

## Ecology of a vulnerable shorebird across a gradient of habitat alteration: Bristle-thighed Curlews (*Numenius tahitiensis*) (Aves: Charadriiformes) on Palmyra Atoll

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### Abstract

Palmyra Atoll, USA, in the Central Pacific, has remained mostly uninhabited since construction and abandonment of a U.S. Naval base during World War II. However, the effects of Navy modifications have persisted, affecting physical conditions and benthic habitat quality of Palmyra's lagoon sand flats. Sand flats provide important nonbreeding habitat for Bristle-thighed Curlews (*Numenius tahitiensis*), a migratory shorebird listed as "vulnerable" by the IUCN. We used camera trapping, observations of focal individuals, and quantification of prey availability and sediment characteristics to assess curlew habitat use across different levels of historical anthropogenic impact. Habitat preferences were not determined by the degree of land reclamation impact on lagoon flat habitat, although the two most preferred sites were both highly impacted. Curlew abundance was most strongly correlated with availability of prey items, such as spionid polychaetes (*Malacoceros* spp.). Our findings provide new ecological information on a shorebird species that is rarely studied, and provides useful information for habitat management at Palmyra Atoll and other curlew wintering grounds.

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## Introduction

Historical accounts of remote Pacific islands evoke landscapes, flora, and fauna profoundly different from those observed today (Dawson 1959, Stoddart 1968). Twentieth-century visitors to these islands introduced alien species, dredged reefs to create boat channels, expanded land masses to construct runways, and left behind debris from wrecked vessels (Magier and Morgan 2012). In one of the first scientific assessments of anthropogenic impacts on a coral reef ecosystem, Dawson (1959) documented the dramatic modifications to the lagoons and vegetation of Palmyra Atoll, USA that accompanied the construction and abandonment of a World War II-era U.S. Naval base. Although the island has remained mostly uninhabited since the abandonment of the base in 1945, the effects of these past alterations persist to the present day (Maragos et al. 2008b).

Today, Palmyra Atoll provides important habitat for several species of resident nesting seabirds and at least four species of migratory shorebirds, three of which are of conservation concern (Engilis and Naughton 2004, Maragos et al. 2008a). Shorebirds inhabit beaches, grasslands, wetlands, and tundra (Brown et al. 2001, Warnock et al. 2001, Colwell 2010) – habitats that are rapidly disappearing due to coastal and agricultural development and pollution (Noss et al. 1995, Junk 2003). Recent evidence suggests that global shorebird populations are in decline (Colwell 2010).

Bristle-thighed Curlews (*Numenius tahitiensis*) are shorebirds that breed in Alaska in the boreal summer and winter on small tropical and subtropical oceanic islands (Kessel 1989, Gill and Redmond 1992, Marks et al. 2002). They are the only species of shorebird that depends exclusively on oceanic islands for feeding during the non-breeding season (Kessel 1989, Gill and Redmond 1992). The IUCN Red List (BirdLife International 2008) classifies this species as “vulnerable” due to its small and declining populations. Declines are driven by predation on

curlews on their wintering grounds by introduced mammals (Gill and Redmond 1992, Marks 1993) as well as by loss of these wintering grounds to land development (Wodzicki 1981, BirdLife International 2008).

While there is substantial information about *N. tahitiensis* from its breeding grounds in Alaska (Gill et al. 1990, Lanctot et al. 1992, Marks et al. 2002), information on habitat use at non-breeding sites is scarce and generally obtained from large-scale bird surveys (Gill and Redmond 1992, Marks and Redmond 1994). Wintering curlews appear to have varied, generalized diets that range from terrestrial insects and bird eggs to fiddler crabs and other intertidal invertebrates. (Bakus 1967, Ely and Clapp 1973, Gill and Redmond 1992, Marks and Hall 1992). In a study conducted on Rangiroa Atoll (Tuamotu Archipelago), curlews were found mostly in saltpan habitats and channels between islets, and, less often, on ocean terraces and sand beaches (Gill and Redmond 1992). Gill and Redmond (1992) suggested that the presence of humans and introduced domesticated and feral animals, not habitat type, might be the most important determinant of curlew distributions on Rangiroa Atoll and in other areas where they have been historically hunted or are at risk of predation.

In addition to being a location of critical importance for Bristle-thighed Curlews (Marks and Redmond 1994), Palmyra offers a unique opportunity to compare habitats with dramatically different histories of human disturbance within a single atoll. Palmyra Atoll hosts one of the largest aggregations of curlews of any Central Pacific Island, with 266 individuals as of 2010 (U.S. Fish and Wildlife Service 2011). Shallow, non-vegetated, intertidal sand and mud flats occupy the margins of Palmyra Atoll's lagoons. Bristle-thighed Curlews forage on these flats during low tides and congregate on the atoll's only remaining airplane runway at high tides (A.S. Guerra, pers. obs.). Palmyra Atoll has been largely uninhabited throughout its history, but the effects of human occupation during World War II persist to the present day (Collen et al. 2009). In the 1930s and 1940s, the US Navy dramatically modified the atoll, cutting a channel through the reef, nearly doubling the total land area of the islets through land reclamation, and restricting water flow to parts of the atoll's inner lagoon and flats by building roads and causeways between them (Collen et al. 2009). The modifications altered natural water flow and increased

lagoon water retention and temperatures, which affects sediment particle size and duration of the flat's submersion during high tides, and permanently lowered water levels in the lagoon, which increased the extent of shallow lagoon flats accessible to intertidal foragers (Maragos et al. 2008b, A.S. Guerra, pers. obs.). This resulted in sand flats with varying levels of impact and differing invertebrate communities along the shores of the lagoon (A.S. Guerra, pers. obs.). In 2010, a plan to restore parts of the atoll to their pre-World War II state by reducing or removing artificial restrictions to water flow through lagoons was proposed to U.S. Fish and Wildlife Service by the Army Corps of Engineers (A. Pollock, USFWS Palmyra Atoll Refuge Manager, pers. comm.). The Corps' proposal was not approved, but such restoration efforts are still being considered, and any restoration aiming to remove artificial water restrictions is likely to substantially change Palmyra's lagoon flats (A. Pollock, USFWS Palmyra Atoll Refuge Manager, pers. comm.). The potential impact of this intervention on shorebirds has not yet been explored.

To examine the potential consequences of past lagoon flats alteration and proposed restoration, we assessed curlew habitat use and feeding behavior across lagoon flat sites with varying degrees of anthropogenic impact due to land modifications. Our goal was to quantify spatial variability in *N. tahitiensis* habitat use on Palmyra Atoll, to elucidate how land alterations made to the Atoll by the U.S. Navy during World War II might have affected availability of lagoon flat habitat for curlews, and to shed light on whether planned restoration efforts might increase or decrease habitat availability for curlews. We observed high abundances of fiddler crabs (one of the preferred prey of curlews on other wintering grounds; Bakus 1967, Gill and Redmond 1992) at sites where effects such as water restriction from land reclamation were acute, and we therefore predicted that curlews would prefer these highly impacted sites relative to other flats. Additionally, sediment size can affect abundances and densities of different prey types (Yates et al. 1993) and shorebird foraging behavior (Colwell 2010). Shorebirds with probing behavior tend to favor fine sediment, while shorebirds such as curlews, which peck at the surface of the sediment, favor coarser sediment (Colwell 2010). Thus we predicted that sites with coarser sediments might be preferred.

We quantified Bristle-thighed Curlew presence and abundance across 12 sites varying in land reclamation impact by using camera traps at each of the sites during low tides. We studied foraging behavior and preferences by observing curlew foraging behavior and sampling macroinvertebrates at each site.

### Methods

We conducted field work on the lagoon sand and mud flats of Palmyra Atoll National Wildlife Refuge (5.86° N, 162.08° W), a tropical atoll in the central equatorial Pacific Ocean. All data were collected between July 18 and August 20, 2012.

