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Growth of *Lampsilis radiata* (Bivalvia: Unionidae) in Sand and Mud: A Reciprocal Transplant Experiment

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To examine the effects of habitat on shell growth and form, freshwater unionid clams (*Lampsilis radiata*) were reciprocally transplanted between a sandy and a muddy site in Inner Long Point Bay, Lake Erie. There were significant differences in the initial shell dimensions of the two populations, with the sand clams being larger and less obese than the mud clams. Pretransplant growth rate analysis, using annual rings, showed that long-term growth in the sand was greater than that in the mud. After 16 wk the transplanted clams were recovered. Overall growth rate was affected by the source of the clams, while transplant destination affected shape change (height growth per unit length growth). This suggests that shell growth rates may be under direct genetic control, while shell shape can be adaptively modified by environmental cues.

Pour examiner les effets de l'habitat sur la croissance et la forme de la coquille, on a transplanté des coquillages unionidés d'eau douce (*Lampsilis radiata*) d'un site sableux à un site boueux et vice versa. L'expérience a eu lieu dans la baie Long Point intérieure du lac Érié. Les dimensions initiales des coquilles étaient très différentes d'une population à l'autre, les coquillages de sable étant plus gros et moins obèses que les coquillages de boue. L'analyse du taux de croissance avant la transplantation, d'après les couches d'accroissement annuel, a montré que la croissance à long terme est plus forte dans le sable que dans la boue. Après 16 sem, on a récupéré les coquillages transplantés. L'origine des coquillages influait sur leur taux de croissance global, alors que le milieu dans lequel ils étaient transplantés conditionnait leur forme (croissance en hauteur par unité de croissance en longueur). Ces résultats portent à croire que le taux de croissance des coquilles est commandé directement par des facteurs génétiques, alors que la forme de la coquille peut subir des modifications adaptatives dictées par les conditions environnementales.

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Many researchers (Isely 1911; Wilson and Clark 1914; Grier 1920; Eagar 1948; Agrell 1949; Negrus 1966; Harman 1972; Green 1972; Kat 1982) have observed correlations between habitat and the growth (inferred from size) and form of unionid clams. However, field experiments are necessary to verify such observational data. Biological monitoring using unionids is receiving increasing attention (Foster and Bates 1978; Curry 1977-78; Forester 1980; McCuaig and Green 1983; Mitchell 1984). A better understanding of the factors affecting the growth and form of unionids will help to assess them as biological monitors of freshwater environments.

On the basis of a field experiment, Kat (1982) determined that growth rates of the freshwater unionid *Elliptio complanata* were reduced on muddy substrates. He hypothesized that on mud substrates clogged filtration systems would cause a reduction in feeding efficiency. Conversely, Newell and Hidu (1982), using a laboratory transplant study, noted that the marine bivalve *Mya arenaria* grew more rapidly in mud than in sand. Their explanation was that food availability was greater in muddy sediments. Reciprocal transplants in the field have recently been used to examine the relative importance of habitat type and genotype on the growth rate of the marine bivalve *Mytilus edulis* (Widdows et al. 1984; Dickie et al. 1984). The purpose of this study was to utilize a reciprocal transplant experiment to show how habitat type affects growth rate and

and shell form in the freshwater unionid *Lampsilis radiata* (Gmelin 1792).

Materials and Methods

Two sites in Inner Long Point Bay, Lake Erie (42°38'N, 80°24'W), were chosen for the study on the basis of substrate type, as reported in Heathcote (1981). One site, located south of St. Williams, Ont. had a muddy bottom whereas the other, located south of Turkey Point, Ont., had sand (Fig. 1). Selected environmental parameters were measured at both sites (Table 1). R. C. Bailey (unpubl. data) sampled 50 sites in the Inner Bay and found that the two sites in this study fell at nearly opposite ends of a sand-mud gradient.

