

## QUANTIFYING VARIATION IN THE STRENGTHS OF SPECIES INTERACTIONS

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**Abstract.** Understanding how the strengths of species interactions are distributed among species is critical for developing predictive models of natural food webs as well as for developing management and conservation strategies. Recently a number of ecologists have attempted to clarify the concepts of “strong-” and “weak-interactors” in a community, and to derive techniques for quantifying interaction strengths in the field, using metrics that are consistent, comparable, and of relevance to theoreticians. In this paper, we examine potential biases in different empirical approaches to quantifying variation in interaction strengths within and among natural communities.

Using both simulated and published data, we explore the behavior of four commonly used or recently proposed empirical measures of the strength of consumer–prey interactions. The type of index used, the experimental protocol, and the underlying model of predator–prey interaction all strongly influence one’s perception of both (1) the distribution of interaction strengths among species (e.g., presence of “keystone” species), and (2) the specific identity of the interactions that appear to be most important. Raw treatment differences tend to emphasize effects on very abundant prey, while the three proportional indices tend to emphasize effects on extremely rare prey. Two of the proportional indices are inherently asymmetric about zero, and they inflate positive or negative effects, respectively. When predators exhibit a saturating functional response, the three proportional measures of per capita effect are biased toward a skewed distribution of interaction strengths dominated by effects on the rarest prey. Predator interference causes the per capita measures to emphasize the effects of rare predators. Estimates of per capita effects are also problematic when (1) the per capita effects are back-calculated from experiments designed to measure collective effects (e.g., predator exclusions), and (2) the collective effect of a predator is constant across a wide range of predator densities, as may be common for keystone predators. Finally, since all of the indices show time-dependent behavior, they are differentially suited for different experimental protocols (e.g., short-term vs. long-term results, or community initially near vs. far from equilibrium). All the indices explored here have the potential to provide useful, complementary information about ecological impacts of species in natural communities. In this analysis, we attempt to clarify what each index actually measures and the conditions under which each is most revealing.

**Key words:** *density dependence; food web; functional response; interaction strength; keystone species; per capita effects; predator–prey interaction; simulation; species impact; species interactions.*

### INTRODUCTION

Understanding how the strengths of species interactions are distributed among species is critical for developing both predictive models of natural food webs (Hall and Raffaelli 1993, Wootton 1997) and management and conservation strategies (Mills et al. 1993,

Power et al. 1996). Species interaction strength (i.e., the magnitude of the effect of one species on the abundance of another) is a key parameter in most dynamic food web models. Due to a lack of empirical data on interaction strengths, theorists have generally assumed that they are drawn from a uniform or symmetrical distribution (Lawton 1992, Hall and Raffaelli 1993). In four recent empirical studies, estimated interaction strengths among a suite of species have all had highly skewed distributions (Paine 1992, Fagan and Hurd

Manuscript received 20 November 1997; revised 22 October 1998; accepted 27 October 1998; final version received 20 November 1998.

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TABLE 1. Empirical indices of per capita consumer–prey interaction strength explored in this study.

Index	Formula <sup>†</sup>	Original intent	Reference
Raw difference	$(N - D)/Y$	Commonly presented in studies to show absolute, untransformed treatment effects	N/A
Paine's Index (PI)	$(N - D)/(DY)$	Quantify effect of consumer on competitive dominant that has potential to form monoculture	Paine 1992
Community Importance (CI)	$(N - D)/(Np_y)$	Quantify effect of a species relative to its abundance (i.e., distinguish “keystones” from “dominants”)	Power et al. 1996
Dynamic Index (DI)	$(\ln(N/D))/Yt$	Quantify an effect of size that is theoretically equivalent to the coefficient of interaction strength in the discrete-time version of Lotka–Volterra equations	Osenberg and Mittelbach 1995, Wootton 1997

<sup>†</sup>  $N$ , abundance of prey in the treatment where predators are present (i.e., “normal condition”);  $D$ , abundance of prey in the treatment where predators are absent (i.e., “deleted”);  $Y$ , abundance of the predator;  $p_y$ , proportional abundance of the predator;  $t$ , time.

1994, Raffaelli and Hall 1996, Wootton 1997). Most species had weak or no detectable effects on the abundances of other species, while a few had strong effects. These patterns are consistent with the observations and intuition of many ecologists that the structure of many communities is likely to be determined by a small subset of species that exert disproportionately strong effects (e.g., Paine 1980, Power et al. 1996). These four recent studies (Paine 1992, Fagan and Hurd 1994, Raffaelli and Hall 1996, Wootton 1997) are unique and valuable contributions for two reasons: (1) some of them use indices of “interaction strength” that can be derived from explicit models of species interaction, and thus could be estimates of parameters describing interaction strength used in these models; and (2) they measure a suite of interactions in an assemblage with a common metric, so that the relative importance of many interactions can be compared.

Using interaction strength indices derived from theoretical models is extremely important, because communication between empiricists and theoreticians has historically been impeded by confusion over the definition of interaction strength and by a discordance between what theoreticians model and what empiricists actually measure (MacArthur 1972, Laska and Wootton 1998). In fact, the empirical studies were partly motivated by recent efforts by ecologists to clarify the concepts of “strong-” and “weak-interactors” in a community and to derive techniques for quantifying interaction strengths in the field that are consistent, comparable, and of relevance to theoreticians (e.g., Paine 1992, Wootton 1994, 1997, Power and Mills 1995, Osenberg and Mittelbach 1996, Power et al. 1996, Ruesink 1998).

Laska and Wootton (1998) reviewed and clarified alternative theoretical concepts of interaction strength, and they evaluated different approaches for empirically estimating the per capita interaction strength coefficients in dynamic models of species interactions. In this paper, we focus on the more empirical problem of

finding a common metric to quantify variation in species interactions in natural communities. Using a common metric in measuring interaction strength has important practical implications, independent of how a given system is modeled, because this practice allows characterization of (1) the patterns of variation in interaction strength among species within a community (i.e., the distribution of interaction strengths among species), (2) the identity of which species, if any, play disproportionately strong roles, and (3) how these vary over space and time. Thus, it is important to understand how our perception of the patterns of interaction strengths is influenced by the inherent mathematical behavior of the index used, including the index's response in prey or predator density to natural variation among species or among sites.

Using both simulated and published data, we explore the behavior of four commonly used or formally proposed indices for quantifying the relative importance of consumer–prey interactions (Table 1): (1) the raw, arithmetic difference in prey abundance in treatments, with and without predators; (2) an index proposed by Paine (1992) and used by Fagan and Hurd (1994) and Raffaelli and Hall (1996) (hereafter “Paine's Index, PI”); (3) an index proposed by Osenberg and Mittelbach (1996) and Wootton (1997) (hereafter “Dynamic Index, DI”); and (4) an index of “community importance” (CI) proposed by Power et al. (1996) to quantify the degree to which a community or ecosystem trait is altered by a species deletion. Since CI exhibited similar behavior to PI, it is not included in all of our analyses. All the indices have the potential to provide useful information about the relative importance of interactions among species. They must be used, however, with a clear understanding of what they actually measure and of the conditions under which one can expect them to be most revealing.

#### EMPIRICAL ESTIMATES OF INTERACTION STRENGTH

In this study, we focus on consumer–prey interactions to explore the behavior of the different empirical

indices of interaction strength. Many field ecologists have historically quantified the strength of consumer impacts by the raw, arithmetic difference in prey abundance between treatments with and without predators ( $N - D$ ), or as the per capita effect  $((N - D)/Y)$ ; where  $N$  (normal condition) is prey abundance in the presence of predators,  $D$  (deleted) is prey abundance in the absence of predators, and  $Y$  is predator abundance (Table 1; e.g., Connell 1961, Dayton 1971, Menge 1976, 1978).

Paine (1992) proposed an index (PI) for quantifying per capita interaction strengths from field experiments (Table 1). In this approach, the interaction strength is estimated as  $(N - D)/(DY)$ . Thus, the index shows the effect of an individual predator on the per capita change in prey abundance. Under equilibrium conditions, it is mathematically equivalent to the per capita interaction strength ( $\alpha$ ) used in a particular formulation of the Lotka–Volterra competition equations (Laska and Wootton 1998). In addition, it is based on variables that field ecologists measure.

In deriving this index, Paine (1992) was interested in quantifying the “magnitude of a consumer’s influence on an entire assemblage,” and, thus, specified that the target species  $x$  be a competitively dominant prey that had the potential to form a monoculture in the absence of its consumer  $y$ . A monoculture of  $x$  was considered to be a “reference state,” and the degree to which  $y$  prevented  $x$  from dominating the assemblage was a measure of the importance of  $y$ . The index has since been applied to two other types of communities for estimating the distribution of per capita direct effects among species and using different experimental protocols (Fagan and Hurd 1994, Raffaelli and Hall 1996).

The community importance index (CI) of a species was proposed as part of an effort to make the definition of a “keystone species” more operational (Table 1; Power et al. 1996). Here, CI is measured as  $(N - D)/(Np_y)$ , where  $p_y$  is the proportional abundance (usually biomass) of species  $y$  before it was deleted from the community. While we focus here on consumer–prey interactions, it is also important to note that CI was conceived as an index of a species impact, not only on the abundance of particular taxa, but also on ecosystem properties such as nutrient retention, productivity, and albedo, or green biomass (Power et al. 1996). The two other differences between CI and PI are as follows: (1) in CI, the intact community ( $N$ ) is considered to be the “reference state” (i.e., the denominator includes  $N$  rather than  $D$ ), and (2) the “collective” effect of a species,  $CI \times p_y$ , when plotted against  $p_y$ , measures how a population’s impact scales with its proportional biomass. Such plots distinguish keystone species as those species that have effects that are large, and much larger than would be predicted by their abundance (Power et al. 1996). While CI does not correspond to any theoretically defined coefficient of interaction

strength, it is ecologically meaningful and has important practical implications for conservation and management by quantifying the degree to which a community is structured by keystone species.

Another empirical measure of per capita interaction strength, which was derived from theory, was proposed by Osenberg and Mittelbach (1996) and Wootton (1997). This index (DI) is based on the discrete-time version of the dynamics described by Lotka–Volterra equations (Table 1). DI is similar to measures used by limnologists to quantify zooplankton feeding rates (e.g., Dodson 1975). This index essentially measures interaction strength as the difference in exponential prey growth rates, with and without predators. It has the advantage that, unlike PI, it makes no assumptions about equilibrium conditions. Thus, it can be calculated before the prey (and predator) population reach an equilibrium state (see also Laska and Wootton [1998]). However, because DI is expressed in units of time, comparisons among different experiments or different systems require that the time scale be specified.