### Site Selection

We selected sites by first delineating impact zones across the entire atoll. Two observers familiar with Palmyra's lagoon flats (ASG and CLW) consulted historical aerial photography (FAB Pearl Harbor (a)), modern satellite imagery (Google Earth V.7.0.3.8542, 2013), and a study of historical geomorphology of the atoll (Collen et al. 2009) to delineate zones of high, moderate, and no land-reclamation impact. Criteria for these categories included the site's proximity to reclaimed land, difference in land area before and after construction, and restrictions to water flow due to construction of the Naval base (Fig. 1; Maragos et al. 2008b, Collen et al. 2009). We then selected a total of 12 sites across impact zones (five high impact sites, four low impact sites, and three no impact or control sites). We selected sites that were composed entirely of sand or mud flat, remained mostly exposed during the two daily low tides, and were accessible to observers (Fig. 2). <<Figure 1 near here>><<Figure 2 near here>><<Figure 3 near here>>

### Prey Abundance

In order to measure the relative availability of potential curlew prey items, we sampled macroinvertebrates using a 20-cm diameter sediment core. We selected coring sites by randomly choosing a cardinal direction (0° to 360° from north) and sampling at a spot 3 m in that direction

from the center point of the site (Fig. 3). Three cores were taken at each site once during the study period and the cored sediment was passed through a nested mesh sieve of 6-mm and 1-mm mesh size. Macroinvertebrates recovered from the sieve were identified to the lowest taxonomic level possible and counted in the field (Colin and Arneson 1997, Gosliner, et al. 1996, Hoover 2006, Madrigal 1999, Severns 2001). We calculated taxon richness as the number of macroinvertebrate species present at each site, and prey abundance as the average abundance of macroinvertebrates at each site.

Since fiddler crabs (*Uca tetragonum*) were not adequately characterized by our sediment core due to their rapid burrowing behavior, we obtained an estimate of relative fiddler crab abundance by having two observers (ASG and CLW) visually estimate percent cover of fiddler crab-inhabited sand flat, distinctive because the crabs form dense colonies of burrows (A.S. Guerra, pers. obs.). Each observer made an independent estimate of the extent of fiddler crab habitat at each site, and we used the average of these two estimates, which were strongly correlated ( $R^2=0.95$ ,  $df = 10$ ,  $P<0.001$ ), as a metric for relative fiddler crab abundance among sites.

#### Sediment

To quantify sediment characteristics, we measured sediment grain size at each site using a 4-cm diameter, 10-cm long sediment core. We took three sediment cores from each site, using the same methodology as used for selecting invertebrate coring sites. In the laboratory, we passed these sediment samples through three nested sieves (1 mm, 500  $\mu\text{m}$ , and 100  $\mu\text{m}$ ) and then dried samples in a drying oven. We then measured the dry weight of the material retained in each sieve to calculate the ratio of large (>1 mm) to small (<100  $\mu\text{m}$ ) sediment grain mass.

## Camera Trapping

We used time-lapse photography to count birds on the flats during low tide. Camera trapping offers several advantages over direct observation: it limits observer bias, provides an objective record, increases the extent of area that can be simultaneously sampled, and is less likely to influence animal behavior than *in-situ* observations by researchers (Cutler and Swann 1999, Silveira et al. 2003, O'Brien and Kinnaird 2008). At each of our 12 sites, we placed time-lapse wildlife cameras (Covert Extreme Black 60 Trail Camera, DLC, Lewisburg, KY) on the demarcated reference area, to capture images of the lagoon flat and any birds present during low tides. Trail cameras were attached to a post in a location where the devices would not be submerged or splashed, and they were therefore placed on the shoreline, at the average level of water at high tide. This results in bias against sighting curlews near the shoreline, a limitation that must be borne in mind when interpreting results. The far boundary of each site was set at 50 m into the lagoon from the high-tide line, the approximate maximum distance at which our cameras (placed at the high-tide line) could provide sufficient resolution to identify a Bristle-thighed Curlew (Fig. 3). At each site, we placed reference markers around the boundary of the camera's triangular field of view out to 50m. These boundaries allowed us to standardize an area of 0.12 ha for each site. Six cameras were deployed and rotated among the sites throughout a five-week study period for an average of  $13 \pm 3.52$  (mean  $\pm$  SE) monitoring periods per site. Each deployment was  $\sim 6.19 \pm 2.16$  (mean  $\pm$  SE) hours long (Table S1 in Supplementary Appendix).

We set out cameras at each of our 12 sites during daytime high tides between July 18 and August 20, 2012. Cameras remained deployed for the entirety of the low tide immediately following the high tide camera deployment, capturing curlews visiting that site for the entire time

that the site was exposed. We then retrieved and downloaded the cameras at the subsequent daytime high tide. All cameras were programmed to record one still photograph every 30 s. We scored photos by recording the number and species identity of all birds present within the 0.12 ha reference area throughout the entire low tide. We considered the beginning of the low tide to be the time at which the first mounds of benthic sediment broke the surface of the water at each site; we considered the end of the low tide to be the time when all sediment at the site was entirely covered by water. This technique allowed us to quantify both curlew presence throughout one camera deployment per site and mean bird abundance across photographs (every 30 s) per low tide per site.

### Focal Sampling

In order to quantify differences in behavior of curlews among sites, we performed direct observations and developed curlew time budgets for each site. During each observation session, we conducted focal observations on five individuals sequentially (Table S2 in Supplementary Appendix). Focal sampling has been used to describe and quantify behavior in a variety of shorebird species (e.g., Burger and Gochfeld 1991, Turpie and Hockey 1993, 1997, Leeman et al. 2001). Each focal individual was observed independently and continuously for up to ten minutes. If no Bristle-thighed Curlews were present at the site, we scanned the site for 40 min before terminating an observation session. When *N. tahitiensis* were present, we used 8x42 mm binoculars to observe behavior and continuously recorded the focal individual's behavior into a digital voice recorder. Noted behaviors included: walking, pecking, eating (swallowing), handling prey, vocalizing, preening, standing, and flying. If a focal individual was lost from sight before ten minutes elapsed, we noted the duration of the observation to that point. We conducted only one observation per bird during an observation session. When there were not enough

curlews present at the site to conduct five observations, we conducted observations on as many curlews as possible without using the same individual more than once.

We analyzed recordings of curlew behavior using quantitative behavioral analysis software (JWatcher 1.0, 2006, University of California Los Angeles and Macquarie University, Sydney), and calculated the proportion of time allocated to each behavior and the number of pecks per minute per focal observation, as well as the proportion of time spent eating at each of the sites. We then used rate of pecking (pecks per min) and time allocated to eating per observation session per site as a proxy for the availability of foraging opportunities at each site.

### Statistical Analysis

We began by comparing environmental characteristics among sites (HI1, HI2, HI3, HI4, HI5, LI1, LI2, LI3, LI4, NI1, NI2, NI3) and impact categories (high, low, and no impact). We used a general linear mixed model for each environmental characteristic of interest: sediment grain size ratio (mass of large sediment grain fraction : mass of small sediment grain fraction) and macroinvertebrate taxon richness. Models included impact category (high, low, and none) as a fixed effect and site as a random effect nested in impact category. This analysis was conducted using the *lmer* function (package *lme4*) in R, and *P* values were extracted with *pvals.fnc* (*language R* package; R 2.14.1 GUI 1.43, R Foundation for Statistical Computing, 2011). We used one-way ANOVAs to investigate variability of sediment grain size ratio and macroinvertebrate taxon richness among sites. We also used linear mixed models, including site as a random effect, to examine the relationship between macroinvertebrate taxon richness and sediment grain size ratio, and the relationship between the abundance of different macroinvertebrate taxa and sediment grain size ratio (using *glmer* function, *lme4* package in R; R 2.14.1 GUI 1.43, R Foundation for Statistical Computing, 2011; generates estimate parameters of model using Laplace method approximation).

Curlew abundance was quantified as number of birds per photo and was averaged among all photos within a camera deployment to generate an average number of birds per photo per deployment. There were many camera deployments in which no curlews were detected, resulting in zero-inflated data. To account for this, we broke curlew data down into two parts: curlew presence/absence and curlew abundance where present.

To compare patterns in curlew presence/absence among sites and impact categories, we used a mixed-effects logistic regression, with impact category as a fixed effect and site as a random effect (using *glmmPQL* function, *MASS* and *stats* packages in R; R Core Team 2015). To assess whether curlew presence/absence was related to the abundance and diversity of invertebrate prey or by sediment characteristics, we ran similar logistic regressions of curlew presence/absence against macroinvertebrate taxon richness, the abundance of each invertebrate taxon, and sediment grain size ratio.

