

## LIFE HISTORIES AND THE STRENGTHS OF SPECIES INTERACTIONS: COMBINING MORTALITY, GROWTH, AND FECUNDITY EFFECTS

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**Abstract.** Interactive effects of one species on another may simultaneously influence mortality, growth, and fecundity. To quantify the strength of an interaction between two species, we must therefore use techniques that integrate these various responses into estimates of overall effect. Demographic models of populations provide such a framework. Here we develop a demographic model describing the life history of a hemimetabolous insect to evaluate the relative importance of predator effects on mortality and growth of damselflies (*Enallagma boreale*) in fishless ponds and mayflies (*Baetis bicaudatus*) in trout streams.

Previous experiments have shown that dragonfly predators in fishless ponds inflict direct mortality and cause reduced growth rates in *Enallagma* damselflies. Parameterization of the demographic model from these data show, however, that only the direct mortality effects of dragonflies should significantly influence damselfly population dynamics. This is because damselfly size at emergence does not influence adult female fecundity, so the effects of dragonflies on damselfly larval growth do not influence adult fecundity. Likewise, both trout and stonefly predators inflict mortality on larval *Baetis* mayflies and cause decreases in growth rates. However, our demographic analyses indicate that the growth effects of both predators should dominate the population-dynamic effects on *Baetis*. This is because size at emergence translates directly into adult fecundity in mayflies. We also present data suggesting that developmental responses to changes in environmental conditions (e.g., predator abundances, resource availabilities) differ between species depending on these same life history parameters.

The biological significance of lethal vs. sublethal predator impacts must be evaluated in a demographic framework to identify whether alterations in growth rate, and the timing of and size at metamorphosis, significantly influence population dynamics. The demographic model used for any particular organism must be tailored to its life history, but the various impacts of interactions with other species can all be integrated into estimates of projected population growth that can then be readily compared among species with different life histories.

**Key words:** damselflies; demographic model; *Engallagma*; interaction strength; *Ischnura*; life history; mayflies; population growth; predator impacts; size at metamorphosis; species interactions; timing of emergence.

### INTRODUCTION

A prime objective of ecology is to quantify how the population dynamics of one species is shaped by interactions with the physical environment and with other species. A necessary component of this endeavor is to quantify the strengths of these interactions. Ecologists have attempted to measure the strengths of interactions among species in a variety of ways, including estimating parameters for generalized models of interactions (e.g., Neill 1974, Bender et al. 1984, Billick and Case 1994) and comparing changes in abundance under various experimental conditions (e.g., Paine 1992).

Although these methods have provided the basis for much stimulating theoretical and empirical research,

they have a number of shortcomings. Methods attempting to estimate parameters for generalized models (e.g., models of the Lotka-Volterra type) do not capture mechanistic features of interactions, which makes the association of parameter estimates to real biological processes difficult (Bender et al. 1984, Yodzis 1989, Billick and Case 1994). Also, because the system must be allowed to reach an equilibrium, application of methods comparing changes in abundance may be impractical (e.g., generation times of organisms may be too long) or impossible (e.g., systems may display random fluctuations, limit cycles, chaos, or truly lack an equilibrium). Finally, species interactions may simultaneously influence survival, growth, and reproduction. Evaluating the relative contributions of these demographic effects to a determination of overall population dynamics is difficult, because they are all measured in

different currencies. A common framework is needed that integrates mortality, growth, and fecundity responses to species interactions, permits mechanistic interpretations of results, and can be applied to short-term as well as long-term studies.

The demography of a population embedded in an ecosystem provides such a theoretical framework. Interactions with the abiotic environment and other species determine the demographic rates (i.e., mortality, growth, and fecundity) of a species. Demographic models integrate these various demographic rates to generate a projection of population dynamics based on current ecological conditions (Caswell 1989a). The effect of eliminating an interaction with another species can be quantified in field experiments (e.g., the measurement the demographic rates of a prey species in the presence and absence of its predator). Comparisons of projected population growth rates in demographic models as a consequence of the manipulation of other species can then be used directly as metrics quantifying the strengths of interactions (see Weinberg et al. 1986, Caswell 1989a, b, and Osenberg and Mittelbach 1996 for related approaches). Also, by using population-growth rate as an estimate of fitness, demographic models provide a direct means to evaluate the consequences of behavioral or developmental plasticity expressed by organisms in response to other species in the community (e.g., foraging rate–predation risk trade-offs [Lima and Dill 1990, Werner and Anholt 1993]). Such methods may also be applied to predict optimal life histories for organisms within certain environmental conditions (Werner and Gilliam 1984, Ludwig and Rowe 1990, Rowe and Ludwig 1991, Abrams and Rowe 1996). Demographic models can therefore provide a common framework for studies of community structure, behavioral and developmental plasticity, and life history evolution.

We have developed a demographic model describing the life history of a hemimetabolous insect, in order to evaluate the relative importance of predator effects on mortality and growth in populations of two prey species: damselflies and mayflies. This model is tailored to the life histories of the organisms considered (i.e., damselflies and mayflies). Similar demographic approaches have been developed for analyzing experimental results in aquatic insects (e.g., Livdahl 1982, Livdahl and Sugihara 1984) and general experimental procedures (Caswell 1989b). The demographic model presented here is a specific example of a more general class of models that have been considered theoretically elsewhere (e.g., Ludwig and Rowe 1990, Abrams 1991, Abrams et al. 1996, Abrams and Rowe 1996). We parameterize this demographic model from the results of our recent field studies of predator effects on damselfly and mayfly populations (McPeck 1990a, 1997, 1998, Peckarsky et al. 1993, Peckarsky and McIntosh 1998). Consistent with previous theoretical predictions, our demographic analysis of data from field experiments

and observations show that similar predator effects on growth and mortality rates can have profoundly different effects on projected population-growth rates depending on species-specific life history parameters. Also, we present data suggesting that developmental responses to changes in environmental conditions (e.g., predator or resource abundances) may also differ between species depending on these same life history parameters.

#### DEMOGRAPHIC MODEL OF A COMPLEX LIFE CYCLE

We first construct a demographic model that incorporates larval growth and survival rates based on the life cycle of a hemimetabolous aquatic insect. For this analysis we assume that all individuals in the population develop synchronously as a cohort (i.e., only one age or stage class is present in the population at any given time) and generations are non-overlapping. This model only strictly applies to the number of females, as the number of eggs laid to begin each generation depends critically on the number and size of adult females in the previous generation. We define the life cycle to begin when eggs are laid, and the model projects the number of eggs in the next generation. Defining  $E(t)$  as the number of eggs at time  $t$ , and  $\lambda$  as the geometric growth rate of the population, the change in the number of eggs between generations is

$$E(t + 1) = \lambda E(t). \quad (1)$$

Our goal is to define a function that describes  $\lambda$  as a function of various ecological conditions.

