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REVIEW

Seven ecological and technical attributes for biofilm-based recovery of shorebird populations in intertidal flat ecosystems

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Abstract

1. Soft-bottomed intertidal flats are essential foraging areas for shorebirds but are severely impacted by threats such as coastal development and climate change. Notwithstanding the urgency for humanintervention (conservation, restoration and creation) of tidal flats, few ecologically based technical guidelines exist for the artificial (clearly intended human intervention) intertidal flats, and none explicitly consider the unique properties of intertidal biofilm as a critical food source for small-bodied shorebirds.
2. We propose that effective human intervention in intertidal flat ecosystems can be developed through mirroring the needs of small-bodied shorebirds. Scientific evidence from intertidal flat recovery projects in Japan is summarized, and foraging requirements of shorebirds are reviewed with a focus on intertidal biofilm as a critical food source.
3. These findings are used to propose the primary goal of intervention, that is maximizing total energy intake for population recovery of small-bodied shorebirds through biofilm. Three sub-goals are presented for creating environmental conditions in which (1) a broad spectrum of food sources is available, but particularly intertidal biofilm; (2) maximizing energy intake rate per individual; and (3) maximizing foraging activity. We then describe seven key ecologically based technical attributes for artificial intertidal flats that promote use by small-bodied shorebirds: depositional environment, complex shoreline, gentle slope, gradient of grain sizes from muddy to sandy, maximum water depth at the lowest tide 5 cm or less, freshwater inflow and unobstructed sight-lines.
4. Critical questions remain for effective intervention in intertidal flat ecosystems, including food web dynamics, variation in the quality and quantity of food sources, especially biofilm, optimal sedimentary environment systems (interaction between grain size, bed slope and elevation), monitoring involving comparisons with appropriate benchmark (control) habitats, quantifying foraging behaviour and the synergy and trade-offs among ecosystem services.

KEYWORDS
creation, food webs, microphytobenthos, restoration, tidal flats

1 | INTRODUCTION

Threats to coastal ecosystems, such as development and climate change, are ongoing (Halpern et al., 2008; Lotze et al., 2006), with an observed decline of about 35% in both marine/coastal and inland natural wetland areas from 1970 to 2015 (Ramsar Convention on Wetlands, 2018). In particular, intertidal flats, defined as open areas of soft sediment that are regularly inundated and exposed by marine tides, lost an average of 16% of their total global area from 1984 to 2016 (Murray et al., 2019). In Japan, approximately 40% of the total area of natural flats was lost from the 1940s to 1980s (Imai et al., 2008). Thus, human intervention (conservation, restoration and creation) in ecosystems is necessary to maintain or restore biodiversity and ecosystem services in a rapidly changing world (Hobbs et al., 2011).

Intertidal flats provide multiple ecosystem services such as improving water quality through removal of pollutants and, via primary producers at the base of benthic food webs, increasing coastal fish and shellfish production (Hope et al., 2020; Okada et al., 2021). Also, the cultural services of intertidal flats and their biota, such as birdwatching opportunities and nature appreciation, co-exist alongside their ecological importance (Green & Elmberg, 2014; Mathot et al., 2018). However, restoration initiatives have had mixed success (Atkinson, 2003; Suding, 2011; Sebastian-Gonzalez and Green 2016). While many studies have targeted specific threats, such as disturbance and invasive species at community and ecosystem scales (Iglecia & Winn, 2021), few have specifically considered intervention in intertidal flat ecosystems (Almeida et al., 2020; Kuwae et al., 2003; Wang et al., 2021). None have fully incorporated the roles of intertidal biofilm – an important, recently discovered food source for small-bodied shorebird species in habitats with various degrees of human intervention (almost natural to artificial habitats) (Kuwae et al., 2012). Recently, Duarte et al. (2020) concluded that rebuilding many components of marine life by 2050 is an achievable challenge but requires immediate action to recover depleted habitats. However, fundamental ecological questions remain unresolved, including how well-recovered habitats mirror the functioning of natural habitats.

Concomitant with habitat losses, the world's shorebirds are suffering steep population declines (Amano et al., 2010, 2018; Clemens et al., 2016; Rosenberg et al., 2019; Studds et al., 2017), which directly link habitat needs with population recovery. For example, in Japan, a grassroots initiative to protect the Fujimae flats for shorebirds and waterfowl resulted in a controversial land reclamation project being discontinued (Environment Agency, 1998; Nagoya City and Nagoya Port Management Association, 1999), making the site a national icon for wetland conservation (Ikeguchi & Okamoto, 2008). Consequently, interventions in intertidal flat ecosystems were instigated within a broader Japanese programme to conserve aquatic habitat and promote ecosystem services (Chan et al., 2006; Kuwae & Crooks, 2021; Kuwae & Miyoshi, 2012).

