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PERSISTENCE OF AN EXTINCTION-PRONE PREDATOR–PREY INTERACTION THROUGH METAPOPULATION DYNAMICS

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Abstract. In theory, predator–prey pairs with extinction-prone local populations can persist through metapopulation dynamics, wherein local populations fluctuate asynchronously, occasionally providing dispersers that prevent permanent extinction in all patches. A few studies have shown that spatial structure can extend predator–prey persistence. However, no studies have unequivocally demonstrated the asynchrony among patches, low dispersal rates, and rescue effects that prove metapopulation dynamics extend persistence. We used a protist predator–prey pair to show that spatial subdivision lengthens persistence through metapopulation dynamics. The pair comprised the predaceous ciliate, *Didinium nasutum,* feeding on the bacterivorous ciliate, *Colpidium* cf. *striatum.* A replicated experiment assessed how habitat subdivision affects persistence. Undivided habitats were of four volumes: 30, 180, 270, and 750 mL. Subdivided microcosms, or "arrays," were groups of nine or 25 linked 30-mL bottles (270 or 750 mL total volume). In arrays, predators and prey persisted for 130 d (602 prey and 437 predator generations), at which point the experiment ended. Predators went extinct in undivided microcosms of equivalent volumes within a mean of only 70 d. Predators persisted for a mean of just 19 d in isolated 30-mL bottles (equivalent to isolated patches of arrays). In a separate experiment, prey were driven extinct in four of 15 isolated 30-mL bottles, and persistence times of predators were broadly similar. We documented the following hallmarks of metapopulation dynamics: (1) asynchronous fluctuations in different subpopulations; (2) frequent local prey extinctions and recolonizations; (3) persistence of protists in arrays, despite extinction of isolated local populations; and (4) rescue effects in predator populations.

Other experiments measured dispersal rates and the effects on local dynamics of immigrant predators and prey, and initial predator : prey ratios. Only a small fraction of protists dispersed within a generation, consistent with metapopulation dynamics. Immigration of predators increased the frequency of local extinctions of prey, and immigration of prey increased the persistence of both predators and prey. Higher initial predator : prey ratios decreased the persistence of prey in undivided volumes.

Although the pair persisted regionally in arrays, data indicated that local extinctions of prey were common. In array patches, predator : prey ratios were higher and predator–prey cycles were shorter than in undivided volumes. Dispersal made local dynamics more prone to extinction, yet promoted regional persistence because the risk of extinction of distant subpopulations became independent.

Key words: dispersal; immigration; metapopulation; persistence; predator–prey; Protista; rescue effects; subdivision; turnover.

INTRODUCTION

In theory, local populations that cannot persist in isolation may be able to persist through metapopulation dynamics, where a collection of extinction-prone local populations are linked by dispersal (Levins 1969, Hanski 1991, Harrison 1991). This dispersal either balances local extinctions with recolonizations, or dispersers may *rescue* local populations from extinction altogether (Brown and Kodric-Brown 1977, review in Harrison and Taylor 1996). Metapopulation theory was first developed for single species, but has also commanded attention as a potential explanation for the persistence in nature of extinction-prone species interactions (Zeigler 1977, Crowley 1981, Reeve 1988, Kareiva 1990, Taylor 1990, 1991, Hassell et al. 1991, Nachman 1991, Tilman 1994, Tilman et al. 1994). Despite widespread theoretical interest, two-species metapopulations have rarely been studied experimentally, and few, if any, of the existing studies have provided the data needed to demonstrate metapopulation dynamics (Kareiva 1990, Taylor 1990, 1991, Harrison and Taylor 1996). Before presenting our experiments, we outline the evidence needed to prove that an extinction-prone interaction persists through metapopulation dynamics, and then briefly discuss the existing studies of predator–prey metapopulations.

To demonstrate that an interaction persists because

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of metapopulation dynamics, it is first necessary to show that the interaction cannot persist in local patches that are isolated from dispersers. It is also essential to show that the interaction cannot persist in undivided habitat of volume equivalent to the total of the subdivided habitat, because large populations generally persist longer than small ones (small populations being more prone to extinction through demographic stochasticity). In addition, patches must be similar enough that the interaction between the species is extinction prone in all patches. Otherwise, populations may persist because one or more of the patches serves as a permanent *refuge* population, which provides a source of colonists. This scenario is not a true metapopulation, but a "core–satellite" or "island–mainland" system in which the populations persist only because of the refuge (Boorman and Levitt 1973, Pulliam 1988, Pulliam and Danielson 1991).

Demonstrating metapopulation dynamics also requires data showing that local population dynamics are asynchronous, and that only a small proportion of the population disperses within each generation. Asynchronous fluctuations in local abundance are necessary for the persistence of metapopulations, because asynchrony reduces the risk of simultaneous extinction of all subpopulations by creating an independent risk of extinction in different patches (Zeigler 1977, Crowley 1981). Asynchrony also permits rescue effects to operate by creating different abundances in nearby subpopulations at any point in time. With asynchrony, individuals may disperse from patches where they are abundant, thereby supporting populations in surrounding patches. Dispersal rates are also crucial to metapopulation dynamics: organisms must disperse at a sufficient rate to balance local extinction with recolonization, but the proportion of the population dispersing cannot be too great or the subpopulations will become synchronous. Additionally, if predators inevitably drive prey extinct locally, predators must disperse at a low enough rate that they cannot colonize all patches and drive all prey subpopulations simultaneously extinct (Taylor 1990, 1991).

Evidence for predator–prey metapopulations is all but lacking in field studies. In extensive reviews of field predator–prey systems, Taylor (1990, 1991) found that most studies had not collected sufficient information to distinguish between population and metapopulation dynamics. In field studies, it is particularly difficult to quantify dispersal, or to prove that refuges are absent and that local populations are truly extinction prone. Of those studies that did collect the required information, most resembled single populations or mainland–island systems. The only clear examples of a predator–prey interaction with a metapopulation component to persistence are semifield experiments on a greenhouse mite predator–prey pair (Nachman 1981*a, b,* 1987*a, b,* 1991). In this system, prey undergo local extinctions lasting for several generations, followed by recolonizations, which is consistent with metapopulation theory. However, it is unclear whether predators persist as a population or metapopulation, because they can disperse across several patches (plants) within a generation, and may disperse in response to low prey densities, making their movements more like foraging behavior (Taylor 1991).

Metapopulation dynamics are easier to demonstrate in laboratory tests than in the field, because patch uniformity and dispersal can be controlled and monitored more readily. Several laboratory studies have shown that habitat subdivision promotes coexistence of predators and prey in systems that would not persist without subdivision (Huffaker 1958, Huffaker et al. 1963, Pimentel et al. 1963, Maly 1978). These innovative investigations were conducted prior to the development of metapopulation theory, and, not surprisingly, did not attempt to distinguish between population and metapopulation dynamics.

We tested how spatial subdivision of microcosms altered the dynamics of a protistan predator–prey pair, and whether or not metapopulation dynamics were important to persistence. The rapid generation times of aquatic protozoans permit dynamics to be easily quantified, so that metapopulation theory can be tested more thoroughly than in other systems. We were also able to study how dispersal modifies local, within-patch dynamics, a subject that has been almost entirely neglected in metapopulation theory (but see Nachman 1987*b,* 1991, Reeve 1988).

