EFFECT OF SAND GRAIN SIZE ON BURROWING BEHAVIOR OF JUVENILE PACIFIC SAND CRABS (*EMERITA ANALOGA)*

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ABSTRACT

Emerita analoga, Pacific coast sand crabs, are an important biological component of the swash zone ecosystem. They have evolved the ability to burrow into sand, and burrowing speed is commonly used as an indicator of performance relevant for fitness in this species. Sand grain size varies among beaches, and crabs may be better adapted to to burrow in some sand types.. We performed a completely crossed 3-factor experiment to determine how the sand grain size associated with beach-of-origin and rearing conditions influence burrowing in coarse and fine sand.. Crabs from a fine sand beach and a coarse sand beach were housed in both fine and coarse sand. The burrowing speed of each crab was tested in fine and coarse sand five times over ten weeks. Crabs were housed individually during the ten weeks, in either coarse or fine sand. We found a significant difference in burrowing times throughout sessions. Crabs from both beaches, housed in both sand types, burrowed faster in coarse sand than in fine sand. However, neither beach-of-origin nor rearing sand type influenced burrowing speed. There was also no difference in mortality among treatments. These results indicate that, although the abiotic factor, sand grain size, influences burrowing speed, this effect is not altered with long term exposure to different sand types.

INTRODUCTION

The swash zone, the area of the intertidal zone above the surf zone, which is characterized by constant tidal flux, is a particularly harsh environment for intertidal organisms (Dugan et al., 2000). Desiccation, exposure to predators, and high wave energy are just some of the stressors to which intertidal organisms must adapt in order to survive (Dugan et al., 2000). Pacific sand crabs, *Emerita analoga*, are a major biological component of the swash zone

ecosystem in California and have adapted to this high-energy zone by the employing the unique ability to burrow rapidly into the sand (Trueman, 1970; Faulkes & Paul, 1998; Dugan et al., 2000). Burrowing is an adaptive behavior that allows the crabs to minimize predation and to anchor in the sand to filter feed. Because faster burrowers can escape dislodgement by wave action and predators more quickly than slower burrowers (Cubit, 1969; Efford, 1966; Trueman, 1970; MacGinitie, 1938), burrowing behavior, specifically burrowing speed, can be an indicator of fitness in this species.

Emerita analoga is found along the Pacific Coast from Alaska to southern Chile. While the crabs spend most of their life in the swash zone, eggs hatch into larvae at sea and recruit on beaches, where they further develop via a series of molts into juveniles and then adults (Sorte et al., 2001).

Burrowing by sand crabs is affected by both abiotic and biotic factors, including sand grain size and parasite infection (Oliva et al., 2008). Specifically, the size of the grains of sand in which burrowing occurs influences a crab's burrowing speed and endurance. Some studies have found that crabs burrow slower after successive trials, suggesting fatigue (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S.Ramadan, M. Zosky, unpublished data); this study also found that crabs burrow slower in coarser sand (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data), consistent with other studies (Brazeiro, 2005; Lastra et al., 2004). A biotic factor that may influence burrowing is infection with parasites. Sand crabs are an intermediate host to the acanthocephalan parasite, *Profilicollis altmani*. Parasitized female crabs tend to burrow more slowly than uninfected crabs (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data), which can increase the chance of predation by shorebirds, the final host for *P. altmani.* Beach morphodynamics has also been

shown to influence the distribution of intertidal species (Borzone et al. 1996). The slope of the beach and the wave action influences not only what type of organisms can inhabit that environment, but also their behavior in that environment. A reflective beach is characterized by a steep slope and high wave height (Miles and Russell, 2004). A dissipative beach is characterized with a wide, flat surf zone (Wright et al., 1979). One study has shown that crabs from finer sand, dissipative beaches burrow faster than crabs from reflective, coarser sand beaches (Brazeiro, 2005).