We define a function for  $\lambda$  by stepping through the life cycle. First, some number of eggs,  $E(t)$ , are laid;  $E(t)$  strictly represents only eggs containing females. Some fraction,  $h$ , of the eggs hatch into first instar larvae ( $hE(t)$ ). Assuming a constant mortality rate for the larvae over the larval period, which seems to be true for many aquatic insects if ecological conditions are held constant (e.g., Lawton 1970, Kerans et al. 1995), the number of adult females,  $A(t + \gamma)$ , that will be produced from  $E(t)$  eggs is

$$A(t + \gamma) = e^{-mD} h E(t) \quad (2)$$

where  $m$  is the larval mortality rate (per day),  $D$  is the duration of the larval phase of the life cycle (in days), and  $\gamma$  is the fraction of the generation time spent as a larva.

Each adult female contributes some number of eggs to start the next generation. The number of eggs that a female lays may depend on her size as an adult, which in turn often depends on her size at metamorphosis to the adult stage (Clifford 1970, Benech 1972, Elliott and Humpesch 1980, Brittain 1982, deMoor 1982, Rosillan 1988, Briegel 1990, Peckarsky et al. 1993, Scrimgeour and Culp 1994). For simplicity of the analysis, we assume that size at metamorphosis does not influence any other adult performance measure (e.g., adult survival), and this assumption seems justified for the

species we consider (see *Evaluating predator-induced mortality and growth effects*). We define the function translating female size into fecundity to be  $f(S)$ . Using mean size to describe the size in the entire population, the number of eggs laid to begin generation  $t + 1$  is then the number of adult females in generation  $t$  multiplied by the function translating size of adult females into eggs:

$$E(t + 1) = f(S)A(t + \gamma) = f(S)e^{-mD}hE(t). \quad (3)$$

The average size,  $S$ , of adults is the initial larval size,  $I$ , multiplied by the mass-specific growth function over the larval period. The form of this function is not well developed for insects. For now, assume that increase in mass is exponential according to

$$S = Ie^{gD} \quad (4)$$

where  $g$  is the mass-specific growth rate. Assuming a geometric relationship between size and the number of eggs produced gives

$$f(S) = \alpha S^\beta \quad (5)$$

where  $\alpha$  and  $\beta$  are scaling constants. Substituting Eq. 4 into Eq. 5 gives

$$f(S) = \alpha(Ie^{gD})^\beta = \alpha I^\beta e^{g\beta D}.$$

Substituting this into Eq. 3 gives

$$E(t + 1) = \alpha I^\beta e^{g\beta D} e^{-mD} h E(t) = \alpha I^\beta e^{(g\beta - m)D} h E(t). \quad (6)$$

For simplicity and because we lack adequate data, we ignore any effects of the timing of metamorphosis (cf. Ludwig and Rowe 1990). From Eq. 6,

$$\lambda = \alpha h I^\beta e^{(g\beta - m)D}. \quad (7)$$

We now have a demographic function describing  $\lambda$  based on mortality and growth rates, duration of the larval phase, and the scaling of final size to fecundity. Eq. 7 can be used to evaluate the demographic consequences of manipulating ecological agents that influence these parameters.

#### EVALUATING PREDATOR-INDUCED MORTALITY AND GROWTH EFFECTS

In addition to inflicting direct mortality on prey, predators often also reduce the feeding rates of their prey. Consequently, the presence of predators often reduces both survival and growth of their prey (McPeck 1990a, 1997, 1998, Peckarsky et al. 1993). Evaluating the relative importance of mortality and growth effects in prey populations is difficult because they are measured in different currencies. The above demographic model enables us, however, to evaluate mortality and growth effects of predators simultaneously. In this section, we analyze the demographic contributions of mortality and growth inflicted by predators on two aquatic insects, *Enallagma* damselflies (Odonata: Coenagrionidae) in fishless lakes, and *Baetis* mayflies (Ephemeroptera: Baetidae) in trout streams.

#### *Damselflies fed upon by dragonflies*

In ponds and lakes that do not support fish populations in eastern North America, large dragonflies (e.g., *Anax*, *Aeshna*, and *Tramea* species) are the primary predators of coexisting damselflies (McPeck 1990a, 1998). For larvae of *Enallagma* damselflies inhabiting these ponds and lakes, dragonfly predation can account for >75% of total larval mortality (McPeck 1990a, 1997, 1998). Also, larval growth rates are reduced in the presence of dragonflies because of reduced feeding (McPeck 1990a, b, 1998). Here we parameterize Eq. 7 using the results of field experiments and literature values to evaluate the relative contributions of mortality and growth effects of dragonfly predators on the damselfly, *Enallagma boreale*.

To evaluate the effects of dragonfly predators, we first must parameterize the model for a natural *E. boreale* population. We use 123 d as an estimate of the duration of the larval phase under ambient conditions. Based on our natural history experience in southwestern Michigan, where the experimental work was performed, we calculate this as follows. First instar larvae appear around 15 August. We consider the period 15 August–31 October to be the fall active period for larvae. By the end of October when water temperatures cool considerably, larvae begin to become inactive for winter (damselflies and dragonflies). Little is known about occurrences during this winter inactive period; we assume here that no mortality or growth occurs during this time. In the spring, larvae resume activity around the middle of April, and continue to grow until they emerge at the beginning of June. We consider the period 15 April–30 May to be the spring active period for larvae. Combining these two active periods into the total amount of time larvae are growing and being killed by predators gives 123 d as the effective larval duration. Larval mortality rates in natural populations are 0.027 d<sup>-1</sup> (McPeck 1990a). Nearly identical mortality rates are obtained in field experiments when actively foraging *Anax junius* dragonfly larvae are placed in cages with *E. boreale* (0.026 d<sup>-1</sup>) (McPeck 1990a, 1997, 1998). We will use this experimentally derived mortality rate (0.026 d<sup>-1</sup>) in our analysis.

Previous studies suggest that size at emergence may have little effect on adult female fecundity or longevity in coenagrionid damselflies, and that adult feeding probably primarily determines adult reproductive success (Anholt et al. 1991, Anholt 1992, Richardson and Baker 1997). For example, Richardson and Baker (1997) found that, in the laboratory, *Ischnura verticalis* female size at emergence was unrelated to fecundity, but instead fecundity was strongly positively related to feeding rate. Also, Anholt (1991) found that adult survival of *E. boreale* females in the wild was not related to size at emergence in one year, and in another year the relationship between survival and size at emergence had a slight negative relationship (Anholt 1991: Fig.

