National Park Service
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Northeast Region
Boston, Massachusetts

The effect of off-road vehicles on barrier beach invertebrates at Cape Cod and Fire Island National Seashores

Technical Report NPS/NER/NRTR—2009/138

ON THE COVER
Off-road vehicle exiting beach at Race Point-South dune cut, Cape Cod
Photograph by: Jacqueline Kluft

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Abstract

The effects of off-road vehicles (ORVs) on invertebrates inhabiting macrophyte debris (wrack) and supratidal sands on energetic beaches in the northeastern United States were studied at Cape Cod (MA) and Fire Island (NY) National Seashores. Cores, wrack quadrats, and pitfall traps were used to sample four study beaches, which all had vehicle-free sections in close proximity to ORV corridors, allowing for paired traffic/no-traffic samples at these sites. A manipulative experiment was also performed by directly driving over nylon-mesh bags filled with eelgrass (*Zostera marina*) wrack that had been colonized by beach invertebrates, then subjected to treatments of high-, low-, and no-traffic.

Pitfall trap samples set at the wrackline had consistently higher overall invertebrate abundances in vehicle-free than in high-traffic zones on all four beaches. Overall abundance of wrack was also higher on beaches free of vehicle traffic. In contrast, both wrack quadrats (with intact wrack clumps) and the cores taken directly beneath them did not show consistent differences in overall invertebrate abundances in areas open and closed to vehicles. The talitrid amphipod *Talorchestia longicornis* and the lycosid spider *Arctosa littoralis*, both of which roam the beach widely by night but burrow diurnally in supratidal bare sands as adults (rather than under wrack as the juveniles do), were always less abundant in beach sections open to vehicle traffic, regardless of the sampling method used. Other invertebrates, such as oligochaetes (family Enchytraeidae) and tethinid flies (*Tethina parvula*), which spend most of their lives within/beneath wrack detritus, showed either no response or a positive response to traffic disturbance.

In the direct impact study the tenebrionid beetle *Phaleria testacea* (85% larvae) was significantly less abundant in disturbed wrack bags than in controls, while *Tethina parvula* (90% larvae) showed increases in disturbed wrack. Nonetheless, ORVs adversely affected beach invertebrates on the whole, in part by either killing or displacing some species, and by lowering the total amount of wrack, which lowered the overall abundance of wrack dwellers. For some interstitial detritivores the amount of vehicle disturbance on these beaches apparently facilitated mechanical breakdown of wrack and possibly sand surface moisture, increasing observed abundances.

Our results suggest that on beaches with moderate levels of beach traffic (as at Cape Cod and Fire Island) alternating opening and closing of adjacent beaches to vehicle traffic can potentially allow recolonization of wrack clumps in newly-closed beaches from two sources: wrack-dwelling species from intact wrack clumps that are missed by ORVs and remain on the disturbed beach and wide-ranging species from adjacent undisturbed beaches. Research on the rapidity of recolonization from these sources is needed to demonstrate that recolonization would be successful, and to optimize scheduling of alternating beach closures for conservation of supratidal invertebrates.

Acknowledgments

We thank the staffs of Cape Cod National Seashore and Fire Island National Seashore for generous logistical support, and for use of laboratory facilities and vehicles. Jeffrey Marion and Jenifer Dugan provided constructive comments on early drafts of the manuscript. This research was funded by the National Park Service NRPP Program and by the U.S. Geological Survey.

Introduction

The biotas of sandy beaches are currently threatened by pressures resulting from coastal development and increased human use of beach resources (Schlacher et al., 2007a & 2008b). Of these pressures, perhaps the most severe form of direct human disturbance on sandy beaches is from off-road vehicles (Schlacher et al., 2008c). Motorized off-road vehicles (ORVs, off-highway vehicles-OHVs, or four-wheelers) are driven on exposed beaches world wide, yet their use is a subject of persistent concern on government-managed beaches. Unfortunately, published studies on the effects of beach driving on invertebrate populations of energetic beaches are often insufficient for beach managers to make informed decisions on conservation policy (Schlacher et al., 2006). Patchy distributions and high variability in time and space (Colombini & Chelazzi, 2003; Defeo & McLachlan, 2005) have made beach invertebrates prohibitively challenging to quantify (Barros, 2001) and led to conflicting or inconclusive results in the measurement of macroinvertebrate response to any chronic, large-scale anthropogenic disturbances (e.g., Zaremba et al., 1979; Schoeman et al., 2000).

Though it was often thought that beach macrofaunal communities can withstand human disturbances (Godfrey, Leatherman, & Buckley, 1978; Jaramillo et al., 1996; Brown, 2000; Schoeman et. al, 2000), because they are already well adapted to their unstable substrata, recent studies have indicated that anthropogenic disturbance effects vary greatly depending on their density, seasonality, and location in conjunction with the specific life histories of the local macrofaunal assemblages (Schlacher et al., 2008b; Schlacher, 2008c). Nonetheless, invertebrates living above the daily swash (in supratidal/backbeach areas) appear to be consistently vulnerable to human disturbances on a global scale (Zaremba et al, 1979; Watson et al., 1996, Gomez & Defeo, 1999; Defeo & Gomez, 2005). Oniscid isopods can be crushed when burrowed supratidally (Van der Merwe & Van der Merwe, 1991), and they decline on highly populated beaches (Brown, 2000), along with talitrid amphipods (Weslawski et al.; 2000a & 2000b) in temperate regions and ghost crabs (e.g., *Ocypodid quadrata*) (Barros, 2001; Gao & Xu, 2002) in milder locations. Ghost crabs are often killed by vehicles, while foraging intertidally (Wolcott and Wolcott, 1984; Moss & McPhee, 2006; Schlacher et al., 2007b). They can be buried during beach scrapings (Peterson et al., 2000), and crushed in their soft-sand back-beach burrows if the burrows aren't deep enough (Schlacher et al., 2007b). ORVs have also been implicated in the historical disappearance of the supratidal northeastern beach tiger beetle (*Cicindela dorsalis dorsalis*) from much of its original geographical range (U.S.F.W.S., 1993). This vulnerability has lead several authors to propose several supratidal species (including Talitrid amphipods and Ocypodid ghost crabs) as effective indicators of ORV traffic (Barros, 2001; Schlacher et al., 2007b; Moss & McPhee, 2006).

In the U.S., beach driving is often limited to the most exposed, energetic beaches, where wrack debris (organic matter consisting of dislodged macrophytes and marsh plants) collects on the backshore and serves as a main source of ecosystem nutrients (Polis and Hurd, 1996; Colombini and Chelazzi, 2003). These wrack deposits are largely spring-tide and storm driven and occur less frequently and in lower abundance than on protected shores. However, they still attract abundant and species-rich invertebrate populations (e.g., Lavoie, 1985; Inglis, 1989; Polis and Hurd, 1996; Dugan et al., 2003), which play a vital role in temperate barrier beach food chains.

While this assemblage of macrophytes or 'the wrack-line' is well-known in the northeastern United States as foraging habitat for shorebirds (especially the federally-protected piping plovers (*Charadrius melodus*) Gibbs, 1986; Hoopes, 1993; Elias et al., 2000), there are only a few invertebrate community studies on these populations (Behbehani & Croker, 1982; Kluft Steinback, 1999; Burlas et. al, 2001). Recent studies have shown that human disturbances such as oil spill clean-ups (de la Huz et al., 2005) and beach rakings or "cleanings" (Engelhard & Withers, 1998; Dugan et al., 2003; Fanini et al., 2005; Llewllyn & Shackley, 2006), which involved wide-spread removal of wrack deposits, can cause immediate reductions in the abundances of semi-terrestrial crustaceans, insects, and their predators (Dugan et al., 2003). In addition, coastal armoring with sea level rise has been predicted to lower deposition and retention of wrack on disturbed beaches, destroy habitat, and lower macroinvertebrate prey availability for shorebirds (Dugan and Hubbard, 2006; Schlacher et. al., 2008b). In light of this known sensitivity of wrack assemblages to human disturbance, a better understanding of wrack community members in the northeastern U.S. and the effects of off-road vehicles on these communities is necessary to help managers set ORV policies that balance recreation with natural resource protection.

In this study, we re-visit two U.S. National Seashores that served as study sites in the late 1970's for investigations into the effects of ORVs on beach/dune systems (Anders and Leatherman, 1981). In these studies, vehicles were shown to crush vegetation and break beach grass rhizomes (Broadhead & Godfrey, 1979, Leatherman & Godfrey, 1979), prevent embryonic dune formation by disturbing wrack debris (Zaremba et al., 1979), and facilitate sand mobility and habitat loss (Visco, 1977; Broadhead & Godfrey, 1979; Anders & Leatherman, 1981, 1987). However, a specific study of the effects of ORVs on the wrack community was inconclusive. Here, we focus on the effects of off-road vehicles on the supratidal invertebrates.

First, we compare four different wrack-laden beaches in the northeastern U.S. (three within Cape Cod National Seashore, one within Fire Island National Seashore) that have neighboring sections of ORV-traveled and ORV-free beach (the 'analytical approach,' Buchanan, 1976), and second, we perform a controlled direct-impact study, in which we drive over colonized, experimental wrack clumps near Ballston Beach, MA, to assess the effects. By replicating our sampling at four beaches (Schoeman et al., 2000) and using several sampling methods, we strove to maximize the chances that observed differences between treatment (traffic) and control (non-traffic) sites were due to ORV activity. In the manipulative experiment, we controlled the level and timing of the traffic that the wrack-associated species received. In addition, we compared accompanying environmental variables that may be good indicators of the effect of traffic on invertebrate habitat.

Methods

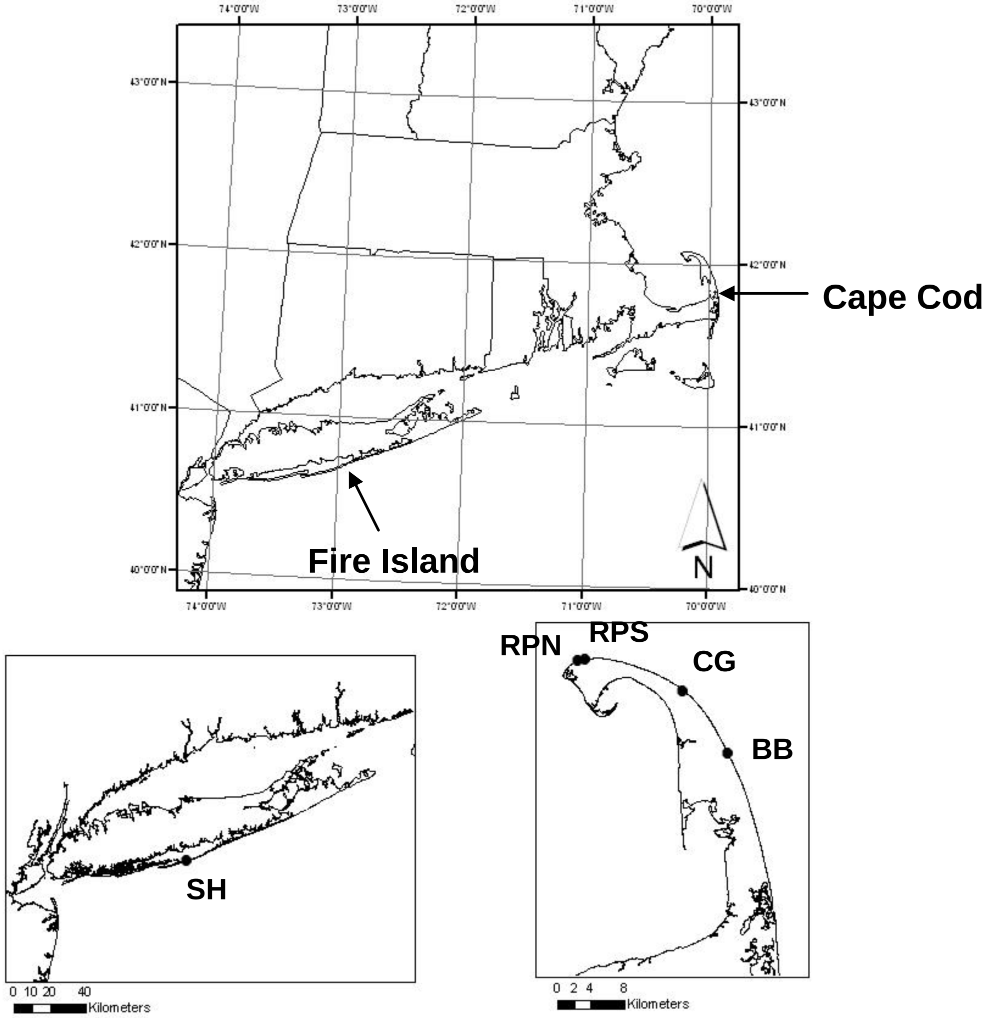
Comparative Study

Study sites

In the summers of 2001-2002, comparative samples were taken from exposed beaches within Cape Cod National Seashore (CACO) (avg. summer temp. 19.5º), a government-protected area along the northeastern edge of Cape Cod, MA (Figure 1). The 8.5-mile off-road driving corridor at CACO is open 24 hours a day from April 15-November 15, with 5,500 – 6,500 annual/weekly permits per year. However, ORV routes can be closed in June and July for nesting piping plovers.

