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GENETIC DIFFERENTIATION IN TRANS-FLORIDIAN SPECIES COMPLEXES OF *SESARMA* AND *UCA* (DECAPODA: BRACHYURA)

Darryl L. Felder and Joseph L. Staton

ABSTRACT

Most nearshore brachyuran crabs of the northern Gulf of Mexico have been treated as conspecifics of those in warm-temperate Carolinian waters on the southeastern Atlantic coast of North America. However, historical physiographic constraints appear to have periodically restricted gene flow between northern Gulf populations and sibling Atlantic coast populations, and contemporary disjuncture of ranges often persists across south Florida. The present examination of intertidal complexes has centered on grapsid crabs presently assigned to *Sesarma reticulatum* and ocypodid crabs assigned to *Uca minax,* 2 species in which we have observed marked variations in coloration over their distributional range. Genetic differentiation between populations has been assayed by allozyme electrophoresis, and resultant data have been evaluated with *F*-statistics and cluster analysis of genetic distance. Allozyme divergence between Gulf and Atlantic populations of the *S. reticulatum* complex is at levels previously reported for speciated populations, while that between trans-Floridian populations of *U. minax* is much less pronounced. In both species, minimal divergence can be measured between 2 widely separated Atlantic coast sample localities that were compared, while more complex grades of differentiation are evident between sample localities compared within the northern Gulf of Mexico. Trans-Floridian divergence of populations for both of these species is compatible with models for periods of contact and subsequent isolation of Gulf and Atlantic stocks during and since peak glacial advances in North America. Less conspicuous patterns of genetic differentiation between sample localities within the northern Gulf of Mexico may reflect a history of glacial and postglacial alluvial events which resulted in contemporary physiography of northern Gulf estuaries.

Prior to recent reevaluations, the coastal warm-temperate Carolinian decapod crustacean assemblage of the western North Atlantic was thought to include a large number of widely distributed and highly adaptable nearshore and intertidal brachyuran species that ranged from the vicinity of Cape Hatteras, North Carolina, into the northern and northwestern Gulf of Mexico (Hedgpeth, 1953; Williams, 1965; Powers, 1977). Even in cases where distributions of species were known to break at the southern extreme of peninsular Florida, close morphological similarity between disjunct populations led most investigators to conclude that little or no differentiation had occurred between such populations. These breaks in distribution were usually assumed to represent nothing more than a contemporary disjuncture of appropriate habitats which accounted for a short break in an otherwise continuous range. While endemism of nearshore species was documented within some brachyuran genera in the Gulf of Mexico, evidence was limited primarily to certain conspicuous cases of apparent relict species (*Uca subcylindrica* (Stimpson), *Platychirograpsus spectabilis* de Man) and some possible isolates of tropical stocks (*Uca spinicarpa* Rathbun, *U. marguerita* Thurman, *Callinectes rathbunae* Contreras). Evidence of a few other endemic nearshore brachyurans could be deduced from published ranges, but there was no clear case for relationship of these or other Gulf endemic species to Atlantic coast siblings and no documentation of trans-Floridian geminate species pairs in this group (Williams, 1965; Felder, 1973; Williams, 1974; Powers, 1977).

Evidence for historical disjuncture of coastal brachyuran stocks across the Florida peninsula and ultimate speciation of those stocks has accumulated in the course of several case studies from the early 1970s to the present. In his separation of the Atlantic xanthid crab *Dyspanopeus sayi* (Smith) from the closely related Gulf of Mexico endemic species *D. texanus* (Stimpson), Abele (1972: 269) discussed the probable role of Miocene through Pleistocene events which alternately submerged and exposed the Florida peninsula and which could have reduced gene

flow between Gulf and Atlantic coast populations of the *Dyspanopeus* complex (treated within *Neopanope* prior to Martin and Abele, 1986) and of "other species pairs among the Decapoda with similar distribution patterns along the Gulf and Atlantic coasts." Subsequently, additional closely related species pairs have been identified that may have diverged from stocks isolated to either side of historical or contemporary distributional breaks in south Florida; these include such Gulf/Atlantic pairings as *Uca panacea* Novak and Salmon/*U. pugilator* (Bosc) (Novak and Salmon, 1974), *Ovalipes floridanus* Hay and Shore/*O. stephensoni* Williams (Williams, 1976), *Panopeus simpsoni* Rathbun/*P. herbstii* Milne Edwards (Williams, 1984a), and *Menippe adina* Williams and Felder/*M. mercenaria* (Say) (Williams and Felder, 1986). Even where contemporary ranges for some of the above may now overlap in the northeastern Gulf, as in the case of *Uca panacea*/*U. pugilator* (Novak and Salmon, 1974; Barnwell and Thurman, 1984), or where, as in the *Menippe* complex, introgressive hybridization may occur (Bert, 1986; Williams and Felder, 1986; Bert and Harrison, 1988), historical events which separated stocks across the Florida peninsula may have facilitated genetic isolation and subsequent speciation.

Recognition of divergent features between closely related trans-Floridian sibling species and populations of the Brachyura has in various instances been facilitated by comparison of morphology, coloration, behavior, physiology, hemocyanin electromorphs, allozyme frequencies, and nucleic acid sequences (as referenced above, see also Fielder *et al.*, 1971; Selander *et al.*, 1971a; Salmon *et al.*, 1979; Sullivan *et al.*, 1983; Neigel *et al.*, 1991). In the present study, we undertake allozyme analyses in trans-Floridian complexes that are presently treated as two brachyuran taxa, the fiddler crab (Ocypodidae) *Uca minax* (Le Conte) and the marsh crab (Grapsidae) *Sesarma reticulatum* (Say). The selection of these species is based upon (i) their classical and continued treatment as Carolinian species that range into the Gulf of Mexico (Hedgpeth, 1953; Barnwell and Thurman, 1984; Abele and Kim, 1986), (ii) the disjuncture in distribution of both of these species across southern Florida, and (iii) the disjuncture of appropriate estuarine habitats for these species across southern Florida. There is, however, some difference in early life history and capacity for dispersal between typical populations of the *U. minax* (five zoeal stages) and *S. reticulatum* (three zoeal stages) complexes, and some difference in habitat preference between *U. minax* (low salinity marshes and banks) and *S. reticulatum* (medium to high salinity marshes and banks) complexes.

Much as color differences first prompted further study and eventual recognition of sibling species in the *Menippe mercenaria*/*M. adina* complex (Williams and Felder, 1986), our observation of differences in coloration between trans-Floridian populations of both the *U. minax* and the *S. reticulatum* complexes has prompted us to undertake genetic characterizations, despite our finding of otherwise striking morphological similarities between Atlantic and Gulf of Mexico populations. However, since in both complexes some color variations were also observed between geographically separated populations within the Gulf of Mexico, an effort has been made to compare populations of both species from throughout their ranges in the Gulf of Mexico. Finally, our interest in genetic examination of the *S. reticulatum* complex has also been prompted by recent studies of reproductive biology (Zimmerman and Felder, 1990, 1991) and osmoregulatory ability (Staton and Felder, 1992) that have uncovered evidence of functional divergence between Gulf of Mexico and Atlantic populations of this group.