TABLE 1. Estimated demographic effects of *Anax* dragonfly predation on *Enallagma boreale* damselfly populations.

Estimate	Larval mortality (d <sup>-1</sup> )	Larval duration (d)	$\lambda$	% change in $\lambda$ †
Natural population	0.0260	123	0.909	...
Growth effects removed	0.0260	115	1.119	23.1
Mortality effect removed	0.0060	123	10.637	1070.5
Mortality and growth effect removed	0.0060	115	11.160	1128.1

Note: All analyses use 22.25 female eggs/female as adult fecundity and 1.0 for hatching success; other parameters are as given in the table body.

† The percentage change in  $\lambda$  as compared to the value for the natural population.

3). In contrast, Banks and Thompson (1987) found a negative relationship between clutch size and female size and a positive relationship between female size and the number of clutches produced over a lifetime for the European conenagrionid, *Coenagrion puella*. We will assume here that size at emergence does not influence female fecundity or adult survival following Anholt's (1991) results for *E. boreale*. Therefore, the only effects of variation in larval growth should be manifested through effects on larval duration. Fecundity of *E. boreale* females has not been quantified; for this analysis we will use the average value of 44.5 eggs/female obtained by Fincke (1986, 1988) for *E. hageni*. Assuming that the sex ratio of larvae is 1:1 (Fincke 1986), this provides an estimate for the number of female eggs produced per female of 22.25 (i.e.,  $f(S) = 22.25$  in all analyses). We also assume for this analysis that all eggs hatch into first instars (i.e.,  $h = 1.0$ ). These assumptions do not affect our main qualitative conclusions, since  $\lambda$  is a simple multiple of  $h$  and  $f(S)$  in this case (see Eq. 7).

Substituting these parameters into Eq. 7 yields an estimate of  $\lambda = 0.909$  (Table 1). Our goal here is not to evaluate whether this population is at or near a steady state (see, e.g., Crowley and Johnson 1992). Instead, our goal is to determine the projected outcome of removing the various effects of dragonfly predation on *Enallagma* population-growth rate.

We can evaluate the relative mortality and growth effects of dragonfly predators by altering the mortality rate and larval duration according to estimates from field experiments and studying the consequences of those alterations in demographic parameters on  $\lambda$ . We will use the results of a field experiment performed in the fall of 1995 to derive estimates of changes in mortality rate and larval duration when dragonflies are removed (McPeck 1997, 1998). When dragonflies were free to forage in cages, damselfly larval mortality rates averaged 0.026 d<sup>-1</sup>, and the head widths of larvae increased at an average rate of 0.0103 d<sup>-1</sup> (assuming exponential increase in size). Increase in head width is

an indicator of the rate at which larvae progress through instars, and thereby is an indicator of larval duration (Lawton et al. 1980). When dragonflies were absent from cages, mortality rates averaged 0.006 d<sup>-1</sup> and head widths of larvae increased on average by 0.0110 d<sup>-1</sup>; the differences in mortality and growth rates between treatments were both statistically significant at the  $\alpha = 0.05$  level (McPeck 1997, 1998). From these data we estimate that damselfly mortality rates should decrease by 77% (i.e., decrease from 0.026 to 0.006 d<sup>-1</sup>), and that larval duration should decrease by 7% in the absence of predators (i.e., decrease from 123 days to 115 days), assuming that larvae grow to a fixed size at emergence. Because size at emergence does not influence adult fecundity, this assumption has minimal effects on our results. Note that the change in growth rate between the predator and no-predator treatments reflects changes in behavioral responses to both predator and damselfly densities.

If both mortality rate and larval duration are altered to their values estimated in the absence of dragonfly predators,  $\lambda$  increases by more than an order of magnitude (Table 1). The separate contributions of mortality and growth in determining  $\lambda$  can be evaluated by altering each in turn. When this is done, it is clear that the projected increase in  $\lambda$  is caused predominantly by the decrease in mortality rate (Table 1). Decreasing larval duration only (which simulates removing predator effects on growth while maintaining predator-inflicted mortality rates) results in only a slight increase in  $\lambda$ , because larvae would be exposed to predators for slightly less time. However, decreasing larval mortality rate only, which simulates removing the predator mortality effect while maintaining the sublethal predator effects on growth, results in a substantial increase in  $\lambda$ . This analysis indicates that dragonfly predation should influence *E. boreale* abundances primarily through inflicting mortality on larvae.

#### *Mayflies fed upon by trout and stoneflies*

*Baetis* mayfly populations in trout streams simultaneously face two predators: trout and stoneflies. Each of these predators inflicts mortality on *Baetis* populations; their presences result in smaller emerging larvae, and the presence of stoneflies causes *Baetis* to lengthen the larval period (Peckarsky et al. 1993, Kerans et al. 1995, Peckarsky and McIntosh 1998). We use data on *Baetis bicaudatus* from natural populations and experiments to examine the effects on mortality and growth imposed by these two predators in populations at the Rocky Mountain Biological Laboratory (RMBL), Crested Butte, Colorado, USA.

As baseline population parameters we use data from the summer generation of a bivoltine population of *B. bicaudatus* in the East River at RMBL in 1990 (Kerans et al. 1995). Based on data from this cohort, we used 42 d as the ambient duration of the larval period and 0.0378 d<sup>-1</sup> as the natural mortality rate of larvae (Ker-

TABLE 2. Estimated demographic effects of trout and stonefly predation on *Baetis bicaudatus* mayfly populations.

Estimate	Larval mortality rate (d <sup>-1</sup> )	Larval final mass (mg)	Larval duration (d)	$\lambda$	% change in $\lambda$ †
Natural population	0.0378	0.2448	42	1.993	...
Stonefly effects					
Growth effects removed	0.0378	0.3665	39	4.776	139.7
Mortality effect removed	0.0355	0.2448	42	2.195	10.1
Mortality and growth effects removed	0.0355	0.3665	39	5.224	162.2
Trout effects					
Growth effects removed	0.0378	0.3665	42	4.264	114.0
Mortality effect removed	0.0300	0.2448	42	2.765	38.8
Mortality and growth effects removed	0.0300	0.3665	42	5.916	197.0
Combined stonefly and trout effects					
Growth effects removed	0.0378	0.3665	39	4.776	139.7
Mortality effect removed	0.0277	0.2448	42	3.045	52.8
Mortality and growth effects removed	0.0277	0.3665	39	7.081	255.4

Note: All analyses assume a hatching success of eggs equal to 0.67, larval duration of 42 d, and a power-functional relationship between the number of eggs produced by a female that will develop into a female and the size of BWP stage larvae: (number of female eggs) =  $206.5 \times (\text{BWP larval mass})^{1.89}$ .