Burrowing is typically used as a performance measurement for sand crabs because it is likely an important component of fitness and because it can be easily quantified. Our study is unique compared to other sand crab burrowing experiments because we tested juveniles rather than adults, and because we repeatedly measured the burrowing speed of the same individuals over the course of weeks. Using juveniles allowed us to raise crabs in different sand types. Our study addressed whether the sand type in which juvenile crabs are reared affects their burrowing and survival.. It has been shown that smaller crabs inhabit the upper swash zone while larger crabs inhabit the lower swash zone (Forward et al., 2005).

To our knowledge, ours is the first 3-way crossed design study to test the influence of sand type on burrowing.. The three variables we expected to influence burrowing speed were the sand type of the crab's native beach, the sand type the crabs were housed in, and the sand type the crabs were tested in. These three factors each included two different sand grain sizes (coarse and fine)..

Our study is based on the general assumption that sand type affects burrowing speed. In a previous study, it was found that crabs burrowed slowest in coarse sand but that crabs from coarse sand beaches were the fastest burrowers (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma,

S. Ramadan, M. Zosky, unpublished data). Based on this finding, we wanted to know if there was an effect of being reared in a sand type other than native sand on burrowing speed. We attempted to answer questions on what population of sand crab would be faster at burrowing, and if the type of sand they were housed in would affect survival. We predicted that crabs that had longer burrowing times would be less fit than those with faster burrowing times, and thus have a higher mortality rate. In support of earlier findings of faster burrowing times in fine sand, we expected to find that crabs from a fine sand population would burrow faster, regardless of sand type.

METHODS

Native Populations

Pacific sand crabs (*Emerita analoga*) were collected from beaches based on the beach morphodynamics. Two beaches were used as collection sites in San Luis Obispo County, California. Hazards Reef at Montaña de Oro State Park (N35°17.433' W120°52.887') is a California State Park beach with coarse sand, while Pismo Beach (N35°13.992' W120°64.465') is a fine sand beach (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data). Montaña de Oro has a mean sand grain size of 0.38 mm and sorting variance of 0.3 mm. Pismo beach has a mean sand grain size of 0.23 mm and a sorting variance of 0.13 mm (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data). The beaches were chosen as collection sites due not only to the sand grain size difference, but also to the proximity to San Luis Obispo, CA. A uniform mixture of sand typical of the swash zone of each site, and a sample of 32 crabs (see details below) were obtained from each of the beaches. Sand crabs were housed for ten weeks at the California Polytechnic State University

pier in Avila Beach, CA (N35°10.695' W120°43.932') (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data).

Crab and Sand Collection

Sand crabs were collected from Montaña de Oro and Pismo Beach in late July, 2009. Crabs were first obtained at Pismo in the morning. Many adult carcasses littered the beach, but few adults could be found. Juveniles were instead collected, approximately 2.5 cm in carapace length and of mixed sexes. Thirty two juveniles were obtained from Pismo. Crabs were collected at Montaña de Oro one week later in the mid-afternoon, and no adults could be found. Thirty two juveniles of mixed sexes were collected with an average carapace length of 2.0 cm.

Crabs were collected using a trowel and a sieve. Sand was scooped up and either dug through by hand or placed into a large sieve. Using the water washing onto the shore, the sand was swept out of the sieve, leaving any sand crabs inside. Crabs were placed in a Styrofoam cooler with sand from the native beach inside. One half inch of water was placed on top of the sand for transport. The crabs were taken to the Cal Poly pier in San Luis Bay where they were housed for ten weeks.

Sand from the beaches was collected and transported to the Cal Poly Pier for the crabs to be housed in, and used as the experimental subjects to obtain information on burrowing speed. To collect at Pismo, sand was shoveled into a large cooler with trowels and loaded into a car for transport to the Cal Poly pier. Sand from Montaña do Oro was collected by shoveling sand into garbage bags with trowels. The garbage bags were placed into backpacks and carried up to the parking lots for transport to the pier.

