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Genetics and shell morphology in a hybrid zone between the hard clams *Mercenaria mercenaria* and *M. campechiensis**

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Abstract

Populations of *Mercenaria mercenaria* (L.) from South Carolina, USA, and *M. campechiensis* (Gmelin) from the Gulf of Mexico, Florida, USA, were sampled in 1987. The two species differed at all of seven enzyme loci tested, as well as in the thickness of shell ridges and nacre color. The difference in lunule shape was not great, although differences in relative shell width, shell weight, and lunule size make morphometric discrimination between the species possible. Shell ridges, nacre color, and multivariate morphometrics in a sample of clams collected from the Indian River Lagoon on the Atlantic coast of Florida in 1985 do not assort independently. Individuals with thick ridges, white nacre, and/or *campechiensis*-like morphometrics have significantly different allele frequencies at most enzyme loci from individuals with thin ridges, purple nacre, and/or *mercenaria*-like morphometrics. The deviations are in the direction predicted from the analysis of the allopatric populations of *M. mercenaria* and *M. campechiensis*. *M. mercenaria* outnumber *M. campechiensis* in the Indian River sample, but the majority of the clams seem to be hybrids.

Introduction

Three criteria have traditionally been used to distinguish the northern hard clam, *Mercenaria mercenaria* (L.), from the southern, *M. campechiensis* (Gmelin) (Abbott 1974). *M. mercenaria* generally has some purple nacre, while *M. campechiensis* is generally pure white. The concentric ridges on the outside of shells of typical *M. mercenaria* are so thin that they often erode to leave smooth patches, while the ridges of *M. campechiensis* are thicker and generally do not erode completely. The lunule, a heart-shaped feature of the shell found anterior to the beaks, is supposed to be at least as wide as it is high in *M. campechiensis*, but narrower in *M. mercenaria*.

Although their ranges overlap broadly, only rarely are the two taxa truly sympatric (Menzel 1988). *Mercenaria mercenaria* occurs from Canada to the central Florida coast, with a subspecies, *M. mercenaria texana*, in the northern Gulf of Mexico. Throughout its range, *M. mercenaria* primarily inhabits shallow, estuarine areas, although it has been found to a depth of 15 m (Kerswill 1941). *M. campechiensis* is only common in shallow, estuarine waters on both coasts of southern Florida (excluding the extreme southern tip around the Keys), in Mexico, and perhaps elsewhere in the Caribbean Sea. It has been found, quite uncommonly, in deeper offshore waters as far north as Cape May, New Jersey (Merrill and Ropes 1967). Isozyme frequencies differ significantly between populations of allopatric *M. mercenaria* and *M. campechiensis* populations (Pesch 1974, Humphrey 1981). Individuals with intermediate characteristics, or mixtures of characteristics, are found in the few areas where *M. mercenaria* and *M. campechiensis* occur together. This led Abbott (1974) to suggest that the two taxa may be only subspecies or forms.

Mercenaria mercenaria can live for weeks out of water under refrigeration, while *M. campechiensis* cannot (Menzel 1988). *M. campechiensis* generally shows more rapid growth under culture (Chestnut et al. 1956, Menzel 1962). Hybridization studies (Loosanoff 1954, Chestnut et al. 1956, Haven and Andrews 1956, Menzel 1962, 1977, Menzel and Menzel, 1965) with parental lines from a great variety of environments have always produced viable hybrids. The F_1 hybrids are interfertile, and can be backcrossed successfully to the parental lines (Menzel 1977). A more complete review of attempts to induce genetic variability in *M. mercenaria* broodstocks is available in Dillon and Manzi (1988).

The purpose of this paper is to establish morphological and isozyme criteria for distinguishing *Mercenaria mercenaria* and *M. campechiensis*, and to apply these criteria to a sample of clams taken from an area where the two species

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co-occur. We show that although *M. mercenaria* and *M. campechiensis* hybridize in the wild, some reproductive isolation seems to exist. We thus consider the taxa valid species.

Materials and methods

A sample of 179 adult hard clams was obtained from commercial fishermen in the fall of 1985 from the Indian River, a lagoon about 150 km long on the central east coast of Florida (27°–29°N; 80°–81°W). The clams were collected on about the same date and without regard to morphology, but we do not have precise locality data. This sample was compared to 224 adult *Mercenaria mercenaria* obtained from a population from a tributary of the Stono River, 15 km south of Charleston, South Carolina in 1987 (32°39′N; 80°00′W) and to 194 adult *M. campechiensis* obtained from Cedar Key, Florida on the northern Gulf of Mexico (29°08′N; 83°03′W).

