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 *PANOPEUS 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); overhanging mat was partly cut from bank with shovel and flipped over onto marsh to expose roots from which many small and some larger crabs were collected, mat then returned to water. 3) Mud bank (banks of hard mud

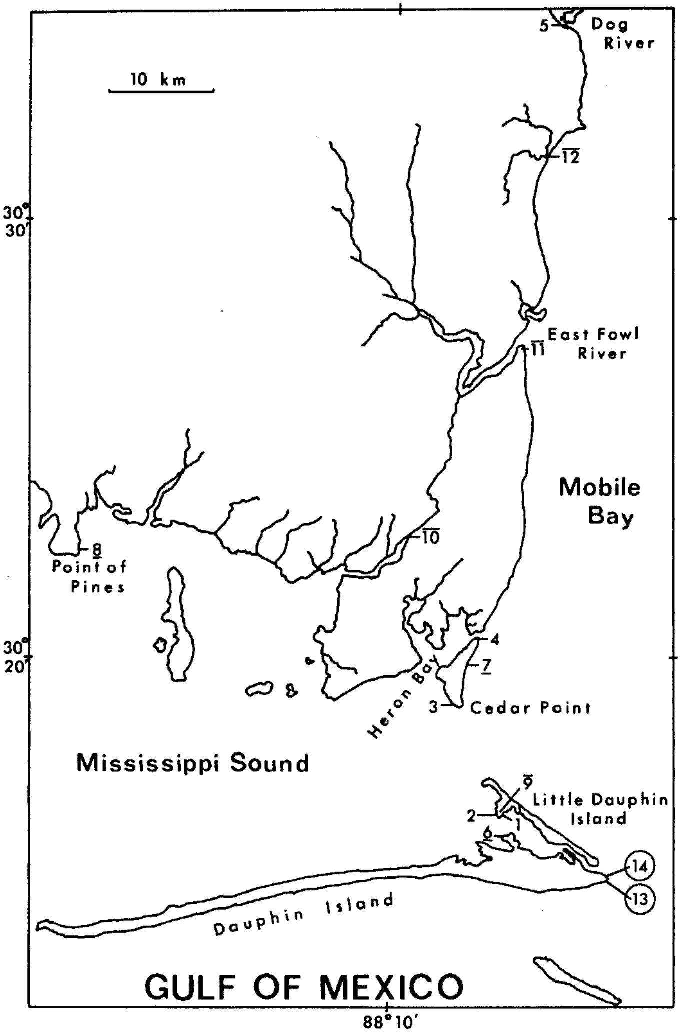

FIGURE 1.—Section of the northern Gulf of Mexico showing southwestern Mobile Bay and eastern Mississippi Sound with indicated prominent physical features and location of numbered sampling stations discussed in text. Station substrate types: unmarked = intertidal rubble and shell beach; underscored = undercut marsh; overscored = mud bank; encircled = jetty.

containing *Juncus* and *Spartina* roots and marsh mussel (*Geukensia*) shells, generally about 1 ft (30 cm) in depth from top of marsh surface to bottom of silty mud along tidal creeks at stations 9, 10, 11, 12); from burrows 2-4 ft (61-122 cm) long × 2-3 in (50-75 mm) in diameter; crabs captured at mouths of burrows, trapped near openings by inserting shovel behind crabs and breaking burrow open, or taken by hand from depths of burrows. 4) Jetty (among boulders and stones at stations 13, 14); crabs captured by hand intertidally, and subtidally with aid of mask and snorkel.

Physical and biological factors, along with color and behavior of mud crabs, were noted at each collection site. Mud crabs were preserved in the field for morphological studies or transported alive to the laboratory and maintained in seawater aquaria until used in feeding experiments. Three kinds of prey—oysters, snails, and crabs—associated with the crabs in nature were presented to both species in the aquaria.

