

INTEGRATING DIRECT EFFECTS AND TRAIT-MEDIATED INDIRECT EFFECTS USING A PROJECTION MATRIX MODEL

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Abstract. In systems where indirect effects are mediated by traits (e.g., behavior) rather than density, direct and indirect effects may be measured in different biological currencies, making it difficult to quantify their relative contributions to a net interaction. For instance, the hydroid *Hydractinia symbiolongicarpus*, which colonizes shells occupied by the hermit crab *Pagurus longicarpus*, affects its host directly by reducing its fecundity and indirectly by modifying the behavior of its predators. In this study, I construct population projection matrices for *P. longicarpus*, which were housed with different assemblages of hydroids and predators. By defining direct and indirect effects as combinations of log-transformed λ 's from these matrices, I translate direct effects on fecundity and indirect effects on survival into a common currency (population growth rate), allowing me to assess the relative strength of these effects. In the presence of a fish predator, strong positive indirect effects countered negative direct effects, producing a net mutualism. In the presence of a crab predator, indirect effects were equivalent in size and magnitude to direct effects, resulting in a net parasitism. These results provide insight into the mechanisms underlying context-dependency and help to explain the geographical and temporal variation observed in outcomes of symbiotic interactions.

Key words: conditional interactions; context-dependency; demographic model; hermit crab; *Hydractinia symbiolongicarpus*; interaction modifications; mutualism; net effects; *Pagurus longicarpus*; symbiosis; trait-mediated indirect interactions.

INTRODUCTION

One of the practical applications of ecology is to predict how changes in abundance of an “associate” species (e.g., from harvest, invasion, or other factors) affect a “focal” species (sensu Miller and Kerfoot 1987). In ecological communities, this net effect is composed of direct and indirect effects (Yodzis 1988). By the definitions of Wootton (1994), direct effects arise from physical interaction between associate and focal species. Indirect effects are transmitted via interactions with “intermediate” species, and therefore arise only in multispecies assemblages. Strong indirect effects may significantly enhance or neutralize direct effects, resulting in a net outcome that is nonintuitive based on knowledge of direct interactions (Yodzis 1988). For this reason, we need to account for both direct and indirect effects when quantifying the net effect of one species on another in a community context.

Ecologists (Miller and Kerfoot 1987, Wootton 1993, Abrams et al. 1996) distinguish between two mechanisms underlying indirect effects. The first, termed a density-mediated indirect interaction (DMII) or inter-

action chain, arises when change in the density of an associate species alters density of an intermediate species, in turn altering the density of the focal species (Fig. 1a). The second, termed a trait-mediated indirect interaction (TMII) or interaction modification, arises when the associate species modifies a trait (e.g., behavior, morphology) of an intermediate species, and this modified trait changes the rate at which intermediate and focal species interact (Fig. 1a). A standard approach for quantifying direct and indirect effects, which is grounded in community matrix theory, implicitly assumes that indirect effects are transmitted by changes in population density. Assuming that all direct effects act on the same time scale, a chain of direct effects (i.e., a DMII) will take longer to manifest than a single direct effect. Thus, changes in population growth rate resulting from a temporary perturbation from equilibrium (a “pulse” experiment) quantifies direct effects only, while changes in equilibrium population density resulting from a sustained perturbation (a “press” experiment) quantifies both direct and indirect effects (Bender et al. 1984).

Applying such an approach to systems that include TMIs is inappropriate, in part because effects are likely to be measured in terms of changes in demographic rates (i.e., fecundity, growth, survival) rather than population density. Direct and indirect effects that act on different demographic rates are measured in different biological currencies, making it difficult to compare their contributions to the net effect. We thus require a