Three study beaches were chosen along the CACO ORV route: 1) Race Point North (RPN)—the only area open to overnight campers/trailers during the study (restricted to 100 vehicles per night), 2) Race Point South (RPS)—located .4 miles south of RPN, and 3) Coast Guard (CG) beach, North Truro, which has been open to night fishing only since 1998. Both Race Point sites are located on the Provincetown barrier spit and have been open to vehicles since the 1960’s (Broadhead and Godfrey, 1979).

A fourth beach, near Sailor’s Haven (SH) on Fire Island National Seashore, NY, was sampled as part of preliminary ORV research in the summer (avg temp. 22º) of 1995. Fire Island is a dynamic barrier island lying just south of Long Island, NY (Figure 1), with vehicle access limited to 245 permitted residents and various personnel (~173), and most driving restricted to early morning and evening hours during summer. Both Cape Cod and Fire Island National Seashores have intermediate-type beaches (Wright & Short, 1983) with semidiurnal, astronomical tides and typical seasonal shifts between storm (winter) and recovery (summer) profiles (*sensu* Komar, 1976) (Table 1). All sites can experience exceptionally high tides during hurricanes and Nor’Easters (Bokuniewicz et al, 1993), however Fire Island is more wave-dominated than the Cape Cod beaches (Table 1).



Fire Island **Cape Cod**

Figure 1. Map of study sites.

Table 1. Background characteristics for the four sampled beaches with vehicle access and the Ballston area where the manipulative experiment study was performed.

	Wave height (m)	Tidal range (m)	Back Beach	Morphology	Exposure	Median grain size (mm)	Longshore drift	Latitude	Longitude
Cape Cod National Seashore									
Race Point North	1.05-1.25	2-4	moderate foredunes (3 m); dense vegetation front	barrier spit	N	1-1.2	W	42º 04’ 46.92” W	70º 13’ 23.16" N
Race Point South	1.05-1.25	2-4	moderate dunes (4-6 m); eroding foredune face	barrier spit	N	1-1.2	W	42º 04’ 53.22" W	70º 12’ 47.16" N
Coast Guard	>1.25	2-4	eroding sea cliffs (16-18 m); north of cut has densely vegetated foredune	glacial outwash	NE	.85-1	NW	42º 02’ 54.96" W	70º 04’ 20.78" N
Ballston Beach	>1.25	2-4	eroding sea cliffs (30 m)	glacial outwash	E	.85-1	N	41º 58’ 54.12" W	70º 00’ 24.12" N
Fire Island National Seashore									
Sailor's Haven	>1.25	<1.0	low dunes (1 m); densely vegetated foredunes	barrier island	S	.2-.4	W	40º 39’ 09.16” W	73º 07’ 08.01” N

Sampling areas

On either side of each vehicle cut (between 100-200m wide), traffic (T) and non-traffic (NT) sample areas were designated by 100m-wide stretches of beach (parallel to the water) that were roughly equidistant from the vehicle entrance-way (after Anders & Leatherman, 1981, Fig. 47). A benchmark (PVC pipe) with known elevation (height above NGVD88, provided by USGS-Woods Hole, MA) was established 50m into each area, at the toe of the dune/bluff closest to the beach, to serve as reference. At SH, height was measured relative to NGVD83. Initial descriptive data on foredune/bluff characteristics, such as height/slope, vegetation composition and cover, and the presence of vegetation fronts (the seaward edge of dune vegetation, Anders & Leatherman, 1981) were collected at least once during each summer of study within the T/NT areas. Foredunes were considered the dunes closest to the water that usually fronted larger primary dunes of higher elevation.

Transects

Samples were taken twice at Cape Cod sites in 2001 (July 19-Aug. 2 & Aug. 10-23) and 2002 (June 3-8 & Aug. 8-14) and three times at SH in 1995 (July 29-31, Aug. 10-11 & Aug. 23-24). Within each 100m-wide sample area, five points were randomly selected for dune toe-to-swash transects. The foredune toe was defined by the point where steep dune slopes soften and merge onto the back beach. Changes in profile slope were measured at roughly 1-m intervals, using a hand-held digital level (SmartTool™, Macklanburg-Duncan, Oklahoma City, OK, USA) run along a tape measure from the dune to swash at low tide. Profiles from transects of the first sampling period were averaged together and plotted to display representative contours of each beach area.

To quantify the overall amount of wrack within each sampling area, any wrack debris along a profile that intersected the tape (and up to roughly 0.5 meter to either side) was recorded for dimensions (l*w*d), % species composition, and an ordinal rating of wrack consistency (1-5), and the mean density/meter ((l*w*d)/meter^2 of beach) was estimated. Since the clump was measured at its largest length and width, and was therefore an overestimate of clump cover, an elliptical surface area, estimated using the standard formula (length/2*width/2*PI), was calculated for more accurate analysis. These surface area estimates (m^2 wrack/meter of beach) for each transect were then used to generate overall % cover for each area (after Dugan et al., 2003).

Invertebrate sampling

Along each profile, a 0.1m^2 quadrat frame was placed over a random wrack clump to delineate a sample. Clumps were randomly chosen from within driving areas first. If there was no wrack within a driving corridor, then samples were taken in the surrounding sample area in proportion to the occurrence of each debris type (e.g., fresh and old) present. Attempts were also made to sample wrack with quadrat cover over 50%, to minimize any bias associated with different sized wrack samples.

Three sampling methods were then used in each transect, in this order:
1) debris samples, where the wrack within the quadrat frame was measured for environmental variables, cut away, and collected in Ziploc™ bags for later sorting of invertebrates; 2) core samples, in which a beveled PVC pipe (15.24 cm diameter*20 cm depth or ~.02 m^2 SA and 3.6*10-3m^3) cored sand below the sampled wrack, which was then sieved through a 1-mm mesh screen, and bagged for later sorting of burrowed fauna, and finally 3) pitfall trap samples: a 16 oz. (0.5 liter) plastic Solo® cup partially filled with soapy water was set (either in the core hole or within few meters landward of it) for 24 hours, to catch mobile, nocturnal animals.

Environmental variables measured within wrack samples included: quadrat percent cover, relative wrack age (categorized qualitatively as fresh, decaying, or old) and % composition (predominantly *Zostera marina* or eelgrass; brown alga--*Ascophyllum nodosum* and *Fucus* spp.; cordgrass or *Spartina alterniflora*; and beach grass, *Ammophila breviligulata*), temperature and humidity at the wrack/sand interface (with a Tri-Sense® meter & RH/Temp probe with sintered bronze filter tip, Cole-Parmer Instrument Co., Vernon Hills, IL, USA), and sand temperature at 10cm depth (w/soil thermometer) beneath wrack. Wrack wet/dry weight, % moisture (water loss upon drying at 60ºC until weights stabilized for 24 hrs), and volume (cubic centimeters were measured by placing wrack in a plastic container of known volume) were determined in the laboratory for CACO samples. Core, wrack, and pitfall trap samples were sorted, and invertebrates were identified to lowest possible taxonomic level. SH samples differed in that the wrack debris was sorted for invertebrates in the field (see Kluft Steinback, 1999), and wrack frequency on the beach, % moisture, dry weight, volume, and temp./RH under wrack were not measured. At both Cape Cod and Fire Island, wrack debris and core samples were pooled, because they tended to catch similar species. However, at Fire Island, wrack debris samples were down-weighted to represent samples of similar surface area to the core samples (Kluft Steinback, 1999).

Analysis

The Fire Island samples consisted of 10 wrack samples and 10-11 pitfall traps taken in three time periods (30 wrack samples/32 pitfall traps in the T and NT areas). CACO samples consisted of 10 wrack and 10 pitfall trap samples taken from each of the six areas (3 Traffic/3 Non-traffic) over two time periods in 2001, and two more in 2002 (12 pitfall traps/area). Therefore, while 2-way ANOVAs (treatment ***x*** sampling period) could be used at the Fire Island site, 3-way ANOVAs (treatment ***x*** site ***x*** period) were used at CACO. ANOVAs were performed using SPSS 16.0, 2007 (SPSS, Inc). When desired, the T-method for multiple unplanned comparisons among means (Sokal & Rohlf, 1995) was then used to determine which sites were significant by treatment. A Levene's Test

(1960) or an F-max test was used to confirm homogeneity of variances, and data with many zeros or outliers were log (x+1) transformed. If data were not normal, then two-way nonparametric ANOVAs (traffic*period) using the Scheirer-Ray-Hare extension of the Kruskal-Wallis Test were run with BIOMstat, version 3.301 (Applied Biostatistics Software, Inc., Pt. Jefferson, NY, USA). This test was chosen, because it is robust against departures from normality. When traffic*site interactions occurred, then two-way ANOVAs were run at each site individually.

Manipulative Study

The manipulative experiment was performed from late June-mid July, 2002, on a remote, undisturbed beach near Ballston, Cape Cod, 1/10 mile north of the Welfleet/Truro line (Table 1). Freshly deposited eelgrass *Zostera marina* was frozen for 48 hours to kill existing invertebrates, soaked overnight in filtered seawater to simulate being washed ashore, and partitioned (150 gm/clumps) into 81 wide-mesh sacs (20" Nylon replacement nets, Pepper Net Co., Inc., Williamson, NY, USA) that could easily be colonized by all invertebrates <2 inches in diameter.

On the morning after the June 25th full-moon, the bags were placed above the spring high tide line on a 50m stretch of beach partitioned into 9 sections, 9 bags per section, and tethered in place using fishing line and stakes. Bags were arranged into 2 rows (2 m long and 2 m apart) per section, perpendicular to the shore, and subjected to one of three treatments (1) high traffic, bags run over 10 times on each sampling day; 2) low traffic, bags run over 2 times/sampling day; 3) control, bags not run over. A Chevrolet Suburban (curb weight 4634 lbs.) with tires (245/75-16) lowered to 12-15 psi and driven at approximately 10 miles/hour, consistent with Park regulations, was used to apply treatments. The layout of the experiment is shown in Figure 2.

