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The Phenology of Sand Crabs, *Lepidopa benedicti* (Decapoda: Albuneidae)

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ABSTRACT

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Albuneid sand crabs are widespread on sandy beaches around the world, but because they conceal themselves by digging in sand and are often found at low densities, little is known about their basic biology. *Lepidopa* species were collected from the beaches of South Padre Island, Texas, on the western coast of Gulf of Mexico, a location that had previously been suggested to act as a population sink. The site contained *Lepidopa benedicti* and *L. websteri*, although the latter was extremely rare (collected three times in 5 years). There was significant variation in abundance across the year, with higher densities in summer and lower in winter. Ovigerous females, carrying up to almost 2000 eggs, were found from late spring through summer, with most of the young of the year appearing in autumn. The sex ratio was biased toward females. The average size of *L. benedicti* in South Texas was smaller than individuals in Florida, but the population density appeared to be higher in Texas. The presence of reproductive individuals and even distribution of size classes weakens an earlier hypothesis that the western Gulf of Mexico acts as a population sink for *L. benedicti*. The changes in abundance suggest that the *L. benedicti* actively repositions itself at different depths in the swash zone at different times of the year, possibly for reproduction.

ADDITIONAL INDEX WORDS: *Beach, life history, colour morph, sex ratio*.

INTRODUCTION

Sand crabs (Family Albuneidae) are small decapod crustaceans that live in fine sandy beaches (Boyko, 2002). All species in this family are obligate diggers as adults. They conceal themselves completely in sand (Dugan, Hubbard, and Lastra, 2000; Faulkes and Paul, 1997, 1998) and leave no traces of their presence visible to observers walking on a beach. Consequently, sand crabs can be difficult to find: Hay and Shore (1918) wrote that they could not find a single live *Lepidopa websteri* even after "a vast amount of digging." This, combined with their low abundance, means that very little is known about the basic life history of any albuneid sand crab.

Albuneid sand crabs provide opportunities to test ecological hypotheses about the macrofauna of sandy beaches. The habitat harshness hypothesis (Defeo, Gomez, and Lercari, 2001; Defeo and Martínez, 2003) predicts that populations occurring on dissipative beaches should have higher abundance, growth, and fecundity than those on harsh reflective beaches because more energy is expended by individuals to maintain baseline metabolic demands on reflective beaches. The source-sink hypothesis (Defeo and McLachlan, 2005) suggests that reflective beaches are more likely to act as population sinks, with recruitment occurring from dissipative beaches acting as sources for new individuals. Source populations are predicted to have a wide representation of size classes, while sink populations are more likely to show irregular distribution of size classes because of irregular recruitment (Defeo and McLachlan, 2005). Previously, Murph and Faulkes (2013) suggested that the dissipative beach of South Padre Island, Texas, might be a population sink for *L. benedicti*. South Padre Island is one of the southernmost locations where this species has been recorded (Figure 1), which is consistent with the hypothesis that this location is marginal habitat for this species. No ovigerous females had been found over 2 years of sampling, and individuals from South Padre Island were smaller than those collected from other regions. These findings run contrary to hypotheses that state that dissipative beaches are unlikely to be sinks. To test these hypotheses, this paper more than doubles the time frame of a previous study (Murph and Faulkes, 2013), thus providing greater resolution into the phenology of this sand crab, particularly its reproductive cycle. This has the incidental benefit of increased probability to find other rare individuals (*e.g.*, rare species and colour morphs). This paper also provides data regarding *L. benedicti* from intermediate beaches on the Atlantic coast of Florida as an initial effort to characterize differences in this species across its range.

