Journal of Environmental Management 262 (2020) 110290

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: http://www.elsevier.com/locate/jenvman

Research article

Shorebird predation on benthic invertebrates after shrimp-pond harvesting: Implications for semi-intensive aquaculture management

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ARTICLE INFO

Keywords:
Shorebird
Predation
Foraging
Exclosures
Benthic invertebrate
Shrimp-farm management

ABSTRACT

How to improve habitat quality for wildlife is of particular importance in areas dedicated to food production, due to increasing pressures of global demands associated to human population growth. Semi-intensive aquaculture ponds can provide a potentially important foraging habitat for migratory shorebirds throughout the non-breeding season. Therefore, understanding the availability of benthic invertebrates in aquaculture ponds will help to identify proper management decisions for shorebird conservation. We used an exclosure experiment during the first three days after shrimp harvesting at semi-intensive aquaculture ponds in north-west Mexico to assess shorebird predation on benthic invertebrates. We found that shorebird predation did not deplete total benthic invertebrate density (particularly polychaete worms), but significantly affected the prey size distributions and biomass in the ponds during a short-time window of just three days. Shorebirds removed 0.6 g ash-free dry weight m^{-2}, equivalent to 43% of the initial biomass and showed high selectivity for polychaetes larger than >40 mm as prey, potentially explaining the absence of large polychaetes at the end of the experiment. This depletion was the likely cause of the daily decrease observed in overall density of foraging shorebirds at recently harvested ponds. These results can serve to identify management actions that allow an extended use of semi-intensive aquaculture ponds as foraging sites for migratory shorebirds during the non-breeding season, with potential applications to develop standards for a friendlier aquaculture management.

1. Introduction

Land-use changes are severely impacting biodiversity at a global scale (Newbold et al., 2015), and coastal wetlands are one of the most threatened habitats worldwide (Duarte, 2009). Migratory shorebirds (O. Charadrii) depend on wetlands during the non-breeding season, and provide an essential link to maintain global biodiversity through trophic and transport effects between very distant areas (Bauer and Hoye, 2014). In spite of large investments during last decades based on international agreements (e.g. Ramsar, African Eurasian Waterbird Agreement, Arctic Migratory Bird Initiative), shorebird populations continue to decline (Rosenberg et al., 2019), mainly because of wetland loss and degradation (Wetlands International, 2012). Conversely, several shorebird species are currently using anthropogenic habitats such as rice fields (Elphick, 2000), saltpans (Masero, 2003) or coastal pastures (Navedo et al., 2013) as alternative foraging grounds. Indeed, increasing suitability of anthropogenic habitats is being recognized as an adaptive management strategy for conservation of migratory shorebird populations (Reynolds et al., 2017), which can help to mitigate the impact of natural wetland loss for biodiversity.

How to improve habitat quality is of particular importance in areas dedicated to food production, due to increasing pressures to meet increasing demands of global markets (FAO, 2018). Aquaculture is one of the fastest expanding global animal food production sectors (Jones et al., 2015; Weitzman, 2019), and the conservation potential of improving aquaculture practices has recently been identified (Green et al., 2015; Walton et al., 2015; Navedo et al., 2017). Although aquaculture has fragmented and deteriorated coastal ecosystems and thus impacted biodiversity (Valiela et al., 2009), harvested ponds can function as an artificial habitat that provide food and shelter for several species of shorebirds (Yasué and Dearden, 2009; Lehnen and Krementz, 2013; Sandiyan, 2017; Basso et al., 2018; Mei-Ling et al., 2018; Jackson et al., 2019). As in other productive systems (e.g. Elphick, 2000; Masero and Pérez-Hurtado, 2001; Navedo et al., 2013), wildlife consumption of

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https://doi.org/10.1016/j.jenvman.2020.110290
Received 25 April 2019; Received in revised form 15 February 2020; Accepted 15 February 2020

resources that become available only after harvesting (i.e. thereby not increasing production costs and/or decreasing harvest) represents a 'win-win' opportunity for adaptive management in aquaculture. Indeed, improving management of aquaculture for the benefit of shorebirds was recently identified a potential tactic within the Pacific Americas Conservation Strategy (Senner et al., 2016).