Sampling and treatments occurred over a three-week period, with samples collected on days 1, 2, 4, 7, 10, 13, 16, 19, & 22. During sampling, one bag was removed from each of the nine beach sections (3 replicates of each treatment), placed into double Ziploc™ bags along with some handfuls of the underlying sand, and left over night in a Berlese funnel to extract colonizing invertebrates. Relative humidity and temperature were measured at the wrack/sand interface, as well as wrack bag dimensions (l*w*d), level of bag burial, and temperature at 10cm below the wrack. Invertebrates were identified, and stored in 75% ethanol. Average invertebrate abundances and abundant species were analyzed using 2-way ANOVAs (treatment ***x*** period).

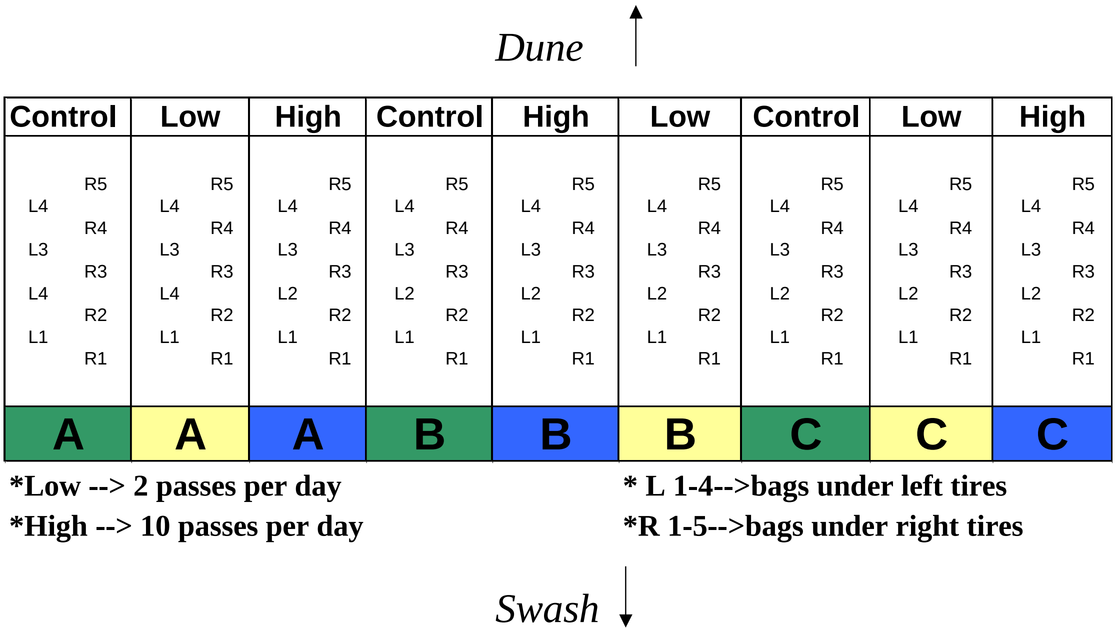


Figure 2. Sketch of the direct experiment layout. One bag was removed from each sample block per sample day, with a total of 9 bags, 3 of each treatment, on 9 sample days.

Results

Comparative Analysis

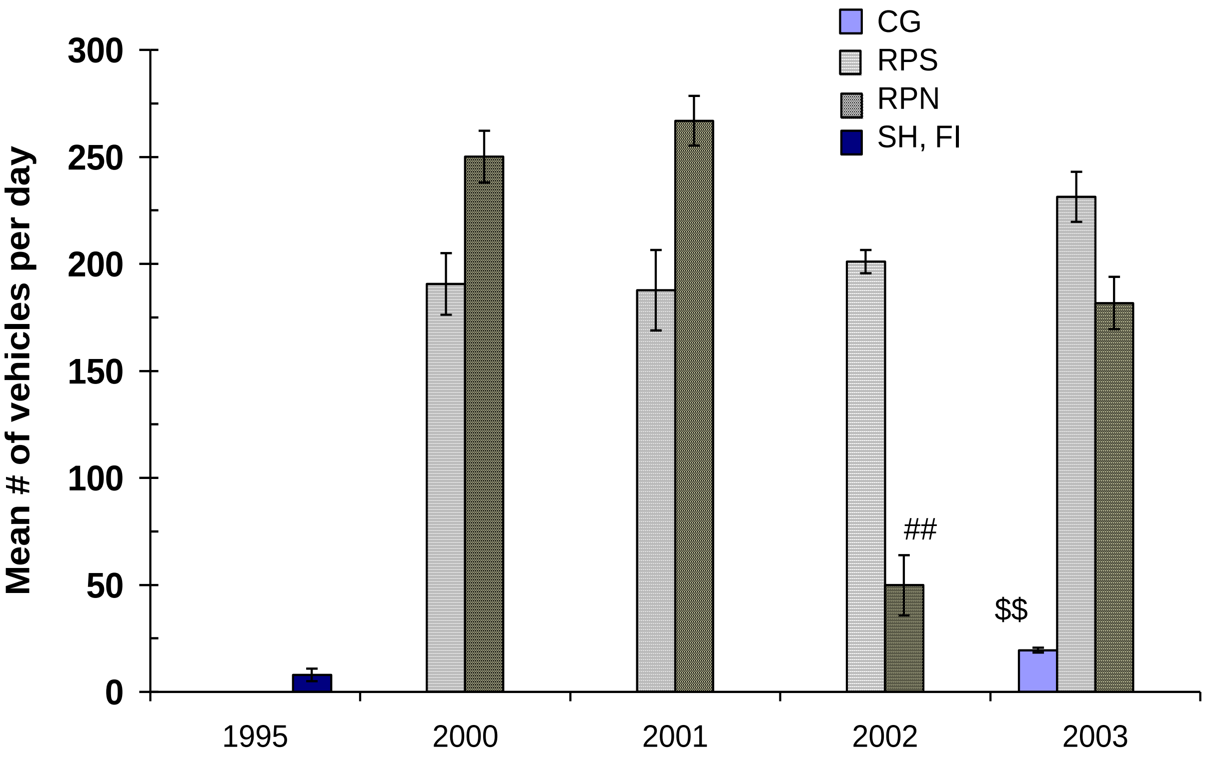
Traffic level

In 2001, traffic-level was highest at the Race Point-North (RPN) site (267±19 cars/day) (mean ± 1 SE), followed by Race Point–South (RPS: 187±12), and Coast Guard (CG) in N. Truro (Figure 3). Traffic level was apparently lowest at Fire Island, but the level was estimated from transect counts of vehicle tracks. Driving at both Cape Cod and Fire Island sites is mostly limited to the back-beach, 10-20 feet from the foot of the dune and 10-feet landward of the berm crest. However, there were some differences among the sites as to exactly where vehicles drove. RPN and CG had relatively narrow driving corridors (~7m and ~5m wide) about 8-10m from their vegetation fronts. At RPN (59m-wide NT beach, 64 T beach), campers parked along the berm top, limiting the ORV corridor width, while at CG (53m NT, 49 T) the ORV corridor was limited by tides. At RPS (77m NT, 78 T), the widest beach, there was no consistent ORV lane, and vehicles could drive along a wide range of the back beach (est. track width at 21±1) (mean ± 1 SE), starting ~18m from the dune vegetation. Finally, at Sailor's Haven (55m NT, 58 T), the track width was not measured, but visible tracks (on average) ran diagonally over the storm wrack that collected at low points between summer and winter berms, about 26m from the profile stake.

Vegetation surveys and profiles

Vegetation surveys showed no consistent differences in dune vegetation between traffic and non-traffic areas. However, at all non-traffic sites, vegetation fronts appeared denser than at their traffic counterparts. This difference was most notable at Coast Guard beach site, where the NT area had a densely vegetated foredune, while the T area had just a few sparse plants. American beach grass (*Ammophila breviligulata* was the most abundant vegetation at all sites, while beach pea (*Lathyrus maritima*) and dusty miller (*Artemisia stelleriana*) occurred intermittently on the CG-NT side and at Race Point North.

The most notable differences in foredune/dune vegetation density occurred among sample sites. Race Point North T and NT sides had densely vegetated foredunes (5-6m high) and vegetation fronts (15m wide) (Figure 4), but at Race Point-South T and NT areas (Figure 5), the foredunes (6-7m high) of Race Point areas were only sparsely vegetated (100% beach grass roots) due to storm erosion, as was the 5 m-wide vegetation front, which consisted of the occasional sea rocket (*Cakile edentula*) or sandwort (*A. peploides)*. CG was the only site with steep (18m high) eroding bluffs, and these were also poorly vegetated (1% T and 3% NT) with beach grass (Figure 6). Though Sailor's Haven dune profiles were not measured, both T and NT areas had low foredunes (~1-2m high), sporting wide, dense beach grass in summer (Figure 7).



$$ Data was not available for all years at Coast Guard, but traffic patterns were similar for 2000-2002. Coast Guard allowed night fishing only.

Race Point North was closed to vehicles in July, 2002, due to nesting piping plovers.

Figure 3. Mean # of vehicles (± 1 SE) using the beach, June-August. Measured by Cuesta Systems TS-601 traffic broken-beam traffic counters installed by the NPS at access points to each driven sample area. SH, FI count was estimated by transect counts of observed vehicle tracks in the sampling area.

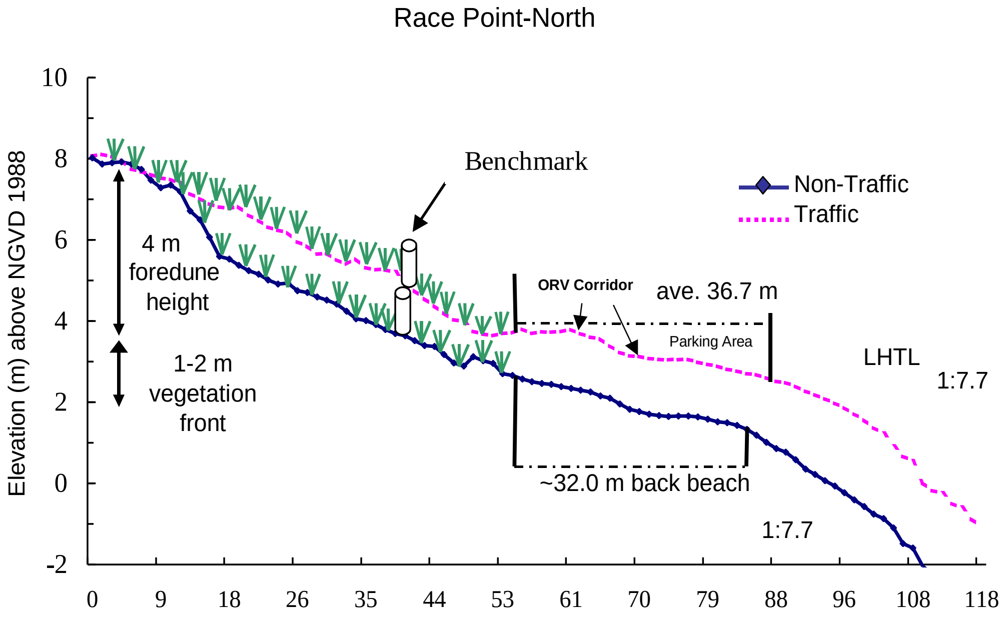


Figure 4. Average Race Point North profiles for traffic and non-traffic areas calculated by averaging transect elevations from sampling period 1.

