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T. F. Duda, Jr.

Genetic population structure of the recently introduced Asian clam, *Potamocorbula amurensis*, in San Francisco Bay

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Abstract The genetic population structure of the recently introduced Asian clam, *Potamocorbula amurensis*, in San Francisco Bay was described using starch gel electrophoresis at eight presumptive loci. Specimens were taken from five environmentally distinct sites located throughout the bay. The population maintains a high degree of genetic variation, with a mean heterozygosity of 0.295, a mean polymorphism of 0.75, and an average of 3.70 alleles per locus. The population is genetically homogeneous, as evidenced from genetic distance values and *F*-statistics. However, heterogeneity of populations was indicated from a contingency chi-square test. Significant deviations from Hardy-Weinberg equilibrium and heterozygote deficiencies were found at the *Lap-1* locus for all populations and at the *Lap-2* locus for a single population. High levels of variability could represent a universal characteristic of invading species, the levels of variability in the source population(s), and/or the dynamics of the introduction. Lack of differentiation between subpopulations may be due to the immaturity of the San Francisco Bay population, the "general purpose" phenotype genetic strategy of the species, high rates of gene flow in the population, and/or the selective neutrality of the loci investigated.

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T. F. Duda, Jr. (✉)
Department of Biology,
San Francisco State University,
1600 Holloway Avenue,
San Francisco,
California 94132, USA, and

U.S. Department of the Interior,
Geological Survey,
Water Resources Division,
345 Middlefield Road (Ms-496),
Menlo Park,
California 94025, USA

Present address: Zoology Department, University of Hawaii, Pacific Biomedical Research Center, Kewalo Marine Laboratory, 41 Ahui Street, Honolulu, Hawaii 96813, USA

Introduction

Information concerning the genetics of invading populations during initial periods of invasion is lacking (Barrett and Richardson 1986). A description of the genetics of a successfully introduced species is pertinent to a more complete understanding of not only the dynamics of the invasion and colonization events, but also of evolutionary concepts, such as founder effects, genetic differentiation, gene flow, genetic drift, mutation, and speciation (Woodruff et al. 1986). Speculation may yield information on a few of these issues; however, most are beyond the scope of a single investigation. This study examined the genetic population structure of the recently introduced Asian clam, *Potamocorbula amurensis*, following its successful invasion and colonization of San Francisco Bay, to allow an analysis of the dynamics of its introduction, comparison of levels of diversity with other successful invading species, insight into the genetic strategy of the population, perception of possible rates of gene flow in the population, and a basis for future genetic work on this species/population.

Potamocorbula amurensis was first discovered in San Francisco Bay in late 1986. It apparently became established in Grizzly and Suisun Bays (see Fig. 1) as a result of the release of *P. amurensis* larvae transported in the ballast water of ship(s) from Asia (Carlton et al. 1990). Within the next year, the range and abundance of the species greatly increased. The species in San Francisco Bay is quite eurytopic, occurring in a wide range of salinities, temperatures, and substrates and in both subtidal and intertidal zones (Carlton et al. 1990). It is also strictly dioecious, with gametogenesis occurring throughout the year for populations in South Bay, and twice a year, in the spring and fall, for northern populations from Suisun Bay [F. Parchaso, U.S. Geological Survey (USGS), personal communication]. Specimens were not immediately observed in South Bay (Fig. 1) until the middle of 1987 (Carlton et al. 1990). It is possible that the southern population originated from a second introduction. Having regard to the differences in the timing of gametogenesis and initial appearances of

specimens in the northern and southern regions, the populations from Suisun and South Bay may represent different genetic stocks. However, these differences may also be attributable to the physical differences between the locations and dynamics of a single introduction.

The purpose of this study was threefold: (1) to measure the degree of genetic variation of *Potamocorbula amurensis*, (2) to determine whether genetic differentiation occurs on a limited geographic scale, and (3) to describe the genetic population structure of the species in San Francisco Bay during the early phases of its colonization.