Seven morphological characters were measured with a metric vernier caliper for statistical analysis (Fig. 2): Carapace, length in midline and greatest width; body depth; third maxilliped, length of merus and ischium; major chela, length and height of palm. Third maxillipeds of crabs with carapace lengths of <9 mm were not measured, nor were newly regenerated chelae. Male gonopods were examined with the aid of a light microscope and scanning electron microscope.

Statistical analyses were performed at the Computer Center of the University of Alabama, Mobile, using the MUSIC STATPAK program (Jarvis 1974),

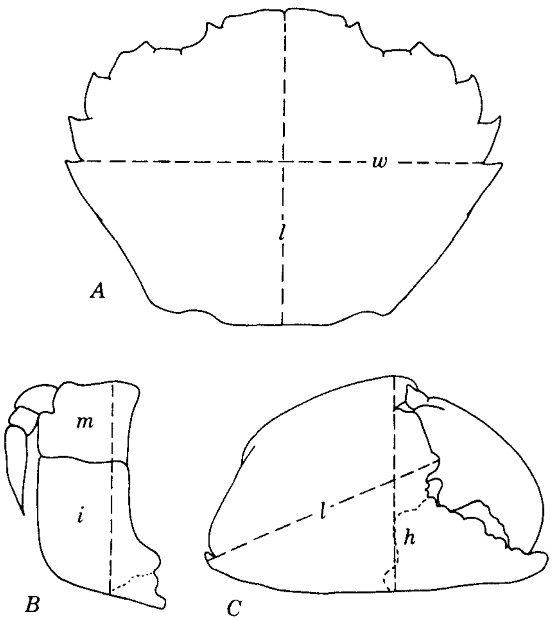

FIGURE 2.—Diagram of measurements made for analysis of morphometry. *A*, carapace, length (*l*), width (*w*); *B*, third maxilliped, length merus (*m*), ischium (*i*); *C*, palm of major chela, length (*l*), height (*h*).

and on the DEC System 10 Computer[1] of the National Marine Fisheries Service (NMFS), using computer programs written and maintained by Joseph L. Russo for the Systematics Laboratory, NMFS. The ANCOVA procedure follows that presented by Zar (1974), with the exception that the probability associated with the calculated value of the *F* statistic, for the purpose of simplification and clarity, is generated by the computer program instead of being calculated as a value of the *F* statistic with its associated numerator and denominator degrees of freedom.

Results

Ecology

Panopeus simpsoni occurs among oysters, rocks, and rubble. The crabs burrow in rubble, clearing out shallow depressions under pieces of cover, each excavation usually having more than one opening. When uncovered, the crabs again bury themselves in the substrate by wedging their flat bodies between loose shells. On jetties, this species occupies burrows, shallow depressions beside pieces of stone, and interstices among rocks and attached oysters. Collection of such individuals is difficult because they rapidly burrow among sharp oyster shells when disturbed.

Undercut marsh and mud bank stations exclusively yielded *P. obesus*. The burrows of this species are tubular, those in mud banks being the most intricate and often consisting of numerous interconnecting galleries. Each burrow generally has one or more openings at the surface of the marsh near the edge of a bank and a lower opening near the interface between hard and silty substrates. From the lower opening, a passage normally penetrates horizontally into the bank. This passage divides into one more or less vertical connection with the upper openings and another branch which angles downward at about 45°. The lower part of most burrows is <1 m long (about an arm's length), the end commonly being filled with soft, silty mud. The mud bank habitat contains many large adult *P. obesus*.

Burrows of larger mud crabs in the undercut marsh connect to both upper and lower surfaces of the marsh mat. Larger burrows are all vertical or nearly so, while smaller burrows are inclined or nearly horizontal. Juveniles (the majority of individuals in this habitat) live in the tangle of marsh roots on the lower surface of the mat.

