

GENETIC VARIATION IN SEVEN WOOD-BORING TEREDINID AND PHOLADID BIVALVES WITH DIFFERENT PATTERNS OF LIFE HISTORY AND DISPERSAL

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ABSTRACT

Intrapopulation genetic variation and genetic distance between populations were investigated for ten populations of seven teredinid and pholadid species in the bivalve superfamily Pholadacea. Genetic variation as measured by allozyme heterozygosity, percent polymorphic loci, and number of alleles per locus tended to be higher in species with planktotrophic larvae, lower in species with brooded larvae. Two introduced populations were genetically impoverished, perhaps due to founder effects and bottlenecks. Most of the 20 loci resolved for all species showed heterozygote deficiency, as has been reported for many marine bivalves. Wahlund effects and inbreeding are not sufficient to explain heterozygote deficiency; natural selection and null alleles may also be causes. Species both with and without planktonic larvae show heterozygote deficiencies. Substantial genetic differentiation exists between populations of one species with planktonic larvae. Patterns of genetic variation could not be correlated with latitude or local environmental factors. The data suggest that breeding structure and larval dispersal influence intra- and interpopulation allozyme variation.

Key words: shipworm; Teredinidae; Pholadidae; Pholadacea; allozymes; heterozygosity; genetic variation; brooding; planktotrophy; dispersal; heterozygote deficiency.

INTRODUCTION

Since the advent of electrophoresis as a tool in population genetics, many researchers have sought to describe patterns in genetic variation at the population and species levels. Some have related genetic variation to heterogeneity or uncertainty of the environment (Levinton, 1973; Selander & Kaufman, 1973), although Johnson (1976) demonstrated the ambiguity of many such studies. High genetic variability has been correlated with geographical range and colonization ability (Nevo, 1978). Species with dispersive larvae are assumed to be outbreeders and good colonizers, hence more variable genetically at the population level, but less genetically differentiated between populations, than species that brood their young or otherwise lack a dispersive larval stage (Crisp, 1978; Ament, 1979; Hamrick *et al.*, 1979). Most of the data supporting these ideas involve several populations of one or two species (Koehn *et al.*, 1976; Ayala & Valentine, 1974; Lavie & Nevo, 1986). Most molluscan data sets include only a few enzyme systems that are usually highly polymorphic (Levinton, 1975; Berger, 1977;

Wilkins and O'Regan, 1980; Beaumont *et al.*, 1980; Badino & Sella, 1980).

The type of larval development in bivalves is related to the ability of the young to disperse; hence it bears a relationship to geographic range, population size, and genetic structure of populations. The positive correlation of genetic variation with these three factors has been supported theoretically and empirically (Soulé, 1976; Snyder & Gooch, 1973), but contradictory evidence was cited by Valentine (1976). Few data are available that delineate genetic patterns in similar species with different types of larval development and different levels of fecundity (Lavie & Nevo, 1986).

This paper reports the electrophoretic analysis of a broad range of enzyme systems for ten populations of seven species of wood-boring teredinid and pholadid bivalves within one superfamily, the Pholadacea. Two populations are introduced; the effects of introduction on population genetic structure was investigated. The genetic distance between populations was compared for two species and related to typical interspecific values. The other purpose of the work was to compare heterozygosity in populations of species with

different life histories and modes of dispersal. Each species has a characteristic development pattern, ranging from completely planktonic to completely brooded development with the release of pediveliger young. Some species follow an intermediate path, with a brooded period followed by a planktonic period. Levels of fecundity are proportional to the amount of time spent in the plankton. The species are otherwise ecologically similar, spending their adult lives burrowing in wood. Some of the species chosen for analysis are congeners. Several species were taken from the same geographical area, so that the degree of environmental variation (e.g., seasonal temperatures and salinities; variation in food and exposure to predators) would not be a major factor explaining the observed differences in genetic variation among taxa.

METHODS

Populations Studied

The populations of Pholadacea that were examined are described in Table 1. The density of each species in the white pine collecting panels indicates the strength of the age-class settlement over the time period of the submergence of the panels. The accuracy of the estimate is lower for species lacking a planktonic larval stage, such as *Teredo bartschi*. Such species are expected to have highly clumped distributions (Hoagland *et al.*, 1981).

The salinity at all sites is seasonally variable. The yearly salinity ranges are based on my observations in the case of the New Jersey sites, and data from laboratories at localities cited in Table 1 for the other sites. All sites are estuarine except Millstone, Connecticut, and Virginia Key, Florida, which have approximately full oceanic salinity for most of the year.

Teredo bartschi is a tropical to subtropical species that was accidentally introduced into the thermal effluents of two nuclear power plants in the cold temperate zone (Hoagland & Turner, 1980). The Fort Pierce, Florida, population is within the natural distribution of the species. The New Jersey and Connecticut populations had been established for seven and five years, respectively.

Life History

Data on the life history of the teredinids from New Jersey were obtained between 1976 and 1981 by submerging wood panels for one to twelve month periods, then retrieving them and submerging new panels monthly at 20 stations in Barnegat Bay (Hoagland, 1983a). In the laboratory, the shipworms were dissected from the wood, identified, measured, and examined for larvae in the gills. Other life historical and ecological data were available in the literature (Turner & Johnson, 1971; Hoagland & Turner, 1981). Temperature and salinity tolerances were determined in the laboratory; details of these experiments are reported elsewhere (Hoagland, 1983b, 1986).

Electrophoresis

Specimens were dissected from the wood while alive, identified, and either electrophoresed immediately or frozen in Tris tissue buffer until they were subjected to electrophoretic analysis. Voucher specimens are on deposit at The Academy of Natural Sciences of Philadelphia (ANSP); catalogue numbers are in Table 1. Horizontal starch-gel electrophoresis followed by staining for specific enzymes was employed to study 23 enzyme systems. The general methods of Ayala *et al.* (1973) were applied to mollusks as amended by Dillon & Davis (1980) and Davis *et al.* (1981). Starch gels (13%) were prepared using 33.5 g of Electrostarch and 250 ml of one of four gel buffers: 1) tris citrate, pH 6.0; 2) tris NaOH borate (Poulik), tray buffer pH 7.6 and gel buffer pH 8.9; 3) tris-EDTA-borate (TEB) pH 8.0; and 4) TEB, pH 9.1. Four enzyme systems were run on TEB of pH 9.1 but with tray buffer of pH 8. Enzymes assayed and electrophoretic conditions are reported in Table 2.

