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Assessing Anthropogenic and Natural Impacts on Ghost Crabs (*Ocypode quadrata*) at Cape Hatteras National Seashore, North Carolina

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ABSTRACT

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This study explores impacts of off-road vehicles on ghost crab populations as a measure of impact from recreational beach use on two beaches of the Cape Hatteras National Seashore and assesses the effectiveness of several alternatives for the use of off-road vehicles (ORVs) on the beach. Ghost crab population size and density have been used as indicators of the environmental quality of beaches and dunes. Data on the creation of an "ORV corridor" in which ORVs can drive on the landward portion of the berm, but not on the beach crest, indicate that it may be possible to preserve ghost crab populations on the beach while still permitting the use of ORVs. Closing the beach crest 24 hours a day may be the optimal solution for preservation of ghost crab populations. High-energy weather events, however, resulted in larger changes to the population dynamics of the ghost crabs. After storms, ghost crabs were able to (re)inhabit areas where their numbers previously had been reduced by the operation of ORVs. While temporary closures of the beach crest may be used to reduce the short-term impacts of ORVs on ghost crab populations on the outer banks of North Carolina, long-term impacts ultimately are controlled by the strength and frequency of storms that reset the system.

ADDITIONAL INDEX WORDS: *Beaches, habitat alteration.*

INTRODUCTION

Ghost Crabs

Ghost crabs (*Ocypode quadrata*) are common on open ocean sandy beaches of the Atlantic and Gulf coasts of the United States and have been studied in other regions including southern Brazil (MILNE and MILNE, 1946; NEVES and BEMVENUTI, 2006). They are primarily nocturnal (DAHL, 1953; HALEY, 1969; WOLCOTT, 1978), but juveniles and the occasional adult may be seen on the surface near their burrows during daylight hours (HALEY, 1969). HILL and HUNTER (1973) state that during the morning, ghost crabs construct new, and repair older, burrows. Then, in the early afternoon they plug the burrows and remain within them until after sunset. In the Carolinas, they spawn from April through July (WILLIAMS, 1984). The zoeal and megalopal larval stages take approximately 60 days and are spent in the water, after which the ghost crabs recruit onto the beaches, generally at low tide (ANSELL *et al.,* 1972; DAHL, 1953). Ghost crabs are one of the top predators on the beach and have been cited as a potentially significant predator on terrapin hatchlings (ARNDT, 1991, 1994 as cited in DRAUD, BOSSERT, and ZIMNAVODA, 2004). According to WOLCOTT (1978, p. 67), ghost crabs consume most of the production of mole crabs, *Emerita talpoida* (Say), and coquina clams, *Donax variabilis* (Say) and "have essentially no terrestrial competitors or predators on the beaches."

Ghost crabs burrow primarily during the daylight hours (WILLIAMS, 1984). They construct burrows 0.6 to 1.2 m long in a zone extending from the high tide line shoreward up to 400 m (WILLIAMS, 1984). HILL and HUNTER (1973) describe the shapes of ghost crab burrows and DUNCAN (1986) describes the orientation of the burrows and determined that burrow diameter increases landward. According to WOLCOTT and WOLCOTT (1984), the width of a burrow is approximately equal to the width of the carapace. Ghost crabs travel up to 300 m while foraging on the foreshore at night and therefore do not return to their original burrows day after day (WOLCOTT, 1978). They can travel at speeds up to 2 m/s (PENNISI, 2007). From October through April, ghost crabs "hibernate" in their burrows (LEBER, 1982).

Owing to their habitat, size, and abundance, ghost crabs

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have been used as an indicator species for measuring the impacts of recreational beach use (Steiner and Leatherman, 1981) and other anthropogenic impacts (Neves and Bemvenuti, 2006). Barros (2001) found the relative spatial density of the Australian ghost crab (*Ocypode cordimana*), as indicated by the spatial density of burrows, to be an effective indicator of the level of human impact. Counting burrows is a simple, rapid technique for estimating crab populations (Barros, 2001) and population density (Hill and Hunter, 1973). The density of ghost crab burrows varies significantly with differing levels of recreation on the beach (Steiner and Leatherman, 1981). The mean number of ghost crabs per 0.1-ha plot at Assateague Island, Maryland–Virginia, was 10 on an undisturbed beach, 19 on a pedestrian-impacted beach, 1 on a light off-road vehicle and pedestrian-impacted beach, and 0.3 on a beach heavily impacted by off-road vehicles (ORVs) (Steiner and Leatherman, 1981). Steiner and Leatherman (1981) hypothesized that off-road vehicles may damage the crabs by crushing or burying them, by interfering with their reproductive cycle, or by altering their environment so that they can no longer survive. As a result, there is likely to be little to no reproduction, and new inhabitants would need to migrate in from other areas (Steiner and Leatherman, 1981). Pedestrians appear to have little detrimental effect on ghost crabs; rather it is likely the crabs are positively impacted by them since they capitalize on the food scraps scattered by tourists (Steiner and Leatherman, 1981). According to Wolcott and Wolcott (1984), the primary effect of ORVs on ghost crabs likely occurs at night when the crabs are feeding on the foreshore.

