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THEORETICAL CONCEPTS AND EMPIRICAL APPROACHES TO MEASURING INTERACTION STRENGTH

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Abstract. Evaluating the strength of interactions among species is an important step in understanding the structure of natural communities and predicting how they will respond to changes in the biotic environment. Where feasible, accurate characterization of interaction strength can shift the theory of multispecies communities from identifying the vast range of possibilities to isolating the most likely possibilities. To derive generality in our understanding of interaction strengths, however, they must be placed within a unified framework, a framework that can be applied to empirical situations. In this paper we first identify four different theoretical concepts of interaction strength prevalent in the literature (community matrix, Jacobian matrix, inverse Jacobian, and removal matrix), showing how they are related to each other and how they are derived. We also demonstrate that their behavior is not necessarily concordant; hence it is important to identify clearly which concept of interaction strength is being discussed. Then we evaluate several observational and experimental approaches to estimating interaction strength empirically, highlighting their ties to theory, if any, and the limitations and strengths of each approach. Finally, we apply several techniques to a simulated data set, based on an intertidal community, evaluating both accuracy and logistical ease of these approaches. We find that per capita interaction strength is often the most useful index to measure, that caution must be exercised in interpreting empirical estimates of interaction strength because of equilibrium assumptions and the potential confounding effect of indirect effects, and that concentrating on evaluating the relationship between empirically observed rates of change and species abundances may be a profitable way to proceed.

Key words: community matrix; competition; dynamic regression; experiment; food web; interaction strength; Jacobian matrix; Lotka-Volterra model; observation; per capita effects; simulation.

INTRODUCTION

One of the central themes in community ecology is the examination of interactions between species (e.g., Connell 1983, Schoener 1983, Ricklefs 1990). Most pairwise interactions, and those embedded in complex food webs, are described in terms of the concept of interaction strength. Interaction strength estimates the magnitude of the effect of one species on another, and is commonly used in both experimental and theoretical approaches. This widely used concept, however, has several different definitions (e.g., MacArthur 1972, Vandermeer 1972, May 1973, Yodzis 1989), and a surprising variety of empirical approaches have been applied to determine its magnitude (e.g., Paine 1980, 1992, Davidson 1980, Bender et al. 1984, Wootton 1993*a*, *b*, 1994*b*, 1997, Menge et al. 1994, Laska 1995, *unpublished manuscript*, Moore et al. 1996; J. Ruesink, *unpublished manuscript*).

The great diversity of approaches and definitions complicates coherent and universal analysis of interactions in food webs. It is important for ecologists to understand interaction strength, because of its dominant role as a descriptor of community parameters (Paine 1992, Wootton 1994*b*, Laska 1995), because it is a critical parameter in many food web models (Pimm 1982, Lawton 1989, Pimm et al. 1991, Lawton 1992), and because it has widespread implications for conservation strategies (Mills et al. 1993, Power et al. 1996). Nonetheless, estimating the most appropriate empirical numbers has been difficult, in part because there are so many variations in the interpretation of interaction strength (e.g., Yodzis 1988, Paine 1992).

Confusion on the concept of interaction strength can be seen even in its earliest treatments. For example, MacArthur (1972) stated that a strong interactor is a species whose "removal would produce a dramatic effect." This definition is in accordance with what many empiricists attempt to measure (e.g., Paine 1966, 1980, 1992, Power et al. 1985, Morin et al. 1988, Marquis and Whelan 1994, Menge et al. 1994, Wootton 1994*b*,

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Laska 1995, Morin 1995, Power et al. 1996), although the relative importance of "strong" vs. "weak" interactors in food webs is somewhat controversial (Menge and Sutherland 1987, Polis 1991, Paine 1992, Goldwasser and Roughgarden 1993, Mills et al. 1993). Yet in his next paragraph, MacArthur (1972) switches his definition, stating that "the competition coefficient, α, measures how strong the interactions [between two species] are." Although presented side by side, these two ideas of strong interactors are not the same. One represents per capita direct effects of a species, whereas the other describes all of the direct and indirect effects of an entire population. At the same time, May (1972, 1973) tied community stability to species diversity, number of interactions within a community, and interaction strength, the latter defined in yet another way, i.e., the per capita direct effect of one species on the entire population of another species near equilibrium.

To facilitate progress in community ecology, empirical measures of the strength of species interactions need to be incorporated into theoretical models of communities and food webs. For this goal to be attained, there must first be a clear understanding of how different types of empirical data relate to various theoretically relevant concepts. In this paper, we clarify alternative definitions of interaction strength, illustrating their differences and relationships with a simple predator–prey model. We then describe various methods by which empiricists have attempted to measure interaction strength. Finally, we examine the strengths and weaknesses of these approaches, applying them to simulated data similar to the sorts of data empiricists might collect, and investigating how well they recapture the actual interaction strengths underlying the simulations.

CONCEPTIONS OF INTERACTION STRENGTH

The various measures of interaction strength can be placed into four theoretical categories: elements in the community matrix (Levins 1968, MacArthur 1972), elements in the Jacobian matrix (May 1973), elements in the inverse Jacobian matrix (Levine 1976, Yodzis 1988), and elements in the "removal" matrix (following MacArthur 1972 and Paine 1992). In the following section we outline these theoretical measures, show how they are derived, and examine relationships between the four measures, using a two-level food chain model to compare them.

Parameters in a model (e.g., community matrix)

The first measure of interaction strength refers to parameters in dynamic models of species interactions. In simple terms, this concept of interaction strength describes the average direct effect that a single individual of one species has on a single individual of another species (i.e., a per capita effect). MacArthur's idea of α as a measure of interaction strength can be extended to a multispecies community using Levins' (1968) derivation of the community matrix, which is the coefficient matrix derived from the generalized form of the Lotka-Volterra equations. For example, consider the following Lotka-Volterra predator–prey functions generalized for consumers (*H,* herbivores) and their prey (*V,* vegetation). Population growth of the vegetation is described by

$$\frac{dV}{dt} = f(V, H) = b_v\left(1 - \frac{V}{K}\right)V - c_hHV - m_vV \quad (1)$$

where c_h is the capture rate of the herbivore, b_v is the birth rate of the vegetation, and m_v is the death rate of the vegetation. Herbivore population growth is described by

$$\frac{dH}{dt} = g(V, H) = b_hc_hVH - m_hH \quad (2)$$

in which b_h is the efficiency with which herbivores convert captured vegetation into new herbivores, and m_h is the death rate of herbivores.

The resulting community matrix (**A**) would be

$$\mathbf{A} = \begin{bmatrix} \frac{-b_v}{K} & -c_h \\ b_hc_h & 0 \end{bmatrix}$$

where the (1, 1) element represents the effects of prey (*V,* vegetation) on prey, the (1, 2) element represents the effects of consumers (*H,* herbivores) on prey, the (2, 1) element represents the effects of prey on consumers, and the (2, 2) element represents the effects of consumers on consumers. In the community matrix, the *i*th row consists of the partial derivatives of $(1/N)dN/dt$ for species *i,* with respect to the density of each of the species in the community. In competitive models, the elements of the community matrix are composed of α's, or the Lotka-Volterra competition coefficients. It is important to note that mechanistic community matrices and competition matrices are not the same thing since competition matrices abstract consumer resource interactions to estimate the indirect, rather than direct, effects of one competitor on another when exploitative competition occurs (Schoener 1986). Mechanistic community matrices have advantages over competition matrices for a variety of reasons (see also Schaffer 1981, Bender et al. 1984). In particular, competition coefficients will change as the community changes because of changes in resource dynamics, species composition, and environmental parameters. Therefore, these types of interaction strengths cannot be easily applied to novel situations, and some methods may be unable to directly estimate them. Most techniques applied to estimate strengths of competitive interactions can, however, be applied to estimate the strength of direct interactions and therefore studies investigating these matrices can be illuminating. The community matrix is often standardized, particularly in competition studies or when all species are assumed to follow logistic growth, by dividing each row *i* by the corresponding elements α_{ii} (Levins 1968, as in Seifert and Seifert 1976, Bender et al. 1984).