Five wicks of No. 3 Whatman filter paper were saturated with homogenized tissue, blotted, and applied, one wick from each individual, to each gel. Five gels were run concurrently; each was then analyzed for three enzyme systems. Each individual was investigated for all enzyme systems over a 2-day period.

Six individuals from a reference population and 25 individuals from the population being tested were run on a single gel. Runs were repeated if the relative position of the reference population was unclear or if results were

TABLE 1. Populations of Pholadacea used in this study.

Species	Population	No. of genomes sampled	Approx. density*	Yearly salinity range (‰)	Comments
<i>Teredo bartschi</i>	Blue Hole, intracoastal waterway near Harbor Branch Laboratory, Ft. Pierce, Florida	98	10 ¹ –10 ²	10–39	Panels submerged May 2, 1980 removed Nov. 20, 1980 in mangrove area. ANSP A9100.
<i>Teredo bartschi</i>	Oyster Creek nuclear generating station, Oyster Creek and Forked River, New Jersey	200	10 ² –10 ³	7–30	Panels submerged from docks and removed in 1979 and 1980. ANSP A8717A-E.
<i>Teredo bartschi</i>	Millstone nuclear generating station, Millstone Point, Niantic Bay, Waterford, Conn.	40	10 ⁰ –10 ¹	28–33	Panels submerged from docks June 17 and removed Nov. 7, 1980. ANSP A8693, A8726C.
<i>Teredo navalis</i>	Oyster Creek nuclear generating station, Oyster Creek and Forked River, New Jersey	180	10 ¹	7–30	Panels submerged from docks and removed in 1980. ANSP A8362.
<i>Teredo navalis</i>	Millstone nuclear generating station, Millstone Point, Niantic Bay, Waterford, Conn.	102	10 ¹	28–33	Panels submerged from docks June 17 and removed Nov. 7, 1980. ANSP A8726A & B.
<i>Bankia gouldi</i>	Oyster Creek and Forked River, New Jersey	214	10 ¹	7–30	Panels submerged from docks and removed in 1980. ANSP A7927E.
<i>Bankia fimbriatula</i>	Rocky Point, 1 mi. S. of "Crossroads" where Intracoastal Waterway meets St. Lucie River, near Hobe Sound, Florida	100	10 ⁰ –10 ¹	~10–30	Dead red mangrove collected Oct. 22, 1979. ANSP A8680A.
<i>Lyrodus floridanus</i>	Rosenstiel School, U. Miami, Bear Cut, Virginia Key, Florida	104	10 ¹	~31–35	From pine panels submerged for 6 months from a dock. Collected Oct. 29, 1980. ANSP A8680B & C.
<i>Lyrodus bipartitus</i>	Little Jim Creek, Ft. Pierce Inlet, near Ft. Pierce, Florida	130	10 ¹ –12 ²	10–39	Panels submerged May 2 and removed Nov. 20, 1980, exposed in red mangrove area. ANSP A8726D.
<i>Martesia striata</i>	Rocky Point, 1 mi. S. of "Crossroads" where Intracoastal Waterway meets St. Lucie River, near Hobe Sound, Florida.	124	10 ²	~10–30	From dead red mangrove collected Oct. 22, 1980. ANSP 353444.

*Order of magnitude estimate per wood volume equivalent to a test panel 2 × 9 × 21 cm.

otherwise ambiguous. Although a sample size of at least 50 individuals per population was sought for each enzyme locus, it was not always reached because a few species were rare. The sample size also varied among enzyme systems for a single population when the zymograms could not be resolved for all

individuals. After preliminary results showed no differences in allelic patterns due to tissue type, entire animals minus brooded larvae were homogenized. All specimens were 4 to 12 months old and most were female. Gels were scored as described in Ayala *et al.* (1973). The alleles of each locus were

TABLE 2. Enzymes assayed, buffers, current, voltage, and duration of electrophoresis.

Enzyme	No. loci	Gel & tray buffer	Current/voltage	Run time (hr)
Acid phosphatase (AcPh)	1	TC6	35 MA	3.5
Adenylate kinase (Adkin)	1*	Poulik	35 MA	3.0
Aldehyde oxidase (AO)	2*	TEB 9	350 V	4.5
Aspartate amino transferase (AAT)	1	TEB 9	350 V	4.5
Esterase NA (EST NA)	3*	TEB 9/8	35 MA	2.0
Glucose-6-phosphate dehydrogenase (G6PDH)	1*	TC 6	35 MA	2.5
Glucose-phosphate isomerase (GPI = PGI)	2*	TC 6	35 MA	2.0
Glutamate dehydrogenase (GDH)	1*	Poulik	35 MA	3.0
Glyceraldehyde-3-phosphate dehydrogenase (G3PDH)	1*	TEB 8	35 MA	3.5
α-Glycerophosphate dehydrogenase (α GPDH)	1*	Poulik	35 MA	3.0
Hexokinase (HEX)	1	Poulik	35 MA	3.0
Isocitrate dehydrogenase (IsDH)	2	TEB 8	35 MA	3.5
Lactate dehydrogenase (LDH)	1	TEB 8	35 MA	3.5
Leucine amino peptidase (LAP)	1	TC 6	35 MA	2.0
Mannose-6-phosphate isomerase (MPI)	1	TEB 9/8	35 MA	2.0
NAD-dependent malate dehydrogenase (NAD-MDH)	2*	TC 6	35 MA	3.5
Peptidase G (Pep G)	3*	TEB 8	35 MA	3.5
Phosphoglucomutase (PGM)	1	TC 6	35 MA	2.0
		TEB 9	350 V	4.5
6-phosphogluconate dehydrogenase (6-PGDH)	1	Poulik	35 MA	3.0
Sorbitol dehydrogenase (SoDH)	1	Poulik	35 MA	3.0
Superoxide dismutase (SOD)	2*	TEB 9/8	35 MA	2.0
Triosephosphate isomerase (TPI)	1*	TEB 8	35 MA	3.5
Xanthine dehydrogenase (XDH)	1	Poulik	35 MA	3.0

*Locus with missing data. (If there are multiple loci, the upper locus has missing data, except for Pep G, where the lowest locus has missing data.)

identified by the distance, in mm, that they migrated with respect to the most common allele of a reference population. *Teredo bartschi* from Oyster Creek, New Jersey, was the reference population because it was abundant and nearly monomorphic. Assignment of electrophoretic patterns to loci and consequent interpretations were made with the aid of data collected on the same enzyme systems for mollusks (Davis *et al.*, 1981) and other organisms (Lewontin, 1974).

