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► **To cite this version:**

Céline Hauzy, Florence Hulot, Audrey Gins, Michel Loreau. Intra- and interspecific density-dependent dispersal in an aquatic prey-predator system. *Journal of Animal Ecology*, 2007, 76, pp.552-558. bioemco-00176014

HAL Id: bioemco-00176014

<https://hal-bioemco.ccsd.cnrs.fr/bioemco-00176014v1>

Submitted on 9 Oct 2007

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**INTRA- AND INTERSPECIFIC DENSITY-DEPENDENT
DISPERSAL IN AN AQUATIC PREY–PREDATOR
SYSTEM**

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ABSTRACT.

Dispersal intensity is a key process for the persistence of prey–predator metacommunities. Consequently, knowledge of the ecological mechanisms of dispersal is fundamental to understanding the dynamics of these communities. Dispersal is often considered to occur at a constant *per capita* rate; however, some experiments demonstrated that dispersal may be a function of local species density.

Here we use aquatic experimental microcosms under controlled conditions to explore intra- and interspecific density-dependent dispersal in two protists, a prey *Tetrahymena pyriformis* and its predator *Dileptus* sp.

We observed intraspecific density-dependent dispersal for the prey and interspecific density-dependent dispersal for both the prey and the predator. Decreased prey density lead to an increase in predator dispersal, while prey dispersal increased with predator density.

Additional experiments suggest that the prey is able to detect its predator through chemical cues and to modify its dispersal behaviour accordingly.

Density-dependent dispersal suggests that regional processes depend on local community dynamics. We discuss the potential consequences of density-dependent dispersal on metacommunity dynamics and stability.

INTRODUCTION

Knowledge of dispersal mechanisms is crucial to understanding the dynamics of spatially structured populations and metacommunities (Leibold *et al.* 2004). Such knowledge may also be useful for explaining the response of communities to fragmentation and climate change. Metacommunity dynamics can be influenced by local processes such as intra- and interspecific interactions (Lotka 1925; Rosenzweig & MacArthur 1963; Volterra 1926) and regional processes such as dispersal, that link the dynamics of several local communities (Cadotte 2006). Dispersal is the movement of individuals from one patch (emigration) to another (immigration). Intermediate intensities of dispersal can increase the persistence of prey–predator metacommunities (Crowley 1981; Holyoak & Lawler 1996a, b; Huffaker 1958; Nachman 1987a; Reeve 1988; Zeigler 1977). Dispersal rate is often considered a constant trait of species, but it may be condition-dependent. In particular, it may depend on the density of species in the local community. Density-dependent dispersal implies a direct interaction between local (population dynamics) and regional (dispersal) processes, which could influence metacommunity dynamics and stability.

Many studies have explored dispersal in the context of a single species. They have shown that dispersal often depends upon a species' own local density (Diffendorfer 1998). We call this effect intraspecific density-dependent dispersal. Dispersal may either increase (positive density-dependent dispersal) or decrease (negative density-dependent dispersal) as population density increases. Positive and negative intraspecific density-dependent dispersal has been observed in mites (Bernstein 1984), insects (Fonseca & Hart 1996) and vertebrates (French & Travis 2001; Le Galliard, Ferrière & Clobert 2003; Matthysen 2005; see for review Matthysen 2005), but not in protists (Holyoak & Lawler 1996a, b). In a mite prey–predator system, Bernstein (1984) found positive intraspecific density-dependent dispersal

in the prey, but not in the predator. Conversely, French & Travis (2001) observed density-independent prey dispersal but density-dependent parasitoid dispersal in a beetle–wasp system.