Then, to compare patterns in curlew abundance where curlews were present (i.e., excluding all camera deployments where curlews were not present), we used general linear mixed models (using *lme* function, *nlme* package in R; R Core Team 2015). The model included impact category as a fixed effect and site as a random effect nested in impact category. We transformed mean curlew abundance data using a fourth-root transformation to conform to the assumption of homogeneity of variance (after Gelman 2007, Kirchner 1995). To assess whether curlew abundance (excluding camera deployments where curlews were not present) was related to the abundance and diversity of invertebrate prey or to sediment characteristics, we ran linear fixed-effects models of curlew abundance (excluding deployments with no curlews) against macroinvertebrate taxon richness, the abundance of each macroinvertebrate taxon, and sediment grain size ratio.

Pecking behavior was quantified as number of pecks per minute observed during focal follows. To account for these zero-inflated data, we broke the pecking rate variable into two variables: pecking behavior present/absent and pecking rate (average number of pecks per minute) for follows in which pecking was observed. To compare patterns in pecking behavior presence/absence among sites and impact categories, we used a mixed effects logistic regression, with impact category as a fixed effect and site as a random effect (using *glmmPQL* function, *MASS* and *stats* packages in R; R Core Team 2015). To assess whether presence/absence of pecking behavior was related to the abundance and diversity of invertebrate prey or by sediment characteristics, we ran similar logistic regressions of pecking behavior presence/absence against macroinvertebrate taxon richness, the abundance of each invertebrate taxon, and sediment grain size ratio.

For the focal follows in which pecking behavior was present, we used general linear mixed models to compare pecking rate across impact categories (using *lme* function, *nlme* package in R; R Core Team 2015). The model included impact category as a fixed effect and site as a random effect. Average pecking rate was also regressed against average abundance of *N. tahitiensis* within each site to test whether pecking rates were influenced by bird densities and possible interference among individual birds,

## Results

We conducted a total of 156 camera sessions, with an average of 13 sessions per site and of 6.2 hr of data per session (Table SI1 in Supplementary Appendix I). Curlews were absent from 124 of the 156 sessions; they were present between 70–75 percent of the time at sites with highest curlew presence and abundance, and absent 100 percent of the time at sites with lowest curlew presence and abundance. We also conducted a total of 30 observation sessions and 38 focal

observations (Table SI2 in Supplementary Appendix I). On average, across sites where curlews were present, the birds spent 40 percent of their time walking, 33 percent standing, 8 percent pecking, 6 percent flying, 4 percent eating, 2 percent preening, 1 percent handling prey, and 0.1 percent vocalizing. Average pecking rate for all focal observations was 4.36 pecks per min.

#### Site Characteristics And Foraging Opportunity Differences

There were no significant differences in sediment grain size ratio between the control (no impact) and high impact categories (estimate=0.42±SE=0.44, df=34,  $t$ -value=0.965,  $P=0.34$ ), or between control and low impact categories (estimate=0.45±0.45, df=34,  $t$ -value=0.971,  $P=0.34$ ). However, sediment grain size ratio was significantly different among sites (ANOVA,  $F_{11,24}=9.85$ ,  $P<0.001$ ). A *post-hoc* Tukey's comparison showed sediment grain size ratio was significantly larger at sites HI1, HI5, LI1 and LI2 than at the remainder of the sites ( $P<0.01$ ; Fig. 4B).

<<Figure 4 near here>>

Average macroinvertebrate taxon richness for all sites was 5.56±0.56 (mean ± standard error [SE]). Macroinvertebrate taxon richness was marginally significantly higher at no impact sites relative to high impact sites (control mean±SE=7.22±0.543, high impact mean±SE=4.467±0.631; estimate=-2.756±1.262, df=9,  $t$ -value=-2.18,  $P=0.06$ ), but there was no difference between no impact and low impact sites (low impact mean±SE=5.667±0.541, estimate=-1.556±1.320, df=9,  $t$ -value=-1.179,  $P=0.26$ ). There was also a significant difference in taxon richness among sites (ANOVA,  $F_{(11,24)}=4.13$ ,  $P=0.002$ ). A *post-hoc* Tukey's comparison showed that macroinvertebrate taxon richness was significantly greater at sites HI3, NI2 and NI3 than at the remainder of the sites ( $P<0.05$ ; Fig. 4A). Macroinvertebrate taxon richness and sediment grain size ratio were not significantly related (estimate=-0.878±0.713,  $t$ -value=-1.232, df=23,  $P=0.23$ ). Sediment grain size ratio was not related to the abundance any macroinvertebrate taxon (Table SI4 in Supplementary Appendix I).

## Curlew Presence/Absence and Abundance

Presence/absence of Bristle-thighed Curlews did not differ between control (no impact) and high impact categories (estimate=0.678±1.188, t-value=0.570, df=9,  $P=0.58$ ), or between control and low impact categories (estimate= -1.101±1.334, t-value=-0.825, df=9,  $P=0.43$ ). However, there was a significant difference among sites, with curlew presence significantly more likely at site HI1 (estimate=2.46±1.04, z-value=2.368, df=155,  $P=0.02$ ) and site HI5 (estimate=2.71±0.97, z-value=2.803, df=155,  $P=0.005$ ) relative to all other sites (Fig. 4C). There was no significant relationship between curlew presence/absence and macroinvertebrate taxon richness (estimate=-0.002±0.260, t-value=0.006, df=10,  $P=0.99$ ). Curlew presence was positively related to the abundance of spinoid polychaetes (*Malacoceros* spp.), but was not significantly related to the abundance of any other macroinvertebrate taxon (Fig. 5, Table 1). The sediment grain size ratio was positively related, although not significantly so, with curlew presence (estimate=1.686±0.779, t-value=2.16, df=10,  $P=0.055$ ; Fig. 6).

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Using only camera deployments where curlews were present, we found that curlew abundance did not significantly differ between control (control mean±SE= 0.003±0.0002) and low impact categories (low impact mean±SE=0.021±0.001; estimate=1.27±0.10, t-value=1.208, df=5,  $P=0.28$ ), between low impact and high impact categories (high impact mean±SE=0.049±0.009; estimate=0.03±0.09, t-value=0.292, df=5,  $P=0.78$ ), or between high impact and control categories (estimate=0.15±0.08, t-value=2.009, df=5,  $P=0.10$ ). We also found no difference in curlew abundance among sites (ANOVA,  $F_{7,24}=2.092$ ,  $P=0.08$ ). There was no significant relationship between curlew abundance and macroinvertebrate taxon richness across sites (estimate=-0.021±0.016, df=6, t-value=-1.326,  $P=0.23$ ). Curlew abundance was not significantly related to the abundance of any macroinvertebrate taxon (Table SI3 in

Supplementary Appendix I) and there was also no relationship between curlew abundance and sediment grain size ratio (estimate=0.048±0.057, df=6, t-value=0.84,  $P=0.43$ ).

### Focal Sampling

Mean peck rate for all the curlews observed was 4.33±1.11 (mean ± standard error) pecks per minute. There was no significant difference in the presence/absence of pecking behavior between control and high impact categories (estimate=28.919±254,817, t-value=0.00011, df= 5,  $P=0.99$ ), between control and low impact categories (estimate=-0.647±1.30, t-value=-0.49892, df=5,  $P=0.64$ ), between high and low impact categories (estimate=-29.566±254,813, t-value=-0.00011, df=5,  $P=0.99$ ), or among the different sites (ANOVA,  $F_{(7,30)}=0.71$ ,  $P=0.66$ ).

Excluding observations without pecking behavior, there was no significant difference in average pecking rate between control and high impact categories (estimate=1.62±2.54, t-value=0.636, df= 5,  $P=0.55$ ), between control and low impact categories (estimate=-1.63±4.01, t-value=-0.41, df=5,  $P=0.69$ ), between high and low impact sites (estimate=-3.259±3.785, t-value=-0.8609, df=5,  $P=0.43$ ), or among sites (ANOVA,  $F_{7,24}=2.28$ ,  $P=0.06$ ). Additionally, average pecking rate was not significantly correlated to *N. tahitiensis* abundance (estimate=-0.002±0.016, t-value=-0.116, df=5,  $P=0.91$ ).