Calculations were made of the allele frequencies at each locus, the average number of alleles per locus (A), the percent polymorphic loci (P), and Nei's genetic distance (D) between populations. A locus was scored as polymorphic if the frequency of the most common allele was <.99. Heterozygosity of each enzyme locus for each population (h) was predicted from the Hardy-Weinberg equilibrium. Heterozygosity was also calcu-

lated directly ($h_{obs.}$). A heterozygote deficiency index was calculated as $(h_{obs.}-h_{pred.})/h_{pred.}$. The average individual heterozygosity per locus was calculated, again using both the Hardy-Weinberg assumptions ($H_{pred.}$) and the direct method ($H_{obs.}$), by averaging the respective h values over all loci.

RESULTS

Genetic variation

The allele frequencies for each population are in the Appendix. Of the 32 loci resolved, 20 yielded consistent results for all populations and were used in the analysis of genetic variation. Fourteen loci were polymorphic in at least one species. At 5 loci (AcPh, SOD, LDH, 6-PGDH and IsDH), one allele was fixed in each of the seven species. Only for XDH

TABLE 3. Pholadacea. Average heterozygote deficiencies.

	Mean $\pm$ S.E. het. def.	No. loci polymorphic	Total no. loci lacking heterozygotes
<i>T.b.</i> Conn.	-1.00	2	2
<i>T.b.</i> N.J.	-0.50	2	0
<i>T.b.</i> Fla.	-0.54 $\pm$.18	7	3
<i>L.b.</i> Fla.	-0.51 $\pm$.11	10	1
<i>T.n.</i> Conn.	-0.36 $\pm$.08	10	0
<i>T.n.</i> N.J.	-0.67 $\pm$.09	11	1
<i>L.f.</i> Fla.	-0.42 $\pm$.15	9	3
<i>B.f.</i> Fla.	-0.38 $\pm$.12	11	1
<i>B.g.</i> N.J.	-0.48 $\pm$.08	14	0
<i>M.s.</i> Fla.	-0.43 $\pm$.12	13	3

was the same allele fixed in all the species. Regardless of the species, genetic variation was consistently higher at some loci (eg., GPI, PGM, MPI) than others.

The heterozygote deficiencies (Table 3) were large at most loci. Lack of heterozygotes occurred at three loci in three populations, but all three populations also exhibit loci in Hardy-Weinberg equilibrium ($d \approx 0$). Loci lacking heterozygotes are not the same in each population. Heterozygote deficiencies ranged widely among populations of one species. The introduced population of *Teredo bartschi* from Millstone, Connecticut, had only two polymorphic loci, and both had complete lack of heterozygotes.

Table 4 summarizes commonly-used indices of genetic variation for the 10 populations. The values of P and A for the Millstone population of *Teredo bartschi* may be underestimated because only 20 specimens were obtained over a 2-year period. Means of the various indices for the Pholadacea were calculated with and without the two introduced populations. In comparing *Teredo bartschi* with other taxa, the latter values should be used. The values for the recently-introduced *T. bartschi* are probably altered by founder effects and are not representative of natural populations (Hoagland, 1983b).

Interpopulation variation is assessed using Nei's genetic distance (D), Table 5. The relationships do not change using other indices. Differences between populations are considerably smaller than those between species. The genetic distance between populations of *Teredo navalis* with planktonic larvae is substantial at 0.29. In fact, the genetic distance between the populations of *T. bartschi* is much less (0.08 to 0.11).

Ecology

Table 6 reviews life historical and ecological information based on field and laboratory work (Turner, 1966; Turner & Johnson, 1971; Hoagland, 1983b, 1986). The most important difference among the species is the type of larval development. Two species, *Teredo bartschi* and *Lyrodus bipartitus*, brood the young in the gill to the pediveliger stage; they produce relatively few yolky eggs. *Teredo navalis* and *L. floridanus* also brood the young, but release them in the straight hinge veliger stage, after which they undergo several more weeks of planktotrophic development. The other three species are completely planktonic; fertilization of up to a million eggs per reproductive event is external, or could involve pseudocopulation, transfer of sperm using the siphons.

Despite these differences, all shipworms can be classified as opportunistic (Turner, 1973), because they colonize wood, an ephemeral substrate and food resource that they themselves destroy. Although the peaks in settlement activity of sympatric species do not coincide, most natural wood collected in Florida contained numerous co-existing species. *Lyrodus massa*, *L. floridanus*, *L. bipartitus*, *Teredo furcifera*, *T. bartschi*, and *Martesia striata* were found together in mangrove wood from the Ft. Pierce Inlet, Florida, although *L. massa* and *T. furcifera* were rare. Most predators on the shipworms that I observed, including nereid polychaetes, flatworms, and protozoa, appeared to be non-selective. All 7 species of shipworms have the same trophic position, eating both wood and algae. I have reared adults and larvae of 4 of the 7 species on the same diet.

TABLE 4. Genetic variation in 10 populations of Pholadacea, 20 loci.

