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PATTERNS IN THE MORPHOLOGY AND DISTRIBUTION OF
GASTROPODS IN ONEIDA LAKE, NEW YORK, DETECTED USING
COMPUTER-GENERATED NULL HYPOTHESES

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Elton (1946) was the first to examine the taxonomic similarity of samples from a large fauna. His analysis of published species lists suggested that communities from smaller habitats have fewer congeneric pairs than the regions from which they were sampled. Elton proposed that competition plays a role in separating congeners, which are morphologically similar and thus would be expected to have similar ecological requirements. However, Williams (1947) pointed out that fewer congeneric pairs are expected in random samples of a species pool. Williams (1951) found evidence of an excess of congeners in published records from African bird communities. In a reexamination of this controversy, Simberloff (1970) found that the species-to-genus ratios of a variety of floras and faunas from 180 islands did not generally differ from the ratios in their presumed source areas. There was a slight tendency, however, toward higher species-to-genus ratios than expected. Simberloff attributed this to the similarity of congeneric species in ecological requirements and dispersal capabilities. Strong et al. (1979) also found little morphological evidence that the species co-occurring on islands are more than random assemblages. Using ratios of morphological measurements between similar pairs of species, they could not distinguish the avifaunas of several island groups from their presumed sources. Strong et al. concluded that, although there had been intense interest in the subject, to date there had been no unequivocal demonstration that the organisms in small samples of large biotas could be significantly more unlike one another than random expectation would suggest.

In this study I test the hypothesis that there are patterns of morphological similarity between the snail species occurring in small samples taken by Baker (1918) from Oneida Lake, New York. I have quantified morphological similarity in two ways, taxonomic relatedness by genus or family, and direct measurement of shell and radula morphology. There are two possible null hypotheses. The first is that the probability of any snail species occurring in a sample is independent of morphology but dependent on its abundance in the lake as a whole. This conforms more realistically to immediate random expectation. However, a second null

hypothesis has been more often examined in published studies, and so will also be tested. This is that the probability of any species occurring in a sample is independent of both its morphology and its abundance. If relative abundances are viewed as a function of recent environmental conditions and the life cycles of the species involved, these abundances may change rapidly. Thus this second null hypothesis may be more appropriate than the first over evolutionary time.

In addition to examining the morphological similarity of co-occurring snails, I address two ancillary questions in this study. One involves the degree to which individual species are randomly distributed throughout the samples (independent of morphology), and the other involves the influence of several environmental variables on morphological similarity.

METHODS

The distributional data used in this study were collected by Baker (1918) in lower South Bay, Oneida Lake, New York. He made 162 quantitative samples of plants and macrobenthos using three methods. On rocky bottoms he lifted whole rocks (average surface approximately 84 cm²) and removed all attached organisms. On softer bottoms in shallow water he used a long-handled dipper that collected 103 cm² of substrate per scoop, and in deep water he pulled a 41-cm dredge 122 cm along the bottom, collecting approximately .5 m² per pull. At each site he recorded depth, substrate, and distance to the shore.

Of the 162 samples, 21 either contained no snails or were omitted from Baker's report. Baker recognized 37 species and subspecies of snails in the remaining 141 samples (5,617 individual snails), but the taxonomic revision of Harman and Forney (1970) recognized only 32 valid species. (Harman and Forney eliminated the several pairs of sympatric subspecies included by Baker.) I collected living specimens of 13 of these species in August, 1978, from Oneida Lake in the vicinity of lower South Bay. Ten more species, collected originally as close as possible to Oneida Lake, were obtained in alcohol from the Academy of Natural Sciences of Philadelphia and the University of Michigan Museum of Zoology. Six species found rarely by Baker were omitted because specimens were unavailable. These species, *Viviparus georgianus*, *Valvata bicarinata*, *Cincinnatia binneyana*, *Gillia altilis*, *Somatogyrus subglobosus*, and *Laevapex fuscus*, accounted for only 35 individuals combined.

The three remaining species, *Amnicola bakeriana*, *A. clarkei*, and *A. oneida*, were very common in 1916 but are unobtainable now. These three species were described in 1918 from specimens collected by Baker in Oneida Lake. Subsequently they have been collected at few if any other localities, and they have become very rare or extinct in Oneida Lake (Harman and Forney 1970). However, because they were so common in 1916, they cannot now be disregarded. Descriptions and type shells suggest that *A. bakeriana*, *A. clarkei*, and *A. oneida* may be shell forms of the much more widespread *A. lustrica*, which also occurred in the lake. I have thus lumped all four of these species together for this analysis. If

they were in fact distinct species, it must be assumed that their lumping will not bias the results of this analysis.

Computer Simulations

Two Monte Carlo simulations based on Baker's sampling process at Oneida Lake were developed. The first was a preliminary simulation, the results of which served as a null hypothesis in the examination of distributional patterns of the snail species independent of morphology. A species pool was created with the probability of drawing each species proportional to its overall abundance in the lake. For example, Baker found 17 individuals of *Campeloma decisum* in his 141 samples, so the probability of *C. decisum* occurrence in this simulation was 17/5,582. (The number, 5,582, is the total 5,617 individual snails minus the 35 individuals of rare species excluded.) This assumes that snail dispersal is unimpeded throughout the study area, an assumption that seems reasonable since lower South Bay is relatively shallow and protected. The area of lower South Bay proper, in which 84% of the samples were made, is only around 4.0 km², and the maximum distance between any pair of samples was around 3.4 km.