Finally, PI, DI, and  $(N - D)/Y$  all measure the per capita effects of a predator on its prey. In theory, the per capita effect of a predator should be less sensitive to variation in ambient predator density than an estimate of the collective impact of the entire predator population (Wootton 1997). This is not the case, however, when per capita predation rates are strongly density dependent (with respect to either the prey or the predator). Another potential problem is that field ecologists often measure the collective effect of excluding a predator, and then back-calculate the per capita effect by dividing by some estimate of predator density. Field measures of per capita effects based on exclusion experiments, therefore, may depend critically on both the reliability of one’s estimate of predator population size and on the assumptions of a linear functional response with respect to prey density and of no interference or facilitation among predators.

#### BEHAVIOR OF THE INDICES

It is important to understand how a given index influences our perception of the ecology of a given system, independent of its correspondence to a particular model parameter. Fig. 1a illustrates a range of possible results observed in a field experiment designed to determine the effect of a consumer species  $y$  on a target species  $x$ . Because three of the indices are undefined when the denominator is zero, we only considered cases with  $x \geq 1$ . In Fig. 1a, the experiment begins with species  $x$  at ambient density (either 100, 90, 10, or 1). In treatment  $N$ , the consumer  $y$  is present at natural density; in treatment  $D$ ,  $y$  is excluded. The top three panels represent cases where  $y$  has a positive effect on  $x$  (Fig. 1a, panels 1, 2, and 3), the bottom three panels represent negative effects of  $y$  on  $x$  (Fig. 1a, panels 4, 5, and 6). Cases 1 vs. 2, and 4 vs. 5 represent situations where the raw difference between treatments is the

same, but the prey densities, and thus the proportional (or per capita prey) differences, are different. Cases 2 vs. 3, and 5 vs. 6 represent situations where the proportional differences among treatments are both relatively large (e.g., almost total suppression of  $x$  by  $y$  under normal conditions in both cases 5 and 6), and the raw differences between treatments are different (e.g., 99 vs. 9).

Fig. 1b illustrates how the different indices translate the experimental results for each case into quantitative estimates of interaction strength. The number in each bar indicates which particular case (1–6) in Fig. 1a is being measured. For simplicity, we assume that the density of predators,  $Y$ , is either equal to unity or is equal under the different scenarios. For ease of comparison, we also calculate CI as a per capita effect rather than per proportional biomass. Compared to the raw difference (Fig. 1b;  $[N - D]/Y$ ), both PI and CI reflect the proportional difference between treatments. For a given raw difference among treatments, the strength of positive effects, as measured by PI, tends to be greater than the negative effects (Fig. 1b). This is because the denominator ( $D$ , the abundance of species  $x$  in the absence of  $y$ ) is smaller (Fig. 1a, cases 1 vs. 4, 2 vs. 5, and 3 vs. 6). Considering just the negative effects (Fig. 1, cases 4, 5, and 6), PI differs from  $(N - D)/Y$  in that the latter considers cases 4 and 5 to be equivalent, while PI, which emphasizes the proportional difference among treatments, measures all cases in which  $y$  essentially eliminates  $x$  as being similar and close to  $-1$  (Fig. 1b, PI cases 5 and 6). The difference between PI and  $(N - D)/Y$  varies with the sign of the interaction, as positive effects measured by PI are progressively larger as  $(N - D)/Y$  increases (Fig. 1, cases 2 and 3). The behavior of CI is analogous to PI, except that CI inflates negative (rather than positive) effects, because the denominator is  $N$  rather than  $D$  (Fig. 1b).

Unlike PI and CI, in this example DI behaves symmetrically about zero (Fig. 1). It emphasizes large proportional differences among treatments. By log-transforming the proportional changes, it solves the problem of bounding the index to  $-1$ , as PI does, or to  $+1$ , as CI does. Thus, DI preserves the difference in magnitude between cases 5 and 6 in Fig. 1. In this case, the response of DI to differences among treatments tends to reflect our ecological intuition: If  $y$  reduces the abundance of  $x$  by 10, its effect should be stronger if this essentially eliminates  $x$  from the community (Fig. 1, cases 5 vs. 4). Similarly, if  $y$  eliminates  $x$  and prevents it from forming a monoculture, this should be a stronger effect than if  $x$  is not very abundant even in the absence of  $y$  (Fig. 1, cases 6 vs. 5).

Fig. 1c illustrates the sensitivity of each index to varying ambient prey abundance, given a constant raw difference (10 individuals) in prey abundance between treatments, with and without predators. As the mean prey abundance decreases, the measured interaction strength increases nonlinearly for all three proportional

indices (PI, CI, and DI). However, both PI and CI behave asymmetrically about zero. In PI, negative effects are bounded by  $-1$ , but positive effects can theoretically be infinite as  $D$  approaches zero. The reverse is true for CI. Given these patterns, if one was to quantify the distribution of interaction strengths among species, and both positive and negative effects were expected, then the distributions of PI and CI are likely to be inherently skewed toward positive and negative effects, respectively. In other words, they may be more likely to characterize a system as being dominated by a few disproportionately strong interactions, simply because the indices are inherently asymmetric. Whether or not this occurs will depend critically on the frequency distribution of the denominator of the index.

Whether one index better reflects the ecological realities of a given community depends on one's question of interest and the particular model of predator-prey interaction that one has in mind. In an experiment where one expects multiplicative population growth of the prey, DI would be more appropriate than raw treatment differences as a measure of interaction strength. Similarly, if data are log-transformed prior to analysis (to satisfy assumptions of statistical tests), then one is implicitly emphasizing proportional effects rather than the change in absolute number of prey (see also Wootton [1994]). On the other hand, measuring absolute changes in prey abundance may be more informative if, for example, one does not expect underlying exponential growth of prey in the experiment, or if one wishes to characterize total energy flow in a system.

#### SIMULATION MODEL

We used a simple predator-prey model to more rigorously explore the following questions: (1) When do the empirically determined interaction strengths correspond to the known theoretical coefficient? (2) How are empirical estimates of variation in per capita interaction strength (among species or over space and/or time) biased by natural variation in prey or predator density? (3) How does the experimental protocol influence the interaction strength that is measured (e.g., short- vs. long-term results; community initially near equilibrium vs. far from equilibrium)?

Our aim was to simulate a typical field experiment measuring the impact of a long-lived predator on the abundance of a prey species that has a much faster generation time. We assume that, over the course of the experiment, the predator density is held constant, but the prey density can change due to reproduction or mortality from predation and other sources. In the simulations, the dynamics of the prey population is described as follows:

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - \frac{aNP}{1 + c_N N + c_P P} \quad (1)$$

where  $K$  is prey carrying capacity,  $r$  is prey per capita intrinsic growth rate,  $a$  is predator attack rate (i.e., in-

