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Comparative behavior of *Eurypanopeus depressus* (Smith) and *Eurypanopeus dissimilis* (Benedict and Rathbun) (Decapoda: Brachyura: Xanthidae).

Humberto A. Garcés B.
Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida, 33431, U.S.A.

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Abstract: A series of experiments and observations were made on two nominate species of mud crabs. Differences were found in desiccation resistance, salinity tolerance, temperature tolerance, dominance and coexistence, aggressiveness, feeding, and response to a new habitat. Data support the scheme of previous classification, which regards them as separate species. It is concluded that *Eurypanopeus depressus* and *Eurypanopeus dissimilis* are two closely related sympatric species isolated by behavioral factors.

The behavioral patterns of the crabs are among the most varied and complex of the crustaceans. Unfortunately, relatively few behavioral accounts exist for brachyurans despite the abundance of crab species and the opportunity for comparative studies of their behavior and ecology.

The genus *Uca* of the family Ocypodidae has received the most ethological attention (Salmon 1967; Crane 1975). Behavioral reports outside the genus *Uca* within the division Brachyura are scarce and almost absent within the Xantid family.

Behavioral studies encountered within the Xanthidae have been made on agonistic and sexual behavior (Savage 1971; Hazlett 1976; and Swartz 1976) and on larval behavior during vertical migration (Forward 1985). Within the genus *Eurypanopeus* there are only a few studies on *E. depressus* and none on *E. dissimilis*. Studies on adult *E. depressus* include the report on desiccation tolerance and the exploitation of microhabitat (Grant and McDonald 1979); electrophoretic variations (Turner and Alyerla 1980); allometric constraints and variables of reproductive effort (Hines 1982); and behavioral basis of depth regulation in hatching and post-larval stages (Sulkin *et al.* 1983). Behavioral responses of the larval stages of *E. depressus* have received some attention, such as: the effects of cadmium and mercury (Mirkes *et al.* 1978) and the response of stage I zoea to gravity and thermal gradients (Kelly *et al.* 1980).

The present investigation was done to detect and contrast differences in behavior of the two closely related species, *E. depressus* (Smith 1869) and *E. dissimilis* (Benedict and Rathbun 1891). Although both are considered different species, *E. dissimilis* has not been reported in the literature since 1930 (Rathbun). It seems that *E. dissimilis* has been overlooked if not confused with *E. depressus* in past studies. There are, however, subtle differences in morphology and distribution between both species. The main morphological characters that separate both species are carapace teeth shape, chela coloration, and size of red spot on third maxilliped. Furthermore, *E. depressus* is mostly a northern species, occuring on both coasts from Massachusetts Bay through Florida and to southern Texas. It has also been reported from St. Martin, Dutch West Indies, Uruguay and Bermuda (Williams 1984). Boca Raton is considered a new locality record for *E. depressus*. According to Rathbun (1930), *E. dissimilis* occurs in the Gulf of Mexico (west coast of Florida only) down to Santa Catarina, Brazil, and in Cuba, Jamaica, Trinidad and Nicaragua. The occurence of *E. dissimilis* is recorded here for the first time since 1930 (Rathbun). The east coast of Florida is considered a new record for distribution and locality of the species.

MATERIAL AND METHODS

Collections: Individuals of *E. depressus* and *E. dissimilis* were collected subtidally from clumps of oyster shell beds on a seawall canal. Sampling was done in the canal between US–1 and the Intracoastal Waterway in northern Boca Raton, Palm Beach County, Florida, U.S.A. during October and November, 1984. The canal fauna was composed mainly of *Crassostrea virginica* Gmelin, the American oyster, growing over the concrete walls, dock pilings, and on the bottom of the canal. The average salinity in the canal (Mohr Titration) was 34.00/00, and the average water temperature was 21.0°C. A summary of the collection is presented in Table 1. Both species of *Eurypanopeus* were identified by morphological characteristics outlined by Rathbun (1930) and Williams (1984). Raymond B. Manning from the National Museum (United States) verified both *Eurypanopeus* species identification. Voucher specimens have been deposited at the United States National Museum (U.S.N.M.): *E. depressus* (U.S.N.M. Cat. Nos. 233535-233537) and *E. Dissimilis* (U.S.N.M. Cat. Nos. 233538 and 233539).