A few studies have experimentally explored how dispersal of one species is affected by the density of another species. We refer to this type of dispersal as interspecific density-dependent dispersal. The presence of a predator or parasitoid has enhanced prey dispersal in some insect communities (Holler *et al.* 1994; Kratz 1996; Wiskerke, Dicke & Vet 1993). By contrast, in aquatic ciliates, dispersal of the prey (*Colpidium striatum*) was not affected by the presence of the predator (*Didinium nasutum*) (Holyoak, personal communication; Holyoak & Lawler 1996a, b). However, these studies considered predator presence or absence and not predator density. Bernstein (1984) showed with terrestrial mites that prey emigration had a positive relationship with predator density and that predator emigration had a negative relationship with prey density. Similarly, Kratz (1996) found that a decrease in prey density enhanced predator emigration in aquatic insect larvae. French & Travis (2001) observed a decrease in parasitoid swap dispersal as prey dispersal increased but no interspecific density-dependent dispersal for the prey. Thus, overall, dispersal seems to be a function of local densities in several experimental models. However, only two studies (Bernstein 1984; French & Travis 2001) have considered the full set of intra- and interspecific effects of density on dispersal in prey–predator systems, in spite of their great interest in the perspective of metacommunity theory.

Interspecific density-dependent dispersal in prey may be considered as a predator-induced defence (Lima & Dill 1990). Other predator-induced responses include morphological changes in vertebrates (Kishida & Nishimura 2006) and invertebrates (Kuhlmann, Kusch & Heckmann 1999; Tollrian & Dodson 1999). Predator-induced dispersal suggests that the prey is able to assess the presence of its predator. Several experiments in aquatic systems showed that prey may detect their predator because of

organic compounds they release in the medium, for instance *Daphnia* (Lampert, Rothhaupt & von Elert 1994; Stibor & Lüning 1994) and ciliates (Karpenko, Railkin & Seravin 1977; Kuhlmann et al. 1999). By contrast, perception in ciliates may require encounter between individuals: two mechanisms have been reported in ciliates: (1) detection of their predators by direct membrane contact (Kuhlmann 1994; Kusch 1993), and (2) detection of local hydrodynamic disturbances created by the motion of cilia (Karpenko et al. 1977). Consequently, interspecific density-dependent dispersal in ciliates may occur through water-born chemical cues or may require direct contact.

Here we explore intra- and interspecific density-dependent dispersal in freshwater protists. These organisms are often patchily distributed in ponds and lakes at the scale of millimetres or centimetres (Arlt 1973; Smirnov & Thar 2003; Taylor & Berger 1980; Wiackowski 1981). We use a prey–predator couple, in aquatic experimental microcosms under controlled conditions and investigate the effects of population density on dispersal, and address three questions. First, does a species’ own density affect its dispersal (intraspecific density-dependent dispersal)? We test this hypothesis for the prey and the predator separately. Second, does prey density affect predator dispersal, and does predator density affect prey dispersal (interspecific density-dependent dispersal)? If prey dispersal is positively related to predator density, our third question investigates the effects of predator organic compounds on prey dispersal. In addition, we explore these effects at low and high initial prey density to assess the interaction between prey and predator densities on prey dispersal.

MATERIALS AND METHODS

Study Organisms

Tetrahymena pyriformis Ehrenberg, a bacterivorous protist, and its protist predator *Dileptus* sp. were obtained from Carolina Biological Supply (Burlington, NC, USA). Prey and predator were cultured in 50 mL microcosms containing medium inoculated with a mixed bacterial suspension. The medium was prepared by sterilizing mineral water with 0.75 g.L⁻¹ of Protozoan Pellet (Carolina Biological Supply). Cultures were maintained at 18.0 ± 0.5 °C under controlled light (14:10 h light:dark cycle). One day after bacterial inoculation, each culture was inoculated with 1 mL of *T. pyriformis* to give about 240 cells.mL⁻¹. Three days later, *T. pyriformis* cultures reached a stationary phase; they were then used to feed *Dileptus* sp. The same culturing method was used in all experiments. Under our standard culture conditions, the minimal generation times of *T. pyriformis* and *Dileptus* sp. were 8,18 h and c. 24 h, respectively (Hauzy C. & Hulot F.D., unpublished data).

Experimental design

To measure dispersal, we used microcosms made of two 100 mL bottles (55 mm internal diameter) connected by a 10 cm tube (5 mm internal diameter). We defined dispersal as migration from a bottle initially containing organisms (donor patch) to a bottle free of organisms (recipient patch).

We conducted six independent experiments according to the following design. The tube of each microcosm was initially clamped and donor patches were assigned randomly.