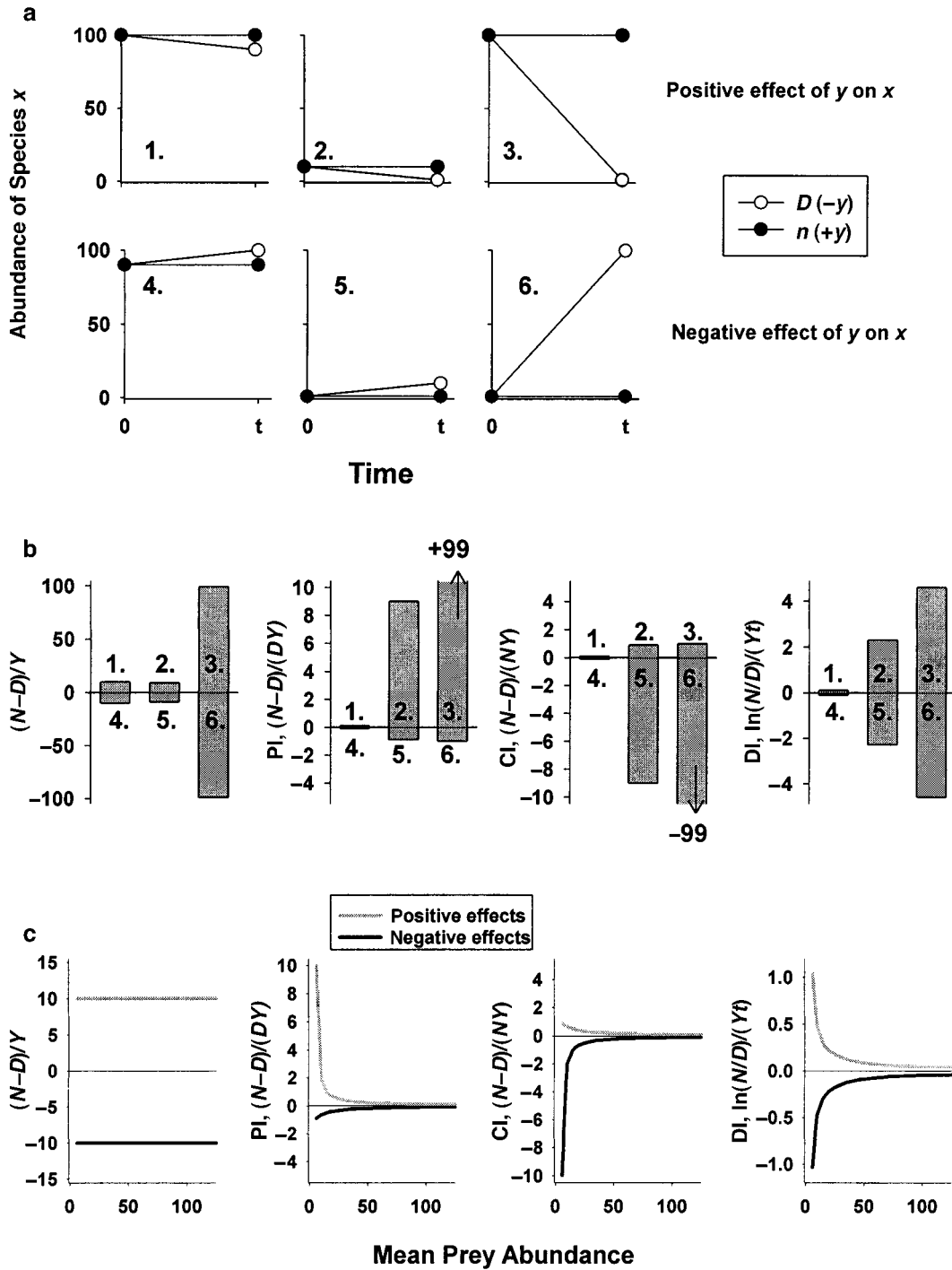


FIG. 1. (a) A range of possible results of an experiment designed to determine the effects of species  $y$  on a target species  $x$ . Each panel shows the abundance of  $x$  in two treatments over the time course of the experiment,  $t$ . In treatment  $N$ , species  $y$  is present. In treatment  $D$ , species  $y$  is excluded (or “deleted”). In all cases,  $x$  is present at the start of the experiment at some ambient density (100, 90, 10, or 1), and subsequent effects of  $y$  on the survival of  $x$  are observed. In addition, all experiments terminate before the abundance of  $x$  is zero, thus the minimum value is 1 for the abundance of  $x$ . The abundance of  $y$  was assumed to be 1, so that all effects represent per capita effects. Cases 1, 2, and 3 represent situations where  $y$  has a positive effect on  $x$ . In cases 4, 5, and 6,  $y$  has a negative effect on  $x$ . See *Behavior of the indices* for details. (b) Different measures of the strength of the effect of  $y$  on the final abundance of  $x$  in (a). The different bars in each panel are spatially arranged to represent cases 1–6 in (a).  $(N - D)$  is the raw difference in the abundance of  $x$  between treatments with and without  $y$ . PI, Paine’s Index (Paine 1992); CI, Community Importance (Power et al. 1996); DI, Dynamic Index (Osenberg and Mittelbach 1996, Wootton 1997). See *Empirical estimates of interaction strength* for details. (c) A simulation illustrating



teraction strength), and  $c_N$  and  $c_p$  are parameters. Throughout the study,  $r = 0.5$ . In the absence of the predator, the prey population undergoes logistic growth, approaching a carrying capacity,  $K$ . If  $c_N = c_p = 0$ , then the predator has a Type I functional response with a constant per capita predator attack rate,  $a$ . If  $c_N > 0$ , then the predator's functional response is a saturating (Type II) function of prey density. In this case, the per capita effect of the predator depends on the density of prey. Likewise, if  $c_p > 0$ , then the predator's functional response is a saturating function of predator density (e.g., predator interference at high predator density). Whether one defines the theoretical coefficient of interaction strength as the per capita attack rate  $a$  (e.g., Laska and Wootton 1998), or as the attack rate relative to the prey intrinsic growth rate (e.g., Holt 1977),  $a$  should scale positively with per capita interaction strength.

The model was simulated using a fourth-order Runge Kutta algorithm with the Solver computer package (Gurney et al. 1996). For each of the cases described below, simulations of the model were run to obtain trajectories of the prey density, with and without the predator. The empirical indices were measured at each time step, to show how the measures of the interaction strength are affected by changes in the duration of the experiment. In each case, the per capita attack rate  $a$  was held constant at  $a = 0.05$ .

To explore the questions outlined above, we quantified "empirical" predator per capita interaction strength under seven different model scenarios (Table 2). Case 1 (simple exponential growth) assessed the degree to which the different indices are sensitive to prey density when there is no self-limitation or other density dependence incorporated in the model. It also evaluated, whether PI or DI approximate the known attack rate coefficient  $a$  under the simplest possible conditions. Cases 2–5 explored the sensitivity of the empirical indices to varying initial prey abundance when prey exhibit logistic growth. In cases 2 and 3, initial prey density varied among runs, but the carrying capacity remained constant. This was analogous to comparing interaction strength estimates for prey density that differ in distance from equilibrium. In case 3, predator consumption saturated at high prey density (i.e., Type II functional response; Holling 1959), while in case 2 the only density dependence explicitly modeled was self-limitation by the prey. Thus, a comparison of cases 2 and 3 assessed the degree to which a dependence on prey density in the predator's functional

response influences the patterns of interaction strengths measured empirically, even when  $a$  is constant in all cases. Cases 4 and 5 were similar to 2 and 3 in that they explored the effects of variable initial prey density. In these cases the predator was added to the system with the prey at its carrying capacity ( $N_0 = K$ ), but different prey species have different carrying capacities. These cases were analogous to comparing empirical interaction strengths among species that differ in ambient equilibrium abundance, or to comparing one interaction among sites that differ in productivity. As in cases 2 and 3, cases 4 and 5 differed from each other in whether or not predator consumption saturated at high prey density. In cases 6 and 7, initial prey density and the carrying capacity were constant across runs, but predator density varied. Case 7 incorporated predator interference at high predator density, while there was no predator density dependence in case 6. These cases assessed the degree to which empirical per capita interaction strengths are sensitive to variation in predator density, both with and without density dependence explicitly present in the model. As in the other cases, the theoretical per capita attack rate  $a$  was constant in all runs.

#### *Exponential growth*

With simple exponential prey growth (Table 2, case 1), both PI and DI are insensitive to variation in initial prey density, while the raw difference is increasingly sensitive over time to the most abundant prey (Fig. 2). Only DI actually measures  $a$ , the attack rate coefficient. Furthermore, DI is constant over the time course of the experiment (see also Laska and Wootton [1998]). PI, however, is extremely time dependent and eventually approaches a value that does not correspond to  $a$  (Fig. 2b).

#### *Variable initial prey density (constant $K$ )*

With logistic prey growth and a constant carrying capacity for all runs (Table 2, cases 2 and 3; Fig. 3), both the raw difference ( $N - D$ ) and PI are insensitive to variation in initial prey density, when they are measured once the prey have reached equilibrium, regardless of whether predator consumption is density dependent with respect to prey (Fig. 3a–d,  $t > 30$ ). At equilibrium, PI settles on a value of  $PI = -a/r = -0.1$ , illustrating that Paine's Index equals the attack rate coefficient  $a$  only for a particular formulation of the underlying model (see Laska and Wootton 1998). Before reaching equilibrium, both the raw difference and

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how the different measures respond to varying ambient prey abundance for the same raw difference between treatments with and without the predator. Ambient prey abundance was measured as the mean of treatments  $D$  and  $N$ , where in each case the difference ( $N - D$ ) was 10 individuals. Note that, for the same absolute treatment difference, the magnitude of the proportional effects (PI, CI, and DI) increase nonlinearly as ambient prey abundance decreases. In addition, PI and CI behave asymmetrically about zero, but in different directions, due to their respective denominators.

TABLE 2. Parameter and variable values for the cases explored in the predator-prey simulation.

Case	Initial prey density, $N_0$	$K$	$P$	$c_N$	$c_P$	$\alpha$
Exponential prey growth						
1	100, 500, 1000, 1500, 2000	N/A	5	0	0	0.05
Varying initial prey density, without and with saturating functional response						
2	100, 500, 1000, 1500, 2000	1000	5	0	0	0.05
3	100, 500, 1000, 1500, 2000	1000	5	<b>0.005</b>	0	0.05
Varying prey carrying capacity, without and with saturating functional response						
4	100, 500, 1000, 1500, 2000	= $N_0$	5	0	0	0.05
5	100, 500, 1000, 1500, 2000	= $N_0$	5	<b>0.005</b>	0	0.05
Varying predator density, without and with predator interference						
6	100	1000	1, 5, 10, 15, 20	0	0	0.05
7	100	1000	1, 5, 10, 15, 20	0	<b>0.1</b>	0.05

Notes:  $N$ , prey density;  $P$ , predator density;  $K$ , prey carrying capacity;  $r$ , prey per capita intrinsic growth rate (set equal to 0.5 throughout);  $a$ , predator attack rate (interaction strength);  $c_N > 0$ , saturating functional response at high prey density;  $c_P > 0$ , predator interference at high predator density. See Eq. 1 for governing relationship.

PI are highly variable and very sensitive to initial prey density. These patterns highlight the fact that the robustness of PI and  $N - D$  depends on equilibrium conditions, and hereafter we focus on the behavior of these measures at equilibrium ( $t > 30$ ; see also Osenberg et al. [1997]). As noted above and by others (e.g., Laska and Wootton 1998), DI does not depend on the assumption of equilibrium. In fact, it performs very poorly at equilibrium, because it approaches zero under all conditions (Fig. 3e and f), thus hereafter we focus on the non-equilibrium patterns of DI ( $t$  near 0; see also Osenberg et al. 1997). Under simple logistic prey growth with no predator saturation (Fig. 3e), DI approximates  $a$  only very early in the experiment and when prey are initially rare (i.e., far from equilibrium where growth rates are closest to exponential). Even when no saturating functional response is incorporated in the model (Fig. 3e), DI varies with initial prey density. When predators exhibit a saturating functional response (Fig. 3f), if one were to compare interaction strengths among prey species that vary in density, the distribution of interaction strengths (measured by DI) would be inherently skewed and dominated by rare prey, despite the fact that  $a$  is constant.

#### Variable initial prey density (variable $K$ )

With logistic prey growth and variable carrying capacities (Table 2, cases 4 and 5; e.g., different prey species with different equilibrium abundances, or different sites varying in productivity), both PI and DI are robust to variation in prey abundance when predators do not exhibit a saturating functional response (Fig. 4c and e). The raw treatment difference, however, varies considerably with prey density, even if the predator functional response is linear (Fig. 4a). When predators exhibit a saturating functional response, all three indices are sensitive to prey abundance in a way that inherently skews the distribution of interaction strengths (among species or among sites) despite the fact that  $a$  is constant (Fig. 4b, d, f). In this case, PI

and DI inherently emphasize effects on rare prey (or in low productivity sites), while raw treatment differences emphasize effects on abundant prey (or in high productivity sites). Again, DI is the only index that approximates  $a$ , but only does so very soon after the perturbation of adding predators and when prey are least abundant.

#### Variable predator density

With logistic prey growth and variable predator density (Table 2, cases 6 and 7), all the empirical measures of per capita interaction strength are sensitive to variation in predator density, *regardless* of whether predator density dependence is explicitly modeled, and despite the fact that  $a$  was constant across all simulations (Fig. 5). In the absence of predator interference, DI again approximated  $a$  only early in the experiment when prey are least abundant (Fig. 5e). DI was also robust to variation in predator density during this time period, but soon thereafter it increasingly emphasized effects of abundant predators. For low predator densities ( $P = 1$  and 5), PI again measured  $-a/r$  at equilibrium. For higher predator densities,  $P > 10$ , the predator drove the prey extinct, and PI reached a value of  $-1/P$  at equilibrium. When predators interfere at high densities, DI was very sensitive to predator density in the nonequilibrium window in which it generally performs best (Fig. 5f). In this case (case 7), all the indices were inherently biased toward emphasizing the per capita effects of rare predators despite a common value of  $a$  (Fig. 5b, d, and f).

