

Evaluation of alternate harvesting strategies using experimental microcosms

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Experimental evidence to evaluate alternate conservation policies for harvested populations is currently meager. We used populations of the ciliate *Tetrahymena thermophila* growing in test tube microcosms to experimentally evaluate the effects of alternate harvesting policies in a controlled, replicable setting. Simple density-dependent models were effective in predicting patterns of ciliate population growth in the microcosms. We evaluated several univariate models, finding that a Ricker logistic model was a better predictor of ciliate population dynamics than Gompertz logistic, non-linear logistic, or random walk models. Using the Ricker logistic model as a demographic skeleton, we modeled ciliate population dynamics with respect to three alternate harvesting policies (fixed quota, fixed proportion, and fixed escapement), each conducted at four comparable levels of harvest intensity. The parameterized demographic models predicted that fixed quota harvesting would lead to lower mean ciliate abundance and higher temporal variability in ciliate abundance than fixed proportion or fixed escapement policies, with an appreciable risk of extinction, even under the controlled environmental conditions of our experimental system. For each harvesting policy, the intensity of harvest had demonstrable effects on population density. Population variability was higher for fixed quota harvesting than the other policies. The stochastic demographic model successfully predicted heightened extinction risk in the fixed quota system, relative to the other management treatments. Our experimental evidence lends support to the theoretical prediction that fixed quota harvesting is riskier than fixed proportion or fixed escapement policies.

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It is estimated that about one-third of bird species and one-half of mammals worldwide are classified as threatened due to overexploitation (Goombridge 1992). As such, there is an urgent need to develop more reliable methods for managing harvested populations. Three alternate policies commonly used to manage harvests of natural resources are fixed quota (removing a constant number of individuals), fixed proportion (removing a constant percent of the population), or fixed escapement (removing individuals when the population is above a threshold density).

Harvesting theory suggests that fixed quota harvesting should cause greater variation in stock density than fixed proportion harvesting or fixed escapement harvesting, leading to an elevated risk of stock collapse (Beddington and May 1977, May et al. 1978, Walters 1986, Lande et al. 1995, Roughgarden and Smith 1996, Ludwig 1998). Historically, fixed quota harvesting has been the most common strategy used in resource management. In recent years, however, policy makers have begun to shift to alternative approaches to harvest management (Ludwig et al. 1993, Hilborn et al. 1995, Pascual and

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Hilborn 1995). Fixed proportion harvesting is currently the most common strategy used in European and North American fisheries (Rosenberg et al. 1993). Fixed escapement harvesting also has the objective of reducing the risk of resource collapse while maintaining high average yields. It is currently being integrated into the management plans of several renewable resources (Lande et al. 1997, Roberts 1997).

Evaluation of alternate harvest policies is severely hampered, however, by the inherent difficulty of performing controlled experimental harvesting trials with adequate replication. Ethical and practical difficulties prevent extensive field testing of alternate harvesting policies. As an alternative, ecologists often use model systems in laboratory microcosms, allowing statistical replication under controlled environmental conditions and clarification of ecological dynamics occurring in more complex natural environments (Lawler 1993, Lawton 1995, Wilbur 1997, Drenner and Mazumder 1999, Mueller and Joshi 2000).

Tetrahymena thermophila is a unicellular freshwater organism found in streams, lakes and ponds and are about 50 μm long and 20 μm wide (Frankel 2000). Under laboratory conditions, these ciliates can reach densities up to 10^5 ml^{-1} in a variety of media, with generation times of 2–3 hours (Orias 1997). *Tetrahymena* is a suitable experimental organism for replicated harvesting experiments, due to the ease with which they can be maintained in the laboratory. *Tetrahymena* has been used as a model organism for numerous previous studies of foraging behavior, interspecific competition, exploitation of patchy environments and to test complex population growth models (Watson et al. 1981, Swift et al. 1982, Fredrickson 1991, Hatzis et al. 1994, Diehl and Feissel 2001, Long and Karel 2002).

Here we develop simple predictive models of population dynamics for the ciliate *Tetrahymena thermophila* and apply them to lab microcosms to evaluate fixed quota, fixed proportion, and fixed escapement harvest policies. Through the observation and manipulation of *T. thermophila* in microcosms, we specifically test whether fixed quota harvesting produces greater population variation, lower mean density, and higher risk of stock collapse than fixed proportion or fixed escapement policies.

