

Ecological consequences of intraspecific variation in lake *Daphnia*

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SUMMARY

1. Although populations harbour considerable diversity, most ecological studies still assume they are homogeneous. However, mounting evidence suggests that intraspecific diversity is not only common, but also important for interactions with community members. Here, intraspecific variation in *Daphnia dentifera* in haemoglobin content is shown to be a marker of hypolimnion use.
2. Hypolimnion use differed substantially within and among *D. dentifera* populations. *Daphnia dentifera* with haemoglobin resided primarily in the hypolimnion, while *D. dentifera* lacking haemoglobin migrated vertically. These 'deep' and 'migratory' *D. dentifera* had different seasonal phenologies and dynamics.
3. Deep and migratory *D. dentifera* had qualitatively different relationships with an important competitor, *Daphnia pulex*. Deep *D. dentifera* density was negatively correlated with *D. pulex* density, whereas migratory density was not correlated with *D. pulex* density.
4. Given that *D. pulex* tends to reside in the hypolimnion, this negative correlation probably reflects competition between *D. pulex* and the deep *D. dentifera*. This pattern would have been missed if only the relationship between the overall lake populations of *D. dentifera* and *D. pulex* had been studied.
5. Abundances of deep *D. dentifera* and *D. pulex* were both correlated with the size of the hypolimnetic refuge from fish predation, but in opposite directions. Lakes with large refuges generally had high *D. pulex* and low deep *D. dentifera* densities.

Keywords: community ecology, community genetics, *Daphnia galeata mendotae*, diel vertical migration, interspecific competition

Introduction

There is substantial diversity among individuals within populations and species (Bolnick *et al.*, 2003; Hughes *et al.*, 2008). This diversity potentially has important consequences for population dynamics (Hairston *et al.*, 2005; Saccheri & Hanski, 2006) as well as for ecological interactions, including competition (Fridley, Grime & Bilton, 2007; Steiner, Cáceres & Smith, 2007), predation (Post *et al.*, 2008) and parasitism (Duffy & Sivars-Becker, 2007; Elderd, Dushoff &

Dwyer, 2008). Nevertheless, most studies of community- and ecosystem-level processes still assume that all individuals within a species are identical (Bolnick *et al.*, 2003). This assumption stems in part from practical needs; when studying interspecific interactions, it may not be feasible to measure the variability within each species. It may also, in part, reflect scepticism regarding the presence of such variation and its importance to ecological interactions (Bolnick *et al.*, 2003).

Here, I present a case where ignoring variation within populations would have obscured evidence for competition among lake *Daphnia*. *Daphnia* have been the focus of well over a century of study and have played a major role in improving our understanding

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of evolutionary and community ecology (Kerfoot, 1980; Kerfoot & Sih, 1987; Lampert, 2006). As a result, we know that *Daphnia* populations can possess substantial variation (e.g. Weider & Lampert, 1985; Leibold, Tessier & West, 1994; Hairston *et al.*, 1999), and that community members (such as predators, competitors and parasites) can strongly influence that variation (e.g. Weider, 1992; Cousyn *et al.*, 2001; Duffy *et al.*, 2008). Yet as is true more generally, the consequences of intraspecific variation in *Daphnia* on interspecific interactions remain largely unexplored.

In this study, I focused on variation in habitat use within a *Daphnia* species. Variation among *Daphnia* species has been well-documented and is associated with differences in population dynamics and interspecific interactions, most notably predation risk (e.g. Stich & Lampert, 1981; Leibold & Tessier, 1997). There is also variation within *Daphnia* species in habitat use (e.g. Weider, 1984; Leibold *et al.*, 1994), and this may also have important consequences for population dynamics and interspecific interactions. For example, if one species uses two different habitats, only one of which overlaps with the habitat used by another species, then the strength of interspecific competition should differ between those habitats. Here, I take advantage of a phenotypic marker of hypolimnion use in *Daphnia dentifera* Forbes to present evidence for such an effect of habitat use on its relationship with an important congener, *Daphnia pulicaria* Forbes.