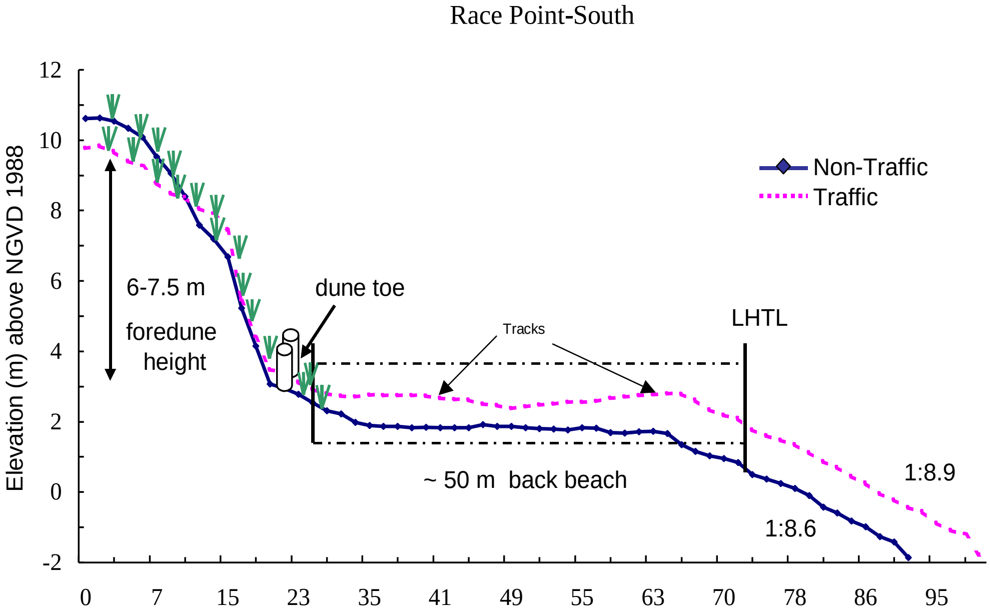


Figure 5. Average Race Point South profiles for traffic/non-traffic areas calculated by averaging transect elevations from sampling period 1.

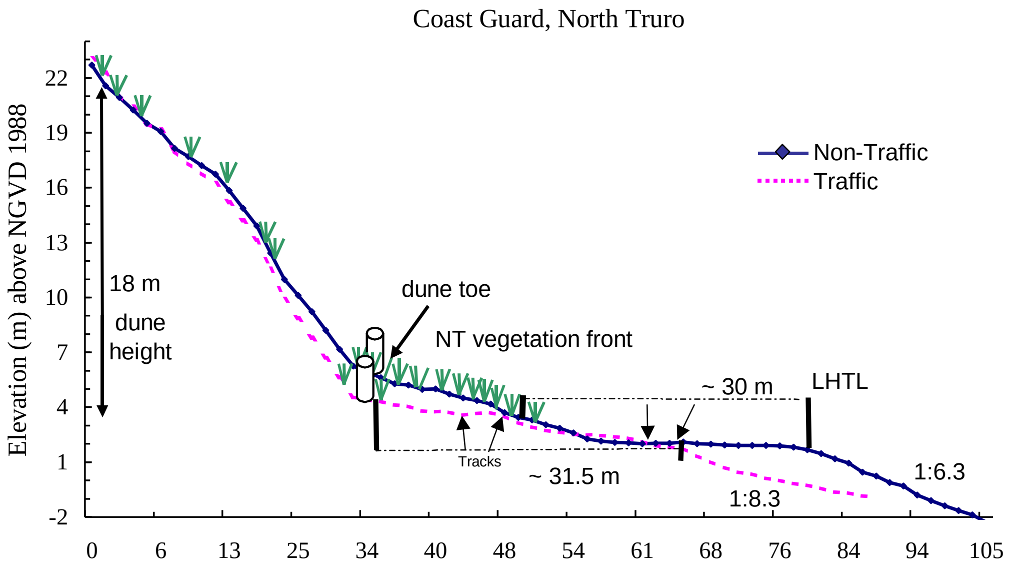


Figure 6. Average Coast Guard profiles for traffic and non-traffic areas calculated by averaging transect elevations from sampling period 1.

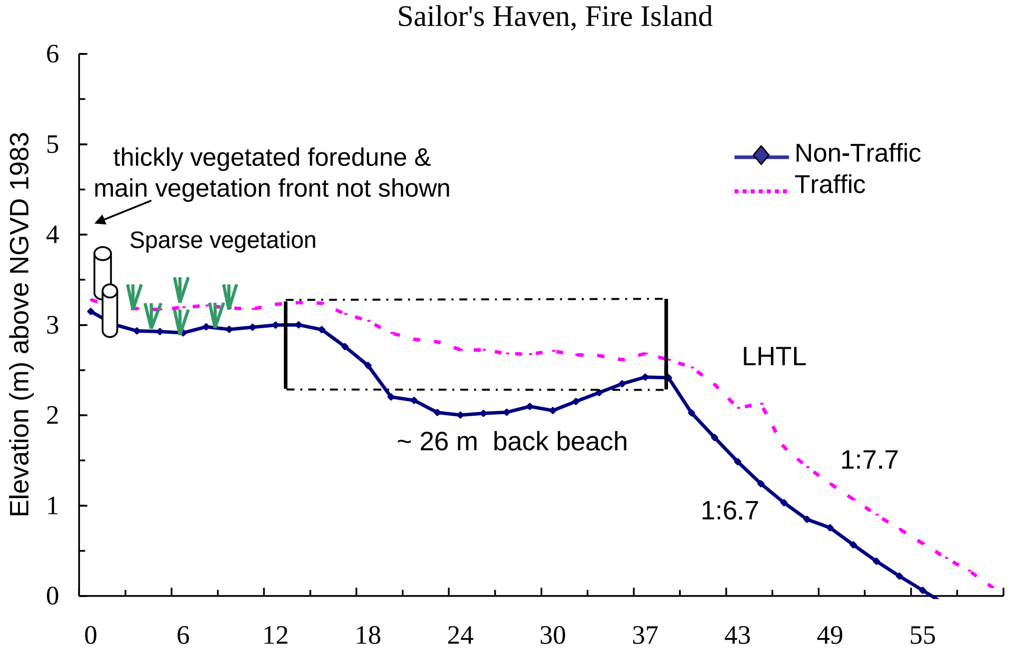


Figure 7. Average Sailor's Haven profiles for traffic and non-traffic areas calculated by averaging transect elevations from sampling period 2.

Profile shapes in T and NT areas were also similar. However, all sites except Coast Guard had higher beach elevations in traffic areas during sampling. In addition, the slopes within traffic areas were generally gentler than within non-traffic areas (ANOVA: overall treatment effect at Cape Cod: F=18.8 df=1, 24 P<0.0002). Mean intertidal slope gradients varied from 1:7.7 NT-1:7.7 T at RPN (Figure 4), 1:8.6 NT-1:8.9 T at RPS (Figure 5), 1:6.3 NT-1:8.3 T at CG (Figure 6), and 1:6.7 NT-1:7.7 T at SH on Fire Island (Figure 7)**.** Overall, Coast Guard was the only site of the four with large differences in beach morphology and vegetation fronts between traffic- and non-traffic areas during the time of sampling.

Environmental variables

Abundance and distribution of wrack differed on beaches with and without traffic. Wrack was significantly less frequent in traffic than non-traffic areas, both on the beach as a whole (mean # of wrack clumps/transect, F= 16.2 df=2, 48 P<0.001) and within ORV corridors (Scheierer-Ray-Hare tests by site: CG: F=6.7 df=1,16 P=0.02; RPS: F=22.6 df=1,16 P<0.002; and at RPN: F=5.2 df=1,16 P=0.04) (Figure 8). Rankings of wrack consistency per clump (i.e. whether the thickness was consistent throughout the sample) and wrack cover {(both within sample quadrats and estimated for the 100m sample area (calculated as frequency of wrack occurrence in 1m^2 quadrats/100 m-long sampling area of beach (m^2))} were also higher in non-traffic areas at Cape Cod (Tables 2 & 3). This difference was not significant at Sailor's Haven (cover, F=1.4 df=1,56 P=0.24). However, other measurements of the amount of wrack on T and NT beaches, such as the average density and surface area per clump, did not differ (Tables 3). Nor did wrack quadrat measurements of volume (l), dry weight (gms), or wrack age at Cape Cod (Table 2) or Sailor's Haven (dry weight, Periods 1, 2, 3: p-values 0.09, 0.09, 0.71; wrack age H: 3.7 P=0.06). The only other significant difference within wrack samples was wrack moisture, which was higher within traffic samples at Cape Cod (Table 2), but not at Sailor's Haven (F=1.7 df=1, 56 P=1.9).

The wrack was composed mainly of *Zostera marina*, *Ascophyllum nodosum*, *Fucus* spp., *Spartina alterniflora*, *Ammophila breviligulata*, and a mixture of filamentous algae (including *Pylaiella, Polysiphonia, Enteromorpha, Rhizoclonium spp*.) (Table 4). 'Other' intermittent components included *Ulva lactuca*, *Phragmites,* and the occasional animal carcass. Though the relative percentage of these components varied among sites and sample dates, there were no consistent differences in wrack relative composition between traffic and non-traffic areas for any individual component, with the exception of the relative abundances of *Zostera marina* and *Spartina alterniflora* at Sailor's Haven (Table 4).

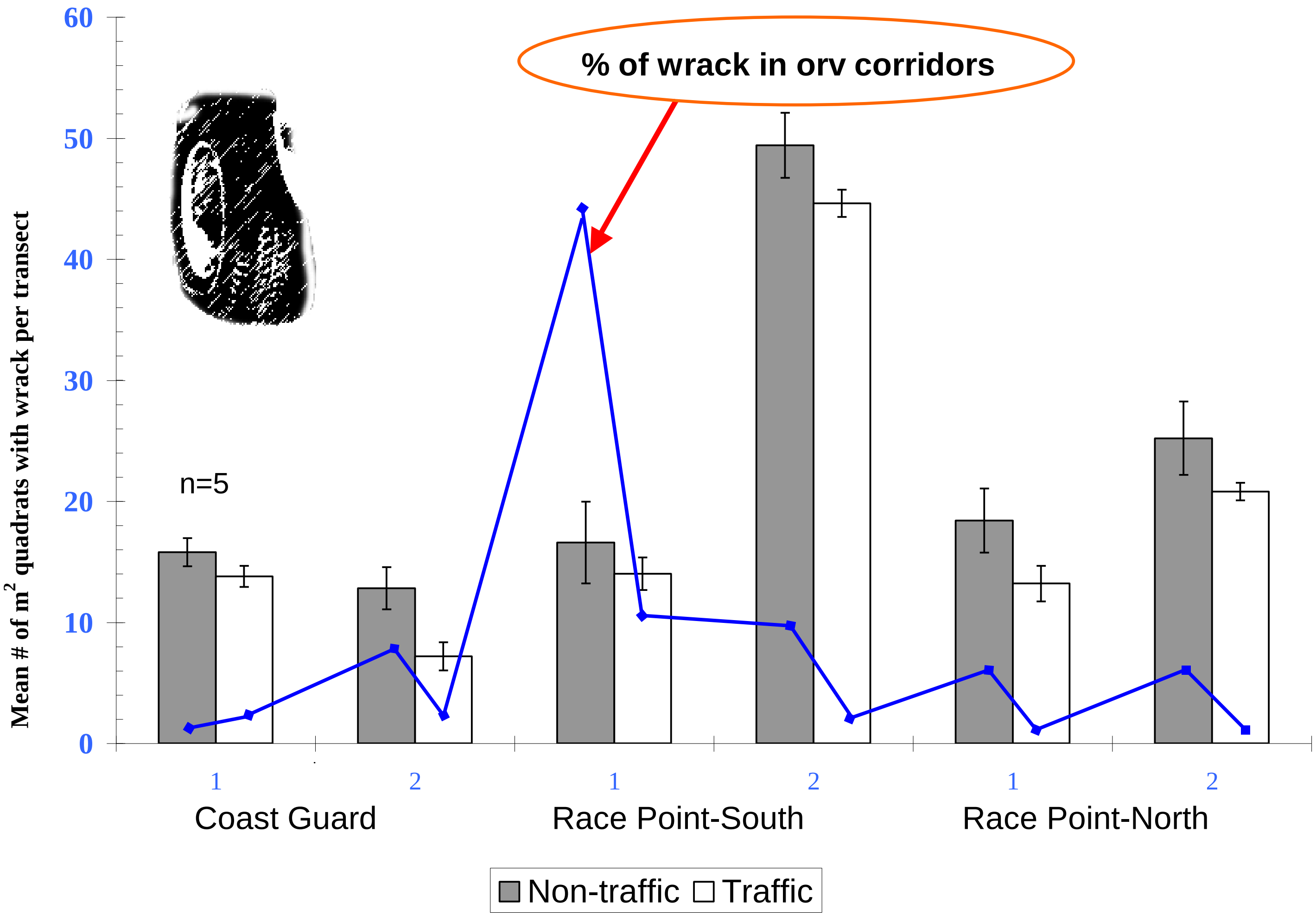


Figure 8. Comparison of mean wrack occurrence/transect (± 1 SE) within traffic/non-traffic areas on CACO beaches: along the entire beach width (the end of vegetation front to the swash at low tide), indicated by histogram, and the mean percentage of that wrack that occurred within the ORV corridors or their projected location if driving had occurred (line).