Material and methods

The study was conducted during May–August 2000. Populations of *T. thermophila* (strain B1975 obtained from Dr. J. Frankel, Univ. of Iowa) were maintained via weekly sterile transfer in 1% proteose peptone, 1% yeast extract, and 0.2% dextrose in a controlled, laboratory environment. The microcosms consisted of 20 ml test

tubes kept out of direct sunlight at room temperature. To prepare the microcosms, sterile test tubes were provided with 10 ml of a culture medium of dried cereal grass leaves and inoculated within 72 h with the bacteria *Enterobacter aerogenes* (obtained from R. Van Twest, Dept of Cell and Molecular Biology, Univ. of Guelph). The cerophyll medium was filtered using Whatman no. 1 paper prior to dilution, autoclaving, and inoculating with bacteria. The test tubes were left for 24 h to allow the bacteria to multiply. A constant volume of 100 μl of a solution of high density ($>20 \mu\text{l}^{-1}$) *T. thermophila* was then added to each microcosm. The microcosms were gently swirled manually once a day to avoid biomass accumulation at the bottom of the test tubes. Test tubes were always mixed manually prior to sampling. While no tests were done to guarantee that other species of bacteria were not present during the trials, the sterile techniques employed would be expected to considerably reduce this possibility.

A preliminary experiment, without harvesting, was done to observe the growth rate of *T. thermophila*, so that we could subsequently predict the outcome of harvesting (Fig. 1). Ten test tubes were provided with 10 ml of culture medium and inoculated with 100 μl of a high density ($>20 \mu\text{l}^{-1}$) stock solution of *T. thermophila*. Counting was done over a period of 124 h, by removing a 20 μl subsample from each microcosm using an eppendorff micropipette and placing it into a triple-spot depression slide. The subsamples were preserved with a few drops of Lugol's fluid to facilitate counting, and viewed at a magnification of $50\times$. When densities were extremely high (i.e. $>20 \mu\text{l}^{-1}$), the subsamples were diluted with a known volume of distilled water and a 20 μl subsample was extracted from this dilution. Unlike the harvesting trials conducted later, there was no replacement of culture medium at each counting episode, which is a potential source of bias in forecasting growth rates.

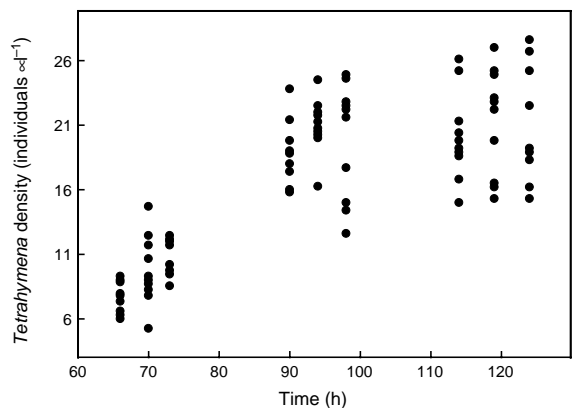


Fig. 1. Changes in population density (individuals μl^{-1}) over time for *Tetrahymena thermophila* growing in 10 ml test-tubes.

Data from the preliminary study were used to estimate the per capita rate of population change ($\lambda_t = N_{t+1}/N_t$) from sequential census data collected every 4 h. These data were then fitted to several alternate demographic models, using least squares minimization, and the residual variation around the demographic model was estimated. Four alternate stochastic models were considered: random walk ($\lambda_t = \mu + \varepsilon_t$), Ricker logistic ($\lambda_t = \exp[a - bN_t + \varepsilon_t]$), Gompertz logistic ($\lambda_t = \exp[a - b \ln(N_t) + \varepsilon_t]$), and non-linear logistic ($\lambda_t = a[1 - bN_t]^0 + \varepsilon_t$). Akaike's information criterion (AIC_c), corrected for small sample sizes, was used to evaluate predictive ability of the models: $AIC_c = -2 \ln(\Lambda) + 2p(n/[n - p - 1])$, where Λ is the likelihood of the model based on normally distributed error, p is the number of model parameters, and n is the sample size (Burnham and Anderson 1998). The results from these preliminary observations were used to determine the carrying capacity of the microcosmal environment of *T. thermophila*. This was necessary in order to choose appropriate harvesting rates. The methods used for sub-sample counting remained the same throughout the preliminary and harvesting studies.