Methods

Study system

I studied *Daphnia* populations in eight glacial lakes in south western Michigan, U.S.A.: Baker, Bassett, Cloverdale, Lawrence, Pine, Sherman, Three Lakes Two ('3L2') and Warner Lakes (Barry and Kalamazoo Counties, MI, U.S.A.). These lakes were chosen for this study because they span a range of productivity (spring phosphorus: 6.4–26.6 $\mu\text{g L}^{-1}$) and depth (max. depth: 9–17 m), but all stratify thermally in summer (Tessier & Woodruff, 2002; Cáceres *et al.*, 2006). These lakes are dominated by two *Daphnia* species, *D. pulicaria* (Tessier & Woodruff, 2002) and *D. dentifera* (Taylor, Hebert & Colbourne, 1996). *Daphnia dentifera* was formerly known as *Daphnia galeata mendotae*. *Daphnia galeata mendotae* was split into *Daphnia rosea*, *Daphnia mendotae* and their hybrids by Taylor & Hebert (1992); *D. rosea*

later became *D. dentifera*. The lakes used in this study contain *D. dentifera* and *D. dentifera* \times *D. mendotae* hybrids (Duffy, Tessier & Kosnik, 2004), but no *D. mendotae* individuals were observed during this study (based on morphology; Taylor & Hebert, 1992; Duffy *et al.*, 2004). In general, *D. pulicaria* is a cold-water specialist, dominating in winter and spring, and occupying the hypolimnion during summer (Tessier & Welsler, 1991). *Daphnia dentifera* predominates in summer and fall, and is generally considered to be migratory, occupying the epilimnion at night and migrating to the hypolimnion during the day to avoid fish predation (Leibold & Tessier, 1997).

Daphnia produce haemoglobin in response to low-oxygen conditions (Fox, Gilchrist & Phear, 1951). Haemoglobin improves physiological performance and fitness in low-oxygen environments (Fox *et al.*, 1951; Heisey & Porter, 1977; Pirow, Baumer & Paul, 2001). It is assumed that there are costs associated with producing haemoglobin, as resources used in the synthesis of haemoglobin are no longer available for growth and reproduction (Pirow *et al.*, 2001). Oxygen levels in stratified lakes vary with depth. The epilimnion is characterised by higher temperatures and high oxygen levels, while the hypolimnion is characterised by colder temperatures and lower oxygen levels (Wetzel, 2001). Given this, differences in habitat use in stratified lakes may correspond with differences in haemoglobin presence. While it is possible to quantify concentrations of haemoglobin (e.g. in comparison with human blood: Fox, 1948; via UV spectrophotometry: Salonen & Lehtovaara, 1992), using these methods would greatly limit the number of individuals per sample, the number of samples per population and the number of populations I could study. Therefore, I chose to use a qualitative measurement (presence or absence of haemoglobin), which enabled me to increase greatly the breadth of the study.

Habitat use

My first aim was to determine whether haemoglobin presence could be used as an indicator of habitat use by *D. dentifera*. To do this, I studied the vertical distribution of *D. dentifera* in Lawrence and Sherman Lakes. These lakes covered the range of haemoglobin prevalence; Sherman had a very high proportion of individuals containing haemoglobin, while Lawrence had a low proportion. Lakes were sampled both at

day and at night, since *D. dentifera* are known to undergo diel vertical migration (DVM) (Leibold & Tessier, 1997). Lawrence Lake was studied on 24 and 28 July 2003 and Sherman Lake on 14 and 16 July. To ensure that the strong observed differences in night-time habitat use did not change in Sherman Lake over the course of the study, I also studied the vertical distribution of *D. dentifera* in Sherman Lake at night on 21 and 31 July and 8 August 2003.

Samples were collected every 1- or 2-m using a 20-L, plexiglass Schindler trap with an 80 μm mesh. Samples were counted live using a dissecting microscope with transmitted light and 25–50 \times magnification. Animals containing haemoglobin are distinguished by a pinkish-red colour, particularly near the heart (Fox *et al.*, 1951). For the analysis, the population was divided into groups comprised of animals with and without haemoglobin to determine whether there were differences in the vertical distribution of the two groups. Samples were also grouped by habitat: the epilimnion was defined as ≤ 4 m depth, corresponding to the thermocline depth in both of these lakes (see Results).

These data were then analysed for significant differences in habitat use between animals with and without haemoglobin. I analysed the data using a split-plot design model, where lake is the plot, and day/night is the sub-plot treatment. Lake, day/night and haemoglobin were all treated as fixed effects. Even though all factors were treated as fixed effects, data were analysed using Proc Mixed in SAS (SAS institute, Cary, NC, U.S.A.) to deal with the unbalanced design (Littell *et al.*, 2006).

