Marine Environmental Research 181 (2022) 105762

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Identifying conservation priorities for a widespread dugong population in the Red Sea: Megaherbivore grazing patterns inform management planning

Abdulqader Khamis [a,*], Teresa Alcoverro [b,c], Elrika D'Souza [c], Rohan Arthur [c], Jordi F. Pagès [b], Junid Shah [d], Tareq Al-Qahtani [e], Ameer Abdulla Eweida [f,g]

[a] Faculty of Biology, University of Barcelona, Av. Diagonal, 643, 08028, Barcelona, Spain
[b] Centre d'Estudis Avançats de Blanes (Spanish National Research Council, CEAB-CSIC), Blanes, Girona, Spain
[c] Oceans and Coasts Programme, Nature Conservation Foundation, Amritha 1311, 12th Cross, Vijayanagara 1st Stage, Mysore, 570017, India
[d] Ajaz Environment Consultants, United Arab Emirates
[e] National Center for Wildlife, P. O. Box 61681, Riyadh, 11575, Saudi Arabia
[f] NEOM, Saudi Arabia
[g] Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, USA

ARTICLE INFO

Keywords:
Dugong
Marine mammal
IUCN vulnerable Species
Seagrass
Habitat
Red sea
Saudi Arabia
Conservation

ABSTRACT

Extensive home ranges of marine megafauna present a challenge for systematic conservation planning because they exceed spatial scales of conventional management. For elusive species like dugongs, their management is additionally hampered by a paucity of basic distributional information across much of their range. The Red Sea is home to a wide-spread, globally important but data-poor population of dugongs. We surveyed the north-eastern Red Sea in the waters of NEOM, Kingdom of Saudi Arabia, to locate feeding sites and determine priority areas for dugong conservation. We conducted large-scale in-water surveys of dugong feeding trails across 27 seagrass meadows that span 0.7 degree of latitude and recorded nine seagrass species and 13 dugong feeding sites. Spread over ~4,061 km^2 of nearshore and offshore waters, many of these sites clustered around five main core feeding areas. Dugong feeding trails were mostly recorded at sites dominated by the fast-growing pioneer seagrasses *Halodule uninervis*, *Halophila ovalis* and/or *H. stipulacea*. Multispecific meadows with pioneer seagrasses tended to be sheltered and shallow, reflecting a similar spatial pattern to the identified dugong feeding sites. Often close to hotels and fishing harbours, these high-use dugong areas are subject to high boat traffic, fishing, and coastal development which places considerable pressures on this vulnerable mammal and its seagrass habitat. The rapidly accelerating coastal development in the northern Red Sea directly threatens the future of its dugong population. Although our sampling focuses on feeding signs in early successional seagrasses, the results are valuable to spatial conservation planning as they will trigger overdue conservation interventions for a globally threatened species in a data-poor area. Urgent dugong conservation management actions in the northern Red Sea should focus on shallow waters sheltered by coastal lagoons, bays and the lee of large islands.

1. Introduction

Large marine herbivores such as green turtles or dugongs, typically occupy large home ranges over which they move between foraging and breeding grounds (Bakker et al., 2015; D'Souza et al., 2013; Kelkar et al., 2013; Littles et al., 2019). Megaherbivore movements are typically mediated by a suite of environmental and biological drivers, such as the availability of shelter and food resources that are often spatially explicit (i.e., seagrass meadows, and macroalgal beds), avoidance of predation, breeding, offspring nurturing and thermoregulation (Acevedo-Gutierrez, 2009; Bakker et al., 2015; Deutsch et al., 2022a; Irvine, 1983; Marsh et al., 1999; O'Shea et al., 2022). Because of these large-scale movements and dispersion dynamics, marine megaherbivores often have to traverse varying regimes of human use and jurisdictional boundaries (Hamann et al., 2010; Sheppard et al., 2006). The heterogeneous spread of environmental drivers and anthropogenic stressors

* Corresponding author. H 1556, R 4647, B 1046, Bahrain.
E-mail addresses: akhamikh14@alumnes.ub.edu (A. Khamis), teresa@ceab.csic.es (T. Alcoverro), elrika@ncf-india.org (E. D'Souza), rohan@ncf-india.org (R. Arthur), jpages@ceab.csic.es (J.F. Pagès), junaidnazir.shah@gmail.com (J. Shah), tareq2700@gmail.com (T. Al-Qahtani), ameer.eweida@neom.com (A.A. Eweida).

https://doi.org/10.1016/j.marenvres.2022.105762
Received 26 May 2022; Received in revised form 24 September 2022; Accepted 26 September 2022
Available online 2 October 2022

across marine megaherbivore ranges leads to a significant challenge for conservation spatial planning and effective management interventions. The long-distance movements of these animals exceeds the spatial scale of conventional conservation and management interventions (Bakker et al., 2015; di Sciara et al., 2016; Dobbs et al., 2008; Marsh and Kwan, 2008). While large-scale marine protected areas or specially designated areas for marine megaherbivores may be an option to address the entire range of the species, they tend to be difficult to implement and manage, involve complex or inadequate transboundary arrangements, and often land up adding to the long list of paper parks (i.e., legally gazetted protected areas with insufficient management or enforcement; Marcos et al., 2021; Wells et al., 2016). However, many marine megaherbivores often spend large periods of time in one or multiple feeding grounds that can be relatively stable and predictable as long as resource stocks last (Anderson, 1981; Kelkar et al., 2013; Littles et al., 2019; Pilcher et al., 2014; Sheppard et al., 2006). This concentrated use of their otherwise vast home ranges is likely a strategy that better increases their chances of persistence (D'Souza et al., 2013; Marsh et al., 2002). Marine conservationists and managers can overcome some of the limitations inherent in large-scale conservation programs by focusing on well-defined feeding sites and designing area-based conservation measures that are cost effective and tailor made for these specific locations (di Sciara et al., 2016; Dobbs et al., 2008; Laist and Reynolds III, 2005; Pilcher et al., 2014; Tol et al., 2016).

The dugong (*Dugong dugon*) is a classic case in point. This large marine herbivore is distributed over a vast geographical range across the tropical and subtropical Indo-Pacific. Its movements can be relatively restricted (<15 km), but is also found to travel over much larger areas (>600 km; de Iongh et al., 2007; Deutsch et al., 2022b; Marsh et al., 1999; Sheppard et al., 2006). What this means is that its home range can be remarkably variable, from less than 1 km^2 to nearly 733 km^2 (Sheppard et al., 2006), occasionally straddling the territorial waters of several countries. Globally listed as vulnerable to extinction (Marsh and Sobtzick, 2019), the dugong continues to be threatened by direct hunting, accidental entanglement in fishing nets, collisions with boats, and degradation of the seagrass habitats on which it primarily feeds (D'Souza et al., 2013; Marsh et al., 2002, 1999; Nasr et al., 2019; Ponnampalam et al., 2022; Preen, 2004; Sheppard et al., 2006). Decades of intense human pressures have reduced dugong populations to remnant individuals or small isolated herds on the brink of local extinction (Marsh et al., 2011; Marsh and Sobtzick, 2019; Tol et al., 2016), with only few remaining sizeable dugong populations primarily found in Australia, New Caledonia, Papua New Guinea, Arabian Gulf and Red Sea (Cleguer et al., 2017; Marsh et al., 2002; Preen, 1989, 2004; Preen et al., 2012). As a result, the global conservation of the dugong faces biological, multi-scalar and jurisdictional challenges that are illustrative of vulnerable large-ranging megaherbivores.

In this study we focused on the relatively unknown dugongs of the Red Sea where a large population (~4,000 dugongs; Preen, 1989; Preen et al., 2012) is dispersed over an extensive seascape (458,620 km^2; Rasul et al., 2019) bordered by a lengthy and geomorphologically complex coastline. Few dated studies exist for this population, but from what is known, the estimated population of dugongs along the Saudi Arabian coast of the Red Sea (1,818 ± 382 individuals) form small groups (mean = 1.43 individual) distributing widely and sparsely across 1,840 km of coastline (Preen, 1989; Preen et al., 2012). In general, the Red Sea dugong population is considered data deficient (Marsh et al., 2002; Marsh and Sobtzick, 2019; Nasr et al., 2019; Preen et al., 2012) hampering conservation planning efforts in this region.

Their elusive nature and long-distanced transboundary movement patterns (Deutsch et al., 2022b; Sheppard et al., 2006) present challenges for obtaining data on the distributional range of dugongs. However, dugongs may leave clear feeding signs, which allow the identification of high-use areas using low-cost non-destructive rapid assessments. Dugongs feed either by excavating or cropping (Anderson, 1981; Aragones et al., 2012; Keith-Diagne et al., 2022; Marsh et al., 2011). Excavating entails uprooting the whole seagrasses from unconsolidated sediment, while cropping removes only the aboveground plant parts (Anderson, 1981; Aragones et al., 2012; Marsh et al., 2011). Excavating is the main mode through which dugongs graze on early successional seagrasses and results in the formation of distinctive meandering lines called dugong feeding trails (D'Souza et al., 2015; Nasr et al., 2019; Preen, 1995; Shawky, 2019a; Tol et al., 2016). In contrast, the marks left by dugong cropping are difficult to recognize in the wild (Budiarsa et al., 2021; Nakanishi et al., 2008). As obligate bottom feeders, dugongs obtain their dietary requirements mainly through excavating when feeding on seagrasses growing in soft sediments, but cropping tends to be the dominant mode when dugongs feed on climax species with fibrous rhizomes or seagrasses growing on hard substrates (Aragones et al., 2012; Keith-Diagne et al., 2022).