† The percentage change in  $\lambda$  as compared to the value for the natural population.

ans et al. 1995). Size at emergence in *Baetis* is strongly related to the fecundity of adult females (Peckarsky et al. 1993). Size at emergence is estimated as the dry mass of black wing-pad stage larvae (BWP larvae). The BWP stage is a 24-h non-feeding larval stage immediately preceding metamorphosis into adults. The relationship between size at emergence and adult fecundity for this population is estimated to be (number of female eggs) =  $413.0 \times (\text{BWP larval mass})^{1.89}$  (data from Peckarsky et al. 1993). Assuming a 1:1 sex ratio, the relationship for the number of eggs that will develop into females is then (number of female eggs) =  $206.5 \times (\text{BWP larval mass})^{1.89}$ . The average mass of BWP female larvae in the baseline cohort (0.2448 mg) was used as our baseline estimate of size in the fecundity relationship. Field data indicate that 67% of oviposited eggs hatch (i.e.,  $h = 0.67$ ; B. L. Peckarsky, unpublished data).

Substituting these parameters into the resulting equation provides an estimate of  $\lambda = 1.993$  for this population in this year (Table 2).

We estimated the mortality and growth effects of *Megarcys stignata* stoneflies and brook trout (*Salvelinus fontinalis*) from experiments done in artificial streams and from observations in natural streams at RMBL (Peckarsky et al. 1993, Peckarsky and McIntosh 1998). Mortality rate due to *Megarcys* predation was estimated to be  $0.0023 \text{ d}^{-1}$  in experiments performed in 1991, 1995, and 1996 in artificial streams of two sizes (small streams are described by Peckarsky and Cowan [1991] and large streams by McIntosh and Peckarsky [1996]). Therefore, for analysis we estimate that removing mortality due to *Megarcys* predation will reduce the overall mortality rate from  $0.0378$  to  $0.0355 \text{ d}^{-1}$  (larval mortality rate [ $\text{d}^{-1}$ ] =  $0.0378 - 0.0023$ , as seen in Table 2).

No reliable estimate of *Baetis* mortality due to trout predation from comparable experiments is available. Therefore we indirectly estimated *Baetis* mortality rates from behavioral experiments on the frequency of drifting events and the probability of capture during drifting by trout. Previous studies suggest that *Baetis* mortality due to trout predation occurs primarily when *Baetis* larvae leave the substrate and drift in the water column (Allan 1978, 1981, Wilzbach 1986, Forrester 1994). From behavior experiments, we estimate that an individual *Baetis* will drift on average 4.00 times a night (assuming 10 h of darkness) and 0.28 times during daylight hours (assuming 14 h of daylight) (B. L. Peckarsky and A. R. McIntosh, unpublished manuscript). From estimates of drift distance (P. R. Ode, unpublished data), trout density and the reaction field size of trout (A. R. McIntosh, B. W. Taylor, and B. L. Peckarsky, unpublished data), we estimate that the probability of a *Baetis* encountering a trout during a drift event is 0.0357. Finally, from flume feeding trials with trout using infrared videorecording, we know that trout capture 0.425 drifting *Baetis* per encounter during the day and 0.025 drifting *Baetis* per encounter during the night (A. R. McIntosh, B. W. Taylor, and B. L. Peckarsky, unpublished data). From these estimates we arrive at an estimate of the daily probability that an individual *Baetis* will die due to trout predation as  $0.0078$  (i.e.,  $[4.00 \times 0.0357 \times 0.025] + [0.28 \times 0.0357 \times 0.425]$ ). The probability that the individual will survive a day is therefore 0.9922, and the overall mortality rate due to trout predation in the population is  $-\ln(0.9922) = 0.0078$ , since  $N(t+1) = N(t) \exp(-m)$ , where  $\exp(-m)$  is the probability that each individual survives each day. This estimate is within the bounds of *Baetis* mortality due to trout predation estimated in other studies (Forrester 1994), and agrees closely with comparisons

of *Megarcys* and brook trout predation made by Allan (1983). Therefore, for analysis, we estimate that removing mortality due to trout predation will reduce the overall mortality rate from 0.0378 to 0.0300 d<sup>-1</sup> (Table 2).

Because mortality rates inflicted by trout and stoneflies are estimated from different sources, and we have no information about how they interact, we will assume here that the mortality rates inflicted by the two predators are additive. Removing mortality by both predators is then estimated to change mortality rate from 0.0378 d<sup>-1</sup> to 0.0277 d<sup>-1</sup> (larval mortality rate [d<sup>-1</sup>] = 0.0378 - 0.0023 - 0.0078, as seen in Table 2).

The effects of stoneflies and trout on *Baetis* size and timing of emergence were quantified in experiments done in large circular streams (Peckarsky and McIntosh 1998). The presence of trout was simulated by dripping water into cattle tanks from another tank housing trout, so that effects on *Baetis* growth could be measured in the absence of predator-inflicted mortality. The presence of stoneflies was simulated by gluing the mouthparts of live stoneflies; these stoneflies continued to forage and to encounter *Baetis* with their natural periodicity (Peckarsky et al. 1993, Peckarsky 1996). In this experiment, the presence of (1) stoneflies, (2) trout, or (3) both predators all depressed the size (dry mass) of BWP larvae by the same amount. From this experiment we conclude that both predators depress *Baetis* size at emergence to the same degree and the combined effect of both is equivalent to the separate effects of either. From the results of this experiment, we estimate size at emergence will increase by 49.7% if the effects of either or both predators are removed.

The presence of only trout had no effect on the timing of emergence (i.e., trout removal is assumed to not affect larval duration), but the presence of stoneflies or both stoneflies and trout increased the time to emergence in this same experiment (Peckarsky and McIntosh 1998). From these results, we estimate that removing the stoneflies will decrease larval duration by 7.7%. The values presented in Table 2 represent how these experimental responses would affect the demographic parameters of the baseline population. Note that these growth effects of the two predators are not additive (Peckarsky and McIntosh 1998).

Again we will evaluate the relative effects on growth and mortality for the two predators by altering each effect in turn. First consider the responses to altering only stonefly effects while leaving trout effects unchanged. Removing all effects of stonefly predators is projected to increase  $\lambda$  for the *Baetis* population by a factor > 2.5 (Table 2). The separate contributions of mortality and growth indicate that this increase in population growth rate would result primarily from the relaxation of effects on *Baetis* growth rate and not from the removal of mortality effects (Table 2). Likewise, the growth effect of the presence of trout is projected to have a substantially larger impact on *Baetis* popu-

lation growth rates than the direct mortality effects (Table 2). Trout are projected to have a larger effect on mortality than stoneflies, resulting from the higher mortality rate estimate, but stoneflies are projected to have a larger effect through growth because they induce both smaller size at emergence and longer time to emergence, whereas trout only affect size at emergence. The combined effect of removing both predators is similar to the individual effect of each (Table 2). Unlike dragonfly predation on *Enallagma* damselflies, trout and stonefly predation are projected to have their greatest impacts on *Baetis* mayfly population dynamics via their effects on altering growth rates and not via inflicting direct mortality.