Population dynamics

I studied the dynamics of *D. dentifera* and *D. pulicaria* in all eight lakes from July to September of 2003. However, the lakes were not all sampled at the same intensity. For logistical reasons, I focused on five of the lakes: 3L2, Baker, Cloverdale, Pine and Sherman; these lakes were sampled, on average, every 4–7 days during the course of the study. Temperature and dissolved oxygen profiles were measured every 2–4 weeks using a Hydrolab Minisonde 4a attached to a Surveyor 4a datalogger (Hach Environmental, Loveland, Colorado, U.S.A.).

I used a 153- μm mesh Wisconsin bucket net to collect four samples on each sampling date. Each of

these four samples constituted a pooling of vertical net hauls taken from the whole water column at four different sites within the deep basin of each lake. Three of the samples were preserved in 60–90% ethanol and later counted for *Daphnia* density. I analysed the remaining live sample immediately to determine haemoglobin prevalence in the *D. dentifera* population, calculated as the number of *D. dentifera* containing haemoglobin divided by the total number of *D. dentifera*. Based on the data collected in the 'Habitat use' study (described above), the prevalence of haemoglobin in the population was used to indicate the proportion of the overall population that was non-migratory (i.e. the 'deep' *D. dentifera*). The prevalence of non-haemoglobin-producing individuals was used to indicate the proportion of the overall population that was migratory (i.e. the 'migratory' *D. dentifera*).

I also studied more intensively the dynamics in two of the lake populations: Baker and Sherman. The density of the deep *D. dentifera* was high enough in these lakes to allow me to estimate instantaneous growth rate (r), birth rate (b) and, by difference, death rate (d) in these lakes. I also used the same sample in which I determined haemoglobin prevalence (see above) to estimate per capita fecundity (number of eggs per individual) for individuals with and without haemoglobin. This per capita fecundity was then combined with temperature-dependent egg development time to calculate the per capita birth rate (b) for each lake date, using the egg ratio method (Paloheimo, 1974; Rigler & Downing, 1984). The temperature used to calculate egg development time was determined based on vertical temperature profiles conducted throughout the study for each of the lake populations, combined with information on vertical migration of the deep and migratory *D. dentifera*. For Sherman Lake, 90% of individuals with haemoglobin were assumed to remain in the hypolimnion at all times, while the other 10% were assumed to be migratory. Forty percentage of the Sherman Lake individuals without haemoglobin were assumed to remain in the epilimnion all day, 30% were assumed to always be in the hypolimnion, and the other 30% were assumed to be migratory. I was unable to do detailed vertical habitat use studies in Baker Lake, because of safety concerns. Instead, I used values that were intermediate between those for Sherman and Lawrence Lakes to estimate the migration of individuals with and without haemoglobin (with haemoglobin: 80% always in hypolimnion, 20% undergoing

DVM; without haemoglobin: 25% always in hypolimnion, 35% undergoing DVM, 40% always in epilimnion). Egg development times were calculated separately for each of these three groups (according to Bottrell *et al.*, 1976), taking into account the differences in temperature experienced by the three groups (because of differences in temperature between habitats), and the amount of time spent in each habitat. I assumed that individuals undergoing DVM migrated to the hypolimnion half an hour before sunrise, and that they migrated to the epilimnion half an hour after sunset. Instantaneous population growth rate (r) between sampling days was calculated as $r_{ij} = (\ln N_j - \ln N_i)/(j - i)$, where $\ln N_i$ and $\ln N_j$ are the natural log of the densities on days i and j . I calculated the instantaneous per capita death rate (d_i) by subtracting growth rate (r_{ij}) from the per capita birth rate (b_i).

To evaluate whether the observed differences in hypolimnion use of *D. dentifera* within (seasonally) and among lakes affected coexistence with *D. pulicaria*, the main competitor of *D. dentifera* in these lakes (Tessier, Leibold & Tsao, 2000), I looked for correlations between the density of *D. pulicaria* and (i) the density of the deep *D. dentifera*, (ii) the density of the migratory *D. dentifera* and (iii) the overall *D. dentifera* population (i.e. the deep + the migratory *D. dentifera*). I looked for these correlations within lake populations for the five lakes for which there were sufficient data (at least five sampling dates). Data were log-transformed prior to the analysis. To deal with cases where the haemoglobin prevalence was estimated to be zero, I replaced this with half the lowest non-zero value (i.e. 0.1%) and multiplied that by the *D. dentifera* density on that date. For *D. pulicaria*, I replaced the density with half the lowest non-zero density (i.e. 44 *D. pulicaria* per m²).