We set out to test whether or not a predator–prey interaction that is known to be extinction prone in undivided microcosms could persist in spatially subdivided habitats, and if so, whether or not metapopulation dynamics were the cause of persistence. To this end, we carried out four experiments. The extinction-prone pair were the predatory ciliate *Didinium nasutum* and the bacterivorous ciliate *Colpidium* cf. *striatum.* In 100-mL bottles, their interaction usually ended with the predator going extinct in <30 d (Morin and Lawler 1996). In an immigration experiment (the third experiment described), we showed that prey were driven extinct in four of 15 replicate 30-mL bottles, and both species persisted for an average of ≤22 d. Both studies found that populations in undivided microcosms of up to 100 mL were extinction prone. In the first experiment, we measured the persistence and spatial dynamics of this predator–prey pair in subdivided and undivided microcosms of equivalent volume. In a second experiment, we quantified predator and prey dispersal rates. Thirdly, we tested whether or not predator and prey immigration altered local persistence and dynamics. Finally, we tested how the predator : prey ratio at the start of experiments affected subsequent persistence of the pair in isolated local populations.

Methods

The study organisms

Didinium nasutum and *Colpidium* cf. *striatum* inhabit freshwater ponds and lakes. Protists are known

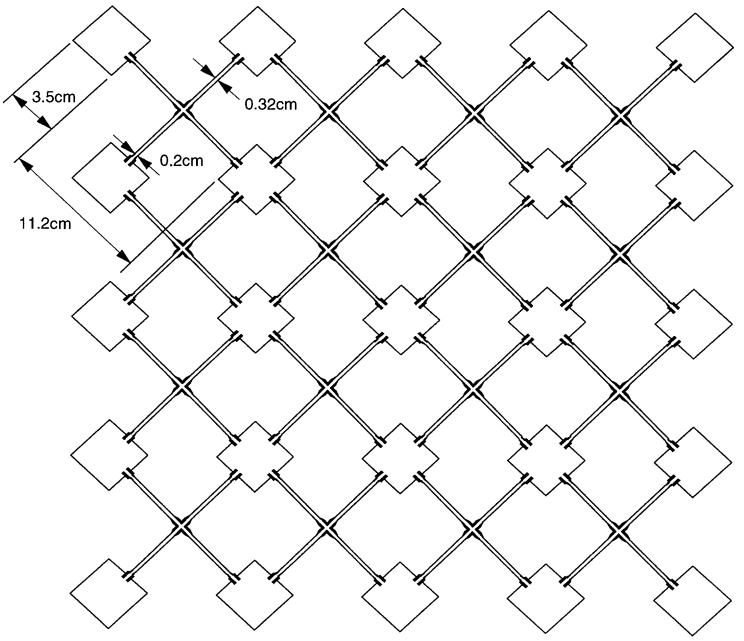

FIG. 1. Plan view of a 25-bottle subdivided array showing the links between bottles. Bottles contained 30 mL of solution, less 0.9 mL for each connecting tube. Each tube between the plastic bottle and the center of the four-way connector (the "X"-shaped piece) contained 0.9 mL. The internal diameter of tubes varied between 0.2 and 0.32 cm because of the connectors.

to be patchily distributed at scales of just centimetres in ponds (Taylor and Berger 1980). *Colpidium* is a bacterivore, and has a high maximum intrinsic growth rate relative to similarly sized ciliates (Taylor 1978). *C. striatum* in our experiments did not and, as far as we know, cannot form resting cysts. *D. nasutum* can encyst when feeding on larger species of *Paramecium* (Beers 1935); however, it did not form cysts (which are easily identified) when feeding on *C. striatum* in any of our experiments, and appears to be unable to do so. *Didinium* is a rapidly swimming, active predator (Laybourn 1977) that feeds primarily in the water column (Berger 1980). *Didinium* accelerates toward currents caused by passing prey and ensnares the prey with trichocysts if contact occurs (Wessenberg and Antipa 1970). *Didinium* increases in cell size upon consuming prey, and divides when ≈18 *C. striatum* have been consumed (M. Holyoak and S. P. Lawler, *unpublished data*) and the cell cycle permits (Salt 1975, Hewett 1980). The length of the predator cell cycle creates a developmental delay that contributes to the nonpersistence of the predator–prey interaction between *Paramecium caudatum* and *D. nasutum* (Maly 1978).

Spatial subdivision experiment

The goals of this experiment were: (1) to test whether or not spatial subdivision could promote coexistence of an extinction-prone predator–prey interaction; and (2) to quantify spatial and temporal dynamics, thereby establishing whether the pair persisted via population or metapopulation dynamics.

The predator *Didinium* and its bacterivorous prey *Colpidium* were supported on a mixed bacterial suspension in semicontinuous batch culture, using aqueous nutrient medium made from Protozoan Pellets (Carolina Biological Supply). Each 30-mL volume also contained a millet seed that provided a slow release of nutrients. Containers were chosen so as to keep volume and air–water surface area constant. Culture vessels were either spatially continuous glass containers (containing 180, 270, or 750 mL of medium at a constant depth), 30-mL polypropylene bottles, or subdivided microcosms constructed by linking arrays of nine or 25 of the 30-mL bottles. Array bottles contained inner connecting nuts and tubes that displaced 0.9 mL of medium, so connecting tubes were cut to a length that contained 0.9 mL of fluid. This gave total volumes of 270 and 750 mL in arrays, respectively. The layout of a 25-bottle array is shown in Fig. 1; nine-bottle arrays were linked in a similar manner. There were three replicates of each volume in subdivided and spatially continuous treatments. Microcosms were kept at room temperature (22 ± 2°C).

Microcosms initially contained sterile protozoan pellet medium. Medium was bacterized by adding a drop (≈0.028 mL) of a mixed inoculum of bacteria to each array bottle and to each 30-mL volume in the 270-mL undivided microcosms. Bacteria were obtained by filtering *Colpidium* cultures through a 5-μm nylon filter, which retains protists but not bacteria. The bacteria species present and their abundances were not quantified. A day later, ≈56 *Colpidium* from a stock culture

were added to each 30-mL volume. After another day, ≈27 *Didinium* were added to a corner bottle of each array and to the undivided volume.

A 1.8-mL sample was taken weekly from each 30 mL (all array bottles, and a sample per 30 mL from undivided microcosms) up to day 54, and at 2-d intervals between day 54 and day 102, to collect a detailed record of spatiotemporal dynamics. After day 102, samples were taken at 2-d intervals, but were only counted on days 110, 120, and 130, when the experiment was halted. Prior to removing samples from arrays, we isolated bottles by tightly closing all lids except from the bottle being sampled; this minimized flow among bottles by creating an air lock. Bottle contents were thoroughly mixed with a Pasteur pipette before samples were withdrawn. Samples were replaced with fresh, sterile nutrient medium. To count *Colpidium* and *Didinium,* we used a binocular microscope to census a three-drop subsample taken from the 1.8-mL sample. If fewer than three individuals were present, the rest of the sample was censused. In preliminary experiments, this sampling procedure yielded a coefficient of variation between samples of ≈0.16 for predators and ≈0.09 for prey (n = 90). Counts were converted to densities per millilitre.

