Ecological Archives E093-056-A1

Spencer R. Hall, Claes R. Becker, Meghan A. Duffy, and Carla E. Cáceres. 2012. A power-efficiency tradeoff in resource use alters epidemiological relationships. *Ecology* 93:645–656.

Appendix A. More data, derivation of the DEB model, and further development of the conversion efficiency mechanism.

In this Appendix, we provide additional information regarding the host susceptibility experiment (Fig. A1), the mechanism used to implement the power-efficiency tradeoff, the experimental results, and the dynamic energy budget model (DEB; Kooijman 1993, Hall et al. 2009a, 2010). This variation on the DEB model adds a semi-mechanistic, feeding rate-based representation of a power-efficiency tradeoff whose signature we observed in the juvenile growth rate assays (Fig. 4C–E). Although we explained its derivation in the text, here we provide more information about the study from which it came (DeMott et al. 2010). Then, we show more model and empirical results.

More on visualizing and implementing the power-efficiency tradeoff

We drew heavily on experimental data to incorporate the power-efficiency tradeoff into our DEB model. The DeMott et al. (2010) study examined feeding rates (ingestion, I), assimilation rates (A), conversion efficiency (ε) of *Daphnia* consuming an array of algae that ranged in quality from highly edible (their lab culture strains) to highly indigestible (their field-isolated strains). They found (in their Fig. 4) that assimilation rate and ingestion rate followed a power function of body length (L), in the form:

$$A(L) = \alpha_1 L^{b_1} \tag{A.1a}$$
$$I(L) = \alpha_2 L^{b_2} \tag{A.1b}$$

where a_j and b_j are slope and power coefficients, respectively (Fig. A2A and B, respectively). Notice that *Daphnia* eat the field-isolated algae (poorer quality, dashed lines) at similar rate as higher quality strains grown in lab culture (solid lines), but much less of that ingested algae becomes assimilated. Since conversion efficiency is the ratio of assimilation rate to ingestion rate, we divided both the power functions for A and I to yield e:

$$\varepsilon(L) = A(L) / I(L) = (\alpha_1 / \alpha_2)L^{(b_1 - b_2)} \tag{A.2}$$

Using DeMott et al.'s coefficients and this equation, we found that conversion efficiency is essentially size invariant for the higher quality algae but is a power function of body size for the lower quality foods (Fig. A2C). Indeed, the negative correlation between intercept (conversion efficiency of a 1 mm animal) and exponent of the power function for each alga summarizes this pattern (Fig. A2D). Higher quality foods (larger intercept) have exponents near zero, while lower quality foods (smaller intercept) have higher exponents. So, again, larger animals digest poor food more easily (Fig. 4C). These patterns justify our use of a minimum function-power function combination to capture the size-dependence of conversion efficiency of poor foods via gut passage time (Eq. 2). Furthermore, ingestion rate increases more quickly with body size (i.e., higher exponent) for lower quality foods (lower intercept of the conversion efficiency power function: this relationship relies on ignoring the outlier denoted with the arrow: Fig. A2E). Using Eq. 2, we also see that a negative relationship between ingestion rate and conversion efficiency arises as animals become larger for six of the seven algal cultures (Fig. A2F).

The dynamic energy budget model

A more complicated model (Hall et al. 2009a) connects genetic variation in the feeding metric and host energetics to other epidemiological parameters. This dynamic energy budget (DEB) model, based on Kooijman (1993), tracks flow of energy from ingestion and assimilation to storage in a "reserve" pool. That reserve energy is used (catabolized) for growth, reproduction (if adult) or reproductive development (if juvenile), and associated metabolic costs. However, parasites take energy from the reserve of hosts and replicate within hosts. Through this energy consumption, parasites exact virulent costs on growth and reproduction of their hosts. Furthermore, the parasite kills its host once parasite mass reaches a certain threshold, a proportion of structural mass of the host (as discussed and justified empirically in Hall et al. 2009a). Before killing it, however, the parasite can inflict energetic stress on its host by drawing down internal energy reserves. The DEB model predicts the implications of this draw-down for growth, reproduction, and survival of hosts.