Elements in a Jacobian matrix

A second concept of interaction strength, advanced by May (1973), are the elements in the Jacobian matrix near equilibrium. Conceptually, elements in the Jacobian matrix represent the direct effect of an individual of one species on the total population of another species at or near equilibrium. This definition has received considerable attention in food web models (e.g., Yodzis 1988, 1989). Furthermore, the PULSE experiments of Bender et al. (1984), which examine community change in response to a small, temporary perturbation of one species from equilibrium, are attempts to measure elements in the Jacobian. The elements in a given cell of the matrix equal the partial derivative of the population growth equation of the species corresponding to row i with respect to the species corresponding to column j, evaluated at equilibrium (see Schoener 1993 for additional discussion). In the above eqs. 1 and 2, then,

$$\mathbf{C} = \begin{bmatrix} \dfrac{\partial f(V^*, H^*)}{\partial V} & \dfrac{\partial f(V^*, H^*)}{\partial H} \\ \dfrac{\partial g(V^*, H^*)}{\partial V} & \dfrac{\partial g(V^*, H^*)}{\partial H} \end{bmatrix}$$

where V^* and H^* represent the equilibrium values of V and H, respectively. For Lotka-Volterra type models, equilibrial values can be obtained by taking the negative inverse of the community matrix described above ($-\mathbf{A}^{-1}$) and multiplying it by a column vector, which contains the density-independent terms in the underlying differential equations (e.g., $b_v - m_v$ and $-m_h$ in Eqs. 1 and 2, respectively). The procedure is repeated for each of the elements in the matrix, which yields the Jacobian matrix (**C**):

$$\mathbf{C} = \begin{bmatrix} \dfrac{-b_v m_h}{K c_h b_h} & \dfrac{-m_h}{b_h} \\ b_h(b_v - m_v) - \dfrac{b_v m_h}{c_h K} & 0 \end{bmatrix}. \tag{3}$$

As in the community matrix, the (1, 1) element represents the effects of prey on prey, the (1, 2) element is the effect of consumers on prey, and so on. However, the effects refer to the direct effect of an individual of one species on the total population of another at equilibrium, rather than per capita direct effects.

The inverted Jacobian matrix

The first two measures above only account for direct effects of one species on another. However, species often have a strong influence on other species in the community via indirect pathways as well (e.g., Paine 1966, Vandermeer 1980, Wootton 1994*c*), so it might be reasonable to derive a measure that incorporates both direct and indirect effects. One such measure is the negative inverse of the Jacobian matrix, as shown by Levine (1976) and others (Lawlor 1979, Yodzis 1988, Stone and Roberts 1991). According to Yodzis (1988; but see discussion below), the negative inverse matrix summarizes the outcomes of all PRESS experiments (where the abundance of a species is held at a constant level away from equilibrium; Bender et al. 1984). To derive the inverted Jacobian matrix, theoreticians simply take the inverse of the Jacobian matrix above after multiplying by -1 (as in Levine 1976, Davidson 1980, Yodzis 1988). This matrix describes the total direct and indirect effects of species i to a constant rate of removal or addition of species j. An assumption of this approach is that the abundance of species j does not drop to zero (i.e., is not completely removed from the system). In the case of the predator–prey model presented above, the inverse of the Jacobian matrix ($-\mathbf{C}^{-1}$) is

$$-\mathbf{C}^{-1} = \begin{bmatrix} 0 & \dfrac{-c_h K}{K c_h b_h (b_v - m_v) b_v m_h} \\ \dfrac{b_h}{m_h} & \dfrac{b_v}{K c_h b_h (b_v - m_v) b_v m_h} \end{bmatrix}. \tag{4}$$

Removal matrix—the empiricist's approach

In empirically based work, Paine (1980) returned to MacArthur's (1972) ideas, to define strong interactors as species whose removal would alter the dominance structure of the community. This conceptualization of interaction strength, which most experimental empiricists investigate, can be summarized in what we call the "removal matrix" (**R**). This can also be thought of as the "differences between treatments" matrix, following the MacArthur (1972)–Paine (1992) definition of interaction strength. In this case, a species is completely removed from a community to determine its effect on the rest of the system (see, e.g., Paine 1966, Power et al. 1985, Morin et al. 1988, Wootton 1994*b*, and Laska 1995, *unpublished manuscript*). Each element in the removal matrix represents the difference in equilibrial abundance between a community with all species present, and the same community with species j removed. In our predator–prey example, the equilibrial values with both species present are given in Eq. 5, the equilibrial value of H in the absence of V is of course 0, and the equilibrial value of V in the absence of H is

$$V_{\mathrm{eq}} = K\left[1 - \frac{m_h}{b_h}\right]. \tag{5}$$

Subtracting the equilibrial values in the presence of both species from the values where one species is removed and substituting the results into a matrix formulation yields

$$\mathbf{R} = \begin{bmatrix} \dfrac{m_h}{c_h b_h} & \dfrac{m_h}{c_h b_h} - K\left(1 - \dfrac{m_v}{b_v}\right) \\ \dfrac{b_v}{c_h} - \dfrac{m_v}{c_h} - \dfrac{b_v m_h}{K {c_h}^2 b_h} & \dfrac{b_v}{c_h} - \dfrac{m_v}{c_h} - \dfrac{b_v m_h}{K {c_h}^2 b_h} \end{bmatrix}. \tag{6}$$

With respect to the removal matrix, we wish to clarify two points. The removal matrix does not have any special mathematical meaning per se, but rather it is a compact way to compare the measures of interaction strength empiricists seek to estimate with other theoretical measures of interaction strength. Second, it superficially appears that the measure is the same as the inverted Jacobian matrix described above, because it includes both direct and indirect effects; however, it is not. Aside from the numerical responses embodied in the inverted Jacobian, the removal matrix also includes properties arising from the structure (i.e., the new pathways of interaction) that species *j* imparts on the food web or community. To see this, multiply the elements in the top row of the inverted Jacobian (Eq. 4) by the equilibrial vegetation abundance, and multiply the bottom row by the equilibrial herbivore abundance. If structural considerations of the community or food web were not important, then the resulting matrix should equal the removal matrix (Eq. 6), however, it clearly does not.

A COMPARISON OF INTERACTION STRENGTH CONCEPTS—METHODS AND RESULTS

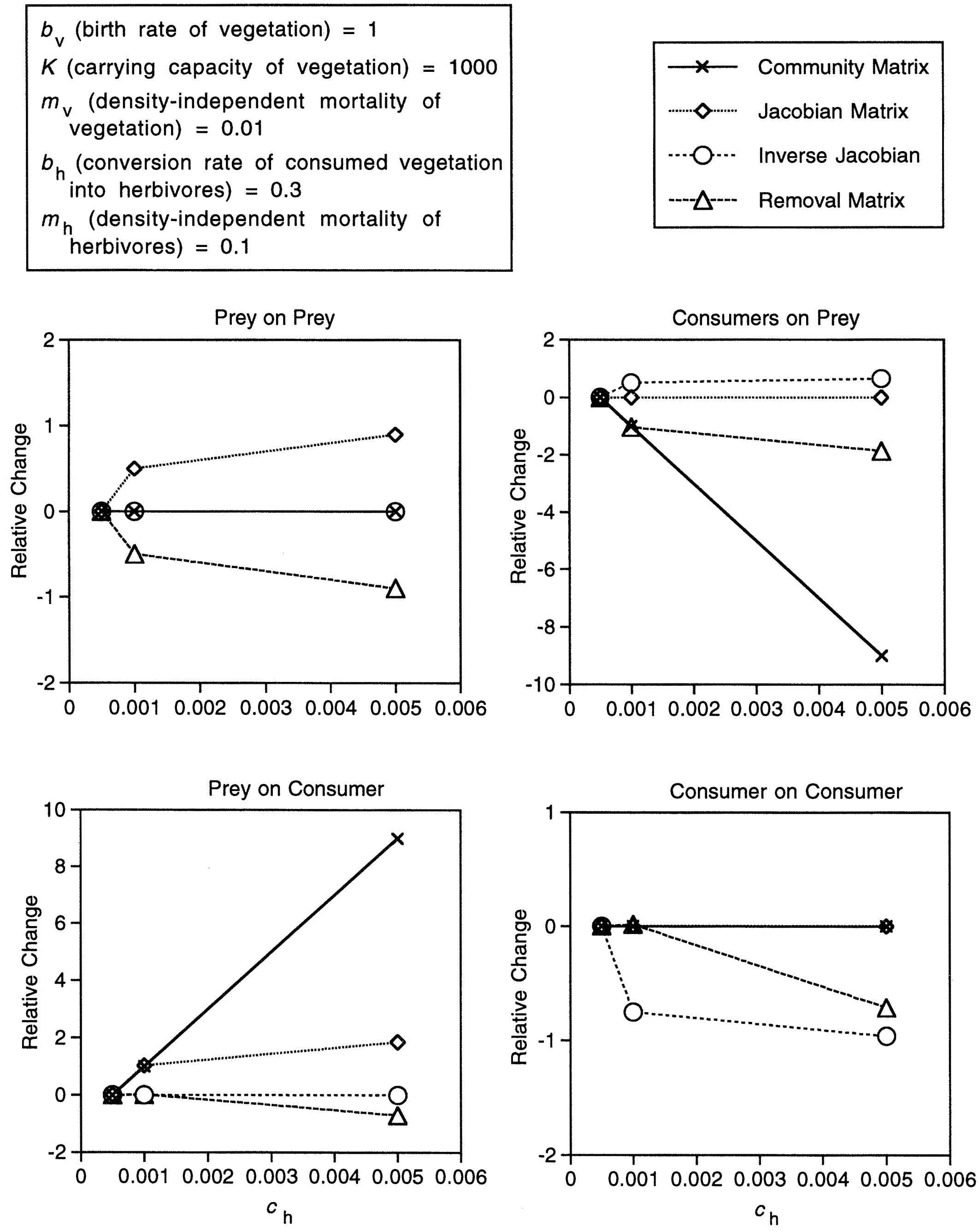
As we described above, there are at least four concepts that reasonably capture various aspects of interaction strength. If these measures are tightly correlated with each other, it is not critical which type of measure is chosen in theoretical or empirical studies. The four concepts of interaction strength, however, do not necessarily track each other. To illustrate this, we provide a numerical example using a two-level food chain model. Specifically, we vary the consumption rate of the herbivore while holding all other parameters constant, and compare how interaction strength changes according to the four different matrix definitions presented above. In our analysis, we set the carrying capacity, K, to 1000, the birth rate, b_v, to 1, and the death rate, m_v, to 0.01. For the herbivore population, birth rate, b_h, is 0.3, and the death rate of herbivores, m_h is 0.1. For comparative purposes, we varied the consumption rate of the herbivore, c_h, between 0.0005 and 0.005, and examined the relative change among the four concepts of interaction strength.

