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# Impact of Off-Road Vehicles on Macroinvertebrates of a Mid-Atlantic Beach

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## *ABSTRACT*

*Potential and actual impacts of off-road vehicle (ORV) use on beach macroinvertebrates were examined on the Cape Lookout National Seashore (North Carolina). Mole crabs* Emerita talpoida *and coquinas* Donax variabilis *were not damaged. Ghost crabs* Ocypode quadrata *were completely protected by burrows as shallow as 5 cm, and therefore were not subject to injury during the day, but they could be killed in large numbers by vehicles while feeding on the foreshore at night. Ghost crab populations on the Seashore were large (10 000 km$^{-1}$ of beach) and a small proportion of the population would be killed by a single vehicle pass. Nevertheless, predicted population mortalities calculated from observed kills of ghost crabs per vehicle-km ranged from 14–98 % for 100 vehicle passes. Currently vehicle use on this beach is light and essentially none occurs on the foreshore after dark. Little impact on beach macroinvertebrates would be expected from this usage pattern. Actual impact on ghost crab populations, assessed by burrow censuses, was negligible. No differences were detected between heavy-use and light-use sites in total population size, average crab size or population change through the heaviest traffic season. However, increases in traffic to levels seen on other beaches, especially night driving, would probably have devastating effects on ghost crab populations. In heavily used areas, banning of ORVs from the foreshore between dusk and dawn may be required to protect this species.*

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# INTRODUCTION

This study was undertaken to assess the effects of off-road vehicle (ORV) operation on beach invertebrates, and to provide data which could be used in managing the Cape Lookout National Seashore and other beach ecosystems subject to vehicular traffic. The paucity of existing data, most in unpublished reports, has been of little help in resolving confrontations between preservationists and ORV users.

The first impression given by a high-energy beach is that 'sand can't be hurt'. Nevertheless, a handful of previous studies have indicated that ORV operation has detrimental effects on beach animals. The displacement of nesting bird species is well documented and is beyond the scope of this paper. Beach invertebrates, on the other hand, have received scant attention. Wheeler (1978) documented significant effects of ORV traffic on populations of sand-flat invertebrates at Cape Cod (Massachusetts). In studies on ocean beaches the ghost crab *Ocypode quadrata* is the only invertebrate species that has been considered, and the data consist of correlations between crab censuses and the amount of vehicle traffic. Ghost crabs burrows were both sparser and smaller in the heavily travelled Back Bay National Wildlife Refuge (Back Bay NWR), Virginia, than at a nearby low traffic area (Leggett, 1975). Similarly, crab burrow densities were lower in the Pea Island NWR (North Carolina) during periods of high ORV usage than across Oregon inlet on Bodie Island. The differences diminished when Bodie Island was opened to ORV usage and disappeared when both islands were closed to all ORV traffic (Florschuts & Williamson, 1978; Smith, 1978). Much lower numbers of ghost crab burrows were found in high traffic areas than elsewhere in the Chincoteague NWR (Virginia), a phenomenon Britton (1979) attributed to displacement of the crab population over several years from high- to low-traffic areas. Steiner & Leatherman (1981) found similar results by counting crabs on the Chincoteague NWR beaches at night, except on a heavy pedestrian use area. Where Britton (1979) found few burrows, they reported high crab activity which they attributed to the edible trash left by picnickers. Although all of these studies found correlations between intensity of vehicular traffic and decreases in ghost crab populations, none documented any direct effect of vehicles upon the crabs. Their speculations about possible mechanisms for population depression by vehicular traffic are not always consistent with ghost crab biology, and they essentially ignore the remaining beach macroinvertebrates.

This study, designed to fill in some of these gaps, had five major facets:

1. Experimental determination of individual vulnerability of the three major mid-Atlantic beach macroinvertebrates (the mole crab *Emerita talpoida*, the coquina clam *Donax variabilis*, and the ghost crab *Ocypode quadrata*) to damage by vehicles.
2. Experimental determination of the population vulnerability of the same species, taking into account normal behaviour and field conditions.
3. Estimating intensity of vehicle use in places and times relevant to the biology and behaviour of the species under study.
4. Calculation of expected population impacts under various levels of vehicular use.
5. Estimation of actual population impact caused by ORV use on various areas of Cape Lookout National Seashore, based on censuses.

## MATERIALS AND METHODS

### Study site

The study was carried out on the Core Banks section of Cape Lookout National Seashore, located in Carteret County, North Carolina (Fig. 1). The study site is a 25-km long, 500-m wide barrier island lying between Cape Lookout and Drum Inlet. At the southwest end are the Cape Lookout lighthouse, National Park Service facilities, a Coast Guard station, and a few inholdings with dwelling houses. The remainder of the island is uninhabited except for a number of rental cabins in fish camps near the middle of the island and a private sportsmen's club near the northeast end. Recreational use of the Seashore includes fishing, beachcombing, and some camping. The sandpit at the southwestern end provides an excellent anchorage and is heavily used by boaters during the summer.

There is no road access to the island. All vehicles used in recreational activities are ferried across by concessionaires landing at the fish camps or the sportsmen's club. The vehicles are operated on the beach or on a series of back roads running parallel to the shore behind the dune line. There is no marked system of crossovers between back roads and the beach, and vehicles may run between or over the dunes at any point.

