Conservation and Restoration of Estuaries and Coasts: Horseshoe Crabs as Flagship Species

Jennifer H. Mattei, Mark L. Botton, Satoquo Seino, Alfredo Quarto, Jaruwan (Ning) Enright, J. Vanitha, Hsu Chia Chi, Lester Tan, Joe Cheung, and John T. Tanacredi

1 Introduction

Many coastal and estuarine habitats: sandy and cobble beaches, saltmarshes, seagrasses, mangroves, and mudflats have been reduced and degraded around the world requiring adaptive management, conservation, and restoration (Zedler 2017). The

J. H. Mattei (✉)
Sacred Heart University, Department of Biology, Fairfield, CT, USA
e-mail: matteij@sacredheart.edu

M. L. Botton
Fordham University, Department of Natural Sciences, New York, NY, USA
e-mail: botton@fordham.edu

S. Seino
Graduate School of Engineering, Kyushu University, Fukuoka, Japan
e-mail: seino@civil.kyushu-u.ac.jp

A. Quarto · J. (. Enright
Mangrove Action Project, Seattle, WA, USA
e-mail: mangroveap@olympus.net

J. Vanitha · H. C. Chi · L. Tan
Nature Society (Singapore), Singapore, Singapore
e-mail: lestertan@nss.org.sg

J. Cheung
Ocean Park Conservation Foundation Hong Kong, Hong Kong, SAR China

The Nature Conservancy Hong Kong Foundation Ltd, Hong Kong, SAR China

J. T. Tanacredi
Department of Earth and Environmental Studies, Molloy College, Rockville Centre, NY, USA
e-mail: jtanacredi@molloy.edu

J. T. Tanacredi et al. (eds.), *International Horseshoe Crab Conservation and Research Efforts: 2007-2020*, https://doi.org/10.1007/978-3-030-82315-3_10

level of ecosystem services provided by these habitats as fish and shellfish nurseries, coastal protection, erosion control, carbon sequestration, water purification, and recreation/tourism are often undervalued and when measured accurately prove more valuable than terrestrial habitats (Barbier 2017; Barbier et al. 2011). With expanding coastal megacities, increasing levels of pollution and shoreline armoring, estuaries need "flagship species" to be recognized that are valued culturally, economically, and ecologically in order to impress upon people the importance of these coastal habitats. One taxonomic group that is important in all of these areas and should take the role of the flagship species for estuaries and coasts is the horseshoe crab.

The concept of a flagship species is often associated with charismatic terrestrial vertebrates (typically mammals), such as pandas, tigers, elephants, lions, or polar bears. Flagship species belong to a larger category of "focal species," which "… for ecological or social reasons, are believed to be valuable for the understanding, management and conservation of natural environments" (Zacharias and Roff 2001, p. 59). Some flagship species have the dual function of "umbrella species," ones whose protections will ensure conservation of other co-occurring species (Kalinkat et al. 2017). By virtue of their size, appearance, perceived threatened status, and familiarity with the public, flagship species are important vehicles in fundraising campaigns and education about the importance of preserving natural resources. By focusing public awareness on the conservation of flagship species, the status of other species which share the habitat may be improved. For instance, large megafauna (e.g., tigers, manatees, dolphins) may be more effective as flagship species for habitats dominated by mangrove trees than the myriad small resident invertebrates and fishes (Thompson and Rog 2019). The challenge in finding suitable flagship or umbrella species in aquatic habitats is that many species of ecological importance are taxonomically very distant from humans (i.e. not mammals), and may be small and/or cryptic (Kalinkat et al. 2017). Shokri et al. (2009) proposed using sygnathid fishes (pipefish and seahorses) as flagship species for the conservation of seagrass habitats. The main appeal of these species is their aesthetics and their use in traditional Chinese medicine but support for the conservation of seagrass has not improved with worldwide losses of seagrass beds estimated to be 1.5% per year (Gómez 2018).

There are four extant species of horseshoe crab, three in Asian coastal habitats: (1) tri-spine horseshoe crab *Tachypleus tridentatus*, (2) coastal horseshoe crab *T. gigas*, and (3) mangrove horseshoe crab, *Carcinoscorpius rotundicauda*. The fourth species, the American horseshoe crab *Limulus polyphemus*, inhabits the coasts of the eastern United States and parts of the Gulf of Mexico. At first glance, horseshoe crabs would appear to be unlikely candidates to enlist as a flagship species for the conservation of coastal and estuarine habitats, as they do not fit the typical profile as a physically attractive animal with features (such as large eyes or fur) that are common to most other flagship species. However, as identified by numerous authors (e.g. Shuster et al. 2005; Chen et al. 2009; Tanacredi et al. 2009; Carmichael et al. 2015, this volume) horseshoe crabs have immense ecological, evolutionary, economic, and cultural significance which serve as a counterweight to this disadvantage. Horseshoe crabs are "living fossils" with remarkable persistence over 445 million years of geological changes (Rudkin and Young 2009). Their evolutionary history of *baúplan* stasis, association with deep time, surviving the past five mass extinctions has fascinated many people from paleontologists to children visiting natural history museums. Horseshoe crab blood products have improved the health of billions of people. Their blood contains a material known as LAL (*Limulus* amoebocyte lysate) that is the worldwide industry standard to detect gram-negative bacterial endotoxins in pharmaceutical products (Krisfalusi-Gannon et al. 2018). The use of LAL for vaccine testing has not only prevented billions of people from becoming ill but has also protected our domesticated companions and agricultural livestock (Beekey and Mattei 2015). LAL and TAL (*Tachypleus* derived amoebocyte lysate) will be used to help test COVID-19 vaccines before being distributed to the world's populations (Gorman 2020). This demonstrates, once again, how important coastal and estuarine habitats are that allow horseshoe crabs to survive and reproduce for the benefit of all people to remain healthy during the current and future pandemics. There has never been a better time to draw peoples' attention to the plight of horseshoe crab habitats. Additional economic benefits include use as bait in commercial fisheries for eels, whelks, and octopus (Smith et al. 2016), and horseshoe crabs are consumed by people in many countries in Southeast Asia (John et al. 2018).

Ecologically, when horseshoe crabs are abundant, they are a dominant species responsible for increased biodiversity/biomass in coastal spawning habitats (Mattei et al. this volume). Various aspects of this food web have been investigated by researchers in North America (Walls et al. 2002; Botton and Shuster 2003; Carmichael et al. 2004; Odell et al. 2005; Botton 2009; Niles et al. 2009) and Asia (Debnath et al. 1989; Kwan et al. 2015; Fan et al. 2017). *Limulus* eggs are vital food for migratory shorebirds, fish, and numerous invertebrate species as observed in the Delaware Bay estuary, USA. Dense aggregations of horseshoe crabs can be significant predators and bioturbators of estuarine habitats (Botton 1984; Kraeuter and Fegley 1994). Predation on adult horseshoe crabs is seldom reported (Botton 2009), with two notable exceptions. *Limulus polyphemus* forms an important part of the diet of federally endangered loggerhead (*Caretta caretta*) and Kemp's Ridley (*Lepidochelys kempii*) sea turtles in the middle Atlantic region of the United States (Keinath et al. 1987; Seney and Musick 2007). *Limulus* that are overturned during spawning activity often fall prey to large seagulls (Botton and Loveland 1989). As large numbers of horseshoe crabs die onshore during spawning events, their carcasses are scavenged by everything from bald eagles to carrion beetles, flies, and worms which in turn expand the food web.

All species of horseshoe crab spend their lives in coastal and estuarine habitats. Spawning generally takes place on sandy and cobble estuarine beaches for the tri-spine horseshoe crab *T. tridentatus*, coastal horseshoe crab *T. gigas*, and American horseshoe crab *L. polyphemus*, and mangrove forests for the mangrove horseshoe crab, *C. rotundicauda*. However, *Limulus* has also been observed, across its North American range, to spawn in saltmarshes, eel grass beds, and mudflats (pers. obs. J. Mattei, M. Botton, C. Chabot, J. Brockman, D. Sasson). In addition, horseshoe crabs have a relatively long juvenile growth and development period that spans

8–10 years. Although juvenile habitat requirements are not well studied, juvenile horseshoe crabs of all four species have been observed foraging in mudflats (Hu et al. 2015), flat sandy areas (at least through 4 years of age), and *Limulus* juveniles have been observed in saltmarsh fens (Mattei, unpublished data; Colón et al. this volume). Thus, throughout their lifetime of over 20 years, horseshoe crab individuals require between two and four different habitat types within coastal and estuarine ecosystems.