Initial densities in all experiments were adjusted by serial dilution in 1-day-old bacterial culture after counting the 3-day-old *T. pyriformis* and the 1-day-old *Dileptus* sp. cultures. Counts were done under a binocular microscope in 10 μ L drops for *T. pyriformis*, and 100 μ L drops for *Dileptus* sp. Several drops were examined until a minimum number of 400 individuals was counted. The donor patch received 50 mL of the experimental treatment culture. The recipient patch received 50 mL of standardized 1-day-old bacterial culture. The experiments were initiated by releasing the clamp off the tube. Organisms dispersed freely during a time that was shorter than the generation time of the species studied. Treatments were replicated five times, except experiment 5, which was replicated four times.

At the end of the experiment, the content of each bottle was fixed with formaldehyde at a final concentration of 0.2%. Because the recipient patches did not contain high population densities, they were concentrated by centrifugation (5 min, 2000 r.p.m., 425 g). Organisms were counted under a binocular microscope in 10 μ L drops for *T. pyriformis*, and 100 μ L drops for *Dileptus* sp. Several drops were examined in accordance with the following two procedures: (1) in experiments 1–4 and 6 (see below) up to 100 or 400 individuals were counted, respectively, and (2) in experiment 5, individuals were counted in 800 μ L. Dispersal was measured by the dispersal rate per capita and per generation, and was calculated as the ratio of the density of the focal species in the recipient patch at the end of the experiment to its initial density in the donor patch. Initial, not final, density in the donor patch was used to avoid the potentially confounding factor of prey depletion in experiments testing prey dispersal in the presence of the predator (see experiments 4, 5 and 6 below).

Intraspecific density-dependent dispersal

In experiment 1 we tested the effect of *T. pyriformis* density on its own dispersal in the absence of *Dileptus* sp. Density treatments corresponded to cultures with 12 700 cells.mL⁻¹, 1270 cells.mL⁻¹ and 43.1 cells mL⁻¹. The dispersal time was 4 h.

In experiment 2 we tested the effect of *Dileptus* sp. density on its own dispersal. Treatments correspond to three levels of density: 61.3 cells mL⁻¹, 30.6 cells.mL⁻¹ and 15.3 cells.mL⁻¹. *T. pyriformis* density was adjusted to 3.3 cells.mL⁻¹ in all treatments. The dispersal time was 18 h.

Interspecific density-dependent dispersal

Experiment 3 tested the effect of *T. pyriformis* density on *Dileptus* sp. dispersal. A *Dileptus* sp. culture was mixed 50:50 with a *T. pyriformis* culture of varying density. We obtained three treatments with the same initial *Dileptus* sp. density (20.8 cells.mL⁻¹) but different initial *T. pyriformis* densities: 5400 cells.mL⁻¹, 540 cells.mL⁻¹ and 54.0 cells.mL⁻¹. The dispersal time was 18 h.

Experiment 4 tested the effect of *Dileptus* sp. density on *T. pyriformis* dispersal. Cultures with different *Dileptus* sp. densities were mixed 50:50 with a *T. pyriformis* culture. *T. pyriformis* initial density was 1120 cells.mL⁻¹ in all treatments, and *Dileptus* sp. densities were 37.5 cells.mL⁻¹, 18.8 cells.mL⁻¹ and 9.4 cells.mL⁻¹. The dispersal time was 5 h.

Mechanism of detection

In order to test whether *T. pyriformis* is able to detect *Dileptus* sp. via a chemical signal, we compared prey dispersal rate in the presence of the predator (treatment «with»),

in a filtered medium of predator culture (treatment «filtered») and in the absence of predator (treatment «without»). This hypothesis was tested independently for two initial *T. pyriformis* densities (experiment 5: 550 cells.mL⁻¹; experiment 6: 6600 cells.mL⁻¹). In the treatment «with», we added the *Dileptus* sp. culture to the *T. pyriformis* culture (initial density of *Dileptus* sp. in experiment 5: 63.5 cells mL⁻¹; in experiment 6: 22.1 cells mL⁻¹). In the treatment «filtered», we replaced the *Dileptus* sp. culture of the treatment «with» with the same *Dileptus* sp. filtered with a 1.2 µm Whatman GF/C filter permeable to chemical compounds and bacteria. In the treatment «without», the *T. pyriformis* culture was diluted with a 1-day-old bacterial culture. Each treatment was replicated five and four times in experiments 5 and 6, respectively. The dispersal time in both experiments was 8 h.