For the harvesting experiments, 20 test tubes were provided with the cereal culture medium and inoculated with *E. aerogenes* and *T. thermophila*. Test tube microcosms were left for approximately four days to ensure that the ciliate populations had grown to at least $5 \mu\text{l}^{-1}$. Subsamples from each population were counted daily to determine the density prior to harvesting. Harvesting was conducted daily for eleven consecutive days, from day 4 to day 15, using a glass pasteur pipette under sterile conditions. All solution removed from the microcosm during harvesting was replaced with an equal volume of culture medium inoculated with *E. aerogenes*.

Five replicates were conducted for each of four harvest intensities, for a total of 20 sample populations per harvest strategy. Harvest intensities, hereafter referred to as low, medium-low, medium-high and high, were kept as similar as possible between strategies, using the following parameters.

Fixed proportion harvesting

The four harvesting rates were 10%, 30%, 50% and 70% of all individuals per day, based on volumetric considerations. The actual numbers of ciliates removed during this procedure were estimated by multiplying density counts by volume removed (Table 1).

Fixed quota harvesting

The four harvesting quotas were 16×10^3 , 55×10^3 , 79×10^3 , and 83×10^3 individuals per day, with quotas comparable to expected yields from the fixed proportion

harvesting procedure (Table 1). Quotas were used to calculate the volume to be removed, by dividing total harvest by ciliate density.

Fixed escapement harvesting

The four threshold densities were identified as 20, 15, 10, and 5 individuals μl^{-1} , based on 100%, 75%, 50% and 25% of the carrying capacity of *T. thermophila* noted during preliminary observations (Fig. 1). If the density of a population was found to be below the threshold, then no harvesting occurred that day. If the population was greater than the threshold, then the appropriate volume was withdrawn to remove excess individuals. Average harvests resulting from this procedure are shown in Table 1.

Although it is sometimes reasonable to use repeated measures or MANOVA to compare data from replicated time series, the acceptable conditions for this procedure were not met in our experiment. Repeated measures approaches are generally inappropriate for the kind of non-linear time series models most consistent with our data (Diggle 1990, Fuller 1996). Moreover, application of repeated measures analysis is only reliable when the number of time steps in each replicate is considerably less than the number of replicates in each treatment category (Diggle 1990). Given the non-linear nature of our system and limited replication, we felt that these assumptions were unsupported.

In light of these issues, we conservatively chose to completely eliminate any statistical bias caused by autocorrelation in the ciliate time series by simply working with mean population density and the variance in population density for each replicate during the period of harvesting (day 4–15). This provided a sample size of five independent replicates at every level of intensity for each harvesting strategy, yielding a total sample size of 60 means and 60 variances for subsequent statistical comparison. Two-factor ANOVAs were then performed to evaluate the overall effects of harvesting strategy versus harvest intensity and to see if the interaction between these two factors affected mean density and/or mean variance. Single-factor ANOVAs were then used separately for each of the three harvesting strategies to test whether intensity

Table 1. Average harvests over 10 days as a result of different harvest strategies and intensities.

		Harvest strategy		
		Fixed proportion	Fixed quota	Fixed escapement
Intensity	low	15 631	16 000	1250
	low-medium	54 654	55 000	15 452
	medium-high	79 300	79 000	28 728
	high	83 377	83 000	60 447

levels had a significant effect on mean density and/or mean variance.

Results

During the preliminary experiment, populations of *Tetrahymena* showed evidence of logistic growth, rapidly increasing from modest densities, then leveling off at densities ranging between 15–28 individuals μl^{-1} (Fig. 1).

Evaluation of the AIC_c values suggested that the Ricker logistic model best explained the variation in λ ($r^2=0.334$), followed by the Gompertz logistic ($\Delta\text{AIC}_c=1.8$; $r^2=0.319$) and non-linear logistic models ($\Delta\text{AIC}_c=3.5$; $r^2=0.323$), with the random walk model very poorly supported ($\Delta\text{AIC}_c=30.9$). The residuals around the fitted Ricker model (Fig. 2), were well-described by a normal distribution. The estimated carrying capacity was 19.4 individuals μl^{-1} , seen as the x-intercept in Fig. 2. The maximum growth rate ($r_{\text{max}}=y$ -intercept of regression of $\ln[\lambda]$ versus N) was 0.109 h^{-1} . While this growth rate may seem somewhat low for lab cultures, which could derive from low pH or low oxygen concentration arising in test tube conditions, we did not see any evidence of unusual mortality when *Tetrahymena* samples were examined visually.