Ridges on the exterior of all 597 clams were scored as either thick, thin, or intermediate. A three-category system was used for nacre color: white, purple, or intermediate (almost entirely white, but with a small amount of purple around the rim). The maximum shell length, shell height (maximum dimension perpendicular to shell length in the plane of the valves), shell width (maximum dimension perpendicular to the valve plane), lunule height (along the line separating the valves), and lunule width (the maximum dimension perpendicular to lunule height) were measured with vernier calipers. Shell weight (both valves) was measured to the nearest gram. The specimens have been deposited in the Academy of Natural Sciences of Philadelphia.

Discriminant analysis on principal component scores was used to classify the individuals (following Dillon 1984). First a principal-component analysis was performed on the correlation matrix of the six measurement variables over all 597 clams (the Princomp procedure, SAS 1985). The covariance matrix was not analyzed because of the differing units of measurement. Since Blackith and Reyment (1971) and Atchley et al. (1976) suggested disregarding variance on the first principal component as a method of factoring-out size variance, certain to be largely non-genetic in populations of mixed ages, we used factor scores on the last five principal components as new variables for discriminant analysis.

Because conventional discriminant-function analysis is based on analysis of variance, the assumption of homoscedasticity is inappropriate for factor scores. We used nearest-neighbor discriminant analysis (The neighbor procedure, SAS 1985), a nonparametric technique that does not involve the calculation of discriminant functions. We analysed the 224 *Mercenaria mercenaria* from South Carolina and the 194 *M. campechiensis* from Cedar Key with the 179 Indian River clams entered as unknowns. A distance in 5-variate space (Euclidean or Mahalanobis) was calculated from each clam to its 596 neighbors. Clams were classified as "merc-metric" if at least nine of the their ten nearest morphological neighbors (of known affinity) were *M. mercenaria*, "camp-metric" if at least nine of their ten nearest neighbors were *M. campechiensis*, or "intermed-metric" if otherwise.

We have identified seven enzyme loci that are highly polymorphic and easily resolved in *Mercenaria* spp. (Dillon 1985). Allele frequencies at these loci were determined for all 597 individuals using protein electrophoresis. Siphon samples were ground in a tris-phosphate tissue buffer and centrifuged, and the supernatant was subjected to electrophoresis in horizontal starch gels using three different buffer systems. The enzymes examined were glucose phosphate isomerase (GPI, EC 5.3.1.9), leucine aminopeptidase (LAP, EC 3.4.11), superoxide dismutase (SOD, EC 1.15.1.1) 6-phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), mannose phosphate isomerase (MPI, EC 5.3.1.8), and phosphoglucomutase (two loci – PGMS and PGMF – EC 2.7.5.1). Simple Mendelian inheritance of codominant alleles has been demonstrated at GPI, LAP, 6PGD, PGMS and PGMF by Adamkewicz et al. (1984). Details of the electrophoretic techniques employed, along with recipes for all buffers and stains, have been published elsewhere (Dillon 1982, 1985, Dillon and Manzi 1987).

Results

South Carolina and Cedar Key populations

The thickness of the shell ridges was the best discriminator between *Mercenaria mercenaria* from South Carolina and *M. campechiensis* from Cedar Key. All of the 224 South Carolina clams had thin, easily eroded ridges, while all but one of the 194 Cedar Key had thick ridges. The remaining individual from the Cedar Key sample had ridges that were intermediate in thickness. 80% of *M. mercenaria* were strongly purple, while 92% of *M. campechiensis* were purely white (Table 1).

