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Hurricane Sandy and engineered response created habitat for a threatened shorebird

Katie M. Walker,[1,†] James D. Fraser,[1] Daniel H. Catlin,[1] Shannon J. Ritter,[1]
Samantha G. Robinson,[1] Henrietta A. Bellman,[1] Audrey DeRose-Wilson,[1,2]
Sarah M. Karpanty,[1] and Steven T. Papa[3]

[1]*Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia 24061 USA*
[2]*Delaware Division of Fish and Wildlife, Delaware Department of Natural Resources and Environmental Control, Smyrna, Delaware 19977 USA*
[3]*Long Island Field Office, U.S. Fish and Wildlife Service, Shirley, New York 11967 USA*

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Abstract. The intensity of Atlantic Ocean hurricanes is predicted to increase, and although disturbance is recognized as a fundamental driver of ecological processes, the benefits of hurricanes to ecological systems are seldom acknowledged. In October 2012, Hurricane Sandy overwashed Fire Island and Westhampton Island, New York. The storm flattened dunes, buried vegetation, and breached the barrier islands in several places. To reduce future overwashing, engineers attempted to stabilize the islands. We studied nest-site selection, suitable habitat, and abundance of a threatened shorebird, the piping plover (*Charadrius melodus*), before and after Hurricane Sandy. Prior to the hurricane, piping plovers selected nest sites ($n = 62$) farther from the ocean ($\bar{x}$ least-cost distance = 82.8 m) and bay ($\bar{x}$ Euclidean distance = 697.7 m; $\bar{x}$ least-cost distance = 24,160.6 m) than would be expected if they were selecting nest sites at random. Following the hurricane, piping plovers selected nest sites ($n = 45$) predominantly in or near storm overwash habitat, which was close to, and had unobstructed walking access to, the ocean ($\bar{x}$ least-cost distance = 123.4 m) and newly created bayside foraging habitats ($\bar{x}$ Euclidean distance = 468.0 m; $\bar{x}$ least-cost distance = 728.9 m). Areas overwashed by the hurricane contained the most suitable piping plover habitat across all new habitat types. Piping plover abundance increased 93% by 2018 from pre-Hurricane Sandy abundances, with most pairs nesting in new habitats. However, only 58% of suitable piping plover habitat was protected from recreational use and few piping plovers used unprotected habitats for nesting. Our results suggest that the ecological benefits of increased storminess may be maximized by coupling coastal stabilization with targeted conservation of storm-created habitats.

Key words: barrier island; conservation; early-successional; habitat change; Hurricane Sandy; piping plover; recreational use; suitable habitat; threatened species.

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† **E-mail:** kmwalker@vt.edu

INTRODUCTION

Sea-level rise has accelerated since 1870 (Church and White 2006), partly due to the expansion of warming oceans (Wong et al. 2014). As hurricane power is positively correlated with sea surface temperatures, an increase in the strength of hurricanes is expected (Emanuel 2005). Some models project nearly double the frequency of category 4 and 5 Atlantic hurricanes by the end of the 21st century compared to late 20th- and early 21st-century frequencies (Bender et al. 2010). Thus, more coastal flooding and erosion are predicted (Wong et al. 2014). While hurricanes and storms can harm (Marsh and Wilkinson 1991, Brown and McLachlan 2002, Sheikh 2005) or induce temporary emigration (Gibson et al. 2018*a*) in organisms, disturbance has long been recognized as a key driver of patterns and processes in natural ecosystems (Turner 2010), and it is unlikely that all hurricane-driven changes are negative.

Barrier islands are narrow, elongate landforms lying parallel to the mainland and separated from the mainland by wetlands, bays, sounds, or estuaries (Oertel 1985, Feagin et al. 2015). They generally have low elevations and are particularly susceptible to hurricane impacts. Barrier islands are resilient yet dynamic systems that move landward as sand is driven by winds, waves, tides, and storm surges (Swift 1975, Schroeder et al. 1979, Sallenger 2000, Hanley et al. 2014, Sopkin et al. 2014). The overwashing process, which transports sand across an island, is largely dependent on ocean shoreline topography relative to oceanic forces (Sallenger 2000), and in extreme cases, overwash-driven sand may bury or uproot vegetation (Schroeder et al. 1979, Hayden et al. 1995, Feagin et al. 2015). Occasionally, in powerful storms, barrier islands breach, creating new channels from ocean to bay (Roelvink et al. 2009). These storm-induced habitat changes can be beneficial to imperiled species that use early-successional island habitats, including seabeach amaranth (*Amaranthus pumilus*, Sellars and Jolls 2007), Northeastern beach tiger beetle (*Cicindela dorsalis dorsalis*, Knisley et al. 1998), and sea turtles (Cheloniidae sp., Garmestani et al. 2000, Mazaris et al. 2006). However, if overwash is not frequent, vegetation may quickly regrow. Vegetation recolonizes through rhizome emergence and seed recruitment from nearby surviving species (Maun 1998, Courtemanche et al. 1999) and persists until overwash or other disturbance occurs, fueling cyclic ecosystem dynamics.

Early-successional barrier island habitats seldom are conserved after their creation due to societal priorities for coastal stabilization projects aimed at protecting human infrastructure (Bulleri and Chapman 2010, Hapke et al. 2013). Prioritizing static conditions in a dynamic ecosystem inhibits landward migration and fuels shoreline erosion. Engineering, such as dune creation, inlet closures, and structural stabilization disrupt processes that barrier islands require to persist and grow (Smith et al. 2008). Anthropogenic modifications prohibit natural coastal responses to storms and sea-level rise, disrupting processes like overwash and sediment transport that maintain shoreline change and island width (Smith et al. 2008, Hapke et al. 2013). Thus, species-specific responses to increased storminess and anthropogenic modifications must be investigated to properly manage coastal wildlife in the face of climate change.

The Atlantic coast piping plover (*Charadrius melodus*) is a shorebird listed as threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1985). The population decline of piping plovers was attributed to habitat loss, recreational land use, and coastal development (Wilcox 1959, Haig and Oring 1985, USFWS 1985, 1996, 2009). Atlantic coast piping plovers nest in small depressions on sparsely vegetated dry sand on barrier islands (Wilcox 1959, Cairns 1982, Cohen et al. 2008), and they reach their highest densities (pairs/hectare) where sand spans the distance from the ocean to the bay shoreline (Cohen et al. 2009). These conditions frequently occur when seas overwash the islands, depositing fresh sand. Suitable piping plover nesting habitat is unlikely to be used in some areas without active management to prevent recreational beach use (Maslo et al. 2018), which may directly or indirectly affect beach-nesting birds (Schlacher and Thompson 2008, Defeo et al. 2009). Thus, the protection of piping plover nesting habitat from off-road vehicle (ORV) and pedestrian beach use is essential for management of the species.

Hurricane Sandy reached the east coast of New Jersey, USA, on 29 October 2012 with sustained winds of 130 km/h (Sopkin et al. 2014). The hurricane was 1770 km in diameter (Halverson and Rabenhorst 2013), and tropical storm-force winds affected most of the U.S. Atlantic coastline (Sopkin et al. 2014). On Fire Island, New York, dunes were eroded by an average of 2 m and a maximum of 5 m (Sopkin et al. 2014). Hurricane Sandy overwashed and breached several locations on Fire Island and Westhampton Island, New York. These geomorphic changes led to coastal engineering by the U.S. Army Corps of Engineers (USACE) to stabilize the islands to protect infrastructure and restore habitat for piping plovers (USFWS 2014). Furthermore, local parks initiated smaller dune-engineering efforts through the placement of snow fencing and Christmas trees, both of which capture blowing sand and thus build dune height. Previous studies have illustrated benefits to the piping plover that follow large-scale disturbance events such as storms (habitat creation; Wilcox 1959, Cohen et al. 2009, Maslo et al. 2019) and floods (habitat creation and demographic success; Hunt et al. 2018). The objectives of this study were to evaluate the effects of natural processes and coastal engineering on a threatened shorebird on two New York barrier islands by (1) modeling piping plover nest-site selection before and after Hurricane Sandy, (2) quantifying piping plover suitable nesting habitat before and after Hurricane Sandy, and (3) estimating the amount of suitable nesting habitat protected from recreational use after the hurricane.

METHODS

Study area

We studied piping plovers on the beaches of two Atlantic coast barrier islands, Fire Island and Westhampton Island, New York. Fire Island is 50 km long and comprises Robert Moses State Park, Fire Island National Seashore, and Smith Point County Park (Fig. 1). Fire Island National Seashore includes Fire Island Lighthouse Beach, Otis Pike Wilderness Area, and encompasses inholdings in the communities from Kismet to Watch Hill (Fig. 1). Fire Island is bordered by Fire Island Inlet in the west, Moriches Inlet in the east, the Atlantic Ocean to the south, and the Great South Bay and Narrow Bay to the north. Cupsogue Beach County Park, located east of Moriches Inlet and south of Moriches Bay on Westhampton Island, is 2.3 km long and was the easternmost portion of our study area (Fig. 1). Both barrier islands contain ocean-front sandy beaches, ephemeral pools, bayside intertidal habitat, low-lying dunes, higher vegetated dunes, and marsh. Across all management units, various levels of recreational ORV and pedestrian use occur throughout the year.

