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Dugong-Seagrass Interactions in the Arabian Peninsula: Dugong Feeding Grounds as a Conservation Management Unit

Abdulqader Khamis

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Interaccions entre dugongs i herbeis a la península aràbiga: Les zones de pastura com a unitats de gestió per la conservació

Abdulqader Khamis

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Dugong-seagrass interactions in the Arabian Peninsula: Dugong feeding grounds as a conservation management unit

Interaccions entre dugongs i herbeis a la península aràbiga: Les zones de pastura com a unitats de gestió per la conservació

Submitted by
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INFORM, that the research studies developed by **Abdulqader Khamis** for his Doctoral Thesis have been organized in four main chapters, which correspond to four scientific papers listed below (two published and two in preparation for publishing), in addition to general introduction, discussion, and conclusion;

and CERTIFY, that the work has been carried out by **Abdulqader Khamis**, participating actively in all the tasks, including:

Chapter 3

- Conceiving and setting the study objectives and plan,
- Developing the sampling design,
- Carrying out the field work (where he stayed onboard two research vessels for 43 days),
- Collecting and analysing samples (e.g. seagrass biomass and shoot density),
- Conducting, conceiving and performing the analyses,
- Producing the GIS maps and figures, and
- Writing the manuscript.

Chapter 4

- Conceiving and setting the study objectives and plan,
- Developing the methods of the boat-based, drone and in-water ecological surveys,
- Preparing the questionnaire for the structured interviews,
- Conducting the literature review,
- Carrying out the field work,
- Undertaking the structured interviews,
- Conducting, conceiving and performing the analyses,
- Producing the GIS maps and figures, and

- Writing the manuscript.

Chapter 5

- Conceiving and setting the study objectives and plan,
- Conducting the literature review,
- Digitalizing the historical records using QGIS,
- Developing the methods of the in-water ecological surveys and sea temperature monitoring,
- Carrying out the field work,
- Undertaking the structured interviews,
- Conducting, conceiving and performing the analyses,
- Producing the maps and figures, and
- Writing the manuscript.

Chapter 6

- Conceiving and setting the study objectives and plan,
- Developing the methods of the in-water ecological surveys and experiments as well as sea water quality monitoring (temperature and salinity),
- Performing the ecological surveys and executing the experiments,
- Collecting and analysing the samples (e.g. seagrass biomass and shoot density),
- Conducting, conceiving and performing the analyses,
- Producing the maps and figures, and
- Writing the manuscript.

and CONFIRM, that **Abdulqader Khamis** participated actively in writing, revising, and submitting to the journals the following manuscripts which correspond to two of the above chapters:

Chapter 3	Khamis, A., Alcoverro, T., D'Souza, E., Arthur, R., Pagès, J. F., Shah, J., Al-Qahtani, T., & Eweida, A. A. (2022). Identifying conservation priorities for a widespread dugong population in the Red Sea: Megaherbivore grazing patterns inform management planning. *Marine Environmental Research*, 181, Article 105762.

https://doi.org/10.1016/j.marenvres.2022.105762 (Impact Factor [2021]: 3.737; Category/Quartile [WoS]: Marine and Freshwater Biology-SCIE [Q1])

Chapter 4	Khamis, A., Abdulla, A., D'Souza, E., Kelkar, N., Arthur, R., Al Khalifa, E., Bader, H., & Alcoverro, T. (2023). Long-term persistence of large dugong groups in a conservation hotspot around Hawar Island, Kingdom of Bahrain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 33(3), 1–14. https://doi.org/10.1002/aqc.3936 (Impact Factor [2021]: 3.258; Category/Quartile [WoS]: Marine and Freshwater Biology-SCIE [Q1])

Finally, I CERTIFY that the co-authors of the publications listed below and that conform this doctoral thesis, will not use these manuscripts in another Doctoral thesis.

Barcelona, 02 October 2023

Main Supervisor

Dr. Teresa Alcoverro Pedrola

Centre d'Estudis Avançats de Blanes

In memory of my

deceased beloved mother and father

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The decision that I made to shift my initial focus from coral bleaching to dugong-seagrass interactions has introduced dramatic changes to my academic life considering how charismatic are dugongs, and how wide are the knowledge gaps hindering adequate understanding of their life history traits in the region. At the end of this journey, what really matters more than any academic rewards is the impact that our team has made in introducing to the world two globally important populations of a legendary elusive marine mammal that have remained unexplored for decades. Millions of people around the globe have enjoyed watching ‘The Dugong Whisperer’ episode on Red Sea’s dugongs and even more are expected to eagerly watch the upcoming documentary on the Arabian Gulf’s large dugong groups, the world’s largest. This is not an individual effort, but a collaborative achievement inspired by teamwork spirit; thank you all for making this happen.

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Dissemination of Thesis Chapters

1 Peer Reviewed Journal Articles

Chapter 3

Khamis, A. [1], Alcoverro, T. [2,3], D'Souza, E. [3], Arthur, R. [3], Pagès, J. F. [2], Shah, J. [4], Al-Qahtani, T. [5], & Eweida, A. A. [6,7] (2022). Identifying conservation priorities for a widespread dugong population in the Red Sea: Megaherbivore grazing patterns inform management planning. *Marine Environmental Research*, 181, Article 105762. https://doi.org/10.1016/j.marenvres.2022.105762 (Impact Factor [2021]: 3.737)

Chapter 4

Khamis, A. [1], Abdulla, A. [6,7], D'Souza, E. [3], Kelkar, N. [8], Arthur, R. [3], Al Khalifa, E. [9], Bader, H. [10], & Alcoverro, T. [2,3] (2023). Long-term persistence of large dugong groups in a conservation hotspot around Hawar Island, Kingdom of Bahrain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 33(3), 1–14. https://doi.org/10.1002/aqc.3936 (Impact Factor [2021]: 3.258)

Chapter 5

Khamis, A. [1], Eweida, A. A. [7], D'Souza, E. [3], Arthur, R. [3], Hameid, N. [11], Al Khalifa, E. [9], Ahmed, M. [10], Stepanenko, K. [6], Pagès, J. F. [2] & Alcoverro, T. [2,3] (2023). *Large dugong groups persist in areas with continuous seagrass meadows despite anthropogenic disturbances around Hawar Island, Bahrain* [Manuscript in preparation]. Department of Evolutionary Biology, Ecology, and Environmental Sciences, University of Barcelona.

Chapter 6

Khamis, A. [1], Eweida, A. A. [7], D'Souza, E. [3], Arthur, R. [3], Aguhob, J. [12], Almuhery, A. [12], Badaam, S. [12], Al Khalifa, E. [9], Al-Bastaki, J., Pagès, J. F. , & Alcoverro, T. [2,3] (2023). *How do seagrass meadows in extreme environments cope with high density megaherbivore populations? Understanding the persistence of dugong feeding grounds in the Arabian Gulf* [Manuscript in preparation]. Department of Evolutionary

	Biology, Ecology, and Environmental Sciences, University of Barcelona.

2 Conference Presentation

Chapters 4-6	Khamis, A. [1] (2023, May 2-4). *Dugong-seagrass research and management initiatives in the Kingdom of Bahrain* [Conference presentation]. Regional meeting on science and management for dugongs of the Arabian Gulf, Abu Dhabi, United Arab Emirates.

3 Documentaries

Chapter 3	Short episode entitled ‘The Dugong Whisperer’ addressing the story of the author of this thesis facing the challenge of searching for elusive sparse dugongs across the extensive seascape of the Red Sea (https://www.youtube.com/watch?v=BEwmTijYqzA)

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Table of Content

List of Tables

List of Figures

List of Supplementary Materials

Tables

Figures

Abstract

The principal challenge of conserving marine megaherbivores is that they typically range over extensive areas that far exceed the spatial scales of conventional management, transcending protected areas, and often moving across political boundaries. In the case of dugong (*Dugong dugon*, Müller 1776) populations, their elusive nature further frustrates our ability to design spatial management that effectively encompasses their entire home range. The dugong is globally vulnerable, and across most of its Indo-Pacific distribution, it exists as remnant populations composed of solitary individuals or small groups. Where their populations are large, dugongs often aggregate to feed in seagrass meadows, where they can spend several months as large groups. These meadows then serve as a vital opportunity for effective spatial management of dugongs. For this, it is critical to first describe which meadows dugongs choose to feed in as well as the corelates of this choice. It is additionally important to determine how seagrass meadows cope with this intense herbivory and what additional threats dugongs and seagrasses face.

This thesis explores dugong-seagrass interactions in the Arabian Peninsula to strengthen the management of its data deficient but globally significant dugong populations. We used a set of complementary approaches (combining key informant interviews and citizen science with in-water ecological studies and spatial analyses) to study dugongs and their seagrass feeding grounds in the north-eastern Red Sea (NEOM, Kingdom of Saudi Arabia) and Arabian Gulf (Jabal Ali Wildlife Sanctuary, Emirate of Dubai, United Arab Emirates as well as Hawar Island, Kingdom of Bahrain). In both seas, we used indirect signs to identify hotspots for dugong foraging by evaluating the presence and density of feeding trails in seagrass meadows (Chapters 3, 4 and 6). These hotspots of dugong use clustered in shallow nearshore meadows, dominated by the fast-growing pioneer seagrasses *Halodule uninervis*, *Halophila stipulacea* and/or *H. ovalis.* While dugongs in the north-eastern Red Sea were relatively sparse, the Arabian Gulf encompasses the most clumped dugong groups in the world. We documented that these dugongs gather in large groups to feed around Hawar Island in Bahrain. Historical records and citizen science reports confirmed that these large dugong groups (>50 individuals) have persistently aggregated almost year-round around the island. At their maximum, we documented a record aggregation of ~700 dugongs, making it the largest dugong group ever recorded worldwide in recent history (Chapter 4). These fluid groups account for not less than ~60% of all dugongs in Bahrain and ~12% of the Arabian Gulf's population, and move in small

area between distinct winter and summer aggregation sites, serving as traditional feeding grounds. The core area occupied by the large dugong groups (~145 km^2) around Hawar straddles the Bahrain-Qatar border, reflecting the transboundary nature of these groups and their habitats. In Chapter 5, we explored the environmental correlates of the large dugong groups around Bahrain. The groups move between areas, largely as a seasonal response, spending roughly half a year in each location. Differences in water temperature between summer and winter months can be extreme (range: 21 °C) and dugongs have to cope with some of the coldest and hottest temperatures anywhere in their range. The main predictor of the distribution of large dugong groups was the availability of extensive seagrass meadows (>760 km^2), which covered approximately 82% of the main dugong occupancy area around Hawar.

Given the high density of dugongs in the Arabian Gulf and the extreme temperature and salinity that the seagrasses have to tolerate, our final chapter explores how these seagrasses cope with the additional pressure induced by intense dugong grazing. We compared seagrass production with dugong consumption at 18 sites across the Arabian Gulf using a combination of observational approaches and experimental grazing studies. For a start, very few seagrass species are able to tolerate the harsh environmental settings of the Arabian Gulf and the meadows are limited to *H. uninervis*, *H. stipulacea*, and *H. ovalis,* which at some sites undergo seasonal die-back cycles. Despite this, these short lived, high turnover species, seem perfectly able to deal with intense megaherbivory pressures. For many locations in the Arabian Gulf, dugongs consumed <2% of seagrass production. However, at meadows around Hawar Island, mean dugong herbivory accounted for 57–87% (and occasionally consuming >100%) of primary production at the large dugong group core feeding grounds. Experimentally, we found that, once grazed, seagrass meadows take between 4–6 months to recover. The seasonal movement that we documented in earlier chapters (Chapters 4 and 5) allows these fast-growing species to recover from and cope with intense megaherbivory induced by large dugong groups. The seagrass meadows' extensive area, species composition, and production regime in addition to the dugong seasonal movement associated with rotational grazing have sustained the year-long persistence of clumped groups of 100s dugongs for >3 decades at spatially confined seasonal feeding grounds around Hawar Island.

Our results indicated that dugong feeding grounds in both Red Sea and Arabian Gulf overlap with high human-use areas with intensifying coastal development, fishing, and boating activities imposing increasing risks on dugongs and their seagrass habitats (Chapter 3, 4, and 5). This underscores the pressing need of integrating the dugong-seagrass interaction dynamics in the management of dugong feeding grounds, to ensure that both dugongs and their key habitats are interdependently conserved through a holistic ecosystem-based management approach. Local fishers should be enlisted as co-managers since they have a large stake in maintaining productivity and health of the seagrass meadows they share with dugongs. Given their transboundary nature, regional collaboration cannot be overemphasized to conserve the dugong feeding grounds and migration corridors by establishing a network of regional dugong protected areas, a crucial requirement if we are to safeguard these globally important enigmatic dugong populations of the Red Sea and Arabian Gulf.

Resum

El principal repte en la conservació de megaherbívors marins és que solen abastar extenses àrees que superen amb escreix les escales espacials de la gestió convencional, transcendint les àrees protegides i sovint traspassant les fronteres polítiques. En el cas de les poblacions de dugong (Dugong dugon, Müller 1776), la seva natura esquiva dificulta encara més la nostra capacitat de dissenyar una gestió espacial que abasti tot el seu territori. El dugong és una espècie altament vulnerable a nivell mundial i, en la major part de la seva distribució Indo-Pacífica, només trobem poblacions residuals compostes per un únic individu o grups petits. Quan les seves poblacions són grans, però, els dugongs sovint s'agreguen en àrees concretes de pastura per alimentar-se d'herbeis dominats per angiospermes marines, on poden passar diversos mesos. Aquests herbeis, o zones de pastura, poden representar espais on realitzar una gestió espacial per la conservació dels dugongs. Per a això, és fonamental descriure primer quins herbeis trien els dugongs per alimentar-se, així com els factors principals que determinen aquesta elecció. A més, és important determinar com els herbeis responen a l'impacte dels herbívors i a quines amenaces addicionals s'enfronten els dugongs i les angiospermes marines.

Aquesta tesi explora les interaccions entre dugongs i els herbeis d'angiospermes marines a la península aràbiga per enfortir la gestió de les poblacions d'aquest megaherbívors que estan en clara regressió a nivell mundial. Per adreçar-ho s'utilitzen una sèrie d'aproximacions complementàries combinant entrevistes a informants clau i ciència ciutadana amb estudis ecològics i anàlisis espacials. L'estudi es centrarà en les àrees de pastura dels dugongs al nord-est del Mar Roig (NEOM, Regne de l'Aràbia Saudita) i el golf d'Aràbia (Jabal Ali Wildlife Sanctuary, Emirat de Dubai, Emirats Àrabs Units; i Hawar Island, Regne de Bahrain). En ambdós mars, s'utilitzen la presència i densitat de les marques d'herbivorisme (feeding trails) dels dugongs que s'observen als herbeis com a senyals indirectes per identificar les àrees de pastura (Capítols 3 i 4). Els resultats en indiquen que les àrees de pastura s'han observat sobre tot en herbeis poc profunds propers a la costa, dominats per les angiospermes marines pioneres, de creixement ràpid, *Halodule uninervis, Halophila ovalis* i/o *H. stipulacea*. El resultats també indiquen que la presència de dugongs al nord-est del Mar Roig es relativament petita, i en canvi el golf Aràbic engloba la segona població de dugongs més gran del món. En concret vaig documentar que aquests dugongs es reuneixen en grans grups al voltant de l'illa de Hawar a Bahrain per pasturar en dos zones diferents a l'estiu i a l'hivern, 6 mesos a cada una, que poden arribar a tenir diferencies de temperatura de més de 21 °C (Capítol

5), les més grans observades en el rang de distribució dels dugongs. Els registres històrics i els informes de ciència ciutadana confirmen que les agrupacions de dugongs (> 50 individus) s'agregen de manera persistent gairebé durant tot l'any en aquesta illa amb una agrupació rècord de ~700 dugongs (Capítol 4) i representen aproximadament el 60% de tots els dugongs de Bahrain i el 12% de la població del golf Aràbig. El principal predictor de la seva distribució és la disponibilitat d'extensos prats d'herbeis (>760 km2), que cobreixen al voltant del 82% de l'àrea d'ocupació principal al voltant de Hawar. L'àrea central ocupada per aquests grups (~145 km2) es troba a cavall entre la frontera de Bahrain i Qatar, reflectint la naturalesa transfronterera d'aquests grups i els seus hàbitats

Tenint en compte l'alta densitat de dugongs al golf Aràbic, i la temperatura i salinitat extremes d'aquesta zona, el meu capítol final explora com les angiospermes marines fan front a les pressions d'herbivoria. En aquest capítol comparo amb mesures *in situ* la producció dels herbeis amb el consum dels dugongs (taxes d'herbivorisme) a 18 llocs diferents al llarg del golf Aràbic. Els resultats ens indiquen que només tres espècies d'angiospermes marines són capaces de tolerar els durs entorns ambientals del golf, i els herbeis es limiten a *H. uninervis, H. stipulacea* i *H. ovalis*, que en alguns llocs experimenten cicles de mortalitat estacional. Malgrat això, aquestes espècies de vida curta i alta productivitat son perfectament capaces de fer front a les intenses pressions megaherbívores. A la majoria de les localitats triades al llarg del golf, els dugongs consumeixen <2% de la producció dels herbeis. No obstant això, els herbeis al voltants de Hawar, experimenten unes taxes d'herbivoria que representen de mitjana entre el 57 i el 87% de la seva producció, consumint ocasionalment > el 100% de la producció al nucli de les zones de pastura dels grans grups de dugongs. Experimentalment, vaig trobar que, un cop consumides, les angiospermes marines triguen entre 4 i 6 mesos a recuperar-se. El moviment estacional dels grans grups de dugongs que he documentat als capítols anteriors (Capítols 4 i 5) permet que aquestes espècies de plantes de creixement ràpid es recuperin i facin front a l'intens herbivorisme. La persistència durant més de 3 dècades dels grups de dugongs (superiors al 100 individus) en aquests nuclis relativament petits al voltat de Hawar es dona gràcies a l'extensa àrea dels herbeis, la composició i la producció de les espècies d'angiospermes que els conformen i al moviment estacional dels dugongs entre zones de pastura molt properes.

Els nostres resultats també indiquen que les zones de pastura dels dugongs tant al Mar Roig com al Golf Aràbic es superposen amb zones molt freqüentades per humans. En aquestes àrees hi ha un desenvolupament costaner intensiu, gran activitat de pesca i navegació que imposen riscs als dugongs i als seus hàbitats (Capítols 3, 4 i 5). Això subratlla la necessitat imperiosa d'integrar les dinàmiques tròfiques dels dugongs en la gestió de les zones de pastura per garantir que tant els dugongs com els seus hàbitats clau es conservin de manera interdependent mitjançant un enfocament de gestió holístic basat en l'ecosistema. Els pescadors locals s'han d'integrar com a cogestors, ja que tenen un gran interès en mantenir la productivitat i la salut dels herbeis que comparteixen amb els dugongs. Atesa la naturalesa transfronterera d'aquests grans mamífers, la col·laboració regional és crítica per tal de protegir aquests hàbitats i els corredors de migració de dugongs. Es proposen l'establiment d'àrees protegides regionals en aquestes zones de pastura, un requisit crucial si volem salvaguardar aquestes poblacions de dugongs d'importància mundial.

1

General Introduction

1 Seagrass as pastures for marine herbivores

Seagrasses are habitat-building marine flowering plants constructing the most widespread vegetated habitat in the world's oceans (>160,000 km^2; Waycott et al., 2009; McKenzie et al., 2020). Despite their limited diversity (<60 species), seagrasses form distinct communities featuring six bioregions that stretch predominantly along the temperate, tropical, and subtropical coastlines (Short et al., 2007). Seagrasses constitute the foundation of a highly productive ecosystem nourishing the world's oceans with flourished marine life, tightly interconnected with other ecosystems both in the sea and on land through trophic and energy transfer trajectories (Valentine & Heck Jr, 1999; Orth et al., 2006). The meadows formed by seagrasses represent important sheltering, feeding, breeding, and nursery grounds indispensable for the survival and persistence of a remarkable diversity of coastal and marine flora and fauna (Short et al., 2007; Hays et al., 2018; Scott et al., 2018; Qurban, et al., 2019a).

The health of seagrass meadows is a function of dynamic ecological processes mediated by a suite of environmental and biological covariates. Among key biotic attributes influencing seagrass diversity, structure, and function is herbivory. For centuries, the role of herbivory had remained overshadowed by theories overwhelmingly stressing the influence of environmental covariates on plant distribution and community structure as well as the controlling role of predators on the populations of herbivorous animals (Hairston et al., 1960; Pagès, 2013; Pausas & Bond, 2019). However, this perception has dramatically changed and evolved over time since the mid 20th century (Hairston et al., 1960). By late 1990s, the importance of herbivory for the seagrass ecosystem started to build momentum with increasing numbers of researchers stressing that seagrass functions and dynamics cannot be fully understood without appreciating the roles of herbivores (Cebrián & Duarte, 1998; Valentine & Heck Jr, 1999; Alcoverro & Mariani, 2004; Buñuel, 2021). Currently, herbivory is increasingly recognised as a critical underlying driver shaping community structure, primary production as well as material and energy transfers in both terrestrial and marine environments (Alcoverro & Mariani, 2002, 2004; Bakker et al., 2015, 2016). While the plant materials removed by grazers per unit time indicates the magnitude of herbivory, it is the total flux of seagrass production to the second trophic level that corresponds to the capacity of a seagrass meadow to sustain a given herbivore population (Cebrián & Duarte, 1998; Cebrian & Lartigue, 2004). The interaction between primary producers and herbivores is governed by an equilibrium between production and consumption enabling primary producers to continue sustaining the dietary requirements of herbivores while, concurrently, meeting their own survival and persistence needs as well as providing other valuable ecosystem services. The health of the entire ecosystem is dependent on maintaining this equilibrium for the benefits of both producers and consumers (Lucero, 2010). Overall, compared to their terrestrial counterparts, aquatic (i.e., freshwater and marine) herbivores take-off higher percentage of primary production (<1% to 100%; Cebrian & Lartigue, 2004; Bakker et al., 2016), underscoring the prominent roles of marine herbivores in cycling energy and materials across ecosystems (Cebrian & Lartigue, 2004).

2 Strategic importance of marine megaherbivores for the health and functions of seagrass ecosystems

Among biota heavily dependent on seagrass habitats are marine herbivores; plant-eating animals occupying the second trophic level in a given marine food web (Nunez-Farfan & Valverde, 2020; Schowalter, 2022). Marine herbivores are taxonomically diverse and include representatives of molluscs, crustaceans, echinoderms, fish, reptiles, birds, and mammals, among others (Valentine & Heck Jr, 1999, 2021; Bakker et al., 2016). Unsurprisingly, therefore, these herbivores vary considerably in their size, feeding behaviour and preferences, aggregation patterns as well as ecosystem functional roles. Of these, marine megaherbivores (body mass: >10 kg; Bakker et al., 2015) are widely distributed across the globe, inhabiting diverse marine habitats. Relative to their terrestrial counterparts, extant marine megaherbivores are less taxonomically diverse with green sea turtle *Chelonia mydas* (Linnaeus, 1758) and dugong *Dugong dugon* (Müller, 1776) dominating seascapes as the largest exclusively marine plant grazers. The fact that these large-bodied grazers are seagrass community specialists underlines the significance of megaherbivory in shaping marine ecosystems, particularly across the tropical and subtropical Indo-Pacific waters where their vast spatial ranges overlap (Valentine & Heck, 1999; Aragones et al., 2012b; Bakker et al., 2016; Marsh et al., 2018; Keith-Diagne et al., 2022).

Due to their dietary preferences and needs, many herbivores are tightly dependent on seagrass as a primary food source through consuming the seagrass leaves, rhizomes and/or roots (Cebrián & Duarte, 1998; Kelkar et al., 2013a; Marsh et al., 2018). For a herbivore, seagrass is less nutritious than other primary producers due to the high fibre content and occurrence of deterrent compounds (Valentine & Heck Jr, 2021). Overall, the nutritional quality of seagrass is widely variable with fast growing species and young leaves of the same species containing higher nutrient and lower fibre contents (Cebrián & Duarte, 1998; Valentine

& Heck Jr, 1999; Marsh et al., 2018). However, compared to other aquatic primary producers, seagrass is featured by high resistance and remarkable adaptation to intense grazing pressures. For instance, seagrasses store tissues and basal meristems in belowground reserves, protecting them from grazers (Valentine & Heck Jr, 1999; Buñuel et al., 2023). This is of particular relevance to dugongs *D. dugon* and green turtles *C. mydas* considering their mass daily dietary needs and destructive feeding modes (Aragones et al., 2006, 2012b; Kelkar et al., 2013a), making seagrass meadows suitable feeding grounds for these animals, but within limits constrained by the seagrass carrying capacity (Gangal et al., 2021). Obligate bottom feeders, dugongs are seagrass community specialists, feeding primarily on at least 17 genera and 26 species of seagrasses in addition to algae. Occasionally, also, dugongs are reported to deliberately feed on invertebrates, including ascidians and polychaetes (Preen, 1992; Aragones et al., 2012b; Marsh et al., 2018; Keith-Diagne et al., 2022). Green turtles tend to be more dietary generic with adults foraging on a bulk of algae and seagrass, but also targeting invertebrates such as hydroids and cephalopods (Ferreira et al., 2006; Demography, 2010; Kelkar et al., 2013b).

By virtue of their extensive distributional range and substantial dietary needs, megaherbivores maintain and potentially alter the functions of their ecosystems through, for instance, occupying important trophic levels, engineering the community structure of primary producers, and modifying the geomorphological environment (Bakker et al., 2015; Valentine & Heck Jr, 2021). Compared to their terrestrial counterparts, the functional roles of aquatic megaherbivores are yet to be further explored despite the fact that they all share a suite of similar life history traits, including: large dietary requirements, generic diet composition, wide spatial ranges, and a tendency to form large aggregations (Unsworth et al., 2007; Bakker et al., 2015). The high consumption rates of megaherbivores exert substantial grazing pressures on primary producers that in extreme cases result in functional extinction of their forage (Kelkar et al., 2013a; Gangal et al., 2021). This is in part because marine megaherbivores not only reduce aboveground standing croup by off-taking upper plant parts, but also target the belowground plant materials (Christianen et al., 2014; Bakker et al., 2016). In fact, consumption of vascular plants is higher in oceans (5–10 folds; Bakker et al., 2016), reaching 30–80% of total leaf production compared to 10–20% of primary production on land (Bakker et al., 2015).

The grazing pressure exerted by herbivores mediates cascadal effects on the structure and functioning of marine primary producer communities. Grazing of the aboveground parts reduces the shoot length and canopy height while specialised belowground feeders, such as dugongs and manatees, increase habitat heterogeneity and patchiness across plant beds (Valentine & Heck Jr, 1999, 2021; Bakker et al., 2015, 2016; Buñuel et al., 2023). Another prominent alternation induced by persistent megaherbivore grazing is the modification in species composition from slow-growing large climax plant stands to those dominated by fast-growing pioneer species. An array of grazers have been reported to induce such shift in community structures in marine ecosystems such as sea urchin; mute, whooper and Bewick swans; green turtles; and dugongs (Valentine & Heck, 1999; Alcoverro & Mariani, 2004; Aragones et al., 2012b; Kelkar et al., 2013b; Bakker et al., 2015, 2016; Gangal et al., 2021; Valentine & Heck, 2021). Changes can be also observed in the structure and chemical compositions of primary producers as reported by Aragones et al. (2006) who detected modifications in the nutrient levels of seagrasses following simulated dugong grazing. Combined, these impacts are cascaded to the ecosystem functioning in the form of modifications in geomorphology, primary production, community structure, nutrient cycling, and seed dispersal, among others. For instance, Hearne et al. (2019) reported reduced diversity and abundance of seagrass and algae in meadows grazed by sea turtles in the Caribbean Sea. In Thailand, dugong grazing at intertidal seagrass meadows induced a 2–3 fold reduction in the density of infaunal and epifaunal invertebrate communities (Nakaoka et al., 2002), conforming with a similar trend recorded following intense fish and waterbird grazing (Bakker et al., 2016). In trading of their direct and indirect impacts, megaherbivores, when in equilibrium with plant beds, can also provide benefits to the primary producers upon which they feed. For example, in Borneo, green turtles grazing has been reported to increase seagrass tolerance to high nutrient loads (Christianen et al., 2012). In the Great Barrier Reef, green turtles and dugongs have been attributed to disperse >500,000 seagrass seeds daily over 650 km. The exerted seeds, also, appear to grow 18–61% faster and record 2–4 times higher germination rates (Tol et al., 2017, 2021). Similar long-distance dispersal of plant seeds and propagules is mediated by other aquatic herbivores such as ducks and fish (Bakker et al., 2016).

3 Megaherbivore movement patterns and grouping behaviour determine the fate of herbivory

The ranging patterns of terrestrial and aquatic megaherbivores are profoundly governed by their distinctive behaviour of migrating over large spatio-temporal scales (Owen-Smith et al., 2010; Bakker et al., 2015; Owen-Smith & Martin, 2015), stretching their vast occupancy range over multiple ecosystems and political jurisdictions. These large-scale movements are typically driven by an array of physiological and behavioural needs, strategic for the survival and persistence of species, including: availability of shelter and food resources, avoidance of predators, breeding, offspring rearing, and thermoregulation (Marsh et al., 1999; Wirsing et al., 2007a; Vanak et al., 2010; Boult et al., 2019; Deutsch et al., 2022a). In some cases, megaherbivore migration is expressed as a shift in range in response to unfavourable conditions or constraints in their local environments (Preen & Marsh, 1995; Bakker et al., 2015; Boult et al., 2019). Altogether, the drivers governing the megaherbivore movements cascade through the herbivory pathways into the ecosystem structure and functions. Wide ranging megaherbivores spread their mass dietary needs across large scales of space and time, alleviating the grazing intensity on primary producers and mediating ecosystem connectivity across seascapes. This, additionally, enhances the resilience of megaherbivore populations toward natural and human-induced stressors; long-distance migratory grazers can avoid depleted food supplies or increasing threats at their local environments by travelling to distant habitats and exploring new food types (Owen-Smith et al., 2010; Aragones et al., 2012b; Bakker et al., 2016).

Almost the same set of covariates mediating log-distance migration of megaherbivores, concurrently, drive another characteristic life history trait, social behaviour. Over their evolutionary history, large terrestrial and marine herbivores have evolved distinctive aggregation patterns encouraging solitary animals to form groups (Bakker et al., 2015; Brakes & Dall, 2016; Joly et al., 2019; Edwards et al., 2021). Acevedo-Gutierrez (2009, p. 511) defines an animal group as "*any set of individuals, belonging to the same species, which remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics*". Increasing fitness benefits are provisioned as the most accepted explanation for why an individual trades-off competition on resources and reproduction opportunities by joining a group (Acevedo-Gutierrez, 2009; Martin et al., 2015; Stutz et al., 2018). On land, group vigilance shown by gregarious wildebeests and antelopes enhances their grazing efficiency through early detection of predators, predator confusion as well as diluting predation risk. In addition, information socially-transmitted among conspecifics further improves the search for high-quality foraging grounds (Stutz et al., 2018). Similarly, enhancing foraging efficiency is consistently reported as a key driver mediating grouping behaviour in other marine mammals, including those occupying higher trophic levels (Acevedo-Gutierrez, 2009; Smith et al., 2012). For instance, individuals of bottlenose dolphins *Tursiops* spp., common dolphins *Delphinus* spp., killer whales *Orcinus orca*, blue whales *Balaenoptera musculus*, and bowhead whales *Balaena mysticetus* increase their chances of persuading and capturing preys by aggregating and foraging in groups (Acevedo-Gutierrez, 2009).

When unifying two key life history traits (such as wide-ranging movement and grouping behaviour) with megaherbivores, we expect profound consequences on herbivory. While long-distance migration spreads herbivory over extensive seascapes, the grouping behaviour intensifies grazing pressures within spatially confined persistent core feeding grounds. Apparently, by virtue of their clumped density and high abundance, grazing exerted by gregarious herbivores mediates more profound effects on ecosystem structures and processes compared to sparse populations belonging to the same species (Cebrián & Duarte, 1998; Bakker et al., 2016). For instance, where they persist in exceptionally high densities, both turtles and swans have been reported to consume >100% of primary production at their feeding habitats (Kelkar et al., 2013a; Bakker et al., 2015). In some cases, such persistent intense herbivory may lead to the collapse of primary producer communities and, hence, the loss of associated ecosystem functional roles and services (Valentine & Heck Jr, 1999, 2021; Arthur et al., 2013). In India, for example, rapid recoveries of turtle populations resulted in intense overgrazing inducing profound impacts on seagrass. Upon the arrival of turtles in large numbers and high densities to a meadow, among the first consequences to recognize was substantial seagrass biomass reduction and ~50% decline in shoot elongation rates. This was followed by dominance shift to the favour of fast-growing species which was associated with dramatic fragmentation and shrink in the meadow areal extent. Within 2–9 years of sustained intense turtle grazing, these impacts ultimately resulted in functional extinct and collapse of seagrass communities (Kelkar et al., 2013a, 2013b; Gangal et al., 2021). Such dramatic changes were later observed as sharp declines in fish abundance and fisheries landing, triggering severe conflicts between local fishers and turtles often leading to targeted killing of turtles (Arthur et al., 2013; Kelkar et al., 2013a, 2013b; Heithaus et al., 2014; Gangal et al., 2021). In addition to their impacts on fisheries, turtle overgrazing led to ~40% loss of belowground organic carbon, constraining the blue carbon sequestration capacity of the seagrass meadows (Gangal et al., 2021).

4 The special case of dugong herbivory

4.1 Dugong dietary needs and grazing behaviour

Following the extinction of Steller's cows (see below), dugongs have dominated the world's oceans as the largest extant exclusively marine megaherbivore (Aragones et al., 2012b; Bakker et al., 2015, 2016). Dugongs are widely distributed across 860,000 km^2 of warm tropical and subtropical Indo-Pacific waters spanning 128,000 km of coastlines that straddle the jurisdictions of 44 countries and territories (Marsh & Sobtzick, 2019; Figure 1.1). With a body spanning up to ~3.3 m long and weighing ~570 kg (Jefferson et al., 2015), unsurprisingly, dugongs have massive daily dietary demands (~28.5–30.5 kg WW d^{-1}; Preen, 1992; Aragones, 1994) entailing that these animals engage in foraging most of the time (Preen, 1995). A dugong in the Red Sea, for instance, spends 54% of its daylight time feeding (Shawky, 2018), relatively comparable to 41% exhibited by single dugongs and mother-calf pairs in Moreton Bay, Australia (Hodgson, 2004; O'Shea et al., 2022). In Australia, Chilvers et al. (2004) estimated that foraging occupied 67% of all dives attempted by 15 dugongs fitted with telemetry transmitters. These examples suggest that dugongs need to spend considerable time in seagrass areas, explaining why seagrass has been consistently reported as a key correlate shaping the distributional patterns of dugongs across their range (Anderson, 1981; Marsh et al., 1999, 2002, 2011; Aragones & Marsh, 2000; Sheppard et al., 2006; Hodgson, 2009, 2011; D'Souza et al., 2015; Ponnampalam et al., 2015; Cleguer et al., 2017; Rabaoui et al., 2021; Derville et al., 2022).

Dugong-seagrass interactions have been explored in a number of localities, including: Australia (Preen, 1995; Aragones, 1996; Burkholder et al., 2012), Philippines (Lucero, 2010), Indonesia (de Iongh et al., 2007), Malaysia (Heng et al., 2022), Thailand (Yamamuro & Chirapart, 2005), India (D'Souza et al., 2015; Prajapati et al., 2022), and Egypt (Nasr et al., 2019; Shawky, 2019a). Various approaches have been employed to explore these complex interactions, such as: examination of mouth parts (Johnstone & Hudson, 1981), stomach analysis (Marsh et al., 1982; André & Lawler, 2003; Adulyanukosol et al., 2004), observation of feeding trails (Preen, 1995; Nakaoka & Aioi, 1999; Adulyanukosol et al., 2003; D'Souza et al., 2015; Mizuno et al., 2017; Apte et al., 2019; Budiarsa et al., 2021), analysis of seagrass chemical composition (de Iongh et al., 1995; Yamamuro & Chirapart, 2005; de Iongh et al., 2007; Sheppard et al., 2007; Burkholder et al., 2012; Tol et al., 2016), visual-acoustic observations (Tsutsumi et al., 2005), and fine-scale matching between dugong and seagrass distribution (de Iongh et al., 2007; Sheppard et al., 2007). All these studies have pointed out that the distinctive feeding behaviour of dugongs makes them crucial engineering agents of seagrass habitats. While both turtles and dugongs feed by cropping above- and below-ground plant parts, the excavating feeding mode of dugongs entails the uprooting of whole plants from the substrate (Aragones et al., 2012b; D'Souza et al., 2015; Keith-Diagne et al., 2022). The bioturbation associated with this destructive feeding mode induces prominent geomorphological modifications to the seabed, mediating an array of ecological changes to seagrass communities and associated flora and fauna (see above). Together, dugong dietary needs and grazing behaviour subject seagrass meadows to substantial herbivory pressures far exceeding those exhibited by other marine herbivores (Bakker et al., 2015; Keith-Diagne et al., 2022; Wirsing et al., 2022).

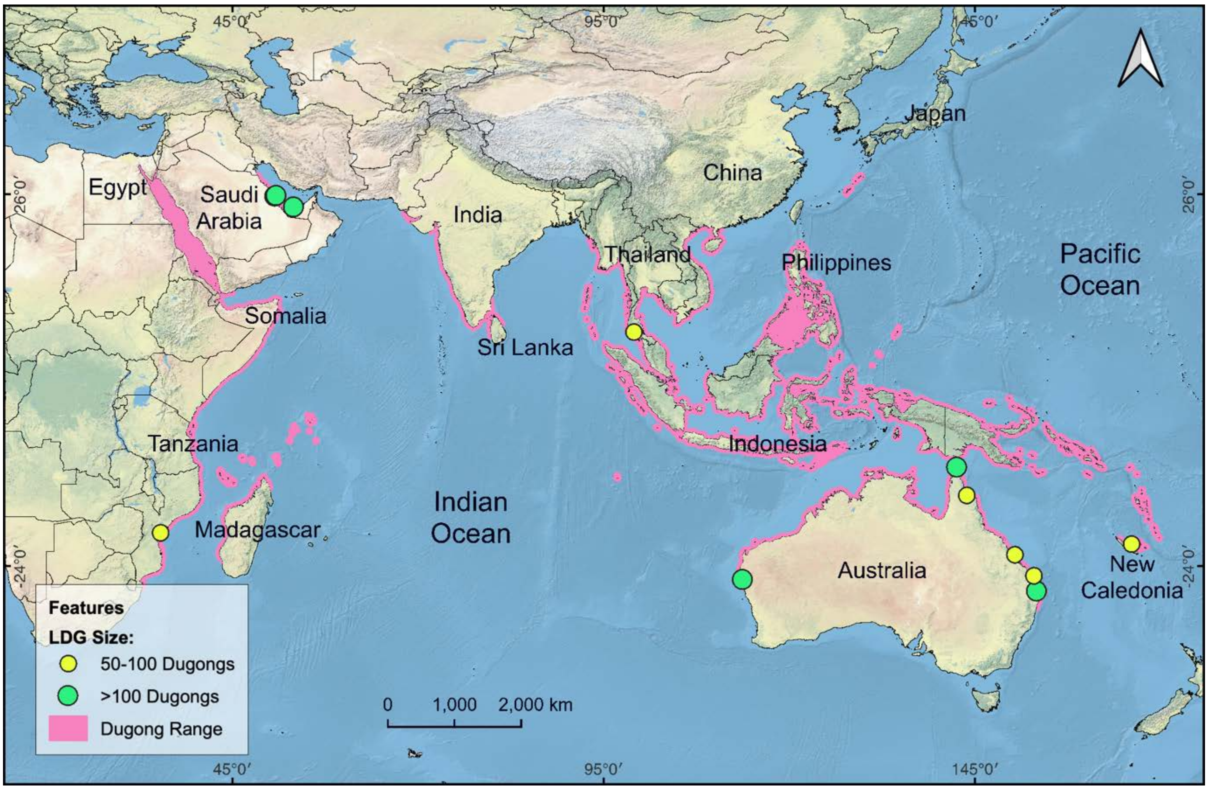


Figure 1.1. The global distributional range of dugongs indicating their preference to warm tropical and subtropical Indo-Pacific waters, superimposed with important areas harboring large dugong groups (LDGs; >50 dugongs), classified into two size categories (50–100 and >100 dugongs). The large dugong group locations are approximate (shapefile of the dugong global distribution: www.iucnredlist.org).

4.2 Dugong herbivory in relation to their movement patterns and grouping behaviour

The areal extent of dugong home ranges varies considerably among individuals and locations. Dugongs exhibit heterogenous movement patterns varying from micro- (<15 km) to meso- (15–99 km) and macro-scales (≥100 km). While some dugongs remain sedentary at particular areas, moving between nearby feeding grounds (<15 km), others undertake directional macro-scale migrations (>600 km). Parts of these movements are ranging with some dugongs returning to the same feeding grounds even after traveling >100 km (Marsh et al., 1999; Sheppard et al., 2006; de Iongh et al., 2007; Deutsch et al., 2022a, 2022b). Sedentary dugongs show noticeable fidelity to .5 km^2 and widely-ranging dugongs occupy an extensive area of up to ~733 km^2 (Sheppard et al., 2006; O'Shea et al., 2022). Obviously, these characteristic movement patterns influence dugong use of seagrass meadows in space and time with meadows grazed by sedentary individuals tend to be exposed to higher and more frequent grazing pressures. The influence of dugong grazing on seagrasses become even more prominent when these animals congregate forming high-density groups with tens or hundreds of dugongs striving to satisfy their massive daily dietary needs at spatially confined feeding grounds. Similar to their movement patterns, the social behaviour of dugongs is a complex trait; while most dugongs spend much of their time solitary, they often aggregate forming sizeable clumped groups of several hundred individuals (Marsh et al., 2002; Preen, 2004; Sobtzick et al., 2017; O'Shea et al., 2022). This fission-fusion group forming behaviour has been so far reported only at certain regions with the size of dugong groups peaking (>100 dugongs) in Australia and the Arabian Gulf (Preen, 1992; Preen & Marsh, 1995; Marsh et al., 2002; Hodgson, 2004; Sobtzick et al., 2017). Smaller but still large groups of dugongs (50–100 dugongs) have been also reported in South Asia, Africa, and New Caledonia (Hines et al., 2005; Findlay et al., 2011; Cleguer, 2015; Figure 1.1). Only few studies have explored the grouping behaviour of dugongs, leaving wide knowledge gaps in our understanding of this phenomenon and, hence, its implications on seagrass communities (Hodgson, 2004; O'Shea et al., 2022).