On June 4, 1984, 183 *L. radiata* were collected from the two sites using SCUBA. Clams were aged by counting annual rings. A letter and number code were scribed onto each shell to identify collection site and individuals. The initial length, height, and width of each individual (as defined in Tevesz and Carter 1980, our "width" measurement is equivalent to their "thickness") were measured using vernier calipers to the nearest 0.01 mm. Half of the clams were randomly chosen and replaced as controls at each site, while the remaining half were taken to the other site. The clams were "replanted" by hand in their normal living position (i.e. anterior end in the sediment). On September 21, 1984, after 16 wk of growth, marked indi-

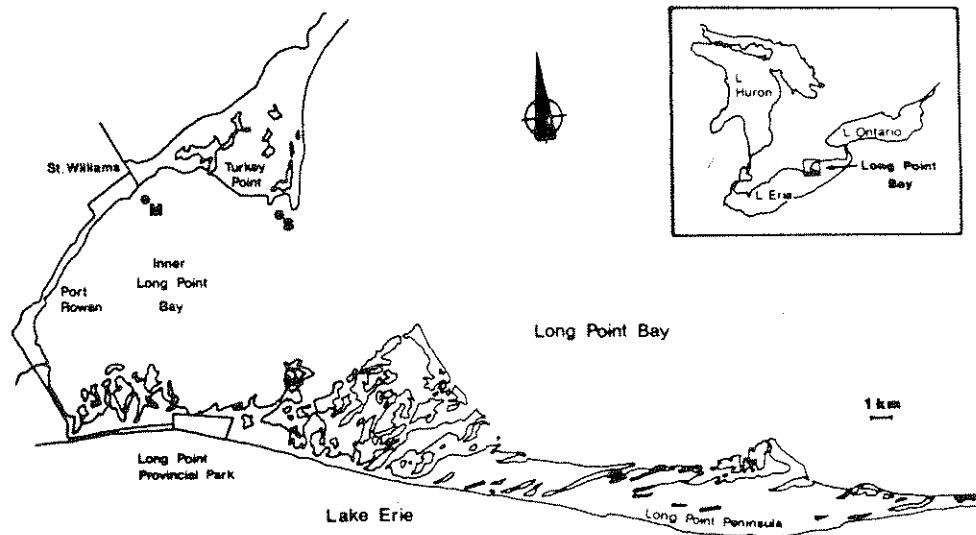


FIG. 1. Inner Long Point Bay showing the mud (M) and sand (S) transplant sites. Inset shows location of bay in Lake Erie.

TABLE I. Means (SD) of environmental measurements from the mud and sand transplant sites. Measurements taken on June 21, 1984.

	Mud site (n = 3)	Sand site (n = 3)
Depth (m)	2.50 (0.06)	1.90 (0.06)
pH	8.44 (0.02)	8.44 (0.04)
Alkalinity (mg · L ⁻¹)	124.33 (0.29)	107.33 (0.76)
Calcium (mg · L ⁻¹)	44.10 (2.44)	37.01 (1.41)
% loss on ignition	2.36 (0.20)	0.64 (0.34)
% sediment sample that did not pass through 75- μ m sieve	20.03 (6.12)	82.47 (2.31)
Macrophyte species present	<i>Vallisneria americana</i> <i>Najas</i> sp. <i>Myriophyllum</i> sp. <i>Potamogeton praelongus</i>	<i>Chara</i> sp.

viduals were recovered from both sites. Final lengths, heights, and widths were remeasured.

The means of the initial log-transformed shell length, height, and width measurements at each site were compared using multivariate analysis of variance (MANOVA). This was followed by calculation of the normalized discriminant vector describing the difference in the mud and sand populations with respect to shell dimensions.

Long-term growth was assessed using analysis of covariance (ANCOVA), which compared growth ring data from the mud and sand populations using the Walford plot model (McCuaig and Green 1983). This model assumes von Bertalanffy growth curves. Growth ring data were collected by measuring lengths of the most legible pair of consecutive annual rings on each clam. This sampling strategy differs from that of McCuaig and Green (1983) and Green et al. (1983) who measured as many pairs of consecutive annual rings on a single clam as possible.

Short-term growth was assessed from the reciprocal transplant experiment data. A factorial multivariate analysis of covariance (MANCOVA) was carried out using final length, height, and width of the clams as the dependent variables and initial length, height, and width as the covariates. This is a multivariate factorial analogue of the Walford Plot ANCOVA utilized and described by McCuaig and Green (1983). It en-

ables one to determine both the statistical significance and the nature of differences in growth along the three dimensions due to the source of the clams, their transplant destination, and the interaction of these two factors.