Shorebird usage of artificial habitats such as fish and shrimp ponds, saltpans and rice fields underscores the potential for artificial habitats to serve similar roles as their natural counterparts (Almeida et al., 2020; Dias et al., 2014; Lei et al., 2021; Navedo et al., 2015; Warnock & Takekawa 1995). Here, we define the term 'artificial' to mean sites with clearly intended human interventions, such as restored and newly created habitats, in contrast to 'natural' sites, which may be subject to indirect and/or unintended anthropogenic effects, such as climate change, but are formed without clearly intended human interventions. The usage of artificial compared with natural habitats may differ in ecological aspects, such as population sizes of target species (Jackson et al., 2020), functional biodiversity (Almeida et al., 2020) and feeding guild and body size (Lei et al., 2021).

If we focus on the recovery of shorebird populations, the value of interventions into artificial intertidal flat ecosystems depends on their capacity to generate the required quantity and quality of food sources at the 'right' time, especially at stopover/staging sites used for re-fuelling during long-distance migration (Canham et al., 2021; Mathot et al., 2018). Consequently, intervention must be founded on sound understanding of food web structure, energy flow and the cycling of nutrients. Here, we propose that effective ecologically based techniques for intervention in artificial intertidal flat ecosystems can be developed through using small-bodied shorebirds as a proxy for ecosystem functionality. Recent advances in understanding the foraging of small-bodied shorebirds, especially the recognition of intertidal biofilm as a critically important food source (Kuwae et al., 2008; 2012; Schnurr et al., 2020) provide novel insights into how ecologically sound intervention can be achieved. Hence, we focus on intertidal biofilm rather than macro- and meio-faunal invertebrates, the traditionally recognized prey of shorebirds (Colwell, 2010; Sutherland et al., 2000), while recognizing the important role of invertebrates in intertidal areas will merit similar consideration in the future.

Although locations and cases are limited, several intertidal flat recovery projects in Japan provide valuable lessons. These findings can be used to set the primary goal and three sub-goals for intervention in artificial intertidal flat ecosystems and identify seven key attributes for recovery of small-bodied shorebird populations through biofilm. Finally, techniques for intervention are evolving and new research directions towards further improving artificial intertidal flats are proposed. We show that some Japanese lagoon-type artificial intertidal flat ecosystems can serve as effective means of human intervention for population recovery; however, if two key conditions mediating the sedimentary environment, that is external forcing (waves and currents) and sediment supply (explained in detail below), are satisfied, the proposed attributes would also be effective for other types of intertidal flats that have similar ecological and geophysical locations to sites in Japan. Given the trophic position of small-bodied shorebirds as both primary and secondary consumers and the role of the sedimentary environment in determining the quantity and quality of their food sources, these birds can be viewed as an ultimate goal and indicator with which to evaluate the success of interventions.