Statistical Analysis

Data were analysed with linear (LM) or linear mixed effects models in R vs. 2.2.0. For experiments 1–4, data were considered as continuous variables whereas data of experiments 5 and 6 were considered categorical. When homoscedasticity of variances (Bartlett's test) was satisfied (experiments 2, 3, 5 and 6), we used the LM procedure. When variances were heteroscedastic (experiments 1 and 4), we used the Generalized Least Squares procedure of the linear mixed effects model, which accounts for heteroscedasticity. The Generalized Least Squares procedure gave the same qualitative results as the LM procedure. Tukey's post hoc tests were used to determine the differences between treatments and groups of treatments.

RESULTS

Intraspecific density-dependent dispersal

In experiment 1, no *T. pyriformis* individuals could be detected in the recipient patch for three of five replicates of the low density treatment. *T. pyriformis* density had a strong significant effect on its own dispersal rate (Fig. 1a; $t = 4.17$, d.f. = 13, $P = 0.001$). The treatment with the highest density (12 700 cells.mL⁻¹), which corresponded to the beginning of the stationary phase, was significantly different ($P < 0.001$) from the lower density treatments (1270 and 43.1 cells.mL⁻¹).

Experiment 2 (Fig. 1d) showed no significant effect of *Dileptus* sp. density on its per capita dispersal rate ($F = 2.45$, d.f. = 14, $P = 0.141$).

Interspecific density-dependent dispersal

In experiment 3 (Fig. 1c), *T. pyriformis* density had a strong significant effect on *Dileptus* sp. dispersal rate ($F = 7.07$, d.f. = 14, $P = 0.019$). The average *Dileptus* sp. dispersal rate was significantly higher at the lowest prey density (54.0 cells mL⁻¹) than at higher prey densities (5400.0 cells.mL⁻¹ and 540.0 cells.mL⁻¹) ($P < 0.0001$).

In experiment 4 (Fig. 1b), the initial *T. pyriformis* density (1120 cells.mL⁻¹) was chosen such that it does not affect its own dispersal rate (see Results of experiment 1). *Dileptus* sp. density had a strong significant effect on the dispersal rate of its prey ($F = 22.28$, d.f. = 14, $P < 0.001$) and the dispersal rate of *T. pyriformis* was significantly higher at the two highest *Dileptus* sp. densities (37.5 cells.mL⁻¹ and 18.8 cells.mL⁻¹) than at the lowest density (9.8 cells mL⁻¹) ($P < 0.0001$).