Intuitively, increasing the consumption rate reflects an increasingly stronger negative interaction of the consumer on its prey, and an increasingly stronger positive interaction of the prey on its consumer. The results of the analysis are described in Fig. 1. To standardize the comparisons, changes are expressed in proportion to their values at $c_h = 0.0005$ [that is, $(N_{c_h=0.0005} - N_{c_h=x})/N_{c_h=0.0005})$]. As can be seen, the different measures of interaction strength do not necessarily correspond to each other, either quantitatively or qualitatively (Fig. 1). For example, increasing the consumption rate of H increases the (1, 1) element of the Jacobian, decreases the (1, 1) element in the removal matrix, and has no effect on the (1, 1) elements in the community matrix or the inverse Jacobian. Additionally, even when elements behave in a qualitatively similar manner (e.g., they all decrease), they may do so in a very nonlinear way. For example, increasing consumption rates decreases the (1, 2) element in the community matrix linearly, but the decline in the corresponding element in the Jacobian matrix becomes progressively smaller as the consumption rate increases (Fig. 1). Consequently, conclusions regarding the effects of interaction strength must be qualified by the concept of interaction strength being considered. For example, May's (1973) analysis of stability in model food webs, based on analysis of the Jacobian matrix, indicated that large interaction strengths were incompatible with speciose and highly linked food webs, which has led to the generalization that, in complex natural communities, interactions among species in general should be weak. Our numerical example shows, however, that the existence of strong per capita interaction strengths can be quite compatible with complex food webs in some circumstances because the elements in the Jacobian matrix may be quite insensitive to such strong per capita effects.

Given the consequences of the differences among the four concepts of interaction strength presented above, it is also important to ask which concept would be most appropriate for empiricists to measure. Depending on the interests of, and the assumptions made by an investigator, valid arguments can be constructed for using any of the four. We advocate concentrating on measuring per capita interaction strength based on the community matrix for two reasons (see also Paine 1992, Fagan and Hurd 1994). First, it is the only one of the four concepts that does not necessarily require an assumption of equilibrium conditions, an assumption that has been questioned for many natural communities (e.g., Wiens 1977, Sale 1977, Connell 1978, Paine and Levin 1981, Hubbell and Foster 1986, McGrady-Steed and Morin 1996). Second, all other concepts of interaction strength ultimately are derived from per capita interaction strengths, whereas it is difficult, if not impossible, to work backwards from many of the other measures.

APPROACHES USED TO ESTIMATE INTERACTION STRENGTH

A range of approaches have been employed to empirically estimate interaction strength in both natural and artificially constructed communities. Three questions are important to consider when assessing these approaches: (1) How do these measures relate to the theoretical concepts presented above? (2) What are their implicit assumptions? and (3) Which seem most appropriate in providing the most accurate estimates of interaction strength? We explore these questions below by providing a general overview of the use of interaction strength in community studies. The problem of estimating interaction strength has been empirically at-



b_v (birth rate of vegetation) = 1
K (carrying capacity of vegetation) = 1000
m_v (density-independent mortality of vegetation) = 0.01
b_h (conversion rate of consumed vegetation into herbivores) = 0.3
m_h (density-independent mortality of herbivores) = 0.1

FIG. 1. Graph of the relative change in four indices of interaction strength given a change in herbivore attack rate, c_h. The four indices of interaction strength examined are elements in: the community matrix, the Jacobian matrix, the inverse Jacobian, and the removal matrix. Relative change is the change in parameter value relative to its value for an attack rate of 0.0005. In these graphs, represented by a 2 × 2 matrix format, the upper left graph represents the (1, 1) element, or the effect of prey on prey, the upper right graph represents the (1, 2) element, or the effect of consumers on prey, the lower left graph represents the (2, 1) element, or the effect of prey on consumers, and the lower right graph represents the (2, 2) element, or the effect of consumers on consumers. The herbivore attack rate, c_h, varies from 0.0005 to 0.001 to 0.005.

tacked in two basic ways: with experimental and observational approaches.

Experimental approaches to estimating interaction strength

Perhaps the first way in which interaction strengths were estimated was through the use of controlled experiments, and this approach has been revitalized in recent years. Gause (1934) pioneered this approach in laboratory experiments comparing the dynamics of yeast and protozoans in single- and multispecies cultures. Gause explicitly tied the results of his experiment to theoretical ideas of interaction strength by assuming an underlying model (Lotka-Volterra competition equations), estimating growth rate and carrying capacities from graphs of the dynamics of single-species cultures, and using those estimates and the observed rates of change in mixed species treatments to derive per capita interaction strength (or, in his terminology, "the coefficient of the struggle for existence"). Many subsequent laboratory studies have followed this procedure (e.g., Vandermeer 1972, Wilbur 1972, Neill 1975, Gilpin et al. 1986) or a variation on it (e.g., Lawler 1993, McMillan 1996). The specific approach used by Gause requires that equilibrium conditions eventually be obtained in order to graphically identify single-species carrying capacities, although modifications of this approach relax this requirement.

With the rise of field experimentation in recent years, ecologists have started examining interaction strength in a more complex, natural context. Application of the Gause (1934) approach to estimating interaction strength in these situations is problematic because it is much more difficult to follow the detailed dynamics of complex communities for sufficient periods to estimate equilibrium densities, and because it is difficult, if not impossible, to perform manipulations of all species combinations (see, for example, Tilman 1987). Initial discussions of interaction strength in a field context were based on comparing the absolute difference in the densities of target species to a manipulated species after some period of time (e.g., Paine 1980, Power et al. 1985, Morin et al. 1988, Menge et al. 1994). Intuitively this is an attractive measure to use because it provides a straightforward index of the total effect of one species on another, thus it often directly reflects responses in which investigators are ultimately interested (for example, the possible consequences of species extinction in a specific situation). However, its use as an index of interaction strength introduces some problems because of a loss of generality. Specifically, it has the potential to change dramatically as the circumstances being examined change. Estimated values depend critically on the length of time over which the experiment was conducted both because of the multiplicative nature of population growth and because of the complication of indirect effects that arise as the dynamics of co-occurring species change (Bender et al. 1984, Wilbur and Fauth 1990, Wootton 1993, 1994*a*). The values may also change depending on the nature of the experimental manipulation—stronger interactions would be indicated by simply removing or adding more individuals of the manipulated species, and outcomes might also be dependent on starting densities of the target species, at least in short-term experiments (Underwood and Petraitis 1993). Consequently, depending on the circumstances examined, this measure might reflect several of the different theoretical concepts described above, or none at all.