The DEB model tracks energy flow through hosts and parasites. Hosts first eat food, then assimilate some fraction of it. Assimilation rate (A), then, is:

$$A = aL^2 X / (h + X);$$
(A.3)

A depends on size-specific assimilation rate, a, which itself is the product of size-specific maximal feeding rate, c, and conversion efficiency, ε; surface area of the host, proportional to L^2; and feeding on algal food (X) following a type-II functional response with a half-saturation constant (h). Assimilated energy is then put into a reserve energy pool (E). Reserve energy (E), in turn, is modeled as the product of energy density (e) and structural mass (W) so that $E = eW$. The change through time of this energy pool, dE/dt, involved two components:

$$\frac{dE}{dt} = \frac{d(eW)}{dt} = W\frac{de}{dt} + e\frac{dW}{dt}$$
(A.4)

First, reserve density per unit structural mass changes (involving the de/dt term), then the host grows more structure (the dW/dt term). Following Kooijman (1993), we assume homeostasis of reserves, meaning that the animal regulates the reserve density at a level related to its feeding rate. Reserve density (e) increases with assimilation and decreases linearly with e (i.e., according to first-order kinetics):

$$\frac{de}{dt} = \frac{A}{W} - \left(\frac{aL^2}{e_M W}\right)e$$
(A.5)

where e_M is the maximum density of energy. Once equations (A.3)-(A.5) are combined, utilization rate (C) of energy becomes:

$$C = A - \frac{dE}{dt} = E\left(\frac{aW^{2/3}}{e_M W} - \frac{dW}{Wdt}\right)$$
(A.6)

Under normal circumstances, the host allocates these catabolized energy reserve towards growth versus reproduction if mature or maturation if juvenile following the kappa (κ)-rule, according to which a fixed proportion (κ) of utilized energy is allocated to growth, and a proportion ($1-\kappa$) towards reproduction. In mathematical terms, the host devotes utilized energy to growth at rate:

$$\kappa C = g(dW / dt) + mW$$
(A.7)

where the first term on the right-hand side denotes growth of structural mass (dW/dt) with associated cost of growing (g), and the second term represents costs to maintain current mass (at rate m). We solved both equations (A.6) and (A.7) for C, set them equal to each other, then solved for the dW/dt term to yield:

$$\frac{dW}{dt} = W\left[\frac{\kappa a L^2 E / (e_M W) - mW}{\kappa E + gw}\right] \tag{A.8}$$

The rest of the catabolized energy reserves, $(1 - \kappa)C$, are used for reproduction and associated costs. The rate of reproduction, dR/dt, is then:

$$dR / dt = (q / E_0)[(1 - \kappa)C - ((1 - \kappa) / \kappa)mW_P] \tag{A.9}$$

where q is the cost of converting energy reserve of the mother into the energy reserve of the offspring ($0 < q < 1$), and E_0 converts energy to offspring. This equation also includes a second term (in brackets) for "maturity maintenance" (see Kooijman 1993; W_P denotes size at maturation). The DEB model for the host, then, consists of equations (A.4), (A.8), and (A.9).

We then add the parasite growing within the host. This parasite (N) feeds on energy reserves of its host (E) according to its own saturating (type II) functional response. Thus, reserve dynamics change (from Eq. A.4) to:

$$\frac{dE}{dt} = W\frac{de}{dt} + e\frac{dw}{dt} - \frac{a_N}{\varepsilon_N}\left(\frac{E}{h_N + E}\right)N \tag{A.10}$$

where consumption by parasites (last term) is governed by a half-saturation constant (h_N), maximal assimilation rate (a_N), and conversion efficiency (ε_N) of the parasite. This parasite then grows according to a classic equation for a resource consumer (Grover 1997):

$$\frac{dN}{dt} = a_N\left(\frac{E_N}{h_N + E_N}\right)N - m_N N \tag{A.11}$$

where m_N lumps various loss rates (e.g., maintenance, death) of the parasite.