Some studies suggest that supratidal areas provide an important food supply where shorebirds forage at high densities and obtain high intake rates (Masero and Pérez-Hurtado, 2001; Rocha et al., 2017). Among these supratidal habitats, aquaculture ponds occur in large areas (Berlanga-Robles et al., 2011; Valiela et al., 2009; Murray et al., 2014) and can provide potentially important foraging habitats for shorebird populations in Europe, Asia and the Americas (Ma et al., 2004; Walton et al., 2015; Navedo et al., 2015). For example, over 25,000 individuals of 25 shorebird species used drained aquaculture ponds for feeding during autumn migration in a coastal wetland in northwestern Mexico (Navedo and Fernández, 2019). Although shorebirds consistently forage at recently harvested shrimp-aquaculture ponds, information about prey availability and food consumption is lacking, thus preventing the adoption of proper management decisions for biodiversity conservation.

Shorebirds are important benthic predators that can substantially impact benthic invertebrate communities in intertidal areas (Goss-Custard, 1980; Christianen et al., 2017). Most shorebird species rely on exposed intertidal mudflats to forage during low tide periods (Granadeiro et al., 2007; Fonseca et al., 2017) to fulfill their daily energy requirements during the non-breeding season (Piersma et al., 1995; Burton et al., 2004). Since shorebirds have high daily energy requirements (Quammen, 1984), they need to forage in areas with high invertebrate availability (Evans, 1976; Goss-Custard, 1980). Several species can potentially feed on the same preys (Philippe et al., 2016; Lourenco et al., 2017), and therefore predation can potentially reduce prey densities and may cause fluctuations in abundance of target prey or given prey sizes (Ahmedou Salem et al., 2014; Navedo et al., 2019).

Several studies have examined the impact of shorebird predation on benthic invertebrates using exclosure experiments (Hiddink et al., 2002; Zharikov and Skilleter, 2003; Mendoca et al., 2007; Rosa et al., 2008; Cheverie et al., 2014; Rocha et al., 2017). Some demonstrated a reduction in prey density up to 90% due to shorebird predation (Székely and Bamberger, 1992), while others failed to find a significant impact on invertebrate numbers (Kalejta, 1993; Sewell, 1996; Hamer et al., 2006). Predation can affect densities of the most abundant species (Schneider, 1978) or change prey size frequencies, usually by reducing the proportion of larger prey (Sánchez et al., 2006). Indeed, invertebrates removed by predation are typically only a small fraction on the available prey (Scheiffarth and Nehls, 1997), being a higher or lower fraction depending on factors that can vary seasonally (Mercier and McNeil, 1994; Thrush et al., 1994; Rodríguez-Pérez and Green, 2012). At intertidal areas with high densities of shorebirds or in periods of the year when their energetic requirements are particularly high (e.g. moulting and migration; Newton, 2008), predation pressure may cause prey depletion (Schneider and Harrington, 1981; Rosa et al., 2008). Hence, at contained systems such as semi-intensive aquaculture ponds that are extensively used as foraging areas by shorebirds (Walton et al., 2015), prey consumption may also cause depletion if profitable prey is limited.

In this study, we used exclosures to evaluate the effect of shorebird predation on benthic invertebrates at semi-intensive aquaculture ponds surrounding a tropical coastal lagoon in north-west Mexico. Shorebirds use ponds intensively for a short period following shrimp harvest (Navedo et al., 2017), and we expected that shorebird predation would significantly reduce prey density and biomass in recently harvested aquaculture ponds. On the basis of optimal foraging theory (Pike et al., 1977), we predicted that shorebirds would select more profitable prey and, consequently, we expected prey of large sizes be substantially reduced. Evaluating the impact and the extent to which shorebirds can affect the benthic community at harvested aquaculture ponds will provide essential information for sustainable management of these widespread anthropogenic habitats.

2. Material and methods

2.1. Study area

Our study was conducted at the shrimp farm "Acuícola Don Jorge" located in Estero de Urías coastal lagoon, Mazatlán, Mexico (23°13′N, 106°25′W; Fig. 1) during the harvesting season in autumn 2015. This wetland complex includes extensive intertidal foraging areas whose availability varies with the predominantly semi-diurnal tides (Fonseca et al., 2017). The shrimp farm has over 50 discrete ponds, covering approximately 300 ha. The shrimp harvesting cycle usually lasts 40 days between late October and throughout November. During this period, ponds are harvested by reducing water depth using a water outlet channel, making ponds available for foraging shorebirds (Navedo et al., 2015, 2017).