Chen et al. (2009) first considered the tri-spine horseshoe crab as a flagship species for marine conservation in Taiwan, and in this chapter, we expand this to include all four species of horseshoe crab as flagship species for the conservation of estuaries and coasts. The three Asian horseshoe crab species are declining in all areas of Asia where studies have been conducted (John et al. 2018; Laurie et al. 2019), and the American horseshoe crab populations are declining in most regions of North America (Smith et al. 2016). There are many factors linked to their decline, including overharvesting for bait, human consumption, biomedical uses, pollution, and shoreline hardening/reclamation (Seino et al. 2003; Smith et al. 2016; John et al. 2018). However, the overarching factor of decline of horseshoe crab populations is the loss of coastal and estuarine habitats.

The workshop on which this chapter is based was held in September 2016 as part of the IUCN World Conservation Congress in Honolulu, Hawaii. The title of this workshop, "Conservation and Restoration of Estuarine, Beach and Mangrove Habitats: Horseshoe Crabs as a Flagship Species," reflects our belief that the broader goals of conservation and restoration of coastal and estuarine habitats can be facilitated by having horseshoe crabs as flagship species due to their dependence on these habitats for their continued existence.

2 Sandy/Cobble Beaches

Beaches form along shorelines where waves deposit sediments, and the beach morphology is shaped by ocean waves during shoaling, breaking, and swash. All beaches consist of sediment ranging in size from sand up to cobbles, and along some shorelines, mixed with larger rock and boulders. In mid-latitudes, beaches are composed of eroded grains of siliceous or quartz sand grains. Tropical beaches are generally composed of carbonate sediment or shell fragments (Short 2012).

2.1 Ecosystem Services of Beaches

Beaches and associated dunes provide protection of the upland from storms by forcing waves to shoal and break before reaching human developments. Beaches are important foraging areas for shorebirds, crabs, and finfish due to the benthic animals and microalgae living on or within the sand (King et al. 2018).

2.2 *What Are the Causes of Loss/Decline of Beaches?*

Changes in sea level associated with global climate change threatens the continued persistence of sandy estuarine beaches which are the primary spawning habitat for three of the world's four horseshoe crab species, *Tachypleus tridentatus*, *T. gigas*, and *Limulus polyphemus*. To protect coastal property and infrastructure, shorelines are frequently armored, an alteration that greatly decreases their ecological value relative to the beaches or marshes they replace (e.g., Dugan et al. 2008). Hardening the shoreline makes it unsuitable as spawning habitat for horseshoe crabs (Botton 2001; Seino 2001; Seino and Uda 2007; Jackson and Nordstrom 2015; Loveland and Botton 2015). Less intrusive methods, such as beach nourishment and living shorelines, are an alternative approach for coastal protection that may cause less damage to biota. The outcome of some of these projects in the United States and Japan may be useful in the design of future shoreline restoration efforts.

Case Study: Shoreline Armoring, the Japanese Experience

Over a half of the Japanese coast (except island areas) were artificialized in the early 1990s for protection of erosion and reclamation (Environmental Agency, Government of Japan 1994). National seashore protection policies were oriented to harmonize with the ecosystem along with amendments of the Seacoast Act in 1999. *Tachypleus tridentatus* was designated as the target species for conservation of estuaries and sandy beaches by national governmental technical guidelines (Seino et al. 2004). However, erosion control of sandy beaches was executed with solid concrete structures. Moreover, the 2011 Great East Japan Earthquake and tsunami spurred the Japanese government to build bigger and wider concrete sea walls. In northeast Japan, efforts to fend off future disasters are focusing on a nearly 402 km chain of cement sea walls, at places nearly five stories high (~15 m, Fig. 1). Opponents of this US$6.8 billion plan argue that the massive concrete barriers will damage the marine ecology and aesthetics of the area, hinder vital fisheries and the protective value to residents is not known; residents are encouraged to relocate to higher ground if possible.

Japan's southern inland sea has experienced urbanization, development, and land reclamation for agriculture. Port construction and waterway dredging have caused deformity and loss of geomorphological continuity of the sea bottom. Every river has dams, weirs, and armored shorelines. Thus, sediment transport downstream has been halted (Seino et al. 2000).

*Tachypleus tridenta*tus, the tri-spine horseshoe crab, is now an endangered species in Japan with a declining population due to the loss of spawning habitats (i.e., coarse sandy beaches) since the 1990s. Sea level rise and coastal erosion are increasing the threat of horseshoe crab extinction in Japan. The ecological restoration of estuaries is needed. The possibility of beach nourishment is being discussed. Small-scale trials of beach nourishment projects have been executed during the 1980s as

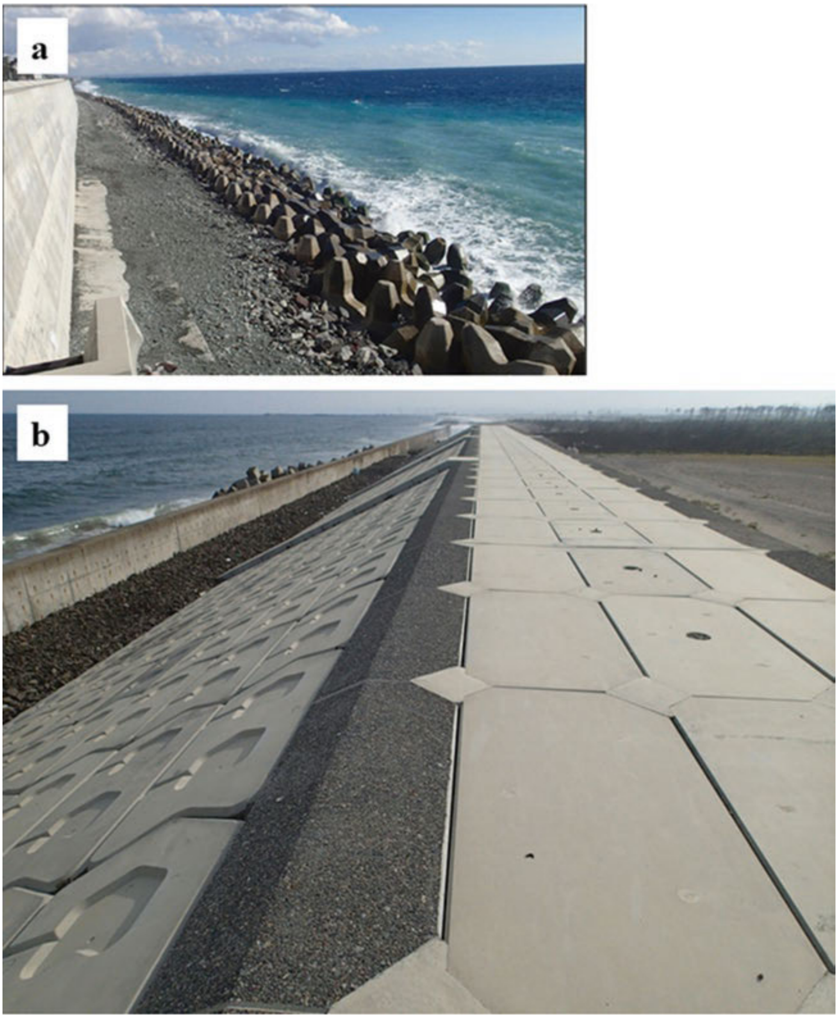

Fig. 1 Some views of coastal Japan. (**a**) typical artificialized beach along the coast of Japan; (**b**) giant sea wall construction after the Great East Japanese Earthquake of 2011

mitigation of reclamation. Continuous extensions of roads and highways have reclaimed many sandy beaches. Often, local inhabitants would request their beaches to be restored through governmental nourishment projects (Ishikawa et al. 2013). Dredged sand from harbors and dam reservoirs may be used but also may have contaminants and/or have high silt components. Very fine-grained sediments may not be the best beach composition for spawning horseshoe crabs. Restoration of sand transport within the watershed and conservation of the sea bottom are essential, but the current social system of water resource and disaster reduction should be modified with nature-based solutions. In recent years, Japanese academics and environmental policies have become to be interested in ECO-DRR (Ecosystem-based Disaster Risk Reduction) and Green Infrastructure. In part, these strategies involve re-thinking the proper placement of revetments to preserve the continuity between the land and sea (Fig. 2). Sandy beaches for horseshoe crab will benefit if we avoid coastal overexploitation.