This model requires a few other pieces of biology before use (see Hall et al. 2009a for the mathematical details). First, an equation for food dynamics follows our experimental protocol (below): non-reproducing food is consumed by hosts but replenished daily. Second, parasite growth within a host can inflict "moderate" and "severe" energetic stress on the host. As parasites draw down energy within a host, they can first stop growth of the host (moderate energetic stress), but then stop reproduction (severe energetic stress). These changes update the kappa-rule for allocation of utilized energy. Third, the parasite kills the host once it reaches a physical threshold ($N = \rho W$, where ρ denotes a mechanical limit of the host to support the parasite). Once this threshold is crossed, the animal stops eating (i.e., $f = 0$). Then, energy reserve (E) drops to zero, and the host dies. (The parasite cannot drop E to zero itself because it's own minimal energy reserve requirements exceed zero). Finally, starting parasite density (P_0) within a host of an initial size (L_0) equaled that consumed over a 24 hour period. Thus, hosts with higher rates of the feeding metric started with more parasite internally than those with lower rates. Parameter values used are summarized in Table A1.

More model results: feeding, fecundity, size, and spore yield

The dynamic energy budget model can produce varying relationships between host susceptibility, as

indexed with feeding rate, and fecundity scaled arithmetically (offspring per day) and with spore yield. When we simulate the model for 16–25 days, we see that feeding rate and fecundity show a mostly negative relationship (Fig. A3A, day 16). By day 25, however, that relationship becomes quite hump-shaped, with large increasing portions. In contrast, feeding rate and instantaneously scaled fecundity (i.e., per capita growth rate, as calculated from the Euler-Lotka equation: see Hall et al. 2009b, 2010 for methodology) always shows a decreasing relationship (as seen in the experiment: $R = -0.68$, $P = 0.063$; Fig. A3B). This discrepancy can be explained by the fact that calculations of instantaneous birth rate this way largely emphasizes early reproduction, a period during which the power-efficiency tradeoff operates most strongly (and hosts with lower feeding rate enjoy higher conversion efficiency: Fig. 4C). Changes in fecundity, on the other hand, qualitatively mirror the shifting relationship between feeding rate and host body size (Fig. A3C). When young, body size largely drops with feeding rate because conversion efficiency is higher for smaller hosts. (We would also expect negative relationships between juvenile growth rate and body size, as seen in the experiment.) As the host continues growing, conversions efficiency elevates, and hosts with higher feeding rate begin assimilating more energy than those with lower feeding rate (since assimilation rate involves the product of conversion efficiency, feeding rate, and body size; Kooijman 1993, Hall et al. 2009a). As a result, the relationship between the two fecundity measures change shape through time. Earlier, we would expect a positive relationship (as seen in the experiment: $R = 0.89$, $P = 0.001$); as time progressed, the relationship would become increasingly *J*-shaped, with portions showing a negative relationship (Fig. A3D).

The model predicts that we should also see shifting relationships between fecundity and spore yield. Fecundity should start off positively (i.e., a spore yield-fecundity tradeoff; Fig. A3E); as time goes on, portions of these curves become increasingly negative. In fact, the curves start looking like what we observed in the lifetable experiment (Fig. 3A). This shift is caused by the increasing hump shape of the fecundity-feeding relationship (Fig. A3A). However, instantaneously scaled fecundity shows little change in relationship: the model robustly predicts a positive relationship (Fig. A3F). Since we saw a negative correlation between spore yield and instantaneously scaled fecundity ($R = -0.72$, $P = 0.03$), it seems unlikely that this the dynamic energy budget model can explain our spore yield-fecundity data. These data to point to interesting relationships between feeding rate, growth (size), and fecundity that warrant attention in future studies of power-efficiency tradeoffs.

The experiment predicts a negative relationship between time until death of infected hosts and susceptibility of hosts (Fig. A4A). This result was predicted by the model (Fig. A5A) and emphasizes that hosts that are most susceptible consume more spores to become infected due to high feeding rate. Hosts that lived longer once infected yielded more spores upon death (Fig. A4B) from larger hosts (Fig. A4C). The survival-spore yield relationship also emerged from the model (Fig. A5B), but the size-spore yield correlation was an assumption of the model, not an outcome.

TABLE A1. Parameter values and ranges of parameters used in simulations in the text and Appendix A. The symbols used correspond directly to those in Hall et al. (2009a), where the dynamic energy budget model is presented in detail.