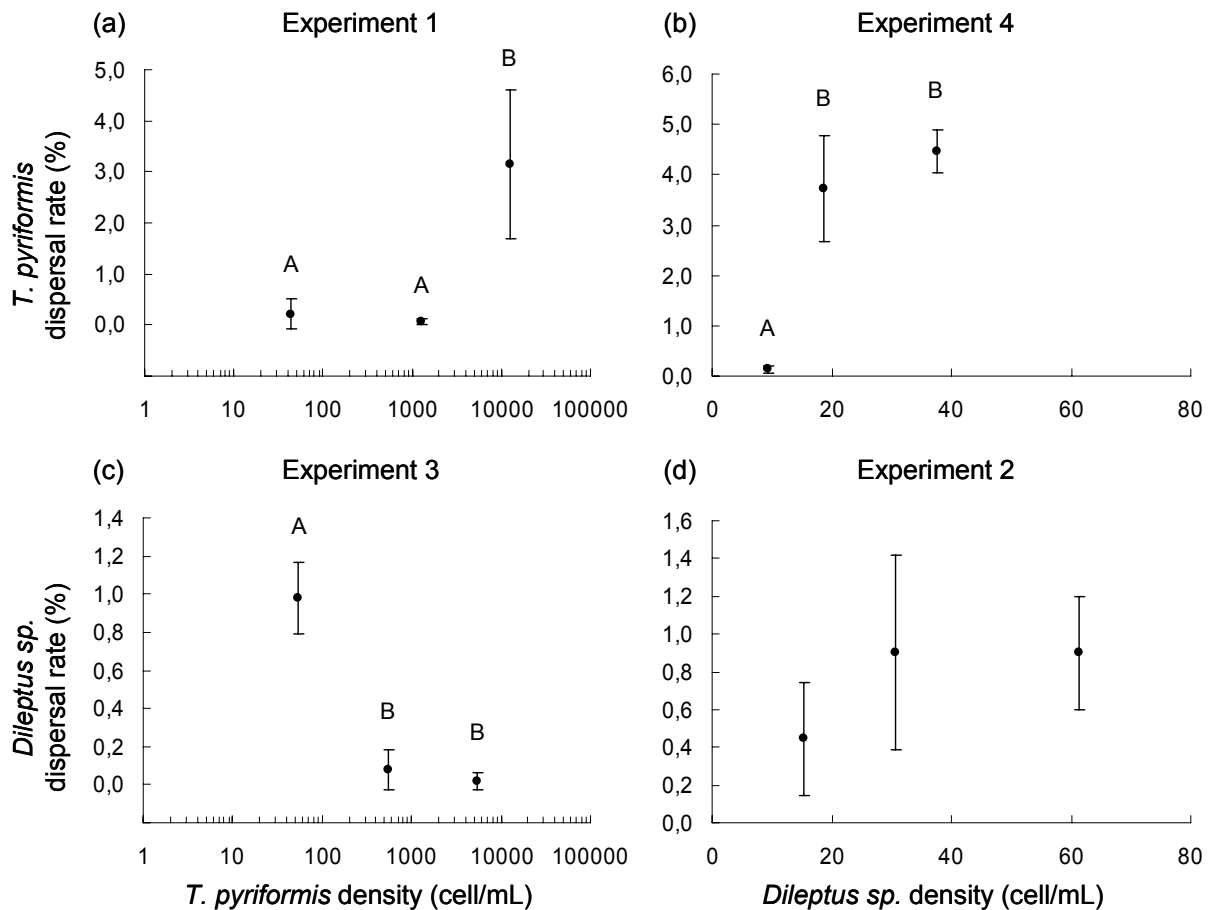


Figure 1. Effects of (a) *Tetrahymena pyriformis* density and (b) *Dileptus* sp. density on *T. pyriformis* dispersal rate, and effects of (c) *T. pyriformis* density and (d) *Dileptus* sp. density on *Dileptus* sp. dispersal (mean \pm 1 SE). Letters indicate significant differences in dispersal rate among density treatments.

Mechanism of detection

Experiments 5 and 6 were conducted at a predator density that induces prey dispersal (see Results of experiment 4). When the density of *T. pyriformis* was low (experiment 5), the differences among treatments on *T. pyriformis* dispersal rate were significant (Fig. 2a; $F = 165.4$, d.f. = 12, $P < 0.001$). Tukey's *post hoc* test indicated that prey dispersal rate in the treatments «filtered» and «with» were significantly higher than in the treatment «without» ($P < 0.001$). Prey dispersal rate was also significantly higher in the treatment «filtered» than in the treatment «with» ($P < 0.005$). When initial *T. pyriformis* density was high (experiment 6), the effects of the treatments «without», «filtered» and «with» on *T.*

pyriformis dispersal rate were marginally significant (Fig. 2b; $F = 3.623$, d.f. = 9, $P = 0.070$). Tukey's *post hoc* test shows that the prey dispersal rate in the treatment «filtered» was marginally higher than in the treatment «without» ($P = 0.060$).



Figure 2. *Tetrahymena pyriformis* detects *Dileptus sp.* presence through chemical cues (mean \pm 1 SE). (a) Low initial density of *T. pyriformis*; (b) high initial density of *T. pyriformis*. Letters indicate significant differences in dispersal rate among treatments.