TABLE 1

Summary of collections from northern Boca Raton, Florida, from October 28 to November 12, 1984. N = Total number of organisms; % = Percentage of relative abundance; CW = Carapace width in cm (mean values ± 1 standard deviation); and Range (CW) = Range of carapace width (cm)

	E. depressus	*E. dissimilis*
N	98	39
%	72	28
CW	1.07 ± 0.25	0.94 ± 0.16
Range (CW)	0.65 – 1.80	0.75 – 1.30

Laboratory maintenance: Both species of *Eurypanopeus* were maintained separately in community tanks (19.5 cm diameter). Each tank contained dead oyster shells for shelter and 600 ml of 34.00/1000 sea water. The water was aerated continuously and changed every 24 hours to prevent the waste build-up. No more than 50 crabs were maintained together in a single tank at any time. During this study, the water temperature range in the laboratory was 15.5 - 22.5 °C, with an average of 20.0 ± 1.5 °C; room temperature range was 15.0 - 22.0 °C, with an average of 20.0± 1.0°C. Crabs were kept in the laboratory at least five days prior to experimentation.

Desiccation tolerance: All desiccation experiments were carried out at room temperature (19.0 - 21.0 °C) in a glass desiccator, containing 50 g of color-indicating $CaSO_4$. Each crab was placed in a 20 ml beaker inside the desiccator to avoid contact with the desiccant. Crabs were weighed on a Cent-O-gram Ohaus balance. After determination of wet weight (initial weight), animals were placed in the desiccator, weighed initially at 60 min. intervals, and then weighed at 30 min. intervals when near death. The time that the crabs spent out of the desiccator was not included in the data. After death, animals were dried at 100 °C for 24 hours, using a Precision Thelco Oven Model 18, and weighed (dry weight). The criterion for determining death was the lack of response of the walking legs to tactile stimulation (Grant and McDonald, 1979). After obtaining the dry weight the crabs were measured with a Bel Art Caliper at the widest part of the carapace to the nearest 0.01 cm. Percentage of body weight composed of water (% Pbw) was calculated by the following formula:

$$\%\,Pbw = \frac{\text{Wet Weight} - \text{Dry Weight}}{\text{Wet Weight}} \times 100$$

Percentage of body water lost (% P 1) due to desiccation at time of death was calculated by the following formula:

$$\%\,Pl = \frac{\text{Wet Weight} - \text{Weight at Death}}{\text{Wet Weight} - \text{Dry Weight}} \times 100$$

The difference between the initial wet weight and the final dry weight was considered to be the water content of the animal. The percent of this water content lost at each time interval was calculated, and mean values were plotted for both species.

Salinity tolerance: Salinity tolerance of both species of *Eucypanopeus* were measured in 0, 5, 17, 34, 45, and 75.00/1000 at room temperature (19.0 - 21.0 C). The activity of each crab was assessed as follows: freely moving and active, 2 points, lethargic and failing to move after gentle prodding, 1 point; dead, 0 points (Shumway, 1983).

Temperature tolerance: Temperature tolerances of both species of *Eurypanopeus* were determined by observing the behavior while increasing or decreasing the water temperature. Five crabs of each species were placed in a glass dish (7.8 cm in diameter) with equal volumes (200 ml) of 34.00/1000. The dish with the crabs was placed inside a bigger dish (15.0 cm in diameter), and hot or cold water was poured at intervals into only the bigger dish. The temperature was meassured with a scale thermometer (0 - 50 °C) placed inside the smaller dish with the crabs. In the decreasing temperature experiments the water temperature was lowered gradually from 19.0 °C to 9.0 °C in 1 hour. In the increasing temperature experiments the water temperature was gradually raised from 19.0 °C to 39.0 °C in 2 hours. The water temperature was raised or lowered until death occured using two crabs per species under similar conditions. Al experiments were carried out in duplicate.