On the basis of these preliminary measurements, we used the Ricker model as the demographic framework for stochastic harvesting models that applied one of the three alternate policies: fixed quota, fixed proportion, or fixed escapement. In each case, we assumed that harvesting occurred once a day, over a course of 10 consecutive days, with unperturbed population growth between harvesting episodes. The stochastic harvesting model

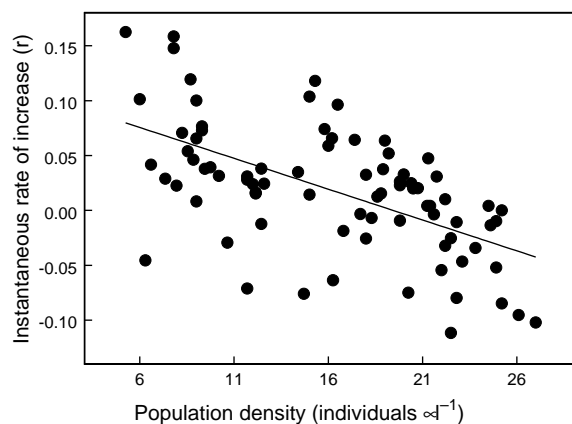


Fig. 2. Population growth rate per 4 h for *Tetrahymena thermophila* growing in 10 ml test-tubes, in relation to population density (individuals μl^{-1}) at the beginning of the 4-h interval. Note that the x-intercept is the carrying capacity (K) and the y-intercept the maximum intrinsic rate of growth (r_{max}) for the population.

was $N_{t+1}=(N_t-H_t)\exp[a-b(N_t)+\varepsilon_t]$, where the stochastic variable ε_t was a random deviate drawn from a Gaussian distribution with mean = 0 and $\text{sd}=0.048$. Note that this model presumes that population growth rate is conditioned on population density immediately preceding the instantaneous harvesting perturbation. The daily harvest (H) was constant in the fixed quota model. In the fixed proportion model, $H=qN$, where q is the proportion of the population harvested at each episode. In the fixed escapement model, $H=N-T$, where T is the population threshold below which harvesting is forbidden. Simulation models were run for 10 days, as per the experimental protocol, with 1000 replicates performed.

Results of these Monte Carlo simulations showed that fixed quota harvesting in this experimental system would be expected to yield higher variation in population density for a given level of average harvest than a fixed escapement or fixed proportion harvest policy, especially at quotas exceeding 7 individuals μl^{-1} (Fig. 3). As a consequence, our stochastic models predicted that there would be a sizeable risk of extinction in the fixed quota treatment (Fig. 4), but virtually no risk of extinction in the systems with fixed proportion or fixed escapement harvest treatments.

Mean densities of *Tetrahymena* in our experimental microcosms were sensitive to harvest policy ($F_{2,48}=30.29$, $P<0.001$), the intensity of exploitation ($F_{3,48}=51.98$, $P<0.001$), and the interaction between these factors ($F_{6,48}=11.27$, $P<0.001$). For all of these policies, mean ciliate density varied significantly with harvest

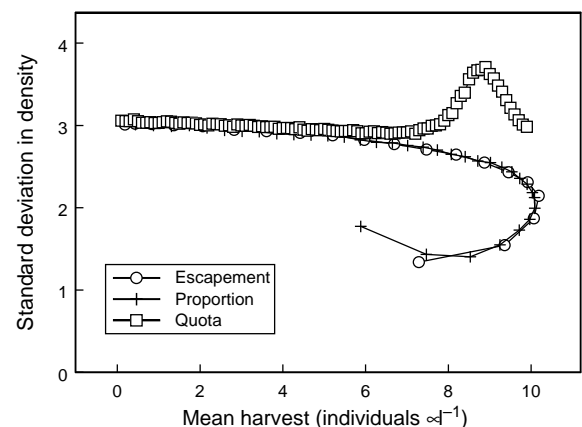


Fig. 3. Predicted standard deviation in population density of the ciliate *Tetrahymena thermophila* in relation to harvest level for three alternate policies: fixed escapement, fixed proportion, and fixed quota. For the fixed proportion and fixed escapement policies, two levels of variability are possible for a given level of harvesting. This is because high harvest proportion (or conversely low escapement) and low harvest proportion (or conversely high escapement) can produce similar harvest levels for some parameter values. Note that fixed quota harvesting yielded higher variation in population density than the other policies at mean harvests >7 individuals μl^{-1} .