As indicated above, it is widely recognized that marine mammals decide to join a group when the fitness benefits they gain through group-living offset the trade-offs associated with competing with other group members for resources and space (Acevedo-Gutierrez, 2009; O'Shea et al., 2022). Drawing on this principle, Preen (1992) and Hodgson (2004) explored several potential fitness benefits that dugongs likely gain through forming sizeable groups in Moreton and Shark Bays, Australia, including: protecting calves from predators, thermoregulation, and foraging efficiency.

Young animals are particularly vulnerable to the risk of predation, which is sometimes diluted by mothers through joining a group. However, based on aerial surveys conducted in the Arabian Gulf and Australia, Preen (1989, 1992) concluded that calf proportion exhibited a linear relationship with dugong herd size. Likewise, Hodgson (2004) speculated that group-living may not enhance the fitness of mother-calf pairs in Moreton Bay considering that they do not position themselves in the centre of the herds. This implies that group living likely does not reduce the predation risk for mother-calf pairs and, hence, cannot fully explain why dugongs form sizeable groups at certain localities.

As thermoregulatory adaptations for aquatic life, sirenians have large body sizes, divergent blubber arrangement, and counter-current heat exchange systems (Marshall et al., 2022). Despite these adaptations, manatees and dugongs, being tropical and subtropical, still cannot tolerate long exposure to low water temperatures. When temperature drops ≤20 ºC, Florida manatees *Trichechus manatus latirostris* migrate to warm-water refugia, otherwise they risk suffering stress syndromes should temperatures drop further to 16–18 ºC (Marshall et al., 2022). In winter, manatees aggregate in hundreds around traditional refugia heated by warm water springs, power plant outfalls, and haloclines formed by freshwater inflow (Irvine, 1983; Reynolds III & Wilcox, 1994; Stith et al., 2012; Littles et al., 2019; Edwards et al., 2021). Similarly, a number of studies showed that dugongs respond to cold water temperatures below 17–18 ºC through daily (e.g., in Moreton Bay) or seasonal (e.g., in Shark Bay) thermoregulatory movements (Preen, 1992; Holley et al., 2006; Sheppard et al., 2006; Marsh et al., 2011; Zeh et al., 2018). Drawing on the well-studied aggregation behaviour of Florida manatees, Preen (2004) hypothesized that low winter temperature is likely the main driver inducing the formation of large dugong groups (>50 individuals) around Hawar Island, Bahrain (see below), (Preen, 1989; Reynolds III & Wilcox, 1994; Laist & Reynolds III, 2005; Preen et al., 2012; Stith et al., 2012; O'Shea et al., 2022).

A consistently reported explanation of dugong social behaviour inducing the formation of sizeable groups in Australia revolves around the 'cultivation grazing hypothesis' speculated by Preen (1992, 1995). This hypothesis suggests that group living provides additional fitness benefits enabling aggregating dugongs to enhance their feeding efficiency, a primary concern for mammals with massive daily dietary needs like dugongs. According to the cultivation grazing hypothesis, dugongs deliberately enhance the quality of their forage through aggregating in clumped groups and repeatedly grazing the same meadows (Preen, 1992). This persistent grazing pressure mediates a number of desirable modifications in seagrass communities: (i) inducing dominance shifts favouring the growth of nutritionally superior pioneer seagrasses, (ii) maintaining seagrasses at a young seral stage with low fibre contents, and (iii) concentrating the forage at areas maximizing harvest success (Preen, 1992, 1995; Aragones & Marsh, 2000; Aragones et al., 2006; Figure 1.2). Terming them as 'feeding aggregations', Hodgson (2004) quantitatively proved that dugongs forming large groups in Moreton Bay spend longer time grazing compared to solitary or scattered animals. Hodgson, also, noted that dugongs tend to form larger and tighter groups while grazing—in comparison to other behaviours—suggesting that members joining large groups benefit from enhanced foraging efficiency compared to solitary individuals. Based on these conclusions, Hodgson (2004) strongly supported the 'cultivation grazing hypothesis' suggested by Preen (1992, 1995) as the primary driver provoking the year-round formation of large dugong groups in Moreton Bay. Due to the rarity of encountering large dugong groups across much of the dugong range, this hypothesis has been examined only in Australia although it has been also suggested as a key driver of the persistent use of seagrass meadows by a sparse dugong population in the Andaman Sea (D'Souza et al., 2015). It yet remains unclear whether the cultivation grazing hypothesis drives, also, the exceptional grouping behaviour of the Arabian Gulf's dugongs (similar to their counterparts in the southern hemisphere), particularly considering that only three pioneer seagrass species grow in this environment.

5 Anthropogenic stressors influence megaherbivory across seascapes

5.1 Seagrass meadows: Critical marine ecosystems in decline

Seagrass meadows represent one of the most threatened marine ecosystems on earth, increasingly experiencing an alarming degradation, severe fragmentation, and extensive loss as a result of sediment and nutrient runoff, coastal development, unsustainable fishing practices, invasive species, disease outbreaks, and extreme climate events (Seddon et al., 2000; Orth et al., 2006; Short et al., 2007; Waycott et al., 2009; Dunic et al., 2021; Marsh et al., 2022). A review by Waycott et al. (2009) estimated that, at global level, the accelerating human-induced declines drive the loss of 110 km^2 yr^{-1} of seagrass meadows, accounting for ~29% contract in the areal extent of seagrass since 1879. A recent assessment conducted by Dunic et al. (2021), similarly, suggested ~19% decline in the global extent of seagrass habitats (equivalent of ~5,602 km^2 since 1880), predominately attributed to accelerating coastal development and deteriorating water quality. In addition to their direct ecological consequences, these reported world-wide declining trajectories may be reflected on the health of the entire ecosystem as well as human well-being. That is because seagrasses provide crucial environmental functions in the form of organic carbon production, nutrient and contaminant cycling, blue carbon sequestration as well as sediment accumulation and stabilization (Unsworth et al., 2019). Of particular importance for human well-being, seagrass meadows sustain food security, create job opportunities, and enhance climate change resilience, among other crucial services to which the livelihoods of many coastal and islander communities are firmly tied (Basson et al., 1977; Orth et al., 2006; Waycott et al., 2009; Erftemeijer & Shuail, 2012; Hays et al., 2018; Dunic et al., 2021; Bennett et al., 2022).

5.2 Intensifying human stressors threaten marine megaherbivores

The large-scale movement and dispersion patterns of megaherbivores entail that their key habitats and occupancy corridors substantially overlap with high human-use areas and straddle various jurisdictional scales, literally exposing these charismatic animals to ever-increasing and intensifying anthropogenic threats (Atwood et al., 2020). Over long history of non-rationale human use, marine megaherbivores have faced alarmingly increasing human-induced pressures in the form of fishing bycatch, direct hunting, poaching, boat strikes and disturbances, invasive species, pollution, climate change as well as habitat degradation, alternation, and loss (Ferreira et al., 2006; Hodgson, 2009; Knight et al., 2011; Pilcher et al., 2014; Abdulqader et al., 2017; Ponnampalam et al., 2022). Combined, these stresses have dramatically reduced megaherbivore abundance and diversity, declining to historical records since the twentieth century, although some recoveries of few species (e.g., green turtles) have been recently reported (Bakker et al., 2016). A prominent example is the human hunting-driven extinction of Steller's cows in 1768, only 27 years after their discovery (Steneck et al., 2017; Wirsing et al., 2022), clearly showing how non sustainable human use can lead to tragic consequences on megaherbivore populations. In some localities, anthropogenic activities mount over the already existing threats imposed by natural stresses on megaherbivores, leading to severe deterioration. For instance, Preen and Marsh (1995) reported 96% decline in the dugong population of Hervey Bay, Australia associated with mass dugong mortality driven by large-scale loss of seagrass beds (>1000 km^2) as a consequence of cyclones hitting the bay in 1992 (Deutsch et al., 2022b). This example demonstrates the consequences on marine megaherbivores if no effective interventions have been undertaken to halt the accelerating human-induced seagrass degradation and loss.

While the direct impacts of anthropogenic stressors on megaherbivore populations and their critical habitats have been well-documented, indirect implications on their grazing behaviour is yet to be fully understood and may have severe consequences on their persistence. For example, large terrestrial mammalian herbivores such as elephants are forced by human disturbances to trade-off their preferred feeding grounds (Selier et al., 2015). In oceans, large

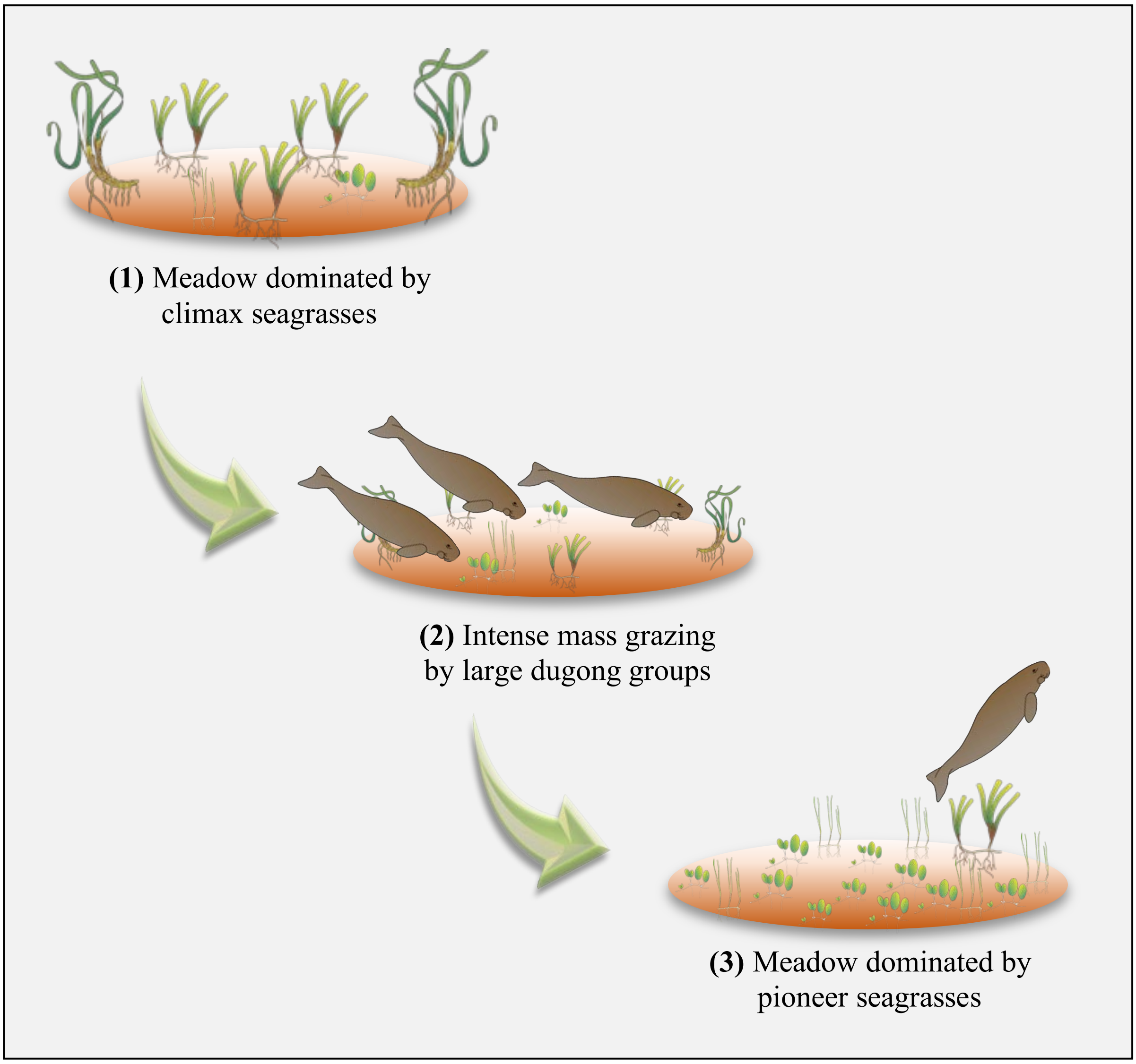


Figure 1.2. Dominance shift in seagrass community structure, favoring the growth of pioneer seagrasses, mediated by persistent mass grazing by large dugong groups (>50 dugongs) as speculated by the cultivation grazing hypothesis suggested by Preen (1995), (Symbols: www.ian.umces.edu/imagelibrary).

dugong groups in Moreton Bay respond to boat disturbance originating from >1 km through a behavioural cascade including suspension of feeding and short distance traveling to nearby feeding spots (Anderson, 1981; Preen, 1992; Hodgson, 2004). Where dugongs are sparse, they have been reported to follow a different strategy through synchronizing their grazing with the quieter time of the day (e.g., at night) when human disturbance is minimal (Shawky et al., 2017; Nasr et al., 2019). Overall, with the combined natural and anthropogenic stresses intensifying across seascapes, there is a pressing need for efficient management to halt the mounting undesirable implications on marine herbivores and their critical habitats (Bakker et al., 2016).

6 Dugongs of the Arabian Peninsula: Megaherbivory under harsh environmental settings

6.1 Globally important sizeable regional dugong populations

The Arabian Peninsula is bordered by two seas protruding from the western Indian Ocean: the Red Sea and Arabian Gulf. The Red Sea measures roughly 458,620 km^2 whereas the smaller Arabian Gulf extends over approximately 250,000 km^2. These subtropical land-locked seas differ remarkably in bathymetry with maximum depth reaching ~2,900 m in the central Red Sea compared to ~100 m in the Arabian Gulf (Krishnakumar et al., 2018; Rasul et al., 2019). In both seas, dugongs have been reported to present in large numbers; the Arabian Gulf dugong population is the second largest after Australia while that of the Red Sea is third worldwide (Preen, 1998; Preen et al., 2012; Marsh & Sobtzick, 2019; Nasr et al., 2019). Geographically, the Red Sea marks the western extreme while the Arabian Gulf represents the northern limit of the global dugong distributional range (Figure 1.1). However, these two populations differ considerably in their spatial distributional patterns. Dugongs are widely spread along almost the entire lengthy Red Sea's coastline forming a sparsely distributed population. In comparison, the Arabian Gulf's dugongs are more concentrated around the southern coast (Preen, 1989, 2004; Preen et al., 2012; Marsh & Sobtzick, 2019; Nasr et al., 2019; Figure 1.3). Moreover, albeit most dugongs in the Arabian Gulf are found as solitary or paired animals (mean group size: 1.33–1.85 dugong; Preen, 2004), which is consistent with the dugong sparse distribution in the Red Sea, they aggregate at specific localities forming clumped large groups (Preen, 1989, 2004; Preen et al., 2012). Further highlighting the global importance of the Arabian Gulf's dugong population, the dugong group comprised of ~670 dugongs, that was sighted by Preen (2004) in 1986 to the north west of Hawar Island, Bahrain has been consistently cited as the largest dugong group ever reported in recent history (Hodgson, 2011; Marsh et al., 2011, 2018; Preen et al., 2012; O'Shea et al., 2022).

6.2 Harsh physical environment constrains marine biological settings

The location of the Red Sea and Arabian Gulf in the subtropics as well as their semi-enclosed nature feature these water bodies with harsh environmental settings mediated by elevated temperature and salinity (Basson et al., 1977; Manasrah et al., 2019; Qurban et al., 2019a; Alosairi et al., 2020; Howells et al., 2020). Considered among the highest in the world, the extreme seawater temperature and salinity levels in the Arabian Gulf fluctuate over a wide annual range imposing additional stresses on local species, further constraining their occurrence, abundance, and distribution (Basson et al., 1977; Price et al., 1993; Vousden, 1995; Manasrah et al., 2007; Howells et al., 2020). The Arabian Gulf, also, experiences low temperatures in winter as a result of its high latitudes and shallowness. This harshness is reflected in the biological settings with the Arabian Gulf encompassing less diversity of marine life compared to the Red Sea. For instance, whereas 12 seagrass species grow in the Red Sea, only three species tolerate the saltier and hotter waters of the Arabian Gulf (Basson et al., 1977; Price & Coles, 1992; Erftemeijer & Shuail, 2012; Al-Bader et al., 2014; El Shaffai, 2016; Qurban et al., 2019a).

Beside surviving in the harshest seas worldwide, the Arabian Peninsula's dugongs occupy high latitudes where the regional dugong distributional range is believed to be constrained by cold winter temperatures (Preen, 1998). Drawing on consistent observations of thermoregulatory behaviours exhibited by manatees and dugongs (see above), Preen (2004) suggested that the broad-distribution of dugongs in the Arabian Gulf is constrained by low winter temperatures (<18 ºC). He further hypothesized that the large dugong groups around Hawar are formed around warm discharges from underground springs (Hodgson, 2009, 2011; Marsh et al., 2011; Preen et al., 2012) to counter the stress imposed by low winter temperatures (annual range: 10–45 °C; Basson et al., 1977; Vousden, 1995; Coles, 2003; Al-Bader et al., 2014; Alosairi et al., 2020). For more than three decades, this hypothesis has not been tested, and, hence, the effects of localized warm water discharges on dugong grouping behavior in the Arabian Gulf has remained an unanswered question.

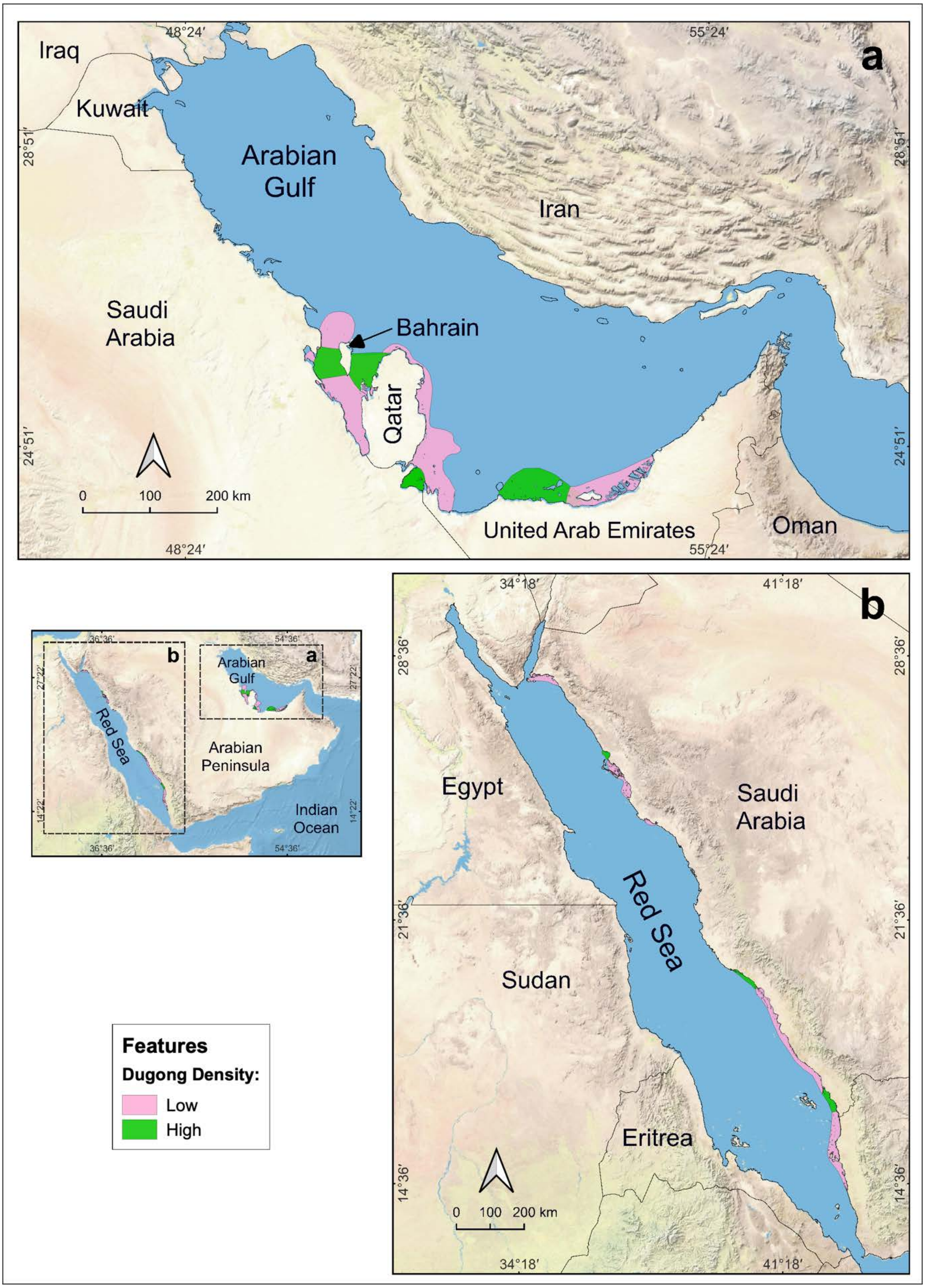


Figure 1.3. Spatial distribution and density of dugongs along the Arabian Peninsula's coastlines in the Red Sea and Arabian Gulf, digitalized from the maps produced by Preen (1989) based on aerial surveys conducted in 1985–1987. The distribution of dugongs along the African coast of the Red Sea is not indicated.

7 Integrating dugong herbivory dynamics in the conservation management strategies in the Red Sea and Arabian Gulf

7.1 Dugong feeding trails: A valuable spatial planning tool to evaluate dugong habitat use

In spite of their global importance, very little is known about the life history, ecology, and habitat use patterns of dugongs of the Red Sea and Arabian Gulf, explaining why both regional populations have been classified by the International Union for Conservation of Nature as ‘data deficient’ (Marsh & Sobtzick, 2019). Scientific research on these populations is scarce and most studies have mostly focused on quantifying their abundance, distribution, and mortality (Preen, 2004; Das, 2007; Environment Agency-Abu Dhabi, 2014). Along the Saudi Arabian coastline of the Red Sea as well as across the entire dugong distribution in the Arabian Gulf, no specialized study has yet explored the dugong feeding ground dynamics. As a result, basic knowledge related to how dugongs in this region use seagrass meadows and the spatial distribution of key dugong feeding grounds across seascapes have remained largely unexplored. This is in part because dugongs are elusive animals that spend much of their time as solitary individuals or mother-calf pairs making spotting and monitoring dugongs in the wild challenging. Added to this complexity is that dugong movement is heterogenous with ranging dugongs reported to travel across hundreds of kilometres. Over decades, these knowledge gaps have hindered the integration of dugong-seagrass interaction dynamics into the conservation management in the Arabian Peninsula forcing a fragmented approach, mostly focusing on the direct anthropogenic stressors threatening dugongs without adequately correlating the spatial planning with the dugong habitat use patterns. Considering all these challenges, the dugong feeding trails emerge as a promising detection tool for dugongs, informing conservation management on dugong occupancy and habitat use, especially where data on dugong feeding grounds is considerably scarce like in the Arabian Peninsula (D’Souza et al., 2013, 2015). In this essence, a number of studies have successfully employed feeding trails to locate high-use dugong areas (de Iongh et al., 1995; Preen, 1995; Aragones et al., 2006). For instance, on the African side of the Red Sea, Shawky and collaborators (2019a, 2019b) identified dugong feeding grounds using feeding trail surveys coupled with photo identification techniques (Nasr et al., 2019). In a similar manner, the spatially explicit dugong feeding ground distribution in the Andaman Sea was determined after observing persistent feeding trails over time (D’Souza et al., 2013, 2015).

7.2 Dugong feeding grounds as high priority conservation areas

Historical records indicate that dugongs have been hunted for their meat, oil, and leather in both the Red Sea and Arabian Gulf (Preen, 1989, 2004; Nasr et al., 2019). While legal protection has succeeded to significantly halt direct hunting, dugong populations around the Arabian Peninsula continue to be threatened by accidental entanglement in fishing nets, collisions with boats, habitat degradation and loss, pollution, and climate change (Hodgson, 2009; Preen et al., 2012; Nasr et al., 2019; Abdulqader et al., 2020; Marsh et al., 2022; Ponnampalam et al., 2022). Currently, these harsh seas are experiencing accelerated coastal developments never witnessed before with lengthy coastlines have been dredged and reclaimed to meet the increasing land demand catering to residential, recreational, commercial, and industrial purposes (Zainal et al., 2012; Burt et al., 2017; Burt & Bartholomew, 2019).

Safeguarding wide-ranging dugongs represents a challenge for conservation management in this region given their tendency to disperse over large spatial scales and, conversely, congregate in high abundance and density at confined traditional aggregation sites. To this extent, dugong feeding grounds can be used as a valuable conservation unit informing spatial planners on where the management efforts should be focused to ensure the persistence of these charismatic megaherbivores and the valuable ecosystem services their main habitats provide. Undoubtedly, the effectiveness of these management interventions is conditional on gaining better understanding of the ecological processes governing dugong feeding grounds and maintaining primary production-herbivore consumption dynamics balanced in the face of mounting anthropogenic pressures (Orth et al., 2006; Unsworth et al., 2019). This is particularly true for the Arabian Peninsula where sizeable dugong populations occupy large spatial scales rendering the conservation efforts challenging, especially where logistic, technical, financial and human resources dedicated to conservation are limited. Identifying potential dugong feeding grounds and migration corridors is critical to focus the conservation efforts on high-priority conservation hotspots. Widely recognized as a ‘flagship species’, the protection of dugongs shall promote the conservation of the seagrass meadows and their associated flora and fauna.

8 Dugong-seagrass interactions in the Arabian Peninsula provide a unique insight into marine megaherbivory

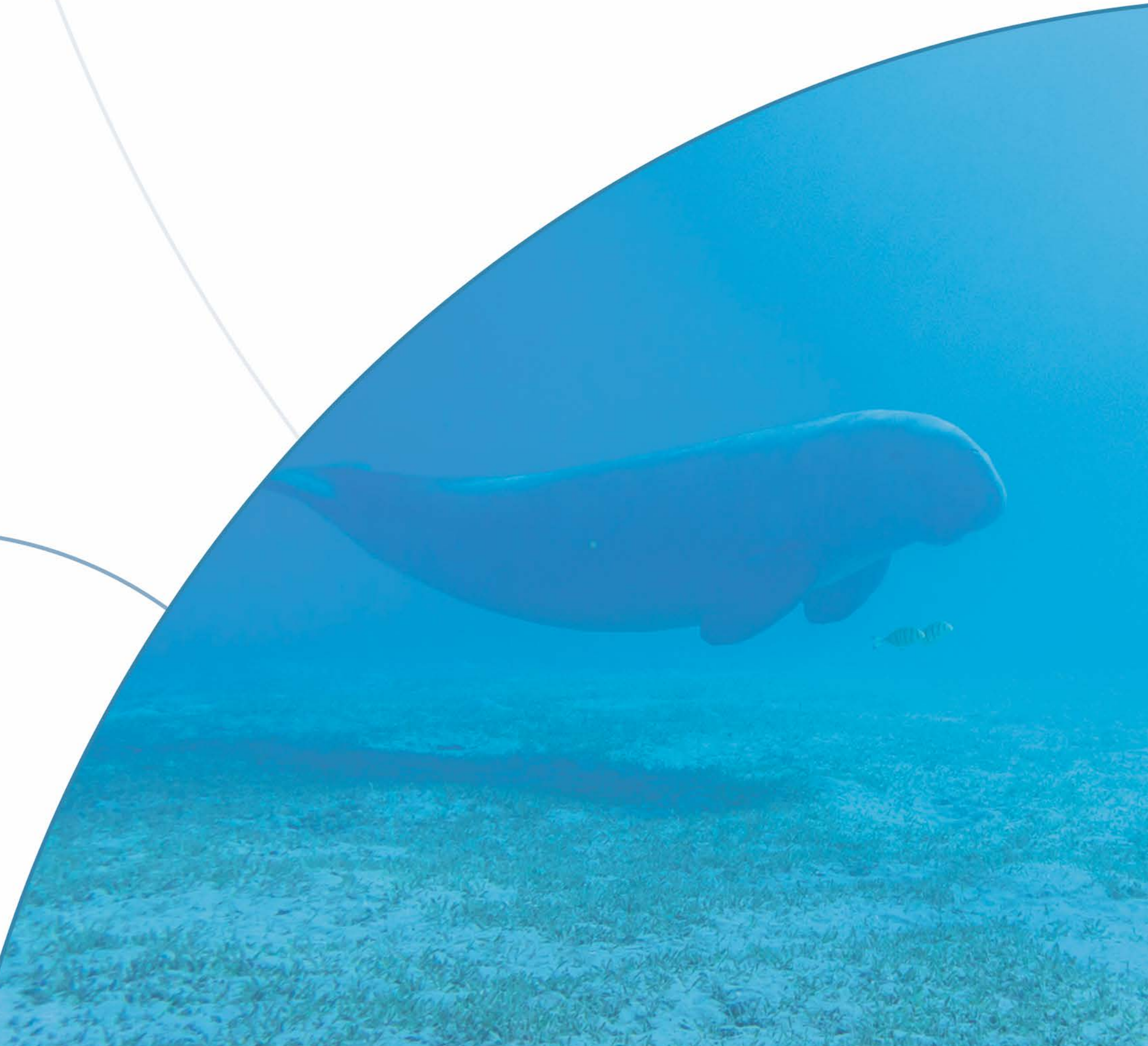
Given their group-forming social behaviour and geographical location in the northern and western dugong distributional limits, the interactions between the Arabian Peninsula’s dugongs and seagrass represent an exceptional case of marine herbivory. For the first, the Arabian Gulf is one of few marine environments around the world where dugongs aggregate forming large groups, potentially feeding on seagrasses, although the persistence of these groups is yet to be confirmed (Preen, 2004; Marshall et al., 2018; Deutsch et al., 2022b). In addition, the fact that both forage (i.e., seagrasses) and megaherbivore (i.e., dugongs) likely survive close to their maximum tolerance thresholds in relation to temperature and salinity (Basson et al., 1977; Price et al., 1993; Vousden, 1995) makes dugong-seagrass interactions in the Arabian Peninsula exceptional from scientific and conservation perspectives. In fact, these seas have been increasingly recognized by scientists as living laboratories projecting how tropical and temperate species may react in response to rising seawater temperatures (Wabnitz et al., 2018; Hereher, 2020; Howells et al., 2020). Therefore, it can be reasonably concluded that dugong herbivory in the Arabian Peninsula models the future fate of marine megaherbivory in the era of global warming, but with herbivore densities mimicking historical sizeable populations. In this essence, the Arabian Gulf represents an exceptional case to study the world's largest and most clumped groups of the biggest extant marine megaherbivore potentially exerting the most intense marine grazing pressures on seagrass meadows experiencing the highest seawater temperature and salinity in the world.

Despite their global importance, there remain wide knowledge gaps hindering adequate understanding of the interactions between dugongs and seagrasses in the harsh environmental settings prevailing around the Arabian Peninsula. For instance, what are the distributional patterns of dugong feeding grounds around the Arabian Peninsula, what do characteristic features make seagrass meadows suitable feeding grounds for dugongs, what are the main anthropogenic activities threatening these feeding grounds, what are the foraging impacts of dugongs on the seagrass meadows, what are the features sustaining the productive capacity of seagrass meadows surviving in such harsh environment to support sizeable megaherbivore populations aggregating at some localities forming large clumped groups, and whether these interactions differ from other parts of the world, have remained largely unexplored.

This thesis attempts to address the current wide knowledge gaps related to dugong feeding ground dynamics in the Arabian Peninsula with an aim of integrating the enhanced understanding of dugong-seagrass interactions in the conservation management strategies in the Red Sea and Arabian Gulf.

2

Research Objectives and Thesis Structure



This thesis aims to enhance the understanding of dugong-seagrass interaction dynamics governing the dugong feeding grounds around the Arabian Peninsula towards optimizing the conservation management of the data deficient regional dugong populations and the associated seagrass meadows. The research spans over two subtropical seas and three countries: Red Sea (NEOM, Kingdom of Saudi Arabia) and Arabian Gulf (Jabal Ali Wildlife Sanctuary, Emirate of Dubai, United Arab Emirates as well as Hawar Island, Kingdom of Bahrain). This regional spatial scope enables the exploration of dugong herbivory over wide gradients of seagrass community structures and abundance, dugong grazing intensity (driven by the heterogenous dugong movement and grouping patterns in the region) as well as anthropogenic stressors.

To achieve the research aim, the thesis is structured into key four chapters focusing on the following specific objectives:

(i) **Objective 1:** Assess the geomorphological, environmental, and ecological characteristic features of key dugong feeding grounds in the northern Saudi Arabian Red Sea to inform the spatial planning on dugong habitats of high conservation priorities.

Chapter 3: Given the sparse distribution of dugongs in the Red Sea, we conducted a large-scale in-water ecological survey to determine the presence/absence of dugongs based on the feeding trails left by a feeding dugong. We correlated the location of dugong feeding areas relative to the shore, determined seagrass species composition and abundance, and estimated dugong grazing intensity to identify the criteria used by dugongs to select their key feeding grounds in the north-eastern Red Sea. These results establish the basis for further research modeling the spatial distribution of dugong high use areas across the Red Sea.

(ii) **Objective 2:** Determine the persistence of large dugong groups and traditional dugong aggregation sites around Kingdom of Bahrain over space and time to advocate a regional approach enhancing dugong conservation management in the Arabian Gulf.

Chapter 4: In this chapter we determined whether dugongs have persisted to aggregate around Hawar Island, Bahrain since the first report of a large dugong group (>50 dugongs) in this region in 1986. We assessed the spatio-temporal patterns of large dugong groups and delineated their seasonal aggregation sites. Considering their transboundary nature and substantial contributions to the dugong population, we discussed the need for a holistic regional approach to safeguard dugongs in the Arabian Gulf. The results of this chapter repentant an important addition to the understanding of dugong grouping behavior given the paucity of studies on this topic worldwide.

(iii) **Objective 3:** Evaluate key environmental and ecological correlates driving the spatial distribution of large dugong groups around Kingdom of Bahrain in relation to mounting anthropogenic pressures with a focus on fishing and boating activities.

Chapter 5: We correlated the distributional patterns of large dugong groups with a suite of environmental and ecological attributes featuring the marine environment around Bahrain to determine the habitat suitability patterns sustaining the persistence of large dugong groups almost year-round. Of particular reference, we assessed the potential impacts of fishing and boating activities on the persistence of large dugong groups and determined whether these intensifying threats have forced the groups to completely abandon their traditional aggregation sites around Hawar Island. The findings of this chapter underscore the importance of integrating the habitat suitability patterns in the dugong conservation management strategies.

(iv) **Objective 4:** Identify key ecological attributes governing the interaction dynamics between dugong herbivory and seagrass primary production in the Emirate of Dubai and Kingdom of Bahrain to inform the management of dugong feeding grounds under the harsh environmental settings in the Arabian Gulf.

Chapter 6: The first of its kind in the Arabian Gulf, this chapter attempts to assess the impacts of low and high dugong herbivory intensities on the abundance, community structure and production of seagrass around Jabal Ali Wildlife Sanctuary, Emirate of Dubai, United Arab Emirates and Hawar Island, Bahrain while determining the recovery turnover of seagrasses in response to dugong grazing. Based on spatially-explicit evaluation of seagrass primary production and dugong herbivory, we explained why seagrass meadows around Bahrain have sustained the massive dietary requirements of large clumped groups of dugongs over decades while congruously coping with the harsh environment of the Arabian Gulf. This study provides exceptional insight on marine megaherbivory informing future research, forecasting the ecological impacts of large clumped megaherbivore populations under future scenarios of seawater temperature rise induced by climate change.

The results obtained from these four chapters are then discussed in **Chapter 7** and summarized in **Chapter 8** to crystalize strategic priorities for the conservation of the globally important dugong populations of the Red Sea and Arabian Gulf through incorporating the dugong-seagrass interaction considerations, with a particular focus on dugong feeding ground dynamics, in the conservation management strategies.

3

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

1 Abstract[1]

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 .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 resorts 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.

Keywords: dugong, marine mammal, IUCN vulnerable species, seagrass, habitat, Red Sea, Saudi Arabia, conservation

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[1] See the original publication in Khamis et al. (2022), Annex-2

2 Introduction

Large marine herbivores, such as green turtles or dugongs, typically occupy large home ranges over which they move between foraging and breeding grounds (D'Souza et al., 2013; Kelkar et al., 2013a; Bakker et al., 2015; 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 (Irvine, 1983; Marsh et al., 1999; Acevedo-Gutierrez, 2009; Bakker et al., 2015; Deutsch et al., 2022b; 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 (Sheppard et al., 2006; Hamann et al., 2010). The heterogeneous spread of environmental drivers and anthropogenic stressors 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 (Dobbs et al., 2008; Marsh & Kwan, 2008; Bakker et al., 2015; di Sciara et al., 2016). 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; Wells et al., 2016; Marcos et al., 2021). 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; Sheppard et al., 2006; Kelkar et al., 2013a; Pilcher et al., 2014; Littles et al., 2019). This concentrated use of their otherwise vast home ranges is likely a strategy that better increases their chances of persistence (Marsh et al., 2002; D'Souza et al., 2013). 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 (Laist & Reynolds III, 2005; Dobbs et al., 2008; Pilcher et al., 2014; di Sciara et al., 2016; 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; Marsh et al., 1999; Sheppard et al., 2006; de Iongh et al., 2007; Deutsch et al., 2022a). 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 & 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 (Marsh et al., 1999, 2002; Preen, 2004; Sheppard et al., 2006; D'Souza et al., 2013; Nasr et al., 2019; Ponnampalam et al., 2022). 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; Tol et al., 2016; Marsh & Sobtzick, 2019), with only few remaining sizeable dugong populations primarily found in Australia, New Caledonia, Papua New Guinea, Arabian Gulf and Red Sea (Preen, 1989, 2004; Marsh et al., 2002; Preen et al., 2012; Cleguer et al., 2017). 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; Preen et al., 2012; Marsh & Sobtzick, 2019; Nasr et al., 2019) hampering conservation planning efforts in this region.

Their elusive nature and long-distance transboundary movement patterns (Sheppard et al., 2006; Deutsch et al., 2022a) 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; Marsh et al., 2011; Aragones et al., 2012b; Keith-Diagne et al., 2022). Excavating entails uprooting the whole seagrasses from unconsolidated sediment, while cropping removes only the aboveground plant parts (Anderson, 1981; Marsh et al., 2011; Aragones et al., 2012b). 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 (Preen, 1995; D'Souza et al., 2015; Tol et al., 2016; Nasr et al., 2019; Shawky, 2019b). In contrast, the marks left by dugong cropping are difficult to recognize in the wild (Nakanishi et al., 2008; Budiarsa et al., 2021). 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., 2012b; 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; J. K. Sheppard et al., 2010; Aragones et al., 2012b) 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 et al., 2011; Aragones et al., 2012b; 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 (Johnstone & Hudson, 1981; Marsh et al., 1982; de Iongh et al., 1995, 2007; Preen, 1995; Nakaoka & Aioi, 1999; Adulyanukosol et al., 2003, 2004; André & Lawler, 2003; Yamamuro & Chirapart, 2005; Sheppard et al., 2007; D'Souza et al., 2015; Tol et al., 2016; Mizuno et al., 2017; Apte et al., 2019; Budiarsa et al., 2021). In the Red Sea, the importance of these seagrasses for dugongs has been underscored through feeding signs (Egypt; Nasr et al., 2019; Shawky, 2019a) 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 (Preen, 1995; D'Souza et al., 2015; Tol et al., 2016; Nasr et al., 2019; Shawky, 2019b). 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.

3 Materials and Methods

3.1 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; Figure 3.1). With a tidal range of about 60 cm (Rasul 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., 2019b). Two key megaherbivores use these waters: green turtles *Chelonia mydas* and dugongs *D. dugon* (Preen, 1989; Baldwin, 2018; Miller, 2018). 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 (Preen, 1989; Baldwin, 2018), 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).