Ecological restoration must be attempted to allow this species to survive in Japan. Mass mortality of *T. tridentatus* was observed at Sone tidal flat in northern

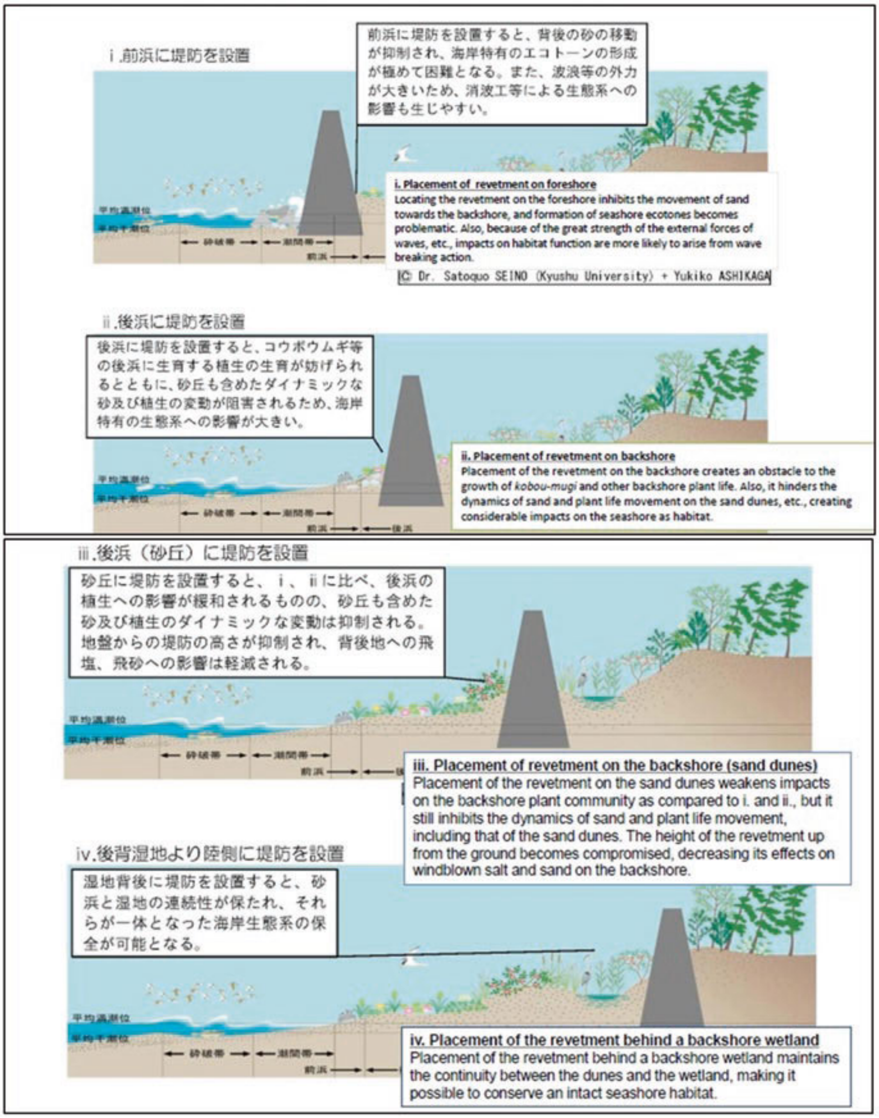

Fig. 2 Strategies for the placement of revetments along the coast of Japan is part of the national guidelines of disaster recovery construction

Kyushu. This population lives at the northern limit in Asia. In 2016, western Japan experienced the hottest summer on record with 1 day in August reaching 41 °C. Global climate change research and studies of local human impacts that affect horseshoe crab biology and ecology are being revealed by international cooperation. In this decade, floods and landslide disasters caused by intense rainstorms had previously been recorded only once a half century or rarely (e.g., every 350 years) are occurring more frequently. Almost all horseshoe habitats in western Japan are impacted by climate changes. In many areas, tidal mudflats that used to be horseshoe crab nurseries have come to be regarded as high-risk areas and become reclaimed lands.

2.3 Restoration of Beaches in General

Sea level rise is coupled with the overall problem of global climate change, and hence to greenhouse gas emissions (IPCC 2018). In the final analysis, we would collectively need to lower our use of fossil fuels, otherwise beach erosion will continue. Building bulkheads and sea walls ends up causing more erosion and attempts to divide the land from the sea which in turn damages and reduces ecosystem services. Large-scale techniques like beach nourishment may slow or delay beach erosion, but are expensive (Thuy et al. 2018).

Beach Nourishment and Horseshoe Crabs: A Case History from New York City, USA

Sea level rise associated with global climate change is a world-wide threat to coastal ecosystems. The materials used in coastal restoration make a difference to the species that use the area. In particular, we provide an example of how the grain size of sediments used during beach nourishment activities may be more important for horseshoe crab spawning and egg development than the volume of sand brought in.

This study took place on Plumb Beach, Jamaica Bay, New York, where we compared spawning abundance and egg density on a beach nourished in 2012, with a nearby reference site beginning in 2011 (pre-restoration) and continuing for 4 years post-restoration (Botton et al. 2018). The lengths of the nourishment site and reference site were similar, 0.9 and 0.85 km, respectively. Shoreline counts of spawning adult crabs took place on 12 dates each spring, that were selected to bracket the new and full moons, which are the anticipated peaks of spawning activity. To assess egg densities, we collected a series of 30 core samples every 2–3 weeks during the spawning season in 2012 (pre-nourishment) and 2013–2015 (post-nourishment). Cores were 3.8 cm in diameter and we sampled to a depth of 20 cm. The hardness of the surface mid-beach sediment was measured using a pocket penetrometer (Forestry Suppliers Inc., model 77,114). Sediment samples from each site were sieved in the laboratory and standard grain-size statistics were calculated (see Botton et al. 1988 for details of all methodologies).

The newly restored beach area sustained very low horseshoe crab density compared to the reference beach, even 4 years after the restoration. There was only a slight increase in the density of spawning females on the restored beach before and after beach nourishment, but spawning densities were consistently higher at the reference site throughout the study. Similarly, beach nourishment in Fall 2012 was not followed by a detectable increase in horseshoe crab egg deposition in the first three post-nourishment seasons, 2013–2015. The nourishment site had significantly fewer horseshoe crab eggs, embryos, and trilobite larvae both before and after the restoration project. These differences in spawning and egg densities between beaches have persisted through 2019 (M. Botton and C. Colón, unpublished data).

We believe that differences in sediment texture between sites may explain the differential use of the restored and reference sites. Hard-packed fine sand of relatively uniform texture was found at the restored beach. In contrast, the reference site has a less compacted, coarser, and more heterogeneous mix of particle sizes. The very dense sand at the restored beach has small pore spaces for oxygen and water exchange, leading to occasional anoxic conditions that are unfavorable for horseshoe crab egg development. These results are consistent with the study by Botton et al. (1988) which showed that horseshoe crabs tend to avoid depositing their eggs on beaches that have high levels of hydrogen sulfide, which is an indicator of anoxic conditions.

In summary, this case history showed that beach restoration at Plumb Beach did not result in significant benefits to horseshoe crabs as assessed by spawning and egg densities. Subtle differences in sediment texture over relatively short distances can be detected by horseshoe crabs and may underlie their selection of specific nesting sites. This study illustrates the importance of selecting the proper type of sediment for beach nourishment projects to create suitable conditions for spawning horseshoe crabs.

3 Saltmarshes, Seagrasses

Saltmarshes and seagrasses are highly productive biodiverse ecosystems, consisting of a variety of plant species that provide important interconnected coastal habitats. Tidal saltmarsh communities are found in gently sloping areas above mudflats between mean high water neap tides and mean high water spring tides. Seagrasses (i.e., submerged aquatic vegetation or SAV) are found further offshore and remain submerged to depths of 1–3 m. Saltmarshes and seagrasses occur worldwide, particularly in middle to high latitudes, in sheltered locations; however, diverse seagrass species are also found throughout the tropics (Short et al. 2007; Mcowen et al. 2017).

3.1 Ecosystem Services of Marshes and Seagrasses

Saltmarshes and seagrasses are extremely valuable ecosystems, contributing to local and global economies. Services include fish/shellfish production, building materials and fodder for livestock, ecotourism, wildlife habitat, carbon sequestration/storage, and protection of coastal areas from natural disasters, such as erosion and storm surges (Short et al. 2007; Mcowen et al. 2017).