2 | THREE CONSIDERATIONS ON INTERVENTION IN INTERTIDAL FLAT ECOSYSTEMS FOR SHOREBIRDS

2.1 | Shorebird foraging

Shorebirds (or waders) are a diverse group characterized by their use of wetlands and shorelines. Their body sizes are among the most varied in birds (Colwell, 2010), encompassing the small-bodied (<30 g), short-billed (<30 mm length) sandpipers to large-bodied (>800 g), long-billed (> 200 mm) curlews. Shorebirds forage using one or more modes (e.g. pecking, probing, grazing) that relate to food availability, body size and bill morphology (Nebel et al., 2005). The traditional view held that shorebirds targeted macro- and meio-faunal invertebrate prey by either probing into sediment or pecking at the surface (Colwell, 2010; Sutherland et al., 2000). However, more recently, four small-bodied shorebird species (western sandpiper, *Calidris mauri*, dunlin, *Calidris alpina*, red-necked stint, *Calidris ruficollis* and semipalmated sandpiper, *Calidris pusilla*) have been shown to graze the thin biofilm layer on the surface of intertidal mudflats (Kuwae et al., 2012; Quinn et al., 2017). Intertidal biofilm is composed of microalgae, especially diatoms, bacteria and other microorganisms, enveloped in a coating of extracellular mucus. The discovery of biofilm as a food source was precipitated by the observation that western sandpipers and dunlin have fine bristles on their tongues suitable for gathering paste-like food, such as biofilm (Elner et al., 2005). Tongue bristles have now been documented in 21 shorebird species, including sandpipers, shanks and plovers, indicating that biofilm-grazing is widespread among shorebirds (Kuwae et al., 2012). Video recordings confirmed that sandpipers ingest biofilm, and parallel studies using stomach samples and stable isotopes revealed that biofilm can account for approximately 45–59% of the total diet or 50% of the daily energy budget of western sandpipers (Kuwae et al., 2008). Reliance on biofilm differs among age classes and sexes of small-bodied shorebirds and can be up to 70% of the total diet (Hall et al., 2021; Kuwae et al., 2012). Bristle distribution and length differences between shorebird species likely reflect functional morphological adaptations to remove biofilm.

The contribution of biofilm to the diet of small-bodied shorebirds appears largest on estuarine mudflats with high biofilm density and fine sediments (Jiménez et al., 2015; Kuwae et al., 2012). Further, sites where biofilm contributed to large proportions of diets also had relatively higher abundances of small-bodied shorebirds (Jardine et al., 2015), indicating their dependence on biofilm availability. As other shorebird species have tongue bristles likely adapted for biofilm feeding (Kuwae et al., 2012), determining the extent to which these other shorebirds forage on biofilm, as well as the functional traits, substrate types and seasonal conditions that allow them to do so, should allow the identification of further focal species to tailor intervention efforts.

The qualitative value of food for small-bodied shorebirds is linked to the provision of macronutrients for long-distance migration (Guglielmo, 2010; Schnurr et al., 2019; 2020; Young et al., 2020), which vary in seasonal abundance between years (Passarelli et al., 2015). The lipid content of biofilm may vary with the biomass of microphytobenthos in the sediment, although Schnurr et al. (2020) demonstrated that total lipid content is not always correlated with total organic matter and chlorophyll-a (the common proxy for biofilm biomass); rather, biofilm quality was not a constant over time, as the total lipid/total organic content ratio peaked during the northward pre-breeding migration of small-bodied shorebirds. Diatoms and other microalgae produce large quantities of lipid under conditions of stress (Sajjadi et al., 2018; Solovchenko, 2012), as occurs during rapidly changing conditions in spring, suggesting that intertidal flats that do not produce adequate lipid during key migratory periods have low value to small-bodied shorebirds. The mechanisms responsible for generating the lipid peak, the relationship between biofilm quality and quantity and implications for other organisms and food webs have become critical research questions (Schnurr et al., 2019). To further understand biofilm quality, field experiments could be conducted. These experiments may involve manipulating temperature and salinity gradients in coastal embayments or artificially enhancing lipid content and then evaluating shorebird responses through foraging observations, or physiological studies such as tracing the uptake of macronutrients labelled by stable isotopes.

2.2 | Sedimentary environment systems

Intertidal flats host complex biological communities exhibiting wide temporal variation in abundance and composition in response to abiotic factors, such as light, salinity, temperature and nutrients (MacIntyre et al., 1996; Montani et al., 2003), as well as biotic interactions (Weerman et al., 2011; Passarelli et al., 2012). Biofilm coating the flats responds to the same abiotic factors. For example, diatoms and other microorganisms in the microphytobenthos exude extracellular polymeric secretions which act to stabilize sediments, retain nutrients and affect light transmittance below the surface (Decho, 2000). In turn, these factors are affected by three characteristics of sedimentary environments, namely elevation, bed slope and sediment grain size (Figure 1). Thus, intertidal flats need to be recognized as integrated sedimentary environments, with the three characteristics directly and indirectly affecting the survival of associated organisms and their interactions.

Usually, the sedimentary environment is in dynamic equilibrium but external forces such as tides, waves and currents and changes in sediment supply can disrupt the equilibrium (Figure 1). The system can rebuild, with dynamic equilibrium re-established after responding to the external forces. Hence, the potential of intertidal flats, whether lagoon or other types, and natural or artificial, to serve as foraging grounds for shorebirds are shaped by their locations that primarily determine these external forces and sediment supply.