Materials and Methods

Animals for genetic analyses were collected over a 2-year period (16 May 1989–1 August 1991) from localities at intervals along the southeastern Atlantic and Gulf of Mexico coasts of the United States (Fig. 1). Within this area, we have concluded that the *Sesarma reticulatum* complex is reliably documented to range in the Gulf of Mexico from Barra del Tordo, Tamaulipas, Mexico (Rabalais *et al.*, 1989; Zimmerman and Felder, 1991) to Sarasota County, Gulf coast of Florida (Abele, 1973), and from Volusia County, Atlantic coast of Florida, to Woods Hole, Massachusetts (Abele, 1992). We have concluded that the *Uca minax* complex ranges in the Gulf of Mexico from near the Neches River at the eastern extreme of the Texas coast (Wurtz and Roback, 1955) into northwestern Florida, perhaps to Yankeetown, Gulf coast of Florida (Salmon, 1967); precise records for both eastern and western extremes of the Gulf range are questionable, since the species

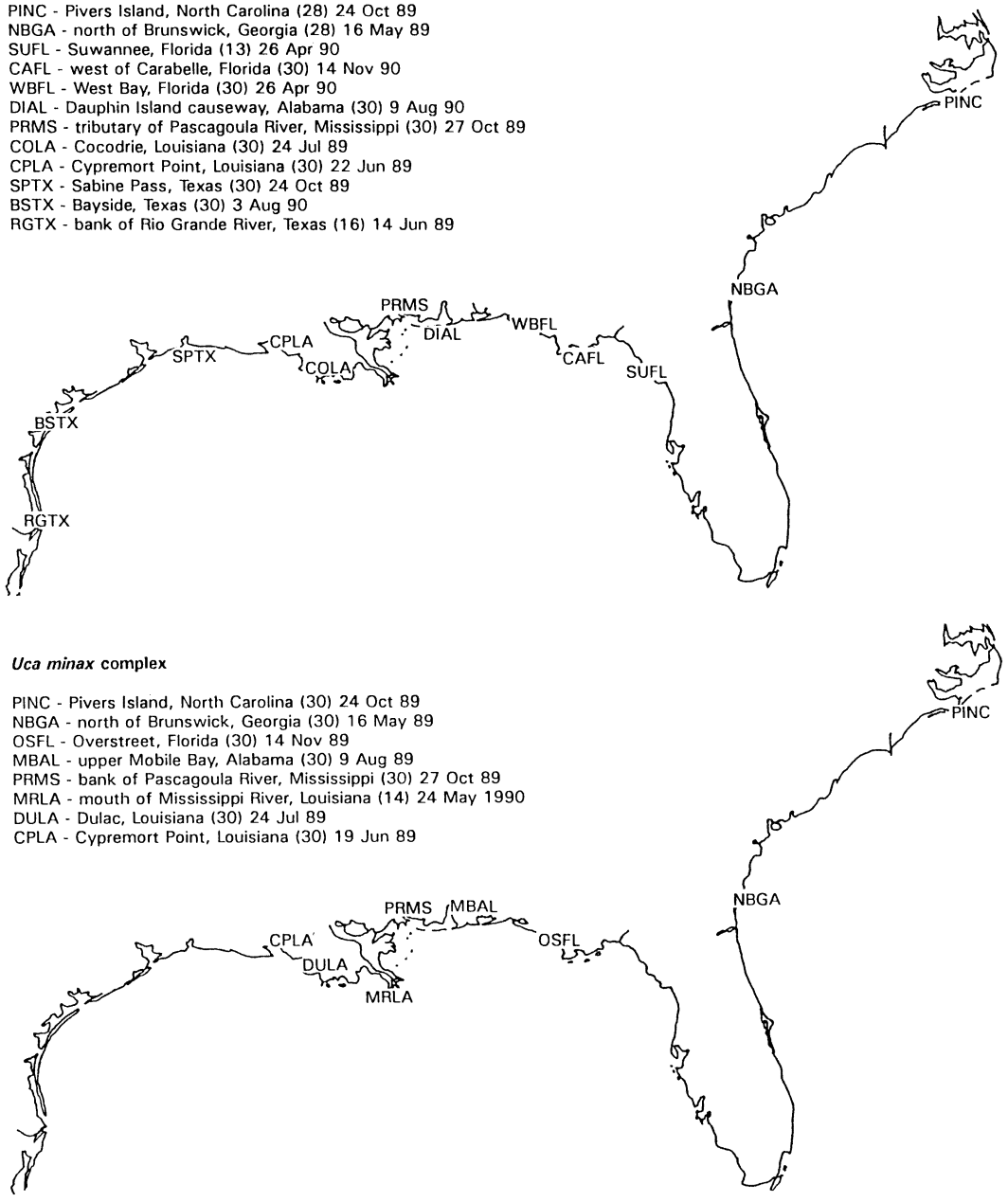

Fig. 1. Sample localities for specimens of the *Sesarma reticulatum* and *Uca minax* complexes. Locality abbreviations listed are each followed by site definition, sample size (N), and date of collection.

has often been confused with a closely related but distinct Gulf endemic species, *Uca longisignalis* Salmon and Atsaides (see Salmon and Atsaides, 1968; von Hagen, 1976; Heard, 1977; Williams, 1984b). On the Atlantic coast, *U. minax* appears to range from northeast Florida to Buzzards Bay, Massachusetts (Williams, 1984b).

Our collection localities along coastlines of the Gulf of Mexico were selected to encompass as much of the distributional ranges as possible, and to represent subpopulations that were known to vary in color or subpopulations that appeared to be segregated by features of coastal physiography. Successful sampling for both complexes within their Gulf ranges was limited to those localities from which adequate sample sizes could be obtained and, therefore, did not represent extreme lim-

Table 1. Enzyme systems and optimal buffer systems used in the analysis of population samples of *Sesarma* (S) and *Uca* (U). E.C. No. refers to index numbers recommended by the Nomenclature Committee of the International Union of Biochemistry (1984). Buffers used in this study were Tris-citrate pH 8.0 (TC 8) and Poulik pH 8.7 (P 8.7).

Enzyme system (locus abbreviation)	E.C. No.	Buffer system
Acid phosphatase (*Acp*)	3.1.3.2	TC 8 (S)
Alanopine dehydrogenase (*Aladh*)	1.5.1.17	TC 8 (S, U)
Arginine kinase (*Ark*)	2.7.3.3	P 8.7 (S, U)
Enolase (*Eno*)	4.2.1.11	TC 8 (U)
Glucose phosphate isomerase (*Gpi*)	5.3.1.9	P 8.7 (S, U)
Glutamic-oxaloacetic transaminase 1 and 2 (*Got*)	2.6.1.1	TC 8 (2-S; 1-U)
Hexokinase (*Hk*)	2.7.1.1	P 8.7 (S, U)
Isocitric dehydrogenase 1 and 2 (*Idh*)	1.1.1.42	TC 8 (S, U)
Lactic dehydrogenase (*Ldh*)	1.1.1.27	TC 8 (S, U)
Leucyl-alanyl peptidase (*PepLa*)	3.4.13.–	TC 8 (S, U)
Leucyl-glycyl-glycyl peptidase (*PepLg*)	3.4.13.–	TC 8 (S, U)
Malic dehydrogenase 1 and 2 (*Mdh*)	1.1.1.37	TC 8 (S, U)
Mannose phosphate isomerase (*Mpi*)	5.3.1.8	P 8.7 (S, U)
6-phosphogluconic dehydrogenase (*Pgdh*)	1.1.1.49	TC 8 (S, U)
Phosphoglucomutase (*Pgm*)	2.7.5.1	P 8.7 (S, U)
Sorbitol dehydrogenase 1 and 2 (*Sdh*)	1.1.1.14	P 8.7 (2-S, 1-U)
Superoxide dismutase (*Sod*)	1.15.1.1	TC 8 (S, U)

its of the reported ranges. Collection localities for both complexes on the Atlantic coast were limited to 2 widely separated sites, and animals of respective species from both sites were similar in coloration. Crabs were captured while they were active outside their burrows or were excavated at low tide. An effort was made to collect at least 30 individuals from each locality for the analysis, and additional intact specimens along with dissected remains were usually preserved as morphological vouchers. Collection localities are identified throughout the remainder of this paper by the abbreviations listed in Fig. 1.

Tissue samples were either frozen in liquid nitrogen in the field, or were dissected from animals transported live to the laboratory; all tissue samples were stored at −70°C until they were processed prior to electrophoresis. Prior to homogenization, subsamples of tissue (excluding hepatopancreas) were placed in 1.5-ml microcentrifuge tubes and refrozen with an equal volume of distilled water. These frozen preparations were homogenized and then centrifuged for 20 min at 15,000 *g*. Samples were electrophoresed in 12.5% starch (Starch*art* Corp., Smithville, Texas, U.S.A.) under the conditions of Selander *et al.* (1971b) and Murphy *et al.* (1990). An initial screening of more than 35 enzymes produced 20 presumptive loci for *Sesarma* and 18 presumptive loci for *Uca* that produced consistently interpretable results (Table 1). Allelic forms of enzymes were designated by letters, and different loci for the same enzyme system were designated by Arabic numerals.