3.2 What Are the Causes of Loss/Decline in General?

Even though the estimates of ecosystem services of global saltmarsh and seagrass habitats range in trillions of dollars, they are declining around the world with estimates at 50% of their global historical coverage (Duarte et al. 2008; Crooks et al. 2011). These coastal habitats are subjected to high levels of disturbance that vary both in frequency and intensity including hurricanes, runoff, sedimentation, sea level rise, as well as coastal development and other human uses including fishing/harvesting, aquaculture, marine trades, and access for recreational activities. Long-term disturbance, historical loss and alteration of habitats, and urbanization have increased the need for coastal habitat restoration (Greipsson 2011; Davis and Kidd 2012).

3.3 Restoration

Case Study: Nature-Based Restoration in Stratford, Connecticut, USA

Restoration of highly disturbed coastal habitats involves activities that include remediation (e.g., removal of contaminants), rehabilitation (e.g., dune construction and prescribed burning), and revegetation (e.g., planting of native beach grasses and upland woody species). Unfortunately, confidence levels are often low regarding the target goals of many restoration projects. This is due to the uncertainty regarding natural variation in temporal and spatial conditions with respect to hydrology, weather, growth and reproduction patterns of plants and animals, effects of natural predators and invasive species, and changes in the surrounding landscape due to human activity (Thom 2000). The development of successful restoration projects requires an understanding of the state of the system, the prognosis for further development, the measures needed to correct problems, and a long-term commitment via monitoring and adaptive management (Mattei 2019).

Living shorelines are nature-based solutions to man-made problems along our highly populated coasts. Coastal development, pollution, and uncontrolled harvest of seafood have changed the conformation of our coastlines. One would need to go back to the late 1700s to find descriptions of what our natural coastal habitats looked like because we have changed every habitat in our coastal ecosystem (Ermgassen et al. 2012). For example, we overharvested the oysters and stripped out nearly all of the oyster beds and reefs. We have filled in and taken out the majority of our saltmarshes and vegetated dunes, many replaced with human developments. These coastal habitats were the natural buffers of wave energy and coastal storms. In the past, wave energy would dissipate well before it hit the shoreline and upland.

Living shorelines can be used for capping heavy metals, slowing coastal erosion, increasing sediment deposition, and increasing wildlife habitat structure and function. Living shorelines in New England, USA, consist of temperate coastal habitats including oyster reef, *Spartina* saltmarsh grasses and upland beach grass, shrubs, and trees. The model used at Stratford Point, Connecticut, employs reef balls (www.reefball.org) operating as artificial oyster reefs, to slow the incoming waves, protect newly restored marsh grasses, and provide fish habitat (Fig. 3). Oysters and blue mussels are slowly colonizing the reef. The sediments that have accumulated 2 years after installation (~30 cm) are now deep enough for horseshoe crab spawning to be successful in the area (Fig. 4). The numbers of spawning horseshoe crabs have increased in the area over the past 4 years and biodiversity has dramatically increased (Mattei 2019).

Fig. 3 Stratford Point living shoreline, August 2019, Connecticut, USA (photo credit: J. Mattei)

Fig. 4 Spawning horseshoe crabs found in accumulated sediments around reef (left). Shellfish colonization of reef (right) (photos by J. Mattei)

4 Mangrove Forest Ecosystem

Mangrove forests are tidal tropical and subtropical coastal wetlands found in estuaries, deltas, lagoons, or surrounding islands found in the Indo West Pacific (58 species) and the Atlantic East Pacific (12 species) along the coastal areas of Mexico, Central America, and parts of the Caribbean. Mangrove trees are uniquely adapted for growth in salt water.

4.1 Relevance of Mangrove Restoration for Conservation of Horseshoe Crabs

Mangrove forests are important for healthy coastal ecosystems in the tropics and sub-tropics. These forest wetlands support an immense array of marine and coastal life, serving as marine nurseries, nesting, and feeding grounds for migratory shore birds, one of the last remaining refuges for Bengal tigers in the Sundarbans of the Bay of Bengal, and a wide variety of other mammals dependent on a healthy mangroves and related habitats including manatees, proboscis monkeys, lemurs, a myriad of insects, amphibians, reptiles, sea turtles, and mangrove horseshoe crabs.

Mangroves also support the health and productivity of coral reefs and sea grass beds by filtering out sediment and absorbing excess nutrients from river water. In addition, mangroves play an important, life-supporting role for countless coastal communities who depend on mangroves for life and livelihoods. Mangroves are recognized for their important role in mitigating climate change, sequestering up to five times more carbon than other forest ecosystems, storing that carbon in their peat soils for hundreds, if not thousands of years (Howard et al. 2017). Mangroves are also living buffers against the forces of storms and waves that can otherwise erode and devastate coastlines (del Valle et al. 2020).

Horseshoe crabs have been around for over 400 million years, evolving in the shallow seas of the Paleozoic Era (540–248 million years ago). Yet these resilient creatures that survived the five previous mass extinction events may not survive the present one because of loss of habitat. For one species of horseshoe crab, that loss intertwines its fate with that of the mangrove forests of Southeast Asia, as industrial shrimp aquaculture, tourism, urban, and agricultural expansion all threaten this habitat. Healthy, intact mangrove forests play an ancient and complex role for *Carcinoscorpius rotundicauda*, popularly called the "mangrove horseshoe crab." These horseshoe crabs are found only in Southeast Asia. The fate of *C. rotundicauda* is tied closely to the decline of mangroves, because this species spawns only along the creek banks in areas of mangroves (Vestbo et al. 2018). The other two species of Asian horseshoe crabs, *Tachypleus gigas* and *T. tridentatus* use sandy beaches for spawning, but the loss of mangroves also impact them indirectly due to altered hydrodynamics, changes in nutrient cycling, erosion of beaches, and altered food webs.

As loss of (mangrove) habitat has been and still is a major driver of horseshoe crab extinction globally, effective conservation of existing primary forests and restoration of degraded forests is essential.

What Are the Causes of Mangrove Decline and Loss?

It is estimated that less than 15 million hectares remain worldwide—less than half their original area (Strong and Minnemeyer 2015). Although the overall losses of mangroves are declining, this average masks regions and countries where mangroves are being converted at 5–8% per annum. In Southeast Asia, this is mainly driven by shrimp aquaculture, rice and oil palm production (Richards and Friess 2016), and also timber and fuel wood extraction, charcoal production, urban expansion, pollution, coastal road construction, and other industrial and infrastructure developments.

Community-Based Ecological Mangrove Restoration: An Effective Approach to Mangrove Restoration

Non-Governmental Organization (NGO) Mangrove Action Project (MAP) (Wodehouse 2020) and others (Lewis 2009; Primavera et al. 2012) have argued that the long-term conservation of primary mangrove forests should be the primary objective, followed by effective restoration of degraded or destroyed mangroves. While efforts to conserve mangroves have increased with the growing awareness of their value, many restoration efforts still fail completely or fail to meet their objectives. Specifically, traditional mangrove restoration efforts (line planting of mid-zone mangrove species, such as *Rhizophora* sp. on all sites and at all elevations relative to sea level) often fail or fail to reach their objectives. Restoration efforts often fail to resolve the underlying problems or stressors that caused their loss in the first place, such as over-exploitation, local poverty, unusually high salinity or disturbed hydrology and fail to understand why a site is not regenerating naturally. Planting projects fail due to poor site selection, poor site-species matching, and a poor understanding of mangrove biology and ecology (Wodehouse 2020). Furthermore, if successful, traditional planting establishes monoculture plantations that lack biodiversity and full mangrove ecosystem function.

Community-Based Ecological Mangrove Restoration (CBEMR) is an alternative, holistic approach to mangrove restoration that tries to mitigate underlying mangrove stressors and works with nature to facilitate natural regeneration if the site is not propagule-limited. This might be done by restoring the hydrology and improving the drainage or adjusting a site's topography so that mangroves may regenerate naturally, resulting in more biodiverse ecosystem (Fig. 5). Key to the success of this process is to conduct a stakeholder analysis at the outside and involve the local communities and other stakeholders with power and interest in the project from the outset.

