ELECTROPHORETIC ANALYSES OF HEMOCYANINS FROM FOUR SPECIES OF MUD CRABS, GENUS PANOPEUS, WITH OBSERVATIONS ON THE ECOLOGY OF P. OBESUS

The mud crab, known until now as Panopeus herbstii H. Milne Edwards, s.l., of the family Xanthidae, has been regarded as a common intertidal species throughout much of its range in the western Atlantic. As such, it commonly has been used in ecological, physiological, and genetic studies (reviewed in McDonald 1977). Four morphological forms (Rathbun 1930) are recognized as species in the paper by Williams (1983), their ranges outlined, and habitat preferences shown.

As part of the study on the genetic control of hemocyanin production, we examined several hundred individuals from coastal North Carolina and found considerable evidence that two of these four forms represent separate gene pools. Additional field observations revealed that these two forms occupy distinct areas in the intertidal zone, exhibit behavioral differences, and consume different prey. However, morphological differences other than color appeared to be slight. Smaller collections of Panopeus were made at Charleston, S.C., Big Pine Key and St. Petersburg, Fla., and Grand Terre Island, La. These included individuals representing the species Panopeus herbstii H. Milne Edwards, s.s., P. lacustris Desbonne, P. obesus Smith, and P. simpsoni Rathbun. Electrophoretic analyses of their hemocyanins provide data that are compatible with taxonomic treatment of each as a distinct gene pool.

Materials and Methods

Crabs were collected by hand at low tide from the intertidal zone. Although ecological studies were confined to the area around Pivers Island, Beaufort, N.C., additional material was collected at Harkers Island and Swansboro, N.C., and at the localities mentioned above. Crabs from Big Pine Key and Grand Terre Island were shipped by air to Beaufort. The remaining crabs were bled at the collecting sites and hemocyanin samples transported on ice to Beaufort. Electrophoretic analysis of hemocyanins was performed following dissociation to monomeric subunits according to the methods of Sullivan et al. (1974) and Sullivan and Tentori (1981). Stomach analyses were made by injecting 1 ml of Formalin into the cardiac region of the crab at the time of collection, and later, following its removal, contents of the cardiac stomach were examined under a binocular dissecting microscope.

Results

In studying the electrophoretic patterns of hemocyanin from the forms of Panopeus herbstii, s.l. (Fig. 1), we associated an aberrant pattern with the color morph now recognized as P. obesus (Williams 1983). Conditions of preparation and electrophoresis of hemocyanins cause the polymeric hemocyanin to dissociate into subunits (Sullivan et al. 1974). The patterns shown in Figure 1 represent monomeric hemocyanin subunits. Six loci are active in a fiddler crab, Uca pugilator (Bosc), but the polypeptides of...
were adjacent. Simpsoni from Louisiana reveals three phenotypic
P. simpsoni P. herbstii All individuals were collected in rocky areas
obesus. Along intertidal where oyster rubble and marsh grass
were present in the lower intertidal where only shells were present, and P. obesus alone was present
in the upper intertidal where Spartina dominated; but in areas of lower salinity it appeared that P.
obesus tended to displace P. herbstii on oyster bars.

Examination of adult females in June showed one ovigerous female out of five P. obesus whereas five of
seven adult females of P. herbstii were ovigerous. Individuals of P. obesus appeared to live in burrows and
would position themselves in the entrances to defend them. In general, P. obesus appeared more aggressive
than P. herbstii. Stomach analyses of P. obesus revealed oyster spats (the primary food source of P.
herbstii), shell and sea urchin fragments, and eggs and walking legs of Uca pugnax (Smith) and perhaps
Sesarma sp., which are all primary food sources for P. obesus. Although the number of crabs examined was
small, the ratio of the cheliped dactyl length (inner length, base to tip) divided by the carapace width
averaged 0.25 for P. obesus and 0.22 for P. herbstii. If P. obesus does prey on other crabs in considerable
numbers rather than mainly on oysters, one might expect a longer dactyl as compared with the oyster-
feeding P. herbstii.