Allelic frequencies and observed heterozygosities (H_{OBS}) for each locus were determined by direct census of the population data. Mean heterozygosity within populations was estimated from average values across all loci. Hierarchical *F*-statistics (Weir and Cockerham, 1984) were estimated for 3 levels of population structure: individuals within localities (F_{IL}), localities within 2 regions, the Gulf coast and the Atlantic coast (F_{LR}), and the 2 regions within the total area sampled (F_{RT}, see Table 2). Theoretically, *F* values range from 0–1 with $F = 1$ being groups fixed for alternate alleles. Preliminary runs of the data produced small negative values, and these were set to zero in subsequent analyses as suggested by Slatkin and Barton (1989). Nei's (1978) unbiased genetic distance (D_N) was calculated and then clustered using the unweighted pair-group algorithm (UPGMA, Unweighted Pair-Group Method Using Arithmetic Averages; Sneath and Sokal, 1973) and the neighbor-joining algorithm (Saitou and Nei,

Table 2. Hierarchical *F*-statistics adapted from Weir and Cockerham (1984) design that utilizes a random-effects nested ANOVA model (after Kwast *et al.* 1990). F_{RT} is genetic differentiation among regions within the total area sampled, whereas F_{LR} and F_{IL} are the levels of genetic differentiation of localities within regions and individuals within localities, respectively.

Level of variation	Variance component	*F*-statistics
Regions (R) within total (T)	σ^2_{RT}	$F_{RT} = \sigma^2_{RT}/\sigma^2_{GT}$
Localities (L) within regions	σ^2_{LR}	$F_{LR} = \sigma^2_{LR}/(\sigma^2_{GT} - \sigma^2_{RT})$
Individuals (I) within localities	σ^2_{IL}	$F_{IL} = \sigma^2_{IL}/(\sigma^2_{GT} - \sigma^2_{RT} - \sigma^2_{LR})$
Genes (G) within individuals	σ^2_{GI}	
Total	σ^2_{GT}	

Table 3. Allele frequencies and heterozygosities for 13 loci in 12 collections of the *Sesarma reticulatum* complex. Alleles are identified by lower case letter; multiple loci are identified by Arabic numeral. H_{OBS} and H_{EXP} represent observed and expected (unbiased) heterozygote frequencies, respectively. "—" indicates absence of heterozygotes for localities with only homozygotes. Locality abbreviations and sample sizes are given in Fig. 1.

	Locality											
Locus	PINC	NBGA	SUFL	ARFL	WBFL	DIAL	PRMS	LCLA	CPLA	SPTX	BSTX	RGTX
Acp-2												
a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
b	1.000	0.982	1.000	1.000	1.000	1.000	1.000	0.983	1.000	1.000	1.000	1.000
c	0.000	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
H_{OBS}	—	0.036	—	—	—	—	—	0.033	—	—	—	—
H_{EXP}	—	0.036	—	—	—	—	—	0.033	—	—	—	—
Aladh												
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.937
b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063
H_{OBS}	—	—	—	—	—	—	—	—	—	—	—	0.000
H_{EXP}	—	—	—	—	—	—	—	—	—	—	—	0.121
Got-1												
a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.017	0.000
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.983	1.000	1.000	0.983	1.000
H_{OBS}	—	—	—	—	—	—	—	0.033	—	—	0.033	—
H_{EXP}	—	—	—	—	—	—	—	0.033	—	—	0.033	—
Got-2												
a	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.017	0.033	0.000	0.017	0.031
b	0.018	0.000	0.577	0.552	0.565	0.934	0.850	0.866	0.850	0.850	0.950	0.875
c	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.033	0.000
d	0.964	0.982	0.423	0.431	0.435	0.000	0.150	0.117	0.117	0.150	0.000	0.094
e	0.018	0.018	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
H_{OBS}	0.071	0.036	0.385	0.552	0.419	0.067	0.300	0.267	0.267	0.233	0.100	0.250
H_{EXP}	0.071	0.036	0.508	0.518	0.500	0.129	0.259	0.238	0.267	0.259	0.098	0.232
Gpi												
a	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	0.000	0.000	0.000	0.000	0.016	0.017	0.000	0.017	0.017	0.017	0.017	0.000
c	0.000	0.000	0.654	0.793	0.758	0.800	0.883	0.850	0.733	0.900	0.900	0.719
d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
e	0.804	0.857	0.346	0.207	0.226	0.183	0.117	0.116	0.250	0.083	0.083	0.281
f	0.178	0.143	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
H_{OBS}	0.250	0.214	0.538	0.414	0.484	0.400	0.167	0.267	0.533	0.133	0.200	0.438
H_{EXP}	0.328	0.249	0.471	0.334	0.380	0.332	0.210	0.268	0.406	0.186	0.186	0.417
Idh-1												
a	0.000	0.000	0.000	0.103	0.032	0.000	0.033	0.000	0.117	0.167	0.100	0.000
b	1.000	1.000	1.000	0.896	0.968	1.000	0.967	1.000	0.883	0.816	0.900	1.000
c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000
H_{OBS}	—	—	—	0.206	0.000	—	0.067	—	0.167	0.300	0.067	—
H_{EXP}	—	—	—	0.189	0.063	—	0.066	—	0.210	0.310	0.183	—
Idh-2												
a	1.000	0.964	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	0.000	0.036	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
c	0.000	0.000	1.000	0.983	0.984	1.000	1.000	1.000	1.000	1.000	0.983	1.000
d	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.017	0.000
H_{OBS}	—	0.071	—	0.034	0.032	—	—	—	—	—	0.033	—
H_{EXP}	—	0.070	—	0.034	0.032	—	—	—	—	—	0.033	—
Mdh-2												
a	0.000	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000
b	1.000	0.982	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.983	1.000
H_{OBS}	—	0.036	—	—	—	—	—	—	—	—	0.033	—
H_{EXP}	—	0.036	—	—	—	—	—	—	—	—	0.033	—

Table 3. Continued.

Locus	Locality											
	PINC	NBGA	SUFL	ARFL	WBFL	DIAL	PRMS	LCLA	CPLA	SPTX	BSTX	RGTX
PepLa-2												
a	0.000	0.036	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	1.000	0.964	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
c	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
H_{OBS}	—	0.000	—	—	—	—	—	—	—	—	—	—
H_{EXP}	—	0.070	—	—	—	—	—	—	—	—	—	—
PepLg-1												
a	1.000	1.000	0.077	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	0.000	0.000	0.923	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000
c	0.000	0.000	0.000	1.000	1.000	0.967	1.000	1.000	1.000	1.000	1.000	1.000
H_{OBS}	—	—	0.000	—	—	0.000	—	—	—	—	—	—
H_{EXP}	—	—	0.148	—	—	0.066	—	—	—	—	—	—
Pgdh												
a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063
b	0.982	0.929	1.000	1.000	1.000	1.000	1.000	0.967	0.967	0.967	1.000	0.937
c	0.018	0.071	0.000	0.000	0.000	0.000	0.000	0.033	0.033	0.033	0.000	0.000
H_{OBS}	0.036	0.071	—	—	—	—	—	0.000	0.000	0.067	—	0.000
H_{EXP}	0.036	0.135	—	—	—	—	—	0.126	0.065	0.065	—	0.121
Pgm												
a	0.000	0.000	0.000	0.017	0.000	0.017	0.017	0.017	0.000	0.000	0.000	0.031
b	0.018	0.000	0.308	0.310	0.516	0.717	0.783	0.833	0.733	0.750	0.867	0.813
c	0.982	1.000	0.692	0.638	0.452	0.266	0.150	0.133	0.200	0.217	0.133	0.156
d	0.000	0.000	0.000	0.035	0.032	0.000	0.050	0.017	0.067	0.033	0.000	0.000
H_{OBS}	0.036	—	0.461	0.483	0.613	0.367	0.333	0.300	0.433	0.367	0.200	0.250
H_{EXP}	0.036	—	0.443	0.504	0.537	0.422	0.367	0.292	0.425	0.396	0.235	0.324
Sdh-2												
a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
c	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.949	1.000	1.000	1.000	1.000
d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
H_{OBS}	—	—	—	—	—	—	—	0.100	—	—	—	—
H_{EXP}	—	—	—	—	—	—	—	0.098	—	—	—	—

1987). Standard errors were calculated as described by Nei *et al.* (1985) and displayed on UPGMA cluster diagrams (± 1 SE).