#### LIFE HISTORY STRATEGIES AND STRENGTHS OF INTERACTIONS

Altering the strengths of interactions influencing mortality rate, growth rate, and duration of the larval period should also influence the developmental and behavioral choices that individuals make (Werner and Gilliam 1984, Werner 1986, Lima and Dill 1990, Ludwig and Rowe 1990, Werner and Anholt 1993, 1996, Ball and Baker 1996). If we use population-growth rate (i.e.,  $\lambda$ ) as an estimate of fitness, we can use the above demographic framework to explore how fitness will be altered in organisms showing behavioral and life history responses to other species in the community (e.g., predators) that change these three demographic parameters. Here, we do not directly incorporate functions relating behavioral and life history phenotypes to demographic parameters (see e.g., Ludwig and Rowe 1990, Werner and Anholt 1993). Rather, we simply consider how changes in the demographic parameters affect  $\lambda$  and qualitatively relate these changes to behavioral and life history decisions that organisms could make (see Ludwig and Rowe 1990, Rowe and Ludwig 1991). To do this, differentiate Eq. 7 with respect to mortality rate, growth rate, and duration of the larval period, in turn:

$$\frac{\partial \lambda}{\partial m} = -\alpha h I^{\beta} D e^{(g\beta - m)D} \quad (8a)$$

$$\frac{\partial \lambda}{\partial g} = \alpha h I^{\beta} \beta D e^{(g\beta - m)D} \quad (8b)$$

$$\frac{\partial \lambda}{\partial D} = \alpha h I^{\beta} (g\beta - m) e^{(g\beta - m)D} \quad (8c)$$

From Eq. 8a, we obtain the intuitively obvious result that decreasing mortality rate always leads to an increase in fitness (i.e.,  $\partial \lambda / \partial m < 0$  for all possible parameter values with  $\lambda > 0$ ).

However, altering the mass-specific growth rate and the duration of the larval period can have variable effects on fitness depending on the exact parameter values. To complement the results for altering interaction strengths presented in the previous section, we will

only consider here the effects of altering  $\beta$ , the parameter scaling size at emergence with fecundity, on fitness. First, consider an organism for which size at metamorphosis influences adult fecundity (i.e.,  $\beta > 0$ ). For such an organism (e.g., mayflies), increasing growth rate always increases fitness: from Eq. 8b,  $\partial\lambda/\partial g > 0$  for all possible parameter values with  $\lambda > 0$ . However, altering the duration of the larval phase can either increase or decrease fitness depending on  $m$ ,  $g$ , and  $\beta$ . With  $m > g\beta$ , fitness is increased by decreasing larval duration (see Eq. 8c); in words, the survival benefit of being exposed to larval mortality agents (like predators) for less time outweighs the fecundity cost of emerging at a smaller size. In contrast, when  $g\beta > m$ , fitness is increased by increasing larval duration (see Eq. 8c); in words, the fecundity benefit of emerging at a larger size outweighs the survival cost of being exposed to mortality agents for more time. For a species that can modulate these parameters through behavioral or developmental plasticity, these calculations imply that the optimal timing of and size at metamorphosis is a complex function of these three parameters and the underlying ecological functions determining their values. The timing of and size at metamorphosis should thus vary according to the environmental conditions larvae experience (see also Abrams and Rowe 1996, Abrams 1991, Abrams et al. 1996).

Now consider an organism for which size at metamorphosis does not influence adult fecundity (i.e.,  $\beta = 0$ ). For this type of organism (e.g., damselflies), altering the mass-specific growth rate has no effect on fitness (i.e., from Eq. 8b,  $\partial\lambda/\partial g = 0$ ), and fitness is always increased by decreasing larval duration (i.e., from Eq. 8c,  $\partial\lambda/\partial D < 0$  for all possible parameter values with  $\lambda > 0$ ). One prediction that follows from this is that if size at metamorphosis does not influence adult performance (i.e.,  $\beta = 0$ ), individuals should always metamorphose at the minimum size that is developmentally possible. No advantages accrue to an individual that grows larger than the minimum size required for metamorphosis, and it will be exposed to larval mortality agents for longer than necessary (see also Blakley 1981, Werner and Gilliam 1984, Anholt et al. 1991, Twombly 1996).

The above analysis predicts that because size at emergence does not influence damselfly adult fecundity (i.e.,  $\beta \approx 0$ ), damselfly populations experiencing different ecological conditions should display similar sizes at emergence. In contrast, size at emergence in mayfly populations are predicted to vary substantially among populations experiencing different ecological conditions, because size at emergence influences adult mayfly fecundity (i.e.,  $\beta > 0$ ). As a first test of these predictions, we compared the sizes at emergence (head capsule widths and dry masses) across populations and through time for two damselfly species and for *Baetis bicaudatus* mayflies.

For damselflies we compared sizes of final instars

collected in the week before populations emerged from ponds and lakes. *Enallagma boreale*, the species considered in *Evaluating predator-induced mortality and growth effects*, were collected from two fishless ponds near the Kellogg Biological Station in Michigan in 1987 and two fishless ponds in Vermont in 1996. *Ischnura verticalis* larvae, a species common to both fish and fishless lakes (Johnson and Crowley 1980, McPeck 1990a, 1998), were collected from both fish and fishless water bodies in Michigan in 1987 and in Vermont and New Hampshire in 1996. We expect that ecological conditions varied among these populations collected in different years and in different geographic regions, especially for *I. verticalis* populations in fish and fishless water bodies (McPeck 1990a, 1998).

We compared black wing-pad larvae of *Baetis bicaudatus* from the East River at the Rocky Mountain Biological Laboratory in Colorado in 1990, 1994, and 1995. *Baetis* is bivoltine in this river, having summer and winter generations. We included BWP larvae from both generations over multiple years in our comparisons. Males and females were analyzed separately for *Baetis*, as the sexes differ intrinsically in size. Water temperatures, resource levels, and predation intensities differed between years and especially between summer and winter generations (B. L. Peckarsky, unpublished data).