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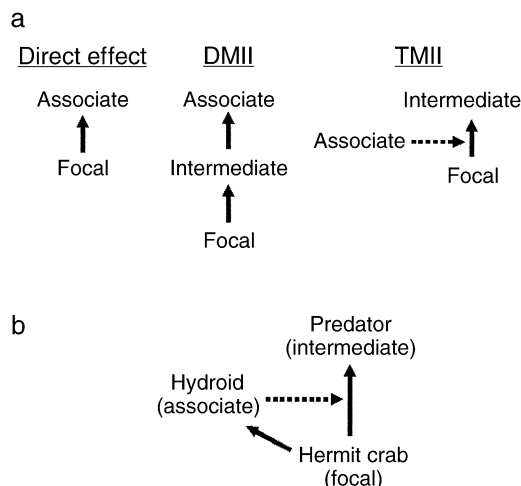


FIG. 1. Species interactions described in this study. Panel (a) is adapted from Wootton (1993) and provides a general schematic of direct effects, density-mediated indirect effects (DMII), and trait-mediated indirect effects (TMII). Solid arrows represent direct effects and point in the direction of energy transfer (directions of arrows may be switched). Dashed lines indicate an effect of an associate species on a trait of an intermediate species, thus changing the rate of direct interaction between intermediate and focal species. Panel (b) illustrates specific direct and indirect effects studied in the hermit crab–hydroid symbiosis. Since the indirect effect arises only in the presence of a hermit crab predator, the predator is considered the intermediate species. Hydroids alter predation rates on hermit crabs by causing a trait shift in predator behavior; thus, they affect their hosts through both a direct effect and a TMII.

method to translate effects that act on different demographic rates into a common currency, to enable comparison and to quantify the net effect that results when direct and indirect effects combine. McPeck and Peckarsky (1998) used a demographic model to integrate predators' lethal and sublethal effects on damselfly prey into an overall direct effect, by translating effects on mortality and growth into the common currency of population growth. In this paper, I develop a similar method to integrate direct and indirect effects using a population projection matrix, and test it by evaluating the direct and indirect effects of a symbiotic hydroid on its hermit crab host.

METHODS

Natural history

On the east coast of the United States, the hydroid *Hydractinia symbiolongicarpus* colonizes snail shells occupied by the hermit crab *Pagurus longicarpus* (see Plate 1), and is thought to benefit from associating with hermit crabs (Brooks and Gwaltney 1993). In this study, I focus on direct and indirect effects imposed by the hydroid (associate species) on its hermit crab host (focal species); these interactions are diagrammed in Fig. 1b. In a previous study, I demonstrated that *H. symbiolongicarpus* imposes direct costs on *P. longicarpus* fecundity (Damiani 2003). However, the pres-

ence of hydroids on a hermit crab's shell can repel some predators (Brooks and Mariscal 1985, Damiani 2000), either by stings from their nematocysts or unpalatable secondary compounds (Stachowicz and Lindquist 2000). This behavioral shift may reduce predation rates, resulting in a TMII on hermit crab survival. For this study, conducted in Beaufort, North Carolina, I developed a demographic method to weigh the relative importance of direct costs on fecundity and indirect benefits on survival in determining the net outcome of the hermit crab–hydroid symbiosis, when indirect effects were mediated by two local predators: striped burrfish *Chilomycterus schoepfi* and blue crabs *Callinectes sapidus*.

A demographic method for comparing relative strength of direct and indirect effects

Hermit crab population dynamics may be described by the matrix equation

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}_{t+1} = \begin{pmatrix} P_1 & F_2 & F_3 \\ G_{21} & P_2 & 0 \\ G_{31} & G_{32} & P_3 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}_t \quad (1)$$

where $n_{i,t}$ is the number of females in size class i at time t , P_i is the fraction of size class i that survive the interval $(t, t + 1)$ and remain in size i , G_{ij} is the fraction of size class j that survive the interval $(t, t + 1)$ and grow into size i , and F_i is size-specific fecundity. The dominant eigenvalue (λ) of the matrix represents geometric growth of the hermit crab population. To compare direct and indirect effects, I constructed annual matrices and calculated λ 's for *P. longicarpus* maintained under four treatments: control (O), hydroid (H), predator (P), and predator + hydroid (PH), where predators were either burrfish or blue crabs. I defined direct effects (DE) as the difference in population growth between hermit crabs with and without hydroids, and net effects (NE) as the difference in growth between populations with predators + hydroids, and populations with predators only. Since net effects are the sum of direct and indirect effects, indirect effects (IE) were equal to net effects minus direct effects. Because effects were defined as differences in population growth, I first log-transformed the λ 's so that population growth was expressed on a linear scale. Thus,

