Gulf of Mexico Science

Volume 15
Number 1 *Number 1*

Article 4

1997

Population Genetics of the Blue Crab *Callinectes sapidus* from the Northwestern Gulf of Mexico

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DOI: 10.18785/goms.1501.04

SHORT PAPERS AND NOTES

Gulf of Mexico Science, 1997(1), pp. 35–39

POPULATION GENETICS OF THE BLUE CRAB *CALLINECTES SAPIDUS* FROM THE NORTHWESTERN GULF OF MEXICO.—

The adult blue crab *Callinectes sapidus* Rathbun inhabits the estuaries and marshes along the Atlantic Ocean and Gulf of Mexico from Nova Scotia to northern Argentina. Such a wide distribution is attributed to the pelagic larval stage and adult migratory behavior (Darnell, 1959; Adkins, 1972; Steele, 1991; Steele and Bert, 1994). This species supports large commercial and recreational fisheries (Moss, 1982; Roberts and Thompson, 1982; Steele, 1982; Perry et al., 1984). Successful harvests depend on many factors, among them survival rates (Heck and Coen, 1995), recruitment pattern back into the estuaries (Epifanio, 1995; Johnson, 1995), and movement of the adults along the coast (Perry, 1975; Steele, 1991). Depletion at one site, due to mortality from pollution, diseases, and overfishing, might lead to a decrease in harvest if populations are locally isolated (Perry et al., 1984).

Blue crab population structures have been studied by several authors. Cole and Morgan (1978) postulated that the homogeneity of the populations in Chesapeake and Chincoteague Bays was due to larval dispersal. In an extensive study of the blue crab populations inhabiting the Atlantic and Gulf of Mexico coasts, McMillen-Jackson et al. (1994) found an overall homogeneity of allelic frequencies superimposed by genetic patchiness; one enzyme, EST-2, exhibited clinal variation that they attributed to selection. Kordos and Burton (1993) found that several adult populations of blue crab along the Texas coast differed temporally and spatially in their GOT and EST allelic frequencies. Moreover, differences between studies were found with PGM, MDH, and ACP among Atlantic coast populations (Cole and Morgan, 1978; Nelson and Hedgecock, 1980; McMillen-Jackson et al., 1994).

The present study was undertaken to compare the genetic structure of blue crab populations from Louisiana, Alabama, and Texas.

Materials and methods.—Forty-eight crabs were collected during late spring 1992 from four localities: (1) Pass Manchac, Lake Pontchartrain, LA; (2) Barataria Bay, LA; (3) Mobile Bay, AL; and (4) Aransas Bay, TX. All crabs were adults with carapace widths ranging from 110 to 176 mm. Samples were a mixture of males and females (69%, 50%, 52%, and 87% males, respectively). Tissue preparations (muscle, gill, and hepatopancreas) and horizontal starch-gel electrophoresis have previously been described in Ayala et al. (1973) and Tracey et al. (1975). Twenty-eight enzymes and proteins were assayed: acid phosphatase (ACP; enzyme number 3.1.3.2), adenylate kinase (AK; 2.7.4.3), aldehyde oxidase (AO; 1.2.3.1), alkaline phosphatase (ALP; 3.1.3.1), aspartate aminotransferase [AAT (formerly GOT); 2.6.1.1], esterase (EST; 3.1.1.-), fumarase (FH; 4.2.1.21), glucose-6-phosphoisomerase (GPI; 5.3.1.9), glutamate dehydrogenase (GLUDH; 1.4.1.-), glucose-6-phosphate dehydrogenase (G6PDH; 1.1.1.49), glycerol-3-phosphate dehydrogenase (G3PDH; 1.1.1.8), 3-hydroxybutyrate dehydrogenase (HBDH; 1.1.1.30), hexokinase (HK; 2.7.1.1), L-iditol dehydrogenase (IDH1; 1.1.1.14), isocitrate dehydrogenase (IDHP; 1.1.1.42), leucine aminopeptidase (LAP; 3.4.11.1), lactate dehydrogenase (LDH; 1.1.1.27), malic dehydrogenase (MDH; 1.1.1.37), malic enzyme (MEP; 1.1.1.40), mannose-6-phosphate isomerase (MPI; 5.3.1.8), octanol dehydrogenase (ODH; 1.1.1.73), dipeptidase (glycylglycyl for substrate) ($DPEP_{gg}$; 3.4.-.-), tripeptidase (leucylglycylglycyl for substrate) ($TPEP_{lgg}$; 3.4.-.-), peroxidase (PERX, 1.11.1.-), phosphogluconate dehydrogenase (PGDH; 1.1.1.44), phosphoglucomutase (PGM; 5.4.2.2), general proteins (PROT), and xanthine dehydrogenase (XDH; 1.1.1.204). AK, AO, G6PDH, G3PDH, HBDH, HK, IDHP, ODH, $DPEP_{gg}$, and PERX could not be scored owing to faint or nonexistent bands. The upper band of ALP matched the upper band of ACP. Because of their indistinct banding patterns, FH and EST were eliminated despite their indications of a high level of variability. A total of 21 loci were successfully assayed.