Population	Percent poly-morphic loci, P*	Average no. of alleles per locus A (S.E.)	Avg. individual observed heterozygosity (S.E.)	Avg. individual predicted heterozygosity (S.E.)
Brooders				
<i>T. bartschi</i> Conn.	10	1.15 (.11)	0 (-)	0.04 (0.03)
<i>T. bartschi</i> N.J.	10	1.15 (.11)	0.004 (0.003)	0.01 (0.01)
<i>T. bartschi</i> Fla.	35	1.35 (.11)	0.008 (0.004)	0.05 (0.03)
<i>L. bipartitus</i>	45	1.95 (.26)	0.082 (0.025)	0.18 (0.05)
Mixed development				
<i>T. navalis</i> Conn.	55	2.20 (.34)	0.150 (0.042)	0.24 (0.06)
<i>T. navalis</i> N.J.	55	2.10 (.32)	0.069 (0.024)	0.21 (0.05)
<i>L. floridanus</i>	45	1.55 (.15)	0.042 (0.020)	0.09 (0.04)
Planktonic larvae				
<i>B. fimbriatula</i>	55	1.90 (.25)	0.138 (0.038)	0.24 (0.05)
<i>B. gouldi</i>	70	2.40 (.28)	0.133 (0.033)	0.27 (0.05)
<i>M. striata</i>	65	2.30 (.29)	0.146 (0.049)	0.25 (0.06)
Mean (S.E.), 10 pops.	44 (07)	1.81 (0.15)	0.077 (0.020)	0.16 (0.03)
Mean (S.E.), excluding introduced populations	53 (04)	1.97 (0.13)	0.096 (0.019)	0.19 (0.03)

*A locus is considered polymorphic if the frequency of the most common allele is less than .99.

TABLE 5. Pholadacea. Nei's Distance Matrix.

	<i>T.b.</i> Fla.	<i>T.b.</i> Conn.	<i>T.n.</i> N.J.	<i>T.n.</i> Conn.	<i>L.f.</i> Fla.	<i>L.b.</i> Fla.	<i>B.g.</i> N.J.	<i>B.f.</i> Fla.	<i>M.s.</i> Fla.
<i>T.b.</i> N.J.	0.11	0.10	0.67	0.88	0.60	0.94	0.95	0.71	1.23
<i>T.b.</i> Fla.		0.08	0.63	0.85	0.57	0.99	1.09	0.89	1.27
<i>T.b.</i> Conn.			0.69	0.82	0.58	1.04	1.07	0.86	1.24
<i>T.n.</i> N.J.				0.29	0.82	0.92	0.82	0.85	1.23
<i>T.n.</i> Conn.					0.98	0.95	0.81	1.09	1.06
<i>L.f.</i> Fla.						0.84	0.90	0.75	1.23
<i>L.b.</i> Fla.							1.07	0.78	1.62
<i>B.g.</i> N.J.								0.48	0.98
<i>B.f.</i> Fla.									1.53

All the species of this study have been found as adults in driftwood. Brooding females are able to reach new sites while carrying larvae. Species such as *Teredo bartschi* and *Lyrodus bipartitus* that brood young during all months of the year are very likely to colonize as adults with larvae. *Teredo bartschi* living in a New Jersey heated effluent retained larvae in the gills through the winter months, although successful settlement did not occur between December and April. Larvae of *T. bartschi* have survived for at least two weeks in the laboratory without growth when either food or temperature was inadequate for metamorphosis. This phenomenon has been reported for many teredinids

(Turner & Johnson, 1971). All populations used in this study lived in water 0.5 to 2 m deep and were exposed to seasonal changes in temperature and salinity (Tables 1, 6). The environment is seasonally variable with regard to temperature in Connecticut, salinity in Florida, and both in New Jersey. Field observations suggest that in New Jersey, adult *Teredo bartschi* and *T. navalis* rarely live more than 18 months. *Bankia gouldi* often lives a full 2 years or longer. Specimens of *T. bartschi* have been found brooding larvae only 4 weeks after they have come in contact with wood, while the other two New Jersey species live in the wood for a minimum of 5 weeks before reaching maturity

TABLE 6. Comparative life history and ecology of seven species of Pholadacea.

	<i>T. bartschi</i> (N.J.)	<i>T. navalis</i> (N.J.)	<i>L. bipartitus</i> (Fla.)	<i>L. floridanus</i> (Fla.)	<i>B. fimbriatula</i> (Fla.)	<i>B. gouldi</i> (N.J.)	<i>M. striata</i> (Fla.)
Breeding season	May–Nov.	June–Oct.	All year	All year	Unknown	June–Aug.	Unknown
Eggs per reproductive event	10 ³ –10 ⁴	10 ⁴ –10 ⁵	10 ³ –10 ⁴	10 ⁴ –10 ⁵	10 ⁶ or more	10 ⁶ or more	10 ⁶ or more
Brooded larval stage (weeks)	3–4	about 2	3–4	about 2	0	0	0
Planktonic larval stage (weeks)	0	about 2	0	about 2	about 4	about 4	about 4
Pediveliger stage (days)	0–14	unknown	unknown	unknown	unknown	unknown	about 16
Year to year variation in population density per test panel							
Known species range	10 ³ Worldwide warm water	10 ² Worldwide cold water	10 ² W. Atlantic warm water	unknown W. Atlantic warm water	unknown Worldwide warm water	10 ² E. Coast N. & S. America temperate	unknown Worldwide warm water
Salinity tolerance ¹ (‰)	7–60	7–45 +	unknown	unknown	unknown	7–45 +	unknown
Temperature tolerance ¹ (°C)	11–35	0–30	unknown	unknown	unknown	0–30	unknown
Field temperatures (°C)	2–31 ²	0–31	12–33	16–31	14–31	0–31	14–31

¹Survival of more than 50% of 100 individuals after 10 days.

²When the power plant in Oyster Creek is not operating, the temperature can drop to 0°C.

as females. Some populations of *Teredo bartschi* and *Lyrodus bipartitus* are highly skewed toward individuals brooding young (as high as 90%). Sex ratios are close to 60% female in *B. gouldi*, *B. fimbriatula*, and *T. navalis*. Although most males are smaller than most females, the largest individuals of all species tend to be male. This fact coupled with the sex ratio bias towards females suggest that pholadaceans undergo alternating sexuality.

The life history characters of the subtropical larviparous species *Teredo bartschi* and *Lyrodus bipartitus*, including shorter generation time, more generations per year, and shorter lifespan, imply a higher population turnover rate than in the species with planktonic larval development. The potential for inbreeding is also greater in the larviparous species because the pediveliger young from one brood often settle together (and with the parents) on the same substratum (Turner & Johnson, 1971; Hoagland & Turner, 1981).