Table 1. *Mercenaria mercenaria* (*Mm*, Charleston, South Carolina) and *M. campechiensis* (*Mc*, Cedar Key, Florida) categorized by shell morphology. Categories camp-, intermed-, and merc-metric are based on Euclidean distance to nearest neighbors, as described in "Materials and methods"

Nacre color	Camp-metric	Intermed-metric	Merc-metric	Total
Charleston *Mm*				
white	0	1	10	11
intermediate	0	0	33	33
purple	3	9	168	180
Total	3	10	211	224
Cedar Key *Mc*				
white	156[a]	23	0	179
intermediate	11	0	0	11
purple	4	0	0	4
Total	171	23	0	194

[a] Includes one individual with "intermediate" ridges

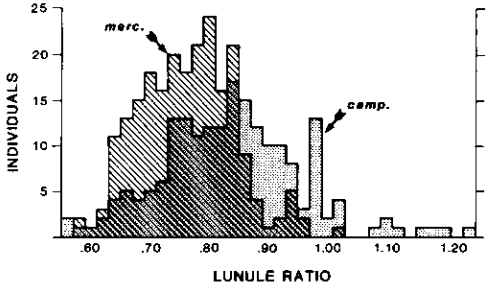

Fig. 1. *Mercenaria* spp. Ratio of lunule width to lunule height in *M. mercenaria* from South Carolina (hatched) and *M. campechiensis* from Cedar Key, Florida (stippled)

Table 2. *Mercenaria* spp. Principal-component analysis of shell morphology in clams Charleston, South Carolina, Cedar Key, Florida and Indian River, Florida ($N = 597$)

Morphological character	Eigenvectors					
	PC1	PC2	PC3	PC4	PC5	PC6
Shell length	0.42	0.00	−0.41	−0.73	0.34	−0.04
Shell height	0.46	−0.10	−0.14	−0.07	−0.86	0.14
Shell width	0.44	−0.35	0.20	0.24	0.10	−0.76
Lunule height	0.33	0.48	0.77	−0.23	0.03	0.10
Lunule width	0.34	0.67	−0.41	0.50	0.13	−0.04
Weight	0.43	−0.44	0.09	0.33	0.34	0.63
Eigenvalue	4.33	0.77	0.58	0.18	0.08	0.06
Cumulative variance	0.72	0.85	0.95	0.98	0.99	1.00

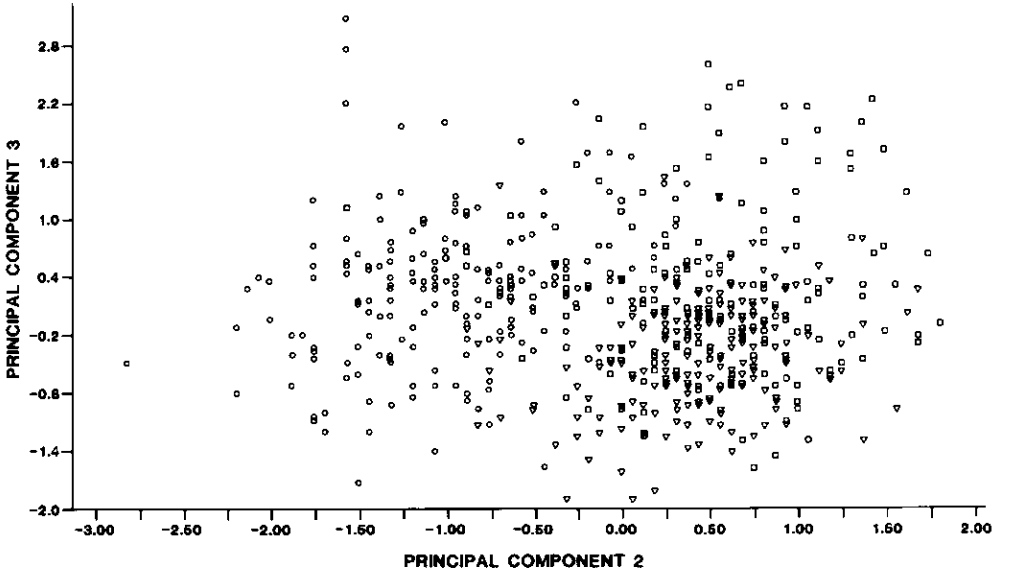

Fig. 2. *Mercenaria* spp. Individuals from South Carolina (▽), Cedar Key (○), and Indian River (□) plotted on Principal Components 2 and 3 from the morphometric analysis. Total of 22 South Carolina, 17 Cedar Key, and 20 Indian River clams are obscured by overlap, and 2 Indian River clams are off the scale on right

The ratio of lunule width to lunule height was of limited utility. Although *Mercenaria mercenaria* tends to have a narrower lunule, the two species *M. mercenaria* and *M. campechiensis* broadly overlap in this character (Fig. 1). Clams with lunules at least as wide as they are high are usually *M. campechiensis*. However, individuals with this trait represent only about 14% of the population of *M. campechiensis* at Cedar Key.

