

# A Reappraisal of Phenotypic Variation in *Daphnia galeata mendotae*: The Role of Interspecific Hybridization

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Seasonal, within-lake, and among-lake variation in helmet size and shape has been reported for *Daphnia galeata mendotae*. The genetic component of this variation was assessed by an allozyme and morphological reanalysis of nine previously studied sites. Genetic associations with morphological variation were found, but all were attributed to *D. galeata mendotae* × *Daphnia rosea* hybridization or to taxonomic confusion with *D. rosea*. The existence of hybrids accounted for spatial polymorphism both within and among lakes. In addition, hybrids contributed to seasonal variation as they increased in abundance from summer to winter. Nevertheless, cyclomorphosis in *D. galeata mendotae* s.s. was real and due largely to phenotypic plasticity. Local hybridization between *D. galeata mendotae* and *D. rosea* was widespread from the midwestern states to Vermont. The distributions and habitat associations of *D. galeata mendotae* and *D. rosea* indicated that ecological segregation at the lake level acts as an important reproductive isolating mechanism. Reinterpretation of previous studies, however, suggests that disturbance followed by one or a few hybridization events often leads to hybrid domination of a lake.

On a signalé une variation saisonnière, au sein d'un lac et d'un lac à l'autre, dans la taille et la forme de la capsule céphalique chez *Daphnia galeata mendotae*. Nous avons évalué la composante génétique de cette variation en étudiant un allozyme et en effectuant une deuxième analyse morphologique de neuf sites étudiées antérieurement. Nous avons découvert des associations entre l'aspect génétique et la variation morphologique, mais elles ont toutes été attribuées à une hybridation de *D. galeata mendotae* × *Daphnia rosea* ou à une confusion taxinomique avec *D. rosea*. L'existence d'hybrides expliquait le polymorphisme spatial tant dans un lac que d'un lac à l'autre. De plus, les hybrides contribuaient à la variation saisonnière du fait que leur abondance augmentait de l'été à l'hiver. Cependant, le cyclomorphisme chez *D. galeata mendotae* s.s. était réel, et dû principalement à la plasticité du phénotype. L'hybridation à caractère local entre *D. galeata mendotae* et *D. rosea* était répandue des États du Midwest au Vermont. Les répartitions et les associations en matière d'habitat de *D. galeata mendotae* et *D. rosea* indiquaient que la ségrégation écologique au niveau du lac constitue un mécanisme important d'isolement pour la reproduction. La réinterprétation des études précédentes semble toutefois indiquer qu'une perturbation suivie par un ou quelques événements d'hybridation conduit souvent à une domination d'un lac par les hybrides.

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Striking morphological variation is common in aquatic invertebrate species. Often, the variation involves defensive structures (e.g., helmets and spines) whose presence is strongly correlated with predation risk (Havel 1987). In cladocerans, the most prevalent pattern of variation is cyclomorphosis — a temporal succession of morphs. Other polymorphic systems lack temporal succession but the morphs are spatially segregated either within water bodies (Green 1967; Zaret 1972) or among water bodies (Riessen and O'Brien 1980).

The freshwater cladoceran *Daphnia galeata mendotae* Birge, 1918 is exceptional in that it exhibits all three of the major polymorphism patterns. The two common morphs are characterized by their differing head size and shape: tall and pointed, and low and rounded. Usually, temporal shifts in the frequencies of these morphs lead to cyclomorphosis, as individuals with tall, pointed helmets are prevalent in the summer and individuals with low, rounded helmets are dominant in the winter (Brooks 1957). Yet, it has been known since Herrick (1884) and Birge (1892) that among-lake spatial polymorphism also exists in *D. galeata mendotae*, as some lakes contain only rounded-head forms

during the warm months. In addition, some lakes contain both the rounded- and pointed-head morphs during the summer (Brooks 1964; Malone and McQueen 1983). In these lakes, Brooks (1964) described spatial segregation with the pointed-head morphs dominating the epilimnion and the rounded-head morphs dominating the deeper strata.

Such polymorphism warrants genetic analysis. The initial investigators of allozyme and morphological variation in *D. galeata mendotae* failed to provide evidence of a strong genetic component to these polymorphisms; instead, phenotypic plasticity was thought to account for most of the observed morphological variation (Jacobs 1961; Brooks 1964; Mort 1986; Stirling and McQueen 1987; Mort 1989). Recently, however, Taylor and Hebert (1992) have shown that interspecific hybridization contributes to all three patterns of polymorphism in *D. galeata mendotae*. Their allozyme analyses showed that interspecific hybrids between *D. galeata mendotae* and *Daphnia rosea* are common in the lakes of Indiana. These hybrids, which always possessed a rounded-head phenotype, often cooccurred and underwent seasonal succession with one parent taxon while

TABLE 1. Summary of morph and allozyme phenotypes from prior studies of *D. galeata mendotae* populations. The "intermediate" and "pointed" helmet morphs of Stirling and McQueen (1987) have been pooled in this table under the angulated/pointed category. Parentheses indicate genotype designations of Stirling and McQueen (1987). Enzyme abbreviations are those recommended by IUBNC (1984).

Lake	Prior studies	Midsummer helmet phenotype (%)			Multilocus genotype frequencies				Our taxonomic reevaluation	
		High, angulated pointed	High, rounded	Low, rounded	<i>AO</i>	<i>sAAT</i>	<i>GPI</i>	<i>PGM-2</i>		
Bantam Lake, Conn.	Brooks 1947; Jacobs 1961	100	0	0	—	—	—	—	<i>D. g. m.</i>	
East Twin Lake, Conn.	Brooks 1964; Zaret 1972	95	—	—	—	—	—	—	<i>D. g. m.</i>	
		—	—	5	—	—	—	—	<i>D. g. m. × D. r.</i>	
Mt. Tom Pond, Conn.	Brooks 1964	2	—	—	—	—	—	—	<i>D. g. m.</i>	
		—	—	98	—	—	—	—	<i>D. g. m. × D. r.</i>	
Queechy Lake, N.Y.	Brooks 1964	0	0	100	—	—	—	—	<i>D. g. m. × D. r.</i>	
Lake Mitchell, Vt.	Mort and Jacobs 1981; Mort 1986	0	0	100	—	—	<i>ss</i>	—	0.024	<i>D. catawba?</i>
		0	0	100	—	—	<i>fs</i>	—	0.803	<i>D. g. m. × D. r.</i>
		0	0	100	—	—	<i>ff</i>	—	0.173	<i>D. r.</i>
Lake Morey, Vt.	Mort and Wolf 1985; Mort 1986, 1989	100	0	0	—	<i>ss</i>	—	—	0.763	<i>D. g. m.</i>
		100	0	0	—	<i>sf</i>	—	—	0.237	<i>D. g. m.</i>
Haynes Lake, Ont.	Stirling and McQueen 1987	0	100	0	<i>fs</i>	<i>mm</i>	<i>mm</i>	<i>sf</i>	1.000	<i>D. g. m. × D. r.</i>
Lake St. George, Ont.	Malone and McQueen 1983; Stirling and McQueen 1987	88	0	12	(1) <i>ff</i>	<i>mm</i>	<i>mm</i>	<i>ss</i>	0.340	<i>D. g. m.</i>
		86	0	14	(2) <i>ff</i>	<i>mm</i>	<i>mm</i>	<i>sf</i>	0.100	<i>D. g. m.</i>
		0	0	100	(3) <i>fs</i>	<i>mm</i>	<i>mm</i>	<i>sf</i>	0.100	<i>D. g. m. × D. r.</i>
		71	0	28	(9) <i>ff</i>	<i>mm</i>	<i>sm</i>	<i>ss</i>	0.140	<i>D. g. m.</i>
Three-Lakes-Three, Mich.	Tessier et al. 1992	0	100?	?	(15) <i>ff</i>	<i>mm</i>	<i>mf</i>	<i>ss</i>	0.100	<i>D. g. m.</i>
		0	100?	?	—	—	—	—	—	<i>D. r.</i>