3.2 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 (Figure 3.1). 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

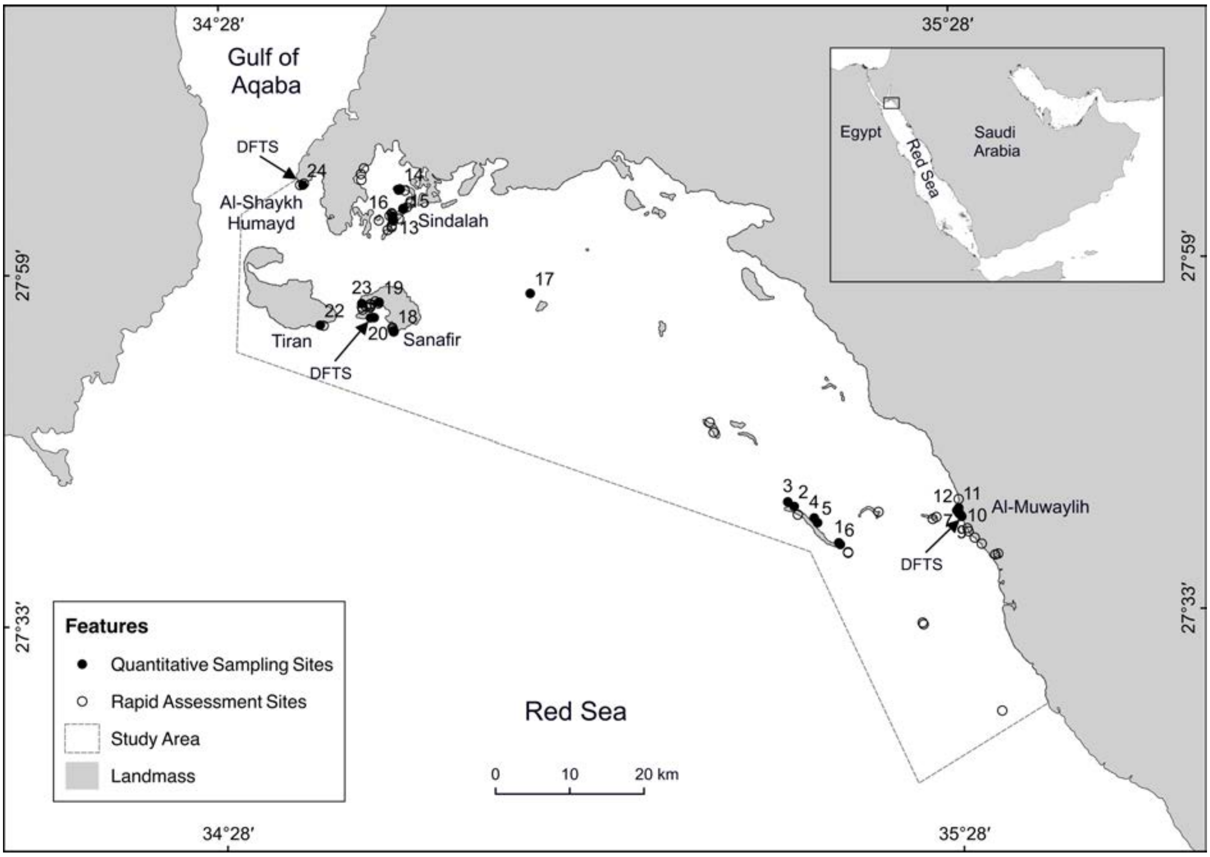

Figure 3.1. Map of the study area showing the sampling sites quantitatively surveyed for the dugong feeding signs and seagrass meadow characteristics, dugong feeding trail measurement sites, and the initial rapid survey sites. The inset map shows the location of the study area in the Saudi Arabian northern Red Sea (DFTS= dugong feeding trail assessment sites, number= quantitative sampling sites).

the 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., 2007b; Deutsch et al., 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 percentage cover was estimated relative to the total seagrass 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 .5 to several meters long, (ii) 6–30 cm wide, and (iii) 2–6 cm deep (Preen, 1992; Nakaoka et al., 2002; Adulyanukosol et al., 2003; D'Souza et al., 2015). 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 (Figure 3.1). 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.

3.3 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 percentage 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 hours and weighing with a microbalance. Biomass was expressed as dry weight of seagrass per surface area (g DW m^{-2}).

3.4 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).

3.5 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], percentagecover, 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 Generalized 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, percentagecover, 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).

4 **Results**

4.1 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 3.1). 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 3.1). 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%).

4.2 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 3.1). 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 with distance interval <5 km: Al-Muwaylih, Sindalah, Sanafir Island, Tiran Island and Ras Al-Shaykh Humayd (Figure 3.2). The spatial extent of the DFSs within the surveyed meadows was relatively small ranging .003 – .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 DFSs were in <10 m waters, but we also recorded distinctive dugong feeding trails at greater depths up to 17.5 m (Table 3.1).

In the sites with dugong feeding trails, the percentagetrail cover varied widely (range: ≤1 –35%) with 69% of all DFSs grazed lightly (trail cover: <3%). 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: .1 – .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 ± .96 cm. Within the assessed trails, dugongs removed an average (± SD) 82.8 ± 5.5% of total seagrass shoots with the removal percentageof *H. stipulacea* being the highest, followed by *H. ovalis* and *H. uninervis* (92.4%, 91.1%, and 67.3%, respectively).

Table 3.1. Characteristics 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*, DFTs= dugong feeding trails, B= boating, D= development, F= fishing, H= hotel, • = present).

Site	**Depth (m)**	**Exposure level**	**Seagrass species composition**									**DFTs**	**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

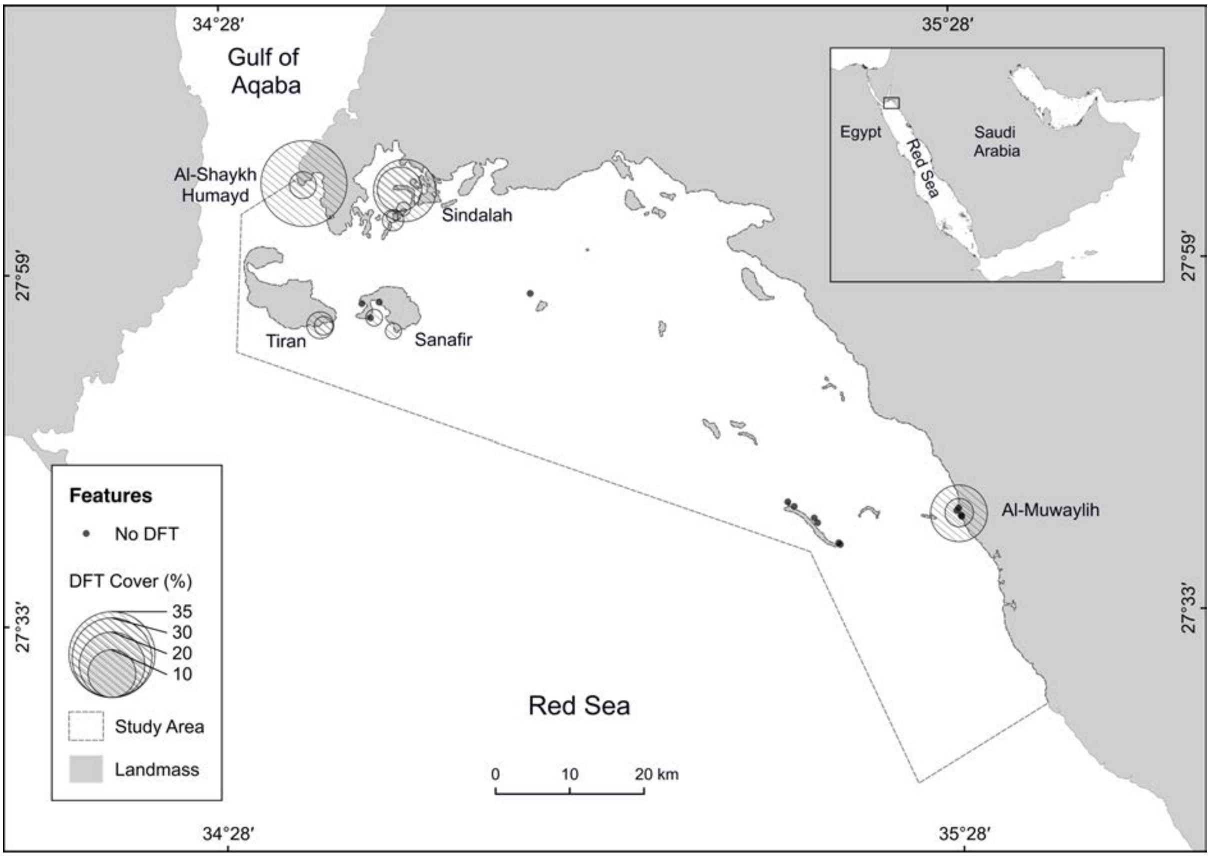

Figure 3.2. Dugong feeding trail cover (%) across the study area superimposed on the sampling sites. The inset map shows the location of the study area in the north-eastern Red Sea (DFT= dugong feeding trail).

Seagrass percentagecover 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 3.2; Figure 3.3). 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 percentagecover, number of seagrass species, and shoot density (Table 3.2). 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 percentagecover (Figure 3.4). 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 (Figure 3.5).

4.3 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 two DFSs were few kilometres from coastal development activities (Table 3.1).

Table 3.2. Summary statistics: (a) comparing species richness (i.e., total number of seagrass species), percentage 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, percentage 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, DFT= dugong feeding trail, * = significant effect).

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

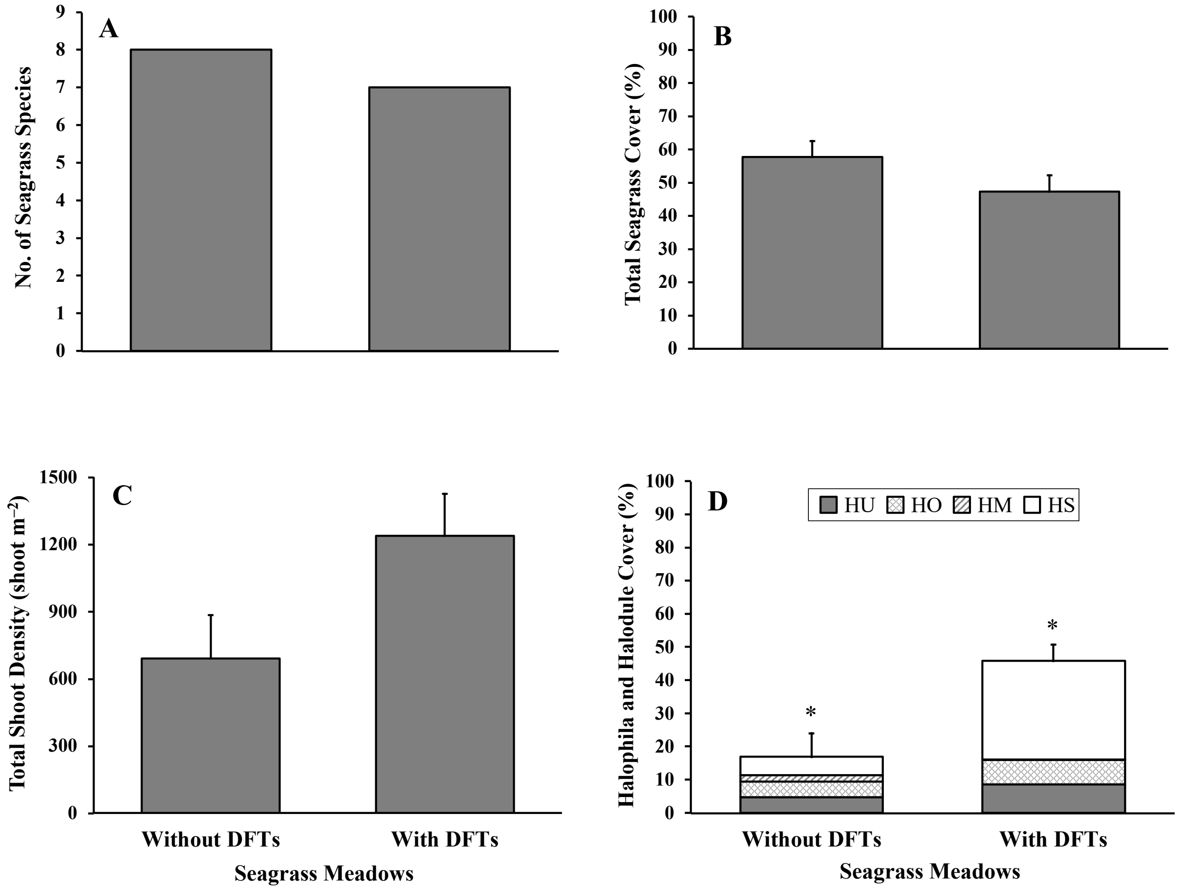

Figure 3.3. Comparison between sites with and without dugong feeding trails based on a suite of seagrass diversity and abundance covariates: (A) number of seagrass species, (B) total seagrass cover (%), (C) total shoot density (shoot m^{-2}), and (D) combined cover (%) of *Halophila* and *Halodule* spp. (HU= *Halodule uninervis*, HO= *Halophila ovalis*, HM= *H. minor*, HS= *H. stipulacea*, bar= standard error, DFTs= dugong feeding trails, * = significant effect).

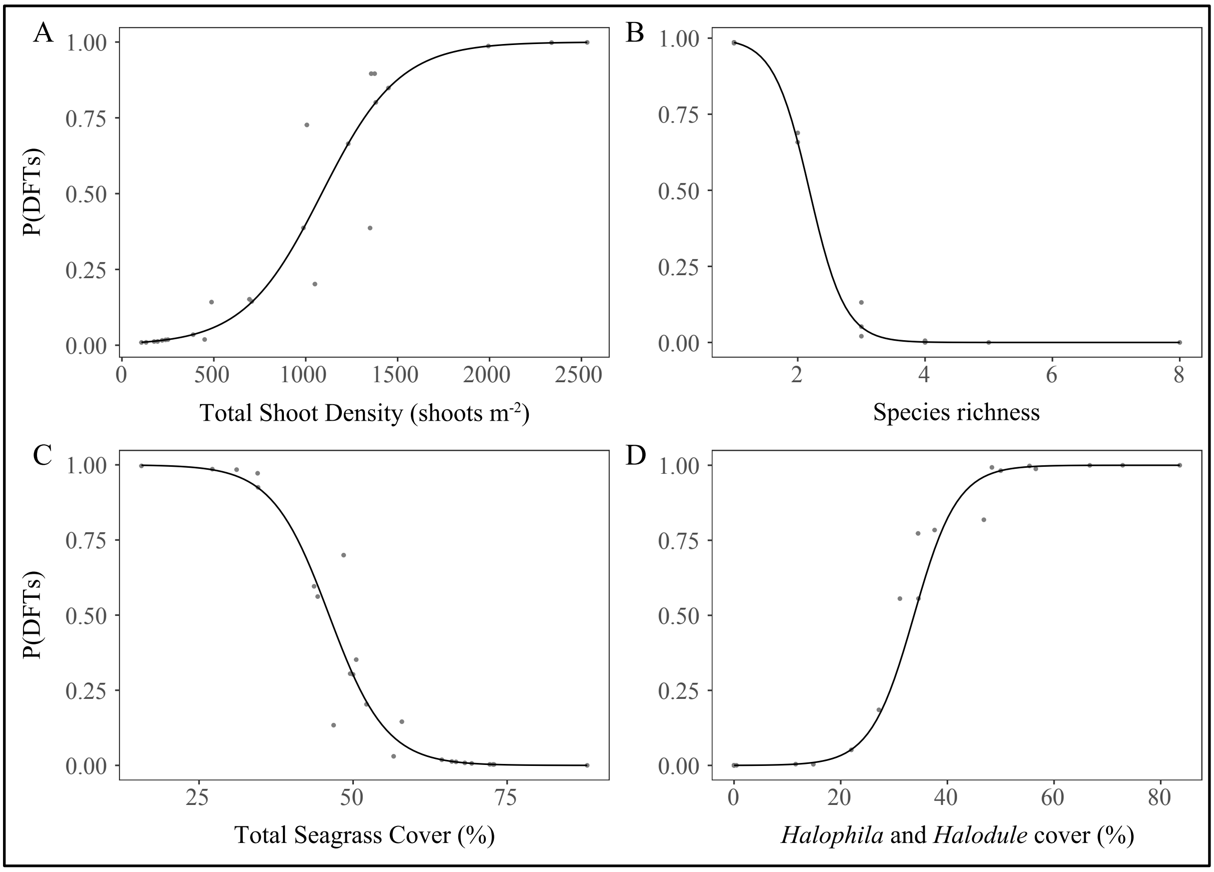

Figure 3.4. Generalised Linear Model (*GLM*) output demonstrating the influence of selected biological factors on the dugong feeding trail detection probability (P(DFTs)) across the study area: (A) total shoot density (shoot m^{-2}), (B) species richness (i.e., total number of seagrass species), (C) total seagrass percentage cover, and (D) combined percentage cover of *Halophila* and *Halodule* spp..

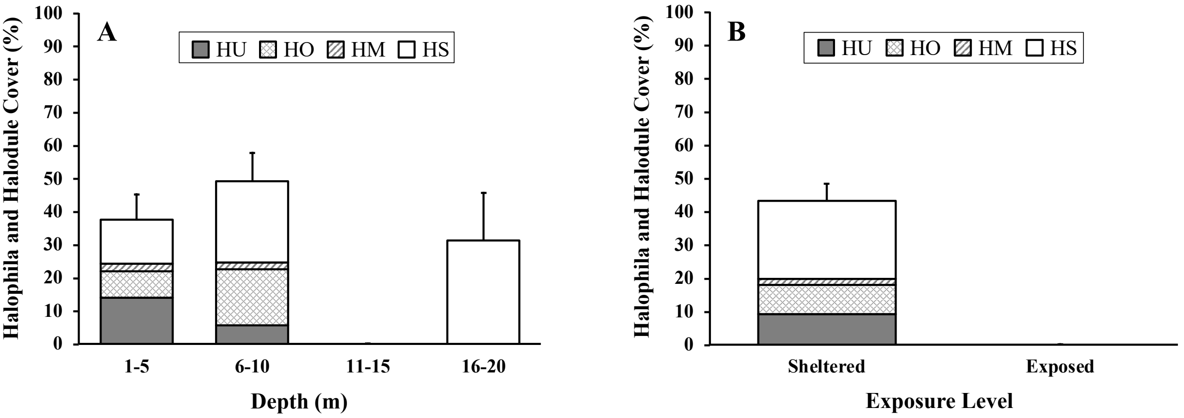

Figure 3.5. Comparison among the sampling sites pinpointing the influence of key environmental factors on the combined cover (%) of seagrasses belonging to the genera *Halophila* and *Halodule*: (A) water depth (m), and (B) exposure to waves and currents (HU= *Halodule uninervis*, HO= *Halophila ovalis*, HM= *H. minor*, HS= *H. stipulacea*, bar= standard error).

5 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.

5.1 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 (Preen, 1989; Preen et al., 2012; Al-Mansi, 2016; Baldwin, 2018; Nasr et al., 2019). 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 (Marsh et al., 1999, 2002, 2011; D'Souza et al., 2013; Derville et al., 2022). 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 potential Important Marine Mammal Areas (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, 2019b). Calves may leave trails ranging 9–14.3 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 trails, 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 (de Iongh et al., 1995; Preen, 1995; Aragones & Marsh, 2000; Aragones et al., 2012b). On average, this recovery could take between 3–7 months (e.g., Australia and Indonesia; de Iongh et al., 1995; Nakaoka & Aioi, 1999; Aragones & Marsh, 2000), but could be considerably faster (<1 month; e.g., India and Thailand; Nakaoka & Aioi, 1999; D'Souza et al., 2015) or slower (>1 year; e.g., Australia and Indonesia; de Iongh et al., 1995; Preen, 1995; Aragones & 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 (Lipkin, 1975; Marsh et al., 1982; Keith-Diagne et al., 2022). 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, 2019b). 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 (Sheppard et al., 2006; Burkholder et al., 2012). 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 et al., 2014; El Shaffai, 2016). 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 dugong foraging grounds 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 (Preen, 1995; Marsh et al., 2011; Burkholder et al., 2012; D'Souza et al., 2015; Nasr et al., 2019; Derville et al., 2022; Deutsch et al., 2022a).

5.2 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).

5.3 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; Nakanishi et al., 2008; Marsh et al., 2011; Keith-Diagne et al., 2022), 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.

5.4 Timely interventions needed to conserve the dugong population of the 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.

6 Acknowledgments

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4

Long-term persistence of large dugong groups in a conservation hotspot around Hawar Island, Kingdom of Bahrain

1 Abstract[1]

Predictable aggregations of large marine mammals are valuable conservation targets, but can also expose aggregated populations to site-level threats. The globally vulnerable *Dugong dugon* has wide distribution but is found in large numbers mainly in Australia and the Arabian Gulf. While Australian dugong populations are well-studied, much less is known of the dugongs in the Arabian Gulf. The spatial and temporal persistence of dugongs around Bahrain, with a focus on large dugong groups (>50 dugongs), was determined using an occupancy modelling framework supported with historical records, structured interviews, citizen science network reports, and small-scale boat and unmanned aerial vehicle surveys. Historical records and current distributional studies confirmed that large dugong groups have been reliably sighted around Hawar Island (Bahrain) since at least 1986, forming large, clumped groups that persist almost year-round. The largest recorded so far in the world, these fluid groups (maximum: ~700 dugongs) account for ~60% of the dugongs found in Bahrain and ~12% of all dugongs in the Arabian Gulf. The delineated occupancy core area of large dugong groups (~145 km^2) straddles the Bahrain-Qatar border, reflecting the transboundary nature of these groups. Careful management of human-induced stressors (in particular fishing, boating, and coastal development) combined with regular monitoring of Hawar Island's large dugong groups and their seagrass habitat is critical to safeguard this globally important population. The effectiveness of any conservation management is predicated on strengthening cooperation among all range states in the Arabian Gulf. A key recommendation of this study is to establish a regional network of marine protected areas encompassing core aggregation sites for dugongs particularly: Hawar Islands in Bahrain, north-western waters of Qatar, Marawah Island in the United Arab Emirates in addition to the shallow waters between Saudi Arabia, Qatar, and United Arab Emirates.

Keywords: Arabian Gulf, conservation, fishing, GIS, grouping behaviour, historical data, marine mammals, memory recalls, seagrass

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[1] See the original publication in Khamis et al. (2023), Annex-2

2 Introduction

The tendency of many large marine mammals to gather in dense aggregations at predictable locations makes these sites hotspots for conservation (Nowacek et al., 2011; Brakes & Dall, 2016; di Sciara et al., 2016). At the same time, their high abundances and clumped distribution make these populations particularly vulnerable to human-induced stresses at their aggregation sites (Anderson, 1981; Laist & Reynolds III, 2005; Schipper et al., 2008; Reeves, 2009; Reynolds III & Marshall, 2012; Magera et al., 2013; Brakes & Dall, 2016). The globally vulnerable dugong *Dugong dugon* (Marsh & Sobtzick, 2019) shows highly variable grouping behaviour (Preen, 1992; Hodgson, 2004; Marshall et al., 2018). Described as facultative herders (Preen, 1992), dugongs are usually found as solitary individuals, mother-calf pairs or small groups (<10 dugongs), but they occasionally aggregate in large groups of several hundreds (Anderson, 1981; Preen, 1992; Hodgson, 2004; Marsh et al., 2011; Marshall et al., 2018; Deutsch et al., 2022b; O'Shea et al., 2022).

Dugongs have experienced considerable reductions across their Indo-Pacific distributional range with reported regional extinctions dating back to 18th century (Marsh et al., 2011; Aragones et al., 2012b; Marsh & Sobtzick, 2019). Yet data on their population status and distribution are still scarce in many regions, even where they are known to be abundant (Marsh et al., 1999, 2002; Marsh & Sobtzick, 2019). Across their range, dugongs are threatened by incidental net entanglement, direct hunting, alteration and loss of their primary seagrass habitats, boat strikes, pollution, and climate change, pushing several geographically isolated populations to the edge of extinction (Marsh et al., 2002; Aragones et al., 2012b; Reynolds III & Marshall, 2012; Marsh & Sobtzick, 2019; Marsh et al., 2022; Ponnampalam et al., 2022). For instance, the dugong population in China has recently been declared functionally extinct. In addition, dugongs in Japan and East Africa are critically endangered while in New Caledonia they are considered endangered (Marsh & Sobtzick, 2019; International Union for Conservation of Nature, 2022; Lin et al., 2022a, 2022b).

The slow reproduction rate and long generation times impede rapid recoveries of depleted dugong populations (Anderson, 1981; Marsh et al., 1999, 2002; Marsh & Kwan, 2008; Marsh, O'Shea & Reynolds III, 2011). This makes areas where dugongs aggregate in large numbers of particular significance. On the one hand, they are ideal areas to conserve the population. On the other, anthropogenic stressors at these key sites can disproportionally affect a large number of breeding adults as well as calves. Therefore, identifying these aggregation sites, and determining how dugongs use them over space, and time are important conservation priorities (Hodgson, 2004; Preen et al., 2012). However, this is often not straightforward. Dugongs are characteristically wide-ranging and elusive animals (Marsh et al., 2002; Sheppard et al., 2006; Marsh et al., 2011), and obtaining reliable population estimates across extensive spatio-temporal scales can be a considerable challenge for conservation planners.

Despite its vast range, spanning around 44 countries and territories across the warm tropical and subtropical Indo-Pacific waters (Marsh & Sobtzick, 2019), large groups of >100 dugongs have been reported in recent times predominantly from two broad regions, Australia (e.g., Moreton Bay, Cape York, and Shark Bay) and the Arabian Gulf (e.g., Bahrain, Qatar, and United Arab Emirates; Preen, 1992, 2004; Marsh et al., 2002; Lanyon, 2003; Hodgson, 2004; Chilvers et al., 2005). Slightly smaller groups of between 50–100 dugongs are more common and have been regularly sighted in Australia (e.g., Moreton Bay, Cape York, Shark Bay, Hervey Bay-Tin Can Bay, Cape Flattery-Princess Charlotte Bay, and Shoalwater Bay) and the Arabian Gulf (e.g., Bahrain, Qatar, and United Arab Emirates; Preen, 1992, 2004; Preen & Marsh, 1995; Marsh et al., 2002; Hodgson, 2004; Sobtzick et al., 2017; O’Shea et al., 2022), but have also been encountered occasionally across a broader range including New Caledonia (Cleguer, 2015), Thailand (Hines et al., 2005), and Mozambique (Findlay et al., 2011). Across this range, however, small groups of 1–2 dugongs are still frequently encountered (O’Shea et al., 2022).

The Arabian Gulf hosts one of the world’s largest dugong populations (~5,800 dugongs; Preen, 2004), second only to Australia (~155,000 dugongs; Clark et al., 2021). The Arabian Gulf’s population is considered the largest in the western and northern regions of the dugong’s distributional range (Marsh et al., 2002; Preen, 2004; Hodgson, 2011; Preen et al., 2012). The population is spread over a wide area and the key to maintaining and conserving the species is identifying hotspots of dugong use, especially those occupied by large groups (Preen, 2004; Preen et al., 2012). To date, however, the management of large dugong groups (LDGs; >50 dugongs) and their primary habitats in the Arabian Gulf has been limited by sparse information. In 1986, Preen (1989, 2004) encountered exceptionally large groups totalling ~670 dugongs in the Arabian Gulf, south east of Bahrain, repeatedly cited as the largest ever reported in the world (Preen, 2004; Hodgson, 2011; Marsh et al., 2011; Preen et al., 2012; O’Shea et al., 2022). After this first record from over 35 years ago, reliable reports of LDGs in the Arabian Gulf are limited to a few sightings from Bahrain and United Arab Emirates (Preen, 2004; Hodgson, 2011; Preen et al., 2012; Environment Agency-Abu Dhabi, 2014). An exception was Marshall et al. (2018) who reported five LDGs in the north-western waters of Qatar near the Bahrain-Qatar border on surveys conducted in the winter of 2015. Given the current wide knowledge gaps, it is difficult to know where LDGs are reliably found in the Arabian Gulf, how persistent they are in these areas, and whether they form seasonally or use the area throughout the year. This baseline information is essential for effective spatial management of aggregating marine mammals such as dugongs.

In this study, current and past distribution of LDGs was evaluated around Bahrain and their persistence since their first encounter in 1986 was determined. For this, a set of complementary methods was used including historical records, structured interviews, citizen science network reports as well as small-scale boat and unmanned aerial vehicle surveys. Consequently, current critical large dugong group areas around Bahrain were identified and a proactive conservation approach has been discussed with a focus on strengthening the role and utility of regional cooperation in managing this globally important dugong population and associated seagrass habitat.

3 Materials and Methods

3.1 Study area

The study covered the territorial waters of the Kingdom of Bahrain (25º 32' – 27º 9' N; 50º 20' – 51º 7' E) that span over ~7,500 km^2 (Al-Zayani et al., 2009). Bahrain is an archipelago comprising more than 36 islands and islets occupying a total landmass area of 778 km^2 (General Directorate of Statistics, 2017). The archipelago is situated in the Gulf of Bahrain, an inlet of the central southern coast of the Arabian Gulf whose southern part forms a shallow bay called Gulf of Salwa (Figure 4.1). Gulf of Bahrain is recognized as an Important Marine Mammal Area, named ‘Gulf of Salwa IMMA’ in recognition of its international importance for marine mammals, particularly dugongs (IUCN-Marine Mammal Protected Areas Task Force, 2021). An aerial survey carried out in 2006 indicated that Bahrain has a large population of 1,164 (95% CI = 530, 1798) dugongs with an average group size of 1.5 (± .22 SE) dugongs (Hodgson, 2009; Preen et al., 2012). The shallow waters surrounding Hawar Island (hereinafter around Hawar) in the south east of Bahrain have been consistently identified as one of the most important areas for the Arabian Gulf’s dugong population (Preen, 2004; Hodgson, 2009; Preen et al., 2012). The area has the highest dugong density in Bahrain (.59 dugong km^{-2}; Hodgson, 2009) and most LDG sightings in the Arabian Gulf have been reported from these shallows.

These include the ~670 dugongs encountered by Preen (2004) on 5 March 1986, that was in fact composed of two nearby groups of ~570 and ~100 dugongs sighted around Fasht Mu’tarid, a small reef complex situated to the north west of Hawar (Preen, 1989; Marsh et al., 2002). In addition, Bell (2001) sighted groups of ~55, ~150, and ~250 dugongs in 2000 and Preen et al. (2012) reported ~300 dugongs in 2005 around Hawar. Hodgson (2009) also encountered in 2006 a LDG comprising >50 dugongs off Fasht Jarim (~80 km from Hawar). In 2015, Marshall et al. (2018) identified five LDGs ranging ~170–510 dugongs in Qatar to the east of the Bahrain-Qatar border.

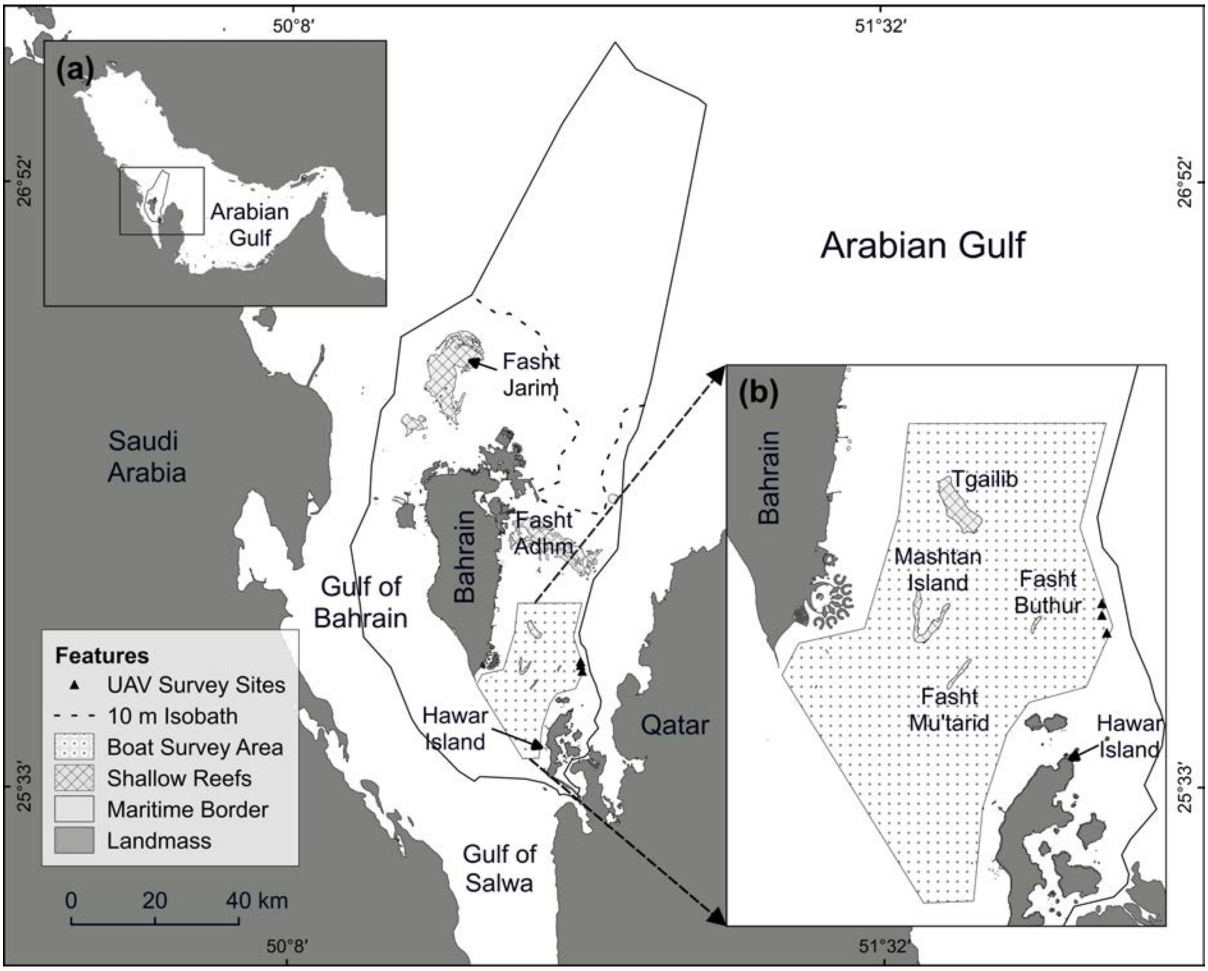

Figure 4.1. Map of the study area showing: (a) the location of Bahrain in the Gulf of Bahrain and the larger context of the Arabian Gulf, and (b) major islands and shallow reef complexes (fashts), boat-based survey area, and large dugong groups (>50 dugongs) surveyed by unmanned aerial vehicles (UAVs). The dashed line represents the 10 m isobath marking the broad-scale distribution of dugongs in the Arabian Gulf delineated by Preen (2004).

3.2 Compilation of past and present data on large dugong groups

Since the definition of a 'dugong herd' is problematic (Hodgson, 2004), we prefer to use the terms 'marine mammal group' as suggested by Acevedo-Gutierrez (2009) and 'scattered dugong group' as defined by Preen (1989) to describe the dugong groups around Bahrain. We consider a dugong group comprising >50 individuals with inter-dugong distance not exceeding 20 body lengths (mean dugong body length: ~2.5 m; Hodgson, 2004) to be a 'large dugong group (LDG)'. All LDG sightings obtained by various methods were categorized according to season, following the classification of Vousden (1995) of the temporal patterns of the marine environment around Bahrain: winter (December-March), spring transition period (April), summer (May-October), and autumn transition period (November). The sightings were then plotted with Geographical Information System (GIS) maps using the software Quantum Geographic Information System (QGIS; Version 3.18; QGIS Association).

The persistence of LDGs around Bahrain was assessed by combining historical records, structured interview surveys and citizen science network reports together with opportunistic small-scale boat and unmanned aerial vehicle surveys. The field surveys and structured interviews were undertaken in accordance with the environmental permit (RH/24/84/2019/AA) and following the guidelines of the Research Ethics Committee of the University of Barcelona, that also approved the interview schedule. Identities of interviewed people were always kept anonymous.

To identify potential large dugong group core areas, LDG sightings recorded by all standardized aerial surveys undertaken thus far in Bahrain were inventoried: (i) March 1986 (Preen, 1989; Preen, 2004), (ii) October 1986 (Preen, 1989; Preen, 2004), (iii) October 2000 (Bell, 2001), and (iv) October 2006 (Hodgson, 2009). These aerial surveys covered nearly all Bahraini waters up to the 10 m isobath marking the broad-scale distribution of dugongs in the Arabian Gulf, delineated by Preen (2004), with the exception of the 2000 survey which focused only on the waters around Hawar (Figure 4.1).

Due to the paucity of historical records of dugongs, the persistence of the dugong population around Bahrain was assessed, with a focus on LDGs, through memory recalls. During 2020–2021, questionnaire-based structured interviews were conducted with local fishermen, tour boat operators, environmentalists, and researchers (*N*= 97). The informants were asked to specify important dugong areas and identify seasonal variations in dugong abundance. To obtain spatial data on dugong occurrence, knowledgeable key respondents (*n*=

41) were presented with a map of the region and requested to mark polygons representing the estimated spatial extent of all dugong sightings that they could remember encountering across all territorial waters of Bahrain. The informants were then asked to rank each polygon (*N*= 149) in terms of: (i) time interval (1–3, 4–15, 16–30, and >30 years), and (ii) size (1–10, 11–50, 51–100, 101–300, 301–500, and >500 dugongs) of the dugong group encountered. Sixteen key informants were chosen as members of a citizen science network and encouraged to report on all dugong sightings that they incidentally encountered across all Bahraini waters. Between October 2019 and February 2022, members of the citizen science network reported the location, timing, and group size (as the best estimated count of dugongs seen on water surface) of each dugong sighting.

A total of 61 LDG boat-based surveys were conducted between December 2019 and February 2022 around Hawar where LDGs had been reported by aerial surveys, structured interviews, and citizen science network (Figure 4.1). During these trips, the boat travelled at 15–20 knots (27.8–37.0 km hr^{-1}) while two observers scanned the surface, unaided or with 10 × 42 binoculars. While this speed was not ideal for observing individual or paired dugongs, it allowed a large area to be covered in search of LDGs, which were the primary focus of these surveys. Although sightings of scattered dugongs were recorded whenever encountered, these records were not included in the analysis since spotting solitary or paired dugongs from a low platform in murky waters is challenging even at slower speeds.

Upon encountering a dugong group, the search was suspended and the boat slowly manoeuvred towards the animals, maintaining ~200 m from the group to minimize disturbance. The estimated geographical coordinates were then obtained with a Global Positioning System (GPS) and the dugongs were observed more closely with binoculars. Since evaluating dugong abundance through boat-based surveys is challenging due to the elusive nature of dugongs and limited water visibility in their habitats (Hodgson, 2011; Aragones et al., 2012a; Keith-Diagne et al., 2022), three independent observers estimated the size of dugong groups encountered during boat surveys. First, the observers estimated the maximum number of dugongs seen on the surface using binoculars. Considering that the number of dugongs counted from a boat fluctuates over short time intervals due to the rapid changes in the predominant group behaviour (e.g., grazing or travelling), each observer continued to scan the dugong group for at least five minutes. After that, each observer estimated the group size, which was averaged across observers.

Three LDGs encountered on 14, 15, and 16 February 2021 were surveyed with two unmanned aerial vehicles (UAVs; DJI Mavic 2 Pro and DJI Inspire 2) equipped with high resolution cameras mounted with wide angle lenses and anti-glare polarizer filters. The UAVs were controlled from a speedboat and flown over the LDGs at a maximum height of 120 m. Still frames were then extracted from the captured UAVs' videos and carefully examined by three observers who obtained independent counts to estimate the average group size and calf proportions. The observers employed image processing software (Adobe Photoshop) to mark (with a coloured dot) and count each shape with recognizable dugong features. The dugong group size and calf count and proportion of the three surveyed LDGs were then averaged between observers.

Dugong group sizes were cross verified by comparing overlapping UAV and boat-based dugong surveys on 14, 15, and 16 February 2021. This enabled the estimation of the number of sub-surface dugongs missed by boat-based observers at the time of counting. During all UAV flights, three observers in a nearby speedboat independently estimated the maximum number of dugongs seen near the water surface using binoculars as described earlier. On the 15 February 2021 survey, also, the percentage of individuals located within two dugong body lengths of nearest neighbours was calculated. To identify habitats in key areas occupied by LDGs, six groups had been observed until they moved away from their feeding spots (as indicated by their repetitive diving and the sediment plume generated by feeding; Hodgson, 2004; Marshall et al., 2018; Keith-Diagne et al., 2022) and then the benthos was visually examined by snorkelling or scuba.

3.3 Current distribution of large dugong groups

The main distributional range of LDGs reported between 2019 to 2022 by the citizen science network and boat-based surveys was determined by computing kernel density estimate heatmaps using QGIS. The resultant heatmaps were then converted to percentage volume contours (PVCs) following the guidelines of MacLeod (2014) to identify where large groups were likely to occur 50% (50% PVC) and 95% (95% PVC) of the time. Shallow reef complexes (locally known as 'fashts') marked on the habitat map produced by Al-Zayani et al. (2009) and islands were considered natural barriers and cropped from the resultant PVCs.

3.4 Spatio-temporal trends of large dugong groups and dugong population

The persistence of LDGs over space and time around Bahrain was first determined visually by examining the GIS maps and observing any distinctive patterns in the spatial or temporal trends using the different methods included in the survey. These trends in persistence of LDGs were then compared to all dugongs around Bahrain to highlight any potential role of LDGs in maintaining the dugong population. To this end, a dynamic occupancy modelling framework (see Royle & Kéry, 2007) was used to estimate dugong occupancy (i.e., percentage of sites occupied), turnover (i.e., persistence), and colonization of all dugongs around Bahrain over time, based on the memory recall data reported by observers in the structured interviews, for the time period from >30 years to the time of data collection (i.e., 2021). It has to be noted that detectable changes in dugong occupancy, persistence and/or colonization do not necessary indicate corresponding changes (i.e., increase or decrease) in population size. A similar approach was also used by D'Souza et al. (2013) to estimate dugong occupancy and changes in distribution in India's Andaman and Nicobar islands. Occupancy modelling allows for the probabilistic estimation of parameters related to species occurrence at specific sites conditional on the probability that all animals of the species may not be perfectly detected by observers. These surveys, conducted in a systematic spatial sampling framework, can prove helpful in estimating past distribution dynamics by addressing issues of imperfect detection inherent to available historical records or in the case of this study, memory recalls. In this model, the probability of detection was estimated through spatial replicates represented by multiple informants in the same grid, who were providing memory recall information. Due to the long intervals between the aerial surveys and the absence of any standardized dugong survey over the last 15 years, only data obtained through interviews (see above) were included in this analysis. First the accuracy of the polygons marked by informants was verified by classifying them based on the time of sighting and dugong group size as described above. Then, polygons were overlaid on the historical dugong encounters recorded by corresponding aerial surveys undertaken in 1986 (Preen, 1989; Preen, 2004), 2000 (Bell, 2001), and 2006 (Hodgson, 2009) before the overlap percentage was calculated.