In summary, the modeling results illustrate how, under most conditions, all the empirical indices are time dependent, with DI performing best when prey are furthest from equilibrium, and the others performing best when prey are at equilibrium (Table 3). In addition, DI is the only index that approximates the theoretical coefficient of interaction strength  $a$ , and this only occurs when the prey are rare and far from equilibrium. Independent of whether the indices actually measure  $a$ ,

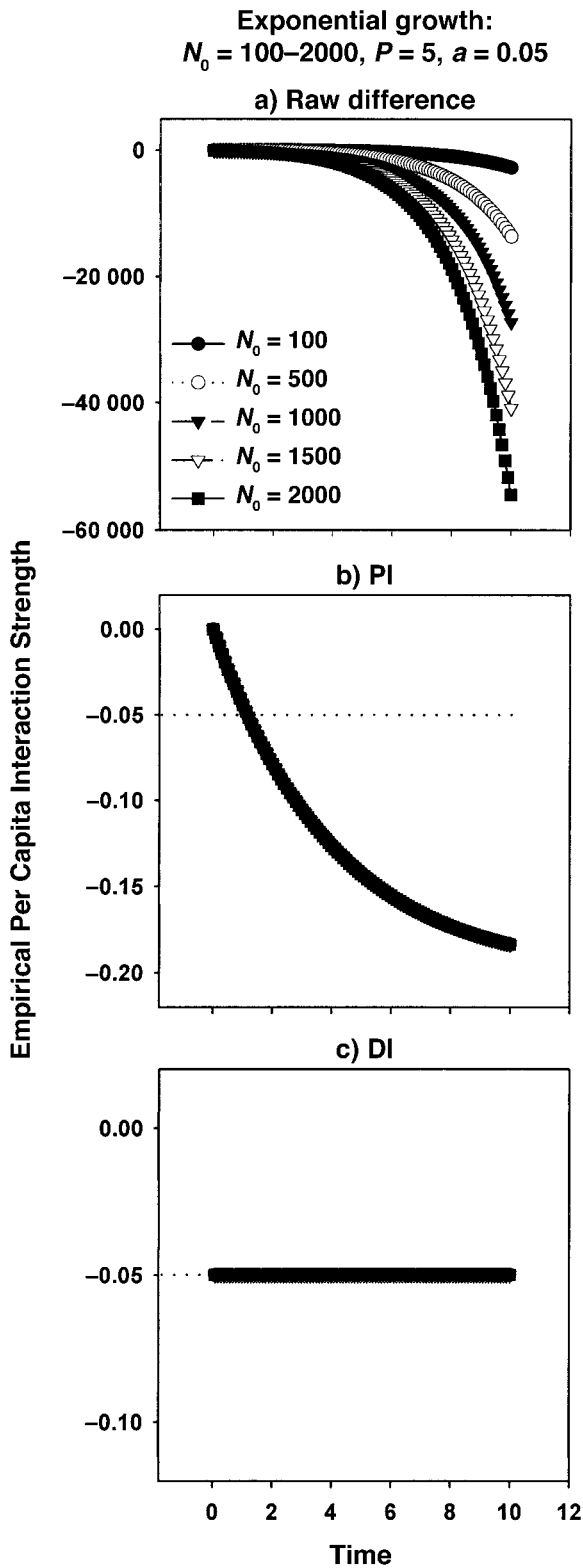


FIG. 2. Temporal trajectories of the per capita interaction strength, as measured by the different empirical indices, estimated from simulations with vs. without predators for case 1 (Table 2), where prey growth was exponential, initial prey density ranged from 100 to 2000, and  $a$  (the theoretical in-

teraction strength coefficient) was constant across all runs. (1) how these strengths respond to natural variation in prey or predator abundances, and (2) how they respond to prey or predator density dependence that commonly occurs in natural systems. Toward this end, the modeling results suggest that all the indices are sensitive to variation in prey or predator density when predator satiation or interference is present, as well as showing sensitivity in some cases where there is no explicit prey or predator density dependence. Thus, when quantifying the distribution of interaction strengths among species or among sites, most empirical measures will be inherently skewed by variation in prey or predator abundance, independent of whether the “true” interaction strength differs.

CASE STUDIES

To better explore these *empirical* challenges to quantifying variation in interaction strength, we reanalyzed data from three case studies that either quantified consumer-prey interaction strengths for a suite of predators and/or prey, or quantified the effects of a given predator across a number of different sites. These studies provide an opportunity to compare how the different indices respond to natural variation among species, or among localities, in ambient prey or predator densities.

Using PI, Fagan and Hurd (1994) estimated the per capita effects of mantid predators on a suite of arthropod prey. This study provides a good example of how different measures of interaction strength respond differently to ambient prey abundance. Mantid predator densities were held constant in enclosures, while the abundance of each prey species varied naturally. The densities of different groups of arthropods in each treatment (predator additions and controls) at the end of the experiment (on day 20) were used to calculate interaction strengths. Using Paine’s Index (PI), they found that the distribution of interaction strengths between mantids and their prey was highly skewed, with most of the impacts being weak or zero except for strong positive effects on certain groups of hemipterans (Figs. 6b and 7b, He and Md). Using their data for intermediate-density predator treatments and predator exclosures, we calculated per capita effects using the dynamic index (DI) and the raw treatment differences  $((N - D)/Y)$  to compare the patterns of interaction strength provided by the three indices. When DI is used, the ranking of mantid impacts on

←  
interaction strength coefficient) was constant across all runs. (a) Raw difference  $([N - D]/Y)$ , (b) PI, Paine’s Index, and (c) DI, Dynamic Index. The different lines represent different initial prey densities. Where only one line is visible, it is because all five lines overlap. The horizontal dotted reference line indicates  $a = 0.05$ .



Variable Initial Prey Density (constant  $K$ )

Linear functional response:

$c_N = 0, c_P = 0, K = 1000$   
 $N_0 = 100-2000, P = 5, a = 0.05$

Saturating functional response:

$c_N > 0, c_P = 0, K = 1000$   
 $N_0 = 100-2000, P = 5, a = 0.05$

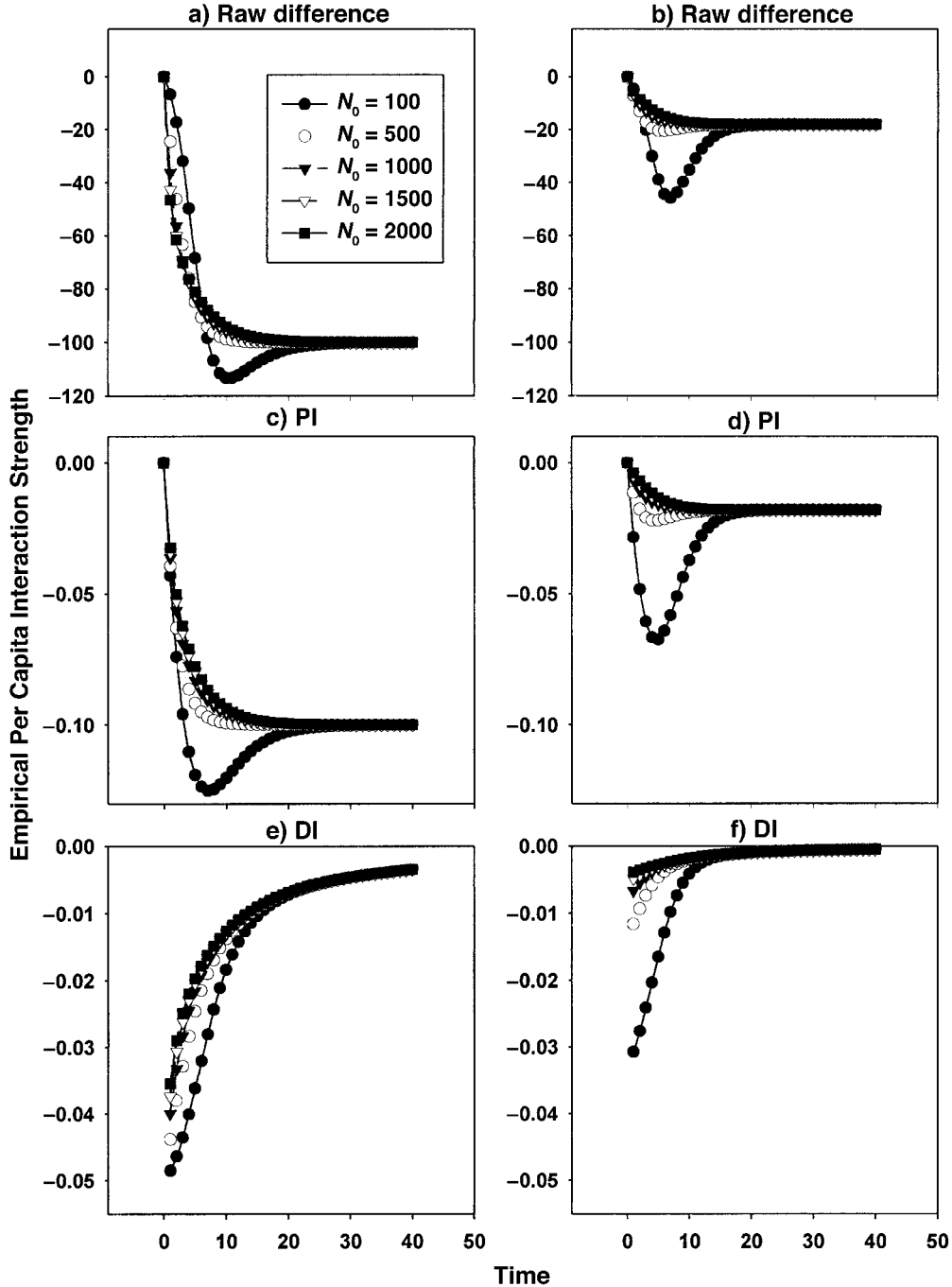


FIG. 3. Temporal trajectories of the per capita interaction strength, as measured by the different empirical indices, estimated from simulations with vs. without predators for cases 2 and 3 (Table 2), where prey exhibit logistic growth, predators had either a linear or saturating functional response, initial prey density ranged from 100 to 2000, carrying capacity  $K$  was constant, and  $a$  (the theoretical interaction strength coefficient) was constant across all runs. (a) and (b) Raw difference ( $[N - D]/Y$ ); (c) and (d) PI, Paine's Index; (e) and (f) DI, Dynamic Index; (a), (c), and (e) show the linear functional response (Table 2, case 2); (b), (d), and (f) show the saturating functional response (Table 2, case 3). The different lines represent different initial prey densities. Where only one line is visible, it is because all five lines overlap.