The histories of the two introduced populations of *Teredo bartschi* are quite distinct. The New Jersey population, founded in late 1973 or 1974, underwent a severe bottleneck in 1976 when the thermal effluent ceased temporarily during winter (Hoagland & Turner, 1980). After rebounding in 1978, another bottleneck and recovery occurred in 1980, when the thermal effluent was absent from January 5 to July 17. Fluctuations of the native *T. navalis* and *Bankia gouldi* were less severe, but the population of *B. gouldi* has been low (about 10 per panel) since the introduction of *T. bartschi*, compared with the 100 to 1,000 per panel in 1971–1973. The Connecticut population of *T. bartschi* has not suffered dramatic bottlenecks but has remained small (fewer than 10 per panel). The native Florida population of *T. bartschi* is patchy and unpredictable in time and space. A few specimens were collected in panels submerged in August, 1979, and retrieved in October, 1979, near Ft. Pierce, while panels submerged at the same locality in May, 1980, and retrieved in November, 1980, contained hundreds of specimens. Panels submerged less than a mile away contained no *T. bartschi*, and none were found in the Miami area. The distribution of *Lyrodus bipartitus* is more extensive and predictable; the species was found in abundance (200/panel) at both localities and in both years. *Bankia fimbriatula* was rare where it was collected, while *Martesia striata* was very common.

DISCUSSION

Patterns of genetic variation at the various enzyme loci

It is reasonable to ask whether methodology is relevant to the interpretation of genetic variation. Sequential electrophoresis and isoelectric focusing have revealed more genetic variation at some loci than simple starch-gel electrophoresis (Ramshaw *et al.*, 1979). However, there is no relationship between the amount of genetic variation uncovered by these newer techniques and the species (Hamrick *et al.*, 1979) or the biochemical function of the enzymes (Jones, 1980). No systematic bias is expected from using the starch-gel method.

The P values in Table 4 are similar to those summarized by Selander (1976) for marine invertebrates (0.587) and for all invertebrates (0.467). Selander's heterozygosity of 0.147 for marine invertebrates and 0.083 for marine snails compare well with the 0.096 for the 7 pholadacean species, excluding the 2 introduced populations.

Electrophoretic results obtained by Cole & Turner (1978) for pholadaceans are not directly comparable with the data reported here. Their H values were higher, and their P values inconsistent with mine. They analyzed a different set of enzymes for each species and obtained results across all 5 species for only 6 highly polymorphic loci of the 22 examined, accounting for their high H values. A similar explanation might account for the high average H value (0.367) calculated by Wilkins (1975) for 12 marine bivalves. Simon & Archie (1985) demonstrated the necessity of using the same enzymes in any comparison of H values across taxa. However, Archie (1985) also pointed out that certain statistical tests to detect differences in heterozygosity between samples are invalid when the same set of (non-random) loci are used. Generally, low values of $\bar{H}$ and loci fewer than 40 make statistical comparisons difficult.

The amount of genetic variation in the pholadaceans was found to differ in a characteristic way for particular genetic loci. The esterases, peptidases, GPI, PGM, LAP, and MPI were highly polymorphic, as has been found for many organisms (Hamrick *et al.*, 1979; Badino & Sella, 1980). Sarich (1977) claimed that the highly polymorphic enzymes accumulated substitutions at a rate ten times that of the less polymorphic enzymes. He

proposed that rapidly-substituting loci should be more polymorphic than slowly-substituting loci at any instant even if polymorphism is due to neutral allele substitutions. But natural selection on individual enzymes could be responsible for maintaining polymorphism in enzymes whose substrates are variable (Gillespie & Langley, 1974), or in enzymes that participate in regulatory reactions (Johnson, 1976).

The heterozygote deficiencies in Table 3 are large. They show no relationship with species-specific life history patterns or the metabolic functions of the enzymes. The lack of heterozygotes at two loci in the Millstone population of *Teredo bartschi* could be due to separate introductions, or simply to small sample size. No species shows a pattern of complete absence of heterozygotes, decreasing the possibility that obligate self-fertilization or parthenogenesis occurs (Selander & Hudson, 1976). No marine bivalves are known to undergo parthenogenesis. In shipworms, plenty of male gametes are present in all populations studied. Circumstantial evidence for self-fertilization has been reported in shipworms (Eckelbarger & Reish, 1972).

Large heterozygote deficiencies have been reported for numerous marine invertebrates, including bivalves. Zouros & Foltz (1984) reviewed the literature and mathematically analyzed the relationship of differential selection in different parts of the life cycle and differential reproduction of heterozygote individuals to heterozygote deficiency. They concluded that, to achieve levels of heterozygote deficiency reported in the literature, selection differentials would have to be very high. Beaumont (1982) and others have suggested a combination of factors could be operating, including inbreeding, selection on juvenile stages, and a Wahlund Effect, although in lab experiments Beaumont *et al.* (1983) implicated selection alone. Inbreeding alone cannot explain the heterozygote deficiencies seen for teredinids, because within a population some loci lack heterozygotes while others are in Hardy-Weinberg equilibrium.

Population subdivision models of heterozygote deficiency have been suggested by Tracey *et al.* (1975). Because many marine populations with large heterozygote deficiency are founded by pelagic larvae, they proposed temporary subpopulations and fine-scale patchiness to explain the genetic structure. Johnson & Black (1984), studying a limpet with planktonic development, sug-

gested that heterozygote deficiency at all 7 loci was due not to temporal variation, but to binomial sampling variance among small local breeding groups plus mixing of larvae on a local scale.

In teredinids, species both with and without planktonic larval dispersal show heterozygote deficiency. Temporal and small-scale local genetic variation could be important for all species of teredinids. Shipworm larvae can travel within an estuary or along a coastline before settlement. It is likely that even pediveligers move far enough to encounter temperature and salinity regimes, with concomitant changes in food and predators, different from those of the parents. But adults also disperse in small groups within driftwood or boats. The extent of the Wahlund Effect may depend upon the life history characteristics of the species, but it could operate in all species.