Term	Units	Definition	Value or range
State Variables			
e	-	Reserve energy density ($= E/W$)	–
E	mg C	Reserve energy mass ($= eW$)	–
N	mg C	Mass of the parasite	–
R	offspring	Reproduction (offspring)	–

t	day	time	–
W	mg C	Structural mass (weight) of the host	–
X	mg C/L	Food (algae)	–
Fluxes			
A	mg C/day	Assimilation rate	–
C	mg C/day	Energy utilization (catabolism) rate	–
Parameters			
a	mg C·mm^{-2}·day^{-1}	SA-specific maximal assimilation rate, εf	4.6×10^{-3}
a_N	day^{-1}	Maximal assimilation rate, parasite, $\varepsilon_N f_N$	0.6
c	mg C·mm^{-2}·day^{-1}	Surface area-specific maximal feeding (consumption) rate	0.009[*] (0.0045-0.01)
c_N	day^{-1}	Maximal feeding rate, parasite	0.75
d_N	day^{-1}	Combined loss rate, parasite	0.08
E_0	mg C	Carbon investment per offspring	0.0021
e_M	–	Maximal energy density	1.0
g	–	Mass-specific cost of growth	0.8
g_v	–	Proportionality constant, gut volume	0.025
h	mg C/L	Half-saturation constant, host	0.1
h_N	mg C	Half-saturation constant, parasite	0.005
L	mm	Size of host; relation to W: $W = aL^3$	--
L_0	mm	Initial size of hosts when exposed to parasite	1.2
m	day^{-1}	W-specific maintenance rate, host	0.2
m_N	day^{-1}	Loss rate of the parasite	0.08
$N_{0,E}$	mg C	Initial spore mass in beaker to which hosts are exposed	0.09, 0.13[‡], 0.17
q	–	Metabolic cost of production of an offspring	0.9
T	days	Interval of food replenishment	1.0
W_P	mg C	Mass at puberty	0.002
φ	mg C/mm^3	Conversion for struct. mass-length regression	1.8×10^{-3}
ε_{max}	–	Maximal conversion efficiency, host	0.7[§]
ε_N	–	Maximal conversion efficiency, parasite	0.8
κ	–	Fraction of energy spent on growth	0.2
ρ	–	Mechanical threshold of infected host	1.68

[*] Range used in Figs. 4 and 5 to produce variation in the feeding rate.

[‡] Masses produced from initial spore doses of 1,000, 1,500, and 2,000 spores per mL, respectively, assuming 174 pg/spore (Hall et al. 2009a). Mass of ingested parasite (N_0 of Hall et al. 2009a) is then calculated for a 1.2 mm size animal as a function of the feeding rate metric.