$$DE = r_H - r_O \quad (2)$$

$$NE = r_{PH} - r_P \quad (3)$$

$$IE = r_{PH} - r_P - r_H + r_O \quad (4)$$

where $r = \ln(\lambda)$, the intrinsic rate of increase. This allowed me to compare the relative strength of direct effects on fecundity and indirect effects on survivorship using a common metric r .

Parameterization of the matrix model

Ideally, transition probabilities would be estimated by following fates of uniquely marked individuals

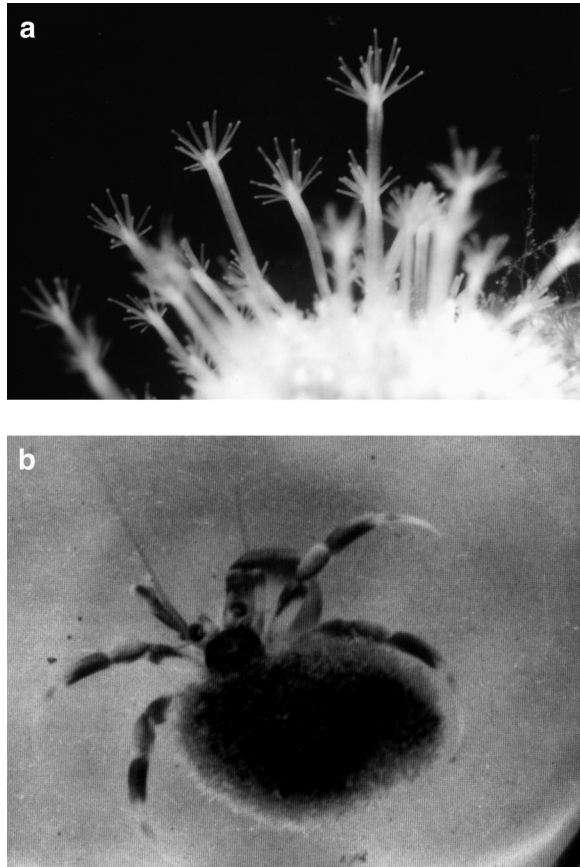


PLATE 1. The hydroid *Hydractinia symbiolongicarpus*, (a) shown under a dissecting scope, and (b) covering the snail shell occupied by its host hermit crab *Pagurus longicarpus*. Photo credit: C. Damiani.

maintained under different treatments for a year, then calculating P_i and G_{ij} by dividing the number of crabs that transition from “state” j to “fate” i during the experiment (m_{ij}) by the initial number of crabs in state j ($m_{.j}$) (Caswell 2001). Three logistical problems prevented me from using this ideal design; consequently, data used to parameterize matrices were gathered from a complex sampling scheme involving multiple studies (Appendix A).

The first limitation was that the tanks in which I conducted mesocosm experiments to estimate P_i and G_{ij} had to be dismantled every three months to repair liners and clear pipes of fouling organisms. I therefore could not run experiments long enough to measure annual demographic rates. Instead, data from six-week experiments, conducted over two years (Appendix B: Table B1), were used to construct matrices for three 18-week seasons: spring/early summer, late summer/fall, and winter. Annual matrices were calculated from the periodic matrix products of these seasonal matrices (Appendix C).