In an effort to circumvent these problems, Paine (1992) proposed estimating per capita interaction strength from experimental manipulations. By estimating per capita interaction strength rather than the total effect of a species, variations in interaction strength resulting from differences in the densities of manipulated and/or target species are circumvented. In this approach, per capita interaction strength is estimated as $(E - C)/CM$, where E (=experimental) is the abundance of the target species in the presence of the manipulated species, C (=control) is the abundance of the target species in the absence of the manipulated species, and M (=Manipulated) is the abundance of the manipulated species in the experimental treatment. Note that this notation differs from convention, but follows the format of Paine (1992). This measure can be derived theoretically from the following argument, based on the logistic equation, where N is the target species and M is the manipulated species. In the control treatment, the dynamics of the target species can be described as

$$\frac{1}{N} \times \frac{dN}{dt} = r\left(1 - \frac{N}{K}\right) \tag{7}$$

whereas in the experimental treatment, they can be described as

$$\frac{1}{N} \times \frac{dN}{dt} = r\left(1 - \frac{N}{K} + \alpha M\right) \tag{8}$$

where r is the intrinsic rate of increase of N at low density, K is the carrying capacity of N in the absence of M, and α is the per capita interaction strength of M on N. Solved at equilibrium, the control and experimental equations become, respectively

$$\begin{aligned} N(= C) &= K \\ N(= E) &= K + K\alpha M. \end{aligned} \tag{9}$$

Applying the Paine (1992) formula and canceling, isolates α, the per capita interaction strength.

The development of the Paine (1992) per capita interaction strength approach has spurred much recent interest in estimating interaction strength, and it has been applied to several types of communities (Paine 1992, Fagan and Hurd 1994, Laska 1995, Raffaelli and Hall 1996). For example, Laska (1995, *unpublished manuscript*) demonstrated a predictive relationship between per capita interaction strength and increasing body sizes of freshwater zooplankton (*Daphnia* spp.) using laboratory microcosm communities. Laska (1995) estimated per capita interaction strength by comparing densities and biomass of a target species in the presence (E) and absence (C) of competing species (M) of varying mean sizes. By regressing the interaction strengths on body sizes, Laska found that per capita interaction strengths were strongest as body size differences increased. It should be pointed out, however, that the assumptions in the theoretical derivation place some constraints on its use as a technique for estimating actual per capita interaction strength. First, Paine's derivation assumes equilibrium conditions, and so may not hold in short-term experiments in field settings. Second, K is represented as a constant between experimental treatments. This means that M can have no indirect effects on N or the resulting estimates will not be α. Although this was not a problem in Laska's (1995) artificially assembled simple laboratory communities, it could be problematic in more complex, natural communities.

An alternative measure of per capita interaction strength based upon experimental manipulation has been advanced to avoid the problems of making equilibrium assumptions (Wootton 1994*a*, 1997, Billick and Case 1994, Osenberg et al. 1997). This approach examines the term $\ln(E/C)/M$, where the notation is the same as that used above. The theoretical justification for this term comes from applying the discrete-time version of the generalized Lotka-Volterra multispecies equation, which may be more appropriate than the usual differential equation formulation because experimental data are taken on numbers or densities after some elapsed experimental period of time, rather than directly as rates of change. The equations for experimental and control treatments in this case are, respectively,

$$E = N_{i,t} = N_{i,0}\exp\left[\left[\left\{r_i + \left(\sum_{i=1}^{s-1} \alpha_{ij}\cdot N_{j,0}\right) + \alpha_{iM}M_0\right\}t\right]\right]$$

$$C = N_{i,t} = N_{i,0}\exp\left[\left[\left\{r_i + \left(\sum_{i=1}^{s-1} \alpha_{ij}\cdot N_{j,0}\right)\right\}t\right]\right] \qquad (10)$$

where $N_{i,t}$ is the abundance of species N at time t (the equation is usually scaled so that $t = 1$), e is the base of the natural logarithm, r_i is the density-independent growth rate of species i, s is the number of species in the community, and α_{ij} is the per capita interaction strength on species i of species j. Applying Eqs. 10 to the formula $\ln(E/C)$ estimates the per capita effect of the total population of species M on species N_i, and dividing by M isolates the per capita interaction strength α_{iM}, assuming that both treatments start with the same number of species N_i (or that $N_{i,0}$ values are known and substituted into the equations). No equilibrial assumptions are required to derive this formulation, so it is potentially applicable to a wide range of situations. Two aspects of this approach need to be noted, however. First, the estimate of interaction strength contains defined units of time (days, years), rather than being scaled to some "instantaneous" time, and therefore interaction strength (but not the dynamics of the equation) may change if the time units are changed. Second, this approach requires that the population dynamics over the course of the experiment depend only upon the densities of community members at the start of the experiment. Therefore, the presence of indirect effects may render these estimates less accurate.

Bender et al. (1984) suggest another approach, termed a PULSE experiment, to estimate per capita interaction strength (see *Conceptions of interaction strength*: *Elements in a Jacobian matrix* section, above). Here a control, assumed to be at equilibrium, is compared with an experimental treatment where the density of a single species is manipulated slightly away from equilibrium and the resulting short-term changes in the other members of the community are noted. The PULSE experimental approach estimates the per capita interaction strength, as used in this paper, with the formula $(dN_e/dt)/E(M_e - M_c)$, where M_e and M_c are the abundance of the manipulated species in the experimental and control treatments, respectively. Bender et al. (1984) do not recommend any particular technique to estimate dN_e/dt from densities at the end of the PULSE experiment, and different estimates used might alter the estimates to some extent. One measure might simply be the difference between starting and final densities of the unmanipulated species in the experimental treatment (or alternatively, between experimental and control treatments, assuming both treatments started at control densities, which is inherent in the equilibrium assumptions). An alternative might be to use $\ln(E_t/C_0)$ as a measure of $(dN_e/dt)/E$, as outlined above. To our knowledge, this approach has not been applied to any empirical situation, probably for a variety of practical reasons related to issues of time scale and statistical power. These include: (1) the manipulated species may recover too quickly for other species to respond, (2) indirect effects may become important before there is sufficient time for some direct effects to have a detectable signal, and (3) the combination of small perturbations and short response times may require so many replicate experiments to obtain sufficient statistical power to uncover the interaction strengths of even a single species that the enterprise is not feasible from a practical standpoint.

A final approach using experimental data to estimate interaction strength is to apply path analysis to experimental results (Johnson et al. 1991, Wesser and Armbruster 1991, Wootton 1994*b*). This approach has proven useful in identifying experimentally documented strong and weak interactions in a rocky intertidal marine community. The measures of "interaction strength" derived from this approach, the path coefficients, represent an index that reflects the relative amount of variation in a target species that can be accounted for by variation in various interaction species. This type of measure, although potentially useful for qualitatively identifying the relative importance of interactions, does not correspond to any theoretically defined index of interaction strength, and so it is of limited value in parametrizing typical community models.

Observational approaches to estimating interaction strength

Several observational techniques have also been proposed to estimate interaction strength. The earliest approaches to this problem were techniques estimating niche overlaps (MacArthur and Levins 1967, Pianka 1973, Schoener 1974*a*), comparing morphological traits (Ricklefs and Travis 1980), static regressions of species abundances on each other in different sites (Schoener 1974*b*, Hallett and Pimm 1979, Rosenzweig et al. 1984, 1985), and static measures of energy flow to different species (Baird and Milne 1981, Patten 1982, Hall et al. 1990, de Ruiter et al. 1995, Raffaelli and Hall 1996). These approaches have been criticized for various reasons and experimental studies have not supported some of their predictions (Seifert and Seifert 1976, Paine 1980, Bender et al. 1984, Hall et al. 1990, Laska 1995, *unpublished manuscript,* Pfister 1995, Wootton 1997).