**Variable Initial Prey Density (variable  $K$ )**

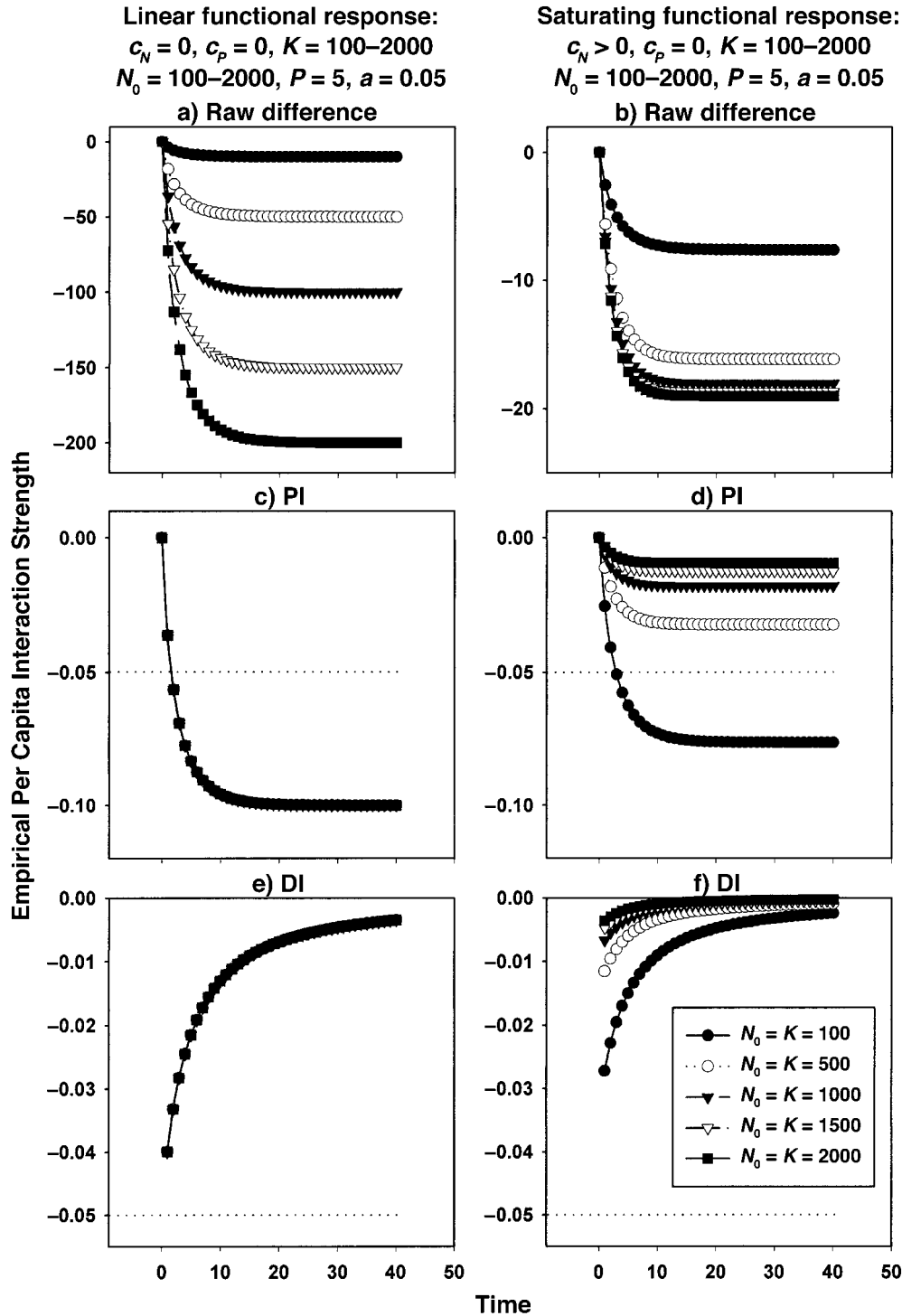


FIG. 4. Temporal trajectories of the per capita interaction strength, as measured by the different empirical indices, estimated from simulations with vs. without predators for cases 4 and 5 (Table 2), where prey exhibit logistic growth, predators had either a linear or saturating functional response, initial prey density was equal to the carrying capacity  $K$ , which ranged from 100 to 2000, and  $a$  (the theoretical interaction strength coefficient) was constant across all runs. (a) and (b) Raw difference  $([N - D]/Y)$ ; (c) and (d) PI, Paine's Index; (e) and (f) DI, Dynamic Index; (a), (c), and (e) show the linear functional response (Table 2, case 4); (b), (d), and (f) show the saturating functional response (Table 2, case 5). The different lines represent different initial prey densities. Where only one line is visible, it is because all five lines overlap. The horizontal dotted reference line indicates  $a = 0.05$ .

**Variable Predator Density**

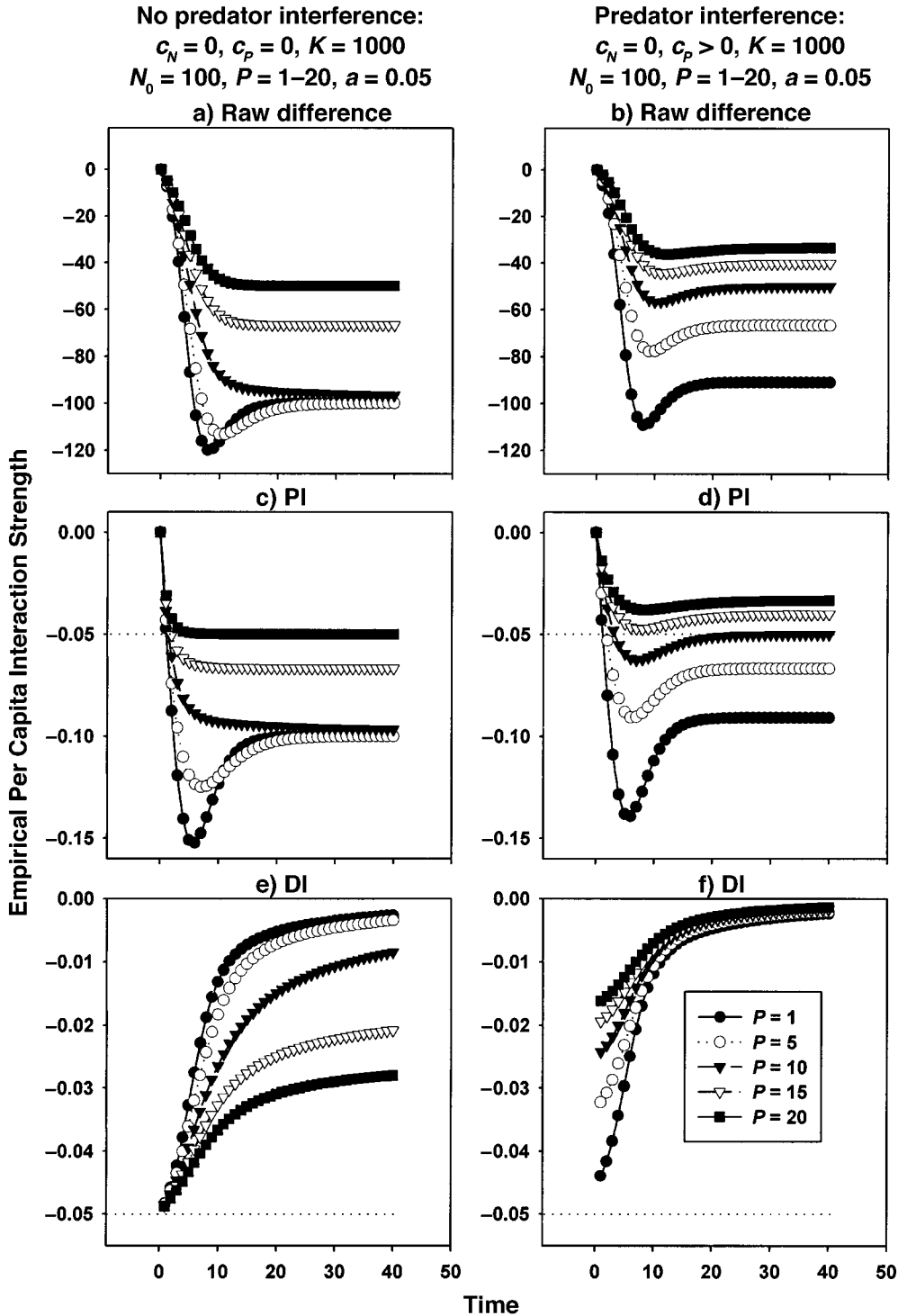


FIG. 5. Temporal trajectories of the per capita interaction strength, as measured by the different empirical indices, estimated from simulations with vs. without predators for cases 6 and 7 (Table 2), where prey exhibit logistic growth, predators either interfere at high densities or not, initial prey density was constant (100), the carrying capacity  $K$  was constant (1000), and  $a$  (the theoretical interaction strength coefficient) was constant across all runs. (a) and (b) Raw difference ( $[N - D]/Y$ ); (c) and (d) PI, Paine's Index; (e) and (f) DI, Dynamic Index; (a), (c), and (e) show the linear functional response (Table 2, case 6); (b), (d), and (f) show the saturating functional response (Table 2, case 7). The different lines represent different initial prey densities. Where only one line is visible, it is because all five lines overlap. The horizontal dotted reference line indicates  $a = 0.05$ .

TABLE 3. Characteristics of the empirical indices of per capita interaction strength explored in this study.