Dominance and coexistence: In the dominance and coexistence experiments different sizes, sexes and species combinations were placed together in a glass dish (7.8 cm in diameter) with 200 ml of 34.00/1000, and their behavior) then observed and recorded. All experiments were carried out at room temperature (19.0 - 21 0 °C) and lasted 30 min. Three combinations were used: 1. *E. depressus* - *E. depressus* interactions; 2. *E. dissimilis* - *E. dissimilis* interaction; and 3 . *E. depressus* - *E. dissimilis* interaction.

Individual behavior differences: Individual behavior differences within both species, were noted and recorded throughout the experimentation period. During experimentation the controls were used for behavioral observation; also, occasional periods of extra observation were carried out (i.e., behavior on sandy bottom dish). In this experiment 5 crabs of both species of *Eurypanopeus* were placed in a glass dish (7.5 cm in diameter) with a small layer of beach sand (1.5 cm in width) on the bottom, and 200 ml of 34.00/1000. All experiments were carried out at room temperature (19.0 °C), lasted 30 min., and were done in quintuplicate.

RESULT AND DISCUSSION

Desiccation: Death by desiccation was substantially different between *E. depressus* (509 min.) and *E. dissimilis* (263 min.), with *E. depressus* surviving over 1 1/2 times as long as *E. dissimilis* (Table 2). The mean percentage of water loss was similar with *E. depressus* showing a mean value of 29.0%, and *E. dissimilis* showing a mean value of 21.0% (Table 2). However, the cumulative percentage of water loss by both species was different. In *E. depressus* 4.0% of water loss vas achieved in the first hour, while *E. dissimilis* lost 11.0% in the same period; by the second hour, *E. depressus* had lost 9.0% of water, while *E. dissimilis* had lost 14.0%, falling under a stress condition (Table 3). The stress condition was observed on *E. depressus* when it lost 17.0% of water after 4 hours of desiccation. The stress condition was characterized by lack of movements and contraction of all the walking legs and chelae toward the body. Both species began with different percentages of body weight due to water (57.0% in *E. dissimilis*, and 64.0% in *E. depressus*), and had lost slightly different amounts of water at the time of death (27.0% in *E. dissimi-*

TABLE 2

Desiccation tolerance. % water loss is amount of wight lost due to desiccation. Survival time is measured from introduction into desiccator until death. Intervals of time needed for successive wighings are not included. Values are means ± 1 standard deviation

	N	Mean Size (g dry wt.)	Mean % Water Loss	Mean Survival Time (min.)
E. depressus	10	0.16	28.9 ± 10.0	508.8 ± 28.3
E. dissimilis	8	0.15	20.5 ± 6.0	262.7 ± 32.4

TABLE 3

Cumulative water loss percentage. (*) Refers to beginning of stress, characterized by lack of movements and contraction of all the walking legs and chelae towards the body

Time (min.)	Cumulative Water Loss (%) *E. depressus*	Cumulative Water Loss (%) *E. dissimilis*
60	4	11
120	9	14*
180	13	22
240	17*	25
300	22	28
360	23	–
420	27	–
480	28	–
540	32	–

TABLE 4

Parameters used in desiccation tolerance experiments.
N = Numbers of crabs; CW = Carapace width in cm; Range (CW) = Range of carapace width (cm); Pbw = Percentage of total body weight due to water; Pl = Percentage of total body water loss at time of death. All values except range are means ± 1 standard deviation

	E. depressus	*E. dissimilis*
N	10	8
CW	1.22 ± 0.19	1.08 ± 0.12
Range (CW)	0.85 – 1.35	1.00 – 1.25
Pbw	64.30 ± 1.54	56.90 ± 1.64
Pl	30.80 ± 1.73	26.60 ± 0.74