A factorial ANCOVA was also run on each dimension (length, height, and width) separately as an aid to showing how growth in each dimension was affected by source and destination. In each of these analyses the final size of the dimension was the dependent variable and the initial size was the covariate.

Results

The initial dimensions of the clams (Table 2) were significantly different (based on Wilks criterion, MANOVA $F(3,104) = 130.14, P < 0.01$). The normalized discriminant vector derived from this analysis (Table 2) indicated that the clams from the sand site were longer and taller but less obese (narrower at a given length) than the clams from the mud. Relative height (height per unit length) was less in the clams from the sand. If the difference in the populations was only a matter of size, then all of the discriminant coefficients would be equal. This is based on an allometric growth model described by Mosimann (1970). The fact that the width coeffi-

TABLE 2. Means (SD) of initial shell dimensions (mm) in the total sample and in each group, and the normalized discriminant coefficients from a comparison of the sand and mud clams.

	Total (n = 107)	Sand (n = 53)	Mud (n = 54)	Normalized discriminant coefficient
Length	58.7 (10.6)	68.0 (5.7)	49.6 (4.3)	0.78
Height	35.2 (6.0)	40.6 (2.6)	29.9 (2.9)	0.58
Width	25.7 (6.0)	30.9 (3.4)	20.7 (2.7)	0.26

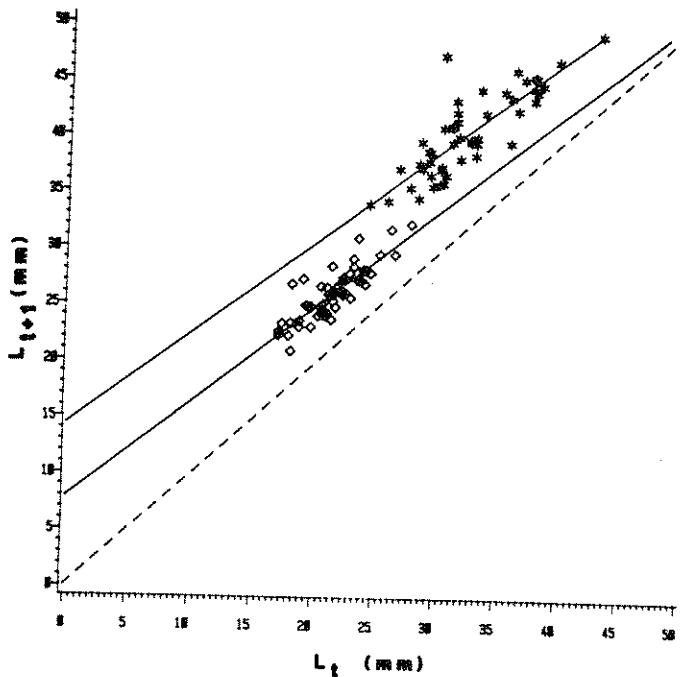


FIG. 2. Walford Plots of the lengths at consecutive annual rings for *L. radiata* from the sand (*) and mud (□) sites. Length at time t is L_t ; length at time $t + 1$ is L_{t+1} .

cient is much smaller than the length coefficient indicates a proportionately smaller increase in width, relative to increase in length, for the clams from the sand.

The mean ages of clams collected from the sand and mud populations were 11.1 ± 1.7 ($\pm 95\%$ confidence limits) and 10.4 ± 1.7 yr, respectively. These means are not significantly different (t -test, $P > 0.05$); therefore, differences in initial shell dimensions are not a result of differences in population age.

Clams from the mud and sand populations have the same relative growth rates (i.e. they approach their asymptotic size at the same age) based on the consecutive annual growth ring data (ANCOVA; Fig. 2). However, the clams from the sand site grow to a greater maximum size (Fig. 3) ($F(1,100) = 290.5$, $P < 0.01$) and thus have a greater absolute growth rate. The growth equations derived from the annual ring data are as follows:

Mud population:

$$L_t = 67.7(1 - e^{-0.111t})$$

Sand population:

$$L_t = 115.3(1 - e^{-0.111t})$$

TABLE 3. Normalized discriminant coefficients and probability levels for factorial MANCOVA of length, height, and width growth of transplanted clams.

