THE ROLES OF SEA TURTLES IN ECOSYSTEM PROCESSES AND SERVICES

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INTRODUCTION

There have been promising reports of the recovery of sea turtle populations around the world due to conservation actions that have reduced bycatch rates and threats to nesting turtles and their eggs (Mazaris *et al*., 2017). However, current populations of sea turtles are still likely to be 15-30% less than historical numbers (Jackson *et al*., 2001; McCauley *et al*., 2015) and this decreased abundance has wider implications than just for population trends. Sea turtles have important ecological roles (functions of an organism in ecosystem processes) that contribute to the ecosystem services or benefits that people receive- and rely on- from ecosystems.

There are four main categories of ecosystem services: cultural, provisioning, regulating, and supporting (MEA, 2003). While there is a moral reason for conserving species for their intrinsic value (Wallach *et al*., 2018), the ecological roles of sea turtles and their contribution to ecosystem services can make a more powerful argument when trying to initiate action and influence policy for their conservation. In this review, we summarise the importance of sea turtles in marine ecosystem processes and services for easy reference by researchers, conservation practitioners, and educators. Where possible, we have drawn examples from countries bordering the Indian Ocean and in Southeast Asia.

CULTURAL SERVICES

Cultural ecosystem services are the non-material benefits that can be derived from an ecosystem and are considered to be life-enriching and life-affirming contributions to human well-being (MEA, 2003; Satz *et al*., 2013). Sea turtles provide a host of cultural services to the communities that engage with them.

Symbols

Sea turtles serve as important sociocultural symbols to the communities that they closely co-exist with, and to other stakeholders such as conservationists, fishers, policy makers etc. One such symbol is that of a "cultural keystone species", which Garibaldi & Turner (2004) define as "culturally salient species that shape in a major way the cultural identity of a people". An example of turtles as a cultural keystone species is seen in the Torres Strait, Australia, where the species are an essential component of culture, identity, and sea life (Kwan *et al*., 2001).

Another symbol often used to signify the cultural and ecological importance of a species is that of a "flagship species", the term bestowed on well known, charismatic animals that can act as representatives of the area they inhabit. Recognition as a flagship species is based less on the biology or ecology of the species, and more on public perception, appreciation, and approval (Dietz, 1994; Frazier, 2005). Sea turtles are flagship species, depicted on the coins, paper currencies and postal stamps of numerous countries around the world (Lopez, 1996; Frazier, 2005).

Identity

The reverence for sea turtles has deep historical roots, as human-turtle interactions have occurred for centuries and spans areas across the globe ranging from South and Southeast Asia, Greece, Latin America, and the Pacific and Caribbean Islands. Millennia-old examples have been found in the Middle East and the Arabian Peninsula, where cylinder seals, decorative stamps for food, reliefs on palace walls, and other cultural artefacts clearly depict sea turtles (Frazier, 2005).

The cultural importance of sea turtles and other species is often expressed by sublimation into a source of identity for the community or region where close human-turtle interactions occur. At a macro-level, sea turtles are regarded as the emblematic animal for the Indian Ocean region (Chandrasekar & Srinivasan, 2013). Contributions of turtles to micro-level community identity can be seen in idols in religious context in the Penghu Islands of Taiwan (Balazs *et al*., 2000), and use of eggs and meat in religious (Voudou) ceremonies in West Africa (Chandrasekar & Srinivasan, 2013).

When the cultural importance of a species and/or practice involving sea turtles is so interwoven with the cultural and religious identity of a community, practices that are harmful to the existence of the turtles are often revered. This can lead to failure of conservation measures undertaken to curb such practices for the protection of the species; for example, a ban on consumption can do little to curb consumption itself as it may be perceived as a threat to the community's identity. This was observed in Baja California Sur, Mexico, where turtle meat was traditionally served at weddings, religious holidays (Christmas and Easter), and other celebrations (Mancini *et al*., 2011). Despite a total ban on the consumption and sale of sea turtles by the government in 1990, officials publicly consumed sea turtles. The meat continues to be a symbol of power among people with authority, and illegal trade of sea turtle products can sometimes be tied to drug trafficking in the country (Mancini & Koch, 2009; Senko *et al*., 2011).

Diplomacy/ Political Significance (Resource Governance)

The cultural significance of sea turtles has facilitated large-scale and trans-border co-operation and conservation efforts. International environmental agreements are signed by numerous signatory states, an example being the Memorandum of Understanding on the Conservation and Management of Marine Turtles and Their Habitats of the Indian Ocean and South-East Asia (IOSEA MoU), with 35 signatory states in 2020 (CMS, 2020).