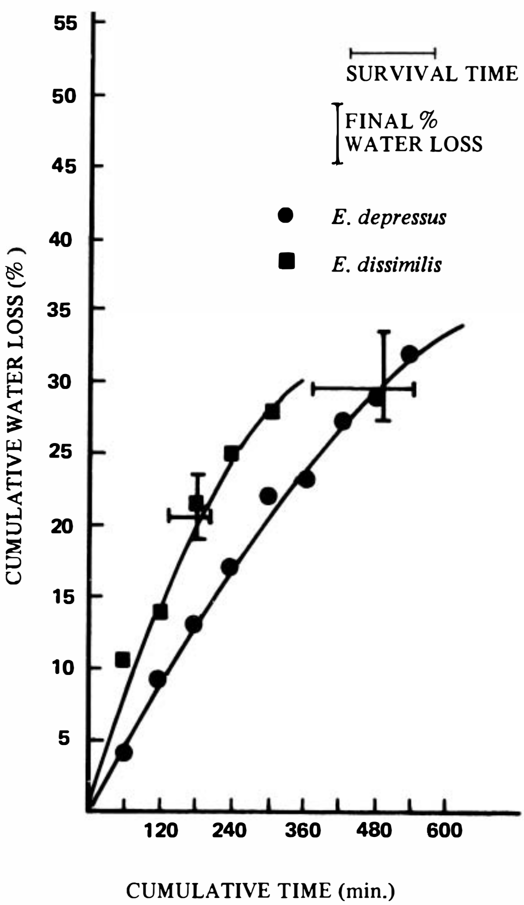

Fig. 1. Desiccation rates for the two Xanthid crab species. Mean values ± 1 standard error for survival time and final % water loss are indicated for each species.

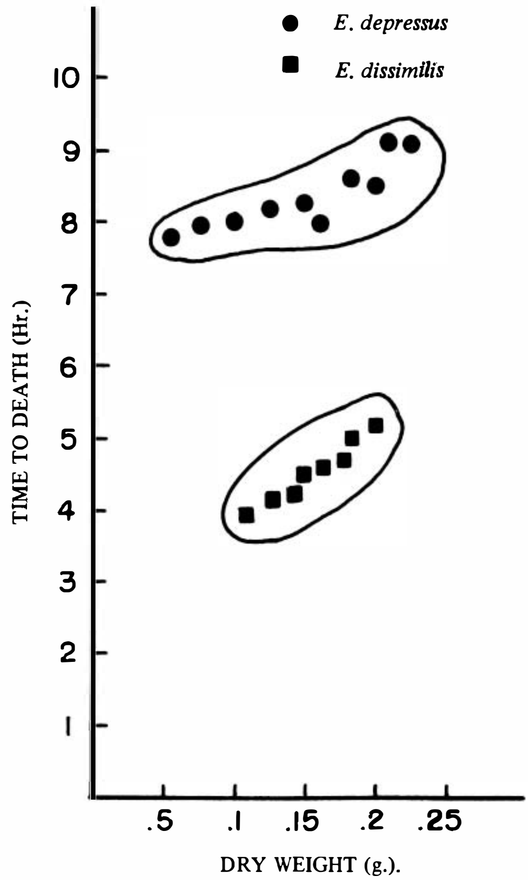

Fig. 2 Scatter diagram of dry weight (g) against time to death (hours).