The first principal component from the analysis of all 597 individuals had uniformly positive, high loadings on all six variables, ranging from 0.33 to 0.46, and accounted for 72.2% of the total variance (Table 2). Variance on this axis can be attributed to size and was disregarded. The 597 clams (minus 61 out-of-range or obscured by overlap) are plotted on Principal Components 2 and 3 in Fig. 2. Although it was not calculated to be a discriminant function, the two populations are very distinct on Principal Component 2. Judging from the factor loadings given in Table 2, with size constant, *Mercenaria campechiensis* has a wider, heavier shell with a smaller lunule. Factor scores on the last five principal components, accounting for 27.8% of the variance, were used in nearest-neighbor discriminant analysis.

The discriminant analysis demonstrated significant morphometric differences between *Mercenaria mercenaria* and *M. campechiensis*. When Mahalanobis distances were used as the metric, 92% of the *M. mercenaria* and 86% of the *M. campechiensis* were categorized correctly. When Euclidean distances were used, 94 and 88%, respectively, were categorized correctly (Table 1). Although no Cedar Key clam was identified to 90% confidence as *M. mercenaria*, three South Carolina clams were misidentified as *M. campechiensis*.

All three of these "camp-metric" *M. mercenaria* had purple nacre (Table 1). In general, nacre color and shell morphometrics assort independently in the South Carolina and Cedar Key populations. For example, the probability of white nacre is 0.049, and that of intermediate nacre 0.147 in South Carolina, and the probabilities are 0.013 and 0.045 for camp-metric and intermed-metric, respectively. Joint probabilities would predict about 1.5 intermediate/intermediate clams and 0.50 white/intermediate clams in 224 samples. No intermediate/intermediate clams and one white/intermediate clam were observed in the South Carolina sample.

Allele frequencies at the seven polymorphic enzyme loci are given in Table 3, using the nomenclature of Dillon and Manzi (1987). Although differences are not fixed, the differences between *Mercenaria mercenaria* from South Carolina and *M. campechiensis* from Cedar Key are highly significant (by chi-square two-sample tests) at every locus. The most common GPI allele in *M. mercenaria* (GPI 100), at a frequency of over 90%, is absent from *M. campechiensis*, and the most common PGMF allele in *M. campechiensis*, (PGMF 97) at a frequency of 64%, is absent from *M. mercenaria*. Eleven alleles were unique to *M. campechiensis* (excluding GPI 60, known from more northerly *M. mercenaria* but not from South Carolina) and four alleles were unique to *M. mercenaria*.

Indian River sample

The 179 Indian River clams were more variable morphologically than either the population of *Mercenaria mercenaria* from South Carolina or *M. campechiensis* from Cedar Key. The sample included many clams which, at least on the two axes graphed, were indistinguishable from *M. mercenaria* from South Carolina, and a few that were indistinguishable from *M. campechiensis* from Cedar Key. Many clams were morphologically quite unlike either *M. mercenaria* or *M. campechiensis* (e.g. scoring high on both principal components graphed).

Table 4 shows the 179 Indian River clams simultaneously classified by the results of the discriminate analysis (based on Euclidean distances to nearest morphometric neighbors), nacre color, and shell ridges. These characters are not independently assorting. Seven individuals have thick ridges, white nacre, and camp-metrics, when only 1.3 individuals would be expected from the product of the marginal probabilities. 22 individuals have thin ridges, purple nacre, and

Table 3. *Mercenaria*. spp. Allele frequencies at seven enzyme loci for South Carolina *M. mercenaria*, for Indian River clams sorted by nacre color, and for *M. campechiensis* from Gulf of Mexico, Florida