METHODS

A population of *L. benedicti* Schmitt, 1935, on South Padre Island are being studied as part of an ongoing, long-term project enacted to understand the basic biology of a representative species of the family (Joseph and Faulkes, 2014; Murph and Faulkes, 2013; Nasir and Faulkes, 2011). Sand crabs were collected at South Padre Island monthly. Collection sites ranged from the beach east of the Exit 6 access road in the north (26°12′3.65″ N, 97°10′42.01″ W) to the beach east of the

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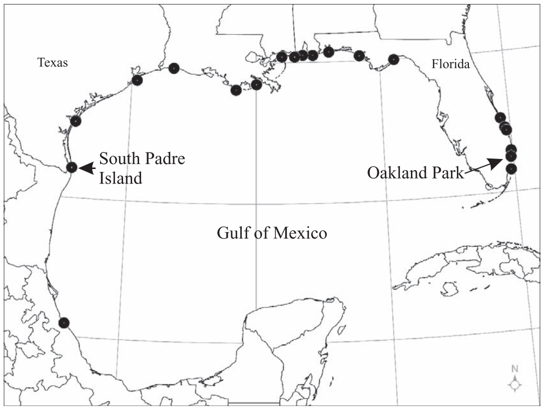

Figure 1. *Lepidopa benedicti* has a discontinuous distribution on the Gulf of Mexico and the Atlantic Ocean. Distribution of *L. benedicti*, based on data from Boyko (2002); one site shown for each U.S. county or parish.

University of Texas Rio Grande Valley's Coastal Studies Lab in the south (26°4′30.59″ N, 97°9′26.59″ W). Previous research found no significant differences in the population between the northern and southernmost collection sites (Murph and Faulkes, 2013), so all locations were pooled in analyses.

The foreshore of South Padre Island is a dissipative to intermediate beach (Houser and Mathew, 2011) with low tides ($<$1 m) and fine sand ($\sim$0.2 mm in diameter) (Houser and Mathew, 2011; Judd, Lonard, and Sides, 1977). Two albuneid species are present at this location: *L. benedicti*, which is relatively common (Murph and Faulkes, 2013), and *L. websteri* Benedict, 1903, which is rare (Faulkes, 2014b). This study includes monthly records of *L. benedicti* from five calendar years (January 2011 to December 2015). Data from January to August 2011 was used in earlier analyses (Murph and Faulkes, 2013; available in Faulkes [2014a]). Using the same methods as the Texas site, sand crabs were also sought at Fort Lauderdale, Oakland Park, and Pompano Beach in Broward County, southern Florida, in November 2012. These locations are intermediate beaches with slightly coarser sand (Benedet, Finkl, and Klein, 2006). Of these three locations, individuals were found only at the beach in Oakland Park. Results refer to the Texas population unless otherwise specified.

Sand crabs were collected by digging 10-m transects parallel to, and slightly above, the waterline of the swash zone. The location of transects was chosen to minimize variation along the dune-to-sea continuum and to maximize the likelihood of encountering animals. Boyko (2002) reported that *L. websteri* appeared to be most abundant at the low-tide waterline. Transects were spaced haphazardly because of local beach conditions (*e.g.*, presence of heavy shell grit making digging difficult). The number of transects dug ranged from 3 to 20 in a month (mean = 6.42 transects per month; standard deviation [SD] = 3.21), depending on weather, and need of animals for other projects (Table 1). Sand was overturned and examined for *Lepidopa*, and any individuals that emerged from the trench after it filled with water were collected. The sex, carapace length, and colour were recorded on site. Sample sizes for these features vary because some sand crabs were damaged by the shovel during collecting or escaped capture. For example, some damaged animals could be sexed but not have the carapace length measured. Sex was determined by examining the pleopods, which are long in adult females and extremely short in adult males. The eggs from ovigerous females were counted in the lab by removing the pleopods and counting the eggs under a stereomicroscope. Individuals less than 5 mm in carapace length could not be sexed and were considered the young of the year.

Table 1. *Sampling effort. Number of 10-m transects dug at South Padre Island, Texas, during each month of the study.*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
2011	5	5	3	6	6	6	4	6	3	5	5	5
2012	4	4	6	6	7	4	12	5	5	8	8	5
2013	9	3	6	6	8	4	9	3	3	10	6	3
2014	5	6	7	8	5	15	17	20	12	6	7	6
2015	6	6	6	6	6	6	6	6	6	6	6	6

To test whether size differences along the range of *L. benedicti* (Murph and Faulkes, 2013) were attributable to the western Gulf of Mexico being a poor habitat for sand crabs compared to the Atlantic Ocean, the size of albuneid species that live in both habitats were compared using records from the literature (Boyko, 2002). Carapace lengths for *L. websteri*, *Albunea gibbesii*, and *A. catherinae* were taken from Boyko (2002).