Using a Tausworthe pseudorandom number generator, 141 samples identical to Baker's samples in number of individual snails collected were drawn from the species pool with replacement. Thus the probability that a particular snail species occurred in a particular sample was determined by the abundance of that species and the number of individual snails in that particular sample. This process was repeated 30 times. By comparing the results of this simulation to Baker's data, it will be possible to determine in one analysis if individuals of the various species are randomly distributed in the samples, or if there is an overall tendency toward regularity or aggregation. The technique of rarefaction has been used to address similar questions from a different perspective (Heck et al. 1975; Simberloff 1978).

The second simulation was designed to provide a null hypothesis to test for patterns in the distribution of snail species with regard to morphology. Two versions of this simulation were done, "weighted" and "unweighted." In the former version, the species pool was created with the probability of drawing each of the 23 species weighted by the overall abundance of that species, as above. For $N = 2-7$, N different snail species were drawn from the pool with replacement using the random number generator. (Although Baker's samples contained up to $N = 10$ snail species, only seven samples contained more than seven species. These seven samples were omitted from the analysis.) If a species already represented in the sample was drawn, the program looped back and drew again. For each sample size, 2-7 species, 100 iterations were made. Methods were identical in the unweighted version of this simulation, except that all species had equal probabilities of being selected regardless of their abundance. That is, the probability that *C. decisum* was drawn in this version was 1/23. The results of the abundance weighted and unweighted simulations were compared to Baker's data

to see if the snails co-occurring in small sites on the bottom of Oneida Lake are morphologically random samples, and if not, whether the snails tend to be more or less similar to each other.

Taxonomic Analysis

The taxonomic analysis was restricted to the 23 snail species for which preserved specimens were available in order to allow comparisons with the morphological analysis. Using the widely recognized taxonomic scheme of Harman and Forney (1970), I counted all congeneric and confamilial pairs in Baker's samples for each of the six classes of species number present. Since only five of Baker's samples contained more than one congeneric pair, all sites with congeneric pairs were lumped regardless of the number of pairs. To analyze confamilial pairs, three categories were established: none present, one pair present, and more than one present. This resulted in the lumping of four samples including three confamilial pairs with the samples including two confamilial pairs. Congeneric and confamilial triplets and quadruplets occurred rarely. Triplets were counted as two pairs and quadruplets as three pairs.

The null hypothesis was that Baker's data and the expected numbers of congeneric and confamilial pairs based on the two simulations were not significantly different. To test this I employed frequency table analysis (BMDP3F, Dixon 1977) to fit a log-linear model to each of the four separate comparisons, Baker's data versus weighted and unweighted simulations in both congeneric and confamilial pairs. Expected frequencies were calculated from the simulations on the basis of all 100 iterations and rounded to the nearest whole number. Since sampling zeros occurred in the tables, .5 was added to each cell before analysis. There are eight effects to be considered when fitting a three-way table. For convenience each of these effects will be given an abbreviation. The three main effects are number of pairs (congeneric or confamilial, abbreviated P), number of snail species present (two through seven, abbreviated S) and run (real vs. weighted or unweighted simulation, abbreviated R). Also included in a complete log-linear model are the overall mean effect, three first order interactions (PS, PR, and RS) and the second order interaction (PSR). The effects of primary interest are the first order interaction between run and pairs (PR) and the second order interaction (PSR).

The contribution of any particular effect to the fit between data and model cannot be assessed independently of other effects. Thus I have used several criteria to establish the importance of PR and PSR. One method is comparison of the best fitting log-linear model including the effect of interest to the best model that does not include this effect. If PR is significant, the best model that includes it should fit the data better (have a lower χ^2) than the best model that does not have PR. In addition, Brown (1976) has suggested tests for partial and marginal association of factors. If PR is significant, χ^2 testing for partial or marginal association of P and R should be large. Using these three criteria, any pattern in the taxonomic similarity of snails from small samples of lake bottom should become apparent.

Morphological Analysis

Eleven morphological measures were made on each of the 23 species, five on the radula and six on the shell (table 1). Five of the shell characters were measured according to Davis (1969). The sixth measure, aperture width, was measured as the maximum distance across the aperture perpendicular to the measure of aperture length. To measure radula characters, the entire radular ribbon was removed from the buccal mass using commercial bleach. Then an ocular micrometer was used to measure its length and its maximum unfolded width. The number of rows of teeth was counted down the length of the ribbon. A single row was arbitrarily selected from the middle of the ribbon and the number of individual teeth in it counted. To quantify dentition on individual teeth, the number of cusps was totaled for the first 30 teeth encountered starting at one end of the arbitrarily chosen row. If the row had fewer than 30 teeth, I continued counting with the next row. For some species it was necessary to tease the teeth apart before beginning this count. Shell length, shell width, aperture length, and aperture width were easily measured with vernier calipers on most specimens; thus 50 individuals of each species were measured for these characters. The seven remaining characters were measured on five individuals of each species. Radula morphology was measured on only three *Promenetes exacuosus* and two *Valvata sincera* because of their unavailability.