Fig. 5 Photo sequence of a successful Community-Based Ecological Mangrove Restoration project that the Mangrove Action Project helped initiate in El Salvador 10 years ago resulting in good mangrove recovery after the blocked hydrology was restored by volunteers from the resident communities. (Association Manglar/Eco-Viva, El Salvador)

5 Intertidal Flats: Important for Juvenile Horseshoe Crab Growth and Development

Found worldwide, intertidal flats are a common feature of many estuarine environments. These habitats occur in relatively protected areas, allowing for the accumulation of fine sands and mud. Mudflats are areas of land that are flooded at high tide and are formed by a buildup of fine sediment carried in by tides and rivers.

5.1 Importance of Mudflats

Despite the rather barren appearance of many sand flats and mudflats, they often harbor abundant benthic infauna that are well-adapted to survive frequent sediment disturbances caused by waves, storms, and bioturbation (Zajac and Whitlatch 2003). At low tide, flats are important feeding and resting habitats for birds (Burger et al. 1977; Fonseca et al. 2017), and at high tide when the flats are submerged, the resident fauna can be preyed upon by rays and other types of fishes (Cross and Curran 2000). Indeed, some intertidal flats have such abundant benthic resources that they are crucial foraging sites for shorebirds in estuaries throughout the world, such as the Bay of Fundy, Canada (Hicklin 1987), Wadden Sea, Netherlands (Kraan et al. 2009), Banc d'Arguin, Mauritania (Lourenço et al. 2015), and Copper River Delta, Alaska (Gill Jr and Handel 1990). Tidal flats provide a wealth of additional ecosystem services, including nutrient cycling, carbon sequestration, wave attenuation, sediment storage, and protection of the shoreline against erosion (Miththapala 2013). These systems are threatened by sea level rise, invasive species, shoreline development, sand extraction, and river diversions that affect the hydrological regime and sediment budget (Miththapala 2013; Itaya et al. this volume).

Tidal flats are a critical link in the life history of horseshoe crabs. During the spring spawning season and well into the summer, adult *Limulus* often aggregate on tidal flats during low tides, where they feed on mollusks and other invertebrates (Botton 1984). Young-of-the-year *Limulus*, as well as juveniles up to about 3 years of age, are commonly found on tidal flats during the summer months (Botton et al. 2003; Colón et al. this volume). Tidal flats are also critical habitats for juvenile Asian horseshoe crab species (Hu et al. 2015; Cartwright-Taylor et al. 2011; Kwan et al. 2016). New hatchlings of *Tachypleus tridentatus* disperse from spawned sandy beaches to neighboring mud tidal flats to settle there and grow (Maeda et al. 2000). Tidal flows are essential to support hatchling ecology. Consequently, modifications of coastal land forms by development can adversely change critical processes of the early life history of horseshoe crabs.

5.2 Restoration and Conservation of Mudflats

The management of tidal wetlands including mudflats has a long history in North America that is summarized by Tiner (2013) but very little information exists on mudflat restoration. The World Bank has called for the worldwide conservation and management of coastal wetlands for "ecosystem mitigation" to help combat sea level rise through carbon sequestration (Crooks et al. 2011) by our estuaries and coastal habitats.

6 Horseshoe Crabs Outreach: Connect People with Their Coastal Environments

6.1 Beaches/Marshes/Seagrasses

The members of the International Union for Conservation of Nature (IUCN) Horseshoe Crab Specialist Group invited researchers and community members from around the world to celebrate the value of horseshoe crabs in our coastal ecosystems and to designate them as "flagship species" for the conservation of estuarine and coastal ecosystems. Many community-based activities have recently been launched and promoted due to the first International Horseshoe Crab Day on June 20, 2020 (https://www.youtube.com/watch?v=bDjqXfEWy4Q&list=PLdrZ71BTGCwwZpDoS1nBNeiu6GM95eiUY). Over 50 videos have been combined and posted from 11 different countries.

Project *Limulus* (www.projectlimulus.org) is a model community research program whose participants learn the ecological importance of horseshoe crabs to the Long Island Sound ecosystem in the United States through hands-on activities such as tagging and conducting spawning surveys. In 2012, a total of 18 nonprofit organizations encompassing more than 400 volunteers participated in 234 horseshoe crab spawning surveys across 30 Connecticut beaches. Volunteers tagged and released approximately 9000 horseshoe crabs (Mattei et al. 2015). Parts of this program have been replicated in Malaysia, Hong Kong, and India (Faridah et al. 2015) and community members have been encouraged to tag and report recaptured horseshoe crabs as well as help with hatching of eggs and juvenile release programs.

6.2 Mangroves

Community-Based Ecological Mangrove Restoration (CBEMR) involves a more methodological ecosystem approach than the usual monoculture restoration efforts, incorporating natural mangrove dispersal and ecological recovery. The key is in the restoration of the hydrology and topography where needed of the area being considered for restoration, and then working with nature itself to help facilitate regeneration of the area's naturally occurring mangrove species. Adequate monitoring and evaluation follow this for 3 the 5 years at each site to assess progress and take corrective action to ensure success,

CBEMR is based on principles of community engagement and empowerment, recognizing that sustainable restoration requires the active participation of the affected local communities. The importance of local community involvement in mangrove conservation and restoration cannot be overstated, as it is these local communities who reside on-site and have most to gain from a healthy, living mangrove buffer, including improved livelihoods from increased wild fisheries and protection from storms and wave surges, These communities also possess important local knowledge of their community base and surroundings and are more able to monitor and assess the status of their mangrove areas on an ongoing basis.

If the mangrove horseshoe crab is to survive this present sixth extinction, surely effective conservation and restoration of its spawning grounds in the mangroves must occur. Hand planting mangrove seedlings in mud flats, seagrass beds, or other inappropriate coastal zones will not accomplish the objectives of long-term, biodiverse habitat restoration. An ecosystem-based restoration and management approach such as represented by CBEMR is urgently needed.

Horseshoe Crabs, Mangroves, and Citizen Science in Singapore

Coastal development has been occurring in Singapore since agricultural times, but the rate at which development has been happening in the last few decades is rapid. Mangrove forests are being cut down for new buildings and ports. A stretch of mangroves adjacent to Sungei Buloh Wetlands Reserve known as Mandai Mangroves (72.8 ha park) is an important habitat for migratory birds and horseshoe crabs. Mangrove horseshoe crabs gather at these mudflats in high densities. It is imperative to preserve what is left in order to prevent the extinction of the mangrove horseshoe crab, *Carcinoscorpius rotundicauda* and preserve other fish and wildlife habitat. In addition to the importance of the mangrove habitats for horseshoe crabs, Mandai mudflats and mangroves have cultural and historical significance. Conserving the habitat is crucial for future generations. Mangrove forests can also prevent coastal erosion and faster recovery from storm events (i.e., resiliency).

Singapore is a small-island city-state of 582 km^2 with about 90% of our shoreline covered by mangroves when it was founded in 1819. Over the years, increase in population and the need for housing, infrastructure, industrial, shrimp farms, other land use development and extensive land reclamation have resulted in the loss of 70–80% of these mangroves. Even now with increasing demand for water for our five million population, the damming of many of our rivers to create water catchment/containment areas has resulted in diminished sedimentation for our vulnerable remaining mangroves.

The past 10 years that our Horseshoe Crab Rescue & Research (HSC R&R) has been monitoring the *C. rotundicauda* population at the Mandai mudflats, we are witness to the gradual degradation of the mudflats and dying back of the adjacent mangrove habitat. Although we still have a sizable population of mangrove horseshoe crabs at the mudflats, we are concerned that without the protective nursery afforded by the roots of the adjacent healthy mangrove habitat, the survival of horseshoe crabs, other fish, and intertidal creature hatchlings will decline. HSC R&R volunteers help release horseshoe crabs that become entangled in ghost fishing nets (Fig. 6) With the possible loss of most, if not all, of the more fragile species in this ecosystem, the impact on the overall biodiversity of this habitat may not only effect the sustainability of the horseshoe crab population, which acts as a flagship species here, but also have adverse consequences on this area as a feeding and foraging area for the shorebirds of our Sungei Buloh Wetland Reserve, located a few kilometers to the west on the same shoreline, and also as an important pit stop for migratory birds on the East Asian Australasian Flyway (EAAF).

On a group of islets off main island Singapore, the authorities have built a surrounding sea wall to create a land fill. Along the shoreline of this sea-walled landfill a mono-culture of mangrove has been planted. As this instant mangrove is meant as a biological barrier to help contain and monitor possible landfill seepage, it does not qualify as mangrove restoration.