Results

The *Sesarma reticulatum* complex was monomorphic across the entire range sampled for seven of the 20 presumptive loci examined (*Ark, Hk, Ldh, Mdh-1, Mpi, Sdh-1,* and *Sod*). In the *Uca minax* complex, five of the 18 loci (*Ark, Eno, PepLg, Mdh-1,* and *Sod*) tested were monomorphic for the entire range sampled. Many loci possessed local rare alleles with frequencies <5% (e.g., *Acp-1, Got-1, Mdh-2,* and *Sdh-2* for the *S. reticulatum* complex (Table 3); *Aladh, Hk, Idh-1, Mdh-2, Mpi, PepLa,* and *Pgdh* for the *U. minax* complex (Table 4)). Atlantic and Gulf of Mexico samples of the *S. reticulatum* complex demonstrated fixed or nearly fixed differences in alleles for *Idh-2, PepLa-2,* and *PepLg-1*. For other loci, the dominant allele in Atlantic samples was present in northwestern Florida samples, but largely absent from western Gulf samples (e.g., for *Got-2,* Atlantic mean = 0.973, Florida mean = 0.430, and western Gulf mean = 0.084). This pattern is repeated in *Got-2, Gpi,* and *Pgm* loci. In the *Uca minax* complex, a similar pattern is distinguishable for the *Idh-2* and *Sdh-1* loci, although the Gulf localities do not show a distinct east to west separation. However, the extreme western Gulf populations from Louisiana do exhibit a distinct allelic shift from $Idh\text{-}2^d$ to $Idh\text{-}2^c$.

While genetic separation in the *S. reticulatum* complex is greater between Gulf and Atlantic regions than in the *Uca minax* complex, *U. minax* possessed a greater av-

Table 4. Allele frequencies and heterozygosities for 13 loci in eight collections of the *Uca minax* complex. Alleles are identified by lower case letter; multiple loci are identified by Arabic numeral. H_{OBS} and H_{EXP} represent observed and expected (unbiased) heterozygote frequencies, respectively. "—" indicates absence of heterozygotes for localities with only homozygotes. Locality abbreviations and sample sizes are given in Fig. 1.

	Locality							
Locus	PINC	NBGA	OSFL	MBAL	PRMS	SPMR	DULA	CPLA
Aladh								
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.933
b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017
c	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050
H_{OBS}	—	—	—	—	—	—	—	0.033
H_{EXP}	—	—	—	—	—	—	—	0.128
Got-2								
a	1.000	1.000	0.983	1.000	0.967	1.000	0.933	0.983
b	0.000	0.000	0.017	0.000	0.033	0.000	0.067	0.017
H_{OBS}	—	—	0.033	—	0.067	—	0.133	0.033
H_{EXP}	—	—	0.033	—	0.065	—	0.126	0.033
Gpi								
a	0.000	0.000	0.051	0.000	0.017	0.036	0.000	0.000
b	0.167	0.167	0.283	0.150	0.200	0.321	0.117	0.267
c	0.650	0.716	0.433	0.567	0.400	0.357	0.567	0.567
d	0.183	0.117	0.233	0.283	0.383	0.286	0.316	0.166
H_{OBS}	0.600	0.533	0.800	0.667	0.600	0.786	0.567	0.567
H_{EXP}	0.524	0.453	0.686	0.586	0.664	0.712	0.574	0.590
Hk								
a	1.000	0.967	1.000	1.000	1.000	1.000	1.000	1.000
b	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000
H_{OBS}	—	0.000	—	—	—	—	—	—
H_{EXP}	—	0.065	—	—	—	—	—	—
Idh-1								
a	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000
b	1.000	1.000	0.950	0.983	1.000	1.000	1.000	0.983
c	0.000	0.000	0.033	0.017	0.000	0.000	0.000	0.017
H_{OBS}	—	—	0.100	0.033	—	—	—	0.033
H_{EXP}	—	—	0.098	0.033	—	—	—	0.033
Idh-2								
a	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.050
b	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.000
c	0.000	0.000	0.083	0.033	0.050	0.036	0.350	0.783
d	0.033	0.000	0.467	0.684	0.567	0.643	0.334	0.167
e	0.950	1.000	0.450	0.283	0.383	0.321	0.250	0.000
f	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000
H_{OBS}	0.100	—	0.400	0.300	0.667	0.428	0.333	0.267
H_{EXP}	0.098	—	0.582	0.459	0.538	0.500	0.713	0.362
Ldh								
a	1.000	1.000	1.000	1.000	1.000	0.929	1.000	1.000
b	0.000	0.000	0.000	0.000	0.000	0.071	0.000	0.000
H_{OBS}	—	—	—	—	—	0.000	—	—
H_{EXP}	—	—	—	—	—	0.137	—	—
Mpi								
a	1.000	1.000	0.983	1.000	1.000	1.000	1.000	1.000
b	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000
H_{OBS}	—	—	0.033	—	—	—	—	—
H_{EXP}	—	—	0.033	—	—	—	—	—

Table 4. Continued.

Locus	Locality							
	PINC	NBGA	OSFL	MBAL	PRMS	SPMR	DULA	CPLA
Mdh-2								
a	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	0.967	0.967	0.983	0.983	1.000	1.000	1.000	1.000
c	0.000	0.033	0.000	0.017	0.000	0.000	0.000	0.000
d	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000
e	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000
H_{OBS}	0.067	0.067	0.033	0.033	—	—	—	—
H_{EXP}	0.066	0.065	0.033	0.033	—	—	—	—
PepLa								
a	1.000	1.000	1.000	1.000	1.000	1.000	0.983	1.000
b	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000
H_{OBS}	—	—	—	—	—	—	0.033	—
H_{EXP}	—	—	—	—	—	—	0.033	—
Pgdh								
a	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000
b	0.983	1.000	0.966	1.000	0.983	1.000	1.000	1.000
c	0.017	0.000	0.000	0.000	0.017	0.000	0.000	0.000
d	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000
H_{OBS}	0.033	—	0.067	—	0.033	—	—	—
H_{EXP}	0.033	—	0.066	—	0.033	—	—	—
Pgm								
a	0.033	0.000	0.000	0.017	0.017	0.036	0.000	0.033
b	0.000	0.000	0.000	0.000	0.000	0.000	0.067	0.000
c	0.834	0.900	0.966	0.833	0.867	0.893	0.717	0.900
d	0.100	0.100	0.000	0.083	0.000	0.000	0.133	0.067
e	0.033	0.000	0.017	0.050	0.066	0.071	0.083	0.000
f	0.000	0.000	0.017	0.017	0.050	0.000	0.000	0.000
H_{OBS}	0.333	0.133	0.067	0.333	0.267	0.214	0.333	0.200
H_{EXP}	0.298	0.183	0.066	0.300	0.246	0.204	0.465	0.187
Sdh-1								
a	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.017
b	0.000	0.050	0.450	0.450	0.350	0.500	0.400	0.517
c	1.000	0.933	0.533	0.533	0.650	0.500	0.566	0.433
d	0.000	0.017	0.017	0.017	0.000	0.000	0.017	0.017
H_{OBS}	—	0.133	0.500	0.633	0.500	0.571	0.700	0.567
H_{EXP}	—	0.128	0.521	0.521	0.463	0.518	0.527	0.553

erage number of alleles (1.64 ± 0.08) and a greater mean frequency of polymorphism (0.215) within populations than did the *S. reticulatum* complex (1.38 ± 0.05 and 0.167, respectively, Table 5). Observed and expected heterozygosities were in relative agreement for both complexes and suggest no heterozygote deficiencies within populations for both species. Mean observed heterozygosities (H_{OBS} ± SE) summed across all individuals and loci were 0.130 ± 0.003 for the *S. reticulatum* complex and 0.134 ± 0.004 for the *U. minax* complex.

Individual loci demonstrated high heterozygote deficiencies (large F_{IL} values, Table 6) which were attributable to single individuals that were homozygous for a rare allele at that locus. The overall jackknife means (Weir and Cockerham, 1984) for F_{IL} were similar for the two species. The *U. minax* complex possessed a significantly higher jackknife mean F_{LR} than did the *S. reticulatum* complex (α = 0.05, Student's *t*-test). The major component of variation in *S. reticulatum* was that between regions (F_{RT}); that of *U. minax* was not statistically different between regions (F_{RT}) or among populations (F_{IL}) according to jackknife means. The *S. reticulatum* complex possessed much higher genetic differentiation on either side of the Florida peninsula (jackknife mean F_{RT} = 0.795 ± 0.090) than did the *U. minax* complex (jackknife mean F_{RT} = 0.118 ± 0.062).