The territorial waters of Bahrain, confined within the Gulf of Bahrain, were partitioned into 2 × 2 nm^2 (~ 3.70 × 3.70 km^2) grid cells (N= 490). From the 490 grids sampled, a re-configured dataset of 151 grids, with 3–4 spatial replicates each based on proximate grids, was used across the four time intervals of memory recalls reported by interviewed informants. The northernmost waters of Bahrain were not included in the modelling as they are further offshore than the 10 m isobath cut-off, as detailed above. The data on dugong occurrence reported by memory recalls were assigned in a 1/0 format to the 151 grids. Reports of confirmed dugong sightings were assigned '1' and reports of not having seen dugongs were assigned '0' from all interviewees for that particular grid. These data represented detections and non-detections, and not true presence or absence of dugongs, as the reported sightings were conditional on: (i) the interviewee's probability of encountering a dugong and correctly reporting it, (ii) the interviewee's ability to accurately recall past sightings, and (iii) internal consistency in reporting sightings for the four time-periods for which information was requested. Clearly, some of these detections are likely to be imperfect. It is also reasonable to expect that recent detections would have a lower uncertainty than past detections. All these caveats and assumptions lent themselves to an occupancy modelling approach. The model was run in the R software (R Core Team, 2020), using the packages 'rjags' and 'jagsUI', through the Bayesian statistical programming module JAGS (Plummer, 2014). For each model, 10,000 MCMC iterations were run in three chains and a burn-in time of 5,000 interactions was used. All model parameter estimates were checked for convergence and their Bayesian credible intervals (95%) were reported.

3.5 Potential transboundary movements of large dugong groups

To highlight likely transboundary movements of LDGs in the Arabian Gulf, LDG sightings, recorded during this study, which are <2 km from the maritime border of Bahrain were examined. In addition, the interval distances between the LDGs in Bahrain and those recorded earlier in Qatar (Marshall et al., 2018) and United Arab Emirates (Preen, 1989; Preen, 2004) were estimated and compared with the dugong movement ranges defined by earlier studies (e.g., Sheppard et al., 2006; Deutsch et al., 2022b).

4 Results

4.1 Current distribution of large dugong groups

Based on data from boat-based surveys and citizen science network between 2019–2022, a number of large dugong groups (LDGs) were identified around Hawar (Figure 4.2a). Kernel density estimate heatmaps indicated that LDGs were distributed over 490 km^2 of the shallow waters surrounding Hawar (i.e., overall distributional range). These shallows encompassed a large dugong group occupancy area (LOA; 144.6 km^2) that is composed of three percentage volume contours (PVCs) indicating where LDGs spend 50% and 95% of their time. Two 50% PVCs were located to the west and north of Hawar, one around Fasht Mu'tarid of 7.9 km^2 and another off Fasht Buthur of 38.3 km^2 (~1% of the latter straddles the Bahrain-Qatar border). The longitudinal axis of the 50% PVCs around Fasht Mu'tarid measured 6.8 km and around Fasht Buthur measured 8.1 km. The linear nearest interval distance between the edges of the two 50% PVCs was 5.2 km. The 95% PVC (i.e., home range) occupied 98.4 km^2 off the western and northern coasts of Hawar with 5.4% of its total area extended easterly beyond the Bahrain-Qatar border. In addition, the distribution of the LDGs shows distinct spatial separation between winter and summer feeding grounds as described below (Figure 4.2b).

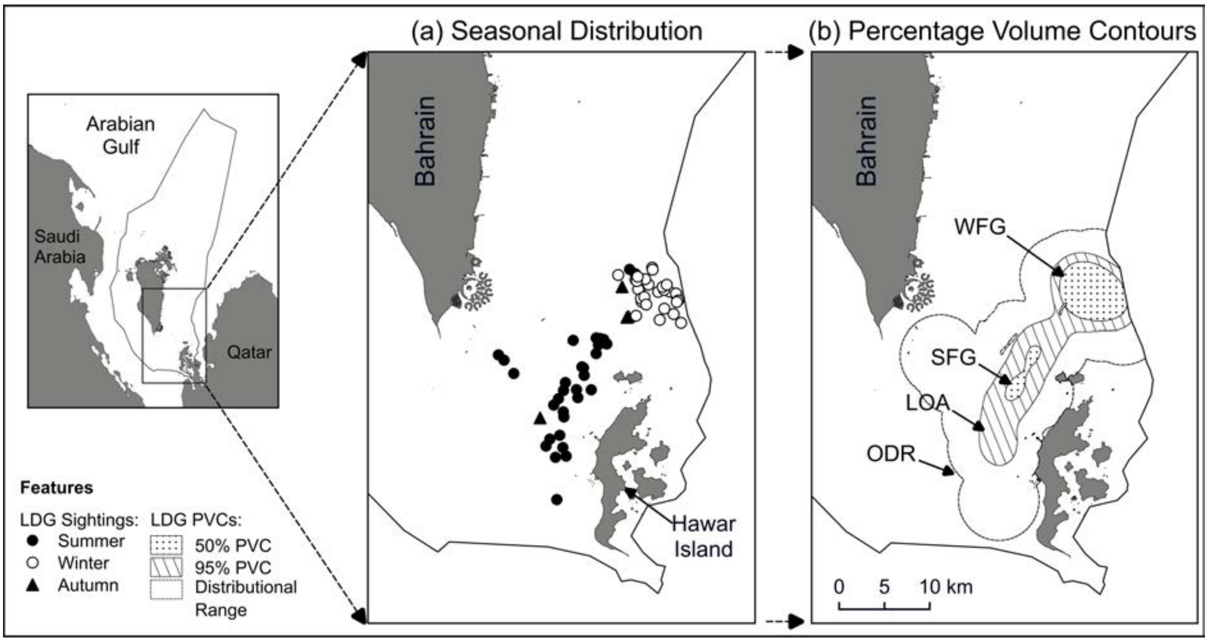

Figure 4.2. Spatio-temporal patterns of large dugong groups (LDGs; >50 dugongs) recorded during 2019–2022 through boat-based surveys and citizen science network: (a) large dugong group sightings classified by season, and (b) spatial extent of the overall distributional range as well as 50 and 95 percentage volume contours (50% and 95% PVC, respectively) of large dugong groups (LOA= large dugong group occupancy area, ODR= overall distributional range, SFG= summer feeding ground, WFG= winter feeding ground).

4.2 Temporal and spatial trends of large dugong groups

Structured interviews showed a clear persistence of LDGs around Bahrain over the last three decades. Thirty-five percent of all respondents reported that they had encountered LDGs during their lifetime although the size of the largest groups they sighted varied considerably (size category: 51–100 [32%], 101–300 dugongs [27%], 301–500 dugongs [19%], and >500 dugongs [22%]; maximum: 1000 dugongs). The informants outlined a total of 25 polygons representing large dugong group sightings; these spanned all time intervals apart from the >30 years. The persistence of these groups in the shallow waters around Hawar was also confirmed by citizen science network reports and boat-based surveys, recording a total of 149 dugong groups, of which 64 (43%) were LDGs. The historical aerial survey records further confirmed that LDGs persisted over the period 1986–2000 within the same core areas they currently occupy (Figure 4.3). In addition to Hawar, both structured interviews and aerial survey records reported LDG sightings (*n*= 3) off Fasht Jarim.

Of the interviewed respondents that recorded LDGs, 27% encountered large groups in both summer and winter while 46% and 27% sighted them either in summer or winter, respectively (Figure 4.4). The citizen science network and boat surveys provided further insight into the seasonal patterns of LDGs. The large groups around Hawar were persistently recorded in each of the 12 calendar months with the exception of April and May, although logistic constraints prevented adequate sampling of the region in April. Additionally, distinctive seasonal patterns were detected in the distribution of these groups around Hawar. In warm months (June-October), LDGs were mostly found in the 50% PVC around Fasht Mu’tarid where they continued to be sighted until October or November. Later, most large dugong group sightings were encountered in the 50% PVC around Fasht Buthur where they persisted throughout the cold-winter months (December-March; Figure 4.2b). Occasionally, however, LDGs moved to the winter ground before the end of summer leading to a slight overlap between the two areas. On all boat surveys, LDGs were sighted either at summer (i.e., around Fasht Mu’tarid) or winter (i.e., around Fasht Buthur) feeding grounds except for two occasions in September when two LDGs were observed concurrently at both feeding grounds.

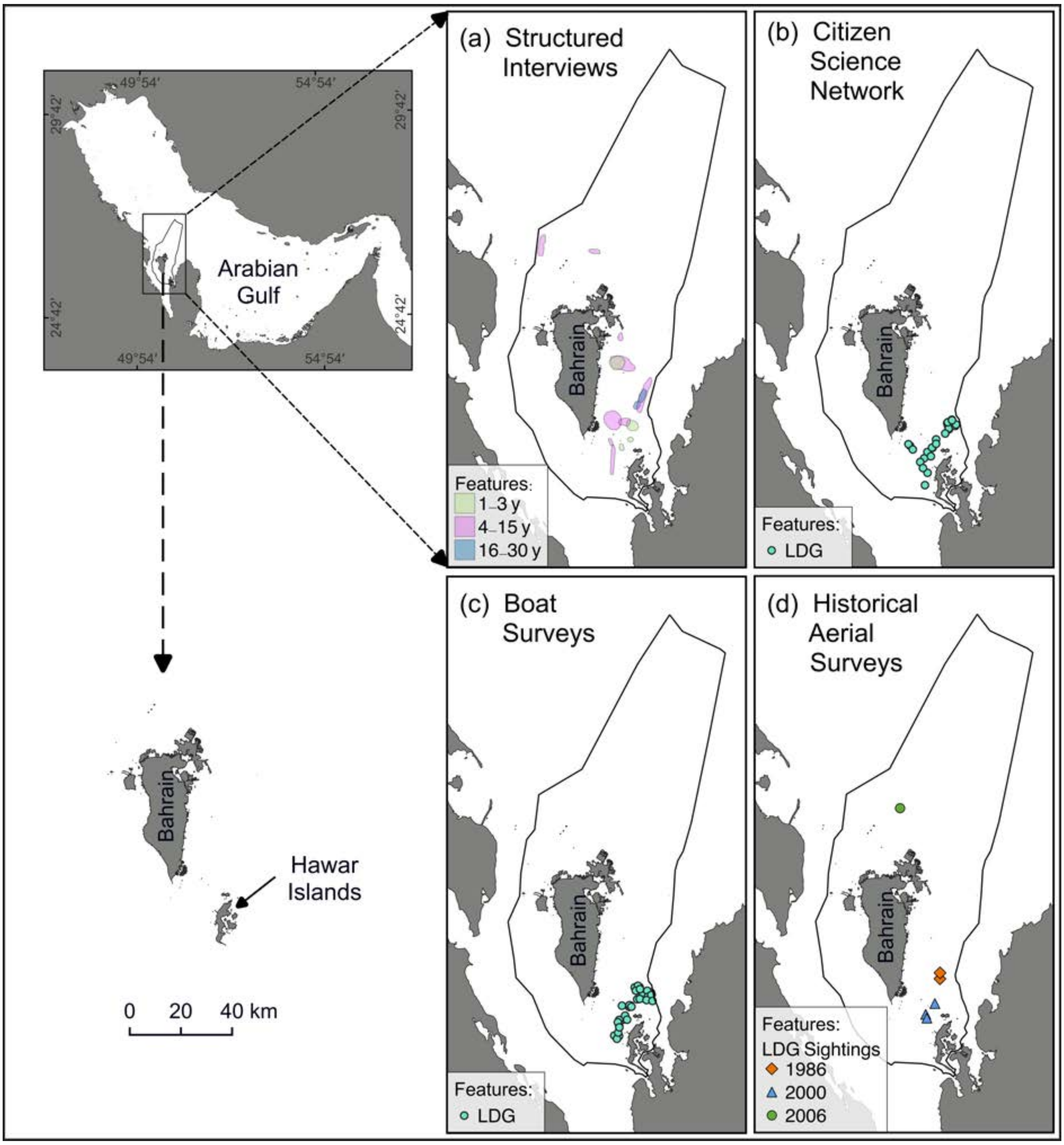

Figure 4.3. Large dugong group (>50 dugongs) sightings recorded by multiple methods: (a) memory recalls obtained through structured interviews (classified according to time intervals: 1–3, 4–15, and 16–30 year), (b) 2019–2022 citizen science network reports, (c) 2019–2022 boat-based surveys, and (d) historical records from 1986 (Preen, 1989; Preen, 2004), 2000 (Bell, 2001), and 2006 (Hodgson, 2009) aerial surveys (LDG= large dugong group, y= year).

Figure 4.4. An aerial photo of a large dugong group (>50 dugongs) encountered in summer (4 October 2021) to the north of Hawar Island, Bahrain indicating the difficulty associated with accurately estimating the group size of large dugong groups (Photo courtesy of Janez Lotric, Diplomatic Protocol Communications).

4.3 Dugong baseline occupancy and changes in spatial distribution

Structured interviews showed that dugongs were unevenly distributed across the waters of Bahrain with dugong sightings (marked as polygons on maps by respondents) highly clustered around Hawar. Two other dugong core areas were recognized around Fasht Jarim and off the south-western coast. Additionally, the respondents reported a number of dugong sightings beyond the 10 m isobath across all time intervals apart from >30 years. Historical dugong sighting records (N= 89) reported from the 1986 and 2006 standardized aerial surveys (N= 3) confirmed these spatial trends with 59% of all encounters around Hawar; Fasht Jarim and the south-western coast accounted for 13% and 9% of encounters, respectively. Confirming the general agreement between the two methods, the memory recall polygons of the corresponding time intervals overlapped with the 1986, 2000, and 2006 aerial survey sightings by 46%, 75%, and 73% respectively (Figure 4.5).

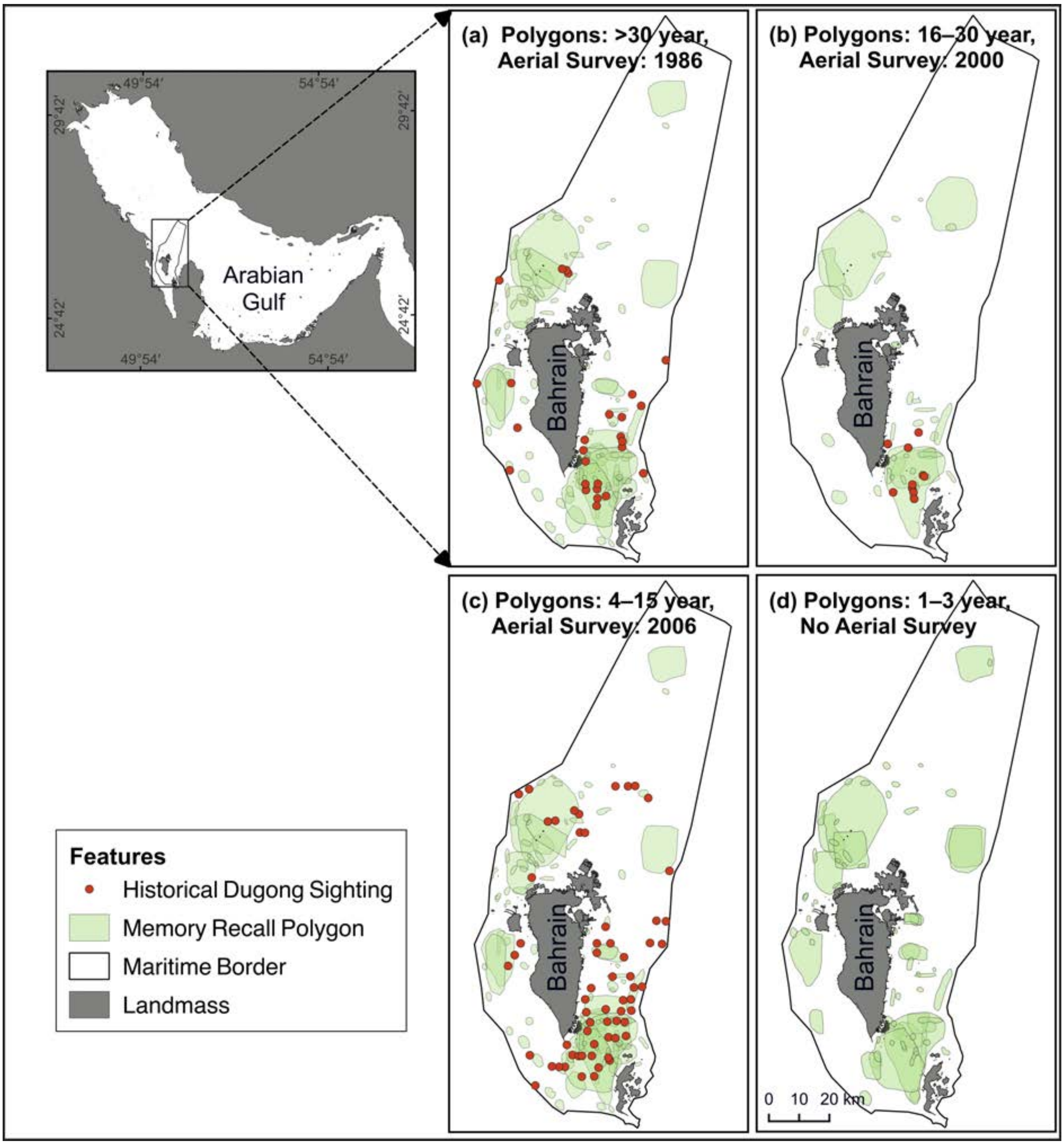

Figure 4.5. Historical dugong occurrence records presented as memory recall polygons (delineated by informants interviewed in 2020–2021), classified according to time intervals: (a) >30 year, (b) 16–30 year, (c) 4–15 year, and (d) 1–3 year. The maps are overlaid with dugong sightings recorded during the 1986 (Preen, 1989; Preen, 2004), 2000 (Bell, 2001), and 2006 (Hodgson, 2009) aerial surveys, respectively. There was no aerial survey conducted during the 1–3 year interval. Unlike the 1986 and 2006 surveys, the 2000 aerial survey covered only the south east of Bahrain.

The occupancy model indicated baseline occupancy (>30 years) of the dugong population around Bahrain at 32% of the total 151 grid cells. In addition, high persistence probability (~95%) of dugongs was detected across the four time intervals. Colonization probability increased over time, with 35% of unoccupied sites recently occupied by dugongs. This increased overall dugong occupancy in 2021 to 55% (i.e., by nearly 23% from the baseline). Detection probability was estimated at 63% based on the memory recalls of interviewed respondents. Table 4.1 presents the parameter estimates and Bayesian credible intervals from the final selected model.

4.4 Additional observations on large dugong group dynamics and habitat

Of all boat surveys with successful LDG sightings (*n*= 54), a single group was most frequently encountered during the survey (83%). On occasions, however, two (15%) and rarely three (2%) groups were observed. When two or more groups were found, the inter-group distance ranged between .2 – 2 km, with a single instance of 17.2 km between sightings. As confirmed by in-water observations, LDGs were found in extensive seagrass areas. These include the three groups surveyed by UAVs on 14, 15, and 16 February 2021 that were located at 3–4.5 m deep seagrass meadows in the winter feeding ground.

Table 4.1. Estimates of occupancy model parameters, with standard deviation and Bayesian credible intervals (95% of posterior distribution of probabilities) from one of the best models explaining dugong occurrence around Bahrain across four time intervals (1–3, 4–15, 16–30, and >30 years) based on memory recall data obtained through structured interviews undertaken in 2020–2021. The credible intervals or posterior distributions of effect sizes do not include zero, indicating a significant effect.

State parameters	Notation	Parameter mean (± SD)	Credible interval (2.5%)	Credible interval (97.5%)
Pr. (occupancy)	ψ	.315 (± .063)	.20	.44
Pr. (persistence)	ϕ	.96 (± .013)	.94	.99
Pr. (colonization)	γ	.36 (± .04)	.30	.44
Pr. (detection)	p	.63 (± .02)	.58	.66

Independent counts of the UAVs' footage estimated the average size of these LDGs as 181 (± 4 SD), 696 (± 5 SD), and 648 (± 8 SD) dugongs, respectively. In addition to their exceptional sizes, LDGs appeared in the aerial footage densely clumped particularly when the groups were grazing or fleeing from approaching boats. For instance, approximately 91% of dugongs in the group sighted on 15 February 2021 were less than two body lengths from their nearest neighbour. The aerial footage further revealed that dugongs often arranged themselves in multiple layers in the water column despite the limited depth. In most cases, the clumped groups occupied an area < .5 km^2. The sea floor was visible in the captured aerial footage in only parts of the surveyed area but mostly was not visible at the spots occupied by the groups possibly due to the sediment clouds generated by their mass grazing (Figure 4.4). Hence, the size of these LDGs may be larger than estimated particularly when surveyed from boat. In this essence, comparing boat and UAV counts estimated on 14, 15, and 16 February 2021 indicated that boat counts were found to underestimate those of the UAV flights by 2.66, 5.15, and 4.47 times, respectively. A total of 11 (± 1 SD) (6.1%), 45 (± 2 SD) (6.4%), and 39 (± 1 SD) (6.0%) calves were counted within the LDGs surveyed on 14, 15, and 16 February 2021, respectively. Further examination of the UAV footage showed that mother-calf pairs were occasionally difficult to recognize in extracted still images due to the murky waters and the elusive behaviour of calves suggesting that the calf proportions could be underestimated. Given that clumped LDGs typically occupied an area of < .5 km^2, the density of dugong calves (i.e., number of calves per unit area) within the foraging area of the LDG was approximately 11–45 calf per .5 km^2.

Structured interviews and boat-based surveys showed that many LDGs encountered in cold winter months were in close proximity to the Bahrain-Qatar border and <2 km from the large groups sighted in Qatar by Marshall et al. (2018). Similarly, interviewees marked LDG sightings off Fasht Jarim, <1 km from the Bahrain-Saudi border (Figure 4.3). At a larger scale, Hawar's LDGs were ~430 km from the dugong core area around Murawah Island in the United Arab Emirates (Figure 4.6).

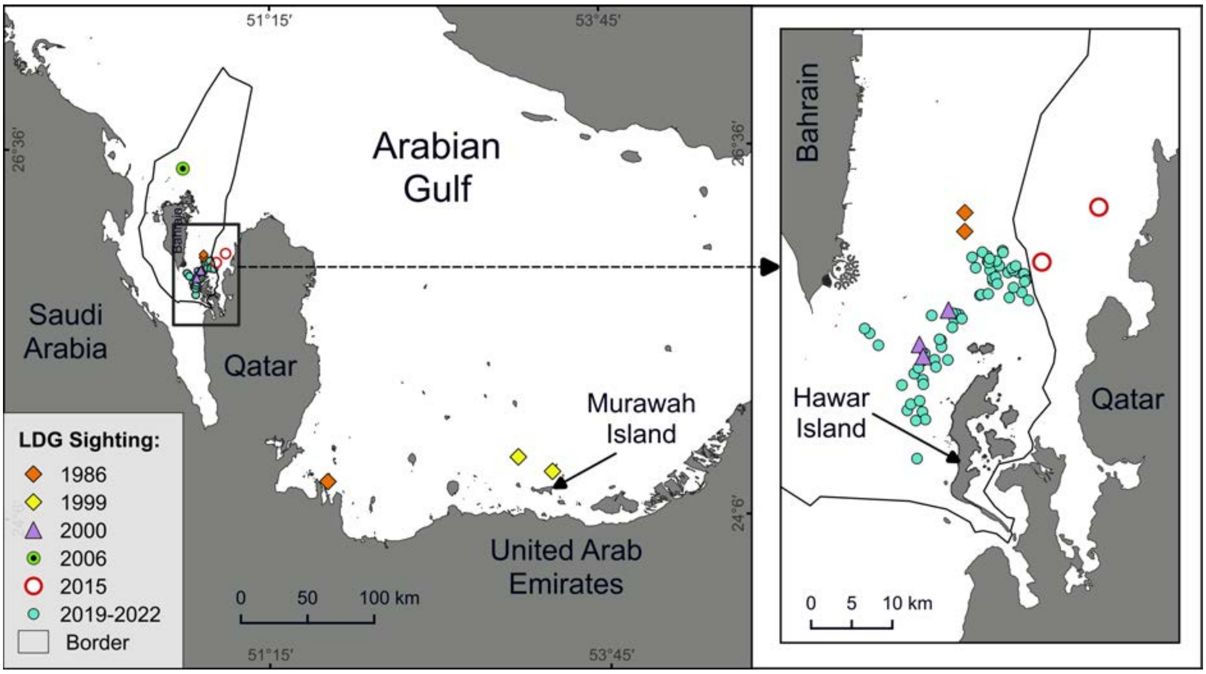

Figure 4.6. Historical and recent large dugong group (>50 dugongs) sightings in the Arabian Gulf, recorded by aerial and boat surveys and citizen science network in 1986 (Preen, 1989; Preen, 2004), 1999 (Preen, 2004), 2000 (Bell, 2001), 2006 (Hodgson, 2009), 2015 (Marshall et al., 2018), and 2019–2022 (this study), indicating their likely transboundary movements. The inset map shows the proximity of the large dugong groups reported in both Bahrain and Qatar to the Bahrain-Qatar border. Arrows indicate the location of Murawah Island (United Arab Emirates) and Hawar Island (Bahrain), the most important core dugong areas in the Arabian Gulf.

5 Discussion

Hawar Island is a globally significant hotspot for dugong conservation, with some of the largest, most persistent and actively reproducing groups of dugongs recorded across its Indo-Pacific range. Combining data from historical and current distributional studies using a mix of approaches, this study confirms that large dugong groups, measuring in the 100s, have used Hawar’s shallow seagrass meadows for at least the last four decades. The models suggest that the occupancy range of the dugong population around Bahrain may be expanding in recent years although large dugong groups are still mostly restricted to the relatively small core occupancy area around Hawar.

In the field, the groups encountered on 15 and 16 February 2021 outnumber all earlier reports from this region (Preen, 1989; Preen, 2004, Marshall et al., 2018) as well as from Australia (Preen, 1992; Lanyon, 2003) making them the largest ever documented in recent times. These findings, however, should be interpreted with caution considering the difficulties associated with accurately estimating the group size of LDGs (see below). As with the LDGs reported in Australia, these groups tended to be highly clumped, and group size extremely fluid, often breaking up into subgroups several kilometres apart that occasionally joined again (Anderson, 1981; Preen, 1989, 1992, 2004; Hodgson & Marsh, 2007; Marsh et al., 2011; Marshall et al., 2018). This characteristic fission and fusion behaviour is common across aggregating species from birds to baboons, and is also seen in many marine mammal groups (Marsh et al., 2011; Tsai & Mann, 2013; Zuluaga, 2013; Díaz López et al., 2018; O'Shea et al., 2022). It is likely that when dugongs were much more abundant in other parts of the Indo-Pacific, large groups were more common, and that the LDGs of the Arabian Gulf and Australia, measuring in the 100s, may be relicts of a once widespread grouping strategy (see Preen, 1992; Hodgson, 2004). Why dugongs still gather in such large numbers at only certain localities is still a matter of some conjecture (Preen, 1992; Marsh et al., 2002; Marshall et al., 2018; O'Shea et al., 2022). Several factors have been examined to explain dugong grouping behaviour including population density thresholds, thermoregulation, calf nursing, predatory defence, grazing efficiency, extreme weather conditions, and social interactions (Anderson, 1981, 1998; Preen, 1992; Hodgson, 2004; Holley, 2006; Cleguer, 2015). Which of these factors play a role in Hawar's LDGs would require detailed, context-specific studies on environmental, population and behavioural triggers. Whatever factors determine this grouping behaviour, it likely plays important social functions including cultural transmission as well as information sharing about resource distributions and reproduction.

The calf proportions of the studied LDGs are lower than earlier LDG reports from this region (15.7%; Preen, 2004) but comparable to proportions reported in the LDGs of Qatar (5.4–9.9%; Marshall et al., 2018). For most reported LDGs, calf proportions tend to fall within average values reported across dugong populations (Preen, 1992; Hodgson, 2004): United Arab Emirates (7.46–8.4%; Das, 2007), Red Sea (1.4–14.9%; Preen, 1989; Preen, 1992), Hervey Bay (1.5–22.1%; Sobtzick et al., 2017), and New Caledonia (4.7–18.0%; Cleguer et al., 2017). In terms of calf density, however, it was remarkably high in Hawar's LDGs (45 calves occupying < .5 km^2) conforming with earlier reports from nearby Qatar (51 calves in <1 km^2; Marshall et al., 2018). These results suggest that persistent aggregation sites of LDGs across their range possibly represent important calf birthing and/or rearing grounds. This is further supported by the multi-decadal persistence of mother-calf pairs around Hawar; a positive sign that the population is likely reproductively healthy given their slow rate of reproduction and the vulnerability of orphaned calves (Anderson, 1981; Preen, 1992; Marsh et al., 1999; Marsh & Kwan, 2008).

Another remarkable feature of Hawar's LDGs is their persistence in space and time. The core area of dugong occupancy around Hawar has had consistent reports of LDGs for >35 years, indicating that these shallow waters are a traditional grouping location for the population. Considering the difficulties inherent in estimating the group size of LDGs (see below), the persistence of sizeable LDGs of almost the same number (~700 dugongs; Preen, 2004; this study) around Hawar for >3 decades further underscores the significance of this area for dugong conservation. The multidecadal persistence of LDGs, also, lends support of the global importance of the Gulf of Salwa IMMA for dugongs (Knight et al., 2011; IUCN-Marine Mammal Protected Areas Task Force, 2021).

Of all historical LDG records in Bahrain (Bell, 2001; Preen, 2004; Hodgson, 2009), 67% were in summer, supporting our findings that dugongs aggregate around Hawar not just in winter as previously thought (Preen, 1989, 2004; Preen et al., 2012; Marshall et al., 2018). To our knowledge, Hawar is second only to Moreton Bay in harbouring groups of >100 dugongs year-round (Preen, 1992; Hodgson, 2004; Chilvers et al., 2005; O'Shea et al., 2022). That said, these fluid groups do show distinctive seasonal movements, but at a highly reduced scale, shifting between distinct but slightly overlapping summer and winter feeding grounds. Highlighting the importance of socially transmitted information (Anderson, 1981; O'Shea et al., 2022), these results add to the evidence from Moreton Bay where large groups repeatedly use the same feeding grounds (Anderson, 1981; Lanyon, 2003) in a systematic manner following predictable seasonal movement routes (Hodgson, 2004). Without more detailed studies on seagrass nutrient contents and temporal patterns of seagrass availability, it is difficult to speculate on the reasons for this seasonal movement. However, these small-scale migrations have important consequences for managing these LDGs. The encounter of LDGs at the winter feeding ground during November-March conforms with the results of Marshall et al. (2018) who reported that LDGs start arriving to the nearby Qatari waters in November and persist until February. These consistent reports highlight the transboundary nature of LDGs and underscore the role of seasonality in shaping their spatial distribution and, hence, the larger Arabian Gulf's population (Preen, 2004; Marshall et al., 2018).

The year-round persistence of LDGs around Hawar enabled the mapping of a well-delineated hotspot where hundreds of dugongs spend their summers and winters in large groups. While this allows managers to focus management efforts on a relatively small and well-defined hotspot for conservation, it also increases the vulnerability of the dugong population to site-level threats. Due to their exceptionally large size, clumped distribution, and high calf density, any significant human-induced stressors to LDGs and/or their primary aggregation sites will have disproportionate impacts on the entire dugong population. Given the global significance of this population, there is a need to urgently put in place a series of management actions with a focus on restricting the use of gillnets and imposing boat speed limits across the LDG occupancy area since bycatch has been identified as a major source of dugong mortality in the Arabian Gulf (Hodgson, 2009; Knight et al., 2011; Environment Agency-Abu Dhabi, 2014; Abdulqader et al., 2017). Also, it is crucial to safeguard the extensive seagrass beds around Hawar from the impacts of accelerating coastal development in the south of Bahrain. Establishing and maintaining a continuous monitoring program is a priority to identify any decline in dugong populations or degradation in seagrass habitats at early stages, allowing timely conservation interventions. In all this, it is vital that local communities are made partners in dugong conservation, to ensure that small-scale fishing can sustainably thrive alongside large dugong groups. There is little doubt that these LDGs cross jurisdictional boundaries and, hence, establishing a regional network of marine protected areas spanning all the Arabian Gulf’s range states is crucial to the effective protection of these groups and the larger dugong population. This network should encompass confirmed and potential core dugong aggregation sites, including: Murawah Island and Al Yasat Island in the United Arab Emirates; Hawar Island, Fasht Buthur, and Fasht Jarim in Bahrain; north-western waters of Qatar in addition to the shallow waters between Saudi Arabia, Qatar, and United Arab Emirates. Of these, only the first three have been officially designated as marine protected areas. The network could be established progressively with the first series of core zones encompassing the designated protected areas (42%), followed by Fasht Buthur and the north-western waters of Qatar (29%). The addition of Fasht Jarim and the shallow waters between Saudi Arabia, Qatar and United Arab Emirates would expand the network by a further 29%. In addition to these core zones, the regional network should promote ecological connectivity by imposing a similar array of interventions on LDG migration corridors and key habitats interconnected with seagrass particularly coral reefs and islands.

This multidisciplinary study has confirmed the persistence of LDGs around Hawar and defined their core occupancy area using cost-effective methods supported by UAV surveys. In interpreting these results, it is important to consider a few important caveats. Given the chosen boat speed, it is possible that some dugong groups may have been missed. In addition, an important source of information was the structured interviews with key informants, and the possibility of inaccurate renditions of encounters due to failing memories cannot be discounted. Despite their large numbers, clumped dugong groups are often difficult to observe from air (Preen, 1989; Pollock et al., 2006; Cleguer, 2015; Cleguer et al., 2021; Trotzuk et al., 2022). This is even more complex for boat-based surveys that depend on surfacing individuals; dugongs resting or feeding underwater make accurately estimating group size a real challenge. Given this difficulty it is possible that LDGs could be more common across the dugong global range than currently reported. Despite these caveats, by using multiple approaches, these results are considered to be robust, and signify the high conservation importance of this region. It is hoped that the enhanced knowledge on the Arabian Gulf's LDGs from ongoing research in Bahrain, Qatar, and United Arab Emirates will inform evidence-based conservation management.

What is remarkable about dugong groups is just how variable they are in size, from solitary or paired individuals to mega-aggregations of 100s of dugongs. A complex set of trade-offs and life-history characters underlie this flexibility (Anderson, 1981; Preen, 1995; Hodgson, 2004; Zeh et al., 2018). This variable grouping behaviour may possibly contract across the dugong's range as accidental bycatch, hunting, seagrass meadow loss, and boat strikes combine to see fragmentation and decline of local populations. What makes the Hawar's large dugong groups so vital is that they represent an important part of the suite of dugong behaviours across its range. Conserving the LDGs around Hawar should be a global priority to preserve the population of the Arabian Gulf and maintain the remarkable behavioral flexibility this species can show across its range.

Given the LDGs we encountered during this study and assuming that the population sizes reported by Hodgson (2009) and Preen (2004) have not changed substantially over time, it is estimated that ~12% of all dugongs in the Arabian Gulf (= ~60% in Bahrain) may aggregate forming large groups around Hawar. As speculated earlier by Preen (2004), the interval distance between Hawar and Murawah Islands is within the large-scale dugong movement range (Sheppard et al., 2006; Deutsch et al., 2022b) suggesting possible contributions of regional migration to the formation of Hawar's LDGs. The extension of the LDG occupancy area beyond the Bahrain-Qatar border further highlights the transboundary nature of the LDGs around Hawar. These reports underscore the significance of LDGs in maintaining sizeable dugong populations, a primary consideration for any dugong conservation or management strategies in the Arabian Gulf (Knight et al., 2011; Preen et al., 2012). For this globally important population to persist, therefore, the LDGs and their core aggregation sites and migration corridors should be effectively conserved through an evidence-based regional conservation plan. Establishing a regional network of marine protected areas and effectively engaging local communities are critical steps if we are to maintain the large dugong groups in their northern distributional limits.

6 Acknowledgments

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5

Large dugong groups persist in areas with continuous seagrass meadows despite anthropogenic disturbances around Hawar Island, Bahrain

1 Abstract

Spatially explicit aggregation sites for threatened marine mammals are natural targets for conservation. Identifying why these sites persistently sustain mammalian aggregations is critical to ensuring they remain suitable as primary habitats for these charismatic animals. Large dugong groups (>50 dugongs) aggregate predictably around Hawar Island, Bahrain using these waters year-round at two core areas, one in summer and the other in winter. In this study we evaluated the main environmental, ecological, and anthropogenic predictors of their distribution. For this, we combined spatially explicit data from historical records, structured interviews, satellite imagery, habitat cartographies, and field ecological surveys. Our results indicated that the core aggregation sites of large dugong groups are characterised by shallow (3–8 m) extensive seagrass meadows (>760 km^2) sheltered by reef complexes and islands. Field behavioural observations confirmed that the summer and winter aggregation sites correspond to seagrass feeding grounds. These grounds had similar temperatures to the surrounding waters, that overlapped with the dugong lower thermal tolerance threshold, with no indication of localized warm water vigorous discharges. Composed of only three pioneer seagrass species, extensive seagrass meadows occupied 82% of the large dugong group occupancy and were the main driver governing their spatial distribution. Almost completely overlapped with boat traffic and fishing grounds, these meadows have been fished over decades subjecting dugongs and their aggregation sites to the threats imposed by fishing gear and boats. We conclude that the future persistence of large dugong groups around Hawar is conditional on the maintenance of extensive healthy unfragmented seagrass meadows and imposing control on intensifying fishing and boating activities. Whereas the large size, clumped density, and massive dietary needs of these groups lends itself to spatially explicit conservation planning focusing on high-use areas, the transboundary nature of their movements and primary habitats as well as anthropogenic threats call for a holistic ecosystem approach stressing the human dimension and regional cooperation in their management.

Keywords: dugong, social marine mammal, Arabian Gulf, habitat suitability, fishing, maritime traffic, conservation management

2 Introduction

Marine mammals are widely distributed across the world's oceans and show a remarkable ability to adapt to a wide range of coastal and marine environments (Olff et al., 2002; Morrison et al., 2007; Schipper et al., 2008; Macdonald et al., 2013). Many of these mammals are group living and use traditional aggregation sites to satisfy strategic needs for this survival (Macdonald et al., 2013; Brakes & Dall, 2016; di Sciara et al., 2016). Group living has a number of fitness benefits to social animals, including increasing food detection, improved forage nutritional quality, diluted predation risk, enhanced reproductive opportunities, better young rearing, and reduced anthropogenic threats (Acevedo-Gutierrez, 2009; Macdonald et al., 2013; Zuluaga, 2013; O'Shea et al., 2022). These benefits do not come without their trade-offs. The high abundance and density of these animals at their aggregation sites make them particularly vulnerable to even small changes in resource availability, environmental fluctuations and/or anthropogenic pressures (Brakes & Dall, 2016; Littles et al., 2019). As a result, few locations can reliably support large marine mammalian aggregations. It is therefore essential to understand what characterizes these aggregation sites where they exist, and to determine potential threats to their persistence.

While many marine mammals aggregate in remote deep water locations, coastal species, such as the dugong *Dugong dugon* (Müller, 1776), prefer shallow water habitats closer to shore, largely overlapping with high human-use areas (Marsh et al., 1999, 2022; Hodgson, 2004; Ponnampalam et al., 2022). Unsurprisingly, therefore, dugongs are increasingly threatened throughout their range by entanglement in fishing gear, vessel traffic and strikes, habitat deterioration and loss, hunting as well as climate change, among others. Of these, incidental drowning in gill nets is principally responsible for dugong mortality in many coastal regions (Hodgson & Marsh, 2007; Cleguer, 2015; Marsh et al., 2022; Ponnampalam et al., 2022). In addition to the risk of serious injury and death (Marsh et al., 2002; Holley, 2006; Hodgson & Marsh, 2007; Cleguer et al., 2015; Moore et al., 2017), acoustic disturbance generated by boats impairs foraging time for a species that needs to meet large energetic demands on a daily basis (Marsh et al., 2002; Hodgson & Marsh, 2007; Ponnampalam et al., 2022).

Despite the vast dugong distributional range extending over 128,000 km of tropical and sub-tropical Indo-Pacific coastlines spanning over 44 countries and territories (Marsh & Sobtzick, 2019), large dugong groups (LDGs; >50 dugongs) have been persistently recorded only at some localities (Preen, 1992, 2004; Marsh et al., 2002; Hodgson, 2004; Chilvers et al., 2005). Where dugongs cluster forming large groups, they tend to predictably return to the same sites year on year (Preen, 1992; Marsh et al., 2002; Hodgson, 2004; Chilvers et al., 2005; Hines et al., 2005; Findlay et al., 2011; Cleguer, 2015), making them particularly susceptible to anthropogenic disturbances (Baldwin & Cockcroft, 1997). Therefore, understanding what characterizes dugong aggregation sites and identifying potential threats is critical for any conservation planning.