Following Hurricane Sandy, the study area comprised numerous habitat types, both naturally created and engineered (Table 1). Storm overwash consisted of sand that was deposited inland during Hurricane Sandy and included portions of the island where overwashing seas

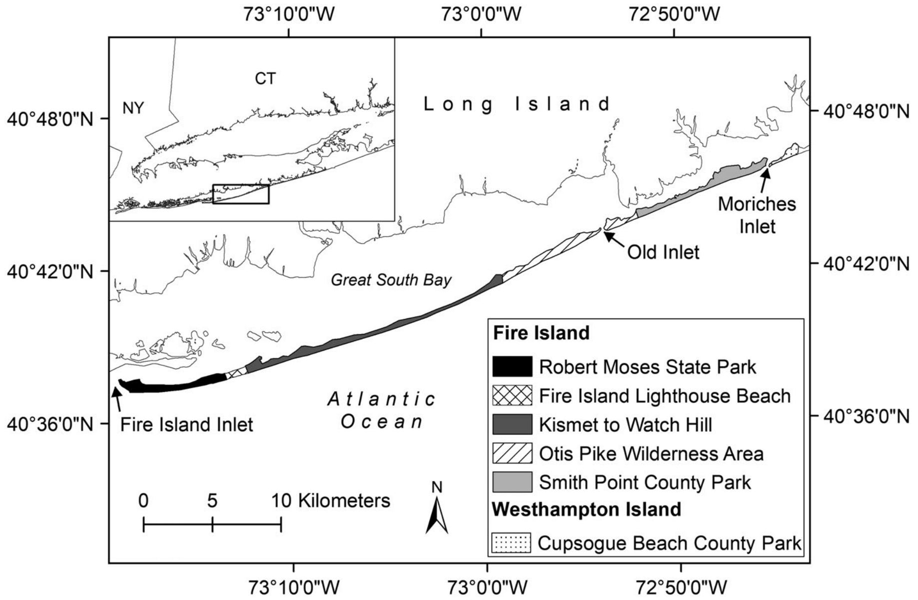

Fig. 1. Fire Island and Westhampton Island, New York. The study area was comprised of Robert Moses State Park, Fire Island Lighthouse Beach, communities stretching from Kismet to Watch Hill, Otis Pike Wilderness Area, Smith Point County Park, and Cupsogue Beach County Park.

reached the bay and formed low-energy, intertidal habitat, and other regions where the storm created expansive overwash fans that did not reach the bay. Two breaches that formed during Hurricane Sandy were promptly filled with dredged sand by the USACE. Another breach, Old Inlet within the Otis Pike Wilderness Area (Fig. 1), remains unfilled. The USACE built dunes and sparsely planted them with American beachgrass (*Ammophila breviligulata*), and local land managers manipulated dunes with snow fencing and Christmas trees to accumulate sand. To mitigate the impact of engineering on breeding piping plovers, the USACE created restoration areas where sand was placed, dunes flattened, or vegetation removed to produce piping plover habitat (USFWS 2014). Portions of beachfront were nourished (widened with dredged sand) before the 2015 piping plover breeding season, and various regions of the islands included dredged sand stockpiles and graded areas (Table 1).

Field methods

*Nest searching.—*Due of the listing status of the species and potential negative interactions with the public, great effort is taken to ensure that all piping plover nests are located and protected early in the nesting cycle. Nest searches were conducted in multiple surveys throughout a breeding season to determine success or failure of nests, to detect new nesting pair arrivals, and to locate renests following failure. Nests were numbered, and locations were plotted or logged to avoid double counting.

We used 2010 data to model pre-Hurricane Sandy nest-site selection because it was the closest pre-Hurricane Sandy year that high-resolution (15-cm pixel) aerial imagery was available. We did not survey our study area until 2013. During 2010, experienced national, state, and county park land managers and trained monitors searched for nests every 1–3 d by walking through potential dry sand nesting habitat and observing piping plover behavior across the whole study area. USFWS Long Island Field Office provided coordinates of 2010 piping plover nest locations. Nest locations within Otis Pike Wilderness Area were collected using Trimble GPS GeoXT, 2005 or 2008 series (Trimble Navigation, Sunnyvale, California, USA), and others were plotted in the field by land managers onto an aerial map (1 in:400 m), using field landmarks and vegetation and were later digitized to obtain coordinates.

We used 2015 data to model post-Hurricane Sandy nest-site selection as it was the first year following the storm that we surveyed piping plovers across the whole study area and obtained 15-cm resolution aerial imagery. Further, the 2015 breeding season was the first in which all proposed post-Hurricane Sandy USACE engineering (USACE 2014) was complete. We searched for nests every 1–3 d by walking transects within potential dry sand nesting habitat and observing piping plover behavior. We searched the entire study area except the

Table 1. Habitat categories used to quantify suitable piping plover habitat on Fire Island and Cupsogue Beach County Park, Westhampton Island, New York, during 2010 and 2015.

Habitat	Definition
Storm overwash	Sand deposited inland during Hurricane Sandy
Restoration area	Piping plover habitat created by the USACE via placement, removal, or devegetation of sand. Elevation changes were made to build nesting habitat (higher elevation) and foraging habitat (ephemeral pools; lower elevation)
Breach fill	Areas that breached during Hurricane Sandy and were filled with dredged sand by the USACE
Planted dune	Engineered dunes planted with American beachgrass (*Ammophila breviligulata*) by the USACE
Manipulated dune	Unplanted dunes created by the USACE and dunes formed by sand accumulation around snow fencing and Christmas trees, which were placed by local land managers
Nourishment	Sand deposited onto the berm and intertidal zone of Smith Point County Park during November 2014–March 2015. Total nourishment was calculated by creating a polygon that encompassed the area between the 2014 and 2015 spring high tide lines
Dredged sand	Stockpiles and graded areas of dredged sand placed by New York State at Robert Moses State Park
Other	Sand that was neither overwashed nor engineered following Hurricane Sandy

developed communities of Fire Island from Kismet to Watch Hill (20 km, Fig. 1) because piping plovers rarely nested in those areas, but National Park Service staff searched those areas for nests using the same search methods used in 2010. During 2015, we collected nest coordinates using a Garmin GPSMAP 78 (Garmin International, Olathe, Kansas, USA; error ± 3.67 m; Garmin International 2013), and during 2016–2018, we used a Trimble GPS Geo7X (Trimble Navigation; error ± 0.95 m, standard error [SE] = 0.13; S. G. Robinson et al., *unpublished manuscript*). During 2015, 77% of nests were found at two eggs (within 3 d of initiation), and 90% were found before full clutch (usually four eggs). We began banding birds in 2013, which enabled identification of individuals at each nest in 2015. Individuals were only assigned to a nest if they were observed incubating that nest.

Pair counts.—During 2010–2012, abundance estimates were based on land managers and monitors searching for pairs in potential dry sand nesting habitat every 1–3 d and midseason breeding censuses conducted from June 1 to 9 (USFWS, *unpublished data*). During 2013–2018, we searched for pairs every 1–3 d using the same methods and banded individuals with field-readable colored leg flags or unique color band combinations. During 2013–2018, the detection probability of banded birds was constant at 0.94 (SE = 0.03; L. F. Hermanns et al., *unpublished data*), estimated with a Barker model (Barker 1997). Because methods and experience of monitors were similar across all years, we believe the detectability of pairs during 2010–2012 was similarly high. Across all years, pair counts were conservative, such that if an unbanded pair had a nest fail where an unbanded pair nested soon after, they would be considered a single pair.

We determined the sex of individuals in-hand using plumage and bill characteristics (Gratto-Trevor et al. 2010) and through behavioral observation (copulation position, territorial flight, courtship displays). During 2013–2017, 21 individuals were sexed by observing copulation. These individuals were further sexed by plumage 1468 times by various observers throughout the breeding seasons. Out of 1468 plumage-based observations, 1437 agreed with copulation-based sexing, resulting in 98% agreement between copulation- and plumage-based sexing. If mate-switching occurred between banded birds, pairs were estimated by counting the number of breeding males because males establish territories and have higher territory fidelity than females (Haig and Oring 1988).

Mapping.—During 2015, we mapped the spring high tide line in the areas most commonly used by piping plovers to approximate the ocean- and bayside limits of useable nesting habitat. Spring tides are semidiurnal tides of increased range that occur twice monthly with new or full moons (Pugh 1987). If a nest was below the spring high tide line, it would likely be flooded during the 34-d laying and incubation period. We mapped the spring high tide lines by foot and ATV using a Trimble GPS Geo7X in May and June of 2015.

Land managers erected symbolic fencing and area-closed signs at the beginning of each breeding season for the protection of piping plover nesting habitat. Symbolic fencing is lightweight string tied between posts to delineate areas where pedestrians and vehicles are prohibited (USFWS 1996); therefore, we considered areas within symbolic fencing to be protected habitat. We were not surveying or mapping the study area in 2010 and therefore were unable to assess the amount of protected habitat in 2010. We mapped pre-nesting symbolic fencing by foot during 2015–2016 using Trimble GPS Geo7X and Trimble GeoExplorer 6000 units.