Panopeus simpsoni occurs both inter- and subtidally (under pieces of rubble); *P. obesus* occurs only intertidally but does occupy habitats of *P. simpsoni* if suitable cover is available. For example, a large *P. obesus* was found among concrete rubble at one station but not burrowed under it as was *P. simpsoni*. Small *P. obesus* (carapace length about 10 mm) were also found among pebbles behind a stone jetty. The presence of young *P. obesus* in rocky *P. simpsoni* habitat tends to contradict the assumption by Benedict and Rathbun (1891) that dorsal curvature in the *P. obesus* carapace results from development in burrows.

Principal associated macroinvertebrates observed were *Sesarma cinereum* (Bosc), *S. reticulatum* (Say), *Uca* spp., and *Littorina irrorata* (Say) in the marsh; *Crassostrea virginica*, *Eurypanopeus depressus* (Smith), and *Balanus* spp. in the intertidal rubble and on jetties.

Stations north of Heron Bay (5, 10, 11, and 12, Fig. 1) had salinities which were too low (<14 ppt) to support populations of either species.

Panopeus obesus fed actively on oysters, snails, and crabs which were offered to them in captivity; *P. simpsoni* consumed the offered prey least actively. Both species fed on small American oysters, *Crassostrea virginica* (up to 5 cm long). A crab would grasp the oyster in its chelae and begin to chip around the edges of the valves with its major chela. As soon as an

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

opening could be found between the valves, the crab would insert fingers of the major chela into the opening and utilize the large basal tooth on the dactyl to repeatedly crush one valve. Once the valves remained open, the crab would pick out the flesh with its chelae.

Panopeus obesus was successful in feeding on the marsh periwinkle, *Littorina irrorata*, but *P. simpsoni* was unable to chip the shell aperture of the snail. *Panopeus obesus* initially chipped at the edge of the snail's shell aperture, and soon inserted fingers of the major chela into the opening which it had created. Repeated crushing with the dactyl opened the shell along a direct line toward and beyond the operculum. Once the crab was able to remove the operculum, it could feed on the flesh. Densities of *L. irrorata* were apparently related to those of *P. obesus*; where large individuals of the crab were abundant, few or no *L. irrorata* could be found.

Large *P. obesus* readily fed on *Sesarma cinereum*, *S. reticulatum*, and species of *Uca*, but less actively on *Eurypanopeus depressus*. Prey was entrapped by means of ambulatory legs and chelae. The less aggressive *P. simpsoni* fed on any of the crabs presented if they were sufficiently small.

Regardless of feeding intervals or molting occurrences, cannibalism in both species always resulted when medium to large individuals remained in a tank for extended periods (2-3 mo).

Only *P. simpsoni* was observed feeding in the field. One individual was observed feeding on algae and bryozoans encrusting rocks by tearing off bits of the encrustation with both chelae and passing these to the third maxillipeds.

Coloration

The two species of mud crabs from Mobile Bay can be identified by differences in coloration. *Panopeus obesus* is dark reddish brown dorsally and cream colored ventrally. The chelipeds exhibit a "veined" pattern extending from upper to lower margins on the external surface of the palm. These pigmentation sites coincide with muscle fiber attachments within the chelae. Fingers are dark brown.

Panopeus simpsoni is variably grayish brown dorsally, with or without a variable cream colored stripe (lacking, simple, broken, or staggered) posterior to the frontal margin; some individuals have a spotted appearance (grayish brown varying to dark brown with yellow-white areolations). Most are white to cream ventrally. Palms of the chelae are mottled with brown, gray, and yellow-white, fading to yellow-white ventrally; fingers are dark brown.

Males of both species of mud crabs have a large proximal red spot on the inner surface of the ischium of the third maxillipeds (color variably persistent after long preservation). The spot is present in all females of *P. obesus* but completely lacking in females of *P. simpsoni*.