However, on another larger islet off main island Singapore, a collaboration, involving National Parks, Singapore, the Geography Department of the National University of Singapore and Nature Society (Singapore) (NSS), known as the Restore Urban Mangroves (RUM) project has just been initiated (Friess 2017). This is a hydrology-based method to guide mangrove restoration of an area of degraded shoreline and NSS volunteers are involved in the replanting effort. We look forward to sharing the results of this project in the near future.

The hallmark of this cycle of climate change is the significant contribution of mankind's excesses to its accelerated and pronounced nature. Flora and fauna that are slow or unable to adapt to the effects of global warming will perish. It is

Fig. 6 Rescuing mangrove horseshoe crabs entangled in discarded fishing nets in Singapore (Nature Society Singapore)

appropriate, opportune, and timely for enlightened governments to provide committed leadership together with the multitude of nature, environmental, and biodiversity conservation NGOs with their many passionate volunteers to employ nature-based solutions to, hopefully, stem the tide of rising sea levels and species loss.

In 2016, the Police Coast Guard erected a fence surrounding the north-western coast of Singapore to keep illegal immigrants out. This has indirectly contributed to the decline of abandoned nets and traps left by fishermen as the mudflats and mangroves are behind the fence. During the same period, an invasive mussel, *Mytella strigata,* hitched a ride into Singapore and established a strong colony throughout the north-western coastline. It has blanketed the mudflats and encroached onto the horseshoe crabs, impairing movements and latching onto its book gills. The population of the mussels has since declined and stabilized within several parts of Singapore. Late in 2018, The National Parks Board (NParks) announced that Mandai Mangrove and Mudflat will be conserved as a Nature Park.

6.3 Mudflats: Horseshoe Crabs and Marine Conservation in Hong Kong

At Ocean Park Conservation Foundation, Hong Kong (OPCFHK), we use juvenile horseshoe crab that are artificially bred in the laboratory at City University of Hong Kong, and then raised in local secondary schools to educate children about the importance of coastal habitats (see Kwan et al. 2017 for details of this program). The children come out to release their horseshoe crab "babies" and see the degraded mudflats (Fig. 7). The children wanted their "babies" to survive so they had incentive and helped pick up oyster farm debris, garbage, and plastics. The children experienced how they could now make a difference in the condition of horseshoe crab habitat and positively affect their survival. Children teach their parents and share to the public of what they experienced and become ambassadors for preserving coastal habitats to save the horseshoe crabs. More attention has been raised among the community by these children which attracted more stakeholders to join us restoring the habitat in recent years.

7 Summary and Conclusions

The four species of extant horseshoe crabs are reliant on an interdependent set of nearshore estuarine and marine habitats, which are under increasing stress from shoreline development and sea level rise. For *Tachypleus tridentatus*, *T. gigas*, and *Limulus polyphemus*, sandy beaches are critical for reproduction and intertidal flats

Fig. 7 At Ocean Park Conservation Foundation, Hong Kong children released laboratory reared horseshoe crabs

and salt marshes for juvenile nursery habitat. Beach nourishment is preferable to hardening the shoreline, but to have maximum benefit, these shore protection projects should consider the texture of the sediment and not merely the quantity of sand added to a beach. Experiences from Japan show that if revetments are needed, they must be properly placed to preserve the continuity between the land and sea. The fate of *Carcinoscorpius rotundicauda* is tightly coupled to the mangrove ecosystems in Southeast Asia. Efforts to restore mangrove forests may be well-intentioned, but if best practices are not observed, the results may be disappointing. Lastly, we are encouraged by the enthusiastic public participation in the United States, Singapore, Hong Kong, and elsewhere which have embraced the concept of horseshoe crabs as a flagship species for coastal conservation.

Acknowledgments This chapter is based on the Knowledge Café roundtable discussion co-sponsored by the IUCN Horseshoe Crab Specialist Group, Mangrove Action Project, and Nature Society (Singapore), which was held on September 3, 2016 in Honolulu, Hawaii, during the IUCN World Conservation Congress. We thank all of the participants at the roundtable for their input. We thank Chang-Po Chen and Hwey-Lian Hsieh for initiating the conversation about using horseshoe crabs as a flagship species for coastal conservation, and D. Wodehouse for his comments on an earlier draft of this manuscript.

References

E.B. Barbier, S.D. Hacker, C. Kennedy, et al., The value of estuarine and coastal ecosystem services. Ecol. Monogr. **81**, 169–183 (2011)

E.B. Barbier, Marine ecosystem services. Curr. Biol. **27**(11), 507–510 (2017)

M.A. Beekey, J.H. Mattei, The mismanagement of Limulus polyphemus in Long Island Sound, U.S.A.: What are the characteristics of a population in Decline? In R. Carmichael, et al., Changing global perspectives on biology, conservation and management of horseshoe crabs. Springer, New York, NY. pp. 433–461 (2015)

M.L. Botton, The importance of predation by horseshoe crabs, *Limulus polyphemus*, to an intertidal sand flat community. J. Mar. Res. **42**, 139–161 (1984)

M.L. Botton, The conservation of horseshoe crabs: What can we learn from the Japanese experience? in *Limulus in the Limelight*, ed. by J. T. Tanacredi, (Kluwer Academic/Plenum Publ, New York, 2001), pp. 41–51

M.L. Botton, The ecological importance of horseshoe crabs in estuarine and coastal communities: A review and speculative summary, in *Biology and Conservation of Horseshoe Crabs*, ed. by J. T. Tanacredi, M. L. Botton, D. R. Smith, (Springer, New York, 2009), pp. 45–64

M.L. Botton, C.P. Colón, J. Rowden, et al., Effects of a beach nourishment project in Jamaica Bay, New York on horseshoe crab (*Limulus polyphemus*) spawning activity and egg deposition. Estuar. Coasts **41**, 974–987 (2018)

M.L. Botton, R.E. Loveland, Reproductive risk: High mortality associated with spawning by horseshoe crabs (*Limulus polyphemus*) in Delaware Bay, USA. Mar. Biol. **101**, 143–151 (1989)

M.L. Botton, R.E. Loveland, T.R. Jacobsen, Beach erosion and geochemical factors: Influence on spawning success of horseshoe crabs (*Limulus polyphemus*) in Delaware Bay. Mar. Biol. **99**, 325–332 (1988)

M.L. Botton, R.E. Loveland, A. Tiwari, Recruitment and survival of young-of-the-year in a commercially exploited population of horseshoe crabs (*Limulus polyphemus*). Mar. Ecol. Prog. Ser. **265**, 175–184 (2003)

M.L. Botton, C.N. Shuster, Horseshoe crabs in a food web: Who eats whom? in *The American Horseshoe Crab*, ed. by C. N. Shuster, R. B. Barlow, H. J. Brockmann, (Harvard Press, Cambridge, 2003), pp. 133–153

J. Burger, M.A. Howe, D.C. Hahn, J. Chase, Effects of tide cycles on habitat selection and habitat partitioning by migrant shorebirds. Auk **94**, 743–758 (1977)

R.H. Carmichael, D. Rutecki, B. Annett, et al., Position of horseshoe crabs in estuarine food webs: N and C stable isotopic study of foraging ranges and diet composition. J. Exp. Mar. Biol. Ecol. **299**, 231–253 (2004)

R. H. Carmichael, M. L. Botton, P. K. S. Shin, S. G. Cheung (eds.), *Changing Global Perspectives on Horseshoe Crab Biology, Conservation and Management* (Springer, Switzerland, 2015)

L. Cartwright-Taylor, Y.V. Bing, H.C. Chi, L.S. Tee, Distribution and abundance of horseshoe crabs *Tachypleus gigas* and *Carcinoscorpius rotundicauda* around the main island of Singapore. Aquat. Biol. **13**, 127–136 (2011)

C.-P. Chen, H.-L. Hsieh, H.-Y. Chen, et al., The conservation network of horseshoe crab *Tachypleus tridentatus* in Taiwan, in *Biology and Conservation of Horseshoe Crabs*, ed. by J. T. Tanacredi, M. L. Botton, D. R. Smith, (Springer, New York, 2009), pp. 543–557

C.P. Colón, M.L. Botton, P. Funch, et al., Ecology of Juvenile American Horseshoe Crabs (*Limulus polyphemus*) at Plumb Beach, Jamaica Bay, New York. In: (this volume)

S. Crooks, D. Herr, J. Tamelander, et al., Mitigating climate change through restoration and management of coastal wetlands and near-shore marine ecosystems: Challenges and opportunities. Environment department papers; no. 121. Marine ecosystem series. World Bank; Washington, DC (2011)