Colpidium shows logistic growth in the absence of *Didinium,* and has never been observed to drive its bacterial prey extinct (Morin and Lawler 1996). We therefore treated *Didinium* and *Colpidium* as a predator–prey system, as previous authors have done with *Didinium* and *Paramecium* (Gause 1934, Luckinbill 1973, 1974, 1979, Salt 1974, 1975, Luckinbill and Fenton 1978, Maly 1978, Hewett 1980, 1987). We calculated persistence times, average densities, the coefficient of variation (CV) of density, and spatial synchrony for predators and prey, the period of predator–prey cycles, and predator : prey ratio. This was done using 20 samples at 2-d intervals starting on day 54. Predator : prey ratios were calculated as the mean predator density per array divided by the mean prey density per array. Mean densities, predator : prey ratios, and CVs were compared between treatments by using Student's t tests and applying a sequential Bonferroni correction to preserve the 0.05 rate of false rejection of the null hypothesis of no difference. To compare mean densities in bottles within subdivided microcosms that had different numbers of tubes, we used one-way ANOVAs to compare ln(mean density + 1), carried out separately for predators and prey. Before applying ANOVAs, we tested means for normality using chi-square tests.

Spatial synchrony was quantified using lag-zero cross-correlation (Hanski and Woiwod 1993), r, measured using 20 samples taken at 2-d intervals (from day 54). If X_i and X_j are the natural logarithms of density + 1 in the bottles i and j of an array at a given time, then r is the correlation between X_i and X_j. When estimating synchrony, it is necessary to remove a bias caused by simultaneously recorded zero density values in pairs of bottles, because these reflect simultaneous extinctions rather than similar densities. To simplify interpretation of how synchrony changes with distance in subdivided arrays, we used multiple regressions of synchrony (r) against distance between bottles (slope b) and numbers of densities that were zero (slope z) in a pair of bottles simultaneously. Separate regressions were carried out for predators and prey in each array. The resulting slope b is a measure of how spatial synchrony changes with the distance between subpopulations, and the intercept a measures synchrony at a distance of zero. Distance was measured in units of the distance between pairs of adjacent bottles. Regressions were weighted for numbers of nonzero abundance values.

The period of cycles was measured by locating maxima and minima using turning point tests (Kendall and Stuart 1969). This method locates the times at which maximum and minimum abundances occur by looking at changes in successive densities. The period of the cycle is then the time period between successive maxima or minima. We did not apply tests for random distribution of periods because these are of low statistical power. Instead, we averaged the periods and used student's t tests to test whether or not the periods of cycles differed between undivided containers and arrays.

We were not able to characterize predator–prey dynamics in the original 30-mL bottles because predators went extinct rapidly, before we began to sample at 2-d intervals on day 54. Instead, we quantified the dynamics in 30-mL control bottles from the immigration experiment. The immigration experiment was set up and sampled in an identical manner. Predator starvation rate was measured in a side experiment. We placed 50 *Didinium* in each of 21 vials containing 3 mL of medium without prey. We destructively sampled and counted the *Didinium* in three vials daily, until no survivors remained.

Dispersal rates

This experiment provided estimates of the dispersal rates of predators and prey in subdivided arrays. Pairs of 30-mL bottles were linked, as in the subdivided microcosms (Fig. 1), and were filled with bacterized medium. Either prey, predators, or both were placed into the first bottle of each pair (Table 1). Either nothing or prey was added to the second bottle (Table 1). Replication is shown in Table 1. After 1 h, numbers of individuals that dispersed to the second bottle were sampled. The first bottle was also sampled, so that the data could be adjusted for any reproduction or predation (Table 1). From numbers dispersing within 1 h and densities in the first bottle, we calculated the proportion dispersing per hour.

We calculated the proportion of individuals that dispersed and tested whether or not dispersal was density dependent. Logistic regression is an unbiased way to

TABLE 1. Dispersal rates of predators (*Didinium nasutum*) and prey (*Colpidium striatum*) in pairs of linked 30-mL bottles. Individuals were placed in the first bottle and dispersed to the second bottle. *n*, number of replicates; *P* for density dependence is the *P* value from a test of density dependence (see *Dispersal rates* section of *Methods*). To adjust values for reproduction during trials, density in the first bottle was estimated as the geometric mean of initial numbers and numbers 1 h later. In each dispersal experiment, prey were at eight different initial densities between 32 and 645/mL, and predators were at eight different densities between 5.2 and 12.4/mL.

Contents of first bottle	Contents of second bottle	*n*	Proportion dispersing per hour ($\bar{X}$ ± SE)	*P* for density dependence
Dispersal of prey:				
Prey culture diluted with bacterized medium†	bacterized medium†	57	0.004 ± 0.0006	≈0.4
Prey and predators in predator culture medium	filtered predator culture medium‡	40	0.017 ± 0.003	≈0.2
Dispersal of predators:				
Predator culture containing prey	filtered predator culture medium‡	40	0.035 ± 0.006	≈0.5
Predator culture containing prey	filtered prey culture medium‡	40	<0.0027§	not applicable

† Medium was bacterized by adding one drop of filtered solution (using a 5-μm nylon filter) from the *Colpidium* culture per 30 mL at 1 h prior to the experiment.

‡ A 5-μm nylon filter was used to remove protists but not bacteria.

§ No predator individuals dispersed in this treatment. A single individual dispersing would have given a dispersal rate of 0.0027/h.

test for density dependence (Hails and Crawley 1992). We regressed the proportion dispersing (per hour) against density in the bottle from which dispersers originated; regressions were carried out exactly as described in Hails and Crawley (1992), except that proportion dying was replaced by proportion dispersing after 1 h, and initial density was the geometric mean of densities after 0 and 1 h in the first bottle. We conducted separate regressions for experiments set up under different conditions of predator and prey abundance, as shown in Table 1.

Immigration experiment

To measure how addition of a single pulse of immigrant predators or prey influences local dynamics in subdivided microcosms, we conducted experiments in isolated 30-mL bottles, which are equivalent to isolated patches in subdivided microcosms.