Crab Housing Treatments

The California Polytechnic State University Center for Coastal Marine Sciences Pier at Avila Beach extends one kilometer into San Luis Bay. The crabs were housed in an animal room with a flow-through seawater system and natural light supplemented by fluorescent lighting during the day. The pier is equipped with a flow-through seawater system from the bay itself. This system has seawater or filtered seawater available for use. The crabs were housed with seawater flowing through to act as their food source, and to simulate wave action.

In order to house each crab separately, cylinders were constructed out of black plastic mesh that was inert and did not leach chemicals. This allowed sand and water to flow through each cylinder. The plastic mesh was cut into rectangles that were 12 inches by 14 inches to make a cylinder that was 4 inches in diameter. The cylinders were 14 inches high, and the sides were tied together using black plastic zip ties. Five zip ties were used per cylinder to hold the sides together. A base rectangle of mesh was cut to be 9 inches by 19 inches. The open ends of the cylinders were zip tied onto the base piece in a two by four cylinder pattern, for a total of eight cylinders per base. Eight base pieces with eight cylinders each were made (Figure 1).

The base structures were each placed in eight 10 inch X 20 inch X 5 inch plastic bins. The bins were set up on one table in a two by four pattern, with the shorter sides against one another (Figure 1). PVC piping was set up to allow the seawater to flow into each bin evenly. Four one inch PVC pipes were linked together linearly with connectors. Both ends of the pipeline were connected to a hose that would run seawater through the piping. Holes were drilled into the piping every inch to allow the water out and into the bins. Two such pipes were made. One pipe was used to flow to the front four bins, and the second pipe was used to flow to the back four bins. Each bin had holes drilled into it near the rim to allow water to flow out while

minimizing sand loss. When the bins and piping were set up, the bins were filled with sand from either Montaña de Oro or Pismo.

In order to test the housing conditions and make sure crabs could not escape through the mesh, a pilot study was performed. One bin was set up with eight mesh cages. One PVC pipe with holes drilled into it every inch was placed across the bin lengthwise and hooked up to hoses for the flow-through system at each side. One crab was placed into each mesh cylinder. Crabs used for the pilot study were of various sizes. Crabs were monitored for two weeks for mortality and burrowing status. The PVC pipe was cleaned regularly. Any crabs that died were removed from the bin. After two weeks of running the pilot study, no crabs had escaped, and the mesh was used as constructed, to set up the 8 bins that constituted the experiment.

Bins were named based on the beach the sand crab came from and the sand with which the bucket was filled. Four buckets were set up containing Pismo sand and four buckets contained Montaña de Oro sand. The buckets were systematically staggered on the table with respect to sand type so that no one population would be subjected to significantly different environmental conditions than the other population. The bins were filled with four inches of sand and 3 inches of water above the sand. The bin was filled with sand after the mesh cages were placed inside to ensure the sand was deep enough inside the cages for the crab to burrow into. Once there was sand in each bin, the flow-through system was turned on, and the bins were left to acclimate for two weeks before crabs were placed into the bins. The bins and sand collection were completed before the crabs were collected.

Crabs were collected as described above and placed into the bins. One crab was placed into each cylindrical cage. Four treatments were established. Crabs that were collected at Pismo were either placed in Pismo sand or Montaña de Oro sand. Crabs that were collected at Montaña

de Oro were placed in either Pismo sand or Montaña de Oro sand. The eight buckets allowed us to have 16 crabs in each treatment. The bins were labeled according to the crab's native population, the sand type in which they were being housed, as well as the treatment number. For example, a bin labeled Pismo M2 contained a crab originally from Pismo that was being housed in Montaña do Oro sand, and was the second of two populations in that condition. The eight bins were: Pismo P1, Pismo P2, Pismo M1, Pismo M2, MDO M1, MDO M2, MDO P1, MDO P2 (in which case MDO stands for Montaña de Oro and P stands for Pismo).