Sea turtles can also aid national level diplomacy. For example, Butler *et al*. (2012) found that the species' cultural value influenced the level of co-management and power-sharing between authorities and local communities in the Torres Strait region of Australia. The wide variety of local, national, and international beneficiaries led to an expansion of stakeholders among governing bodies, an example being expansion of the Torres Strait Protected Zone Joint Authority (PZJA) to include Torres Strait Islanders in addition to government representatives. In addition, the cross-cultural resource governance of the flagship sea turtles encouraged co-management of keystone species, which have essential ecological roles but are less publicly recognised, such as sea cucumbers and *Trochus* sea snails. Thus, sea turtles can play an important role in shaping local governance, formulating international policy, and even in facilitating multilateral relations.

PROVISIONING SERVICES

Sea turtles provide a multitude of provisioning ecosystem services, i.e., tangible resources or goods at a micro- to macro-scale, that enrich human lives. Historically, sea turtles have provided food (meat, eggs, and oil) and other commodities (including shell, bone, leather, and medicine) to coastal peoples (Chandrasekar *et al*., 2013). With recent conservation efforts, most countries now regulate the consumptive use of sea turtles in these ways. However, illegal harvest and exploitation still occurs due to poor knowledge of existing laws, poor policy implementation and/or enforcement, and lucrative black-market opportunities.

Food

The most used consumptive resources from sea turtles in current times are eggs and meat. Eggs can be harvested directly from the beach or purchased from collectors or markets, and the motive for consumption may be nutritional and/or cultural (Frazier, 2005; IOSEA, 2014). Meat usually originates from bycatch turtles (e.g., Sri Lanka; Rajakaruna *et al*., 2020), but targeted fisheries also operate (e.g., Madagascar; Golding *et al*., 2017). Consumption of turtle meat may also be for nutritional (IOSEA, 2014) and/or ritual (e.g., Madagascar; Lilette, 2006) purposes, and can be culturally regulated to minimise the risk of chelonitoxism (turtle poisoning) (Limpus, 1987; Aguirre *et al*., 2006).

Ornaments

Tortoiseshell combs, jewellery, sunglasses and other items, and taxidermied turtles have been available for sale throughout the region (e.g., Islam, 2001; Tisdell & Wilson, 2003; IOSEA, 2014). Traditional ornamental and ceremonial (and utilitarian) uses of tortoiseshell in Papua New Guinea is also known (Kinch & Burgess, 2009). Japan imported ~114,500kg of raw bekko (Japanese for tortoiseshell) for carving and ~160,500kg of worked bekko (mainly stuffed hawksbill turtles) for ornaments from 1979-1981 alone, including from countries in the Indian Ocean and southeast Asia region (e.g., Indonesia, Kenya, Maldives, Philippines, Seychelles, Singapore, and Tanzania) (Mack, 1983). (See also Miller *et al*. (2019) and section on Trade below.)

Medicine

Medicinal uses of sea turtle by-products include oil in Tanzania (West, 2010) and Eritrea (Mebrahtu, 2013), blood in India (Silas & Rajagopalan, 1984), and meat in Tanzania (West, 2010).

Trade

Traditional products from sea turtles (Frazier, 1980) and emerging products, including hatchlings for the pet trade in Pakistan (Kiani *et al*., 2021), can be lucrative sources of income. Trade in sea turtle products can result from traditional practices, factors like poverty and lack of food security, and/or the desire for economic gain. Sea turtles may be caught deliberately or accidentally (as bycatch) and then traded legally or illegally for their numerous consumptive uses. Illegal markets may be local, regional, and international in scale (see Senko *et al*., 2011). Such a wide scale of markets might result in dependence of local communities on provisional services provided by the sea turtles, and even act as a primary source of income for the members of such coastal communities.

Tourism

Meletis & Campbell (2007) propose that tourism is another consumptive use of sea turtles, as the industry consumes/extracts environmental resources. Sea turtle tourism has delivered economic, conservation, and/or education benefits in many countries, including Australia (Tisdell & Wilson, 2001; Wilson & Tisdell, 2001, 2003), India (Katdare, 2012), South Africa (Poultney & Spenceley, 2001) and Sri Lanka (Tisdell & Wilson 2003). Similar ecotourism initiatives have also been proposed for countries such as Indonesia (Haryati *et al*., 2016; Budiantoro *et al*., 2019; Nurhayati *et al*., 2022), and Oman (Al Busaidi *et al*., 2018). Note that the conservation benefits of some sea turtle tourism, such as hatcheries in Sri Lanka which operate illegally but openly and have long been an important local tourist attraction and source of income, has been questioned (Richardson, 1996; Hewavisenthi, 2001; Rajakaruna *et al*., 2013; Phillott *et al*., 2017).