Not much is currently known why dugongs choose particular areas to aggregate in large numbers since these locations are not common or easy to locate across the dugong vast range. Much of what we know about dugong grouping behaviour comes from Australia, in particular from Moreton and Shark Bays, where reports of LDGs go back >130 years (Preen, 1992; Hodgson, 2004, 2011; Chilvers et al., 2005; O'Shea et al., 2022). Several hypotheses have been proposed to explain the formation and persistence of LDGs including: thermoregulation, calf nursing, predatory defence, grazing efficiency, social interactions as well as unfavourable weather conditions (Anderson, 1981, 1998; Preen, 1992; Hodgson, 2004; Holley, 2006; Cleguer, 2015). In the Arabian Gulf, dugongs regularly gather in some of the largest dugong groups (maximum: ~700 dugongs) ever recorded in modern times (Preen, 2004; Hodgson, 2011; Marsh et al., 2011; Preen et al., 2012; O'Shea et al., 2022). In particular, the shallow waters around Hawar Island (off the south-eastern coast of Bahrain; hereafter 'around Hawar') have persistently harboured LDGs for over 35 years (Hodgson, 2011; Marsh et al., 2002; Preen, 2004; Preen et al., 2012; Chapter 4) with distinct spatially explicit summer and winter aggregation sites. After more than three decades since they were first reported, however, little is known of the factors determining the spatial distribution of these LDGs. From the sparse information available, the Arabian Gulf's cold winter temperature (annual range: 10–45 °C; Basson et al., 1977; Price & Coles, 1992; Vousden, 1995; Coles, 2003; Al-Bader et al., 2014; Alosairi et al., 2020) overlaps with the reported lower thermal tolerance threshold of dugongs (Sheppard et al., 2006; Deutsch et al., 2022a). As such, it has been hypothesized that dugongs aggregate around Hawar during winter cold months near warm submerged springs that heat the surrounding waters (Preen, 1989, 2004).

There is increasing evidence that cold water temperature mediates thermoregulatory movements and social behaviour in sirenians (Deutsch et al., 2022a; Marshall et al., 2022; Ponnampalam et al., 2022). For instance, in response to winter temperature falling below 20 ºC, Florida manatees *Trichechus manatus latirostris* cluster around thermal refugia (e.g., warm-water springs and power plant outfalls) forming sizeable aggregations of several hundred

(Irvine, 1983; Reynolds III & Wilcox, 1994; Littles et al., 2019; Edwards et al., 2021; O'Shea et al., 2022). Similarly, dugongs tend to avoid prolonged exposure to temperatures of ≤18 ºC, although at some localities they occasionally tolerate 15.4–17 ºC (Preen, 1992, 2004; Lanyon et al., 2005; Sheppard et al., 2006; Marsh et al., 2011; Cleguer, 2015; Zeh et al., 2018; Marshall et al., 2022). In addition to temperature, it is likely that LDGs in the Arabian Gulf distribute themselves in relation to a host of other factors including food availability, social and reproductive interactions and/or anthropogenic disturbances that yet to be explored. Due to these wide knowledge gaps, no appropriately targeted strategies have been developed to address the conservation management needs of the Arabian Gulf's LDGs.

In this study, we evaluated the main environmental, ecological, and anthropogenic correlates of large dugong groups over the last decades in Bahrain with a particular focus on the shallow waters around Hawar. For this, we compiled spatially explicit data on seawater temperature, depth distribution, distance to the coast, habitat type, seagrass meadow size, boat traffic as well as fishing activities, and then related it to the presence of LDGs. Data on large dugong groups and fishing activities was obtained using historical records, structured interviews, and field observations. The rest of the data was sourced from maps, satellite imagery, and rapid seagrass ecological assessment surveys. Our key objectives were to: (i) determine the main environmental and ecological attributes driving large dugong group spatial distribution around Bahrain, and (ii) identify key anthropogenic stressors core dugong aggregation sites face, with a special focus on fishing and boating activities. Based on these results, we discuss strategic priorities for conserving the globally significant dugong groups in the Arabian Gulf.

3 Materials and Methods

3.1 Study area

The study was conducted in the Gulf of Bahrain which forms a shallow inlet of the Arabian Gulf. With a landmass of ~778 km^2 (General Directorate of Statistics, 2017), Bahrain is surrounded by ~7,500 km^2 of territorial waters (Al-Zayani et al., 2009) comprising ~41% of the 'Gulf of Salwa Important Marine Mammal Area' (IUCN-Marine Mammal Protected Areas Task Force, 2021). The later area harbours globally important dugong habitats where LDGs have been consistently recorded over the last four decades (Bell, 2001; Preen, 2004; Preen et al., 2012). Between 2019–2022, for instance, 64 large dugong groups were encountered almost year-round over 490 km^2 of shallow waters marking the LDG overall distributional range (ODR). This range encircles the main large dugong group occupancy area (LOA, ~145 km^2), that is composed of three percentage volume contours (PVCs) indicating where LDGs spend 95% (95% PVC) and 50% (50% PVC) of their time (Figure 5.1). The two 50% PVCs represent the core dugong aggregation sites, alternately used by LDGs as distinct winter and summer feeding grounds (WFG and SFG, respectively). Extending easterly beyond the Bahrain-Qatar border, the LOA is surrounded by a number of islands and reef complexes (locally known as '*fasht*') including the 200 km^2 Fasht Adhm, one of the largest reefs in the Arabian Gulf (Burt et al., 2013). Additionally, the large dugong groups are occasionally sighted around Fasht Jarim, ~80 km to the north west of Hawar. Indicative of its productivity and socio-economic significance, the marine environment around Bahrain sustains an expanding artisanal fishing fleet which landed a total of 12,215 metric tons in 2015 (General Directorate of Statistics, 2017). This fleet fishes mostly for finfish and crab, serving as an important source of protein for a population of 1.4 million people (2016 cencus; General Directorate of Statistics, 2017).

3.2 Large dugong group spatial distribution and core areas

To determine the spatial distribution of large dugong dugongs around Bahrain we inventoried all historical and recent LDG sightings reported using: (i) historical records from 1986 (Preen, 1989, 2004), 2000 (Bell, 2001), and 2006 (Hodgson, 2009) aerial surveys; (ii) structured interviews carried out in 2020–2021 with fishers, tour operators, researchers, and environmentalists; (iii) 2019–2022 citizen science network reports; (iv) 2019–2022 boat-based surveys; and (v) opportunistic unmanned aerial vehicle (UAV) surveys (see Chapter 4 for detailed methods). We used the combined data on presence/absence of LDGs to map their spatial distribution around Bahrain over four time intervals: (i) 1–3 year (2019–2021), (ii) 4–15 year (2006–2018), (iii) 16–30 year (1991–2005), and (iv) >30 year (1990 and before).

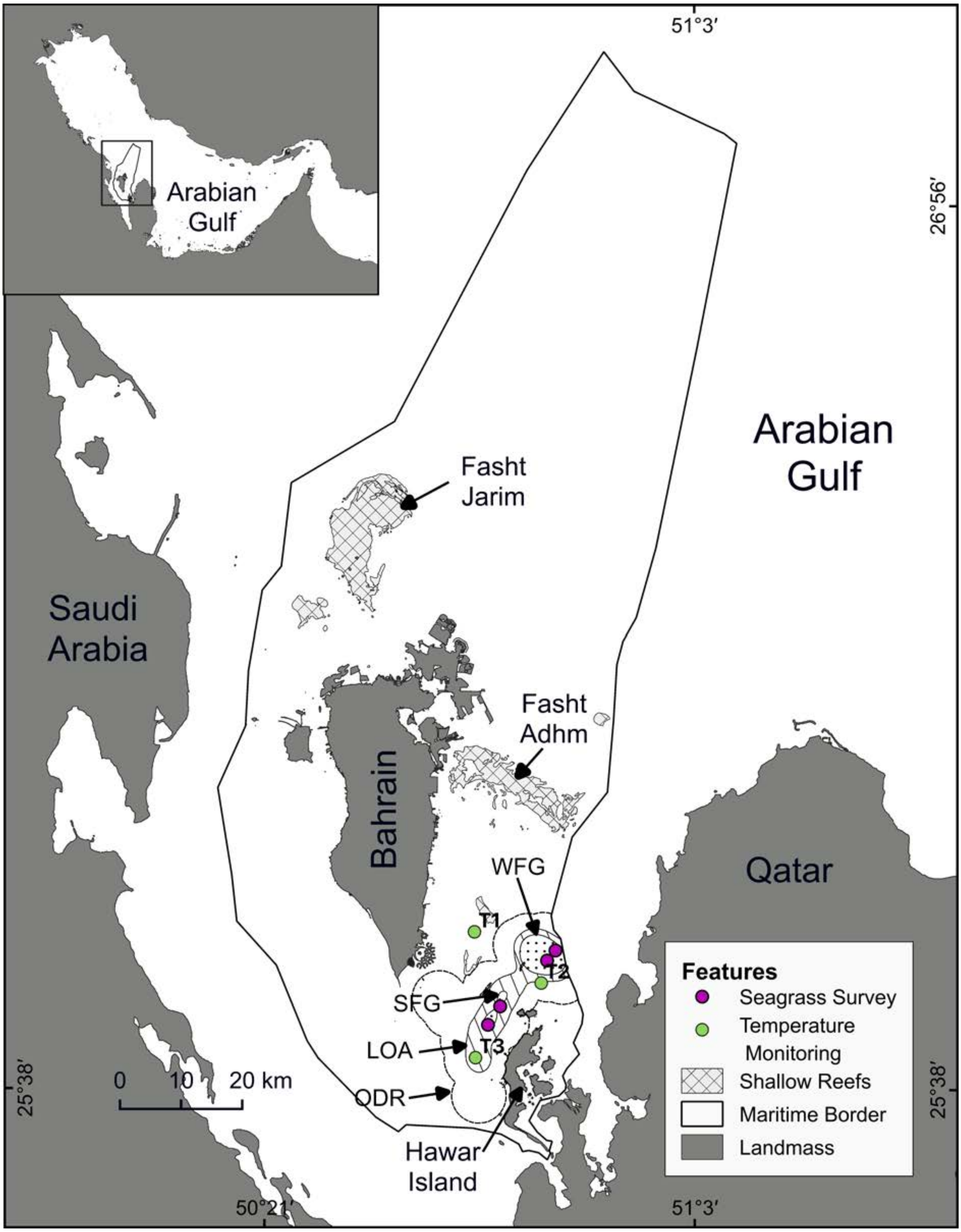

Figure 5.1. Map of the study area showing the location of Bahrain in the Arabian Gulf, the areal extent of the overall distributional range and main aggregation sites of large dugong groups (LDGs; >50 dugongs) around Hawar Island, sampling sites of the rapid seagrass ecological survey as well as temperature monitoring sites (ODR= overall distributional range, LOA= main large dugong group occupancy area, WFG= winter feeding ground, SFG= summer feeding ground, T= temperature monitoring site).

3.3 Environmental correlates of large dugong group distribution

Bathymetric contours were sourced from navigation charts corrected to Chart Datum (Survey Directorate, 1997) which enabled us to estimate water depth to the nearest 1 m. In addition, we employed maximum tidal current velocity charts modelled over a 24-hour average spring tidal cycle (Erftemeijer et al., 2004) to rate water velocity on a 4-grade scale: ≤ .25, .25 – .50, .51 – .75, and ≥ .75 m s^{-1}. We assessed the spatial gradients in sea surface temperature (SST) across the Gulf of Bahrain and over six months representing two seasons. Six satellite images were acquired to determine seasonal patterns in SST that were classified to: (i) summer (images dated 10 October 2020 and 11 June 2021), and (ii) winter (images dated 20 December 2020, 13 January 2021, 23 February 2021, and 18 March 2021). The images were obtained from Sentinel-3 satellite using OLCI (Ocean and Land Colour Instrument) with 1 km resolution for thermal channels (Donlon et al., 2012). The images were subset to cover the central southern coast of the Arabian Gulf, re-projected and converted to a fine resolution of ± .5 ºC using ArcView GIS (Version 10.8.2). To facilitate visual comparison, the SST raster images were converted to contour polygons and visually assessed to detect any distinctive signs of localized warm water discharges around Hawar or large-scale thermal patterns differentiating the LDG distributional range or LOA from the rest of the Gulf of Bahrain. In parallel, we deployed temperature loggers (Odyssey Xtreem Submersible Temperature logger; Dataflow Systems, New Zealand) to measure seawater temperature *in situ* at three shallow-water locations (depth range: 3.1–3.4 m), two of which were within LOA (Figure 5.1). The loggers were configured to record a temperature reading every 10 minutes for the two coldest months of the year (i.e., January and February 2021). The obtained means were then compared to the corresponding monthly means measured around Bahrain by Vousden (1995).

3.4 Ecological correlates of large dugong group distribution

Habitat types were determined based on the habitat classification of Al-Zayani et al. (2009) who identified 12 benthic categories, including seagrass and seagrass mixed with other habitats. In addition, within LOA, seagrass characteristics were evaluated by rapid in-water ecological surveys. Two sampling sites at the summer and other two at the winter feeding grounds (*N*= 4) were assessed using three transects (50 m), haphazardly deployed at each site, along which seagrass species composition as well as relative and total seagrass cover were identified to the nearest centimetre.

3.5 Anthropogenic correlates of large dugong group distribution

Maps of fishing grounds targeted by fishers in 1992, 1996, 2000, and 2006 (Al-Zayani, 2003; Zainal & Abdulqader, 2009) were digitized using Quantum Geographic Information System (QGIS; Version 3.18; QGIS Association). Since all available fishing maps were outdated, we produced an updated fishing ground chart by interviewing experienced local fishermen (*N*= 6) who were asked to delineate polygons on maps, marking the boundaries of all fishing grounds targeted around Bahrain between 2019–2021. For all maps, we classified polygons according to the fishing gear used: (i) line (e.g., hook, longline, and troll), (ii) wire cages (e.g., cylindrical crab and hemisphere finfish cages), (iii) nets (e.g., trawl and gill nets), and (iv) unclassified.

We included temporal information to assess variations over time in spatial overlaps between fishing grounds and dugong sightings reported through the aforementioned methods. The fishing maps were reproduced for three time intervals and superimposed on the corresponding dugong spatiotemporal data while referring to 2021 as benchmark (see above): (i) 1–3 years (2019–2022 citizen science network reports and boat-based survey sightings overlaid on 2019–2021 fishing chart), (ii) 4–15 years (2006 aerial survey sightings overlaid on 2006 fishing chart), and (iii) 16–30 years (2000 aerial survey sightings overlaid on 1992/1996/2000 fishing charts). Then, we calculated the overlap percentage between dugong spatial distribution and fishing activities over time. To further explore potential interactions between LDGs and fishers, we overlaid LOA on the 2019–2021 fishing chart, and the overlap percentage was estimated. During the boat-based surveys, we recorded qualitative field observations on the distribution and type of fishing boats and gear around Hawar, particularly at LOA. In addition, we evaluated the maritime traffic density around Hawar using traffic density maps and direct qualitative observations. All non-military vessels registered in Bahrain are legally-mandated to have an automatic identification system (AIS) fitted (Ministry of Interior, 2017), allowing continuous monitoring of marine vessel movements. We determined the range of boat traffic intensity (route .5 km^{-2} $year^{-1}$) based on marine traffic maps of the year 2019 generated from AIS acquired data (www.marinetraffic.com; zoom level: 10). We further examined these maps to determine whether particular types of vessels (e.g., fishing boats and ferries) substantially contributed to the marine traffic at LOA.

During the boat surveys conducted in 2019–2021, we recorded field observations on the behavioural responses of dugongs towards approaching boats and boat noise traveling over distance. We focused on two key dugong behaviours: grazing and traveling—based on the dugong behaviour classification of Hodgson and Marsh (2007)—since other behaviours (e.g., resting and socializing) are difficult to unequivocally determine from the boat (Hodgson, 2004). We further examined this response behaviour in aerial footage captured by UAVs overflying LDGs in proximity to fishing boats. We developed a set of observations to identify the grazing behaviour of LDGs from boat: (i) the LDG remained at nearly the same spot for >15 min, (ii) a number of dugongs near the surface were repetitively diving by lifting their peduncles at ≥45° (see Anderson, 1981), and (iii) the water column was murky with a distinctive sediment plume. We confirmed these criteria with the UAV aerial footage and in-water observations by snorkelling and SCUBA. Additionally, we used a towed-video camera system (Splashcam Deep Blue, Ocean Systems, USA), snorkelling and/or SCUBA surveys to examine the benthos immediately after a LDG had moved away, to locate distinctive fresh dugong feeding trails as described by D'Souza et al. (2015). A total of six groups were sampled for grazing signs following this method.

3.6 Analysing key drivers of large dugong group distribution

We ran an analysis to assess the drivers governing the spatial distribution of LDGs. For this, we first gridded the territorial waters of Bahrain, south of 26° 38' N, into 2 × 2 nm^2 (~ 3.70 × 3.70 km^2) grid cells ($N = 490$). We did not include the northern offshore waters in this sampling design due to the unavailability of marine habitat maps for and absence of LDG sightings in these waters. In each grid cell, we determined the presence/absence of LDGs reported in 2019–2022 by structured interviews, citizen science network reports and boat-based surveys (see Chapter 4). In addition, we classified each cell based on its bathymetry (m), summer SST (22 October 2020; °C), winter SST (13 January 2021; °C), distance to nearest reef/island (m), distance to nearest large seagrass meadow (m), water velocity (4-grade scale: $\leq .25$, $.25 - .50$, $.51 - .75$, and $\geq .75$ m s^{-1}), habitat type (5-grade scale: unconsolidated sediment, hard bottom/corals, algae, seagrass, and deep water), maritime traffic (3-grade scale: 0–26, 27–243, and >243 route .5 km^{-2} year^{-1}), in addition to fishing line, cages, and nets (2-grade scale: present or absent). To establish the distance to the nearest large seagrass meadow, cells were further assessed based on the habitat map of Al-Zayani et al. (2009). We considered a cell occupied by >50% seagrass and surrounded by at least three cells similarly covered by >50% seagrass as being located in a large seagrass meadow. After all this data had been obtained for each grid, we ran a Generalised Linear Model (*GLM*) in R software environment (R Development Core Team, 2021), where the presence of LDGs was the dependent variable and the remaining variables presented above were included as independent variables. We started model selection from a full model including all independent (predictor) variables. Then, each effect was dropped one by one, and we selected the best model using the Akaike Information Criterion and the likelihood ratio test statistic (Zuur et al., 2009). Predictors dropped during model selection are not presented in the final output, as they were considered not important in influencing the dependent variable (Table 5.1). Tukey Honestly Significant Difference (HSD) post hoc tests were undertaken using the package multcomp (Hothorn et al., 2008) to determine level-specific differences within significant variables. Normality and homogeneity of variances were checked graphically by inspecting residuals and fitted values.

4 Results

4.1 Environmental correlates of large dugong group distribution

The main large dugong group occupancy area was characterised by shallow depth contours, of which 50%, 47%, and 3% was located in 1–5 m, 6–10 m, and 11–15 m waters, respectively. Water depth at SFG and WFG ranged between 3.1–8.8 m and 2.7–7.6 m, respectively. Nearly 77% of LOA experienced current velocity ranging .25 – .50 m s^{-1} while 20% was situated at calmer waters (< .25 m s^{-1}), and only 3% of LOA experienced currents reaching .51 – .75 m s^{-1}. Large dugong group sightings were also in proximity to reef complexes and/or islands with a maximum linear distance ranging 151–4932 m and averaging 1763 (± 1055 SD) m.

The SST satellite images detected neither persistent localized warm spots (indicative of active warm water discharges) around Hawar, nor a distinctive large-scale thermal trend substantially differentiating the ambient waters around Hawar from the rest of the Gulf of Bahrain. In fact, in all studied months, SST levels at the overall distributional range and main occupancy area of large dugong groups were mostly within ± 2 °C of the gradients across the nearshore and offshore waters of the Gulf of Bahrain (Figure 5.2). This low variability was also confirmed by the *in situ* temperature loggers. Monthly mean seawater temperature varied slightly across sites during the coldest winter months ranging between 19.2–19.9 °C and 19.3–19.8 °C for January and February 2021, respectively. The minimum and maximum values across the logged period were 16.9 °C and 21.9 °C, respectively. These readings are even below the corresponding monthly means of seawater temperature recorded by earlier studies around Bahrain (difference: .94 – 1.59 °C; Figure 5.3).

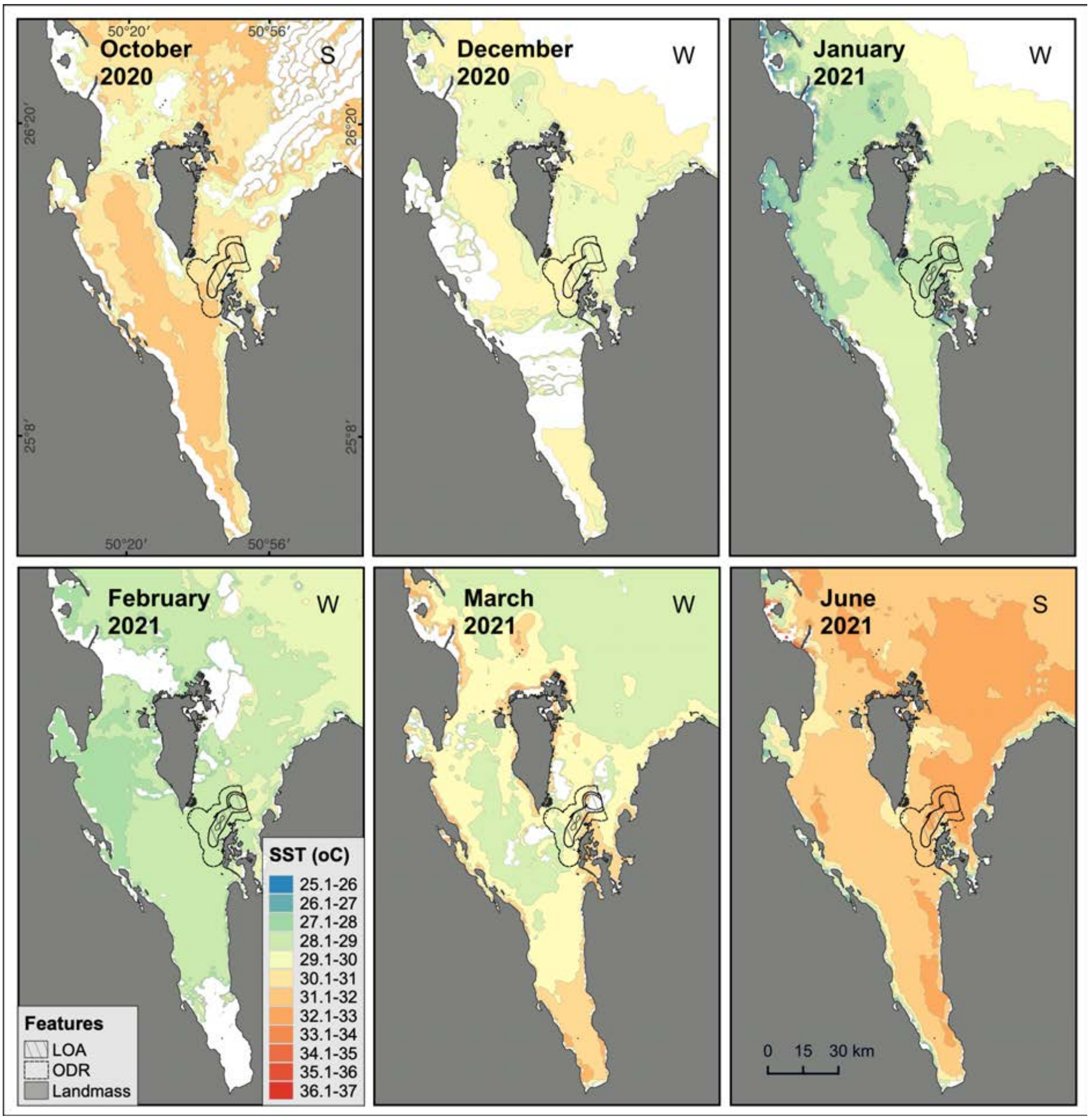

Figure 5.2. Spatiotemporal variations in sea surface temperature (SST; °C), recorded over six selected calendar months in 2020–2021, comparing SST within the overall distributional range and main occupancy area of large dugong groups (LDGs; >50 dugongs) around Hawar Island relative to nearshore and offshore waters across the Gulf of Bahrain in the Arabian Gulf. White spaces represent clipped cloud cover (ODR= overall large dugong group distributional range, LOA= main large dugong group occupancy area, S= summer, W= winter).

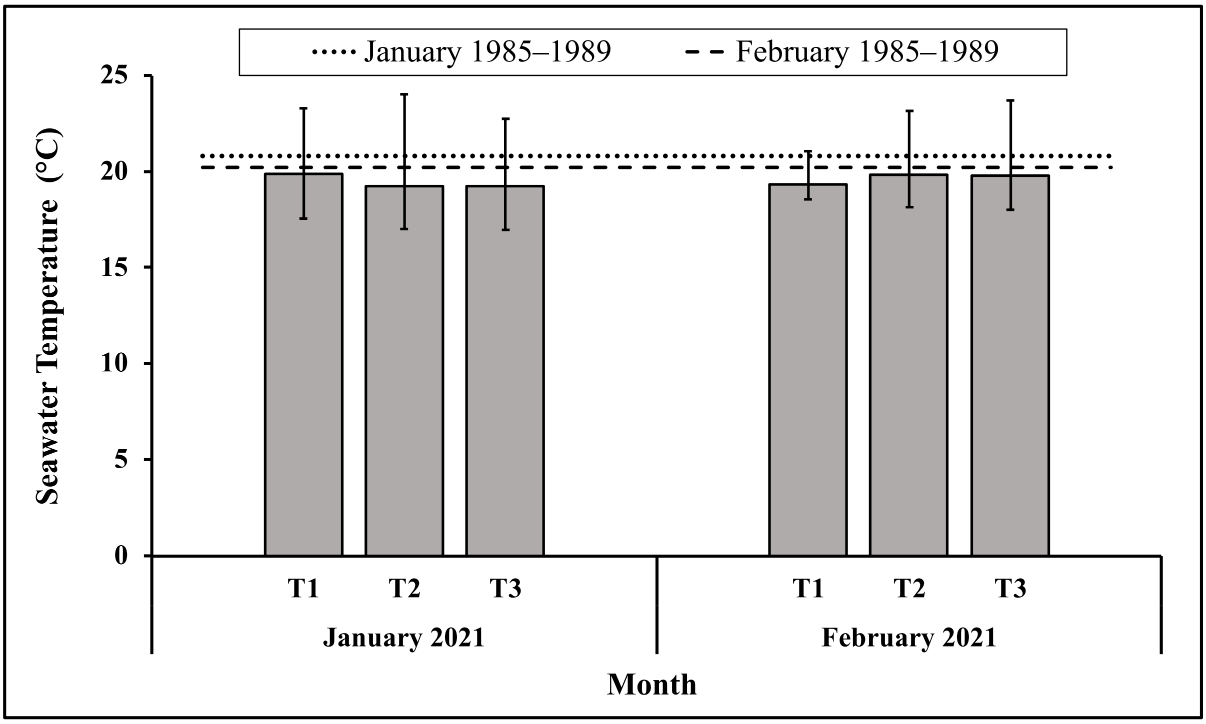

Figure 5.3. Monthly mean, minimum and maximum seawater temperatures recorded in the months of January and February 2021 by three temperature loggers, deployed around Hawar Island, compared to the corresponding monthly means measured by Vousden (1995) around Bahrain during 1985–1989 (T= logger number, bars= minimum and maximum temperature values).

4.2 Ecological correlates of large dugong group distribution

Of all LDG sightings, 92% were encountered in seagrass meadows and the remaining (*n*= 5) were all <430 m from the nearest seagrass area. Likewise, the seabed across LOA was 82% covered by seagrass, of which only 1% was seagrass mixed with other habitats (i.e., rocks, coral, sand, and algae). The habitat map showed that the seagrass at LOA is part of extensive meadows stretching over ~765 km^2 from Fasht Adhm to the southern tip of Hawar Island (Figure 5.4). These meadows appear to extend easterly beyond Bahrain-Qatar border as suggested by the satellite images (Google Earth Pro, n.d.). The in-water ecological surveys further confirmed that the meadows at WFG and SFG were prevalently covered by seagrasses (mean total cover: 69 [± 10% SD]), composed of only three species: *Halodule uninervis*, *Halophila stipulacea*, and *H. ovalis* (relative cover: 34%, 29%, and 6%, respectively; Figure 5.5). All boat surveys conducted close to WFG and SFG revealed that LDGs were actively feeding, which was also confirmed by in-water surveys of dugong feeding trails.

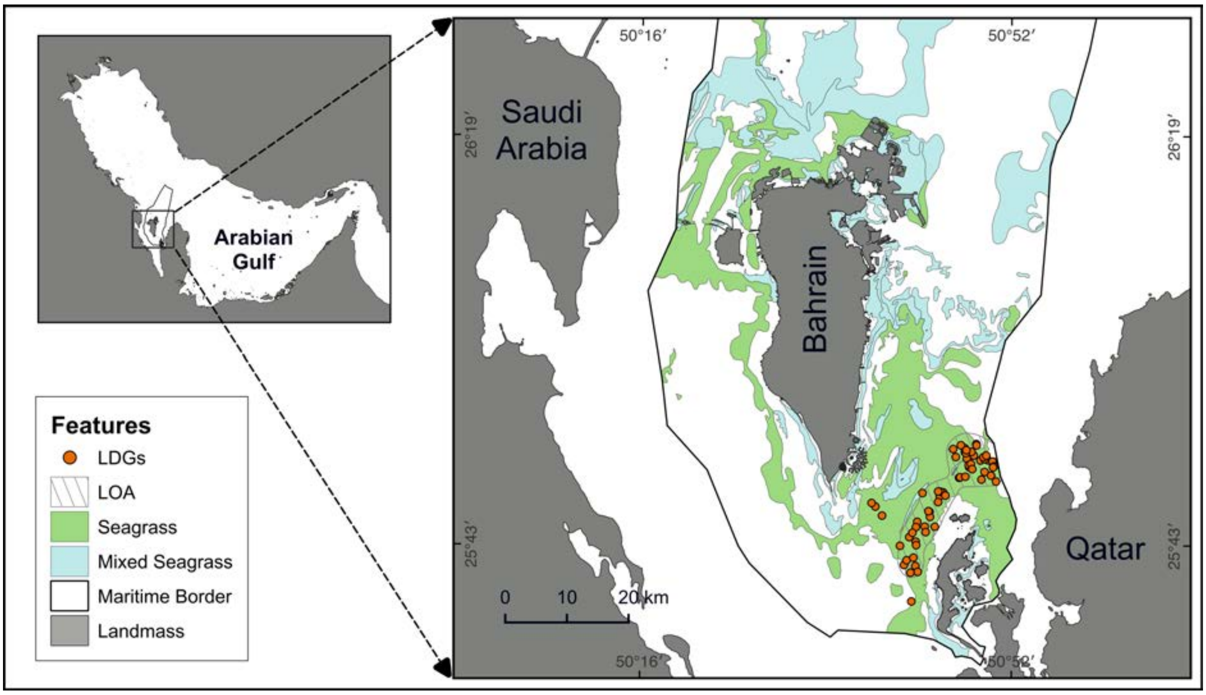

Figure 5.4. Overlap between the main large dugong group occupancy area (LOA) as well as large dugong group sightings (LDGs), recorded during 2019–2021 through citizen science network and boat-based surveys, with seagrass and mixed seagrass habitats digitalized from the marine habitat map of Al-Zayani et al. (2009).

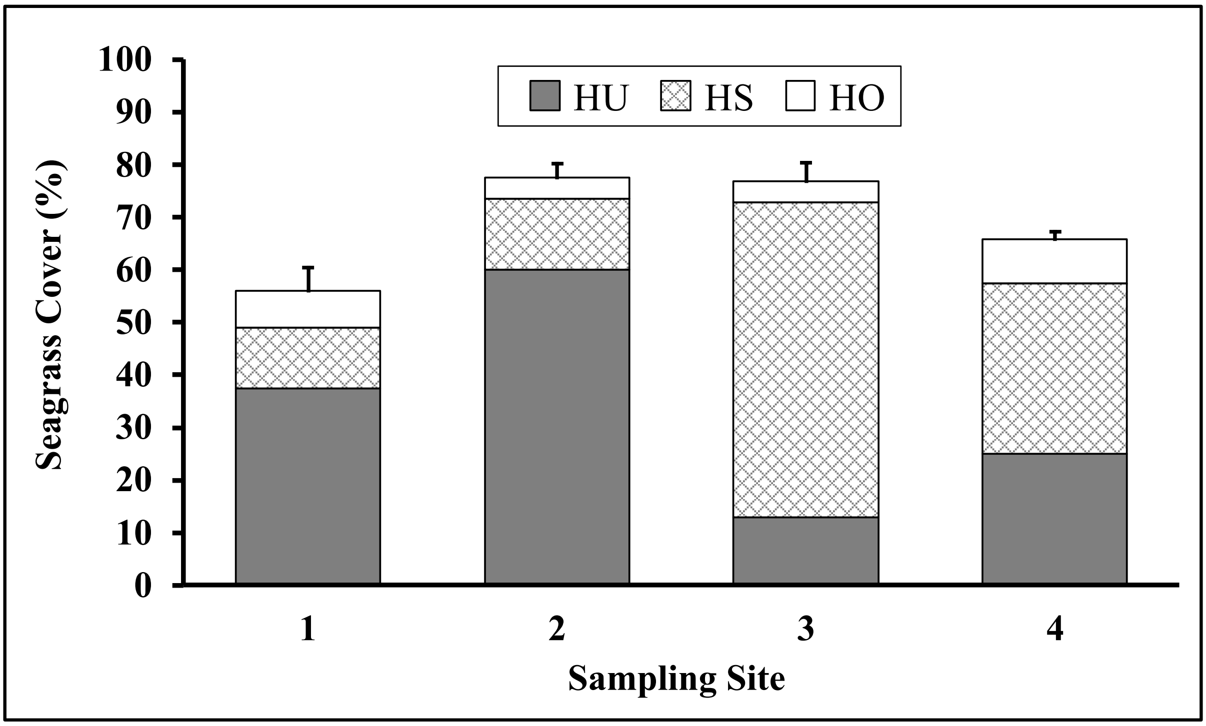

Figure 5.5. Seagrass species composition as well as total and relative cover (%) at selected sites sampled in the summer (site: 1–2) and winter (site: 3–4) feeding grounds of large dugong groups (>50 dugongs) around Hawar Island, Bahrain (HU= *Halodule uninervis*, HS= *Halophila stipulacea*, HO= *H. ovalis*).

4.3 Anthropogenic correlates of large dugong group distribution

The territorial waters of Bahrain have been extensively fished over the last three decades with fishing intensity increasing over time. Across time intervals, fishing grounds mitch-matched considerably with important dugong areas as both historical and recent dugong sightings overlapped with the corresponding fishing charts: 92% overlap, 1–3 years; 91% overlap, 4–15 years; and 36% overlap, 16–30 years (Figure 5.6). Throughout dugong distribution around Bahrain and across all time intervals, fishers used multiple fishing gear including lines, wire cages, and nets. Nearly 87% of LOA overlapped with productive fishing grounds primarily targeted in 2019–2021 for finfish and crabs using hemisphere and cylindrical wire cages, gillnets, and line (Figure 5.7). The large fleet observed fishing at these grounds was mostly comprised of small speedboats equipped with a single outboard engine. Although featured with less boat traffic intensity compared to some other areas around Bahrain, the shallow waters surrounding Hawar experienced high maritime traffic that ranged on average <3, 4–17, 18–100, and 101–467 route .5 km^{-2} $year^{-1}$ at 11%, 53%, 16%, and 21% of LOA, respectively. Confirming our field observations, fishing boats accounted for the bulk of this traffic occupying 96% of the areal extent of LOA whereas 14% of this area overlapped with a ferry line (~ 3–103 route .5 km^{-2} $year^{-1}$).

We regularly observed LDGs grazing while they were <1 km from slow moving fishing boats. These groups, however, got disturbed after the approaching vessel had sailed at higher speeds or approached closer (<500 m). In particular, LDGs were considerably sensitive towards the noise generated from starting the boat engines or changing the mechanical throttle control. The sequential behavioural response of LDGs to approaching vessels consisted of an initial tail slapping of the water surface followed by mass diving and short distance directional movement (~150–500 m) before the group settled again and promptly resumed grazing. However, on few occasions when animals were repeatedly harassed by boats, we observed LDGs swimming away at high speeds to >1.5 km with repeated tail slapping. Unlike LDGs, all solitary or paired dugongs (n= 69 sightings) encountered during the boat surveys fled after spotting the boat from distance and did not resume grazing.

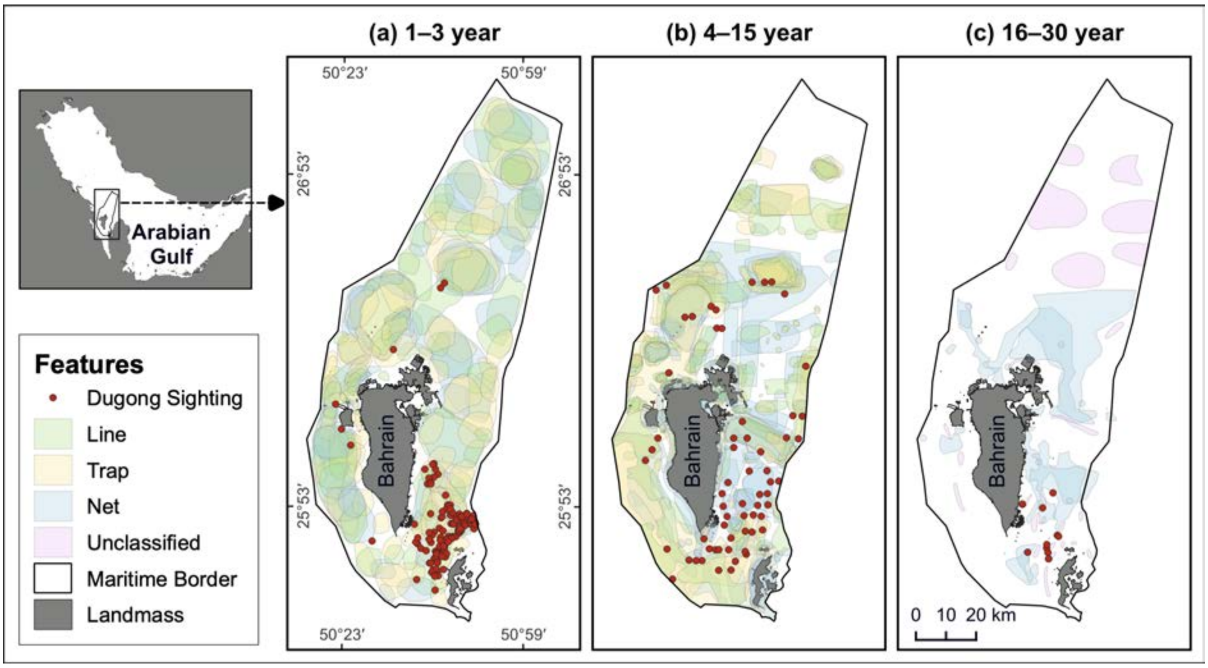

Figure 5.6. Fishing grounds across the territorial waters of Bahrain marked with the main fishing gear used. The polygons are classified to three time intervals and overlaid with dugong sightings recorded by the corresponding aerial and/or boat surveys as well as citizen science reports: (a) 1–3 year (2019–2021 citizen science network and boat-based surveys overlaid on 2019–2021 fishing map developed through structured interviews), (b) 4–15 year (2006 aerial survey (Hodgson, 2009) overlaid on 2006 fishing maps (Zainal & Abdulqader, 2009)), and (c) 16–30 year (2000 aerial survey (Bell, 2001) overlaid on 1992/1996/2000 fishing map (Al-Zayani, 2003)). The 2000 aerial survey covered only the shallow waters around Hawar Island.

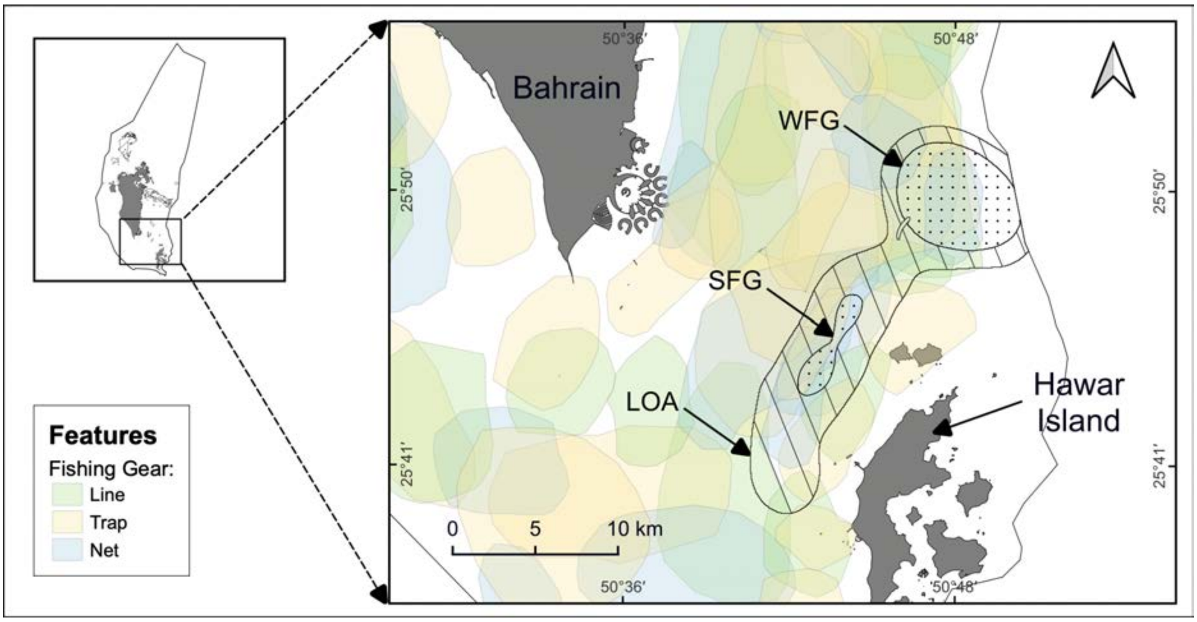

Figure 5.7. Overlap between 2019–2021 fishing grounds marked with the main fishing gear used, and the extent of the main occupancy area of large dugong groups (>50 dugongs) around Hawar Island, Bahrain (LOA= main large dugong group occupancy area, WFG= winter feeding ground, SFG= summer feeding ground).