Each bin was labeled with its population on the front of the bin and on the top rim of the bin. The bins were arranged, from left to right and front to back (bottom to top in Figure 1) Pismo M1, MDO P1, Pismo P1, MDO M1, MDO P2, Pismo M2, MDO M2, Pismo P2. The bins were staggered for randomization. Within each bin, the cylinders were labeled one to eight from left to right and front to back (bottom to top in Figure 1). Thus, a crab that had an identification of MDO M1 5 was a crab originally from Montaña de Oro, was housed in Montaña de Oro sand, was one of two populations, and was in the fifth cylinder cage. The crabs were allowed to acclimate for two weeks in their housing cages prior to the start of data collection.

The bins required little cleaning or maintenance, but the PVC piping was cleaned weekly. Each week, the piping was taken apart at the connectors and test tube cleaners were used to brush the insides of the tubes. Toothbrushes were used to clear the drilled holes that allowed water into the bins. The water pressure was turned to high to force sediment out of the tubing. The bins that contained Pismo sand were replenished with sand every two weeks, as the fine sand grains were lost with the water more so than the coarse sand grains. Bins that contained sand from Montaña de Oro were refilled occasionally throughout the experiment, but not as often as bins that contained sand from Pismo.

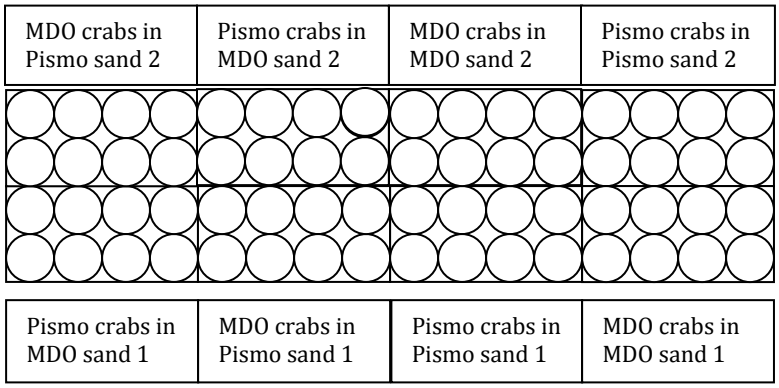

Figure 1. Rearing treatments for the sand crab experiment. Rectangles represent the bins that consisted of a single sand type and circles represent the individual cylinders each crab was housed in. Rectangles are labeled with the specific treatment. In every case, "MDO" sand is coarse and "Pismo sand" is fine, and "MDO crabs" and "Pismo crabs" refer to the beaches of origin.

Burrowing Measurement Procedures

Burrowing times of each crab were recorded in each sand type, as described below, every two weeks for 10 weeks. Digital calipers were used to measure carapace length in mm to 0.01 mm. Sex was determined by the presence or absence of pleopods, five pairs of thin ventral appendages that are used to hold eggs in females (MacGinitie, 1938).

Crabs were tested one at a time, beginning with the front left chamber within a bin, and proceeding through that bin in numerical order (1-8), then moving to the bin behind it. This was repeated, testing the front bin first, followed by the back bin, moving left to right. Although this meant that crabs were tested in the same order each time, the arrangement of crabs from different sites and in different sand types ensured that there was no systematic bias with respect to either of those variables. Each crab underwent four burrowing trials per testing day: two trials per sand

type. A coin toss determined the sand type of the first trial; subsequent trials alternated sand type. Two cylindrical opaque plastic tubs were used in the burrowing experiments, each filled with approximately 18 cm of either Pismo or MDO sand and 5 cm of filtered seawater. The seawater was changed after each trial. After a crab was selected from its housing chamber, it was held underwater in the tester's hand in the randomly selected trial tub for a count of five seconds, and then released. Burrowing time was defined as the time from initiation of digging by the crab's uropods to the time the crab's carapace was completely submerged in the sand; if the crab did not submerge completely, the end time was counted as when the crab stopped covering itself with sand and ceased digging (Lastra et al., 2004). The crab was then scooped out of the sand and sand was removed from the crab with gentle swirling in water. This method was repeated in alternating sand types for a total of four trials per crab. A crab was not tested if it had recently molted and still had a soft carapace, though this occurred rarely. Some crabs refused to burrow and instead swam around in the trial tub; in this case, crabs were recaptured and held again for five seconds, then re-released. Over the course of ten weeks some crabs inevitably died of unknown causes, in which case data acquisition was stopped for that crab.