Thirty bottles with predators and prey were started in a manner similar to the previous experiment, except that initial densities were ≈12 *Colpidium* and exactly four *Didinium*. Additionally, predators were added 2 d after prey, not 1 d, as in the spatial subdivision experiment. Two additional bottles were set up containing prey but no predators. Four days after the addition of *Didinium,* extra immigrant predators, prey, or both were added to each of five bottles. The remaining 15 bottles were controls that received no extra predators or prey. The number added was 10% of the maximum density of predators and prey observed during the first 4 d after addition of *Didinium*; numbers were ≈3314 *Colpidium* and ≈49 *Didinium* in 2.86 mL. The same volume (2.86 mL) of sterile medium was added to the 15 controls. The experiment was sampled every 2 d using the same procedure as in the spatial subdivision experiment. Additionally, if no predators or prey were recorded in the sample, the entire 30 mL was checked to confirm presence/absence. Presence/absence of predators and prey was confirmed on the days between samples by pouring the bottle contents into a sterile petri dish and observing it under a binocular microscope; this enabled persistence times to be assessed more accurately. Sampling continued until either *Didinium* or *Colpidium* and *Didinium* went extinct. Samples were used to calculate the mean and CV of predator and prey density, persistence times, predator : prey ratio, and the period of predator and prey cycles, as in the previous experiment. Statistical methods were identical to those in the spatial experiment, except that we used *G* tests to compare the proportions of bottles in which predators and prey went extinct in the different treatments. Additionally, ln(persistence times) in different treatments were compared using one-way ANOVAs conducted separately for each species; lumped ln(persistence times) for either predators or prey did not differ from normality in chi-square tests.

The time series of abundances from the controls of this experiment contained zero values; some of these represented confirmed extinctions and some were due to sampling error. We used these time series to calculate the probability that one or more zero values represented a confirmed extinction. To do this, we calculated the proportion of observations of a given number of consecutive zero densities that represented true extinctions. This allowed us to judge the probability that sequential zero abundances in array bottles represented local extinctions. Because of the links between bottles, we could not confirm extinctions in the arrays without disrupting the experiment.

We estimated generation times of the protists, using data from all 30 microcosms during the first 48 h after each species was added to the microcosms. Populations peaked at 96 h, so these estimates represent a period of rapid growth. The number of prey divisions in 48 h

was calculated as [ln(final density) − ln(initial density)]/ln(2). Generation time was 48/total number of divisions, averaged across microcosms. This method could underestimate generation times in the main experiment, where the medium was older. Therefore, we performed a side experiment to measure the generation times of *Colpidium* in aged medium. We placed a single *Colpidium* in each of 32 vials containing 2 mL of medium taken from array samples on day 100 of the spatial experiment. The medium was filtered to exclude protists but not bacteria. The resulting populations were killed 20 h later with Lugol's Iodine and censused. Nine vials that had no *Colpidium* were eliminated from calculations because the original cell was inviable or lost. This method could still underestimate generation times in arrays if generation times were density dependent and mean prey densities were high, but, as we will demonstrate, prey densities were extremely low in arrays. Our estimate of predator generation times may be low if predators are strongly density dependent, because predators were sometimes abundant in arrays.

Initial predator : prey ratio experiment

To test whether or not high predator : prey ratios could change the ability of the pair to persist in isolated populations, we conducted an experiment in which we started undivided microcosms with a range of predator : prey ratios. The experiment was conducted in 30-mL bottles and used predator : prey ratios selected from the values seen in individual array bottles. The predator : prey ratios used were high enough to cause predator and prey abundances to decline very rapidly once predators were added, making it difficult to accurately measure dynamics. Therefore, we analyzed only the times for predators and prey to reach a minimum density.

Bottles were started as in the previous experiments, except that predator and prey densities differed. Predator densities were calculated to give an initial predator : prey ratio of 0.05 (two bottles), 0.2 (four bottles), 0.6 (four bottles) and 1.0 (five bottles). Replication was idiosyncratic because of difficulty in obtaining the large numbers of predators needed to set up this experiment. Dynamics were monitored daily, as described in the immigration experiment. Because of the discreteness of persistence times, we used linear models to compare ln(persistence time) of predators and prey in the different treatments; we weighted for sample size and assumed a Poisson distribution of persistence times. Lumped persistence times from all treatments for predators or prey did not differ from Poisson distributions in chi-square tests.

Results

Persistence in subdivided and undivided microcosms

The predator–prey interaction persisted for only short periods of time in undivided microcosms of 30-mL volume; these are equivalent to isolated patches in the subdivided arrays. In the experiment on spatial subdivision, prey persisted in all three replicates, but predators went extinct in only 18 ± 1 d (mean ± 1 SE; Fig. 2). Extinctions also occurred in all of the controls from the immigration experiment that were started under similar conditions. Prey went extinct before predators in four of 15 replicates (27%); in the remainder (73%) of bottles, predators went extinct but prey persisted to the end of the experiment. The mean persistence time of predators in this experiment was 22.6 d (95% CI = 21.2–24.0 d) in replicates where predators did not drive prey extinct. The mean persistence time of prey in replicates where they went extinct was 14.0 d (95% CI = 12.0–15.7 d).

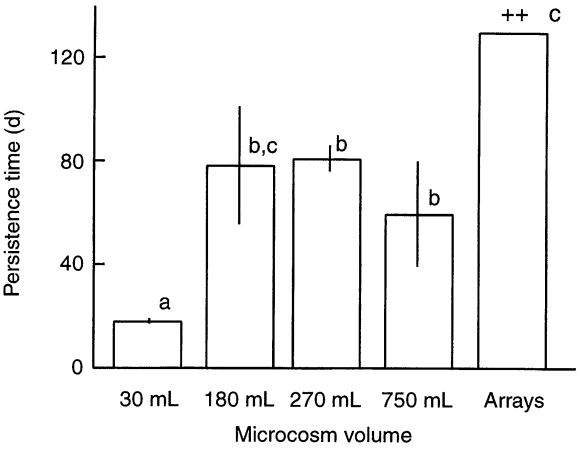

FIG. 2. Mean persistence times of predators, *Didinium,* in subdivided and undivided microcosms of various volumes. "Arrays" represents both nine- and 25-bottle subdivided microcosms. Error bars show ± 1 SE; there were three replicates per treatment. The ++ symbol indicates that no extinctions occurred in either nine- or 25-bottle arrays when the experiment was halted on day 130. Bars with the same letter above them did not differ in Student's *t* tests. For comparisons of 30 and 270 mL, or 30 and 750 mL, or 270 and 750 mL, df = 4; for comparison of the arrays with any of the undivided treatments, df = 7. We applied a sequential Bonferroni correction to preserve the Type I error rate of 0.05.

In the larger undivided microcosms, 270 and 750 mL, with total volume equivalent to the subdivided arrays, predator *Didinium* persisted for 70.2 ± 10.5 d (mean ± 1 SE). This is substantially longer than in the smaller 30-mL bottles (Fig. 2).

Spatial subdivision dramatically changed the ability of *Didinium* and *Colpidium* to coexist. Although predators went extinct in undivided microcosms of equivalent total volume to the arrays (270 and 750 mL) in a mean of just 70.2 d, they did not go extinct in all bottles of the arrays during the 130-d experiment. Data from the immigration experiment show that this represents ≈602 prey generations and ≈437 predator generations (generation times for prey: 5.18 ± 0.02 h, mean ± 1 SE; for predators: 7.14 ± 0.02 h; generation time of prey on aged medium: 5.18 ± 0.03 h). Mean

TABLE 2. Spatial synchrony of population density fluctuations in arrays (three replicates, Rep.). Spatial synchrony was measured using lag-zero cross-correlation, r (Hanski and Woiwod 1993), which is simply Pearson's correlation between densities in bottles that are a distance d apart, through 20 consecutive densities at 2-d intervals (from day 54). The column labeled r_1 gives the mean correlation between adjacent pairs of bottles. The rest of the table gives the results of a multiple regression† of r against distance (slope b) and the number of density values that were simultaneously zero in both bottles of a pair (slope z), which represents a source of bias. n, total no. r values used in multiple regression. All values in the table were significant at $P < 0.05$; NS indicates nonsignificant values ($P > 0.05$).

