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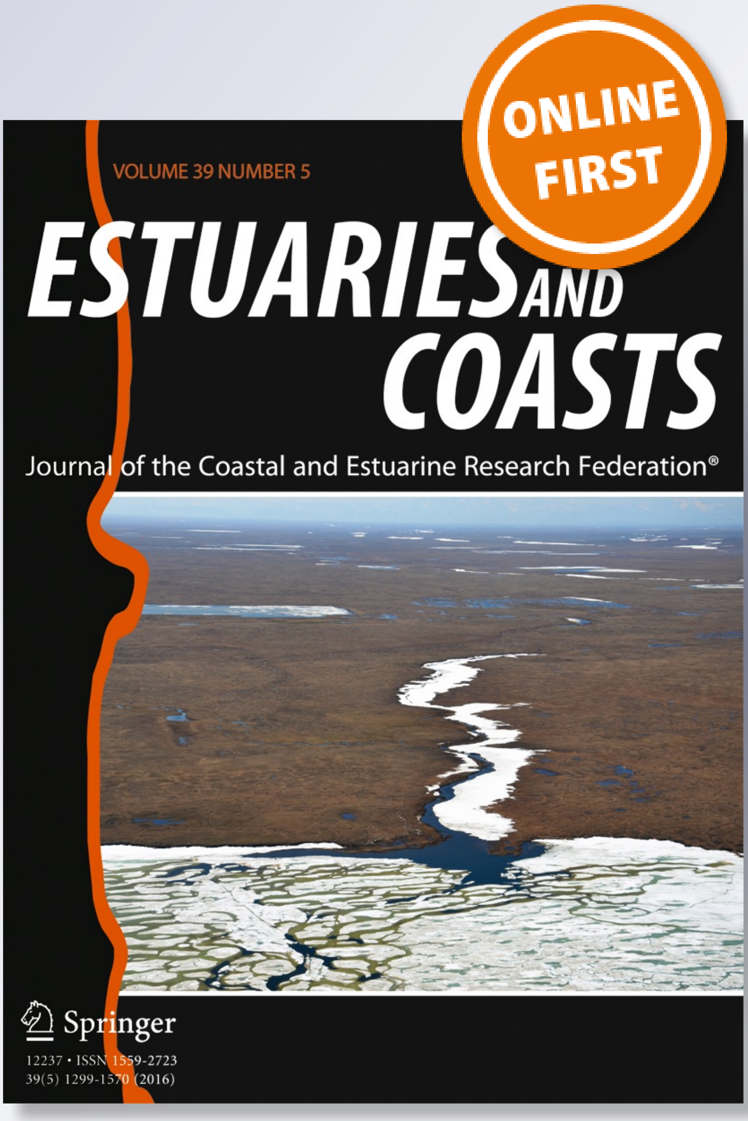

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Importance and Function of Foraging and Roost Habitat for Wintering American Oystercatchers

Janell M. Brush[1] · **Amy C. Schwarzer**[1] · **Peter C. Frederick**[2]

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Abstract With changing climate and increased human populations, oyster reefs have been negatively affected by excessive wave action; contamination; overharvesting; decreased freshwater inputs; and shifts in oxygen, salinity, and turbidity regimes. In Florida's Big Bend, intertidal reefs dominated by the eastern oyster (*Crassostrea virginica*) have experienced a net decline in area of 66 % since the 1980s, a loss likely to have substantial impacts on reef-dependent wildlife. Our study examined the use of intertidal oyster reefs by wintering American oystercatchers (*Haematopus palliatus*) in this area. The minimum foraging time required to meet daily caloric needs was conservatively estimated at 37 min per adult oystercatcher, indicating that at present, foraging habitat is not a limiting factor within our study area. We found high-tide roosts to be away from all vegetation and limited in number. They were located in offshore oyster reef habitat, which has experienced an 88 % decline in area over the past 30 years. We suggest that offshore, high-tide roost habitat is a limiting factor and worthy of further attention.

Keywords American oystercatcher · *Crassostrea virginica* · Eastern oyster · Estuary · *Haematopus palliatus* · Oyster reef

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Introduction

Rapid changes in marine and estuarine habitats such as seagrass beds, coral reefs, and salt marshes may have wide-ranging implications for the flora and fauna that depend on these communities. Understanding the specific attributes of these habitats that the organisms depend on is key to quantifying and projecting effects on different species. Here, we consider the characteristics of oyster reefs important to roosting and foraging by American oystercatchers (*Haematopus palliates*) and the susceptibility of these different reef habitats to ongoing loss.

With an estimated 85 % decline globally, oyster reef communities are among the most heavily degraded and endangered marine habitats (Beck et al. 2011). Oyster communities dominated by the eastern oyster (*Crassostrea virginica*) are highly sensitive to a number of threats, including excessive wave action; contamination; overharvesting; and shifts in oxygen, salinity, and turbidity regimes (Bahr and Lanier 1981; Beck et al. 2009; Seavey et al. 2011; Wall et al. 2005). Elevated salinity as a result of decreased freshwater input leads to increased vulnerability to disease and predation, and freshwater flow regime has been strongly linked to productivity and survival of oyster stocks in a number of estuaries in the USA (Kimmel et al. 2014; Livingston et al. 1997; Pollack et al. 2011; Wilbur 1992). Although the Florida Big Bend (Crystal River to Panacea; Fig. 1) is a highly conserved and undeveloped part of the Gulf Coast (Main and Allen 2007), there has been a 66 % net decline in the extent of the oyster reefs there since the 1980s (Baker et al. 2003; Bergquist et al. 2006; Seavey et al. 2011). These reefs are more than 3000 years old (Grinnell 1972), which suggests that the rapid decline is a consequence of a recent fundamental change in the