R.E. Cross, M.C. Curran, Effects of feeding pit formation by rays on an intertidal meiobenthic community. Estuar. Coast. Shelf Sci. **51**, 293–298 (2000)

J. Davis, I.M. Kidd, Identifying major stressors: The essential precursor to restoring cultural ecosystem services in a degraded estuary. Estuar. Coasts **35**, 1007–1017 (2012)

R. Debnath, S.K. Nag, A. Choudhury, et al., Feeding habit and digestive physiology of the Indian horseshoe crab, *Tachypleus gigas* (Muller). Indian J. Physiol. Allied Sci. **43**, 44–49 (1989)

A. del Valle, M. Eriksson, O. Ishizawa, et al., Mangroves protect coastal economic activity from hurricanes. Proc. Natl. Acad. Sci. **117**(1), 265–270 (2020)

C.M. Duarte, W.C. Dennison, R.J.W. Orth, T.J.B. Carruthers, The charisma of coastal ecosystems: Addressing the imbalance. Estuar. Coasts **31**(2), 233–238 (2008)

J.E. Dugan, D.M. Hubbard, I.F. Rodil, et al., Ecological effects of coastal armoring on sandy beaches. Mar. Ecol. **29**(suppl. 1), 160–170 (2008)

Environmental Agency, Government of Japan. Seacoast Survey Report in The 4th National Survey on the Natural Environment (in Japanese) http://www.biodic.go.jp/reports2/4th/kaigan/4_kaigan.pdf (1994)

P.S.E.Z. Ermgassen, M.D. Spalding, B. Blake, et al., Historical ecology with real numbers: Past and present extent and biomass of an imperiled estuarine habitat. Proc. R. Soc. B **279**, 3393–3400 (2012)

L.-F. Fan, C.-P. Chen, M.C. Yang, et al., Ontogenetic changes in dietary carbon sources and trophic position of two co-occurring horseshoe crab species in southwestern China. Aquat. Biol. **26**, 15–26 (2017)

M. Faridah, N. Ismail, B. Ahmad, et al., The population size and movement of coastal horseshoe crab, *Tachypleus gigas* (Muller) on the east coast of Peninsular Malaysia, in *Changing Global Perspectives on Horseshoe Crab Biology, Conservation and Management*, ed. by R. H. Carmichael, M. L. Botton, P. K. S. Shin, S. G. Cheung, (Springer, New York, 2015), pp. 213–228

J. Fonseca, B. Baso, D. Serrano, J.G. Navedo, Effects of tidal cycles on shorebird distribution and foraging behaviour in a coastal tropical wetland: Insights for carrying capacity assessment. Estuar. Coast. Shelf Sci. **198**, 279–287 (2017)

D.A. Friess, Mangrove rehabilitation along urban coastlines: A Singapore case study. Reg. Stud. Mar. Sci. **16**, 279–289 (2017)

R.E. Gill Jr., C.M. Handel, The importance of subarctic intertidal habitats to shorebirds: A study of the central Yukon-Kuskokwim Delta, Alaska. Condor **92**, 709–725 (1990)

C. Gómez, Seagrass Meadows: The Marine Powerhouses. IUCN news releases: https://iucnrle.org/blog/seagrass-meadows-the-marine-powerhouses/ (2018)

R. Gorman, Atlantic horseshoe crabs and endotoxin testing: Perspectives on alternatives, sustainable methods, and the 3Rs (replacement, reduction, and refinement). Front. Mar. Sci. 7, 1–11 (2020)

S. Greipsson, *Restoration Ecology* (Jones & Bartlett Learning, Sudbury, MA, 2011)

P.W. Hicklin, The migration of shorebirds in the Bay of Fundy. Wilson Bull. **99**, 540–570 (1987)

J. Howard, A.E. Sutton-Grier, D. Herr, et al., Clarifying the role of coastal and marine systems in climate mitigation. Front. Ecol. Environ. **15**(1), 42–50 (2017)

M. Hu, B.K.Y. Kwan, Y. Wang, S.G. Cheung, et al., Population structure and growth of juvenile horseshoe crabs *Tachypleus tridentatus* and *Carcinoscorpius rotundi*cauda (Xiphosura) in Southern China, in *Changing Global Perspectives on Horseshoe Crab Biology, Conservation and Management*, ed. by R. H. Carmichael, M. L. Botton, P. K. S. Shin, S. G. Cheung, (Springer, Switzerland, 2015), pp. 167–180

IPCC, Global warming of 1.5°C. intergovernmental panel on climate change, 616 p. https://www.ipcc.ch/sr15/download/#full. Accessed 2 Aug 2020 2018

M. Ishikawa, S. Seino, H. Tomida, Improvement of a horseshoe crab spawning site, in *Proceeding of the Global Congress on ICM: Lessons Learned to Address New Challenges*, vol. 1, (2013), pp. 569–579

S. Itaya, T. Wada, M. Shuuno, Cumulative modifications of the endangered horseshoe crab *Tachypleus tridentatus* habitat by small scale developments at Tsuyazaki Cove in Fukuoka, Japan. In: (this volume)

N.L. Jackson, K.F. Nordstrom, Strategies to conserve and enhance sandy barrier habitat for horseshoe crabs (*Limulus polyphemus*) on developed shorelines in Delaware Bay, United States, in *Biology and Conservation of Horseshoe Crabs*, ed. by J. T. Tanacredi, M. L. Botton, D. R. Smith, (Springer, New York, 2015), pp. 399–416

B.A. John, B.R. Nelson, H.I. Sheikh, et al., A review on fisheries and conservation of Asian horseshoe crabs. Biodivers. Conserv. **27**, 3573–3598 (2018)

G. Kalinkat, J.S. Cabral, W. Darwall, et al., Flagship umbrella species needed for the conservation of overlooked aquatic biodiversity. Conserv. Biol. **31**, 481–485 (2017)

J.A. Keinath, J.A. Musick, R.A. Byles, Aspects of the biology of Virginia's sea turtles: 1979–1986. Va. J. Sci. **38**, 329–336 (1987)

P.G. King, C. Nelsen, J.E. Dugan, et al., Valuing beach ecosystems in an age of retreat. Shore Beach **86**, 1–15 (2018)

C. Kraan, J.A. van Gils, B. Spaans, et al., Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. J. Anim. Ecol. **78**, 1259–1268 (2009)

J.N. Kraeuter, S.R. Fegley, Vertical disturbance of sediments by horseshoe crabs (Limulus Polyphemus) during their spawning season. Estuaries **17**, 288–294 (1994)

J. Krisfalusi-Gannon, W. Ali, K. Dellinger, et al., The role of horseshoe crabs in the biomedical industry and recent trends impacting species sustainability. Front Mar Sci **5**, 185 (2018). https://doi.org/10.3389/fmars.2018.00185

B.K.Y. Kwan, S.G. Cheung, P.K.S. Shin, A dual stable isotope study for diet composition of juvenile Chinese horseshoe crab *Tachypleus tridentatus* (Xiphosura) on a seagrass-covered intertidal mudflat. Mar. Biol. **162**, 1137–1143 (2015)

B.K.Y. Kwan, J.H.Y. Cheung, A.C.K. Law, et al., Conservation education program for threatened Asian horseshoe crabs: A step towards reducing community apathy to environmental conservation. J. Nat. Conserv. **35**, 53–65 (2017)

B.K.Y. Kwan, H.-L. Hsieh, S.G. Cheung, P.K.S. Shin, Present population and habitat status of potentially threatened Asian horseshoe crabs *Tachypleus tridentatus* and *Carcinoscorpius rotundicauda* in Hong Kong: A proposal for marine protected areas. Biodivers. Conserv. **25**, 673–692 (2016)

K. Laurie, C.-P. Chen, S.G. Cheung, et al., *Tachypleus tridentatus* (errata version published in 2019). The IUCN Red List of Threatened Species 2019: e.T21309A149768986. https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T21309A149768986.en (2019)

R.R. Lewis, Methods and criteria for successful mangrove forest restoration, in *Coastal Wetlands: An Integrated Ecosystem Approach*, ed. by G. M. E. Perillo, E. Wolanski, D. R. Cahoon, M. M. Brinson, (Elsevier, Oxford, UK, 2009), pp. 787–800

P.M. Lourenço, T. Catry, T. Piersma, J.P. Granadeiro, Comparative feeding ecology of shorebirds wintering at Banc d'Arguin, Mauritania. Estuar. Coasts **39**, 855–865 (2015)