Allele	*M. mercenaria*	Indian River clams		*M. campechiensis*
		purple	white	
GPI				
110	0.023	0.030	0	0
105	0.014	0	0	0
100	0.901	0.783	0.515	0
90	0.021	0.036	0.029	0.008
85	0	0.006	0	0.023
80	0.002	0.018	0.176	0.221
70	0.038	0.066	0.162	0.432
65	0	0	0	0.013
60	0	0.060	0.088	0.271
50	0	0	0.029	0.031
(*N*)	(213)	(83)	(34)	(192)
LAP				
104	0.095	0.108	0.162	0.074
100	0.412	0.440	0.352	0.127
96	0.463	0.410	0.397	0.333
94	0.019	0.042	0.088	0.407
90	0.012	0	0.015	0.059
(*N*)	(215)	(83)	(34)	(162)
SOD				
100	0.768	0.703	0.650	0.018
90	0.232	0.297	0.350	0.702
80	0	0	0	0.281
(*N*)	(114)	(79)	(30)	(114)
6PGD				
110	0.030	0.049	0.079	0.084
100	0.622	0.605	0.619	0.517
95	0	0	0	0.011
90	0.348	0.346	0.302	0.388
(*N*)	(201)	(81)	(32)	(179)
MPI				
110	0	0	0	0.032
108	0.059	0.149	0.167	0.484
105	0.389	0.474	0.450	0.267
100	0.300	0.247	0.383	0.174
95	0.253	0.130	0	0.043
(*N*)	(144)	(77)	(30)	(187)
PGMS				
103	0.012	0.019	0.015	0
100	0.844	0.772	0.471	0.161
97	0.043	0.082	0.103	0.078
95	0	0	0	0.075
92	0.077	0.076	0.382	0.578
87	0.024	0.051	0.029	0.056
82	0	0	0	0.035
77	0	0	0	0.016
(*N*)	(208)	(79)	(34)	(186)
PGMF				
105	0	0.030	0.030	0
103	0.148	0.120	0.197	0.061
100	0.852	0.825	0.652	0.282
97	0	0.024	0.121	0.636
97	0	0	0	0.021
(*N*)	(209)	(83)	(33)	(189)

Table 4. *Mercenaria* spp. Indian River categorized by shell morphology

Ridges and nacre color	Camp-metric	Intermed-metric	Merc-metric	Total
Thick				
white	7	13	4	24
intermediate	6	11	2	19
purple	3	6	8	17
Intermediate				
white	0	5	3	8
intermediate	4	8	22	34
purple	0	11	31	42
Thin				
white	0	0	2	2
intermediate	0	3	6	9
purple	1	1	22	24
Total	21	58	100	179

Table 5. *Mercenaria* spp. Values of chi-square and degrees of freedom comparing samples of Indian River clams with different shell morphology. * ** *** Values significant at 0.05, 0.01, and 0.001 levels, respectively

Locus	Shell ridges	Nacre color	Discriminant analysis
	thick = 60, thin = 35	white = 34, purple = 83	camp-metric = 21, merc-metric = 100
GPI	13.84**, 3	33.08***, 4	19.75***, 1
LAP	2.63, 3	3.84, 3	9.11*, 3
SOD	6.21*, 1	10.16**, 1	10.63**, 1
6PGD	0.0, 1	0.41, 1	0.0, 1
MPI	13.02**, 3	11.70**, 3	10.87*, 3
PGMS	16.24***, 2	31.02***, 2	13.26**, 2
PGMF	4.87, 2	10.99**, 2	5.95, 2

merc-metrics, when only 9.1 would be expected. The most striking deficit is the presence of only 14 individuals with thick ridges and merc-metrics, when 33.5 such individuals would be expected.

Individuals with thin ridges, purple nacre, or merc-metrics were significantly different at most enzyme loci from thick, white, or camp-metric individuals (Table 5). Example data comparing the 34 Indian River clams with white nacre to the 83 such clams with purple nacre are given in Table 3 (setting aside the 62 intermediates). The purple-nacred clams tend to genetically resemble *Mercenaria mercenaria* from South Carolina, and the white-nacred clams are genetically similar to *M. campechiensis*. These differences are significant at the 0.001 level in some cases (Table 5).

Discussion

Although *Mercenaria mercenaria* and *M. campechiensis* have broadly overlapping ranges, the populations from South Carolina and Cedar Key are distinct. This is indicated by the fidelity of the shell-ridges character and the independent assortment of the nacre color and morphometric characters in the two populations. The complete absence of the GPI 100 allele from the Cedar Key population suggests that no gene flow occurs from *M. mercenaria* to *M. campechiensis* in the Gulf of Mexico. In a random sample of 194 diploids, one has a 95% chance of seeing at least one copy of any allele present at a frequency of 0.008 or greater.