	Length	Height	Width	P
Source	0.429	0.895	0.142	0.023
Destination	-0.593	0.803	0.049	0.008
Source \times destination	0.490	0.867	0.096	0.284

TABLE 4. Probability levels for factorial ANCOVA's of length, height, and width growth of the transplanted clams ($df = 1,103$).

	Length	Height	Width
Source	0.096	0.004	0.365
Destination	0.121	0.018	0.786
Source \times destination	0.202	0.095	0.781

where L_t = length at time t and t = time in years.

We recovered 58% of all marked individuals: 64% from the sand site and 54% from the mud. The factorial MANCOVA of the pre- and post-transplant data (Table 3) showed that both the source of the clams and their destination had significant effects on their shell growth in the reciprocal transplant experiment. There was no interaction between source and destination. The discriminant coefficients indicate that the "source" effect is on overall growth rate (i.e. all coefficients are positive). Clams from the sand site grew faster than those from the mud site. Destination affected growth in height relative to growth in length (i.e. the length and height coefficients have opposite signs). Both control and transplanted clams placed at the mud site grew more in relative height (height growth per unit length growth) than control and transplanted clams placed at the sand site.

The ANCOVA's of each dimension (Table 4) show similar results. The adjusted growth of each group of clams along each of the three dimensions was determined from these ANCOVA's (Table 5). To obtain these, the mean final size of each dimension for each group was adjusted by the ANCOVA for differences among the clams in initial size, and then subtracted from the initial size of the dimension.

Discussion

We determined from initial shell sizes that clams from the sand are longer, taller, and less obese than those from mud. Analysis of annual growth rings shows that clams from the sand grow faster than those from mud although both groups reach their asymptotic size at the same age. The results from the transplant experiment also indicate that clams from the sand grow faster than those from mud. These three independent analyses all result in a similar conclusion: *L. radiata* from sand grow faster and are less obese than those from mud.

Clams from the sand habitat had greater lengths and heights than those from the mud. Kat (1982) speculated that a similar trend observed in the lengths of *E. complanata* from muddy substrates resulted from a reduction in feeding efficiency caused by fine sediments clogging the clams' filtration system. Stansbery (1970), however, suggested that muddy substrates reflect reduced water flow regimes, and therefore a reduction in available food may be a cause of reduced unionid growth in muddy habitats.

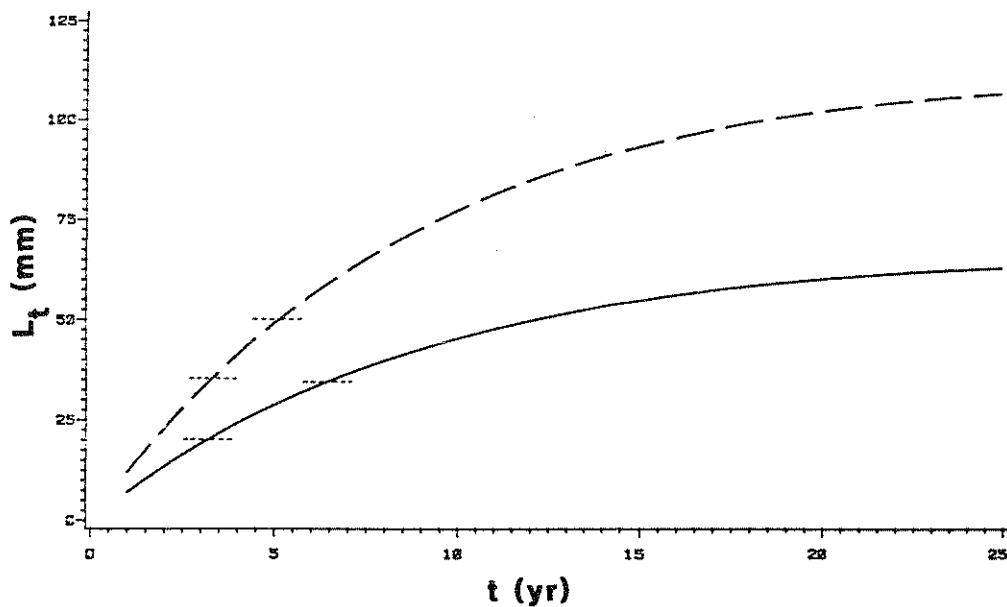


FIG. 3. Growth curves for *L. radiata* from the sand (---) and mud (—) sites. The ranges of data used to derive these curves are indicated by horizontal broken lines on each curve.