Calculation of standard summary statistics (*e.g.*, mean, SD), chi-squared tests, *t*-tests, and analyses of variance (ANOVA) and their associated post-hoc means comparisons (Tukey's post-hoc tests) were completed using Origin 2016 (OriginLab Corporation, Northampton, Massachusetts, U.S.A.). To avoid pseudoreplication, analyses for differences between months of the year were based on the average of all transects per month per year. That is, the sample size for each month is five (one for each year of the project). The proportion of young over the course of a year was analyzed using a nonparametric Kruskal Wallis test on SPSS 23.0.0.0 (IBM Corporation, Armonk, New York, U.S.A.) because many the observations were zeroes and were not normally distributed.

RESULTS

Lepidopa benedicti were most abundant and reproduced during late summer. During this study, a new colour morph of *L. benedicti* was found, and the rare species *L. websteri* was recorded again at this study site.

Variation in Population Abundance and Sex

Lepidopa benedicti were collected in every month of the year ($n = 1222$ individuals collected). The abundance significantly varies throughout the year in Texas (ANOVA, $F_{11,44} = 5.43$, $p = 0.000022$), being low in winter and peaking in late summer (Figure 2A). The abundance of individuals in Florida was less than Texas. The abundance of *L. benedicti* was 1.63 individuals 10 m^{-1} transect (SD = 0.75, $n = 5$ months) in Texas for the month of November, but only 0.071 individuals 10 m^{-1} transect in Florida for the same month ($n = 1$ month), even though the total number of transects dug in Florida (42 transects) was greater than Texas (32 transects).