Allelic frequencies, mean number of alleles per locus (n_a), average number of animals studied per locus (N), mean observed (H_o) and expected (H_e) heterozygosities, and proportion of polymorphic loci were calculated using the stringent (frequency of the common allele <95%, P_{95}) level for each population using the Biosys-1 statistical program (Swofford and Selander, 1981). Deviations of observed genotypic proportions from Hardy-Weinberg expected values were tested with chi-square goodness-of-fit analysis using Levene's formula for small sam-

TABLE 1. Allelic frequencies at the nine variant loci in four *Callinectes sapidus* populations. The numbers in the allele column refer to the distance of migration relative to the most common allele, noted as 100. N is the number of sampled individuals at each locus. The monomorphic loci, ACP-2, IDH1, LAP-1, MEP, MPI, $TPEP_{1gg}$, PROT-1, PROT-2, PROT-3, PROT-4, PGDH, and XDH, are not listed.

	Population			
Allele	Lake Pontchartrain	Barataria Bay	Mobile Bay	Aransas Bay
AAT				
94	0.28	0.36	0.39	0.27
100	0.72	0.64	0.61	0.73
ACP-1				
96	0.02			
100	0.98	1	1	1
N	48	48	48	41
GLUDH				
99		0.02		
100	—	0.98	1	1
N		46	48	24
N	48	44	45	46
GPI				
95				0.01
100	0.97	0.98	1	0.94
106	0.03	0.02		0.05
N	48	48	48	48
LAP-2				
100	1	0.98	1	0.99
104		0.02		0.01
N	17	40	48	46
LDH				
100	0.98	1	1	1
104	0.02			
N	24	45	48	24
MDH-1				
100	1	0.95	1	0.98
104		0.05		
106				0.02
N	39	48	48	24
MDH-2				
100	1	0.98	1	1
103		0.02		
N	48	48	48	48
PGM				
95				0.02
100	1	1	1	0.98
N	39	46	48	30

ples and Fisher's exact test for 2 × 2 contingency table (Biosys-1). Because many genotypes were present in small numbers, allelic rather than genotypic frequencies were used for tests of independence between populations using the G statistic with Williams' correction for small samples (Sokal and Rohlf, 1981).

Results and discussion.—Allelic frequencies for the tested proteins indicated that genetic variation among the four populations of *C. sapidus* was very low. Nine of the 21 loci visualized were polymorphic. Variants were found with AAT (GOT), ACP, GLUDH, GPI, LAP, LDH, MDH-1, MDH-2, and PGM (Table 1). The average number of alleles per locus ranged from 1.1 in the Mobile Bay population to 1.3 in the other populations. Polymorphism varied from a maximum of 13.3% in the Lake Pontchartrain population to 5.6% in the Mobile Bay population.

DOI: 10.18785/goms.1501.04

TABLE 2. Summary of genetic parameters in four *Callinectes sapidus* populations. Abbreviations are as follows: L, number of loci in each population; $\bar{N}$, mean sample size per locus; $\bar{n}_a$, mean number of alleles per locus per population; P_{95}, stringent polymorphic index; $\bar{H}_o$ and $\bar{H}_e$, observed and expected mean percentages of heterozygotes per locus, respectively, with standard error of the mean (SEM).