Materials and methods

During January and early February of 1992, a minimum of 100 specimens of *Potamocorbula amurensis* was collected from each of five locations in San Francisco Bay. These sites comprised a subtidal site in the upper reaches of Suisan Bay (USGS Station 4.1), a subtidal site (USGS Station 8.1) and an intertidal site (M1) in the lower reaches of Suisun Bay, and two subtidal sites in South Bay (USGS Stations SM47 and D3) (Fig. 1). Subtidal specimens were collected aboard the USGS R.V. "Polaris" using a 0.1 m^2 Van Veen grab. Intertidal specimens were collected by hand from the upper surface of the mudflat at low tide.

Site 4.1 is in the middle of the shipping channel in Suisun Bay; the sediment at this site is typically sand; salinity in 1991 ranged from 0 to 13‰. Site 8.1 is in the shipping channel at the western end of Suisun Bay; sediment at this site ranges from sand to mud; salinity at 8.1 in 1991 ranged from 12 to 24‰. Site M1 is located on the mudflats within 1 km of Site 8.1 and has sediments of sandy mud. Site SM47 is located in the South Bay offshore from Redwood City; the sediment at this site is typically mud; in 1991 salinity ranged from 25 to 32‰. Site D3 is at the southern extreme of South Bay near Coyote Creek; the sediment at this site is also mud; salinity in July 1992 was 26‰. Ancillary data for 4.1, 8.1, and SM47 were taken at Sites 4.0, 8.0 and 32 (USGS physical data collection-sites in close proximity to the sites used for benthic collection), respectively (Wienke et al. 1992).

The procedure for starch-gel electrophoresis was adapted from Schaal and Anderson (1974), Richardson et al. (1986), Pasteur et al. (1988), and Hillis and Moritz (1990). Eight proteins (encoded by a total of 13 presumptive loci) were stained: adenylate kinase (ADK), glucosephosphate isomerase (GPI), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucomutase (PGM), 6-phosphogluconic dehydrogenase (6-PGD), and a peptidase (leucylglycylglycine, LGG). The enzymes and the buffer systems used were found to give readable results in preliminary investigations.

Genetic statistics were calculated using the BIOSYS-1 program (Swofford and Selander 1981). A locus was considered polymorphic if the most common allele was present with a frequency of < 0.95. Heterozygosity values were calculated by direct count and using an unbiased estimate (Nei 1978). Genotype frequency fit to Hard-Weinberg equilibrium was determined using chi-square tests with and without pooling [with Levene's (1949) correction of expected genotypic frequencies, Yates' (1934) correction for small sample size, and the Bonferroni technique (Lessios 1992)] and using exact probabilities. Nei's (1978) unbiased genetic identities and distances were computed. Distance values were also tested for being significantly equal to zero using Nei's (1987) test of significance. A contingency chi-square test was conducted to test for heterogeneity of populations. For the loci that show significant heterogeneity, a randomization test was conducted using a variation of the technique for data randomization suggested by Roff and Bentzen (1989). *F*-statistics were calculated.

