

Assessing conservation conflict: Does intertidal oyster aquaculture inhibit foraging behavior of migratory shorebirds?

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Abstract. Conservation is increasingly in conflict with human activities due to global human population growth, particularly in areas that support threatened species. Conflicts often impede effective implementation of needed conservation measures and also have implications for social inequality, resource use and economic development. Bivalve molluscan shellfish aquaculture is commonly considered one of the least impactful forms of protein production worldwide but, in some locations, may interfere with essential activities of threatened species such as the stopover ecology of migrating shorebirds. Here we assess the impact of oyster aquaculture as practiced in Delaware Bay (New Jersey, USA) on the presence and foraging behavior of migratory shorebird species of conservation concern. We conducted counts and behavioral observations of shorebirds across a 4.8-km stretch of the Delaware Bay and tested the effect of regulated aquaculture structures and activities on shorebird presence relative to various environmental factors. We also evaluated differences in mean peck rates for each species within and away from aquaculture areas, and we examined multiple factors influencing foraging rates for each species. For all species, we found that oyster tending reduced the probability of shorebird presence by 1–7%, whereas the untended aquaculture structures had no detectable impact. Foraging rates were mostly influenced by environmental conditions, particularly the presence of competitors (gulls or other shorebirds), and the foraging substrate. None of the focal species substantially altered their time budget or foraging rates in the presence of tended or untended oyster aquaculture. This evidence suggests that intertidal oyster aquaculture and migrating shorebirds can co-utilize the resource rich intertidal areas on which they occur.

Key words: aquaculture; evidence-based conservation; red knot; ruddy turnstone; semipalmated sandpiper; stopover ecology.

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INTRODUCTION

Conservation is increasingly in conflict with human activities due to global human population growth, especially within regions that house

high numbers of threatened species or are global biodiversity hotspots (Jackson and Wangchuk 2001, Harvey et al. 2008, Marini et al. 2009). These conflicts often impede the effective implementation of needed conservation measures,

and because they often have implications for social inequality, resource use and economic development, they are considered one of the most intractable problems in conservation biology (Redpath et al. 2013). In addition, there is continued human expansion into coastal areas raising the prospect for increasing rates of such conflicts arising (Lockwood and Maslo 2014). Here we assess the impact of intertidal oyster aquaculture on the presence and foraging behavior of a suite of shorebirds that are of conservation concern (Andres et al. 2012). The shorebirds are long-distance migrants that forage on invertebrates of intertidal habitats at multiple stopover sites on their way to their breeding grounds. If migrating individuals fail to sufficiently refuel, they may delay remaining migratory movements (further migration) or arrive on breeding grounds in such poor energetic condition that their breeding success is reduced (Inger et al. 2010, Morrison et al. 2013, Shoji et al. 2015). These same resource rich intertidal environments support low-input production of commercially valuable oysters, which sustains a growing local aquaculture industry (Jarvinen 2000). A central step in finding shared solutions is building an evidence base surrounding the outcomes of conflicting demands on this shared resource (Redpath et al. 2013).

Delaware Bay, located along the mid-Atlantic coastline of the USA, includes several critical habitats for both resident and migratory birds leading to its designation as a Ramsar Wetland of International Importance, an Audubon Important Bird Area, and its inclusion within the Western Hemisphere Shorebird Reserve Network and the U.S. Environmental Protection Agency National Estuary Program. Intertidal beaches and mudflats of Delaware Bay are critical stopover sites for several globally declining shorebird species, including the *rufa* subspecies of the red knot *Calidris canutus rufa*, ruddy turnstone *Arenaria interpres*, sanderling *C. alba*, and semipalmated sandpiper *C. pusilla*. These species visit Delaware Bay during their spring migration north from their wintering grounds and rely heavily on the lipid-rich eggs deposited by spawning horseshoe crabs (*Limulus polyphemus*) to gain enough weight to complete their migration and begin their breeding season in the Arctic (Clark et al. 1993, Botton et al. 1994, Duijns et al.

2017). Horseshoe crabs deposit eggs over a 3 to 7-week window each spring (Smith et al. 2002), and the timing of these shorebird migrations typically allows them to take advantage of this energetically rewarding food source during the brief period of their stopover (Tsipoura and Burger 1999, Niles et al. 2014).

Red knots were listed as endangered in Canada in 2007, and threatened under the U.S. Endangered Species Act in 2015 due to multiple threats (McGowan et al. 2015, Wikelski and Tertitski 2016). A significant factor contributing to red knot population recovery is horseshoe crab egg abundance in the Delaware Bay (Baker et al. 2004, McGowan et al. 2011, Loveland and Botton 2015). While red knots have received the most conservation attention, several additional sandpipers rely heavily on horseshoe crab eggs during their stopover in Delaware Bay (Gillings et al. 2007, Mizrahi and Peters 2009, but see Tucker et al. 2019) and have also experienced notable declines that have been associated with the reduction of horseshoe crab eggs (Haramis et al. 2007).

Aquaculture is the fastest growing segment of agriculture in the world, and production now equals fishery production globally (FAO 2018). Commercial intertidal oyster aquaculture (hereafter, oysterculture) is practiced on many continents and is a burgeoning industry in the USA, with production in some states just beginning to level off following a decade of exponential growth (Hudson 2018). Unlike other forms of aquaculture, oysterculture typically requires no addition of food, fertilizer, antibiotics or pesticides, making it a relatively environmentally benign source of dietary protein (Hilborn et al. 2018). Structures used to cultivate oysters may function as artificial reefs that are initially populated with oysters and subsequently colonized by a diverse array of species including algae, invertebrates and vertebrates, both mobile and sessile (Dealteris et al. 2004). Oysterculture typically involves rack and bag systems (or trestles) that are placed directly on intertidal sandflats with little direct alterations to the substrate or surrounding area. Overcolonization by some organisms leads to fouling that can slow growth and reduce survival of the oysters. Thus, routine maintenance of oyster bags (typically via powerwashing) is required to keep fouling from impeding flow of water to the oysters.