### Discussion

According to our data, degree of historical land impact did not influence Bristle-thighed Curlew habitat choice. But while curlews did not systematically prefer one impact category over another, they were significantly more likely to be found in two of the 13 sites (HI1 and HI5), and both of these preferred flats were in the high-impact category. These two sites had higher abundances of *Malacoceros* polychaetes, suggesting that this polychaete may be an important prey item. Curlew presence was also positively correlated, although not significantly so, with coarse sediment. The

highest sediment ratios occurred at sites HI1, HI5, LI1, and LI2, but the latter two sites had low abundance of *Malacoceros* polychaetes.

Contrary to our predictions, curlew presence/absence and abundance were not significantly correlated with fiddler crab abundance, suggesting that fiddler crabs may not be a preferred prey item on Palmyra. It is possible that fiddler crab abundance may be high enough that curlews do not need to forage at sites with the highest crab densities to meet their dietary requirements. Alternately, curlews may be foraging for fiddler crabs at night, with patterns of nighttime habitat use differing from the ones we detected during their diurnal foraging. While we incidentally captured some nighttime foraging with the camera traps, we excluded these data from analysis because the bright flash and limited visibility of the trail camera would have biased our measures of curlew abundance. Because it seems that curlews do forage on the flats at night, it would be worthwhile to design sampling to capture these behaviors and compare them to patterns observed during daylight.

Curlew presence was positively related to the presence of *Malacoceros* sp. polychaetes. Although no past studies have documented polychaetes in *N. tahitiensis* diets, the birds are known to prey on a broad range of invertebrates and to be fairly opportunistic in prey choice (Bartsch 1922, Bakus 1967, Ely and Clapp 1973, Gill and Redmond 1992, Marks and Hall 1992). Other species of curlews, such as Long-Billed Curlews (*N. americanus*) and Whimbrels (*N. phaeopus*), are known to feed on marine polychaetes in mud and sand flats at nonbreeding sites (Velásquez and Navarro 1993, Perez-Hurtado et al. 1997, Leeman et al. 2001). On Palmyra Atoll, Bristle-thighed Curlews were often observed handling both worms and fiddler crabs on sand flats (A.S. Guerra and C.L. Wood, pers. obs). Therefore, it is possible that curlews prefer sites HI1 and HI5 due to greater prey availability.

Although curlew presence was more likely at sites with high abundance of potential prey

items, pecking rate was not higher at these sites. Pecking is a searching and prey-capture attempt behavior in shorebirds, and not all pecks are successful in capturing prey (Turpie and Hockey 1993). Sandpipers have been found to have an increased ratio of successful to unsuccessful pecks in areas of high prey biomass relative to areas of low prey biomass (Goss-Custard 1970). In whimbrels (*Numenius phaeopus*), prey capture is unrelated to pecking rate and hypothesized to be associated with tactile foraging when foraging in mud (Turpie and Hockey 1997). In our study, we could not distinguish between successful and unsuccessful pecks, and it is therefore possible that physical characteristics of the flat led to similar patterns of tactile foraging, but different foraging success rates.

The positive (although only marginally significant) relationship between ratio of large to small sediment and *N. tahitiensis* presence ( $P=0.055$ ) suggests that curlews may choose to forage at sites with coarser sediment. Grain size can alter sediment's resistance to the movement of bird bills, thus influencing bird distributions by affecting their foraging success. Past studies have found that the abundance and distribution of invertebrate prey varies with the physical characteristics of the tidal habitat (Quammen 1982, Velásquez and Navarro 1993, Danufsky and Colwell 2003), though we found no significant correlation between the abundance of *Malacoceros* sp. polychaetes and sediment grain size. However, particle size of substrates may affect foraging behavior of shorebirds; probing shorebirds favor fine sediment, while shorebirds such as curlews that peck at the surface prey found on coarser sediment (Colwell 2010). This is consistent with our finding of higher curlew abundance at sites with coarser sediment. Eastern Curlews (*Numenius madagascariensis*) feeding on intertidal flats in Eastern Australia were found predominantly in coarser sand sediment as it offers less resistance to pecking behavior than finer substrates (Finn et al. 2001). Therefore, larger sediment grain size might allow for an increased foraging efficiency at HI1 and HI5.

Our results suggest that a combination of factors, such as prey availability and sediment characteristics, may determine *N. tahitiensis* habitat preferences. Although the degree of land reclamation impact on a site was not significantly related to the presence/absence or abundance of curlews, it is important to consider that the two sites that were preferred by curlews were both highly impacted. Our study highlights the importance of considering shorebird habitat preferences when planning conservation measures. With regard to future restoration initiatives on Palmyra Atoll, our study suggests that lagoon restoration might decrease Bristle-thighed Curlew habitat. In particular, the data reveal the importance of sites HI1 and HI5 for curlews. The lack of significant difference in curlew abundance among sites where curlews were present could indicate a flexibility to move on to another foraging site once one becomes unsuitable. We suggest that care should be taken with restoration near these sites, to ensure that they are not substantially altered in any restoration project, as they might provide important foraging habitat; their alteration could reduce the overall value of the atoll as a foraging ground for curlews. Further research should focus on predicting the potential for change in curlew carrying capacity that could result from restorations of the entire lagoon. More information on habitat use of Bristle-thighed Curlews is necessary to fully assess the potential impacts of restoration on the availability of curlew habitat on Palmyra, particularly studies across the entire winter season and with an effort to identify specific prey types on Palmyra Atoll.

Notably, our results appear to suggest that Bristle-thighed Curlews are relatively adaptable to past intertidal disturbance, as their preferred sites were ones that were highly impacted; this is a positive prognosis for this vulnerable bird. However, more information is needed on the effects of ongoing human disturbance and whether the key factor in their success at Palmyra Atoll is that human disturbance remains only as a legacy effect.

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We thank Lee Tibbitts for her information on curlews, advice on study design, and comments on the manuscript. We also thank Felicity Arengo, Mark Denny, and Brett Sandercock for their comments on earlier versions of the manuscript, Jim Breeden and Amanda Pollock for information on Bristle-thighed Curlews of Palmyra Atoll, Amanda Zerbe for field assistance, John McLaughlin for invertebrate identifications, and Joe Wible and John Collen for obtaining historical aerial photographs. The authors also gratefully acknowledge the staff of The Nature Conservancy and U.S. Fish and Wildlife Service. Funding was provided by Stanford University Vice Provost for Undergraduate Education, Palmyra Atoll Research Consortium, and the Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust.

Tables

Table 1. Results of general linear mixed model for the relationship between the abundance of various invertebrate species and bristle-thighed curlew presence.

Taxonomic		Estimate	± SE	t -value	df	p
Invertebrate spp.	group					
Holothurid sp. 1	sea cucumber	-0.0047	0.0306	-0.153	10	0.88
Polychaete sp. 2	polychaete	0.0495	0.0832	0.596	10	0.57
Polychaete sp. 3	polychaete	-0.0329	0.0246	-1.340	10	0.21
<i>Ptychodera flava</i>	hemichordate	0.1351	0.1909	0.708	10	0.5
<i>Malacoceros</i> sp. <i>Chiridota</i>	polychaete	0.0906	0.0315	2.875	10	0.02 *
<i>hawaiiensis</i>	sea cucumber	-0.0145	0.3885	-0.037	10	0.97
Hemichordate sp. 2	hemichordate	0.1529	9.2230	0.685	10	0.51
Tellinid sp. 1	bivalve	-0.5070	0.3996	-1.269	10	0.23
Polychaete sp. 4	polychaete	0.0097	0.2721	0.356	10	0.73
<i>Uca tetragonum</i>	crab	0.0598	1.6043	0.037	10	0.97