Regarding the possibility of gene flow from Gulf of Mexico *Mercenaria campechiensis* populations to *M. mercenaria* in South Carolina, we found that the South Carolina allele frequencies differed little from those obtained from the same seven loci in Virginia and Massachusetts clams (Dillon and Manzi 1987). The South Carolina population seems to be missing the rare Virginia and Massachusetts allele GPI 60, and shows a low frequency of the previously unknown allele LAP 90. Deleting rare alleles for the purposes of chi-square tests, the Virginia and the South Carolina populations at five of the seven loci do not differ significantly. Significant differences are apparent only in the higher frequency of MPI 95 and the lower frequency of PGMS 87 in South Carolina. Both of these findings are the opposite of what one would expect if South Carolina populations outcrossed with *M. campechiensis*.

These findings confirm those of Pesch (1974), who reported a significant difference in allele frequencies at the SOD locus ("TO") between four populations of *Mercenaria mercenaria* (Prince Edward Island, Maine, Rhode Island, and South Carolina) and two of *M. campechiensis* (North Carolina, Gulf of Mexico). Humphrey (1981) compared several populations of the two species at six of the seven loci we report here. Her *M. mercenaria* populations were from Massachussets, Virginia, Georgia, and the east coast of Florida, and her *M. campechiensis* were from Tampa Bay and Port St. Joe, Florida. Humphrey also detected significant differences at GPI, SOD, PGMS, and PGMF, but missed the less striking differences at LAP and 6PGD, possibly due to smaller sample sizes.

The disequilibrium between the several morphological characters and the allele frequencies observed in the Indian River sample may result from the fact that *Mercenaria mercenaria* and *M. campechiensis* co-occur, and often hybridize, but that some reproductive isolation is present. Differences in spawning time or habitat may be responsible. Regarding the latter, dispersal capabilities of *Mercenaria* spp. should be high. Dillon and Manzi (1987) found only one significant difference in allele frequencies between Massachusetts and Virginia clams over seven loci. Here we report but two differences between Virginia and South Carolina. Although the Indian River lagoon is large, any differences in the distribution of *M. mercenaria* and *M. campechiensis* would be more likely due to differing success in various habitats than to dispersal barriers. Such habitat segregation is generally considered an effective reproductive isolating mechanism (Mayr 1963: p. 92).

Of the 15 enzyme alleles unique to one species or the other, 6 occur in the Indian River, 3 from each species. Interestingly, only one of the seven white, thick-ridged individuals with *campechiensis*-like morphometrics had no copies of the diagnostic *M. mercenaria* alleles GPI 110, GPI

100, or PGMS 103. Thus, only this one clam can be considered purely *M. campechiensis*. In contrast, 21 of the 22 purple, thin-ridged individuals with *mercenaria*-like morphometrics were free of the diagnostic *M. campechiensis* alleles GPI 85, GPI 50, and PGMF 97.

In the Indian River sample, 157 individuals have mixtures of morphologies and/or mixtures of alleles. These are probably hybrids. Because there is some morphological overlap between the pure populations and the mechanism of inheritance for these characters is unknown, morphological criteria cannot be used to identify hybrids unequivocally. Lamb and Avise (1987) have reviewed the problems associated with hybrid indices based on morphology. However, 18 individuals have at least one allele diagnostic of *Mercenaria mercenaria* and one allele diagnostic of *M. campechiensis*. These must be hybrids. Included among these are seven clams homozygous for the diagnostic allele GPI 100 of *M. mercenaria* and carrying the allele PGMF 97 diagnostic of *M. campechiensis*. One GPI 110/100 heterozygote carried PGMF 97, and two PGMF 97 homozygotes carried GPI 100. These ten individuals must be hybrids and cannot be F_1 progeny. Thus, in the wild as in the nursery (Menzel 1977), F_1 hybrids are not sterile.

If *Mercenaria mercenaria* and *M. campechiensis* are to be considered geographic races or subspecies, one must hypothesize that the current situation in the Indian River is transitory. However, a very large migration imbalance from a pure source population or populations into the Indian River would be required to produce such a high hybrid percentage over a population large enough to support a commercial fishery. Although one could postulate a high selective advantage for the immigrant genome, and/or population growth, to complement a migration imbalance, such a combination of events seems less likely than simple reproductive isolation between two species.

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