Predator effect†	Raw difference	PI	CI	DI
Relationship to theoretical interaction strength				
...	None	Only at equilibrium and for certain underlying models.	None	Only when prey exhibit exponential growth.
Inherent bias in comparing positive and negative effects				
...	None (symmetric).	Emphasizes positive effects.	Emphasizes negative effects.	None (symmetric).
Bias when comparing effects on prey that vary in density				
WOS	Emphasizes abundant prey, or high productivity sites.	Robust to prey density at equilibrium.	Robust to prey density at equilibrium.	Emphasizes prey far from equilibrium; robust to different $K$ 's
WS	Emphasizes abundant prey, or high productivity sites.	Emphasizes rare prey, or low productivity sites.	Emphasizes rare prey, or low productivity sites.	Emphasizes prey far from equilibrium, rare prey, or low productivity sites.
Bias when comparing effects of predators that vary in density				
WOI	Robust to predator density.‡	Robust to predator density.‡	Robust to predator density.‡	Emphasizes abundant predators.
WI	Emphasizes rare predators.	Emphasizes rare predators.	Emphasizes rare predators.	Emphasizes rare predators.
Conditions when most informative				
...	Long term experiment.	Long term experiment.	Long term experiment.	Short term experiment.
	Prey initially abundant and near equilibrium.	Prey initially abundant and near equilibrium.	Prey initially abundant and near equilibrium.	Prey initially rare and far from equilibrium.
	Comparing both positive and negative effects.	Comparing only negative effects.	Comparing only positive effects.	Comparing both positive and negative effects.

† WS, with predator saturation; WOS, without predator saturation; WI, with predator interference; WOI, without predator interference.

‡ Robustness fails when prey are driven extinct at equilibrium.

different prey is similar to PI (Fig. 6c), but the distribution of interaction strengths is comparatively less skewed and more symmetrical about zero (Fig. 7c). This is consistent with our observations that PI tends to highlight positive effects (Fig. 1). When mantid effects are measured as the per capita raw difference between treatments  $((N - D)/Y)$ , the rank order of mantid impacts is altered (Fig. 6a), and the distribution of interaction strengths is skewed in the opposite direction to that for PI (Fig. 7a). The per capita raw difference index characterizes the impacts of mantids as generally weak, except for one disproportionately strong negative effect on homopteran prey (Fig. 7a). This pattern was due to the fact that the homoptera were generally an order of magnitude more abundant than the other prey (157.5 per 4-m<sup>2</sup> plot for "Other Homoptera" vs.  $16 \pm 1$  SE per 4-m<sup>2</sup> plot on average for all other taxa in predator exclusions). Therefore, large absolute differences in homopteran abundance between treatments (Fig. 6a,  $[N - D]/Y = -5.9$  for Oh) were divided by large ambient prey density to estimate DI and PI, resulting in relatively small proportional effects (Fig. 6b,  $PI = -0.04$  for Oh; Fig. 6c,  $DI = -0.05$  for Oh). In contrast to the raw treatment differences, the strongest effects measured by DI were on the least abundant prey (Nabidae [Nb],

2.5 per 4-m<sup>2</sup> plot). These results are consistent with the modeling results that demonstrate that, under some conditions, DI will inherently emphasize effects on rare prey, while raw differences will emphasize effects on abundant prey (e.g., Fig. 4b vs. f).

Raffaelli and Hall (1996) recently used PI to estimate the distribution of per capita effects of six predators on six invertebrate prey in the Ythan River estuary in Scotland. While Fagan and Hurd (1994) focused on the effects of one predator enclosed at fixed densities, Raffaelli and Hall (1996) used exclosures to quantify the effects of a suite of predators all at different ambient densities. That study, therefore, provides an opportunity to examine how per capita effects measured by the different indices are sensitive to estimates of predator density (as opposed to prey density). Using PI (per capita effects), they observed the strengths of predator impacts to be mostly weak or zero, with a few disproportionately strong negative effects of shorebirds on five of their prey (Figs. 8b and 9b). In this case, when the per capita effects are measured as DI or as the raw difference between treatments, the distribution of interaction strengths remains dominated by the strong negative effect of shorebirds, although the specific interactions that dominate the distribution are different for the raw differences (Figs. 8a, c and 9a, c).

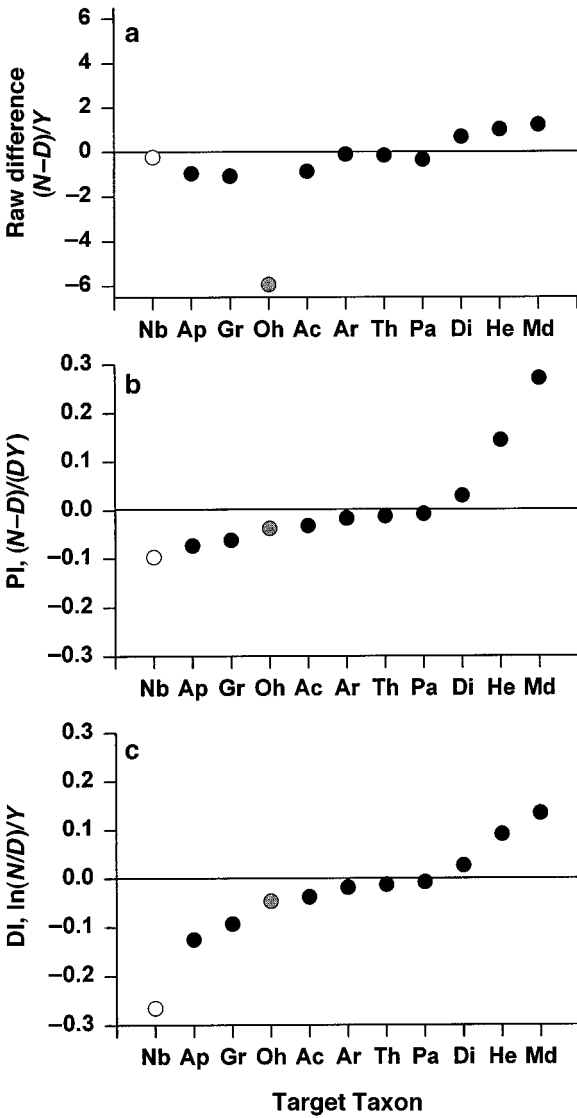


FIG. 6. Per capita interaction strengths measuring a mantid's impact on a suite of arthropod taxa (from Fagan and Hurd [1994]). (a) Interaction strength measured as the per capita raw difference in prey abundance between treatments with and without mantids. (b) Interaction strength measured as Paine's Index (PI), as in Fagan and Hurd (1994). (c) Interaction strength measured using the Dynamic Index (DI). Rankings are all based on panel (b), with PI as a measure of interaction strength. Data were taken from Tables 1, 4, and 5 in Fagan and Hurd (1994), using "control" treatments without mantids and "medium density" mantid treatments. Taxon codes are as in Fig. 4 of Fagan and Hurd (1994): Ap, Aphids; Gr, Gryllids; Oh, Other Homoptera; Ac, Acarina; Pa, Parasitoid Hymenoptera; Ar, Araneida; Di, Diptera; Th, Thysanoptera; He, Hemiptera (pooled); Md, Miridae; Nb, Nabidae (Md and Nb are the most abundant families of Hemiptera). Gray circles highlight the effects of mantids on the most abundant prey. Open circles highlight effects on the least abundant prey. Black circles represent prey of intermediate abundance.

The strong apparent per capita effects of shorebirds were partly due to the fact that shorebirds were two to five orders of magnitude less abundant than the other predators ( $0.004$  shorebirds/ $m^2$  vs.  $43 \pm 9$  other predators/ $m^2$  [mean  $\pm$  SE]), so the treatment differences for shorebirds are divided by an extremely small number. These results are consistent with the modeling results that demonstrate that per capita interaction strengths can be strongly influenced by predator density (Fig. 5).

When per capita effects are compared with collective impacts, the rank order of predator impacts is considerably altered (Fig. 8 and right vs. left panels). For

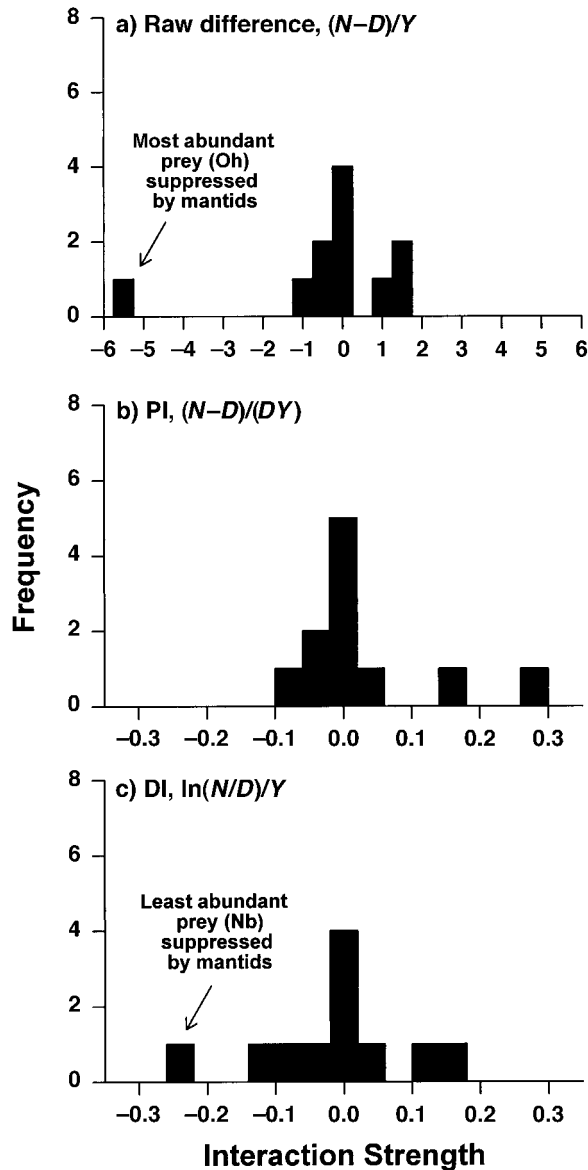


FIG. 7. The frequency distributions of different measures of interaction strength for the effect of predatory mantids on a suite of arthropod taxa (from Fagan and Hurd [1994]). See Fig. 6 legend for details.