lis, and 31.0% in *E. depressus*) (Table 4). These three percentages are apparently not a function of size because the entire range of carapace widths remained constant with only a slight standard deviation (1.1 ± 0.12 cm in *E. dissimilis*, and 1.2± 0.19 cm in *E. depressus*) (Table 4). *E. depressus* showed a greater resistance to desiccation than *E. dissimilis.* with a greater survival time, and a slightly higher value for final percentage of water loss (Figure 1). This resistance to desiccation was true although the mean dry weights (g) were very similar (0.16 g in *E. depressus*, and 0.15 g in *E. dissimilis*) (Table 2). When time to death was plotted against dry weight (g) a clear separation on the scatter diagram was obtained for both species (Figure 2). Both species of *Eurypanopeus* studied seem to be sensitive to desiccation, having lost about 27.0 - 31.0% of body water at time of death. Young (1978), using identical methods, found a

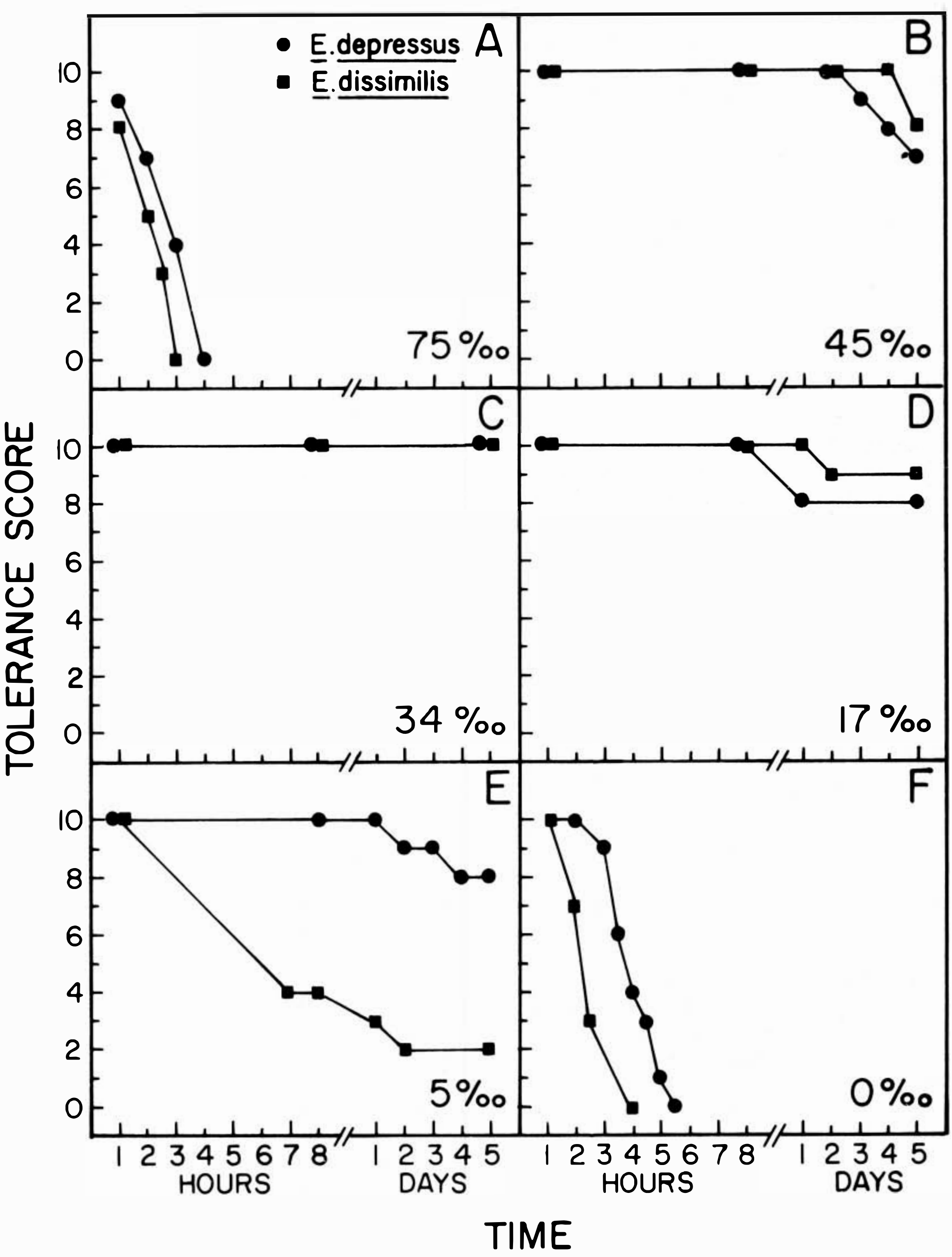

Fig. 3 Mean tolerance scores in 0, 5, 17, 34, 45, and 75.00/1000. Tolerance scored as 2 points for each active animal, 1 point for each lethargic, and 0 for each dead animal.

50.3% water loss at death in the intertidal hermit crab *Clibanarius vittatus* (Bosc) with shell removed, a value larger than the one obtained for both species of *Eurypanopeus*. Grant and McDonald (1979), using similar methods, found a 30.1% water loss at death for intertidal populations of *E. depressus*, and 32.0% for subtidal populations a value very close to the one found here for *E. depressus*. Their experiments suggest that within the intertidal zone, low desiccation tolerance may be indicative of the greater importance of the microhabitat for a given species, and this was particularly important to *E. dissimilis*. It is speculated that without the protection of the substrate (oyster shell beds) from desiccation extremes, neither species of *Eurypanopeus* could live intertidally.