Morphology

The carapace of *P. obesus* appears wider in relation to its length, is more convex dorsally along the anterior-posterior axis, and is armed with generally blunter anterolateral teeth than that of the relatively less bulky *P. simpsoni* (Rathbun 1930; Williams 1983). While differences in carapace morphology and color usually suffice to distinguish living or freshly preserved individuals of the two species, variations among individuals within the study area and throughout the entire geographic range indicate that these and other possible differences should be rigorously evaluated (Smith 1869; Rathbun 1930; Williams 1965).

The ecological interface between the two sympatric forms was considered to be the best place to test for possible differences between them, since it is the area in which intergradation might most likely occur. Nearly all of the measured mud crabs were collected at random from habitats in the intertidal zone. However, by imposing this limitation on the samples, the proportion of older (and larger) individuals in them may not reflect true proportions in the natural populations. (Larger individuals of *P. simpsoni* may occur subtidally but normally *P. obesus* did not occur there.) An intertidal rubble station in proximity to a mud bank sheltered many *P. simpsoni* as well as a small number of *P. obesus*. Intertidal mud banks yielded about 22% of the *P. obesus* (mainly larger individuals), but the overwhelming proportion of this form came from undercut marsh (mostly smaller individuals).

The means for each character except those of the palm (Table 1) were significantly greater ($P = 0.05$) in the *P. obesus* samples, although the smallest specimen of *P. simpsoni* was only 1 mm shorter than its *P. obesus* counterpart. The relationships between carapace length and width, carapace length and body depth, length of merus and ischium of the third maxilliped, and length and height of the palm of the major chela (Fig. 2) were analyzed by regression analysis (Table 2) and the ANCOVA procedure (Table 3). The coefficients of determination (Table 2) were >0.94 in all cases except one. The ANCOVA procedure (Table 3) showed a highly significant statistical difference between the species in each of these

TABLE 1.—Elementary statistics for samples of *Panopeus obesus* ($N = 209$) and *P. simpsoni* ($N = 200$) from Mobile Bay, Ala.; measurements in mm.

Character	Mean	SD	Max.	Min.
P. obesus				
Carapace				
Length	16.6	7.60	38.9	5.7
Width	23.2	10.99	55.8	7.7
Body depth	10.9	5.29	27.8	3.7
Third maxilliped				
Length merus	2.5	0.86	4.8	1.2
Length ischium	4.5	1.58	9.4	2.4
Major palm				
Length	12.3	6.50	33.7	3.8
Height	8.2	4.44	23.2	2.4
P. simpsoni				
Carapace				
Length	14.8	4.38	26.2	4.7
Width	19.7	5.94	35.2	6.1
Body depth	9.0	2.96	16.7	2.4
Third maxilliped				
Length merus	2.1	0.45	3.8	1.0
Length ischium	3.9	0.88	6.7	2.0
Major palm				
Length	11.3	4.13	22.2	2.8
Height	8.2	3.15	16.6	1.9

TABLE 2.—Regression statistics for samples of *Panopeus obesus* and *P. simpsoni* from Mobile Bay, Ala.; measurements in mm. First variable of each pair is independent (x).

Character	Data pairs	*Y*-intercept	Regression coefficient	SE regression coefficient	SE estimate	Coefficient of determination
P. obesus						
Carapace						
Length: width	209	−0.88316	1.44504	0.005	0.507	0.998
Length: body depth	209	−0.33666	0.67624	0.011	1.256	0.945
Third maxilliped (length)						
Merus: ischium	183	0.10077	1.77387	0.032	0.376	0.943
Major palm						
Length: height	181	−0.16787	0.68115	0.003	0.303	0.996
P. simpsoni						
Carapace						
Length: width	209	−0.24887	1.35075	0.008	0.515	0.992
Length: body depth	209	−0.66950	0.65737	0.007	0.446	0.976
Third maxilliped (length)						
Merus: ischium	183	0.69728	1.52849	0.064	0.435	0.755
Major palm						
Length: height	181	−0.35777	0.75729	0.006	0.312	0.990

pairs of attributes except for the slope of carapace length: body depth, but the *Y*-intercepts of those two lines differed significantly.