Dugong foraging choices are still a matter of some debate, largely attributed to variations in sampling design. While there is evidence to suggest that dugongs selectively target pioneer seagrasses (e.g., Preen, 1992, 1995; Nakanishi et al., 2006; Sheppard et al., 2010; Aragones et al., 2012) other studies point to them being generalist feeders consuming a wide range of suitable forage available in their local environments (e.g., Marsh et al., 1982; Tol et al., 2016). It is likely that dugong dietary preferences vary between localities depending on type and availability of forage as well as time of grazing (e.g., season or tidal cycle; Sheppard et al., 2007; Marsh, O'Shea & Reynolds III, 2011; Aragones et al., 2012; Keith-Diagne et al., 2022). Despite unresolved doubts on dietary preferences, early pioneering species (particularly *Halophila* and *Halodule* spp.) are clearly important components of the dugong diet across much of its range (Adulyanukosol et al., 2004, 2003; André and Lawler, 2003; Apte et al., 2019; Budiarsa et al., 2021; D'Souza et al., 2015; de Iongh et al., 2007, 1995; Johnstone and Hudson, 1981; Marsh et al., 1982; Mizuno et al., 2017; Nakaoka and Aioi, 1999; Preen, 1995; Sheppard et al., 2007; Tol et al., 2016; Yamamuro and Chirapart, 2005). In the Red Sea, the importance of these seagrasses for dugongs has been underscored through feeding signs (Egypt; Nasr et al., 2019; Shawky, 2019b) and analysis of digesta (Gulfs of Aqaba and Suez; Lipkin, 1975). The tendency of dugongs to excavate these pioneer seagrasses allows for indirect inference that one or more grazing dugong(s) had been present in areas where feeding trails have been visually recognized.

In this study, we conducted a rapid large-scale survey along the north-eastern Red Sea to identify priority conservation areas for the dugong population. Our objectives were to (i) identify current feeding areas that dugongs graze through excavating in the north-eastern Red Sea, and (ii) determine what characterises grazed seagrass meadows in order to inform conservation initiatives in this region. For the first objective, we used indirect signs of dugong feeding (i.e., distinctive dugong feeding trails) as an indication of dugong presence and habitat-use (D'Souza et al., 2015; Nasr et al., 2019; Preen, 1995; Shawky, 2019a; Tol et al., 2016). We then characterised the surveyed seagrass sites based on their oceanographic characteristics, seagrass species composition and abundance and potential anthropogenic stressors. Together, this information can assist in identifying important areas for dugong foraging that can be used for effective conservation planning.

2. Materials and methods

2.1. Study area and study design

We undertook a large-scale expedition to survey seagrass meadows to determine the distributional patterns of dugong feeding trails and the characteristics of the associated seagrass. Additionally, we assessed potential anthropogenic stressors at each of the surveyed sites. The study was conducted over six weeks during October–November 2020.

Our study area (~4,061 km^2) covered the north-eastern Red Sea in the waters of NEOM, Kingdom of Saudi Arabia, stretching from the mouth of the Gulf of Aqaba to the south of Duba Port (28° 6' – 27° 21′ N and 34° 30' – 35° 36′ E; Fig. 1). With a tidal range of about 60 cm (Rasul

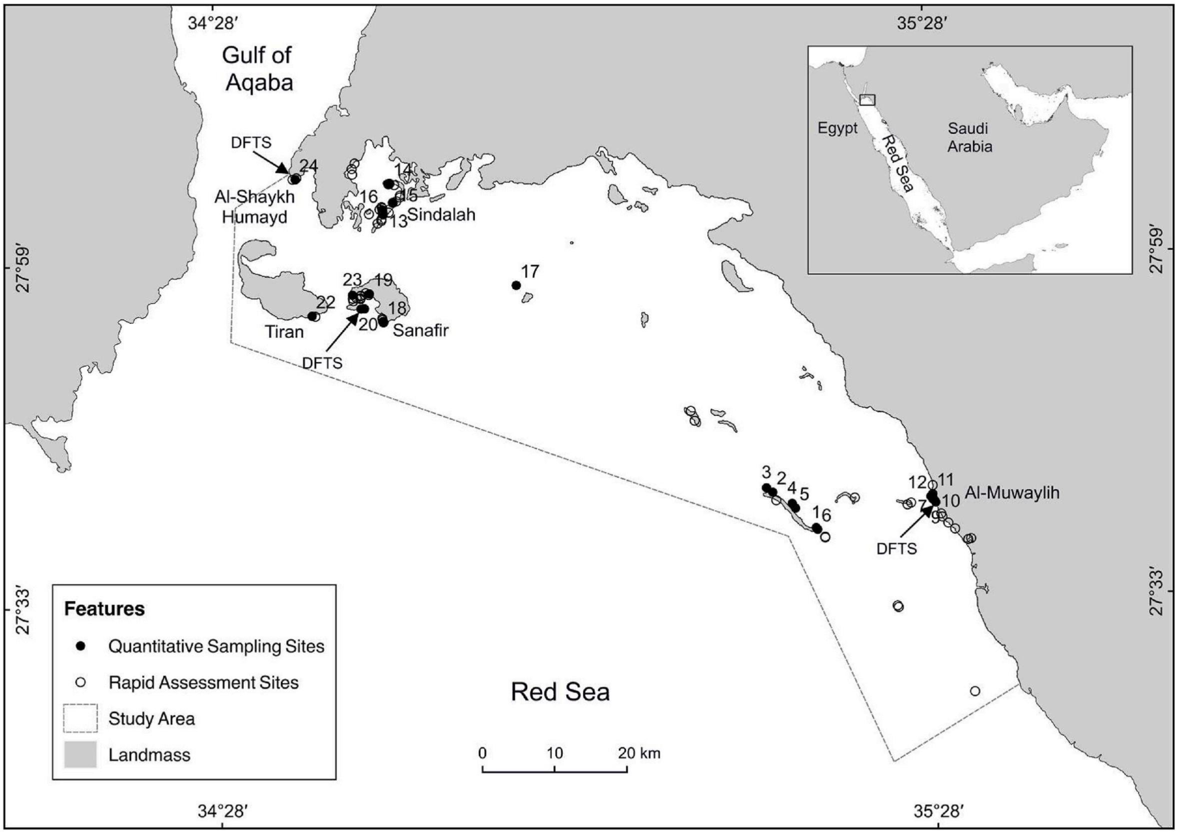

Fig. 1. Map of the study area showing the sampling sites quantitatively surveyed for the dugong feeding signs and seagrass meadow characteristics, dugong feeding trail measurement sites, and the initial rapid survey sites. The inset map shows the location of the study area in the Saudi Arabian northern Red Sea (DFTS = dugong feeding trail assessment sites, number = quantitative sampling sites).

et al., 2019), this part of the Red Sea encompasses deep water communities and a mosaic of shallow water continental shelf habitats, including: sandy beaches, rocky shores, coral reefs and seagrass meadows. The seagrass meadows in the study area are patchy and distributed across a series of reefs, atolls, shoals, lagoons and islands (El Shaffai, 2016; Qurban et al., 2019). Two key megaherbivores use these waters - green turtles (*Chelonia mydas*) and dugongs (*D. dugon*), (Baldwin, 2018; Miller, 2018; Preen, 1989). The standardized dugong aerial survey conducted in July–August 1987 by Preen (1989) highlighted the historical significance of the study area for dugongs. A recent aerial census carried out in April 2018 indicated that the substantial local dugong population (~98 dugongs [95% CI 54–141] in the northern half of the study area; Baldwin, 2018) is widespread across this part of the north-eastern Red Sea. Although dugong sightings are typically of solitary individuals (Baldwin, 2018; Preen, 1989), mother-calf pairs and small groups (<10 dugongs) are occasionally encountered (Baldwin, 2018). Key anthropogenic stressors threatening marine megaherbivores in the study area include fishing, oil exploration and exploitation, maritime traffic and coastal development (Baldwin, 2018; Nasr et al., 2019).

2.2. Dugong feeding sites

To identify seagrass meadows where feeding grounds could be present, we initially conducted a rapid survey of a total of 85 sites, widely distributed across the study area. The geographical coordinates of each site were marked with a hand-held global positioning system (GPS). The sites were rapidly assessed for the presence of seagrasses on SCUBA or snorkel, depending on the depth. Later, we selected a subset of 27 sites covered by seagrasses, and systematically sampled them for the presence of dugong feeding trails and for seagrass meadow characteristics (Fig. 1). To identify key covariates of seagrass meadows excavated by foraging dugongs, we distributed sampling sites across wide gradients of bathymetry, exposure, substrate type as well as seagrass composition and cover. We measured water depth and categorized the sampling sites to: (i) 0–5 m, (ii) 6–10 m, (iii) 11–15 m, and (iv) 16–20 m deep. We classified sites based on their exposure to waves and currents: (i) sheltered (in a lagoon or the leeward of main landmass or large islands), and (ii) exposed (around offshore shoals or in the windward of islands).

At each site, we randomly placed three 50 m benthic transects using fibreglass measuring tapes along the transverse axis of the meadow. For small meadows that could not accommodate the full length of the transects, the transects were located ~1.5 m from the periphery of the meadow to avoid edge effects. It should be noted that dugongs in some localities (e.g., Shark Bay, Australia) reportedly graze at the edges of meadows; a behavior speculated to be an adaptation to minimize predation risk (see Wirsing et al., 2007; Deutsch et al., 2022a, 2022b). During our survey, we carefully examined meadow edges for dugong feeding signs, but did not observe any. Along the transect line, we surveyed a belt of 10 m (50×10 m^2) that was carefully examined for any signs of characteristic dugong feeding trails whose percent cover was estimated relative to the total area of the belt transect. Upon encountering dugong feeding trails, we examined the seagrass species composition at the edges of each trail. Based on the presence/absence of the dugong feeding trails, the sampling sites were classified as: (i) with trails, and (ii) without trails. We identified dugong feeding trails as straight or meandering lines which were: (i) from 0.5 to several meters long, (ii) 6–30 cm wide, and (iii) 2–6 cm deep (Adulyanukosol et al., 2003; D'Souza et al., 2015; Nakaoka et al., 2002; Preen, 1992). We took opportunistic advantage of an underwater encounter and direct observation of a dugong foraging at one of our sampling sites to familiarize ourselves with the distinctive characteristics of dugong feeding trails in this region. Our direct field observations of dugong feeding confirmed that the scars identified at the surveyed seagrass meadows had been left by foraging dugongs.