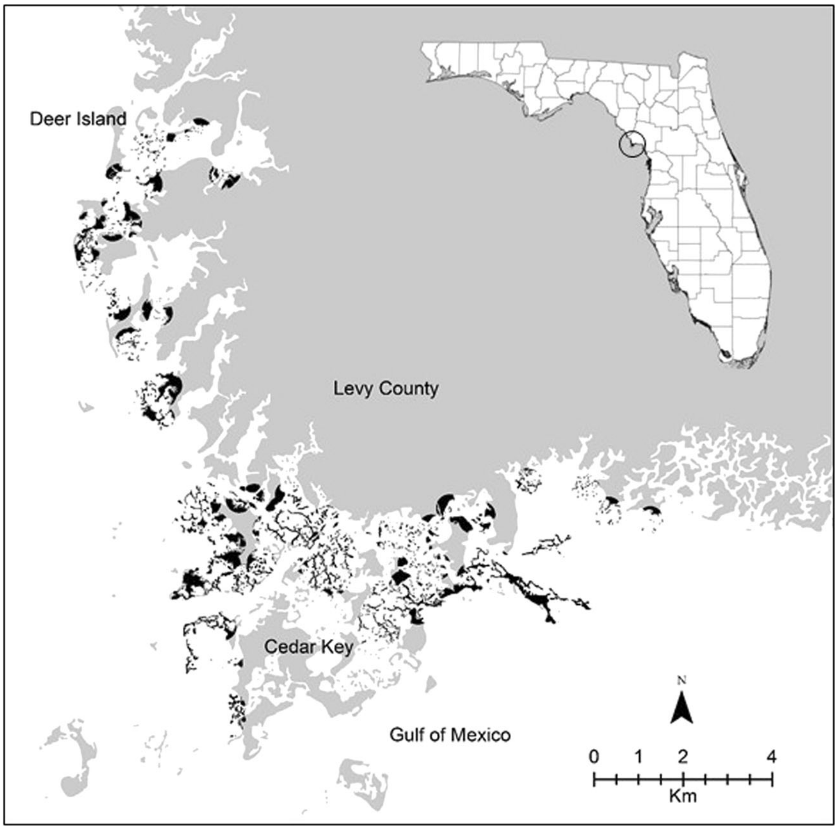

Fig. 1 Map of study area in the Big Bend of Florida. The intertidal oyster reef complex included in the project is shaded *black*

hydrological conditions that maintain the reefs. The causes are probably multiple, but the dominant mechanism is increased disease and predation effects resulting from high salinities, stemming from reduced freshwater input. The increasing length and frequency of low-freshwater discharge events has led to poor recruitment and survival of oysters, erosion of oyster reefs, and, ultimately, irreversible loss of substrate appropriate for oyster settlement (Baker et al. 2003; Seavey et al. 2011).

Oyster reefs provide crucial foraging and roosting opportunities for many coast-dependent wintering shorebirds. The American oystercatcher (hereafter oystercatcher) feeds primarily on marine bivalves and depends on coastal areas that support intertidal shellfish beds (Nol and Humphrey 1994). The US population of oystercatchers consists of ca. 11,000 individuals (Brown et al. 2005) and is listed as a species of high conservation concern in the US Shorebird Conservation Plan (Brown et al. 2001). Major threats to the oystercatcher include widespread habitat loss, increased anthropogenic pressure, and several effects of climate change, particularly sea-level rise (Schulte et al. 2010). Oystercatchers migrate from northern Atlantic breeding sites to coastal wintering areas on both the South Atlantic US coast and the Gulf of Mexico (Nol and Humphrey 1994). Two main, geographically separate winter aggregations of the Eastern population exist, at Cape Romain, South Carolina (16 % of the estimated total population size), and in Florida's Big Bend (8 % of the estimated total population size). The Big Bend has been estimated to support more than 900 individuals from nearly all Atlantic coastal states during the winter (Schulte et al. 2010). While considerable research has been focused on breeding habitat conditions, little has been devoted to understanding or improving wintering habitat (American Oystercatcher Working Group et al. 2012; Schulte et al. 2010).

The oystercatcher is a long-lived bird, and its population trajectories are particularly sensitive to adult survival rates, which may be affected by winter habitat suitability (American Oystercatcher Working Group et al. 2012; Hitchcock and Gratto-Trevor 1997; Yasue 2006). In winter, avian survival is usually sensitive to availability of food, refuge from predation, and local weather events (Placyk and Harrington 2004; Sherry and Holmes 1996). Although foraging is critical for survival, roosting and its associated activities such as rest, digestion, and maintenance are also important (Conklin et al. 2008). Roost quality is typically associated with proximity to feeding habitats because of the energetic costs of commuting (van Gils et al. 2006). For coastal birds, roost quality is also affected by tidal conditions and protection from strong winds, high surf, precipitation, and predation (Colwell 2010; Cresswell 1994; Gill et al. 2001; Rogers et al. 2006). Shorebirds and seabirds tend to roost in open areas where predators are visible (Clemens et al. 2008).

The rapid decline of oyster reefs in the Big Bend region could have significant effects upon a substantial portion of oystercatcher overwintering habitat. Loss of oyster reefs in the Big Bend has been disproportionately focused on offshore reefs, with much of the inshore habitat mosaics remaining in relatively good condition (Seavey et al. 2011). Offshore reefs were defined as those that were more than 1 km from the coastline and also were not protected from open gulf waters by any other landform. Inshore reefs were defined as those that were less than 1 km from the shoreline or were part of the marsh behind the shoreline and were protected from open water by at least one landform (marsh, sandbar, mudflat, oyster reef). Within these mosaics, it is unclear what habitat features are used most by oystercatchers for feeding and roosting and why.