More recently, a second class of observational approaches has been advanced, in which data are collected that specifically match the units of interaction strength used in theoretical models. For example, Wootton (1997) combined data on consumption rates, predator behavior, prey densities, and predator densities to derive per capita estimates of interaction strength; predictions derived from these measures successfully matched independent experimental manipulations. Similarly, Goldwasser and Roughgarden (1993) combined data on consumption rates with estimates of predator densities to estimate the instantaneous total impact of predators on prey species (e.g., the $-c_h VH$ term in Eq. 1) in a Caribbean island food web.

A slightly different approach combines selected observational estimates of per capita interaction strength having appropriate theoretical units with theoretical analysis (Moore et al. 1993, 1996, de Ruiter et al. 1996). In this approach, the food web model is initially specified and solved for the equilibrium abundance of species. The community is then sampled for the abundance of different species, and these values, assumed to be equilibrial abundances, are substituted into the model solutions. Specific estimates of per capita interaction strength (e.g., conversion efficiencies, consumption rates) are then derived from observation or mensurative experiments and applied to the model solutions until the model can be solved for all unknown interaction strength parameters. The predictions of this interesting approach have yet to be evaluated experimentally, although the assumption of equilibrium may limit the application of this approach to some situations (see above).

A final approach is to examine time series data of species abundance in communities that are not at equilibrium (Wootton 1994*c*, Pfister 1995, Chase 1996), or what might be termed dynamic regression analysis. This approach involves estimating population growth rates of each species over a series of time intervals, and applying multiple regression techniques to estimate per capita interaction strength. This is a variant on the same approach as described in Eq. 10. For example, starting with Eq. 10, taking logs and rearranging, one obtains the equation

$$\ln(N_{i,t}/N_{i,0})/t = r_i + \sum_{j=1}^{s} \alpha_{ij} N_{j,0} \qquad (11)$$

which fits directly into a linear multiple regression format. Pfister (1995) applied the dynamic regression approach to a group of competing tide pool sculpins and found that the predictions derived from this approach matched the predictions of manipulative experiments. This method works best if there is substantial variation in species abundances over time, which will occur in nonequilibrial situations. Consequently, this technique is particularly powerful when applied to communities recovering from disturbances of different ages. Furthermore, the variation introduced into communities by experimental manipulations can also improve the power of this approach, making it a potentially useful method to apply to experimental data as well as observational data. For example, Seifert and Seifert (1976, 1979) used this general approach to examine insect communities in *Heliconia* bracts, with the difference that rates were estimated as linear differences over time rather than as log ratios, and only one time interval was used to make their estimates. Several features of this approach are worth noting. First, it does not require that the community of interest be at equilibrium, and indeed works best if it is well away from it. For example, this approach could be substituted for the graphical analysis of Gause (1934) to avoid making equilibrium assumptions. Second, it shares the features of Eqs. 10 above, in that the per capita interaction strengths are derived for a specific time unit and the interval between sampling is assumed to be sufficiently short that the dynamics can be described as functions of species abundances at the beginning of the time interval.

COMPARING RELATIVE ACCURACY OF APPROACHES—RESULTS AND DISCUSSION

As discussed above, all current approaches have particular limitations. Given the limitations of each approach, it is worth asking how well they apply to simulated data and what types of data might best be col-

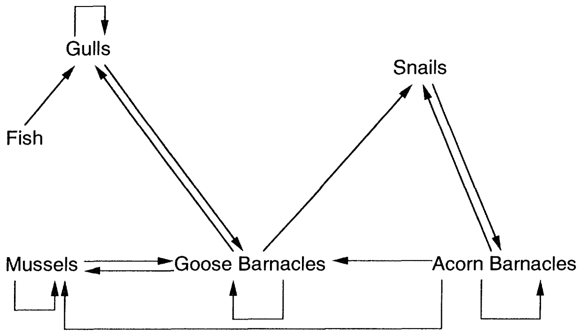


FIG. 2. Diagram of model community used in the simulations to assess different methods of estimating interaction strength from population data (after Wootton 1994*b*). Arrows pointing completely up represent effects of resources on consumers, with the arrow pointing in the direction of energy flow. Arrows pointing down represent the effects of consumers on resources. Arrows pointing (at least partially) horizontally and arrows that circle back to the same variable represent inter- and intraspecific interference interactions, respectively, with arrows pointing to the winner.

lected to minimize the limitations. We evaluated the four approaches that are most directly tied to theoretical measures of interaction strength: per capita differences between removal treatments and controls, PULSE experimental analysis, and dynamic regression analysis applied to either PULSE experiments or newly disturbed communities both with and without species removal treatments.

A seminatural model community

Ideally, we would want to test the different approaches using a model of a real community with empirically estimated values of all parameters. To our knowledge, no such community model exists. Therefore, we evaluated the approaches against a model containing some elements of realism but with some parameters set to make the model behave in a realistic manner. The model structure (Fig. 2) follows the pattern of interactions determined from the middle-intertidal community of Tatoosh Island, Washington State, as presented in Wootton (1994*b*). Therefore the pattern of interactions is representative of a natural, but somewhat simplified, community. The model community consisted of Glaucous-winged Gulls (*Larus glaucescens, l*), dogwhelk snails (*Nucella* spp., *n*), acorn barnacles (*Semibalanus cariosus, a*), California mussels (*Mytilus californianus, z*), and goose barnacles (*Pollicipes polymerus, p*). The community was modeled as follows:

$$dl/dt = (f + \alpha_{lp}p + \alpha_{ll}p + r_l)l$$

$$dp/dt = I_p + (r_p + \alpha_{pp}p + \alpha_{pz}z + \alpha_{pl}l)p$$

$$dz/dt = I_z + (r_z + \alpha_{zp}p + \alpha_{zz}z)z$$

$$da/dt = I_a + (r_a + \alpha_{aa}a + \alpha_{ap}p + \alpha_{az}z + \alpha_{an}n)a$$

$$dN/dt = (\alpha_{na}a + \alpha_{np}p + r_n)n \tag{12}$$

where α_{ij} is the per capita effect of species j on species i, r_j is the net-density independent growth and mortality rate, and I_j is the immigration rate of species j from outside of the community. Several aspects of the model are worth mentioning. First, the system is open for sessile species because these species recruit from the plankton. Second, gull populations are supported, in part, by pelagic fish (f) derived from outside the system, and there are limited intraspecific aggressive interactions around the nesting territory. Third, the results of Wootton (1994*b*) indicate that although snails gain some benefit from feeding on goose barnacles, they have no appreciable effect on the amount of space covered by goose barnacles, hence a negative effect of snail consumption on goose barnacles is not included. The model was simulated using STELLA II simulation software (High Performance, Hanover, New Hampshire) with a Runge-Kutta 4 estimation procedure and a time step (*dt*) of 0.1.

The model was parametrized using a multistep process to produce realistic dynamics. Initially, a dynamic regression procedure was carried out on the data presented in Wootton (1994*b*) to provide an initial set of parameter estimates for the model. Because the available data spanned a short time period, and therefore covered a limited range of the observed dynamics of this community, we did not expect that these parameter estimates would all be accurate, and indeed, initial simulations produced some unrealistic patterns of species abundance. Second, we tuned the parameters until the equilibrial populations sizes in the model reflected the population sizes observed in the natural community (Wootton 1994*b*, 1997, and *unpublished data*). Tuning was largely concentrated on those parameters whose estimated values seemed least likely to be accurate, based upon the structure of the data and/or the biological implausibility of the estimates (e.g., those with the wrong sign or inappropriate magnitude). The behavior of the tuned model also captured the natural community in two other aspects: (1) successional dynamics from bare space followed the same temporal patterns observed in the community (Paine and Levin 1981, Wootton 1993*b*), and (2) the community response to the removal of gulls from the model was similar to that observed in actual experimental gull removals (Wootton 1993*b*, 1994*b*). Because the tuning was carried out largely without reference to these latter two patterns, we have reason to believe that the parameter estimates might reflect those in the natural community.

The simulations were conducted on the model in a variety of ways, as dictated by the data requirements of the different approaches being evaluated. For the equilibrial treatment comparison method (Paine 1992), we systematically removed each species from the model and simulated the outcome after 200 iterations, applying the formula $(P - A)/(AM)$ to the final population sizes in the control ($=P$) and the species removal ($=A$)

TABLE 1. Estimates of per capita interaction strengths estimated by five different approaches, as compared to actual values in a simulated food web model.