Curative Agent/Sealant

Oil or fat from turtles was historically used as a curative agent and/or sealant for wooden boats in the Indian Ocean region (see Bhaskar, 1979; Frazier, 1980; Thorbjarnarson *et al*., 2000). There have been no recent reports of continued use for this purpose.

REGULATING SERVICES

Sea turtles contribute to regulating services, which are benefits derived from ecosystem processes that moderate natural phenomena and include biodiversity regulation and habitat modification.

Biodiversity Regulation

Sea turtles play the role of regulators as they shape ecosystem structures through top-down modifications. Healthy seagrass beds are maintained by green turtles through grazing (Bjorndal & Jackson, 2002; Teelucksingh *et al*., 2010; Heithaus *et al*., 2014; Lovich *et al*., 2018). The consumption of seagrass results in increased water flow and aeration of sediments, thereby preventing sediment anoxia (Heithaus *et al*., 2014; Johnson et al., 2017). The removal of seagrass biomass through consumption also decreases self-shading (Teelucksingh *et al*., 2010), and reduces the likelihood of eutrophication by lowering the availability of organic matter that might support algal and epiphyte blooms (Christianen *et al*., 2012; Heithaus, 2013; Heithaus *et al*., 2014). By consuming the seagrass, sea turtles provide an alternate pathway for decomposition of organic matter, thereby allowing for a quicker detritus cycle (Thayer *et al*., 1982). Note also that overgrazing by sea turtles, due to high population numbers, can have negative impacts on seagrass beds (reviewed by Heithaus, 2013).

Hawksbill turtles play a similar role in regulating reef ecosystems through spongivory. Through selective feeding on sponges, they can affect succession and reef diversity by influencing competition for space and other resources (Bjorndal & Jackson, 2002; Teelucksingh *et al*., 2010). As sponges are competitively superior to corals, this allows for improved coral health and species richness (Lovich *et al*., 2018).

The same applies to leatherback turtles that predominantly prey on jellyfish. Owing to overfishing and other threats to marine vertebrates, jellyfish are positioned to dominate marine ecosystems; however, predation by leatherbacks acts as a check on their populations (Teelucksingh *et al*., 2010).

By reducing the populations of species of seagrass, sponges and jellyfish, these consumptive activities of sea turtles also have indirect effects on organisms that may be dependent on these species, thereby producing trophic cascades within ecosystems (Heithaus, 2013).

Habitat Modification

Sea turtles also carry out habitat modifications through their foraging and nesting behaviours. The processes of body pitting, egg chamber construction, and filling in the nest all result in soil disturbance as well as the uprooting, burial and damage of coastal vegetation (Lovich *et al*., 2018). Seedlings near the edges of dunes can be dug up, and thus, prevent the encroachment of vegetation near the shoreline (Heithaus, 2013). Some organisms even use sea turtle nests as habitats (Madden *et al*., 2008), such as machrochelid mites (Mast & Carr, 1985) and seed corn maggots (Saumure *et al*., 2006).

Modification of benthic environments occurs during sea turtle foraging. Loggerhead turtles have been observed practising infaunal mining to find prey (Bjorndal & Jackson, 2002). While digging deep pits, they feed on invertebrates that are displaced from the sediment (Lovich *et al*., 2018). This can have the effect of uncovering fresh substrate and/or restructuring benthic communities (Teelucksingh *et al*., 2010). It also facilitates bioturbation, whereby reduced particle sizes and greater surface area of prey remains leads to reduced decomposition times, thereby maintaining high biological activity in marine sediments. In addition to this, the foraging behaviour of sea turtles displaces invertebrates, small particles, and pieces of prey that are consumed by a variety of fish that follow them, including pilot fish and angelfish (Heithaus, 2013).

SUPPORTING SERVICES

In addition to the direct benefits that humans can derive from sea turtles, the species' also play supporting roles that facilitate other ecosystem services.

Host to Epibionts, Parasites and Pathogens

Sea turtles act as hosts to parasites and pathogens and as substrates to epibionts (Bjorndal & Jackson, 2002). These roles provide a food source for a variety of cleaning organisms, including fish that consume parasites, dead skin or algae that grows on sea turtle carapaces. In offshore waters, some bird species use sea turtles as perching platforms and feed on fish that gather under them (Heithaus, 2013).