Based on previous work on oystercatchers, we hypothesized that use of foraging habitat would be focused on oyster reefs (a) with high densities of live oysters in a size range that oystercatchers typically eat (American Oystercatcher Working Group et al. 2012; Hand 2008); (b) that were far from vegetative cover or perches that could harbor aerial or ground predators (Yasue 2006); (c) that were far from artificial structures (docks, roads, or buildings) that could lead to increased disturbance; (d) that had a high edge-to-area ratio that afford a high proportion of edge feeding habitat where oysters are inundated (shells open) at water depths accessible to oystercatchers, which forage by inserting their bills into open oysters, tearing the muscle at the hinge to prevent the oysters from closing; (e) that had a high density of surrounding foraging habitat, which would reduce costs of flight among foraging sites; and (f) that were close to roosting sites, which would again reduce costs of flight (van Gils et al. 2006). For roosting habitat, we expected that oystercatchers would use reefs that were (a) high in elevation and large in area, which would provide both shelter from adverse weather conditions and a better view of predators (Clemens et al. 2008); (b) far from vegetative cover for mammalian predators and perches for avian predators; (c) distant from artificial structures; (d) far from shallow water and close to deep water, which would discourage mammalian predators capable of fording shallow expanses of water; and (e) close to surrounding foraging habitat. We examined oystercatcher use of foraging and roosting habitat in relation to landscape and microhabitat features to understand how current and projected losses of oyster reefs might affect this declining species.

Materials and Methods

Study Area

The study was conducted in coastal waters from Cedar Key to Deer Island in Levy County, Florida (Fig. 1). While oyster reef density and coverage vary greatly in the Big Bend region, the study area was large enough to include reef systems representative of the area, with largely intertidal reef structure, a gradient of inshore marsh to isolated offshore reefs, and a lack of protective barrier islands. Offshore reefs were defined as those that were more than 1 km from the coastline and also were not protected from open gulf waters by any other landform. Inshore reefs were defined as those that were less than 1 km from the shoreline or were part of the marsh behind the shoreline and were protected from open water by at least one landform (marsh, sandbar, mudflat, oyster reef).

Foraging Habitat

We estimated the total number of oystercatchers in the study area and identified oyster reefs used by foraging oystercatchers by performing six ground surveys between October 2011 and February 2012. Each survey was conducted by two or three teams using airboats, covering the entire study area in 1 day. Surveys were conducted during tides of varying amplitudes within 1.5 h either side of low tide. Teams followed non-overlapping designated routes that allowed 100 % coverage of the oyster reefs in the survey area. Teams recorded the approximate locations (within 75 m) of oystercatchers using a handheld GPS unit. We also recorded the number of oystercatchers, their behavior (foraging, non-foraging, or both), and the substrate type of the reef (sandbar, marsh–oyster, sand–oyster).

In order to characterize the oystercatcher foraging habitat, in ArcMap 10.0 (Esri 2010), we created a fishnet grid (200 × 200 m) on a map of the entire study area. Grid squares were randomly selected for sampling of foraging habitat. Grid squares corresponding to locations at which no foraging oystercatchers had been observed were eliminated from consideration for random selection.

When surveying oyster reefs in the field, the randomly selected grid squares were sampled for the presence of foraging adult oystercatchers. Once detected, the physical location on the oyster reef where the oystercatcher was foraging (in water, waterline, top of reef, etc.) was documented. We also recorded surface elevation using a laser level from the top of the reef and later linked those relative elevations to true elevation benchmarks established in the study area. We collected the following microhabitat data: slope of the oyster reef at the foraging location, distance to any non-woody emergent vegetation on the reef (typically short form *Spartina alterniflora*), and substrate type (mud, sand, shell, mud–shell, sand–shell). Oyster density (living and dead) and presence of mussels within a 0.25-m^2 quadrat were determined 1 m from the oystercatcher location, in each cardinal direction. Shell length, the longest distance from hinge to shell edge (mm), was measured for all oysters in one randomly selected quadrat. We also characterized nearby foraging habitat by selecting six random points within 10 m of the oystercatcher location, where we recorded oyster density (living and dead) and presence of mussels. In every other 0.25-m^2 quadrat, we recorded shell length for all of the oysters within the quadrat.

We also compared characteristics of reefs used for foraging to those of randomly selected reefs to evaluate selection of foraging habitat. We recorded percent cover of oysters, vegetation, and substrate type on each reef. A laser range finder was used to measure distance from the center of the reef to both the nearest woody (typically mangroves or pines) and the nearest non-woody emergent vegetation. Methods used to sample microhabitats depended on the size of the oyster reef. Small oyster reefs (<75 m, longest linear distance) were sampled along the long axis of the reef. Large oyster reefs (>75 m, longest linear distance) were sampled along transects perpendicular to the long axis of the reef. Randomly generated distances (range 1–5 m) were used to determine the starting point of sampling as well as each sampling point along each transect. We recorded the following microhabitat information within a 0.50-m^2 quadrat at each sample point: percent cover of vegetation, oysters, and open substrate by type (mud, sand, shell, mud–shell, sand–shell); percent living and dead oysters; and presence or absence of mussels. In addition to the field data, landscape-level feature data were analyzed in ArcMap10.0. These data included area (ha) of the oyster reef, reef shape (0.25 × perimeter)/$\sqrt{}$area), distance to shallow (0.9–1.8 m) and deep (1.9–3.7 m) waters based on the most recent bathymetric charts, distance (m) to the closest known high-tide and intermediate-tide (available only below mean high tide) roost sites, and density of oyster reefs (m^2/ha) within a radius of 250 m.