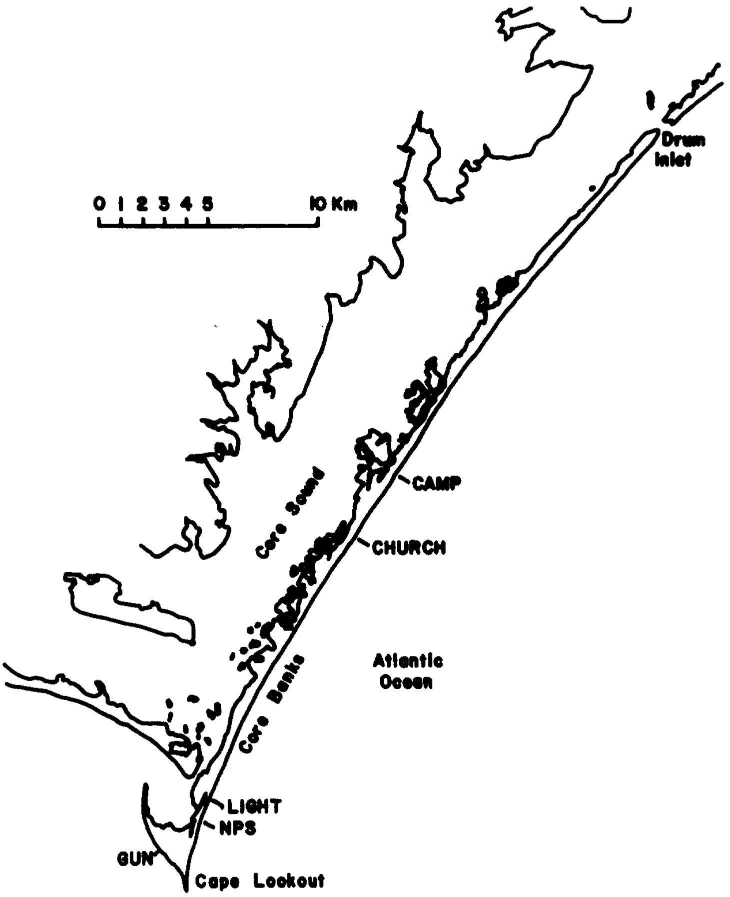

**Fig. 1.** Core Banks section of Cape Lookout National Seashore, showing census locations.

## Individual vulnerability

Damage to mole crabs *Emerita talpoida* and coquinas *Donax variabilis* was assessed in August 1980 on the ocean beach near the park service facilities. Fishermen's vehicles passing on the wet foreshore were used (without their knowledge) as the experimental vehicles. Immediately after passage of a vehicle a sand sample (about 5 × 15 × 5 cm deep) was gently removed from the tyre track with a small trowel, and a similar sample taken from the adjacent undisturbed sand. The macroinvertebrates were wet-sieved (2 mm mesh) from the sand, inspected for obvious damage, and released into a bucket of fresh sea water. Only if they swam actively (mole crabs) or burrowed quickly into the sand in the bottom of the bucket (both species) were they scored as undamaged. The number of intact and damaged animals was recorded for each experimental/control pair of samples. This method was chosen over a quantitative sediment-sampling technique (e.g. coring) due to the large number of mole crabs injured in preliminary sampling when care was not taken to avoid transecting them with the trowel. Samples were obtained from tracks of several vehicles at several levels of the foreshore.

The vulnerability of ghost crabs in their burrows was tested with crabs which had been collected the previous night and held in 500 ml plastic boxes. Artificial burrows, 5 cm in diameter by 20 cm deep, were excavated with a plastic corer. The crabs were held in a $CO_2$ atmosphere until immobilised (about 2 min), placed 5, 10 or 15 cm deep in the holes, and run over with a 4-wheel drive truck. They were then carefully unearthed, inspected for external damage, and returned to their individual boxes. Lids were left off, and crabs which clambered out of the boxes and either left the area or commenced new burrows were scored as survivors.

The vulnerability of ghost crabs on the beach surface required no testing. These crabs rely upon speed rather than armour for defence and their fragile exoskeletons are easily crushed by the lightest vehicle.

## Population vulnerability

Estimating population vulnerability required consideration of behaviour only in the case of ghost crabs. The immobile mole crabs and coquinas in the preceding experiments were exhibiting normal behaviour for the times they would be at risk, and population vulnerability is the aggregate of individual vulnerability. The estimates for ghost crabs were obtained by driving a pair of vehicles (Honda ATC-90 all-terrain three-wheel cycles) on the beach at or near the time of night low tides. The first vehicle proceeded over a prescribed course at 10–15 km $h^{-1}$; the second vehicle followed closely and the driver counted crabs obviously crushed by the first vehicle or injured seriously enough to be immobilised. Spot checks confirmed that such animals were mortally wounded. Preliminary runs with red-filtered headlights, intended to minimise a shadow reflex causing the crabs to dart toward the approaching vehicle, showed no obvious effects of filtering. White headlamps like those of conventional ORVs were therefore used to permit safer driving and easier counting of kills. The runs were made at biweekly intervals from late August 1981 (before the major traffic period coinciding with the autumn fishing season) until the end of the crabs' active season in mid-October.

To avoid biased results caused by crabs being herded toward or away from another section of the beach profile, runs were made in the following sequence (see Fig. 1):

1. Low foreshore from near the National Park Service facilities (NPS) to the point of Cape Lookout.
2. Backshore, from the point to NPS.
3. Backshore, from NPS to the Lighthouse (LIGHT).
4. Low foreshore, from LIGHT to NPS.
5. Back road, from NPS to LIGHT.

A random sequence, although possibly preferable, was not feasible within the span of a single low tide period.

The number of 'confirmed kills' per run was divided by the distance between the landmarks, determined from charts and aerial photographs, to calculate kills per vehicle-kilometre.