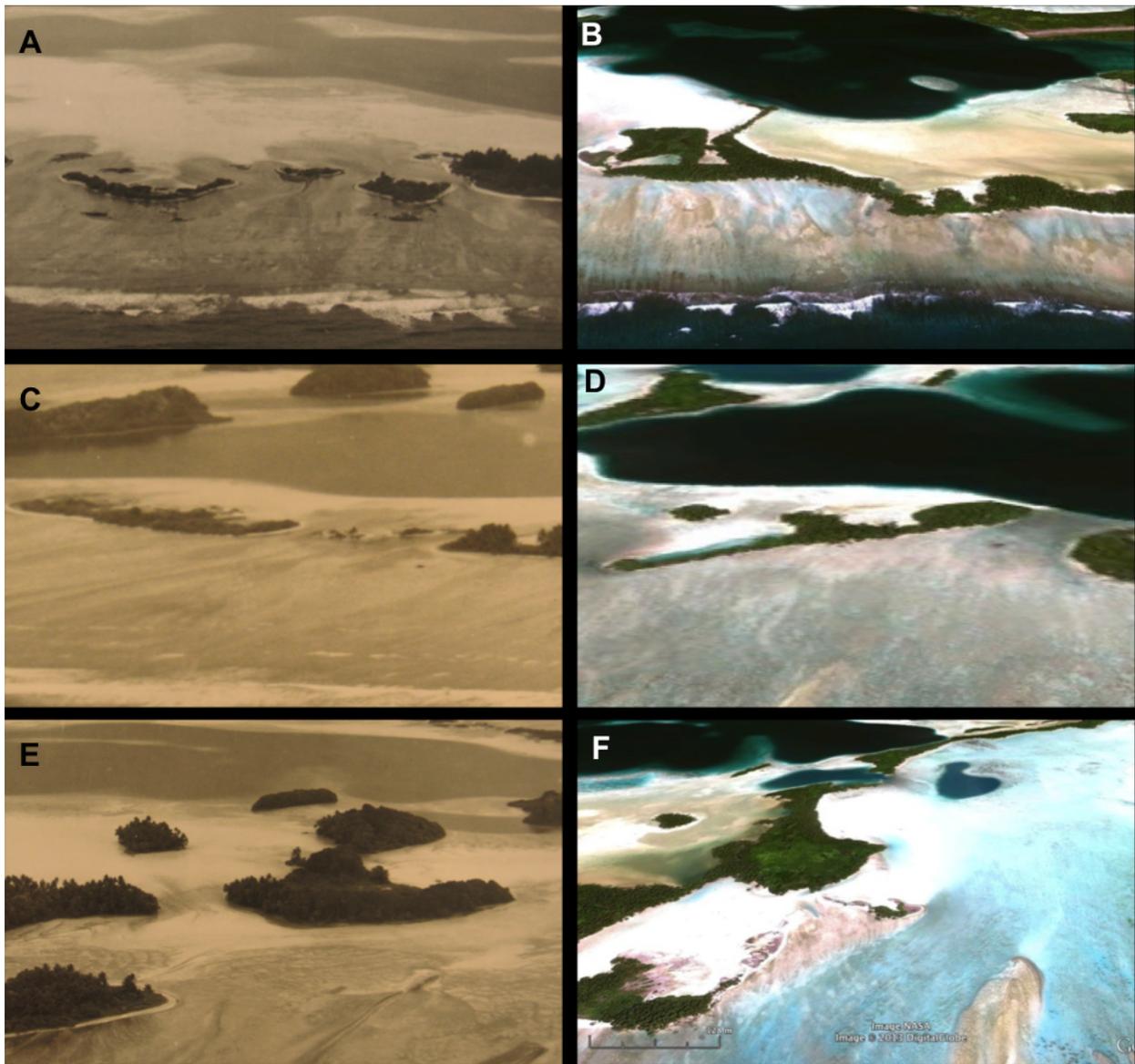


Figure 1. General aspect of lagoon flat habitats prior to the construction of the Naval base (left column) and general aspect of the lagoon flat habitats in 2009 (right column) at a high impact site (HI3 and HI2; A–B), low impact site (C–D), and no impact site (NI1; E–F). Photo: FAB Pearl Harbor (b-c), Google Earth V.7.0.3.8542, 2013.

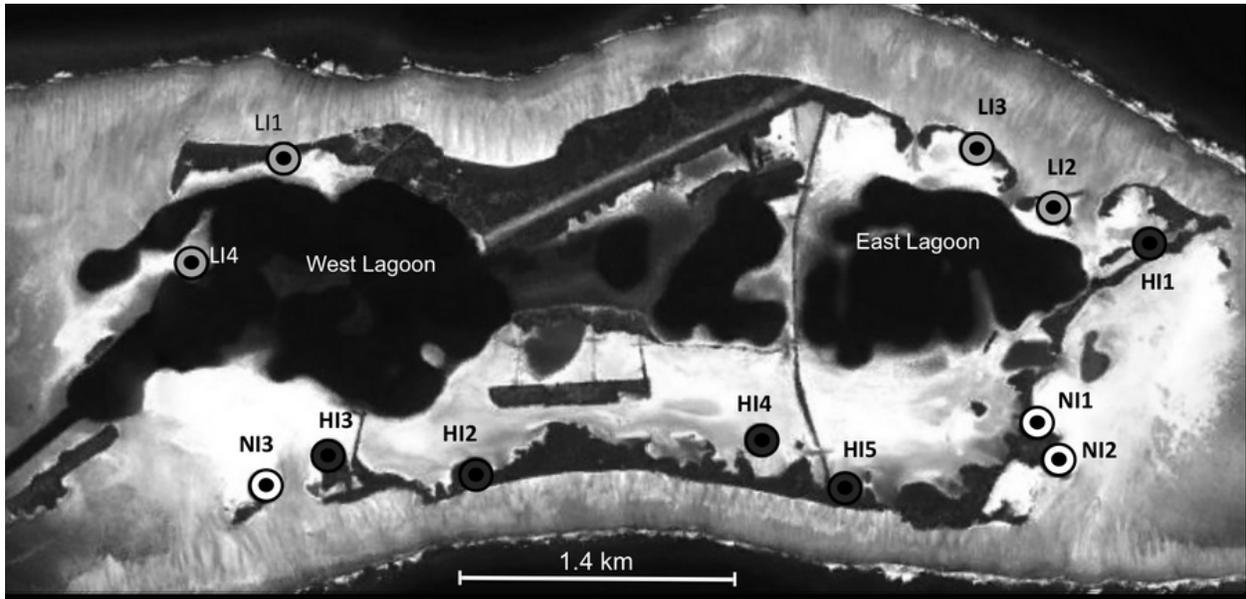


Figure 2. Map of Palmyra Atoll showing 12 study sites named after their determined level of impact: High Impact (HI) in dark gray, Low Impact (LI) in light gray, and No Impact/Control (NI) in white.