		Prey (*Colpidium*)				Predators (*Didinium*)			
Rep.	n	a‡	b	z	r_1§	a‡	b	z	r_1§
1	300	0.367 ± 0.027	NS	NS	0.367	0.222 ± 0.024	−0.033 ± 0.011	0.144 ± 0.039	0.189
2	300	0.371 ± 0.040	−0.042 ± 0.013	0.041 ± 0.010	0.329	0.466 ± 0.018	−0.054 ± 0.009	0.055 ± 0.023	0.412
3	300	0.227 ± 0.039	−0.032 ± 0.015	0.045 ± 0.013	0.195	0.284 ± 0.023	−0.061 ± 0.011	NS	0.223

† The regression equation was: synchrony = $a + b \times$ distance + $z \times$ number of zero densities.
‡ If r did not decline with either distance or number of zeros, then a is arithmetic mean (and SE) of r.
§ r_1 values were estimated from regression from equations assuming no zero densities.

persistence times of predators in the spatial subdivision experiment are shown in Fig. 2. Taking 130 d as the mean persistence time for arrays, mean persistence times differed between arrays and undivided microcosms ($t_{10} = 5.67$, $P < 0.001$). Furthermore, the increases in persistence time in subdivided arrays were over and above those caused by increases in volume between 30- and 270–750-mL bottles, showing that increased persistence time in the subdivided arrays is not merely an effect of increased volume. Prey did not go extinct in any of the undivided microcosms in the spatial subdivision experiment, or in all bottles of any of the arrays.

The spatial experiment: evidence for metapopulation dynamics

Dynamics in 270- and 750-mL microcosms were similar, so we illustrate the mode of persistence in arrays with results from the 750-mL microcosms. Metapopulations of predators and prey were indicated by the following points:

1) Prey and predator population fluctuations in adjacent bottles were only partially synchronous (see r_1 values in Table 2), and synchrony declined with the distance between array bottles in five of six cases (Table 2).

2) Dynamics in individual 30-mL bottles were similarly extinction prone, so that the arrays were unlikely to persist through "island–mainland" dynamics. Predators went extinct in all isolated 30-mL bottles in a mean of 18 ± 1 d in the spatial experiment. There were 15 more replicates of this treatment in the immigration experiment, in which predators went extinct in a mean 19 ± 6.4 d; this figure differs from that in the previous section because it includes replicates where predators drove prey extinct.

3) Prey frequently went locally extinct and recolonized individual patches of arrays. We could not directly confirm local extinctions in the arrays without disrupting the experiment, but we often observed series of several zero sample densities from individual bottles. Data from the immigration experiment show that series of recorded zero densities are strongly correlated with extinctions confirmed by examining the entire bottle contents (Fig. 3A). For example, in each array there was a mean of 20 observations of three consecutive zero prey densities in various bottles. In the immigration experiment, 73% of such observations were actual extinctions.

4) Predator extinctions probably occurred, but were less common. Sequential zero values for predators were rare in arrays. In 500 observations, there was a mean of only 21 single zero values in each array; data from control bottles of the immigration experiment indicate that each one had a 0.491 probability of representing an extinction (Fig. 3B). There was a mean of only 3.3 sequential zeros in each array, each with a probability of ≥0.79 of being an extinction.

5) That local dynamics were extinction prone in arrays was further indicated by relatively high variability in prey densities (measured as CV of density) in single array bottles. Population variability of prey was at least as great in individual bottles of subdivided arrays as in isolated 30-mL bottles, in which 27% of populations went extinct (data for isolated 30-mL bottles from the immigration experiment; Fig. 4A, B).

Dynamical differences in arrays vs. continuous volumes

The spatial experiment also showed intriguing differences in predator–prey cycles between arrays and undivided volumes that may relate to the risk of extinction. As mathematical stability (sensu Case and Casten 1979) declines, there is a theoretical progression from a point equilibrium, to simple cycles of increasing amplitude or reduced period, to cycles of increasing complexity, until chaos ensues (May 1973). In subdivided microcosms, the mean density of predators and prey across all subpopulations did not show clear cycles, which is consistent with dynamics that have high mathematical stability (Fig. 5A). Predator populations were also more abundant (Fig. 5B) and showed lower amplitude fluctuations in arrays than in undivided 750-mL microcosms (as indicated by lower CVs for regional

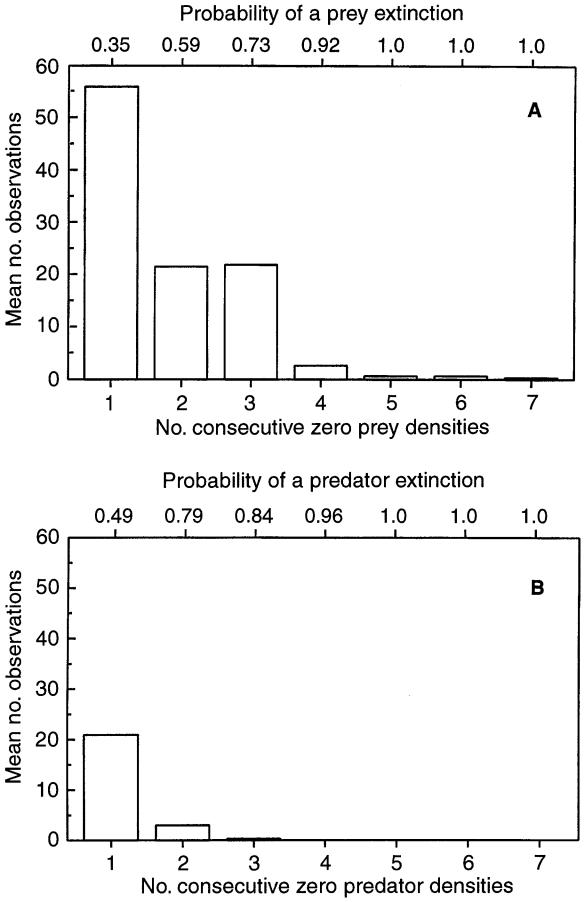

FIG. 3. The frequency of zero densities recorded for prey (A) and predators (B). The bars show the total number of observations of a given number of sequential zero density values in bottles of 5 × 5 arrays, and the probability of extinction represented by each observation. The probability of extinction was calculated from isolated 30-mL control bottles used in the immigration experiment, where extinctions were confirmed by examining the entire bottle contents. Note that the scale on upper axes is nonlinear.