The effects that ORVs have on the beaches and the ecology of the beaches has been well documented, including changes in the sediment, populations of animals, and plant communities (Barros, 2001; Burger, 1981, 1994; Godfrey and Godfrey, 1976, 1980; Hobbs, 1977; Kutiel, Zhevelev, and Harrison, 1999; Liddle and Moore, 1974; McAtee, 1981; Perry, 2002; Steiner and Leatherman, 1981; Wolcott and Wolcott, 1984). Off-road vehicle usage on the beaches can dramatically alter the physical aspects of the environment, including increasing compaction (Perry, 2002), thereby decreasing sediment moisture content available to the ghost crabs (Steiner and Leatherman, 1981).

Suggestions for mitigating the impact of ORVs on the ecology of the beach system include closing the foreshore to ORVs during night hours to regulate for ghost crab populations (Wolcott and Wolcott, 1984) and creating an "ORV corridor" between the foreshore, which is accessed by ghost crabs, and the back edge of the beach, which is often used by nesting birds and turtles (Godfrey and Godfrey, 1980).

Peterson, Hickerson, and Johnson (2000) studied the response of several organisms including the ghost crab to beach nourishment and beach bulldozing, which have much different physical consequences on the beach when compared with ORV use. While confirming "that it is possible to successfully conduct manipulative experiments on exposed sandy beaches," Schoeman, McLachlan, and Dugan (2000, p. 869) note that the natural dynamics of the beach contribute to both spatial and temporal variations in the response of the macrobenthos to the anthropogenic forcings of the experiment. As will be discussed, the occurrence of substantial coastal storms during the course of this study both complicated the assessment of the impact of ORVs on ghost crabs and highlighted the role natural physical processes play in the ecology of organisms that dwell in the beach. Defeo and McLachlan (2005) consider the response of beach macrofauna to passive sorting and transportation by swash or to elevated water levels but do not address the more dramatic situation of an extremely rapid change in beach form that accompanies strong storms. The occurrence of high-energy weather events during the course of the study truncated the study of ORV impacts but permitted the analysis of the changes in ghost crab population dynamics before and after the passage of the storms.

The purpose of the present work is to assess potential restrictions to ORV use on the beaches of Cape Hatteras as a means of reducing the detrimental ecological impacts. The study is intended to assist in the development of an ORV management plan required under federal executive orders (Federal Register, 2006) and is needed since the lack of a formal plan has resulted in inconsistent management of ORV use. The Federal Register notice states that "the management of ORV at (Cape Hatteras National) Seashore has been controversial" and that the ORV management plan must "allow for a variety of visitor use experiences" while minimizing "conflicts between ORV use and other uses," which would include environmental considerations (p. 71,553). The notice further states that conflicts between park visitors desirous of using ORVs and those seeking other experiences have increased.

METHODS

Site Description and Study Design

Two beaches within Cape Hatteras National Seashore, one at Coquina Beach and one just south of Avon, North Carolina ("Coquina" and "Avon," respectively in Figure 1a, 1b), were chosen with the assistance of U.S. National Park Service personnel in order to reduce the impacts of differing levels of human recreation on the beaches, as well as to represent typical beach habitats found within the park. Within each region, four separate sites were designated: one site that remained vehicle free, one site that remained open to ORV use, one site from which ORVs were to be restricted from the seaward ~20 m of the beach at all times, and one site from which ORV use on the seaward ~20 m of the beach was to be forbidden from 2000 to 0600 hours, for a total of eight study sites (Figure 1). The sites were separated by several hundred meters of beach on which the use of ORVs was not restricted. For clarity of discussion, sites are designated "no ORVs" or "ORV," respectively. Analyses of the newly restricted zones are designated "24-h closure" and "PM closure," respectively. The latter two were established in early August 2003. This created an "ORV corridor," delineated with signs, in which vehicles could be operated between the base of the fore dune and the regulatory signs that were placed about 20 m shoreward of the high water line. Access to the water was obtained by parking behind the signs and walking across the no-ORV