Statistic	Population			
	Lake Pontchartrain	Barataria Bay	Mobile Bay	Aransas Bay
L	15.0	20.0	18.0	18.0
$\bar{N}$	35.0	43.0	47.1	35.1
SEM	3.5	2.0	0.8	2.8
$\bar{n}_a$	1.3	1.3	1.1	1.3
SEM	0.1	0.1	0.1	0.1
P_{95}	13.3	10.0	5.6	11.1
$\bar{H}_o$	3.8	3.5	3.1	3.5
SEM	2.6	2.3	3.1	2.5
$\bar{H}_e$	4.1	3.7	2.7	3.4
SEM	2.8	2.3	2.7	2.3

The average observed heterozygosities ranged from 3.1% in the Mobile Bay population to 3.8% in the Lake Pontchartrain population and were comparable to the expected heterozygosities (Table 2). All four populations showed a good fit to the expected Hardy-Weinberg genotypic proportions ($0.038 < \chi^2 < 1.12$, df = 1, n.s.). Tests of independence of the populations based on allelic frequencies of all variant loci showed no significant differences among the four populations. A low level of genetic variation is common in many crustacean species. Nelson and Hedgecock (1980) observed a heterozygosity of 8.0% in *C. sapidus* from South Carolina. The same parameter was estimated at 8.3% and 7.1% in blue crab populations from Chincotegue and Chesapeake bays, respectively (Cole and Morgan, 1978) and at 4.0% in the survey by McMillen-Jackson et al. (1994).

In the current study, polymorphism was consistently present at only one locus, AAT (GOT), with two alleles present in this dimeric enzyme. The frequencies of the most common allele varied between 61.1% and 72.8% in the Mobile Bay and Aransas Bay populations in this study. Comparisons of AAT (GOT) data among populations inhabiting the Chesapeake Bay area (Cole and Morgan, 1978), South Carolina (Nelson and Hedgecock, 1980), and the northwestern Gulf of Mexico locations from this study do not show any significant differences in the AAT (GOT) allelic proportions (G = 6.09, df = 4, n.s., pooled data). However, spatial and temporal differences among several populations along the Texas coast were found by Kordos and Burton (1993). This enzyme was monomorphic or nearly monomorphic in 16 populations located from Amityville, NY, to Brownsville, TX (McMillen-Jackson et al., 1994).

However, the lack of genetic difference among this study's four populations suggests that at the time of sampling, they formed a common breeding population with genetic exchange both unimpeded by physical or physiological barriers and large enough to offset any differentiation brought about by selective forces. Larvae and megalopae, found offshore year-round (Rabalais et al., 1995), are subjected to currents transporting them considerable distances (Perry, 1975; Perry and Stuck, 1982; Scheltema, 1986; Sulkin and Van Heukelem, 1986; Epifanio, 1988, 1995; Johnson and Hester, 1989). In addition, adult migratory behavior further promotes genetic exchange between these neighboring populations (Oesterling, 1976; Osterling and Adams, 1982; Steele, 1991).

Thus, major anthropogenic events, such as overfishing, oil spills, and accidental chemical discharges from industries and municipalities, should not result in a collapse of the blue crab population in any one of the localities in this study. Larval dispersal and/or adult migration from the other unspoiled locations should ensure replenishment in the affected area. However, the variability of AAT (GOT) along the Texas coast (Kordos and Burton, 1993) remains intriguing. Additional electrophoretic surveys of larval, juvenile, and adult populations along the northern Gulf coast need to be completed to confirm this variability. If present, AAT (GOT), the only consistently poly-

morphic locus in this study, would be a possible candidate for monitoring spatial and temporal distributions of the blue crab populations within the Gulf of Mexico.