[§] Default used in all figures; this is the value used for *Scendesmus*.
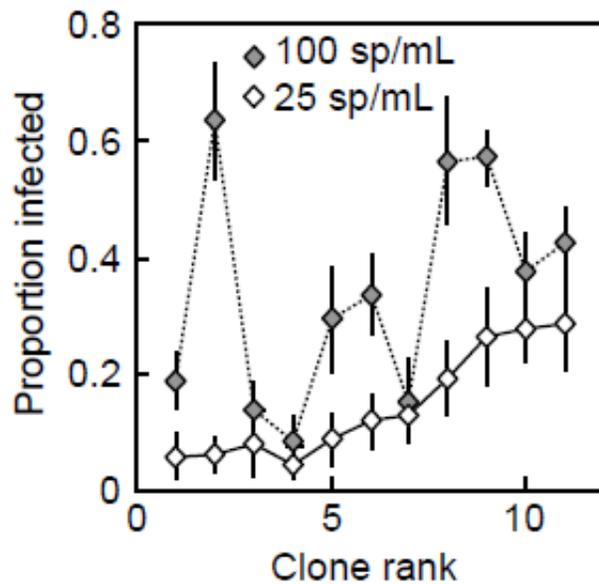
FIG. A1. Raw prevalence (proportion infected) data for each genotype exposed to either a lower (25 spores/mL, white diamonds) or higher (100 spores/mL, grey diamonds) spore density. Genotypes are ranked from lowest to highest prevalence seen in the low spore treatment. Points are means ± one standard error.
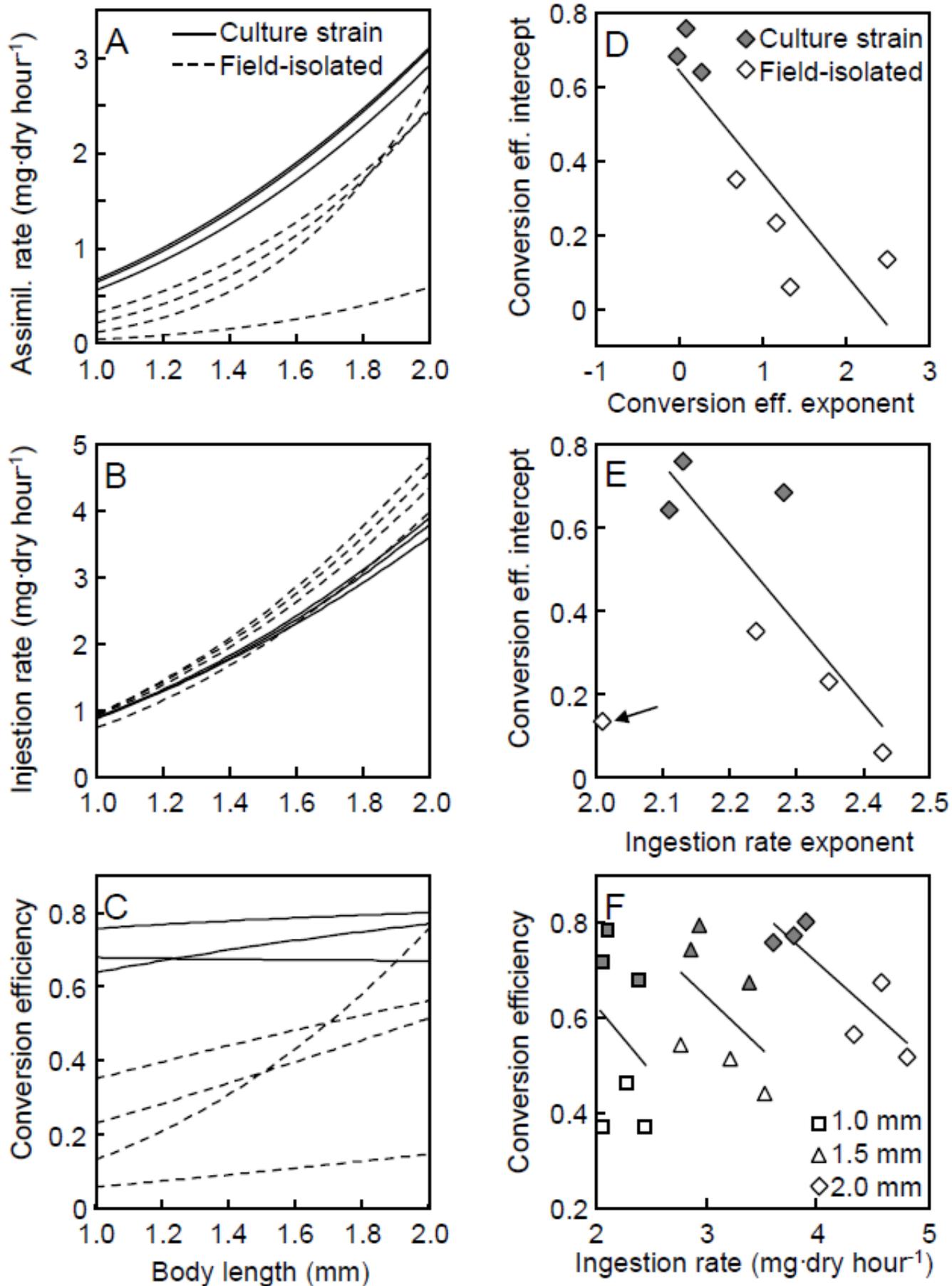
FIG. A2. Summary of DeMott et al.'s (2010) results linking body size (length, mm) with ingestion rate,