Where dugong feeding trails were abundant (e.g., Al-Muwaylih, Sindalah and Ras Al-Shaykh Humayd), we measured the spatial extent of five dugong feeding sites using manta-tow and snorkelling. The estimated area of the grazed meadows was identified by marking the start and end points (using a hand-held GPS) along the longitudinal and transverse axes. In one location, Al-Muwaylih, we analysed a total of 14 fresh dugong feeding trails to identify seagrass species grazed by dugongs through excavating (Fig. 1). First, the feeding trails were measured for their total length (one replicate) and width (four replicates) using a fiberglass measuring tape. Subsequently, a 20 × 20 cm quadrat was deployed outside (four replicates) and inside (four replicates) each trail. Shoot density (shoot m^{-2}) was calculated by counting the shoots of each seagrass species inside the quadrat. Later, seagrass removed by dugongs along each feeding trail was calculated as the difference between the average shoot density estimated outside and inside the trail and expressed as a percentage. Seagrass diversity around the dugong trails (~2 m from the trail edges) was carefully examined for any species not sampled by the quadrats.

2.3. Seagrass composition and abundance

We assessed the meadow characteristics of the sampling sites surveyed through the three benthic transects deployed for estimating the dugong feeding trail cover (see above). To establish seagrass percent cover and fragmentation along each transect, we measured transitions in substrate and benthic habitat types as well as seagrass species composition and abundance to the nearest centimetre. We visually assessed and classified the habitat to four broad categories (seagrass, algae, coral and substrate), and the substrate to seven grades (mud, fine sand, medium sand, coarse sand, gravel, rock, and rock with sand veneer). We identified seagrasses *in situ* to the species level following the guidelines of El Shaffai (2016). Whenever necessary, seagrass specimens were collected to verify the identification.

To evaluate the spatial variations in aboveground seagrass biomass, we deployed two replicates of a 20 × 20 cm quadrat at each site and carefully harvested all seagrasses within the quadrat. The seagrass samples were collected in mesh bags, transferred to labelled plastic bags and frozen at – 5 °C. Later, the aboveground portion of the seagrass samples was thoroughly rinsed with freshwater and manually sorted into species to measure relative and total aboveground biomass and shoot density. For all *Halophila* species, each leaf pair was considered a shoot. Whenever necessary, the seagrass shoots and rhizomes covered with sediment particles or epiphytes were carefully cleaned using lab wipes or blades. The aboveground biomass was then calculated by drying the sorted seagrass subsamples in an oven at 60 °C for 36 h and weighing with a microbalance. Biomass was expressed as dry weight of seagrass per surface area (g DW m^{-2}).

2.4. Anthropogenic stressors

To assess the presence of anthropogenic stressors at each site, we recorded direct observations of human activities (e.g., boat traffic and fishing) while conducting the ecological survey. In addition, we quantified the linear distance between a sampling site and key human presence (e.g., fishing ports and coastal development) through Geographical Information System (GIS) maps using Quantum Geographic Information System (QGIS; Version 3.18; QGIS Association).

2.5. Data analysis

We compared sites in relation to the presence or absence of dugong feeding trails (dependent variable) relative to a subset of biological independent variables (i.e., total number of seagrass species [i.e., species richness], percent cover, shoot density and combined cover of *Halophila* and *Halodule* spp.) with one-way ANOVAs after averaging the replicates of each site. We graphically inspected residuals and fitted values to check model assumptions for each variable. The variable aboveground biomass was heteroscedastic as a result of the two grazing levels having contrasting variances. We therefore introduced this variance structure as weights in a Generalised Least Squares model (GLS), using the package nlme in the R software environment (Pinheiro et al., 2011).

To determine which variables best explained the spatial patterns of dugong feeding trail cover across the study area, we used a Generalised Linear Model (GLM) with a binomial distribution. We modelled the presence/absence of dugong feeding trails (dependent variable) as a function of the total number of seagrass species, percent cover, shoot density, and combined cover of the pioneer seagrasses belonging to the genera *Halophila* and *Halodule* (most frequent and abundant seagrasses along dugong feeding trails). Each explanatory variable was then sequentially dropped and the best model was selected using the Akaike Information Criterion and the likelihood ratio test statistic (Zuur et al., 2009). Model validation was assessed by inspecting model residuals and fitted values. Data analysis was performed using R statistical software (Version 4.0.3; R Development Core Team, 2021).

3. Results

3.1. Seagrass species diversity increases in sheltered shallow nearshore waters

Most seagrass meadows surveyed were found in coastal lagoons and around offshore shoals and islands. Sheltered meadows represented 67% of the total, while exposed meadows represented the remaining. Water depth across sampling sites ranged from 1.2 to 17.5 m (Table 1). Within surveyed meadows, seagrass represented the dominant habitat, followed by corals and algae (53.6%, 2.3% and 1.9%, respectively) while 42.2% of seabed was occupied by bare substrate. The sea bottom was primarily comprised of sand and, to a lesser extent, hard substrate (gravel, rock, and rock with sand veneer) and mud (84.2%, 9.4% and 6.4%, respectively). Among the unconsolidated sediment grades, coarse and medium sand were the most dominant (relative cover = 56.6% and 22.9%, respectively).

We recorded a total of nine seagrass species across all sampling sites with species richness varying considerably between sites (1–8 species; Table 1). Of all sites, 38% encompassed monospecific meadows while 54% harboured three or more seagrass species. Seagrass species diversity peaked at the shallow nearshore meadows while deep and exposed meadows were predominantly monospecific and, to a less extent, bispecific. Shallow nearshore waters, sheltered in coastal lagoons and the lee of islands, included multispecific seagrass communities dominated by fast-growing pioneer species. Around 92% of meadows with three or more species (n = 13) were found in sheltered waters. In contrast, deep and exposed meadows tended to have much lower species diversity with later successional seagrasses dominating exposed meadows. Seagrass species diversity dropped considerably relative to increasing depth with 82% of all meadows located in >10 m deep waters (n = 11) being monospecific. The deeper nearshore monospecific meadows were dominated by *H. stipulacea* while exposed offshore meadows were dominated by *Thalassodendron ciliatum*. The seagrass *H. stipulacea* was the most frequently encountered across all sampling sites (71%), followed by *H. ovalis* (58%) and *T. ciliatum* (54%).

3.2. Early successional seagrasses are important forage for dugongs

We recorded distinctive dugong trails at 13 feeding sites (i.e., seagrass areas grazed by dugongs) out of the 27 sampling sites that were surveyed in the north-eastern Red Sea (Table 1). Within this vast range (~98 km linear distance), the dugong feeding sites (DFSs) were clustered around five core areas that encompassed a number of feeding sites

Table 1
Characteristic of the sampling sites in terms of water depth, exposure to waves and currents, occurrence frequency of seagrass species, presence of dugong feeding trails and key human-induced stresses (Hu = *Halodule uninervis*, Ho = *Halophila ovalis*, Hm = *H. minor*, Hs = *H. stipulacea*, Cs = *Cymodocea serrulata*, Cr = *C. rotundata*, Tc = *Thalassodendron ciliatum*, Th = *Thalassia hemprichii*, Si = *Syringodium isoetifolium*, DFT = dugong feeding trail, B = boating, D = development, F = fishing, H = hotel, • = present).

Site	Depth (m)	Exposure level	Seagrass species composition									DFT	Human Stress
			Hu	Ho	Hm	Hs	Cs	Cr	Tc	Th	Si		
1	11.7	Exposed							•				F, B
2	16.0	Exposed							•				F, B
3	15.8	Exposed							•				F, B
4	13.7	Exposed							•				F, B
5	11.6	Exposed							•				F, B
6	13.4	Exposed							•				F, B
7	5.6	Sheltered	•	•	•	•						•	F, B
8	3.9	Sheltered	•	•	•	•							F, B
9	2.2	Sheltered	•	•	•	•	•		•	•	•		F, B
10	3.6	Sheltered	•	•		•			•		•		F, B
11	6.4	Sheltered	•	•	•	•							F, B
12	7.8	Sheltered	•	•	•	•							F, B
13	1.4	Sheltered	•	•		•						•	H, B
14	1.6	Sheltered	•	•		•		•				•	D, B
15	16.6	Sheltered				•						•	D, B
16	17.5	Sheltered				•						•	H, B
17	12.2	Exposed							•				F, B
18	1.3	Sheltered	•			•			•	•		•	
19	1.2	Sheltered	•	•		•				•			
20	12.2	Exposed		•		•			•				
21	16.1	Sheltered		•		•						•	
22	5.7	Sheltered		•		•						•	
23	3.9	Sheltered		•		•			•			•	
24	2.7	Sheltered	•	•		•			•			•	B

with distance interval <5 km: Al-Muwaylih, Sindalah, Sanafir Island, Tiran Island and Ras Al-Shaykh Humayd (Fig. 2). The spatial extent of the DFSs within the surveyed meadows was relatively small ranging from 0.003 to 0.034 km^2. All identified DFSs were in shallow nearshore waters sheltered in coastal lagoons or the lee of islands while no dugong feeding trails were observed at the exposed meadows. Nearly 77% of all