2.2. Exclosure experiment

Exclosure experiments were conducted in four ponds (ranging 1.0–8.2 ha) during the first three days after shrimp harvesting, because this is the time-window during which ponds serve as foraging grounds by shorebirds (Navedo et al., 2017). Within each freshly harvested pond (i.e., at day 0), we deployed six (3 m × 3 m) exclosures that prevented birds from foraging inside. Parallel to these exclosures (2.5 m away), we set up six control plots of the same size (Fig. 1). Since dryness within ponds varied depending on their specific spatial configuration and location, we placed exclosures and controls surrounding the water channel within each pond to ensure that the area remained available for foraging shorebirds throughout the experiment (i.e., 3 days).

Our exclosure design consisted of a set of four wooden stakes (length: 60 cm, diameter: 5 × 2 cm) buried in each corner of the plot with 20 cm remaining above the surface of the sediment (following Rosa et al., 2008). Then we stapled a mesh as a roof (5 mm light-diameter to minimize shading) to the top of the stakes, and strung three nylon ropes (4, 8 and 12 cm above the ground) around the stakes to act as barriers to prevent birds from entering (Fig. 1A). In control plots, four stakes were placed in exactly the same manner, but without the mesh and ropes thus allowing birds to forage there (Fig. 1B).

2.3. Invertebrate sampling

Immediately before the exclosure and control plots were deployed, we collected three sediment samples from random locations within each exclosure and control plots, repeating exactly the same sampling at the end of experimental period (Sánchez et al., 2006). A core sample (38.5

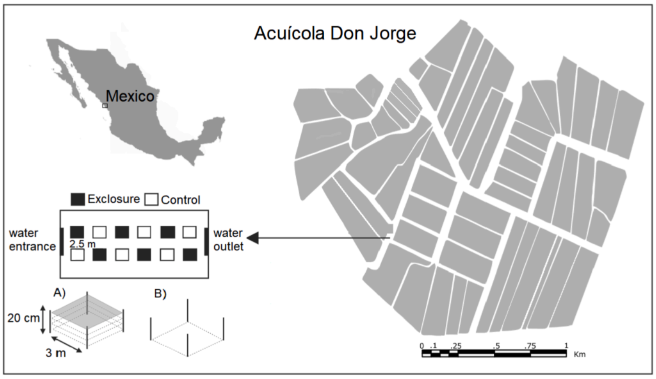

Fig. 1. Study area near Mazatlán, Sinaloa, Mexico. The picture shows an example of the position of the treatment of exclosure (A) and control (B) plots within a pond and its design.

cm^2) was used to collect the top 10 cm of substrate. To avoid disturbing the surface, we minimized stepping in the exclosure and control plots. At the time of sampling, all plots experienced the same amount of disturbance, and thus we assumed that any decrease in prey abundance is the direct result of predation. Because other potential benthic invertebrate predators (i.e., fish and blue crabs within shrimp-ponds) (Rosa et al., 2008) are also removed during pond-harvesting, predation after pond harvesting is mainly due to shorebirds. We obtained prey items by washing each sample with a 500 μm sieve *in situ* and stored the content in 70% alcohol. In the laboratory, we then counted each prey retained and measured the length of each individual using the image analyzer AxioVision Release 4.7.2. Biomass expressed as ash free dry weight (AFDW) for each sample was calculated as the difference between the dry weight (obtained after exposing the organisms to 60 °C for 24 h) and the weight of the ash remaining after the organisms had been burned for 2 h at 500 °C (Micael and Navedo, 2018), and finally estimated actual invertebrate biomass ($AFDW{\cdot}m^{-2}$).