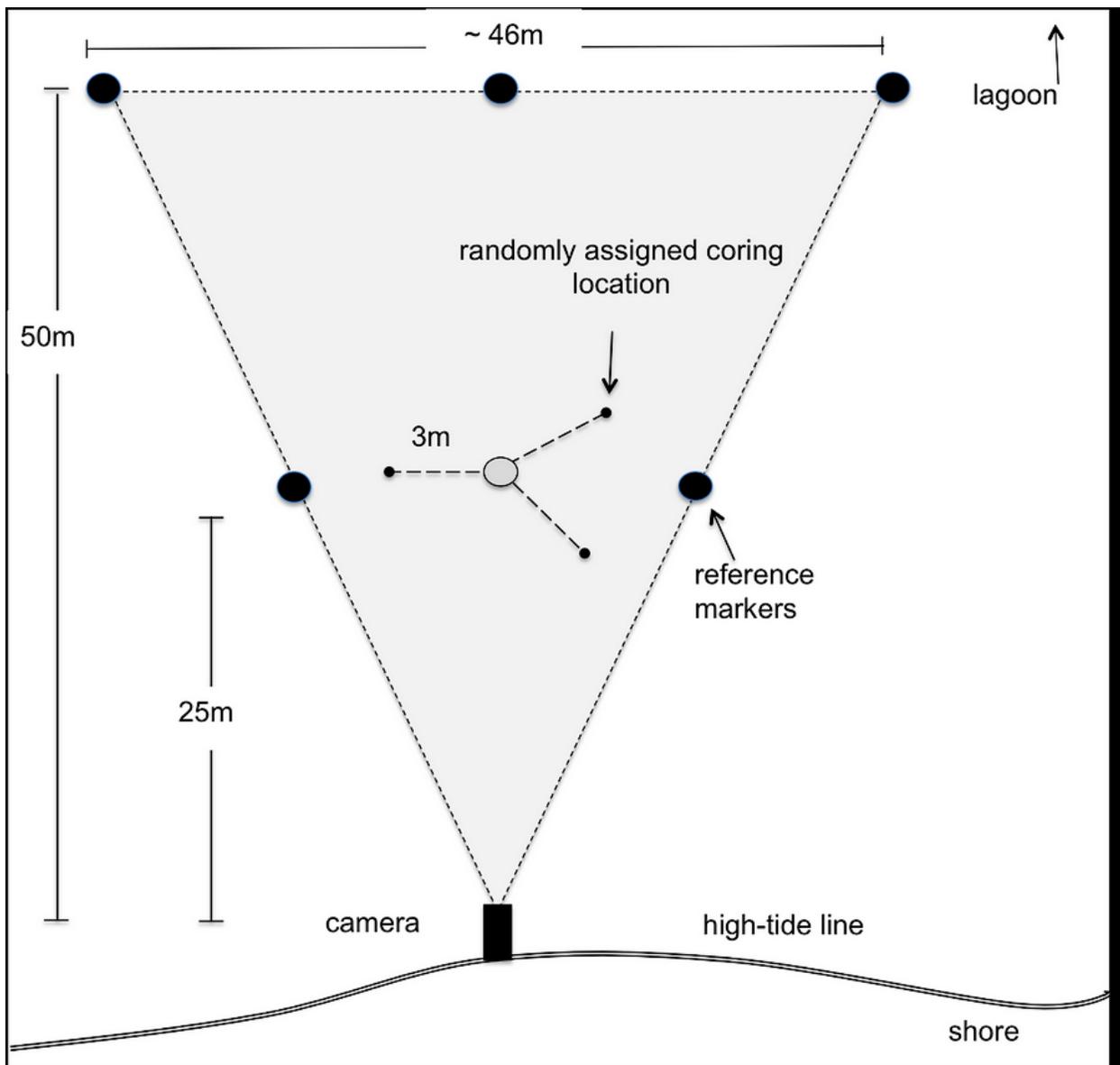


Figure 3. Generalized layout of sites showing placement for camera and reference markers as well as orientation relative to the lagoon and shoreline. An example of three random coring locations within a site is also shown.

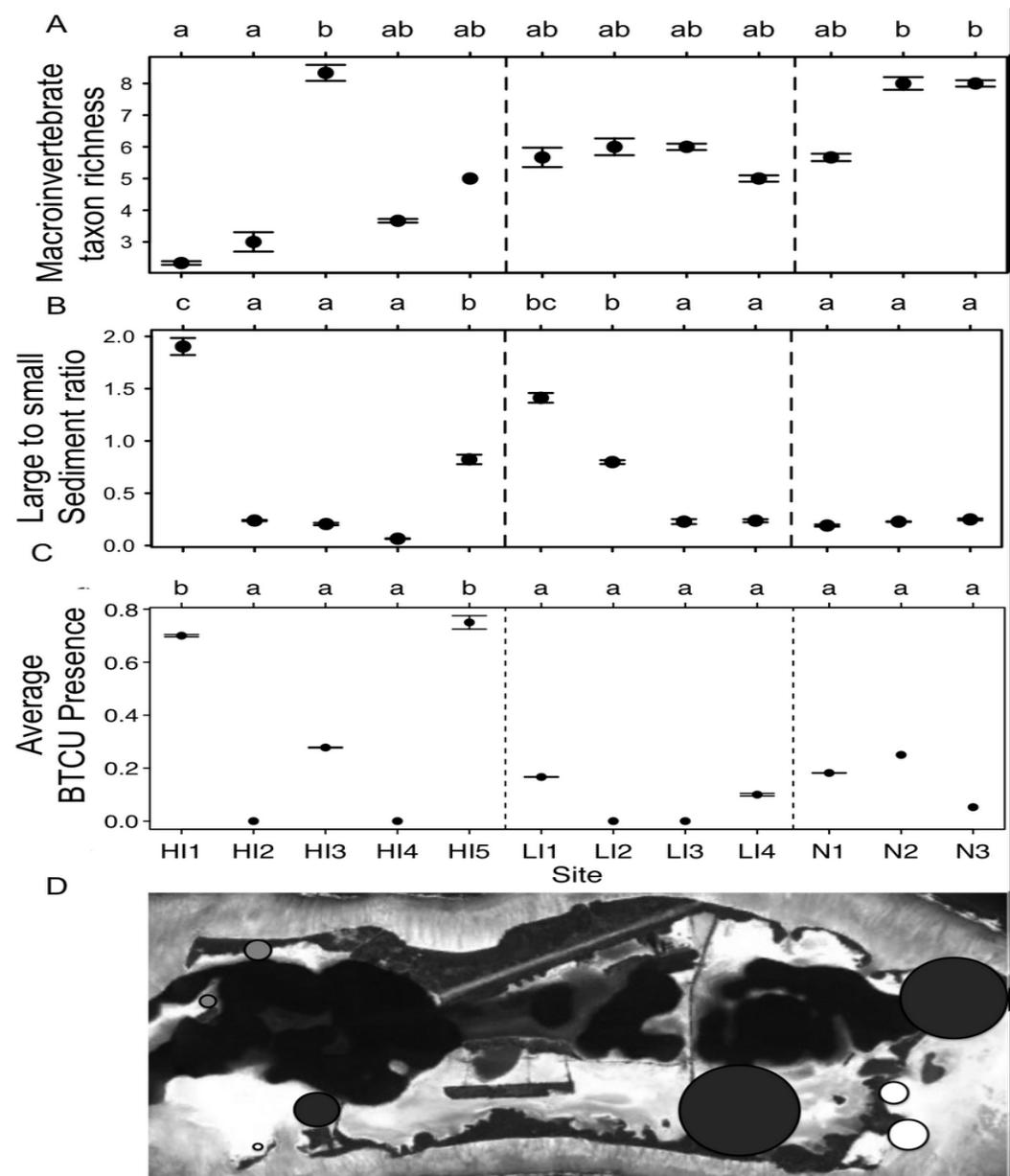


Figure 4. A) Macroinvertebrate taxon richness averaged (with 95% confidence interval) within low tide at each site B) Large to small sediment ratio averaged within low tide at each site. C) Presence of Bristle-thighed Curlews (BTCUs) averaged over all low tides at each site. D) Map shows the relative proportion of the average presence of curlews at sites based on the diameter of the circles. Hues represent level of impact: high impact (dark gray), low impact (light gray), no impact (white).

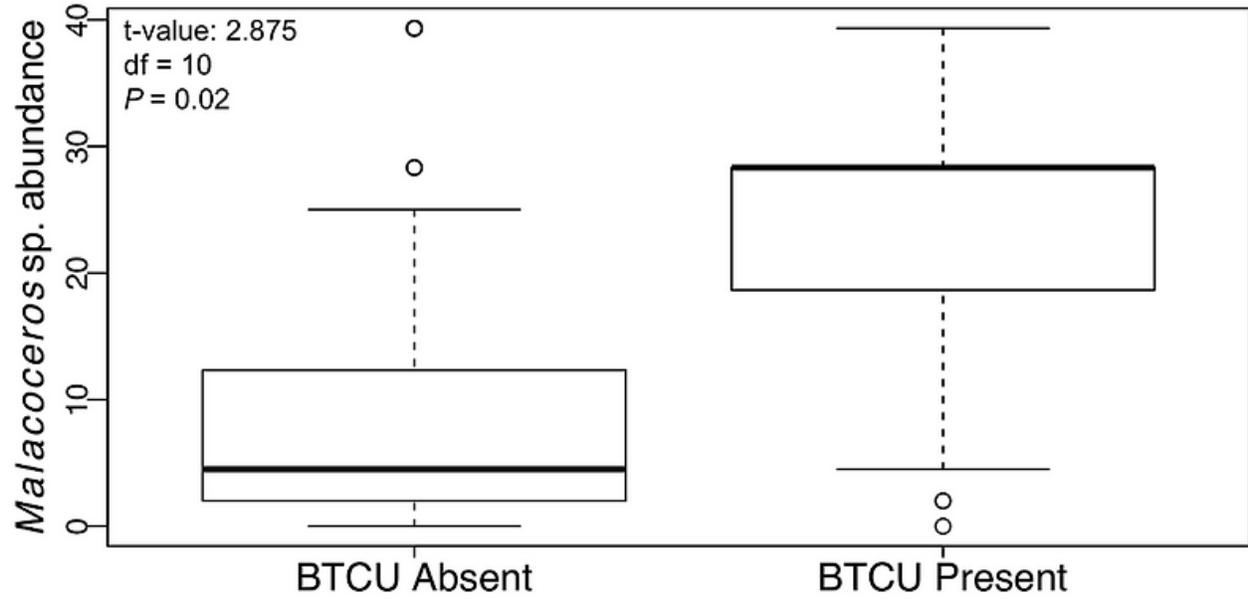


Figure 5. Presence of Bristle-thighed Curlews (BTCUs) averaged over all low tides at each site for *Malacoceros* polychaetes.