One factor that might have influenced the relationships between *D. pulicaria* and *D. dentifera* is the size of the hypolimnetic refuge from fish predation (Tessier & Welser, 1991). The hypolimnetic refuge is the region between the thermocline and the zone of anoxia; the most common fish predator in these lakes, the bluegill sunfish, does not cross the thermocline, making the oxic regions below the thermocline a refuge from fish predation (Tessier & Welser, 1991). To calculate refuge size, I calculated the difference between the depth of the thermocline and the depth of anoxia (defined as dissolved oxygen concentrations

<1.0 mg L⁻¹). For each lake, I calculated the mean refuge size, and the means of the densities of deep *D. dentifera*, migratory *D. dentifera*, total *D. dentifera* and *D. pulicaria*. I expected there to be correlations between mean refuge size and mean population densities of deep *D. dentifera* and *D. pulicaria* (which live primarily in the deep habitat) but not between mean refuge size and mean migratory *D. dentifera* density.

Results

Daphnia dentifera that contained haemoglobin lived deeper than *D. dentifera* that did not contain haemoglobin ($F_{1,16} = 281.24$, $P < 0.0001$; Fig. 1; Tables 1 & 2). This difference was especially pronounced at night; most (c. 70–90%) of the animals with haemoglobin remained in the hypolimnion at night, whereas only few (c. 15–30%) of the animals without haemoglobin remained in the hypolimnion at night, and this pattern was consistent through time. Thus, haemoglobin is an indicator of hypolimnion use by *D. dentifera*.

The density of *D. dentifera* occupying the hypolimnion ('deep' *D. dentifera*, estimated as the density of *D. dentifera* containing haemoglobin) varied within and among lakes (Fig. 2). The deep *D. dentifera* were quite common in some lakes (e.g. Sherman), but

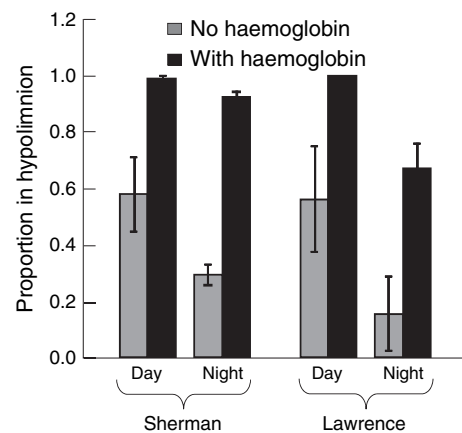


Fig. 1 Proportion of *Daphnia dentifera* in the lake hypolimnion. Data are shown for two lakes (Sherman and Lawrence) for day and night and for individuals with haemoglobin (black bars) and those without haemoglobin (grey bars). Both lakes were sampled on multiple dates. Error bars represent ± 1 standard error; during the day, individuals with haemoglobin were always observed in the hypolimnion in Lawrence Lake.

Table 1 Summary of habitat use by individuals with and without haemoglobin in Lawrence and Sherman Lakes (see also Fig. 1)

Lake	Haemoglobin?	% Always in hypolimnion	% Always in epilimnion	% Undergoing diel vertical migration
Lawrence	Yes	c. 70	0	c. 30
Lawrence	No	c. 15	c. 40	c. 45
Sherman	Yes	c. 90	0	c. 10
Sherman	No	c. 30	c. 40	c. 30

Table 2 ANOVA results for habitat use analysis. The model included three fixed effects: lake, day versus night ('DayNight') and haemoglobin production ('haemoglobin'). The effect of these factors on habitat use (i.e. proportion in the deep habitat) was modelled using a split-plot design, as described in the methods. 'd.f.', degrees of freedom

Effect	d.f.	F	P
Lake	1,1	0.68	0.56
DayNight	1,1	7.41	0.22
Haemoglobin	1,16	281.24	<0.0001
DayNight*Haemoglobin	1,16	0.01	0.93

relatively rare in others (e.g. 3L2). Thus, there is substantial variation in hypolimnion use by *D. dentifera* within lakes (seasonally), as well as among lakes.

The dynamics of the deep and migratory *D. dentifera* also differed through time (Fig. 2, Table 3). The density of the deep *D. dentifera* increased in all five lakes, whereas, in most lakes, there was no significant log-

linear trend in the density of the migratory *D. dentifera*. This difference in dynamics between the deep and migratory *D. dentifera* can be ascribed to differences in death rate (Fig. 3). In July, the deep *D. dentifera* in Baker and Sherman had substantially lower death rates (d) and higher population growth rates (r) than the migratory *D. dentifera*. As expected given the colder temperature of the hypolimnion, the birth rates (b) of the deep *D. dentifera* were also generally lower than those of the migratory *D. dentifera*, though this difference was smaller than the difference in death rates (Fig. 3).