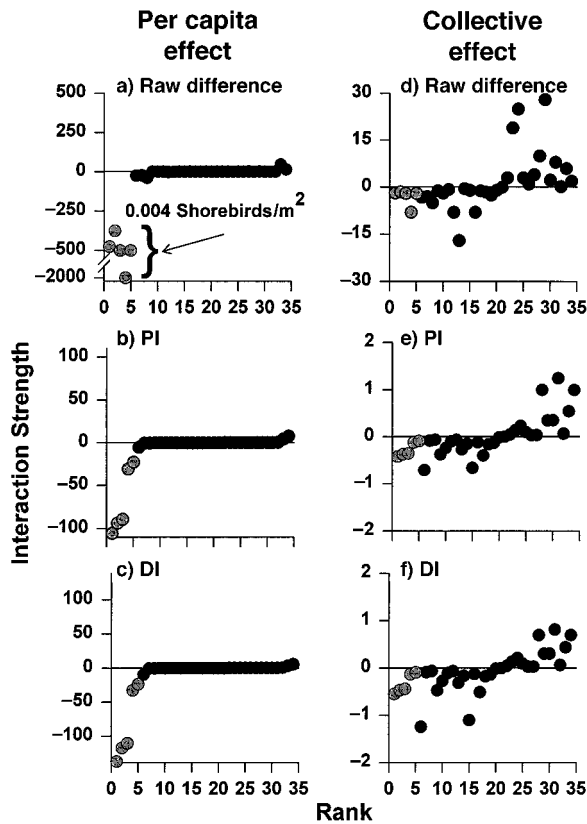


FIG. 8. Different measures of interaction strengths characterizing effects of six predators on six invertebrate prey in the Ythan river estuary in Scotland (from Raffaelli and Hall [1996]). Panels (a)–(c) represent per capita effects based on ambient densities of each predator  $y$ . Panels (d)–(f) represent collective, population-level effects. (a) and (d) Interaction strength measured as the raw difference in prey abundance between treatments with and without predators. (b) and (e) Interaction strength measured as Paine's Index (PI), as in Raffaelli and Hall (1996). (c) and (f) Interaction strength measured using the Dynamic Index (DI). The gray circles highlight the effects of shorebirds on five of their prey. Rankings are all based on panel (b), with PI as a measure of per capita interaction strength as in Raffaelli and Hall (1996). Data were taken from Table 17.1 in Raffaelli and Hall (1996).

example, the large per capita effect of shorebirds contrasts with their modest collective impact on prey populations. In addition, the distribution of collective effects is much less skewed than that for per capita effect, for all three measures of interaction strength used here (Fig. 9, right vs. left panels). Since the per capita effects here are back-calculated from the collective effects, these patterns highlight the fact that all three measures can be sensitive to estimates of predator density, as well as to the reliability of those estimates. In the case of rare, highly mobile predators that exhibit aggregating behavior, density estimates may be very sensitive to the spatial or temporal extent of the sampling area.

In the rocky intertidal zone of the coast of Oregon, USA, Navarrete and Menge (1996) examined variation in the effects on one prey species (the mussel, *Mytilus*

*trossulus*) of two predators, the classic “keystone” predator (Paine 1969), *Pisaster ochraceus* (a starfish), and whelks of the genus *Nucella*. Experiments involved transplanting mussels to experimental plots where either, both, or neither of the predators was removed. This manipulation was repeated at four localities differing in ambient predator densities (among other factors). A separate study at a fifth site, examined whelk effects on similarly transplanted mussel patches, where whelks were either excluded or enclosed at two different densities (E. L. Berlow, unpublished data.). Thus, in this case, prey abundance was initially the same among treatments, while predator abundance for both a keystone and a nonkeystone predator varied among sites or enclosures (Fig. 10a). When one looks at the raw, collective effect of each predator on mussel survival rates, starfish were able to consistently locate and rapidly eliminate the transplanted mussels at all sites (Fig. 11). The effects of whelks on overall mussel survival rates were generally weaker and more variable

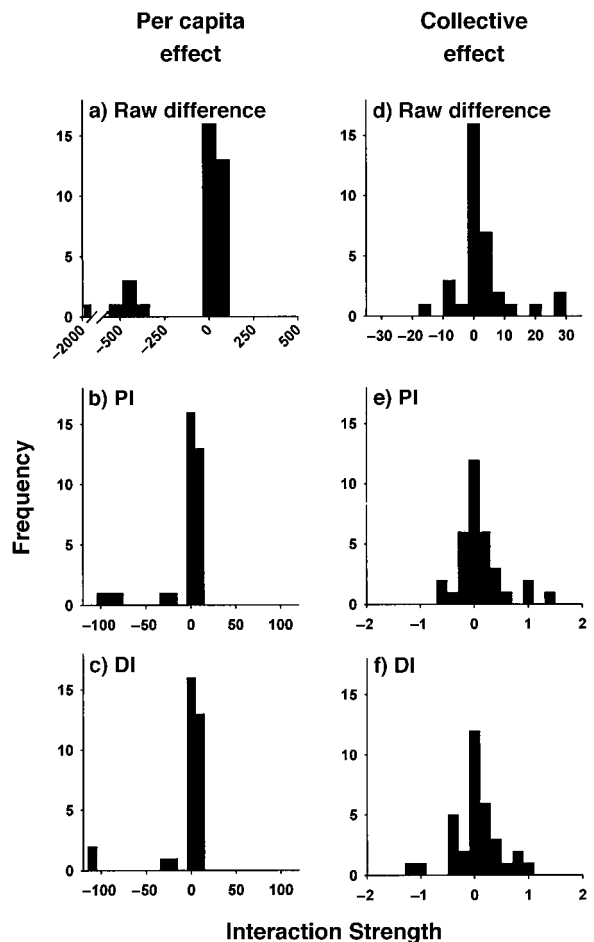


FIG. 9. The frequency distributions of different measures of interaction strength for the effects of six predators on six invertebrate prey in the Ythan river estuary in Scotland (from Raffaelli and Hall [1996]). See Fig. 8 legend for details.

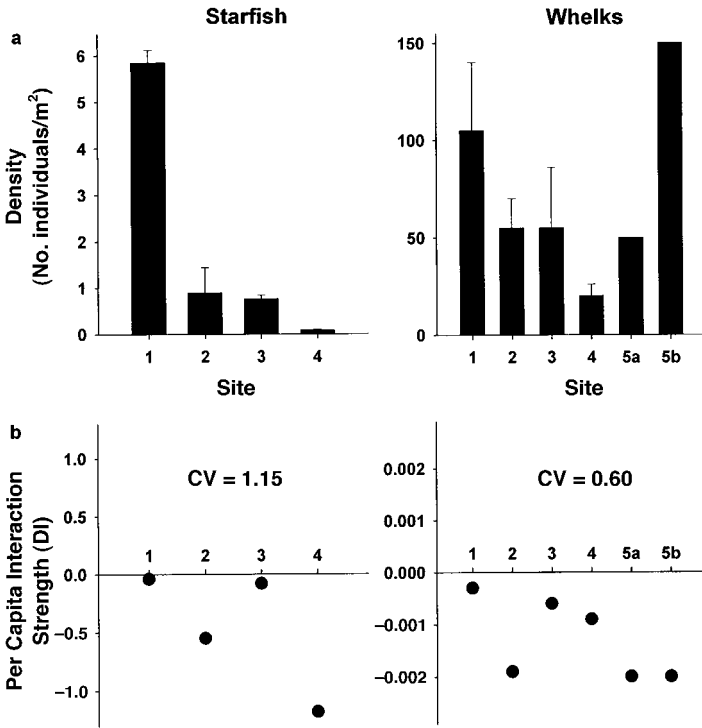


FIG. 10. (a) Mean densities (+1 SE) of starfish and whelks at different localities. There are no error bars for Site 5a and b, because it was a separate experiment where whelks were held in enclosures at different but constant (i.e., variance was 0) densities (0, 50, and 150 whelks/m<sup>2</sup>). (b) Mean per capita interaction strength of the effect of starfish and whelks on mussel prey at the same five sites as in (a). Interaction strength is measured as DI (PI could not be accurately calculated with the data available).

among sites (Fig. 11). These patterns are consistent with other studies demonstrating that *Pisaster* is a “strong-interactor” in this system and that *Nucella*’s collective impacts can be weak and variable (Menge et al. 1994, Navarrete 1996, Berlow 1997).

When the predator impacts are measured as per capita effects using DI (in this case, PI could not be ac-

curately calculated with the data available) the patterns of variation in predator impacts across sites were reversed (Fig. 10b). In contrast to the consistently strong collective impact of starfish on mussel survival rates (Fig. 11), their per capita interaction strengths were quite variable among sites (Fig. 10b). The site with the highest density of starfish had the weakest per capita

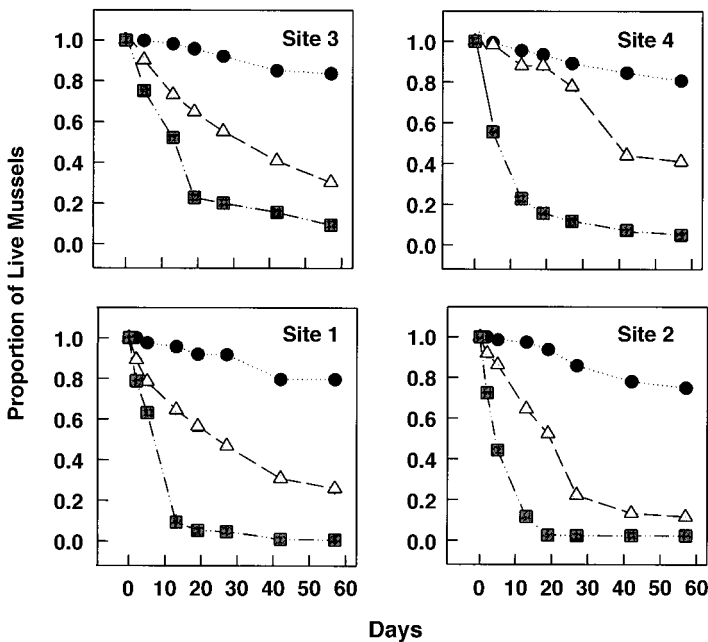


FIG. 11. Mean survival of transplanted mussel prey over time at the four sites where both starfish and whelks were manipulated (see Fig. 10 legend). Circles indicate treatments where both predators were removed. Triangles indicate treatments where whelks were present and starfish removed. Squares indicate treatments where starfish were present and whelks removed. (Figure adapted from Navarrete and Menge [1996]).

effects, and the site with the lowest density of starfish had the strongest per capita effects (Fig. 10). The per capita effects of whelks on mussels were generally two orders of magnitude weaker. In contrast to the variable collective impacts of whelks (Fig. 11), the per capita effects varied less among sites than those for starfish (Fig. 10b; coefficient of variation of DI across sites = 0.60 for whelks vs. 1.15 for starfish).