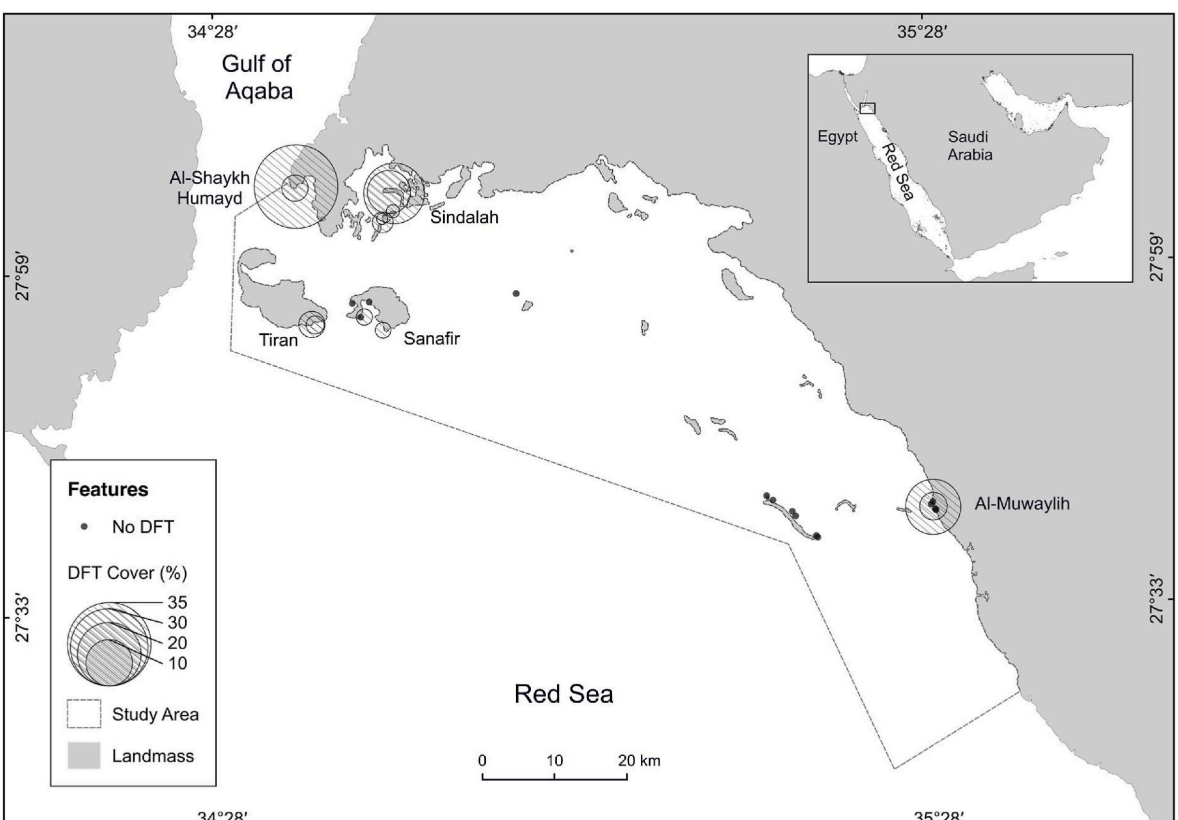

Fig. 2. Dugong feeding trail cover (%) across the study area superimposed on the sampling sites. The inset map shows the location of the study area in the north-eastern Red Sea (DFT = dugong feeding trail).

DFSs were in <10 m waters, but we also recorded distinct dugong feeding trails at greater depths up to 17.5 m (Table 1).

In the sites with dugong feeding trails, the percent trail cover varied widely (range = ≤ 1%–35%) with 69% of all DFSs grazed lightly (trail cover = < 3.0%). All moderately grazed DFSs (trail cover = 14.7%–35%) were in <10 m waters while those located in >15 m waters were lightly grazed (trail cover = 0.1%–0.5%) with the total feeding trail count ranging 2–3 trails across the entire meadow. Many dugong feeding trails at Al-Muwaylih seemed fresh as evident from their deep centre and recognizable edges. Concurrently at this site, also, we recorded other trails which were at early and advanced stages of recovery. In contrast, the trails observed at other dugong feeding areas all appeared old.

We encountered five different seagrass species growing around the edges of the dugong feeding trails across DFSs: *Halodule uninervis*, *Halophila stipulacea*, *H. ovalis*, *H. minor,* and *Cymodocea rotundata*. Among these species, three were more frequently grazed by dugongs: *H. stipulacea* was present in 100% of DFSs, followed by *H. ovalis* (70%) and *H. uninervis* (50%). The seagrasses *H. minor* and *C. rotundata* were found only at one DFS. Examining seagrass species composition along the dugong feeding trails assessed at Al-Muwaylih confirmed a similar trend. At this site, dugongs left feeding trails that averaged (±SD) 3.54 ± 1.28 m (range = 2.14–7.13 m) in total length and 19.25 ± 2.34 cm in transverse width. Exceptionally narrow trails (n = 2) were encountered at this site with mean (±SD) width measuring 12.25 ± 0.96 cm. Within the assessed trails, dugongs removed an average (±SD) 82.8 ± 5.5% of total seagrass shoots with the removal percent of *H. stipulacea* being the highest, followed by *H. ovalis* and *H. uninervis* (92.4%, 91.1% and 67.3%, respectively).

Seagrass percent cover was not significantly different between sampling sites with and without dugong feeding trails. Compared to sites without trails, seagrass shoot density at sites with trails was slightly but not significantly higher, while aboveground biomass was significantly lower at sites with trails. The combined cover of *Halophila* and *Halodule* spp. was significantly higher at sites with trails. The total number of seagrass species encountered at sites with trails ranged from 1 to 4 species and did not significantly differ from those recorded at sites without trails (see Table 2; Fig. 3). All meadows with dugong feeding trail cover >10% were multispecific (range = 3–4 species). The GLM confirmed some of these trends. The distribution of dugong feeding trails across the study area was best explained by the combined cover of *Halophila* and *Halodule* spp. (i.e., most encountered seagrasses around the trails), seagrass percent cover, number of seagrass species, and shoot density (Table 2). Specifically, the probability of encountering dugong feeding trails increased with increasing combined cover of *Halophila* and *Halodule* spp. and seagrass shoot density whereas it decreased with increasing number of seagrass species and seagrass percent cover (Fig. 4). Seagrasses belonging to the genera *Halophila* and *Halodule* were mostly present in shallow sheltered habitats; their combined cover and species diversity dropped considerably at exposed and >10 m deep sites, respectively (Fig. 5).

3.3. Dugong feeding sites vulnerable to anthropogenic stressors

During the survey, we observed boats fishing with gillnets around offshore islands where we also found abandoned fish pots underwater. The DFS at Al-Muwaylih was in proximity (~140 m) of a fishing harbour which included ~35 speed boats at the time of the survey. Similarly, the DFS at Ras Al-Shaykh Humayd was ~360 m away from a major jetty (~50 boats). The boats at Al-Muwaylih were mostly operated by fishers, while those at Ras Al-Shaykh Humayd were mainly used for artisanal fishing and picnicking (Thamer Habis, personal communication, November 2020). Additionally, two DFSs were close to hotels and other

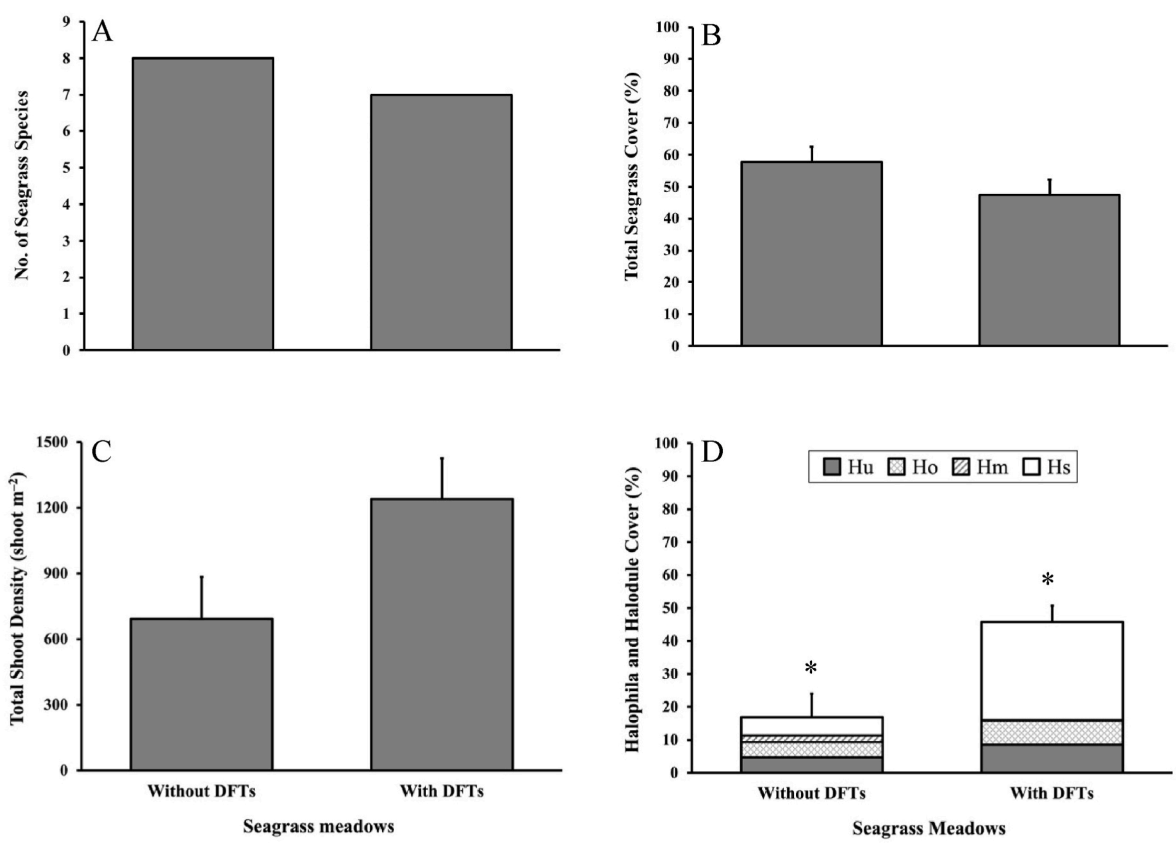

Fig. 3. Comparison between sites with and without dugong feeding trials based on a suite of seagrass diversity and abundance covariates: (A) number of seagrass species, (B) total seagrass cover (%), (C) total shoot density (shoot m^{-2}), and (D) combined cover (%) of *Halophila* and *Halodule* spp. (Hu = *Halodule uninervis*, Ho = *Halophila ovalis*, Hm = *H. minor*, Hs = *H. stipulacea*, bar = standard error, DFTs = dugong feeding trails, * = significant effect).

Table 2
Summary statistics: (a) comparing species richness (i.e., total number of seagrass species), percent cover, shoot density, combined cover of *Halophila* and *Halodule* spp. and aboveground biomass between sites with and without dugong feeding trails; and (b) Generalised Linear Model explaining the presence/absence of dugong feeding trails across the study area as a function of total seagrass species richness, percent cover, shoot density and seagrasses belonging to the genera *Halophila* and *Halodule* (LM = Linear Model, GLS = Generalised Least Squares model, GLM = Binomial Generalised Linear Model, Df = degree of freedom, DFTs = dugong feeding trails, * = significant effect).