Salinity: There were no adverse effects on either species at 34.00/1000 (control) (Figure 3C), and after 16 days they still were alive and healthy. The tolerance level diminished, while reducing the salinity from control, at 17, 5, and 0.00/1000, in both species with *E. dissimilis* showing a slightly lower level of tolerance than *E. depressus* (Figure 3D, 3E, and 3F). In increasing water salinity from control, both species presented a reduced level of tolerance at 45 and 75.00/1000, with *E. dissimilis* showing a slightly lower level of tolerance than *E. depressus* (Figure 3A and 3B). In general, *E. depressus* has the greater resistance to salinity changes with higher tolerance to both salinity extremes (0 and 75.00/1000). Experimental results were consistent with past reports (Shumway 1983). Adults have been captured between 4.5 - 52.00/1000 (Rouse 1970; Williams 1984) Costlow and Bookhout (1961) reared *E. depressus* larvae in a wide salinity range (12.5 -31.00/1000) under laboratory conditions. For *E. dissimilis*, salinities of 5.00/1000 seemd to be near their lower limit of tolerance. For this reason it is suggested that their limit is reached at a higher salinity between 5 and 17.00/1000). Thus, they can be found *in situ* from there through 45.00/1000.

Temperature: *E. depressus* showed a narrower normal range of temperature (22.0 °C) which they can withstand without distress than *E. dissimilis* (28.0 °C) (Figure 4), but *Eurypanopeus depressus* showed a wider range toward warmer temperatures (above 20 °C). The best temperature range in which *E. depressus*

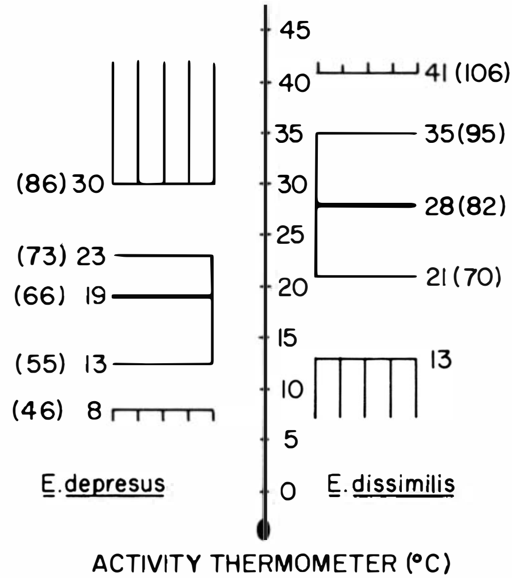

Fig. 4 "Thermogram" showing the best temperature range, upper and lower lethal limits, and optimal temperature. °F is shown in parentheses.