The presence of null alleles is a possible explanation of heterozygote deficiency, one that is difficult to verify without breeding experiments. Thus, natural selection, null alleles, inbreeding, sampling error, and Wahlund Effects can all contribute to heterozygote deficiency; the values in Table 3 suggest that more than one factor is involved. Mis-identification of specimens can lead to artificially high heterozygote deficiencies if there are loci with fixed alternate alleles in the confounded species. The only species that was difficult to identify was *Lyrodus floridanus*, which is easily confused with *L. pedicellatus* when not brooding young. Since many animals were brooding, and no specimens of *L. pedicellatus* were identified in the material, it is unlikely that those species were confused. Morphologically similar species have been identified electrophoretically; in fact I have found undescribed species of *Crepidula* via electrophoretic analysis (Hoagland, 1984a). In such cases, certain specimens show a consistent pattern; they are fixed for alternate alleles at one or more loci. This situation has not been found in the data set reported upon here.

Correlation of genetic variation with life history and other possible factors

Comparing the genetic variation (Table 4) with life history (Table 6), an imperfect but suggestive trend of greater genetic variation with longer larval life in the plankton can be seen (Fig. 1). If means are calculated sepa-

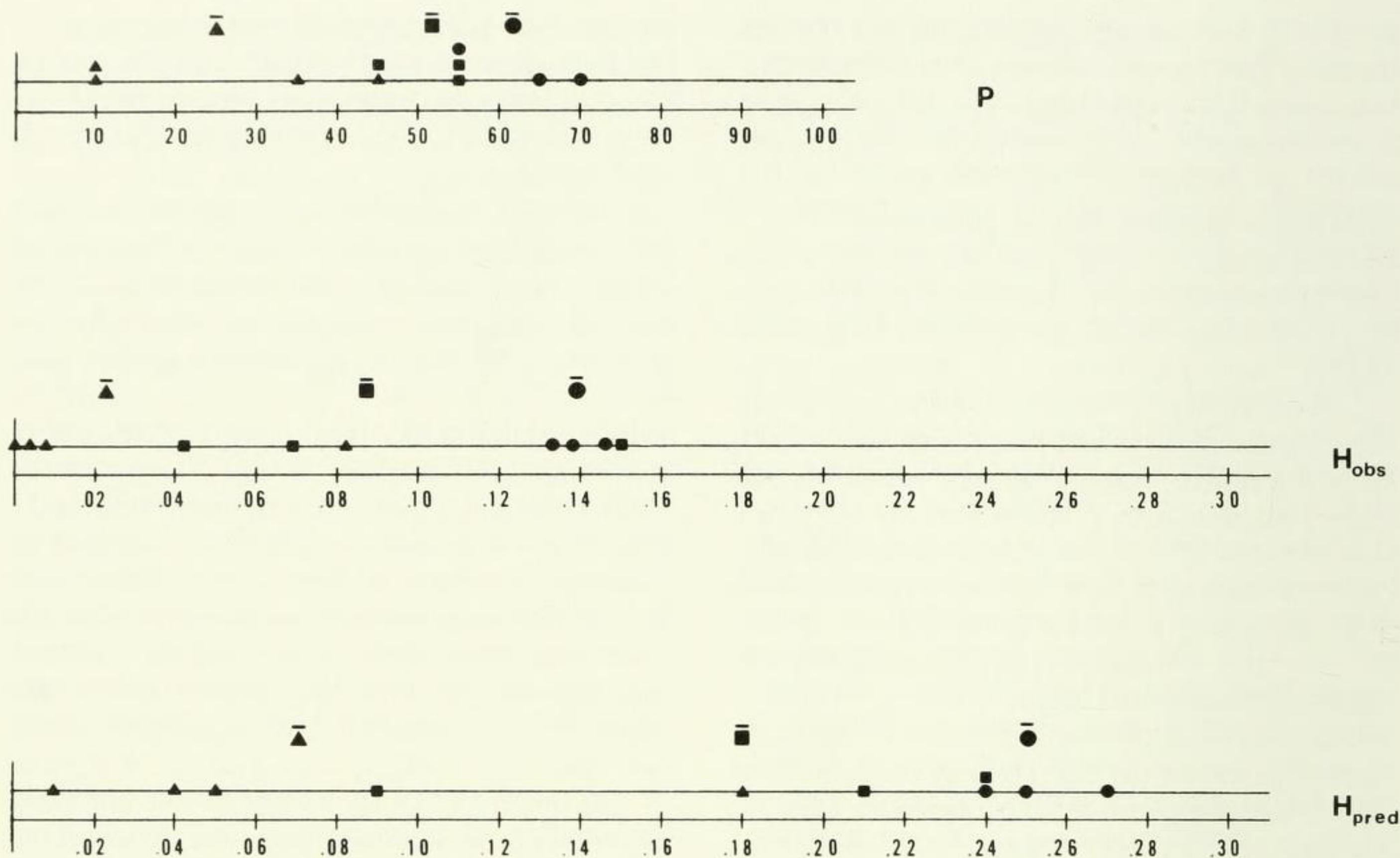


FIG. 1. The values of predicted heterozygosity (H_{pred}), observed heterozygosity (H_{obs}) and percent polymorphic loci (P) for populations of species with the three types of larval development. Δ = brooded development, release of pediveliger. $\bullet$ = planktonic development, release of eggs and sperm. $\blacksquare$ = mixed brooded and planktonic development, release of straight-hinge larvae. The original data are in Table 4. Averages of data for each larval type are indicated by the symbols with bars above.

rately for the introduced populations, the natural populations of larviparous species, the populations with mixed development, and those with pure planktonic development, these life history categories representing increasing opportunity for dispersal and outbreeding fall in the order of increasing heterozygosity (Table 7). The data suggest that the level of heterozygosity and genetic polymorphism in general may be related to life history characteristics. If so, this could be an example of population structure influencing the level of polymorphism.