Effect	Response variable	Model	Df	Statistic	P-value
(a) Comparison between sites with and without dugong feeding trails					
Species richness	DFTs	LM	1 22	$F = 0.006$	.941
Total seagrass cover	DFTs	LM	1 22	$F = 2.244$	.148
Shoot density	DFTs	LM	1 22	$F = 3.927$	.060
Halophila & *Halodule* cover	DFTs	LM	1 22	$F = 9.443$	.006*
Aboveground biomass	DFTs	GLS	1	$\chi^2 = 7.401$	.006*
(b) Binomial Generalised Linear Model					
Probability of detecting DFTs	Species richness	GLM	1	$\chi^2 = 5.434$	.020*
	Percent cover	GLM	1	$\chi^2 = 6.210$	.013*
	Shoot density	GLM	1	$\chi^2 = 4.160$	.041*
	Halophila & *Halodule* cover	GLM	1	$\chi^2 = 9.946$	.002*

two DFSs were few kilometres from coastal development activities (Table 1).

4. Discussion

Although sparse, dugongs of the Red Sea represent a globally important population occupying the western extreme of the dugong's global distributional range. Studies on this population are few and far between, leaving managers with little to use for conservation planning. Our study used a rapid survey approach based on secondary signs (i.e., dugong feeding trails) to identify a number of seagrass meadows grazed by dugongs, and to determine the oceanographic and ecological factors that characterize these sites. We encountered dugong feeding sites across the north-eastern Red Sea with the majority clustering around five feeding core areas in shallow sheltered waters along the mainland and the leeward sides of islands. During our survey, we also had direct underwater observations of a dugong foraging at one of our sampling sites that confirmed that the foraging marks seen at the identified DFSs had been left by dugongs. A number of these locations were subject to high human activity by boats, fishing, and coastal development which will need careful management if this population is to be protected. While on their own, dugong feeding core areas are natural targets for strategic conservation management, immediate interventions should focus more broadly on protecting sheltered shallow nearshore meadows composed of early successional seagrasses with distinctive dugong feeding trails. This is vital if we are to protect important dugong feeding grounds in the northern Red Sea from rapidly accelerating development.

4.1. *Dugong feeding sites along the mainland and leeward of islands*

Dugong feeding sites that we identified by feeding trail signs were patchy and distributed over an extensive area of shallow waters extending from Ras Al-Shaykh Humayd in the north to Al-Muwaylih in the south. These spatial patterns match the broad-scale dugong distribution found historically across the eastern coast of the Red Sea where solitary or small groups of dugongs are sparsely-spread across shallow sheltered waters (Al-Mansi, 2016; Baldwin, 2018; Nasr et al., 2019; Preen, 1989; Preen et al., 2012). Across much of their range, dugongs show spatially explicit preferences, choosing shallow sheltered waters in coastal bays, mangrove channels and the lee of large islands to frequent (D'Souza et al., 2013; Derville et al., 2022; Marsh et al., 2011, 2002, 1999). Our results confirm the significance of dugong important areas identified earlier in the north-eastern Red Sea by Preen (1989; 'Tiran Zone Area') and Baldwin (2018; 'Liveability Area'). In addition, six of dugong feeding sites identified by this study overlap with the Strait of Tiran Area of Interest, listed for further assessment as a potential

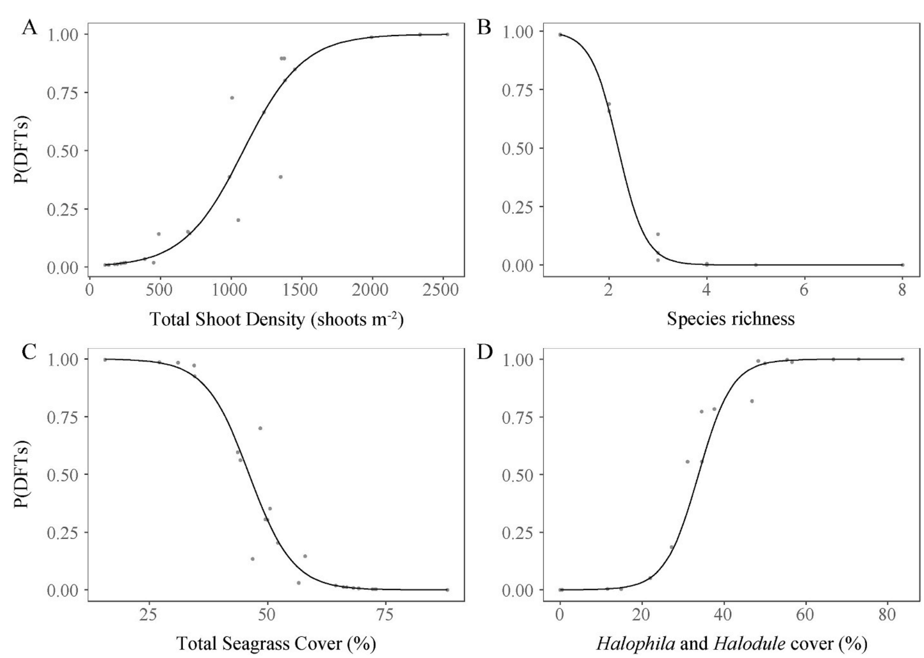

Fig. 4. Generalised Linear Model (GLM) output demonstrating the influence of selected biological factors on the dugong feeding trail detection probability (P (DFTs)) across the study area: (A) total shoot density (shoot m^{-2}), (B) species richness (i.e., total number of seagrass species), (C) total seagrass percent cover, and (D) combined percent cover of *Halophila* and *Halodule* spp.

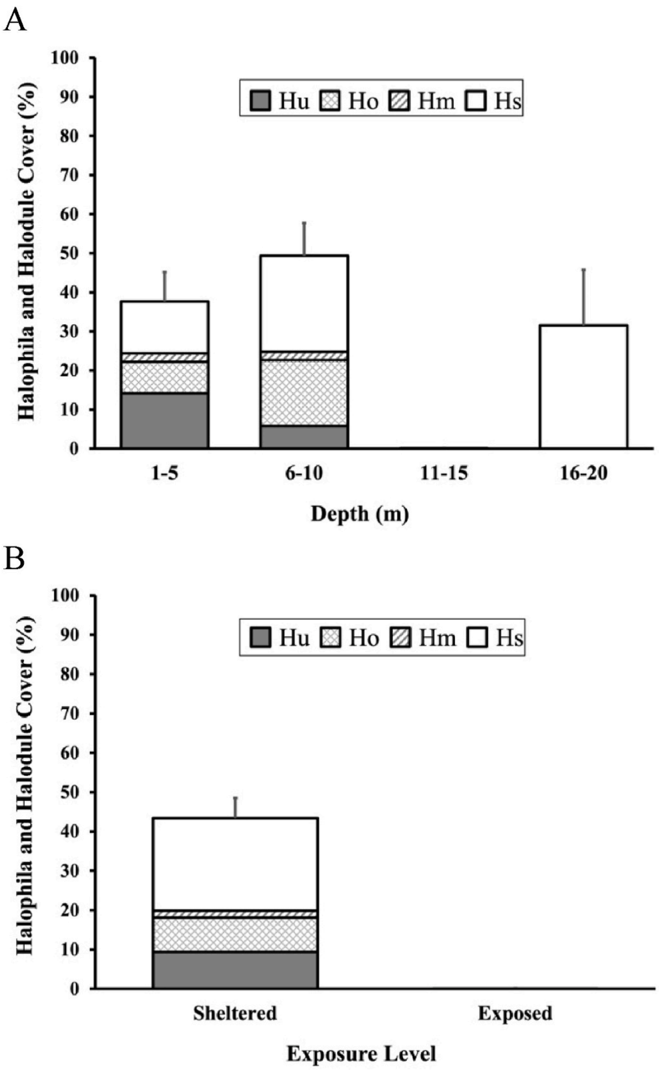

Fig. 5. Comparison among the sampling sites pinpointing the influence of key environmental factors on the combined cover (%) of seagrasses belonging to the genera *Halophila* and *Halodule*: (A) water depth (m), and (B) exposure to waves and currents (Hu = *Halodule uninervis*, Ho = *Halophila ovalis*, Hm = *H. minor*, Hs = *H. stipulacea*, bar = standard error).

Important Marine Mammal Area (IUCN-Marine Mammal Protected Areas Task Force, 2019).

The trail measurements provide insights into the group structure of dugongs at Al-Muwaylih. With a mean width of 19.25 cm, most trails recorded at this site were likely from adult dugongs. The mean trail width of an adult dugong may average 17.4–19.8 cm (Adulyanukosol et al., 2003; Tsutsumi et al., 2005) although widths >28 cm have been also reported (Apte et al., 2019; Shawky, 2019a). Calves may leave trails ranging 9.0–14.3 cm wide (Adulyanukosol et al., 2003; Tsutsumi et al., 2005). The narrow trails measured at Al-Muwaylih fall within this range pinpointing Al-Muwaylih as a potential dugong calving area. Within meadows that had feeding trials, dugong grazing intensity varied markedly across the north-eastern Red Sea confirming similar spatial trends in the Indian Ocean (3.8%–42%; D'Souza et al., 2015). With the exception of Al-Muwaylih, the feeding signs at the other DFSs were not recent indicating likely seasonal grazing patterns; a trend similarly recorded along the western coast of Red Sea (Shawky et al., 2017) and Indonesia (de Iongh et al., 2007).