Table 2. Selected environmental variables measured for wrack/core samples within traffic and non-traffic areas of Cape Cod National Seashore during the 2001 field season (means ± 1 SE). An X under the P-value indicates that significant 3-way interactions of treatment ***x*** site ***x*** period rendered the 3-way ANOVA invalid. An @ indicates that site means were significantly different at the 0.05 value.

Cape Cod 2001: AVERAGED ENVIRONMENTAL VARIABLES FOR ALL THREE SITES

Within sample quadrats	CG-NT	CG-T	RPS-NT	RPS-T	RPN-NT	RPN-T	All Sampling sites		F-value	df	P
% Cover of sample wrack in quadrat	44.5 ± 2.7	32.5 ± 10.7	69.5 ± 3.0	56.0 ± 17.7	62.0 ± 5.2$^{@}$	36.5 ± 11.5	58.7 ± 3.9	41.7 ± 13.2	8.9	1, 44	**0.004**
Wrack volume (l) per sample	1.3 ± 0.4	1.0 ± 0.3	2.4 ± 0.5	1.9 ± 0.5	1.4 ± 0.2	1.0 ± 0.2	1.7 ± 0.2	1.3 ± 0.2	1.8	1, 44	0.19
Wrack dry weight (gm) per wrack sample	115 ± 47	90 ± 33	307 ± 71	333 ± 136	141 ± 22	112 ± 31	193 ± 33	185 ± 53	0.02	1, 44	0.90
Average % moisture loss per wrack sample	20.1 ± 3.0	31.5 ± 5.6	22.8 ± 4.0	24.7 ± 3.2	16.5 ± 2.4	25.3 ± 4.5$^{@}$	19.8 ± 1.9	26.8 ± 2.5	7.1	1, 44	**0.01**
Mean ranking of wrack age (1-fresh, 2-decaying, 3-old, 4-very old)	2.2 ± 0.4	2.3 ± 0.4	3.0 ± 0.3	2.9 ± 0.4	3.2 ± 0.4	3.4 ± 0.5	2.8 ± 0.2	2.9 ± 0.3	0.04	1, 48	0.85
Relative humidity (%) at wrack/sand interface	74.9 ± 2.7	81.0 ± 2.6	85.0 ± 3.0	84.0 ± 2.9	80.2 ± 5.2	76.2 ± 6.6	80.0 ± 2.3	80.4 ± 2.6	0.02	1, 48	0.89
Sample temperature (°C) at wrack/sand interface	28.6 ± 1.7$^{@}$	21.9 ± 0.9	23.6 ± 1.4	29.7 ± 1.4$^{@}$	27.5 ± 1.3	28.5 ± 2.5	26.6 ± 0.9	26.7 ± 1.2	0.22	1, 48	**X**
Sample distance (m) from dune vegetation	11.4 ± 2.2	13.1 ± 2.3	19.2 ± 3.3	22.7 ± 1.0	12.9 ± 1.7	15.6 ± 3.8	14.9 ± 1.6	17.1 ± 1.0	1.8	1, 48	0.19

Table 3. Selected environmental variables measured along whole beach transects within traffic and non-traffic areas of Cape Cod National Seashore during the 2001 field season. An X under the P-value indicates that significant 3-way interactions of treatment *x* site *x* period rendered the 3-way ANOVA invalid. An @ indicates hat site means were significantly different at the 0.05 value.

On the whole beach	CG-NT	CG-T	RPS-NT	RPS-T	RPN-NT	RPN-T	All Sampling sites		F-value	df	P
Average elliptical surface area per wrack clump (m^2)	0.40 ± 0.10$^{@}$	0.04 ± 0.01	0.50 ± 0.1	0.47 ± 0.1	0.18 ± 0.02	0.27 ± 0.1	0.38 ± 0.05	0.34 ± 0.03	2.4	1, 1168	**X**
Average density (m^3) $*10^{-3}$ per wrack clump	5 ± 1$^{@}$	2 ± 0.3	5 ± 1	7 ± 1	5 ± 1	5 ± 1	5 ± 1	6 ± 1	0.05	1, 1168	0.82
Mean ranking for consistency of thickness (1-low, 2-medium, 3-high, 4-very high)	2.0 ± 0.1$^{@}$	1.7 ± 0.1	2.2 ± 0.1$^{@}$	1.9 ± 0.1	2.2 ± 1.0	2.2 ± 1.0	2.2 ± 0.1	1.9 ± 0.1	7.3	1, 1142	**0.007**
Average density (m^3) per meter^2 of beach $*10^{-3}$	1 ± 0.3$^{@}$	0.2 ±0.1	2.7 ± 0.7	2.4 ± 0.4	1 ±0.3	0.9 ± 0.2	1.7 ± 0.3	1.2 ± 0.2	7.3	1, 48	**X**
Estimated % cover for 100m sample area	1.9 ± 0.4$^{@}$	0.6 ± 0.2	1.5 ± 0.2	1.6 ± 0.2	3.4 ± 1.2	2.9 ± 1.0	2.3 ± 0.4	1.7 ± 0.4	4.6	1, 48	**0.04**

Table 4. Relative contribution of the different macrophyte species in the wrack samples (given as the percentage wet weight of each taxon at the sample sites indicated).

	Zostera marina		*Ascophyllum nodosum*		*Spartina alterniflora*		*Fucus spp.*		*Ammophila breviligulata*		Filamentous algae		Other	
	NT	***T***	***NT***	***T***	***NT***	***T***	***NT***	***T***	***NT***	***T***	***NT***	***T***	***NT***	***T***
Coast Guard														
Period 1	23.8	38.5	42.3	32.1	12.1	5.8	14.4	18.1	49.0	1.5	0.6	1.2	2.0	2.8
Period 2	3.1	25.8	29.1	24.0	9.0	11.2	0.1	13.0	5.6	3.4	11.0	2.1	42.1	10.5
Race Point South														
Period 1	18.5	13.9	54.8	63.2	7.8	2.5	5.8	7.7	5.7	2.3	0.1	1.3	7.3	9.2
Period 2	19.7	0.6	40.6	73.8	2.5	0.4	7.8	5.0	1.3	5.6	24.6	10.0	3.5	4.6
Race Point North														
Period 1	3.3	15.0	46.4	29.0	2.4	8.4	24.2	4.0	4.5	19.0	2.5	2.8	16.7	21.8
Period 2	30.2	20.0	51.6	37.2	1.2	4.6	4.2	21.8	5.8	7.6	0.0	0.0	7.0	8.8
ANOVAS on treatment (df=1, 56)	F=0.33 P=0.57		F=0.009 P=0.92		F=0.15 P=0.90		F=0.27 P=0.61		F=0.59 P=0.45		F=1.2 P=0.28		F=0.66 P=0.42	
Sailor's Haven														
Period 1	13.0	23.5	16.5	4.1	66.5	31.0	4.0	4.5					0.0	36.9
Period 2	33.0	53.5	9.5	12.5	54.5	29.6	3.0	2.5					0.0	1.9
Period 3	30.0	64.6	11.8	3.2	37.7	29.5	2.7	1.8					9.3	18.2
ANOVAS on treatment (df=1, 56)	F=5.7 **P=0.02**		F=1.1 P=0.29		F=6.2 **P=0.02**		F=0.05 P=0.83						F=0.38 P=0.85	

Beach invertebrate abundances

Abundances of beach invertebrates in wrack/core samples did not differ consistently within traffic and non-traffic areas at either Sailor's Haven (ANOVA treatment: F=0.62 df=1,56 P=0.44) or the Cape Cod sites (F=0.46 df=1,56 P=0.50) (Figure 9). In contrast, abundances in pitfall trap samples were consistently lower in traffic areas than in non-traffic areas at the Cape Cod sites (Figures 10b, 10c) (2001 treatment, F=17.39, df=1,48 P<0.001; 2002 treatment: F=8.9 df=1,60 P=0.004). This difference was not significant at Sailor's Haven (F=1.4, df=1, 58 P=0.25), but the trend was consistent with the Cape Cod results (Figure 10a). At Cape Cod, the average number of species per sample also varied within pitfall traps (9.6 ±0.5 NT, 7.1 ±0.5 T; ANOVA: treatment effect, F=13.1 df=1,60 P=0.001), but not within wrack/core samples (6.7 ±0.7 NT, 5.4 ±0.7 T; ANOVA: treatment effect, F=1.9 df=1,48 P=0.17). Dominant taxa, listed in order of abundance (Table 5), included oligochaetes, tethinid flies, talitrid amphipods, and beach-inhabiting coleoptera.

Some species were consistently more abundant in areas without traffic. For example, the beach hopper *Talorchestia longicornis* (Table 6) and the wolf spider *Arctosa littoralis* (Table 7) were less common in traffic areas when sampled using both wrack/core (*T. longicornis* at SH, treatment: F=1.1 df=1, 56 P=0.30; at Cape Cod, treatment: F=6.3 df=1, 44 P=0.02; *A. littoralis* at SH, treatment: F=9.6 df=1, 56 P=0.01; at Cape Cod F= 4.1 df=1,44 P<0.05) and pitfall trap methods (*T. longicornis* at SH, treatment: F=1.2 df=1, 58 P=0.29; at Cape Cod 2001, treatment: F=85.0, df=1,48 P<<0.001, 2002, treatment: F=23.5 df=1, 60 P<0.0001; *A. littoralis* SH, treatment: F=9.4 df=1, 58 P=0.003, but heterogeneous variances, so run by periods 1, 2, 3: P-values 0.13, 0.03, 0.12; at Cape Cod 2001 treatment: F=19.5 df=1,48 P<0.0001; 2002 heterogeneous, so run by sites CG, RPS, RPN: P-values: 0.4, 0.01, 0.02). However, other species showed no consistent difference in traffic and non-traffic areas or were sometimes higher in traffic areas, such as the tethinid *Tethina parvula* (Table 8: SH pitfall trap treatment: F=0.005 df=1, 58 P=0.94; Cape Cod 2001 wrack/core, treatment: F=0.001 df=1, 48 P=0.98; Cape Cod pitfall traps 2001, treatment: F=2.4 df=1, 48 P=0.13; 2002, treatment: F=0.002 df=1, 60 P=0.97) and enchytraeid oligochaetes (Table 5; SH core/site; F=4.2 df=1,56 P=0.05; Cape Cod wrack/cores 2001: treatment F=0.41, df=1,44 P=0.53).