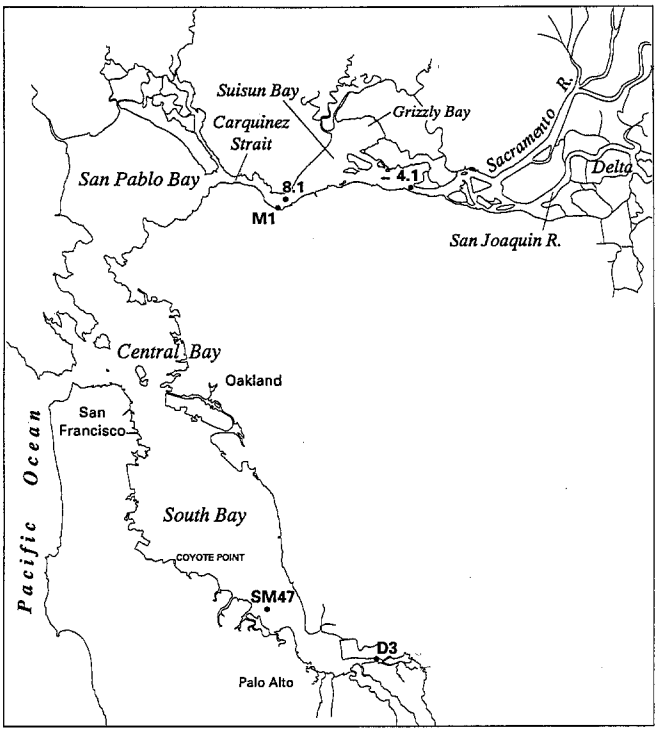

Fig. 1 San Francisco Bay, showing locations of sites used (Site 4.1: 38°03′06″N, 121°52′31″W; Site 8.1: 38°01′54″N, 122°08′24″W; Site M1: 38°01′33″N, 122°09′28″W; Site SM47: 37°31′36″N, 122°09′08″W; Site D3; 37°27′48″N, 122°01′40″W). (Map courtesy of D. Jones, USGS)

Results

Six of the eight proteins investigated in *Potamocorbula amurensis* could be reliably scored: GPI, LAP, MDH, ME, PGM, and 6-PGD. ADK and LGG showed activity but the observed banding patterns could not be interpreted. From the six proteins, nine presumptive loci were inferred: *Gpi, Lap-1, Lap-2, Mdh-1, Mdh-2, Me-1, Me-2, Pgm*, and *6-Pgd. Mdh-1* was unacceptable for use in analysis of population structure due to an unexplainable excess of heterozygotes at this locus. The large homozygote deficiency at this locus was considered too great to be encountered by an assumed non-selfing species in which none of the other loci displayed such a deficiency. It is likely that this locus was either misinterpreted when scored or is subject to post-translational modifications. *Mdh-2* and *Me-1* were monomorphic; the remaining six loci were all polymorphic. Protein structures were similar to those reported in Pasteur et al. (1988).

Allele-frequencies are presented in Table 1. As a whole, the populations from San Francisco Bay had 3.70 (standard deviation=0.19) alleles per locus. Each population was polymorphic at 75.0% of the loci examined (Table 1). The average unbiased expected heterozygosity (H_u) was 0.372 (SE=0.004). By direct count, the average heterozygosity was 0.295 (SE=0.005) (Table 1).

Chi-square tests for Hardy-Weinberg equilibrium indicated significant deviation from Hardy-Weinberg expecta-

Table 1 *Potamocorbula amurensis.* Allelic frequencies and heterozygote deficiencies in San Francisco Bay. (*N*): sample size; *H*: observed number of heterozygotes; H_e: expected number of heterozygotes; D: $(H_0 - H_e)/H_e$; *: significant deviation form Hardy-Weinberg expectations, H_{dc}: mean direct-count heterozygosity; H_u: mean unbiased heterozygosity; P: proportion of polymorphic loci; A/L: mean number of alleles per locus