Foraging Behavior, Prey Selection, and Foraging Energetics

Foraging adult oystercatchers were observed in order to document their prey items and estimate average search and handling time. From a distance of 15–50 m, we observed adults within the same randomly selected grid squares for which we had made foraging habitat observations. When multiple oystercatchers were present, we selected the foraging individual closest to us in the direction associated with a randomly generated compass degree and observed the bird for 5 min or until it left the area. Oystercatcher behavior type (e.g., probing, eating, preening) and duration were recorded. The size of any identified prey item was estimated as a fraction of the length of the foraging oystercatcher's bill. The average oystercatcher bill length (American Oystercatcher Working Group et al. 2012) was later used to estimate prey length.

In order to estimate the energy contained in the oysters the oystercatchers consumed, we measured mass and length of oyster meats (longest distance of freshly shucked meat attached to bottom valve) of 81 oysters collected from the areas where oystercatchers had been seen foraging. Oysters ranged from 22.4 to 104.5 mm in total shell length. We used this information to develop an equation that explained the relationship between fresh meat length and mass of meat (wet mass = 0.2522 e$^{0.0663 \text{ (meat length)}}$, R^2 = 0.91). We then used equations developed by Dame (1972a) to convert the masses of oyster meats consumed to dry mass (dry mass = 0.1664 × wet mass$^{0.97}$), and from estimated dry mass of meats, we then estimated total caloric content (5.066 kcal/g dry mass; Dame 1972b).

Roosting Habitat

We identified roosts during high and intermediate tides. High-tide roosts were defined as those available to birds at mean high tide (Cedar Key gauge) or higher. Intermediate-tide roosts were defined as those available only below mean high tide, typically used at low tide when water levels fell below the oyster line and birds ceased foraging. Oystercatchers forage almost exclusively below the waterline on partially opened oysters presumably because they are easier to manipulate and eat. We located and surveyed all high-tide roosts monthly from August 2011 to February 2012. Intermediate-tide roosts were identified during the six comprehensive ground surveys. Whenever we encountered oystercatchers, we recorded time, weather conditions, and tide stage. In addition, we recorded percent cover of oysters and vegetation, as well as substrate type on each reef. We also recorded distance from the center of the oyster reef to vegetation (both woody and non-woody) using a laser rangefinder, and maximum elevation was derived using survey-grade real-time kinetic GPS equipment corrected with local benchmarks. We collected the same landscape-level features (reef area, distance to shallow and deep water, etc.) that we collected for foraging reefs.

Statistical Analyses

In order to characterize oystercatcher foraging habitat, we compared 40 randomly selected oyster reefs with 40 oyster reefs known to support foraging oystercatchers. We examined the effect of the following spatial and physical variables on the presence of foraging oystercatchers: distance from the reef center to nearest woody and non-woody vegetation, distance to the nearest high-tide roost, distance to shallow and deep waters, and distance to nearest artificial structure (building or road); highest elevation on the reef; percent cover of vegetation and of oysters; average percentage of oysters that were alive; reef shape; density of surrounding reef (area of adjacent oyster reefs within 250 m); and interaction terms between the variables.

In order to characterize oystercatcher roosting habitat, we compared 40 random oyster reefs with 28 intermediate-tide roosts and 13 high-tide roosts. We sampled all the roosts available that had been identified through systematic and opportunistic observations. We separated high-tide roosts from intermediate-tide roosts because of strong differences in temporal availability and bird densities at these two roost types. The following spatial and physical variables were included in the analyses: distance from the center of the reef to nearest woody and non-woody vegetation, distance to shallow and deep waters, and distance to nearest structure (building or road); highest elevation on the reef; percent cover of vegetation; reef area and shape; area of adjacent oyster reefs within 250 m; and interaction terms between the variables.

Before analysis, all explanatory variables were tested in a pairwise fashion for correlation to preclude issues with multicollinearity. In cases where variables had a correlation of $r \geq 0.50$, one of the variables was excluded from analysis. We used backward stepwise logistic regression (Bewick et al. 2005; Hosmer and Lemeshow 2000) in Program R (R 2012) to analyze separately the effect of the variables on use of each class of reef (foraging, high tide, intermediate tide). All independent variables were included in the initial model; then, variables with an alpha level greater than $P = 0.10$ were removed one at a time, starting with the least significant variable. Since the habitat we studied was completely open and entirely accessible to the observers via airboat, and because oystercatchers are extremely conspicuous in these habitats, we did not incorporate estimates of detectability in our analyses.

We used Akaike's information criterion to judge whether reduced models were an improvement over the full model (Burnham and Anderson 2002). The model with the smallest Akaike's information criterion (AIC) value was the model most strongly supported by the data. If one or more models were <2 AIC from the top model, the model with the fewest number of parameters was considered to be the most parsimonious. The selection of simpler models over more complex models when there is no clear difference in explanatory power is well discussed and has been supported by examples, in which simpler models have higher predictive value than more complex models (Bolker 2008). All parameters within the most parsimonious models were significant at $P \leq 0.10$ unless otherwise reported.

Results

Foraging Habitat

The number of oystercatchers documented during the six surveys ranged from 988 to 1176 (average = 1076; SE = 40.4). We observed the behavior of 163 foraging oystercatchers and collected microhabitat data on 91 oyster reefs. Average oyster density at foraging sites was 86.8 oysters/m^2 (SE = 2.744 oysters/m^2, range 0–660 oysters/m^2, $n = 1620$). Average oyster shell size at foraging sites was 37.8 mm (SE = 0.17 mm, range 2.3–118.0 mm, $n = 10{,}504$).