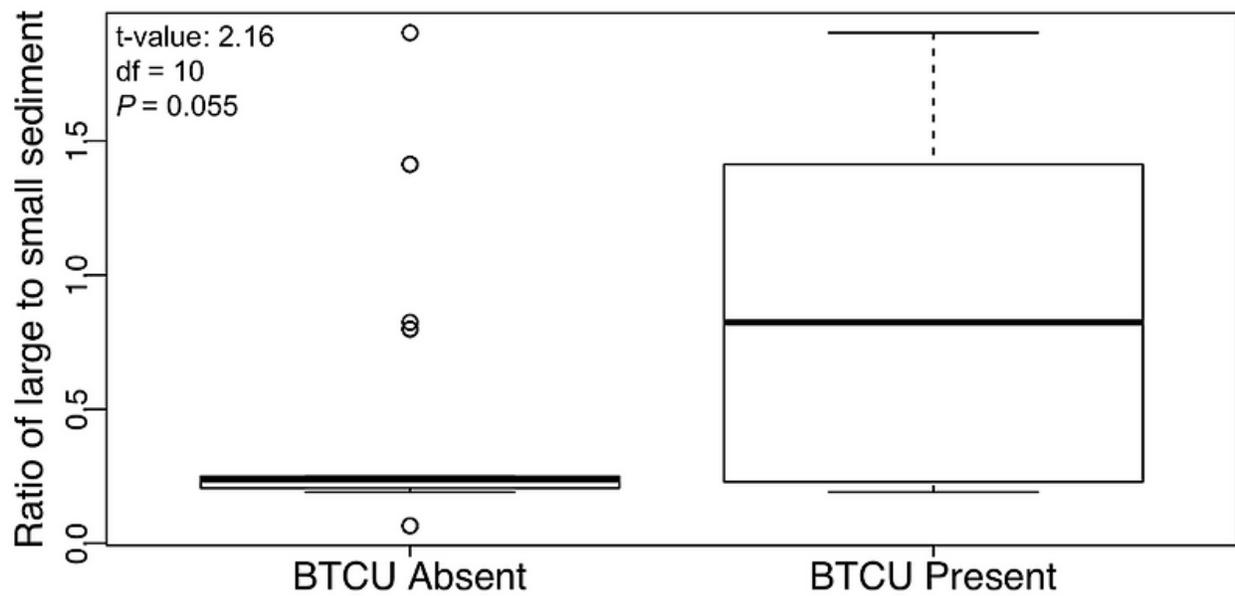


Figure 6. Presence of Bristle-thighed Curlews (BTCUs) averaged over all low tides at each site for ratio of large to small sediment grain size.

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## SUPPLEMENTAL MATERIALS

## Supplementary Appendix I

Table SI1. Number and length of camera deployment at  
each of the 12 sites.

Site	Number of deployments	Mean length of deployments [hr]
HI1	10	8.63
HI2	14	10.13
HI3	18	5.35
HI4	16	5.93
HI5	16	5.97
LI1	12	5.11
LI2	11	4.15
LI3	11	6.72
LI4	10	3.12
NI1	11	4.77
NI2	8	9.43
NI3	19	4.98

Table SI2. Number of observation sessions, total number of focal observations done at each of the 12 sites, and average length of follows at each site.

Site	Number of observation sessions	Total number of focal observations	Average length of focal observations (min)
HI1	2	5	8.4
HI2	5	2	10
HI3	3	8	6.8
HI4	2	0	0
HI5	3	4	7.5
LI1	2	0	0
LI2	2	0	0
LI3	2	0	0
LI4	3	4	8.5
NI1	4	3	4.7
NI2	3	2	5.5
NI3	4	10	7.1

Table SI3. Results of general linear mixed model for the relationship between the abundance of various macroinvertebrate taxa and bristle-thighed curlew abundance only for sites where curlews were present.

Invertebrate spp.	Taxonomic group	Estimate	± SE	t-value	df	<i>p</i>
<i>Chiridota</i>						
<i>hawaiiensis</i>	sea cucumber	-0.0460	0.0208	-2.215	6	0.07
Hemichordate						
sp. 2	hemichordate	0.0194	0.0116	1.670	6	0.14
Holothurid sp. 1	sea cucumber	-0.0039	0.0017	-2.266	6	0.06
<i>Malacoceros</i> sp.	polychaete	0.0021	0.0027	0.785	6	0.46

Polychaete sp. 2	polychaete	-0.0043	0.0045	-0.952	6	0.38
Polychaete sp. 3	polychaete	-0.0026	0.0030	-0.874	6	0.41
Polychaete sp. 4	polychaete	-0.0001	0.0020	-0.041	6	0.97
<i>Ptychodera flava</i>	hemichordate	-0.0056	0.0147	-0.381	6	0.72
Tellinid sp. 1	bivalve	-0.0492	0.0297	-1.656	6	0.15
<i>Uca tetragonum</i>	crab	-0.0597	0.1137	-0.526	6	0.62

Table SI4. Results of general linear mixed model for the relationship between the abundance of various macroinvertebrate taxa and sediment grain size ratio.

Invertebrate spp.	Taxonomic group	Estimate	± SE	t -value	df	p
<i>Chiridota</i>						
<i>hawaiiensis</i>	sea cucumber	-0.495	0.455	-1.088	23	0.29
Hemichordate						
sp. 2	hemichordate	-0.236	0.871	-0.270	23	0.79
Holothurid sp. 1	sea cucumber	-2.150	7.720	-0.278	23	0.78
<i>Malacoceros</i> sp.	polychaete	-0.878	0.713	-1.232	23	0.23
Polychaete sp. 2	polychaete	0.074	1.637	0.045	23	0.96
Polychaete sp. 3	polychaete	-5.307	7.802	-0.680	23	0.50
Polychaete sp. 4	polychaete	-4.490	7.733	-0.581	23	0.57
<i>Ptychodera</i>						
<i>flava</i>	hemichordate	-0.774	1.018	-0.761	23	0.45
Tellinid sp. 1	bivalve	-0.307	0.516	-0.595	23	0.56
<i>Uca tetragonum</i>	crab	-0.231	0.516	-0.449	10	0.66

## Supplementary Appendix II

### Supplementary analysis: Generalized linear mixed effects model with zero-inflated negative binomial distribution

To supplement our analysis based on presence/absence data and curlew abundances for deployments where curlews were present, we also conducted an analysis studying the relationship between curlew abundance and site characteristics across all deployments, not just those where curlews were present. The results from this supplemental analysis parallel those from the presence/absence analysis, indicating that presence of curlews, rather than abundance, is what might be driving these results.

### Statistical Analysis Methods

We used a generalized linear mixed model with negative binomial error and zero-inflated counts to compare the average number of curlews per camera deployment among each impact category (*glmmADMB* package). The model included impact category (high, low, and none) as a fixed effect, and site as a random effect nested in impact category. Because the effect of site, within impact categories, was always significant, we also used a one-way ANOVA to investigate variability among sites. Before ANOVA, we transformed mean curlew abundance data using a sixth root transformation to conform to the assumption of normality of variance (Gelman 2007), and we used a Tukey's comparison of means *post-hoc* test.