the other parent taxon was absent or rare. These abundance patterns generated seasonal changes in morphology that mimicked cyclomorphosis. Among-lake spatial polymorphisms occurred during the summer because some lakes contained only hybrids (with rounded helmets) whereas other lakes contained only *D. galeata mendotae* (with pointed helmets). When both hybrids and *D. galeata mendotae* coexisted within a lake, a dimorphic pattern resulted.

Hybrids between *D. galeata mendotae* and *D. rosea* in Indiana were detected in 17 of the 22 Indiana lakes studied. Given that these species are neighbouringly sympatric (sensu Grant 1981) throughout much of North America, it is unlikely that hybridization is restricted to Indiana. Allozyme diagnosis of hybrids is straightforward because both fixed allelic differences and marked gene frequency divergences exist between their parent species. The present study reevaluates previous reports of phenotypic polymorphisms in *D. galeata mendotae* from lakes in eastern North America and assesses the role of interspecific hybridization as a source of this variation. To our knowledge, we have included lakes from all prior studies that examined the extent of morphological and genetical variation in "*D. galeata mendotae*" at the population level. We provide allozyme and morphological evidence that both *D. galeata mendotae* × *D. rosea* hybridization and misidentification of *D. rosea* are important in accounting for spatial (both within and among lakes) and seasonal patterns of phenotypic diversity in these populations.

## Materials and Methods

Populations of *D. galeata mendotae* and *D. rosea* from Indiana (Taylor and Hebert 1992) were used as genetic reference material for the present study. Additional samples of typical *D. rosea* were collected from both Ontario (Guelph) and Vermont (Lake Mitchell) for evaluation of regional variation in allozyme markers. Prior work on morphological and genetic diversity in populations of *D. galeata mendotae* has been limited to nine sites in eastern North America (Table 1). *Daphnia* were collected from these lakes between June 14 and July 9 in either 1990 or 1992. Two of these lakes were sampled again on April 17, 1991 (Bantam Lake and Mt. Tom Pond), for genetic assessment of temporal polymorphisms. Duplicate vertical hauls were conducted with a 30-cm-diameter plankton net (200- $\mu$ m mesh) and the resulting *Daphnia* samples were frozen in liquid nitrogen. *Daphnia* species were identified according to Brooks (1957).

## Electrophoretic Analysis

Individuals of the *D. galeata mendotae* complex were characterized under a dissecting microscope according to helmet shape (round, angulated, pointed) and size (low, high). Cellulose acetate electrophoresis was then conducted using standard methods (Hebert and Beaton 1989). Ten variable loci were used including the following nine loci that Taylor and Hebert (1992) found useful in separating *D. galeata mendotae* from *D. rosea*; aldehyde oxidase (*AO*, 1.2.3.1) aspartate aminotransferase

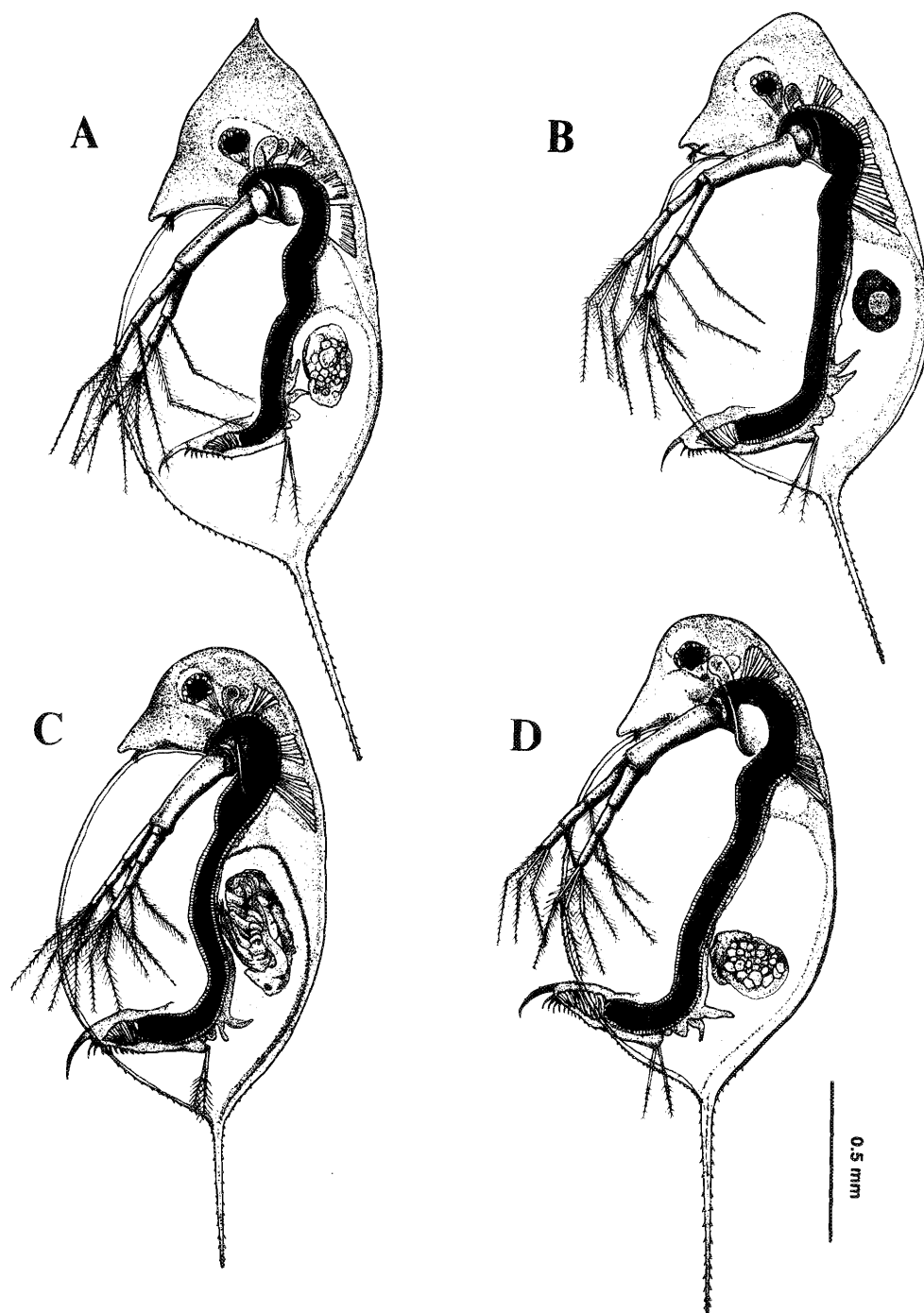


FIG. 1. Midsummer morphs of *D. galeata mendotae*. (A) tall, pointed morph from Lake St. George, Ont., June 19, 1990; (B) tall, angulated morph from same sample; (C) short, rounded morph from same sample; (D) short, rounded morph from Lake Mitchell, Vt., July 9, 1990. Illustrations represent adult females in lateral view.