The sizes of final-instar larvae of *E. boreale* differed among the four populations (multivariate analysis of variance [MANOVA] including head width and dry mass as response variables,  $F$  approximation of Wilks' lambda,  $F_{6,68} = 3.91$ ,  $P < 0.001$ ; Table 3). However, when the variation in these measures were partitioned into separate components, only 9.7% of the variation in head width and 17.6% of the variation in dry mass was attributable to differences among *E. boreale* populations; the rest was attributable to within-population variation. *I. verticalis* populations also differed significantly in final-instar size (MANOVA  $F_{14,140} = 3.41$ ,  $P < 0.0001$ ; Table 3), but populations in fish vs. fishless water bodies did not consistently differ in size (MANOVA with populations nested within habitats,  $F_{2,2} = 0.11$ ,  $P > 0.89$ ). As with *E. boreale*, only a small proportion of the variation in these variables was attributable to differences among *I. verticalis* populations (head width, 32.1%; dry mass, 6.9%). This was also evident in the fact that the coefficients of variation (CV) calculated for the pooled data on a species were not outside the range of the CV's for the individual populations (Table 3).

In contrast to the damselflies, head widths and dry masses varied substantially among years and generations in the same population of *Baetis bicaudatus* mayflies (males and females were analyzed separately for *Baetis* because the sexes differ greatly in size at the BWP stage: MANOVA females— $F_{8,200} = 50.64$ ,  $P < 0.0001$ ; males— $F_{8,140} = 58.96$ ,  $P < 0.0001$ ; Table 3). For females, head width and dry mass differed signif-

TABLE 3. Head widths and dry masses for (A) two species of damselflies and (B) one species of mayfly across multiple populations and years.

Species	Population	Year	N	Head width (mm)		Dry mass (mg)		
				Mean $\pm$ 1 SD	CV	Mean $\pm$ 1 SD	CV	
A) Damselflies								
<i>Enallagma boreale</i>	Turkey Marsh, Hickory Corners, Michigan	1987	8	3.54 $\pm$ 0.04	1.20	9.23 $\pm$ 0.82	8.84	
	Duck Marsh, Yankee Springs, Michigan	1987	2	3.55 $\pm$ 0.00	0.00	7.84 $\pm$ 0.80	10.20	
	Johnson Pond, Norwich, Vermont	1996	22	3.48 $\pm$ 0.10	2.88	9.95 $\pm$ 1.43	14.42	
	Childs Pond, Thetford, Vermont	1996	7	3.44 $\pm$ 0.09	2.74	10.62 $\pm$ 1.77	16.72	
	Combining all populations		39	3.49 $\pm$ 0.09	2.64	9.81 $\pm$ 1.48	15.05	
<i>Ischnura verticalis</i>	F—Three Lakes II, Richland, Michigan	1987	9	3.18 $\pm$ 0.06	1.93	6.42 $\pm$ 0.85	13.30	
	F—Palmatier Lake, Yankee Springs, Michigan	1987	13	3.12 $\pm$ 0.05	1.44	5.59 $\pm$ 1.57	28.09	
	F—Connecticut River, Hanover, New Hampshire	1996	2	3.18 $\pm$ 0.03	0.84	5.79 $\pm$ 0.81	13.95	
	F—Post Pond, Lyme, New Hampshire	1996	21	3.16 $\pm$ 0.08	2.56	5.02 $\pm$ 0.54	14.69	
	FL—Turkey Marsh, Hickory Corners, Michigan	1987	9	3.12 $\pm$ 0.08	2.65	5.81 $\pm$ 0.53	9.05	
	FL—Ferson Road Marsh, Lyme, New Hampshire	1996	3	3.22 $\pm$ 0.09	2.70	5.96 $\pm$ 0.87	14.67	
	FL—Sherrard Pond, Norwich, New Hampshire	1996	13	3.15 $\pm$ 0.04	1.17	5.09 $\pm$ 1.31	25.76	
	FL—Childs Pond, Thetford, Vermont	1996	9	3.28 $\pm$ 0.07	1.99	5.85 $\pm$ 2.01	34.45	
	Combining all populations		79	3.17 $\pm$ 0.08	2.46	5.53 $\pm$ 1.25	22.56	
	B) <i>Baetis bicaudatus</i> Mayflies, RMBL							
Female	Summer	1990	6	0.69 $\pm$ 0.04	6.16	0.25 $\pm$ 0.05	21.73	
		1994	9	0.82 $\pm$ 0.06	7.70	0.44 $\pm$ 0.11	25.82	
		1995	25	0.92 $\pm$ 0.07	7.07	0.71 $\pm$ 0.14	19.67	
	Combining years		40	0.86 $\pm$ 0.11	12.20	0.58 $\pm$ 0.22	37.27	
	Winter	1989–1990	3	0.96 $\pm$ 0.14	14.43	1.10 $\pm$ 0.81	73.77	
		1993–1994	31	0.93 $\pm$ 0.08	8.21	0.81 $\pm$ 0.15	18.35	
		1994–1995	35	1.09 $\pm$ 0.08	7.72	1.80 $\pm$ 0.34	18.71	
		Combining years		69	1.01 $\pm$ 0.11	11.23	1.33 $\pm$ 0.57	43.00
	Combining years and generations		109	0.96 $\pm$ 0.13	13.83	1.06 $\pm$ 0.60	56.44	
	Male	Summer	1990	6	0.72 $\pm$ 0.07	9.70	0.29 $\pm$ 0.05	18.20
1994			13	0.93 $\pm$ 0.03	3.43	0.49 $\pm$ 0.06	12.01	
1995			19	1.02 $\pm$ 0.05	4.51	0.69 $\pm$ 0.08	12.20	
Combining years			38	0.95 $\pm$ 0.12	12.16	0.56 $\pm$ 0.16	29.08	
Winter		1993–1994	19	1.07 $\pm$ 0.06	6.03	0.71 $\pm$ 0.11	15.01	
		1994–1995	19	1.16 $\pm$ 0.06	5.08	1.33 $\pm$ 0.22	16.6	
Combining years			38	1.11 $\pm$ 0.08	6.83	1.02 $\pm$ 0.36	35.20	
Combining years and generations			76	1.03 $\pm$ 0.13	12.44	0.79 $\pm$ 0.36	45.61	

Note: For each population of each species, the number of larvae sampled ( $N$ ), means  $\pm$  1 SD, and coefficients of variation for the two variables are given. For *I. verticalis*, populations are identified as coexisting with fish (F) or existing in a fishless (FL) body of water.