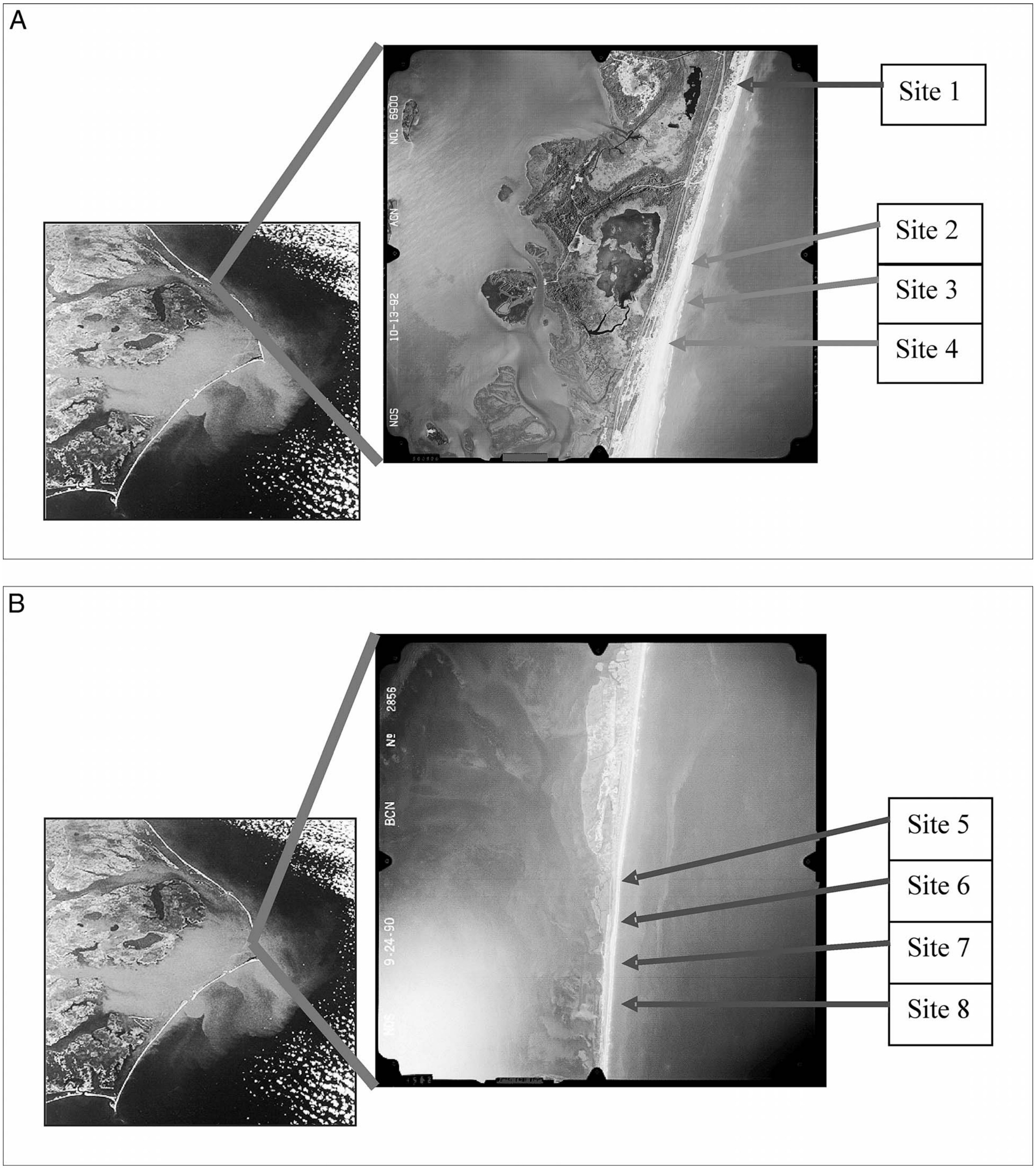

Figure 1. (A) Coquina Beach, North Carolina. Site 1: ORV free at all times. Site 2: ORVs restricted from the seaward 20 m of the beach 24 hours a day. Site 3: ORVs restricted from the seaward 20 m of the beach from 2000 to 0600 hours. Site 4: open to ORV use. (B) Avon, North Carolina. Site 8: ORV free at all times. Site 7: ORVs restricted from the seaward 20 m of the beach 24 hours a day. Site 6: ORVs restricted from the seaward 20 m of the beach from 2000 to 0600 hours. Site 5: open to ORV use.

corridor to the water. The restricted portion of the beach was designated as the "beach crest." During the summer, the closure signs were not moved in response to beach growth.

Both Coquina and Avon beaches are wave-dominated, microtidal environments. The mean tide range at Nags Head, roughly 10 km north of Coquina, is 1.0 m, and at Cape Hatteras, roughly 10 km south of Avon, it is 1.1 m (NOAA, 2007). Both sites are open to the Atlantic Ocean. Coquina Beach faces the northeast, whereas Avon faces east; the sites are about 50 km apart.

Ghost Crab Burrow Densities and Sizes

Within each of the eight sites, burrow use, density (number of burrows per unit area), length, and width were measured and recorded. Within each site, three randomly assigned belt transects, 5 m wide, were designated for each collection period. Each transect was perpendicular to the water line and stretched from the crest of the dune to the water line. Burrow and sediment data were collected at 4.5-m intervals in the belt across the beach from the crest of the fore dune to the water line. Compaction of the sand was measured with a Spectrum Technologies soil compaction meter. Burrow length was determined by inserting a thin, flexible tube marked at centimeter increments into the burrow until resistance suggesting the bottom was met. Data were collected during eight periods at 2- to 3-week intervals from early June and through November 2003.