The recovery of dugong feeding trails through seagrass re-colonization varies significantly between localities, and is influenced by a number of factors including seagrass species composition around the trails as well as timing (i.e., season), frequency (i.e., repeated grazing disturbance) and intensity of dugong grazing (Aragones et al., 2012; Aragones and Marsh, 2000; de Iongh et al., 1995; Preen, 1995). On average, this recovery could take between 3 and 7 months (e.g., Australia and Indonesia; de Iongh, Wenno & Meelis, 1995; Nakaoka and Aioi, 1999; Aragones and Marsh, 2000), but could be considerably faster (<1 month; e.g., India and Thailand; Nakaoka and Aioi, 1999; D'Souza et al., 2015) or slower (>1 year; e.g., Australia and Indonesia; de Iongh, Wenno & Meelis, 1995; Preen, 1995; Aragones and Marsh, 2000), depending on the location. Although *H. ovalis* has been reported to increase its abundance within 80–100 days following simulated grazing (Nasr et al., 2019), more studies are needed to estimate the recovery period of seagrasses following dugong grazing in the Red Sea. This will allow us to estimate the time interval of the presence of dugong(s) more accurately at grazed sites.

Dugongs have a varied diet and may occasionally even consume non-plant material (Keith-Diagne et al., 2022). All seagrass species recorded at our study area have been reported to be grazed by dugongs across much of their global range (Keith-Diagne et al., 2022; Lipkin, 1975; Marsh et al., 1982). No distinctive feeding signs were detected at meadows dominated by later successional seagrasses which could be attributed to the difficulty in recognizing dugong cropping signs in the wild, or absence of grazing. The dugong feeding trails were mostly restricted to patches characterised by few fast-growing early-successional species particularly *H. uninervis*, *H. ovalis* and/or *H. stipulacea*. As species richness increases, the meadows tend to be dominated by later successional seagrasses which lowers the probability of detecting dugong feeding trails despite that the presence of these seagrasses increases seagrass cover and aboveground biomass.

This study confirms the importance of *Halophila* and *Halodule* spp. as forage for dugongs, reported earlier in the north-western Red Sea (Nasr et al., 2019; Shawky, 2019a). As revealed by stomach content analysis, also, dugongs in the Gulfs of Aqaba and Suez graze mainly on *H. uninervis*, *H. ovalis* and *H. stipulacea*, despite they often take small amounts of *C. rotundata* and *T. ciliatum* (Lipkin, 1975). This would help predict the distribution of dugong feeding grounds grazed by excavating. The distributional patterns of megaherbivores is indirectly governed by the same set of underlying factors controlling their forage (Burkholder et al., 2012; Sheppard et al., 2006). Our results suggest that exposure to waves and currents possibly led to significant limits on seagrass species composition in the study area, which conforms with earlier observations in the Red Sea (El Shaffai, 2016; El Shaffai et al., 2014). Across the study area, multispecific meadows harbouring *Halophila* and *Halodule* spp. were found almost exclusively in shallow sheltered nearshore waters. We speculate that by exerting control on the distribution of *Halophila* and *Halodule* spp., exposure indirectly determines the spatial patterns of important foraging dugongs dominated by pioneer seagrasses in the north-eastern Red Sea. The intensity of dugong grazing also decreased with water depth, confirming trends reported elsewhere showing that dugongs prefer grazing in shallow waters (Burkholder et al., 2012; D'Souza et al., 2015; Derville et al., 2022; Deutsch et al., 2022b; Marsh et al., 2011; Nasr et al., 2019; Preen, 1995).

4.2. Dugong feeding sites vulnerable to anthropogenic stressors

Our results showed that seagrass meadows used by dugongs overlapped with areas of high human use. While dugongs may not be hunted in the north-eastern Red Sea, the proximity of DFSs to harbours and hotels makes dugongs vulnerable to the risk of boat strikes and entanglement in fishing nets (Nasr et al., 2019). In such high dugong use areas, measures like reducing speed and wake size, controlling boat numbers, restricting fishing net usage and training fishers on how to deal with entanglement can go a long way to protecting dugong populations. Also, the rapidly-accelerating development projects in the Red Sea (Manasrah et al., 2019) puts DFSs at high risk. Although dugongs have been reported to graze at high human-use and urbanized areas (Marsh et al., 2011; Ng et al., 2022; Ponnampalam et al., 2022), coastal development represents a serious threat considering that many DFSs were mostly small and located in shallow nearshore waters. These are typically among the first areas drastically impacted by coastal development and other land-based anthropogenic activities (Marsh et al., 1999, 2002; Ponnampalam et al., 2015, 2022; Tol et al., 2016).

4.3. Surveying dugong feeding trails is a valuable conservation planning tool but has limitations

Our rapid assessment is of immediate importance for the management of the dugong population of the north-eastern Red Sea. We identified a number of DFSs in our study area that clustered around five feeding core areas. Foraging signs indicated that the dugong population in this area are reproducing with evidence of at least one calf foraging in one of the meadows. In general, these findings suggest that dugong feeding trail surveys can be used as a valuable spatial planning tool enabling the identification of dugong high-use areas for immediate conservation interventions to halt severe deterioration or loss. However, this method has its own limitations which restricts its universal applicability. Feeding trail surveys detect presence but cannot confirm absence of grazing dugong(s) limiting its suitability to only seagrass meadows dominated by pioneer species. For instance, due to the difficulty in recognizing the dugong cropping scars in the field (Anderson, 1981; Keith-Diagne et al., 2022; Marsh et al., 2011; Nakanishi et al., 2008), it is likely that we missed dugong feeding sites at patches dominated by later successional seagrasses particularly considering that stomach analyses (N = 4) conducted by Lipkin (1975) confirmed that dugongs in the northern Red Sea graze on *T. ciliatum*. Similarly, since dugongs do not excavate trails on hard substrate, our method was not designed to detect dugong feeding signs on seagrasses growing on rocky bottoms. Additional research is needed to highlight seasonal variations in dugong grazing patterns and link the distribution of feeding sites with the abundance of foraging dugongs since a group of feeding tails could be left by one or more dugong(s). It is worth clarifying that extending the benthic transects to the edge of meadows and increasing the replicates of biomass and shoot density samples would have increased the variability captured in our sampling design.

4.4. Timely interventions needed to conserve the dugong population of Red Sea

Our results indicated that feeding sites grazed by dugongs through excavating tend to distribute along the mainland and the leeward of islands, exposing these charismatic mammals to intensifying human-induced stresses. This is further complicated by the rapid development being undertaken in the Red Sea at scales seldom witnessed before. The dugong population in the Red Sea is regionally and globally important. Losing it to lack of knowledge would lead to a range contraction for this species and a loss from a poorly connected body of water from which natural recovery would be very difficult. While it is imperative to bolster our understanding of this population with further, more in-depth studies, developing conservation interventions must be undertaken with urgency if we are to protect this enigmatic western population of dugongs. Focusing conservation planning efforts on shallow nearshore waters sheltered by coastal lagoons, embayments and the lee of large islands will support the immediate interventions needed to conserve this vulnerable large-ranging megaherbivore at its western distributional limits.

CRediT authorship contribution statement

Abdulqader Khamis: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Teresa Alcoverro:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Supervision. **Elrika D'Souza:** Conceptualization, Methodology, Writing – review & editing. **Rohan Arthur:** Writing – original draft, Writing – review & editing, Visualization. **Jordi F. Pagès:** Formal analysis, Writing – review & editing, Visualization. **Junid Shah:** Formal analysis, Writing – review & editing. **Tareq Al-Qahtani:** Investigation, Writing – review & editing. **Ameer Abdulla Eweida:** Methodology, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Abdulqader Khamis reports financial support, administrative support, and travel were provided by BEACON, King Abdullah University of Science and Technology, Kingdom of Saudi Arabia. Abdulqader Khamis reports administrative support and equipment, drugs, or supplies were provided by NEOM, Kingdom of Saudi Arabia (This work was performed as a part of subregional multidisciplinary scientific expedition organized by NEOM).

Data availability

The authors do not have permission to share data.

Acknowledgments

This study was conducted as part of the NEOM – OCEANX Expedition (October–November 2020) funded and organized by NEOM, Kingdom of Saudi Arabia (http://neom.com). We are grateful to all staff of NEOM, OceanXplorer (https://oceanxplorer.oceanx.org) and Cyclone (https://tornadomarinefleet.com) who facilitated the surveys. We deeply thank BEACON Development Company at King Abdullah University of Science and Technology, Kingdom of Saudi Arabia, for their support. Special thanks are due to Simon Paker, Thamer Habis and Mubarak Al-Jedani for their valuable assistance during field work.

References

Acevedo-Gutierrez, A., 2009. Group behavior. In: Perrin, W.F., Wursig, B., Thewissen, J. G.M. (Eds.), Encyclopedia of Marine Mammals. Academic Press, pp. 511–520.

Adulyanukosol, K., Boukaew, P., Prasitthipornkul, A., 2004. Analysis of stomach contents of dugongs (*Dugong dugon*) from Gulf of Thailand. In: Proceedings of the International Symposium on SEASTAR2000 and Bio-Logging (The 5th SEASTAR2000 Workshop). Graduate School of Informatics, Kyoto University, pp. 45–51.

Adulyanukosol, K., Thongsukdee, S., Poovachiranon, S., 2003. An observation of dugong behaviors from aerial surveys and feeding trails of a cow-calf pair in seagrass habitat. J. Environ. Resour. Mahidol Univ. 1, 112–118.

Al-Mansi, A., 2016. Status and ecology of sirenian, cetaceans and marine turtles in the farasan bank, red sea, Saudi Arabia. J. King Abdulaziz Univ. - Mar. Sci. 26, 1–8. https://doi.org/10.4197/Mar.26-1.1.

Anderson, P., 1981. The behavior of the dugong (*Dugong dugon*) in relation to conservation and management. Bull. Mar. Sci. 31, 640–647.

André, J., Lawler, I.R., 2003. Near infrared spectroscopy as a rapid and inexpensive means of dietary analysis for a marine herbivore, dugong *Dugong dugon*. Mar. Ecol. Prog. Ser. 257, 259–266. https://doi.org/10.3354/meps257259.

Apte, D., Parasharya, D., Patel, B., 2019. Feeding trails of dugong *Dugong dugon* (müller, 1776) (mammalia: sirenia: dugongidae) in the Gulf of kachchh, western coast of India. J. Threat. Taxa 11, 13151–13154. https://doi.org/10.11609/jott.4315.11.1.13151-13154.