Battaglia *et al.* (1978), working with six species of crustaceans, also found that some oviparous species had higher heterozygosities than a brooded species. Unfortunately, information on the type of larval development was not given for all six species. Nevo *et al.* (1984) and Snyder & Gooch (1973) reported a correlation between species heterozygosity and dispersal. Hamrick *et al.* (1979) noticed higher variation in widespread outcrossing and wind-pollinated plants, relative to regionally-distributed plants. They also found that fecundity was positively correlated with

genetic variation. Fecundity is positively correlated with both the length of planktonic life and heterozygosity in Pholadacea (Table 6). Lavie & Nevo (1986) attributed higher heterozygosity in *Cerithium scabridum* than in *C. rupestre* to greater niche-width in the former species due to its high intertidal position. However, *C. scabridum* also has higher fecundity, correlated with planktonic larvae lacking in *C. rupestre*. Dispersal rather than niche-width at any one locality might be responsible for the high heterozygosity of populations of *C. scabridum*.

Soulé (1976) suggested that life cycle heterogeneity should be reflected in high genetic variation. If so, planktonic developers should have higher genetic variability than brooders, and this is so. But we might also expect the species with mixed brooded-planktonic development like *Teredo navalis* to have the highest genetic variation; this is not so.

Animals with pelagic larvae are expected to have similar gene frequencies throughout their ranges (Soulé, 1976), yet I found considerable genetic distance between two populations of *T. navalis* (Table 5). Perhaps it is

TABLE 7. Pholadacea. Heterozygosity values averaged over populations with the same type of larval development. Number of populations in parentheses. Data from Table 6.

	H observed	H predicted	P	A
Introduced brooders (2)	.002	.025	10	1.15
Brooders, natural populations (2)	.045	.115	40	2.08
Mixed strategy (3)	.087	.180	52	1.95
Planktotrophic species (3)	.139	.253	63	2.20

due to the patchy distribution of wood substratum in the Northwestern Atlantic, which effectively isolates populations despite the pelagic larvae. Burton (1983) also made the point that substantial genetic differentiation has been observed between populations of marine invertebrates supposed to have high dispersal capabilities.

The proximal cause of greater intrapopulation genetic diversity in populations of species with planktonic larvae has been cited as the larger gene pool (Selander, 1976). The data for pholadaceans are in agreement. The smaller population size of *Bankia fimbriatula* may explain its lower genetic variation compared with *B. gouldi*. Fuller & Lester (1980) showed that heterozygosity was proportional to effective population size as well as to the potential for immigration; Motro & Thomson (1982) showed a large effect of repeated bottlenecks on level of heterozygosity. The high percentage of animals brooding eggs in some populations suggests that *Teredo bartschi* might be a simultaneous hermaphrodite, which would influence the effective population size. Richards *et al.* (1980) found hermaphrodite gonads in a large percentage of *T. bartschi*, unlike *Bankia gouldi* and *T. navalis*, which are usually either male or female. Even if selfing is rare and alternating sexuality is the rule as in *T. navalis* and *B. gouldi* (Hoagland, 1984b), the population structure of *T. bartschi* in which offspring (males) settle on the same wood as parents (females) leads to inbreeding. Dispersal of adults in wood does occur regularly, but large groups of closely-related individuals move together in the same piece of wood. Pediveligers of *T. bartschi* are capable of swimming and crawling before metamorphosis, but field studies in Barnegat Bay indicate that most settle near the parents.

The pholadacean data show that species with brooded development such as *Teredo bartschi* can be widely distributed and have low genetic variability within and between

populations yet have isolation of populations and high potential for inbreeding, compared with the planktonic developers. Similarly, Davis *et al.* (1981) found that some widespread, phenotypically uniform species of freshwater mussels (Unionidae) have low genetic variation within and between isolated populations. Selander & Kaufman (1975) and Selander & Hudson (1976) found monomorphism yet good colonization ability in the widespread introduced self-fertilizing land snail *Rumina decollata*; McCracken & Selander (1980) found the same pattern in selfing populations of introduced slugs.

Teredo bartschi fits the "general purpose genotype" model of Selander & Hudson (1976) for species with broad physiological tolerances despite reduced genetic variability. There are no differences in breadth of tolerance in the 10 populations of shipworms that can be related to levels of genetic variation. *T. bartschi* of New Jersey has as broad a tolerance for temperature and salinity as the Florida population (Hoagland, 1986).

There is no detectable relationship between the level of genetic variation and latitude of the pholadacean populations. The three sympatric species of New Jersey differed much more in levels of genetic variation than did the congeners *Bankia gouldi* and *B. fimbriatula*, which are temperate and tropical respectively, but which have similar patterns of larval development and dispersal. Redfield *et al.* (1980) also found no correlation between latitude and genetic variation.

Nelson and Hedgecock (1980) implicated a heterogeneous diet in levels of enzyme heterozygosity. No differences in diet or parasite infection are known that correlate with enzyme polymorphism in the Pholadacea. The anatomical data for the six Teredinidae of this study (Turner, 1966) reveal a similarity in the size of the gill versus the caecum compared with some other teredinid genera, suggesting a similar diet.

Populations introduced in thermal effluents

Nevo *et al.* (1977) found lower heterozygosity for barnacles in a thermal effluent than at a control station. Such a trend is not evident in my data except as due to founder effects and bottlenecking (Table 7). *Teredo navalis* from a thermal effluent actually had a higher heterozygosity than a population from just outside such an effluent (Table 4). There is some evidence that enzymes such as α GPDH in invertebrates have greater variability in thermally variable environments (Johnson, 1976). The thermal effluent of a nuclear power plant is actually a variable environment because of frequent plant outages. Genetic similarity of the introduced populations of *T. bartschi* (Table 5) could confirm the identity of the species but not the pathway of introduction. It is quite likely that the introductions were independently derived from the Floridian or other natural populations.

CONCLUSION

The ecological requirements of the pholadaceans of this study are similar. All face a temporally unstable environment over more than one generation. Some species show high polymorphism within populations, while others are nearly monomorphic as determined by electrophoresis of enzymes. The sympatry of some of the species with differing levels of population heterozygosity is due in part to factors other than the physical environment. The degree of genetic variability is related to the breeding structure and type of larval development and dispersal of the species. Species of Pholadacea with completely planktonic larval development have higher genetic variability, higher fecundity, more constant population size, and probably more outbreeding than do larviparous species. Larviparous species are more likely to be monomorphic through inbreeding and local bottlenecks; their distribution is patchy. I hypothesize that constraints of life history and population structure affect the genetic structure (i.e., level of polymorphism) of populations.