(*sAAT*, *mAAT*, 2.6.1.1), dipeptidase (*PEPA*, 3.4.13.11), fumarate hydratase (*FUM*, 4.2.1.2), lactate dehydrogenase (*LDH*, 1.1.1.27), phosphoglucosomutase (*PGM-2*, 5.4.2.2), phosphoglucosomerase (*GPI*, 5.3.1.9), and proline dipeptidase (*PEPD*, 3.4.13.9). Reinterpretation of phenotypic diversity at an additional locus (*PGM-1*) provided another diagnostic difference between *D. galeata mendotae* and *D. rosea* and this locus was also scored in this study. Substrates for *PEPA* and *PEPD* were

L-leucylglycine and L-phenylalanyl proline, respectively. Alleles were assigned ascending letter designations with the slowest mobility (relative to the anode) assigned to "a". Individuals from clonal laboratory cultures of typical *D. galeata mendotae* and *D. rosea* from Indiana were used as electrophoretic standards. Nonmetric multidimensional scaling (MDS) of a Cavalli-Sforza and Edwards (1967) chord distance matrix was used to examine the genetic intermediacy of putative hybrid populations.

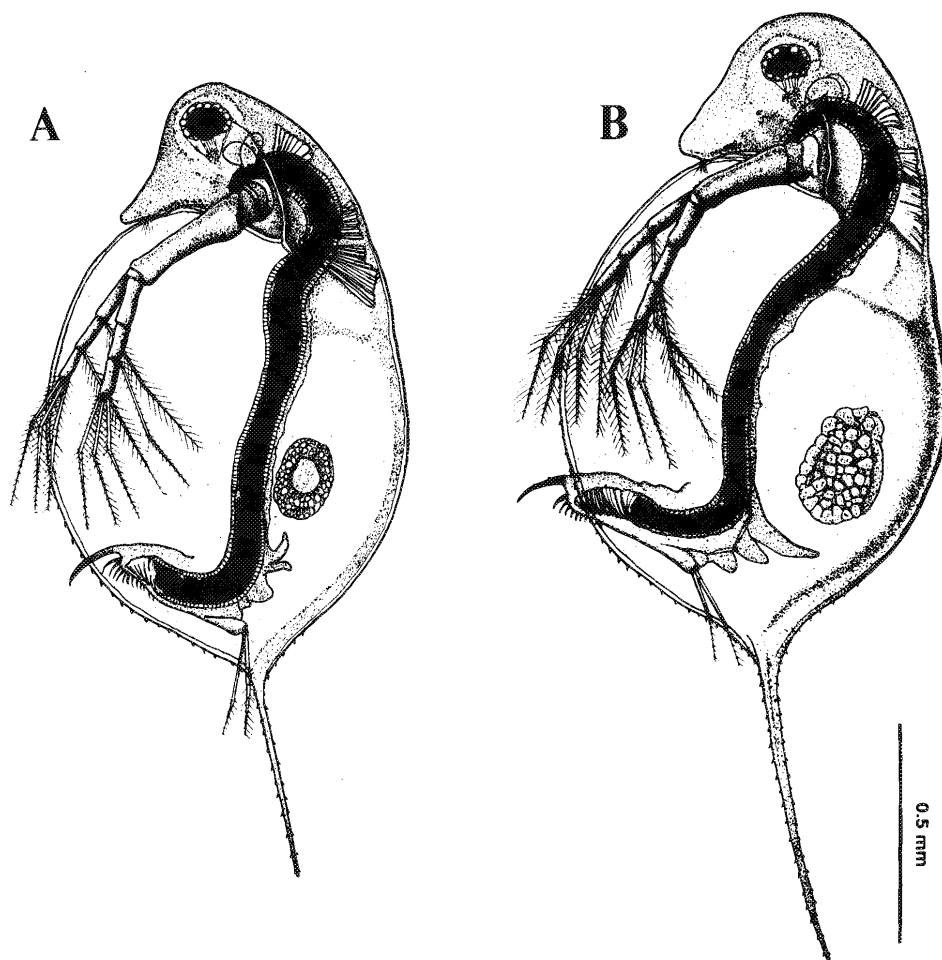


FIG. 2. (A) Mature female of *D. rosea* from Lake Mitchell, Vt., July 9, 1990; (B) mature female of short, rounded morph of *D. galeata mendotae* from Mt. Tom Pond, Conn., April 17, 1991.

## Results

### Morphological Analysis

The *D. galeata mendotae* s.l. in our samples were assigned to three morphs on basis of helmet size and shape. Individuals possessed either tall, pointed helmets (Fig. 1A), tall, angulated helmets (Fig. 1B), or short, smoothly rounded helmets (Fig. 1C and 1D). *Daphnia galeata mendotae* were absent in our samples from Queechy Lake was collected from the other eight lakes that have been the subject of prior studies. Haynes Lake and Three-Lakes-Three samples contained specimens with low, rounded heads. Our samples from Lake Mitchell also contained a low-, rounded-helmet morph of *D. galeata mendotae* s.l. (Fig. 1D) in addition to *D. rosea* (Fig. 2A). Lake St. George contained all three morphs, while the remaining midsummer samples (Bantam, East Twin, Morey, and Mt. Tom) consisted entirely of specimens with tall, pointed helmets. In contrast, April samples of Bantam Lake and Mt. Tom Pond consisted entirely of *Daphnia* with short, smoothly rounded helmets (Fig. 2B).

### Allozyme Analysis

The supplemental reference populations of eastern *D. rosea* (Lake Mitchell and Guelph) possessed similar allelic arrays to those of conspecific Indiana populations (Table 2). They differed

from the Indiana populations of *D. rosea* only by the absence of *LDH<sup>a</sup>* and the presence of *PGM-2<sup>c</sup>* and *PGM-2<sup>f</sup>*. Likewise, many individuals from Haynes Lake and Three-Lakes-Three exhibited allozyme profiles that were typical of *D. rosea* (Table 3). Nevertheless, 61% of Haynes Lake and 15% of Three-Lakes-Three individuals were either backcrosses or advanced generation hybrids, as they possessed either the *AO<sup>b</sup>* or *PEPA<sup>c</sup>* alleles that are diagnostic of *D. galeata mendotae*. Morphs with high, pointed, or angulated helmets (Bantam, East Twin, St. George, Morey, and Mt. Tom) possessed allelic arrays typical of *D. galeata mendotae* (Table 2). Only the *sAAT* locus showed marked gene frequency differences between Indiana and these test populations of *D. galeata mendotae*. Some alleles not detected in *D. galeata mendotae* from Indiana were, however, present in the test populations (*GPI<sup>a</sup>*, *PGM-2<sup>a</sup>*, *LDH<sup>b</sup>*, *LDH<sup>d</sup>*, and *PEPA<sup>b</sup>*).