Discussion

Genetic variability at the hemocyanin loci in all populations of Panopeus which we have sampled
complicates comparisons. Such variability is characteristic of many, but not all, temperate xanthid
species (unpubl. data). Additionally, there are shifts in allelic frequencies in geographically separated
populations, and the occurrence of local alleles is not unusual. However, in all areas where we have sam­
pelled two species, hemocyanin patterns can be designated as specific in spite of the "within-species"
variability. Repeated sampling of the same individual over time has always yielded identical pat­
terns, and the alleles at each locus are invariably in Hardy-Weinberg equilibrium.

We believe the evidence for the existence of two gene pools is very strong. In addition to hemocyanin
data, Turner and Lyerla (1980) found unique alleles at the amylase, esterase, and malate dehydrogenase
loci in the two South Carolina species. For instance, the most abundant amylase allele in P. obesus was not
even present in adjacent populations of P. herbstii.

Habitat preferences are very clear in the Carolinas, at or near the northern limit of range for P. obesus. In
western Florida, P. obesus is more abundant than it is in North Carolina and may occupy a broader range of
habitats. Feeding habits in the two regions appear to

Our original samples (n = 246) of Panopeus from Beaufort, N.C., contained about 2% P. obesus. At
Charleston, S.C., (n = 38) the frequency was 24%, and at St. Petersburg, Fla., (n = 19) it was 89% P.
obesus. All individuals were collected in rocky areas or on oyster bars. Turner (1979) and Turner and
Lyerla (1980) indicated that P. obesus was common in the upper intertidal at North Inlet, S.C., where the
marsh grass, Spartina, grew in abundance. At Beaufort, N.C., our upper intertidal samples yielded
virtually 100% P. obesus. A transect of an intertidal region containing both oyster rubble and Spartina
revealed overlap for the two species only in the mid­dle intertidal where oyster rubble and marsh grass
were adjacent. Panopeus obesus was associated with burrows at the base of Spartina clumps; P. herbstii
was in and under oyster shells. Panopeus herbstii

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be dissimilar and breeding times may also differ. Detailed studies of the life histories of all the species in this complex are likely to reveal considerable differences. Unfortunately, the “forms” of *P. herbstii*, s.l., have been considered a single species and it is seldom possible to determine which “form” (= species) has been used in physiological, ecological, and behavioral experiments (McDonald 1977). The existence of four such similar species over a large range will undoubtedly provide an excellent opportunity for studies of their displacement and comparative biology.

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**MUD CRABS OF THE PANOEPEUS HERBSTII H. M. EDW., S.L., COMPLEX IN ALABAMA, U.S.A.**

The mud crab, *Panopeus herbstii*, s.l. (sensu Rathbun 1930), occupies two distinct habitats in the Mobile Bay region of Alabama—the intertidal marsh and intertidal to subtidal oyster (*Crassostrea virginica* (Gmelin)) reef (Heard 1982). This paper presents an analysis of morphological attributes and ecological associations of these mud crabs, showing that the populations observed correspond to two sympatric species, *P. obesus* Smith and *P. simpsoni* Rathbun (Williams 1983).

**Methods**

Collection of mud crabs for morphological comparisons and feeding experiments was limited to 14 stations along southwestern Mobile Bay, Ala., and nearby eastern Mississippi Sound, from Dog River to Point of Pines, including Dauphin Island (Fig. 1), where *P. herbstii*, s.l., commonly occurs in a salinity range of 14 to > 20 ppt (May 1974). Figure 1 shows the location of stations which were sampled for crabs before destructive Hurricane Frederick struck in September 1978. The crabs, most numerous in waters with salinity > 20 ppt, were sampled on four general types of substrate as follows: 1) Intertidal rubble (pieces of broken concrete over shell hash and silty sand at stations 1, 3, 4, 5, and oyster shell beach at station 2); collected by hand and in small mesh net from beneath pieces of cover. 2) Undercut marsh (mud eroded from beneath floating overhang of vegetation at edge of marsh leaving mat still attached to marsh sod at stations 6, 7, 8); collected by hand and in small mesh net from beneath pieces of cover. 3) Mud bank (banks of hard mud