After the fifth and final testing day, the crabs were individually packed into plastic bags labeled with a unique ID number and placed in a -80° C freezer at the California Polytechnic State University campus. Approximately one week later the crabs were dissected to determine *Profilicollis altmani* (parasite) cystacanth load (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data). Each crab was dissected after the final burrowing trial in session five and any cystacanths found were removed and saved in a different Ziploc bag. The cystacanths appear as small, white oval-shaped structures that are most often found directly

under the carapace (Amin, 1992; Nichol et al., 2002). Because parasites were found in so few crabs, parasite load was not included in the data analysis.

Data Analysis

To analyze mortality as a function of the beach of origin and housing sand type, we constructed two separate contingency tables and performed two separate chi-square tests. Contingency tables were constructed by totaling the number of crabs living versus the number dead in session five.

Factors affecting burrowing speed were analyzed using JMP Version 7 statistical software at an alpha level of 0.05. We used a square root transformation to normalize the data prior to analysis. A repeated measures analysis of covariance (ANCOVA) was performed on the normalized data. The covariates for the analysis were the categorical variable sex (male, female) and the continuous variable carapace length. Session and sand type the crabs were tested in were repeated measures. Non-repeated factors included the crab's native beach and the sand type in which the crab was housed. The model included interaction terms and retained only those that were deemed biologically important; the interactions that were not significant were omitted. The interactions that were retained are shown in Table 1.

RESULTS

Factor	Term in Model	F-statistic	P-value
Session	Repeated Measure	3.2047 (4, 221)	0.0139
Sand Type Tested	Repeated Measure	5.3854 (1, 221)	0.0212
Population Sand Type	Fixed Effect	0.6073 (1, 221)	0.4366
Sand Type Housed	Fixed Effect	3.875 (1, 221)	0.0503
Session x Sand Type Tested		1.9699 (4, 221)	0.1001
Sand Type Tested x Population Sand Type		0.0069 (1, 221)	0.9337
Sand Type Tested x Sand Type Housed		0.008 (1, 221)	0.929
Carapace Length	Covariate	2.0744 (65, 221)	0.0001
Sex	Covariate	1.8357 (1, 221)	0.1768

Table 1. Factors in the repeated measures analysis of covariance model, F-statistic, and P-value.

Mortality

The contingency table for mortality of crabs based upon the beach of origin, or native sand type, did not give significant results ($\chi^2 = 0.68$, p= 0.46, N= 64). The mortality of the crabs throughout the testing period was not significantly different between populations from Pismo and populations from Montaña de Oro (Figure 2). Based on the contingency table for mortalities based on the sand type crabs were housed, there was no significant difference between the crabs housed in coarse sand and the crabs housed in fine sand ($\chi^2 = 0.68$, p= 0.46, N= 64).