Low-, rounded-helmet *D. galeata mendotae* s.l. from Lake St. George and Lake Mitchell possessed allozyme patterns that are consistent with *D. galeata mendotae* × *D. rosea* hybridization (Tables 2 and 3). Specifically, fixed heterozygosity patterns were observed at *AO*, *mAAT*, and *PGM-1* for alleles that are unique markers of the parental genomes. In addition, high heterozygosity was present at other loci (i.e., *PEPD*, *PGM-2*, and *PEPA* in Lake St. George and *PEPD*, *PGM-2*, and *GPI* in Lake Mitchell). Such heterozygotes consisted of alleles that differ

TABLE 2. Allelic frequency comparison at 10 polymorphic loci among Indiana *D. galeata mendotae* (mean of eight populations), Indiana *D. rosea* (nine populations), eastern *D. rosea* (two populations), and *D. galeata mendotae* reexamined in this study. Numbers in parentheses are sample sizes. ND, no data available.

Locus	Alleles	<i>D. galeata</i> (Indiana)	<i>D. rosea</i> (Indiana)	<i>D. rosea</i> (eastern)	Bantam	East Twin	Morey	Mt. Tom	St. George
<i>mAAT</i>	<i>a</i>	— (269)	1.00 (291)	1.00 (178)	— (37)	— (26)	— (67)	— (99)	— (117)
	<i>b</i>	1.00	—	—	1.00	1.00	1.00	1.00	1.00
<i>sAAT</i>	<i>a</i>	0.20 (321)	1.00 (669)	1.00 (154)	0.9 (154)	0.90 (195)	0.92 (174)	0.96 (119)	1.00 (138)
	<i>b</i>	0.80	—	—	0.03	0.10	0.08	0.04	—
<i>AO</i>	<i>a</i>	— (418)	1.00 (900)	1.00 (184)	— (154)	— (175)	— (132)	— (110)	— (145)
	<i>b</i>	1.00	—	—	1.0	1.00	1.00	1.00	1.00
<i>FUM</i>	<i>a</i>	0.30 (336)	— (484)	— (110)	— (176)	— (175)	— (132)	— (110)	— (66)
	<i>b</i>	0.70	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>GPI</i>	<i>a</i>	— (249)	— (775)	— (243)	— (154)	0.03 (176)	0.24 (196)	— (110)	0.03 (180)
	<i>b</i>	0.96	1.00	1.00	1.00	0.97	0.76	1.00	0.90
	<i>c</i>	0.04	—	—	—	—	—	—	0.07
<i>LDH</i>	<i>a</i>	— (430)	0.11 (981)	— (200)	— (65)	— (172)	— (44)	— (110)	— (125)
	<i>b</i>	—	—	—	0.03	0.15	—	—	—
	<i>c</i>	1.00	0.89	1.00	0.97	0.79	1.00	1.00	1.00
	<i>d</i>	—	—	—	—	0.06	—	—	—
<i>PEPA</i>	<i>a</i>	0.07 (291)	1.00 (291)	1.00 (182)	— (175)	— (114)	0.03 (141)	0.16 (93)	— (179)
	<i>b</i>	—	—	—	—	0.35	0.02	0.03	0.08
	<i>c</i>	0.93	—	—	1.00	0.65	0.95	0.81	0.92
<i>PEPD</i>	<i>a</i>	0.81 (289)	— (301)	— (207)	0.55 (122)	0.98 (142)	0.75 (186)	1.00 (98)	0.97 (188)
	<i>b</i>	0.19	1.00	1.00	0.45	0.02	0.25	—	0.03
<i>PGM1</i>	<i>a</i>	— (87)	1.00 (209)	1.00 (140)	ND	ND	— (32)	ND	— (31)
	<i>b</i>	1.00	—	—	—	—	1.00	—	1.00
<i>PGM2</i>	<i>a</i>	— (296)	— (876)	— (106)	0.07 (152)	0.02 (192)	0.05 (131)	0.46 (109)	— (191)
	<i>b</i>	0.60	—	—	0.57	0.72	0.90	0.41	0.80
	<i>c</i>	—	—	0.05	—	—	—	—	—
	<i>d</i>	0.40	0.90	0.33	0.36	0.26	0.05	0.13	0.20
	<i>e</i>	—	0.10	0.41	—	—	—	—	—
	<i>f</i>	—	—	0.21	—	—	—	—	—

greatly in frequency between *D. rosea* and *D. galeata mendotae*. Genotypic diversity of the hybrids was low, as only one multilocus genotype was found in Lake Mitchell whereas one hybrid genotype constituted 96% of the Lake St. George sample. No backcrosses or introgressants were detected in either lake.

Both of these hybrid populations possessed the allelic arrays that are expected of hybridization involving local populations of parent species. For example, the Lake Mitchell hybrids had the *Pgm<sup>c</sup>* allele which was detected only in Lake Mitchell *D. rosea*. In addition, alleles that were found in eastern hybrids of this study (*GPI<sup>a</sup>* and *GPI<sup>c</sup>*) were detected in nearby parent populations but not in Indiana *D. galeata mendotae* or *D. rosea*. Similarly, the *FUM<sup>a</sup>* and *LDH<sup>a</sup>* alleles were found in Indiana parent species and hybrids (Taylor and Hebert 1992) but were absent in both hybrid and parent populations of Ontario and New England. Finally, the possession of the *sAAT<sup>aa</sup>* genotype by all hybrids in this study also supports the notion of local hybridization, as nearby *D. galeata mendotae* were nearly fixed or fixed for *sAAT<sup>a</sup>* whereas *D. galeata mendotae* in Indiana were nearly fixed for *sAAT<sup>b</sup>*.

A spatial summary of these genetic relationships was provided by MDS (Fig. 3). Populations of *F<sub>1</sub>* hybrids from Indiana were intermediate to their parental populations (Indiana *D. rosea* and *D. galeata mendotae*) in dimension 1. We therefore interpreted

this dimension as a hybrid index containing most of the among-species genetic variation. We interpreted dimension 2, on the other hand, as representing genetic variation within taxa because the Indiana populations were separated from their eastern populations. In dimension 1, Lake Mitchell and Guelph *D. rosea* were grouped with Indiana *D. rosea*, while the *D. galeata mendotae* with high, pointed helmets (Bantam, East Twin, St. George, Morey, and Mt. Tom) grouped with the Indiana *D. galeata mendotae*. Dimension 1 showed the genetic intermediacy of the Lake Mitchell and Lake St. George hybrid populations between *D. rosea* and *D. galeata mendotae*. Similarly, Haynes Lake, which contained several introgressants, was intermediate between *D. rosea* and hybrid populations. In dimension 2, the Lake Mitchell and Lake St. George hybrid populations grouped with the eastern populations of parent species whereas 13 of 14 Indiana hybrid populations grouped with Indiana populations of parent species.