At foraging sites, oysters were arranged in continuous mats, in clumps separated by substrate, or, occasionally, as single oysters embedded in the substrate. Oystercatchers were most strongly associated with clumps of oysters (94 % of observations), where oyster density is greatest. In addition, oystercatchers foraged almost exclusively (99 % of observations) at or below the waterline, where the oysters are open and easier to access. Oystercatcher foraging areas were composed mainly (57 %) of mixed mud and shell.

Based on our predictions, we tested a set of seven candidate models to compare reefs used for foraging with randomly selected reefs (Table 1). The most parsimonious model included a positive correlation for distance to woody vegetation, negative correlations for distance to nearest high-tide roost and nearest artificial structure, and a positive correlation with average percent live oysters (Fig. 2).

Foraging Behavior and Energetics

We observed 62 foraging oystercatchers during two winter seasons. Of the prey items we observed being consumed, 72 % were identified. The majority were oysters (95 %), mussels accounted for 5 %, and other prey items accounted for <1 %. Many of the unidentified items were probably also oysters, given the lack of mussels in many parts of the study area, but mussels and crabs are common prey items of the oystercatcher in other parts of its range (Hand 2008; Tuckwell and Nol 1997). Average search time, the time between ingestion and locating a new prey item, was 35.2 s (SE = 2.07 s, range 1–202 s); average handling time was 11.4 s (SE = ±0.76 s, range 1–50 s, $n = 62$).

The average bill length in oystercatchers was 86.64 mm (data from multiple North American sites and both sexes; SD = 5.59 mm; American Oystercatcher Working Group et al. 2012). Mean oyster meat length in our study averaged 28 % of bill length (SE = 0.01, range 0.1–0.66, $n = 144$). Using bill length as a guide, this suggests that the average length of oyster meat consumed was 24.3 mm. We found that the fresh mass of 81 local oysters was related to shell length as $\text{mass} = 0.02552\ e^{0.0663\ \text{length}}$. We used this metric to determine that the average fresh mass of oyster meat consumed by oystercatchers in this study was 1.27 g. By equations relating wet to dry mass in oysters found in Dame (1972a) and calorific content found in Dame (1972b), the average oyster eaten was estimated to contain 4.43 kJ. Based on multiples of basal metabolic rate for different activities, daily energy expenditure (DEE) for breeding male and female oystercatchers has been estimated at 207 and 226 kJ/14 h/day, respectively (Nol 1985). Given the average of approximately 47 s that an oystercatcher required to capture and consume an oyster (search time plus handling time), we calculated that an oystercatcher in our study area would require roughly 37 min of continuous foraging per day to satisfy energy needs. This estimate is likely

Table 1 Number of parameters (#Par), AICc values, and log-likelihood (LL) for candidate models comparing foraging reefs with randomly selected reefs

Model	#Par	AICc	ΔAICc	AICc weight	LL
Dist_Woody + Dist_HiRoost + Dist_Structure + avg_live	5	100.45	0	0.31	−44.82
Dist_Woody + Shape + Dist_HiRoost + Dist_Structure + avg_live	6	100.55	0.1	0.29	−43.69
Dist_Woody + Shape + Shallow + Dist_HiRoost + Dist_Structure +	7	101.28	0.83	0.2	−42.85
Dist_Woody + Shape + Shallow + Dist_HiRoost + Dist_Structure + Dist_Non-Woody + avg_live	8	101.97	1.52	0.14	−41.96
Dist_Woody + Shape + Shallow + Dist_HiRoost + Dist_Structure + Dist_Non-Woody + Dist_Non-Woody × Dist_Woody + avg_live	9	104.39	3.94	0.04	−41.89
Dist_Woody + Total_Veg + Shape + Shallow + Dist_HiRoost + Dist_Structure + Dist_Non-Woody + Dist_Non-Woody × Dist_Woody + avg_live	10	106.88	6.42	0.01	−41.82
Dist_Woody + Total_Veg + %_oys + Shape + Shallow + Density + Dist_HiRoost + Dist_Structure + Dist_Non-Woody + Dist_Non-Woody × Dist_Woody + avg_live	12	112.34	11.88	0	−41.8

Variables include distance to woody vegetation (Dist_Woody), distance to non-woody vegetation (Dist_Non-Woody), distance to high-tide roost (Dist_HiRoost), distance to artificial structure (Dist_Structure), distance to shallow water (Shallow), percent cover of oysters (%_oys), average number of live oysters/m^2 (avg_live), percent cover of all vegetation (Total_Veg), shape (Shape), and density of oyster reefs (m^2/ha) within 250 m (density)

high, since the DEE we used was for breeding rather than individuals wintering in Florida.