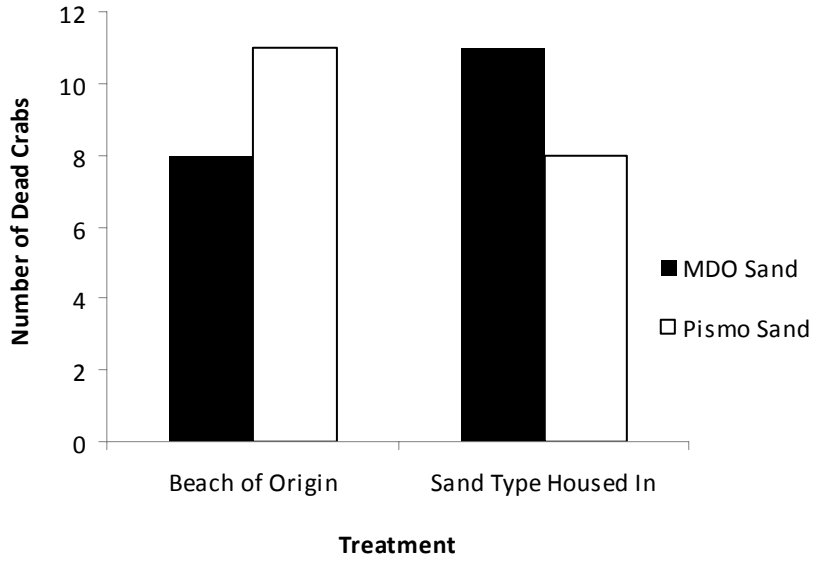

Figure 2. Number of crabs that did not survive to session five as a function of native sand type and housing sand type (Pismo = fine, MDO = coarse).

Factors Affecting Burrowing Speed

Burrowing speed varied significantly with session (Table1). A Tukey's post-hoc test revealed that crabs burrowed significantly slower in session 3 than in session 4 (Table 1, N= 35). All other sessions were not significantly different from each other; however, there was a slowing trend among sessions one, two, and three, followed by faster burrowing in session four (Figure 3).

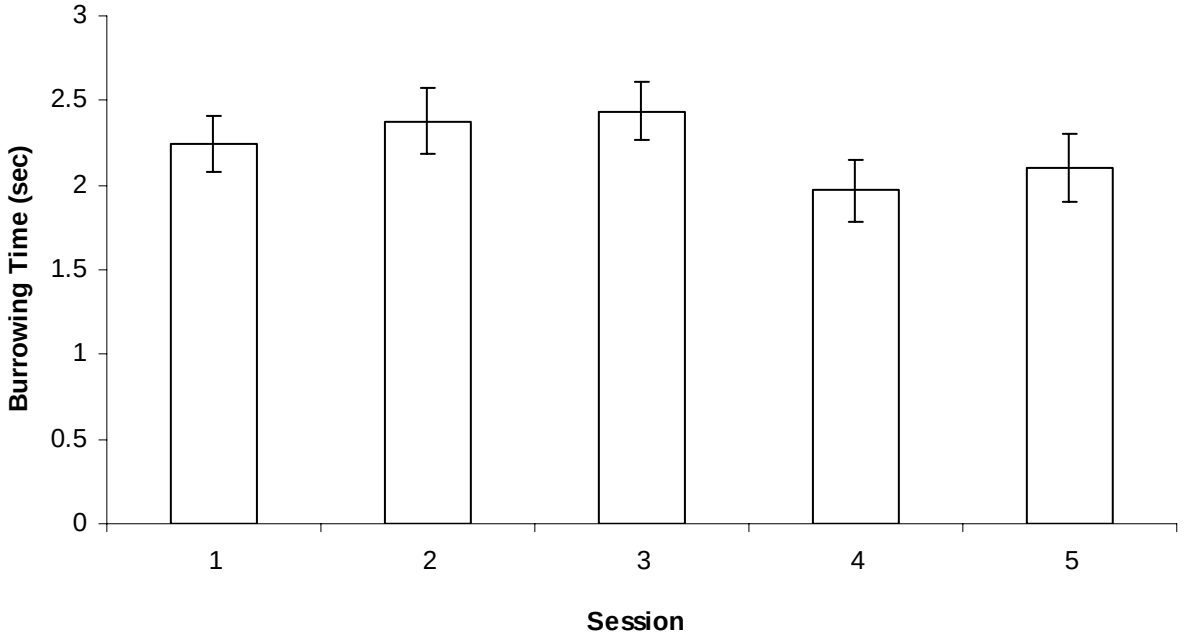

Figure 3. Average burrowing time as a function of session. Sessions were spaced apart by 2 weeks. Untransformed least squared means and standard errors are shown.

Crabs burrowed significantly faster in coarse sand than in fine sand (Table 1; Figure 4).