DISCUSSION

The results of our study suggest that in aquatic prey–predator systems, the dispersal of a species can be a plastic trait that depends on population densities. We observed intraspecific density dependence in dispersal for the prey *T. pyriformis*. By contrast, there was no significant intraspecific density dependence in dispersal for the predator *Dileptus sp.* Interspecific density-dependent dispersal was observed for both the prey and the predator. A decrease in *T. pyriformis* density led to a significant increase in *Dileptus sp.* dispersal rate, while *T. pyriformis* dispersal was higher when *Dileptus sp.* density was higher.

The two previous studies (Bernstein 1984; French & Travis 2001) that have exhaustively explored density-dependent dispersal in a prey–predator system revealed two different patterns (Fig. 3). French & Travis (2001) observed that predator dispersal

depended on its own density and on prey density, but prey dispersal was density-independent. By contrast, Bernstein (1984) showed interspecific density-dependent dispersal for both the prey and the predator, and intraspecific density-dependent dispersal for the prey only. Our results follow the same pattern as Bernstein's (1984). Thus, only two patterns of density-dependent dispersal in prey-predator systems have received experimental support. An increase in the prey dispersal rate when predator density increases, suggests that the prey is able to detect its predator and avoid it. Studies on ciliates' perception have shown that two different detection mechanisms are possible: recognition through chemical cues released in the medium (Karpenko et al. 1977; Kuhlmann et al. 1999; Seravin & Orlovskaja 1977) and recognition that requires direct contact (Karpenko et al. 1977; Kuhlmann 1994; Kusch 1993). Our results suggest that the prey is able to detect its predator through chemical cues. At a low initial prey density, prey dispersal was significantly higher when prey was in the presence of predators or in the presence of a filtered medium of predator cultures than in the control. At a high initial prey density, prey dispersal was marginally higher when prey was in the presence of a predator-filtered culture than in the control or in the presence of the predator. The difference in prey dispersal between the predator-filtered culture and the predator culture may be a result of prey depletion by the predator in the latter treatment.

Two hypotheses may explain the discrepancy between the experiments at low and high densities. First, at a low initial prey density ($550 \text{ cells.mL}^{-1}$), there is no effect of prey density on its own dispersal (see experiment 1, Fig. 1a). The dispersal observed in the presence or simulated presence of the predator is only due to the predator. By contrast, at a high initial prey density ($6600 \text{ cells.mL}^{-1}$), prey density may have an effect on its own dispersal. Therefore, in the absence of the predator, prey dispersal is high and the effect of a predator (whether real or simulated) on dispersal is reduced in comparison with the prey's intraspecific density effect. This result suggests an upper bound on prey dispersal. Second,

the discrepancy between the two experiments might be a consequence of different predator densities in experiments 5 ($63.5 \text{ cells.mL}^{-1}$) and 6 ($22.1 \text{ cells.mL}^{-1}$). However, these two densities are both in the range of predator densities that induce prey dispersal (see experiment 4, Fig. 1b). Therefore the latter hypothesis is not supported by our data.

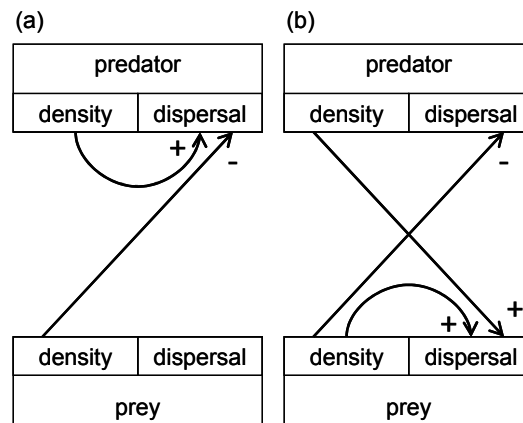


Figure 3. Density-dependent dispersal patterns in prey-predator systems. Arrows indicate positive (+) or negative (-) significant effect of density on dispersal observed in (a) French & Travis (2001), and in (b) Bernstein (1984) and present experiments.