The second limitation was that individuals were difficult to mark, since *P. longicarpus* exchange shells

frequently and molt every 2–3 weeks. For the winter 1996 mesocosm experiment, I estimated P_i and G_{ij} from individuals that were marked with an acetate tag and a colored thread (Appendix D), and checked every two weeks to replace lost tags or threads. However, I discontinued this method, because of the time involved in retagging. For subsequent experiments, I knew the number of crabs in each size class at the beginning ($m_{.j}$) and end ($m_{.i}$) of the experiment. However, because crabs were not marked, I could not unambiguously assign fates to individuals. For instance, I could not determine whether a size class 2 crab collected at the end of the experiment had grown from size class 1 (and therefore should be counted in m_{21}) or had remained in class 2 throughout the experiment (and therefore should be counted in m_{22}). With estimates of size-specific mortality (q_j) and transitions from size class j into class 3 (t_j), it is possible to disentangle survival and growth transition probabilities. I therefore conducted supplemental studies to collect these data.

The third limitation was the difficulty in directly measuring fecundity rates, defined as the number of female offspring, per adult female, that survive to size class 1. *P. longicarpus* can produce multiple clutches in a year and larvae are planktonic, making it difficult to measure annual reproductive output of an individual crab. I therefore estimated F_i for each 18-week season indirectly, by defining it as the product of size-specific propensity to produce a clutch within that season (b_i), probability of clutch success (γ), clutch size (μ), fraction of female offspring per clutch (ρ), and larval survival to size class 1 (σ). I estimated b_i from individuals in the mesocosms, γ and μ from a laboratory study, and ρ from a field census. The parameter σ was estimated indirectly by assuming equilibrium conditions for the control population.

Below, I briefly describe the experiments used to estimate matrix parameters. Additional details on the methods for these experiments may be found in Appendices B–E.

Mesocosm experiments.—Survivorship and growth transition probabilities (P_i , G_{ij}) and breeding propensity (b_i) were estimated from experiments conducted at the Duke University Marine Laboratory (DURL), in which *P. longicarpus* were kept in outdoor flow-through seawater tanks. Tanks were randomly assigned to each of six treatments: control (O), hydroid (H), fish (F), fish + hydroid (FH), crab (C), and crab + hydroid (CH), according to the design in Appendix B: Table B1. In control tanks, all hermit crabs occupied bare shells. In tanks with hydroids (H, FH, CH), ~50% of the hermit crabs occupied hydroid-colonized shells, corresponding to the high end of hydroid frequency observed in the field. Tanks assigned to predator treatments each received one predator for 12 h, twice per week, with the predator being a burrfish (15–18 cm standard length) for treatments F and FH, and a blue crab (9–17 cm carapace width) for treatments C and CH. Pred-

ator treatments were not run in winter, because burrfish and blue crabs were absent from the local habitats occupied by hermit crabs in this season.

For each treatment, I counted the number of crabs in each size class $i = j = 1-3$, pooled over all replicate tanks in a given season, at the beginning (m_{ij}) and end (m_{ir}) of each experiment. At the end of the experiment, I also checked pleopods of each female for eggs or larvae, and used the fraction of ovigerous (i.e., bearing eggs or larvae) females in each size class as an estimator of b_r . Data on m_{ij} and m_{ir} were combined with q_j and t_j (see *Methods: Mortality and growth estimates*) to calculate m_{ij} according to the procedure described in Appendix D. Each m_{ij} was then divided by its respective m_{ir} to calculate 6-week P_i 's and G_{ij} 's.

Mortality and growth estimates.—Probabilities of mortality (q_j) and transition-to-size-3 (t_j) used to solve for m_{ij} were estimated from crabs in bare shells, and adjusted with scaling factors to fit the data for each treatment (see Appendix D). For the winter 1997 data set, q_j and t_j were estimated respectively as the fractions of marked size class j individuals in the winter 1996 mesocosm experiment that died or grew into class 3. Data to calculate q_j and t_j for late summer/fall were collected from a study in which I monitored hermit crabs kept in individual chambers (Appendix E). For spring/early summer, I assumed that hermit crabs experience vital rates similar to winter for half the season, and similar to late summer/fall for half the season. I therefore calculated spring/early summer q_j and t_j from the pooled data of the winter 1996 mesocosm and late summer/fall mortality and growth studies.