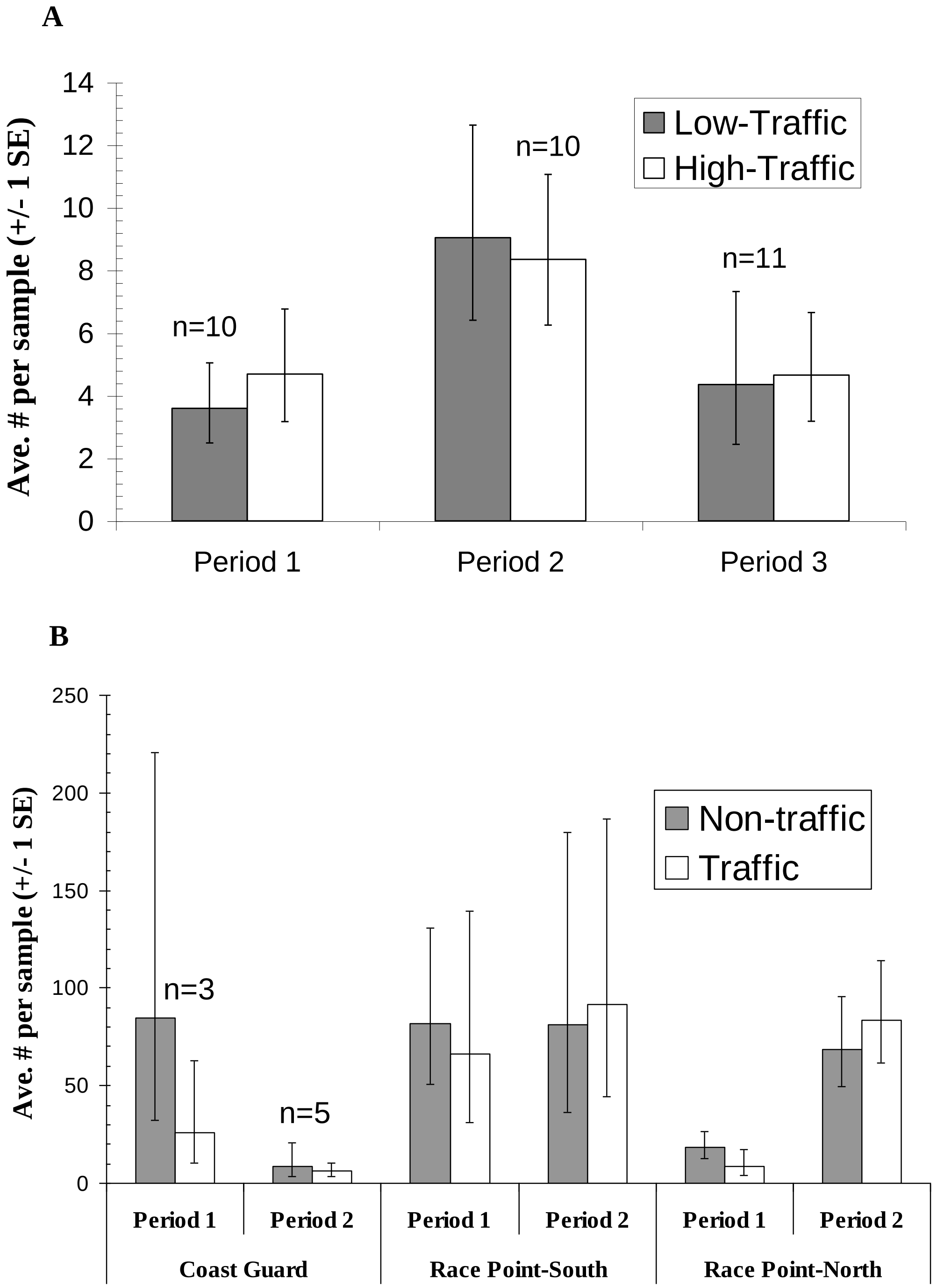


Figure 9. Average wrack/core abundances from a) Sailor's Haven, Fire Island in 1995 (with adjusted means, see **Methods**), and from b) Cape Cod beaches in 2001.

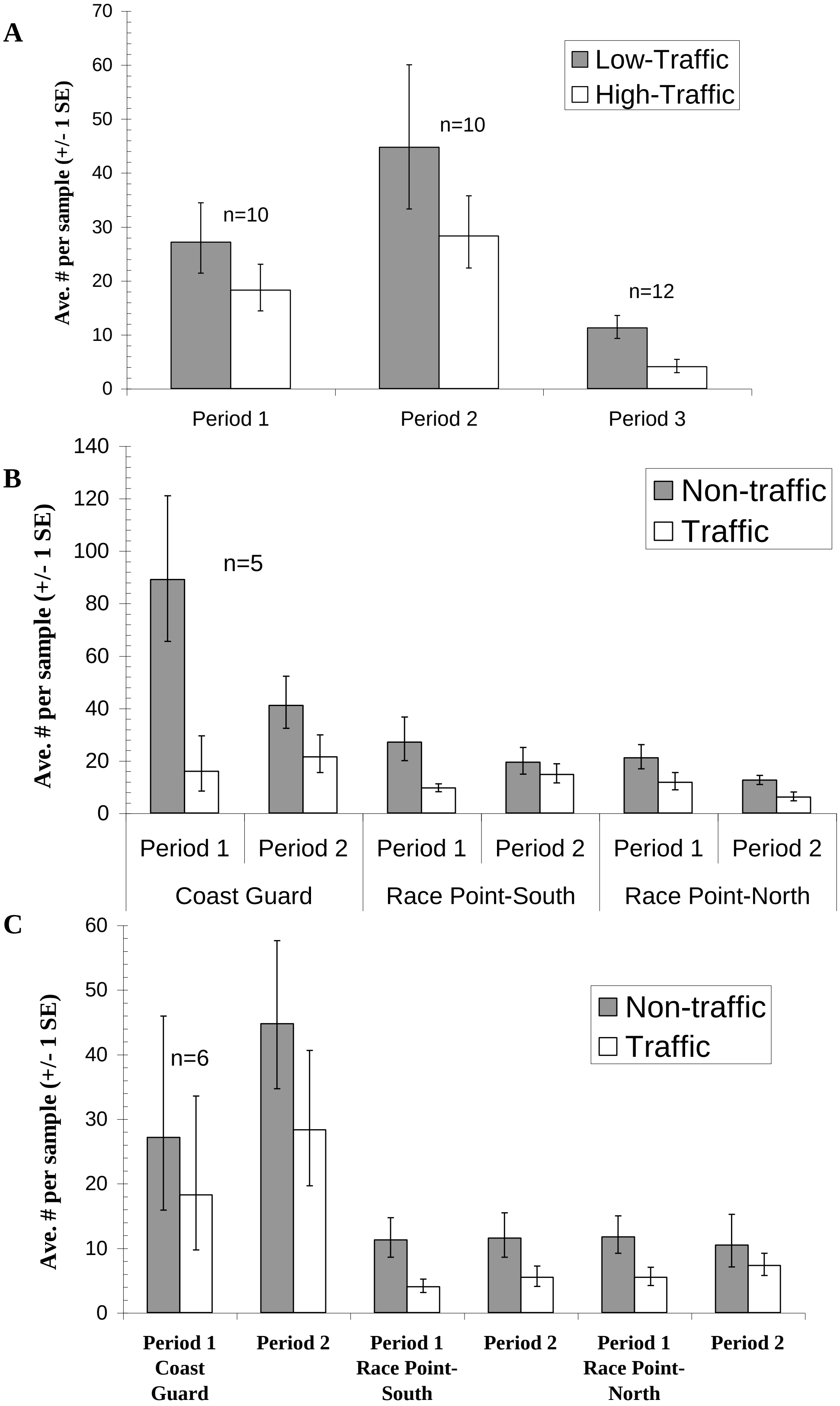


Figure 10. Average pitfall trap abundances from a) Sailor's Haven, Fire Island in 1995, and from Cape Cod beaches in b) 2001 and c) 2002.

Table 5. Average abundances (± 1 SE) per sample of dominant taxa; wrack/core and pitfall trap samples at the three CACO study sites in 2001.

	WRACK		**CORE**		**PITFALL**		**% of**
	NT	**T**	**NT**	**T**	**NT**	**T**	**total**
Oligochaeta: *Enchytraeidae sp.*	34 ±16	37 ±15	15 ±9	16 ±4	0.5 ±0.4	2.6 ±1.7	40.1%
Tethinidae: *Tethina parvula*	3.9 ±1.5	8.3 ±3.6	4.6 ±1.3	5.6 ±1.8	2.3 ±0.7	4.8 ±2.1	11.4%
% larvae/pupae	88%	94%	95%	90%	3%	1%	
% adults	12%	6%	5%	10%	97%	99%	
Hydrophilidae: *Cercyon littoralis*	5.9 ±0.3	2.4 ±0.9	15 ±14	0.9 ±0.5	0.2 ±0.1	0.2 ±0.1	9.2%
% adults	98%	92%	97.5%	58%	100%	100%	
% larvae	2%	8%	2.5%	42%	0	0	
Sphaeroceridae: *Thoracochaeta*	0.2 ±0.2	2.6 ±1.9	0.9 ±0.8	0.1 ±0.1	0.9 ±0.5	0.4 ±0.2	2.0%
brachystoma % adults	0	100%	4%	100%	100%	100%	
% larvae/pupae	100%	0	96%	0	0	0	
Staphylinid: *undetermined spp.*	1.6 ±0.9	0.6 ±0.3	1.0 ±0.4	0.3 ±0.1	0.1 ±0.1	0	1.4%
Anthomyiidae: *Fucellia tergina*	0.4 ±0.1	2.0 ±1.6	0.2 ±0.1	0.9 ±0.5	0.5 ±0.3	0.1 ±0.1	1.6%
% larvae	60%	91%	40%	69%	0	25%	
% adults	30%	1.8%	0	0	100%	75%	
% pupae	10%	7%	60%	31%	0	0	
Anthicidae: *undetermined sp.*	1.1 ±0.4	0.6 ±0.3	0.2 ±0.1	0.04 ±0.04	0.2 ±0.2	0.3 ±0.2	1.0%
Amphipoda: *Talorchestia*	1.5 ±0.9	0.1 ±0.1	1.9 ±1.1	0	21 ±6	0.9 ±0.5	10.3%
longicornis < than 14 mm	98%	100%	93%	0	30%	50%	
mature	2%	0	7%	0	70%	50%	
Talorchestia megalopthalma	0	0	0	0.1 ±0.1	2.0 ±2.0	2.9 ±2.0	2.7%
Lycosidae: *Arctosa littoralis*	0.3 ±0.1	0.1 ±0.1	0	0	1.3 ±0.4	0.2 ±0.1	0.6%
Histeridae: *Hypocaccus fraternus*	0.2 ±0.1	0.1 ±0.1	0.4 ±0.3	0.3 ±0.2	3.1 ±0.7	1.4 ±0.4	2.3%
Ephydridae: *Hecamede albicans*	0	0.5 ±0.2	0.1 ±0.1	0.4 ±0.3	0.3 ±0.2	0.7 ±0.3	0.8%
% adults	0	61.5%	0	10%	100%	100%	
% pupae	0	38.5%	100%	90%	0	0	
Tenebrionidae: *Phaleria testacea*	0.3 ±0.2	0.1 ±0.1	0.6 ±0.3	0.04 ±0.04	0.2 ±0.2	0	0.5%
% larvae	75%	50%	50%	100%	50%	0	
% adults	25%	50%	50%	0	50%	0	
Empididae: *Chersodromia inusitata*	0.04 ±0.04	0.1 ±0.1	0	0	0.2 ±1.0	0.5 ±0.2	0.3%
Others	9.9 ±1.1	7.1 ±1.2	6.9 ±0.9	4.3 ±0.6	9.8 ±1.1	5.6 ±1.2	15.9%
Totals	**1656**	**1720**	**1300**	**800**	**1227**	**612**	**7315**
# of listed species	**12 of 31**	**13 of 37**	**11 of 30**	**11 of 29**	**14 of 50**	**12 of 52**	**79**