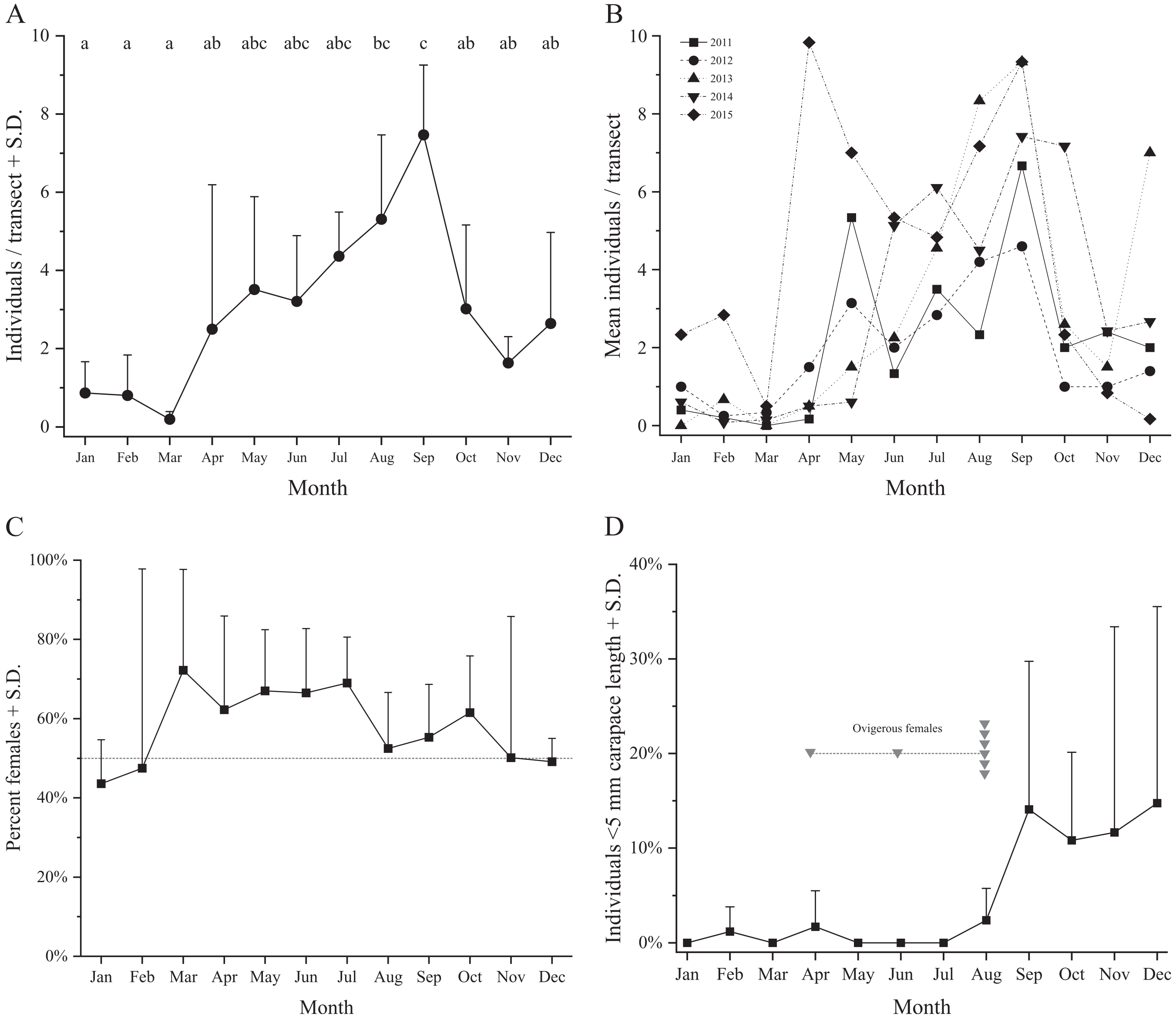

Figure 2. *Lepidopa benedicti* population size and composition varies over a year, despite living in the South Texas region, which experiences moderate seasonal climate changes. (A) Average monthly abundance over 5 years. Months that share a letter are not statistically different from each other (Tukey's post-hoc test). (B) Average abundance for each month. (C) Average monthly sex ratio over 5 years. (D) Reproduction. Average monthly proportion of young of the year (*i.e.* individuals with carapace length less than 5 mm) over 5 years. Each triangle represents one ovigerous female collected during this study.

The sex ratio of *L. benedicti* is significantly uneven, as previously reported (Murph and Faulkes, 2013): 55.85% of the crabs were female ($\chi^2 = 14.98$, df $= 1$, $p = 0.0001$). The sex ratio does not vary significantly over the year (ANOVA, $F_{11,43} = 0.67$, $p = 0.76$; Figure 2C).

Eight ovigerous females were found during this study, six of which were collected in early August (Figure 2D). The earliest was collected on 19 April, and the latest was collected on 14 August. The smallest ovigerous female was 7.52 mm in carapace length. The number of eggs ranged from 536 to 1942 ($n = 6$ ovigerous females).

The proportion of young of the year varies significantly over the course of a year (Kruskal Wallis test, $p = 0.016$) and are most often found from August to December (Figure 2D).

Variation in Size

The mean carapace length of individuals ranged from 2.42 mm to 17.92 mm, with a mean of 8.45 mm (SD $= 2.03$, $n = 1045$). Females are significantly larger than males ($t_{926} = -6.96$, $p < 0.001$), although the mode carapace length for both males and females was between 8.0 and 8.5 mm (Figure 3). Thus, the sexual size difference is mainly attributable to the rarity of males over 11 mm in carapace length.

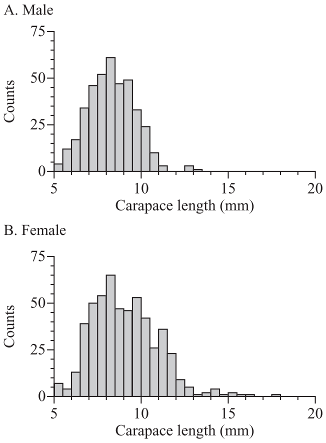

Figure 3. The largest *Lepidopa benedicti* are typically female. (A) Males. (B) Females. Excludes young of the year (*i.e.* those less than 5 mm in carapace length).