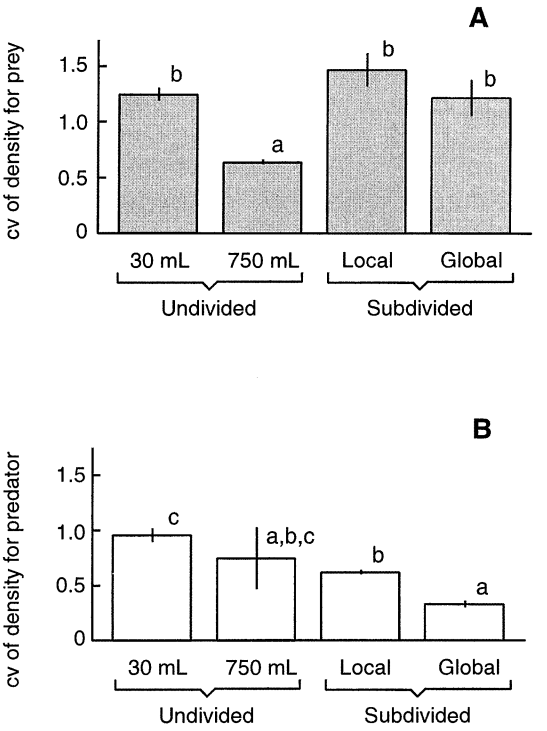

FIG. 4. Population variability of prey (A) and predators (B) in subdivided and undivided microcosms. Plots show the mean coefficent of variation (CV) across microcosms and its standard error from three replicates of 750-mL undivided microcosms or 750-mL arrays from the spatial subdivision experiment, or 15 replicates of isolated 30-mL bottles from the immigration experiment. Global (array-wide) CVs were calculated using a single time series from each array, where mean densities (no./mL) were calculated across bottles within dates. Local values come from the dynamics within individual bottles in 750-mL arrays. A CV value was taken from a time series for each of the 25 bottles in each array; the mean value represented variability in local densities. In both cases, the mean and standard error were then taken across the three replicates. Bars with the same letter above them did not differ in Student's t tests; degrees of freedom are the sample size − 2; we applied a sequential Bonferroni correction to preserve the Type I error rate of 0.05. Time series were seven samples at 2-d intervals, starting at day 54 for treatments other than 30-mL bottles, and starting at day zero in 30-mL bottles.

dynamics in Fig. 4B). In isolated 30-mL bottles, predators and prey cycled with high amplitude and a period of 10–11 d (cycles determined by turning point tests; Fig. 5C). Despite these indications that regional dynamics were less extinction prone in arrays, individual subpopulations in arrays had even lower mathematical stability than those in isolated 30-mL bottles; the period of predator–prey cycles was only 6–7 d (Fig. 5B; $t_{16} = 7.10$, $P < 0.001$ for prey, and $t_{16} = 7.17$, $P < 0.001$ for predators, comparing isolated 30-mL bottles and within-bottle values in arrays).

It is unlikely that rapid cycles were caused by fast starvation of predators once prey were depleted. A side experiment showed that it took a maximum of 4 d for all of 50 *Didinium* to starve when prey were absent, with a mean of 38% surviving after 2 d of starvation. This rate of decline is lower than the mean rate at which *Didinium* disappeared from local patches within arrays, where *Didinium* numbers declined at an average rate of 77% *per day* after a population peak (e.g., Fig. 5B). There was direct evidence that predators dispersed among array bottles, and that this dispersal "rescued" local patches from extinction. Predators often increased in density in patches where prey were absent or rare for many days (e.g., the bottom right panel in Fig. 5B). Further evidence of predator emigration comes from tracking the size of predators in different bottles. At the peak of predator–prey cycles, predators were large (mean 3×10^5 μm³ vs. mean of 1.3×10^5 μm³ during the first 2 d of a cycle; M. Holyoak and S. P. Lawler, *unpublished data*). Such large predators often showed

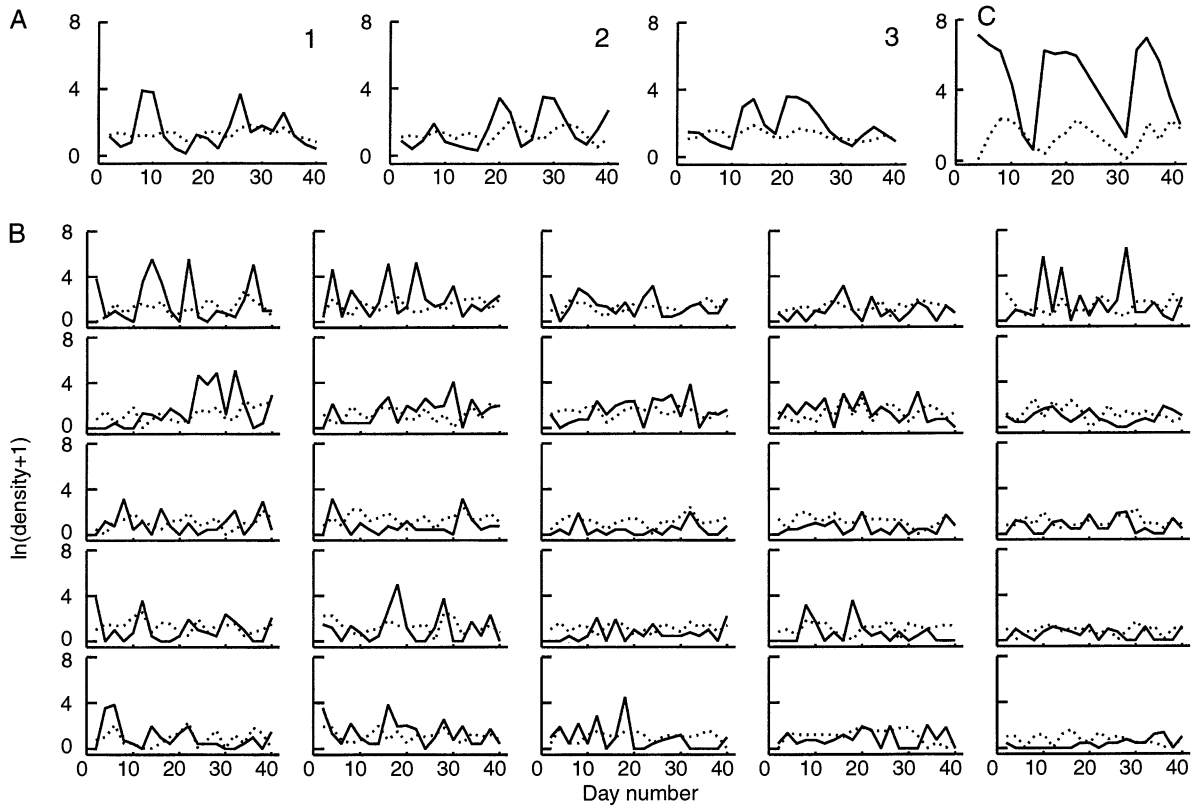

FIG. 5. Plots of the natural logarithm of (density + 1) vs. time (day number) in 750-mL subdivided microcosms. Solid lines represent prey densities, and dotted lines represent predators. (A) gives the mean, or regional, dynamics for each of the three replicates, which are numbered 1–3. (B) gives the densities within the 25 individual array bottles of replicate number 3. Each panel is in the position of a bottle within the array. (C) shows part of an unusually long time series (predators went extinct after 51 d) from a 30-mL "control" bottle of the immigration experiment, to illustrate the form of cycles in isolated 30-mL bottles. The mean persistence time of predators in isolated 30-mL bottles was 22.6 d. In (A) and (B), series were collected at 2-d intervals from day 54, and in (C), the series started on day zero (the day of predator addition). Series were truncated to 40 d from the onset of sampling, because this is the period sampled at 2-d intervals in 5 × 5 arrays. Counts were no./mL.

up in bottles where prey had been scarce or absent, and predators had previously been absent or small. This indicated dispersal rather than growth within the bottle.