Loss or degradation of intertidal shorebird habitat is a significant cause of migratory shorebird declines globally (Stillman et al. 2005, Murray et al. 2014, Piersma et al. 2016, Studds et al. 2017, Weiser et al. 2017). In some areas, intensive shellfish farming has been shown to deplete prey resources (Stillman et al. 2001, Goss-Custard et al. 2004). Where direct harvesting does not occur, oysterculture practices can impact shorebird populations through displacement of shorebirds from prime foraging grounds (Gittings and O'Donoghue 2012, Szabo et al. 2016). Racks could also physically exclude shorebirds from foraging grounds between and under them (Kelly et al. 1996), or the tending activities (i.e., cleaning, harvesting) could also potentially generate sufficient disturbance to behaviorally exclude birds both from within the footprint of the rack system as well as the surrounding area (Kelly 2001, Forrest et al. 2009). Shorebirds may not abandon the area entirely, but instead experience reduced feeding rates due to altered benthic habitat (Connolly and Colwell 2005), increased vigilance and other predator avoidance behaviors of foraging birds (Thomas et al. 2003) or overcrowding of birds displaced by the racks and growers (Kelly 2001). Under some conditions, birds may simply avoid oyster racks when other suitable foraging habitat is nearby (Burger and Niles 2017). Alternatively, oysterculture could positively impact shorebirds by increasing the availability of benthic or other prey taxa (Escapa et al. 2004), or by the cultured oysters (or the invertebrate species using oyster racks) serving as a prey resource themselves (Caldow et al. 2003, Żydelis et al. 2009). Indeed, some studies have shown increased shorebird foraging around intertidal aquaculture operations (Hilgerloh et al. 2001, Connolly and Colwell 2005, Lehnen and Kremenetz 2013). Finally, oysterculture may be considered a neutral industry whereby habitat use and feeding rates are not affected (Hilgerloh et al. 2001).

Here we assess the impact of oysterculture as practiced in Delaware Bay off-bottom, intertidal rack and bag operations on the presence and foraging behavior of red knots, ruddy turnstones, semipalmated sandpipers, and sanderlings. Our focus on foraging behavior reflects the need for these shorebirds to quickly gain sufficient energy reserves for the remainder of their migration.

Alterations to behavior are often early-warning signs of detrimental changes in key demographic rates including reproduction and survival (Greggor et al. 2016). We specifically ask whether the presence and foraging rates of these shorebirds on the tidal flats are altered due to the presence of oyster racks or oyster tending activities. Lower shorebird presence in intertidal habitat near oysterculture sites relative to areas without oysterculture would suggest that shorebirds avoid oyster racks and/or tending activities. In contrast, equal or higher shorebird presence in intertidal habitat near oysterculture may suggest that shorebirds are attracted to aquaculture areas (i.e. racks provide microhabitat for benthic invertebrates; Erbland and Ozbay 2008) or that shorebirds arriving at Delaware Bay are taking more risks (by feeding near oyster racks or oyster growers) due to their depleted energy stores following migration (Houston and McNamara 1982, Myers 1983). In the latter case, quantifying differences in mean peck rates as an index of foraging energetics could provide further insight into the overall impact of oysterculture on shorebirds that use intertidal habitat for stopover refueling.

METHODS

In 2016 and 2017, we conducted behavioral observations of foraging red knots, ruddy turnstones, semipalmated sandpipers, and sanderlings across a 4.8-km stretch of Delaware Bay, USA extending from Kimbles Beach south to Green Creek (Fig. 1). We separated the study area into three distinct zones, based upon the conditions of the intertidal habitats extending perpendicular to the shoreline: aquaculture zones, creek mouths, and tidal flats. We classified aquaculture zones as intertidal habitat extending ~90 m in each cardinal direction from the edge of a rack-and-bag system, which follows the regulatory definition of such zones as designated by the United States Fish and Wildlife Service (USFWS 2016). Our study area included five distinct aquaculture zones (representing 13% of the total study area), which included private leaseholds and other racks tended within the New Jersey Department of Environmental Protection Aquaculture Development Zone. We classified creek mouths as tidal creek drainage areas