Aragones, L.V., Lawler, I., Marsh, H., Domning, D., Hodgson, A., 2012. The role of Sirenians in aquatic ecosystems. In: Hines, E.M., Reynolds III, J.E., Aragones, L.V., Mignucci-Giannoni, A.A., Marmontel, M. (Eds.), Sirenian Conservation: Issues and Strategies in Developing Countries. University Press of Florida, Florida, USA, pp. 4–11. https://doi.org/10.2307/j.ctvx079z0.

Aragones, L.V., Marsh, H., 2000. Impact of dugong grazing and turtle cropping on tropical seagrass communities. Pacific Conserv. Biol. 5, 277–288. https://doi.org/10.1071/PC000277.

Bakker, E.S., Pagès, J.F., Arthur, R., Alcoverro, T., 2015. Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems. Ecography 38, 1–18. https://doi.org/10.1111/ecog.01651.

Baldwin, R., 2018. NEOM Aerial Survey of Marine Mammals (Summer). Five Oceans Environmental Services, Muscat, Oman.

Budiarsa, A.A., de Iongh, H.H., Kustiawan, W., van Bodegom, P.M., 2021. Dugong foraging behavior on tropical intertidal seagrass meadows: the influence of climatic drivers and anthropogenic disturbance. Hydrobiologia 848, 4153–4166. https://doi.org/10.1007/s10750-021-04583-0.
Burkholder, D.A., Heithaus, M.R., Fourqurean, J.W., 2012. Feeding preferences of herbivores in a relatively pristine subtropical seagrass ecosystem. Mar. Freshw. Res. 63, 1051–1058. https://doi.org/10.1071/MF12029.
Cleguer, C., Garrigue, C., Fuentes, M.M.P.B., Everingham, Y., Hagihara, R., Hamann, M., Payri, C., Marsh, H., 2017. Drivers of change in the relative abundance of dugongs in New Caledonia. Wildl. Res. 44, 365–376. https://doi.org/10.1071/WR16133.
D'Souza, E., Patankar, V., Arthur, R., Alcoverro, T., Kelkar, N., 2013. Long-term occupancy trends in a data-poor dugong population in the Andaman and Nicobar Archipelago. PLoS One 8, e76181. https://doi.org/10.1371/journal.pone.0076181.
D'Souza, E., Patankar, V., Arthur, R., Marbà, N., Alcoverro, T., 2015. Seagrass herbivory levels sustain site-fidelity in a remnant dugong population. PLoS One 10, e0141224. https://doi.org/10.1371/journal.pone.0141224.
de Iongh, H.H., Kiswara, W., Kustiawan, W., Loth, P.E., 2007. A review of research on the interactions between dugongs (*Dugong dugon* Müller 1776) and intertidal seagrass beds in Indonesia. Hydrobiologia 591, 73–83. https://doi.org/10.1007/s10750-007-0785-4.
de Iongh, H.H., Wenno, B.J., Meelis, E., 1995. Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. Aquat. Bot. 50, 1–19. https://doi.org/10.1016/0304-3770(94)00438-R.
Derville, S., Cleguer, C., Garrigue, C., 2022. Ecoregional and temporal dynamics of dugong habitat use in a complex coral reef lagoon ecosystem. Sci. Rep. 12 https://doi.org/10.1038/s41598-021-04412-3. Article 552.
Deutsch, C.J., Castelblanco-Martínez, D.N., Cleguer, C., Groom, R., 2022a. Movement behavior of manatees and dugongs: II. Small-scale movements reflect adaptations to dynamic aquatic environments. In: Marsh, H. (Ed.), Ethology and Behavioral Ecology of Sirenia. Springer, Cham, Switzerland, pp. 233–298. https://doi.org/10.1007/978-3-030-90742-6.
Deutsch, C.J., Castelblanco-Martínez, D.N., Groom, R., Cleguer, C., 2022b. Movement behavior of manatees and dugongs: I. Environmental challenges drive diversity in migratory patterns and other large-scale movements. In: Marsh, H. (Ed.), Ethology and Behavioral Ecology of Sirenia. Springer, Cham, Switzerland, pp. 155–232. https://doi.org/10.1007/978-3-030-90742-6.
di Sciara, G.N., Hoyt, E., Reeves, R., Ardron, J., Marsh, H., Vongraven, D., Barr, B., 2016. Place-based approaches to marine mammal conservation. Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 85–100. https://doi.org/10.1002/aqc.2642.
Dobbs, K., Fernandes, L., Slegers, S., Jago, B., Thompson, L., Hall, J., Day, J., Cameron, D., Tanzer, J., Macdonald, F., Marsh, H., Coles, R., 2008. Incorporating dugong habitats into the marine protected area design for the great barrier reef marine park, queensland, Australia. Ocean Coast Manag. 51, 368–375. https://doi.org/10.1016/j.ocecoaman.2007.08.001.
El Shaffai, A., 2016. Field guide to seagrasses of the red sea. In: International Union for Conservation of Nature, second ed. Total Foundation, Gland, Switzerland; France.
El Shaffai, A., Hanafy, M.H., Gab-Alla, A., 2014. Distribution, abundance and species composition of seagrasses in wadi El gemal national park, red sea, Egypt. Indian J. Appl. Res. 4, 1–9.
Hamann, M., Godfrey, M.H., Seminoff, J.A., Arthur, K., Barata, P.C.R., Bjorndal, K.A., Bolten, A.B., Broderick, A.C., Campbell, L.M., Carreras, C., Casale, P., Chaloupka, M., Chan, S.K.F., Coyne, M.S., Crowder, L.B., Diez, C.E., Dutton, P.H., Epperly, S.P., FitzSimmons, N.N., Formia, A., Girondot, M., Hays, G.C., Cheng, I.J., Kaska, Y., Lewison, R., Mortimer, J.A., Nichols, W.J., Reina, R.D., Shanker, K., Spotila, J.R., Tomás, J., Wallace, B.P., Work, T.M., Zbinden, J., Godley, B.J., 2010. Global research priorities for sea turtles: informing management and conservation in the 21st century. Endanger. Species Res. 11, 245–269. https://doi.org/10.3354/esr00279.
Irvine, A.B., 1983. Manatee metabolism and its influence on distribution in Florida. Biol. Conserv. 25, 315–334. https://doi.org/10.1016/0006-3207(83)90068-X.
IUCN-Marine Mammal Protected Areas Task Force, 2019. Important Marine Mammal Areas: Strait of Tiran AoI [WWW Document]. URL. https://www.marinemammalhabitat.org/imma-eatlas/, 9.20.22.
Johnstone, I.M., Hudson, B.E.T., 1981. The dugong diet: mouth sample analysis. Bull. Mar. Sci. 31, 681–690.
Keith-Diagne, L.W., Barlas, M.E., Reid, J.P., Hodgson, A., Marsh, H., 2022. Diving and foraging behaviors. In: Marsh, H. (Ed.), Ethology and Behavioral Ecology of Sirenia. Springer, Cham, Switzerland, pp. 67–100. https://doi.org/10.1007/978-3-030-90742-6.
Kelkar, N., Arthur, R., Marba, N., Alcoverro, T., 2013. Green turtle herbivory dominates the fate of seagrass primary production in the Lakshadweep islands (Indian Ocean). Mar. Ecol. Prog. Ser. 485, 235–243. https://doi.org/10.3354/meps10406.
Laist, D.W., Reynolds III, J.E., 2005. Florida manatees, warm-water refuges, and an uncertain future. Coast. Manag. 33, 279–295. https://doi.org/10.1080/08920750590952018.
Lipkin, Y., 1975. Food of the red sea dugong (mammalia: sirenia) from sinai. Isr. J. Zool. 24, 81–98.
Littles, C.J., Bonde, R.K., Butler, S.M., Jacoby, C.A., Notestein, S.K., Reid, J.P., Slone, D. H., Frazer, T.K., 2019. Coastal habitat change and marine megafauna behavior: Florida manatees encountering reduced food provisions in a prominent winter refuge. Endanger. Species Res. 38, 29–43. https://doi.org/10.3354/ESR00933.
Manasrah, R., Abu-Hilal, A., Rasheed, M., 2019. Physical and chemical properties of seawater in the Gulf of Aqaba and red sea. In: Rasul, N., Stewart, I. (Eds.), Oceanographic and Biological Aspects of the Red Sea. Springer, Cham, Switzerland, pp. 41–73. https://doi.org/10.1007/978-3-319-99417-8_1.
Marcos, C., Díaz, D., Fietz, K., Forcada, A., Ford, A., García-Charton, J.A., Goñi, R., Lenfant, P., Mallol, S., Mouillot, D., Perez-Marcos, M., Peubla, O., Manel, S., Perez-Ruzafa, A., 2021. Reviewing the ecosystem services, societal goods, and benefits of marine protected areas. Front. Mar. Sci. 8 https://doi.org/10.3389/fmars.2021.613819. Article 613819.
Marsh, H., Channells, P.W., Heinsohn, G.E., Morrissey, J., 1982. Analysis of stomach contents of dugongs from Queensland. Aust. Wildl. Res. 9, 55–67. https://doi.org/10.1071/WR9820055.
Marsh, H., Eros, C., Corkeron, P., Breen, B., 1999. A conservation strategy for dugongs: implications of Australian research. Mar. Freshw. Res. 50, 979–990. https://doi.org/10.1071/MF99080.
Marsh, H., Kwan, D., 2008. Temporal variability in the life history and reproductive biology of female dugongs in Torres Strait: the likely role of sea grass dieback. Continent. Shelf Res. 28, 2152–2159. https://doi.org/10.1016/j.csr.2008.03.023.
Marsh, H., O'Shea, T.J., Reynolds III, J.E., 2011. Ecology and Conservation of the Sirenia: Dugongs and Manatees (Conservation Biology 18). Cambridge University Press, Cambridge, United Kingdom. https://doi.org/10.1017/CBO9781139013277.
Marsh, H., Penrose, H., Eros, C., Hugues, J., 2002. Dugong: Status Report and Action Plans for Countries and Territories (UNEP Early Warning and Assessment Series). United Nations Environment Programme, Nairobi, Kenya.
Marsh, H., Sobtzick, S., 2019. *Dugong Dugon* (Amended Version of 2015 Assessment). IUCN Red List Threat. Species 2019 Article eT6909A160756767. https://doi.org/10.2305/IUCN.UK.2015-4. RLTS.T6909A160756767.en.
Miller, J., 2018. Saudi Arabia. In: Phillott, A.D., Rees, A.F. (Eds.), Sea Turtles in the Middle East and South Asia Region: MTSG Annual Regional Report 2018. IUCN-SSC Marine Turtle Specialist Group, pp. 99–134.
Mizuno, K., Asada, A., Matsumoto, Y., Sugimoto, K., Fujii, T., Yamamuro, M., Fortes, M. D., Sarceda, M., Jimenez, L.A., 2017. A simple and efficient method for making a high-resolution seagrass map and quantification of dugong feeding trail distribution: a field test at Mayo Bay, Philippines. Ecol. Inf. 38, 89–94. https://doi.org/10.1016/j.ecoinf.2017.02.003.
Nakanishi, Yoshiei, Adulyanukosol, K., Arai, N., Hosoya, S., Nakanishi, Yoshiko, Kotani, K., Katsukoshi, K., 2008. Dugong grazing scars confirmed in *Enhalus acoroides* meadows. J. Adv. Mar. Sci. Technol. Soc. 14, 1–8.
Nakanishi, Yoshiei, Hosoya, S., Rai, N., Nakanishi, Yoshiko, Katsukoshi, K., Adulyanukosol, K., 2006. The distribution of seagrass meadows and dugong feeding trails in the dry season around Talibong Island, Trang Province, Thailand. In: Proceedings of the 3rd Intenational Symposium on SEASTAR2000 and Asian Bio-Logging Science (The 7th SEASTAR2000 Workshop). Graduate School of Informatics, Kyoto University, pp. 55–62.
Nakaoka, M., Aioi, K., 1999. Growth of seagrass *Halophila ovalis* at dugong trails compared to existing within-patch variation in a Thailand intertidal flat. Mar. Ecol. Prog. Ser. 184, 97–103. https://doi.org/10.3354/meps184097.
Nakaoka, M., Mukai, H., Chunhabundit, S., 2002. Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed. Ecol. Res. 17, 625–638. https://doi.org/10.1046/j.1440-1703.2002.00520.x.
Nasr, D., Shawky, A.M., Vine, P., 2019. Status of red sea dugongs. In: Rasul, N., Stewart, I. (Eds.), Oceanographic and Biological Aspects of the Red Sea. Springer, Cham, Switzerland, pp. 327–354. https://doi.org/10.1007/978-3-319-99417-8_1.
Ng, S.Z.H., Ow, Y.X., Jaafar, Z., 2022. Dugongs (*Dugong dugon*) along hyper-urbanized coastlines. Front. Mar. Sci. 9 https://doi.org/10.3389/fmars.2022.947700. Article 947700.
O'Shea, T.J., Beck, C.A., Hodgson, A., Keith-Diagne, L.W., Marmontel, M., 2022. Social and reproductive behaviors. In: Marsh, H. (Ed.), Ethology and Behavioral Ecology of Sirenia. Springer, Cham, Switzerland, pp. 101–154. https://doi.org/10.1007/978-3-030-90742-6.
Pilcher, N.J., Antonopoulou, M., Perry, L., Abdel-Moati, M.A., Al Abdessalaam, T.Z., Albeldawi, M., Al Ansi, M., Al-Mohannadi, S.F., Al Zahlawi, N., Baldwin, R., Chikhi, A., Das, H.S., Hamza, S., Kerr, O.J., Al Kiyumi, A., Mobaraki, A., Al Suwaidi, H.S., Al Suweidi, A.S., Sawaf, M., Tourenq, C., Williams, J., Willson, A., 2014. Identification of important sea turtle areas (ITAs) for hawksbill turtles in the Arabian region. J. Exp. Mar. Biol. Ecol. 460, 89–99. https://doi.org/10.1016/j.jembe.2014.06.009.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Development Core Team, 2011. Nlme: Linear and Nonlinear Mixed Effects Models.
Ponnampalam, L.S., Izmal, F.J.H., Adulyanukosol, K., Ooi, J.L.S., Reynolds III, J.E., 2015. Aligning conservation and research priorities for proactive species and habitat management: the case of dugongs *Dugong dugon* in Johor, Malaysia. Oryx 49, 743–749. https://doi.org/10.1017/S0030605313001580.
Ponnampalam, L.S., Keith-Diagne, L.W., Marmontel, M., Marshall, C.D., Reep, R.L., Powell, J., Marsh, H., 2022. Historical and current interactions with humans. In: Marsh, H. (Ed.), Ethology and Behavioral Ecology of Sirenia. Springer, Cham, Switzerland, pp. 299–350. https://doi.org/10.1007/978-3-030-90742-6.
Preen, A., 2004. In: Distribution, Abundance and Conservation Status of Dugongs and Dolphins in the Southern and Western Arabian Gulf. Biol. Conserv, vol. 118, pp. 205–218. https://doi.org/10.1016/j.biocon.2003.08.014.
Preen, A., 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. Mar. Ecol. Prog. Ser. 124, 201–213. https://doi.org/10.3354/meps124201.
Preen, A., 1992. Interactions between dugongs and seagrasses in a subtropical environment. Doctoral dissertation. James Cook University, p. 351.
Preen, A., 1989. The Status and Conservation of Dugongs in the Arabian Region (MEPA Coastal and Marine Management Series, Technical Report No. 10). Meteorological and Environmental Protection Administration (MEPA), Saudi Arabia.
Preen, A., Das, H., Al-Rumaidh, M., Hodgson, A., 2012. Dugongs in Arabia. In: Hines, E. M., Reynolds III, J.E., Aragones, L.V., Mignucci-Giannoni, A.A., Marmontel, M.