showed normal activity was found to be between 13.0 - 23.0 °C. The lethal temperature limits for *E. depressus* were 30.0 °C and 8.0 °C. The best temperature range for *E. dissimilis* was between 21.0 - 35.0 °C, with lethal temperature limits of 41.0 °C and 13.0 °C. It was found that *E. depressus* did best at 19.0 °C, and *E. dissimilis* at 28.0 °C. In general, *E. depressus* tolerated cooler temperatures much better than *E. dissimilis*. It is suggested that *E. dissimilis* was studied near their lower limits of best temperature range. *E. depressus* is reported to be found in a very wide temperature range, 16.0 - 32.0 °C (Lyons, *et al.* 1971; Godcharles and Jaap 1973). From the current experimental results, it is expected that *E. depressus* may be found at cooler temperatures than those reported.

Dominance and Coexistence: *E. depressus* - *E. depressus* interaction: Adult males stayed away from one another most of the time. When encountering each other, usually the first crab that attacked dominated the other, causing it to move away, regardless of size. Adult males were dominant over juveniles, but no signs of aggressivenes were shown against ovigerous and non--ovigerous females. Juveniles were aggressive and usually the first that attacked dominated.

TABLE 5.

A survey of ethograms, based on laboratory observation. (*) Indicates elevation of the last two pairs of walking legs

Ethograms	Species showing pattern:	
Act Pattern	*E. depressus*	*E. dissimilis*
I. Body Postures		
1. Normal	yes	yes
2. Rearing*	no	yes
II. Direct Movements		
1. Move toward	yes	yes
2. Move away	yes	yes
III. Chelipeds		
1. Non-contact display	yes	yes
2. Contact display	yes	yes
IV. Walking Legs		
1. Non-contact	yes	yes
2. Contact ('pushing')	yes	yes
V. No Response ('freeze')	no	yes

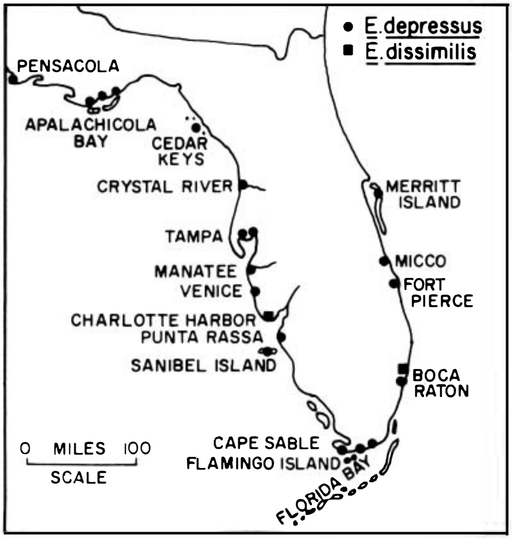

Fig. 5. Known reports for *Eurypanopeus depressus* and *Eurypanopeus dissimilis* in Florida. Location of the Boca Raton collection site is also shown.

E. dissimilis – E. dissimilis interaction: Ovigerous females are dominant over non-ovigerous females and juveniles of both sexes. Adult males showed no aggressiveness toward females.

E. depressus – E. dissimilis interaction: Larger adult males of *E. depressus* were dominant over smaller adult and juvenile *E. dissimilis* males and ovigerous and non-ovigerous *E. dissimilis* females. However, larger *E. dissimilis* ovigerous females were dominant over smaller juveniles and adult *E. depressus* males. If equal in size, *E. depressus* females were dominant over *E. dissimilis* males. There was aggressive behavior between males and females of different species. Ultimately, one caused the other to move away. with *E. depressus* being the more dominant. Although encounters are possible in nature because of the same habitat, it is suggested that interpecific mating is avoided. In either case, males and females of each species showed no signs of acceptance of a foreign species in its territory. A survey of the ethograms observed for both species is presented in Table 5.