### Estimation of vehicle use

The numbers of vehicles ferried to Core Banks by concessionaires were obtained from NPS files. The vulnerability studies revealed a need for additional information about the distances, times and locations of vehicle operation. NPS staff were unable to provide estimates of vehicle activity based on track counts due to the confused patterns left by multiple passes. ORV operators and the concessionaire expressed willingness to fill out and collect a questionnaire, which was printed and delivered to the concessionaire for distribution. Unfortunately, not a single copy was completed and returned, and we had to rely on personal observations and interviews with fishermen, NPS and Coast Guard personnel for the needed information. The Coast Guard lookouts spent every night in a cupola overlooking the beach and were able to offer unbiased impressions of ORV use patterns. Although these sources of information were qualitative, all were consistent with one another.

## Calculation of expected impact on ghost crab populations

Kills per vehicle-km at each biweekly sampling period were compared with census data (see below) to obtain an estimate of the proportion of the ghost crab population killed by a single vehicle pass. In calculating expected population mortality, we assumed that traffic would be infrequent enough to allow the surviving crabs to revert to their normal distribution on the beach, and that passage of a subsequent vehicle would therefore kill a similar proportion of the remaining population. The percentage of the total population remaining after N vehicle passes is then described by the equation:

$$\%\,\text{Surviving} = 100(1 - (1 - \text{M})^{\text{N}})$$

where M is the proportion of the population killed by a single pass.

Extrapolating from mortalities caused by ATCs to those expected from the trucks usually driven on the National Seashore required some adjustments. The low-pressure (2 psi) tyres of the ATCs crushed all large crabs on impact but often passed over 1-cm crabs without damaging them, apparently by straddling them with the tread lugs. This, and the relatively low visibility of the smallest crabs, undoubtedly led to underestimates of mortality in the smallest size classes. Since crabs of all size classes would be crushed by the higher-pressure (20–40 psi) truck tyres, the population mortalities calculated from ATC transits were conservative. Nevertheless, because most truck tyres are only about half as wide as the ATC tyres, a correction factor of 0·5 was applied to the mortality estimates obtained with ATCs. No correction factor was used for the differences between the ATCs' short triangular wheelbase and the longer rectangular wheelbase of trucks, because the effects on mortality could not be predicted. The rear tyres of trucks follow in the tracks of the front tyres, whereas the triangular wheelbase of the ATCs results in three tracks and a larger swept area. On the other hand, the crabs tend to run about when disturbed, and this can carry them under either the front or rear tyres of a larger vehicle. To them the truck may resemble a pair of two-wheeled vehicles travelling in tandem, and the larger number of wheels may compensate for the smaller swept area.

## Estimation of actual impact on ghost crab populations

Ghost crab populations were censused indirectly at five sites subjected to varying intensities of vehicle use (see Fig. 1), listed below in order from the centre of Core Banks to Cape Lookout and in approximate order of decreasing ORV traffic.

CAMP is located 20·4 km northeast of the point, near the island terminus of the ferry service and the fish camp, a collection of shacks and cabins providing most of the lodging available to fishing parties. The beach near the camp is more heavily disturbed by vehicular activity than any other section of the island.

CHURCH, marked by a dwelling misnamed because of its cupola, is 17·2 km northeast of the point. Because of its proximity to the fish camp, this section of beach is heavily used by ORVs.

LIGHT is marked by the Cape Lookout lighthouse 3·8 km northeast of the point. This site receives moderate vehicle use; most vehicles traversing the area bypass the beach and use back roads to reach the point.

NPS is located near the National Park Service facilities 2·6 km from the point. Most drivers passing this area are using back roads on their way to fish at the point.

GUN is located at old fortifications on the southwest beach 2·0 km past the point. The only vehicular traffic is Coast Guard and NPS pickup trucks and occasional fishermen visiting the hook of the cape. It is probably the lowest-traffic site.

The indirect censuses at these sites relied on three replicate counts of ghost crab burrows showing signs of recent occupation (excavated sand, fresh tracks) in 5 m wide transects running perpendicularly from the waterline to the limit of ghost crab habitat (margin of scrub vegetation). Burrow diameters, which predict crab size (Wolcott, 1978) were estimated to the nearest cm. This technique, although requiring subjective distinction between active and abandoned holes, was chosen because it relies on stationary structures which provide information on population size/age structure. It also approximates the total population, rather than the proportion active at a given time and thus available for visual censusing. Quantitative nocturnal counts of surface-active crabs are extremely difficult due to the rapid movements of the animals, and may give much lower population estimates (Steiner & Leatherman, 1981; Wolcott, 1978 compared with Leber, 1982). Our burrow censuses were not restricted to selected areas of the beach as in previous studies, because ghost crabs show little burrow fidelity. Disturbance (e.g. by storms) can result in large apparent changes in local population density when crabs either remain underground or move to burrows farther inland (Wolcott, 1978). Censusing the entire width of ghost crab habitat from the waterline to the scrub line (often several hundred metres inland) accounted for all crabs maintaining open burrows. This minimised the chances of underestimating populations, hence of overestimating vehicle impact.

The total population estimates and average crab size at different sites were compared by analysis of variance (ANOVA, Steel & Torrie, 1960) and Duncan's Multiple Range Test (Steel & Torrie, 1960). Relative frequencies of various size classes were compared between sites by a General Linear Models procedure (Helwig & Council, 1979). Changes in crab densities occurring through the peak traffic period were compared between grouped heavy use (CAMP, CHURCH) and light-use (LIGHT, NPS, GUN) areas by ANOVA.

## RESULTS

The coquina *Donax variabilis* apparently is not susceptible to damage from ORVs. No injured individuals were found in over 30 samples.