Implications for prey-predator metacommunities

In a seminal paper, Huffaker (1958) showed that prey–predator interactions persist longer in a large fragmented landscape than in a small fragmented landscape or isolated patches. His experiment stimulated theoretical studies that have explicitly addressed the role of spatial heterogeneity in the persistence of prey–predator interactions that are prone to extinction when isolated (de Roos, 1991 #29; Hassell, 1991 #30; Sabelis, 1988 #31; Sabelis, 1991 #32}. Several experimental studies showed that individuals’ migration between local communities allows regional persistence because of the asynchrony of local dynamics (Holyoak & Lawler 1996a; Janssen *et al.* 1997; Taylor 1990; van de Klashorst *et al.* 1992). Theoretical studies focused on the essential role of dispersal intensity in prey–predator

metacommunities (Crowley 1981; Nachman 1987a, b; Reeve 1988; Zeigler 1977). These models (reviewed in (Holyoak & Lawler 1996a, b) predict that an intermediate dispersal level of prey and predator enables metacommunity persistence. A low dispersal rate reduces the probability of recolonization of locally extinct patches and cannot prevent local extinctions, whereas a high dispersal rate tends to synchronize local dynamics (Brown & Kodric-Brown 1977; Levins 1970; Yodzis 1988). Experiments have confirmed that moderate dispersal extends the persistence of prey–predator systems (Holyoak & Lawler 1996a, b). However, in these theoretical studies the dispersal ability of species from one patch to another is regarded as an unconditional process described by a single parameter. Our results add to the body of experiments (Bernstein 1984; French & Travis 2001; for review see Matthysen 2005) that show that dispersal is density-dependent, and hence that regional processes depend upon local population dynamics. This strong interaction between local and regional processes is likely to affect the dynamics and stability of communities and metacommunities.

Recent models that incorporate density-dependent dispersal behaviour show different community-level effects of dispersal (reviewed in Bowler & Benton 2005). Most of these models explored the effects of intraspecific density-dependent dispersal on the stability of single-species metapopulations. Models that incorporate positive density-dependent dispersal behaviour, as we showed here with *T. pyriformis*, have found a stabilizing effect of dispersal on population dynamics, whereas models that have simpler dispersal rules do not observe stabilizing effects (Janosi & Scheuring 1997; Ruxton & Rohani 1999; but see Ruxton 1996). Other models have shown that the form of the relationship between dispersal and density is important for predicting its consequences for stability (Amarasekare 1998; Ruxton 1996; Ylikarjula *et al.* 2000).

The effects of interspecific density-dependent dispersal on the stability of prey–predator metacommunities are still unclear. French & Travis (2001) parameterized a model

and found no differences in species persistence and community dynamics between a fixed mean dispersal and interspecific density-dependent dispersal for the predator (parasitoid). By contrast, taking into account intra- and interspecific density-dependent dispersal improves the ability of prey–predator metacommunity models to predict metacommunity dynamics in experiments (Bernstein 1985; Ellner *et al.* 2001; Nachman 1987a, b). Thus, density-dependent dispersal may be fundamental for our understanding of prey–predator metacommunity dynamics. At present, several questions remain unanswered. Is there an interaction between the effects of intra- and interspecific density-dependent dispersal on prey–predator metacommunities? Do different density-dependent dispersal patterns (Fig. 3) have different effects at the metacommunity level? What are the implications of the interaction between local and regional processes for conservation and biological control?

CONCLUSIONS

Our microcosm experiments demonstrate that the dispersal of prey and predator protists can depend on both intra- and interspecific density. Our results may be fundamental and general because they were obtained with relatively simple organisms (unicellular eukaryotes). We further show that prey can detect predator presence through organic compounds that the predator releases in the medium. Therefore chemical signals among organisms may play an important role in species dispersal, and density-dependent dispersal may be a pivotal process in metacommunity dynamics. Understanding and testing the effects of density-dependent dispersal on metacommunity dynamics, is a challenge for future studies.

ACKNOWLEDGEMENTS

We thank M. Huet for her help in maintaining the protist cultures and T. Tully for advice on the statistical analysis. We thank G. Lacroix, S. Leroux and anonymous reviewers for their remarks that permit progress of the manuscript. C.H. thanks B. Boublil for his constant support.

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