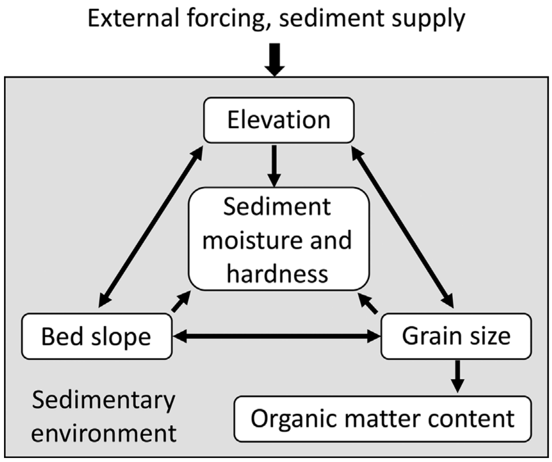

FIGURE 1 Relationships between external forcing (tides, waves and currents), sediment supply and sedimentary environmental systems, all of which regulate the dynamic equilibrium of intertidal flat topography

2.3 | Intertidal food webs

Food web structure controls the dynamics of the component populations (Bascompte, 2010). Within food webs, organisms interact through multiple dimensions, such as in predator–prey and competitive relationships, as well as respond to the surrounding environment. The discovery that small-bodied shorebirds feed directly on intertidal biofilm resulted in the identification of a 'missing link' and a revision of the trophic position of shorebirds from predators to predator/competitors with biofilm-feeding invertebrates (Kuwae et al., 2012). Further, microphytobenthos in intertidal biofilm is a foundation to estuarine ecosystems, contributing to overall photosynthetic activity and carbon sequestration (up to 50%; Saint-Béat et al., 2013; Underwood & Kromkamp, 1999), sediment stabilization and provisioning of consumers (Serôdio et al., 2020). How all these factors can be manifested in intertidal flats remains a work in progress and the search for other links is ongoing (Passarelli et al., 2018). The answers will help elucidate a central issue in ecology, that is how missing links and the behaviour of organisms affect the stability and dynamics of food webs (Kuwae et al., 2012). In addition, this ecological research should contribute to biodiversity conservation and help reverse shorebird declines (Amano et al., 2018; Rosenberg et al., 2019; Studds et al., 2017;).

3 | SEVEN KEY ECOLOGICALLY BASED TECHNICAL ATTRIBUTES OF SHOREBIRD FORAGING

Here we discuss the key ecologically based technical attributes of an idealized artificial intertidal flat that serves as a feeding ground to achieve the primary goal of intervention, that is maximizing total foraging opportunities for small-bodied shorebird population recovery through biofilm. Based on the Energy Maximization Premise (Emlen, 1966; Hughes, 1979), shorebirds should select foraging modes and feeding areas that maximize their rate of energy intake (Bautista et al., 2001; Kuwae et al., 2010) and move between patches within an area as the energy intake rate for a given patch falls below the average for the area (Charnov, 1976; but see van Gils et al., 2006). Accordingly, a shorebird's use of an intertidal flat depends on three sub-goals of intervention: (1) creating environmental conditions in which a broad spectrum of food sources, particularly biofilm, is available, (2) maximizing energy intake rate per individual and (3) maximizing foraging activity (% foraging individuals) (Alerstam & Lindström, 1990). The underlying prediction is that total energy intake by shorebird communities (energy intake rate per individual × foraging activity × number of individuals) is maximized at sites where the three sub-goals are achieved (Figure 2).

An artificial intertidal flat configuration to realize the three sub-goals for serving as a high value foraging ground for small-bodied shorebirds can be achieved through seven key attributes: (1) depositional environment, (2) complex shoreline, (3) gentle slope, (4) gradient of grain sizes from muddy to sandy, (5) maximum water depth at the lowest tide 5 cm or less, (6) freshwater inflow and (7) unobstructed sight-lines (Figure 2). This proposal assumes a spatial scale of several hundred metres to several kilometres; however, the principles can be applied at other scales if there are no trade-offs between habitat management targeting for biodiversity and a given animal group (in this case shorebirds). To make the relationships between the goal, sub-goals and configurations for intervention more comprehensive, the goal here is to maximize the total energy intake. However, 'maximization' may not necessarily be the correct goal, since extremely high foraging by small-bodied shorebirds may interfere with food web sustainability (e.g. depletion). In this latter case, redefining the term 'maximization' to 'optimization' and adjusting each item of the configuration accordingly would be appropriate.