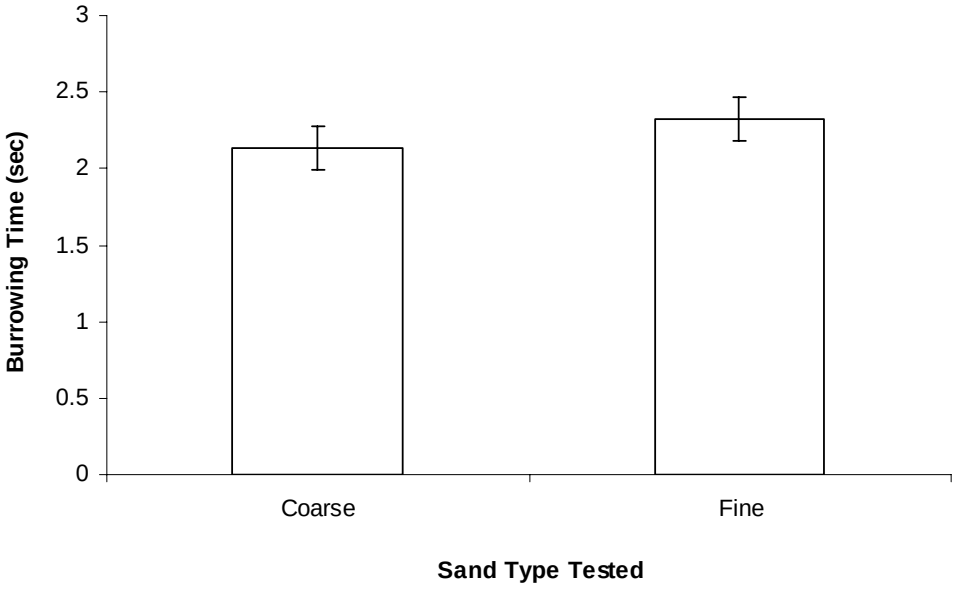

Figure 4. Average burrowing time as a function of sand type tested. Untransformed least squared means and standard errors are shown.

Burrowing speed did not differ with native sand or with sand type in which the crabs were housed (Table 1).

DISCUSSION

We found that crabs burrowed fastest in coarse sand, and slowest in fine sand, which contradicts the idea that *Emerita analoga* is a sediment generalist (Dugan et al., 2000). Crabs showed significant variation in burrowing speed depending upon the sand type in which they burrowed. Other beach crustaceans have been reported as sediment generalists, while bivalves are considered to be substrate sensitive (Dugan et al., 2000). Our results indicate that crab burrowing times are variable across studies, providing evidence that burrowing times are not readily consistent among crabs over time. Our results may be inconsistent with others because we tested juveniles rather than adults. Juveniles have more variable body sizes and are undergoing more rapid growth than adults. These differences seem to have an effect on burrowing speed in specific sand types.

Mortality

Because mortality did not differ with native sand type or sand type the crabs were housed in, we can infer that there is no difference in burrowing between sand crab populations in Pismo and Montaña de Oro. As sand crabs have a larval form capable of recruitment (Sorte et al., 2001), the populations are likely intermixed and not genetically different from one another. Recruitment allows the larvae to settle on beaches ranging along the Pacific coast, which

indicates little genetic difference among these populations. Because the crabs were collected as juveniles and taken out of their natural environment, beach morphodynamics played a minimal role in their development, thus there was no difference in mortality in crabs based on native population.

There was no significant difference in mortality between crabs reared in fine sand and crabs reared in coarse sand. We expected to find significantly higher survival of crabs housed in fine sand because burrowing in coarse sand should be more energetically expensive and thus potentially reduce survival. The high energy required to constantly burrow through coarse sand should be more than that required to burrow into fine sand, and should result in a higher mortality rate in those crabs that must burrow in coarse sand. These results were not observed, indicating that coarse sand may not have a higher energy cost. Crabs taken from Pismo, a fine sand beach, did equally well when reared in coarse sand as in fine sand. Similarly, crabs taken from Montaña de Oro, a coarse sand beach, survived equally well in fine sand and in coarse sand.