Roosting Habitat

We identified 41 oyster reefs used by oystercatchers during intermediate ($n = 28$) and high tides ($n = 13$). We tested a set of six models to compare features of random oyster reefs with high-tide roosts (Table 2). The most parsimonious of six models comparing random reefs and high-tide roosts included positive correlations with elevation, distance to woody vegetation and area of reef, and a negative correlation with distance to the nearest artificial structure (Fig. 3). The term for distance to the nearest artificial structure was insignificant in this

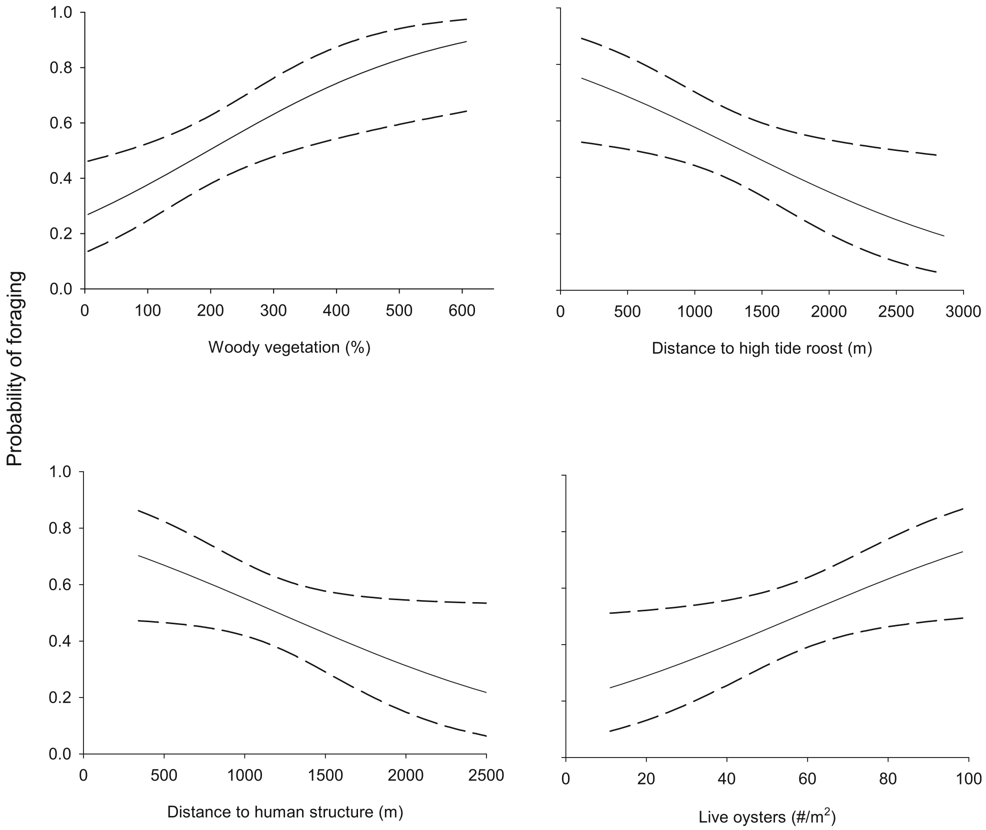

Fig. 2 Probability of oystercatchers selecting an oyster reef for foraging related to the variables included in the most parsimonious model (Table 1). The *solid lines* indicate the model-based predictions for each variable with all other variables held at their mean values. The *dashed lines* indicate the 95 % confidence intervals. All variables are plotted from the 5th to 95th percentiles of the observed values

Table 2 Number of parameters (#Par), AICc values, and log-likelihood (LL) for the models comparing high-tide roosts with randomly selected reefs

Model	#Par	AICc	ΔAICc	AICc weight	LL
Elevation + Dist_Woody + Area + Dist_Structure	5	23.29	0	0.53	−6.01
Elevation + Dist_Woody + Dist_Non-Woody + Area + Dist_Structure	6	24.71	1.41	0.26	−5.44
Elevation + Dist_Woody + Dist_Non-Woody + Area + Shallow + Dist_Structure	7	26.3	3.01	0.12	−4.91
Elevation + Dist_Woody + Area	4	27.87	4.58	0.05	−9.52
Elevation + Dist_Woody + Dist_Non-Woody + Area + Shallow + Deep + Density + Dist_Structure	9	28.91	5.61	0.03	−3.36
Elevation + Dist_Woody + Dist_Non-Woody + Total_Veg + Area+ Shallow + Deep + Density + Dist_Structure	10	31.96	8.66	0.01	−3.36

Variables include distance to woody vegetation (Dist_Woody), distance to non-woody vegetation (Dist_Non-Woody), distance to artificial structure (Dist_Structure), distance to shallow water (Shallow) and deep water (Deep), maximum elevation (Elevation), percent cover of all vegetation (Total_Veg), reef area (Area), and density of oyster reefs (m^2 /ha) within 250 m (Density)

model; however, removal of this term resulted in a model fit >2 AIC below the most parsimonious model. The small sample size of the high-tide roosts resulted in large confidence intervals in the results.

We tested a set of four models to compare features of random oyster reefs with intermediate roosts (Table 3). The most parsimonious model included positive correlations for distance to woody vegetation, non-woody vegetation, and shallow water. Intermediate-tide roost habitat was negatively correlated with density of oyster reefs within 250 m and positively correlated to the interaction term between distance to woody vegetation and distance to non-woody vegetation (Fig. 4).

Discussion

The average prey search and handling times of wintering adult oystercatchers were very similar to those observed in the Cape Romain region of South Carolina (Hand et al. 2010; Sanders et al. 2013), where the largest US population of wintering American oystercatchers resides. Our estimates indicated that