Lepidopa benedicti collected in Florida were significantly larger than Texas individuals (Figure 4A; $t_{12} = 2.44, p = 0.031$), controlling for sex (all female) and month of collection (all collected in November). In contrast, no significant size difference occurred between archival records of individuals collected in the Atlantic Ocean and the Gulf of Mexico in either *L. websteri* (Figure 4C; $t_{76} = -0.97, p = 0.33$) or *A. catherinae* (Figure 4D; $t_{95} = 1.59, p = 0.11$). Archival records of *A. gibbesii* showed those collected from the Atlantic Ocean were significantly larger (Figure 4B; $t_{81} = 3.38$, $p = 0.001$) than those collected from the Gulf of Mexico (Figure 4B).

New Orange Morph

The carapace of *L. benedicti* was previously described as grey or white (Nasir and Faulkes, 2011). Two orange individuals were found during this study (Figure 5): an 11.14-mm carapace length female collected on 22 December 2013 and a 9.92-mm carapace length male collected on 31 July 2014. The orange colour was visible over the entire dorsal surface, including the ocular peduncles, in both individuals. The pigmented eye spots were the normal black (Figure 5C). The ventral surface was not noticeably coloured (Figure 5D), similar to individuals with grey or white carapaces (Nasir and Faulkes, 2011). The exoskeleton was firm and gave no indication that this animal had recently molted, which can sometimes affect carapace