During the September 12 data collection period, high waves passed over the closure signs and often crashed on the base of the dunes, limited sampling to the dune region. The active burrows in each transect were counted and measured. Inactive or filled burrows also were counted. Active burrows were differentiated from inactive burrows by their appearance; burrows were deemed active if tracks were present around the opening where the crab traveled in and out of its burrow or piles of sediment that had been removed from the inside of the burrow were found. Inactive burrows quickly fill with sand, especially when the weather is windy or stormy, and often have a layer of sand just inside the burrow that can be blown there even by a light wind. During later data analysis, spatial densities were normalized to an area of 100 m^2.

Analyzing the Impact of High-Energy Weather Events

Three high-energy weather events, Tropical Depression Henri, Hurricane Fabian, and Hurricane Isabel, occurred during the study. Hurricane Henri weakened to a depression and moved up the East Coast of the United States toward the outer banks of North Carolina. The depression passed approximately 250 km east of the study area, sending high waves to the beaches on September 7 and 8. September 10 and 11, Hurricane Fabian passed approximately 250 km east of the study sites, causing high wind and waves on the study beaches. Hurricane Isabel made landfall as a category 2 hurricane just south of Avon on September 18 with a storm surge that reached 2–2.5 m above the normal tide level. Many of the dunes were scoured by the storm, and all those remaining were scarped or cut through. Beaches were closed to ORVs for several weeks because of both the closure of the roads and scarping of the beach face. Data collection continued in October and November in order to assess the impacts of the high-energy weather events on ghost crab populations.

Statistical Analysis

Analysis of variance (ANOVA, Matlab) was used to compare variations in mean burrow density through the field season, between sites, between regions, and between locations on the beach profile. Analysis of variance also was used to analyze variations in mean burrow lengths and widths for the above tests. Variations in compaction and sediment grain size were analyzed through the field season, among the regions, and between driven and not driven sites using ANOVA.

RESULTS

Off-Road Vehicle Regulation and Burrow Density

Mean burrow densities in the beach crest, midbeach, and dune regions of the beach were compared between the preregulation dates (June 4, June 25, July 7, and August 3) and the postregulation collection date (August 23) to determine impacts of the new vehicle-free zones on ghost crab population density.

At Coquina, restricting the use of ORVs on the beach crest 24 hours a day resulted in a significant increase in mean burrow density (ANOVA, $p = 0.007$, df = 4, 78, $F = 3.81$), though no significant increase occurred in the area restricted to ORV use from 2000 to 0600 hours (ANOVA, $p = 0.113$, df = 4, 56, $F = 1.96$), as compared with previous study dates. Mean burrow density on the beach crest in site 2 (24-h restriction) increased by approximately 4.4 burrows per 100 m^2, or approximately double the density that was found earlier in the field season.

At Avon, restricting the use of ORVs on the beach crest 24 hours a day and from 2000 to 0600 hours resulted in significant increases in mean burrow density within those areas (ANOVA, $p = 0.049$, df = 3, 72, $F = 2.75$; ANOVA, $p = 0.015$, df = 3, 81, $F = 4.045$, respectively) as compared with previous study dates. Mean burrow density on the beach crest in site 7 (24-h restriction) and site 6 (PM closure) increased by approximately 2.2 burrows per 100 m^2.

Mean burrow densities were highly variable and varied significantly among the sites during the field season and varied from approximately 2 to 13 burrows per 100 m^2. At Coquina, site 1 (no ORVs) had significantly more burrows than sites 2 through 4 (all ORV) by an average of 8.8 burrows per 100 m^2 over the entire field season (ANOVA, $p = 0.008$, df = 3, 23, $F = 5.03$). At Avon, site 8 (no ORVs) had significantly more burrows than sites 5 through 7 (all ORV) (ANOVA, $p = 0.007$, df = 3, 23, $F = 5.18$). Mean burrow density was not significantly different between site 1 (no ORVs) and site 8 (no ORVs) (ANOVA, $p = 0.198$, df = 1, 14, $F = 1.82$). Mean burrow densities at the driven sites (ORV) at Coquina (sites 2 through 4) and the driven sites (ORV) at Avon (sites 5 through 7) were not significantly different (Figure 2) (ANOVA, $p = 0.007$, df = 3, 23, $F = 5.18$). After the passage of Hurricanes Henri, Fabian, and Isabel, mean burrow density increased at all sites (Figure 2).

Burrow Sizes

Mean burrow width varied significantly among the sites (ANOVA, $p < 0.001$, df = 7, 2295, $F = 0.87$). Burrow widths were smaller in sites 4 through 6 (all ORV) than in any other sites throughout the field season, which is indicative of the presence of smaller crabs.