3.1 | Depositional environment

Low-energy environments (those less affected by external forces such as waves) provide locations where fine particles are more likely to be deposited. These environments restrict the resuspension and the outflow of fine sediment, contribute to the retention of organic matter (detritus) and biofilm and increase food density for small-bodied shorebirds (Figure 1).

In the lagoon-type situation, one of the typical depositional environments, the intertidal flat is separated from the sea by a narrow opening resulting in a delay in tidal phase between the open coast and the flat. Thus, the flat remains exposed after foraging opportunities outside the lagoon become curtailed due to high tide. Notwithstanding their locations and small areas, some artificial intertidal flats found in Japanese urbanized areas that are used by small-bodied shorebirds as feeding grounds have a lagoon-type shape (Kuwae et al., 2012; Otani & Endo, 2019; Waterfront Vitalization and Environment Research Center [WAVE], 2001; Figure 3). Further, studies into the relationship between shorebird use and the topographic characteristics of the wider Japanese coastlines have identified that sites with inner bays

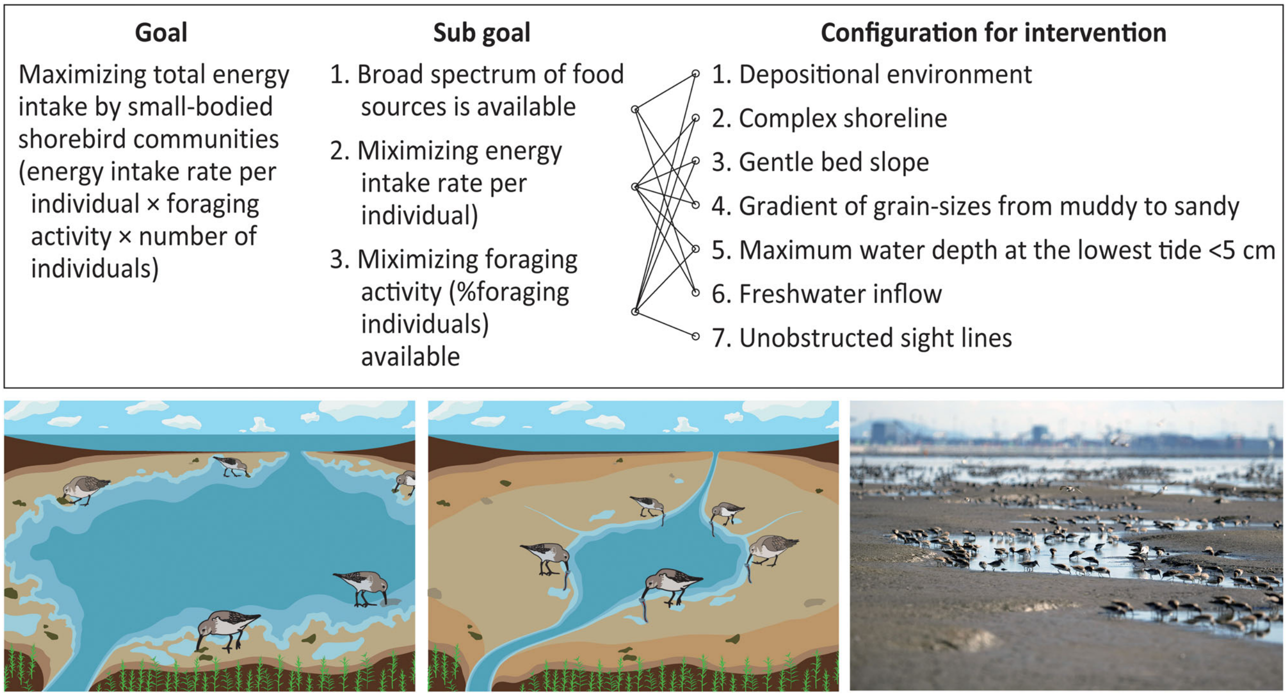

FIGURE 2 Relationships between the primary goal, three sub-goals and the seven attributes of intervention in artificial intertidal flat ecosystems for biofilm-based small-bodied shorebird population recovery (modified from Kuwae & Miyoshi, 2012). Bottom left and center panels depict an intertidal flat during high and low tides, respectively. Water colour depicts water depth (deeper shades = deeper water), and sediment colour depicts the elevation for intertidal zones. The dark colour at the upper part of the intertidal zone indicates biofilm on muddy substrates. Bottom right panel depicts small-bodied shorebirds foraging in tide pools at Roberts Bank, British Columbia, Canada in 2005 (Photo: T. Kuwae)

with narrow openings and fine-grained substrates serve as critical habitats for several shorebird species (Arakida et al., 2011), indicating the lagoon-type is a useful configuration for restoration efforts.