Locus	Population (Site No.)				
	4.1	8.1	M1	SM47	D3
Gpi (*N*)	(99)	(100)	(100)	(100)	(100)
A	0.040	0.065	0.060	0.065	0.055
B	0.010	0.015	0.030	0.045	0.025
C	0.364	0.425	0.315	0.380	0.415
D	0.056	0.040	0.065	0.075	0.055
E	0.096	0.055	0.075	0.080	0.060
F	0.424	0.385	0.395	0.345	0.370
G	0.010	0.015	0.060	0.010	0.020
H_0	70	63	63	73	72
H_e	66.692	66.185	72.680	71.820	68.020
D	0.050	–0.048	–0.133	0.016	0.059
Lap-1 (*N*)	(77)	(77)	(87)	(84)	(89)
A	0.227	0.286	0.086	0.161	0.073
B	0.565	0.455	0.483	0.494	0.573
C	0.110	0.227	0.241	0.256	0.174
D	0.084	0.019	0.103	0.077	0.140
E	0.013	0.013	0.075	0.000	0.039
F	0.000	0.000	0.011	0.012	0.000
H_0	28*	24*	28*	23*	32*
H_e	46.928	50.786	59.580	55.310	54.708
D	–0.404	–0.527	–0.530	–0.584	–0.415
Lap-2 (*N*)	(92)	(95)	M1	SM47	D3
A	0.000	0.000	0.005	0.010	0.020
B	0.174	0.132	0.153	0.128	0.140
C	0.723	0.784	0.745	0.801	0.754
D	0.103	0.084	0.097	0.061	0.095
H_0	29	18*	30	26	32
H_e	40.168	34.258	40.610	33.148	41.595
D	–0.278	–0.475	–0.261	–0.216	–0.231
Mdh-2 (*N*)	(100)	(100)	(100)	(100)	(100)
A	1.000	1.000	1.000	1.000	1.000
Me-1 (*N*)	(100)	(100)	(100)	(100)	(100)
A	1.000	1.000	1.000	1.000	1.000
Me-2 (*N*)	(96)	(96)	(98)	(79)	(99)
A	0.255	0.313	0.199	0.494	0.697
B	0.745	0.688	0.801	0.506	0.697
H_0	41	44	29	30	19
H_e	36.495	41.250	31.240	39.494	41.818
D	0.123	0.067	–0.072	–0.240	–0.235
Pgm (*N*)	(96)	(98)	(100)	(98)	(100)
A	0.005	0.000	0.040	0.041	0.035
B	0.115	0.092	0.135	0.077	0.090
C	0.630	0.673	0.530	0.622	0.600
D	0.156	0.148	0.185	0.163	0.160
E	0.089	0.056	0.065	0.071	0.075
F	0.000	0.020	0.025	0.020	0.025
H_0	43	47	53	48	50
H_e	53.510	50.219	65.980	56.138	59.860
D	–0.196	–0.064	–0.197	–0.145	–0.165
6-Pgd (*N*)	(95)	(90)	(83)	(81)	(93)
A	0.0.26	0.039	0.054	0.025	0.022
B	0.053	0.067	0.030	0.031	0.048
C	0.874	0.822	0.861	0.901	0.892
D	0.047	0.072	0.054	0.043	0.038
H_0	21	25	16	15	19
H_e	21.942	28.150	20.843	14.932	18.532
D	–0.043	–0.112	–0.232	–0.005	–0.025
Mean					
H_{dc}	0.310	0.293	0.281	0.290	0.303
H_u	0.363	0.369	0.384	0.374	0.368
P	0.750	0.750	0.750	0.750	0.750
A/L	3.5	3.5	3.9	3.8	3.8

Table 2 *Potamocorbula amurensis.* Nei's (1978) unbiased genetic identities (above diagonal) and distances (below diagonal) of populations in San Francisco Bay

	4.1	8.1	M1	SM47	D3	Mean
4.1		0.9971	0.9956	0.9865	0.9982	0.9943
8.1	0.0029		0.9909	0.9925	0.9938	0.9936
M1	0.0044	0.0092		0.9816	0.9972	0.9913
SM47	0.0136	0.0075	0.0186		0.9924	0.9882
D3	0.0018	0.0063	0.0028	0.0076		0.9954
Mean	0.0057	0.0065	0.0088	0.0118	0.0046	

tions at *Lap-1* for all populations and at *Lap-2* for the population from Site 8.1. The large heterozygote deficiencies at these loci for these populations probably accounted for the deviations (Table 1).

Nei's (1978) unbiased genetic identity and distance values were computed to determine the degree of genetic differentiation among populations (Table 2). Values for genetic distance ranged from 0.0018 to 0.0186. Only two of the distance values were not significantly different from zero: 4.1–8.1 and D3–M1.

Genetic differentiation was also investigated with contingency chi-square analysis (Table 3). Over all loci, there are significant differences between populations ($P<0.001$). However, *Lap-1* and *Me-2* are the only loci where significant differences exist. The total chi-square value is considerably inflated by the chi-square values estimated for these loci; if *Lap-1* and *Me-2* are not included in the analysis, the total chi-square value is not significant ($P>0.05$). Randomization tests for both loci were significant with 17/1000 ($p=0.017$) and 7/1000 ($p=0.007$) randomizations showing chi-square values greater than that from the original data set for *Lap-1* and *Me-2*, respectively.