As in Ricklefs and Travis (1980), the mean for each species character was log transformed, because this was found by inspection to lessen skewness. Then a principal component analysis (BMDP4M, Dixon 1977) was performed on the species using the correlation matrix of their log-transformed character means. This seemed desirable because correlation among morphological measurements was expected to be high. The correlation matrix was used because the measurements were made in a variety of units. Significance tests on principal components are unreliable when the sample size (23) less the number of variables (11) is as low as 12. Although it is customary to accept only those principal components with eigenvalues greater than one, I believed that such a policy might result in an excessive loss of variance. Because the goal of this analysis was an elimination of intercorrelation and not an increase of economy as such, I stipulated a priori that components would be accepted only until 95% of the total variance was accounted for. The morphology of each species was subsequently represented by K factor scores.

Two measures of morphological diversity were calculated for each of Baker's samples and for samples generated in the Monte Carlo simulations. First, if there were some tendency for morphologically similar species to be more or less likely to co-occur in samples, it seemed possible that this tendency should be strongest in most-similar species. Thus a measure of the similarity of the most-similar species, mean nearest morphological neighbor distance ($\overline{\text{NMND}}$), was used as a measure of overall morphological diversity (Ricklefs and Travis 1980). Where N species were present in a sample, $\overline{\text{NMND}}$ was calculated as the average of the N Euclidean distances to nearest neighbors in K -dimensional space. Another possi-

TABLE 1
 SNAIL SPECIES COLLECTED BY BAKER FROM ONEIDA LAKE, THEIR ABUNDANCES,
 AND MEANS FOR MORPHOLOGICAL MEASUREMENTS

	No.	No. Sites	Simulated Samples ($\bar{X} \pm SD$)	Shell Ht. (cm)	Shell Width (cm)	Aperature Length (cm)	Aperature Width (cm)	Body Whorl Length (cm)	Spire Angle (deg.)	Radula Length (cm)	Radula Width (cm)	Radula Rows	Teeth per Row	Cusps per 30 Teeth
Subclass Prosobranchia														
Viviparidae														
<i>Campeloma decisum</i>	17	10	13.3 ± 3.2	1.93	1.30	.96	.61	1.52	53	.192	.030	36	7	30
Valvatidae														
<i>Valvata sincera</i>	49	6	31.9 ± 3.5	.28	.33	.17	.16	.25	110	.029	.014	21	7	840
<i>V. tricarinata</i> *	545	36	97.5 ± 5.0	.26	.36	.17	.16	.23	97	.046	.019	21	7	712
Hydrobiidae														
<i>Amnicola limosa</i> *	39	2	24.5 ± 3.6	.39	.32	.26	.17	.32	76	.180	.027	62	7	562
<i>A. lustrica</i> †	2,841	78	133.6 ± 1.9	.33	.22	.15	.10	.24	57	.076	.021	44	7	450
Bithyniidae														
<i>Bithynia tentaculata</i> *‡	220	15	70.4 ± 5.3	.99	.57	.41	.29	.74	32	.144	.023	64	7	351
Pleuroceridae														
<i>Goniobasis livescens</i>	82	11	42.8 ± 4.6	1.57	.71	.52	.34	.18	33	.239	.034	56	7	217

Subclass Pulmonata

Physidae

<i>Physa integra</i> *	210	22	69.5 ± 5.0	.96	.59	.63	.28	.84	67	.222	.157	107	162	170
<i>P. sayii</i>	160	38	62.6 ± 4.1	1.53	.93	1.09	.47	1.35	74	.178	.189	83	181	325

Lymnaeidae

Lymnaea cata-

<i>scopium</i> *	455	72	95.0 ± 4.4	1.45	.85	.86	.50	1.28	61	.251	.100	96	41	127
<i>L. columella</i>	17	2	13.4 ± 3.1	1.41	.75	.92	.49	1.28	61	.221	.093	79	51	157
<i>L. haldemani</i>	6	2	5.1 ± 2.0	1.62	.32	.67	.22	1.29	13	.130	.043	80	33	112
<i>L. humilis</i> *	3	1	2.8 ± 1.4	.60	.36	.30	.16	.45	34	.134	.046	76	36	125
<i>L. stagnalis</i>	20	1	16.3 ± 4.3	4.12	1.88	2.13	1.04	3.29	49	.338	.154	105	67	125

Planorbidae

<i>Gyraulus deflectus</i> . .	1	1	1.2 ± 1.0	.16	.50	.12	.17	.13	130	.064	.014	101	26	137
<i>G. hirsutus</i> *	47	18	30.7 ± 4.3	.14	.55	.12	.19	.14	163	.069	.019	94	31	128
<i>G. parvus</i> *	581	60	99.1 ± 4.6	.10	.31	.08	.09	.08	166	.080	.015	110	24	112
<i>Helisoma anceps</i> * . .	44	23	28.8 ± 4.0	.58	.99	.51	.28	.58	180	.115	.051	103	30	217
<i>H. campanulata</i> . . .	67	24	37.9 ± 5.0	.50	1.15	.43	.30	.44	149	.188	.098	116	45	203
<i>H. trivolvis</i> *	50	12	29.6 ± 6.9	1.16	2.05	1.03	.57	1.16	174	.282	.093	128	40	164
<i>Planorbula jenksii</i> . .	1	1	1.1 ± 1.0	.22	.62	.18	.20	.22	173	.158	.038	136	41	150
<i>Promenetes ex-</i> <i>cuosus</i> *	82	34	41.8 ± 4.3	.12	.52	.10	.22	.12	96	.122	.033	136	39	167