2.4. Shorebird counts

In each of the ponds we conducted daily surveys to estimate the abundance of each shorebird species from the start (harvesting day; day 0) to the end of the experiment (~96 h after; day 3). All shorebirds were identified to species level, except for Short-billed dowitcher (*Limnodromus griseus*) and Long-billed dowitcher (*Limnodromus scolopaceus*), which could not be reliably distinguished in the field, and thus were grouped together as *Limnodromus* spp. On each day, a bird count was performed in each pond every hour over a 3-h period (counts lasted 10–20 min), always from 7 to 11 a.m., thus accounting for the potential variability associated with the tide cycle (both low and high tide combined) (Navedo et al., 2017; Basso et al., 2018). During each count, we recorded the abundance of shorebird species foraging in the experimental ponds. We averaged the abundances over the three counts, then calculated the density of foraging shorebirds based on the area of each pond (i.e., we assumed that the entire pond was available for foraging; e.g. Basso et al., 2018). The same observer (J. Fonseca) using binoculars (10x42) and a telescope (20–60 x) performed all counts.

2.5. Statistical analyses

Prior to analysis, we averaged the three benthic samples taken within each exclosure and control plots. We removed a single pair of exclosure/control data from analyses because we observed two individual shorebirds in an exclosure that was broken, thus potentially adding noise to our treatment. Since exclosure and control plots showed no differences at the beginning of the experiment in prey density ($U = 262$, $P = 0.95$), biomass ($U = 228$, $P = 0.42$) or prey size ($U = 98{,}189$, $P = 0.19$), we combined the exclosures and control plots at the start of the experiment as a measure of initial food supply. Consequently, we tested one treatment with three levels in our statistical analyses: start of experiment (i.e., at day 0) and after the experiment (i.e., at day 3) in the exclosures and control plots. We employed generalized linear mixed models (GLMMs) with Gaussian error structure and an identify link function to analyze the effects of our treatment on two response variables: invertebrate density and biomass. Pond and treatment (nested within ponds) were included as random factors using the “lme” function in the *nlme* package (Pinheiro et al., 2019) in R 3.3.1 (R Core Team, 2016). We log-transformed our response variables to meet normality assumptions. Moreover, Kolmogorov-Smirnov test were used for comparisons between the initial distribution of prey size with exclosures and control plots.

To examine for potential prey selection, we grouped prey size into 10 mm-length classes and compared the prey sizes found in the control plots after 3 days with those found at the start of the experiment. Prey selectivity was then measured using Jacobs' index (Jacobs, 1974), calculated as

$$J = (r - p) / (r + p - 2rp)$$

where r is the fraction of each prey size-class predated (estimated from the difference between prey sizes before and after in control plots) and p is the fraction of prey size-class available. J varies from −1 to +1. We considered that a given prey size-class was selected if it J was positive and avoided if it was negative. Index values of 0 indicated that prey sizes are consumed in proportion to their abundance.

Finally, daily density of foraging shorebirds within each experimental pond throughout the experiment was analyzed using ANOVA test. We used a post-hoc Tukey test to evaluate the difference between factor levels (0–3 days). Since two species (Western sandpiper *Calidris mauri* and Willet *Tringa semipalmata*) encompassed 79% of overall shorebird abundance, we conducted separate analysis for each of these species. All results are presented as means ± SE.

3. Results

3.1. Prey density

Polychaetes were the only prey present in our samples. Of these, 96% were *Laeonereis watsoni* (a recently described species in the study area; de León-González et al., 2018), and the remaining 4% belonged to Family Capitellidae. Overall, polychaete density within plots did not significantly change over the course of the experiment (GLM, $F_{2,\ 57} = 2.97$, $P = 0.11$; Fig. 2A). At the start of the experiment, prey density was 1781.6 ± 257.5 $ind{\cdot}m^{-2}$ and remained similar in the control plots after the experiment ($P > 0.05$), while in the exclosures it tended to increase, albeit not significantly ($P > 0.05$). In fact, prey density within exclosures increased 31% relative respect to the start and 34% compared to the control plots.

3.2. Prey biomass

Polychaete biomass significantly changed over the experimental period (GLM, $F_{2,\ 57} = 5.94$, $P < 0.05$; Fig. 2B). At the start of the experiment, prey biomass was 1.4 ± 0.1 g $AFDW{\cdot}m^{-2}$ and decreased to 0.8 ± 0.1 g $AFDW{\cdot}m^{-2}$ in the control plots at the end of the experiment ($P < 0.001$). In contrast, prey biomass within exclosures did not significantly decrease with respect to the initial biomass ($P > 0.05$; Fig. 2B). There were significant differences at the end of the experiment between exclosure and control plots ($P < 0.001$; Fig. 2B). Shorebirds removed in three days 0.6 g $AFDW{\cdot}m^{-2}$, equivalent to 43% of the initial biomass.