F-statistics are presented in Table 4. The mean F_{ST}, an estimate of the degree of genetic differentiation between the populations, was 0.014. The largest F_{ST} values were calculated for *Lap-1* (0.021) and *Me-2* (0.046).

Discussion

Potamocorbula amurensis populations in San Francisco Bay are characterized by (1) high variability within populations, (2) low variation among populations, and (3) deviation from Hardy-Weinberg equilibrium resulting from heterozygote deficiencies at the *Lap-1* locus in all populations and at the *Lap-2* locus for the population at Site 8.1

Table 3 *Potamocorbula amurensis*. Contingency chi-square analysis for heterogeneity of populations in San Francisco Bay

Locus	No. of alleles	Chi-square	*df*	*P*
Gpi	7	33.923	24	0.08604
Lap-1	6	89.412	20	0.00000
Lap-2	4	12.830	12	0.38155
Me-2	2	39.185	4	0.00000
Pgm	7	30.580	24	0.16628
6-Pgd	4	10.677	12	0.55682
Totals		216.606	96	0.00000

Table 4 *Potamocorbula amurensis*. Summary of *F*-statistics at all loci for populations in San Francisco Bay. F_{IS}: genetic variance within populations; F_{IT}: genetic deviation in total population (whole set of samples); F_{ST}: deviations due to differences in gene frequencies between populations

Locus	F_{IS}	F_{IT}	F_{st}
Gpi	0.013	0.017	0.005
Lap-1	0.495	0.505	0.021
Lap-2	0.289	0.292	0.003
Me-2	0.081	0.123	0.046
Pgm	0.156	0.161	0.006
6-Pgd	0.083	0.087	0.005
Mean	0.198	0.209	0.014

Mean genetic-diversity values for *Potamocorbula amurensis* are at the upper extreme for molluscs (Table 5). The values are also comparable with those of recently introduced populations of *Dreissena polymorpha* from the Great Lakes (Hebert et al. 1989; Garton and Haag 1991; May and Marsden 1992; Boileau and Hebert 1993). Moreover, no consistent pattern exists regarding the degree of genetic variability in introduced populations of bivalves from San Francisco Bay (Table 5). *Macoma balthica*, suggested to have been introduced into the bay during the 19th century from the North Atlantic (Meehan et al. 1989), maintains levels of variability similar to those of *P. amurensis*. Yet the degree of variability of *Corbicula fluminea*, first observed in the bay in 1945 (Hanna 1966), is very low (McLeod 1986). The measures of diversity for the introduced populations of *M. balthica* and *C. fluminea* do not differ significantly from the levels of variability of the proposed source populations (Meehan et al. 1989; Kijviriya et al. 1991, Tsoi et al. 1991).

The high levels of genetic diversity of *Potamocorbula amurensis* in San Francisco Bay is a result of the introduction of a genetically diverse assortment of larvae. This may be due to (1) several independent introductions, (2) a single introduction that contained larvae from genetically distinct populations, or (3) an introduction from a source population that maintains a high degree of genetic variation. These hypotheses could be tested with a genetic survey of Asian populations.

Ehrlich (1986, 1989) suggested that high levels of genetic diversity should be possessed by successful invaders. The observed levels of variability in populations of *Potamocorbula amurensis* from San Francisco Bay support this hypothesis. However, the correlation of high levels of genetic diversity in invading species could also be explained by the assumption that a successfully invading species is widespread and gregarious in its native habitat (also two of Ehrlich's "successful invader" attributes) and thus may have a large effective population size in which

Table 5 Comparison of genetic variability data (standard deviations in parentheses) in populations of bivalves. nv: no values given; –: study only examined polymorphic loci. Abbreviations as in Table 1