Factors Affecting Burrowing Speed

Burrowing speed changed over the course of the experiment, showing a peak during session four, and a decrease again at session five. This burrowing speed decrease over time could indicate a developmental change in morphology that allowed the crabs to burrow more quickly in all sand types. The growth could be in the form of an increase in carapace, hind leg, and/or telson length (Dugan et al., 2000). *Emerita analoga*'s larger telson in comparison to other *Emerita* species contributes to its ability to burrow well in a variety of sand grain sizes as a substrate generalist (Dugan et al., 2000).

Contradictory to expectations, all crabs burrowed significantly faster in coarse sand than in fine sand. Other studies found that adult crabs burrowed faster in fine sand than they did in coarse sand (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data; Brazeiro, 2005; Lastra et al., 2004). One possible reason for the discrepancy between those studies and ours is that we tested juvenile crabs rather than adults. Our results could indicate that there is an inherent difference, perhaps a morphological one, between juveniles and adults, that makes juveniles more adept at burrowing in coarser sand than adults.

The decrease in burrowing time in session four could also be evidence for an acclimation to the sand types in which the crabs were burrowing. Crabs were only removed from their chambers in order to be tested, and therefore could have become conditioned to the testing conditions. By session four, the crabs were most likely used to these trials. In the first three sessions, before becoming acclimated to the trials, stress may have played a role in burrowing behavior, causing burrowing to be slower by having a marked effect on metabolism. Studies on stress response in lower invertebrates and crustaceans consistently show a physiological response to handling, from changed blood pH and immune system response (Fotedar et al., 2006) to severely lowered metabolic rate and arrested development (Lant and Storey, 2010). The crabs in our experiment did not grow at the rate expected, nor was there much molting observed, which supports the idea that our crabs may have been under stress due to a number of factors, including low nutrients and space (Lant and Storey, 2010; Dugan et al., 2004).

We expected crabs native to the fine sand beach (Pismo) to be able to burrow faster in both sand types than crabs native to the coarse sand beach (MDO), which would support the findings of several other studies on Pacific sand crabs (G. Kolluru, Z. Green, L. Vredevoe, M. Kuzma, S. Ramadan, M. Zosky, unpublished data; Brazeiro, 2005; Lastra et al., 2004).

However, we found no such difference, indicating no effect based upon native beach. Because crabs have a larval form, they are able to recruit to beaches near each other (Sorte et al., 2001). Our results are consistent with the idea that the populations at Montaña de Oro and Pismo Beach could be genetically similar, thus exhibiting no genetic difference in burrowing speed.

We also expected crabs housed in fine sand to have faster burrowing times in both sand types than crabs housed in coarse sand. There was no difference in burrowing times between the treatments. These results could indicate that coarse sand is not more energetically expensive to burrow in, and that there is not a physiological difference between crabs in either sand type.

Error and Future Directions

While the scope of our study did not include the repeatability of burrowing behavior in individual crabs, it would be intriguing to look into this aspect of burrowing behavior. An animal's behavior can vary considerably given such factors as age, sex, environmental conditions, and intervals between measurements (Bell et al., 2009). It would be important to understand how sand crabs vary in burrowing times over the course of weeks, and if this behavior is predictable. Finding out how average burrowing speed among individuals changes over time would be an important contribution to this field.

Many of the crabs in our study exhibited bodily damage by the end of the ten week period, in the form of carapace dents and missing limbs. These damages were likely a result of crabs trying to burrow out of the chambers in which they were kept and causing resultant damage. This supports the finding that these invertebrates are limited by space, and need a larger area in order to thrive (Dugan et al., 2004). Invertebrates have been found to adapt to captivity in a way that would not allow them to be re-established into the wild (Lewis and Thomas, 2001).

The damage the crabs sustained could account for the inconsistent results on burrowing speed between our study and others, as outlined above. In order to reduce error from damage, chambers could be made larger to allow more room for the crabs to burrow. Chambers could also be coated with a material that would not allow the crabs to scrape their carapace against the mesh. If given more space and exposed to less damaging conditions, these crabs may exhibit more normal growth and show more pronounced differences in burrowing speed with sand grain size.

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