Acknowledgments.—We are grateful to Gary W. Childers (Southeastern Louisiana University) for his support. We thank Hayden Reno (Turtole Cove Environmental Research Station), Cameron Pratt and Scott Holt (University of Texas Marine Science Institute), Chris Camardelle (Grand Isle, LA), and Maurice, Gayle, and Richard Ryan (Dauphin Island, AL) for the crab collections. This study was funded by Faculty Development Grant 1267 from the Office of Sponsored Research of Southeastern Louisiana University.

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RANGE EXTENSION OF *MOBULA TARAPACANA* INTO THE NORTHWESTERN GULF OF MEXICO.—During the second week of August 1993, what appeared to be a pair of manta rays (*Manta birostris*) were videotaped in the daytime swimming at a depth of 24 m over the coral reef on the West Flower Garden Bank (WFGB) (27°52′N, 093°49′W) in the northwestern Gulf of Mexico. Upon careful inspection of this video footage, one animal was identified as *M. birostris,* and the second was determined to be *Mobula tarapacana,* the first occurrence recorded for this region of the western North Atlantic.

The timing of this observation coincided with the annual mass spawning of corals (August and September; e.g., Hagman et al., 1997), and the warmest bottom temperatures (mid-July to mid-September) at the Flower Garden Banks National Marine Sanctuary (FGBNMS) (K. J. P. Deslarzes, pers. comm.). The horizontal visibility over the reef and the average bottom temperature for the observation day were 25 m and 29.5 C, respectively. The WFGB comprises 40.4 ha of submerged reefs that crest at 19 m. The bank has approximately 130 m of relief. The East Flower Garden Bank and the WFGB contain the northernmost coral reefs on the North American continental shelf and are sites of extensive biogenic coral communities (46% live cover; Gittings et al., 1992) of Caribbean origin that have developed atop two salt domes (Bright et al., 1974).

Mobula tarapacana at the Flower Garden Banks.—The August 1993 video footage of the ray in question showed a medium-sized mobulid ray (2.1 m estimated disc width) with a long neck, short caropteres, and a relatively short filamentous tail (approximately 0.9 m). The dorsal surface was dark brown, and the ventral surface was white, with dark blotching and gray shading along the trailing margin of the pectoral and pelvic fins. No white coloration was evident on the dorsal fin or tail, and no caudal spine was apparent. A cigar-shaped fleshy appendage appeared to protrude from the dorsal surface near the base of the dorsal fin, extending approximately 10 cm beyond the pelvic fins. I believe this to be an ectoparasite, possibly an echeneid, and not a vestigial spine. The video also recorded a *Remora remora* attached to the mobula's dorsal surface above the left eye.

Based on the observed morphological characters, this animal is best identified as *Mobula tarapacana.* Its size is twice that known for *Mobula hypostoma,* which also frequents the Flower Garden Banks earlier in the year (unpubl. data). *Mobula japanica* and *M. mobular,* two medium to large mobulids thought possibly to range into the western North Atlantic, each possess a caudal spine, and a very long tail with a row of white denticles along both sides to the tip (Notarbartolo-di-Sciara 1987). Morphological characteristics of the observed individual (long neck, short caropteres, a relatively short filamentous tail, no evident white denticles on the side along the tail, and no caudal spine) all negate the identification of this animal as *M. japanica* or *M. mobular.* The long neck is characteristic of *M. tarapacana,* relative to other mobulid rays.

This *M. tarapacana* was observed swimming approximately 3 m above and 1.5 m behind the *M. birostris* (1.8 m estimated disc width, 0.8 m tail length), passing 2 m directly above the diver, and the two animals continued swimming in their original direction.

Another sighting of *M. tarapacana* at the WFGB was made on 21 Aug. 1995, when divers observed a single individual over a 6.5-hr time interval (1200 to 1830 hr) swimming within a 0–18 m depth range and close to the mooring line of their dive boat. This individual, recorded on video, is a medium-sized mobulid ray (2.1 m disc width) with a narrow mouth, short caropteres, a long neck, and a very truncated filamentous tail (estimated at 10 cm). Its dorsal surface was green and its ventral side bore dark shading. The video of this animal, however, is of poor quality. This sighting also coincided