assimilation rate, and conversion efficiency of another species of *Daphnia* (a *D. pulex-pulicaria* hybrid, the "Geedey" clone). (A) Assimilation rate and (B) ingestion rate increase as a power function of body size. Notice that *Daphnia* eat the field-isolated algae (poorer quality, dashed lines) at a higher rate than higher quality strains grown in lab culture (solid lines), but much less of that ingested algae becomes assimilated. (C) Conversion efficiency (from eq. A.2) is essentially size invariant for the higher quality algae but is a power function of body size for the lower quality foods. (D) A negative correlation between intercept (conversion efficiency of a 1 mm animal) and exponent of the power function summarizes this pattern in (C). Higher quality foods (higher intercept, filled in diamonds) have exponents near zero, while lower quality foods (white diamonds) have higher exponents. (E) Ingestion rate increases more quickly with body size (i.e., higher exponent) for lower quality foods (lower intercept of the conversion efficiency power function; note the exception pointed to with an arrow). (F) A negative relationship between ingestion rate and conversion efficiency arises as animals become larger for six of the seven algal cultures. Different symbols correspond to different lengths: squares: 1.0 mm length; triangles: 1.5 mm; diamonds: 2.0 mm
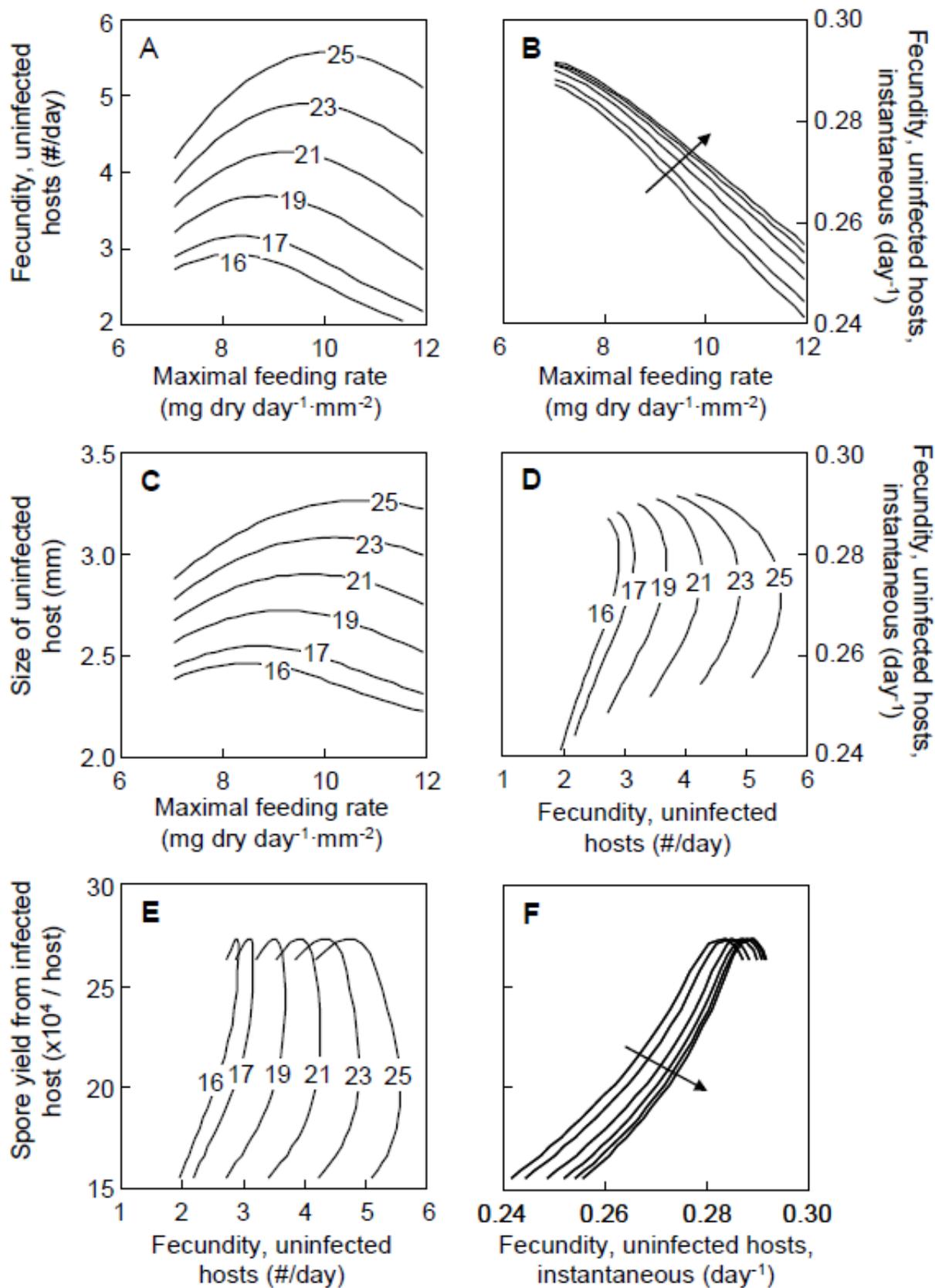
FIG. A3. More simulation results from the DEB model implementing the power-efficiency tradeoff. (A)-(C) *Feeding rate*: relationships between feeding rate and fecundity and size of uninfected hosts. Fecundity is indexed as number of offspring per day in (A), and instantaneously (as *r* from the Euler-Lotka equation) in (B). (C) shows body size at different days, ranging from 16 to 25, of the simulation. (D) Relationships between the two fecundity measurements started relatively positive but then bended out. (E) – (F) *Spore*