The mole crab *Emerita talpoida* is similarly immune to ORV damage. Only one of 73 crabs was damaged in 16 sand samples dug from vehicle tracks; none of the 88 crabs from the 16 control samples were injured. The estimated 1·4 % mortality in mole crab populations under the tyre track is not significantly different from the estimated control value using the 95 % binomial confidence interval (Steel & Torrie, 1960, Appendix II). The single case of injury may be attributable to the tool used to dig up the sample; less gentle preliminary sampling injured many mole crabs.

The ghost crab *Ocypode quadrata* is very susceptible to crushing when on the beach surface, but is virtually immune to damage while in its burrow. Driving over immobilised crabs placed in artificial burrows in a packed area of the backshore caused no mortality or injury (Table 1). Since even the shallowest burrow depths (5 cm) provided complete protection, a second set of experiments was conducted in a presumably higher-risk area, soft unpacked backshore, with all of the crabs placed at 5 cm depth. Again all crabs recovered and moved away spontaneously except for one control animal which was inadvertently asphyxiated in the $CO_2$. Two experimental crabs received eyestalk injuries. These were probably an artefact caused by the failure of $CO_2$-immobilised crabs to fold their eyestalks in the burrows. When the crab's centre was 5 cm deep

**TABLE 1**

Direct Impact of ORVs Driven Over Immobilised Ghost Crabs in Burrows (Injuries on soft backshore were minor (eyestalk damage) and probably due to experimental artefact (see text). The control mortality was caused by excessive $CO_2$ narcotisation.)

| | *Depth in burrow* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *5 cm* | | | *10 cm* | | | *15 cm* | | |
| | *Injured* | *Killed* | *N* | *Injured* | *Killed* | *N* | *Injured* | *Killed* | *N* |
| Hard backshore | 0 | 0 | 6 | 0 | 0 | 6 | 0 | 0 | 6 |
| Soft backshore | 0 | 0 | 5 | | | | | | |
| | 1 | 0 | 5 | | | | | | |
| | 1 | 0 | 5 | | | | | | |
| Control | 0 | 1 | 5 | | | | | | |

in the burrow, the upper eyestalk extended nearly to the sand surface and was presumably subjected to shear forces as the surface sand layers deformed under the passing tyre.

## Population vulnerability to ORV damage

The vulnerability of coquina and mole crab populations is predicted by the measures of individual vulnerability since these were obtained with naturally 'behaving' populations. No damage to coquina populations would be predicted, and 1·4 % mortality would be expected in the portion of the mole crab population actually run over.

The vulnerability of ghost crab populations is low during the day when they are in their burrows or within sprinting distance of them. At night, however, their behaviour makes them highly vulnerable. They congregate on the packed foreshore to feed on mole crabs and coquinas (Wolcott, 1978). This area is relatively smooth and is therefore both the substrate against which the crabs would most easily be crushed and the preferred area of the beach for driving. The crabs had no effective escape behaviour from approaching vehicles. They usually responded to headlights by 'freezing', and only bolted when the vehicle came within a few metres.

Their flight was in seemingly random directions which often carried them under the wheels.

The number of nocturnal kills was influenced by the density of active crabs at each site and period. It was generally at least an order of magnitude higher on the foreshore where the animals congregated to feed than on the backshore or back roads. At one period of unusually high crab activity, over 500 crabs were killed by a single vehicle pass from the lighthouse to the point of the cape (Table 2).

TABLE 2

Mortality (kills km$^{-1}$) of Ghost Crabs Caused by a Single Pass of a Three-Wheeled Vehicle (Honda ATC 90) on Segments of Foreshore, Backshore and Back Roads Near the Time of Night Low Tides

| *Date* | *Kills per vehicle–kilometer* | | | | |
|---|---|---|---|---|---|
| | *Foreshore* | | *Backshore* | | *Back roads NPS–LIGHT* |
| | *Point–NPS* | *NPS–LIGHT* | *Point–NPS* | *NPS–LIGHT* | |
| 25 August | 21·6 | | 3·8 | 0 | 0 |
| 6 September | 31·5 | 43·3 | 4·6 | 9·2 | 3·3 |
| 21 September | 102·7 | 193·3 | 10·0 | 0·8 | 0 |
| 5 October | 52·7 | 94·1 | 1·1 | 1·7 | 1·7 |
| 19 October | No crabs active | | | | |

## Estimates of vehicle use

The seasonal pattern of vehicular traffic on Cape Lookout National Seashore is reflected by the number of vehicles transported to the island (Fig. 2). Driving is minimal during the winter, modest during the spring and summer, and heaviest during the autumn fishing season (September–November). Ghost crabs are exposed to heavy ORV use only during the early part of the peak fishing season because they go underground for the winter in mid-October. Detailed patterns of vehicle use were not obtainable by counting tracks on the beach or by analysing returned questionnaires. From personal interviews and observations it became clear that typical daytime use consisted of driving along back roads until the approximate destination for fishing was reached, then detouring onto the beach and parking. During a day's fishing a vehicle might move a few km along the beach. At the end of the day, usually well

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**Fig. 2.** Number of vehicles ferried to or from the Core Banks section of Cape Lookout National Seashore by concessionaire during each month of 1981 (data provided by NPS).

before dark, the fishermen would return by back roads to the fish camp. Nocturnal operation of ORVs was virtually nil. Our observations, and reports of both NPS and Coast Guard personnel, indicated that the few vehicles moving at night were fishermen returning from the point to the fish camp along the back roads. Interviewed fishermen confirmed that in most cases they would avoid the risk of unseen scarps on the beach by using back roads for all night driving. Most gave a maximum estimate of one nocturnal trip per year on the foreshore from either inlet to the fish camp. During our work on the cape we saw no nocturnal beach driving whatever, with the exception of NPS ACTs used in turtle nesting surveys.