icantly among both generations (univariate ANOVA results, head width— $F_{1,103} = 97.38$ ,  $P < 0.001$ ; dry mass— $F_{1,103} = 226.53$ ,  $P < 0.001$ ) and years (ANOVA head width— $F_{4,103} = 29.12$ ,  $P < 0.001$ ; dry mass— $F_{4,103} = 70.11$ ,  $P < 0.001$ ). Differences among generations and years accounted for 74.6% of the variation in head widths (generations, 48.8%; years, 25.8%) and 87.5% of the variation in dry mass for females (generations, 59.0%; years, 28.5%). Likewise for males, head width and dry mass differed significantly among

both generations (ANOVA head width— $F_{1,71} = 175.73$ ,  $P < 0.001$ ; dry mass— $F_{1,71} = 223.14$ ,  $P < 0.001$ ) and years (ANOVA head width— $F_{3,71} = 54.57$ ,  $P < 0.001$ ; dry mass— $F_{3,71} = 83.36$ ,  $P < 0.001$ ); differences among generations and years accounted for 87.0% of the variation in head width (generations, 49.5%; years, 37.5%) and 90.1% of the variation in dry mass for males (generations, 58.1%; years, 32.0%). These results are reflected in the larger CV's for both sexes when all larvae across years and generations were combined

as compared to the  $CV$ 's for individual cohorts (Table 3). These observations concur with predictions from our analysis that size at emergence of mayflies should be more variable than that of damselflies.

#### DISCUSSION

The results of this study indicate that statistically significant mortality and growth effects obtained separately in field experiments may not necessarily translate into biologically significant effects on population dynamics. A prime mediating factor identified by this study is whether differences in size at metamorphosis influence adult fecundity. Both growth and mortality effects on *Baetis* mayflies are translated into differences in population dynamics, because size at metamorphosis critically determines adult female fecundities (Peckarsky et al. 1993, Scrimgeour and Culp 1994). Moreover, our analysis indicates that *Baetis* population dynamics should be much more influenced by the sublethal effects of the presence of both stonefly and trout on growth than by direct mortality inflicted by these two predators (Table 2). In contrast, although damselfly growth rates are depressed by the presence of threatening predators, these growth responses should have little effect on population dynamics (Table 1); direct mortality inflicted by dragonfly predators predominantly influences population dynamics. Growth responses should only influence damselfly population dynamics through effects on the time required to reach the minimum size for metamorphosis, and thus the time that larvae are exposed to dragonfly predation.

Sublethal predator effects on growth and metamorphosis have now been identified in a number of taxa besides damselflies and mayflies (frogs—Van Buskirk 1988, Skelly and Werner 1990, Wilbur and Fauth 1990, Werner 1991, Skelly 1992, 1995; snails—Crowl and Covich 1990; bluegill sunfish—Werner et al. 1983; mosquitoes—Juliano 1989; chironomids—Ball and Baker 1996). The biological significance of these sublethal predator impacts must be evaluated in a demographic framework to identify whether alterations in growth rate and the timing of and size at metamorphosis significantly influence population dynamics. The demographic model used for any particular organism must be tailored to its life history, but the various impacts of an interaction with another species can all be integrated into estimates of projected population growth (Caswell 1989a). These estimated effects on projected population-growth rates can then be readily compared among species having any life histories (e.g., semelparous vs. iteroparous organisms, age-dependent vs. stage-dependent life histories, etc.).

Paine (1992) proposed to quantify the per capita interaction strength of one species on another as the percentage change in abundance of one species when another is experimentally removed, and Paine standardized this quantity by dividing it by the natural abundance of the removed species (see also Raffaelli and

Hall 1996). The use of demographic methods to evaluate the strengths of species interactions, as we have in this paper, has some advantages over Paine's method (see also Osenberg and Mittelbach 1996). First, demographic methods estimate quantities that form the basis of mechanistic models of species interactions (i.e., mortality, growth and fecundity rates), and they use changes in projected population-growth rates to estimate the relative strengths of interactions. For example, from our analysis we conclude that interactions with trout and stoneflies have relatively equivalent effects on overall *Baetis* population dynamics. However, one cannot simply compare underlying demographic rates directly; e.g., direct mortality imposed by trout is 239% greater than that imposed by stoneflies, whereas the total effect of trout on  $\lambda$  is projected to be only about 30% greater than stonefly effects (Table 2). Also, studies quantifying strengths of interactions by measuring changes in demographic rates will usually require less time than studies quantifying strengths of interaction as changes in abundances. For example, even though the demographic approach we outline here requires that the treatments be sustained over the duration of the experiment ("press" treatment sensu Bender et al. 1984), we were able to measure short-term changes in demographic rates. In contrast, differences in abundance can only be meaningfully interpreted as strengths of interactions if the replicates of an experiment have come to some kind of community equilibrium. This approach also requires a "press" experiment but may take many generations of the component organisms to reach the equilibrium (Paine 1992, Raffaelli and Hall 1996).

Because these two approaches to quantifying the strengths of interactions are implemented over different time scales, they necessarily capture somewhat different aspects of a system. Paine's metric of interaction strength is influenced by the combination of the direct and all indirect effects propagated through the community from one species to another. Also, as communities in replicates lacking a specified species come to the new equilibrium, other regulatory mechanisms become important in the determination of the abundance of the species of interest. Note that this will generate problems of the kind discussed by Yodzis (1988). It may be very difficult to disentangle the contributions of direct and indirect interactions from the contributions of new regulatory mechanisms in determining the new equilibrium abundance of the species of interest (Yodzis 1988, 1996). In contrast, short-term experiments to quantify changes in demographic rates will generally not be performed long enough for indirect effects caused by changes in the abundances of other species (Miller and Kerfoot 1987, Wootton 1994) to be significantly manifested (Yodzis 1988, 1996), although other regulatory processes (e.g., competition, other predators) may become significant: e.g., damselflies competed via interference competition in the pred-

ator-free treatment of the experiment used to parameterize the demographic analyses given in Table 1 (McPeck 1998). However, demographic parameters will reflect indirect effects caused by interaction modifications (e.g., changes in feeding behavior). For example, in experiments testing growth effects of trout and stoneflies on *Baetis*, fish odor modified the effects of stoneflies on mayfly growth (Peckarsky and McIntosh 1998). Thus, the presence of one predator influenced the effect of another predator on a common prey, and the sublethal effects of stoneflies and trout on *Baetis* fitness were not additive. This example illustrates why pairwise species interactions may not provide accurate predictions about the nature of the entire community, and so also identifies a limitation of our analysis. The ability to isolate direct from indirect effects completely remains a difficult task for this alternative methodology as well. The appropriate experimental design will (as always) depend on the question being asked.