Ancylidae

<i>Ferrissia par-</i> <i>allela</i>	45	17	29.1 ± 6.9	.23	.12	.23	.46	.23	180	.068	.022	70	33	350
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* Re-collected from Oneida Lake in August, 1978.

† Includes *A. bakeriana*, *A. clarkei*, and *A. oneida*. Measurements taken on *A. lustrica*, *s.s.*

‡ Baker's report of 1,364 *B. tentaculata* at the 62 cm² site 4 is believed to be in error and emended to 100.

bility was that any tendency for morphologically similar species to be more or less likely to co-occur in samples would be strongest in clusters that had the smallest overall dimensions. Thus a measure of the similarity of the most dissimilar species, mean furthest morphological neighbor distance ($\overline{\text{FMND}}$), was calculated in a manner analogous to $\overline{\text{NMND}}$. Taken together, $\overline{\text{NMND}}$ (which increases as points become more regularly dispersed) and $\overline{\text{FMND}}$ (which increases as outliers become more severe) should give a good estimate of the morphological diversity in each sample.

To test the hypothesis that the morphological diversity of small samples of snails from Oneida Lake was not random, $\overline{\text{NMND}}$ and $\overline{\text{FMND}}$ in Baker's samples were compared to $\overline{\text{NMND}}$ and $\overline{\text{FMND}}$ calculated from the simulations. The values taken by these two measures of morphological diversity are functions of the number of species represented in a sample, so each of the four comparisons, Baker's data versus two simulations in $\overline{\text{NMND}}$ and $\overline{\text{FMND}}$, was performed using paired t -tests (two-tailed, assuming unequal variances) for each of the six classes of species represented (2–7). Because variance in morphological neighbor distance is expected to decrease as number of species present in the sample increases, two-way analysis of variance was inappropriate. To examine the possibility that variances were significantly heterogeneous within classes of species represented, an F -test was performed along with each t -test. Thus each comparison of Baker's data with the results of a simulation was based on six values of t and six values of F .

Environmental Effects

Stepwise linear regression analysis was performed to explore the relationship between each of the two measures of morphological diversity, $\overline{\text{NMND}}$ and $\overline{\text{FMND}}$, and six environmental and sampling variables measured at each site. Baker collected a total of 111 samples with from two to seven snail species present. At most sites he recorded the area sampled in square inches, water depth, substrate type, and distance to the shore. I quantified Baker's substrate categories as follows: 1, rock; 2, gravel; 3, sand; 4, sandy clay; 5, clay; and 6, mud. Baker also recorded the presence or absence of a great variety of plants in each sample. As a measure of vegetational species richness, I totaled the number of the 16 most common macrophyte species present. Since mean nearest and furthest morphological neighbor distance are related to the total number of snail species present, the number of species was included as the sixth independent variable.

Baker did not record the distance to shore for his 17 samples dredged from the middle of the lake, and failed to record the sample area at one other site. Data from these sites were excluded from the analysis. The distribution of Baker's 93 remaining sites over the eight variables was examined using BMDP2D, detailed data description (Dixon 1977). After transformation, these distributions were neither significantly skewed nor kurtotic when two sites with extremely high $\overline{\text{NMND}}$ and two sites collected a great distance from shore were excluded. Shore distance, sample area, and number of plant species present required square root transformation, and $\overline{\text{FMND}}$ required log transformation. Depth, substrate, num-

ber of snail species, and \overline{NMND} were not transformed. Two stepwise multiple regressions (BMDP2R, Dixon 1977) were run to determine if area, vegetational diversity, substrate diversity, or any other variable could be shown to influence the morphological similarity of snail species co-occurring in small samples of lake bottom.

RESULTS

Within-Species Distributional Pattern

Figure 1 shows Baker's samples categorized by the number of snail species they contained. Also shown is the result of the first Monte Carlo simulation described in the methods section. Clearly Baker's samples are much less diverse than one would expect from the simulation, suggesting that individuals of most species tend to clump at particular sites. Only seven of Baker's samples contained more than seven snail species, and none contained more than 10, but sites with 12 and 14 species occurred commonly in the simulation. That this trend is general across all snail species in Oneida Lake can be seen in table 1. Table 1 shows the number of sites at which Baker collected each species. This number can be compared to the mean number of samples in which each species occurred during the 30 iterations of the first Monte Carlo simulation. The expected number of samples is significantly larger than the observed number for nearly every species. The observation that individuals of most species are clumped does not necessarily imply that their free migration is somehow impeded, and thus does not invalidate my assumption that there are no barriers to snail dispersal in lower South Bay.