Individual behavior differences: Aggressiveness: *E. depressus* in general showed a greater aggressiveness. When disturbed this species opened wide both chelae while raising the anterior part of the body to a 45° angle. Adult males of *E. depressus* made jerky movements with the entire body while waving their big chelae and jumping over other crabs when irritated. *E. dissimilis,* in general, showed less aggressive behavior. When disturbed they displayed a typical stress position, placing all their walking legs and both chelae closely toward the body, forming the body into a retracted configuration. If disturbed by an approaching aggressive crab, *E. dissimilis* retreated against the wall of the dish and showed a rearing position, raising the first two pairs of walking legs and holding that posture for a time. According to Warner (1971), this signal communicates the threat of an attack.

Sandy bottom dish: *E. depressus* either stayed in the same place without movement, or moved carefully, staying above the sand. On the other hand, *E. dissimilis* either moved actively and fed on small particles for a few minutes and then began burrowing, or it began burrowing immediately. The burrowing behavior consisted of making a hole with the walking legs first, then introducing its body backwards into the sand, and while the sand was thrown away with both chelae the body of the crab was pushed into the sand. After 5 minutes 1/3 of the carapace was visible and after 15 minutes, just 1/4. This burrowing behavior has not been reported for any xanthid species and may be a factor affecting *E. dissimilis* distribution in certain available areas.

Feeding: *Eurypanopeus depressus* was seen feeding at any time between 12:30 p.m. and 11:00 p.m., showing more activity at night. *E. dissimilis* was found feeding in two periods: between 10 - 11 a.m. and 10 - 11 p.m., when the temperature was higher (21.0 - 22.5 °C). *E. depressus* was observed to feed on suitable size detritus particles on the bottom of the community tank, on fish pellets, and on eggs of ovigerous *E. depressus* and *E. dissmilis* females. *E. dissimilis* fed on the smallest detritus particles and eggs of ovigerous *E. depressus* females. The slight differences in food supplies encountered suggests a spatial partition of their microhabitat in terms of food supplies and space. Thus, this enables them to coexist in the same area.

CONCLUSIONS

Based on all the information obtained from this research and all other sources, *E. depressus* and *E. dissimilis* are maintained as different species. The primary differences being the following:

1. **Morphological:** Carapace tooth shape (first and second teeth fusion), lobiforme in *E. depressus* and dentiforme in *E. dissimilis;* color of propodal finger, not continued onto palm in *E. depressus* and color spreads upward in *E. dissimilis;* red spot present on inner surface of third macilliped ischium, oval and bigger (2/3 of structure) in *E. depressus* and round and smaller (1/3) in *E. dissimilis;* male abdominal segments (third and fourth segments), fused in *E. depressus* and not fused in *E. dissimilis;* and chelae height ratio (minor to major manus), higher ratios (2/3) on *E. depressus* than in *E. dissimilis* (1/2).

2. **Distributional:** *E. depressus* is a mostly northern species, while *E. dissimilis* prefers warmer localities.

3. **Behavioral:** Differences were found in desiccation, salinities and temperature tolerances; dominance and coexistence; aggressiveness, feeding and response to a new habitat (sandy bottom dish).

From all this information it can be concluded that *E. depressus* and *E. dissimilis* are two distinct species that live sympatrically on the locality studied.

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RESUMEN

Una serie de experimentos y observaciones fueron hechas en dos especies de cangrejos Xanthidae. Se encontraron diferencias en su resistencia a la desecación, tolerancia a diferentes salinidades y temperaturas, dominancia y coexistencia, agresividad, alimentación, y respuesta a un nuevo habitat. Los resultados comprueban el previo esquema de su clasificación que considera a ambas como especies distintas. Se concluye que *Eurypanopeus depressus* y *Eurypanopeus dissimilis* estan relacionadas simpátricamente y se mantienen separadas por diferencias en comportamiento.

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