## Calculated population impact of ORV traffic

In calculating the expected population impact of various levels of ORV usage, only nocturnal driving on the foreshore was considered. Driving during the day, or on other parts of the island, would not be expected to cause significant mortalities. The proportion of the crab population killed by a single ATC pass at each sampling period was calculated by dividing

TABLE 3
Percentage of Ghost Crab Populations Killed by a Single Vehicle Pass (Corrected for Truck Tyre Width) on Various Parts of the Cape Lookout National Seashore Beach

| *Date* | *Foreshore* | | *Backshore* | | *Back roads* |
|---|---|---|---|---|---|
| | *Point–NPS* | *NPS–LIGHT* | *Point–NPS* | *NPS–LIGHT* | |
| 25 August | 0·291 | | 0·051 | | 0 |
| 6 September | 0·268 | 0·374 | 0·040 | 0·079 | 0·029 |
| 21 September | 0·853 | 1·606 | 0·083 | 0·007 | 0 |
| 5 October | 0·703 | 1·225 | 0·015 | 0·023 | 0·023 |
| 19 October | | | No crabs active | | |

the observed kills per km by the average population density (crabs per km) during that period at the nearest census sites (NPS, LIGHT). Population mortalities ranged from 0·3% to 1·6% per ATC pass (Table 3).

Expected population mortalities resulting from 100, 200 and 500 truck passes, calculated for the average and extreme values of M (from Table 3, corrected for truck tyres), ranged from 14 to 98% (Table 4).

## Estimates of actual ORV impact on populations

Burrow censuses indicated a large ghost crab population at all sites (Fig. 3), averaging about 10 000 crabs km$^{-1}$ of shoreline over the entire

TABLE 4
Predicted Population Mortality (%) After Various Numbers of Vehicle Passes, at Mortalities Per Pass Ranging from the Lowest to Highest Observed in This Study
(Average mortality/pass on the foreshore was 0·7%, producing an expected 30% population mortality in 100 passes)

| *% of population killed per pass* | *Number of passes* | | |
|---|---|---|---|
| | *100* | *200* | *500* |
| 0·05 | 4·9 | 9·5 | 22·1 |
| 0·15 | 13·9 | 25·9 | 52·8 |
| 0·30 | 25·9 | 45·2 | 77·7 |
| 0·80 | 55·2 | 79·9 | 98·2 |
| 1·60 | 80·1 | 96·0 | 99·97 |

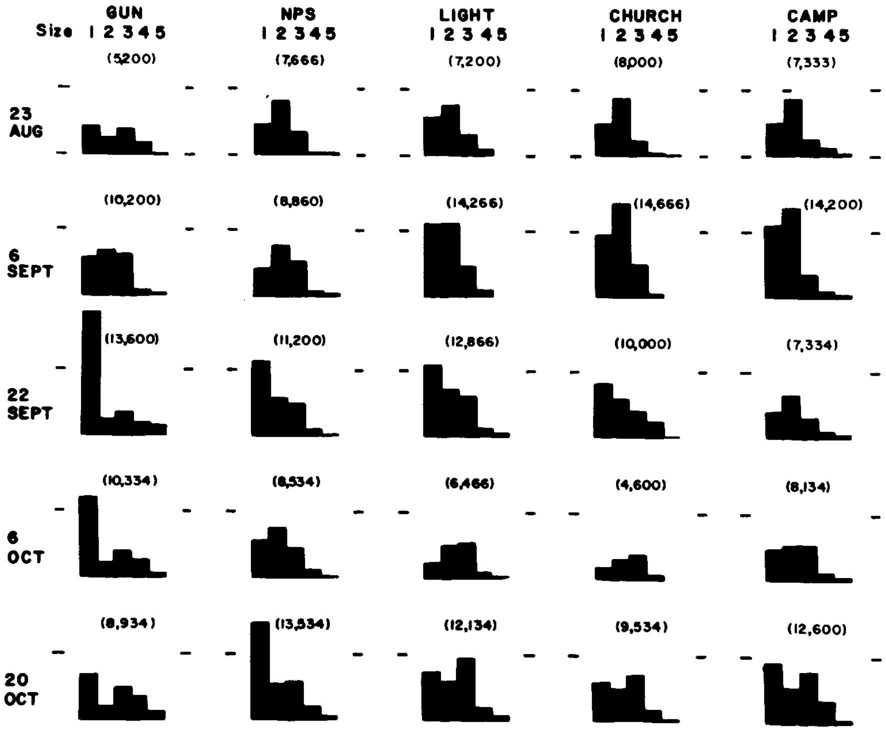

Fig. 3. Density and composition of ghost crab populations at each site and census period. Histograms show numbers of each size class (by carapace width in cm) per km of beach; marks on vertical axes correspond to 5000 km$^{-1}$. Total population density (crabs km$^{-1}$) appears in parentheses.

**TABLE 5**

Analysis of Variance Comparing Burrow Density and Size at Five Sites on Cape Lookout National Seashore

(Site was not a significant factor; see text for discussion of Size and Site–Size terms)

| Source | DF | ANOVA SS | F Value | Pr > F |
|---|---|---|---|---|
| Site | 4 | 68·72 | 0·38 | 0·821 4 |
| Size | 4 | 16 809·68 | 93·49 | 0·000 1 |
| Site–Size | 16 | 1 912·00 | 2·66 | 0·000 6 |

study. Neither significant differences in crab population densities, nor meaningful differences in size distribution, were detectable between sites over the study as a whole, using either ANOVA or Duncan's Multiple Range Test (Tables 5 and 6). General Linear Models analysis (Helwig & Council, 1979) indicated that the significant site–size interaction in the ANOVA is largely due to more 1-cm and fewer 2-cm burrows at the GUN site than at CHURCH and CAMP. The differences are not large, the small holes are the ones most likely to be overlooked or obliterated by wind. The total population estimates are not significantly different. We therefore do not regard these differences as biologically significant.