4.4 Analysing key drivers of large dugong group distribution

The *GLM* pinpointed that the main variable governing the probability of sighting LDGs was the presence of large seagrass meadows while it decreased sharply with increasing distance from nearest seagrass patch (Figure 5.8). The influence of boat traffic was nearly significant (Table 5.1). In contrast, neither seasonal seawater temperature, bathymetry, water velocity, habitat type nor fishing gear influenced the probability of sighing LDGs around Bahrain.

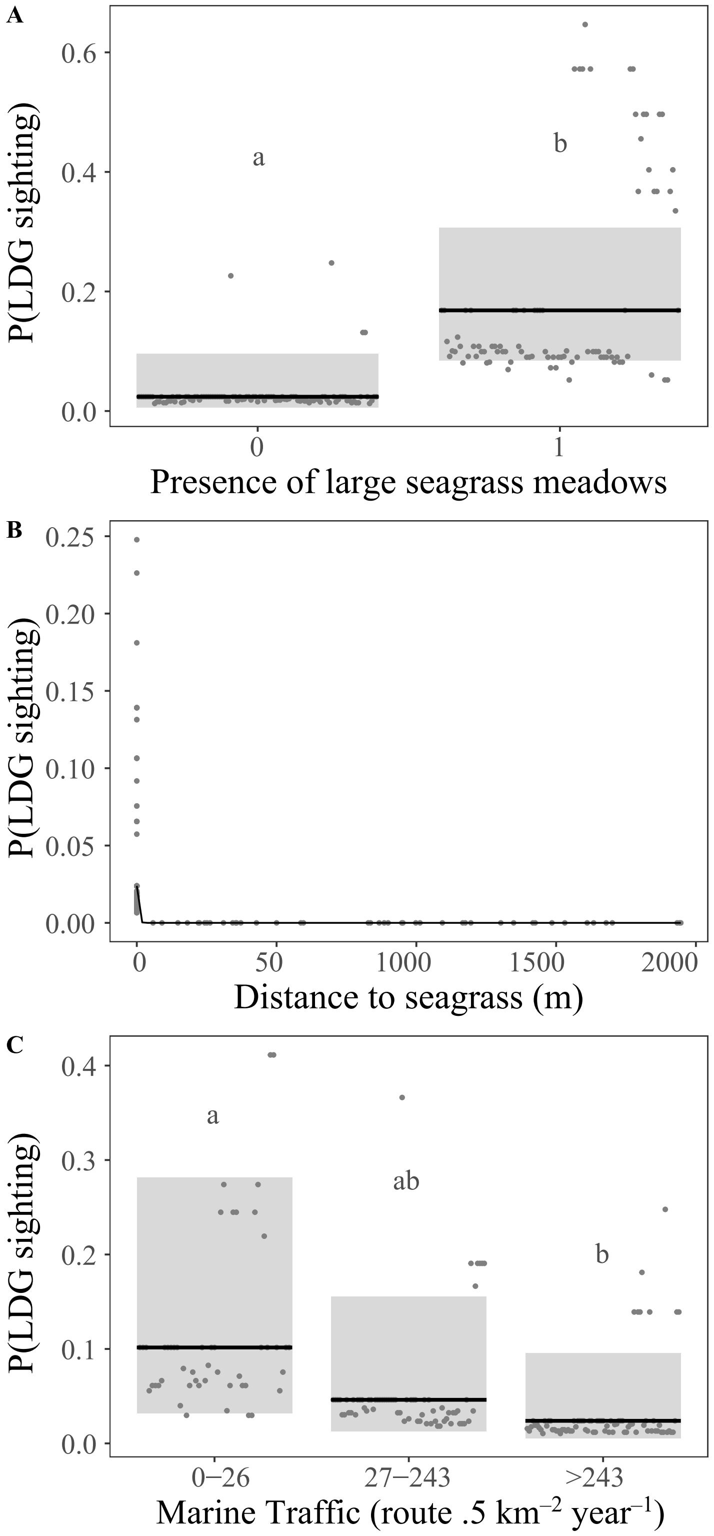

Figure 5.8. Key covariates influencing the probability of sighting large dugong groups (LDG; >50 dugongs) around Bahrain determined by Generalized Linear Models (*GLMs*), conducted on spatial explicit large dugong group sighting data obtained during 2019–2022 through structured interviews, citizen science network and boat surveys.

Table 5.1. Output of the Generalised Linear Models (*GLMs*) illustrating the environmental, ecological, and anthropogenic covariates (independent variables) governing the spatial distribution of large dugong groups (>50 dugongs) around Bahrain.

Independent Variable	**LR Chisq**	**DF**	**p$^{\#}$**
Summer Sea Surface Temperature	2.282	1	.131
Large seagrass meadows	13.617	1	< .001 **
Distance from seagrass	8.964	1	.003 **
Fishing nets	2.853	1	.091 .
Boat Traffic	6.009	2	.049 .

$^{\#}$ Significance codes: '***'= 0, '**'= .001, '*'= .01, '.'= .05

5 Discussion

Hawar Island harbours some of the largest persistent groups of dugongs worldwide that congregate in distinct winter and summer aggregation sites. In situ observations confirmed that these sites were used mostly as feeding grounds for hundreds of dugongs aggregating in clumped groups. The main large dugong group occupancy area was characterised by large contiguous stretches of shallow dense seagrass meadows that, according to our models, appear to be the main factor determining the LDG distribution. Other factors including seawater temperature, currents, and depth did not help predict where dugongs aggregate around Bahrain forming LDGs. Unfortunately, these areas overlapped almost completely with productive fishing grounds persistently fished for at least the last 30 years.

Dugongs around Hawar have occupied the same core areas for >35 years (Preen, 1989, 2004; Vousden, 1995). Unsurprisingly, these groups aggregate around resource concentrations (O'Shea et al., 2022), characterised by extensive shallow sheltered seagrass meadows as observed elsewhere (Preen, 1992; Hodgson, 2004). Their year-long persistence over decades despite their large dietary requirements (~ 28.5–30.5 WW d^{-1} per dugong; Preen, 1992; Aragones, 1994, 1996) suggests that these core areas are likely productive enough to support such constant grazing pressure. Unlike the areal seagrass coverage, our model indicated that the presence/absence of seagrass alone could not predict the LDG distribution. For the LDG habitats to sustain such high densities of dugongs through time, meadows need to be large, productive and with high nutritional values in order to maximize the energy dugongs can extract per unit area (Preen, 1995; Marsh et al., 1999; Sheppard et al., 2007; Burkholder et al., 2012). We found that LOA harboured extensive meadows, characterised by the fast-growing, nutrient rich seagrass genera, *Halophila* and *Halodule* (Preen, 1995; Marsh et al., 1999; Sheppard et al., 2007; Burkholder et al., 2012). Although LDGs have been reported to graze on other seagrasses, pioneer species in this genera are an important forage for these groups across their range (Preen, 1989, 1992, 1995; Anderson, 1998; Holley, 2006), potentially influencing their spatial and grouping patterns (Hodgson, 2004). These pioneering species are also among the best adapted to offset dugong grazing pressure; thanks to their rapid growth and re-colonization abilities (de Iongh et al., 1995; Preen, 1995; Nakaoka & Aioi, 1999; Sheppard et al., 2007; D'Souza et al., 2015). That said, given the high densities of LDGs around Hawar (~700 dugongs < .5 km^{-2}) and the average daily dugong consumption rate of seagrass, the LDGs' daily foraging requirements could be between 19–21 ton WW d^{-1}, making them particularly susceptible to habitat deterioration and loss.

The dependence of LDGs on extensive contiguous meadows makes the developmental plans for this region particularly worrying. A slew of mega development projects have been proposed in south-east Bahrain that involve intense reclamation and dredging operations (Hodgson, 2011; Preen et al., 2012; Zainal et al., 2012; Al-Abdulrazzak & Pauly, 2017; Burt & Bartholomew, 2019). This could result in large-scale deterioration and fragmentation of the meadows around Hawar, making them increasingly unable to support LDGs. Habitat decline may force the large dugong groups to move to more distant, potentially less productive foraging grounds (Preen & Marsh, 1995; Hodgson, 2004; Deutsch et al., 2022a) or a breakup of large groups into more disperse aggregations. Given the transboundary nature of this population (Preen, 2004; Marshall et al., 2018), LDGs are likely to be affected by developments in other neighbouring range states as well, highlighting how important regional management coordination is for wide-ranging marine species like dugongs. Habitat decline and reduced seagrass availability could also have flow-on fitness consequences for the population, with dugongs reported to reduce their investment in reproduction in response to seagrass loss (Preen & Marsh, 1995; Marsh et al., 2002; Marsh & Kwan, 2008).

The distribution of LDGs around Bahrain largely overlapped with shallow sheltered seagrass meadows (Preen, 1989, 2004; Vousden, 1995), confirming a general trend for both scattered dugongs and large groups across the Indo-Pacific (Anderson, 1981; Preen, 1989, 1992; Marsh et al., 1999, 2002, 2011; Aragones & Marsh, 2000; Hodgson, 2004, 2009, 2011; Sheppard et al., 2006; D'Souza et al., 2015; Ponnampalam et al., 2015; Cleguer et al., 2017; Rabaoui et al., 2021; Derville et al., 2022). Another important result of our work is that seawater temperature did not reliably predict the core distributional areas of LDGs, and the waters around Hawar were not influenced by persistent localized warm water discharges. This is unexpected given that these discharges have long been proposed as a strong driver inducing the formation of LDGs in the Arabian Gulf (Preen, 1989, 2004; Preen et al., 2012; Deutsch et al., 2022a). In fact, the minimum temperatures we recorded around Hawar were below the 18 ºC lower thermal threshold that dugongs normally tolerate (Sheppard et al., 2006; Marsh et al., 2011). That said, our results do not necessary rule out the potential role of thermoregulation in shaping the dugong grouping behaviour around Hawar, particularly considering the observed tendency of dugongs to form larger and tighter groups in cold months.

The long-term coexistence between dugongs and fishers indicates that the risk of net entanglement in addition to boat strikes and disturbances are all prominent anthropogenic features of dugong habitats around Bahrain, including LOA. In particular, given the high abundance and clumped density of large dugong groups, the illegal use of long drift gillnets (Hodgson, 2009; Preen et al., 2012) could result in mass dugong mortality if practiced around Hawar, adding evidence to the mounting threats of bycatch on dugongs in the Arabian Gulf (Knight et al., 2011; Environment Agency-Abu Dhabi, 2014; Abdulqader et al., 2017).

Several studies describe that, when approached by a boat, LDGs stop feeding, and initiate short distance coordinated mass movements after signalling with alarm calls, returning to feed only when the vessel has retreated to a safe distance (Anderson, 1981; Preen, 1992; Hodgson & Marsh, 2007). This matches our field observations for large dugong groups around Hawar which remarkedly differed from the reactions of scattered dugongs. Similarly, other group-living animals have sentinel individuals that respond to perceived risks with alarm signals; the collective vigilance benefits this provides helps maximize energy intake and is an important advantage of group living (Acevedo-Gutierrez, 2009; Zuluaga, 2013; Brakes & Dall, 2016). As such, the observed vigilance behavioural adaptation seems an added fitness benefit enabling aggregating dugongs around Hawar to maximize their energy intake budget at traditional feeding grounds experiencing intense maritime traffic. This adaptation has likely been essential to LDGs around Hawar co-existing with fishers over decades, reducing the risks of collision with fishing boats. However, this strategy seems conditional on the availability of unfragmented extensive seagrass meadows. Large meadows enhance the resilience of LDGs

(Hodgson, 2004), because when these groups decide to move in response to disturbances, they can still find nearby high-quality feeding spots without bearing the cost of traveling over long distances (Hodgson & Marsh, 2007). That said, the fleeing behaviour of some LDGs in response to repeated harassment suggests that these groups survive close to their maximum disturbance tolerance. If the mounting pressures of fishing and motorised boats continue unchecked in these waters, dugongs are likely going to be increasingly stressed and suffer significant lethal and sublethal consequences to their population.

The multidisciplinary assessment conducted in this study has provided insight on attributes featuring LDG distribution. However, the study design was limited by some caveats that should be considered while interpreting the results. The exclusions of the northern offshore waters from the sampling grid, and the inaccuracy inherently associated with structured interviews have introduced limitations to the *GLM* modelling outcomes. Also, updated fine-scaled mapping of seagrass meadows across the entire Gulf of Bahrain would have enabled better understanding of the role of seagrasses in shaping the LDG distributional patterns.

The large dugong group habitat correlates identified in this study provide clear insights informing their conservation. Crucial for the maintenance of the globally important Arabian Gulf's dugong population, the future persistence of these groups is dependent on the maintenance of extensive unfragmented healthy seagrass meadows and imposing control on intensifying fishing and boating activities. Local fishers need to be enlisted as co-managers in this process, given that both fishers and dugongs share an interest in maintaining the productivity and health of the seagrass meadows around Hawar. Like all wide-ranging species that move across jurisdictions and are dependent on habitat condition, the conservation of dugong populations will need coordination and cooperation at every level, with fishers, coastal businesses as well as local and regional governments coming together to make common cause to protect this enigmatic species in the Arabian Gulf.

6 Acknowledgments

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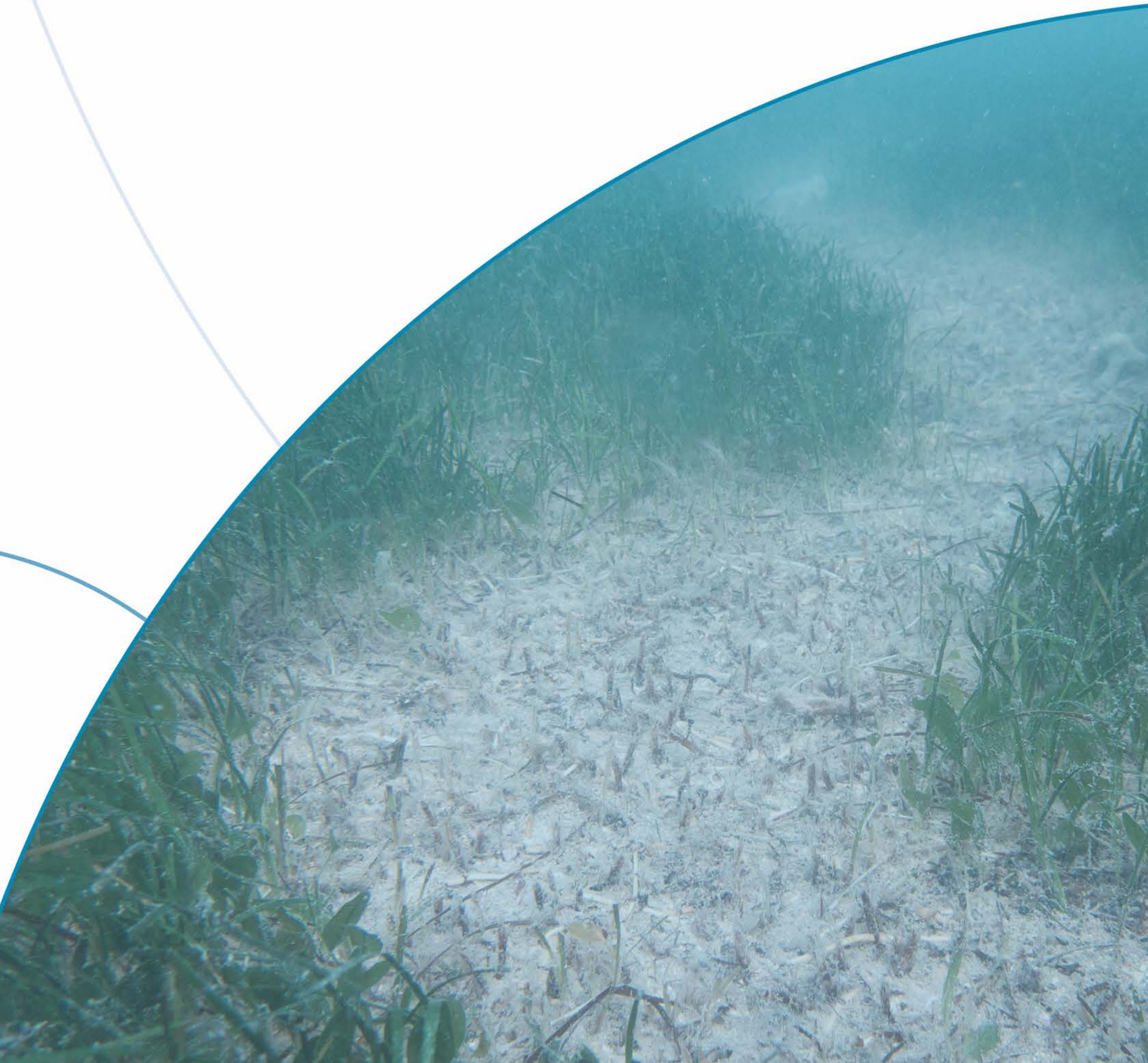
6

How do seagrasses in extreme environments cope with dense megaherbivore populations? Understanding the persistence of dugong feeding grounds in the Arabian Gulf



1 Abstract

The survival of marine megaherbivores, such as dugongs, is conditional on the capacity of their feeding grounds to persistently sustain their mass dietary needs. This coping ability is constrained where seagrass meadows survive under extreme conditions, and megaherbivores congregate forming large aggregations. Understanding how seagrasses cope with such multiple pressures is critical to support evidence-based conservation management. We explored dugong feeding ground dynamics in the Arabian Gulf, where seagrass meadows experience some of the harshest temperature and salinity worldwide, and grazed by the world's largest dugong groups. We compared dugong herbivory with seagrass primary production at 18 seagrass sites around Jabal Ali Wildlife Sanctuary (United Arab Emirates) and Hawar Island (Bahrain). At each site, we used secondary dugong foraging signs (i.e., feeding trails) to estimate seagrass area consumed by dugongs. In parallel, we monitored seawater temperature and salinity, and experimentally tracked simulated trails to determine post-grazing seagrass recovery. Temperature and salinity ranges (15.8–36.7 ºC and 41.9–53 psu, respectively) were considerably broader than the corresponding optima for seagrass species, reported in other regions. Nevertheless, primary production was generally within the global range, and dugong consumption across most sites was well below the production rates (<2%). However, at two feeding grounds, persistently grazed by dugong groups of hundreds, the consumption occasionally exceeded primary production (mean: 57–87%; maximum: 109%), raising the question of how Hawar Island's meadows cope with such sustained intense dugong herbivory. Both areas were foraged only seasonally, as dugong groups make small-scale seasonal movements between winter and summer feeding grounds. Experimental trails regained cover within 4–6 months, indicating fast recovery of the alternately grazed seasonal feeding grounds. Our results showed that despite harsh environmental settings, both production regimes and dugong seasonal movements ensure that feeding grounds cope well with intense seasonal dugong grazing, allowing clumped large dugong groups to persist around Hawar Island for decades. Given the global importance of dugongs in the Arabian Gulf and their persistence in space and time, it is crucial that regional efforts place seagrass meadow conservation front-and-centre of dugong management efforts to ensure that key feeding grounds continue to sustain such large megaherbivore population.

Keywords: dugong, marine mammal, Arabian Gulf, seagrass, herbivory, climate change, conservation management

2 Introduction

The dugong (*Dugong dugon*, Müller, 1776) is the largest exclusively marine megaherbivore (>10 kg; Bakker et al., 2015) alive today (Aragones et al., 2012b; Bakker et al., 2015, 2016; Keith-Diagne et al., 2022; Marshall et al., 2022). These charismatic animals occupy warm tropical and subtropical Indo-Pacific waters with distributional range spanning over 128,000 km of coastline (Marsh et al., 2011; Marsh & Sobtzick, 2019). Globally considered as vulnerable to extinction (Marsh & Sobtzick, 2019), dugongs have contracted substantially in distribution and declined dramatically in abundance as a result of long history of indirect and direct human impacts, resulting in local extinction of a number of sub-regional populations (Marsh & Sobtzick, 2019; International Union for Conservation of Nature, 2022; Lin et al., 2022a, 2022b). Across much of their Indo-Pacific distribution, dugongs are threatened by incidental drowning in fishing nets, degradation of primary habitats, collisions with boats, land- and sea-based pollution as well as climate change (Hodgson, 2009; Reynolds III & Marshall, 2012; Marshall et al., 2018; Marsh & Sobtzick, 2019; Deutsch et al., 2022b; Marsh et al., 2022; Ponnampalam et al., 2022). However, as much as it is increasingly assigned high priority by range states, the conservation of dugongs is equally challenging given that these wide-ranging mammals occupy extensive home ranges, sometimes straddling several political jurisdictions. A pragmatic approach to address these challenges, at least in part, is through identifying and managing high-use areas, particularly where dugongs persistently forage (Garrigue et al., 2008; Pilcher et al., 2014; di Sciara et al., 2016; Tol et al., 2016; Cleguer et al., 2020).

Dugongs spend much of their time (>40%) grazing in seagrass meadows (Chilvers et al., 2004; Hodgson, 2004; Shawky, 2018; O’Shea et al., 2022), where they tend to persist in time and space within traditional feeding grounds (D’Souza et al., 2013, 2015; Marsh et al., 2022; O’Shea et al., 2022). How seagrasses cope with dugong herbivory pressure influences the dugong habitat use and persistence patterns within these grounds. Seagrass meadows themselves are experiencing intensifying anthropogenic stressors leading to large-scale deterioration, fragmentation, and losses across seascapes (Seddon et al., 2000; Orth et al., 2006; Waycott et al., 2009; Unsworth et al., 2019; Dunic et al., 2021). With both marine megaherbivores and their key seagrass habitats witnessing drastic human-induced declines, understanding complex seagrass-megaherbivore interactions at the feeding grounds is critical to inform effective conservation and evidence-based spatial planning (Aragones & Marsh, 2000; Bakker et al., 2015; Scott et al., 2018). This enables managers to clearly define high-use areas, crucial for the survival of both seagrasses and dugongs as well as sustaining the valuable services they both provide.

The dietary needs of megaherbivores exert substantial grazing pressures on seagrasses which results in modifications in canopy height, structural complexity, regeneration time, productivity, reproductive strategies, and population dynamics, among others (Preen, 1992; Nakaoka & Aioi, 1999; Aragones et al., 2012b; Kelkar et al., 2013b; Bakker et al., 2015, 2016; Scott et al., 2018). These impacts are density-dependent, profoundly intensifying where megaherbivores aggregate in large numbers to feed (Aragones & Marsh, 2000; Heithaus et al., 2014; Bakker et al., 2015, 2016; D'Souza et al., 2015; Hays et al., 2018; Scott et al., 2018; Marsh et al., 2022; O'Shea et al., 2022). Eventually, the long-term coexistence between megaherbivores and seagrass meadows is conditional on maintaining primary production at a rate exceeding biomass consumption. Over the last few decades, there has been an increasing recognition of the role of feeding grounds as a conservation unit for marine megaherbivores. For example, feeding grounds have been increasingly the focus of intensive research following unprecedent booms in a number of green turtle populations (Heithaus et al., 2014; Christianen et al., 2021; Meylan et al., 2022). Where rapid recoveries of local green turtle populations have occurred, their foraging has induced large-scale degradation of seagrass ecosystems, leading in extreme cases to the functional collapse of feeding grounds (Kelkar et al., 2013a; Heithaus et al., 2014; Bakker et al., 2015; Scott et al., 2018; Hearne et al., 2019; Gangal et al., 2021). Similarly, overgrazing is of a serious concern for dugongs particularly considering their destructive excavating feeding mode that entails the uprooting of whole seagrasses from the substrate and the generation of clouds of fine sediment (Aragones et al., 2012b; Bakker et al., 2015; D'Souza et al., 2015; Keith-Diagne et al., 2022). Such impacts can be detected even when dugongs are in low numbers such as in the Andaman Sea where a sparse dugong population has been reported to consume substantial amounts of seagrass production (D'Souza et al., 2015). Where dugongs form dense groups, the associated mass grazing has been reported to modify seagrass species composition, and suggested to maintain seagrasses at a young seral stage. Termed 'cultivation grazing', this strategy has been hypothesized to enhance foliage quality for the benefit of foraging dugongs (Preen, 1992, 1995; Aragones & Marsh, 2000; Hodgson, 2004; Aragones et al., 2006).

Seagrass primary production varies considerably in relation to local environmental conditions and is strongly influenced by light, nutrients, and temperature, among other abiotic and biotic factors (Alcoverro et al., 1995; Vermaat et al., 1995; Fourqurean et al., 2001; Collier et al., 2012; Bennett et al., 2022). Environmental tolerance, also, varies with localities and seagrass species, and as local conditions get harsher, some species become increasingly unable to cope. Even relatively hardy species perform best within a certain optimum range, whereas their production progressively declines beyond a turning point (McMillan, 1984; Ralph, 1998; Wesselmann et al., 2020). Generally, prolonged exposure to extreme conditions may mediate profound fitness costs resulting in reduced seagrass growth and reproduction as well as increased mortality (Georgiou et al., 2016; Collier et al., 2018; Wesselmann et al., 2020; Nguyen et al., 2021). For instance, whereases *Zostera muelleri* in the Great Barrier Reef shows substantial reduction in photosynthesis at 33 °C, this temperature is optimal for *Halodule uninervis* which almost doubles its photosynthesis compared to 27 °C (Collier et al., 2011). In Tanzania, the growth of *Halophila ovalis* records optima at 25–26 °C, while with temperatures rising beyond 30 °C, its growth shows a sharp declining trend followed by shoot mortality at >33 °C (John et al., 2016). In the Red Sea, *H. stipulacea* survives across a broad thermal range (8–36 °C) but its growth declines with temperature dropping below 17 °C (Wesselmann et al., 2021).

In harsh environments, dugong herbivory may place a disproportionate additional burden on seagrasses making feeding grounds experiencing environmental extremes likely less capable of supporting intense dugong grazing. This is why seagrass meadows in the Arabian Gulf are so intriguing. These meadows are exposed to some of the harshest environmental conditions anywhere in their range and have to deal with extreme levels and wide ranges of temperatures (10–45 °C) and salinity (38–70‰; Basson et al., 1977; Price & Coles, 1992; Kenworthy et al., 1993; Vousden, 1995; C. Sheppard et al., 2010; Al-Wedaei et al., 2011; Erftemeijer & Shuail, 2012; Al-Bader et al., 2014; Qurban et al., 2019b; Alosairi et al., 2020; Howells et al., 2020). The only three seagrass species that tolerate such harsh conditions create extensive meadows (>7000 km^2; Erftemeijer & Shuail, 2012; Qurban et al., 2019a), home to the second largest dugong population in the world (Marsh et al., 2002; Preen, 2004; Hodgson, 2011; Preen et al., 2012). While many of the Arabian Gulf's dugongs are solitary or in small groups, they aggregate forming some of the world's largest dugong groups (~700 dugongs; Preen, 2004; Marsh et al., 2011; Preen et al., 2012; O'Shea et al., 2022). How these meadows cope with the additional pressure of dugong herbivory is an open question. Scarce little is known of seagrass-dugong interactions in this environment and how the Arabian Gulf′s feeding grounds are faring under the pressure of sustained intense grazing. Clearly, this is a wide gap in our ability to plan conservation management strategies as any unbalance may impose unpredictable consequences on this globally important dugong population.

In this study, we report on the dugong feeding ground dynamics across 18 seagrass sites in the Arabian Gulf. We compared seagrass production with dugong herbivory rates along wide gradients of dugong grazing, including sites around Hawar Island, Bahrain where large dugong groups (LDGs; >50 dugongs) have been regularly sighted. To this extent, we combined spatially explicit seasonal seagrass production and secondary signs of dugong grazing (i.e., visible feeding trails) to compare primary production with seagrass area consumed by dugongs. Additionally, in a subset of the studied meadows, we tracked the recovery of experimentally simulated feeding trails to determine post-grazing seagrass recovery under the harsh environmental conditions these meadows are subject to. In light of these results, we discuss the relationship between primary production and dugong herbivory as well as the persistence patterns of large dugong groups while emphasizing the need to integrate feeding ground ecology in the conservation management of marine megaherbivores and their key habitats.

3 Materials and Methods

3.1 Study area

This study was carried out along the southern coast of the Arabian Gulf at Jabal Ali Wildlife Sanctuary (JAWS), Emirate of Dubai, United Arab Emirates and around Hawar Island, Kingdom of Bahrain (hereinafter ‘around Hawar’). A subtropical marginal young sea protruding from the Indian Ocean, the shallowness and land-locked nature of the Arabian Gulf mediates the prevalence of harsh environmental settings (Basson et al., 1977; Price et al., 1993; Vousden, 1995). Nevertheless, the Arabian Gulf harbours a diversity of coastal and marine habitats including mudflats, mangroves, saltmarshes, algal beds, seagrasses, and coral reefs (Basson et al., 1977; Price & Coles, 1992). Of these, the environmentally and socioeconomically significant seagrass habitat (dominated by three early successional species: *H. uninervis*, *H. stipulacea, and H. ovalis*) is the most dominant forming vast meadows extending along the southern and western coasts (Vousden, 1995; Al-Zayani et al., 2009; Abdelbary & Al Ashwal, 2021). These meadows harbour a sizeable dugong population (~5,800 dugongs; Preen, 2004) unevenly distributed off Saudi Arabia, Bahrain, Qatar, and United Arab Emirates. The selected study locations (i.e., JAWS and Hawar, Figure 6.1) represent contrasting dugong abundances. At JAWS, dugongs are sparse and occupy relatively small seagrass meadows. In contrary, the extensive seagrass meadows surrounding Hawar encompass the second important dugong area in the Arabian Gulf (Preen, 2004; Hodgson, 2011; Preen et al., 2012; Marshall et al., 2018). Of global significance, dugongs around Hawar aggregate forming the largest dugong groups worldwide. These groups have persisted for several decades at the large dugong group occupancy area almost year-round. This area extends over ~145 km^2 of mostly seagrass beds encompassing 95 percentage volume contours (95% PVC; hereinafter home range) in addition to 50% percentage volume contours (50% PVC) representing distinct winter and summer feeding grounds (WFG and SFG, respectively) across which LDGs alternately graze (Figure 6.1). These areas, also, are productive fishing grounds, targeted by a sizeable fishing fleet, exposing LDGs to the risks of gill net entanglement and boat strikes.

3.2 Study design and site selection

To explore seagrass production-dugong herbivory dynamics under the extreme environment of the Arabian Gulf, we followed two main approaches: (i) large-scale field-based surveys of seagrass primary production and dugong grazing across 18 sampling sites, and (ii) in-water experiments to estimate post-grazing seagrass recovery where we simulated dugong feeding trails in a subset of the surveyed seagrass meadows. The first approach determined seagrass primary production under the environmental extremes and dugong herbivory pressures across the study area, crucial to understand the potential persistence of LDGs at particular feeding grounds. The second approach provided an insight on how seagrasses cope with dugong herbivory in such harsh environment, whether dugong herbivory induces any detectable modifications in seagrass communities as well as how long it takes for a given seagrass meadow to fully recover following dugong grazing.

We conducted large-scale rapid assessment surveys by snorkelling, SCUBA, and a towed video camera system (Splashcam Deep Blue, Ocean Systems, USA) to identify seagrass areas along wide gradients of dugong feeding trail cover, water depth, substrate type as well as seagrass species composition and abundance. Based on these results, a total of 18 sites (hereafter sampling sites) in JAWS and Hawar were selected and assessed for dugong herbivory and seagrass ecology (Figure 6.1). At each sampling site, we marked the geographical coordinates using a hand-held global positioning system (GPS) and measured water depth through the boat's or hand-held echosounder (Hondex PS-7, Honda Electronics, Japan).

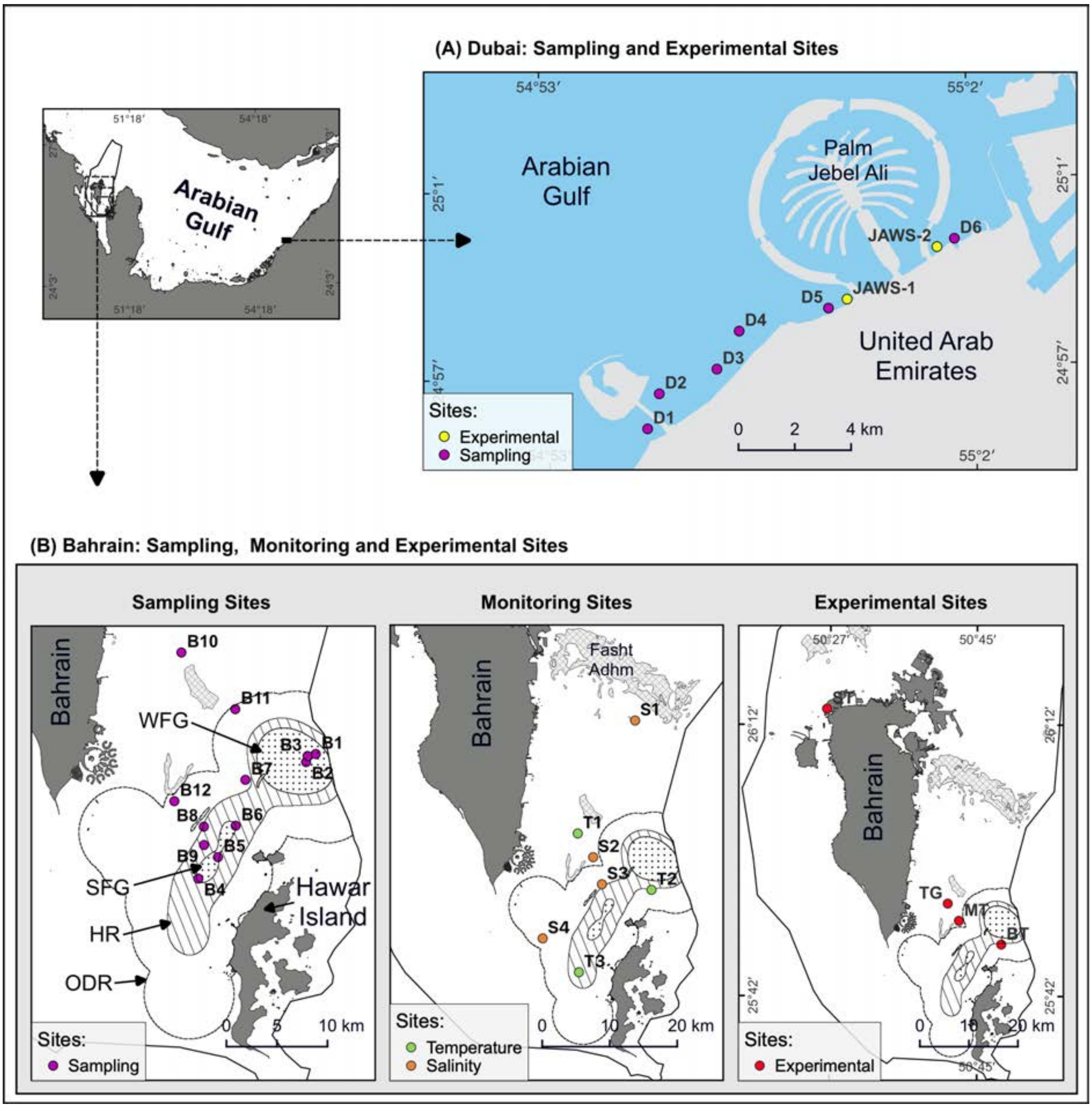


Figure 6.1. Location map of the study area around: (A) Jabal Ali Wildlife Sanctuary (JAWS, Dubai, United Arab Emirates), and (B) Hawar Island (Bahrain), showing the sampling, water quality monitoring, and experimental sites in addition to the large dugong group (>50 dugongs) main occupancy area around Hawar (B= sampling site around Hawar, D= sampling site at Jabal Ali Wildlife Sanctuary, HR= home range, WFG= winter feeding ground, SFG= summer feeding ground, ODR= overall distributional range of large dugong groups, T= temperature monitoring site, S= salinity monitoring site, ST= Salman Town, TG= Fasht Tgailib, MT= Mashtan Island, BT= Fasht Buthur).

All sampling was undertaken from June 2019 to October 2022 and repeated over two main seasons: winter (December-March) and summer (May-October; see Vousden, 1995) to account for potential seasonal variations in seagrass primary production and dugong herbivory. Exceptionally, two sites around Hawar (i.e., B5 and B6) and one site in JAWS (i.e., D3) were surveyed only in one season due to logistic constrains (Figure 6.1).

3.3 Dugong herbivory and primary production across sampling sites

At each sampling site and across seasons, we deployed three random 50 m transects, with ~20 m distance intervals, along which both dugong herbivory and primary production were assessed. To estimate dugong herbivory, we obtained the following variables at the transect level: dugong feeding trail cover, age of the feeding trails as well as biomass consumed by dugongs. Along the deployed three transects, we established 50 × 10 m^2 visual belt transects which were carefully inspected for any dugong feeding trails (D'Souza et al., 2015). Upon encountering distinctive trails, we calculated their percentage cover through dividing the estimated total area occupied by dugong feeding trails (m^2) by the total seagrass aerial extent observed within the transect (m^2), and then multiplied it by 100. The resultant percentages were then averaged for each sampling site for a particular season. In parallel, a trained observer estimated the age of the dugong feeding trails observed along the belt transects based on a 3-grade ordinal scale. To this extent, we fist used the results obtained from the simulated trail experiment to transform the seagrass regrowth percentages, estimated while tracking the recovery of the simulated trails, to time (see below for more details). Following this approach, we estimated the age of the dugong feeding trails encountered *in situ* along the transects as follow: (i) recent trails: 15 days, <5% seagrass recovery; (ii) medium trails: 45 days, <30% seagrass recovery; and (iii) old trails: 75 days, >30% seagrass recovery.

We collected 15 × 15 cm biomass quadrats, equally distributed across the deployed transects (replicates: 6 and 3 per site for a given season at JAWS and Hawar, respectively). When the deployed quadrat corresponded to bare substrate or other habitats, we sampled the nearest seagrass area along the transect. Using a handheld scrapper, all seagrass shoots, rhizomes, and roots inside the quadrat frame were carefully harvested and transferred to mesh bags. The collected samples were thoroughly rinsed with freshwater to remove salt, sediment particles, and epiphytes and frozen at –5 °C. Later, seagrass shoots were sorted into species, differentiated into apical (i.e., growing apices) and lateral (i.e., secondary) shoots, and counted.

Total and relative seagrass shoot density was estimated as the number of shoots per unit area (shoot m^{-2}). The sorted shoots were then separated into aboveground (i.e., blades and petioles) and belowground (i.e., rhizomes and roots) parts, dried in an oven at 60 °C for 48 hours, and weighed to the nearest milligram using a microbalance (see Dawes & Kenworthy, 1990). Total and relative seagrass biomass was then calculated and expressed as dry weight of seagrass per unit area (g DW m^{-2}).

To estimate the average removal percentage of seagrass biomass within a feeding trail by a grazing dugong around Hawar, we had followed four LDGs while grazing until they moved to other feeding spots and then examined the left feeding trails on SCUBA (Figure 6.1). Using a fiberglass measuring tape, we estimated the length (one replicate) and width (four replicates) of 20 fresh dugong feeding trails. The freshness of the trails was recognized from their steep edges and loose surface sediment, exposed seagrass roots and broken rhizomes as well as the smothering of seagrasses growing along their edges (Preen, 1992; D'Souza et al., 2015; Budiarsa et al., 2021). Later, we estimated the seagrass grazed by dugongs within each trail through establishing 15 × 15 cm quadrats inside (four replicates) and outside (four replicates) the trail. We identified all seagrass species within the quadrats and calculated relative and total shoot density (shoot m^{-2}). Difference in average shoot density between outside and inside the trail was then calculated and expressed as total and relative percentages of seagrass shoots removed by a grazing dugong. The obtained percentages were then multiplied by the average shoot count and the trail's areal extent to estimate the count of shoots off-taken by dugongs along each trail. This was further multiplied by the average biomass per shoot for a given seagrass species (see below) to estimate total seagrass biomass removed by a grazing dugong per trail. At JAWS, we examined the seagrass species composition and shoot density along the edges of a set of 10 trails following the same quadrat method.

All above obtained results were then used to calculate the overall dugong herbivory (g DW m^{-2} d^{-1}) at the transect level for each site. To this extent, we first calculated total seagrass biomass off-taken by dugongs by multiplying average total seagrass biomass (g DW m^{-2}) within the transect by average seagrass removal percentage (%) and total dugong feeding trail cover (%). The resultant estimate was then divided by the average trail age and multiplied by 100. If more than one trail age class was observed along a given transect, we multiplied the corresponding trail cover of each grade by their respective age. After obtaining dugong herbivory for the three transect replicates, the estimates were then averaged to calculate overall dugong herbivory at the site level for a particular season.

To estimate primary production (g DW m^{-2} d^{-1}) across sampling sites, we first obtained the following variables at the transect level: total seagrass cover (m^2), relative new shoot production rate (shoot $apical^{-1}$ d^{-1}), relative apical shoot density (apical m^{-2}) as well as relative shoot biomass (mg DW $shoot^{-1}$). We estimated the production from the apical shoots only since the three seagrass species present in the study area generate primary production mainly by adding new apical shoots. Along the three benthic transects deployed to explore dugong herbivory at the sampling sites (see above), we measured the transition in the substrate type (7-grade scale: mud, fine sand, medium sand, coarse sand, gravel, rock, and rock with sand veneer), and determined seagrass species composition and relative/total percentage cover (%) to the nearest centimetre. During the survey, also, we examined the seagrass patches for any signs of seasonal dieback which we recognized as unusual leaf browning (or also whitening for *H. stipulacea*; Vousden, 1995; Seddon et al., 2000).