The deep and migratory *D. dentifera* had qualitatively different relationships with the density of *D. pulicaria* (Fig. 4; Table 4). There was a negative correlation between the densities of deep *D. dentifera* and *D. pulicaria*, but there was no consistent relationship between the densities of the migratory *D. dentifera* and *D. pulicaria*; there was also no consistent relationship between the overall density of *D. dentifera* and the

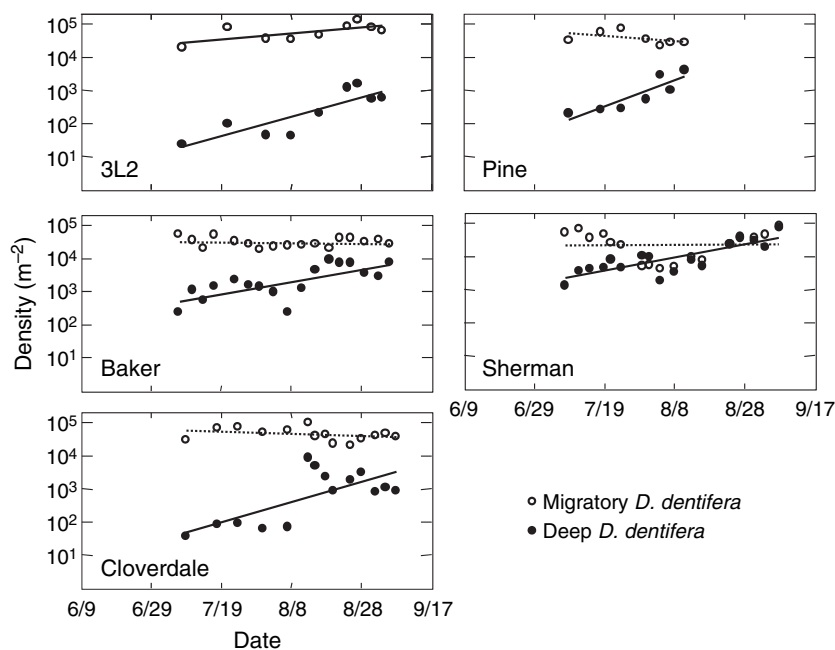
**Fig. 2** Seasonal dynamics of migratory and deep *Daphnia dentifera* in five lake populations. Data for the 'migratory' (without haemoglobin) *D. dentifera* are shown with open symbols; data for the 'deep' (with haemoglobin) *D. dentifera* are shown with closed symbols. Linear fits are shown for each. Solid lines indicate significant correlations between Julian day and log density; dotted lines indicate non-significant correlations (see Table 3).

Table 3 Summary of regressions between Julian Day and the (log) densities of deep and migratory *Daphnia dentifera*. Data cover time periods shown in Fig. 2

Lake	Deep <i>D. dentifera</i>			Migratory <i>D. dentifera</i>		
	Slope	<i>r</i>	<i>P</i>	Slope	<i>r</i>	<i>P</i>
3L2	0.068	0.855	0.003	0.020	0.677	0.045
Baker	0.043	0.723	0.001	-0.002	0.109	0.678
Cloverdale	0.070	0.709	0.004	-0.008	0.335	0.241
Pine	0.091	0.879	0.009	-0.018	0.497	0.257
Sherman	0.045	0.809	<0.001	0.002	0.032	0.904

density of *D. pulicaria*, nor between the densities of the two morphs of *D. dentifera*.

The abundances of deep *D. dentifera* and *D. pulicaria* were correlated with the size of the hypolimnetic refuge from fish predation, though in opposite directions. Lakes with large refuges generally had relatively large *D. pulicaria* populations (correlation between mean refuge size and mean *D. pulicaria* density: $r = 0.66$, $P = 0.08$; Fig. 5), but relatively low densities of deep *D. dentifera* (correlation between mean refuge size and mean deep *D. dentifera* density: $r = -0.75$, $P = 0.03$). There was no significant correlation between mean refuge size and mean migratory *D. dentifera* density ($r = 0.004$, $P = 0.99$) or mean overall *D. dentifera* density ($r = -0.13$, $P = 0.75$).

