpha_1\gamma_G\mu_G}{\alpha_1 + \mu_G B_G} - \delta_G$$

$$\cong \frac{\phi_{21}\alpha_1\gamma_G\mu_G}{\mu_G B_G} - \delta_G$$

$$\cong \phi_{21}\alpha_1\gamma_G\frac{1}{B_G} - \delta_G \tag{A.9}$$

where the final expression is valid for $\alpha_1 \ll \mu_G B_G$, providing a linear dependence of growth on $1/B_G$.

Diggers-only system.—1. *Algal response.*—When only

diggers inhabit the system, $B_G = 0$ and the total resource density is given by

$$A_T(B_D, 0) = \frac{\dfrac{\alpha_1\phi_2}{\alpha_0} + \dfrac{\mu_D}{\alpha_0}\left(\phi_1 + \dfrac{\alpha_1\phi_0}{\alpha_0}\right)B_D + \phi_0\left(\dfrac{\mu_D}{\alpha_0}\right)^2 B_D^2}{\left(1 + \dfrac{\mu_D}{\alpha_0}B_D\right)\left(\dfrac{\alpha_1}{\alpha_0} + \dfrac{\mu_D}{\alpha_0}B_D\right)}.$$

(A.10)

Series expansion for high digger density follows the calculation performed for the grazers-only case,

$$A_T(B_D, 0)$$

$$= \frac{\left(\dfrac{\alpha_1\phi_2}{\alpha_0} + \dfrac{\mu_D}{\alpha_0}\left(\phi_1 + \dfrac{\alpha_1\phi_0}{\alpha_0}\right)B_D + \phi_0\left(\dfrac{\mu_D}{\alpha_0}\right)^2 B_D^2\right)\left(\dfrac{\alpha_0}{\mu_D B_D}\right)^2}{\left(1 + \dfrac{\mu_D}{\alpha_0}B_D\right)\left(\dfrac{\alpha_1}{\alpha_0} + \dfrac{\mu_D}{\alpha_0}B_D\right)\left(\dfrac{\alpha_0}{\mu_D B_D}\right)^2}$$

$$= \frac{\phi_0 + \left(\phi_1 + \dfrac{\alpha_1\phi_0}{\alpha_0}\right)\dfrac{\alpha_0}{\mu_D B_D} + \dfrac{\alpha_1\phi_2}{\alpha_0}\left(\dfrac{\alpha_0}{\mu_D B_D}\right)^2}{\left(1 + \dfrac{\alpha_0}{\mu_D B_D}\right)\left(1 + \dfrac{\alpha_1}{\mu_D B_D}\right)}$$

$$\cong \left(\phi_0 + \left(\phi_1 + \dfrac{\alpha_1\phi_0}{\alpha_0}\right)\dfrac{\alpha_0}{\mu_D B_D}\right)\left(1 - \dfrac{\alpha_0}{\mu_D B_D}\right)\left(1 - \dfrac{\alpha_1}{\mu_D B_D}\right)$$

$$\cong \phi_0 + \dfrac{\alpha_0}{\mu_D}(\phi_1 - \phi_0)\dfrac{1}{B_D}.$$

(A.11)

2. *Digger growth.*—When in isolation from grazers, the digger's biomass changes according to

$$\frac{1}{M_D}\frac{dM_D}{dt} = \gamma_D\mu_D\frac{\phi_{10}\alpha_0\mu_D B_D + \phi_{20}\alpha_0\alpha_1}{(\alpha_0 + \mu_D B_D)(\alpha_1 + \mu_D B_D)} - \delta_D$$

$$\cong \gamma_D\mu_D\frac{(\phi_{10}\alpha_0\mu_D B_D)}{(\mu_D B_D)(\mu_D B_D)} - \delta_D$$

$$\cong \gamma_D\phi_{10}\alpha_0\frac{1}{B_D} - \delta_D$$

(A.12)

where the final expression is valid for high digger densities.

Invading single-consumer systems

Our analysis assumes a very limited and strict definition for coexistence: if in each steady-state, single-consumer system, the other consumer would have a positive growth rate, then the two species coexist.