3.3. Prey size distribution

Polychaete size class distribution significantly changed throughout the experiment (Fig. 3), both at control plots (Kolmogorov-Smirnov, test, $D = 0.09$, $P < 0.01$) and exclosures (Kolmogorov-Smirnov, test, $D = 0.12$, $P < 0.001$). However, size class distributions were similar among exclosures and control plots (Kolmogorov-Smirnov, test, $D = 0.07$, $P = 0.10$). Available polychaete sizes ranged between 2 to and 128.2 mm. Based on Jacobs' index, shorebirds clearly selected polychaetes with a length up to 40 mm ($J > 0.75$; Fig. 3B). By contrast, polychaetes with a length smaller than 40 mm (i.e., $J = -1$, in all cases) were avoided.

3.4. Shorebirds

We recorded 15 shorebird species within experimental ponds (Table 1). All 15 species were observed feeding in shrimp ponds, whereas only six were observed feeding inside control plots (Table 1). Western sandpiper was the most abundant species with 51% of the total abundance, followed by Willet with 28%, while the rest of the species accounting for 21% (Table 1). Overall, average density of foraging

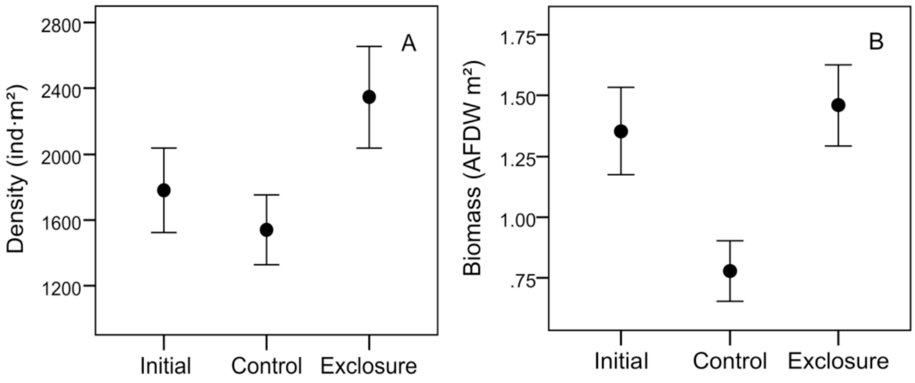

Fig. 2. Density (A) and biomass (B) of polychaetes (average ± SE) at the start (day 0) and end (day 3) of experiment in control and exclosure treatments at shrimp ponds.

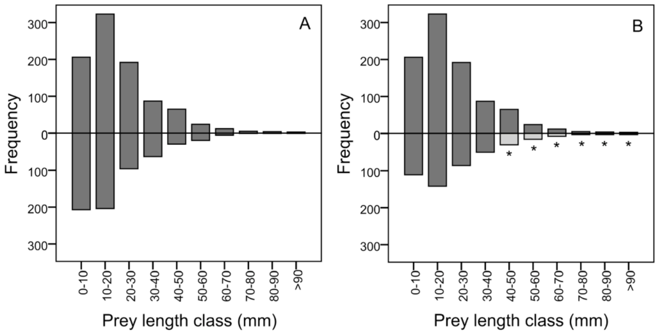

Fig. 3. Polychaete sizes class distribution at the start (A, B; upward bars) in comparison with the size distributions in exclosures (A; downward bars) and control plots (B; downward bars) at the end (day 3). The light grey bars (downwards) represent the polychaete sizes predated. * indicate positive preference of the prey size determined by Jacobs' index. The sizes were grouped into 10 mm-length classes.

Table 1
Feeding density of shorebirds ± SE (birds·ha^{-1}) in shrimp ponds. * Species seen feeding in control plots.