Prey Item

Owing to their high biomass, sea turtles serve as prey to other species (Lovich *et al*., 2018). Eggs, hatchlings, post-hatchlings, and small juvenile turtles are predated upon by a variety of species, including insects, birds, mammals, large lizards, crocodiles and crabs. On entering the ocean, hatchlings also face threats from birds, sharks and other fish, and squid. Predation of adult sea turtles by non-human species is infrequent because of their large size. However, their recorded predators include terrestrial mammals such as jaguars, crocodiles, marine mammals such as monk seals and killer whales, and, most frequently, sharks. As they constitute a large part of the diets of a variety of predator species, sea turtles play an important role within food chains and their removal from ecosystems can result in trophic cascades (Heithaus, 2013).

Nutrient Transport and Nutrient Cycling

Sea turtles are important biological transporters, introducing marine nutrients and energy to nutrient-stressed coastal ecosystems, including islands. They carry out cross-ecosystem transport in the form of eggs deposited on nesting beaches that carry nutrients from widely dispersed foraging grounds (Lovich *et al*., 2018). Though a proportion of these nutrients and energy return to the marine ecosystem as hatchlings, the remains in the nests are incorporated into the nutrient cycle through detritivores and decomposers, nest predators, and plant roots (Bouchard & Bjorndal, 2000). Marine-derived energy and nutrients are important additions to beach habitats as they support dune vegetation and predator populations (Heithaus, 2013). Sea turtles also partake in nutrient cycling within foraging grounds, consuming older and less productive seagrass biomass, and redistributing digested nutrients throughout the habitat as faeces (Teelucksingh *et al*., 2010).

ENSURING SEA TURTLE POPULATIONS FULFIL ECOLOGICAL ROLES AND PROTECT ECOSYSTEM SERVICES IN THE INDIAN OCEAN AND SOUTHEAST ASIA

Ongoing conservation and monitoring efforts are important, even if sea turtle populations appear stable and/or increasing (see Mazaris *et al*., 2017). In the Indian Ocean and Southeast Asia region, recent examples of these efforts include: investigating consumption of turtle eggs in Malaysia (Poti *et al*., 2021) and turtle meat in Madagascar (Rothamel *et al*., 2021), and the call for a complete ban on egg trade in Terengganu (Mohd Jani *et al*., 2020); assessing vulnerability of sea turtles to the Indian Ocean tuna fisheries (Williams *et al*., 2018); using tracking data to understand migratory pathways and habitat usage by sea turtles (Pilcher *et al*., 2020, 2021a, b; Fossette *et al*., 2021) and inform conservation policy and management (Hays *et al*., 2019, 2021); identifying interventions to curb illegal harvest, use and trade in sea turtle products (Lopes *et al*., 2022); assessing threats of anthropogenic structures (Wilson *et al*., 2019), industry operations (Whittock *et al*., 2017), marine debris (Yaghmour *et al*., 2021), persistent organic pollutants (Yaghmour *et al*., 2020), oil spills (Yaghmour, 2020) and light pollution (Wilson *et al*., 2018, 2022) to sea turtles; and, facilitating collaborations among researchers, conservation practitioners, and civil society for sea turtle research, conservation and monitoring

(Stelfox *et al*., 2021). Conservation and monitoring in the region, such as demonstrated in the examples above, is also important because the largest groups of sea turtle regional management units (RMUs) in the Indian Ocean and Australasia (which includes Southeast Asia) have been scored as high risk-high threat (Wallace *et al*., 2011), and nesting populations of olive ridley turtles in Pakistan (Khan *et al*., 2010) and leatherback turtles in Malaysia (Liew, 2011) have been extirpated.

Research to understand past and present role(s) of sea turtles in the ecosystem has been identified as a global research priority (Hamann *et al*., 2010) in need of quantitative studies of all species in oceanic, neritic, and terrestrial habitats (Rees *et al*., 2016). Recent research in the region addresses green turtles as ecosystem engineers in the Lakshadweeps (Gangal *et al*., 2021; Kale *et al*., 2022), loggerhead and leatherback turtles as nutrient transporters in South Africa (Le Gouvello *et al*., 2017), and the role of green turtles as consumers in the Seychelles (Stokes *et al*., 2019), Western Australia (Stubbs *et al*., 2022), and Indonesia (Tapilatu *et al*., 2022), and olive ridley turtles in Oman (Rees *et al*., 2021). More work across different species, life stages, and locations is needed to understand the importance of ecosystem services provided by sea turtles (summarised in Table 1) in the Indian Ocean and Southeast Asia.

Table 1. A summary of the ecosystem services provided by sea turtles.

Category of Ecosystem Service	Sea Turtle Contribution
Cultural	Symbol Identity Diplomacy/political significance
Provisioning	Food Ornaments Medicines Trade Tourism Curative agent/sealant
Regulating	Biodiversity regulation Habitat modification
Supporting	Host to epibionts, parasites and pathogens Prey item Biological transporter Nutrient cycling

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