Comparison of population density and size structure by month in heavy-use (CAMP, CHURCH) and light-use (LIGHT, NPS, GUN) areas by ANOVA (Table 7) indicated no significant short- or long-term vehicle impact. The lack of a significant Group–Month–Size interaction indicates that neither population density nor average crab size is depressed in heavy-use areas. A significant Month term reflected

**TABLE 6**

Duncan's Multiple Range Test Comparing Population Densities (Burrow Frequencies in 5 m Transects) Over the Entire Study Period (Mean frequencies at all sites were statistically indistinguishable (alpha level = 0·05)

| *Site* | *N* | *Mean number of burrows* | *Grouping* |
|---|---|---|---|
| GUN | 75 | 9·52 | A |
| NPS | 75 | 9·83 | A |
| LIGHT | 75 | 10·51 | A |
| CHURCH | 75 | 9·32 | A |
| CAMP | 75 | 10·16 | A |

**TABLE 7**

Analysis of Variance, Comparing Ghost Crab Population Size and Structure in Heavy-Use (CHURCH, CAMP) and Light-Use (GUN, NPS, LIGHT) Areas by Month. GROUP was not a Significant Variable

(See text for discussion of significant interaction terms)

| Source | DF | ANOVA SS | F Value | Pr > F |
|---|---|---|---|---|
| Month | 2 | 1 075·00 | 14·54 | 0·000 1 |
| Group | 1 | 4·01 | 0·11 | 0·742 0 |
| Size | 4 | 16 809·68 | 113·69 | 0·000 1 |
| Month–Group | 2 | 110·10 | 1·49 | 0·227 0 |
| Size–Month | 8 | 2 666·25 | 9·02 | 0·000 1 |
| Size–Group | 4 | 716·56 | 4·85 | 0·000 8 |
| Size–Month–Group | 8 | 388·78 | 1·31 | 0·234 8 |

population increases due to recruitment through the study period, particularly in September. The significant Size term simply reflects the obvious fact that there are more small crabs than large ones. The Size–Month interaction reflects higher numbers of 1-cm burrows in August and September than in October and fewer 2 cm burrows in September than in October. The Size–Group interaction indicates that more 1-cm and fewer 2-cm burrows are found in light-use than in heavy-use areas. As indicated above, the small differences in the observed densities of the smallest burrows are not biologically meaningful, and no other effects of heavier vehicle use are statistically demonstrable.

## DISCUSSION

The primary objective of this study was to provide information useful in projecting impact of ORV traffic on Cape Lookout National Seashore and other mid-Atlantic beaches. This required examination of the mechanisms by which ORVs might damage invertebrates. Projection of future impact was not possible from the data collected by previous workers because although they drew correlations between vehicular use of the beach and depression of invertebrate populations, they did not demonstrate that the relationships were causative. The papers of Florschuts & Williamson (1978) and Smith (1978) taken together present the most convincing case because they document correlated temporal changes in ghost crab densities and vehicular usage. Nevertheless, their data cannot be used to refute the hypothesis that the changes in crab densities are attributable to some other unmeasured causative factor. The only published study involving experimental subjection of invertebrate populations to ORV traffic (Wheeler, 1978) showed that 1000 passes over 20 days eliminated soft-shell clams *Mya arenaria* of two size-classes from experimental plots on Cape Cod sandflats.

The ghost crab *Ocypode quadrata* is the principal beach invertebrate considered in the remaining studies which show lower crab densities in areas of high ORV traffic. The indications of adverse population effects led Leggett (1975) to postulate several mechanisms of damage. These speculations have been repeated and extended by subsequent workers (Florschuts & Williamson, 1978; Smith, 1978; Britton, 1979; Steiner & Leatherman, 1981) to include direct crushing, behavioural derangement (affecting mating behaviour or reproductive output, confusing orientation, or hindering escape from predators), and physiological stress resulting from sediment compaction and changes in water content. No evidence has been presented, however, that any of these mechanisms actually affect natural populations. Existing knowledge about the species' biology and behaviour allowed us to dismiss most of these hypothetical damage mechanisms when examining the vulnerability of coquinas *Donax variabilis*, mole crabs *Emerita talpoida*, and ghost crabs *Ocypode quadrata* to damage by ORVs.

In the case of coquinas and mole crabs, none of the proposed mechanisms seemed plausible. Behavioural derangement is unlikely because the individuals at risk are those that have remained in the exposed intertidal rather than migrating seaward with the receding tide. Their immobilisation in the drained sand precludes feeding, locomotion, spawning and other behaviour during the period when they might be subjected to ORV traffic. Physiological problems caused by habitat modification are also unlikely; exposure of the intertidal is too short to allow drying, and any compaction of the sand will last only until the next tide's waves rework the sediment.