Target: effector‡	Actual value	Estimation approach				
		PULSE	P_{ah}	EC	DR	DR_{ah}
p:z	−1.83 (−3)	−1.74 (−3)	−1.74 (−3)	−1.04 (−2)	−1.74 (−3)	−1.77 (−3)
p:l	−4.00 (−5)	−3.72 (−5)	−3.72 (−5)	−3.00 (−4)	−1.93 (−5)	−3.04 (−5)
z:p	−8.04 (−4)	−6.80 (−4)	−6.80 (−4)	−4.30 (−3)	−1.36 (−3)	−1.07 (−3)
a:p	−4.00 (−3)	−2.54 (−3)	−2.54 (−3)	−6.00 (−3)	−3.49 (−3)	−7.89 (−3)
a:z	−4.00 (−3)	−3.41 (−3)	−3.41 (−4)	1.80 (−3)	−3.50 (−3)	−3.39 (−3)
a:n	−1.65 (−3)	−1.04 (−3)	−1.04 (−3)	−1.39 (−1)	−1.43 (−3)	−7.80 (−4)
n:p	3.00 (−4)	2.40 (−4)	2.40 (−4)	−4.23 (−2)	−3.43 (−4)	2.05 (−4)
n:a	2.00 (−3)	1.74 (−3)	1.74 (−3)	+∞	1.98 (−3)	1.97 (−3)
l:p	1.00 (−3)	9.17 (−4)	9.17 (−4)	1.25 (−2)	9.48 (−4)	9.80 (−4)
Shared comparisons						
r		0.986	0.986	0.015†	0.986	0.994
Mean % diff.		8.25	8.25	3.18 (3)†	4.27 (1)	1.42 (1)
Mean |diff.|		3.65 (−4)	3.65 (−4)	2.64 (−2)†	2.89 (−4)	2.02 (−4)
All comparisons						
No. treatments		8	8	5	2	2
% parameters estimated		85	85	61	100	100
r		0.989	0.986	0.188†	0.996	0.979
Mean % diff.		5.58 (5)	1.75 (1)	8.32 (7)†	1.93 (6)	1.42 (1)
Mean |diff.|		2.42 (−4)	3.65 (−4)	1.20 (−2)†	1.49 (−4)	2.02 (−4)

Notes: PULSE = PULSE experiments, P_{ah} = PULSE experiments with a priori hypothesis of which species interact, EC = comparisons between control and removal treatments at equilibrium, DR = Dynamic regression applied to mussel PULSE and removal experiments, DR_{ah} = Dynamic regression applied to mussel PULSE and removal experiments with an a priori hypothesis of which species interact. Measures of fit for each technique include the correlation coefficient (*r*), the difference between estimated and actual values as a percentage of the actual value (% diff.), and the mean magnitude of the difference between estimated and actual values (|diff.|). Values in parentheses indicate powers of 10 in scientific notation.

† Calculated only using noninfinite estimates.

‡ Codes are the variables used in Eq. 12.

runs, using the equilibrial value of the manipulated species (*M*) in the control run.

For the PULSE approach (Bender et al. 1984), starting conditions included a control near equilibrium, and PULSE manipulations (initial reductions from equilibrium) for each species. The PULSE approach was originally derived for a closed community. Consequently, we had to derive a new series of formulas to estimate parameters in the case of an open system (Appendix). These formulas require that two experiments be conducted on each species with outside immigration, thus a total of eight PULSE runs were required. The initial PULSE conditions were: (1) 1% cover goose barnacles (83% reduction), (2) 3% cover goose barnacles (50% reduction), (3) 1% cover mussels (99% reduction), (4) 35% cover of mussels (50% reduction), (5) 1% cover of acorn barnacles (96% reduction), (6) 12% cover of acorn barnacles (50% reduction), (7) 2 snails/m^2 (79% reduction), and (8) 2000 gulls (42% reduction). For terms estimating interspecific interactions, or intraspecific interactions in closed populations, we compared the estimated rate of change over the first time tick of the PULSE run with that of the control run. Because the PULSE technique applies to instantaneous rates of change, but empirical measurements are taken over discrete time, one must first assume a functional relationship between the two and provide an appropriate transformation to move from an abundance value to a rate of change (Wootton 1994*a*). We assumed exponential growth, so applied the transformation $(1/N_{x,0})(dN_x/dt) = \ln(N_{x,1}/N_{x,0})$ to the PULSE formula $(1/N_p)(dN_p/dt)/\Delta M$, where N_p is the initial value of the target species in the PULSE treatment, and ΔM is the difference in the manipulated species between the control and PULSE treatments. For those species with outside immigration, we used the formulas in the Appendix to calculate the immigration rate and intraspecific interference effects.

For the dynamic regression approach, we again estimated $(1/dN_x)(dN_x/dt)$ as $\ln(N_{x,1}/N_{x,0})$, and applied multiple linear regression to estimate the per capita interaction strengths (α_{ij}), net density-independent growth rates (r_x) and immigration rates (I_x) in the equation $\ln(N_{x,1}/N_{x,0}) = I_x/N_{x,0} + r_x + \Sigma\ \alpha_{ij}N_{j,0}$. Because, in principle, the dynamic regression approach has the advantage that it requires fewer experimental treatments, the approach was only applied to results from treatments where the California mussel, the dominant species in the community, was manipulated, or to a simulated natural disturbance and subsequent recovery. The dynamic regression approach requires large dynamical changes in the system to maximize its power and accuracy, so manipulating the community dominant would a priori seem likely to produce large dy-

TABLE 2. Comparison of the performance of different types of data sets in the dynamic regression approach.

Data set	CS/I	PULSE/D	MR (+/−)	AH (+/−)	r	% diff.	$\lvert$Diff.$\rvert$	Rank
1	I	PULSE	+	+	0.996	1.42 (1)	2.02 (−4)	1
2	CS	PULSE	+	+	0.997	4.53 (1)	2.34 (−4)	2
3	I	PULSE	···	+	0.996	3.29 (1)	3.67 (−4)	3
4	I	PULSE	+	···	0.996	1.93 (2)	4.19 (−4)	4
5	I	PULSE	···	···	0.996	1.60 (6)	3.40 (−4)	5
6	CS	PULSE	···	+	0.996	9.58 (1)	1.37 (−3)	6
7	I	D	+	+	0.979	2.90 (1)	6.50 (−4)	7
8	I	D	···	+	0.982	8.35 (1)	1.24 (−3)	8
9	I	D	+	···	0.982	2.22 (6)	3.77 (−4)	9
10	I	D	···	···	0.987	1.03 (7)	8.83 (−4)	10.5
11	CS	PULSE	···	···	0.995	1.33 (7)	1.37 (−3)	10.5
12	CS	D	+	+	0.965	5.95 (2)	1.55 (−2)	12
13	CS	PULSE	+	···	0.974	1.39 (7)	7.84 (−4)	13
14	CS	D	···	+	0.949	1.50 (3)	2.48 (−2)	14
15	CS	D	+	···	0.929	1.06 (8)	1.55 (−2)	15
16	CS	D	···	···	0.110	5.38 (8)	9.73 (−2)	16
χ^2_1	4.0	4.0	0	4.0				
P	<0.05	<0.5	NS	<0.05				

Notes: CS = continuous sampling, I = interval sampling, D = disturbance, MR = mussel removal treatment present, AH = a priori hypothesis of species interactions used. Contingency table statistics at bottom compare the distribution of different data categories in the top vs. the bottom eight performing data sets (based on mean rankings in the three different fit measures). Abbreviations of different metrics of fit to actual parameters are the same as in Table 1. Ellipses refer to "absent" as in no removal treatment or no a priori hypothesis.

namical responses in most natural situations. To gain insight into the type of data best suited for the dynamic regression technique, we applied the technique to a variety of different scenarios. Basic scenarios included: (1) a PULSE manipulation of mussels (to 1% cover), (2) the combination of a PULSE manipulation of mussels and a mussel removal treatment, (3) a community that experienced natural disturbance (equivalent to a PULSE reduction to 1% cover for each sessile species, two snails and 2000 gulls), and (4) a community that experienced natural disturbance, with both unmanipulated and mussel removal treatments. For each of these scenarios, data were taken in two ways: (1) the first 30 (for scenarios without a mussel removal treatment) or 20 (for scenarios with a mussel removal treatment) sequential time points (t = 0.1–3.0), which we will refer to as "continuous" data, and (2) changes over 15 short-term time intervals (dt = 0.1) spaced out at integer points through the simulation (t = 0.0–0.1, 1.0–1.1, . . . , 14.0–14.1), which we will refer to as the "interval" data. Finally, we applied the dynamic regression to each scenario/data combination using either an underlying a priori hypothesis of which interactions occur in the community, based on natural history observation, or a "naive" hypothesis in which parameters were estimated for all possible pairwise interactions.