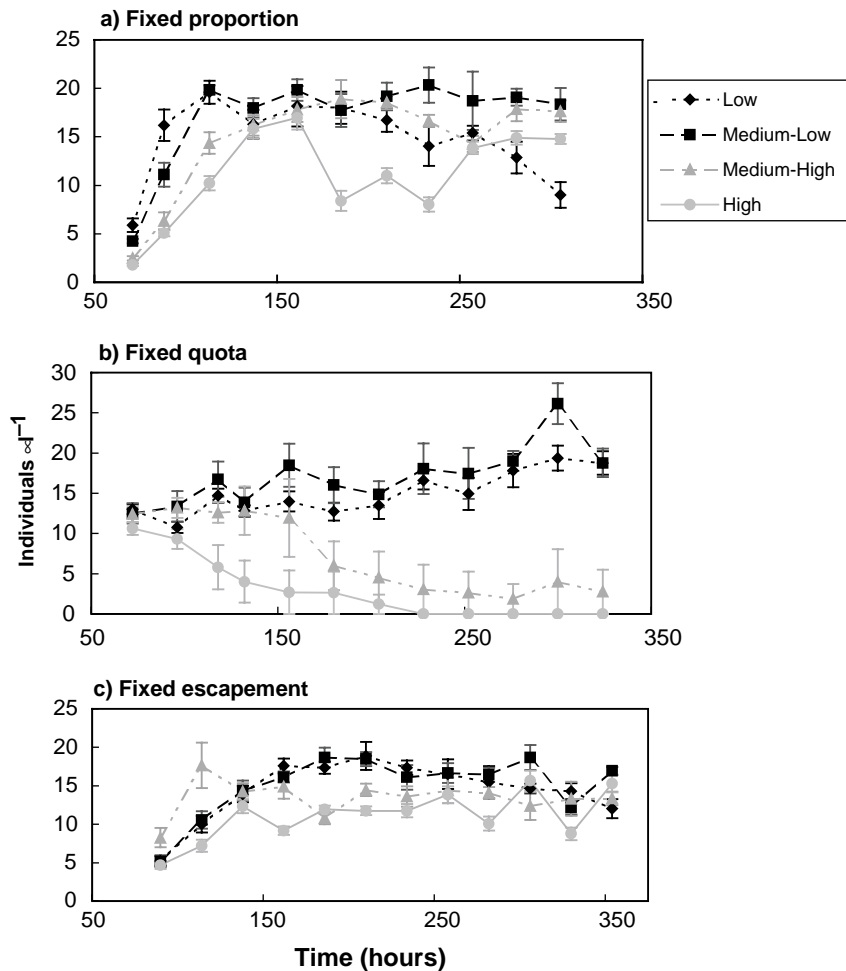


Fig. 5. Observed mean densities over time of five replicate populations of the ciliate *Tetrahymena thermophila* raised in 10 ml test-tubes. Ciliates were harvested at each at four different intensities (low, medium-low, medium-high, and high) using (a) fixed-proportion, (b) fixed quota, and (c) fixed escapement strategies.

intensity (fixed quota: $F_{3,16}=31.66$, $P<0.001$; fixed proportion: $F_{3,16}=23.81$, $P<0.001$; fixed escapement: $F_{3,16}=31.87$, $P<0.001$).

Variability in *Tetrahymena* densities in our experimental microcosms was also sensitive to harvest policy ($F_{2,48}=6.17$, $P<0.05$), but was unaffected by harvest intensity ($F_{3,48}=1.86$, $P=0.150$) or the interaction between harvest policy and harvest intensity ($F_{6,48}=1.64$, $P=0.156$). Fixed escapement harvesting produced the least variability in population density (Fig. 5). The densities in that treatment fluctuated around means of 11–18 individuals μl^{-1} and rarely dropped below 10 individuals μl^{-1} (Fig. 5c). Fixed proportion harvesting induced intermediate variation in *Tetrahymena* density over the span of the experiment, with densities dropping to below half the carrying capacity at times (Fig. 5a). Note that the model predicted essentially equal levels of population variability in the fixed escapement and fixed proportion treatments, which was inconsistent with the

difference in variability observed in the trials. As predicted, the fixed quota treatment had the highest variability in resource levels (Fig. 5b).

Fixed quota harvesting was the only strategy that caused populations to collapse (Fig. 4, 5). After eight fixed quota harvesting events, all the populations harvested at the high intensity and several at the medium-high intensity went extinct. The stochastic harvesting model successfully predicted a high degree of population persistence in the low and medium-low treatments, with increased extinction risk in systems with medium-high and high levels of exploitation intensity (Fig. 4).