It is also apparent that species tend to clump in different samples. If all the species clumped into the same subset of samples, two peaks would be evident in Baker's data shown in figure 1. These two peaks would represent the class of samples from highly favorable sites, where a large number of species occur, and the remaining class of samples from unfavorable sites. The absence of a set of

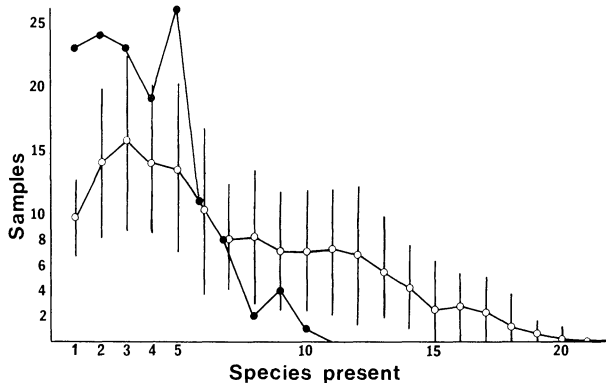


FIG. 1.—The no. of snail species present in samples from Oneida Lake. Closed circles are Baker's (1918) data; open circles are the result of the random simulation of Baker's sampling process described in the text. Bars represent 95% confidence limits.

highly diverse samples, though the individuals of the various species are generally clumped, suggests that the snails co-occurring in Oneida Lake tend to specialize on different habitats or resources.

Taxonomic Analysis

The frequencies of congeneric and confamilial pairs in Baker's samples and the two simulations are presented in table 2. No evidence for a significant second order interaction among all three variables was found in any of the four frequency table analyses performed. Likelihood-ratio chi-squares from tests of partial and marginal association were insignificant for the PSR effect in all four analyses; thus the remainder of this discussion will be concerned with the significance of the PR effect.

In all four analyses, the best fitting model including PR was *PS,PR*. This model includes all three main effects, P, S, and R, and two interactions, PS and PR. In all four analyses, the best fitting model excluding PR was *PS*, including just two main effects and their interaction. Table 3 shows no evidence that Baker's samples and either simulation are different in number of congeneric pairs. Model *PS* fits the data better than model *PS,PR* in these two cases, but these two tests must be insensitive to any tendency for real samples to contain less taxonomic diversity than random expectation. Very few congeneric pairs are expected in samples of less than eight species from the Oneida Lake species pool. Tests for a difference in confamilial pairs should therefore be more sensitive.

Model *PS* is very nearly as good as model *PS,PR* in the comparison of real and weighted simulation confamilial pairs. However, the PR effect does seem to be important in the comparison of confamilial pairs in Baker's sample and the unweighted simulation. The fit of the data to the model improves from 77% to 93% confidence with the inclusion of the run/confamilial pairs interaction (table 3). These results are corroborated in table 4. The test for a partial association of P with R gave a significant χ^2 in the analysis of confamilial pairs in Baker's data and the unweighted simulation. None of the other three analyses resulted in significant PR partial or marginal associations. Table 2 shows that there are systematically more confamilial pairs in the unweighted simulation than in the actual samples of Oneida Lake. In sum, there is good evidence that this difference is real.

Morphological Analysis

Table 1 presents the means of the 11 shell and radula characters for each of the 23 species. Although these means were log transformed to remedy some of the skewness before analysis, distributions on several of these variables were not normal. In particular, the seven prosobranch snails all have seven teeth per row, while the pulmonates ranged from 24 to 181. The number of radular rows was much lower and the number of cusps per 30 teeth generally much higher in the prosobranchs. Nevertheless, I felt that the seven prosobranchs were too similar to the other snails to be separated into a second analysis. Results of the principal

TABLE 2
 NUMBER OF CONGENERIC AND CONFAMILIAL PAIRS PRESENT IN SAMPLES OF SNAILS FROM
 ONEIDA LAKE AND IN TWO MONTE CARLO SIMULATIONS

		CONGENERIC PAIRS																	
		Zero						More than Zero											
No. species present	..	2	3	4	5	6	7	2	3	4	5	6	7						
Real	24	21	17	14	4	1	0	2	2	12	7	7						
Weighted simul.	23	22	14	17	5	3	1	1	5	9	6	5						
Unweighted simul.	..	22	22	13	12	4	2	2	1	6	14	7	6						
		CONFAMILIAL PAIRS																	
		Zero						One						More than One					
No. species present	..	2	3	4	5	6	7	2	3	4	5	6	7	2	3	4	5	6	7
Real	24	21	13	9	1	0	0	2	6	11	6	2	0	0	0	6	4	6
Weighted simul.	23	21	13	12	3	1	1	2	5	13	6	4	0	0	1	1	2	3
Unweighted simul.	...	20	17	7	5	1	0	4	6	9	14	4	2	0	0	3	7	6	6

TABLE 3
COMPARISON OF MODELS *PS** AND *PS,PR** IN ABILITY TO FIT THE DATA

	Real vs. Weighted Simulation	Real vs. Unweighted Simulation
Congeneric pairs		
PS χ^2	4.25	4.80
df	12	12
Probability9785	.9645
PS,PR χ^2	4.05	4.07
df	10	10
Probability9449	.9440
Confamilial pairs		
PS χ^2	7.99	13.35
df	18	18
Probability9788	.7701
PS,PR χ^2	3.91	7.90
df	15	15
Probability9980	.9277

* See text.

component analysis are presented in table 5. The first six components were used because they were the minimum required to account for 95% of the variance.