3.2 | Complex shoreline

Tide pools and hummocks on an intertidal flat increase the foraging area for small-bodied shorebirds (photo in Figure 4) and can mitigate interference competition between individuals (Colwell, 2010). Such topographical features are formed through external forcing, such as currents and waves, combined with internal dynamic processes, such as bioturbation, the disturbance of sedimentary deposits by living organisms. As the topography of mudflats is constantly changing due to complex interactions among external forces, sediment supply and sedimentary environment systems (Figure 1), a focus on post-construction maintenance (adaptive management) rather than proactively designing features is advised.

3.3 | Gentle slope

A wide intertidal zone is preferable because the biomass of food, particularly biofilm, will be higher than on a narrower flat due to the larger area of available habitat. One means to widen the intertidal is to engineer a shallow-sloping surface, which maintains a high groundwater level, suppresses suction and keeps the sediment soft (Sassa & Watabe, 2007). Thus, a gentle slope not only increases foraging opportunities for sandpipers grazing biofilm but also probing for prey (Kuwae et al., 2010).

3.4 | Gradient of grain sizes from muddy to sandy

The need for careful consideration of the grain size distribution of sediment on intertidal flats was demonstrated in comparing a series of recovery projects in Nishiura flat, Mikawa Bay, Japan, where lower numbers of shorebirds were observed at restored flats relative to natural flats. The finding may be attributed to the sediment on the restored flats (approximately 3% silty clay) being too coarse, resulting in a relatively lower food density (Kuwae et al., 2003; Kuwae & Miyoshi, 2012) (Figure 4). Advances in ecological geotechnics have identified the role of suction dynamics – the interaction between elevation and bed slope, influencing the water table depth, and sediment grain size, influencing the permeability of the substrate (Sassa et al., 2013; Figure 1), which in turn determines the distribution of available food sources and, thus, the foraging activities of shorebirds (Kuwae et al., 2010). A geotechnical approach can provide specifications for sediment grain sizes and site design that link directly to the biodiversity targets for interventions (Sassa et al., 2013).

Microphytobenthos, particularly diatoms, are major components of biofilm and develop in shallow areas with sufficient light for

FIGURE 3 Examples of recovered intertidal flats used by small-bodied shorebirds as feeding grounds in Japanese urbanized areas: Osaka-Nanko Wild Bird Park, Tokyo Port Wild Bird Park, Koshien-hama and Yatsu. Note: all have a lagoon-type shape

photosynthesis, that is the upper intertidal zone (Jesus et al., 2009; Underwood & Paterson, 2003). Therefore, fine-grained, muddy sediment should be positioned near shore to increase biofilm productivity. In the lower intertidal zones, where the water is relatively deeper, biofilm production can be presumed to be poorer and less-muddy sediments in these zones to favor other potential food sources (invertebrates).

3.5 | Maximum water depth at the lowest tide 5 cm or less

Within a shallow lagoon, the constricted exchange of seawater with the outside ocean can result in anoxic water masses. Possible solutions include increasing oxygen supply by creating a large pool of shallow water at the lowest tide, which results in a large surface area/volume ratio to maximize gas exchange rate with the air, or increasing the seawater exchange rate (assuming the oxygen concentration in seawater outside the intertidal flats is high). A permanently submerged sub-tidal zone is preferable in order to increase habitat diversity and available food sources. Also, as shorebirds are constrained to shallows less deep than their leg length (Baker, 1979; Colwell, 2010; Ntiamoa-Baidu et al., 1998), the water depth in the subtidal zone should be less than 5 cm for small-bodied shorebirds and up to 30 cm for large-bodied shorebirds (Ma et al., 2010; Taft et al., 2002). Finally, a sluice gate at the lagoon opening may be an option to regulate water depth.