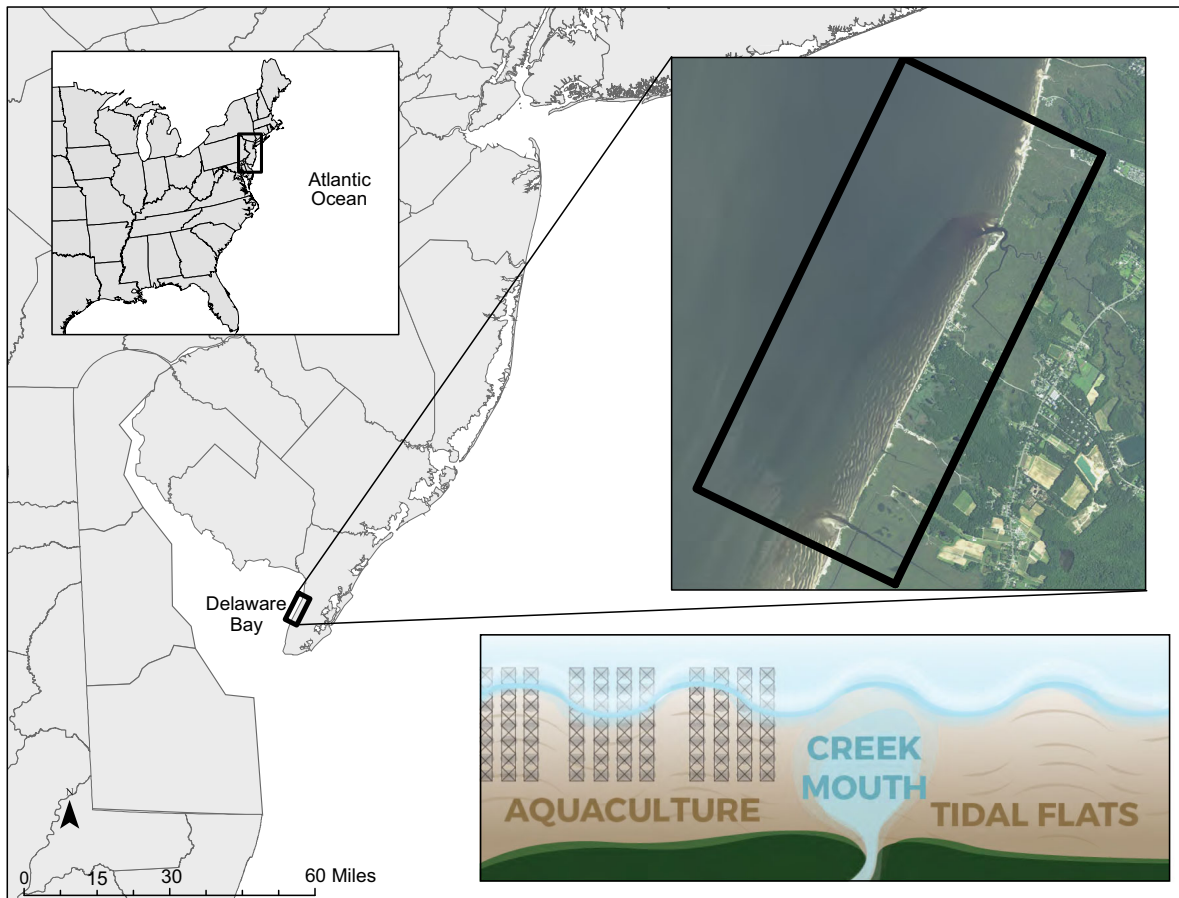


Fig. 1. The study occurred along a 4.8-km stretch of the Delaware Bay, New Jersey, USA extending from Kimbles Beach south to Green Creek. Observations occurred in three distinct zones (aquaculture, creek mouth, tidal flat), based upon the conditions of the intertidal zone extending perpendicular to the shoreline. Aquaculture zones included buffer areas extending ~ 90 m in each cardinal direction from the edge of an oyster rack-and-bag system.

surrounded by sandbars and shoals; the study area contained four creek mouths. We classified remaining intertidal areas as tidal flats without aquaculture. Creek mouths are considered high-quality foraging habitat for migratory shorebirds due to the exchange of nutrients from the tidal creeks and the accumulation of horseshoe crab eggs (Botton et al. 1994), thus serving as a baseline from which to compare foraging rates within aquaculture zones and other intertidal habitat.

Counts of shorebird flocks

From May 4 to June 5 in both study years, we conducted three daily counts (2 h per count) of the entire study area to determine the number

and location of shorebird flocks present. Shorebird counts occurred daily between the hours of 06:00–21:00 and were scheduled to capture low tide, defined as the 2.5-h period on either side of the daily predicted low tide. It is during this time that the oyster racks are exposed from the water, and thus present on the landscape and able to be detected by birds. It also spans the 4-h time interval (2 h on either side of low tide) when oyster-culture personnel are legally permitted to initiate and complete all tending activities. For counts, intertidal habitat zones were further subdivided into 30-m segments extending perpendicularly from the mean high tide line to ~ 100 – 200 m at the narrower northern section up to ~ 375 m at

the widest portions in the southern section. This subdivision allowed for higher resolution in determining, for each shorebird species, a probability of presence for a given census location. For each flock observed, we estimated the number of individuals per species. We recorded the distance from the flock edge to the nearest aquaculture structure. Within aquaculture zones, we recorded whether individuals were between the racks of an oysterculture system, and if not, at what distance from the rack they were foraging (<15 m, 15–30 m, 30–60 m, 60–90 m, or >90 m); these distance categories were based upon published recommended human disturbance buffer distances (Thomas et al. 2003, Koch and Paton 2014). We also noted whether the nearest aquaculture structure was being tended at the time of the survey. We considered a structure to be tended when oyster growers were physically present within the aquaculture zones. Tending restrictions in effect during the study period are detailed in the USFWS Biological Opinion (USFWS 2016). Generally, these regulations allowed tending to occur during the four hours centered around low tide up to five days per week. Tending operations typically involved 1–10 oyster growers and 0–2 ATVs accessing a rack and bag system and consisted of sorting oysters among bags, power-washing fouling material off of bags, and driving all-terrain vehicles across the tidal flats.

To compare the relative magnitude of potential oysterculture impacts with environmental conditions, we also collected data on a suite of metrics hypothesized to influence shorebird presence (Appendix S1: Table S1). Because the timing of shorebird arrival on the breeding grounds is temporally phased and varies each year, we recorded the day of the calendar year for each survey record. We accounted for potential differences in habitat suitability by recording the adjacent shoreline type (dune, *Spartina* marsh, *Phragmites*, woodland, or bulkhead) of each survey segment (i.e., predation risk may be greater in areas of dense vegetation; Yasué 2006). We also noted the presence of low-flying planes that passed over the segment in which the birds were located during the count (there is a banner plane airport in the southern portion of the study area), and whether humans and/or dogs passed within 100 m of the segment being surveyed. The

presence of either disturbance may cause shorebirds to refrain from foraging close by and influence our data between survey segments (Burger et al. 2007, Weston and Stankowich 2013). Finally, to incorporate potential influences of competitors on shorebird presence within survey segments, we counted the total number of non-target shorebird species (i.e., not one of our four focal species) and gulls present in a survey segment at the time of census counts. In particular, laughing gulls (*Leucophaeus atricilla*) are a common predator of horseshoe crab eggs in Delaware Bay (Botton 1984, Karpanty et al. 2006).

We performed an ANOVA of the size of flocks observed within each intertidal habitat zone to assess whether there were significant differences in flock size for each species. Because we were specifically interested in the effect of oyster tending on flock size, we separated observations within aquaculture zones based upon whether or not tending was occurring at the time of the observation. For statistically significant ANOVAs, we performed pairwise Tukey's honest significant difference (HSD) tests to identify differences between habitat zones and/or tending status.