Both the clogged filtration system and the nutritive-stress hypotheses might have been used to explain variability in *L. radiata* growth rates. However, they can not explain greater shell obesity in the clams from muddy sediments. Variation in shell dimensions may represent morphological adaptations to the environment. Large and long shells will assist the clam in maintaining its position in and moving through sandy, more turbulent areas. Smaller, more obese shells will permit the clam to present a broad surface in nonturbulent, soft-silt areas thereby enabling the clam to maintain its position by reducing the amount of sinking.

Horn and Porter (1981) noted that in Lake Waccamaw, obesity of *Lampsilis* sp. was positively correlated with percent organic matter of the sediment. Tevesz and McCall (1979), after observing a similar phenomenon in *L. radiata siliquoidea* in western Lake Erie, suggested that this characteristic enhances buoyancy and helps preclude sinking in soft sediments. The result from the present study agree with those of Tevesz and McCall.

Adaptations of a species to different habitats can be environmentally induced (phenotypic plasticity) or directly inherited characteristics. Results from the reciprocal transplant experiment suggest that both phenomena are occurring in *L. radiata*. The source of the transplants was most important in predicting variation in overall shell growth, indicating a genotypic adaptation of shell growth rate to the clam's original environment. Variability in relative height growth, however, was a function of the clam's destination. Clams that were left in the mud tended to grow relatively taller regardless of their source. A similar response in shell form was observed by Newell and Hidu (1982) for transplanted *M. arenaria*. They suggested that greater relative shell heights in transplants to mud is an adaptive characteristic that would reduce clam sinkage in soft substrates. Although greater relative width growth (increase in obesity) might have been predicted in clams that were transplanted to the mud, there is so little growth in width in adult clams over one season that such differences were hard to detect.

The argument for a genetically controlled growth rate is

TABLE 5. Adjusted growth (mm) of length, height, and width of transplanted clams.

Source:	Sand		Mud	
	Sand	Mud	Sand	Mud
Length	1.82	1.39	1.12	1.08
Height	1.58	1.68	0.41	0.94
Width	0.80	0.80	0.36	0.48

based on the "source" effect from the transplant experiment. Environmental effects on gene expression could have occurred early in the lives of these clams, and thus the "source" effect may not necessarily represent genetic differences between the two populations. However, preliminary electrophoretic data (R. C. Bailey, unpubl. data) suggest differences in allelic frequencies between mud- and sand-dwelling *L. radiata* sampled from Inner Long Point Bay.

Differential selection pressures may be present in the different habitats. Thus, genetic differences in growth rates could arise between the mud and sand populations of *L. radiata*. These differences may be maintained through reduced gene flow between the populations as a result of habitat preferences among fish hosts of the glochidia (parasitic larval clams). Alternatively the transplants may have been exhibiting "phenotypic latency." The potential for phenotypic responses in growth rates of the transplants to their new environment may have existed, but the length of exposure was not sufficient for these responses to be elicited.

Any adaptation would be expected to optimize morphological and physiological responses of a population to its environment (Gartner-Kepkay et al. 1980). This phenomenon has important implications for unionid biomonitoring studies. These studies usually entail taking clams from a relatively "clean" source and transplanting them to areas where trace contaminant levels are to be determined. If investigators do not consider the fact that genetically different populations of a monitor species can exist, comparisons of studies over time

could produce misleading results, since contaminant uptake may be related to genetically determined growth rates. For instance, a study measuring uptake of a contaminant using clams taken from a sandy habitat may not be comparable with another year's study using the same species of unionid taken from a silty habitat. Standardizing the source and genotype of the unionid biomonitors could make results of these studies more comparable. This may be possible through laboratory culturing of the clams, which is now possible without fish hosts (Isom and Hudson 1982; Hudson and Isom 1984).

Research is needed to determine the effects of differential trace contaminant uptake in populations of unionids taken from different habitats. Until such results have been evaluated, data from many unionid biomonitoring studies are not comparable.

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