Organism	H_{dc}	*P*	A/*L*	Source
46 mollusc species	0.148 (0.170)	0.468 (0.287)	nv	Nevo et al. (1984)
Dreissena polymorpha				
Lake St. Clair[a]	0.316	0.739	3.1	Hebert et al. (1989)
Put-in-Bay, Ohio[a]	0.307	–	3.43	Garton and Haag (1991)
The Great Lakes	0.347 (0.035)	–	2.58 (0.15)	May and Marsden (1992)
	0.464[b] (0.058)	–	2.75 (0.13)	Boileau and Hebert (1993)
Macoma balthica				
San Francisco Bay[a]	0.395[b]	0.818	4.4	Meehan et al. (1989)
Corbicula fluminea				
San Francisco Bay[a]	0.000	0.143	1.14	McLeod (1986)
Potamocorbula amurensis San Francisco Bay	0.295 (0.011)	0.750 (0.000)	3.80 (0.17)	Present study

[a] Values based on one population, therefore no standard deviations were computed
[b] Unbiased estimate (may be larger than direct count value, calculated from data in source article

high levels of variability could be expected (Kimura (1983).

As is the case with most plants and animals (Barrett and Richardson 1986), in molluscs there appears to be no clear relationship between genetic variability and the ability to colonize. Introduced populations of several species display relatively high levels of genetic diversity, including: *Biomphalaria straminea* (Woodruff et al. 1985), *Crepidula onyx* (Woodruff et al. 1986), *Dreissena polymorpha* (Hebert et al. 1989), *Macoma balthica* (Meehan et al. 1989), *Mytilus galloprovincialis* (Grant and Cherry 1985), and *Potamocorbula amurensis* (present study). However, low levels or significant reductions in genetic variability in introduced populations have been observed for several other species, including: *Achatina fulica* (Selander and Ochman 1983), *Cepaea nemoralis* (*Selander and Ochman 1983*), *Corbicula fluminea* (Smith et al. 1979; McLeod 1986), *Littorina saxatilis* (Knight et al. 1987), and *Theba pisana* (Johnson 1988). Ward (1989) suggested that the reduction in genetic variability from source to introduced populations may be due to the mode of reproduction of the species and not necessarily the number of initial colonists. That is, organisms which are capable of high rates of intrinsic growth (e.g. produce veliger larvae) would be more apt to recover from a bottleneck as opposed to organisms with low rates. This follows from Nei et al. (1975), who suggested that the reduction of genetic diversity in introduced populations is related to the number of colonizers and the population's growth rate. For the most part, the characteristics of the source population are also those of the introduced population [e.g. *Corbicula fluminea* (Kijviriya et al. 1991; Tsoi et al. 1991), *Crepidula onyx* (Woodruff et al. 1986), *Dreissena polymorpha* (Boileau and Hebert 1993), *Macoma balthica* (Meehan et al. 1989), and *Mytilus galloprovincialis* (Grant and Cherry 1985)].

The amount of genetic differentiation among *Potamocorbula amurensis* populations in San Francisco Bay is quite small and may be insignificant. Alleles with low frequencies were absent from some of the populations; however, since these alleles are rare in those populations in which they are present, it is probable that they would not be observed unless larger sample sizes were used. Genetic-distance values showed very little differentiation between populations. The largest genetic-distance value of 0.0182 is quite small and is within the expected range of distances between local races of a species (Nei 1987). Given the overall small distance-values, an estimate of the true relationships between the populations would be non-informative due to sampling error (Nei 1987). The degree of genetic differentiation among populations, as measured by F_{ST}, was also very low, as would be expected of undifferentiated populations. Values of F_{ST} between 0.05 and 0.15 indicate moderate differentiation (Hartl 1980), well over the mean value of 0.014 obtained for *P. amurensis*.

Contingency chi-square analysis, however, indicated heterogeneity of populations of *Potamocorbula amurensis*. The randomizations of the data for the loci that are responsible for the significance also support this. It is possible that some unknown factor (sampling error, misinterpretation of gels, selection at the locus) affecting these loci may be responsible for the significance of this test (see Paragraphs 10 and 11 of this section).