Analytical methods

We used the maximum-likelihood classification tool in ArcMap 10.2 (Environmental Systems Research Institute, Redlands, California, USA) to classify each 15-cm pixel of 4-band multispectral aerial imagery as dry sand, wet sand, vegetation, or water in imagery from 2010 and 2015 (Axis Geospatial, Easton, Maryland, USA). We used April imagery to ensure that the vegetation stage approximately matched the vegetation that existed when piping plovers returned to the breeding grounds in March and April to select territories. All classifications were clipped to the respective years' spring high tide lines. Because we did not field map in 2010, spring high tides were digitized from imagery taken 1 April 2010 (New York State 2010), when the highest high tide was within 8 cm of the spring tide (NOAA 2009). Although LiDAR was available in 2010 (NOAA 2010), we had no ground reference for the elevation of the spring tide line; therefore, spring high tides were estimated by delineating the wet–dry and wrack lines, and where the tide had washed over ORV tracks. In areas not mapped on foot in 2015, we estimated the spring high tide line by reclassifying LiDAR to digitize the elevation of the field-mapped spring high tide lines.

To compare the characteristics of nest sites, all of which were in classified dry sand, with available piping plover habitat, we compared them with randomly selected points in dry sand (second-order selection; Johnson 1980). The number of random points corresponded to the number of nests in each year and was >50 m away from the nearest random point. We created an ArcGIS-based dataset using eight variables thought to influence piping plover nest-site selection (Table 2, Fig. 2). We created raster layers for each variable and obtained values for nests and random points from those rasters in ArcMap using the Extract Multi Values to Points tool (Table 2).

LiDAR (1-m resolution) was collected in August and April of 2010 and 2015, respectively. We digitized all areas of human development such as roads, buildings, parking lots, and boardwalks and measured the minimum Euclidean distance from each nest and random point to the nearest development. Piping plovers often forage on bayside intertidal areas where invertebrate prey is abundant and they often select nest sites close to those habitats (Loegering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009). Piping plovers also may select nest sites some minimum distance from the ocean to avoid flooding. Thus, we measured the Euclidean distances from every dry sand pixel to both the ocean and bay spring high tide lines. Additionally, we estimated the minimum distance a walking piping plover (i.e., a flightless chick) would traverse to get from any dry sand location to ocean and bay spring high tide lines, such that the path did not pass through a classified pixel of vegetation or water (barriers to chick movement assuming chicks would not pass through a 15-cm^2 area classified as vegetation or water), using the Path Distance tool in ArcMap. We termed this the least-cost distance.

Atlantic coast piping plovers select nest sites in open areas of sparsely vegetated dry sand

Table 2. Summary statistics for candidate variables for logistic regression to determine nest-site selection of piping plovers on Fire Island and Cupsogue Beach County Park, Westhampton Island, New York, before Hurricane Sandy (2010) and after Hurricane Sandy (2015).

	Nest			Random		
Variable	Mean	SE	Range	Mean	SE	Range
2010						
Elevation	2.4	0.1	0.7–4.5	3.0	0.1	0.0–6.0
Distance to development	795.6	99.1	17.7–2460.7	444.7	89.3	6.8–3032.2
Distance to ocean	88.2	18.0	2.2–695.1	30.6	2.9	0.8–96.9
Distance to bay	697.7	92.6	10.1–2644.9	450.3	36.5	49.9–1428.7
Least-cost distance to ocean	82.8	20.7	0.7–794.7	19.7	2.6	0.2–84.3
Least-cost distance to bay	24,160.6	2702.9	11.1–53,042.4	18,147.0	2054.0	93.7–53,485.2
Dry sand within 500 m (ha)	9.8	0.7	3.0–22.2	7.3	0.5	1.6–20.0
Backshore width	77.8	6.5	17.7–197.3	44.2	4.7	6.1–197.9
2015						
Elevation	2.2	0.2	0.5–7.2	2.8	0.2	0.5–7.4
Distance to development	1444.4	127.7	50.4–3113.6	912.2	133.3	2.2–2787.7
Distance to ocean	115.1	15.0	−7.4 to 386.4	80.1	11.8	1.5–644.2
Distance to bay	468.0	75.4	6.8–1786.6	503.1	62.3	9.9–2025.3
Least-cost distance to ocean	123.4	16.8	−7.4 to 455.7	94.8	23.0	1.5–806.9
Least-cost distance to bay	728.9	120.9	7.1–3948.1	3870.4	566.0	10.0–12,084.8
Dry sand within 500 m (ha)	16.2	0.9	6.8–28.2	11.2	0.9	1.3–29.9
Backshore width	177.1	15.6	40.5–419.4	80.1	17.6	11.3–369.4

Notes: SE, standard error. Values are in meters unless otherwise stated. Nests with negative values were below the spring high tide line.

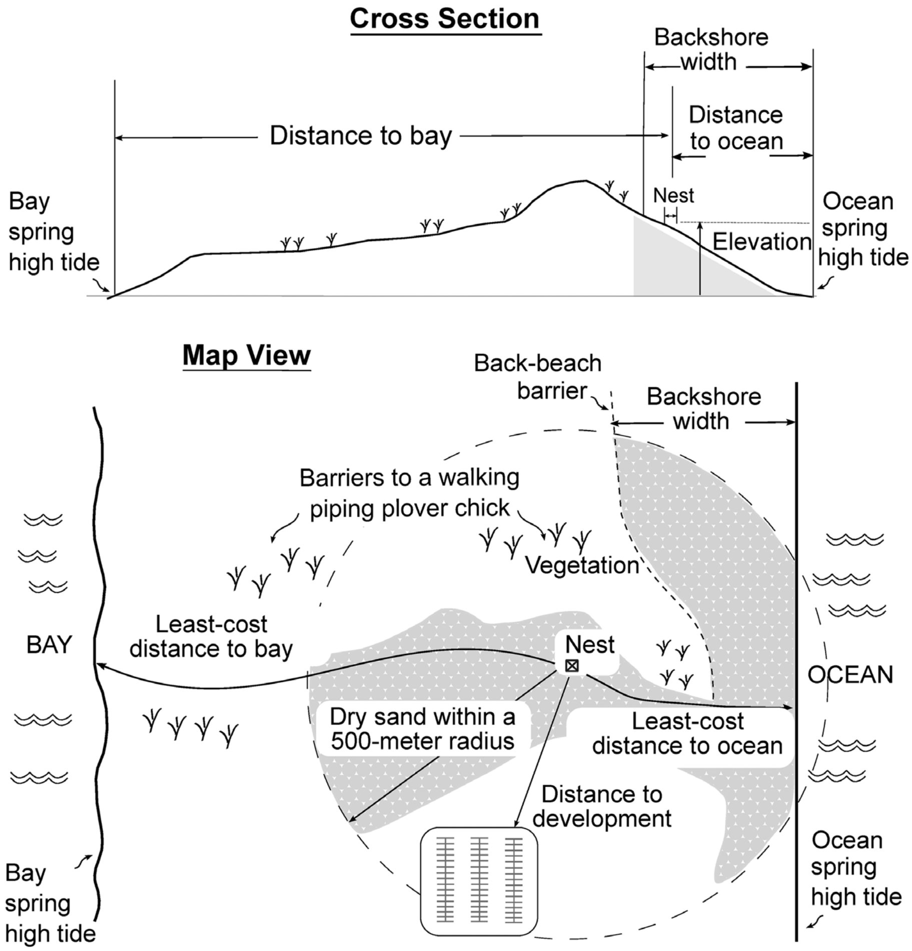

Fig. 2. Cross section and overhead diagram illustrating the eight candidate variables used for logistic regression analysis to determine piping plover nest-site selection on Fire Island and Cupsogue Beach County Park, Westhampton Island, New York, before Hurricane Sandy and after Hurricane Sandy.

(Cohen et al. 2008), enhancing their ability to see approaching predators while remaining cryptic (Anteau et al. 2012, Wiltermuth et al. 2015) and increasing the area that a predator must search to detect them (Fraser and Catlin 2019). Additionally, nest-site selection may require balancing the perils of predation and tidal flooding (Burger 1987). To obtain an index of open dry sand near nests and random points, we created a 500-m buffer around each point using the R (R Development Core Team 2016) package raster (Hijmans 2017) to count hectares of dry sand within each buffer. A wide backshore enables piping plovers to be far from the ocean (reducing probability of flooding) and far from dunes and vegetation near the island's center (reducing probability of predation by a terrestrial predator). We defined backshore width as the distance perpendicular from the shoreline to the nearest back-beach barrier (Fig. 2). We defined the back-beach barrier as a feature that would block piping plover chick movement, including steep dunes (approximately 3–4 m), vegetation, water, or development. We digitized the back-beach barriers for each year using respective imagery and LiDAR. We created 10-m wide polygons that were perpendicular to the shoreline in ArcMap using the Create Fishnet tool. The length of those polygons was the backshore width for all underlying pixels.