Across six experimental sites in Dubai and Bahrain established for the simulated trail experiment (see below; Figure 6.1), we tagged ~30 and ~20 shoots, respectively, of each available species using plastic-coated steel wires that were carefully twisted around the rhizome at the third node from the growing apex. Care was taken while digging for and tagging shoots to minimize disturbance to substrate and seagrasses; tagged shoots were returned and buried as the pre-tagging condition as much as possible. Depending on weather conditions and logistics, the tagged shoots were recovered after 12–21 and 19–42 days in Dubai and Bahrain, respectively, and the increase in shoot count was calculated. To account for any potential seasonal variations in primary production, seagrass shoot tagging was carried out at each experimental site in summer and winter. Recovery success of the marked shoots (n= 45 and 200 in Dubai and Bahrain, respectively) varied considerably according to site and species with the lowest was for *H. ovalis* due to its bristle rhizomes and prominent dieback cycles observed at the experimental sites. Shoot production rate per apical shoot per unit time (shoot $apical^{-1}$ d^{-1}) was then calculated for each retrieved tagged shoot. Due to the low number of *H. ovalis* shoots recovered, we pooled the shoot production rates and averaged them for all sites for a given season and species.

To estimate the overall seagrass production at the transect level, we first calculated the average dry biomass of individual shoots of each species (mg DW $shoot^{-1}$) by dividing the relative biomass (including both above- and belowground parts) on the relative shoot count (shoot m^{-2}) that we obtained earlier form the biomass samples (see above). This was followed by averaging the apical shoot density (apical m^{-2}) of each seagrass species which was calculated from the seagrass shoot samples collected along the same transect. The obtained apical shoot density (apical m^{-2}) was then multiplied by the shoot production rate per apical (shoot $apical^{-1}$ d^{-1}) to calculate relative and total seagrass shoot production rates which were expressed as the total number of shoots produced per unit area per unit time (shoot m^{-2} d^{-1}). The resultant shoot production rates of each species were further multiplied by the corresponding average dry biomass of individual shoots to obtain the relative biomass production rates which were then combined to estimate the total seagrass production rate at the transect level. The later was averaged across the three transects deployed at the same site to obtain site-specific mean total seagrass primary production rate which was expressed as total seagrass dry biomass produced within unit area per unit time in a given season (g DW m^{-2} d^{-1}).

To determine whether the studied seagrass meadows were overgrazed, we compared the estimated seagrass production with dugong herbivory rates across all sampling sites in JAWS and Hawar. In this regard, the percentage of dugong herbivory relative to seagrass production was estimated across: (i) all sampling sites (JAWS and Hawar), (ii) all seasons (JAWS and Hawar), and (iii) LDG main feeding grounds (i.e., WFG and SFG) during the corresponding grazing season (Hawar).

3.4 Species-specific post-grazing seagrass recovery

We conducted an in-water experiment to: (i) estimate the time interval taken by seagrasses to recover following simulated intense dugong grazing, and (ii) examine any potential grazing-induced modifications in seagrass species composition and/or dominance. This experiment was repeated in winter and summer to account for any seasonal variations underpinning the post-simulated grazing regrowth of seagrass.

Two and four sites (hereinafter experimental sites) were established in Dubai and Bahrain, respectively, in shallow areas (depth: <4 m) where shoot production rate was also measured (see above; Figure 6.1). At each experimental site, we excavated (using handheld shovels) three ~ 2 × .20 m lines with ~2 m distance interval to mimic natural dugong feeding trails. We removed ~95% and ~75% of above- and belowground seagrass parts, respectively, from the excavated lines to simulate intense dugong grazing (see de Iongh et al., 1995; Preen, 1995). The simulated trails were then monitored periodically every 1–2.5 months, and the regrowth inside the trails was assessed in terms of relative and total seagrass cover that was estimated in comparison to the corresponding cover around the trail's edges. During each assessment round, also, the trails were photographed and the photos were later examined to enable visual estimation of the dugong feeding trail age (i.e., recent, medium, and old trails) through transforming the regrowth percentages to time (see above). We also reported any distinctive signs of seasonal seagrass dieback or recent dugong feeding in a 10 m radius from the simulated trails. Only one site in Bahrain (i.e., Mashtan Island) was grazed by dugongs during the course of the experiment, but none of the natural dugong feeding trails intersected with the simulated ones.

Monitoring of the trails simulated at two of the experimental sites in Dubai (i.e., JAWS-1 and JAWS-2) and one site in Bahrain (i.e., Salman Town) was suspended after 36–46 days after >80% of seagrasses within and around the trails had disappeared due to mass dieback and/or erosion likely driven by strong seasonal currents. As such, the results of JAWS-2 and Salman Town were not reported. On the other hand, the simulated trails at the three remaining experimental sites in Bahrain were monitored until seagrass had regrown to a percentage cover comparable to the edges of the trails. To account for within site variations, the mean recovery time was averaged to the nearest month across the trails at a given site and season. The trails at a given experimental site were considered recovered when at least one trail exhibited approximately 100% recovery and the average recovery of the other trails in the same subset exceeded 90%. Finally, after the trails had fully recovered and following the elapse of 244–475 days from the onset of the simulated grazing experiment, we examined the potential changes in seagrass species composition and abundance. A 15 × 15 cm quadrat was deployed to estimate the difference in shoot density between inside and outside the trails for each species (following the same method described earlier for the natural trails) that was expressed as average increase/decrease percentages for a given site and season.

3.5 Seawater temperature and salinity

We assessed the harshness of the physical environment in which both dugongs and their main forage (i.e., seagrasses) survive in the Arabian Gulf through measuring seawater temperature and salinity around Hawar. We chose Hawar due to its location at the mouth of the Gulf of Salwa, one of the hottest and saltiest bays worldwide and considering that these shallows encompass a sizeable dugong population, clumped large dugong groups and extensive seagrass meadows. We deployed *in situ* temperature loggers (OXLTEMPS, Odyssey Xtreem

Submersible Temperature logger; Dataflow Systems, New Zealand) at three selected sites around Hawar, of which two were experimental sites located within the areas frequented by large dugong groups. The water quality monitoring sites were 3.1–3.4 m deep that is comparable to the dominant depth across the nearby main dugong feeding grounds. The loggers were configured to measure ambient seawater temperature every 10 minutes for 16, 17, and 28 months at Fasht Mu'tarid, Fasht Buthur, and Mashtan, respectively (Figure 6.1). The obtained measurements were sorted for each monitoring site and the monthly mean, minimum, and maximum temperatures were then calculated. In parallel, seawater salinity was similarly measured using in-water loggers (ODYCT80, Odyssey Conductivity and Temperature Logger; Dataflow Systems, New Zealand) at four monitoring sites (depth: 2.8–3.7 m). The loggers were programmed to record a reading every 10 minutes, but were kept for only five successive days in any monitoring round to avoid likely inaccuracies induced by biofouling and sediment accumulation. At each site, this procedure was repeated over two rounds in between which the loggers were cleaned from biofouling organisms and sand particles. After that, mean, minimum, and maximum salinity levels were calculated from the obtained data.

4 Results

4.1 Physical environment

Sampling sites across the study area were all in sheltered nearshore waters or in proximity to reefs and/or islands. Water depth was averagely shallow ranging 1.8–10.2 m (Table 6.1). Across all sampling sites at JAWS, the seabed was predominantly composed of coarse sand followed by mud, fine sand, and medium sand (54.2%, 39.2%, 6.3%, and .3%, respectively). A similar trend was detected around Hawar where the sea bottom was composed of coarse sand, mud, medium sand, fine sand, and to less extent rock, rock with sand veneer, and gravel (81%, 9.1%, 4.1%, 2.2%, 1.8%, 1.2%, and .6%, respectively). Mean monthly seawater temperature across the monitoring sites varied over a wide range (18.1–35.3 ºC) peaking to maxima in August and dropping to minima in January (36.7 and 15.8 ºC, respectively). Mean salinity exhibited a southerly increasing trend around Hawar fluctuating between 43.5–51.9 psu and recording minimum and maximum values of 41.9 and 53 psu, respectively (Figure S1).

4.2 Seagrass species composition and abundance

Total seagrass cover was variable averaging 43.6 (± 4.4% SE) and 70.9 (± 1.7% SE) at JAWS and around Hawar, respectively. Across the study area, *H. uninervis* and *H. ovalis* were the most frequently seagrass species. In comparison, *H. stipulacea* was found in 78% of all sites, but was rare at JAWS, found at only one sampling site (Table 6.1). Total seagrass biomass was higher in JAWS and dominated by the belowground part, accounting for 84% and 64% of total biomass in JAWS and Hawar, respectively (Figure 6.2). Due to its thick rhizome/root mats, *H. uninervis* dominated seagrass biomass across the study area accounting for 96% and 69% of total biomass around JAWS and Hawar, respectively.

At a number of sampling sites, algae, epiphytes, and colonial ascidians were seen in abundance on seagrass shoots (particularly on *H. uninervis*), including those growing along the dugong feeding trails. In-water observations, also, revelated that some sampling sites around both JAWS and Hawar (*n*= 2 and 3, respectively) exhibited distinctive signs of seagrass dieback in winter. In addition, several sampling sites undergone seasonal dieback in summer which around Hawar was mostly preceded by the predominance of dense epiphytic growth (cover: >90%; Table 6.1). These observations were further confirmed by the repeated monitoring of the experimental sites with two sites in JAWS showing signs of mass dieback in winter and other three in Bahrain undergoing winter and summer dieback cycles (see below). It is important to note that the seasonal seagrass dieback was site-specific with some meadows exhibiting winter and/or summer dieback cycles, while others in proximity (often <300 meters) remained intact.

4.3 Dugong feeding trails

Four out of six sampling sites at JAWS were grazed by dugongs with maximum dugong feeding trail cover not exceeding 1.5% (mean ± SE: .3 ± .1%). Dugong feeding trail cover around Hawar (mean ± SE: 10 ± 1.9%) fluctuated widely ranging from .3% to 52.7% across grazed sampling sites (75% of all sites; Figure 6.3A). The dugong feeding trails measured around Hawar were averagely 2.1 (± .73 SD) m long and .21 (± .04 SD) m wide. Along the trails measured at JAWS, *H. uninervis* was the dominant seagrass followed by *H. ovalis* (96.1% and 3.9% of all seagrass shoots, respectively) with no trails were surrounded by *H. stipulacea*.

Table 6.1. Spatial variations in bathymetry, mean (± SE) seagrass apical shoot density, mean (± SE) seagrass shoot dry weight, and occurrence of seasonal dieback cycles across the sampling sites at Jabal Ali Wildlife Sanctuary (Dubai, United Arab Emirates) and around Hawar Island (Bahrain), (B= sampling site around Hawar, D= sampling site at Jabal Ali Wildlife Sanctuary, HU= *Halodule uninervis*, HS= *Halophila stipulacea*, HO= *H. ovalis*, W= seagrass seasonal dieback observed in winter, S= seagrass seasonal dieback observed in summer).

Sampling Site	**Depth (m)**	**Apical shoot density (apical m^{-2})**			**Seagrass shoot dry weight (mg DW shoot^{-1})**			**Seasonal dieback**
		HU	**HS**	**HO**	**HU**	**HS**	**HO**	
B1	5.4	118.5 ± 66.6	259.3 ± 38.8	7.4	79.3 ± 50.1	23.6 ± 3.5	5.1 ± 2.6	W
B2	5.5	259.3 ± 72.1	400 ± 150.1	7.4	46.7 ± 4.1	18.1 ± 2.3	6.8 ± 1.3	
B3	4.9	362.9 ± 72.9	429.6 ± 84.9		46.3 ± 7.7	21.7 ± 1.2	7.3	
B4	10.2	414.8 ± 124.5	555.6 ± 145	125.9 ± 57.9	43.2 ± 4.3	19.1 ± 3	10.2 ±2	
B5	5.8		755.6 ± 142.9	14.8	32.1 ± 4.2	11 ± 1.7	1.7	
B6	6.3	355.6 ± 266. 7	651.8 ± 392.8	237 ± 156.8	33.1 ± 6.4	8.6 ± .4	7.2 ± .3	
B7	10.1	192.6 ± 37.5	177.8 ± 81.2	7.4	44.5 ± 5.6	7.6 ± 2.8	6.1 ± 1.6	
B8	8.2	333.3 ± 89.4	162.9 ± 92.3	118.5 ± 50.9	76.6 ± 34.8	8.2 ± 3.2	7.2 ± 1.2	
B9	8.6	237.1 ± 67.6	429.6 ± 141.8	37 ± 24.1	36.3 ± 1.8	11.5 ± 2.1	6.4 ± .9	
B10	3.9	807.4 ± 310. 6	88.9 ± 60.7	37 ± 24.1	73.1 ± 23.7	9 ± 5.3	7.7 ± 2.5	W
B11	7.3	296.3 ± 55.8	14.8 ± 9.4	44.4 ± 28.1	49.2 ± 4.4	15.3 ± 10.6	7.4 ± 1.6	

Sampling Site	Depth (m)	Apical shoot density (apical m^{-2})			Seagrass shoot dry weight (mg DW shoot^{-1})			Seasonal dieback
		HU	HS	HO	HU	HS	HO	
B12	5.3	66.7 ± 29.8	651.9 ± 190.2		73.4 ± 21.5	17.6 ± 3.6		W, S
D1	3.8	400 ± 136.3	66.7	163 ± 83.8	46.9 ± 6.5	37.8	8.3 ± .7	
D2	8.4	47.1 ± 13.5		258.9 ± 39.1	126.9 ± 37.1		12.8 ± 3.3	
D3	6.6	903.7 ± 204.5		111.1 ± 51	49.5 ± 4.9		10.2 ± 2.5	S
D4	7.9	540.7 ± 88		55.6 ± 24.5	40.6 ± 6.9		7.3 ± 2.4	S
D5	2.1	1944.4 ± 218.1		70.4 ± 25.3	71.2 ± 2.3		11.5 ± 4.5	W
D6	1.8	1925.9 ± 285.7		700 ± 161.1	47.5 ± 4.9		7 ± .8	W

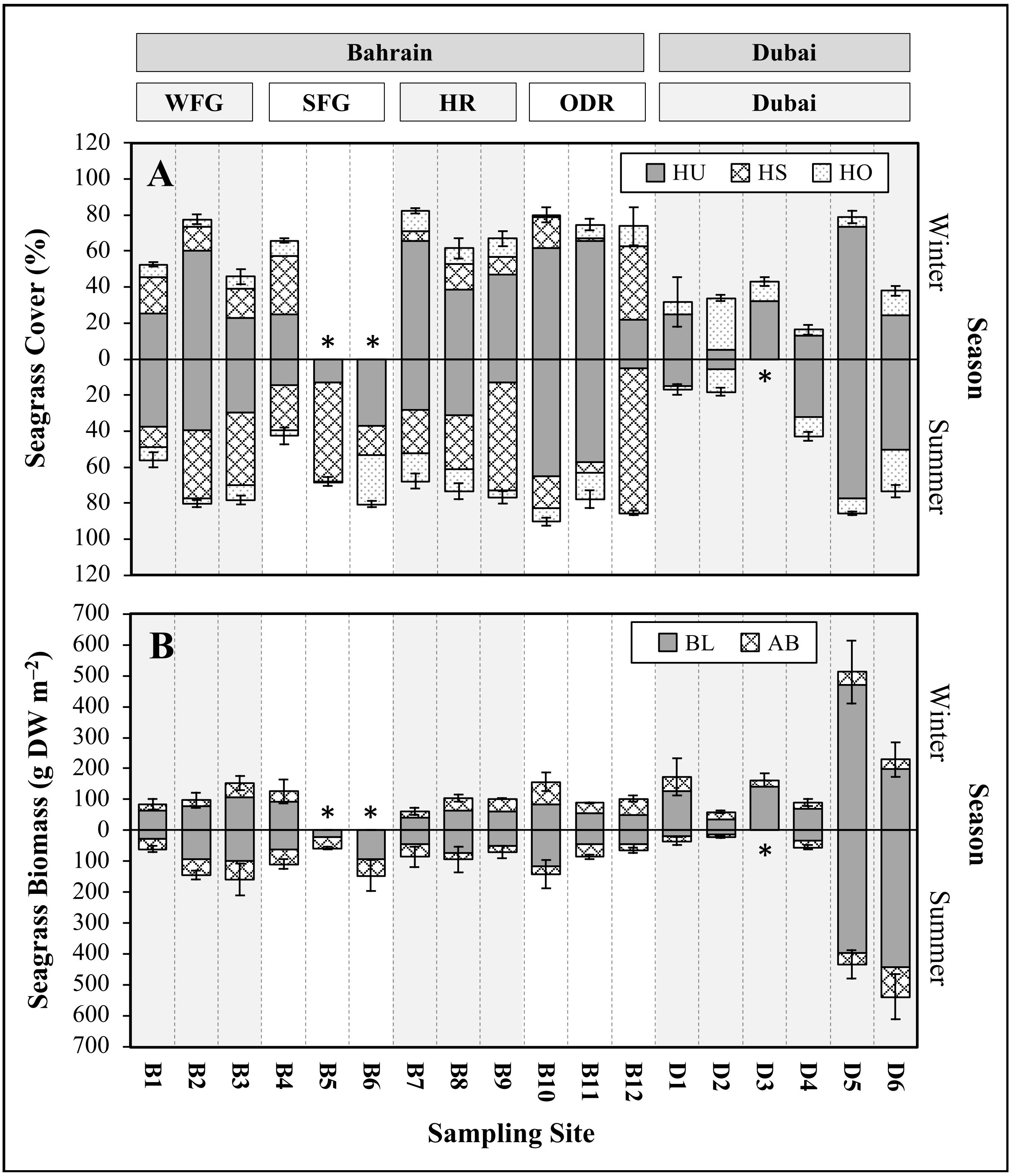


Figure 6.2. Comparison among sampling sites surveyed at Jabal Ali Wildlife Sanctuary (Dubai) and around Hawar Island (Bahrain) across winter and summer seasons in terms of selected seagrass community covariates: (A) relative and total seagrass percentage cover, and (B) relative and total seagrass biomass. Sampling sites are classified into key zones, including key large dugong group aggregation areas (B= sampling site around Hawar, D= sampling site at Jabal Ali Wildlife Sanctuary, HU= *Halodule uninervis*, HS= *Halophila stipulacea*, HO= *H. ovalis*, WFG= winter feeding ground, SFG= summer feeding ground, HR= home range, ODR= overall distributional range of large dugong groups, AB= aboveground biomass, BL= belowground biomass, bar= standard error of mean total, * = site not surveyed during a particular season).

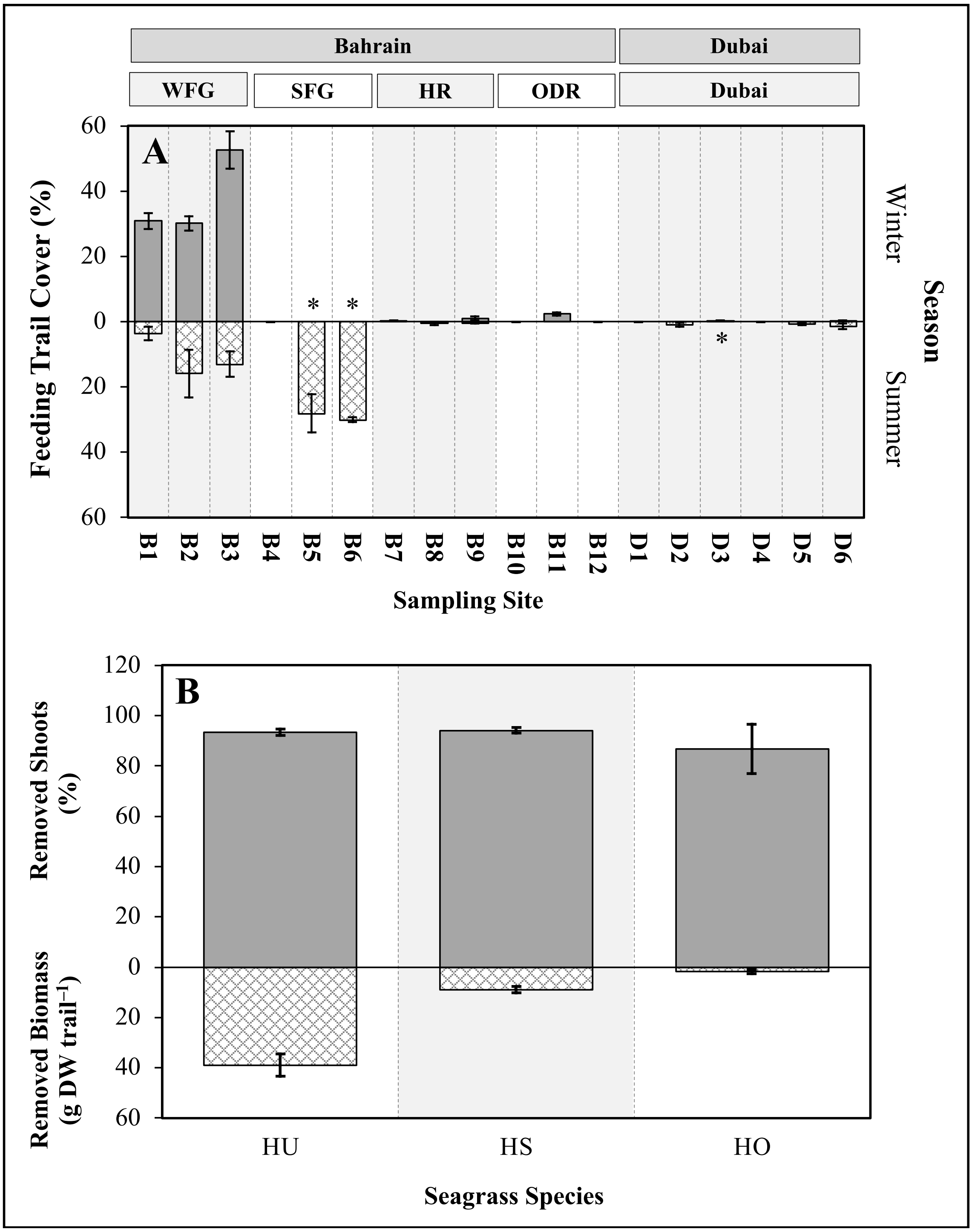


Figure 6.3. Spatio-temporal patterns of dugong grazing across the sampling sites (classified into key zones, including main large dugong group aggregation areas) demonstrated as: (A) mean dugong feeding trail cover across sampling sites and seasons at Jabal Ali Wildlife Sanctuary (Dubai) and around Hawar Island (Bahrain), and (B) mean percentage of seagrass shoot and the corresponding seagrass biomass removed by a dugong from each seagrass species in a given feeding trail (*N*= 20) around Hawar Island (B= sampling site around Hawar, D= sampling site at Jabal Ali Wildlife Sanctuary, HU= *Halodule uninervis*, HS= *Halophila stipulacea*, HO= *H. ovalis*, WFG= winter feeding ground, SFG= summer feeding ground, HR= home range, ODR= overall distributional range of large dugong groups, bar= standard error, * = site not surveyed during a particular season).

Around Hawar, similarly, *H. uninervis* was the most abundant along the measured trails followed by *H. stipulacea* and *H. ovalis* (54.6%, 39.1%, and 6.3% of total seagrass shoots, respectively). Dugongs around Hawar removed ~94 (± 5% SD) of all seagrass shoots within a feeding trail. This accounts for ~48.2 (± 23.8 SD) g DW of seagrass per feeding trail, of which 79% was *H. uninervis* (Figure 6.3B).

4.4 Dugong herbivory rates

Dugong herbivory rate was widely variable across sampling sites, averagely recording ~47 folds around Hawar compared to JAWS (mean ± SE: .611 ± .170 and .013 ± .006 g DW m^{-2} d^{-1}, respectively). Among the sampling sites grazed by dugongs, similarly, herbivory rates fluctuated widely ranging .01 – .09 and .03 – 5.22 g DW m^{-2} d^{-1} in JAWS and Hawar, respectively. Mean dugong herbivory rates peaked around Hawar recording 2.91 (± .73 SE) g DW m^{-2} d^{-1} at WFG and 1.28 (± .51 SE) g DW m^{-2} d^{-1} at SFG during the corresponding LDG grazing seasons (i.e., winter and summer, respectively; Figure 6.4).

4.5 Seagrass production rate

Shoot production per apical measured at the experimental sites varied widely across species with the highest recorded by *H. stipulacea* followed by *H. ovalis* and *H. uninervis* (mean ± SE: .241 ± .019, .152 ± .023, and .121 ± .007 shoot $apical^{-1}$ d^{-1}, respectively; Figure S2). Across sampling sites, total apical shoot density was variable (mean ± SE: 1215 ± 137 and 696 ± 52 apical m^{-2} around JAWS and Hawar, respectively). This trend was also reflected in total shoot production measured at the sampling sites (mean ± SE: 157 ± 22 and 125 ± 10 shoot m^{-2} d^{-1} around JAWS and Hawar, respectively). Seagrass biomass production rate was also spatially variable, recording 2.8 folds around JAWS relative to Hawar (mean ± SE: 7.7 ± 1.2 and 2.8 ± .2 g DW m^{-2} d^{-1}, respectively; Figure S3). In general, seagrass meadows across the large dugong group occupancy area around Hawar produced approximately 367 ton DW d^{-1} of seagrass that is equivalent to 134,112 ton DW yr^{-1}.

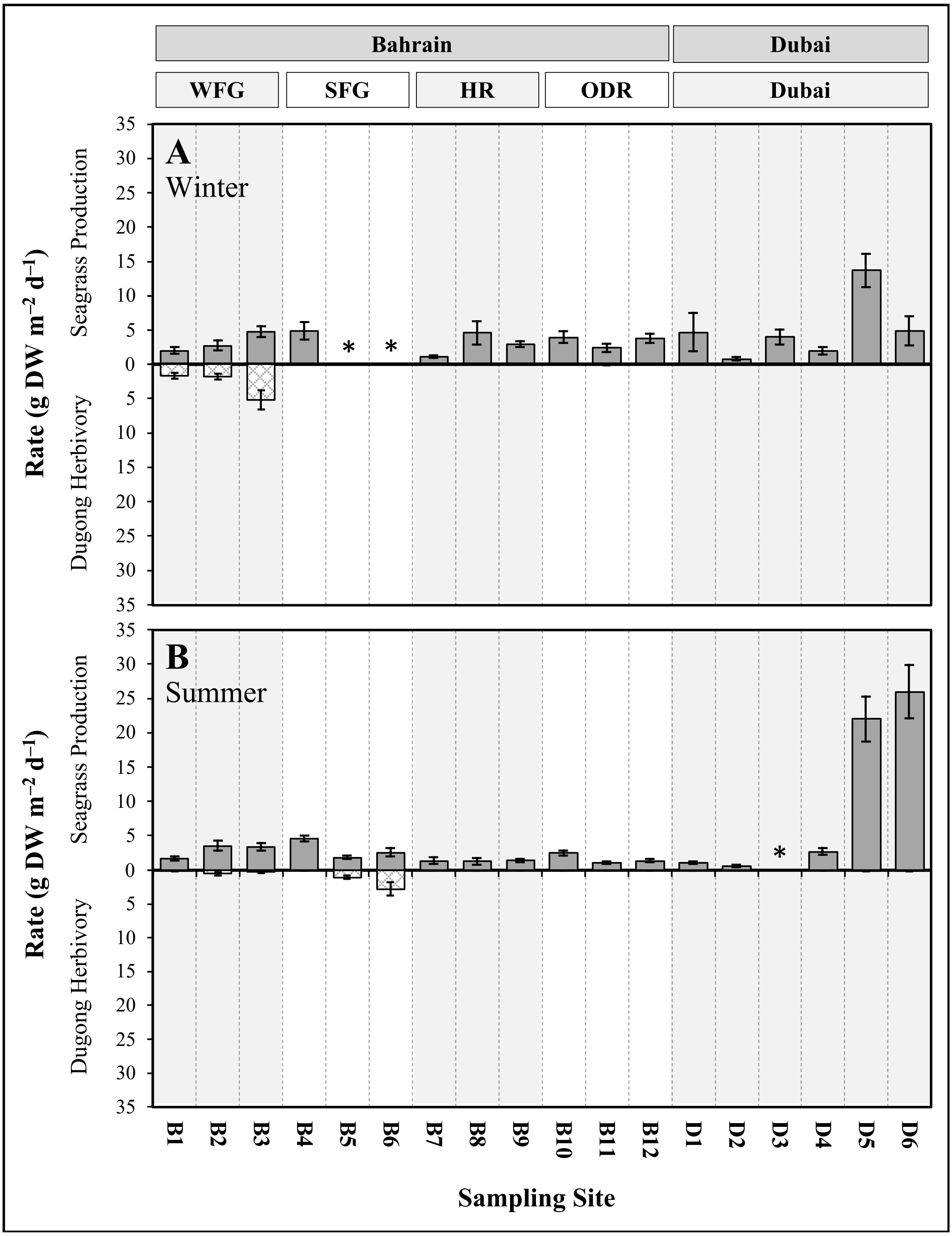


Figure 6.4. Comparison between total seagrass production and dugong herbivory rates (estimated based on dugong feeding trail cover) across sampling sites at Jabal Ali Wildlife Sanctuary (Dubai) and around Hawar Island (Bahrain) during: (A) winter, and (B) summer seasons. Sampling sites are classified into key zones, including key large dugong group aggregation areas (B= sampling site around Hawar, D= sampling site at Jabal Ali Wildlife Sanctuary, WFG= winter feeding ground, SFG= summer feeding ground, HR= home range, ODR= overall distributional range of large dugong groups, bar= standard error, * = site not surveyed during a particular season).

4.6 Dugong herbivory compared to seagrass production

Averaged across sampling sites and seasons, mean percentage of dugong herbivory relative to seagrass primary production rates fluctuated widely recording .14 (± .05% SE) and 21 (± 4.8% SE) around JAWS and Hawar, respectively. Across seasons, the mean percentage at the site level recorded maxima of 109 (± 17% SE) in winter at WFG while it peaked in summer at SFG recording 107 (± 16% SE), (Figure 6.4). At the feeding ground level, dugongs around Hawar consumed substantial percentage of primary production measuring 87 (± 9% SE) and 57 (± 17% SE) at WFG and SFG, respectively, during the corresponding grazing season (winter and summer, respectively).

4.7 Post-grazing seagrass recovery

Recovery of individual simulated trails varied widely from 4 to 9 months and at the experimental site level, mean seagrass recovery ranged 4–6 month (mean: 5 month), hinting likely within and among sites variability. Mean recovery at experimental sites that did not exhibit seagrass seasonal dieback (i.e., Buthur) was averagely 1–2 month faster compared to sites with clear signs of winter and/or summer dieback cycles (i.e., Tgailib and Mashtan; Figure 6.5). The recovered simulated trails did not exhibit modifications in seagrass species composition compared to the seagrass growing along their edges. However, the species percentage cover and shoot density varied considerably favoring the dominance of *H. stipulacea* and *H. ovalis* compared to *H. uninervis* within the recovered trails. Even after the elapse of >15 months since the onset of the simulated grazing experiment, seagrass regrowth across most experimental sites and seasons consistently exhibited considerable declines in the shoot count of *H. uninervis* versus increases in those of *H. stipulacea* and *H. ovalis* (mean ± SE: 37 ± 11% [decrease], 63 ± 31% [increase], and 209 ± 91% [increase], respectively; Figure 6.6).

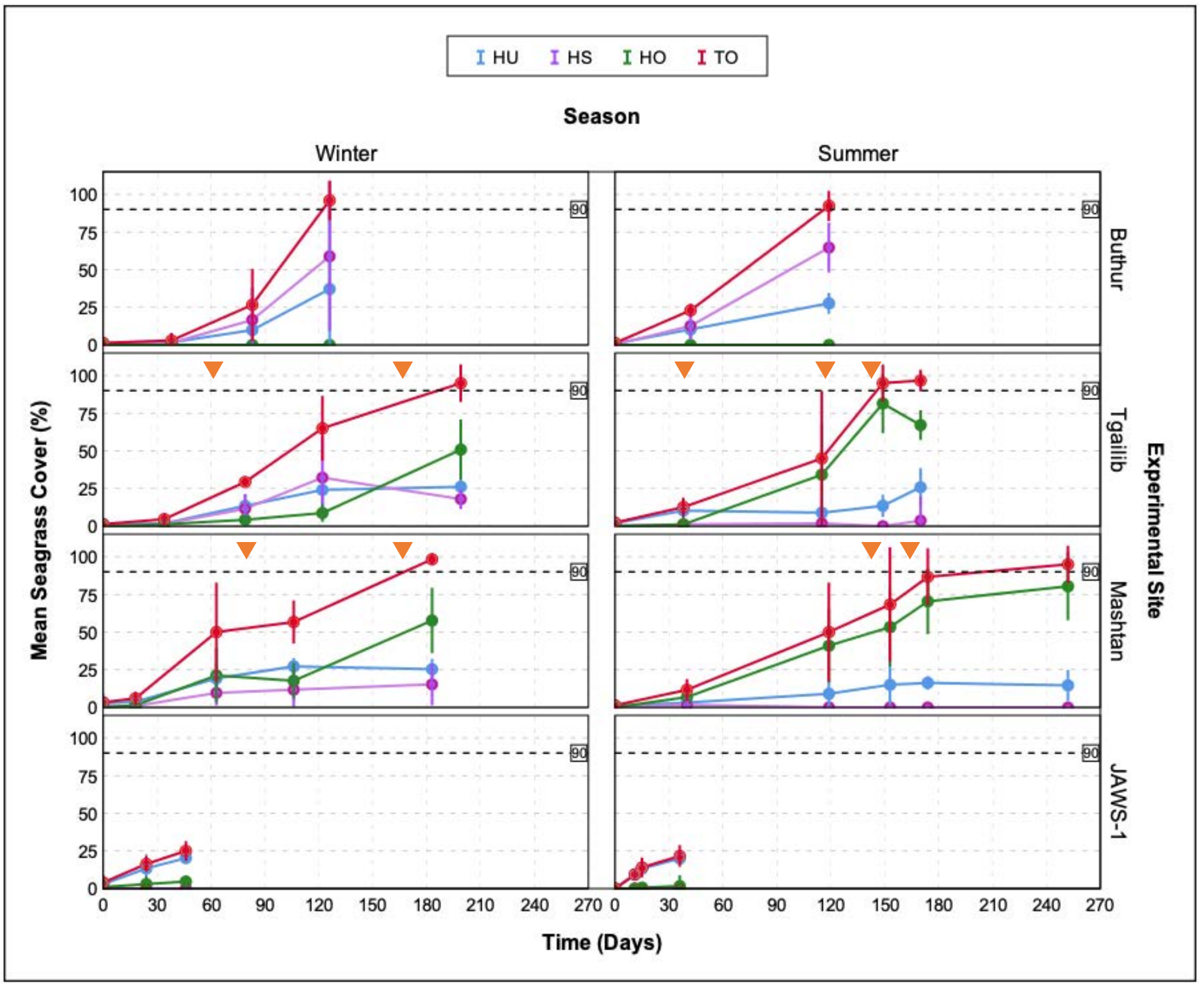


Figure 6.5. Mean recovery time interval of experimental feeding trails excavated to simulate intense dugong grazing during winter and summer at four experimental sites at Jabal Ali Wildlife Sanctuary, Dubai (JAWS-1) and around Hawar Island, Bahrain (Buthur, Tgailib, and Mashtan) alongside any observed seagrass seasonal dieback. The trail subset (*n*= 3) at a particular site and a given season was considered fully recovered when at least one trail exhibited 100% recovery of seagrass cover, and the average recovery of all trails in the same subset exceeded 90% (HU= *Halodule uninervis*, HS= *Halophila stipulacea*, HO= *H. ovalis*, TO= total seagrass cover, 90= 90% recovery of seagrass cover averaged across the trails in a given subset, bar= standard error; ▼ = seagrass seasonal dieback).

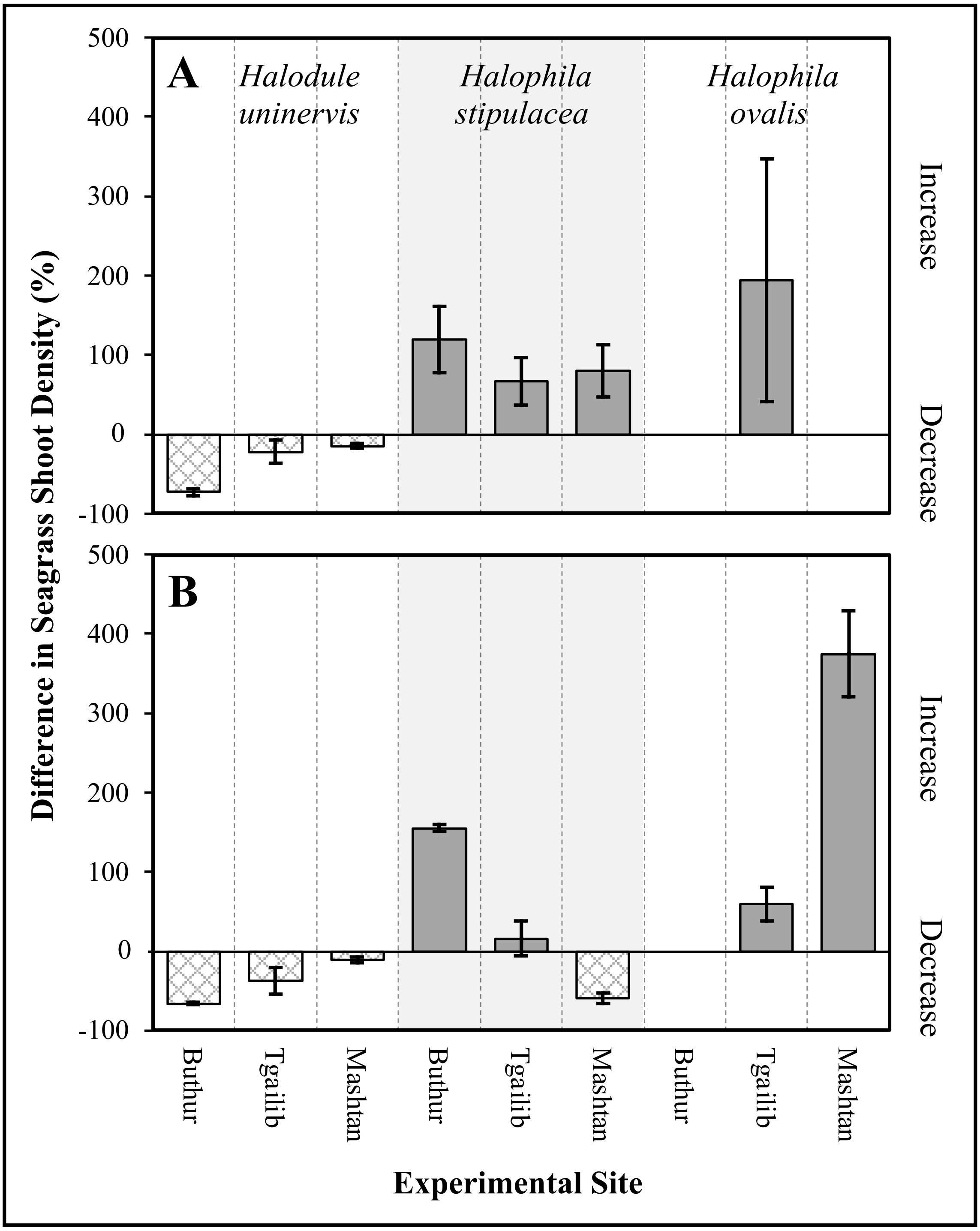


Figure 6.6. Simulated grazing-mediated seagrass species dominance shift, measured as the difference in relative seagrass shoot density between inside and outside fully recovered simulated dugong feeding trails excavated at three experimental sties around Hawar Island, Bahrain during: (A) winter, and (B) summer seasons. The trails were assessed after 359, 475 and 459 days at Fasht Buthur, Fasht Tgailib, and Mashtan Island, respectively, following the onset of the simulated grazing experiment (*n*= 3 replicates at each site at a given season, positive percent= increase in shoot density inside compared to outside the trail, negative percent= decrease in shoot density inside compared to outside the trail, bar= standard error).

5 Discussion

It would be reasonable to assume that seagrass meadows in the Arabian Gulf could support only a relatively small population of foraging dugongs. These meadows are routinely exposed to extreme environmental conditions, both in temperature and salinity. For several months, seagrasses in this region have to deal with sustained stressful conditions as seasonal water temperatures plummet and soar beyond the optimal ranges for most seagrass species, resulting in occasional diebacks of seagrass patches. Yet the Arabian Gulf has one of the most important global populations of dugongs, stably inhabiting shallow seagrass meadows in herds that range from solitary individuals to some of the largest groups recorded anywhere. We found that where dugongs did not form large groups, their foraging did not constitute too much of an additional stress for seagrasses. In contrast, around Hawar, where dugongs can number in the hundreds, the pressure of grazing is much higher, consuming the bulk of seasonal production. The fact that these high-aggregation meadows have persisted to support intense dugong foraging despite the extreme conditions, was likely to the fact that these meadows were large and had high primary production, and dugongs undertook short-range seasonal movements between locations. This short distance rotational foraging between winter and summer feeding grounds gave seagrasses sufficient time to recover from intense grazing pressure at even the densest dugong aggregation sites.