Table 5. Estimation of genetic variability for 20 loci within 12 demes of the *Sesarma reticulatum* complex and 18 loci within eight demes of the *Uca minax* complex. $\bar{N}_a$ = mean number alleles per locus ± standard error; frequency of polymorphism determined by the 95% criterion (locus is polymorphic if frequency of most common allele does not exceed 0.95). Observed (H_{OBS}) and expected (H_{EXP}) heterozygote frequencies are means summed across all loci ± standard error.

Collection	$\bar{N}_a$	Frequency polymorphism	H_{OBS}	H_{EXP}
		Sesarma reticulatum complex		
PINC	1.30 ± 0.17	0.050	0.020 ± 0.005	0.023 ± 0.015
NBGA	1.35 ± 0.11	0.100	0.023 ± 0.006	0.032 ± 0.020
SUFL	1.20 ± 0.09	0.200	0.069 ± 0.016	0.078 ± 0.021
ARFL	1.40 ± 0.18	0.200	0.084 ± 0.011	0.079 ± 0.017
WBFL	1.35 ± 0.15	0.150	0.077 ± 0.011	0.076 ± 0.013
DIAL	1.35 ± 0.17	0.150	0.042 ± 0.008	0.047 ± 0.018
PRMS	1.30 ± 0.16	0.150	0.043 ± 0.008	0.045 ± 0.019
COLA	1.70 ± 0.25	0.200	0.050 ± 0.009	0.054 ± 0.023
CPLA	1.40 ± 0.17	0.200	0.070 ± 0.010	0.069 ± 0.021
SPTX	1.40 ± 0.17	0.200	0.055 ± 0.009	0.061 ± 0.022
BSTX	1.45 ± 0.15	0.150	0.033 ± 0.007	0.040 ± 0.021
RGTX	1.35 ± 0.15	0.250	0.047 ± 0.012	0.061 ± 0.029
		Uca minax complex		
PINC	1.55 ± 0.23	0.111	0.063 ± 0.010	0.057 ± 0.020
NBGA	1.39 ± 0.16	0.167	0.048 ± 0.009	0.050 ± 0.020
OSFL	1.89 ± 0.24	0.167	0.113 ± 0.014	0.118 ± 0.018
MBAL	1.67 ± 0.27	0.222	0.111 ± 0.013	0.107 ± 0.019
PRMS	1.61 ± 0.24	0.222	0.118 ± 0.014	0.112 ± 0.018
MRLA	1.50 ± 0.22	0.278	0.111 ± 0.020	0.115 ± 0.025
DULA	1.78 ± 0.31	0.278	0.117 ± 0.014	0.136 ± 0.019
CPLA	1.72 ± 0.24	0.278	0.094 ± 0.012	0.105 ± 0.022

Table 6. *F*-statistics for sampled populations of the *Sesarma reticulatum* and *Uca minax* complexes. F_{IL} = level of genetic differentiation among individuals within localities (positive values indicate a reduced number of heterozygous individuals in a locality); F_{LR} = level of genetic differentiation among localities within regions (Atlantic and Gulf of Mexico); F_{RT} = level of genetic differentiation among regions within total range sampled. Estimates for each locus are summed across all alleles for that locus. Means over all loci are arithmetic means across all alleles and loci. * signifies locus not scored for that species. — signifies that locus is monomorphic for that species; *F*-statistics are undefined for monomorphic loci.

	S. reticulatum complex			*U. minax* complex		
Locus	F_{IL}	F_{LR}	F_{RT}	F_{IL}	F_{LR}	F_{RT}
Acp	0.001	0.000	0.008	*	*	*
Aladh	1.000	0.035	0.000	0.744	0.031	0.000
Got-1	0.002	0.000	0.000	*	*	*
Got-2	0.042	0.147	0.674	0.000	0.017	0.000
Gpi	0.016	0.020	0.623	0.013	0.019	0.031
Hk	—	—	—	1.000	0.000	0.112
Idh-1	0.217	0.051	0.017	0.000	0.008	0.000
Idh-2	0.001	0.001	0.984	0.245	0.364	0.224
Ldh	—	—	—	1.000	0.051	0.000
Mpi	—	—	—	0.001	0.001	0.000
Mdh-2	0.001	0.000	0.004	0.000	0.000	0.023
Pgdh	0.658	0.006	0.008	0.000	0.001	0.000
PepLa	1.000	0.000	0.994	0.001	0.000	0.000
PepLg	1.000	0.052	0.994	—	—	—
Pgm	0.033	0.160	0.534	0.047	0.027	0.002
Sdh-1	—	—	—	0.000	0.126	0.112
Sdh-2	0.001	0.009	0.000	*	*	*
Mean	0.086	0.097	0.788	0.080	0.144	0.109
Jackknife mean	0.071	0.101	0.795	0.072	0.150	0.118
SE	0.046	0.043	0.090	0.060	0.101	0.062

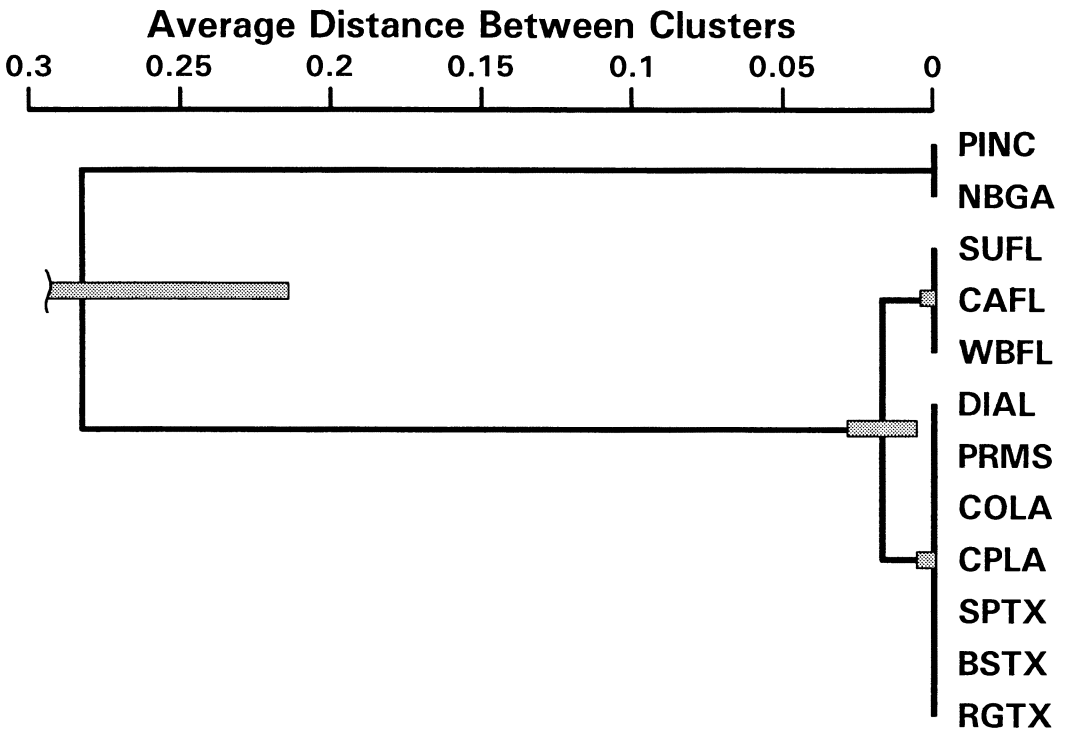

Fig. 2. Dendrogram of UPGMA cluster analysis for sample localities of *Sesarma reticulatum* complex based on D_N derived from 20 presumptive loci. Locality abbreviations identified in Fig. 1. Error bars represent ± one standard error. Long bars are truncated at 0 or left margin.

Where variation between regions was large, it could have served to inflate the overall F_{IT}, which in turn could have led to overestimation of other F statistics because of its relationship with F_{IL} ($F_{RT} = (F_{IT} - F_{IL})/(1 - F_{IL})$; where R refers to regional level). As only *Sesarma* demonstrated a large F_{RT}, the analysis of F_{LR} for *Sesarma* was repeated while artificially restricting the data set to only the Gulf of Mexico samples. The resultant F_{LR} (jackknife mean 0.081 ± 0.013) was not markedly different from the F_{LR} determined in analysis of the combined Gulf and Atlantic samples.