Discussion

Our results support predictions made from a number of earlier theoretical models that a fixed quota harvesting

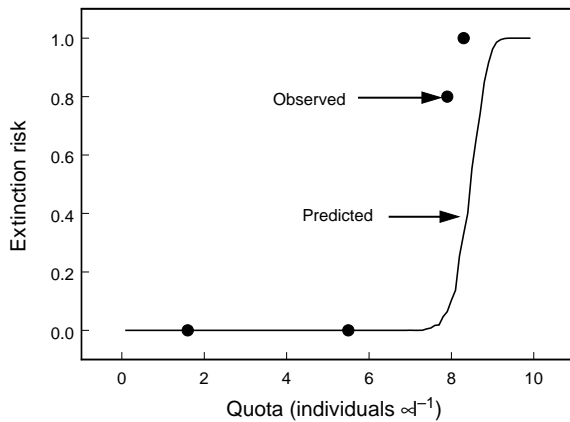


Fig. 4. Observed vs predicted risk of local extinction of the ciliate *Tetrahymena thermophila* growing in 10 ml test-tubes, as function of fixed harvest quota. Note that the predicted and observed risks of extinction were higher at medium-high and high quotas than at the low and medium-low quotas.

policy is more likely to lead to wide variation in population density and elevated probability of extinction than fixed proportion or fixed escapement policies. Although the fixed quota approach is central to the theory and practice of many resources (especially fisheries), a fixed quota policy does not provide a compensatory mechanism to accommodate environmental variation that will inevitably occur. For any quota below the maximum sustainable yield, there are two deterministic nontrivial equilibria: an upper equilibrium that is locally stable and a lower equilibrium that is locally unstable (Beddington and May 1977, May et al. 1978, Clark 1981). If stochastic environmental conditions cause population abundance to fall below the lower unstable equilibrium, then resource collapse becomes likely. Collapse of an exploited population is often countered by the imposition of a moratorium on harvests. Nonetheless, the economic and social costs of such a moratorium are severe. Fixed quota harvesting has been blamed for the depletion of several fisheries around the world. Clark (1981) likens constant quotas to invitations to disaster in a world of varying environments and imperfect data sets.

Our experimental results support the utility of fixed proportion and fixed escapement harvesting policies. Provided that the harvested proportion does not exceed the maximum per capita rate of change, then the deterministic equilibrium for the harvested population should be locally stable. This is because the magnitude of the harvest is scaled to resource abundance: the smaller the stock size, the smaller the harvest. Fixed escapement harvesting also has a built-in mechanism to accommodate environmental variability in vital rates, because harvesting is curtailed whenever the population falls below the threshold (Lande et al. 1997). Due to experience with past management failures, some harvesting plans now require the maintenance of a minimum

population density to ensure replenishment of that resource (Roberts 1997). One drawback to both of these harvesting methods, however, is that population size must be known in advance of harvesting to determine exactly how many individuals to remove. Moreover, both fixed proportion and fixed escapement policies produce higher temporal variability in harvests than does a fixed quota policy, so there is a political and economic cost to enhanced ecological sustainability.

We modeled the population dynamics of *Tetrahymena* using a simple, single-species logistic equation. This representation is obviously a considerable simplification of the true 3-link food chain: detritus, bacteria, and a predator of bacteria (*Tetrahymena*). It is common, indeed typical, for management of harvested resources to be based on single species models that are caricatures of the true foodweb relationships. In our experimental system, there was an additional wrinkle: harvesting required removal of detritus and bacteria as well as *Tetrahymena*. The fact that a single species logistic model captured most of the observed dynamics suggests that food chain dynamics are quite stable in this system. There is no reason to expect this to be generally the case, however, so successful application of such a demographic simplification in this case may have been simply fortuitous.

Despite these caveats, the density-dependent, single species model captured much of the observed variation in growth rates in the preliminary study. This simple demographic model was also able to predict the risk of stock collapse under the kind of controlled exploitation available in the lab. Such prediction was made possible by extensive sampling of population growth rates over a wide range of densities. This yielded not only reliable estimates for demographic parameters, such as the maximum rate of growth and ecological carrying capacity, but also a meaningful estimate of the residual variability in growth rates around fitted demographic relationships. This is essential information for useful estimates of population viability, regardless of whether the population is being harvested or not (Ludwig 1998). Replicated sampling of growth rates over a wide range of densities is a challenging problem, however, in most natural systems (Walters 1986, Hilborn et al. 1995, Nichols et al. 1995), making projections of long-term viability a perilous proposition (Ludwig 1999).

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