Prior to statistical modeling, we standardized all covariate data by dividing covariate values by two standard deviations of a respective predictor mean. Doing so allowed for the interpretation of all regression coefficients in the same way as binary inputs (Gelman 2008). We constructed 23 a priori models to test both univariate relationships, as well as additive relationships, of the various covariates (Appendix S1: Table S2) and ran them using a Bayesian formulation of generalized linear mixed models in R using the package rjags (Plummer 2014). For all models, we included year and survey segment as random effects to account for a lack of temporal independence in count data (i.e., three counts were made of each survey segment in a given day and multiple counts were made of the same segment in a given study year). To test for general goodness of fit of the various model formulations, we used Bayesian *P*-values (Kéry and Schaub 2011). We ran our candidate model set and ranked them by the deviance information criterion (DIC), a measure of predictive accuracy of Bayesian models (Speigelhalter et al. 2002). We considered the best model for each species as the one with lowest

DIC value. Where multiple models within a given species-specific model set returned a $\Delta\text{DIC} < 10$, we model-averaged the regression coefficients using the BMA package in R.

Behavioral observations of foraging shorebirds

After each count, we conducted three simultaneous 45-min periods of observations of separate foraging flocks we had observed. Using a video-enabled camera connected to a 60 × spotting scope, we randomly selected focal individuals within observed flocks of target species to record behaviors for a period of 45 s from an unobtrusive distance (>150 m). Our study was designed to capture differences in foraging behavior at the scale of individual birds, rather than flock-level responses to potential disturbances (i.e., frequency of flushing). We prioritized red knots because of their legal conservation status (federally listed), followed by ruddy turnstones, semipalmated sandpipers, and sanderlings. If the individual, during its typical foraging behavior, temporarily moved out of view (i.e., behind another individual or vegetation), we continued the observation if it returned to view within 20 s and we were certain that it was the same bird. In cases where the individual remained out of view for longer periods of time, or we could not definitively recognize the same individual, we aborted the observation attempt. Duplicate observations of the same individuals in a given day were unlikely because either the flock was dispersed enough for us to keep track of focal individuals during our observation period, or the flock was sufficiently large enough that the probability of selecting the same focal bird for two or more observations was extremely small.

For each observation, we recorded the intertidal habitat zone in which the focal individual was foraging (aquaculture, tidal flat, creek mouth). As above, we noted whether the oyster-culture rack system nearest to the focal individual was being actively tended. To examine potential influence of habitat conditions on peck rates, we recorded the foraging location of each focal individual (beach, mudflat, shoal, slough, or open water), foraging substrate on which it moved (mud, peat, sand, wrack line, or oyster bag), and the wind speed associated with the observation of the focal individual (see Appendix S1: Table S1 for descriptions of

predictor variables). Finally, we noted the location of the focal individual within the flock (edge, center, or solitary) and the total number of shorebirds and gulls (separately) in the flock in which the focal individual was feeding.

We downloaded videos using VLC Media Player 2.2.6 (VideoLAN, videolan.org) and played back each sample at one-quarter speed (to maximize counting accuracy) to document the activity of the focal individual in each recording and retained only the low tide observations. The resolution of our videos were adequate for evaluating foraging behavior; however, we could not reliably determine capture success and therefore did not measure foraging efficiency. During high tide, the oyster racks and tidal flats are completely inundated, and thus not used by foraging birds and unavailable for tending activities.

We prepared a foraging time budget for each focal individual observed foraging during low tide, noting the time of the 45-s sequence each individual engaged in foraging (probing the ground, pecking at organic matter, or scanning the ground for prey items); being vigilant (standing erect, visually scanning the surroundings; or watching a specific perceived threat), running or walking away from an apparent threat (discernible from short-distance walks between pecking bouts), and flying away (from a perceived threat). In most cases, the observer maintained sight of focal individuals that flushed and returned to the same area to resume foraging. When the focal individual left the immediate foraging location completely, the observer recorded it flying away until the 45-s sample period concluded. Time spent engaged in any additional activities, such as preening, was recorded as other.

We calculated the pecking rate (pecks/s) of each individual during the observation period as an index of foraging rate. Because it was not possible to definitively document successful prey captures in many of the video samples, we did not quantify foraging efficiency. We used a one-way analysis of variance (ANOVA) and Tukey's HSD to evaluate differences in mean peck rates for each species within each habitat zone, with significance evaluated at the $\alpha = 0.05$ level.

We performed multiple linear regression using the glm function using the Poisson family in R to explain variation in mean peck rate for each

species (R Core Development Team 2013). We developed 29 a priori candidate models containing explanatory variables alone or in various combinations (Appendix S1: Table S3). Because the Delaware Bay beaches are closed to the public during the migratory stopover period, we recorded < 5 observations of humans walking with or without dogs; therefore, we excluded these variables from the regression analysis. To test for goodness of fit, we calculated the coefficient of multiple determination for the global model for each species (Appendix S1: Table S4), and we used small-sample corrected Akaike's Information Criterion (AIC_c) to rank candidate models (Burnham and Anderson 2002). To reduce model selection bias and uncertainty, we averaged all models returning a $\Delta AIC_c < 2$ using the `modavg` package in R and calculated parameter estimates based on weighted averages of the parameter estimates in the top models (Burnham and Anderson 2002, Burnham et al. 2011).

RESULTS

Predictors of shorebird presence

Shorebird abundance for all species varied considerably within each survey segment and across the study period, with group sizes ranging from one to ~3700 individuals. Because aquaculture zones comprised only 13% of the total study area, direct comparisons of the total number of shorebird observations among intertidal habitat zones (aquaculture areas, tidal flats, and creek mouths) were not informative. However, the percentage of total observations for each target species within aquaculture zones ranged from 21% for sanderlings to 24% for semipalmated sandpipers, which is higher than if shorebirds were distributed randomly across the study area. For red knots, we found no significant differences in flock size among the habitats, regardless of tending activities ($df = 5$, $F = 0.935$, $P = 0.458$). For ruddy turnstones, flock sizes were significantly greater in creek mouths than aquaculture areas and tidal flats ($P < 0.01$), regardless of whether tending was occurring nearby. For semipalmated sandpipers, we found that flock sizes were significantly larger in creek mouths than in tended flats ($P < 0.01$) and untended aquaculture areas ($P < 0.01$), as well as tidal flats ($P < 0.01$).