R.E. Loveland, M.L. Botton, Sea level rise in Delaware Bay: Adaptations of spawning horseshoe crabs (*Limulus polyphemus*) to the glacial past, and the rapidly changing shoreline of the bay, in *Changing Global Perspectives on Horseshoe Crab Biology, Conservation and Management*, ed. by R. H. Carmichael, M. L. Botton, P. K. S. Shin, S. G. Cheung, (Springer, Switzerland, 2015), pp. 41–63

K. Maeda, S. Seino, S. Nishihara, A. Hino, Ecology of hatched larvae of the horseshoe Crab *Tachypleus tridentatus* (Leach) in relation to the physical environment. Benthos Res. **55**, 15–24 (2000)

J.H. Mattei, M. Botton, M. Beekey, C. Colón, Horseshoe crab research in urban estuaries: Challenges and opportunities, in *Changing Global Perspectives on Horseshoe Crab Biology, Conservation and Management*, ed. by R. Carmichael, M. L. Botton, S. G. Cheung, (Springer, Switzerland, 2015), pp. 537–555

J.H. Mattei, Audubon CT In-Lieu Fee Fund Final Report. Regulatory Division US Army Corps of Engineers, 696 Virginia Road, Concord, MA (2019)

J.H. Mattei, J.M. Kasinak, S. Senbel, K. Bartholomew, The power of citizen science: 20 years of horseshoe crab community research merging conservation, education and management. In: (This Volume)
C.J. Mcowen, L.V. Weatherdon, J.W. Van Bochove, et al., A global map of saltmarshes. Biodivers Data J. (5), e11764 (2017)
S. Miththapala, Tidal Flats. Coastal Ecosystem Series (Volume 5). Columbo, Sri Lanka, IUCN. iii + 48 pp (2013)
L.J. Niles, J. Bart, H.P. Sitters, et al., Effects of horseshoe crab harvest in Delaware Bay on Red Knots: Are harvest restrictions working? Bioscience **59**, 153–164 (2009)
J. Odell, M.E. Mather, R.M. Muth, A biosocial approach for analyzing environmental conflicts: A case study of horseshoe crab allocation. Bioscience **55**, 735–748 (2005)
J.H. Primavera, J.P. Savaris, B.E. Bajoyo, et al., Manual for Community-Based Mangrove Rehabilitation, 1st ed, London, Zoological Society of London, Mangrove Manual Series. ZSL, London, UK (2012)
D.R. Richards, D.A. Friess, Rates and drivers of mangrove deforestation in Southeast Asia, 2000–2012. Proc. Natl. Acad. Sci. **113**, 344–349 (2016)
D.M. Rudkin, G.A. Young, Horseshoe crabs – An ancient ancestry revealed, in *Biology and Conservation of Horseshoe Crabs*, ed. by J. T. Tanacredi, M. L. Botton, D. R. Smith, (Springer, New York, 2009), pp. 25–44
S. Seino, Flows related to morphology and ecology of horseshoe crab. Nagare **20**(5), 365–374 (2001). The Japanese Society of Fluid Mechanics (in Japanese) Nagare. https://archive.iii.kyushuu.ac.jp/public/kRhQAAYIakAwHMBhMFzLinrUjm6wKW1l1zyYysTEUFu
S. Seino, T. Uda, Y. Tsuchiya, et al., Field observation of geomorphological features of the spawning site and dispersion of hatchlings of the horseshoe crab *Tachypleus tridentatus*-towards mitigation planning for the rare species- Ecol. Civil. Eng. **3**(1), 7–19 (2000). https://archive.iii.kyushu-u.ac.jp/public/pR88AAvILs-AclgBMVNzrgTrh9C6z1q1crXwGZDTs4vi
S. Seino, T. Uda, Y. Tsuchiya, K. Tsuchiya, Conservation history of horseshoe crab *Tachypleus tridentatus* and its spawning ground, a designated natural monument in Kasaoka Bay in Okayama Prefecture. Asian Pacific Coasts **18**, 551–556 (2003)
S. Seino, T. Uda, S. Sato, et al., Threatened species habitat conservation methodology based on ecological engineering in nature-oriented coastal affairs. Annual J. Coastal Eng. JSCE **51**(2), 1341–1345. (in Japanese) DOI (2004). https://doi.org/10.2208/proce1989.51.1341
S. Seino, T. Uda, Conservation planning for endangered species of horseshoe crab in terms of geomorphology of habitats and life history. Proc. 4th Int. Conf Asian Pacific Coasts **2007**, 2075–2086 (2007). https://archive.iii.kyushu-u.ac.jp/public/CR18AANIQo-AuEABkgxzJhPrx2-6cme1NuzqB9FIK642
E.E. Seney, J.A. Musick, Historical diet analysis of loggerhead sea turtles (*Caretta caretta*) in Virginia. Copeia **2007**(2), 478–489 (2007)
M.R. Shokri, W. Gladstone, J. Jelbart, The effectiveness of seahorses and pipefish (Pisces: Syngnathidae) as a flagship group to evaluate the conservation value of estuarine seagrass beds. Aquat Conserv **19**, 588–595 (2009)
F. Short, T. Carruthers, W. Dennison, M. Waycott, Global seagrass distribution and diversity: A bioregional model. J. Exp. Mar. Biol. Ecol. **350**, 3–20 (2007)
A.D. Short, Coastal processes and beaches. Nat. Educ. Knowled. **3**(10), 15 (2012)
C. N. Shuster, R. B. Barlow, H. J. Brockmann (eds.), *The American Horseshoe Crab* (Harvard Press, Cambridge, 2005)
D.R. Smith, H.J. Brockmann, M.A. Beekey, et al., Conservation status of the American horseshoe crab, (*Limulus polyphemus*): A regional assessment. Rev. Fish Biol. Fish. **27**, 135–175 (2016)
A. Strong, A. Minnemeyer, Satellite data reveals state of world's mangrove forests. World Resources Institute. https://www.wri.org/blog/2015/02/satellite-data-reveals-state-world-s-mangrove-forests (2015)
J. T. Tanacredi, M. L. Botton, D. R. Smith (eds.), *Biology and Conservation of Horseshoe Crabs* (Springer, New York, 2009)

R. Thom, Adaptive management of coastal ecosystem restoration projects. Ecological Engineering, **15**, 365–372 (2000)

M.T.T. Thuy, T. Nagasawa, H. Tanaka, N.T. Viet, Sandy beach restoration using beach nourishment method: A case study of Nha Trang Beach, Vietnam, in *Tropical Coastal and Estuarine Dynamics. Journal of Coastal Research*, Special Issue No. 81, ed. by R. Almar, L. P. Almeida, N. Trung Viet, M. Sall, (2018), pp. 57–66

B.S. Thompson, S.M. Rog, Beyond ecosystem services: Using charismatic megafauna as flagship species for mangrove forest conservation. Environ Sci Policy **102**, 9–17 (2019)

R. Tiner, Tidal Wetland Conservation and Management, in *Tidal Wetlands Primer: An Introduction to Their Ecology, Natural History, Status, and Conservation*, (University of Massachusetts Press, Amherst, MA, 2013)

S. Vestbo, M. Obst, F.J.Q. Fernandez, et al., Present and potential future distributions of Asian horseshoe crabs determine areas for conservation. Front. Mar. Sci. **5**(164), 1–16 (2018)

E.A. Walls, J. Berkson, S.A. Smith, The horseshoe crab, *Limulus polyphemus*: 200 million years of existence, 100 years of study. Rev. Fish. Sci. **10**, 39–73 (2002)

D.C.J. Wodehouse, Towards successful community mangrove management and rehabilitation. Thesis for the Degree of Doctor of Philosophy, MSc, B. Comm. (Hons.), Tech Cert. School of Natural Sciences, Bangor University College of Environmental Sciences and Engineering, Bangor, Gwynedd. LL57 2UW (2020)

M.A. Zacharias, J.C. Roff, Use of focal species in marine conservation and management: A review and critique. Aquat. Conserv. **11**, 59–76 (2001)

R.N. Zajac, R.B. Whitlatch, Community and population-level responses to disturbance in a sandflat community. J. Exp. Mar. Biol. Ecol. **294**, 101–125 (2003)

J.B. Zedler, What's new in adaptive management and restoration of coasts and estuaries? Estuar. Coasts **40**, 1–21 (2017)