The protection afforded by the sand, coupled with the morphology of mole crabs and coquinas, suggested that even direct crushing was unlikely. These animals are found in soft sand or on the beach surface only when sea water is washing across it and vehicles are absent. When ORVs are operated on the tidally exposed foreshore, the animals are imbedded in sand which is so resistant to deformation that truck tyres sink only a few millimetres. The transmission of shear forces to depths of

25 cm and the acceleration of drying by mixing of the surface layers, which can occur higher on the beach (Brodhead & Godfrey, 1979), are not problems in the swash zone (i.e. the area being washed at any given time by shallow water from wave run-up). Both mole crabs and coquinas have an ovoid body form which minimises potential damage from shear movements in the sediment, and the clam is also heavily armoured. All of these factors led us to predict that mole crabs and coquinas would be virtually immune to ORV damage.

As expected, observed mortality of these species in ORV tracks was negligible. No damage whatever was detected in the case of coquinas. A single injured individual of *E. talpoida* was recovered from one track sample. Assuming that it was not a sampling artefact leads to a predicted mortality of 1·4% within the track area, statistically indistinguishable from that predicted for control areas. We emphasise that even if this mortality were statistically significant it would be biologically meaningless because it applies only to the miniscule proportion of the total population lying under the track. Most of the mole crabs and coquinas migrate with the tide and remain in the swash, out of reach of vehicles. Even if ORVs were operated recklessly on the foreshore, so as to churn up the sand and thereby possibly increase mortality in the tracks, the population impact upon mole crabs would probably remain negligible due to the high reproductive capacity of the animals (Diaz, 1975).

These results contrast with those of Wheeler (1978) on Cape Cod sand flats. He demonstrated direct kills of two size-classes of the soft-shell clam *Mya arenaria* by 50 ORV passes per day over 20 days (1000 passes total). It is not clear why the clams were more vulnerable to vehicle traffic than the high energy beach macroinvertebrates of this study. The sand-flat sediment may be less resistant to deformation and confer less protection than hard beach sand. Even low mortalities per pass would result in large population effects at the high traffic levels used.

In the case of ghost crabs, direct crushing is the only plausible damage mechanism. Interference with ghost crab 'nesting' or 'hatches' (Florschuts & Williamson, 1978) can be dismissed; the females release larvae into the sea and recruitment to the beach population occurs after a 6-week planktonic larval phase. Any interference with copulatory behaviour, which occurs on the beach surface (personal observation) will probably occur only by direct crushing. Copulating crabs are nearly oblivious to milder distractions (personal observations). Physiological stress due to habitat modification is unlikely. Ghost crabs dig easily out of burrows that have been collapsed; their emergence holes commonly appear in tyre tracks. Desiccation due to accelerated drying of disturbed sand is not a problem; ghost crabs are able to obtain water *ad libitum* from the damp sand deeper in their burrows (Wolcott, 1976). Mortality due to ORV ruts hindering rapid escape from predators is unlikely to be important for a species which appears to occupy the top of its food chain (Wolcott, 1978).

Crushing of ghost crabs by ORVs rarely occurs during the day for behavioural and physical reasons, most crabs remaining underground during the day. The crabs have acute vision (Cowles, 1908) and a precise memory of their burrow location. Those that venture above ground dart into their burrows well before the arrival of a vehicle approaching at normal speed. When the crabs are as little as 5 cm below the surface, in either soft or packed sand, the burrow provides essentially complete protection (Table 1). Beach burrows are typically 20–60 cm deep (determined by probing and by making burrow casts), providing protection even from ORVs operated so as to churn up deep ruts. It must be emphasised, however, that the low vulnerability of ghost crabs to damage from ORVs is restricted to daylight hours.

During the night, ghost crabs are highly susceptible to damage. They congregate to feed on the other macroinvertebrates (Wolcott, 1978) on the hard, smooth foreshore where vehicles are most likely to drive. They have exoskeletons so thin that they break if dropped 1 m onto a hard surface (personal observations). They would certainly be injured or crushed if struck by even the lightest vehicle. They have no effective escape response in the dark. Their usual response to headlights is immobility, or occasionally running toward the light source. Red filtering has no noticeable effect. The crabs seem to respond principally to substrate vibration. They are capable of detecting and running away from a point source of vibration such as a finger scratching the sand (M. Salmon, pers. comm.; personal observations), but seem unable to localise a large vibration source such as a vehicle. Apparently unable to determine an appropriate escape direction, they often run directly under the approaching wheels.

The structure and behaviour of ghost crabs indicated that large numbers could be killed by nocturnal vehicle operation on the foreshore. This was dramatically demonstrated by beach transits with ATCs; on one occasion over 500 crabs were killed by one vehicle in a single pass from the lighthouse to the point (Table 2). The significance of this mortality to the population depends on two factors: total population size and the amount of nocturnal foreshore traffic.

The ghost crab population on Cape Lookout National Seashore is large; estimates ranged from 4600 to above 14 000 crabs $km^{-1}$ of beach during the study (Fig. 3). The lower figure is certainly an underestimate; the count on 6 October 1981, particularly of smaller burrows at the northern sites, was substantially affected by high winds which obliterated tracks and burrows. The highest figures may be somewhat inflated by counts of unoccupied burrows, but we are confident that average crab densities are at least 10 000 $km^{-1}$ throughout the study area. These populations are comparable with those censused by Florschuts & Williamson (1978) and Smith (1978): about 5000–10 000 crabs $km^{-1}$. Population estimates from this study cannot be compared with those of Britton (1979) and Steiner & Leatherman (1981) due to the very different census techniques used.

The large population sizes imply that vehicles could have a serious impact on crab densities only if each pass killed many crabs. The proportion of the population killed by a single pass is in fact small (Table 3). Nevertheless, significant population impacts are predicted after as few as 100 passes. This is true even at the lowest observed mortality rates (Table 4). Even modest amounts of night driving on the foreshore of Cape Lookout National Seashore would be expected substantially to reduce the ghost crab population.