#### Allozyme–Morph Covariation within *D. galeata mendotae* s.s.

The two high-helmeted morphs (angulated and pointed) in Lake St. George, which possessed typical *D. galeata mendotae* allelic arrays, were genetically different. A total of 17 multilocus genotypes (hereafter clones) were apparent from the analysis of four variable loci. Two clones, which differed only at *PGM-2*,

TABLE 3. Genotype frequencies at 10 polymorphic loci in low-, rounded helmet morphs. Bantam and Mt. Tom samples are from April whereas all other lake samples are from midsummer.  $n$  = sample size.

Locus	Observed genotypes	Lake St. George	$n$	Lake Mitchell	$n$	Mt. Tom	$n$	Bantam	$n$	Three-Lakes-Three	$n$	Haynes Lake	$n$
<i>mAAT</i>	<i>aa</i>	—	55	—	65	—	66	—	49	1.000	33	1.000	42
	<i>ab</i>	1.000		1.000		—		—		—	—	—	
	<i>bb</i>	—		—		1.000		1.000		—	—	—	
<i>sAAT</i>	<i>aa</i>	1.000	60	1.000	35	0.984	63	1.000	55	1.000	33	1.000	44
	<i>ab</i>	—		—		0.016		—		—	—	—	
<i>AO</i>	<i>aa</i>	—	57	—	107	—	62	—	54	0.850	33	0.425	40
	<i>ab</i>	1.000		1.000		—		—		0.150		0.500	
	<i>bb</i>	—		—		1.000		1.000		—		0.075	
<i>FUM</i>	<i>bb</i>	1.000	34	1.000	9	1.000	22	1.000	22	1.000	33	1.000	44
<i>GPI</i>	<i>ab</i>	—	66	1.000	117	—	62	—	33	—	33	—	44
	<i>bb</i>	0.955		—		1.000		1.000		1.000		1.000	
	<i>bc</i>	0.045		—		—		—		—		—	
<i>LDH</i>	<i>cc</i>	1.000	52	1.000	95	1.000	62	1.000	54	1.000	33	1.000	44
<i>PEPA</i>	<i>aa</i>	—	62	1.000	78	—	51	—	32	1.000	33	0.386	44
	<i>ac</i>	1.000		—		—		—		—		0.477	
	<i>bc</i>	—		—		0.098		—		—		—	
	<i>cc</i>	—		—		0.902		1.000		—		0.137	
<i>PEPD</i>	<i>aa</i>	—	66	—	105	0.850	60	—	20	—	33	—	
	<i>ab</i>	1.000		1.000		0.134		0.900		—		—	
	<i>bb</i>	—		—		0.016		0.100		1.000		1.000	
<i>PGM-1</i>	<i>aa</i>	—	13	—	40	—	22	—	11	1.000	33	1.000	44
	<i>ab</i>	1.000		1.000		—		—		—		—	
	<i>bb</i>	—		—		1.000		1.000		—		—	
<i>PGM-2</i>	<i>ab</i>	—	66	—	110	0.742	62	0.039	52	—	33	—	44
	<i>ad</i>	—		—		0.016		0.019		—		—	
	<i>bb</i>	—		—		0.242		0.231		—		—	
	<i>bc</i>	—		1.000		—		—		—		—	
	<i>bd</i>	0.970		—		—		0.346		—		—	
	<i>dd</i>	0.030		—		—		0.365		1.000		1.000	

constituted 68% of the sample. The two alleles we detected at this locus were probably the same as the “*s*” and “*p*” alleles of Stirling and McQueen (1987), as these were the only common alleles found in *D. galeata mendotae* s.s. (Table 2). Helmet morphology differed between these two clones (*G*-test of independence = 15.27, *df* = 1,  $P < 0.005$ ), as one (*PGM-2<sup>bb</sup>*) was associated with a pointed helmet (46 pointed versus 21 angulated) and the other (*PGM-2<sup>bd</sup>*) was associated with an angulated helmet (18 pointed versus 36 angulated). The same relationship was apparent when the 15 less common clones were pooled into *PGM-2* groups (*bb* or *bd*). *PGM-2<sup>bb</sup>* clones (28 pointed versus 14 angulated) were more likely to possess pointed helmets than *PGM-2<sup>bd</sup>* clones (3 pointed versus 13 angulated), ( $G = 11.21$ , *df* = 1,  $P < 0.005$ ). Overall, 68% of the *PGM-2<sup>bb</sup>* individuals had pointed helmets. No significant relationships existed between the other loci and helmet morphology for the genotypes that were abundant enough to test.

#### Seasonal Variation

Despite exhibiting low, rounded helmets, no evidence of hybridization was detected in the spring populations of Bantam Lake and Mt. Tom Pond (Table 3). The allelic arrays of these samples were nearly identical with those of the *Daphnia* with

pointed helmets from the same lakes in midsummer. Although allele frequencies differed significantly between April and July samples in the two lakes (*PGM-2* and *PEPD* in Mt. Tom, and *PGM-2* in Bantam; *G*-tests of independence,  $P < 0.005$  in each case), each allele fluctuation was less than 20%. Genotypic changes were also significant (*G*-tests of independence,  $P < 0.005$  in each case) at these loci, but again, the genotypes that were prevalent in July were still prevalent in April.

#### Reinterpretation of Allozyme Variation

A summary of allozyme variation in prior studies is presented in Table 1. Data on alkaline phosphatase (Mort and Wolf 1985) and amylase (Stirling and McQueen 1987) variation were omitted because these loci were not examined in our study.

#### Lake St. George and Haynes Lake

As heterozygosity at *AO* and *PGM* is diagnostic of hybrids in the present study of Lake St. George, our allozyme reanalysis suggests that Stirling and McQueen’s (1987) genotype 3 in Lake St. George and in Haynes Lake was an interspecific hybrid between *D. galeata mendotae* and *D. rosea*. Genotype 3 was also the only common multilocus genotype to possess exclusively

rounded helmets during the summer (Stirling and McQueen 1987). This summer phenotype is characteristic of hybrids but not of *D. galeata mendotae* (Taylor and Hebert 1992). The remaining genotypes (1, 2, 9, and 15) had diagnostic characters of pure *D. galeata mendotae*, as they were fast homozygotes at *AO* and possessed tall, pointed helmets in the summer.<sup>1</sup>

#### Lake Mitchell

Morphological and allozyme evidence in the present study suggests that *D. galeata mendotae* from earlier Lake Mitchell studies were actually *D. galeata mendotae* × *D. rosea*. The hybrids from the present study closely resemble the drawing of “*D. galeata mendotae*” from Lake Mitchell by DeMott (1981) and both possessed low, rounded helmets during midsummer. This was the only morph of “*D. galeata mendotae*” present in the lake during prior studies (W.R. DeMott, Indiana University – Purdue University, personal communication). In their Lake Mitchell allozyme study, Mort and Jacobs, (1981) detected 3 *GPI* genotypes (*ss*, *fs*, and *ff*) of *D. galeata mendotae*. The *GPI<sup>fs</sup>* genotype prevailed in the lake with a frequency of 0.803. Although we had similar sample sizes to Mort and Jacobs (1981), we found only the heterozygous genotype (*GPI<sup>fb</sup>*). As only two alleles at *GPI* have been detected in *D. galeata mendotae* from the eastern United States (this study; D. Taylor, unpublished data) with *D. rosea* monomorphic for the faster of these alleles, it is probable that the *GPI<sup>fs</sup>* genotype of Mort and Jacobs (1981) is the same as the *GPI<sup>fb</sup>* genotype in the present study.