Species	Days after harvest			
	0	1	2	3
American avocet *Recurvirostra americana**	1.6 ± 0.5	1.9 ± 1.1	1.6 ± 1.1	2.2 ± 1.1
American oystercatcher *Haematopus palliatus*	0.4 ± 0.3	0.3 ± 0.3	–	–
Black-bellied plover *Pluvialis squatarola*	1.6 ± 0.8	1.0 ± 0.5	1.0 ± 0.4	0.4 ± 0.3
Black-necked stilt *Himantopus mexicanus*	8.4 ± 4.7	4.4 ± 3.1	3.0 ± 1.9	2.9 ± 1.3
Dowitchers *Limnodromus* spp*	3.7 ± 3.3	0.1 ± 0.1	0.5 ± 0.3	0.2 ± 0.2
Greater yellowlegs *Tringa melanoleuca*	0.2 ± 0.1	0.1 ± 0.1	–	0.5 ± 0.5
Lesser yellowlegs *Tringa flavipes*	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Long-billed curlew *Numenius americanus*	–	–	0.1 ± 0.1	0.1 ± 0.1
Marbled godwit *Limosa fedoa**	8.2 ± 2.4	5.4 ± 2.9	4.8 ± 1.9	0.9 ± 0.8
Semipalmated plover *Charadrius semipalmatus**	7.2 ± 3.2	5.3 ± 1.9	0.4 ± 0.3	3.5 ± 2.8
Spotted sandpiper *Actitis macularius*	0.1 ± 0.1	0.1 ± 0.1	–	0.2 ± 0.2
Stilt sandpiper *Calidris himantopus*	–	–	–	0.1 ± 0.1
Western sandpiper *Calidris mauri**	41.9 ± 21.5	125.8 ± 48.8	25.7 ± 21.4	4.7 ± 2.8
Whimbrel *Numenius phaeopus*	0.2 ± 0.1	0.6 ± 0.4	1.9 ± 1.0	0.7 ± 0.3
Willet *Tringa semipalmata**	63.4 ± 14.9	13.2 ± 6.5	22.1 ± 7.8	18.7 ± 12.8
Total	145.8 ± 13.7	157.9 ± 53.3	60.9 ± 23.3	35.0 ± 14.7

shorebirds decreased rapidly from 145 ind·ha^{-1} once the pond was harvested to 35 ind·ha^{-1} only 3 days after harvesting (Table 1). Specifically, density of foraging western sandpipers changed significantly over time after shrimp harvest (ANOVA, $F_{3,\ 15} = 3.54$, $P < 0.05$) showing the maximum peak in day 1 ($P < 0.05$, Fig. 4A). By contrast, willets showed no significant changes in density throughout the first three days after harvesting (ANOVA, $F_{3,\ 15} = 2.62$, $P = 0.09$; Fig. 4A). Density of the other shorebird species (grouped) overall tended to decrease throughout the three days after harvesting (Fig. 4B), albeit with no statistically significant differences (ANOVA, $F_{3,\ 15} = 1.36$, $P = 0.30$).

4. Discussion

Our results demonstrate a selective predation by shorebirds on large prey found at aquaculture ponds in the first few days after harvest. By contrast, prey densities were not affected. This indicates that selective consumption of large-size prey, rather than prey densities, explains the day-by-day decrease observed in overall density of foraging shorebirds within semi-intensive aquaculture ponds (Navedo et al., 2017). Hence, some management actions of these ponds could offer a promising approach to semi-intensive aquaculture management to benefit migratory shorebird populations.

4.1. *Impact of shorebird predation*

Our results showed that shorebird predation significantly reduced invertebrate biomass up to 43%, with larger size-classes being virtually absent after a very short-time period. Exclusion experiments have shown that shorebirds can deplete a significant fraction of the production of benthic invertebrates in intertidal flats (Székely and Bamberger, 1992; Zharikov and Skilleter, 2003), but in some cases the effects of predation are masked by prey growth and reproduction (Kalejta, 1993; Hamer et al., 2006). However, in closed systems such as semi-intensive shrimp-aquaculture ponds and other ponds (e.g. Sánchez et al., 2006; Walton et al., 2015; Rocha et al., 2017), benthic recruitment events after harvesting are limited because flow gates remain locked shut until the growing cycle is resumed. Therefore, even with the high evaporation rate that drastically changed day-by-day habitat availability within harvested ponds at tropical areas (Navedo et al., 2017; Navedo and Fernández, 2019), depletion of selected prey is probably the main cause of the daily overall decrease observed in density of foraging shorebirds at recently harvested ponds within shrimp-farms.