Mean nearest and furthest morphological neighbor distances in Baker's samples and the two simulations are compared in figures 2 and 3, respectively. The means of both of these measures of morphological diversity are clearly much higher in Oneida Lake snail samples than expected from the weighted simulation. Table 6 shows that Baker's samples are significantly more diverse morphologically than the weighted simulation in six of the 12 comparisons. (In one comparison, the simulation was significantly more diverse.) Seven of the 12 comparisons also show variances in NMND or FMND significantly greater in Baker's samples. (The *F*-ratios shown in table 6 were all formed with variance from the simulations in the denominator.) Snail species that co-occur in small samples of Oneida Lake seem to be much more different from one another in morphology than random expectation if the species occurred according to their abundances alone.

TABLE 4
LIKELIHOOD-RATIO CHI-SQUARES FROM TESTS OF THE PARTIAL OR MARGINAL ASSOCIATION OF RUN AND CONGENERIC OR CONFAMILIAL PAIRS

	CONGENERIC PAIRS			CONFAMILIAL PAIRS		
	Partial	Marginal	df	Partial	Marginal	df
Real vs. Weighted simulation26	.20	1	5.29	4.07	2
Real vs. Unweighted simulation	1.01	.72	1	8.78*	5.45	2

* Significant at the .05 level.

TABLE 5

EIGENVALUES AND FACTOR LOADINGS FOR THE FIRST SIX PRINCIPAL COMPONENTS IN ANALYSIS OF SHELL AND RADULA MORPHOLOGY OF ONEIDA LAKE GASTROPODS

	1	2	3	4	5	6
Shell height	.869	-.438	.093	.015	.076	-.118
Shell width	.790	.143	-.070	-.401	.139	.312
Aperture length	.946	-.235	.162	-.006	.027	-.117
Aperture width	.856	-.034	.232	-.275	-.210	-.080
Body whorl length	.886	-.267	.161	.062	-.048	-.213
Spire angle	-.012	.752	.523	-.344	-.126	-.023
Radula length	.870	-.026	-.211	.037	.209	.198
Radula width	.894	.173	.138	.331	.024	.169
Number rows	.330	.760	-.254	.007	.404	-.288
Teeth per row	.550	.607	-.020	.478	-.291	.061
Cusps per 30 teeth	-.466	-.102	.770	.232	.335	.082
Eigenvalue	5.975	1.891	1.115	.752	.492	.338
Cumulative proportion of variance	.543	.715	.816	.885	.930	.960

This difference is not apparent when comparing Baker's data to the abundance unweighted simulation. Reference to table 6 shows that these two runs are nearly indistinguishable in mean NMND and FMND. If there is any tendency it is toward less morphological diversity than expectation based on equiprobable species occurrence. In three comparisons with the unweighted simulation, however, the variance in NMND and FMND is significantly less in Baker's samples. The effect of assuming that all species are equally likely to occur in samples may be to introduce a greater variety of snail morphologies into the samples.

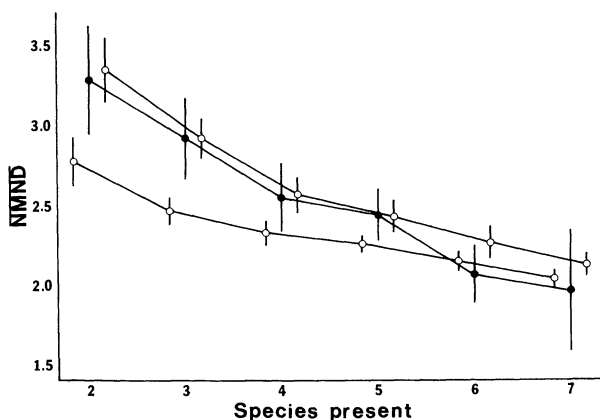


FIG. 2.—Mean nearest morphological neighbor distance as a function of no. of snail species present in samples from Oneida Lake. Distance is Euclidean after principal components analysis. Baker's (1918) samples are graphed as closed circles; results of the two simulations are open circles; upper (leading) curve is the result of the abundance-unweighted simulation; lower (trailing) curve is from the weighted simulation. Bars are 95% confidence intervals for the mean.

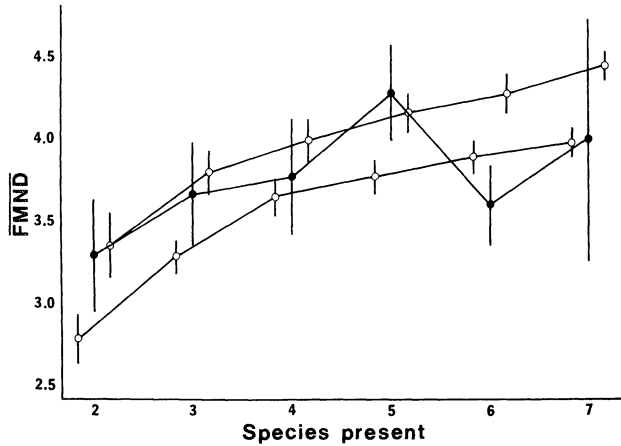


FIG. 3.—Mean furthest morphological neighbor distance as a function of no. of snail species present in samples from Oneida Lake. Symbols as in fig. 2.