Results and discussion of analyses of simulated data

The different approaches to estimating per capita interaction strength varied in their success at recapturing the values underlying our simulated data (Table 1). Fits were assessed using three measures with various strengths and weaknesses: correlation coefficients between actual and estimated values, the mean absolute value of the deviation between actual and estimated values, and the percentage deviation of the estimated value from the actual value. Comparing only the parameters directly estimated by all of the techniques (i.e., excluding those where one or more of the techniques either could not make an estimate or where values were set to 0 in a priori hypotheses), the PULSE technique and dynamic regression techniques provided good parameter estimation. In contrast, the equilibrial comparison approach provided several very poor estimates, and in one case predicted an infinite value. Comparing the performance of the different techniques across all parameters was also instructive. Again, PULSE and dynamic regression approaches provided reasonable fits to the data, whereas the equilibrial comparison approach did not (Table 1). Furthermore, an approach combining PULSE experiments and an a priori hypothesis of which species interact with each other provided more accurate estimates of parameters than did the PULSE experiment without an a priori hypothesis, although the degree of improvement depended on the measure of fit being applied. For example, the percentage deviation values are highly sensitive to deviations from zero (for calculation purposes estimated values were compared to 1×10^{-9} rather than zero to avoid division by zero) and errors in models attempting to estimate zero values were magnified. From a practical standpoint, the approaches also differed substantially in their ease of application. First, only the dynamic regression approach was able to estimate all of the parameters in the model: neither alternative approach estimates the density-independent rates of populations, and the equilibrial comparison approach also cannot estimate any self-interference terms. Second, the dynamic regression approach required the implementation of many fewer experimental treatments to obtain reasonable estimates (0–2) compared with the equilibrial comparison approach (5) or the PULSE approach (8), although it required studies of longer duration than those of PULSE experiments.

Within the dynamic regression approach, certain types of data were more likely to provide good estimates of interaction strength (Table 2). We categorized the specific variants of dynamic regression approaches in terms of fit, comparing characteristics of the best eight to the other eight using a chi-square contingency analysis to determine whether certain features of the data examined tended to promote more accurate estimates. The time pattern of data being examined strongly influenced the dynamic regression approach: six of the eight best-fitting variants had data taken at separate intervals (10 intervening time steps between points), whereas six of the eight data sets giving poorer fits involved data taken at sequential points ($P < 0.05$). This result arises because data collected at more spread-out points in time involve a wider range of species abundance combinations, whereas sequential points are likely to be less independent and to covary over the short-term following recovery from either an experimental or natural perturbation (Fig. 3). One way to insure that this pitfall is avoided when taking a dynamic regression approach is to examine the pattern of temporal autocorrelation among data points, and use data spaced out at the interval where autocorrelation ceases to become significant (at $t = 1.0–1.4$ for the data from the simulation, Fig. 4). A second factor that affected the model fits was the use of an a priori structural hypothesis of which interactions occurred within the community. Six of the eight best-fitting analyses used a priori hypotheses in our analysis. As discussed previously, this result arises because the percentage deviation index of fit inflates errors in attempts to estimate parameters of value zero. Therefore, this may be an unfair comparison of the performance of analyses using a priori hypotheses (which make no attempt to estimate zero parameters) to those that do not use a priori hy-

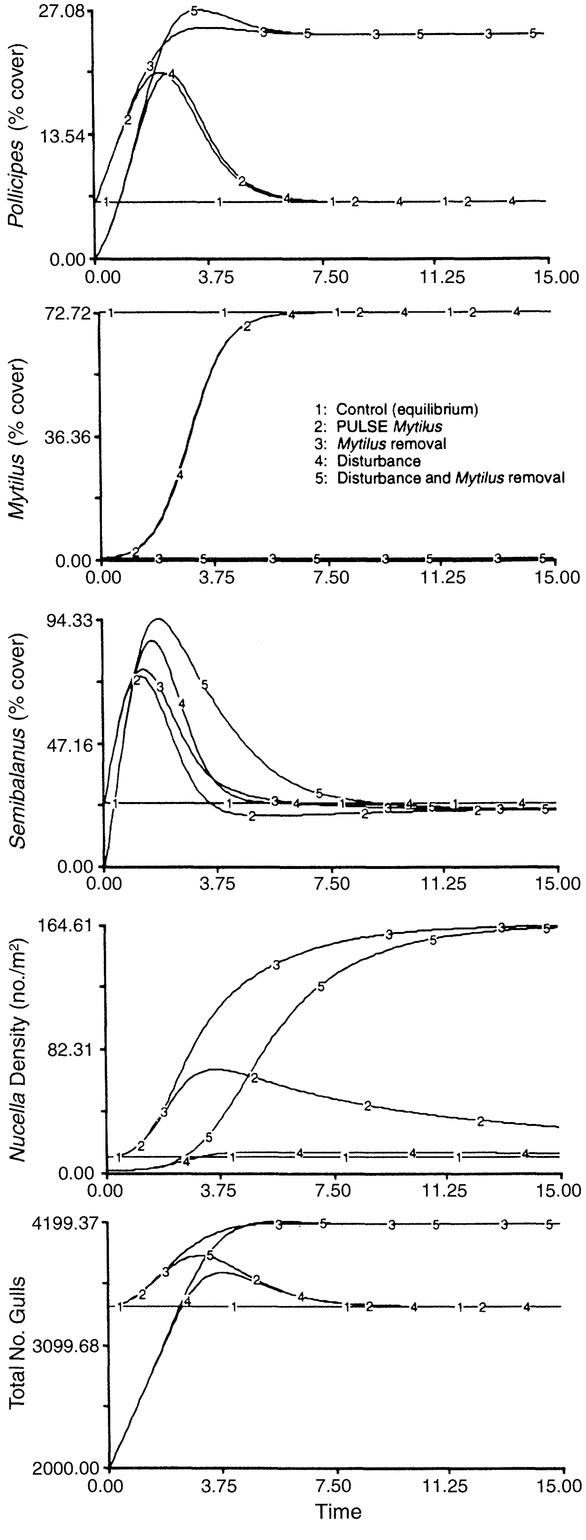


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FIG. 3. Dynamics of the model community to perturbations in mussels in the simulations used to assess different methods of estimating interaction strength. From top to bottom, graphs illustrate the dynamics of goose barnacles, mussels, acorn barnacles, predatory snails, and gulls. Five trajectories are given for each graph representing different types of situations: (1) control treatment at equilibrium, (2) PULSE experiment on mussels, (3) complete removal of mussels, (4) initially disturbed community, and (5) initially disturbed community with the removal of mussels.