We standardized our dataset prior to analyses and checked for collinearity. When any two variables had a correlation coefficient $|r| > 0.7$, we retained only one to avoid issues of multicollinearity (Dormann et al. 2013). In both years, there was little vegetation between nest sites and the ocean spring high tide line. Therefore, distance to ocean and least-cost distance to ocean were highly correlated ($r = 0.99$). Backshore width and dry sand within a 500 m radius also were correlated ($r = 0.79$). We retained least-cost distance to ocean and backshore width as variables because we believed them to be the most biologically relevant to piping plover nest-site selection. The 500 m radii frequently included fragmented dry sand pockets behind primary dunes, whereas backshore widths encompassed a contiguous area of dry sand surrounding nest sites and were therefore a more appropriate predictor of nest-site selection.

Male piping plovers create numerous scrapes within their territory, and females make the final nest-site selection by laying the first egg (Cairns 1982). If the first nest is unsuccessful, the individuals, together or apart, may renest (Cairns 1982, Haig and Oring 1988). To explore the effect of individuals nesting more than once in the 2015 season ($n = 9$), we ran a mixed effects logistic regression with 2015 data, testing for the random effect of female, with the R (R Development Core Team 2016) package lme4 (Bates et al. 2015). Including female as a random effect in the model, Akaike's information criterion (AIC) value was 99.4, compared to an AIC of 97.36 with the random effect removed. Therefore, we considered renest locations of females to be independent of the locations of their first nests and considered the habitat attributes of all nests to be independent in both years.

We conducted logistic regression in R (R Development Core Team 2016) to evaluate the potential influence of geomorphic variables on the suitability of any 15-cm dry sand pixel as piping plover nesting habitat (1 = suitable, 0 = unsuitable). We developed a global model consisting of six non-correlated variables and included an interaction of year with each variable. Variables were considered influential if their 95% confidence intervals did not overlap zero. We assessed the fit of the full model with a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989). We measured the predictive power of our model using McFadden's pseudo-R^2 (values between 0.2 and 0.4 represent excellent model fit; McFadden 1979) and tested for overdispersion.

Suitability maps

We created standardized rasters of retained, uncorrelated variables. Using Raster Calculator in ArcMap, we generated suitability rasters for 2010 and 2015, with a value (0–1) assigned to each dry sand pixel. The 2010 suitable habitat map was produced using the 2010 intercept, beta estimates, and aerial imagery. The 2015 suitable habitat map was created under the assumption that habitat characteristics found suitable in 2010 did not become unsuitable during 2015, but that some habitat may have been more preferable than others following the hurricane. To account for piping plover nest-site selection and nesting habitat suitability pre- and post-Hurricane Sandy, we first created a suitability map using the 2010 intercept and beta estimates on the 2015 imagery. We separately applied the 2015 intercept and beta estimates on the 2015 imagery. To derive the 2015 intercept, we added the 2010 intercept to the 2015 beta estimate. We added each variable's main effect to the interactive effect with 2015 to derive 2015 beta estimates. For each suitability map, we used a suitability threshold of 0.5, at which the model had the highest percentage of nest and random points correctly classified. All dry sand pixels within each suitability map were then classed as suitable ($P \geq 0.5$) or unsuitable ($P < 0.5$). We merged the two suitability maps created using the 2015 imagery into one, such that all suitable pixels, whether geomorphically suitable based on 2010 or 2015 nest-site selection, were combined and weighted equally as 2015 suitable piping plover habitat.

We quantified dry sand and suitable pixels by habitat category (storm overwash, restoration area, breach fill, planted dune, manipulated dune, nourishment, dredged sand, and other; Table 1). Dry sand that was neither overwashed nor engineered following the storm was categorized as other. The USACE provided polygons delineating restoration areas (USACE 2014), and we generated polygons for all additional habitat categories. Some overwashes and engineered habitat were manipulated by engineering following their formation. For example, planted dunes were built atop previously overwashed sand, and manipulated dunes were constructed over breach fills. We considered engineered and natural habitats to be distinct throughout our analysis; therefore, for our estimates, we categorized dry and suitable sand into the most recent habitat category, and no dry sand pixel was counted twice.

Protected areas

Before territory selection and nesting began (early April), land managers in our study area closed some areas to ORV and human use using symbolic fencing (USFWS 1996). Symbolically fenced areas generally occurred on the backshore and at inlets of the islands, allowing for vehicle and pedestrian traffic between protected nesting habitat and the ocean intertidal zone. Beaches remain open to ORV use throughout the incubation period, but ORV use is generally prohibited after chicks hatch. We estimated the amount of protected suitable habitat early in the 2015 breeding season when piping plovers were beginning to set up territories. In areas not fully bordered by symbolic fencing, natural barriers (e.g., large primary dunes, dense vegetation) were considered the boundary from human use because they precluded easy access. Polygons were created based on field-mapped symbolic fencing and natural barriers. We clipped 2015 suitable habitat to those polygons using the Clip tool in ArcMap. To explore the effectiveness of protected areas, we compared the proportion of piping plover nests initiated within protected areas to the expected proportion, given the area, if piping plovers nested randomly across available dry sand using a chi-square test.

RESULTS

We modeled piping plover nesting habitat using a total of 107 nest locations and 107 random points from 2010 ($n = 62$ nests) to 2015 ($n = 45$ nests). Under the selected suitability threshold, 78% of nests were correctly classified and 77% of all points were correctly classified. Our model fit the data well ($\chi^2 = 11.57$, df = 8, $P = 0.17$), predicted well (McFadden's pseudo-$R^2 = 0.31$), and was not overdispersed ($\hat{c} = 1.03$).

During 2010, least-cost distance to ocean had the highest β estimate, indicating it was the strongest predictor of nest-site selection, with piping plovers nesting farther (least-cost distance) from the ocean than expected at random (Tables 2, 3). Piping plover nest-site selection was positively associated with distance to bay and least-cost distance to bay and was negatively associated with elevation, but this result was not statistically significant (Table 3). During 2015, piping plovers selected nest sites at closer least-cost distances to the bay and ocean than during 2010 (Table 3).

Dry sand increased by 47% between 2010 and 2015 (Table 4), including 72 ha created by Hurricane Sandy overwashes and 63 ha that was engineered (Table 4). Suitable habitat increased 1.5-fold between 2010 and 2015 (Fig. 3, Table 4). Hurricane Sandy and subsequent engineering produced 119 ha of suitable nesting habitat, 67 ha generated through Hurricane Sandy overwash, and 52 ha produced by engineering (Table 4). Piping plover abundance decreased by

Table 3. Standardized estimates (β), standard errors (SE), and lower (LCL) and upper 95% confidence intervals (UCL) for variables of the global logistic regression model comparing nest sites selected by piping plovers to random points on Fire Island and Cupsogue Beach County Park, Westhampton Island, New York, before Hurricane Sandy (2010) and after Hurricane Sandy (2015).

Variable	β	SE	UCL	LCL
Intercept†	1.26	0.51	0.27	2.26
2015	−11.98	4.99	−21.76	−2.21
Least-cost distance to ocean	4.03	1.41	1.27	6.79
Least-cost distance to bay	0.55	0.27	0.01	1.08
Distance to bay	0.77	0.30	0.17	1.36
Distance to development	−0.12	0.34	−0.79	0.54
Backshore width	0.48	0.64	−0.77	1.73
Elevation	−0.54	0.31	−1.15	0.07
2015 × Least-cost distance to ocean‡	−4.34	1.43	−7.15	−1.53
2015 × Least-cost distance to bay	−16.10	7.24	−30.29	−1.91
2015 × Distance to bay	−0.80	0.52	−1.82	0.22
2015 × Distance to development	−0.03	0.47	−0.95	0.89
2015 × Backshore width	0.43	0.72	−0.98	1.85
2015 × Elevation	0.81	0.44	−0.05	1.67

Note: Least-cost distances were measured as the shortest distance a piping plover could walk between the nest and the ocean or bay without passing through vegetation or water.

† 2010 intercept.

‡ The × indicates an interaction with the main effect.

Table 4. Dry sand (ha) and suitable piping plover habitat (ha and percentage) created by storm overwash, engineering, and other methods on Fire Island and Cupsogue Beach County Park, Westhampton Island, New York, before Hurricane Sandy (2010) and after Hurricane Sandy (2015).

	2010			2015		
Habitat	Dry sand (ha)	Suitable (ha)	Suitable (%)	Dry sand (ha)	Suitable (ha)	Suitable (%)
Storm overwash	0	0	–	72	67	93
Restoration area	0	0	–	15	7	47
Breach fill	0	0	–	3	3	100
Planted dune	0	0	–	7	7	100
Manipulated dune	0	0	–	10	10	100
Nourishment	0	0	–	12	10	83
Dredged sand	0	0	–	16	15	94
Other†	304	100	33	312	131	42
Total	304	100	33	447	250	56

Notes: Estimates rounded to the nearest hectare. Dashes indicate not applicable. Dry sand was calculated for each year by classifying high-resolution multispectral aerial imagery. Suitability was determined using logistic regression comparing used nest sites with randomly selected dry sand sites in both years.

† Sand that was neither overwashed during Hurricane Sandy nor engineered following the storm.