If dispersal controls local densities of predators within subdivided microcosms, predators should be more abundant in bottles that have a greater number of connections with other bottles, because more tubes should allow more dispersal. We observed this pattern in the 750-mL subdivided microcosms, as shown in Fig. 6A; the difference between bottles with one tube and bottles with a greater number of tubes was significant ($F_{2,6} = 5.21$, $P < 0.05$ in a one-way ANOVA). Prey showed the opposite pattern, that is, they were most abundant in bottles with the fewest tubes (Fig. 6B; $F_{2,6} = 7.60$, $P < 0.05$). This is consistent with predators controlling local prey density, either through predation or by causing prey emigration.

Further insight into how dispersal changes local dynamics is obtained by comparing the within-bottle dynamics in spatial arrays with the dynamics in isolated 30-mL bottles. Average densities of both predators and prey were lower in individual bottles of 750-mL arrays than in isolated 30-mL bottles (Fig. 7A, B). However, prey density decreased far more than predator density, causing predator : prey ratios in individual bottles of spatial arrays to be more than double those in isolated 30-mL bottles (Fig. 7C).

Prey densities were extraordinarily low in both arrays and undivided volumes: mean prey density was 1.51 ± 0.11 prey/mL (mean ± 1 SE) in arrays, and 0.58 ± 0.04 prey/mL in undivided volumes. In the two 30-mL bottles from the immigration experiment without predators, mean density over 56 d was 1203.6 ± 0.3 prey/mL.

Dispersal results

Separate experiments on prey and predator dispersal showed that the dispersal rates were low enough to prevent synchronous dynamics throughout the microcosm, consistent with predictions of metapopulation theory (Table 1). Only 1.8–8.6% of the prey population dispersed to adjacent bottles in a generation,

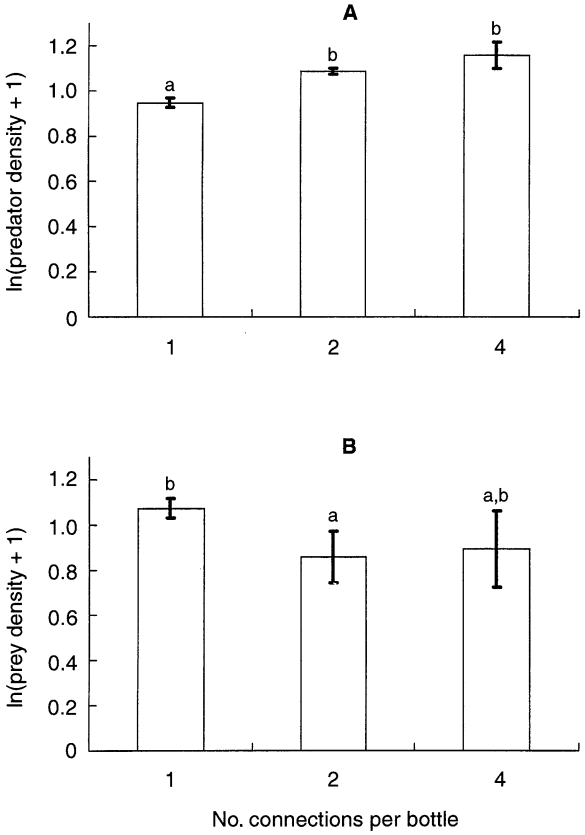

FIG. 6. Mean densities of predators (A) and prey (B) in bottles within 750-mL subdivided microcosms that have different numbers of tubes connecting with other bottles. More tubes allow more dispersal. Bars show standard errors (± 1 SE) from the three replicates. Bars with the same letter above them did not differ in Student's t tests (with df = 4); we applied a sequential Bonferroni correction to preserve the Type I error rate of 0.05. Means were taken from all bottles of a given type within arrays from 20 samples at 2-d intervals, beginning on day 54. Each bar (and 1 SE) represents the mean of the three array means.

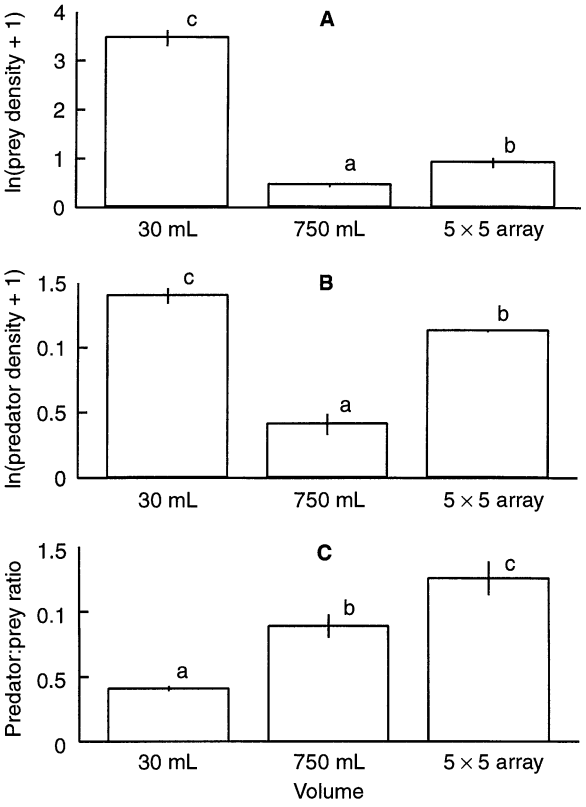

FIG. 7. Mean densities of predators and prey, and predator:prey ratios in subdivided and undivided microcosms. (A) gives the mean ln(prey density + 1), (B) gives the mean ln(predator density +1), and (C) gives the mean predator: prey ratio. Error bars show standard errors (± 1 SE) from the three microcosms for 750-mL and 5 × 5 arrays, and from 15 replicates of the immigration experiment controls for 30-mL bottles. Bars with the same letter above them did not differ in Student's t tests (df = 4 for 750-mL divided vs. undivided habitats; df = 16 for other comparisons); we applied a sequential Bonferroni correction to preserve the Type I error rate of 0.05. In subdivided and undivided 750-mL microcosms, mean predator and prey densities (and predator : prey ratios) were taken from all bottles of a given type within arrays from 20 samples at 2-d intervals beginning on day 54. A mean ± 1 SE (value shown in bars) was then taken from each of the three array means. Because of extinctions in 30-mL bottles from the immigration experiment, we used a variable number of samples and excluded the last sample prior to any recorded extinctions within each bottle.

and this rate was not dependent on prey population density. However, prey dispersal was greater when predators were present than when they were absent (Table 1). Predator dispersal rates were 1.9–25.0% per generation and were independent of predator density. The fraction of predators moving between nonadjacent patches in a generation should therefore be small (<6.3%). Additionally, when predators were first introduced to subdivided arrays, they dispersed to neighboring bottles only every 5–7 d (17–24 generations). These results suggest a substantial degree of subdivision.