Diggers invading grazers.—When the grazers exist alone and are at equilibrium, the grazer biomass achieves a steady-state value K_G determined by $g(0, K_G) = 0$, or,

$$\frac{1}{M_G}\frac{dM_G}{dt} = 0 \Rightarrow \frac{\delta_G}{\gamma_G\mu_G} = \frac{\phi_{21}\alpha_1}{\alpha_1 + \mu_G K_G}$$

$$K_G = \frac{\alpha_1(\phi_{21}\mu_G\gamma_G - \delta_G)}{\mu_G\delta_G}.$$

(A.13)

Under these conditions, diggers face a growth rate given by $f(0, K_G)$ (Eq. A.6a), which must be positive for successful invasion,

$$\frac{1}{M_D}\frac{dM_D}{dt} = \gamma_D\mu_D\frac{\phi_{10}\alpha_0(\mu_G K_G) + \phi_{20}\alpha_0\alpha_1}{\alpha_0(\alpha_1 + \mu_G K_G)} - \delta_D > 0$$

$$\gamma_D\mu_D\frac{\left(\phi_{10}\left(\dfrac{\phi_{21}\alpha_1\gamma_G\mu_G}{\delta_G} - \alpha_1\right) + \phi_{20}\alpha_1\right)\delta_G}{\phi_{21}\alpha_1\gamma_G\mu_G} > \delta_D$$

$$\phi_{10} + \frac{\delta_G}{\gamma_G\mu_G} > \frac{\delta_D}{\gamma_D\mu_D}$$

$$\phi_{10} + \phi_{21}A_2(0, K_G) > \frac{\delta_D}{\gamma_D\mu_D}.$$

(A.14)

The ratios of metabolic rate to resource utilization represent each snails' resource availability required for persistence. Digger invasion of the grazer-only system occurs if inequality (A.14) is satisfied, and requires that the digger's persistence level be less than the equilibrium resource available to it. In this case, resource available to the digger is composed of two parts: the resource at the middle level, which is unused by the grazer, and the equilibrium resource density at the high-resource level, shared with the grazer.

Grazers invading diggers.—Grazers will be able to invade the equilibrium digger-only system if

$$\frac{1}{M_G}\frac{dM_G}{dt} = \gamma_G\mu_G\phi_{21}A_2(K_D, 0) - \delta_G > 0$$

$$\frac{\delta_G}{\gamma_G\mu_G} < \phi_{21}A_2(K_D, 0)$$

(A.15)

where K_D is the steady-state digger biomass and $A_2(K_D, 0)$ is the equilibrium high-level resource fraction of the digger-only system. Thus, this invasion condition requires that the equilibrium high-level resource fraction left behind by the diggers be greater than the persistence level of the grazers. This grazer invasion condition requires solving the full set of equations determining the digger equilibrium,

$$\frac{dA_1}{dt} = 0 \Rightarrow \alpha_0(1 - A_1(K_D, 0) - A_2(K_D, 0))$$

$$= (\alpha_1 + \mu_D K_D)A_1(K_D, 0)$$

(A.16a)

$$\frac{dA_2}{dt} = 0 \Rightarrow \alpha_1 A_1(K_D, 0) = \mu_D K_D A_2(K_D, 0)$$

(A.16b)

$$\frac{1}{M_D}\frac{dM_D}{dt} = 0 \Rightarrow \phi_{10}A_1(K_D, 0) + \phi_{20}A_2(K_D, 0)$$

$$= \frac{\delta_D}{\gamma_D\mu_D}$$

(A.16c)

which yields

$$A_2(K_D, 0) = \frac{1}{\phi_{20}}\left(\frac{\delta_D}{\gamma_D\mu_D} - \phi_{10}A_1(K_D, 0)\right)$$

(A.17)

where

$$A_1(K_D, 0) = \frac{1}{2x}\sqrt{y^2 - 4xz} - \frac{y}{2x}$$

$$x = \frac{\phi_{21}}{\phi_{10}}\left(\frac{\alpha_1}{\alpha_0}\frac{\phi_{20}}{\phi_{10}} - 1\right)$$

$$y = \frac{\delta_D}{\phi_{10}\gamma_D\mu_D}\frac{\phi_{20}}{\phi_{10}}\left(1 + \frac{\alpha_1}{\alpha_0}\right) + \frac{\phi_{20}}{\phi_{10}} - \frac{2\delta_D}{\phi_{10}\gamma_D\mu_D}$$

$$z = \frac{\delta_D}{\phi_{10}^2\gamma_D\mu_D}\left(\frac{\delta_D}{\gamma_D\mu_D} - \phi_{20}\right).$$