Discussion

Phenotypic variation within populations is common, yet is still generally overlooked in community ecology. This study found variation within *D. dentifera* lake populations in hypolimnion use. Specifically, lakes appeared to contain two distinct morphs of *D. dentifera*, one that migrates vertically and one that resides primarily in the hypolimnion. While other studies have also found within- and among-population variation in habitat use (e.g. Weider, 1984; Leibold *et al.*, 1994; King & Miracle, 1995; De Meester & Weider, 1999; Ringelberg, Van Gool & Brehm, 2004), this study additionally demonstrated that this variation can have important consequences for population dynamics and interspecific competition.

Deep-living and migratory *D. dentifera* differed substantially in their seasonal dynamics. Within lakes, migratory *D. dentifera* had relatively constant densities, while deep *D. dentifera* showed increased densities over the course of the study. This increase in deep *D. dentifera* density appears to have been driven largely by the relatively low death rates of deep *D. dentifera*. However, in Sherman Lake in late July and August, the birth rates of the deep *D. dentifera* exceeded those of the migratory *D. dentifera*, which is

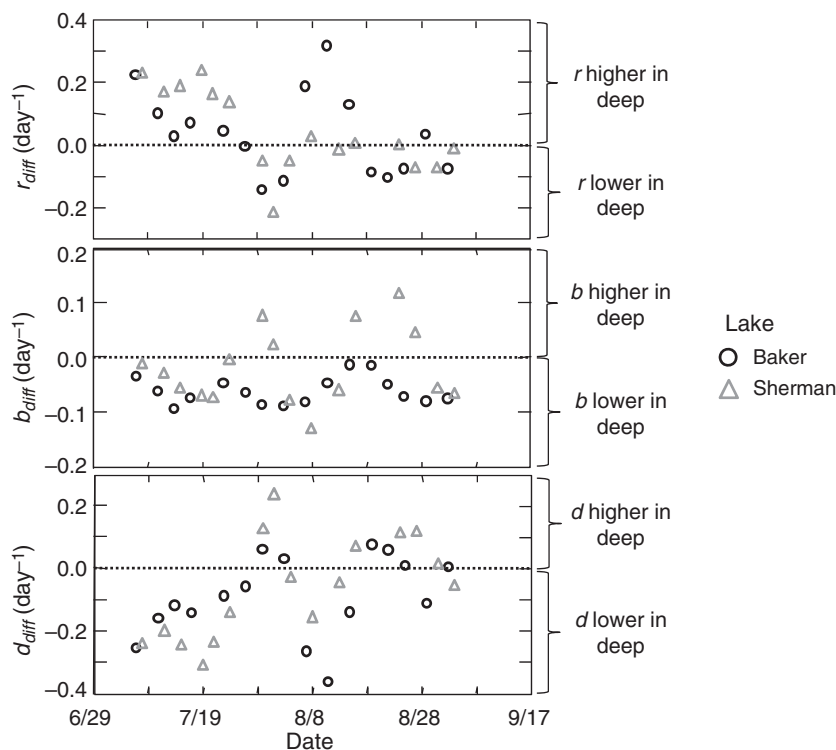


Fig. 3 Population dynamics for two *Daphnia dentifera* populations with high haemoglobin prevalence, Baker and Sherman Lakes. The top panel shows the difference between the instantaneous population growth rate (r) of the deep (with haemoglobin) and migratory (without haemoglobin) *D. dentifera*. The middle panel shows data for population birth rate (b), and the bottom panel shows data for population death rate (d). For each panel, the dotted line indicates no difference; points above this line indicate a higher rate in the deep *D. dentifera*.