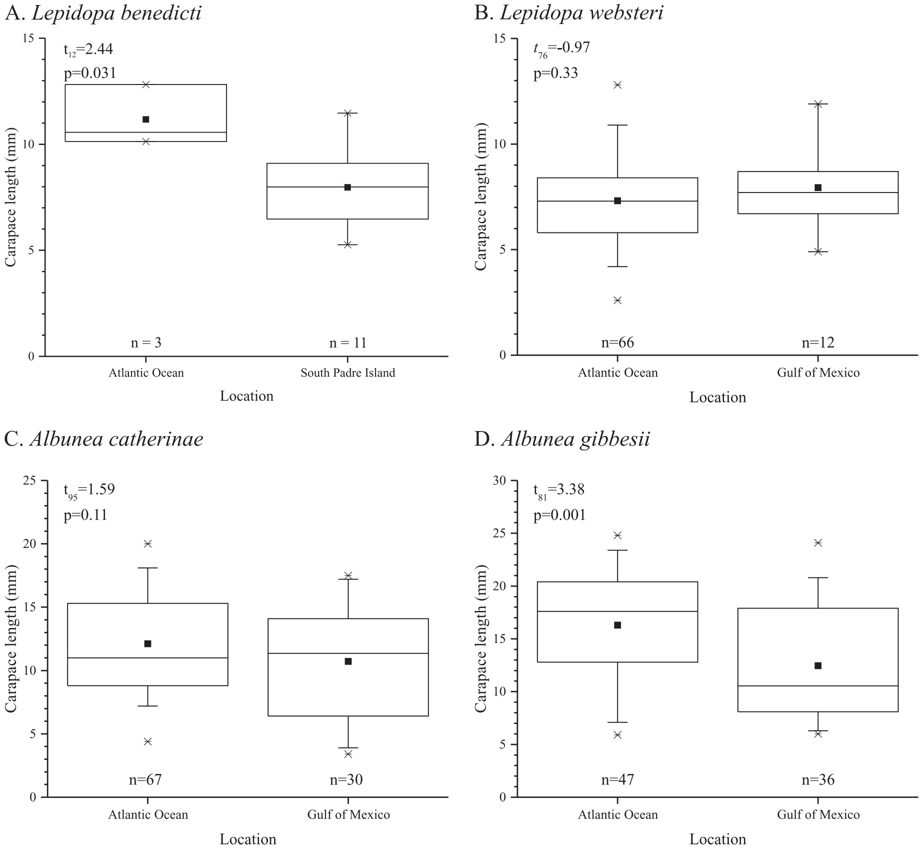

Figure 4. Sand crabs of difference species are not consistently different sizes in the Gulf of Mexico and the Atlantic Ocean. (A) *Lepidopa benedicti*, this study, matching sex and month. (B) *Lepidopa websteri*. (C) *Abunea gibbesii*. (D) *Albunea catherinae*. Data for (B)–(D) are from Boyko (2002). Mean = dot; median = horizontal line; box = 50% of data; whiskers = 95% of data; crosses = minimum and maximum. Note differences in *Y* axis scale.

Figure 5. A new orange colour morph of *Lepidopa benedicti*. (A), (B) Orange individuals next to more common grey and white morphs. Individual in (B) is same individual shown in (C), (D), but different from (A). (C) Close-up of ocular peduncles, showing typical eyespot pigmentation. (D) Ventral view of orange individual, showing typical white colour of exoskeleton; compare to Figure 1C in Nasir and Faulkes (2011).

colour. The individual collected in December 2013 remained the same colour until it died on 10 January 2014 from unknown causes.

New Records of *L. websteri*

Lepidopa websteri was collected three times during this study. The first, collected 23 July 2012, was previously reported as a range extension (Faulkes, 2014b). A nonovigerous female with a carapace length of 10.32 mm was collected 3 August 2015 on the beach east of beach access road Exit 6 (26°12′3.65″ N, 97°10′42.01″ W). A male with a carapace length of 8.55 mm was collected on 10 September 2016 on the beach east of beach access road Exit 4 (26°9′24.67″ N, 97°10′20.49″ W). All individuals had white carapaces.

DISCUSSION

The *L. benedicti* population in South Texas shows several cycles over the course of a year, despite that the location is in a subtropical climate with relatively modest weather changes. Abundance is high in summer, when reproduction occurs, and low in winter. This variation in abundance is not simply a matter of recruitment of the young of the year because most of the young of the year settle from September through December, after the peak in abundance. These facts suggest that *L. benedicti* shift their position relative to the water line during the year. *Lepidopa benedicti* has been collected in waters up to 3 m deep (Boyko, 2002), indicating that this species is not confined to the swash zone. The combined data on cycles over a year in abundance and young of the year suggests the following hypothesis. In winter, individuals live slightly below the water line, reducing their recorded abundance. In spring, individuals position themselves slightly higher in the beach. In many crustacean species, males locate females using olfactory cues (Bauer, 2011; Gleeson, 1980). If sand crabs use pheromones, a position higher on the beach, where receding waves might cause a pheromone to spread down a beach in a directional way, could allow males to locate females more easily than a lower position on the beach, where wave action might spread a pheromone in a more random pattern. After mating and release of eggs, both sexes tend to reposition below the water line.

The hypothesis that South Padre Island is a population sink for *L. benedicti* (Murph and Faulkes, 2013) is weakened by new observations here. First, the size distribution of individuals is relatively even, suggesting continuous recruitment expected of a source location instead of sporadic recruitment expected of a sink location (Defeo and McLachlan, 2005). Second, *L. benedicti* appear to be more abundant at South Padre Island than in the Florida locations surveyed. Third, both ovigerous females and very young individuals were found at South Padre Island, which had not been found in a previous 2-year study (Murph and Faulkes, 2013). Ovigerous females are difficult to collect, however. Their rarity might occur because females retain their eggs only for a short time; the only recorded hatching of *L. benedicti* eggs occurred within a day of collection (Stuck and Truesdale, 1986). Alternatively, the rarity of ovigerous females may be because, as previously suggested, South Padre Island acts as a population sink. Currently, only crude estimates regarding the proportion of females that must reproduce to maintain a population are possible. A single female *L. benedicti* can generate nearly 2000 eggs (this study), and under lab conditions, 31.25% of larvae survive to the megalopa stage (Stuck and Truesdale, 1986). Under that assumption, a single large female could have about 600 offspring survive to the settlement stage, although there is undoubtedly predation during the 14–17-day larval stage (Stuck and Truesdale, 1986) that further reduces larval survival in the wild. Further tests of the sink-source hypothesis could involve examining larval dispersal and performing genetic analyses of individuals from different locations. Given that the South Texas location is one of the more southern locations where this species has been recorded, more northern populations, nearer the center of the species recorded distribution (Figure 1), might be predicted to be potential sources.