yield: relationship between spore yield and (E) fecundity and (F) instantaneous fecundity of uninfected hosts Arrows point in direction of increasing length of simulation. Simulation results assume that hosts were exposed to 1,000 spores per mL (as in Fig. 5).
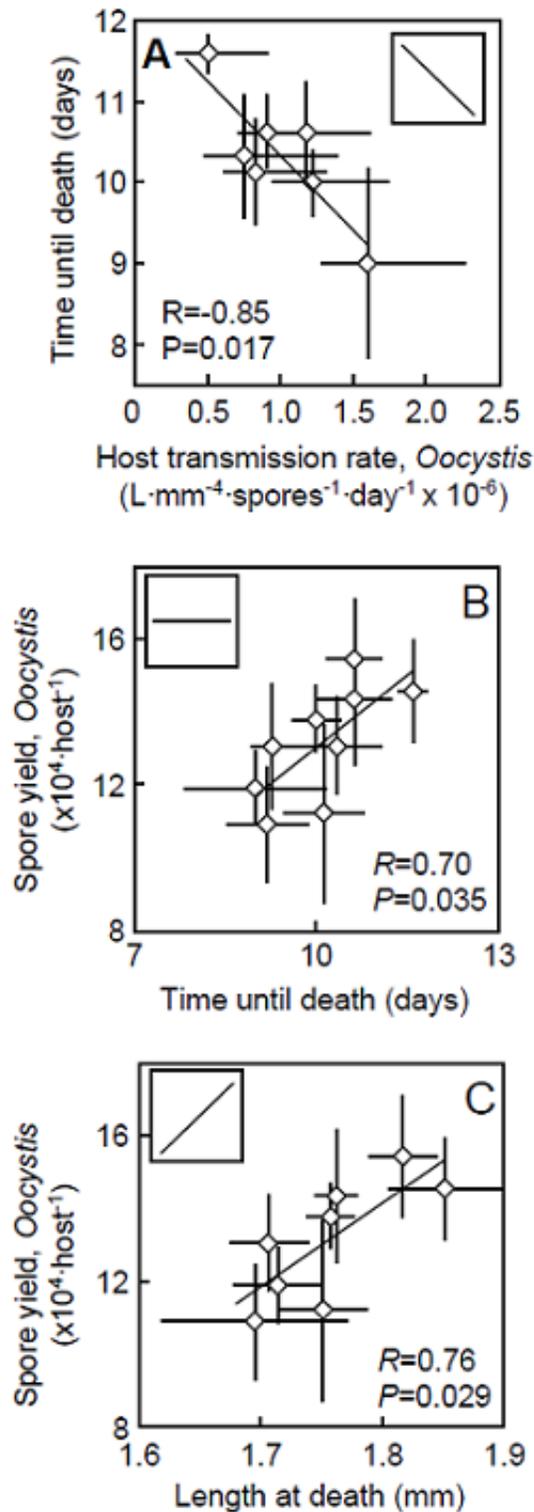
FIG. A4. More results from the life table experiment with the poorer quality algal resource, *Oocystis*. (A)