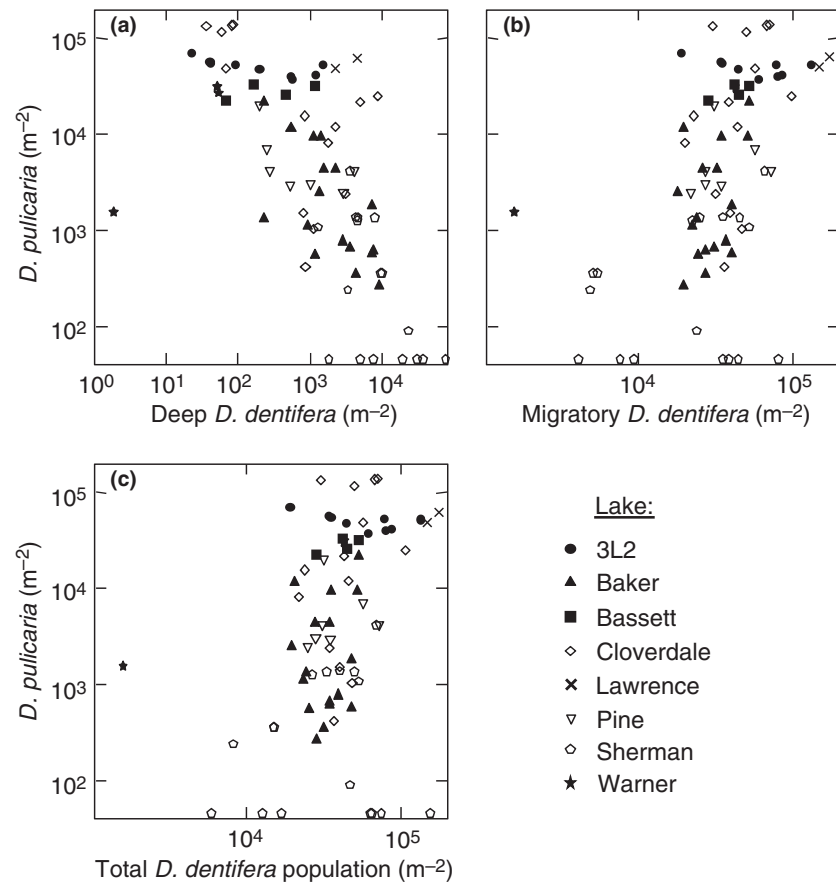


Fig. 4 Relationships between *Daphnia pulicaria* density and (a) the density of the deep (with haemoglobin) *Daphnia dentifera*, (b) the density of the migratory (without haemoglobin) *D. dentifera* and (c) the total *D. dentifera* population. Data are shown for eight lakes. Each symbol represents the densities for a given lake date.

Table 4 Summary of within-lake correlations between the densities of deep *Daphnia dentifera*, migratory *D. dentifera*, total *D. dentifera* and *Daphnia pulicaria* density (m^{-2}). All four variables were log-transformed prior to analysis. Within-lake correlations are not shown for Bassett, Lawrence or Warner Lakes, which both had <5 sampling dates

Correlation	Lake	<i>n</i>	Deep <i>D. dentifera</i> – <i>D. pulicaria</i>		Migratory <i>D. dentifera</i> – <i>D. pulicaria</i>		Total <i>D. dentifera</i> – <i>D. pulicaria</i>		Deep <i>D. dentifera</i> –migratory <i>D. dentifera</i>	
			<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
	3L2	9	–0.75	0.02	–0.61	0.08	–0.61	0.08	0.88	0.002
	Baker	17	–0.65	0.005	0.36	0.15	0.17	0.52	0.02	0.95
	Cloverdale	14	–0.59	0.03	0.35	0.22	0.33	0.25	–0.14	0.64
	Pine	7	–0.63	0.13	0.21	0.65	0.17	0.72	–0.71	0.07
	Sherman	17	–0.54	0.03	0.24	0.35	0.09	0.75	0.32	0.21

surprising given that temperature strongly influences birth rate (Bottrell *et al.*, 1976) and temperatures are colder in the hypolimnion. This higher birth rate of the deep *D. dentifera* was driven by much higher fecundity of deep females (M. A. Duffy, unpubl. data). Research on nearby small stratified lakes indicates that food quality improves with depth (Demott, Edington & Tessier, 2004), which may help explain

the relatively high egg ratios of deep *D. dentifera* in Sherman.

Whether the deep and migratory *D. dentifera* are genetically differentiated subpopulations remains to be determined. *Daphnia pulicaria* has also been shown to vary in vertical habitat use (Leibold & Tessier, 1997), because of a combination of heritable differences in habitat use and acclimation to a particular