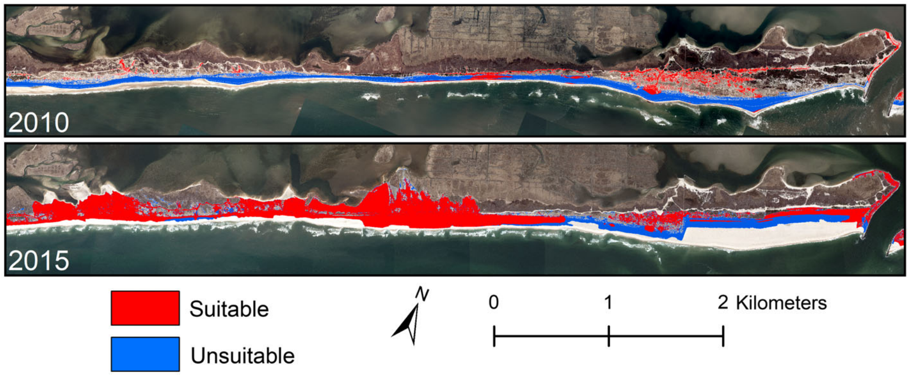

Fig. 3. Suitable and unsuitable piping plover habitat on Smith Point County Park, Fire Island, New York, before Hurricane Sandy (2010) and after Hurricane Sandy (2015) based on logistic regression modeling of nest-site selection. Classified dry sand above the spring high tide line was modeled for suitability.

24% between 2010 and 2011 and remained low during 2012 (Fig. 4). However, following Hurricane Sandy, breeding pairs increased by 93% between 2012 and 2018 (Figs. 4, 5).

Fifty-eight percent of suitable habitat was protected from recreational use during 2015 (Fig. 6). All suitable sand within restoration areas was protected. Suitable storm overwash habitat was 81% protected, and suitable breach fill habitat was 93% protected. Planted and manipulated dunes were 99% and 75% protected, respectively. Across all engineered habitats, nourishment had the least suitable habitat protected (51%, Fig. 6). However, across all habitats, other was the least protected (39%, Fig. 6). Six of 151 nests (4%) were initiated in unprotected areas during 2015–2017 compared to an expected 83 if nests had been placed randomly with respect to protection (chi-square, $\chi^2 = 158.85$, df = 1, $P < 0.001$).

DISCUSSION

Piping plovers selected for hurricane-created habitats following Hurricane Sandy, indicating preference for those areas and highlighting the importance of storm-induced disturbance to this early-successional species. During 2010, when most available sand was in narrow beaches

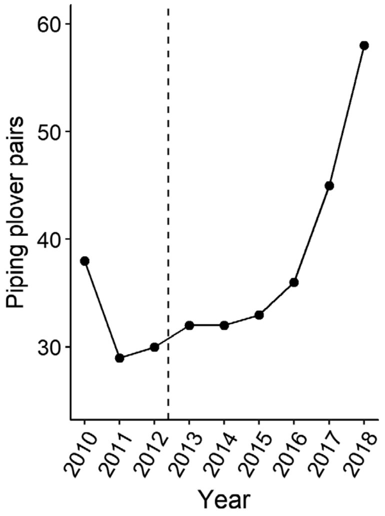

Fig. 4. Breeding piping plover pairs on Fire Island and Cupsogue Beach County Park, Westhampton Island, New York, 2010–2018. Pair counts during 2010–2012 were estimated using breeding census data of unbanded pairs (USFWS, *unpublished data*). Pair counts during 2013–2018 were estimated using banded individuals. Hurricane Sandy (October 2012) is marked as a dashed vertical line.

adjacent to the ocean, piping plovers selected nest sites farther from the ocean than expected at random, which likely reduced the probability of tidal flooding of nests. These results are consistent with nest-site selection in New Jersey, where piping plovers selected nest sites closer to dunes and vegetation and farther from the ocean along a 200-m wide beach abutted by primary dunes and backed by development (Burger 1987). During 2010, nests were farther than expected at random from the bay, measured as a bird would fly (distance to bay) and as a bird would walk on unvegetated sand (least-cost distance to bay). This pattern resulted from piping plovers spreading themselves out along the ocean, so many nests were in the middle (east to west) of the islands, often where the islands were widest (north to south) and where bay access was not immediately accessible to walking broods. There was some evidence to suggest that piping plovers selected lower elevation sand than what was available at random during 2010, probably because much of the higher elevation sand was in dunes where topography and vegetation can obscure approaching predators, such as red foxes (*Vulpes vulpes*; Cavallini and Lovari 1994).

During 2015, piping plover nest sites shifted to Hurricane Sandy overwashes, which provided proximate, unimpeded access to bay and ocean shorelines. Nest-site selection was most strongly associated with a brood's ability to access bay-side foraging, where arthropod prey is plentiful (Loegering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009). While piping plover nest-site selection studies have commonly investigated microhabitat during the nesting phase (Burger 1987, Prindiville Gaines and Ryan 1988, Flemming et al. 1992, Cohen et al. 2008, Anteau et al. 2012), our results highlight a link in habitat selection between the nesting and brooding phases of the breeding cycle on a course scale. Piping plovers may have selected sites to optimize both nest survival and chick survival because broods did not have to travel far to reach food resources along the bay, where previous studies have shown high invertebrate prey densities, leading to faster piping plover chick growth and higher survival relative to other foraging habitats (Loegering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009). In this study, we only quantified suitable nesting habitat; however, bay intertidal foraging habitat increased from approximately 16.14 km of shoreline during 2010 to 19.69 km during 2015, 2.06 km of which was produced by Hurricane Sandy overwash. Indeed, the formation of intertidal habitat benefits many shorebirds, which are impacted by diminishing foraging habitat along migratory routes (Galbraith et al. 2002). We observed twenty-five species of migratory shorebirds, including threatened red knots (*Calidris canutus*), foraging within bay intertidal zones of our study area during 2014–2016 (A. M. Carey et al., *unpublished data*), suggesting that early-successional overwash habitats may benefit migratory, in addition to breeding, shorebirds.

Overwash also may produce foraging habitat in other ways. On Assateague Island, Maryland, managers cut notches through a dune to facilitate overwash, which benefitted piping plovers by creating low-elevation foraging pools (Schupp et al. 2013). In our study, ephemeral pools developed in some overwash fans and were occasionally used as foraging habitat by adults and broods. A previous study encompassing our study area found

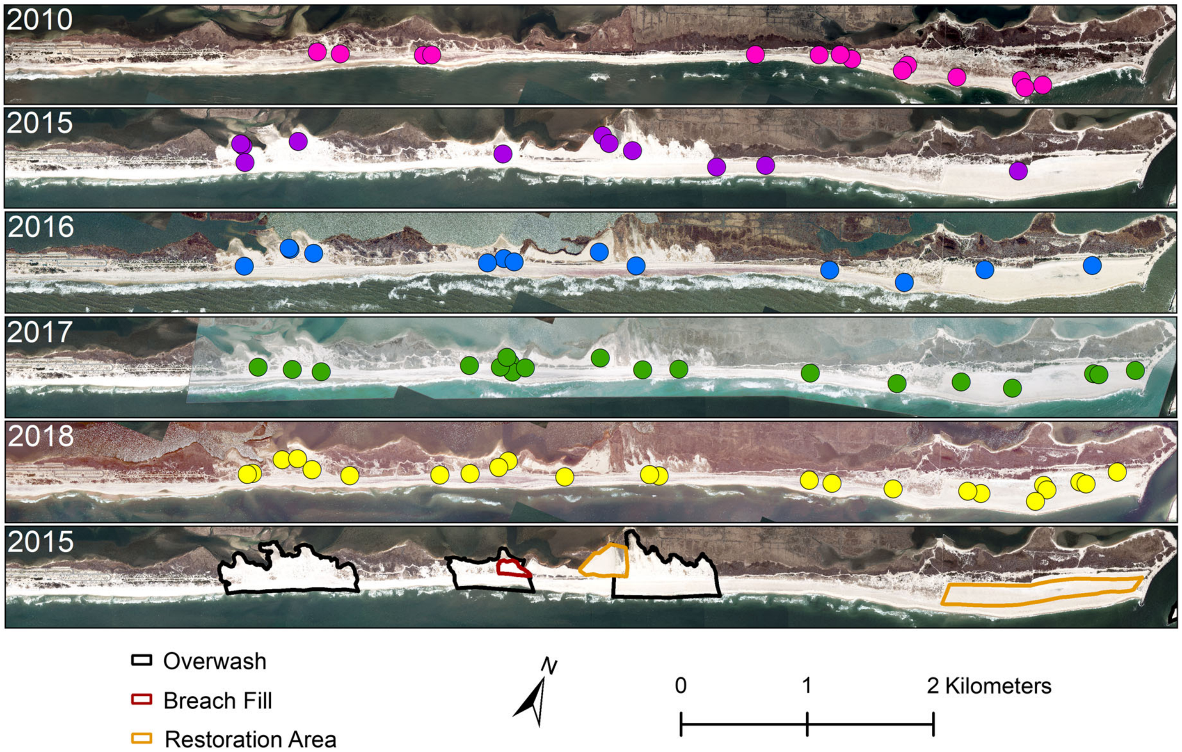

Fig. 5. Smith Point County Park, Fire Island, piping plover pair locations during 2010 and 2015–2018, illustrating the shift in piping plover nest-site selection from habitat farther from the ocean and the bay during 2010, to ocean-to-bay storm-created overwashes and USACE-created habitat during 2015 onward. Outlines of Hurricane Sandy overwashes, breach fills, and restoration areas are shown above 2015 imagery.

that broods preferred ephemeral pools to ocean intertidal, wrack, backshore, and dune habitats (Elias et al. 2000); therefore, it is likely that ephemeral pools provided an important foraging habitat in pre-Hurricane Sandy years when bayside habitat was not available. Being transient in nature, these pools are difficult to quantify and predict as they fluctuate based on season, rainfall, and island morphology. If feasible in future studies, it would be beneficial to investigate the influence of low-elevation ephemeral pools on piping plover nest-site selection, especially where bayside habitat is not available.