Within aquaculture zones, we consistently recorded more observations of birds near untended racks than when oyster tending was occurring (Fig. 2). We did observe all focal species foraging in between racks during tending operations on rare occasions (2–9% of all observations of the four species within aquaculture zones). For all focal species, birds were most frequently observed between the rack system and the high tide line.

The top-ranked models for all species included tending as a significant predictor of presence within a survey segment (Appendix S1: Table S5). In the absence of tending, the probability of presence within a given segment of the entire study area was generally low, ranging from ~17% for red knots and sanderlings to ~50% for semipalmated sandpipers (Fig. 3). When the nearest rack was tended, probability of presence in associated surveys dropped by 1.6–7.0% depending on the species (Fig. 3; Appendix S1: Table S6). The total number of shorebirds also strongly predicted presence of red knots, ruddy turnstones and sanderlings within a survey segment, with effect sizes ranging from 1.240 (CI 0.974, 1.283) for sanderlings to 3.529 (CI 3.164, 3.904) for ruddy turnstones (Appendix S1: Table S6). Effect sizes of total number of shorebirds on species presence were positive and an order of magnitude greater than for presence of tending (negative impact) in all cases. The number of gulls was also a top predictor of semipalmated sandpiper presence within survey segments (0.165; CI 0.063, 0.267).

Time budgets and foraging rates

During the study period, we retained 856 foraging (peck rate) observations across the four species. The majority of our observations were of foraging red knots ($N = 507$) and ruddy turnstones ($N = 231$), with fewer observations of semipalmated sandpipers ($N = 99$) and sanderlings ($N = 19$). On average, individuals of all species spent the majority (86.4–95.3%) of time within our recordings actively foraging (Fig. 4). We found no significant differences in time individuals spent foraging among creek mouths, tidal flats, and aquaculture zones (red knots, $P = 0.816$; ruddy turnstones, $P = 0.624$; semipalmated sandpipers, $P = 0.936$; sanderlings, $P = 0.667$). Individuals of all species spent < 14%

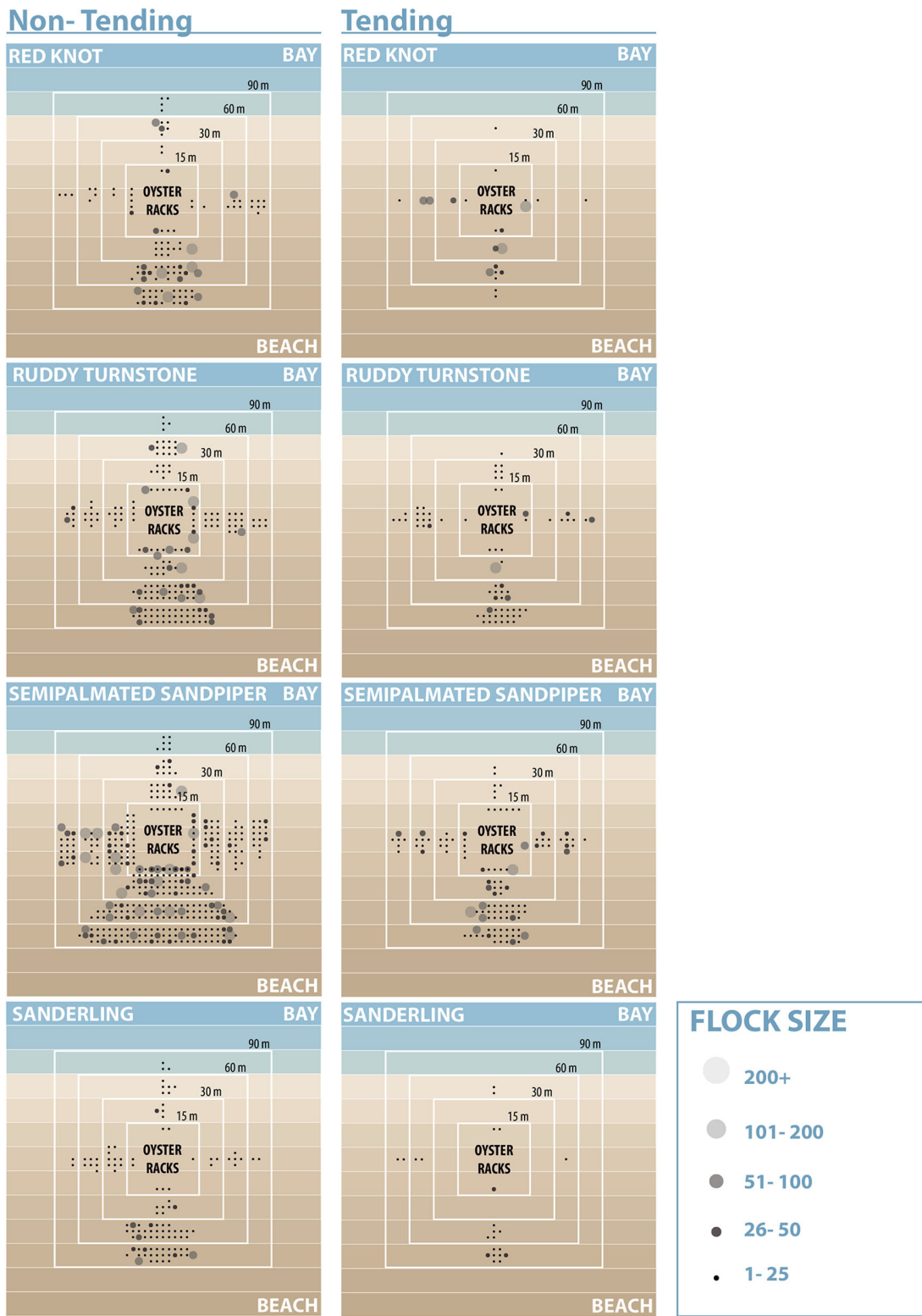


Fig. 2. Graphical representation of the total number of observations of target migratory shorebirds within