Immigration results

The immigration experiment showed that the frequency of prey extinctions was increased by adding immigrant predators to isolated 30-mL bottles (G_1 = 16.0, $P < 0.001$). The 30-mL bottles are equivalent to isolated patches within arrays. Predators drove prey extinct in 27% of 15 replicates of a control treatment to which no immigrants were added, and in 80% of five replicates of a treatment to which immigrant predators were added.

Although adding immigrant predators to isolated 30-mL bottles increased the frequency of prey extinctions, adding additional prey, or both prey and predators, did not change the frequency with which either species went extinct (G tests, $P > 0.05$). However, the persistence times of both *Colpidium* and *Didinium* were increased by adding extra immigrant prey. In control

treatments, prey persisted for a mean of 14.0 d (n = 4), compared to 23.5 d (n = 2) in prey addition treatments (considering only replicates where prey went extinct). Equivalent figures for predators were 22.6 d (n = 11) and 34.7 d (n = 4), respectively. For predators and prey these differences were significant ($P < 0.05$ in one-way ANOVAs comparing ln[persistence time]).

Predator : prey ratio results

Higher initial predator : prey ratios caused more rapid declines in prey abundance, but the range of ratios used did not alter the rate of decline of the predator. Mean times for *Colpidium* to reach a minimum abundance were 2.0 d with the highest ratio of 1.0, 4.0 d at ratios of 0.2 and 0.6, and 5 d with a ratio of 0.05 ($P < 0.001$, $\chi^2 = 23.3$, df = 3, from a linear model of logarithmic persistence times with Poisson errors). *Didinium* took $\approx 6.5 \pm 0.5$ d to reach minimum densities (or go extinct), regardless of the initial predator : prey ratio. With the exception of one outlier, all predator populations in this experiment went extinct within 8 d, demonstrating that these different initial conditions did not make the interaction persistent.

Discussion

We have demonstrated that spatial subdivision increases the persistence times of *Colpidium* and *Didinium* from a mean of 70 d to $\geq$130 d, representing $\approx$600 prey generations and 400 predator generations. Metapopulation dynamics underlie the increased persistence times of predators and prey in arrays, as evidenced by the spatial asynchrony of populations, low dispersal rates of predators and prey, frequent extinctions and recolonizations of prey, and rescue effects in predator populations. We were able to rule out island–mainland dynamics as a means of regional persistence because we controlled patch uniformity, and demonstrated that the predator–prey interaction was unable to persist in 18 bottles identical in manufacture to array bottles. Prey persisted as an archetypal "blinking-lights" metapopulation (e.g., Harrison 1991), where local extinctions and recolonizations occurred frequently. Predators seemed to persist through rescue effects (Brown and Kodric-Brown 1977); they showed fewer local extinctions in arrays than did prey, and there was evidence that dispersing predators supported local predator populations. Since predators starve rapidly without prey, we expected local extinctions of predators to be frequent because there were numerous prey extinctions; however, predators usually persisted via immigration.

Intriguingly, using the predator–prey dynamics observed in undivided microcosms, we could not have predicted that the local persistence of prey in arrays was dependent on metapopulation dynamics. In the immigration experiment, prey persisted in 73% of replicates of the predator–prey treatments that received no immigrant predators, and did not go extinct at all in the absence of predators. This might lead us to expect that prey would form persistent local populations. However, when immigrant predators were added, prey went extinct in 80% of replicates. This cautions against predicting whether or not a population would persist, based on local dynamics. We need to know how the immigration of prey, predators, and intraspecific competitors affects local dynamics before we can predict the likelihood of local extinctions.

The metapopulation structure in arrays had opposite effects on the local persistence of predators and prey. The ability of predators to disperse among local populations decreased the local persistence of prey, while increasing the local persistence of predators. In undivided microcosms, predators tended to overexploit prey and go extinct, but a few prey usually survived through the bottleneck and prey extinctions were rare. In contrast, local extinctions of prey were common in arrays. Two different mechanisms may have produced these extinctions. In arrays, a constant supply of immigrant predators might prevent local prey populations from surviving the bottleneck, since immigrant and resident predators would not starve simultaneously. We also observed that prey dispersed more frequently when predators were present (in the dispersal experiment), so emigration could have contributed to local prey extinctions.

Dispersal substantially changed local dynamics, beyond the changes in extinction rates. Predator : prey ratios in arrays were greatly increased over those in undivided microcosms, and prey exhibited more rapid cycles in arrays than in undivided microcosms. The predator : prey ratio experiment showed that higher ratios could cause faster prey declines, and rapid declines could lead to faster cycles. Predators also displayed more rapid cycles in arrays, but this was not because they starved more quickly than in undivided microcosms. Predators responded to prey declines by dispersing to neighboring bottles, as was shown by their appearance in bottles that had no prey, and by their greater mean density in bottles with more connecting tubes.

Although regional persistence was enhanced by metapopulation structure, local dynamics in array bottles appeared to be at least as extinction prone as in undivided microcosms. A hallmark of increased risk of extinction is increased temporal variability (May 1971, 1973, Connell and Sousa 1983, Taylor 1992). Additionally, lower mathematical stability (sensu Case and Casten 1979) is indicated by shorter period population cycles (May 1973). The decreased period of predator–prey cycles in single array bottles compared to undivided microcosms could indicate decreased persistence in individual array bottles. However, more work is needed to judge whether or not our experimental system meets assumptions of the models that relate fast cycles to low persistence. Population variability of local prey populations in arrays was just as high as in

undivided microcosms, where the predator–prey interaction did not persist. This decrease in within-bottle persistence while regional persistence increases is consistent with metapopulation theory (Kareiva 1990, Taylor 1990).

The system included some features of dispersal that differ from those of classical metapopulations. Prey dispersed more frequently when predators were present. This might allow prey to experience a lower rate of predation by dispersing to areas where predators are less abundant. Even when predators were present, however, the dispersal rate of prey was low enough to prevent synchrony. Thus, prey dispersal is broadly consistent with metapopulation dynamics. In future work, we will examine the implications of directed dispersal to spatial dynamics by constructing a metapopulation model that is parameterized for our system. This study demonstrates the need for development of contingent models that include realistic departures from conventional metapopulation scenarios (as discussed by Harrison and Taylor 1996), such as changes in local dynamics caused by dispersal (e.g., Nachman 1987*a, b,* Reeve 1988). In the past, investigation of the effects of subdivision on persistence and dynamics has been greatly aided by models (reviews in Taylor 1988, 1990, 1991, Hastings 1990, Kareiva 1990, Hanski 1991, Levin 1992, Holt 1993, Hastings and Harrison 1994, Harrison and Taylor 1996).

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