The amount of suitable piping plover nesting habitat on Fire and Westhampton Islands, New York, increased following Hurricane Sandy. Our model assessed selection two years prior to the storm and three years after because we were limited by nest data and imagery during 2011, 2013, and 2014. We believe two years before the storm was an appropriate sample of pre-hurricane conditions because there were no major overwashing events on the islands between 2010 and Hurricane Sandy. Hurricane Irene hit Fire Island in August 2011 and impacted the island with steady winds and moderate wave heights; however, the storm transferred sand from the foreshore to the upper beach and near-dune regions, resulting in a beachfront elevation shift rather than dune overwash (Brenner et al. 2018). Indeed, our post-Hurricane Sandy estimates may underestimate the amount of suitable habitat created by the storm because overwashes were manipulated by engineering between 2012 and 2015 and vegetative succession occurred. Unlike breaching, which may eliminate root systems, overwashing often buries plants, allowing their persistence and reemergence of rhizomes (Schroeder et al. 1979). This process, however, coupled with seed recruitment from nearby plants (Courtemanche et al. 1999), requires time. Vegetative succession and wind and wave

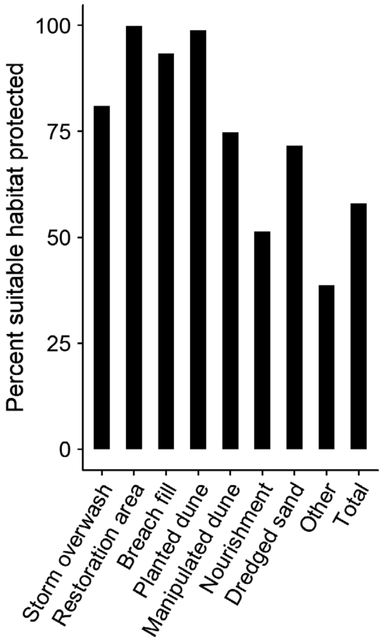

Fig. 6. Percent suitable piping plover habitat protected from recreational use on Fire Island and Cupsogue Beach County Park, Westhampton Island, New York, during 2015. Protected areas were regions closed to human use by symbolic fencing erected by land managers at the beginning of the piping plover breeding season.

dynamics would have affected our study area between Hurricane Sandy and 2015, but we do not believe this considerably affected our estimates of suitable nesting habitat. Following Hurricane Sandy, piping plover habitat also increased along the New Jersey coast but New Jersey piping plovers predominantly nested in pre-storm habitat in the three seasons following the storm (Maslo et al. 2019). These results vary from ours and illustrate that piping plover response to storm-created habitat varies by system and may be largely due to the condition of pre-storm habitat and the degree of storm-induced change.

Piping plover colonization of new habitat was slow in the years following Hurricane Sandy. This delay was consistent with lags in other piping plover populations following the creation of habitat by storms (Wilcox 1959, Cohen et al. 2009, Maslo et al. 2019) and engineering (Catlin et al. 2011). Although an individual's discovery of new habitat may take time, colonization also may be limited by the number of second-year birds (first-time breeders) returning (Catlin et al. 2015). Cohen et al. (2006) estimated that New York piping plovers need to produce about 1.25 fledglings/pair to balance normal mortality when at carrying capacity. However, New York state reproductive output was only 0.72, 0.71, and 1.30 fledglings/pair during 2012, 2013, and 2014, respectively (USFWS 2016). State-wide productivity increased to 1.52 and 1.72 fledglings/pair during 2015 and 2016, respectively (USFWS 2016), contributing to the increased abundance in our study area during 2016–2018 (Fig. 4). Piping plovers continued to colonize Hurricane Sandy-created habitat during 2016–2018, and we expect that if reproductive output and survival remain high, piping plover abundance will continue to grow in response to the increase in suitable habitat until it reaches carrying capacity.

Similar to most Atlantic coast barrier islands, our study area is a heavily modified system where anthropogenic pressures for stabilization and storm protection drive management practices. Following Hurricane Sandy, engineered habitats with the most suitable sand included restoration areas, breach fills, planted dunes, and manipulated dunes. Great Gun restoration area, a site in the easternmost portion of Smith Point County Park, experienced a seven-pair increase between 2015 and 2018 (Fig. 5). This trend is likely due to increasing pair densities in and near overwashes, constraining younger birds to territories in habitats without bayside access for broods. USACE dunes were built above overwashed areas to reduce future overwash, and manipulated dunes often were built along planted dune edges. Due to their location, these dunes provided suitable habitat with access to both ocean and bay foraging habitats. Following the construction of artificial dunes along the Florida Atlantic coast, Martin et al. (2017) found that state-threatened gopher tortoises quickly occupied the man-made features and tortoise densities rose higher in man-made dunes compared to natural. In that system, dune construction may therefore prove to be a valuable management strategy to combat tortoise habitat loss (Martin et al. 2017). Despite the suitability of some engineered dunes in our system, dune development should not be considered a management strategy for sustaining breeding piping plovers, especially because the construction of most dunes in our system required eliminating overwash habitat. All habitats in our study area have become increasingly vegetated following Hurricane Sandy and subsequent engineering, and there has been neither large-scale vegetation removal nor a major disturbance event to restore early-successional habitats.

In our system, suitable habitat may be only as good as the measures enacted to protect the piping plovers that use it. Protection of suitable habitat is critical to the conservation of early-successional coastal species, especially where anthropogenic pressures are high (Maslo et al. 2011, 2018, 2019, DeRose-Wilson et al. 2018). Indeed, the benefits of naturally created habitats to piping plovers may be completely unexploited if they are not prioritized and protected by land managers (Maslo et al. 2019). We show that forty-two percent of post-Hurricane Sandy suitable piping plover habitat was open to human use and was avoided by piping plovers. Many unprotected areas had frequent ORV traffic, boaters landing on the shore, and pedestrian use. Pedestrian and ORV use can alter invertebrate communities (Schlacher et al. 2008, 2016) and disturb nesting and foraging birds directly (e.g., moving vehicles, pedestrians) and indirectly (tire ruts; Schlacher and Thompson 2008; Fig. 7). In our study area, tire ruts predate piping plovers' arrival on the islands, and beaches are driven on daily during March–May when birds are establishing territories. Piping plovers cannot successfully defend territories, attract mates, and select nest sites in areas where nesting substrate has

Fig. 7. Photograph of Great Gun Beach, Smith Point County Park, New York, on 3 May 2018 illustrating the difference in substrate between areas open for recreational use and driving and those behind symbolic fencing (right) that prohibits human use.

been destroyed, disturbance is constant, or nests may be run over. ORV use may limit available habitat for beach-obligate species; thus, protection from ORV use may increase the carrying capacity for these species. Williams et al. (2004) found that one year following the ban of ORVs on South African beaches, the number of near-threatened African black oystercatcher (*Haematopus moquini*) breeding pairs nearly doubled. In the absence of ORVs in the same study area, endangered Damara terns (*Sternula balaenarum*) increased breeding productivity (Williams et al. 2004). Maslo et al. (2018) simulated a scenario where piping plover habitat along the New Jersey coast was entirely protected from recreational use and predicted a 2.6-fold increase in suitable habitat. Conversely, under an unprotected scenario (where no human disturbance protections existed), only a fraction of suitable habitat remained (Maslo et al. 2018). Further, human disturbance is negatively associated with body condition and survival in nonbreeding piping plovers (Gibson et al. 2018*b*) and is negatively associated with chick survival in our system (DeRose-Wilson et al. 2018). We underline the importance of protecting geomorphically suitable habitat from ORV use before the breeding season begins so that substrate remains intact for nest-laying and breeding grounds remain undisturbed throughout nesting and brooding phases.