To assess whether curlew abundance was determined by the abundance and diversity of invertebrate prey or by sediment characteristics, we ran linear fixed-effects models regressing curlew abundance against the macroinvertebrate taxon richness, the abundance of each invertebrate species, as well as against the sediment grain size ratio.

Table SIII. Results of general linear mixed model for the relationship between the abundance of various macroinvertebrate taxa and Bristle-thighed Curlew abundance. Significance level was adjusted for multiple comparisons using a Bonferroni correction ( $\alpha=0.005$ ).

Taxonomic		Estimate	$\pm$ SE	<i>t</i> -value	df	<i>P</i>	
Invertebrate spp.	group						
Holothurid sp. 1	sea cucumber	-0.0022	0.0024	-0.91	154	0.36	
<i>Malacoceros</i> sp.	polychaete	0.0075	0.0027	2.84	154	0.005	*
Polychaete sp. 2	polychaete	-0.0004	0.0072	-0.054	154	0.96	
Polychaete sp. 3	polychaete	-0.0011	0.0013	-0.88	154	0.38	
Polychaete sp. 4	polychaete	0.00001	0.0022	0.006	154	0.99	
<i>Ptychodera</i>							
<i>flava</i>	hemichordate	0.0051	0.0152	0.333	154	0.74	
Hemichordate							
sp. 2	hemichordate	0.0148	0.0179	0.827	154	0.41	
<i>Chiridota</i>							
<i>hawaiiensis</i>	sea cucumber	-0.0201	0.0315	-0.639	154	0.52	
Tellinid sp. 1	bivalve	-0.0296	0.0245	-1.21	154	0.23	
<i>Uca tetragonum</i>	crab	-0.0148	0.1230	-0.114	154	0.91	

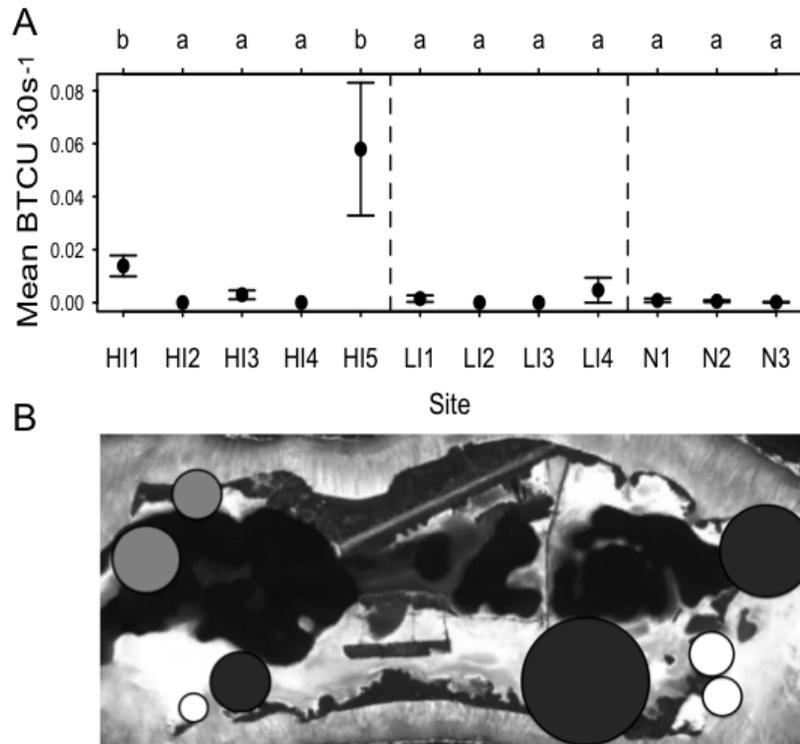


Figure SIII. A) Average number of Bristle-thighed Curlews (BTCUs) per 30 s time-lapse photograph averaged within low tide at each site B) Map shows the relative proportion of the number of curlews (fourth root transformation) at sites where curlews were present based on the diameter of the circles. Hues represent level of impact: high impact (dark gray), low impact (light gray), no impact (white).





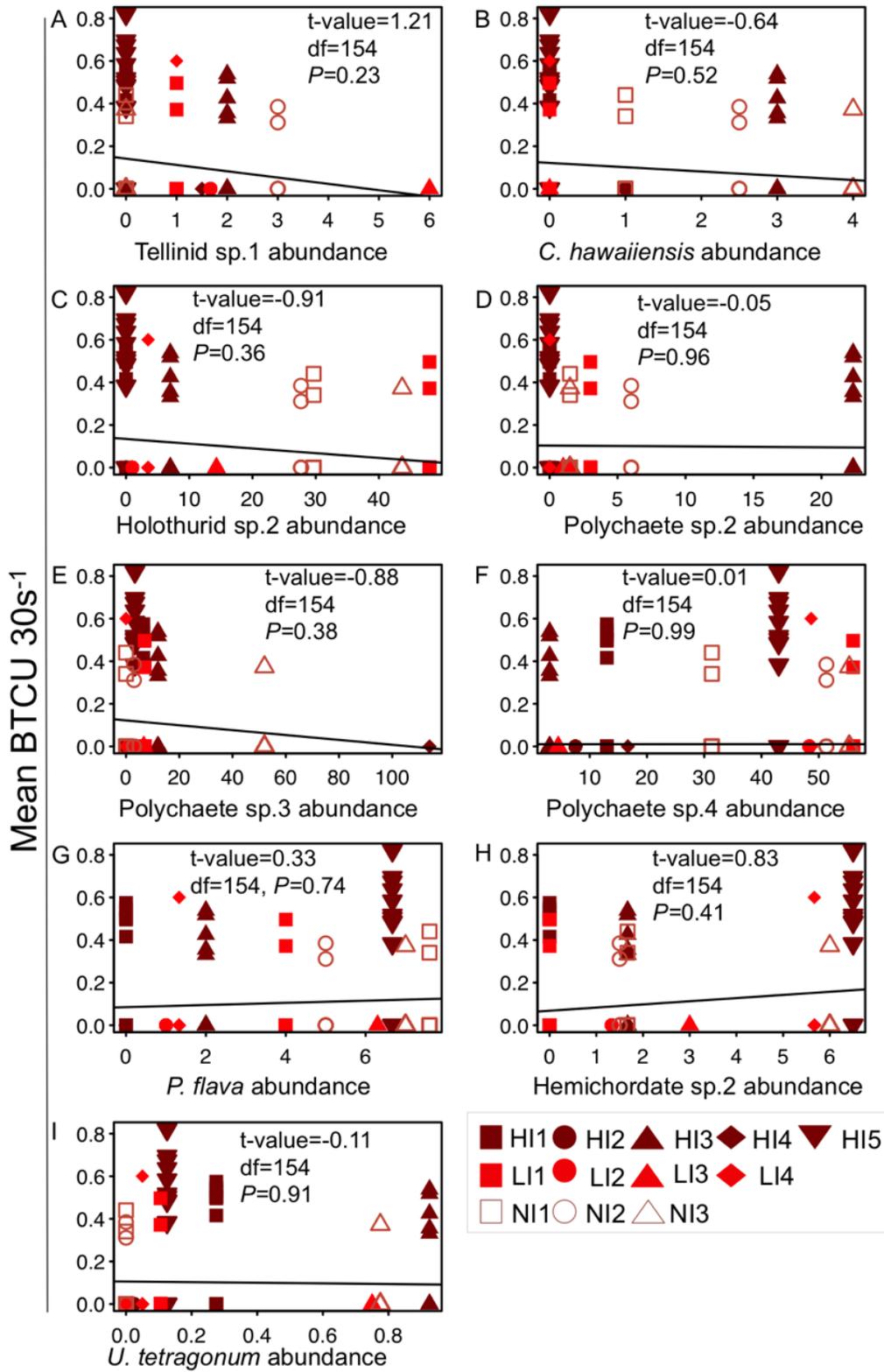


Figure SII4. Average number of Bristle-thighed Curlews (BTCUs) per 30 s time-lapse photographs averaged within low tide at all 12 sites for nine macroinvertebrate taxa.