While UPGMA and neighbor-joining analyses demonstrated similar trends in the data set, some authors have argued recently for the superiority of the neighbor-joining method (Nei, 1991). By either analysis, a large discontinuity was shown to occur between Atlantic and Gulf populations of the *Sesarma reticulatum* complex (Figs. 2, 3). The allelic composition of Atlantic and Gulf populations was found to be diverged at an average D_N of 0.276 ± 0.009 with a range from a minimum D_N of 0.206 between Pivers Island, North Carolina, and Suwannee, Florida, populations and a maximum D_N of 0.323 between Brunswick, Georgia, and Bayside, Texas, populations (Figs. 2, 3). However, allelic composition comparisons between Atlantic populations (Pivers Island and Brunswick) were essentially the same ($D_N = 0$) over a straight line distance of greater than 1,100 km. Within the Gulf of Mexico, smaller clusters of sample localities were distinguishable within eastern and western Gulf extremes of the population. Populations of the *Uca minax* complex showed some evidence of this same pattern of divergence between the Gulf and Atlantic but at much lower levels of significance and to a much lesser degree (mean $D_N = 0.0394$ ± 0.004 for all pairwise comparisons of trans-Florida sites) than in *Sesarma,* and they exhibited no distinct subclusters of sample localities within eastern and western Gulf populations (Figs. 4, 5).

Discussion

Isolation of Atlantic populations from Gulf of Mexico populations of the *Sesarma*

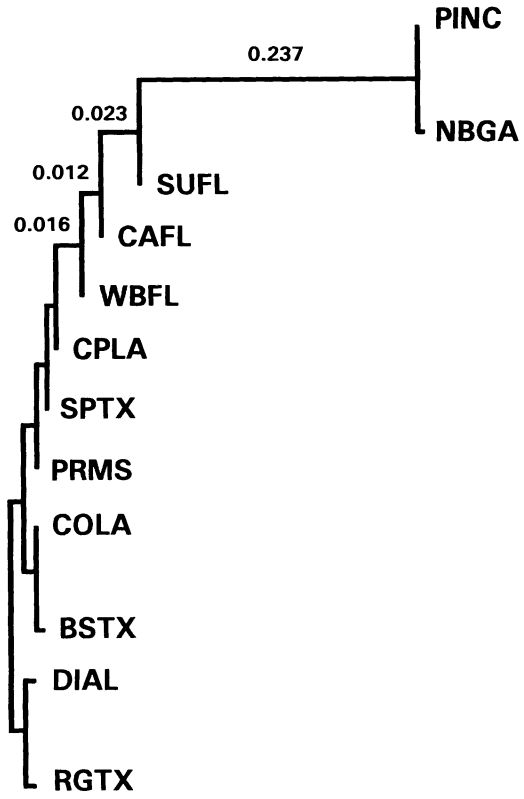

Fig. 3. Dendrogram derived for sample localities of the *Sesarma reticulatum* complex by the neighbor-joining algorithm based on 20 presumptive loci. Locality abbreviations identified in Fig. 1. Numbers above transverse bars indicate genetic distances; distances <0.01 are not shown.

reticulatum complex is evident in our analyses, in terms of both differential fixation for diagnostic alleles in the separate populations and in the high mean F_{RT} calculated for all polymorphic loci. Genetic distances measured between Atlantic and Gulf populations of *Sesarma* exceed those reported by Bert (1986) to separate *Menippe mercenaria* from *M. adina,* and fall within the range of values previously reported in interspecific comparisons of many other decapod crustaceans (see Hedgecock *et al.,* 1982; Lavery and Fielder, 1993). While our genetic analysis of Atlantic and Gulf populations of the *Uca minax* complex do not exhibit a strong differentiation, such as that seen in populations of *Sesarma,* a similar genetic pattern is inferred where subpopulations are separated across the Florida peninsula. Low numbers of alleles and small genetic distances in this complex, given the limitations of our sample size, preclude our assigning statistical significance to a trans-Florida separation in this species, at least on the basis of our present genetic approach. However, we note from ongoing genetic analyses of other species of the subgenus *Minuca* in our laboratory (*Uca longisignalis* and *Uca rapax* (Smith); unpublished data) that low heterozygosity and small genetic distances may be characteristic of allozyme analyses for species in this subgenus. Genetic distance separating regional populations of *Uca minax,* as in other populations of *Minuca* that are under study, is substantially less than that reported in the interspecific comparison of two members of the subgenus *Celuca, Uca speciosa* (Ives) and *Uca spinicarpa* Rathbun (D = 0.70, I = 0.50), by Salmon *et al.* (1979). However, those higher values for genetic distance are also perhaps not surprising for the *U. speciosa/ U. spinicarpa* comparison, given striking morphological and ecological characteristics that also separate those two well-diverged species (Heard, 1977; Barnwell and Thurman, 1984; DLF, unpublished data). This is not to say that correspondence is always to be found between allozymic analysis and morphology or behavior in species of *Uca,* especially in the subgenus *Minuca.* Salmon and Kettler (1987) argued in particular for the resurrection of "*Uca virens*" from the *Uca* (*Minuca*) *rapax* complex on the basis of behavioral evidence, despite apparent isozymic and morphological identity of the populations in question (though we conclude that design limitations of their behavioral study leave that issue yet to be resolved).

In both the *S. reticulatum* and *U. minax* complexes, Atlantic populations are nearly identical genetically between two widely separated localities, while Gulf populations appear to be more complexly structured over such geographic distances. In Gulf populations of the *S. reticulatum* complex, this structure appears limited to grouping of localities from the extreme eastern Gulf of Mexico (all samples from northwest Florida) separately from those ranging over the remainder of the northern and western Gulf, albeit at a relatively low level of separation. Similarly, but at much lower levels of significance, sampled localities of the *U. minax* complex from the eastern to midnorthern

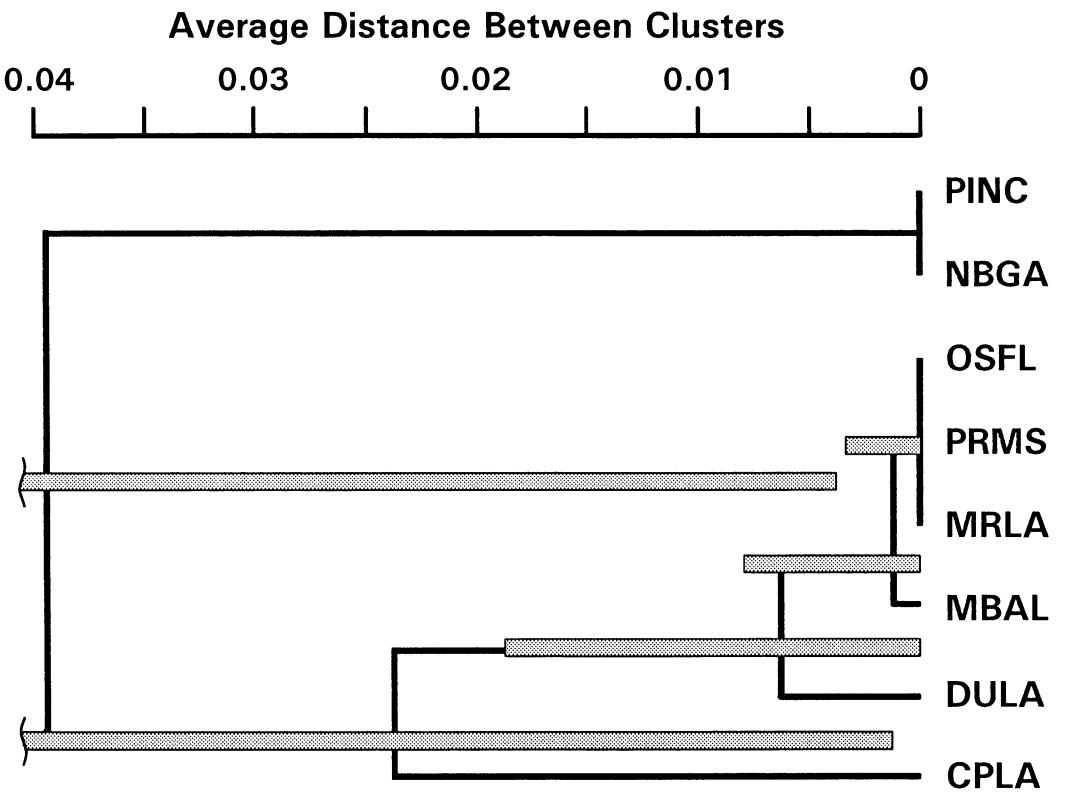

Fig. 4. Dendrogram of UPGMA cluster analysis for sample localities of the *Uca minax* complex based on D_N derived from 18 presumptive loci. Locality abbreviations identified in Fig. 1. Error bars represent ± one standard error. Long bars are truncated at 0 or left margin.