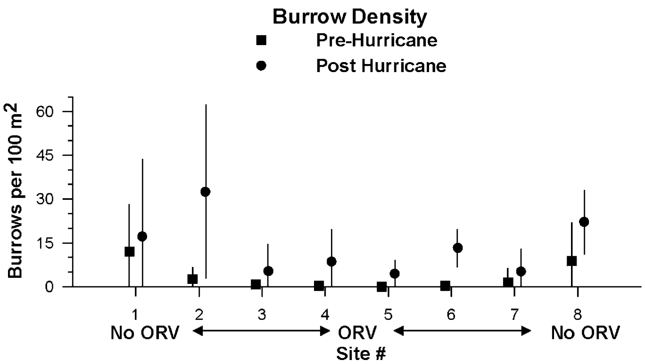

Figure 2. Mean burrow density (and standard deviation) within all eight sites, averaged over the prehurricane and posthurricane study periods. Sites 1 and 8 were closed to all ORV use. Sites 2 and 7 were open to ORVs except for a ~20-m wide corridor near the water from which ORVs were prohibited at all times. Sites 3 and 6 were open to ORVs except that ORVs were prohibited in the ~20-m corridor from 2000 to 0600 hours. Sites 4 and 5 were fully open to ORV use.

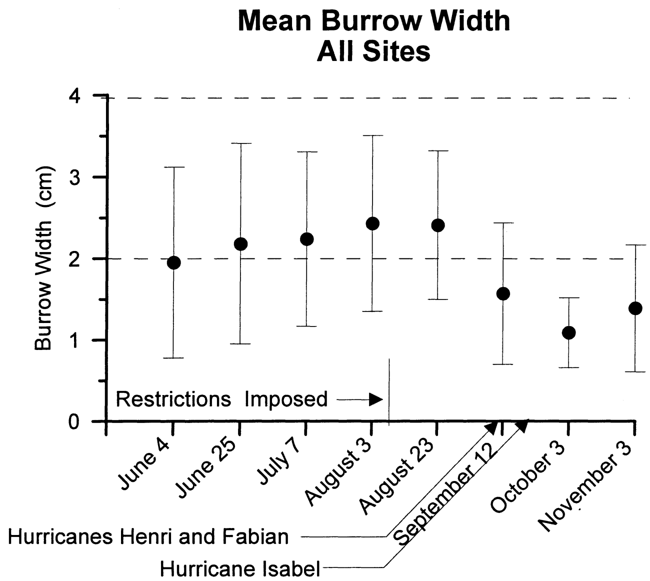

Figure 3. Variations in mean burrow width through the field season. The error bars indicate one standard deviation each side of the mean.

Mean burrow width also changed significantly through the field season (ANOVA, $p < 0.001$, df = 7, 2295, $F = 71.93$). Mean burrow width increased from June 4 through August 3. A decrease in mean burrow width was noted for the September 12 collection period, when waves from Hurricanes Henri and Fabian were impacting the region. A decrease in mean burrow width also occurred prior to the October 3 data collection period, which was the first collection period after Hurricane Isabel. Mean burrow width increased between the October 3 and November 3 data collection periods but remained well below earlier widths (Figure 3).

Mean burrow length did not differ significantly between site 1 (no ORVs) and site 8 (no ORVs) (ANOVA, $p = 0.247$, df = 1, 1473, $F = 1.34$). Mean burrow length for sites 1 and 8 varied over time and changed significantly through the field season (ANOVA, $p < 0.001$, df = 6, 1495, $F = 5.89$). The longest burrows occurred during both August periods (August 3 mean = 37.6 ± 11.6 cm, August 23 mean = 37.7 ± 17.9 cm) and the November 3 period (mean = 35.8 ± 28.1 cm), but the variance was high.

Sediment Compaction

Compaction differed significantly (ANOVA, $p < 0.001$, df = 7, 757, $F = 16.18$) among sites, with measured values ranging from 145 to 220 N cm^{-2} (211 to 320 pounds per square inch [psi]) with the sediments at Coquina more compacted than at Avon. Of the four sites at Avon, site 3 (ORVs not permitted on the seaward ~20 m of the beach at night) on average was the most compact, 220 N cm^{-2} (320 psi), whereas sites 1 and 4 (closed to ORVs and fully open to ORVs, respectively) were almost equally compact, 187 and 195 N cm^{-2} (271 and 283 psi). At Avon, the average compaction of site 8 (closed to ORVs) was 145 N cm^{-2} (211 psi), substantially lower than at the other sites.