Fecundity laboratory experiment.—To estimate clutch success (γ) and clutch size (μ), I collected egg-bearing females in bare ($n = 12$ crabs) and hydroid-colonized ($n = 16$) shells from the field, and kept them in bowls of seawater until their eggs hatched (for a detailed description of this study, see Damiani 2003). Within each treatment, γ was the fraction of females whose eggs successfully hatched, and μ was the average number of larvae produced per successful clutch. Estimates of γ and μ from crabs in bare shells were used for O, F, and C matrices. Because hydroid treatment mesocosms contained 50% hydroid-colonized shells, γ and μ were averaged over crabs in bare and hydroid-colonized shells for the H, FH, and CH matrices.

Field census.—I was unable to determine sex of larvae by examining their morphology, so I used the fraction of females in field-collected samples of size class 1 hermit crabs to estimate the fraction of larvae that are female (p). In a series of field censuses (Damiani 2003), I collected 123 size 1 hermit crabs (6 in July 1996, 21 in November 1996, 5 in January 1997, 14 in March 1997, 13 in September 1997, and 64 in June 1998). Little information exists on developmental time for hermit crab larvae to reach size class 1, so I could not determine with certainty the seasons in which these

individuals were produced. I therefore pooled the class 1 individuals across all censuses, calculated the fraction of females in this pool, and applied this value of p to all seasons and treatments.

Estimating σ by assuming $\lambda_0 = 1.0$.—The last parameter needed to construct the matrices is juvenile survival to class 1 (σ). Maternal size did not correlate with larval size (Damiani 2003), a factor that probably influences larval survival. I therefore assumed that σ is independent of adult size. Larvae disperse rapidly from the mother, so I assumed that survival is independent of hydroids or predators near the adult and applied one value of σ to all sizes and treatments.

Because larvae are small and cryptic, I was unable to estimate empirically the survival of a cohort of larvae associated with a given mother. An alternative, used by Ebert (1999:153) to estimate survival of sea urchin larvae, and which I adopted, is to assume that the population is stable and vary σ in an annual matrix containing estimates of all other parameters until λ approximates 1.0. A matrix parameterized in this way cannot be used to forecast field population growth rates. However, the focus of this study was not to predict hermit crab dynamics in the field, but to examine the differences in λ 's from different treatments relative to a control, in order to quantify direct and indirect effects. I therefore assumed that λ for *Pagurus longicarpus* was ~ 1.0 for the control population, and used the associated value of σ to parameterize matrices for all treatments.

Estimating confidence intervals for direct, indirect, and net effects

Using estimates of P_i , G_{ij} , and F_i from the studies described previously, I constructed 54-week annual matrices and calculated λ 's for all treatments (Appendix C). I then calculated direct, indirect, and net effects using Eqs. 2–4. For each effect 90% and 95% confidence intervals were generated using a bootstrap procedure, which replicated the sampling scheme of the original study (Appendix F). These confidence intervals were generated using the percentile method and a bootstrap sample size of 3000, and were corrected for bias (Caswell 2001:307).

RESULTS

Annual matrices for each treatment (Appendix G) yielded the following population growth rates: $\lambda_0 = 1.010$, $\lambda_H = 0.767$, $\lambda_F = 0.267$, $\lambda_{FH} = 0.435$, $\lambda_C = 0.716$, and $\lambda_{CH} = 0.412$. Fig. 2 contains the estimated direct, indirect, and net effects and their bootstrapped confidence intervals. Although the confidence interval for direct effects encompassed both positive and negative effects, direct effects tended to be negative, on average reducing population growth by 28%. **Burrfish-mediated indirect effects of hydroids on hermit crabs were consistently positive and more than twice the magnitude of direct effects.** Thus, strong positive in-