Fortunately for the ghost crabs, present patterns of vehicle use on the Seashore include only minor amounts of night driving, essentially none of it on the beach. Interviews with ORV operators, park rangers and Coast Guard lookouts indicate that most ORV operators never drive on the beach at night due to the risk of striking an unseen scarp or becoming mired in soft sand. A few drivers indicated they might drive on the foreshore after dark to return to the fish camp from either inlet, but only if the tide was low at the time; they would normally use the back roads. No night driving was observed on the beach during the course of this study. Apparently the foreshore is currently subjected to less than 20 nocturnal vehicle passes per year. If these usage patterns remain unchanged, the risk to beach invertebrate populations appears negligible.

As would be expected from the low level of nocturnal vehicle use in the study area, no population effects were detectable in the most vulnerable species examined, the ghost crab. There were no significant differences between total populations at the five sites throughout the study period

(Table 3), nor were changes in population density through time different in high-use areas (CAMP, CHURCH) relative to low-use areas (LIGHT, NPS, GUN) (Table 4).

This conclusion is in pronounced contrast to those of previous workers. Leggett (1975) found up to ten-fold differences between ghost crab populations in Back Bay NWR and a nearby control area. Florschuts & Williamson (1978) reported four-fold differences between populations on Bodie Island, where ORV use was prohibited, and the heavily-used Pea Island NWR. The differences decreased to two-fold when Bodie Island was opened to ORVs. When both beaches were closed to ORVs due to heavy erosion, differences in their ghost crab populations disappeared, with both islands supporting numbers similar to those of pre-ORV Bodie Island surveys (Smith, 1978). Britton (1979) found only one-thirteenth as many ghost crab burrows on a beach heavily used by ORVs on Assateague Island as on a nearby control area, but he expressed some doubt whether his census technique (number of burrows within 0·4 ha plots) adequately estimated crab densities. It probably did not, in that it failed to take into account the tendency of ghost crab populations to move out of areas where many burrows have been obliterated (Wolcott, 1978). Some of the apparent differences Britton observed were probably due to displacement of the ORV-area population from the beach into the dunes. Steiner & Leatherman (1981) reported up to 33-fold differences, between heavy-traffic and control areas, in nocturnally active crabs counted by a quadrat technique similar to Britton's. The principal difference between their results and Britton's is the large number of crabs Steiner & Leatherman (1981) found feeding in a heavy pedestrian use area. They attribute this anomaly to the food scraps left by picnickers.

The contrast between Cape Lookout National Seashore, where no ORV impact on invertebrate populations is detectable, and the previous barrier island study sites is undoubtedly due to marked differences in total vehicular use. Unfortunately, quantification of ORV traffic has proved difficult for all workers. Florschuts & Williamson (1978) report an average of 9 ORVs sighted $\text{km}^{-1}$ during the autumn fishing season, or 300 vehicles $\text{day}^{-1}$ on the Pea Island NWR. We never saw more than about 0·25 ORV $\text{km}^{-1}$ on Core Banks. Over 4000 ORVs visited the Chincoteague NWR site studied by Britton (1979) and Steiner & Leatherman (1981) during the autumn fishing season of 1978. Only about 350 ORVs were transported to the Core Banks section of Cape Lookout National Seashore during the same period in 1981 (Fig. 2).

Although the time a vehicle arrives or leaves the Seashore is not necessarily a measure of when it is actually driven, most vehicles are brought over by fishing parties for the duration of their stay (typically a week), and the ferry data are probably an adequate estimator of total vehicle use. Only in Leggett's (1975) study at Back Bay NWR are actual traffic volumes available. His high-traffic site sustained 18–87 passes day$^{-1}$ during his study period, and up to 250 passes day$^{-1}$ in previous years. On Cape Lookout, probably less than 5 vehicles day$^{-1}$ drive the length of the beach from either inlet to the fish camp. Clearly the 'heavy use' areas of previous studies were subjected to pressures far beyond any seen at Cape Lookout during this study.

The impacts on ghost crab populations described by earlier workers cannot be accounted for by higher traffic volumes alone, because the ghost crabs are so well protected by their burrows. Unfortunately, no data on the temporal and spatial patterns of vehicle use are available for any of the study sites, but it seems probable that nocturnal driving was responsible for the observed effects at at least two of them. The Back Bay NWR was, during Leggett's (1975) study, traversed by commuters who lived on the NC Outer Banks and worked in Norfolk, Va. Much of their driving would have occurred during hours of dusk or darkness, especially on short autumn days, and presumably would have been done on the hard foreshore. The Chincoteague NWR regulations appended to Britton (1979) indicate that some nocturnal use of the ORV area was permitted. Given the small number of passes required to produce substantial population mortality (Table 4), it seems reasonable to conclude that the observed population differences were due to the fraction of ORV use occurring after dark.

The results of this study indicate that the macrofauna of high energy beaches can tolerate moderate levels of diurnal ORV traffic on the foreshore. The filter-feeding infaunal species are protected so well by the sand that they are virtually immune to damage. Larger organisms, however, become vulnerable if they emerge from their burrows. On mid-Atlantic North American beaches the nocturnal ghost crabs are at risk while foraging on the foreshore. Conservative estimates of the population vulnerability indicate that as few as 20–50 vehicles driving along the foreshore at night during the crabs' active season (April–November) would substantially reduce ghost crab populations. The protection in high-use areas may require a ban on such use. If ORV operations were transferred from the foreshore to the backshore the impact on ghost crabs would be greatly reduced. Shifting night driving off the beach entirely, onto back roads, would probably be equally acceptable to ORV users and would have the added benefit of minimising disturbance to nesting sea turtles.

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