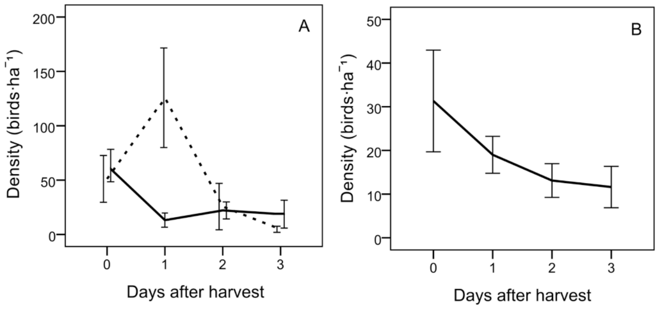

Fig. 4. Average density of feeding shorebirds ± SE (birds·ha^{-1}) in our four study ponds in the shrimp farm Acuícola Don Jorge. A) The dotted line represents the density of Western sandpiper and the solid line represents the density of Willet. B) Density of the rest of the species in the shrimp ponds.

Polychaetes were the only invertebrate prey present in our benthic samples. Although other prey such as crabs and mussels are also present, they are located at very specific areas within the ponds (J. Fonseca unpub. data) and were not covered by our sampling design. Polychaetes are the dominant macroinvertebrates in environments with high organic matter content (e.g. shrimp culture ponds; Soares et al., 2004), and are found at high quantities during the growing cycle and serve as a food source for farmed shrimp (de Paiva and da Silva, 1998). Once the ponds are harvested, benthic polychaetes became an important trophic subsidy for migratory shorebirds, the main predators at anthropogenic wetlands such as low-salinity coastal salt-pans (Rocha et al., 2017) or other aquaculture ponds (Walton et al., 2015). Overall, we found that prey density was lower than densities reported in other anthropogenic habitats, dominated by comparatively smaller prey items (Fam. Chironomidae; Sánchez et al., 2006; Rodríguez-Pérez and Green, 2012; Rocha et al., 2017), but within of the mean range recorded for the adjacent Estero de Urías coastal lagoon (Ferrando and Méndez, 2011). However, prey biomass was much more similar to such areas, probably driven by the dominance of comparatively larger prey (i.e. Nereidae) in our study area.

Contrary to our prediction, shorebirds did not reduce prey densities at ponds during first three days after harvesting. Indeed, we observed a slight increase in prey density within exclosures compared to control plots. Because closed gates overall prevent the entrance of polychaetes (Navedo et al., 2017), and harvested ponds have a gradual drying process that prevents their reproduction, this increase seems to reflect the movement of surrounding polychaetes to exclosures making them less vulnerable to predation (Goss-Custard, 1980). By contrast, a strong effect of shorebirds in prey biomass at control plots was observed, as we predicted, leading to a near absence of large polychaetes (i.e. >40 mm) after three days. Large polychaetes do not have a relevant handling or digestion time compared to other large prey such as crabs or bivalves (Piersma et al., 1993), and are highly profitable for shorebirds (Zwarts and Wanink, 1993) and so were quickly depleted. In addition, we observed a slight effect on mean prey size, with a marginal decrease after three days but similar in the exclosures and control plots. This can be explained due to the high number of small prey found in the exclosures that partially masked the differences with control plots. Therefore, our results supported a strong size-selective predation on large polychaetes by shorebirds (Goss-Custard, 1977; Duijns et al., 2013) that entails a functional depletion of the most profitable prey at harvested aquaculture ponds in a short time-window.