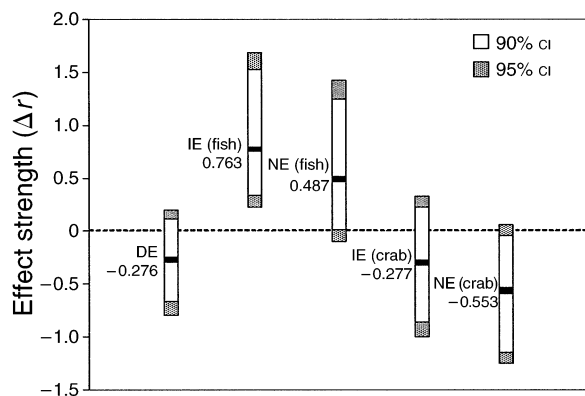


FIG. 2. Direct, indirect, and net effects of *Hydractinia symbiolongicarpus* on *Pagurus longicarpus*. Values indicated are baseline estimates (denoted by black bars) of direct (DE), indirect (IE), and net effects (NE), which are mediated by burrfish (fish) or blue crabs (crab). These estimates were calculated from the original data. White and shaded bars indicate bootstrapped, bias-corrected 90% and 95% confidence intervals, respectively.

direct effects tended to oppose direct effects, producing a net outcome that was generally positive, although its 95% confidence interval slightly overlapped zero.

When mediated by blue crabs, indirect effects ranged widely from positive to negative, but were, on average, equal in sign and magnitude to direct effects. They therefore tended to reinforce negative direct effects, resulting in a net outcome that was negative in >90% of the bootstrap replicates. All effects were associated with wide confidence intervals, making it difficult to determine whether they differed significantly from zero or each other.

DISCUSSION

The role of indirect effects in context-dependency

When analyzed using a projection matrix, **hydroids'** effects on hermit crab fecundity translated into **negative direct effects** on *P. longicarpus* population growth. Strength and sign of indirect effects varied with the species of predator mediating the effect. Burrfish attacked hermit crabs by crushing shells in their mouths. Upon contact with hydroids, they spit shells out, and quickly learned to avoid hydroid-colonized crabs by sight (*personal observation*). This aversion to *H. symbiolongicarpus* is consistent with results that, when mediated through burrfish, strong indirect effects opposed the direct costs of associating with hydroids. On the other hand, blue crabs used their claws to chip at the shell aperture until they could extract the hermit crab (*personal observation*), and this strategy made them less susceptible than burrfish to hydroid defenses. Accordingly, blue crab-mediated indirect effects were weaker and more likely to be negative than burrfish-mediated indirect effects. Consequently, when indirect effects combined with direct effects, the net interaction

tended to be more mutualistic in the presence of burrfish than in the presence of blue crabs.

Direct, indirect, and net effects in this study exhibited a high degree of variation in magnitude and sign. Studies that used the standard "inverse community matrix" approach to analyze press/pulse experiments (Yodzis 1988, Schmitz 1997) have also reported high levels of uncertainty in their results, suggesting that wide confidence intervals may be more common than not in studies of multispecies interactions. This variation may arise from two sources. First, the outcome of a net effect may be sensitive to values of its component parts, each of which might be naturally variable or difficult to measure (and therefore prone to error). For example, variation in blue crab-mediated indirect effects may be an artifact of variation in treatment strength. Hydroid-colonized shells are weaker and easier for blue crabs to crush (Buckley and Ebersole 1994), which should result in a negative effect. However, small blue crabs were more likely to extract hermit crabs with their mouthparts (*personal observation*), making them more susceptible than larger conspecifics to hydroid defenses. Thus, magnitude and sign of indirect effects may depend on size as well as species of predator. Since I used an assortment of crab sizes according to field availability, variation in treatment effect may have hindered my ability to determine the strength and sign of the indirect effect with finer precision.