*GPI* homozygotes may have become extinct since 1979. Yet the *GPI<sup>fs</sup>* genotype is not likely to be the result of *D. galeata mendotae* × *D. rosea* because we have not detected the *GPI<sup>fs</sup>* allele in any *D. rosea* population. The possibility of the *GPI<sup>fs</sup>* being created by  $F_1 \times F_1$  also seems remote because the study of Mort and Jacobs (1981) occurred during the first summer of hybrid colonization. Moreover, the presence of only one multilocus hybrid genotype in our study is inconsistent with successful  $F_1 \times F_1$  matings. Interestingly, the *GPI* homozygotes recorded for *D. galeata mendotae* by Mort and Jacobs (1981) electrophoretically match those of the other two *Daphnia* species in Lake Mitchell. In our samples, both *D. rosea* and *Daphnia catawba* Coker, 1926 were present and *D. rosea* has a *GPI<sup>ff</sup>* genotype whereas *D. catawba* has a *GPI<sup>ss</sup>* genotype. As these *Daphnia* species and the *D. galeata mendotae* × *D. rosea* hybrids are strikingly similar in size and appearance, it is likely, then, that the uncommon genotypes present in the Mort and Jacobs (1981) study were actually *D. catawba* and *D. rosea*. The existence of homozygotes in Mort and Jacobs’ (1981) data can be explained if misdiagnosis occurred 13.6% of the time (82/603). Fixed differences at other enzyme loci indicate that *D. catawba* do not hybridize with either *D. rosea* or *D. galeata mendotae* (D. Taylor, unpublished data).

#### Lake Morey

No evidence of hybridization was found in the genetic data for Lake Morey *D. galeata mendotae*. Our reevaluation of this population does, however, provide insight into Lake *Daphnia* population genetics. From 1981 to 1982, Mort and Wolf (1985) found genotypic frequencies at *sAAT* to be very stable in the lake. Assuming that the two alleles at *sAAT* in Mort and Wolf (1985) are the same two alleles that we found for *D. galeata mendotae*,

<sup>1</sup>Stirling and McQueen (1987) indicated that genotype 2 was heterozygous at *AO*, but it is clear from Stirling (1987) that this was a typographical error and that *AO<sup>ff</sup>* is the original and correct assignment.

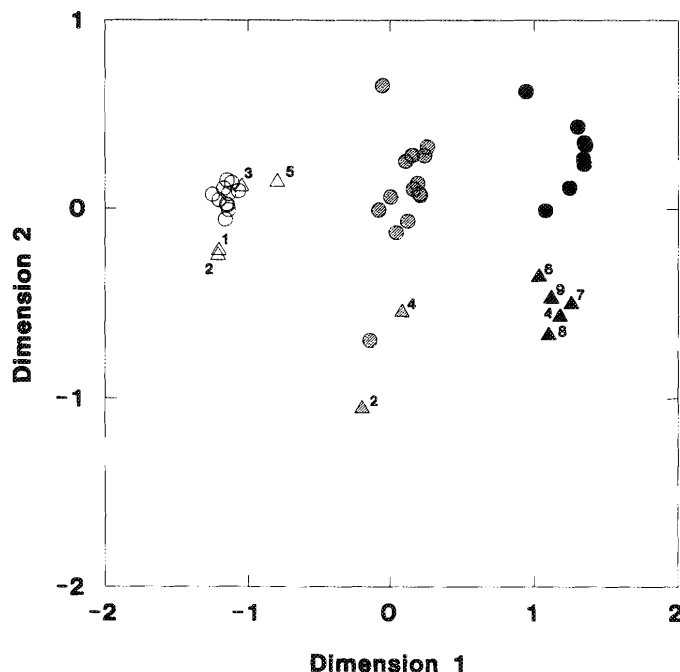


FIG. 3. Nonmetric multidimensional scaling of genetic distances (chord) derived from nine variable loci in the *D. galeata mendotae* complex ( $R^2 = 0.993$ ). *PGM-1* was not included, as it was not available for all populations. Circles represent known populations of *D. galeata mendotae* (solid), *D. rosea* (open), and hybrids (hatched) from Indiana (Taylor and Hebert 1992). Triangles are filled in the same patterns and represent populations reexamined in this study. These are numbered as follows: 1, Guelph Pond, Ont.; 2, Lake Mitchell, Vt.; 3, Three-Lakes-Three, Mich.; 4, Lake St. George, Ont.; 5, Haynes Lake, Ont.; 6, Bantam Lake, Conn.; 7, East Twin Lake, Conn.; 8, Mt. Tom Pond, Conn.; 9, Lake Morey, Vt.

then the genotypic frequencies are not significantly different 9 yr later ( $G = 3.74$ ,  $df = 1$ ,  $P > 0.05$ ). Although *sAAT* variation showed continued stability, *GPI*, which was invariant in 1981, now showed two alleles with the less common allele having a frequency of 0.24.

#### Within-Lake Spatial Distribution of Morphs

Malone and McQueen (1983) described two morphs of *D. galeata mendotae* from Lake St. George as possessing either a “very rounded head capsule” or a “head capsule produced into a point.” Our reanalysis of Stirling and McQueen’s (1987) data provides evidence that the polymorphism was created by hybrids coexisting in the lake with *D. galeata mendotae*. For the following reasons, it is probable that Malone and McQueen’s (1983) rounded morph was also of hybrid origin whereas the pointed morph was true *D. galeata mendotae*. First, hybrids possess very rounded helmets at all times and Malone and McQueen (1983) sampled on October 11, a period when true *D. galeata mendotae* genotypes in Lake St. George rarely possess rounded helmets (Stirling and McQueen 1987). Second, hybrids (i.e., genotypes 3 and iii) are dominant in the fall (Stirling and McQueen 1987).