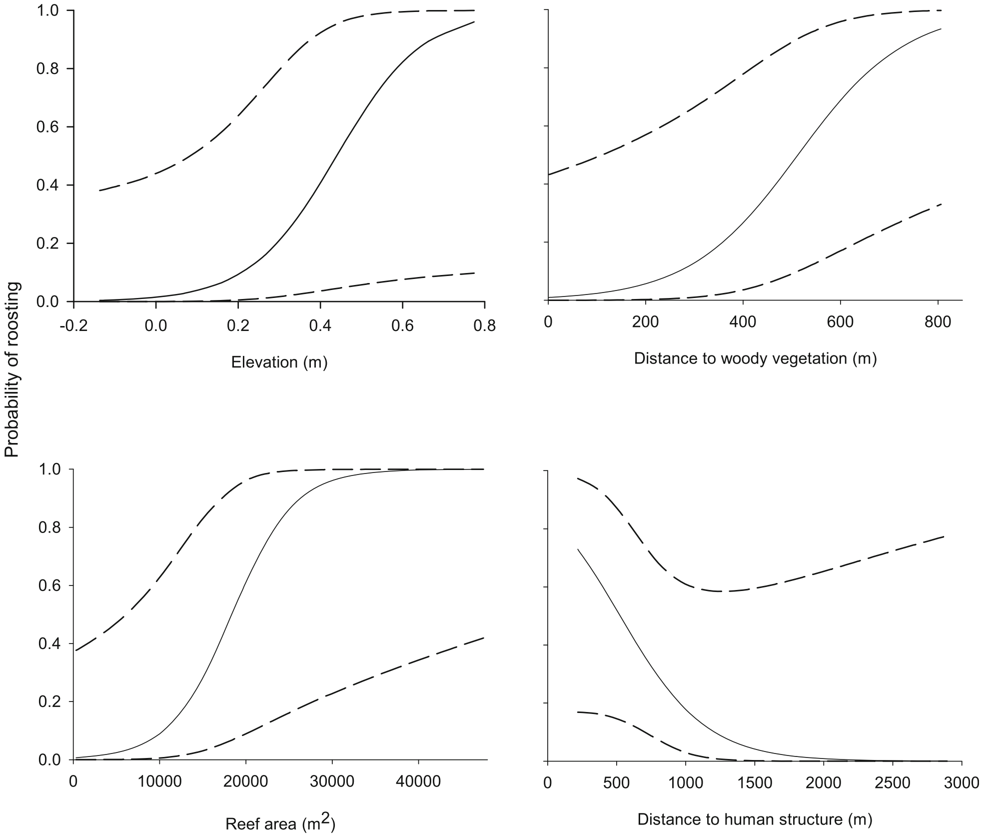

Fig. 3 The probability of oystercatchers selecting an oyster reef as a high-tide roosting location related to the habitat variables included in the most parsimonious model (Table 2). Elevation in the *first graph* is relative to mean sea level. The *solid lines* indicate the model-based predictions for each variable with all other variables held at their mean values. The *dashed lines* indicate the 95 % confidence intervals. All variables are plotted from the 5th to 95th percentiles of the observed values

Table 3 Number of parameters (#Par), AICc values, and log-likelihood (LL) for the models comparing intermediate roosts with randomly selected reefs

Model	#Par	AICc	ΔAICc	AICc weight	LL
Dist_Woody + Dist_Non-Woody + Area + Shallow + Density + Dist_Non-Woody × Dist_Woody	7	71.79	0	0.34	−27.96
Dist_Woody + Dist_Non-Woody + Shallow + Density + Dist_Non-Woody × Dist_Woody	6	72.01	0.22	0.31	−29.31
Dist_Woody + Dist_Non-Woody + Total_Veg + Area+ Shallow + Density + Dist_Non-Woody × Dist_Woody	8	72.24	0.45	0.27	−26.9
Dist_Woody + Dist_Non-Woody + Total_Veg + Area+ Shallow + Density + Dist_Structure + Dist_Non-Woody × Dist_Woody	9	74.65	2.86	0.08	−26.77

Variables include distance to woody vegetation (Dist_Woody), distance to non-woody vegetation (Dist_Non-Woody), distance to artificial structure (Dist_Sturcture), distance to shallow water (Shallow) and deep water (Deep), maximum elevation (Elevation), percent cover of all vegetation (Total_Veg), reef area (Area), and density of oyster reefs (m^2 /ha) within 250 m (Density)

an oystercatcher would need to forage for 37 min daily to satisfy energy requirements in Florida. Since this estimate was based on daily energy requirements during the breeding season, we believe it to be a liberal estimate of winter energy requirements. This finding suggests that prey availability is not a limiting factor for this wintering population. Nevertheless, most of the foraging areas used by oystercatchers were on the nearshore and inshore reefs; many of which are sinking or exhibiting low accretion rates (Seavey et al. 2011). Given the rapid loss of reef area in the region (>66 % in 30 years), this preferred foraging habitat may soon be at risk (Seavey et al. 2011), limiting foraging habitat for this wintering population.

Intermediate-tide roosts were used only when the water level had dropped below that of the oysters on the reefs used for foraging. Since intermediate-tide roosts were interspersed among foraging areas, the threats facing this complex of reefs are probably similar to those facing foraging reefs. Oyster reefs selected as intermediate-tide roosts differed in important ways from reefs selected for foraging. Foraging oystercatchers tolerated non-woody vegetation, but roosting oystercatchers preferred roosts without, and distant from, non-woody vegetation. Intermediate-tide roosts were also located a greater distance from shallow water, although this effect was weak (Fig. 4). This preference may relate to avoidance of terrestrial predators capable of swimming short distances. All of these features suggest that intermediate-tide roosts tend to be farther from the coastline than random reefs. Intermediate-tide roosts, however, were still located within the matrix of nearshore reefs, unlike high-tide roosts, which were located offshore. Nearshore reefs are less likely than offshore reefs to be lost under current conditions (Seavey et al. 2011).