Environmental Effects

No evidence was found that water depth, substrate, shore distance, sample area, or vegetational species richness influences the morphological similarity of co-occurring snail species. In both of the stepwise regression analyses using mean nearest or furthest morphological neighbor distance as dependent variable, the number of snail species present was highly correlated with $\overline{\text{NMND}}$ or $\overline{\text{FMND}}$, as expected (table 7). Once this variable was entered into the regression, none of the remaining variables were significantly partially correlated with the dependent variable. Table 7 shows the correlations of $\overline{\text{NMND}}$ and $\overline{\text{FMND}}$ with each of the six independent variables at the outset of the stepwise procedure and the correlations of the five remaining variables once "species present" was partialled out.

TABLE 6

RESULTS OF TESTS THAT MORPHOLOGICAL DIVERSITY IN BAKER'S SAMPLES IS THE SAME AS DIVERSITY IN THE TWO SIMULATIONS

No. of Species	WEIGHTED SIMULATION				UNWEIGHTED SIMULATION			
	$\overline{\text{NMND}}$		$\overline{\text{FMND}}$		$\overline{\text{NMND}}$		$\overline{\text{FMND}}$	
	<i>t</i>	<i>F</i>	<i>t</i>	<i>F</i>	<i>t</i>	<i>F</i>	<i>t</i>	<i>F</i>
2	2.89**	1.03281	.641
3	3.66**	1.86*	2.46*	2.00*	.015	.870	.779	1.14
4	2.09*	1.44	.692	1.74*	.195	.654	1.25	1.32
5	2.24*	1.85*	3.43**	1.93*	.172	.556*	.788	1.35
6	1.08	.743	2.54*	.492	2.26*	.292*	48.2**	.351*
7	.408	2.98*	.124	3.76**	1.48	1.44	1.48	3.93**

* Significant at the .05 level.

** Significant at the .01 level.

TABLE 7
RESULTS OF TWO STEPWISE MULTIPLE REGRESSION ANALYSES OF ENVIRONMENTAL
AND SAMPLING VARIABLES WITHIN BAKER'S SAMPLES OF SNAILS

	NMND		FMND	
	Step 1 Correlation	Step 2 Partial Correlation	Step 1 Correlation	Step 2 Partial Correlation
Species present	-.634**423**	...
Sample area	-.204	-.094	.073	-.018
Depth	-.047	-.046	-.065	-.080
Substrate052	.196	.172	.119
Shore distance137	.014	-.073	.012
Plant species richness	-.094	.060	.062	-.035

** Significant at the .01 level.

DISCUSSION

Small bottom samples from Oneida Lake, New York, generally contain fewer snail species than one would expect from chance alone. The snail species that do co-occur in the small samples are more morphologically different from one another than random expectation. The null hypothesis that morphological diversity is random when snail species are selected for each site according to their abundance in the lake can be rejected using direct measurement of shell and radula characters as the criterion for morphological similarity. The null hypothesis that morphological diversity is random when all snail species have equal probability of occurring at each site can be rejected using taxonomic relatedness as the criterion for morphological similarity. The former null hypothesis seems more realistic for current distributions, while the latter might be more appropriate in an evolutionary time scale. The conclusions are the same.

There are numerous possible interpretations of these results. Suppose two co-occurring species, A and B, are found to be unusually dissimilar. It is possible that character displacement has occurred between A and B, caused by competition in the present or past. However, the unusual dissimilarity of A and B might not be the direct result of interaction between the two species. Other factors may have been responsible for the phenotypes of A and B, so that now they can coexist without competition. Suppose next that two unusually similar species, B and C, do not co-occur. This might be the result of current, ongoing competition where B cannot survive in areas occupied by C, and vice versa; or it could result from competition between B and C in the past, so that the two species have specialized on resources found in different areas and currently do not move into each other's area. It is also possible to explain unusual similarity of species that do not co-occur without invoking competition at all. For example, B and C may have diverged from a single ancestral species that occupied two distinct habitats. The two species may evolve by specializing on these two habitats while remaining

similar because of their common ancestry. Any of these processes may contribute to the morphology and distribution of Oneida Lake gastropods.

Given that the snails in Baker's samples are indeed more diverse than random expectation based on either null hypothesis, it is valid to examine the reasons that some tests did not uncover significant differences. For example, Baker's data agree well with the results of the unweighted simulation in the analysis of shell and radula morphology. The implication is that many of the morphologically unusual species are rare, or they are specialized on some particular habitat type not adequately sampled by Baker. Also, Baker's samples seemed to have the same number of confamilial pairs as the results of the weighted simulation. This might result from a tendency for each family to contain one or two very common species and the rest rare. Table 1 shows some evidence of this.