DISCUSSION

Management Implications

This is the first report of possible mitigation strategies for ORV impacts on ghost crab populations. Restricting access by ORVs to portions of the beach resulted in a small but significant increase in the number of ghost crabs and their burrows at the beaches of Coquina. Restricting ORVs from the beach crest 24 hours a day resulted in a significant increase of approximately 4.4 burrows per 100 m^2 in mean burrow density. While this increase was small, it was statistically significant and was approximately double the density of ghost crab burrows that had previously been found. Burrow density within the 24-hour closure at Coquina increased significantly only on August 23 and was not as variable as the changes in burrow density found in site 1 (no ORVs). These increases in mean burrow density therefore likely were a result of restricting ORVs from this portion of the beach. On the basis of burrow width, immigrant crabs that inhabited this area were recruited from adjacent dune areas that had restrictions to ORV use. Burrows typically were large and not indicative of smaller crabs that would have been found after settlement. These crabs may have migrated into the newly regulated region at night while foraging on the foreshore, since ghost crabs can move as much as 300 m in one night while feeding on the foreshore (WOLCOTT, 1978). The crabs may also have migrated through the water while breeding or spawning (WILLIAMS, 1984). At Coquina, banning ORVs from the beach crest from 2000 to 0600 hours did not result in a significant increase in the ghost crab population in that area. The continued use of ORVs during the day may have reduced the ability of the ghost crabs to burrow. Simply restricting ORVs from certain portions of the beach at Coquina during night hours when the ghost crabs were most likely to be out of their burrows and foraging on the foreshore as WOLCOTT and WOLCOTT (1984) suggested was not sufficient to allow the crabs to populate that area.

At Avon, restricting ORVs from portions of the beach also resulted in a significant increase in the densities of ghost crabs. Restricting ORVs from the beach crest at Avon for both 24 hours a day and from 2000 to 0600 hours resulted in a small, but significant, increase in mean burrow densities. Mean burrow density at site 8 (no ORVs) was highly variable. As was found at Coquina, the ghost crabs that inhabited the newly regulated portions of the beach were likely recruits from other regions that had prior restrictions to ORV use. Restricting ORVs from the beach crest at night (site 6) may have permitted the ghost crabs to populate the area. During the August 23 study period, this site experienced little ORV traffic during the day (Landry, personal communication). The reduced traffic may have resulted in a modest immigration of ghost crabs that would not have occurred if the region had been more heavily used by ORVs, as was the case at Coquina.

Ghost Crabs

Ghost crab populations at Coquina and Avon had similar mean burrow densities. Burrow densities and sizes were similar for both the driven upon and not driven upon sites in both areas. While no statistically significant differences were found between the burrow densities at Coquina and Avon, there were slightly lower mean burrow densities at site 8 (Avon—no ORVs) relative to site 1 (Coquina—no ORVs). This could be related to the coarser sand and steeper beaches at site 8 (no ORVs). GAULD and BUCHANAN (1956) found that steeper beach slopes and coarser mean sediment grain sizes, as found at Avon, may cause increased drainage rates and therefore may increase the risks of dehydration to the beach organisms, which can be detrimental to the survival of the ghost crabs (WEINSTEIN, 1998; WEINSTEIN, FULL, and AHN, 1994; WOLCOTT and WOLCOTT, 1984). MCLACHLAN (1996) also found that increased sediment grain size might correlate with a decrease in species richness and abundance. Sediment characteristics are important to the habitat use and population size of *Uca* species and other closely related ocypodid crabs (GIBBS, 1978; ICELY and JONES, 1978; THURMAN, 1984).

Prior to the high-energy weather events, off-road vehicles were shown to have a detrimental impact on the density of ghost crabs (*O. quadrata*) at Cape Hatteras National Seashore. The study sites in which vehicles were permitted to drive on the beaches had significantly lower densities of ghost crab burrows than those sites remaining vehicle free. STEINER and LEATHERMAN (1981) showed that ghost crabs can be killed or mortally injured by ORVs driving over them and altering their environment. Whereas WOLCOTT and WOLCOTT (1984) found no real impact of ORV use on ghost crab populations, the effects shown in this study may be due to higher ORV use at Cape Hatteras than at Cape Lookout, an area that WOLCOTT and WOLCOTT had defined as "low-usage," in addition to possible changes in the magnitude of ORV use since the previous study was conducted.

STEINER and LEATHERMAN (1981) found that in a region that is heavily impacted by ORVs, there will be approximately 0.3 ghost crabs per 1000 m^2, and in a region impacted by pedestrians, there will be approximately 19 ghost crabs per 1000 m^2. In this study, we found approximately 2.2 ghost crab burrows per 100 m^2 within the regions impacted by ORVs, which is significantly higher than the densities found by STEINER and LEATHERMAN (1981). We also found approximately nine burrows per 100 m^2 within the regions impacted by pedestrians, but not ORVs, which again is significantly higher than the densities found by STEINER and LEATHERMAN (1981). While both their and our results show that ORV usage on the beaches had a detrimental impact on the density of ghost crabs on the beach, the discrepancies in the scale of the impacts may be due to differences in the sampling methods and location. STEINER and LEATHERMAN (1981) counted the number of crabs within a circle of light at night as an approximate census of the burrow density, while we used daytime burrow counts. LEBER (1982) found that burrow counts in 1976 were nearly an order of magnitude greater along the upper beach than crab counts along swash zone transects. WOLCOTT and WOLCOTT (1984) described counting burrows as a method that, while requiring subjective distinction between active and inactive burrows, has the ability to describe population size and age structures. Counting burrows also approximates the total population, rather than the proportion active at a given time (WOLCOTT and WOLCOTT, 1984). Quantitative nocturnal counts of surface-active crabs are extremely difficult because of the rapid movements of the crabs and may yield much lower population estimates (LEBER, 1982; STEINER and LEATHERMAN, 1981; WOLCOTT, 1978; WOLCOTT and WOLCOTT, 1984).