4.2. *Effect of food supply reduction on shorebird densities*

Shorebird densities decreased daily after harvest, with initial densities of the most abundant shorebird species foraging within aquaculture ponds in our study being also similar to, and following the general temporal pattern observed at shrimp-farms in Mexico (Navedo et al., 2017; Navedo and Fernández, 2019). However, shorebird densities differed between ponds, thus indicating that pond characteristics and location within the shrimp-farm also influenced their use (Basso et al., 2018). As many other *Calidrids*, western sandpipers are highly gregarious (Fernández and Lank, 2008), and move in large flocks between ponds, depending on disturbances (i.e. immediate post-harvesting activities; J. Fonseca pers. obs.) and perceived predation danger by Peregrine falcon *Falco peregrinus* (Basso et al., 2018). This avoidance behavior can explain why this species showed the highest abundances on day 1 after pond harvesting rather than on day 0 (Fig. 4). In contrast, willets showed a high trophic niche width (Haram et al., 2018), opportunistically exploiting other food resources also present within harvested ponds (e.g. crabs and mussels). Hence, willets showed similar densities during the first, second and even the third day after pond harvesting. This pattern probably reflects a much lower effect of depletion of large polychaetes in comparison with other shorebird species, whose densities indeed decreased gradually day-by-day. Overall our results indicate that quick depletion of large prey can strongly affect shorebird densities within recently harvested aquaculture ponds, particularly for substrate-probing birds using tactile methods (Finn et al., 2008).

4.3. *Use of the aquaculture ponds and management implications*

Shrimp ponds are intensively used by foraging shorebirds, but their use can be limited to specific time windows during the harvesting season (Navedo et al., 2015; Navedo and Fernández, 2019). Recent research indicated that increasing substrate moisture within harvested ponds prolongs their use by shorebirds (Navedo et al., 2017). However, our results indicate that remaining food supply after three days once ponds are harvested may be mainly composed of unprofitable prey that will not help birds to meet their energetic demands during non-breeding season, particularly for medium-large substrate-probing species (Quammen, 1984) such as dowitchers and godwits. Although ponds remained humid, the relatively slow growth rate of polychaetes (e.g., mean growth rate 0.27 mm·day^{-1} for *Nereis diversicolor*; Arias and Drake, 1995) will thus not directly increase prey biomass for shorebirds but may result in increases of availability of low-profitable prey. As a recommendation within a dynamic conservation strategy (e.g. Reynolds et al., 2017), we suggest shrimp-aquaculture managers to prioritize a sequential pond harvesting regime that can extend harvesting cycle through time to increase the overall available area harboring profitable prey available at recently (<2 days) harvested ponds. Other management actions (e.g. adjusting water depth or sequentially flooding and emptying ponds after harvesting) may offer a promising approach to aquaculture management which would also benefit shorebirds. For future certification standards of more ‘friendly’ shrimp production, these recommendations would imply an adaptive linking of daily shrimp-pond harvesting with the goal to extend the harvesting cycle within each farm.

4.4. *Conclusions*

Our results support a significant reduction of the available food supply directly related to size-selective predation within recently harvested semi-intensive aquaculture ponds, probably influencing day-by-day decreasing densities of foraging shorebirds. Given that aquaculture is the fastest growing food production industry around the world (Jones et al., 2015; Weitzman, 2019) impacting significantly wetland loss (Ottinger et al., 2016), an appropriate management of these sites alongside sustainable measures and regulations can help to mitigate their negative impacts on coastal wetlands and wildlife (e.g. Green et al., 2015; Walton et al., 2015; Navedo et al., 2017; Froehlich et al., 2017; Jackson et al., 2019). Therefore, our findings contribute to the knowledge about aquaculture ponds as foraging sites for shorebirds during the non-breeding season, with potential relevant applications to develop standards for a friendlier aquaculture management within conservation plans (Froehlich et al., 2017).

CRediT authorship contribution statement

Juanita Fonseca: Conceptualization, Methodology, Formal analysis, Writing - original draft, Project administration, Software. **Juan G. Navedo:** Resources, Data curation, Writing - review & editing, Visualization, Supervision, Funding acquisition.

Acknowledgments

We would like to thank Eliseo Salazar for his help during bird surveys and sediment sampling, and Sergio Rendón for allowing us to use the facilities of the Laboratorio de Biología de Crustáceos of the Instituto de Ciencias del Mar, UNAM to analyze benthic invertebrates. We also thank Guillermo Fernández for providing logistic support and Mark Drever for his fruitful comments on an earlier version of the manuscript. We thank the Acuícola Don Jorge shrimp farm for allowing us to work in their facilities. JGN was funded by CONICYT grant #1161224 (Gobierno de Chile) while writing. This study is part of the PhD dissertation of J. Fonseca funded by CONACyT (n° 248103).

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