Table 6. Average abundances (± 1 SE) per sample of the amphipod *Talorchestia longicornis.*

	Core/site		*Pitfall*	
	NT	***T***	***NT***	***T***
Sailor's Haven				
1995-Period 1	0.52 +/-0.3	0.41 +/-0.3	19.0 +/-5.2	16.0 +/-4.3
1995-Period 2	4.3 +/-2.1	1.7 +/-0.7	55.6 +/-21	40.1 +/-9.2
1995-Period 3	1.9 +/-1.5	1.5 +/-0.9	5.7 +/-2.0	4.1 +/-1.4

	Wrack/core		*Pitfall*	
Coast Guard				
2001-Period1	2.0 +/-4	0.0	58.6 +/-18.1	0.48 +/-0.6
2001-Period 2	1.3 +/-1.4	0.25 +/-0.28	27.8 +/-7.5	2.3 +/-1.6
Race Point South				
2001-Period 1	1.8 +/-2.3	0.43 +/-0.33	27.1 +/-4.7	4.8 +/-0.72
2001-Period 2	0.0	0.0	9.5 +/-0.16	0.15 +/-0.16
Race Point North				
2001-Period 1	0.15 +/-0.16	0.00	0.74 +/-0.45	0.0
2001-Period 2	0.00	0.00	0.64 +/-0.36	0.0

	Pitfall	
Coast Guard		
2002-Period1	17.2 +/-10.3	1.9 +/-0.75
2002-Period 2	20.4 +/-15.4	5.9 +/-5.1
Race Point South		
2002-Period 1	5.2 +/-3.1	0.12 +/-0.13
2002-Period 2	3.6 +/-2.5	0.0
Race Point North		
2002-Period 1	0.81 +/-0.70	0.0
2002-Period 2	0.94 +/-0.43	0.26 +/-0.19

Table 7. Average abundances (± 1 SE) per sample of the lycosid spider *Arctosa littoralis.*

	Core/site		*Pitfall*	
	NT	***T***	***NT***	***T***
Sailor's Haven				
1995-Period 1	0.06 +/-0.06	0.0	0.32 +/-0.15	0.07 +/-0.07
1995-Period 2	0.26 +/-0.29	0.0	0.32 +/-0.15	0.0
1995-Period 3	0.0	0.0	0.41 +/-0.22	0.06 +/-0.06

	Wrack/core		*Pitfall*	
Coast Guard				
2001-Period1	0.82 +/-0.59	0.26 +/-0.29	3.4 +/-1.3	0.43 +/-0.33
2001-Period 2	0.15 +/-0.16	0.25 +/-0.28	0.52 +/-0.26	0.0
Race Point South				
2001-Period 1	0.0	0.15 +/-0.20	1.1 +/-0.4	0.32 +/-0.22
2001-Period 2	0.0	0.0	0.15 +/-0.33	0.0
Race Point North				
2001-Period 1	0.32 +/-0.23	0.0	0.43 +/-0.33	0.32 +/-0.23
2001-Period 2	0.32 +/-0.23	0.0	0.88 +/-0.54	0.0

	Pitfall	
Coast Guard		
2002-Period1	0.0	0.0
2002-Period 2	0.31 +/-0.70	0.44 +/-0.91
Race Point South		
2002-Period 1	0.0	0.0
2002-Period 2	0.23 +/-0.59	0.0
Race Point North		
2002-Period 1	0.13 +/-0.12	0.0
2002-Period 2	0.34 +/-1.0	0.0

Table 8. Average abundances (± 1 SE) per sample of the tethinid fly *Tethina parvula.*

	Core/site		*Pitfall*	
	NT	***T***	***NT***	***T***
Sailor's Haven				
1995-Period 1			0.07 +/-0.08	0.0
1995-Period 2			0.28 +/-0.22	0.54 +/-0.23
1995-Period 3			0.16 +/-0.12	0.06 +/-0.06

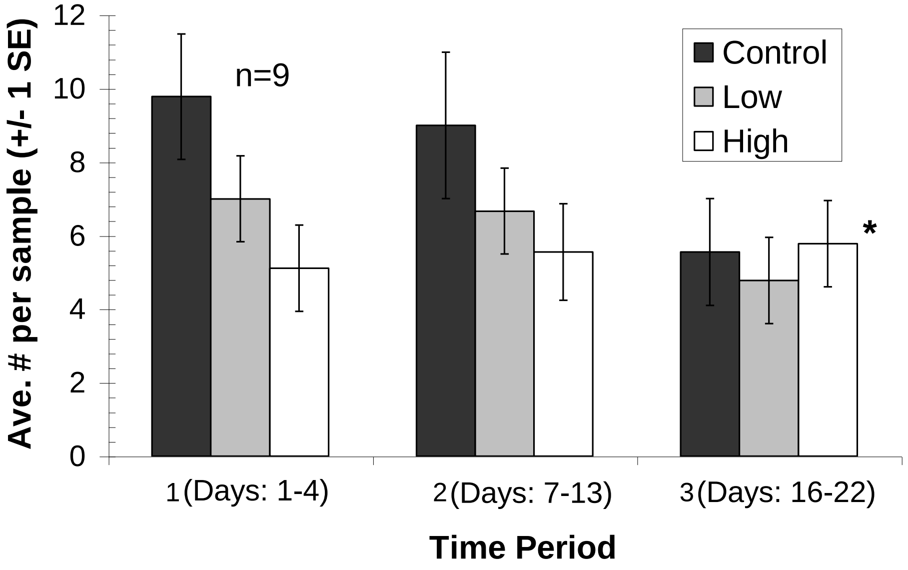
	Wrack/core		*Pitfall*	
Coast Guard				
2001-Period1	2.8 +/-3.2	2.1 +/-0.9	2.7 +/-1.8	2.3 +/-2.8
2001-Period 2	0.82 +/-0.55	0.38 +/-0.45	0.59 +/-0.63	4.4 +/-1.2
Race Point South				
2001-Period 1	5.7 +/-2.5	4.1 +/-4.4	0.64 +/-0.36	1.6 +/-1.3
2001-Period 2	10.0 +/-5.7	16.7 +/-17.2	2.2 +/-1.6	3.5 +/-1.1
Race Point North				
2001-Period 1	1.7 +/-0.8	1.3 +/-1.5	0.78 +/-0.45	1.8 +/-0.83
2001-Period 2	9.6 +/-5.4	7.5 +/-4.4	1.5 +/-0.67	1.2 +/-0.18

	Pitfall	
Coast Guard		
2002-Period1	0.82 +/-0.80	0.51 +/-0.29
2002-Period 2	2.3 +/-0.93	2.4 +/-0.73
Race Point South		
2002-Period 1	0.0	0.12 +/-0.13
2002-Period 2	1.5 +/-0.82	1.6 +/-0.81
Race Point North		
2002-Period 1	0.26 +/-0.19	0.0
2002-Period 2	0.62 +/-0.52	1.1 +/-0.57

Experiment results

Average abundances were 8.1 (± 1.0 SE) in the control bags, 6.1 (± 0.7) in the low-traffic bags, and 5.5 (± 0.7) in the high-traffic bags (Figure 11a), but these treatment differences were only marginally significant (ANOVA: treatment effect, F=2.7, df=2,72, P=0.07). The relative frequencies of the taxa differed among treatments (G=77.3, $P=8.9*10^{-11}$), but these differences were primarily the ecolosion of tethinid fly larvae in period three (which were significantly more abundant in the high-traffic bags ANOVA: treatment, F=5.6, df=2,24, P=0.01), because the relative frequencies without flies formed a non-significant subset (G=15.4). Therefore, the ANOVA was run without the *Tethina* larvae, and treatment was significant (ANOVA: treatment, F=4.2 P=0.02). Larvae of the tenebrionid beetle *Phaleria testacea*, the most abundant species in all three treatments (31% of all individuals), were significantly lower in the bags subjected to traffic (ANOVA: treatment, F=4.8, df=2,72, P=0.01) (Figure 11b). Other abundant species included various microlepidoptera (not common wrack dwellers) and a species of collembola (Entomobryidae). The only environmental variables showing significant differences between treatments were bag volume and % of wrack clumps buried (Table 9).

A. Invertebrate abundances within wrack bags over time



*indicates an abundance of tethinid sp. larvae (23% of sample) found in the high-traffic area during the third period.

B. *Phaleria testacea* (Tenebrionidae) larval abundances within wrack bags over time

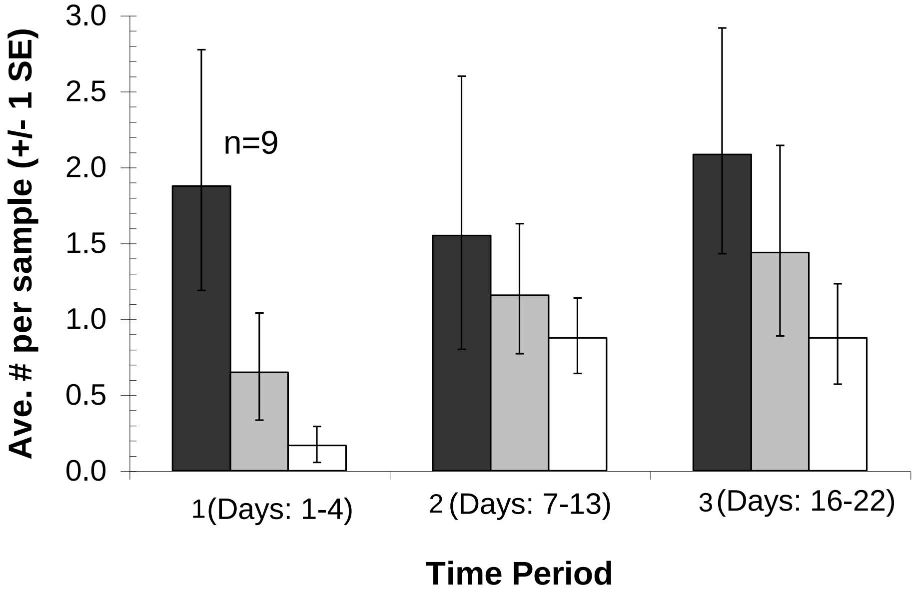


Figure 11. Manipulative study.

Table 9. Environmental variables (means ± 1 SE) measured from high-, low- and control treatment bags in the direct impact study. Days were grouped into three periods, and two-way ANOVAs (treatment*period) were performed.

Variable Measured	**Treatments** Control	Low-traffic	High-traffic	P-value
Bag dimensions (cm^3)	1521 ± 84	920 ± 96	881 ± 90	**<0.001**
Temperature (°C) at the wrack/sand interface	27.2 ± 1.0	27.3 ± 1.0	27.9 ± 1.1	0.88
Relative humidity (%) at the wrack/sand interface	69.3 ± 1.8	70.4 ± 2.5	70.1 ± 2.2	0.94
Temperature (°C) at 10cm depth	23.8 ± 0.5	23.7 ± 0.4	23.9 ± 0.4	0.96
Percentage of wrack clumps fully buried	11.1	40.7	40.7	**0.02**

Discussion

Abundances of beach macroinvertebrates captured in pitfall traps were consistently lower on sandy beaches subjected to off-road vehicle traffic in this study (Figure 10). Although invertebrate abundances in intact or undisturbed wrack clumps did not differ between traffic and non-traffic beaches at our sites, our direct impact experiment showed that traffic can lower wrack invertebrate abundances as well, and in incremental amounts with traffic level (Figure 11). Since both wrack frequency and percent cover were consistently lower on beaches open to off-road vehicles (Figure 8, Tables 2 & 3), driven beaches could be expected to have lower overall abundances of wrack invertebrates in addition to the lower abundances actually seen in pitfall trap samples.