Mean burrow width at Coquina was highly variable with regard to the distribution of larger ghost crabs among the sites and showed no apparent pattern. At Avon, the largest burrows were found at site 8 (no ORVs), which was designated vehicle free, and the smallest burrows were found in site 5 (ORV) which had the greatest traffic, being closest to the ORV ramp onto the beach (Figure 1B). Off-road vehicle use on the beaches may therefore limit the size of ghost crabs in certain sites, possibly affecting the survival of larger crabs and reducing the life expectancy of crabs in those sites and, therefore, resulting in smaller mean burrow widths (STEINER and LEATHERMAN, 1981). Alternatively, ORV use may affect all sizes of crab equally, and the observed differences reflect recruitment and/or immigration of smaller crabs.

The specific processes by which ORVs impact ghost crabs remain unclear. A quick review of unpublished photographs of trenches dug across beaches suggests that the disturbance of the natural structure of the beach by tires is roughly limited to the top 20 cm. This would agree with "back-of-the-envelope" calculations, which suggest that the pressure applied to the beach by a motor vehicle is not great. For example, ORVs usually operate with relatively low tire pressures, perhaps 140 KPa (~20 psi). The pressure exerted on the ground is the same as the air pressure in the tire, and the soil pressure would decrease with depth. A 2700 kg (~6000 lb) vehicle would have a 1900 cm^2 (~300 in^2) contact patch. So, while the total load might be large, the pressure transmitted through the beach sand would be relatively small. However, one might expect that the dynamic nature by which the pressure is applied by rolling wheels might enhance the effects. Nevertheless, compressive closure of shallow, horizontal, as opposed to deeper or more vertical, burrows has to be considered a factor, as does actual physical trauma to the ghost crabs when they are on the beach surface.

Hurricane Impacts on Ghost Crab Populations

While there was no significant variation in overall burrow densities throughout the field season, burrow density at site 1 (no ORVs) increased dramatically by the November 3 sampling period compared with the other study sites. On November 3, at Avon (site 8 [no ORVs]) mean burrow width (1.7 ± 0.6 cm) was substantially greater than at Coquina (site 1 [no ORVs]) (1.2 ± 0.6 cm). The increased presence of larger ghost crabs at Avon after the passage of three hurricanes suggests several possibilities. The higher density of larger surviving crabs at Avon may have resulted in greater predation on the smaller ghost crabs found in that region (WOLCOTT, 1978), whereas higher settlement at Coquina may have been due to the reduced numbers of larger crabs, and therefore reduced levels of competition and predation; alternatively, differences in the physical habitats such as sediment grain size and compaction may have resulted in the differences between Coquina and Avon.

The impact of high-energy weather events on ghost crab populations has not been well documented. Mean burrow densities at Coquina and at Avon changed dramatically after the passage of Hurricanes Henri, Fabian, and Isabel (Figure 2) as did mean burrow width (Figure 3). The increase in burrow densities in the ORV sites after the storms may possibly be due to the restricted ability of ORVs to access the beaches during and immediately following the storms. The high water and waves damaged or destroyed vehicle access ways to the beach, keeping ORVs off of the study area. Storm damage to the main highway served to limit general access to the Outer Banks, thus temporarily decreasing the number of potential ORV users. The entire beach was closed for approximately 2 weeks but prestorm levels of access did not return for 2 to 4 weeks after that. Mean burrow densities also increased in site 1 (no ORVs), but not at site 8 (no ORVs). After the three hurricanes, burrow densities in each site were highly variable. Even after the occurrence of the storms, mean burrow densities in regions open to ORVs were less than those with restrictions on ORV use. It is possible that in the sites that remained vehicle free throughout the season (sites 1 and 8), some larger ghost crabs were able to survive the storms, perhaps by retreating into the dunes, whereas in regions that were open to ORV use, there was little to no competition for the settlement of juvenile ghost crabs.

The erosion that accompanied the storms fully reset the burrow density to zero at all sites. Since the storms substantially eroded the beach, removing all the existent burrows, all the burrows recorded in the October 3 survey must have been excavated after the passage of Hurricane Isabel on September 18.

Settlement of juvenile ghost crabs at Coquina and Avon occurred after the hurricanes and was particularly evident in October and November. Settlement of *Uca* species, a closely related *Ocypodidae,* occurs in clusters or waves (JONES and EPIFANIO, 1995), with larvae developing in the open ocean for approximately 60 days (WILLIAMS, 1984) prior to being driven ashore by transport mechanisms such as tides, winds, and currents (BRUBAKER and HOOFF, 2000; FORWARD *et al.,* 2004; GARLAND, ZIMMER, and LENTZ, 2002; JONES and EPIFANIO, 1995). Such waves of settlement resulting from wind-driven transport explain the large increases in small crabs after the hurricanes.