The genetic uniformity of *Potamocorbula amurensis* in San Francisco Bay, as indicated by genetic distance values and mean F_{ST}, is consistent with Mayr's (1965) observation that colonizing species are typically homogeneous during their initial period of invasion. *P. amurensis* has only been present in San Francisco Bay since 1986 and may still be in its primary phase of range expansion within the bay. Lack of differentiation between populations may exist because (1) the alleles from the examined loci (except possibly *Lap-1* and *Lap-2* as discussed later in this section) are selectively neutral and are only representative of the levels of diversity in the source population(s) and/or (2) similar gene frequencies between populations are indicative of a highly panmictic San Francisco Bay population. Although there is no information on the length of the planktonic larval phase for *P. amurensis*, if it is comparable to that of *P. laevis* in Asia (~5 wk; Wei 1984; Wei and Guan 1985, 1986; all cited by Carlton et al. 1990), then gene flow in San Francisco Bay could be very extensive.

The observed lack of genetic differentiation between populations of *Potamocorbula amurensis* in San Francisco Bay is comparable to the reported genetic homogeneity of *Dreissena polymorpha* in the Great Lakes (May and Marsden 1992). Preliminary studies also indicate the lack of genetic differentiation between populations of another dreissenid species recently discovered in the Great Lakes (J. E. Marsden, Illinois Natural History Survey, personal communication). This condition could be reflective of the genetic structure of populations of opportunistic species such as these. However, this hypothesis is weakened by the recent report of several unique allelic variants of *D. polymorpha* in the Great Lakes (Boileau and Hebert (1993).

Significant deviations from Hardy-Weinberg equilibrium occurred at the *Lap-1* locus for all populations and at the *Lap-2* locus for the population from Site 8.1 due to an excess of homozygotes. Excess homozygotes have been observed for several marine molluscs (see Volckaert and Zouros 1989). Numerous hypotheses have been developed to account for these observations; Gaffney et al. (1990) presented six of them: (1) molecular imprinting, (2) null alleles, (3) misinterpretation of gels, (4) aneuploidy, (5) selection, and (6) the Wahlund effect.

It is difficult to rule out any of these hypotheses without further genetic analysis. The effects of the first two hypotheses would probably be evident in all populations. However, since the populations at Sites 4.1, M1, SM47, and D3 were in Hardy-Weinberg equilibrium and did not display significant heterozygote deficiencies at *Lap-2*, it is unlikely that molecular imprinting is taking place or that null alleles occur at this locus. The Wahlund effect is also not probable as it would require a rather large variance of allelic frequencies between populations (Gaffney et al. 1990). The only apparent explanations left for the homozygote excesses and subsequently the deviations from Hardy-Weinberg equilibrium are scoring errors, selection at this locus against heterozygotes, and aneuploidy.

Since all populations at *Lap-1* display significantly large heterozygote deficiencies and the first five hypotheses are all probable, only the Wahlund effect is an unlikely cause (for reasons mentioned in the foregoing paragraph). However, as stated in Paragraph 7 of this section, heterogeneity of populations was also found, based on the contingency chi-square test, at this locus. Hilbish and Koehn (1985) identified a means by which *Lap* alleles were selected against in relation to salinity. It is possible (many further analyses would be necessary to prove this) that selection could be responsible not only for the heterozygote deficiencies but also for the heterogeneity of populations at this locus.

In conclusion, *Potamocorbula amurensis* displays remarkable genetic diversity in San Francisco Bay. This feature may be important to the ability to successfully invade, colonize, and reside in a variety of environments such as those present in San Francisco Bay. However, it may also simply reflect the levels of variation in the source population(s). Based on two out of three tests, no differentiation is apparent between populations throughout the bay, possibly indicating the continued initialization of the colonization event, the "general purpose" phenotype genetic strategy of the species, and/or high rates of gene flow in San Francisco Bay. Deviation from Hardy-Weinberg equilibrium and significant heterozygote deficiencies which occur at the *Lap-1* locus in all populations and the *Lap-2* locus in a subtidal population from the lower reaches of Suisun Bay may indicate scoring errors, selection, or aneuploidy in association with these loci. Future work on this species should involve the description of the genetic population structure of Asian populations and seasonal and more intense genetic examinations of the San Francisco Bay population.

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