Reexamination of Malone and McQueen’s (1983) data provides evidence for vertical partitioning of hybrids and *D. galeata mendotae* in Lake St. George. They took 20 samples at each of four depths and recorded abundances of the two morphs of *D. galeata mendotae*. They concluded that the two morphs were acting as a “unispecies patch” because their abundances were

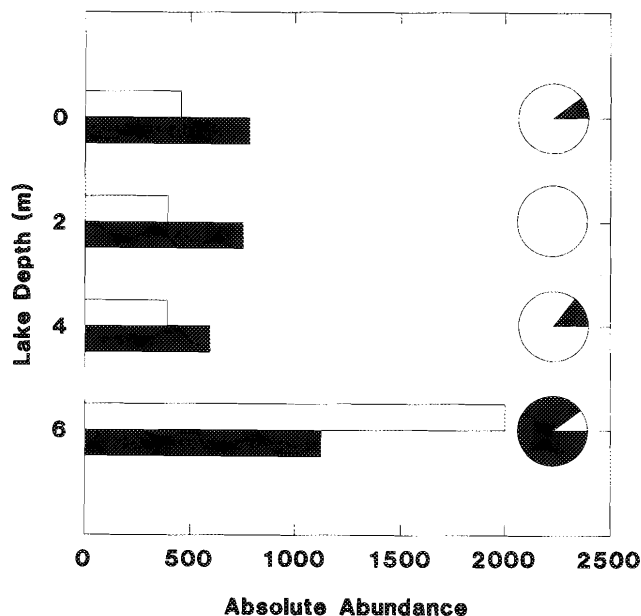


FIG. 4. Relationship between lake depth and abundance (in 500 L of water) of rounded-head (solid bars) and pointed-head (open bars) morphs in Lake St. George (data from Malone and McQueen 1983). Pie graphs indicate the proportion of 25-L samples (20 samples for each depth) across a horizontal grid in which a morph dominated.

correlated along horizontal sampling grids at three depths. Nevertheless, an examination of vertical distribution reveals heterogeneity of morph distributions (Fig. 4). The pointed-head morph (*D. galeata mendotae*) was significantly more abundant than the rounded-head morph (hybrids) at 10 cm, 2 m, and 4 m (Wilcoxon's signed ranks tests,  $z = 3.57-3.92$ ,  $P < 0.001$  for each depth). At 6 m, however, the rounded-head morph was more abundant than the pointed-head morph ( $z = 2.95$ ,  $P = 0.003$ ). The dominance relationship between morphs was consistent across the horizontal grid in the lake, as one morph prevailed in 85–100% of the samples for a given depth (Fig. 4).

## Discussion

Our results show that the hybrid zone between *D. galeata mendotae* and *D. rosea* extends north into Ontario and east into Vermont. Thus far, southern Illinois marks the southern and western extremities of the zone (D. Taylor, unpublished data). Yet the entire hybrid zone is probably much larger because we have examined only a small portion of the region where *D. galeata mendotae* and *D. rosea* are sympatric. Possession of local parental alleles by hybrids further suggests that hybridization in this complex is due to local hybridization rather than dispersal of hybrids following their synthesis. Such widespread hybridization is rare in animals, as zones of sympatry between parent taxa are usually narrow (Harrison 1990).

### Hybridization and Patterns of Morphological Variation

The existence of *D. galeata mendotae* × *D. rosea* hybrids accounts for among-lake spatial morphological variation in both Ontario and Vermont studies. During the midsummer, Haynes Lake (Ontario) and Lake Mitchell (Vermont) may contain only hybrids, while nearby lakes (Lake St. George and Lake Morey) are dominated by *D. galeata mendotae*. A spatial polymorphism

results because hybrids possess rounded helmets, while *D. galeata mendotae* possess pointed or angulated helmets. Artificial polymorphism may also result when rounded-helmet *D. rosea* are identified as *D. galeata mendotae* (e.g., Three-Lakes-Three).

Interspecific hybrids also contribute to within-lake polymorphisms. The coexistence of low-, rounded-head hybrids with tall, pointed/angulated *D. galeata mendotae* in Lake St. George creates a dimorphic pattern under stratified conditions. Vertical partitioning of hybrids and *D. galeata mendotae* appears to occur and coincides with the metalimnion in Lake St. George (McQueen et al. 1989). Our reanalysis suggests that *D. galeata mendotae* dominate within the epilimnion, while hybrids dominate at greater depths. Brooks (1964) attributed such patterns to phenotypic plasticity and concluded that *D. galeata mendotae* develop helmets only when living in the warm epilimnion; individuals living below this layer were thought to lack helmets because of exposure to slow growth conditions.

Although we did not detect low-, rounded-helmet morphs in our reexamination of Brooks' (1964) study sites, there is evidence to suggest that his samples contained *D. galeata mendotae* × *D. rosea* hybrids. The juveniles depicted by Brooks (1964) in Queechee Lake possessed small anterodorsal denticles which are diagnostic of *D. galeata mendotae* × *D. rosea* hybrids in Indiana (Taylor and Hebert 1992). In addition, the drawing of a rounded-helmet adult from Brooks' (1964) study of Mt. Tom Pond is more similar to the hybrids from Lake St. George (in head and carapace shape, head width, and relative tail spine length) than to *D. galeata mendotae* that develop under low temperature conditions in Mt. Tom Pond (Fig. 2B). The low-, rounded-head morph in East Twin Lake was also probably of hybrid origin, as Brooks (1964) found the helmet dimorphism to be genetically controlled in this lake.

Hybridization can also distort patterns of seasonal polymorphism in *D. galeata mendotae*. Probable hybrid genotypes (Stirling and McQueen's iii and 3) increased in abundance relative to *D. galeata mendotae* from summer to winter in Lake St. George in both 1984 and 1985 (Stirling and McQueen 1987). The fall decay of helmets is exaggerated by treating hybrids and *D. galeata mendotae* as one taxon. The same abundance shifts occur in Indiana lakes where *D. galeata mendotae* coexist with hybrids (Taylor and Hebert 1992). The reanalysis of Bantam Lake and Mt. Tom Pond, however, reveals that hybrid-parent succession is not the sole explanation for seasonal polymorphism in *D. galeata mendotae*. The parent taxon is capable of expressing both the maximum and minimum helmets in these lakes. There was also no evidence of genotypic succession causing seasonal polymorphism from these lakes, as genotypic fluctuations were small.

Is there a genetic component to cyclomorphosis with *D. galeata mendotae*? Stirling and McQueen (1987) are the only investigators who have reported an association between allozyme and helmet phenotypes within a *Daphnia* species. We have shown, however, that this association was due to their inclusion of interspecific hybrids. Nevertheless, we did find a different association in Lake St. George, as the *PGM-2<sup>bb</sup>* genotype was more often associated with a pointed-head shape than the *PGM-2<sup>bd</sup>* genotype. The fast allele is the most common allele in *D. rosea* whereas the slow allele is the most common in *D. galeata mendotae* (Table 2). Such a pattern suggests that the *PGM-2<sup>bd</sup>* genotype may, in some clones, mark the introgression of *D. rosea* alleles into *D. galeata mendotae* genomes. We have



found evidence that asymmetric introgression of this kind is widespread between *D. rosea* and *D. galeata mendotae* (Taylor and Hebert 1992; D. Taylor and P. Hebert, unpublished data). If helmet shape is under polygenic control, then introgression may affect helmet expression according to alien gene dosage. Thus, some *D. galeata mendotae* in Lake St. George may have attenuated helmets as a result of the introgression of *D. rosea* alleles for smaller, rounder helmets. Nevertheless, we found no association between introgressed alleles and cyclomorphosis in Bantam Lake and Mt. Tom Pond populations. Consequently, our results support earlier investigations in concluding that the phenomenon of cyclomorphosis in pure *D. galeata mendotae* is due to phenotypic plasticity while acknowledging that different genotypes may have different norms of reaction (Jacobs 1961; Mort 1989).