(Fig. 2. *Continued*)

90 m of untended and tended oyster racks along the Delaware Bayshore, 2016–2017. Circle size and shading is an indicator of flock size. Circle position represents the general flock location (in front, along the side, or behind racks) within each distance category (not drawn to scale). Size and shading of circle indicates flock size. Observations of birds within the footprint of the rack system are included in the 0–15 m distance category. The 90 m distance along the shoreline is at or near the high tide line. Distances closer to the bay were exposed for shorter periods of time.

engaged in other behaviors (Appendix S1: Table S7). We found notable differences in time budgets among species. For example, recorded red knots and semipalmated sandpipers spent very little time engaged in vigilance behaviors or running away. Instead, when these species showed signs of disturbance, they flew up and circled briefly before returning to the same location or flew away from our observation sites. In

contrast, ruddy turnstones flew less frequently in response to apparent disturbance, spending more time running away. Sanderlings appeared least sensitive to disturbance, but our sample size was small. Red knots foraged at significantly higher rates near tended aquaculture as compared to tidal flats (Fig. 5). In contrast, ruddy turnstones foraged at a significantly lower rate in tended aquaculture zones as compared to when

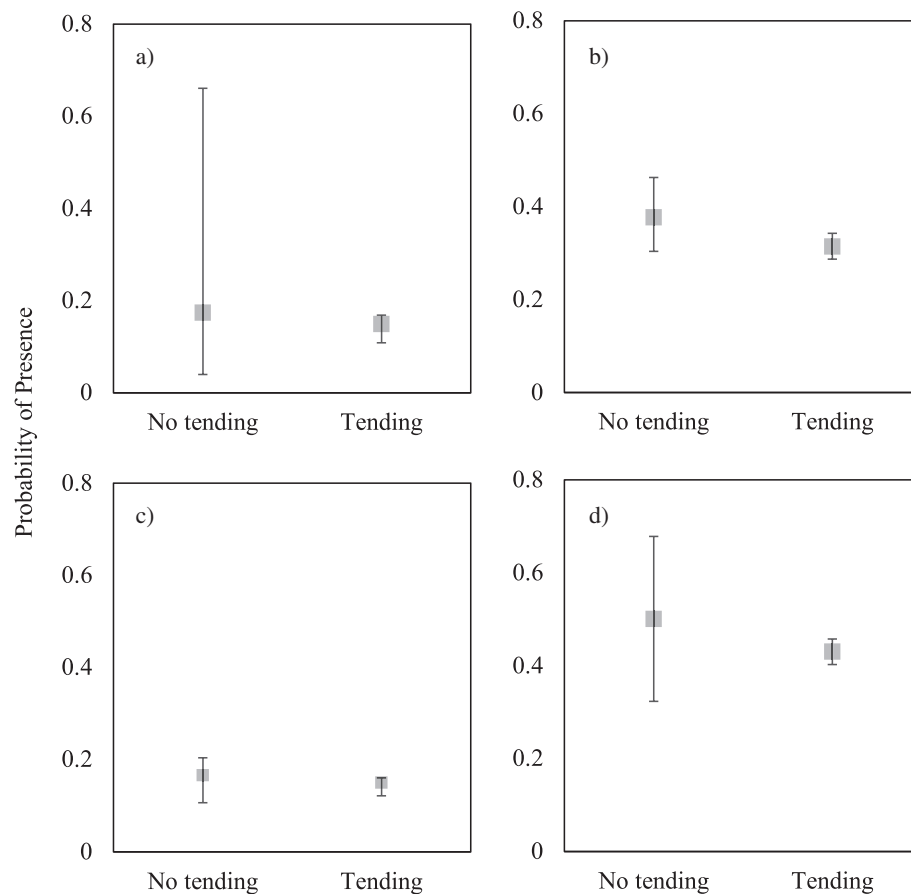


Fig. 3. Probability of presence by (a) red knots, (b) ruddy turnstones, (c) sanderlings, and (d) semipalmated sandpipers of a given survey segment along our entire study area as a function of oyster tending. Probabilities are derived from conversion of regression coefficients (including 95% credible intervals) of the top-ranked Bayesian linear regression models (logit scale).

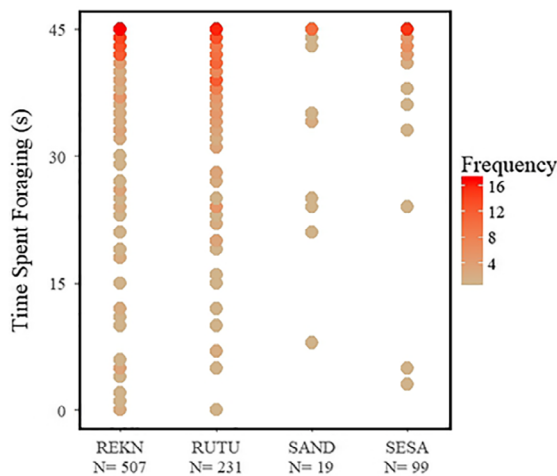


Fig. 4. Density plot illustrating the time red knots (REKN), ruddy turnstones (RUTU), sanderlings (SAND), and semipalmated sandpipers (SESA) spent foraging during each observation, 2016 and 2017.

they were near creek mouths. Semipalmated sandpiper peck rates were similar in all habitats.