(Eds.), Sirenian Conservation: Issues and Strategies in Developing Countries. University Press of Florida, Florida, USA, pp. 91–98. https://doi.org/10.2307/j.ctvx079z0.

Qurban, M.A., Karuppasamy, M., Krishnakumar, P.K., Garcias-Bonet, N., Duarte, C.M., 2019. Seagrass distribution, composition and abundance along the Saudi Arabian coast of Red Sea. In: Rasul, N., Stewart, I. (Eds.), Oceanographic and Biological Aspects of the Red Sea. Springer, Cham, Switzerland, pp. 367–385. https://doi.org/10.1007/978-3-319-99417-8_1.

R Development Core Team, 2021. R: A Language and Environment for Statistical Computing.

Rasul, N., Stewart, I., Vine, P., Nawab, Z.A., 2019. Introduction to oceanographic and biological aspects of the Red Sea. In: Rasul, N., Stewart, I. (Eds.), Oceanographic and Biological Aspects of the Red Sea. Springer, Cham, Switzerland, pp. 1–9. https://doi.org/10.1007/978-3-319-99417-8_1.

Shawky, A.M., 2019a. Evidence of the occurrence of a large dugong in the Red Sea, Egypt. Egypt. J. Aquat. Res. 45, 247–250. https://doi.org/10.1016/j.ejar.2019.08.001.

Shawky, A.M., 2019b. Analysis of Feeding Trails Provides Evidence of the Number of Dugongs Excavating Seagrass at Key Habitats Seasonally in the Egyptian Red Sea. The Rufford Foundation.

Shawky, A.M., Sallam, W.S., Alwany, M.A., Mohammad, D.A., Mohamed, S.Z., 2017. Photo identification of dugongs in marsa alam and wadi El gemal national park, Egyptian coast of the red sea. Al Azhar Bull. Sci. 28, 1–10.

Sheppard, J.K., Lawler, I.R., Marsh, H., 2007. Seagrass as pasture for seacows: landscape-level dugong habitat evaluation. Estuar. Coast Shelf Sci. 71, 117–132. https://doi.org/10.1016/j.ecss.2006.07.006.

Sheppard, J.K., Marsh, H., Jones, R.E., Lawler, I.R., 2010. Dugong habitat use in relation to seagrass nutrients, tides, and diel cycles. Mar. Mamm. Sci. 26, 855–879. https://doi.org/10.1111/j.1748-7692.2010.00374.x.

Sheppard, J.K., Preen, A., Marsh, H., Lawler, I.R., Whiting, S.D., Jones, R.E., 2006. Movement heterogeneity of dugongs, *Dugong dugon* (Müller), over large spatial scales. J. Exp. Mar. Biol. Ecol. 334, 64–83. https://doi.org/10.1016/j.jembe.2006.01.011.

Tol, S.J., Coles, R.G., Congdon, B.C., 2016. *Dugong dugon* feeding in tropical Australian seagrass meadows: implications for conservation planning. PeerJ 4. https://doi.org/10.7717/peerj.2194. Article e2194.

Tsutsumi, C., Ichikawa, K., Akamatsu, T., Arai, N., Shinke, T., Hara, T., Adulyanukosol, K., 2005. Monitoring dugong feeding behavior in a tidal flat by visual and acoustic observation [Paper presentation]. In: Arai, N. (Ed.), Proceedings of the 2nd International Symposium on SEASTAR2000 and Asian Bio-Logging Science (The 6th SEASTAR2000 Workshop). Graduate School of Informatics, Kyoto University, pp. 37–42.

Wells, S., Ray, G.C., Gjerde, K.M., White, A.T., Muthiga, N., Creel, J.E.B., Causey, B.D., McCormick-Ray, J., Salm, R., Gubbay, S., Kelleher, G., Reti, J., 2016. Building the future of MPAs – lessons from history. Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 101–125. https://doi.org/10.1002/aqc.2680.

Wirsing, A.J., Heithaus, M.R., Dill, L.M., 2007. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. Anim. Behav. 74, 93–101. https://doi.org/10.1016/j.anbehav.2006.11.016.

Yamamuro, M., Chirapart, A., 2005. Quality of the seagrass *Halophila ovalis* on a Thai intertidal flat as food for the dugong. J. Oceanogr. 61, 183–186. https://doi.org/10.1007/s10872-005-0030-6.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA. https://doi.org/10.1007/978-0-387-87458-6 e-.