Gulf (western Florida to the Mississippi River) group together, though rare alleles from sample localities west of the Mississippi River may indicate more isolation of that subpopulation, either historically or by contemporary barriers to gene flow.

The pronounced genetic separation between Atlantic and Gulf populations of the *Sesarma reticulatum* complex correlates well with a striking difference that we observed in their coloration. Among several common names that have been applied to the Atlantic coast population, the often used "purple marsh crab" is particularly appropriate. Dorsally, ground color of the carapace in this group ranges from deep purple to bluish-black or dark slate gray, usually with some spots or reticulations of white or pale yellow; anteroventrally on the carapace, on anterior and posterior surfaces of the walking leg meri, and on much of the chelipeds, lighter shades of this ground color may range to violet or wine colors. By contrast, dorsal ground color of the carapace in almost all animals taken in the Gulf of Mexico ranges from reddish brown to rust, or occasionally dark salmon; anteroventrally on the carapace, on anterior and posterior surfaces at the walking leg meri, and on much of the chelipeds, lighter shades of this ground color may vary between vermilion red, orange, salmon, yellow orange, or yellow. Routine occurrences of anomalously colored specimens in the Gulf population were limited in our collections almost exclusively to the three Florida sites, which also tended to group genetically. These anomalous color morphs (alluded to by personal communication from DLF as one of two color morphs "in the Gulf of Mexico" by Abele, 1992: 1,7) typically had a broken coverage of ground color, with light and dark patches dorsally, and occasionally had anteroventral areas of the carapace of a deep coral, or reddish-violet coloration; however, overall ground color still tended to be much nearer

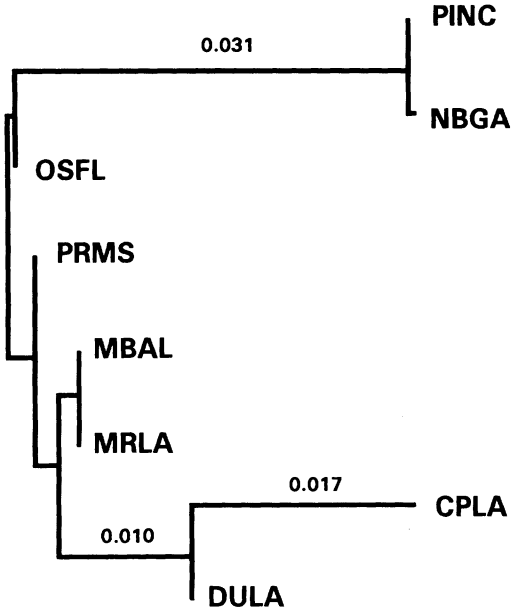

Fig. 5. Dendrogram derived for sample localities of the *Uca minax* complex by the neighbor-joining algorithm based on 18 presumptive loci. Locality abbreviations identified in Fig. 1. Numbers above transverse bars indicate genetic distances; distances <0.01 are not shown.

orange or reddish brown, than it did shades of purple or violet. While we found these color morphs to somewhat resemble patterns in juvenile specimens of the tropical species *Sesarma curacaoense* de Man (as was also reported to occur in populations of *S. reticulatum* from southeastern Florida; Abele, 1992) and agree that additional study is needed in these range extremes, we do not find that presently known differences in color, morphology, or allozymes support recognition of eastern Gulf populations as a separate species from the remainder of the Gulf of Mexico population. Rather, in accord with the species separation suggested in our previous reports (Zimmerman and Felder, 1990, 1991), the color distinction which supports recognition of separate species (Felder and Zimmerman, in preparation) is that which separates Gulf of Mexico from Atlantic populations.

In addition to divergent coloration in the two populations of *Sesarma,* possible divergence at a functional level has been reported in reproductive biology (Zimmerman and Felder, 1991) and in osmoregulatory ability (Staton and Felder, 1992). In the former case, differences in timing and phase-setting of reproductive events suggest possible adaptation to higher seasonal temperatures of the Gulf populations, while in the latter case osmoregulatory differences suggest a possible divergence in adaptive strategy to accommodate contemporary or historical differences in the salinity structure and tidal range of the Gulf and Atlantic habitats. In both these studies, differences between the Atlantic and Gulf populations were deemed to warrant treatment of Gulf populations under the label "*Sesarma* sp. (nr. *reticulatum*)," as opposed to *S. reticulatum* which was applied to the Atlantic populations. Since, in both studies, only animals from the western Gulf (Louisiana) were used for comparisons to Atlantic populations, it is unknown whether the observations reported apply equally well to the eastern Gulf subpopulation (Florida).

Appropriate salt, brackish, intermediate, and fresh marsh habitats (*Spartina, Juncus, Scirpus, Sagittaria, Vigna,* and shrubs along tidal stream banks) are widely available along most of the northern and northwestern Gulf shoreline for colonization by the *S. reticulatum* complex. Even though larval life history is restricted to three zoeal stages in these animals (lasting about 17 days; Zimmerman and Felder, 1991), close proximity of adjacent habitats would appear to maintain gene flow between sample localities over most of the Gulf range. Only west of Cape San Blas in northwestern Florida, and perhaps in extreme south Texas, are there substantial distances devoid of appropriate habitat. The former of these breaks may favor maintenance of a slight genetic separation that we observed between Florida demes and the remainder of the Gulf population. As for the two widely separated Atlantic coast localities, both color and allozyme characteristics appear to be very similar, and this may relate to relative continuity of appropriate habitat and effectiveness of longshore dispersal within this region. However, inclusion of additional sample localities from the Atlantic coast range of *S. reticulatum* will be required in order to more fully understand dynamics there.

Relationship of coloration to evidence for genetic separation in the *U. minax* complex is less apparent than in *Sesarma.* Typical

coloration with striking deep red markings at articulations between articles of the chelipeds and walking legs (a pattern most developed in males), was characteristic of specimens from the Atlantic population (as previously described by Williams, 1965; 1984b; Crane, 1975) and was also well developed in animals from the three westernmost localities (Louisiana) of the Gulf population (as previously noted by Felder, 1973). This articular coloration was very weak to absent in almost all animals taken from Overstreet, Florida, and was weakly developed in almost all animals comprising samples from Alabama and Mississippi. In comparison to our genetic grouping of the Gulf of Mexico localities, it was poorly developed in at least three of the four localities that formed the eastern to midnorthern Gulf group. Except for this divergence in coloration and the limited evidence for genetic divergence that we can presently measure between Atlantic and Gulf populations of the *U. minax* complex, little else is known to reflect trans-Floridian divergence. In both the Atlantic and Gulf populations, larval life history encompasses five planktonic zoeal stages, which at least in the Gulf population complete development within about 20 days (Hyman, 1920; Flynn and Felder, in preparation). The tidal stream bank and marsh habitats occupied are similar in most respects between all sampled localities of the Atlantic and Gulf populations, except that those of upper Mobile Bay and at the two sites west of the Mississippi River appear to be more isolated within upper estuaries than are others east of the Mississippi River and those of the Atlantic coast. Such physical isolation may at least in part account for a slight genetic separation of these demes from the remainder of the Gulf population.