In addition to piping plovers, we observed least terns (*Sternula antillarum*), common terns (*Sterna hirundo*), American oystercatchers (*Haematopus palliatus*), willets (*Tringa semipalmata*), herring gulls (*Larus argentatus*), and killdeer (*Charadrius vociferus*) nesting within protected Hurricane Sandy-created habitat. Elsewhere along the Atlantic coast, black skimmers (*Rynchops niger*; Maslo et al. 2016) and Wilson's plovers (*Charadrius wilsonia*; DeRose-Wilson et al. 2013) nest in similar early-successional habitat. Wide backshores, a result of storm overwash, have been identified as an important predictor variable in nest-site selection of endangered loggerhead sea turtles (*Caretta caretta*) in Florida, USA and Western Greece, as they provide finer substrate and more available nesting sites than narrower beaches (Garmestani et al. 2000, Mazaris et al. 2006). Seabeach amaranth, a threatened plant endemic to Atlantic barrier islands, relies on storm erosion and dune movement to disperse seeds across the landscape (Sellars and Jolls 2007). Furthermore, the threatened Northeastern beach tiger beetle occupies high-energy, wide ocean beaches (Knisley et al. 1998), which are often maintained through overwash.

As hurricane power is projected to increase (Emanuel 2005, Bender et al. 2010, Villarini and Vecchi 2013), we emphasize the potential habitat benefit hurricanes may provide for early-successional coastal species. The natural instability of barrier island ecosystems (Feagin et al. 2010) provides important and dynamic habitat for a suite of disturbance-dependent species. Storm-created habitat will remain a key component to piping plover recovery (USFWS 1996) and will continue to benefit other early-successional species. We expect ecological benefits will be paramount on unstabilized and undeveloped coastlines, which permit habitat succession and island retreat (Galbraith et al. 2002, Seavey et al. 2011, Hapke et al. 2013, Iwamura et al. 2013). In the future, management of barrier island systems should be adaptive and focus on balancing anthropogenic needs with natural ecosystem processes (Schlacher et al. 2007, Feagin et al. 2010, Naylor et al. 2012, Harris et al. 2015, Maslo et al. 2018). Coastal engineering aimed at mitigation should outline clear ecological goals and habitat requirements, and prioritize the conservation and protection of early-successional habitat generated by storms. Engaging in storm response to protect infrastructure without considering the needs of early-successional species will likely reduce or inhibit increase in populations of those species.

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LITERATURE CITED

Anteau, M. J., M. H. Sherfy, and M. T. Wiltermuth. 2012. Selection indicates preference in diverse habitats: a ground-nesting bird (*Charadrius melodus*) using reservoir shoreline. PLoS ONE 7:1–9.

Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53:666–677.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bender, M. A., T. R. Knutson, R. E. Tuleya, J. J. Sirutis, G. A. Vecchi, S. T. Garner, and I. M. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science 327:454–458.

Brenner, O. T., E. E. Lentz, C. J. Hapke, R. E. Henderson, K. E. Wilson, and T. R. Nelson. 2018. Characterizing storm response and recovery using the beach change envelope: Fire Island, New York. Geomorphology 300:189–202.

Brown, A. C., and A. McLachlan. 2002. Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. Environmental Conservation 29:62–77.

Bulleri, F., and M. G. Chapman. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. Journal of Applied Ecology 47:26–35.

Burger, J. 1987. Physical and social determinants of nest-site selection in piping plover in New Jersey. Condor 89:811–818.

Cairns, W. E. 1982. Biology and behavior of breeding piping plovers. Wilson Bulletin 94:531–545.

Catlin, D. H., J. D. Fraser, and J. H. Felio. 2015. Demographic responses of piping plovers to habitat creation on the Missouri river. Wildlife Monographs 192:1–42.

Catlin, D. H., J. D. Fraser, J. H. Felio, and J. B. Cohen. 2011. Piping plover habitat selection and nest success on natural, managed, and engineered sandbars. Journal of Wildlife Management 75:305–310.

Cavallini, P., and S. Lovari. 1994. Home range, habitat selection and activity of the red fox in a Mediterranean coastal ecotone. Acta Theriologica 39:279–287.

Church, J. A., and N. J. White. 2006. A 20th century acceleration in global sea-level rise. Geophysical Research Letters 33:L01602.

Cohen, J. B., J. D. Fraser, and D. H. Catlin. 2006. Survival and site fidelity of piping plovers on Long Island, New York. Journal of Field Ornithology 77:409–417.

Cohen, J. B., L. M. Houghton, and J. D. Fraser. 2009. Nesting density and reproductive success of piping plovers in response to storm- and human-created habitat changes. Wildlife Monographs 173:1–24.

Cohen, J. B., E. H. Wunker, and J. D. Fraser. 2008. Substrate and vegetation selection by nesting piping plovers. Wilson Journal of Ornithology 120:404–407.

Courtemanche, R. P., M. W. Hester, and I. A. Mendelssohn. 1999. Recovery of a Louisiana barrier island marsh plant community following extensive hurricane-induced overwash. Journal of Coastal Research 15:872–883.

Defeo, O., A. McLachlan, D. S. Schoeman, T. A. Schlacher, J. Dugan, A. Jones, M. Lastra, and F. Scapini. 2009. Threats to sandy beach ecosystems: a review. Estuarine, Coastal, and Shelf Science 81: 1–12.

DeRose-Wilson, A., J. D. Fraser, S. M. Karpanty, and D. H. Catlin. 2013. Nest-site selection and demography of Wilson's plovers on a North Carolina barrier island. Journal of Field Ornithology 84:329–344.

DeRose-Wilson, A. L., K. L. Hunt, J. D. Monk, D. H. Catlin, S. M. Karpanty, and J. D. Fraser. 2018. Piping plover chick survival negatively correlated with beach recreation. Journal of Wildlife Management 82:1608–1616.

Dormann, C. F., et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Elias, S. P., J. D. Fraser, and P. A. Buckley. 2000. Piping plover brood foraging ecology on New York barrier islands. Journal of Wildlife Management 64:346–354.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686–688.

Feagin, R. A., J. Figlus, J. C. Zinnert, J. Sigren, M. L. Martínez, R. Silva, W. K. Smith, D. Cox, D. R.

Young, and G. Carter. 2015. Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. Frontiers in Ecology and the Environment 13:203–210.

Feagin, R. A., W. K. Smith, N. P. Psuty, D. R. Young, M. L. Martínez, G. A. Carter, K. L. Lucas, J. C. Gibeaut, J. N. Gemma, and R. E. Koske. 2010. Barrier islands: coupling anthropogenic stability with ecological sustainability. Journal of Coastal Research 26:987–992.

Flemming, S. P., R. D. Chiasson, and P. J. Austin-Smith. 1992. Piping plover nest site selection in New Brunswick and Nova Scotia. Journal of Wildlife Management 56:578–583.

Fraser, J. D., and D. H. Catlin. 2019. Habitat ecology and conservation of *Charadrius* plovers. Pages 217–243 *in* M. A. Colwell and S. M. Haig, editors. The population ecology and conservation of *Charadrius* plovers. CRC Press, Boca Raton, Florida, USA.

Galbraith, H., R. Jones, R. Park, J. Clough, S. Herrod-Julius, B. Harrington, and G. Page. 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds 25:173–183.

Garmestani, A. S., H. F. Percival, K. M. Portier, and K. G. Rice. 2000. Nest-site selection by the loggerhead sea turtle in Florida's Ten Thousand Islands. Journal of Herpetology 34:504–510.

Garmin International. 2013. GPSMAP 78 series owner's manual. https://static.garmincdn.com/pumac/GPSMAP_78_OM_EN.pdf

Gibson, D., T. V. Riecke, T. Keyes, C. Depkin, J. Fraser, and D. H. Catlin. 2018*a*. Application of Bayesian robust design model to assess the impacts of a hurricane on shorebird demography. Ecosphere 9:e02334.

Gibson, D., et al. 2018*b*. Impacts of anthropogenic disturbance on body condition, survival, and site fidelity of nonbreeding piping plovers. Condor 120:566–580.

Gratto-Trevor, C. L., J. P. Goossen, and S. M. Westworth. 2010. Identification and breeding of yearling piping plovers. Journal of Field Ornithology 81:383–391.

Haig, S. M., and L. W. Oring. 1985. Distribution and status of the piping plover throughout the annual cycle. Journal of Field Ornithology 56:334–345.

Haig, S. M., and L. W. Oring. 1988. Mate, site, and territory fidelity in piping plovers. Auk 105:268–277.

Halverson, J. B., and T. Rabenhorst. 2013. Hurricane Sandy: the science and impacts of a superstorm. Weatherwise 66:14–23.

Hanley, M. E., et al. 2014. Shifting sands? Coastal protection by sand banks, beaches, and dunes. Coastal Engineering 87:136–146.

Hapke, C. J., M. G. Kratzmann, and E. A. Himmelstoss. 2013. Geomorphic and human influence on large-scale coastal change. Geomorphology 199:160–170.

Harris, L., R. Nel, S. Holness, and D. Schoeman. 2015. Quantifying cumulative threats to sandy beach ecosystems: a tool to guide ecosystem-based management beyond coastal reserves. Ocean & Coastal Management 110:12–24.

Hayden, B. P., M. C. F. V. Santos, G. Shao, and R. C. Kochel. 1995. Geomorphological controls on coastal vegetation at the Virginia Coast Reserve. Geomorphology 13:283–300.

Hijmans, R. J. 2017. Raster: geographic data analysis and modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York, New York, USA.

Hunt, K. L., J. D. Fraser, M. J. Friedrich, S. M. Karpanty, and D. H. Catlin. 2018. Demographic response of piping plovers suggests that engineered habitat restoration is no match for natural riverine processes. Condor 120:149–165.

Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proceedings of the Royal Society B: Biological Sciences 280:1–8.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Knisley, C. B., J. M. Hill, and C. A. Schulz. 1998. Distribution and abundance of *Cicindela dorsalis dorsalis*, the northeastern beach tiger beetle, along the western shoreline of the Chesapeake Bay in Virginia. Banisteria 12:23–29.

Loegering, J. P., and J. D. Fraser. 1995. Factors affecting piping plover chick survival in different brood-rearing habitats. Journal of Wildlife Management 59:646–655.

Marsh, C. P., and P. M. Wilkinson. 1991. The impact of Hurricane Hugo on coastal bird populations. Journal of Coastal Research 8:327–334.

Martin, S. A., R. M. Rautsaw, R. Bolt, C. L. Parkinson, and R. A. Seigel. 2017. Adapting coastal management to climate change: mitigating our shrinking coastlines. Journal of Wildlife Management 81:982–989.

Maslo, B., S. N. Handel, and T. Pover. 2011. Restoring beaches for Atlantic coast piping plovers (*Charadrius melodus*): a classification and regression tree analysis of nest-site selection. Restoration Ecology 19:194–203.

Maslo, B., K. Leu, C. Faillace, M. A. Weston, T. Pover, and T. A. Schlacher. 2016. Selecting umbrella species for conservation: a test of habitat models and niche overlap for beach-nesting birds. Biological Conservation 203:233–242.

Maslo, B., K. Leu, T. Pover, M. A. Weston, B. L. Gilby, and T. A. Schlacher. 2019. Optimizing conservation benefits for threatened beach fauna following severe natural disturbances. Science of the Total Environment 649:661–671.

Maslo, B., K. Leu, T. Pover, M. A. Weston, and T. A. Schlacher. 2018. Managing birds of conservation concern on sandy shores: How much room for future conservation actions is there? Ecology and Evolution 22:10976–10988.

Maun, M. A. 1998. Adaptations of plants to burial in coastal sand dunes. Canadian Journal of Botany 76:713–738.

Mazaris, A. D., Y. G. Matsinos, and D. Margaritoulis. 2006. Nest site selection of loggerhead sea turtles: the case of the island Zakynthos, W Greece. Journal of Experimental Marine Biology and Ecology 336:157–162.

McFadden, D. 1979. Quantitative methods for analysing travel behaviour of individuals: some recent developments. Pages 279–318 *in* D. Hensher and P. Stopher, editors. Behavioural travel modelling. Croom Helm, London, UK.

Naylor, L. A., M. A. Coombes, O. Venn, S. D. Roast, and R. C. Thompson. 2012. Facilitating ecological enhancement of coastal infrastructure: the role of policy, people, and planning. Environmental Science & Policy 22:36–46.

New York State. 2010. Suffolk County direct download (2010). http://gis.ny.gov/gateway/mg/2010/suffolk/

NOAA [National Oceanic and Atmospheric Administration]. 2009. Tide tables 2010: high and low water predictions East coast of North and South America: including Greenland. North Wind Publishing, Brewer, Maine, USA.

NOAA [National Oceanic and Atmospheric Administration]. 2010. 2010 USACE NCMP topobathy lidar: Atlantic Coast (NY) - A point cloud files with orthometric vertical datum North American vertical datum of 1988 (NAVD88) using GEOID12B. https://coast.noaa.gov/htdata/lidar2_z/geoid12b/data/8624/

Oertel, G. F. 1985. The barrier island system. Marine Geology 63:1–18.

Prindiville Gaines, E., and M. R. Ryan. 1988. Piping plover habitat use and reproductive success in North Dakota. Journal of Wildlife Management 52:266–273.

Pugh, D. T. 1987. Tides, surges, and mean sea-level. John Wiley & Sons, Chichester, UK.

R Development Core Team. 2016. R: a language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna, Austria.

Roelvink, D., A. Reniers, A. van Dongeren, J. van Thiel de Vries, R. McCall, and J. Lescinski. 2009. Modelling storm impacts on beaches, dunes and barrier islands. Coastal Engineering 56:1133–1152.

Sallenger, A. H. 2000. Storm impact scale for barrier islands. Journal of Coastal Research 16:890–895.

Schlacher, T. A., L. K. Carracher, N. Porch, R. M. Connolly, A. D. Olds, B. L. Gilby, K. B. Ekanayake, B. Maslo, and M. A. Weston. 2016. The early shorebird will catch fewer invertebrates on trampled sandy beaches. PLoS ONE 11:1–13.

Schlacher, T. A., J. Dugan, D. S. Schoeman, M. Lastra, A. Jones, F. Scapini, A. McLachlan, and O. Defeo. 2007. Sandy beaches at the brink. Diversity and Distributions 13:556–560.

Schlacher, T. A., D. Richardson, and I. McLean. 2008. Impacts of off-road vehicles (ORVs) on macrobenthic assemblages on sandy beaches. Environmental Management 41:878–892.

Schlacher, T. A., and L. M. C. Thompson. 2008. Physical impacts caused by off-road vehicles to sandy beaches: spatial quantification of car tracks on an Australian barrier island. Journal of Coastal Research 24:234–242.

Schroeder, P. M., B. Hayden, and R. Dolan. 1979. Vegetation changes along the United States east coast following the great storm of March 1962. Environmental Management 3:331–338.

Schupp, C. A., N. T. Winn, T. L. Pearl, J. P. Kumer, T. J. B. Carruthers, and C. S. Zimmerman. 2013. Restoration of overwash processes creates piping plover (*Charadrius melodus*) habitat on a barrier island (Assateague Island, Maryland). Estuarine, Coastal, and Shelf Science 116:11–20.

Seavey, J. R., B. Gilmer, and K. M. McGarigal. 2011. Effect of sea-level rise on piping plover (*Charadrius melodus*) breeding habitat. Biological Conservation 144:393–401.

Sellars, J. D., and C. L. Jolls. 2007. Habitat modeling for *Amaranthus pumilus*: an application of light detection and ranging (LiDAR) data. Journal of Coastal Research 23:1193–1202.

Sheikh, P. A. 2005. The impact of Hurricane Katrina on biological resources. Congressional Research Service Report for Congress. https://digital.library.unt.edu/ark:/67531/metacrs8477/m1/1/high_res_d/RL33117_2006Feb22.pdf

Smith, C. G., S. J. Culver, S. R. Riggs, D. Ames, D. R. Corbett, and D. Mallinson. 2008. Geospatial analysis of barrier island width of two segments of the Outer Banks, North Carolina, USA: anthropogenic curtailment of natural self-sustaining processes. Journal of Coastal Research 24:70–83.

Sopkin, K. L., H. F. Stockdon, K. S. Doran, N. G. Plant, K. L. M. Morgan, K. K. Guy, and K. E. L. Smith. 2014. Hurricane Sandy: observations and analysis of coastal change. U.S. Geological Survey, Reston, Virginia, USA.

Swift, D. J. P. 1975. Barrier-island genesis: evidence from the central Atlantic shelf, eastern U.S.A. Sedimentary Geology 14:1–43.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

USACE. 2014. Fire Island to Moriches Inlet, New York plans for construction of stabilization project. U.S. Army Corps of Engineers, New York, New York, USA.

USFWS. 1985. Determination of threatened and endangered status for the piping plover. U.S. Fish and Wildlife Service, Washington, D.C., USA.

USFWS. 1996. Piping plover (*Charadrius melodus*) Atlantic coast population revised recovery plan. U.S. Fish and Wildlife Service, Hadley, Massachusetts, USA.

USFWS. 2009. Piping plover (*Charadrius melodus*) 5-year review: summary and evaluation. U.S. Fish and Wildlife Service, Hadley, Massachusetts and East Lansing, Michigan, USA.

USFWS. 2014. Fire Island to Moriches Inlet Stabilization Project Biological Opinion. U.S. Fish and Wildlife Service, Hadley, Massachusetts, USA.

USFWS. 2016. Abundance and productivity estimates – 2016 update Atlantic coast piping plover population. U.S. Fish and Wildlife Service, Hadley, Massachusetts, USA.

Villarini, G., and G. A. Vecchi. 2013. Projected increases in North Atlantic tropical cyclone intensity from CMIP5 models. Journal of Climate 26:3231–3240.

Wilcox, L. 1959. A twenty year banding study of the piping plover. Auk 76:129–152.

Williams, A. J., V. L. Ward, and L. G. Underhill. 2004. Waders respond quickly and positively to the banning of off-road vehicles from beaches in South Africa. Wader Study Group Bulletin 104:79–81.

Wiltermuth, M. T., M. J. Anteau, M. H. Sherfy, and A. T. Pearse. 2015. Habitat selection and movements of piping plover broods suggest a tradeoff between breeding stages. Journal of Ornithology 156:999–1013.

Wong, P. P., I. J. Losada, J.-P. Gattuso, J. Hinkel, A. Khattabi, K. L. McInnes, Y. Saito, and A. Sallenger. 2014. Coastal systems and low-lying areas. Pages 361–409 *in* C. B. Field et al., editors. Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK; New York, New York, USA.