High-tide roosts in the study area were used both day and night and have a critical function for the oystercatchers. Although high-tide roosts were significantly more elevated than randomly selected reefs, many are already threatened by overwash and erosion during the normal tidal cycle. Between 1982 and 2011, Florida's Big Bend had an average of 66 % net loss of oyster reef area. Offshore reefs had an even higher rate of loss at 88 % (Seavey et al. 2011). Eight of 13 high-tide roosts and all but one of the roosts used at night are located on offshore reefs, indicating that in the study area, high-tide roosting habitat is likely at greater risk of decline than is intermediate-tide roost habitat. Given the small number of available roosts (13 high-tide roosts versus 28 intermediate-tide roosts) and their immediate vulnerability, the amount of high-tide roosting habitat is likely to be a limiting factor for this population. In addition, there are no areas on the Gulf Coast of Florida that resemble the wintering habitat used by oystercatchers in Cedar Key, making it impossible to find similar habitat elsewhere if the habitat in Cedar Key becomes compromised.

Our analysis suggests that oystercatchers use roosting sites that are far from or lacking woody vegetation; this may be attributed to woody vegetation's providing cover for mammalian predators (e.g., mink, raccoons) and perches for raptors (Yasue 2006). Predation by raptors is an important source of adult mortality (American Oystercatcher Recovery Working Group 2012). Peregrine falcons (*Falco peregrinus*) and bald eagles (*Haliaeetus leucocephalus*) have frequently used some of these preferred roosts. If oystercatchers are forced to use suboptimal roosting locations, there could be survival and energy costs associated with increased predation and increased antipredator behaviors (Rogers et al. 2006). Oystercatchers also face further competition for optimal high-tide roost sites as human recreational use of these few exposed reefs at high tide continues to increase. Florida has documented a 20 % increase in tourism over the past 10 years (VISIT FLORIDA research 2016), and many of these tourists use marine resources.

We suggest that in the Big Bend, oystercatchers are forced to choose between rapidly declining optimal roost habitat in offshore areas and more abundant but suboptimal high-tide roost habitat closer to shore. Oyster reef habitat in the region of Cape Romain region is also declining (Sanders et al. 2004). Oyster reef habitat is more extensive in Cape Romain than it is

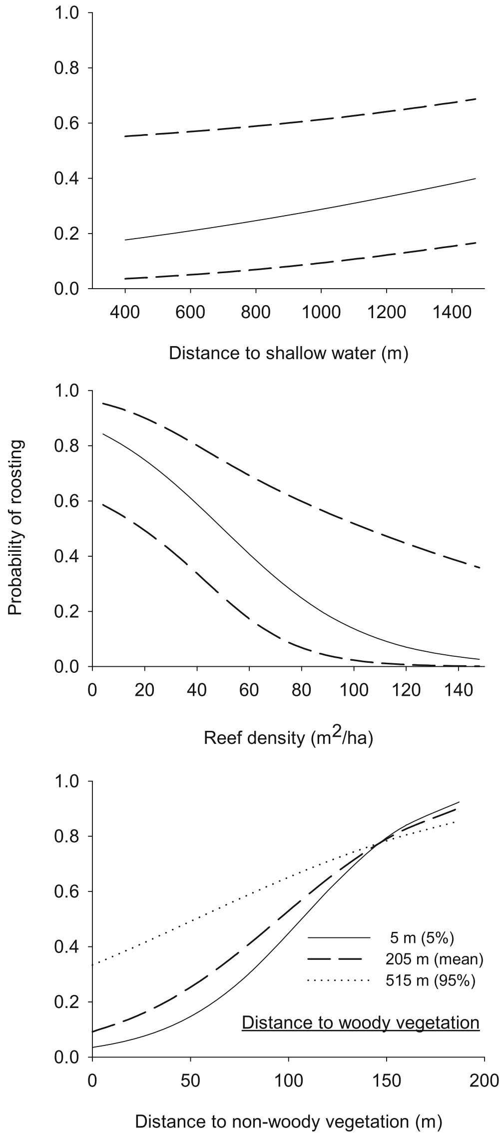

Fig. 4 The probability of oystercatchers selecting an oyster reef as an intermediate-tide roosting location related to the habitat variables included in the most parsimonious model (Table 3). The *solid lines* indicate the model-based predictions for each variable with all other variables held at their mean values. The *dashed lines* indicate the 95 % confidence intervals. All variables are plotted from the 5th to 95th percentiles of the observed values. In the *graph* representing the interaction term, the *lines* represent the effect size of distance from non-woody vegetation at given distances from woody vegetation. Confidence intervals were excluded for visual clarity

in the Big Bend of Florida, and while Cape Romain also accommodates a larger population of wintering oystercatchers, existing high-tide roost habitat is more than sufficient for that population's needs.

Since oyster reefs can grow vertically much faster than sea level is rising (Rodriguez et al. 2014), the loss of habitat is probably not due primarily to sea-level rise. Ultimately, the loss of oyster populations is linked to reductions in freshwater inputs to estuaries, a result of changing freshwater management upstream (Seavey et al. 2011). While efforts are being made to conserve upstream water resources and reduce anthropogenic impacts on frequency or severity of low-flow events, these policies may take decades to enact. In this context, an effective conservation strategy is to minimize the likelihood of further losses in oyster reefs used as high-tide roosting habitat for oystercatchers by adding durable substrate to the degraded reefs. This is likely to allow repeated recolonization of reefs by oysters following episodic die-offs. There is no apparent shortage of larvae in this nearshore ecosystem (Frederick and Sturmer, *unpublished data*), probably because mainland marsh or tidal creek oyster populations have not declined as much as offshore reefs (Seavey et al. 2011). The existence of durable substrate would allow oysters to repeatedly recolonize reefs, making them resilient in the long term to fluctuations in freshwater flow.

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