Factors influencing foraging rates of shorebirds

Regression models for red knots, semipalmated sandpipers, and sanderlings returned a single top model from among the candidate set (Appendix S1: Table S8). Higher wind speeds negatively impacted the foraging rates of red knots (-0.16 , 95% CI -0.26 , -0.06) and sanderlings (-0.44 , 95% CI -0.64 , -0.24); the presence of gulls slightly increased red knot foraging rates (0.004 , 95% CI 0.003 , 0.006 ; Appendix S1: Table S9). Semipalmated sandpipers, in contrast, showed slightly reduced foraging rates in the presence of gulls (-0.02 , 95% CI -0.04 , -0.01). For these species, the proximity or tending condition of an oyster rack had no influence on foraging rate, as demonstrated from the absence of these covariates within the top models (Appendix S1: Table S8).

Ruddy turnstone foraging rate was influenced by multiple factors, including wind speed, habitat zone, foraging location and foraging substrate. Relative to creek mouths, ruddy turnstones foraged at higher rates in tidal flats and aquaculture zones (Appendix S1: Table S9). Sloughs (shallow pools of water left by the tide) and the wrack line had clear negative impacts on foraging rates, but results from other foraging

locations and substrates, respectively, were equivocal. Consistent with red knots, semipalmated sandpipers and sanderlings, the distance to an oyster rack and its tending status had no influence on ruddy turnstone foraging rates (Appendix S1: Table S9).

DISCUSSION

The intertidal habitats of Delaware Bay are a prime example of cases where human activities are simply occupying, and not altering, the same spaces used by species of conservation concern (Burger and Niles 2017), rendering ecological impacts subtle and difficult to quantify. We show here that oysterculture racks, located away from prime foraging areas as prescribed in conservation measures, have little influence on the distribution of migratory shorebirds along Delaware Bay. Oyster tending activities do reduce the probability of presence by ~ 1.6 – 7% ; however, these slight reductions in probability of presence are considerably smaller than the effects of gull and shorebird numbers within the same area. This result is consistent with Burger et al. (2018), which also identified total shorebirds as a significant predictor of red knot, ruddy turnstone, semipalmated sandpiper and sanderling presence in Delaware Bay. During our 7-week study periods, both gulls and shorebirds are intensively exploiting the pulsed horseshoe crab egg resource (Shuster and Botton 1985, Burger and Gochfeld 1991b, Niles et al. 2014). Thus, it is intuitive and consistent with other studies that larger shorebird flocks would result in a higher likelihood that individuals of a focal species would be present. We did not survey horseshoe crab egg abundance or density due to the survey intensity required to achieve meaningful results (Smith et al. 2002, Munroe et al. 2017), but Munroe et al. (2017) found no discernable impact of oysterculture racks on horseshoe crab activity. In addition, shorebird abundance was greatest in the area between the oyster racks and high tide line, likely because it is here where horseshoe crab nests occur in high densities and where exhumed eggs tend to accumulate on the beach surface (Botton et al. 1994, Nordstrom et al. 2006). This intertidal zone is also exposed for the longest period of time during each tidal cycle. Thus, our findings support other studies linking the

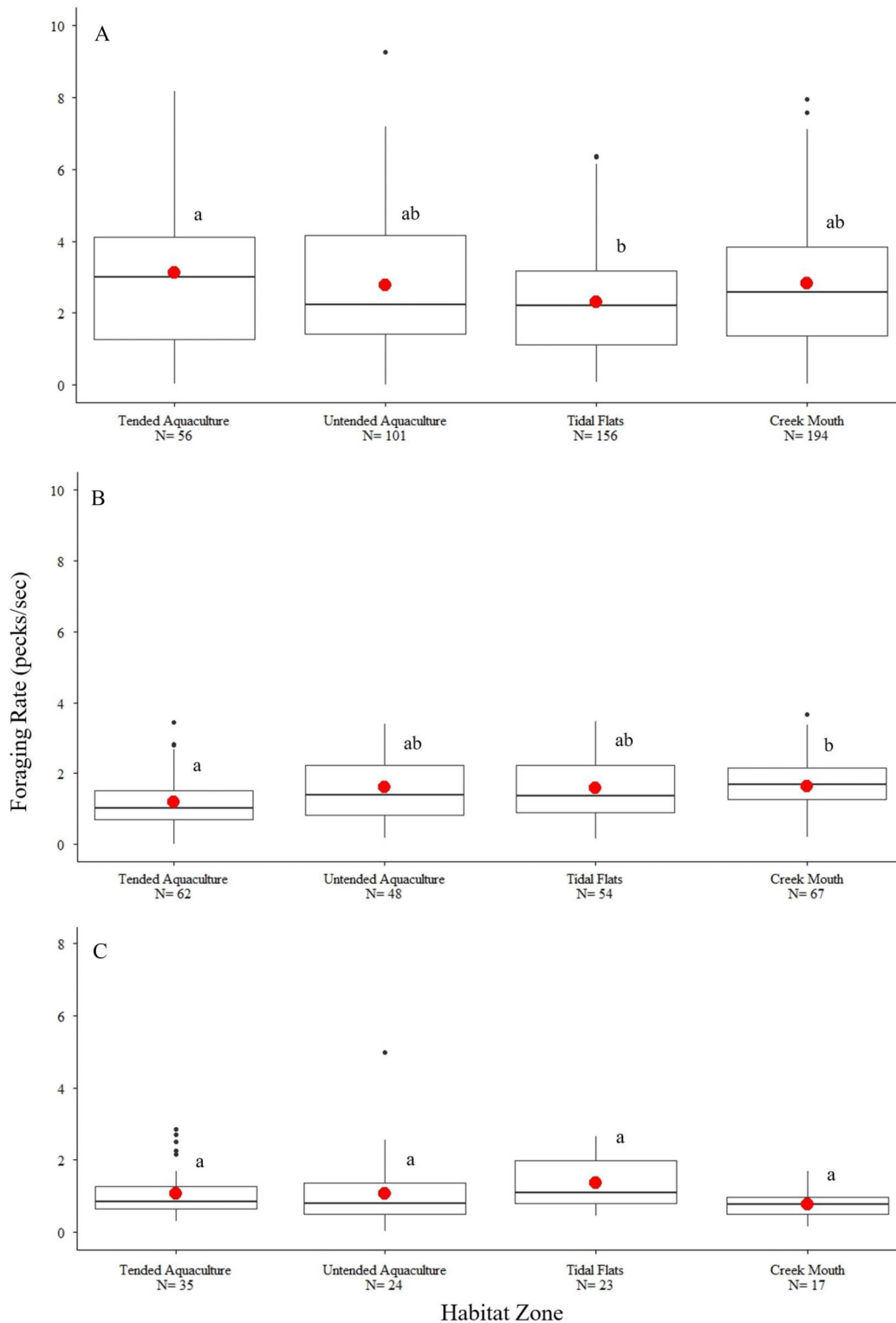


Fig. 5. Differences in mean peck rates of (A) red knots, (B) ruddy turnstones, and (C) semipalmated sandpipers foraging in creek mouths, tidal flats, and untended and tended aquaculture sites during low tide.