A second source of variation lies in the biotic context in which the interaction(s) of interest are embedded. When communities are generated using Monte Carlo methods, each permutation yields a suite of direct and indirect effects that differs in composition and strength, resulting in a range of potential net effects. Similarly, we might expect the net outcome of a given interaction to vary among natural communities that differ in species composition. For example, in Florida, *P. longicarpus* experience predation pressure from burrfish and blue crabs, so we expect the net effect to incorporate negative direct effects, positive indirect effects mediated by fish, and weak indirect effects mediated by crabs, possibly resulting in a commensal relationship. In North Carolina burrfish are rare relative to blue crabs (*personal observation*), so strong positive indirect effects mediated by fish might drop out of the equation, resulting in a parasitic net interaction. Variation in the biotic context in which this symbiosis is embedded may result in variation in strength and sign of indirect effects, causing the qualitative net outcome of an interaction to shift over space and time. This mechanism likely underlies the "conditionality" or "context-dependency" of interactions that are observed to shift between mutualism and antagonism, according to changes in abundances of other species in the community (see Bronstein 2001).

A demographic approach for integrating direct and indirect effects

Methods that use inverse community matrices to identify and measure indirect effects may be inappropriate for TMIs for a couple of reasons. First, the assumption that direct effects will be detected faster than indirect effects does not necessarily hold true for TMIs (Abrams 1995, Werner and Peacor 2003). For the hermit crab–hydroid symbiosis, direct effects on reproduction take a generation to be expressed at the population level, while indirect effects on survival appear more quickly. Thus, in this system, it would be difficult to distinguish direct and indirect effects from analysis of press/pulse experiments.

Second, mechanistic studies on an organism's entire life cycle may be required to capture effects that act on traits. However, for some species it may not be possible to capture effects on an entire life cycle in a single experiment. For species with long generation times, press experiments may need to be applied on the order of decades before the system reaches equilibrium. For species with cyclic or chaotic dynamics, the system might not reach equilibrium at all (McPeck and Peckarsky 1998). In addition, different life stages of some species may be dispersed among different habitats or geographic locations. For example, hermit crabs have planktonic larvae, which drift for weeks in tidal currents and may settle out in different locations from the adults. In my study, analysis of the mesocosm experiments alone would not have captured direct effects on reproduction, which were an important factor in this system. I thus required multiple studies to capture direct and indirect effects on the entire life cycle of the hermit crab. In such cases, the projection matrix may provide a useful framework for integrating data from different experiments.

When indirect effects are trait-mediated and multiple experiments are required to capture all effects of interest, direct and indirect effects might be measured in different biological currencies that are not directly comparable. Because projection matrices integrate survival, growth, and fecundity into a single measure, a demographic approach allows us to translate direct and indirect effects on different demographic rates into a common metric that directly assesses the impact of those effects at a population level (McPeck and Peckarsky 1998).

Admittedly, the matrix method is not a perfect solution. Parameterizing the model requires collection of large amounts of data, and predictions are associated with high levels of uncertainty, perhaps reflecting compounded sensitivity to variation in model parameters. Despite these limitations, the matrix approach provides an alternative method for measuring direct and indirect effects in conditions that standard methods are not equipped to deal with, and is worth developing and improving with future studies.

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APPENDIX A

An overview of the population projection matrix for one treatment and sources of data used to estimate matrix parameters are available in ESA's Electronic Data Archive: *Ecological Archives* E086-108-A1.

APPENDIX B

Additional details on the methods for the mesocosm experiment are available in ESA's Electronic Data Archive: *Ecological Archives* E086-108-A2.

APPENDIX C

Additional details on the methods for construction of annual matrices and estimation of σ are available in ESA's Electronic Data Archive: *Ecological Archives* E086-108-A3.

APPENDIX D

Details on the calculation of m_{ij} are available in ESA's Electronic Data Archive: *Ecological Archives* E086-108-A4.

APPENDIX E

Additional details on the methods for the late summer/fall mortality and growth study are available in ESA's Electronic Data Archive: *Ecological Archives* E086-108-A5.

APPENDIX F

Additional details on the methods for the bootstrap are available in ESA's Electronic Data Archive: *Ecological Archives* E086-108-A6.

APPENDIX G

Baseline annual projection matrices constructed from the original data set are available in ESA's Electronic Data Archive: *Ecological Archives* E086-108-A7.