More susceptible host genotypes die more quickly once infected. This result parallels that seen in the previous experiments with higher quality algae, *Scendesmus* (Hall et al. 2010). Genotypes that yielded more spores upon death (B) lived longer and (C) grew to larger size. A positive length-spore yield relationship emerged with higher quality algae. Each point is a clonal mean ± 1 standard error except for the susceptibility estimates (± 95% CIs). Inset boxes denote trends of these factors detected in a companion study (Hall et al. 2010).
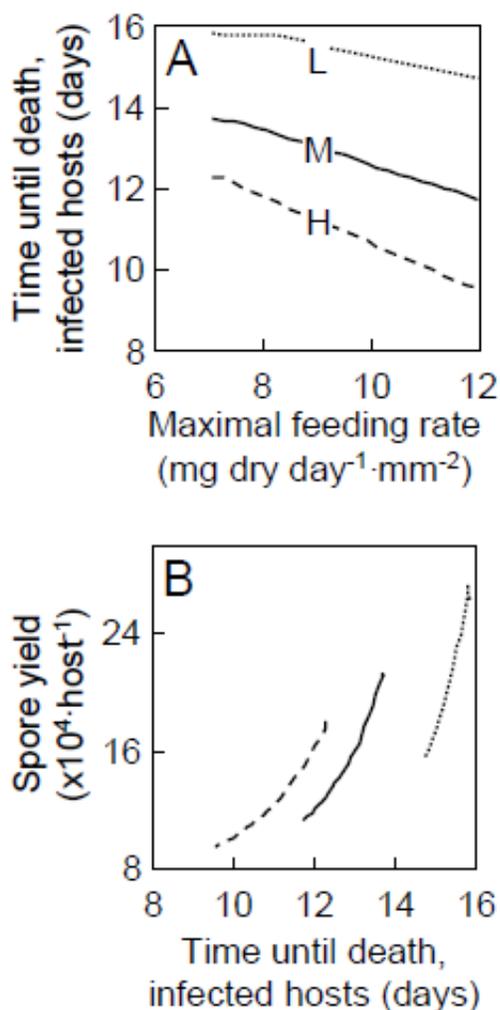
FIG. A5. More results from the DEB model. The model anticipates results seen in Fig. A4. (A) More susceptible hosts, i.e., those with faster feeding rate, should die more quickly once infected. (B). Hosts that live longer while eating poor quality resources should produce more spores. Contours correspond to lower (dotted, L; 1000 spores/mL), intermediate (solid, M; 1,500 spores/mL), and higher (dashed, H; 2,000 spores/mL) levels of spores to which hosts were initially exposed in the simulations.

LITERATURE CITED

DeMott, W. R., E. N. McKinney, and A. J. Tessier. 2010. Ontogeny of digestion in *Daphnia*: implications for the effectiveness of algal defenses. Ecology 91:540–548.

Hall, S. R., J. L. Simonis, R M. Nisbet, A. J. Tessier, and C. E. Cáceres. 2009a. Resource ecology of virulence in a planktonic host-parasite system: an explanation using dynamic energy budgets. American Naturalist 174:149–162.

Hall, S. R., C. M. Knight, C. R. Becker, M. A. Duffy, A. J. Tessier, and C. E. Cáceres. 2009b. Quality matters: food quality and the course of epidemics in a planktonic host-parasite system. Ecology Letters 12:118–128.

Hall, S. R., C. R. Becker, M. A. Duffy, and C. E. Cáceres. 2010. Genetic variation in resource acquisition and use among hosts creates key epidemiological tradeoffs. American Naturalist 176:557–565

Kooijman, S. A. L. M. 1993. Dynamic energy budgets in biological systems. Cambridge University Press.

[Back to E093-056]