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Locus	Allele	Populations									
		<i>T.b.</i> N.J.	<i>T.b.</i> Conn.	<i>T.b.</i> Fla.	<i>T.n.</i> N.J.	<i>T.n.</i> Conn.	<i>L.f.</i> Miami	<i>L.b.</i> Ft. Pierce	<i>B.g.</i> N.J.	<i>B.f.</i> Fla.	<i>M.s.</i> Fla.
AcPh	98	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	100	1.00	1.00	1.00	0.00	1.00	0.00	0.09	1.00	0.00	1.00
	103	0.00	0.00	0.00	0.00	0.00	1.00	0.91	0.00	1.00	0.00
AO I	85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	97	0.00	0.42	0.00	0.00	0.73	0.43	0.00	0.29	0.00	0.00
	100	1.00	0.58	1.00	1.00	0.27	0.57	0.82	0.71	0.85	0.00
	102	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.15	0.00
AAT	78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
	80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22
	82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.70
	93	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.86	0.05	0.00
	95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.69	0.00
	97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00
	99	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	100	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00
EST NA I	93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98
	95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	98	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100	0.96	1.00	0.98	0.96	0.50	0.96	1.00	0.16	0.00	0.00
	102	0.02	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
	103	0.00	0.00	0.00	0.04	0.00	0.04	0.00	0.84	1.00	0.00
	104	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
EST NA II	98	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.68
	100	0.96	0.13	0.00	0.00	0.00	0.00	0.90	0.74	1.00	0.32
	101	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	102	0.04	0.79	1.00	0.84	0.45	0.04	0.05	0.26	0.00	0.00
	103	0.00	0.00	0.00	0.08	0.00	0.96	0.00	0.00	0.00	0.00
	105	0.00	0.00	0.00	0.08	0.55	0.00	0.00	0.00	0.00	0.00
GPI I	100	1.00	1.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	102	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.05
	103	0.00	0.00	0.53	0.00	0.00	0.00	0.63	0.00	0.00	0.00
	105	0.00	0.00	0.00	0.51	0.19	0.20	0.37	0.57	0.70	0.50
	107	0.00	0.00	0.00	0.34	0.74	0.76	0.00	0.02	0.00	0.35
	109	0.00	0.00	0							

Locus	Allele	Populations									
		<i>T.b.</i> N.J.	<i>T.b.</i> Conn.	<i>T.b.</i> Fla.	<i>T.n.</i> N.J.	<i>T.n.</i> Conn.	<i>L.f.</i> Miami	<i>L.b.</i> Ft. Pierce	<i>B.g.</i> N.J.	<i>B.f.</i> Fla.	<i>M.s.</i> Fla.
LDH	96	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	0.00	0.00	1.00	0.00	0.00	0.25	0.00
	101	0.00	0.00	0.00	1.00	1.00	0.00	0.00	1.00	0.75	0.00
LAP	96	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.07	0.00	0.00
	99	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00
	100	1.00	0.00	0.09	0.64	0.34	0.00	0.00	0.51	0.56	0.00
	101	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00
	102	0.00	1.00	0.00	0.10	0.15	0.02	0.28	0.26	0.44	0.13
	103	0.00	0.00	0.91	0.00	0.01	0.00	0.00	0.00	0.00	0.00
	104	0.00	0.00	0.00	0.12	0.48	0.98	0.50	0.16	0.00	0.00
	105	0.00	0.00	0.00	0.04	0.01	0.00	0.09	0.00	0.00	0.28
	106	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
	108	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
MPI	92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.15	0.00
	94	0.00	0.00	0.00	0.19	0.02	0.70	0.36	0.66	0.65	0.00
	96	0.00	0.00	0.00	0.25	0.73	0.00	0.08	0.14	0.00	0.00
	98	0.00	0.00	0.00	0.45	0.25	0.23	0.38	0.11	0.20	0.11
	100	1.00	1.00	0.98	0.11	0.00	0.07	0.18	0.00	0.00	0.16
	102	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.73
MDH I	95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00
	97	0.00	0.00	0.00	1.00	1.00	0.00	0.03	0.00	0.00	0.00
	100	1.00	1.00	1.00	0.00	0.00	1.00	0.00	0.02	1.00	0.00
	101	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	103	0.00	0.00	0.00	0.00	0.00	0.00	0.91	0.00	0.00	0.00
	104	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98
	105	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00
	109	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Pep G II	98	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100	1.00	1.00	0.96	0.25	0.36	0.00	0.00	0.03	0.21	0.00
	103	0.00	0.00	0.00	0.00	0.02	0.00	0.08	0.50	0.69	0.54
	105	0.00	0.00	0.00	0.00	0.58	1.00	0.82	0.16	0.06	0.28
	106	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00
	107	0.00	0.00	0.00	0.75	0.04	0.00	0.00	0.31	0.04	0.12
	109										

APPENDIX (Continued)

Locus	Allele	Populations									
		<i>T.b.</i> N.J.	<i>T.b.</i> Conn.	<i>T.b.</i> Fla.	<i>T.n.</i> N.J.	<i>T.n.</i> Conn.	<i>L.f.</i> Miami	<i>L.b.</i> Ft. Pierce	<i>B.g.</i> N.J.	<i>B.f.</i> Fla.	<i>M.s.</i> Fla.
6-PGD	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.92
	101	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
	105	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
SoDH	94	0.00	0.00	0.00	0.86	1.00	0.06	1.00	0.03	1.00	0.00
	98	0.00	0.00	0.00	0.14	0.00	0.94	0.00	0.83	0.00	0.80
	100	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.14	0.00	0.20
SOD I	95	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00
	100	1.00	1.00	0.98	0.00	0.00	1.00	1.00	0.96	1.00	0.00
	102	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.04	0.00	1.00
	106	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
XDH	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Revised Ms. accepted 10 April 1986