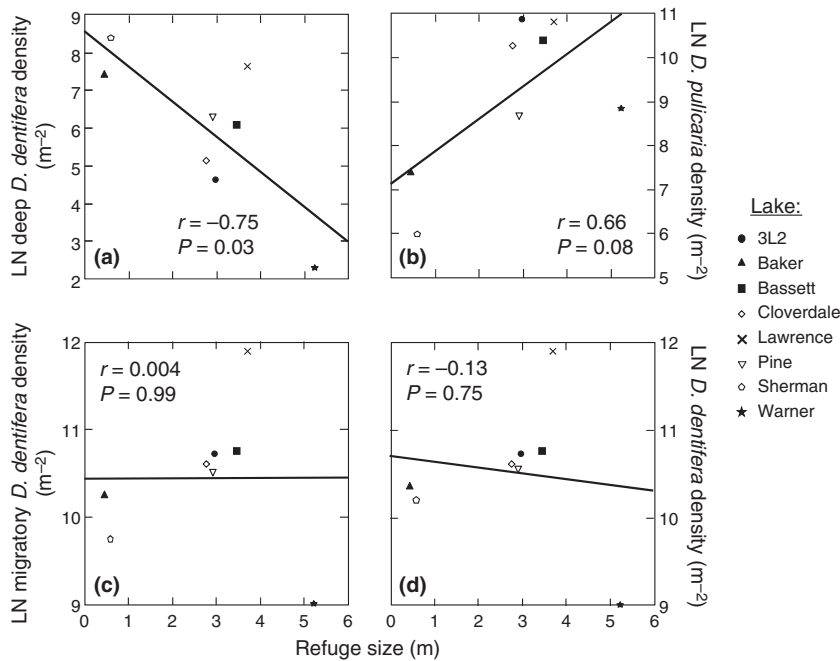


Fig. 5 Relationships to mean refuge size of natural log (LN) of mean (a) deep *Daphnia dentifera* density, (b) *Daphnia pulicaria* density, (c) migratory *D. dentifera* density and (d) total *D. dentifera* density. Lakes are shown with different symbols, as indicated in the legend. Regression lines and correlations are also shown.

habitat (Leibold *et al.*, 1994). A study on a single population of *Daphnia pulex* found differences among genotypes in the presence of haemoglobin and ability to tolerate low-oxygen conditions (Weider & Lampert, 1985). Additionally, a study on *Daphnia longispina* in a Spanish lake showed that the population was dominated by two clones; one of these clones showed strong DVM, while the other remained in deeper water (King & Miracle, 1995). Finally, substantial differences in migration behaviour and habitat use were found among genotypes in the *D. galeata/longispina* complex (Ringelberg *et al.*, 2004). Thus, there is substantial evidence for differences in migration behaviour and habitat use being linked with genotypic differences, so the deep and migratory *D. dentifera* may indeed be different subpopulations. Future studies to determine whether there are genetic differences between the deep and migratory *D. dentifera*, and how much genetic variation is contained within these two groups, would be valuable.

Regardless of whether they were genetically distinct subpopulations, deep and migratory *D. dentifera* showed clear differences in their interspecific interactions. Specifically, only deep *D. dentifera* showed a negative relationship with *D. pulicaria* density. This relationship would have been missed had I only looked at the overall relationship between *D. dentifera* and *D. pulicaria*. The negative relationship between

deep *D. dentifera* and *D. pulicaria* (which also produces haemoglobin) probably reflects competition between these two taxa. Competition was experimentally demonstrated in a study on *D. pulicaria* and *D. dentifera* (then called *D. galeata mendotae*) in a nearby lake population (Hu & Tessier, 1995). That study found a seasonal shift in the outcome of competition; *D. pulicaria* had stronger negative effects on *D. dentifera* in early summer, while *D. dentifera* had stronger negative effects on *D. pulicaria* in late summer (Hu & Tessier, 1995). In both the Hu and Tessier study and the current one, competition appeared to be mediated by the size of the hypolimnetic refuge from fish predation, suggesting that differences in habitat structure among lakes and seasonal changes within lakes may be important to determining the outcome of competition. One factor that was correlated with the size of the hypolimnetic refuge in this study was the temperature of the hypolimnion (lakes with larger refuges had colder hypolimnia; M. A. Duffy, unpubl. data). This may explain the observed patterns between refuge size and the densities of *D. pulicaria* and *D. dentifera*, since *D. pulicaria* prefer colder temperatures than *D. dentifera* (Threlkeld, 1980).

Intraspecific variation in habitat use by *D. dentifera* may influence interactions with other community members as well. Certainly, variation in habitat use should affect interactions with predators, particularly

fish predators. Bluegill sunfish are the dominant fish predators in these lake populations. The thermocline represents an effective barrier to fish, so individuals living below the thermocline (i.e. the deep *D. dentifera*) should have greatly reduced risk of fish predation. This may help explain the substantial difference in the death rates of the deep and migratory *D. dentifera* observed at the beginning of this study.

Overall, this study extends a growing body of literature demonstrating the importance of intraspecific variation (Bolnick *et al.*, 2003; Hughes *et al.*, 2008; Post *et al.*, 2008). The causes of intraspecific variation have been the focus of studies for decades, yet its consequences for interspecific interactions have largely been ignored. However, this study, along with other recent studies, suggest that the tradition in community ecology of simply studying population means can be misleading, and that intraspecific variation must be considered.

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