3.6 | Freshwater inflow

Nutrient supplies from terrestrial sources, such as sewage outflows or groundwater discharges, can improve primary production by phytoplankton and microphytobenthos on intertidal flats, and, in turn, benefit biofilm (bottom-up effect). However, if seawater flowing onto an intertidal flat is already nutrient-rich, then additional sources of nutrients may not be necessary. The mixing of freshwater with seawater is a key attribute of functional intertidal flats (Canham et al., 2021). Increased bird use at created intertidal flats at the Osaka Nanko Bird Sanctuary in Osaka Bay and Komuke Lagoon on the coast of the Sea of Okhotsk has been linked to enhancement of freshwater/seawater exchange through the maintenance or creation of open channels between the flats and the sea (WAVE, 2001; Watanabe & Kuwae, 2021) (Figure 4). Moreover, although apart from energy maximization, springtime changes in water chemistry (i.e. salinity and nutrients)

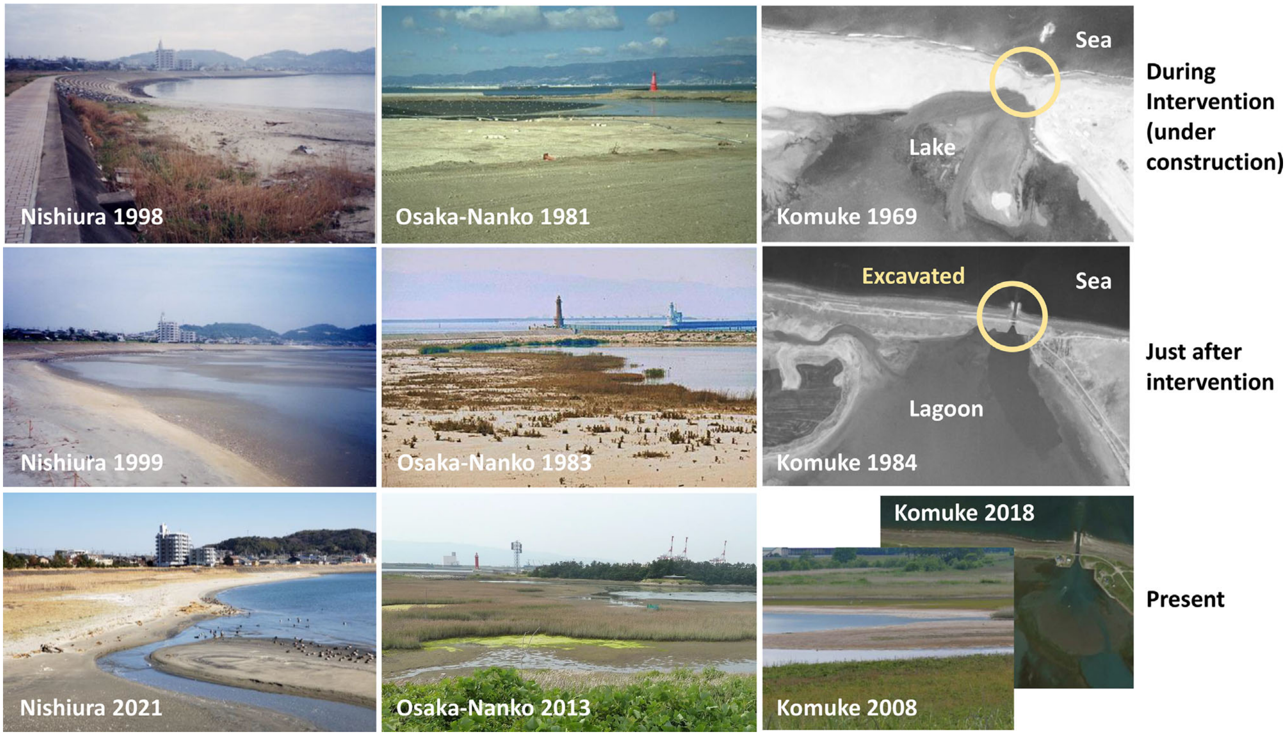

FIGURE 4 Examples of human intervention in intertidal flat ecosystems in Japan. Photo credits: for Nishiura: Mikawa Port Office, Chubu Regional Development Bureau, Ministry of Land, Infrastructure, Transport and Tourism, Japan; Osaka-Nanko: Hiroshi Takada

and temperature can trigger the production of higher overall total lipid/fatty acid content in mudflat biofilms by inducing a lipid-accumulation response in diatoms (Schnurr et al., 2020). Therefore, careful attention needs to be paid to freshwater dynamics to ensure tidal flats provide valuable nutrients for shorebirds.