The differences in abundance and size between *L. benedicti* in Texas and Florida suggest that ecological differences in the two populations exist. These differences may be attributable to phenotypic plasticity in response to the physical characteristics of the beach, similar to the mole crab *Emerita analoga* (Veas, Hernández-Miranda, and Quiñones, 2014). The Texas site has dissipative beaches with finer sand than the intermediate beaches of the Florida sites. The habitat harshness hypothesis (Celentano and Defeo, 2006; Defeo, Lercari, and Gomez, 2003) predicts that animals on dissipative beaches should be larger than those on more energetic (*e.g.*, reflective) beaches because animals on reflective beaches must divert energy into maintenance, not growth or fecundity. Thus, the habitat harshness hypothesis predicts that sand crabs should be larger in Texas than in Florida; however, this was not the case. This suggests that factors other than the physical characteristics of the beach are responsible for differences in the Texas and Florida populations; however, the lower abundance of individuals in Florida is consistent with the predictions of the habitat harshness hypothesis because a harsh habitat is predicted to support fewer individuals.

The orange colour morph in *L. benedicti* is reminiscent of some rare, bright colour morphs of crayfish sold in the pet trade (Faulkes, 2015) or commercially fished crustaceans, such as American clawed lobsters (*Homarus americanus*), which will often make national news (CBC News, 2013; Harish, 2013; White, 2013). In the news media, the probability of finding a red or orange lobster in the wild is usually estimated as being one in 10 million (CBC News, 2013; Harish, 2013; Lobster Institute, 2011; White, 2013), although how this estimate has been calculated is unclear. The probability of *L. benedicti* being orange appears to be about 1 in 600 (two orange individuals found out of 1222 collected during this study). Crustacean colour is determined both by genetics and environment (Black and Huner, 1980; Bowman, 1942; Kent, 1901; Tlusty and Hyland, 2005). Some crustaceans can change their colour to some degree (Barnard *et al.*, 2012; Wade *et al.*, 2012); these include hippid sand crabs (Bauchau and Passelecq-Gérìn, 1987; Stevens *et al.*, 2015; Wenner, 1972), which can change their colour to match the sand they live in. The rarity of the orange morph, plus its stability in adults, suggests that this colour is a rare recessive allele or mutation in both *L. benedicti* and lobsters. Because *L. benedicti* are obligate diggers that effectively spend all their adult lives submerged in sand, colours are unlikely to have any major signaling functions, either to conspecifics or other species (*e.g.*, predators) (Nasir and Faulkes, 2011). Thus, unusual colour morphs in *L. benedicti* may be under less selection pressure than unusual morphs in benthic crustaceans and thus more common. This is consistent with the discovery of this orange sand crab after sampling hundreds of individuals, rather than the millions that might be expected for lobsters.

The finding of additional *L. websteri* individuals suggests this is a normal, albeit extremely rare, species at this study site. That all *L. websteri* individuals were found in summer suggests their abundance, like *L. benedicti*, might vary over the course of a year.

CONCLUSIONS

Populations of *L. benedicti* collected at the shoreline can show cycles in abundance and reproductive status over the course of a year, despite living in subtropical regions with relatively mild climate changes. Changes in abundance are hypothesized to result from individuals repositioning themselves in the swash zone during the year for reproductive purposes. The hypothesis that South Padre Island acts as a population sink for *L. benedicti* is weakened by the findings of reproductive females and juveniles at this location.

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