### Dynamics of Hybridization

Because the *GPI<sup>f</sup>* allele is rare in *D. galeata mendotae* and absent in *D. rosea* (Table 2), the finding of the same dominant hybrid genotype *GPI<sup>sm</sup>* in Lake Mitchell in both 1979 and 1990 suggests that hybrid clones can persist from year to year. Certainly, hybrid genotypes in Lake St. George and Haynes Lake overwinter as free-swimming *Daphnia*. The observation of low clonal diversity in both of these hybrid populations as well as their potential to overwinter may indicate that dominant clones are not only persistent but also may arise from only a few hybridization events (Brooks 1957). Unfortunately the contribution of selection to these observed patterns is unknown.

Of course, a hybrid clone that can neither disperse nor respond rapidly to environmental change has a rather limited evolutionary potential. We have provided evidence that hybrid clones once dominated both Queechy Lake and Haynes Lake but have since become rare or extinct. Yet such hybrid clones are not necessarily the "evolutionary dead-ends" that Fryer (1991) suggested. Haynes Lake now contains *D. rosea* with alleles that are typical of *D. galeata mendotae*. Thus introgression may be the evolutionary legacy of hybrids that act as conduits for gene flow between *D. galeata mendotae* and *D. rosea*.

### Reevaluation of *D. galeata mendotae* Ecology

If our interpretation of Mort and Jacobs' (1981) data is correct, then their manipulation experiments indicated ecological differences between *D. rosea* and the interspecific hybrid *D. galeata mendotae* rather than among genotypes of *D. galeata*. Mort and Jacobs (1981) reported a relative increase in the *GPI<sup>fs</sup>* genotype over *GPI<sup>f</sup>* after increasing density either directly or by adding nutrients (C, N, P). Our reinterpretation suggests that "ff" genotypes represented *D. rosea* and "fs" genotypes represented hybrids. Therefore the experiments provided evidence that hybrids are more fit than *D. rosea* under these conditions. Mort and Jacobs (1981) suggested that the increased fitness was due to heterosis at the *GPI* locus, but this relationship is untenable if the *GPI<sup>fs</sup>* genotype marked an entire hybrid genome. It is worth noting that Mort et al. (1989) found no genotypic responses at *GPI* to density during similar manipulations with European *Daphnia galeata mendotae*. There was, however, a relative increase in *D. galeata mendotae* × *Daphnia hyalina* hybrids compared with the parent taxa (see Mort 1990), producing results that parallel our reinterpretation of Mort and Jacobs' (1981) experiments. It should also be noted that only hybrid genotypes were detected on two of three sampling dates in the enclosure station of Stirling and McQueen (1987).

Mort (1986) also performed a series of experiments with the invertebrate predator *Chaoborus* to gain insight on the adaptive significance and maintenance of helmet polymorphism in *D. galeata mendotae*. *Daphnia galeata mendotae* from Lake Morey were used to represent the pointed-helmet phenotype and *D. galeata mendotae* from Lake Mitchell were used to represent the low-helmeted phenotype. The experiments revealed that high-helmeted *D. galeata mendotae* from Lake Morey was more difficult for *Chaoborus* to capture and ingest than the low-helmeted morph of Lake Mitchell. Our study reveals that the low-helmeted morphs of *D. galeata mendotae* were probably F<sub>1</sub> hybrids. Therefore the data actually provided evidence that hybrids are more susceptible than *D. galeata mendotae* (with pointed helmets) to *Chaoborus* predation. Invertebrate predation might then be an important factor in determining the success of interspecific hybrids.

Taylor and Hebert (1992) found that *D. rosea* were associated with lakes that are smaller in surface area than lakes associated with *D. galeata mendotae*. In this present study, *D. rosea* also occurred in the small water bodies (Guelph pond, Three-Lakes-Three, Haynes Lake, Lake Mitchell), while *D. galeata mendotae* tended to occur in large lakes (Lake St. George being the exception). This pattern of neighbouring sympatry is obviously due to ecological rather than dispersal limitations, as habitat associations exist across broad areas of North America that both species have colonized since deglaciation. Moreover, our finding of widespread local hybridization between these species indicates that populations of each species are often within dispersal range of one another.

The exact nature of the ecological forces that segregate *D. galeata mendotae* and *D. rosea* remain to be addressed. Yet, as species replacements have occurred within the same lake (D. Taylor, unpublished data), we agree with Brooks (1957) that habitat associations based on size of water bodies are most probably due to food availability, competition, and predation rather than to abiotic factors. These biotic forces are presumably responsible for differences in species composition between the adjacent small, hardwater kettle lakes, Haynes Lake and Lake St. George. *Daphnia rosea* are prevalent in Haynes Lake but absent in Lake St. George, whereas *D. galeata mendotae* are prevalent in Lake St. George but absent in Haynes Lake (Stirling and McQueen 1987; this study). *Daphnia* in Lake George are exposed to greater planktivore pressure (from yellow perch (*Perca flavescens*) and golden shiner (*Notemigonus crysoleucas*)) and more eutrophic conditions than *Daphnia* in Haynes Lake (Mazumder et al. 1990; Lafontaine and McQueen 1991). If this ecological pattern were widespread, it might be concluded that intense planktivory prohibits *D. rosea* from becoming established in *D. galeata mendotae* dominated lakes, while intense competition prevents *D. galeata mendotae* from becoming established in *D. rosea* dominated lakes. Indeed, studies from across North America (where taxonomy is not in question) do suggest that *D. rosea* are a strong exploitative competitor in lakes where vertebrate predation is negligible (Clark and Carter 1974; DeMott 1983; Neill 1985). The success of *D. galeata mendotae*, on the other hand, has been associated with intense vertebrate predation, and it is often replaced by other *Daphnia* species when predators (e.g., yellow perch, cisco (*Coregonus artedii*), and golden shiner) become scarce (Zaret and Suffern 1976; Mills and Forney 1988; Rudstam et al. 1993).

Hybrids between *D. galeata mendotae* and *D. rosea* have been detected only in lakes where one or both parent species are absent

or rare. Because the hybrids are locally produced and often more abundant than coexisting parent taxa, hybrid clones must be fitter than one or both parents under certain environmental conditions. Investigations of hybridization among Eurasian lake *Daphnia* suggest that a combination of differential use of the environment (temporal and spatial) and hybrid vigor contributes to their success (Wolf and Mort 1986; Wolf 1987; Mort 1990; Weider and Wolf 1991). Likewise, our reevaluation suggests that some *D. galeata mendotae* × *D. rosea* clones respond differently than parent taxa with respect to vertical segregation, invertebrate predation, and nutrient enrichment. As these phenomena involved only a few hybrid clones, however, it is unclear whether such patterns represent general hybrid features or unique features of these clones that arose as a consequence of selection.

The ecological conditions that separate *D. galeata mendotae* and *D. rosea* and that lead to hybrid success need to be investigated by multilake studies. Although these two species have been prominent in past limnological studies, taxonomic confusion reduces their value for comparative biology. Nevertheless, we have shown that when genetic and morphological information is available, successful reinterpretation of existing studies is possible. We therefore recommend that investigators genetically compare individuals from their study sites and individuals of a known taxon. This study reveals that such a comparison is especially important in lakes where rounded-helmet *D. galeata mendotae* occur in summer months and where *D. galeata mendotae* are thought to coexist with *D. rosea*.

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