3.7 | Unobstructed sight-lines

Shorebirds prefer open landscapes for foraging and roosting because they allow early detection of predators (Pomeroy et al., 2006). Hence, there should be minimal tall marsh vegetation, trees or buildings abutting intertidal flats. In addition, foraging time can be expected to be longer on open intertidal flats where shorebirds can have advance warning of approaching predators.

4 | FUTURE CHALLENGES

A comprehensive ongoing monitoring scheme based on goals and expected outcomes is crucial for decades after intervention on artificial habitats (Lyons et al., 2008; Wauchope et al., 2021). Small-bodied shorebirds might avoid artificial intertidal flats immediately post-construction but numbers may increase with time. Also, increases in species diversity at artificial intertidal flats tend to be slower than increases in abundance (Moreno-Mateos et al., 2012). For post-intervention monitoring, a multi-factor programme should include observing shorebird behaviour, especially grazing, pecking and probing (Mander et al., 2013) to measure intake rate, in addition to surveying shorebird species and numbers, plus, if possible, assessing demographic parameters such as shorebird survival rates (Armitage et al., 2007; Lindell, 2008; Berger-Tal et al., 2011), as well as measuring the quantity and quality of biofilm and other food sources. The general assumption is that intertidal flats with higher shorebird foraging rates provide better habitat than flats with slower shorebird feeding rates, but a site with large numbers of birds may not always be suitable for foraging, for example, the area may be providing refuge from predators or acting as a supplementary feeding habitat only when primary habitats are unavailable (Masero, 2003).

Assessments of the value of interventions only provide reliable inferences when compared to appropriate benchmark (control) habitats. To date, few comparisons have been made of bird usage on artificial versus natural flats (Almeida et al., 2020; Armitage et al., 2007; Brusati et al., 2001; Lei et al., 2021; Kuwae et al., 2003; Wang et al., 2021). Such comparisons provide insight into the ecological equivalency of the habitats, and foraging observations can be placed in a regional context (Masero, 2003; Navedo et al., 2015). In addition to the seven technical factors reviewed for intervention in artificial intertidal flat ecosystems, other considerations include insights from historical records (sites that once had intertidal flats or larger numbers of birds are likely to be successful), spatial heterogeneity (coastal ecosystem and landscape diversity) and effective maintenance practices (e.g. managing competitors, such as gastropods, for biofilm, cutting tall vegetation, adjusting microtopography and sediment grain size)

(Armitage et al., 2007; Athearn et al., 2012). Finally, the proposed seven key attributes are focused on the foraging ecology of small-bodied shorebirds, and the extent of harmonization with other ecosystem services remains to be evaluated. In particular, a dichotomous relationship can occur between ecosystem services, where the increase in one service occurs at the expense of the other. In such cases, the parties involved need to form a consensus on goals and outcomes.

Historically, intertidal flats were viewed as wastelands and, consequently, low-value, disposable habitat (Mathot et al., 2018). However, realization of their ecological complexity and services have forced a re-appraisal of their worth, especially given the synergies between small-bodied shorebirds and intertidal flats (Murray et al., 2019). Small-bodied shorebirds are excellent indicators of the quality and quantity of intertidal biofilm and the technical design (shape, composition and arrangement) of flats can be tailored to their needs by incorporating understanding of optimal foraging, food webs and diet. Accordingly, the abundance and foraging activity of small-bodied shorebirds can serve to track success of interventions within such habitats. The proposed configuration of seven key attributes for biofilm-based shorebird population recovery is grounded in decades of experience with intervention projects in Japan, ecological theory and the most recent understanding of small-bodied shorebird foraging on biofilm. However, the configuration requires further validation, as understanding of how artificial intertidal flats can serve the needs of shorebirds is handicapped by gaps in understanding of, variously, food web structure, seasonal dynamics in the quantity and quality of food sources, sediment environmental systems and post-construction management.

Finally, for clarity, we do not advocate the transformation or modification of existing high-value foraging sites for shorebirds and fully recognize that effective shorebird conservation relies on retaining such sites along migration flyways. The seven key attributes relate to intervention programmes to either create new sites or improve low-value foraging sites for supporting small-bodied shorebird foraging. In doing so, we build on the approach recommended by Jackson et al. (2020), that conservation efforts of flyways with high rates of habitat loss must rely on the integration of artificial habitats alongside the preservation of natural wetlands.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

TK and MD conceived the idea. TK, MD, RE and TA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This study does not include any data.

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