The two methods of measuring morphological similarity, taxonomic relatedness and character measurement, seem to differ in their power of resolution. When the number of co-occurring species is small, very few congeneric or confamilial pairs are expected, and it will be difficult to determine if there are any patterns of taxonomic relatedness. The criterion taxonomic relatedness strengthens as the number of co-occurring species increases. By contrast, direct measurement of morphology is most sensitive to differences between observed and expected results when the number of co-occurring species is low. The number of characters measured and their variance will set upper and lower boundaries on the amount by which groups of species can vary morphologically, and these boundaries converge as the number of species increases. For example, where $N = 2$ the maximum NMND is 4.0 on the scale of figure 2, and the minimum is 0.5. Where $N = 7$, these boundaries are around 3.3 and 0.6, and where $N = 23$ they have converged to 1.7.

Although there is little prior evidence that competition has played a role in determining the distribution and abundance of snails in lakes, considerable attention has focused on possible mechanisms for their coexistence. There is evidence that certain snail species are most numerous on particular macrophyte species (Pip and Stewart 1976) or substrate types (Harman 1972; Clampitt 1973; Harris and Charleston 1977). Clampitt (1970) found that water depth was important in separating the habitats of a pair of *Physa* species. Calow (1973) showed that the rocky, exposed shores of an English tarn have a different gastropod fauna from the weedy, protected shores. Calow and Calow (1975) found great variability in the cellulase activity of 14 freshwater snail species, and suggested that physiological differences may play a role in their coexistence. There seems to be no scarcity of potential mechanisms to reduce competition among snails in lakes.

There is also a sizable literature supporting the contention that organisms with similar morphology have similar ecological requirements (Hespenheide 1973; Karr and James 1975). In snails, attention has focused on the relationship between susceptibility to predation and shell size, shape, and ornamentation (Vermeij 1974; Vermeij and Covich 1978). Relationships between the habits of snails and their shell and radula morphology have been found in numerous studies (Radwin and Wells 1968; Gould 1969; Solem 1973; Vermeij 1973; Cain 1978; Linsley 1978; Dillon 1980). Fenchel (1975) found evidence of character displacement in body size where two *Hydrobia* species occur sympatrically in Europe. In animals

generally, findings have been that co-occurring, related species tend to be morphologically diverse (Brown and Wilson 1956; Hutchinson 1959; Schoener 1965; Ashmole 1968; M'Closkey 1976; Ricklefs and Cox 1977; Ricklefs and Travis 1980). Many of these studies have been strongly criticized, however (Grant 1972; Dunham et al. 1979).

Although I have made the assumption that there are no barriers to dispersal in the lake, this study is similar to many island biogeographical works where islands are treated as samples of a mainland biota. In particular, the two null hypotheses I have tested are analogous to "null hypothesis I" and "null hypothesis II" of Connor and Simberloff (1978). Their first null hypothesis was that all species had equal probabilities of dispersal and their second was that dispersal probabilities varied as a function of the observed distributions. In testing null hypothesis II, Connor and Simberloff weighted probability of occurrence on any particular island by the number of islands on which the species occurred. They found much greater numbers of species or genera shared between islands than expected from either null hypothesis, and concluded that neither null hypothesis was adequate. In contrast, I have found the first null hypothesis (abundance unweighted) quite adequate to explain the diversity of shell and radula of co-occurring snail species but inadequate to explain their taxonomic diversity. The second null hypothesis (weighted) gave opposite results.

It must be emphasized that Baker's samples may have been made over a period of several months, and that a great amount of temporal variation occurs in lake snail populations. Several generations may pass during the summer, and wholesale migrations may occur. Lassen (1975) has found evidence that species turnover in the snail faunas of freshwater lakes may be high. Although little study has been devoted to the question, one might expect the snail fauna of a 103 cm² plot to change hourly, particularly in heterogeneous areas. Notice too that I have measured only adult snails in this study, but surely a large portion of Baker's records were of juveniles. One would expect these variables to introduce considerable error into this analysis.

However, in conclusion, there is strong evidence of distributional pattern in the snails of Oneida Lake with respect to one another, although it is currently impossible to choose among numerous explanations for this pattern. Further research will focus on particular pairs or groups of species whose distributions suggest interaction, and variation in particular morphological characters that suggests adaptation for coexistence.

SUMMARY

Individuals of 23 snail species in Oneida Lake, New York, are clumped into small subsets of 141 bottom samples made by F. C. Baker (1918). The sites preferred by the 23 species seem to differ, so that the number of species present in any sample is generally much lower than expected from chance alone. The snail species that do co-occur in individual samples are more morphologically diverse than expected. The morphological similarity of snail species at a site was assessed in two ways, taxonomic relatedness (number of congeneric or confamilial pairs)

and direct measurement of shell and radula (mean nearest or furthest morphological neighbor distance). Two null hypotheses were also tested, with the probability of occurrence in a sample weighted or unweighted by overall species abundance. The abundance weighted null hypothesis was rejected when shell and radula morphology were the criteria for similarity, and the unweighted null hypothesis was rejected when taxonomic relatedness was considered. No relationship was found between the morphological similarity of co-occurring species and the size of the plot, its depth, substrate, distance from shore, or plant species richness.

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