The strengths of interactions filtered through the life cycle of an organism should in turn influence how natural selection molds behavioral and developmental plasticity within lineages. Demographic analyses therefore also provide a framework for evaluating and predicting these plastic responses to changes in interaction strengths. A number of models have been analyzed to explore how changes in demographic rates will influence age and size at maturity in complex life cycles with various features (Roff 1992, Stearns 1992). Gilliam (1982) and others (Werner and Gilliam 1984, Werner 1986, Gilliam and Fraser 1987, Rowe and Ludwig 1991) have analyzed models in which both larval and adult stages have size-specific growth and mortality functions. Abrams and coworkers (Abrams 1991, Abrams et al. 1996, Abrams and Rowe 1996) have analyzed more generalized forms of the model we present in this paper. All of these models explore how trade-offs in growth and mortality can influence behavioral and developmental choices.

Our analysis of this generalized insect demographic model highlights that the translation of fitness-determining traits from larval to adult stage can dramatically shift the type of behavioral and life history strategies that will be favored by natural selection. If size at metamorphosis influences adult fecundity ( $\beta > 0$ ), larvae should modulate their behavior and development to balance the conflicting demands of feeding and avoiding predators. Mayflies do not feed as adults (Edmunds et al. 1976, Brittain 1982), and consequently adult female fecundity is largely determined by size at metamorphosis; larger females produce more eggs (Brittain 1982, Butler 1984, Sweeney 1984, Peckarsky et al. 1993, Scrimgeour and Culp 1994). Consistent with these model predictions, when predatory fish are present, *Baetis* larvae spend much of their time in safe areas under rocks when they are well fed or food availability is low; but they spend more time foraging on the tops

of rocks, where predation risk is high, when food is abundant or they are hungry (Kohler and McPeck 1989, see also Soluk and Collins 1988, Scrimgeour and Culp 1994, Scrimgeour et al. 1994, Peckarsky and Cowan 1995, Peckarsky 1996). In the laboratory, size and timing of metamorphosis of *Baetis* larvae are also influenced strongly by food availability and predation risk (Scrimgeour and Culp 1994).

Our field data also show that different generations of the same population vary greatly in size at metamorphosis (Table 3). The variation among generations within a year is probably largely due to differences in the ecological environment in which the generations develop. The winter generation of *Baetis* grows and develops slowly in a period when stream temperatures, food resources, and predator activity are very low, and its members attain much larger sizes than those in the summer generation (Table 3). However, the winter generation is subjected to intense predation pressure at the very end of their larval stage (early summer), and responds by taking fewer risks (nocturnal periodicity, Cowan and Peckarsky 1994, Peckarsky 1996). Larvae of the summer generation, on the other hand, are present in the stream during periods of high water temperatures, high food levels, and high predation rates. Their behavioral and developmental plasticity enables them to grow very quickly (4–6 wk duration for the summer generation vs. 8–9 mo for the winter generation). In the summer generation, intense pressure from predators, mermithid parasites (Vance and Peckarsky 1996), and the imminent onset of winter results in accelerated rates of development and emergence at dramatically reduced sizes (Table 3), which may represent a threshold for size at metamorphosis. This speculation is corroborated by the observation that at any one site, size at metamorphosis declines for winter-generation *Baetis* over the duration of the emergence period, but the size of emerging summer-generation *Baetis* is constant and similar to that of the smallest-sized winter *Baetis* (B. L. Peckarsky, unpublished data). These results are consistent with model predictions that alterations in larval behavior and development, which balance the conflicting demands of feeding and predator avoidance, can increase fitness if size at metamorphosis influences adult fecundity (i.e.,  $\beta > 0$ ) and parallel those of other studies of bivoltine insects (Forrest 1987). Obviously, though, further experimentation is needed to separate the effects of changes in vital rates between generations within a year from potential effects of the suitability of different periods of the year for emergence (e.g., Ludwig and Rowe 1990).

In contrast to mayflies, damselfly female size and fecundity are thought to be uncorrelated (i.e.,  $\beta = 0$  in our model). When considered in the demographic framework, such organisms are expected to attempt only to decrease the total mortality that they experience as larvae (see also Anholt et al. 1991, Rowe and Ludwig 1991, Berrigan and Charnov 1994, Juliano and

Stoffregen 1994). Consistent with this, damselfly species display less variation in size at emergence among populations than do mayflies (Table 3), suggesting that damselflies only grow to the minimum size required for metamorphosis (also see Anholt [1991] for a discussion of this issue). Along with this, damselflies alter their behavior in response primarily to the presence of predators (e.g., Pierce et al. 1985, McPeck and Crowley 1987, McPeck 1990a, Richardson and Anholt 1995); alterations in prey abundance have little effect on their behavior (Johansson 1993, Richardson and Anholt 1995, Schaffner 1996). However, more rigorous tests of whether damselflies will modulate their behavior and development under contrasting food and predation regimes are needed. No study to our knowledge has explicitly tested whether damselfly larvae display compensatory behavioral responses to food and predators like those seen in mayflies. Also, we did find statistically significant variation in size at emergence between populations for both damselfly species, and damselfly size at emergence can be experimentally increased to some degree by food addition (Anholt 1990). It may be the case that damselflies do not have a value for  $\beta$  exactly equal to zero, but rather just substantially less than the  $\beta$  value for mayflies (e.g., see Banks and Thompson 1987). Obviously, further experimentation and better data on lifetime reproductive success are sorely needed. For any prey species, the value of  $\beta$  should modulate the relative contributions of direct mortality and sublethal growth effects of predators on the determination of its overall population growth rate.

Just as we do not expect a given organism to behave similarly under different ecological conditions, we also should not expect different species to respond similarly to changes in environmental conditions. Our analysis suggests one important feature of a life cycle that should strongly influence the types of responses favored by natural selection, namely the degree to which larval characters influence fitness components of adults. A fruitful avenue for progress on these issues is to compare the responses of taxa that vary in this translation from larva to adult. The phenotypes of metamorphosing individuals influence the fitness components of adults in a number of taxa and many of these taxa have also been shown to vary in size and timing of maturity or metamorphosis (Reisen and Emory 1977, Wilbur 1977, 1980, Blakley 1981, Suleman 1982, Prout 1984, Prout and McChesney 1985, Forrester 1987, Semlitsch et al. 1988, Crowl and Covich 1990, Feltmate and Williams 1991, Werner 1991, Peckarsky et al. 1993, Juliano and Stoffregen 1994, Scrimgeour and Culp 1994, Sweeney et al. 1995, Twombly 1996, Werner and Anholt 1996). In contrast, taxa such as damselflies, which do not have strong fitness linkages between larval phenotypes and adult fecundity, are expected to balance the conflicting demands of predator avoidance and food acquisition in a very different way. We suggest that more comparative studies are needed

implementing demographic analyses to provide a strong, mechanistic linkage between the processes structuring communities and life history evolution of component taxa.

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