The effect of hurricanes on mean burrow width of the ghost crabs was first noted on September 12, when size classes decreased to more frequent 1-cm burrows. The high wind and wave energy of Henri and Fabian apparently removed or displaced the larger crabs when the waves passed over the beach crest and midbeach regions scouring the beach and removing, burying, or suffocating small organisms. The larger crabs may also have migrated to the dune field behind the fore dune to wait out the storm (LEBER, 1982). If migration into the dunes occurred, only a few crabs then reemerged back onto the beach face after the storm. Hurricane Isabel also dramatically changed the beach profile, decreasing the width and lowering the berm. Since most or all of the burrows were removed by the hurricane, many of the larger crabs that were able to survive Henri and Fabian probably were removed from the system after Isabel. By November there was a small, but apparent, increase in 2-, 3-, and 4-cm burrows, which suggested a migration of the larger ghost crabs back into the study sites, presumably from the back dune areas that were protected from high winds and waves.

High-energy weather events cause a significant amount of sediment movement, through both the wind and the water moving across the beach face, likely filling established burrows (HILL and HUNTER, 1976). It is possible that during periods of fair weather, as the beach face elevation increased, the burrow length also increased, indicating a change in surface height rather than in burrow depth. This possibility was not addressed through the work of this study.

Burrow lengths recorded in the dune region for this study during or after high-energy weather events were greater than in other regions of the study area. LEBER (1982) suggested that ghost crabs may migrate back toward the dune and burrow there during periods of foul weather. Therefore, the increase we observed is likely due to the crabs moving to the dunes and inhabiting those burrows for shelter from the storms. These burrows may also have been kept open due to the increased usage of migrating crabs. Ghost crabs may migrate back toward the dune and burrow there during periods of foul weather (LEBER, 1982).

CONCLUSIONS

Both off-road vehicles and high-energy weather events negatively affected ghost crab populations at Cape Hatteras National Seashore. Off-road vehicles reduced the density of ghost crabs in the areas where the vehicles were operated. Vehicle use has the potential to decrease or limit repopulation. Rapid beach erosion accompanying severe storms removes all existent crab burrows forcing the ghost crabs, which likely temporarily relocated into the dunes, to reoccupy the beach and excavate new burrows. The occurrence of major storms in conjunction with the prime settlement period for the crabs changed the dynamics of the populations and permitted settlement of juvenile ghost crabs.

Through closing the beach crest to ORVs 24 hours a day, the ghost crabs were able to migrate into and inhabit the landward portions of the beach. Although closing the seaward ~20 m of the beach at Coquina to ORVs from 2000 to 0600 hours was not sufficient to permit the ghost crabs to repopulate this region, the nightly ban of ORVs did permit ghost crabs to reinhabit the beach crest at Avon.

High-energy weather events have significant impacts on the beach ecosystem, including the dynamics of ghost crab populations. Storms erode the beaches, removing ghost crab burrows and, apparently, removing larger ghost crabs. Ghost crab populations essentially are reset by the storms. The storms and associated beach erosion reduce the presence of larger ghost crabs and allow subsequent colonization by smaller juvenile crabs into the beach habitat.

Long-term and short-term processes affect the presence of ghost crabs on the beaches of Cape Hatteras National Seashore differently. Short-term impacts such as the use of ORVs on the beach face can cause a marked decrease in the density of ghost crab burrows. Long-term processes on ghost crab populations, such a high-energy weather event, have the ability to reset the system, allowing the settlement of ghost crabs into regions that were previously barren of ghost crab burrows. While ORV use on the beaches during the summer may decrease the density of ghost crab burrows, the occurrence of high-energy weather events in the fall essentially removes all of the ghost crabs, setting the stage for resettlement. When managing for long-term impacts on ghost crab populations and allowing ORVs to drive on the beaches, anticipating the onset of a high-energy weather event to reset the system may be an option. Managers also must keep in mind that if all beaches are fully open to ORVs, the ghost crab population may be reduced, simultaneously reducing the numbers of the crabs available to repopulate the beach after the storm.

In 1980, Godfrey and Godfrey recommended that if vehicles are to be permitted on the beaches, they should be restricted to an "ORV corridor" between the beach crest and the upper drift lines, except where birds and turtles are nesting. The results of this project lead to a similar conclusion. Within the realm of this project, restricting ORVs from the corridor along the beach crest 24 hours a day was sufficient to permit a significant increase in the habitation of ghost crabs, even when ORVs were allowed on the more landward portions of the beach at both Coquina and Avon. Wolcott and Wolcott (1984) suggested that restricting the use of ORVs on the beach crest between dusk and dawn might allow ghost crabs to inhabit an area; our results support their conclusion at Avon, but possibly not at Coquina. Further study is required to analyze the applicability of this method of preserving ghost crab populations on the Outer Banks of North Carolina, especially since the high-energy events prematurely ended the collection of data where restrictions on ORV use had been imposed.

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