A number of other characters compared in preliminary tests are not included in this discussion because they provided minimum information for defining differences between *P. obesus* and *P. simpsoni*. These characters included statistical comparisons of the fifth pereopods of dactyl and propodus lengths, third maxilliped ischium and merus widths, major chelae, dactyl lengths and widths, frontal and frontoorbital widths, and shape of male gonopods.

Conclusions

Rathbun (1930) considered forms of the mud crab, *Panopeus herbstii*, s.l., to be distinct but unacceptable for subspecific status. After field observations in southwestern Alabama, it was apparent that the two forms which she recognized in that area differ markedly from each other, although no obvious external feature will distinguish every individual.

Color

There is a difference in the dorsal coloration of living animals, *P. obesus* being generally russet in tone whereas *P. simpsoni* is mottled gray. The chelae of *P. obesus* exhibit a "veined" pattern over the external surface of the palm whereas those of *P. simpsoni* are mottled brown, gray, and yellow-white, fading to cream color ventrally. The inner surface on the ischium of the third maxilliped bears a large, proximal red spot in both male and female *P. obesus*. The color of this spot is persistent in fluids which are commonly used for preserving study specimens, although it may fade after periods of storage. Males of *P. simpsoni* possess this spot but females lack it.

TABLE 3.—F statistics for results of ANCOVA comparing measured characters from samples of *Panopeus obesus* and *P. simpsoni* from Mobile Bay, Ala.

Character	df	Slope	*Y*-intercept
Carapace length:width	405	99.6812**	
Carapace length:body depth	405	1.9055(NS)	39.8751**
Third maxilliped, length merus:ischium	365	12.4791*	
Major palm, length:height	354	130.1565**	

* = significant at $P = 0.05$.
** = significant at $P = 0.01$.
NS = Not significant.

Morphometry

Panopeus obesus is a wider, deeper bodied form than *P. simpsoni*, with relatively less massive chelae than the latter. Statistically, there is a significant ($P = 0.05$) difference between the two crabs (independent of size) in length and width of carapace, length and depth of body, length of merus and ischium of the third maxilliped, and length and height of the major palm.

Habitat

There is a relatively effective isolation of the two mud crabs by habitat. *Panopeus simpsoni* occurs intertidally or subtidally in association with the American oyster, but not usually in the marsh bank environment. *Panopeus obesus* occurs in marsh banks, but not subtidally. Both species inhabit intertidal rubble areas.

Feeding

Though food type for both species is similar, *P. obesus* is much more aggressive in capturing and consuming prey.

These findings reinforce the conclusion of Williams (1983) that *P. obesus* and *P. simpsoni* are specifically distinct.

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EFFECT OF TEMPERATURE ON RATE OF EMBRYONIC DEVELOPMENT OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*

Recent studies by the Northwest and Alaska Fisheries Center Auke Bay Laboratory of the National Marine Fisheries Service, Auke Bay, Alaska, have focused on causes underlying mortality of eggs and larvae of walleye pollock, *Theragra chalcogramma*, a species of considerable economic importance in Alaskan waters. One aspect of these studies is to predict age of walleye pollock embryos in samples from surveys at sea. Knowledge of age of embryos is necessary for estimating peak spawning time and daily production of eggs, and for predicting abundance and distribution of spawning fish. Because length of the incubation period is dependent on temperature of the water mass in which the eggs are developing (Hamai et al. 1971), embryo age (hours since fertilization) can be estimated provided water temperature is known.

In this study, we determined the relation between temperature and rate of development of walleye pollock embryos at constant incubation temperatures and at fluctuating temperatures (simulated). We then derived equations and a contour plot for estimating the age of an embryo (time from fertilization, in hours) at a given incubation temperature and stage of development. We also derived an equa-