Abundances of common species in traffic samples were consistently lower than in non-traffic areas at all four sample sites, over several years, and using both manipulative and natural experiments. Therefore, our results indicate that ORV traffic lowered the abundances of beach invertebrates on these beaches, even though the level of traffic on Cape Cod is comparatively lower than on other beaches that have found traffic to be a factor in abundances (Schlacher et al., 2008a). The species most strongly affected were amphipods (e.g., *Talorchestia longicornis*) and predators (e.g., the wolf spider *Arctosa littoralis*) that roam widely on the beach. Though the actual mechanism lowering these abundances was not tested, these species could have been affected by vehicle traffic in either a density-mediated (e.g., mortality by crushing) or trait-mediated (e.g., avoidance of vehicles themselves or the beaches disturbed by vehicles) manner. Certain species clearly reacted to off-road vehicles more than others (in both the manipulative and natural experiments), and, therefore, a multi-faceted approach might be needed in studying ORV impacts on beach invertebrates.

Many recent studies have clearly established that wrack removal lowers the diversity and abundance of all beach invertebrates on disturbed sites, including those that do not occur predominantly within wrack (e.g., De la Huz et al., 2005; Dugan et al., 2003; Yaninek, 1980). Our study further demonstrates the importance of wrack beach invertebrate habitat (with higher invertebrate abundances occurring in wrack than on other areas of the beach-Kluft Steinback, 1999), even on high-energy beaches with sparse, ephemeral deposits. Therefore, our study findings also imply that frequency or cover of wrack might be used as an indicator of ORV traffic.

Our results suggest several possible mechanisms for the effects of off-road traffic on invertebrate populations. Even the species burrowing in bare sand on our beaches utilized the wrack in various aspects of survival (e.g., as foraging habitat or cover). Therefore, one mechanism for the lower invertebrate abundances in traffic areas is that traffic lowers the overall amount of the most essential resource (wrack) on these beaches—by crushing, scattering or burying it. Zaremba et al. (1979) found that wrack clumps run over by vehicles were more scattered, shredded, or dispersed than control clumps. Schlacher and Thompson (2007, 2008) documented substantial physical effects of ORV traffic on the upper beach and disturbance of the drift line at a site in Australia. On our driven beaches, this would ultimately result in less wrack available for both surface colonization and sampling. Dry scattered remains of wrack were often seen in our traffic areas, especially at Race Point North, which received the highest level of traffic in a condensed area. We also found that wrack that was run-over was more likely to be flattened in deep tire ruts and buried by wind-blown sand (Table 9).

There are also several reasons why certain species were more affected by ORVs than others. For instance, in the wrack/core samples, which did not show differences between traffic and non-traffic areas, the two most common taxa were tethinid fly larvae/pupae and enchytraeid oligochaetes (comprising 37% of wrack/core abundances combined). Both of these taxa are detritivores, which were highly localized to the moist, fresh wrack at our sites. The abundance of these taxa in high-traffic areas could have resulted from the greater destruction of older wrack by vehicles on high-traffic beaches, because vehicles generally drove on the upper beach. This would have left more of the freshest wrack available for sampling. Higher moisture content recordings were found in the wrack samples taken from high-traffic (Table 2), indicating that the high-traffic samples may have been more favorable habitat for these taxa. It is also possible that rather than being fresher, intact clumps, the wrack sampled in the traffic area might have been temporarily moistened by vehicle impact, because it was compressed in vehicle ruts. Anders and Leatherman (1987) found that sand in vehicle ruts could actually be temporarily moistened, as interstitial water was forced to the surface by compaction. However, under continued disturbance, this wrack would be dried out much faster than undisturbed wrack, as moistened sand is mixed with surface sand and exposed to summer temperatures (Zaremba et al., 1979). Ultimately, this would lead to faster degradation of the wrack habitat.

In the traffic experiment, in which naturally colonized wrack bags were directly run over, the same two taxa, tethinid fly larvae and enchytraeid oligochaetes, again showed a preference for wrack subjected to traffic treatments. For the tethinid fly larvae, the traffic effect was significant, with larvae limited exclusively to wrack bags receiving the highest level of traffic. Oligochaetes were present in extremely low numbers, but showed the same trend. The fact that these two taxa were higher in bags that were run-over further supports the hypothesis that traffic alters the wrack in some way that provided more suitable habitat for these species, at least in the short-term.

Detritivores have been shown to prefer macrophytes that are broken into smaller pieces, moister, and/or buried (Edwards & Heath, 1963). Since Zaremba et al. (1979) found that vehicle impact breaks up organic material, temporarily increasing the surface area and moisture for colonization and decomposition by bacteria, the high-traffic areas in this study may have had wrack that was both more available and more nutritious for detritivores (e.g., Tenore et al., 1982). Since moisture was not measured in the direct impact study, we cannot be certain that moisture was higher in the traffic bags in this experiment, as it was in the comparative study. Nonetheless, run over wrack bags in the traffic experiment did have a higher burial rate than controls, perhaps helping the treatment bags to maintain more moisture than control bags exposed to summer sun. Despite the preference of these taxa for the high-traffic bags, overall abundances and the most dominant species in the colonized wrack bags, the tenebrionid beetle *Phaleria testacea* larvae, were still highest in the control treatments (Figure 11). *Phaleria* larvae were also associated with higher elevations (i.e., control wrack which was usually not buried) and drier wrack, probably due to a greater risk of drowning than adults. Thus, despite the rise in a few detritivores in traffic bags, our direct impact study indicates that ORV traffic will lower wrack overall invertebrate densities in addition to the observed pitfall trap invertebrate densities.

Species that responded negatively to traffic were caught most effectively by pitfall trap samples in the comparative study. Two common pitfall trap species that were less abundant in high-traffic areas were the beach hopper *Talorchestia longicornis* and the wolf spider *Arctosa littoralis* (comprising 38.5% of total pitfall trap abundances). These species, like many others caught in our pitfall traps, were highly mobile invertebrates that wander the beach at night, but that burrow in the back-beach or under decaying wrack diurnally. Our observations were that the talitrid *T. longicornis* spent daylight hours burrowed at (juveniles) or above (adults) the last high-tide line, but left burrows at night to feed on fresh, moist wrack deposits of eelgrass (*Z. marina*) in the intertidal zone. On our study beaches, these back-beach areas received the most vehicle traffic especially during daylight hours, by park regulation. Therefore, vehicles could have directly crushed these soft-bodied arthropods in their shallow supratidal burrows.

Some investigators have reported nocturnally active crustaceans run over while foraging in the intertidal (Wolcott & Wolcott 1984) or killed in their back-beach burrows (Van der Merwe & Van der Merwe, 2001; Schlacher et al., 2007b). Schlacher and Thompson (2007) documented abundant vehicle traffic at the upper portion of Australian beaches near the foredunes, where numerous burrowing species could be affected. Other investigators have found lower abundances of talitrids in areas of human activity (Weslawski et al., 2000a, Veloso et al., 2008) and vehicle traffic (Wheeler, 1979). Barca-Bravo et al. (2008) found increased asymmetry of talitrid amphipods on disturbed beaches, suggesting environmental stress during development. Two alternative possibilities are that these species might have simply avoided the areas disturbed by vehicles or that the physical location of the corridors impeded their nightly migrations.

Pitfall traps were more effective than the wrack/core samples at catching both juvenile and adult *T. longicornis* beach hoppers—at ratios of 5:1 and 40:1 respectively—and the wolf spider *A. littoralis*—at a ratio of 4:1. Because these species are promising indicator species for the effects of off-road vehicles, it is worth discussing their life histories in more detail. The adults of both of these species spend most of the day in moist, supratidal burrows on temperate back-beaches, either in bare sand or under decaying or older wrack. Very small juveniles and immatures, with thinner exoskeletons and higher surface to volume ratios, usually seek shelter closer to or underneath the most recent high-tide wrack, due to their higher risk of desiccation (van Senus & McLachlan, 1985). Wrack cover probably provides substrate stability as well, so that juveniles are not washed out with the tides (Marsden, 1991).

T. longicornis juveniles can be active diurnally as well, moving about the water's edge at high tide, presumably displaced by rising tides. Adults of *T. longiconis* hop all over the beach nocturnally to feed on fresh, soft or yeast-laden wrack. This behavior of feeding on fresh wrack as it washes in has been observed in other *Talorchestia spp.* (Griffiths & Stenton-Dozey, 1981). During the day, adult *Talorchestia* were buried mostly in bare sand, anywhere from 4-20 cm deep, and inland of the wrack (Smallwood, 1903). *A. littoralis*, as one of these amphipod's main predators, can burrow up to 25 cm deep, and also uses a wide range of beach to hunt at night. Both species were easily caught during these migrations in pitfall traps left 1 m landward of wrack deposits for 24 hours. Therefore, pitfall traps are probably the most effective and simplest sampling method for monitoring ORV effects on beaches using similar species.

Previous studies of the effects of beach traffic on erosion and fore front vegetation have shown that traffic can effectively lower dune elevation, alter profile shape, and impair growth of back-beach vegetation. Though such effects were not observed consistently at all four treatment sites, some traffic sites did show expected signs of ORV impacts on beach profiles. Nevertheless, since profile differences were not consistent between high- and low- traffic areas, they cannot explain the consistent differences in invertebrate fauna observed at the four sample sites.

From a management standpoint, these results indicate that the levels of vehicle disturbance at Cape Cod and Fire Island can lower beach invertebrate numbers, but that the current practice of alternating on/off use of beaches is potentially sufficient to sustain sandy beach invertebrate populations within these national seashores. It is important to emphasize that our results apply to beaches with the moderate levels of ORV traffic that currently exist at Cape Cod and Fire Island (Figure 3). Studies of beaches with greater ORV traffic (e.g., Schlacher et al. 2008a) have found considerably more severe effects, with substantial declines in invertebrate activity on heavily disturbed beaches. Therefore, if ORV traffic were to increase, the strategy of alternate opening and closing of beaches to ORV traffic would presumably be less likely to succeed, given the damage to beach faunas that has been documented on other beaches with more traffic.

In our study, the effect of vehicle traffic differed depending on whether the invertebrate species were primarily wrack-inhabitants or were frequently found on open-sand habitats. Wrack inhabitants were equally abundant within intact wrack clumps on beaches both open and closed to off-road vehicles. Therefore, on beaches that are intermittently closed to traffic, new wrack clumps brought in by the tides can be colonized by wrack species, such as tenebrionid beetles, that inhabit older, undisturbed wrack clumps already on these beaches, as well as by other species, such as tethinid flies, that come from new wrack on nearby undisturbed beaches. Damage to wrack clumps by vehicles on beaches with ORV traffic can potentially be limited by setting drive lanes that avoid the wrack line, and/or by providing signage and educational materials to drivers informing them to avoid driving over wrack.

Open-beach species, such as *Talorchestia longicornis* and *Arctosa littoralis,* whose adults burrow in the back-beach and brood their young, were directly impacted by beach traffic, and therefore source populations from undisturbed beaches are important for recolonization. For this reason, proximity of undisturbed beaches to high-traffic beaches is apparently important to sustain populations of these species. In order to set effective guidelines for the timing of beach openings and closures, it is important to understand the rapidity of recolonization from these two sources (undisturbed local wrack clumps and nearby undisturbed beaches). Additional studies suggest that the lunar cycle within the active season sets the timing of recolonization of fresh wrack clumps (Kluft Steinback, 1999). We recommend studies of recolonization by both wrack-dwelling and bare-beach organisms on disturbed beaches after cessation of ORV traffic to determine how much time is needed for beaches to return to pre-disturbance conditions. These studies can provide the information needed to set guidelines for the timing of beach closures.

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