Based on these results, Navarrete and Menge (1996) suggested that collective effects of keystone predators, such as starfish, may be characteristically consistent across sites. This is partly due to the fact that their per capita effects vary with, and compensate for, a wide range of predator, due to steep functional responses (e.g., Robles et al. 1995). On the other hand, nonkeystone predators, like whelks, may be characterized by consistently weak per capita effects that translate into collective effects varying with local predator density. In other words, the collective effect of keystone species, typified by strong per capita effects overall (Power et al. 1996), should rise rapidly with predator density until it saturates (Fig. 12a). This could be due, for example, to interference at high densities, high mobility or voracity of individuals at low densities, or complete elimination of prey at intermediate predator densities. Once the collective effect saturates, then the per capita effect, estimated from experiments that directly measure the collective effect, should decline with increasing predator density (Fig. 12b). In contrast, the collective effect of a non-keystone species, typified by weaker per capita effects overall, would be expected to increase more slowly with predator density and may never saturate across the range of naturally occurring densities (Fig. 12a). In this case, the per capita effects would remain comparatively consistent across that range of predator density (Fig. 12b).

#### DISCUSSION

Of the indices explored here, only the dynamic index (DI) provides estimates for the attack rate coefficient  $a$ , which was considered by Laska and Wootton (1998) to be the theoretical coefficient of interaction strength. This only occurs under the following limited set of conditions: when prey are initially rare, far from equilibrium, and exhibiting exponential growth. Whether or not it actually measures the coefficient of interaction in a population model also depends critically on whether the system at hand meets the assumptions of the model (see also Wootton [1997], Laska and Wootton [1998]). For example, DI assumes exponential prey growth, and all of the measures assume no density dependence in the interaction strength with respect to prey or predators (e.g., satiation or interference). Here, we have illustrated that violation of these assumptions can lead to strong biases in estimates of interaction strength. Similarly, what one defines as the “correct” model coefficient

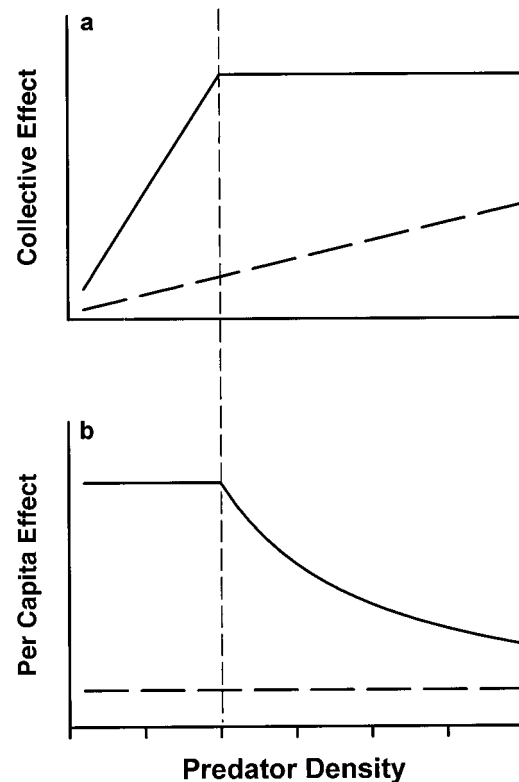


FIG. 12. A hypothetical response curve for (a) the collective, population-level impact and (b) the per capita effect of a predator, as predator density increases. The solid line represents the pattern for a keystone predator with generally strong per capita effects. The dashed line represents the pattern for a non-keystone predator with weaker per capita effects.

that equals “interaction strength” will depend on what one is interested in measuring. This may variously be the effect strength on *maximum* per capita prey growth rate at low prey density (e.g.,  $a$ ; Laska and Wootton 1998), the effect strength on per capita prey growth at ambient prey density at a particular site and time, the consumption rate of the predator relative to prey intrinsic growth rate (e.g., Holt 1977), predator impact on total energy flow, or other predator impacts.

Even if these indices are not directly translatable into model parameters, it is clear that they can provide ecologically meaningful information about how interaction strengths are distributed among species in a given community and how these patterns vary among different communities. This information can guide natural resource management and suggest potential consequences of a species loss. The different indices explored here provide different, complementary information. Furthermore, they have different constraints that make them individually better suited to different situations and types of questions. We now present a summary of some of the characteristics of

these indices, their potential biases, and the conditions under which they are likely to be most informative (Table 3):

1) All of the indices are inherently time dependent under most conditions. The raw treatment difference and Paine's Index (PI) (as well as community importance [CI]) perform best at or near equilibrium, while DI performs best far from equilibrium. Thus, in a comparison of interaction strengths among different experiments, DI should be more appropriate for comparing short-term results, and the others will excel when comparing long-term results (see also Osenberg et al. [1997]).

2) Both PI and CI behave asymmetrically about zero, and they tend to inflate positive and negative effects, respectively, due to the difference in the denominator of the index ( $D$  vs.  $N$ ; Fig. 1). For example, if a prey species is rare in the presence of a predator (small  $N$ ), it is more likely to register as a very large effect when measured as CI vs. PI. In contrast, if a prey species is extremely rare when the predator is absent (small  $D$ ), then even a very small increase in the presence of the predator will register as a large facilitative effect when measured as PI vs. CI. Therefore, we advise caution when using PI or CI to compare a suite of interactions where both positive and negative effects are anticipated. It is important to note, however, that PI was originally conceived to measure the impact of a consumer on a prey species that has the potential to dominate the community in the absence of the consumer (Paine 1992). In this situation, where primarily negative effects are anticipated and where  $D$  is expected to be large (e.g., by release of a competitive dominant in the absence of its consumer), PI is a useful measure of the negative impacts of different consumers. The fact that PI is bounded by  $-1$  makes it easily comparable among different species within an assemblage, different studies, or different systems. The ecological value of CI lies in its ability to distinguish systems structured by "keystone" species from those structured by "dominants," which exert their influence by making up a large proportion of the biomass (Power et al. 1996). However, because it tends to produce left-skewed distributions of interaction strengths, extremely strong negative effects identified by CI should be examined to see if the pattern is being driven by an extremely small  $N$  in the denominator. If both negative and positive effects are being compared, DI is the best measure of proportional effects, because it behaves symmetrically about zero.

3) When comparing interactions among species or among sites, all indices are potentially biased, a priori, by variation in prey density, especially if the interaction is inherently density dependent with respect to the prey (e.g., predator satiation). How the bias occurs is different for DI than the other indices. In order for DI to estimate the theoretical predator attack rate  $a$  prey growth must be approximately exponential. If prey den-

sity is near equilibrium, DI will underestimate this coefficient. Therefore, DI inherently emphasizes effects on prey that are initially far from equilibrium (Fig. 3). The starting densities of prey in the experiment have no effect on the measures of PI, CI, or raw differences, as long as the experiment is allowed to reach equilibrium. Predator satiation will reduce the measured per capita effect on abundant prey, and cause PI, CI, and DI to emphasize the effects on rare prey. Raw differences, on the other hand, always emphasize effects on abundant prey. If there is no inherent density dependence in the interaction, PI, CI, and DI appear to be robust to variation in prey abundance due to differing carrying capacities (Fig. 4). Under these conditions, any of these three indices may be better measures of comparison across sites of differing productivity than the raw treatment differences.

4) Measuring interaction strengths as per capita effects, rather than collective effects, has the advantage of potentially facilitating comparisons among predator species or among localities that vary naturally in predator abundance (e.g., Paine 1992, Wootton 1997). Our results suggest, however, that per capita effects for all the indices, potentially can be sensitive to predator density, regardless of whether the interaction is inherently density dependent and regardless of whether  $a$  is constant (Fig. 5). If predators interfere at high density, all the indices emphasize effects of rare predators. In the absence of predator density dependence, PI, CI, and the raw difference are all robust to differences in predator density. An exception to this occurs if the predator drives the prey extinct at equilibrium, leading the indices to emphasize effects of the rare predators (e.g., Fig. 5b and c, where  $P > 10$ , raw difference =  $K/P$ , and  $PI = 1/P$ ). DI emphasizes effects of abundant predators (unless the effects are measured very early in the experiment; Fig. 5e).

In addition, if per capita effects are back-calculated from collective effects, as in predator exclusion/removal experiments, then the perceived per capita effect will depend on how predator density is estimated (e.g., over what area or what time scale?). Finally, if the collective effect is constant across a wide range of predator density, which may be typical of keystone predators, the per capita effect would be expected to decline with increasing predator density (Fig. 12). We thus recommend that studies of interaction webs should be explicit about predator densities, so that both per capita and collective measures can be estimated. Together both measures provide complementary information about the ecological importance of a given predator, or about variation in impacts of different predators within or among communities.

5) Because of their differential sensitivity to equilibrium vs. nonequilibrium conditions, different indices may be more appropriate for different experimental protocols. DI is a more informative metric for short-term results of "colonization experiments," where the

prey are initially rare and far from equilibrium. On the other hand, PI and CI are more appropriate measures of long-term results or of experiments that begin with an "intact" community (i.e., near equilibrium) and where prey are initially abundant (but, see caveats raised in point (3), above).

6) While raw treatment differences are likely to be sensitive to prey density and to emphasize effects of abundant prey, we believe that these absolute effects can provide important complementary information and add perspective to the proportional effects measured by PI, CI, and DI. Absolute and proportional measures are differentially sensitive to particular prey species that are either extremely rare or very abundant. For example, an extremely rare prey species that becomes even more rare in the presence of a predator will register as a very large proportional effect, although the absolute change in prey abundance is extremely small. Conversely, if an extremely abundant prey species suffers large absolute losses in the presence of a predator, that effect will dominate the distribution of raw treatment differences even if the prey remains relatively abundant. If an effect is large both in absolute and proportional terms, one can more confidently conclude that it is also ecologically important.

This analysis suggests that the type of index used, the experimental protocol, and the underlying model of interaction can all strongly influence our perception of both (1) the pattern of distribution of interaction strengths among species, and (2) the specific interactions that appear to be most important. In this paper we have illustrated the limitations of the various empirical approaches to measuring interaction strength and have highlighted the conditions under which the different measures can be most useful.

#### ACKNOWLEDGMENTS

This study was motivated in part by a thought-provoking symposium entitled "Theoretical, Empirical, and Statistical Approaches to Measuring Interaction Strength" organized by M. S. Laska and J. T. Wootton at the 1997 Annual Meeting of the Ecological Society of America in Albuquerque, New Mexico, USA. It has also benefited enormously from stimulating discussions with R. T. Paine and J. T. Wootton and from comments by J. Bengtsson, M. A. McPeck, and an anonymous reviewer. This work was supported in part by an NSF Postdoctoral Fellowship to E. L. Berlow, FONDAP O&MB #3 and FONDECYT 1971263 to S. A. Navarrete, NSF DEB-9615175 to M. E. Power, and grants from NSF (OCE88-11369, OCE92-17459) and the Andrew W. Mellon foundation to B. A. Menge.

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