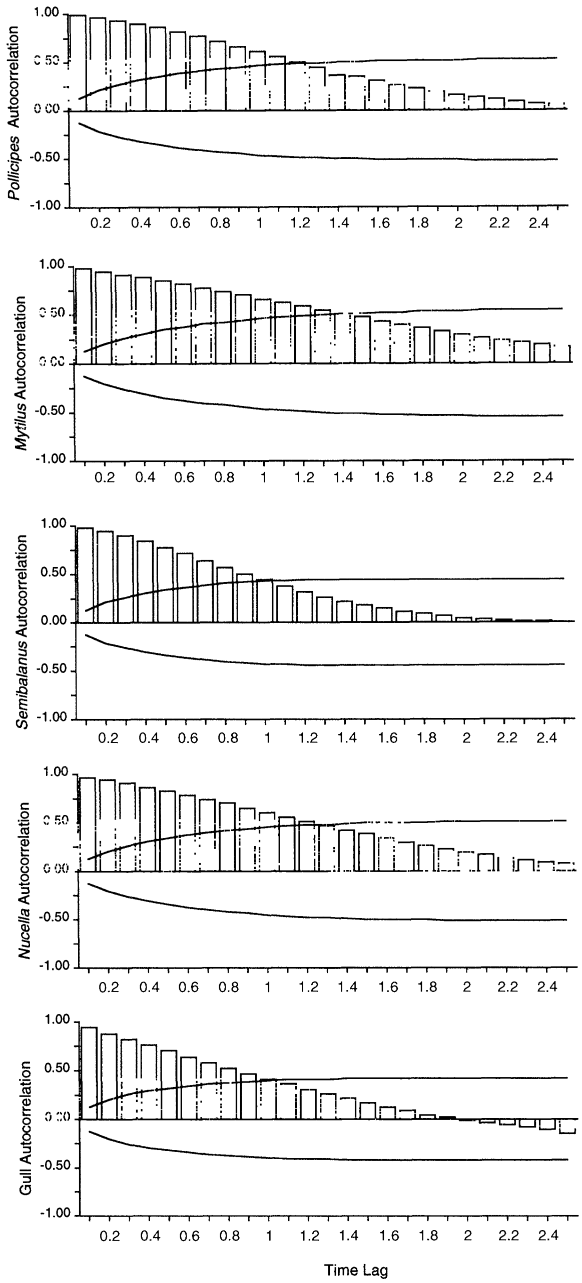

FIG. 4. Temporal autocorrelation in the trajectories of the different variables in the simulation used to assess the effectiveness of different methods for estimating per capita interaction strength in the disturbance simulation. Autocorrelations generally become nonsignificant between 1 and 2, indicating that a separation in the collection of data by similar time periods will yield better estimates of interaction strength than analysis of continuously collected data because of an increase in the independence between observations.

potheses. Indeed, other measures of fit were similar between analyses with and without a priori hypotheses (Table 2), as were all measures of fit when estimates of zero were dropped from the evaluation. Third, the means by which dynamics were introduced into the system affected model fit. The recovery dynamics following an experimental PULSE manipulation tended to give better fits than the recovery dynamics following a disturbance event (Table 2, $P < 0.05$). This result probably occurred because when all species are reduced below equilibrium levels, they will all tend to move in the same direction, thereby introducing inaccuracies due to colinearity. It should be noted, however, that the various measures of model fit associated with disturbance in combination with interval sampling were not much worse than fits associated with PULSE experiments, so examining the long-term dynamics following disturbance may still be useful when PULSE experiments are not possible. One factor did not play a strong role in determining the overall fit of dynamic regression analyses ($P > 0.05$): the presence of a complete species removal treatment.

CONCLUSIONS

The strengths of interactions among species in natural communities are important to measure for several reasons. Without them, predictions and insights into the nature and dynamics of complex food webs or communities are crude at best. Furthermore, multispecies models with sufficient complexity can predict virtually any type of dynamics possible (e.g., Yodzis 1996), so estimates of interaction strength shed light into the realm of likely scenarios by placing constraints on model behavior. Successfully applying interaction strength to specific scenarios or generating an understanding of general patterns of interactions strengths in natural communities requires indices of interaction strength that have tangible ties to theoretical concepts, are empirically relevant, and ideally take the same common form. Currently there are a wide array of theoretical and empirical concepts of interaction strength and their relationships are rarely made. We have identified at least four different, and perfectly valid, concepts of interaction strength in the context of traditional models of multispecies communities. Because of the discordant behavior of these different measures, conclusions based upon one metric of interaction strength may not apply to other concepts, and therefore it is critical that the particular metric being investigated be made clear. We advocate concentrating on per capita parameters in dynamic models in investigations of interaction strength, both because they are less sensitive to variations in species densities and violations of equilibrium assumptions. This is not to say that other indexes of interaction strength are not of interest. For example, many ecologists have a great interest in the consequences of omitting species from a community, and so ultimately may be more interested in terms in a "removal matrix." Per capita interaction strengths underly such measures and therefore may be useful to concentrate on even if other concepts of interaction strength are ultimately of more interest.

A number of empirical approaches have been proposed to estimate interaction strength in the field taking both experimental and observational approaches. Because all approaches have both strengths and limitations, it is important to recognize them and try to insure that the data to which they are applied are appropriate to the particular assumptions and limitations where possible. Many approaches implicitly assume equilibrium conditions, and the effectiveness of all experimental approaches depends on avoiding strong confounding effects of indirect interactions. Further research is required to determine whether there are other effective approaches to estimating interaction strength while avoiding indirect effects. One way is to give more emphasis to observational approaches, since they are usually not affected by indirect effects. Additionally, extensive experimentation may not be feasible from a practical standpoint, so it is important to be able to supplement experimental estimates with observational estimates where possible. It is important to note, however, that our results generally indicate that some degree of experimentation is required to produce the best estimates of interaction strength. Ultimately a combined experimental, theoretical, and observational approach will be needed not only to directly estimate interaction strength but to evaluate different approaches. Experimental manipulations are important to validate observational approaches where possible (e.g., Wootton 1994*b*, 1997, Pfister 1995). Furthermore, analyses of simulated data sets may also be a powerful means for evaluating the effectiveness of different experimental approaches. For example, our analyses of simulated data indicate that PULSE experiments and dynamic regression approaches provide reasonable estimates of interaction strength. They also demonstrate that logistically it may be easier to carry out the dynamic regression approach and that such an approach is best employed in nonequilibrium situations where measures are taken at separate time intervals to avoid bias due to interdependence of closely spaced sampling periods.

In conclusion, estimating interaction strength in natural communities and evaluating the consequences of the resulting patterns represent difficult but important tasks. By making explicit the definition of interaction strength under investigation, the assumptions underlying its investigation and the ties between theoretical and empirical approaches, a more unified understanding of interaction strength will begin to emerge.

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APPENDIX

Derivation of a PULSE Experimental Protocol for an Open Population

Consider the following equation, expressed in per capita form:

$$\frac{1}{N_1} \times \frac{dN_1}{dt} = \frac{I_1}{N_1} + r_1 + \alpha_{11}N_1 + \sum_{j=2}^{s} \alpha_{1j}N_j.$$

This equation takes the form of the generalized mutlispecies form of the Lotka-Volterra equations, but with an additional term (I_1) describing the immigration of individuals from outside the local population. The intraspecific density-dependent effects have been separated from interspecific effects to facilitate the subsequent calculations. If we apply the PULSE protocol outlined by Bender et al. (1984), we obtain two results, one for the control at equilibrium and one for an experimental PULSE treatment where species 1 is perturbed from equilibrium to the value N_1':

control at equilibrium:

$$\frac{1}{N^*_1} \times \frac{dN_1}{dt} = \frac{I_1}{N^*_1} + r_1 + \alpha_{11}N^*_1 + \sum_{j=2}^{s} \alpha_{1j}N^*_j = 0$$

PULSE treatment:

$$\frac{1}{N'_1} \times \frac{dN_1}{dt} = \frac{I_1}{N'_1} + r_1 + \alpha_{11}N'_1 + \sum_{j=2}^{s} \alpha_{1j}N^*_j$$

where N^*_j represents the density of species j at equilibrium. Subtracting the control treatment from the PULSE treatment yields

$$\frac{1}{N'_1} \times \frac{dN_1}{dt} = \frac{I_1}{N'_1} - \frac{I_1}{N^*_1} + \alpha_{11}(N'_1 - N^*_j)$$

which leaves one equation with two unknowns (I_1) and α_{11}), so the conventional PULSE approach is not sufficient to estimate the intraspecific parameters. The problem can be remedied by including another PULSE treatment, to N_1'', and again subtracting the equilibrium equation, which yields

$$\frac{1}{N''} \times \frac{dN_1}{dt} = \frac{I_1}{N''_1} - \frac{I_1}{N^*_1} + \alpha_{11}(N''_1 - N^*_j).$$

Substituting, and rearranging the equations describing both PULSE treatments yields

$$\alpha_{11} = \left(\frac{\frac{1}{N''_1} \times \frac{dN_1}{dt} N''_1}{N^*_1 - N''_1} - \frac{\frac{1}{N'_1} \times \frac{dN_1}{dt} N'_1}{N^*_1 - N'_1} \right) \Big/ (N'_1 - N''_1)$$

$$I_1 = \left(\alpha_{11} - \frac{\frac{1}{N'_1} \times \frac{dN_1}{dt}}{N^*_1 - N'_1} \right) N^*_1 - N'_1.$$