Distributions of both the grapsid and the ocypodid crab populations that we have here examined are conspicuously habitat-dependent. Within slight ranges of variation (as noted above), their contemporary preferred habitats are warm-temperate intertidal vegetated banks and peaty soils of estuaries, typically within or adjacent to marshes of varied salinity. As for historical origins of divergent trans-Floridian populations in either group, divergent populations may have been derived from partitioning of a once panmictic, polymorphic group distributed within a formerly continuous area of warm-temperate habitat. While the contemporary expanse of appropriate habitat is interrupted in southern Florida by calcareous substrates, tropical waters, and absence of typical warm-temperate marsh vegetation, there is evidence that salt-marsh habitats, appropriate sedimentary facies, and warm-temperate climatic conditions formerly extended across southern reaches of the Florida peninsula, perhaps persisting into the Holocene transgression (see review by Barnwell and Thurman, 1984). It appears even more probable that such continuous habitats would have prevailed during earlier periods, perhaps during a peak of glacial advance, when warm-temperate environments were generally displaced to the south. Of particular significance for intertidal species, winter temperatures during peak glacial advance plummeted at latitudes north of 30°, while they fell only slightly in tropical seas (McIntyre *et al.*, 1976), and it is thus doubtful that appropriate climate for warm-temperate marsh-dwelling forms would have persisted during this period either in the northern Gulf of Mexico or along much of the southeastern seaboard of the United States. Evidence suggests that, at 18,000 ybp, winter surface-water temperatures along the continental margins of the Gulf averaged 4–5°C lower than at present, and the 20° winter isotherm was displaced into the southern Gulf of Mexico (Brunner, 1982). It has been hypothesized that such changes would have shifted ranges of both temperate and tropical intertidal crabs to relatively lower latitudes, perhaps into refugia of the southern Gulf of Mexico (Barnwell and Thurman, 1984). With sea-level and coastal sea temperature rise during the Holocene transgression, and increase in both these parameters during the "post-glacial optimum" to levels even greater than at present (Gribbin and Gribbin, 1990: 123), it is likely that panmictic warm-temperate intertidal assemblages moved north and that gene flow became, to various degrees, restricted by discontinuity of warm-temperate habitats across southern extremes of the Florida peninsula. With a slight subsequent fall in both sea-level and sea temperatures during the last 7,000 years, there appears to have been both more extensive emergence of the

Florida peninsula and some reextension of warm-temperate habitats to the south (Scholl and Stuiver, 1967; Field *et al.*, 1979), which could, in the first case, have favored further isolation of partitioned populations or, in the latter case, have facilitated some increased gene flow between them.

Thus, a complex set of physical dynamics, both during and following peak glacial advance, could account for the trans-Floridian genetic partitioning we observe in contemporary populations. A less conspicuous but complex genetic structure within the Gulf may then reflect the history of genetic segregation in subpopulations which postglacially dispersed from panmictic southern (glacially displaced warm-temperate) populations northward along western Gulf shorelines. Regardless of whether such subpopulations may have originated by such a western Gulf tract or were later isolates of the eastern Gulf population, the history of gene flow between sites in the northern Gulf would almost certainly have been impacted by postglacial alluvial flow and sedimentary events that were key determinants of contemporary physiography and hydrology in the northern Gulf of Mexico. From changes in major river courses to changes in the distribution of coastal sediments and vegetation, an array of factors has likely impacted present distribution and partitioning of northern Gulf populations.

In studies of trans-Floridian divergence in the *Menippe* complex, another nearshore brachyuran crab genus, much earlier historical events (12–2 mybp) have been suggested to explain isolation of two species and subsequent hybridization between them (Bert, 1986; Bert and Harrison, 1988). These events, such as periodic opening of the Suwannee Straits during the Miocene or Pliocene, were invoked to explain genetic relationships in large part because of their congruence with divergence times estimated from allozyme data. However, it is questionable whether divergence times can be predicted with reliability for these stocks from allozyme data. While neutral theory predicts divergences between protein and DNA sequences of species to occur at nearly a constant rate (Wilson *et al.*, 1977; Kimura, 1983), detection of this variation at the allozyme level is confounded by silent substitutions, substitutions for similarly charged amino acids, and fluctuating stochastic population parameters which contribute synergistically to variation among populations. Although several researchers have correlated allozymic distances with albumin immunological distances (Wilson *et al.*, 1974; Case *et al.*, 1975; Sarich, 1977; Maxson and Maxson, 1979; Wyles and Gorman, 1980), the majority of these correlations involve parameters estimated from data on herpetofauna and may not be readily applicable to a wide range of phylogenetic groups. We conclude that, while allozyme patterns may greatly enhance studies of biogeography, it is not possible to derive adequate estimates of divergence times for species or populations on the basis of an allozyme "clock" as was earlier done by McCommas (1982) and others. It is also noteworthy that the very existence of a "molecular clock" is questionable (see Gillespie, 1991: 139–141).

In the course of their studies on trans-Floridian partitioning of *Hydractinia* populations (commensal hydroids of hermit crabs), Cunningham *et al.* (1991) have also argued that contact must have predated peak glacial advances, since ranges of nearshore cold-temperate Carolinian ostracods were not found to have extended south of northeastern Florida during these glacial periods (Cronin, 1988). However, this observation must be examined in the full context of glacial events as they affected eastern Florida, including changes in sea level during peak glaciation that would have placed the shoreline over 100 m lower than present eustatic levels (Stanley, 1986). Given the narrowness of the eastern Florida shelf, a significant drop in sea level would effectively eliminate a shallow-water region on the eastern margin of Florida, since the coast would give way directly to the Blake Plateau. At this lower stand of sea level, depths adjacent to shoreline here would have been near 650 m or greater (Sheridan and Enos, 1979). Therefore, for absence of appropriate habitat, a shallow, cold-temperate Carolinian continental shelf ostracod fauna might not be expected to occur off eastern Florida during peak glacial advance, regardless of whether or not warm-temperate species were being displaced to the south. Even without this complication of the record, we would argue that measurable paleotransitions of an offshore continental shelf ostracod as-

semblage would not necessarily reflect conditions directly impacting shallow coastal or intertidal faunal distributions during peak glacial advance. Strong evidence for cold, dry climates in terrestrial environments of the southeastern United States between 23,880 and 14,600 ybp (Watts and Stuiver, 1980) suggests that shallow coastal environments would also have been considerably colder during this period than at present. Average January temperatures in the southeastern United States were perhaps 17°C lower than at present, and "evidence suggests that tropical conditions disappeared in seas fringing the Florida peninsula" (Stanley, 1986).

It is difficult to envision any historical scenario for evolution of intertidal and nearshore trans-Floridian species complexes that would not involve major impacts of glacial activity, especially given extensive evidence for latitudinal displacements in water-surface temperatures, pluvial effects on coastal habitats, sea level changes, changes in distributions of coastal vegetated habitats, and periodic massive coastal discharges of glacial meltwaters that appear to have occurred in the northern Gulf of Mexico and southeastern United States during the last 200,000 and especially the last 20,000 years (see Cronin *et al.*, 1981; Brunner, 1982; Barnwell and Thurman, 1984). Even assuming that the genetic character of intertidal and nearshore trans-Floridian populations was impacted by periodic contacts and subsequent separations dating from the Miocene or Pliocene, it appears likely that genetic signatures of those prior events would be obfuscated by a series of much later glacially modulated population displacements and resultant episodes of population contact and separation. Whether by latitudinal displacements of warm-temperate populations or physiographic modification of habitats, glaciations would appear to have periodically altered effectiveness of the Florida Peninsula as a barrier to gene flow, especially for intertidal and nearshore marine populations.

Finally, we conclude that allozyme analyses can contribute effectively toward resolving genetic consequences of such isolation events. Previous to this study, allozymic differences between Gulf and Atlantic invertebrates were addressed only for certain anemones (McCommas, 1982), stone crabs (Bert, 1986), slipper shell gastropods (Hoagland, 1984), and mussels (Sarver *et al.*, 1992). However, several other studies have documented divergence of Gulf and Atlantic populations of invertebrates on the basis of DNA analyses; these include studies of horseshoe crabs, *Limulus* (see Saunders *et al.*, 1986); oysters, *Crassostrea* (see Reeb and Avise, 1990); hydrozoans, *Hydractinia* (see Cunningham *et al.*, 1991); and hermit crabs, *Pagurus* (see Cunningham *et al.*, 1992). Reeb and Avise (1990) provided evidence that results from allozyme and DNA investigations can exhibit discordant and irreconcilable patterns, and Karl and Avise (1992) suggested that, in some instances, the balancing selection among allozymes may prevent them from differentiating in parallel with mitochondrial DNA and single copy nuclear DNA. Yet, we observe that, where significant patterns are demonstrated by allozyme data in divergent Atlantic and Gulf populations, they are in some general ways concordant with those based upon DNA. We note certain overall similarities among patterns from the analysis of allozyme and mtDNA data for *Crassostrea* (see Karl and Avise, 1992: fig. 2B, C; note that FL2, Stuart, Florida, is an Atlantic locality), the pattern for *Menippe* (see Bert, 1986: fig. 2B), that for *Sesarma* (present study; Figs. 2, 3) and, to a lesser extent, that for *Uca* (present study; Figs. 4, 5). All suggest a unique western Gulf of Mexico group, differentiation of populations between the northeastern and western Gulf, and relative homogeneity of Atlantic populations.

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