distribution of migratory shorebirds with crab egg densities (Karpanty et al. 2006).

That shorebirds do not substantially avoid oyster racks and are only modestly affected by tending activities does not confirm a neutral impact of oysterculture on vulnerable shorebird populations. Long-distance migrants reduce their digestive organs for migratory flights, leaving them only 10–12 d to double body weight before they must complete their migration to the Arctic (Baker et al. 2004). Birds arrive in Delaware Bay physically stressed and rely heavily on horseshoe crab eggs as a food source to gain needed body mass to continue migration (Jehl 2007, Mizrahi and Peters 2009, Andres et al. 2012). Therefore, small differences in the probability of presence does not by itself indicate a lack of impact.

Rather, response to a disturbance depends largely on the perceived severity of the threat (risk of mortality) and the cost of responding, measured in lost food or energy (Frid and Dill 2002, Yasué 2005). Presence of individuals despite a disturbance makes them appear tolerant of the disturbance but can result from poor body condition leading to riskier decision-making (Houston and McNamara 1982). Individuals typically are more sensitive to human disturbance if they are in good body condition because they can afford to expend energy (Burger and Gochfeld 1991a, Gill et al. 2001, McGowan et al. 2002). In contrast, energetically stressed individuals may prioritize energy gains over predator avoidance as they may incur a significant (and potentially insurmountable) cost of abandoning a foraging site (Yasué 2005, Yasué et al. 2008). Alternatively, individuals will abandon a foraging site more quickly if other suitable foraging habitats are available (Fretwell 1972, Yasué 2005). Thus, for our observations to reflect no cost to the entire stopover population, individuals present in sites with oysterculture must forage at rates equal to that of other suitable non-oysterculture foraging habitats.

The species we observed did not substantially alter their foraging rates in the presence of tended or untended rack-and-bag oysterculture. We found instead that foraging rates were mostly influenced by environmental conditions, particularly the presence of competitors (gulls or other shorebirds) and the foraging substrate. Despite some minor statistical significance

among habitat zones and tending activities, mean peck rates were generally consistent regardless of whether birds foraged near untended or tended oyster racks, tidal flats or creek mouths. These patterns were consistent across individuals regardless of their location in the flock, which is important given that a seemingly tolerant group of animals may consist of less sensitive individuals closest to the disturbance and more sensitive individuals farther away (Samia et al. 2016). The most discernable effect of tending was observed in ruddy turnstones, which foraged at lower rates in tended aquaculture zones than at creek mouths, which are considered prime foraging habitat. However, turnstone individuals did forage at statistically similar rates within tidal flats without aquaculture, and there were no differences in time spent foraging across habitat zones at low tide. Notably, individuals of our focal shorebird species spent the majority of their time engaged in foraging behaviors, with few differences in vigilance or fleeing (walking or flying away from a disturbance) among the habitat zones.

The evidence presented here suggests that intertidal oysterculture at its current density and with current buffer zones can successfully co-utilize these resource rich intertidal areas with migrating shorebirds. The degree to which this co-use may represent a lack of impact on the shorebird populations regardless of the scale of oysterculture operations, however, awaits two informational inputs. First, the energetic intake resulting from our observed foraging rates must be sufficiently large that individuals are likely to survive the rest of their migration north and be able to initiate breeding. We could not reliably determine capture success of foraging individuals which could be higher or lower near oysterculture operations. The percentage of individuals reaching the mass threshold has varied greatly over the last 15 yr, likely due to multiple factors; thus, potential effects of oysterculture on shorebird weight gain remains unknown and could vary if there are significant differences in prey capture efficiency even though foraging rates are essentially unaffected. Second, oysterculture along the Delaware Bayshore is currently at low densities. Our observations on shorebird use and foraging rates of intertidal areas around oysterculture racks may be due to this currently small

oysterculture footprint. Knowledge of how impacts change with increasing intensity or spatial coverage of oysterculture will be critical for determining the threshold density at which shorebird populations are demographically impacted. Our observations here can serve as a foundation for acquiring a strong empirical evidence-base for strengthening linkages between these tradeoffs and for informing energetic population models for these species (West et al. 2002, Studds et al. 2017).

CONCLUSIONS

Relative to other forms of animal protein production, oysterculture is one of the least impactful enterprises for feeding a rapidly expanding human population (Hilborn et al. 2018), and it provides many environmental benefits including water filtration, nitrogen removal, and the provisioning of near-shore habitat similar to natural oyster reefs (Coen et al. 2007, Dumbauld et al. 2009, Maslo 2014). As a significant contributor to global food security and economic growth, oysterculture will almost certainly remain a growing commercial industry. At the same time, global migratory shorebird populations continue to decline worldwide from multiple anthropogenic causes (Piersma and Lindström 2004, Sutherland et al. 2012). The degree to which oysterculture practices conflict with the conservation of migratory shorebirds relies on the identification and direction of impacts, and the ability to determine if a balance in tradeoffs between food production and biological conservation is necessary and achievable. Our results suggest such a trade-off is possible for Delaware Bay at present levels of oysterculture, and our data can guide further work to scale up research to whole-population dynamics.

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