The extreme temperature and salinity of the Arabian Gulf likely place constraints on the ability of its seagrass meadows to cope with the additional pressure of megaherbivory. Our recorders logged salinity values upward of 41‰ at all sites, and temperatures that dropped below 16 °C in winter and rose above 35 °C at the peak of summer. The years of our sampling were relatively moderate (Meteorological Directorate, 2021), and seawater temperatures in the Arabian Gulf are known to range even more widely with shallow inshore waters can routinely experience >40 ºC (Vousden, 1995; Al-Wedaei et al., 2011; Abdelbary & Al Ashwal, 2021). These conditions are likely much too extreme for most seagrass species and strong environmental filtering limits the assemblage to three highly stress tolerant seagrasses. For instance, the most abundant species in the Arabian Gulf *H. uninervis* is a particularly known extremophile, tolerating temperatures above 40 °C and salinities exceeding 65‰ (Basson et al., 1977; Price & Coles, 1992; Vousden, 1995; Campbell et al., 2006; Al-Wedaei et al., 2011; Erftemeijer & Shuail, 2012; Qurban et al., 2019a; Abdelbary & Al Ashwal, 2021). Despite their remarkable tolerance, however, laboratory and field-based studies indicate that *Halophila* and *Halodule* spp. have well-defined optima beyond which their photosynthetic activity, production rates and growth typically decline (Campbell et al., 2006; Georgiou et al., 2016; Wesselmann et al., 2020). In this regard, our results revealed that seagrass dieback occurs during summer, supporting the results of Al-Bader et al. (2014) in Kuwait, but contrasting widely stated generalization that this phenomenon is confined in the Arabian Gulf to winter (Basson et al., 1977; Vousden, 1995; Qurban et al., 2019a).

Our measured rates of seagrass production do not differ from normal ranges across the tropics (see Preen, 1992; de Iongh et al., 1995; Nakaoka & Aioi, 1999; Aragones & Marsh, 2000; Budiarsa et al., 2021), suggesting that seagrasses of the Arabian Gulf cope fairly well with the harsh conditions, at least in terms of growth. Of equal concern is how dugongs themselves deal with these extreme conditions, of both heat and cold. While the coldest temperatures recorded around Hawar overlap with the lower thermal tolerance threshold of dugongs reported elsewhere (Sheppard et al., 2006; Marsh et al., 2011; Cleguer, 2015; Deutsch et al., 2022a , 2022b), dugongs in this environment also have to cope with some of the highest temperature and salinity encountered across the dugong's distribution (Preen, 1989). What the energetic costs of dealing with this wide temperature range are for dugongs is unknown, but it could likely influence rates of summer and winter feeding, reproductive success, growth, and movement patterns. While all evidence points to both seagrasses and dugongs coping well with environmental extremes in the Arabian Gulf, they are likely very close to their respective metabolic thresholds (Basson et al., 1977; Price et al., 1993; Vousden, 1995; Erftemeijer & Shuail, 2012; Al-Arbash et al., 2016). As a result, this system may have a limited capacity to deal with major fluctuations in conditions; either a further increase/decrease in seawater temperature or a reduction in meadow size and production.

Ultimately, the ability of seagrass meadows to support dugong herbivory depends predominantly on the relationship between seagrass production and dugong consumption. Across the Arabian Gulf, this relationship varied considerably, tracking the highly heterogenous distribution of dugongs (Preen, 2004; Hodgson, 2009; Preen et al., 2012). While at JAWS (where dugong numbers were typically very low) dugong herbivory was <2% of seagrass production, the consumption around Hawar accounted for >50% of production. This large variation in production/herbivory ratios is not unusual and has been recorded from other areas across the dugong range, including from areas where populations are very sparse (e.g., Andaman Sea: 4–42%; D'Souza et al., 2015), and where dugongs aggregate in sizeable groups (e.g., Moreton Bay: 1–28% of total annual production; Preen, 1992).

Our results indicated that at some core aggregation sites around Hawar, herbivory by dugongs exceeded total seagrass production. Many seagrass species deal with herbivory by compensatory growth, drawing on rhizome stores to offset herbivory losses (McGlathery, 1995; Christianen et al., 2019; Smulders et al., 2022). However, while short-lived species of seagrass can deal with occasional periods of overconsumption, they do not have the rich resources of long-lived species. Instead, pioneer seagrasses rely mainly on their fast growing capacities to cope with sustained grazing. Nevertheless, the cumulative impacts of intense herbivory could be energetically unsustainable for these species. In our simulated grazing experiments, *H. uninervis* took longer to gain cover than *Halophila* spp., indicating that it responds slower to the megaherbivory pressure as has been documented elsewhere (Aragones & Marsh, 2000).

The fact that Hawar's meadows have supported large dugong groups for at least several decades is thanks to the dynamic relationship between seagrass production and recovery rates as well as dugong movement behaviour. These clumped groups have been sighted around Hawar year-round. However, there are distinct seasonal shifts in where the large groups are reported, as they appear to move between summer and winter feeding grounds in the south and north of Hawar, respectively. Both feeding grounds are extensive (occupying an area of 38.3 km^2 [WFG] and ~7.9 km^2 [SFG]) and have dense stands of early successional seagrass species. Large groups of dugongs in other regions (notably Moreton Bay, Australia), also, undertake seasonal movements between meadows, although the scale of those movements is much larger (Preen, 1995; Deutsch et al., 2022b). The LDGs around Hawar do not stray very far from the island and the summer and winter feeding grounds are separated by merely ~5 km, well within the dugong's daily movement range (<15 km; Sheppard et al., 2006). However, this small-scale seasonal rotation is critical to the persistence of these groups around Hawar. Led by *Halophila* spp., our simulated grazing experiments showed that it takes between 4–6 months before seagrass recovers after a dugong grazing event, that falls within the overall recovery range reported across the dugong distribution (Table S1). The fact that LDGs shift seasonally between meadows gives these pioneer seagrasses the time they require to regain cover ahead of the next dugong grazing season. Although mainly attributed in other localities to cultivation grazing (e.g., Moreton Bay; Preen, 1995; Aragones & Marsh, 2000), in the Arabian Gulf it is more likely that environmental extremes, more than grazing itself, selectively maintain the assemblage of early successional seagrass species, dominating traditional dugong feeding grounds. The remarkable plasticity of *Halodule* and *Halophila* spp. in tolerating intense herbivory pressures (Nakaoka & Aioi, 1999; Aragones & Marsh, 2000; Aragones et al., 2012a; D'Souza et al., 2013; Bakker et al., 2015; Cleguer, 2015; Scott et al., 2018) and the predominance of unconsolidated sediment further enhance the capacity of the Arabian Gulf's meadows to sustain intense dugong herbivory. Additionally important in the long-term persistence of LDGs around Hawar are the production and areal extent of its meadows. The seagrass stands encompassing the winter and summer dugong feeding grounds around Hawar are both sufficiently large and productive to support the considerable nutritional requirements of hundreds of dugongs for several months at a time. Smaller, more fragmented meadows may not have been able to support this population, particularly since dugong groups tend to avoid or abandon patchy fragmented meadows (D'Souza et al., 2015). It is possible that rotational grazing is nutritionally driven, with dugongs shifting between seasonal feeding grounds as they deplete at the end of the season. Clearly, multiple factors, including seagrass species composition and production regimes, meadow size as well as dugong behaviour, all act together to ensure that large dugong groups persist in a relatively small area around Hawar.

In more ways than one, the Arabian Gulf is a global hotspot for dugong conservation. Despite its extreme conditions, between production regimes, seagrass extent and dugong behavioural adaptations, locations like Hawar Island still harbour dugong groups that can grow to >600 individuals. The set of circumstances that allow these megaherbivore aggregations to persist in such a spatially explicit and predictable manner makes it an opportunity and a challenge for conservation. On the one hand, it allows for effective spatial management of a wide-ranging species, focused on its principal feeding grounds. On the other, it places disproportionate importance on maintaining the seagrasses of this region in a healthy productive and unfragmented state. Local anthropogenic pressures from coastal development, eutrophication, boat traffic, and fishing could all reduce the capacity of these habitats to support LDGs, if they result in increased meadow fragmentation or reduced production. Of particular importance is to ensure that seasonal corridors are kept functionally open for dugongs, given how critical these are for rotational grazing. All developmental projects need to be evaluated not merely for their direct impacts on nearshore meadows, but also for their offshore consequences to dugong migration corridors. This, also, highlights how critical transboundary arrangements are, considering that LDGs constantly move across political boundaries in their seasonal movements. Given the extreme conditions, it is uncertain how both meadows and dugongs would respond metabolically to further rises in sea temperatures induced by climate change. Increased temperatures may trigger more frequent diebacks, reduced production, and community-wide reassembly for seagrass, while for dugongs it could mean increased nutritional demands, thermoregulatory costs, and energetic consequences that may impinge movement. Importantly, these factors could interact with each other in unexpected ways, making it all the more important that local stressors are kept at a minimum.

Despite being globally threatened, dugongs of the Arabian Gulf are a testament to their resilience. Both seagrass and dugongs survive here in some of the harshest environments anywhere in their range. At most locations in the Arabian Gulf, seagrass habitats are large and productive enough to support the small dugong numbers that frequent the meadows. In these meadows, herbivory constitutes a negligible component of total consumption. However, where dugongs aggregate forming large groups, consumption can often outstrip production. At these locations, dugong groups continue to persist as a result of the seagrass meadow size, species composition, and inherent productive capacity as well as a rotational grazing strategy that gives meadows sufficient time to recover after an entire season of intense grazing. Given how spatially explicit dugong groups are, management efforts need to focus much more on the effective conservation of dugong feeding grounds. Growing as they do in extreme conditions, these meadows may be unable to deal with additional anthropogenic pressures. Managing these local stressors may be the most feasible and effective means to secure the future for these critical hotspot dugong populations.

6 Acknowledgments

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7

General Discussion

Dugong grazing represents a special case of marine megaherbivory. Few other species have as high a daily dietary requirement as the dugong, and its unique grazing behaviour places a strong pressure on seagrass meadows. The high dependence of dugongs on seagrass meadows makes dugong feeding grounds critical conservation areas, and it is imperative to locate their distribution, understand their dynamics, determine how they have persisted in space and time, and identify potential anthropogenic threats to their resilience. This information is crucial for managing and eventually protecting these sensitive habitats through evidence-based spatial planning. This is especially relevant to areas where dugongs aggregate forming large groups within persistent feeding grounds. These feeding grounds are particularly vulnerable to intensifying pressures and need even more careful management. To determine dugong persistence in these grounds it is necessary to understand patterns of seagrass meadow use by dugongs and how seagrasses respond and adapt to intense dugong grazing. This thesis attempts to fill these critical knowledge gaps for a region that has some of the largest populations of dugongs in the world, but paradoxically, very little else is known. In this thesis, we identified a number of dugong feeding grounds across the Red Sea and Arabian Gulf, the western and northern distributional limits of dugongs, respectively, and explored production-herbivory dynamics. We determined the main anthropogenic disturbances threatening these feeding grounds in order to inform the conservation management of the globally sizeable, but data deficient regional dugong populations inhabiting the warm waters of the Arabian Peninsula.

The four main chapters comprising this thesis attempted to: (i) demonstrate how indirect measures of megaherbivory can be employed as a spatial planning tool to identify key feeding grounds of a sparsely-distributed dugong population, (ii) determine the long-term persistence of globally important large dugong groups and their key aggregation sites, (iii) identify the main habitat attributes and principal anthropogenic threats governing the spatial patterns of large dugong groups, and (iv) determine the dugong-seagrass interaction dynamics within the dugong feeding grounds of a sizeable dugong population for the purpose of integrating them in conservation management.

This thesis provides support to the growing body of evidence stressing the critical role of herbivory in influencing the production and structure of the ecologically and socioeconomically important seagrass meadows. The fact that dugongs are the largest extant exclusively marine herbivores underscores their function as crucial engineering agents in the marine realm. Overall, our study of dugong feeding grounds in the Red Sea and Arabian Gulf provides a unique insight into the interactions between the largest extant megaherbivore and seagrasses surviving under harsh environmental settings, projecting the fate of marine herbivory in warming oceans. More importantly, this thesis stresses the need of focusing spatial planning efforts on dugong feeding grounds as a key conservation management unit for both dugongs and seagrass. With the dramatic population declines that these elusive animals experience, understanding dugong feeding ground distribution, dynamics, and traits becomes increasingly crucial to address their spatially explicit conservation needs. The following key results obtained during the course of this study add an extra layer of understanding of dugong-seagrass interactions in the Arabian Peninsula, and provide guidance on how to best use the findings in this thesis to advocate dugong and seagrass conservation management:

1 Locating and understanding dugong feeding grounds

The substantial dietary needs of dugongs require these large-bodied mammals to spend much of their time in seagrass meadows, facilitating the detection of these normally elusive animals in shallow waters accessed by researchers and hunters, alike (Marsh et al., 2002; Ponnampalam et al., 2022). In addition, the dugong's excavating feeding mode leaves distinctive signs in grazed meadows that indicate the presence of a dugong or a group of dugongs even months following a grazing event. Feeding trails have been widely used to locate key dugong feeding grounds across the Indo-Pacific (Preen, 1995; Aragones & Marsh, 2000; Adulyanukosol et al., 2003; D'Souza et al., 2015; Mizuno et al., 2017; Apte et al., 2019; Budiarsa et al., 2021). We used these trails to measure habitat use by a sparse dugong population, distributed over extensive seascapes in the Red Sea. Similarly, we successfully used these secondary signs to locate core aggregation sites of a gregarious dugong population in the Arabian Gulf. That said, this approach has limitations and may not detect habitat use by dugongs feeding on seagrass through cropping (Nakanishi et al., 2008; Budiarsa et al., 2021). Employing multiple methods to identify dugong feeding grounds that combine boat-based surveys (this study), aerial surveys (Preen, 1992; Cleguer et al., 2020) and/or satellite telemetry (Preen, 1992; Holley, 2006; Sheppard et al., 2006) with feeding trail surveys shall provide better insights on the spatial distribution of dugong feeding grounds.

Once identified, an important question to answer from a management perspective is whether dugong feeding grounds have persisted in space and time. Our results underpinned the importance of integrating the freshness of dugong feeding trails, assessed based on pre-defined criteria, as a key parameter in any feeding trail survey. Applying this approach to the north-eastern Red Sea, for instance, we differentiated between feeding grounds that dugongs graze occasionally or seasonally from those used across multiple seasons in a given year.

The spatial distribution and persistence in time and space of these grounds is largely dependent on their environmental, ecological, and anthropogenic covariates determining whether these critical habitats continue to satisfy the dugong's survival needs. While dugong feeding grounds in the north-eastern Red Sea and Arabian Gulf share common attributes (e.g., being shallow, nearshore, sheltered, covered by seagrasses, and threatened by human activities), we detected some spatially explicit differences. In comparison to those in the Arabian Gulf, dugong feeding grounds in the north-eastern Red Sea tend to be located closer to the shore; have wider bathymetric ranges; encompass higher diversity, but lower abundance of seagrass; and feature smaller seagrass meadows. The extensive areal coverage of the shallow seagrass meadows is a remarkable feature of dugong feeding grounds in the Arabian Gulf, and a key factor underlying the distributional patterns of large dugong groups.

2 Dugong movement and herbivory reflect key life-history traits of a facultative herder grazer

The movement patterns of dugongs are mediated by their need to search for and spend much of their time within high quality feeding grounds to satisfy their substantial dietary requirements (Marsh et al., 2002; Ponnampalam et al., 2022). In this regard, we speculate that the lightly-grazed feeding grounds identified in the north-eastern Red Sea, spreading over large spatial scales, had been possibly exploited by dugongs travelling across vast ranges along the fringing reefs (Preen, 1989), while residentiary animals likely grazed across a cluster of meadows with <15 km distance intervals (Sheppard et al., 2006). The high cover of feeding trails reported at two of the feeding grounds in the north-eastern Red Sea was, unexpectedly, within the range exerted by the large dugong groups around Hawar, suggesting that solitary dugongs or small dugong groups may induce herbivory pressures comparable to that of clumped groups if they persistently graze small meadows covered by sparse seagrass. The magnitude of marine herbivory and its implications on seagrass habitat is thus a function of the grouping behaviour of the grazer. While the sparsely distributed dugongs in the north-eastern Red Sea and Dubai dilute their grazing pressures over large seascapes, the grouping behaviour of dugongs around Hawar intensifies herbivory within small confined feeding grounds. Given the larger harvested seagrass area and biomass by the latter, we expect more profound modifications to the seagrass structure and dynamics, including dominance shifts in seagrass species composition (Preen, 1995; Aragones et al., 2006). In addition to the substantial dietary needs and distinctive grazing behaviour, it can be concluded that dugong herbivory is generally mediated by two other key life history traits: the tendency of dugongs to migrate over large seascapes, and aggregate at confined small areas.

3 Dugong grouping behavior in the northern latitudes of dugong distribution

As facultative herders, dugongs aggregate forming sizeable groups at only certain localities with the largest groups have been so far recorded in the Arabian Gulf and Australia (Preen, 1992, 2004; O'Shea et al., 2022; Gole et al., 2023). However, why these predominantly solitary mammals occasionally form groups, and what are the characteristic features of the gregarious populations and their aggregation sites is still unknown (Hodgson, 2004; O'Shea et al., 2022). This thesis represents a rare opportunity to explore dugong grouping behaviour at the northern limits of its global distribution. Interestingly, our results confirmed earlier observations in Australia despite the extended distance interval (>8,750 km), the genetic isolation between the two populations (Plön et al., 2019; Srinivas et al., 2021), and the distinct environmental settings. The large dugong groups reported in Moreton Bay and around Hawar share similar traits of social behaviour; at both localities these groups: (i) account for ~60% of the local dugong population (Preen, 1992), (ii) form fission-fusion groups occasionally breaking into smaller ones (Anderson, 1981; Preen, 1992; Hodgson, 2004), (iii) persist year-round (Preen, 1992; O'Shea et al., 2022), (iv) show a strong fidelity to certain seagrass meadows (Anderson, 1981; Preen, 1992; Hodgson, 2004), (v) follow a predictable migration path while moving between traditional feeding grounds (Anderson, 1981; Hodgson, 2004), and (vi) respond to boat disturbance with coordinated directional short distance mass movements (Hodgson & Marsh, 2007). However, the grouping behaviour of these distinct populations differs in other attributes, considering that they: (i) form larger groups around Hawar (Preen, 1992), (ii) tend to be more clumped around Hawar (Hodgson, 2004), (iii) arrange themselves in multiple layers in the water column around Hawar; (iv) graze in shallower waters in Moreton Bay (Preen, 1992), (v) are more sensitive to boat engines around Hawar (Anderson, 1981; Hodgson, 2004), and (vi) graze on a richer diversity of seagrass species in Moreton Bay. Overall, it appears that the dugong group-forming behaviour at the northern latitudes is a reflection of general traits governing dugong social behaviour reported elsewhere. At the same time, this behaviour shows some site-specific modifications, suggesting that gregarious dugong groups have the ability to adapt their behaviours to the local environment.

4 The challenge of sighting and estimating the size of large dugong groups

Another important finding of our study is highlighting the challenges associated with spotting large dugong groups from low platforms, such as boats, confirming similar difficulties encountered from air during aerial surveys conducted in the same waters around Hawar (Preen, 2004). Similarly, estimating the size of large dugong groups is extremely challenging, particularly in the Arabian Gulf where dugongs form clumped groups and arrange themselves in multiple layers, and where seawater tends to be murky. This may explain why LDGs comprised of >300 dugongs had not been consistently reported around Bahrain over the last three decades. If a conservative correction factor of 2.00 has been applied to account for the sub-surface dugongs missed by boat-based observers, it is likely that a significant proportion of the LDGs recorded during our boat-based surveys would comprise of >100 dugongs. Our definition of a 'large dugong group' (>50 dugongs; boat-based estimation) would then conform with the 'large dugong herd' (>100 dugongs) defined by Hodgson (2004). Unlike other studies (e.g., Preen, 1992; Hodgson, 2004), we prefer to term the dugong sizeable assemblages in the Arabian Gulf 'groups' rather than 'aggregations'. That is because dugongs exhibit evident social interactions among conspecifics as revealed by the coordinated response of LDGs towards boat disturbance (see Acevedo-Gutierrez, 2009). In general, these findings point to the possibility that dugong grouping behaviour may be more common across the dugong range than currently reported, stressing its potential importance in sustaining a number of regional and sub-regional dugong populations. With unmanned aerial vehicles becoming more readily available for dugong researchers (Hodgson et al., 2013; Infantes et al., 2020), more LDG sightings are expected to be reported in other regions, which shall enable better understanding of the dugong grouping behaviour.

5 Drivers inducing large dugong group formation in the Arabian Gulf

Although determining the drivers mediating the grouping behaviour of dugongs in the Arabian Gulf is not among the objectives of this thesis, we recorded field observations that merit additional research. In his study of dugong social behaviour, Preen (1992) hypothesized that 'cultivation grazing' is the main underlying driver inducing dugong group formation in

Moreton Bay, but not in the Arabian Gulf, considering that the latter comprises only pioneer seagrass species. Alternatively, Preen speculated the warm water discharge hypothesis as an explanation for the dugong grouping behaviour around Hawar (Preen, 2004). Our results did not provide any compelling evidence verifying that the exceptional dugong grouping behaviour around Hawar is mediated by localized warm-water discharges. In fact, this hypothesis was primarily drawn on observations of similar aggregation behaviour exhibited by Florida manatees *T. manatus latirostris* around thermal refugia (Reynolds III & Wilcox, 1994; Littles et al., 2019; Edwards et al., 2021). However, our results showed that the geomorphology and hydrodynamics of the dugong aggregation sites around Hawar are distinct from those of manatees. Manatees aggregate around relatively confined sheltered thermal refugia allowing the build-up of warm discharges from power outfalls and natural springs, in addition to salinity stratification formed in sheltered canal systems (Laist & Reynolds III, 2005; Stith et al., 2012; Edwards et al., 2021). In comparison, the dugong aggregation sites around Hawar are located in open offshore waters, driven by semi-diurnal tidal currents, some of which feature medium water velocities. For underwater springs to induce significant increases in ambient seawater temperature in such open waters, the discharges should be vigorous and continuous. This is unlikely considering that underground water in Bahrain has been severely depleted over the last decades due to overexploitation of underground aquifers (Zubari & Lori, 2006; Al-Ansari, 2013; Al-Zubari et al., 2018). Other factors, too, do not seem to adequately explain the dugong grouping behaviour around Hawar. For instance, predation dilution cannot be counted as a key driver given that the waters around Hawar have not been reported to harbour dugong predators, such as big sharks or killer whales *Orcinus orca*. Similarly, calf nursing and rearing cannot help in explaining this phenomenon since the large groups around Hawar encompassed calf proportions within the normal ranges reported across the Indo-Pacific (Preen, 1992; Hodgson, 2004).

As indicated earlier, a number of studies suggested that LDGs in Moreton Bay are feeding aggregations that enhance their feeding efficiency through mass grazing, as speculated by the cultivation grazing hypothesis (Preen, 1995; Hodgson, 2004; Aragones et al., 2006). This thesis addresses the first study outside Australia exploring mass herbivory induced by clumped large dugong groups, and in different environmental and ecological settings. At a first glance, the cultivation grazing strategy may not seem applicable to the LDGs around Hawar due to the fact that only three seagrass species grow in this environment, all are pioneer. However, our results detected dominance shifts between the three pioneer seagrass species with *H. uninervis* being overgrown by the fast-growing *H. stipulacea* and *H. ovalis*. Whether this modification in seagrass species relative abundance in response to dugong grazing is deliberately induced by dugongs to increase their feeding efficiency—as speculated by the cultivation grazing hypothesis (Preen, 1995) —or it occurs as an inevitable consequence of grazing (due to the differences in shoot production rates between species), is yet to be clarified. What is clear is that this dominance shift does not seem conditional on mass dugong grazing as speculated by the cultivation grazing hypothesis. That is because our *in situ* field observations of recovering dugong feeding trails, and the simulated grazing experiments both in Dubai and Bahrain clearly showed that this dominance shift can be induced even at the micro scale of an individual feeding trail. In general, our results provide the first empirical evidence confirming that dugong grazing induces modifications in seagrass dominance in the Arabian Gulf. This proves the crucial roles of dugongs as seagrass ecosystem engineering agents in the Arabian Gulf, supporting similar findings reported elsewhere (Preen, 1995; de Iongh et al., 1998; Nakaoka et al., 2002).

Why dugongs form large groups at spatially delineated aggregation sites around Hawar has remained an answered question although our results point at potential fitness benefits of this grouping behaviour. Through our research, we demonstrated how LDGs around Hawar exhibited a behavioural adaption similar to predator vigilance, enabling aggregating dugongs to continue grazing while maintaining a minimum buffer distance from continuously moving fishing boats (Anderson, 1981; Hodgson & Marsh, 2007; O'Shea et al., 2022). In contrast, solitary dugongs flee upon spotting a boat from distance. This behavioural adaptation seems an added fitness benefit gained by aggregating dugongs, enabling these individuals to maximize their energy gain at high quality, but intensely fished feeding grounds, while minimising the risks of being struck by boat propellers. Whether the intense marine traffic itself is a potential driver mediating the dugong grouping behaviour around Hawar remains an intriguing, but unanswered question and merits particular consideration to inform conservation management. Importantly, this study confirms the multidecadal persistence of LDGs around Hawar year-round, and not just in winter as previously thought (Preen, 1992, 2004). This finding further highlights the global importance of the dugong population in the Arabian Gulf, and can be used to advocate the conservation management of these charismatic animals and their seagrass habitat in the face of accelerating coastal development.

6 Primary production-megaherbivore consumption dynamics in relation to the rotational grazing strategy of dugongs

Comparing the average dugong feeding trail cover around Hawar with that in Dubai demonstrates how massive can be the grazing pressures mediated by large-bodied herbivores should they aggregate in hundreds at spatially confined feeding grounds. Yet, dugongs aggregating around Hawar did not reduce much seagrass cover as their counterparts in Moreton Bay (95%; Preen, 1995). This was unexpected since LDGs around Hawar, relative to those in the southern hemisphere, are larger and more clumped, and occupy smaller aggregation sites (Preen, 1992; Hodgson, 2004). Perhaps, the denser seagrass meadows, composed of only pioneer species, around Hawar provide higher energic returns per unit area compared to the sparser meadows grazed by LDGs in Moreton Bay (Preen, 1992; Hodgson, 2004; Holley, 2006). In general, our work shows the critical importance of primary production-herbivore consumption dynamics in enhancing the understanding of how megaherbivores interact with their foraging grounds. While the removal percentages of seagrass cover/shoots implied that dugong grazing impacts were intense at the feeding ground level, our work shows that seagrass meadows across the study area can cope with this large grazer population. This suggests that the production-consumption relationship is a critical target, placing the feeding ground persistence at a centre of dugong management.

We detected seasonal use of feeding grounds by the sparsely distributed dugong population in the Red Sea and Dubai as well as the clumped large dugong groups around Hawar, conforming with similar trends reported elsewhere (Marsh et al., 2022; O'Shea et al., 2022). Rotational grazing has been reported to enable fast recovery of grazed meadows (Preen, 1995; Aragones et al., 2006), sustaining their capacity to persistently support the local dugong population. This behavioural adaptation, in turn, hints the importance of the lengthy dugong calving interval (3–7 years; Marsh & Kwan, 2008) and grouping behaviour in transmitting traditional knowledge, informing conspecifics on where high quality feeding grounds are, and when grazing should be shifted to other meadows to avoid forage depletion.

7 Adaptation of dugongs and seagrasses to the harsh environmental settings in the Arabian Peninsula

Dugongs and seagrasses in the Arabian Gulf experience the highest seawater temperature and salinity levels worldwide. In addition to these extremes, both grazers and forage are subject to wide annual thermal fluctuations, with cold winter temperatures overlapping with the lower thermal tolerance threshold of dugongs. That said, the multidecadal and year-round persistence of LDGs around Hawar underlines remarkable dugong adaptations towards these temperature and salinity extremes and fluctuations (Preen, 1989). These harsh conditions have not forced dugongs to abandon their traditional feeding grounds, nor they have constrained the capacity of seagrass in sustaining sizeable clumped dugong groups, despite that the meadows undergo seasonal dieback cycles. In fact, our results unexpectedly showed that seagrasses in the Arabian Gulf recovered following simulated dugong grazing within the timeframe reported in other less-stressed marine environments (de Iongh et al., 1995; Preen, 1995; Aragones et al., 2006). Contrary to our expectations, also, the results further suggest that this adaptation is likely enhanced by the harsh temperature and salinity levels, selectively promoting the dominance of only pioneer seagrasses, well adapted to disturbance and grazing, across the dugong feeding grounds. In comparison, although seawater temperature and salinity in the Red Sea are elevated compared to other marine environments, they are not too extreme to considerably constrain seagrass diversity as is the case in the Arabian Gulf. In the Red Sea, the extension of the fringing reefs along most of the coastline limits the prevalence of unconsolidated sediment in nearshore shallow waters, impeding the establishment of extensive meadows dominated by pioneer species (Preen, 1998; El Shaffai, 2016). This is not the case in the Arabian Gulf where the shallow waters fringed by islands and reefs around Saudi Arabia, Bahrain, Qatar, and United Arab Emirates favour the establishment and persistence of extensive meadows, a key factor governing the distribution of large dugong groups.

8 Dugong feeding grounds overlap with high human use areas: Implications on dugong herbivory

The substantial dietary needs of the large-bodied dugongs necessitates that they spend much of their time in nearshore waters, where shallow sheltered seagrass meadows are present. This brings these slow-reproducing animals in direct contact with humans, exposing them to multiple anthropogenic stressors (Hodgson & Marsh, 2007; Cleguer et al., 2015; Ponnampalam et al., 2022). We detected a consistent trend across all localities covered by this study (i.e., northern Saudi Arabian Red Sea, Dubai, and Bahrain), where dugongs had continued to graze in proximity to humans. In the Red Sea, dugong feeding trails were observed near to fishing harbours and coastal construction activities, while in Dubai grazing dugongs left distinctive trails off a beach resort bordering an industrial harbour. In Bahrain, dugongs were sharing their traditional feeding grounds with tens of boats and hundreds of fishing gear, almost daily. This trend, also, has been reported across the dugong distributional range (Preen, 1992; Hodgson & Marsh, 2007; Ponnampalam et al., 2022). For instance, Ng et al. (2022) detected dense dugong feeding trails in inshore meadows close to urbanized areas in Singapore, conforming with our observations in Dubai.

We observed dugongs grazing, during the daytime, in proximity to anthropogenic activities across all studied localities. This suggests that dugongs in the Arabian Peninsula risk their health and lives while searching for and grazing on seagrass. As such, the implications of human-induced disturbances on dugong herbivory should not be underestimated (Preen, 1992; Hodgson & Marsh, 2007; Ponnampalam et al., 2022). This merits a particular conservation consideration given the substantial seagrass biomass that a dugong has to graze on daily basis to satisfy its energetic requirements. The experimental study of Hodgson and Marsh (2007) is the only quantitative assessment of the feeding time budget lost by dugong groups forced to suspend their feeding in response to boat disturbance. Our direct observations suggested that LDGs can tolerate boat disturbance only from specific distance and to a certain threshold, beyond which they promptly suspend grazing before leaving their traditional feeding grounds. Undoubtfully, there is a need to replicate this study in the Arabian Peninsula on both solitary dugongs as well as large dugong groups.

9 The pressing need for regional collaboration to strengthen dugong and seagrass conservation in the Arabian Peninsula

Our results highlighted the transboundary nature of dugongs along both sides of the Arabian Peninsula. In the north-eastern Red Sea, the identified feeding grounds around Ras Al-Shaykh Humayd, Sanafir Island, and Tiran Island are within the daily movement range of dugongs, reported by Sheppard et al. (2006), from the Egyptian coast. It is speculated, therefore, that dugongs may migrate across the northern Red Sea in between the feeding grounds in Saudi Arabia and Egypt as suggested earlier by the occasional sightings of dugongs traveling across offshore deep wates (Baldwin, 2018). Along the Egyptian coast, dugongs have been, also, reported to seasonally migrate between feeding grounds >35 km apart (Shawky et al., 2017; Nasr et al., 2019), confirming earlier observations along the Saudi Arabian coasts (Preen, 1989). In the Arabian Gulf, our direct field observations of large dugong groups transversing the Bahrain-Qatar border prove that these groups cross jurisdictional boundaries. The seasonal movements of LDGs between their winter and summer feeding grounds further demonstrate the significance of migration corridors in maintaining this life history trait.

The crucial role of regional collaboration in strengthening the conservation management of wide-ranging slow-breeding marine mammals, like dugongs, have been consistently emphasised by other studies, and transboundary dugong protected areas have been proposed in the Arabian Gulf since decades (Preen, 1989, 2004; Hodgson, 2009; Knight et al., 2011; Preen et al., 2012). The delineation of a number of Important Marine Mammal Areas encompassing dugong core habitats in the Red Sea and Arabian Gulf (IUCN-Marine Mammal Protected Areas Task Force, 2021) further underscores the role of regional partnership in addressing common challenges and shared opportunities pertaining to dugong management. Dedicated regional dugong and seagrass conservation plans, developed in accordance with the ecosystem-based management approach, can serve as an overarching umbrella bringing together all key players to identify regional strategic conservation management priorities. These may include: (i) regional networks of transboundary dugong protected areas, (ii) collaborative seasonal management of dugong migration corridors, (iii) collective control of key anthropogenic activities threatening dugongs and seagrass, and (iv) regional monitoring programs for the dugong populations and their key habitats. The rapidly intensifying coastal development along the Arabian Peninsula's coastlines underlines how crucial it is for all range states to collaborate if we to safeguard the globally important dugong populations and their seagrass habitats in the Red Sea and Arabian Gulf.

10 Future directions

Through this thesis, we have identified the following key knowledge gaps that shall be considered for future research to enhance the understanding of dugong-seagrass interactions in the Arabian Peninsula:

10.1 Dugong herbivory in relation to dugong movements in the Red Sea and Arabian Gulf

Although dugong movement patterns have been studied in other dugong range states across the Indo-Pacific (Sheppard et al., 2006; Cleguer et al., 2020; Deutsch et al. 2022a, 2022b), very little is known about how dugongs distribute themselves in space and time, and the resultant influences on dugong grazing strategies in the Red Sea and Arabian Gulf. In this thesis, we delineated the core aggregation sites of large dugong groups around Hawar and identified their habitat characteristics. However, there is a need to better understand the movement patterns of dugongs in both Red Sea and Arabian Gulf to inform the conservation management on where dugongs spend much of their time and which migration corridors connect core dugong areas. To this extent, satellite and acoustic telemetry has been widely used in Australia to determine dugong home ranges and migration patterns, along with time spent in different seagrass meadows (Marsh & Rathbun, 1990; Preen, 1992; Sheppard et al., 2006; Zeh et al., 2015, 2016; Cleguer et al., 2020). However, extreme care should be taken before attempting these studies in the Arabian Peninsula considering the harsh environmental settings that may increase the vulnerability of dugongs to stress caused by capturing and restraining (Lanyon et al., 2006). Such studies should be only undertaken by experienced experts in this field and under strict animal welfare regulations. By overlaying the resultant dugong distribution heat maps and marine habitat charts, the correlation between the dugong movement patterns and core areas (e.g., feeding grounds and migration corridors) can be determined. This shall inform conservation management on the time dugongs spend in core areas and reveal any seasonality in their use of space.

10.2 The underlying drivers mediating dugong grouping behavior in the Arabian Gulf

In this study, we proved that the Arabian Gulf is home to the largest dugong groups on earth, and discussed the potential roles of thermoregulation, boat disturbance, areal extent of seagrass meadows, and rotational grazing in inducing the formation of large dugong groups. However, our results did not explicitly determine what factors govern such exceptional dugong social behaviour. Identifying these covariates and exploring whether they directly or indirectly influence seagrass production-dugong consumption dynamics shall underscore dugong conservation management priorities in the region.

10.3 Modeling the spatial distribution and carrying capacity of dugong feeding grounds in the Arabian Peninsula

We identified the habitat characteristics of key dugong feeding grounds in the Red Sea, and determined the geomorphological, environmental, ecological, and anthropogenic correlates of LDG habitats in the Arabian Gulf. These findings can form the basis for developing spatially explicit models projecting the spatial distribution of dugong feeding grounds in the Red Sea and Arabian Gulf. The models, also, could identify key dugong aggregation sites in the Arabian Gulf, which are likely governed by a different suite of covariates compared to solitary animals or small groups. Alongside, the dugong carrying capacity of key dugong feeding grounds and aggregation sites can be modelled through incorporating spatially explicit seagrass production-dugong consumption dynamics.

10.4 The extent to which seagrass seasonality influences dugong herbivory in the Arabian Peninsula

Our results clearly demonstrated that seagrasses in the Arabian Gulf, in particular, are dynamic and governed by profound seasonal variations that include repeated dieback cycles. These fluctuations appeared site-specific and varied considerably even at small spatial scales. Our findings highlighted that we are far from fully understanding the dynamics of seagrasses surviving in extreme environments like the Red Sea and Arabian Gulf. Seagrass meadows around the Arabian Peninsula experience some of the hottest seawater temperatures on earth, and even small increases in temperature could be critical for the persistence of seagrasses and the dugongs dependent on them. There is, therefore, a pressing need to better understand the seasonal variations in seagrass abundance and community structure across wide spatial, environmental, and ecological gradients and identify the factors governing these variations. This study could also provide insight on the implications of seagrass seasonal variations on dugong-seagrass interactions, and clarify the extent to which these dynamic cycles influence dugong grazing strategies and associated movement patterns.

10.5 The influence of boat disturbance on dugong herbivory in the Arabian Peninsula

This thesis identified behavioural adaption of large dugong groups towards intense maritime traffic in the Arabian Gulf. However, wide knowledge gaps hinder our understanding of the factors governing the interactions between dugongs and boats, including the distance interval between dugongs and approaching vessels as well as vessel speed and direction. Similarly, the maximum tolerance thresholds of LDGs to repeated boat disturbances is largely unknown. Our observations indicated that solitary and paired dugongs, in particular, respond to boat disturbance by immediate fleeing and thus inducing unquantified losses in dugong feeding time budgets. Also, the proximity of some dugong feeding grounds in the north-eastern Red Sea to fishing harbours highlights how important it is to understand the response of grazing dugongs to approaching vessels. This knowledge could inform spatial planners on the areal extent and design of dugong protected areas, overlapping with boating and fishing activities.

10.6 Dugong-seagrass interactions in the era of global warming

Both the Red Sea and Arabian Gulf are characterised by harsh environmental conditions that provide an opportunity to project dugong-seagrass interactions under future scenarios of climate change-induced rising seawater temperatures. Some key research questions that could be addressed are what structural, physiological, and morphological adaptations enable seagrasses to survive in these environments, and whether these adaptations have any influences on dugong herbivory. Additionally, it will be interesting to explore the implications of dugong herbivory on the blue carbon sequestration capacity of seagrass meadows in the Red Sea and Arabian Gulf.

8

General Conclusions

This section brings together key findings drawn from the previous chapters to crystalize evidence-based conclusions enhancing the understanding of dugong feeding ground dynamics in the Arabian Peninsula and determine strategic priorities informing the conservation management of the globally sizeable dugong populations of the Red Sea and Arabian Gulf, as follows:

- Secondary feeding signs resulting from the excavating grazing mode of dugongs can be employed as a valuable spatial planning tool to determine key feeding grounds of sparse and dense dugong populations.
- The dugong conservation management efforts in the north-eastern Red Sea should focus on high-use dugong areas mainly located in nearshore shallow sheltered coastal lagoons, bays, and the lee of large islands.
- The extensive shallow seagrass meadows around Hawar Island, Bahrain harbor the world's largest dugong groups ever recorded in recent history that have persisted in these waters almost year-round for more than three decades.
- Dugongs and seagrasses in the Arabian Peninsula survive under harsh environmental settings, likely leaving only limited room for additional pressures induced by anthropogenic stressors.
- The spatial distribution of large dugong groups around Bahrain is correlated with healthy dense extensive seagrass meadows that have been intensely fished over decades and need to be protected from potential fragmentation associated with future development in the region.
- The proximity of dugong feeding grounds along the western and eastern coasts of the Red Sea as well as the straddling of core dugong aggregation sites across the Bahrain-Qatar border suggests the transboundary nature of dugongs in the Arabian Peninsula.
- The multidecadal co-existence between fishers and dugongs indicates how important it is to enlist local fishers as co-managers and advocators of seagrass and dugong conservation in the Arabian Gulf.
- Effective conservation management of dense megaherbivore populations, such as the large dugong groups around Hawar Island, is conditional on the persistence of their traditional feeding grounds which necessitates maintaining the overall primary production persistently higher than megaherbivore consumption.

- Ensuring that migration corridors are kept functionally open for dugongs is crucial to maintain the dugong rotational grazing between seasonal feeding grounds that, in turn, enables seagrass meadows to cope with the intense dugong grazing pressures.
- Considering the substantial dietary needs of dugongs that entail them to spend much of their time in seagrass meadows, dugong feeding grounds should be incorporated as a key unit in dugong conservation management strategies.
- Conserving the sizeable dugong populations in the Red Sea and Arabian Gulf should be a global priority, requiring regional collaborative management between all range states, which shall include establishing a regional network of effectively managed marine protected areas encompassing dugong key aggregation sites, feeding grounds and migration corridors.

9

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10

Annex-1
Supplementary Materials

Table S1. Comparison between seagrass recovery time interval as well as dugong grazing-mediated seagrass species dominance shift, recorded around Hawar Island (Bahrain) with other dugong habitats across the dugong range including large dugong group (>50 dugongs) feeding grounds (HU= *Halodule uninervis*, HS= *Halophila stipulacea*, HO= *H. ovalis*, * = large dugong group feeding ground).

Locality	**Post-grazing seagrass recovery**		**Reference**
	Time interval	**Seagrass dominance shift**	
Andaman and Nicobar Archipelago, India	9 days	Dominance of pioneer seagrasses	D’Souza et al. (2015)
Koh Bae Na, Thailand	<20 days		Nakaoka and Aioi (1999)
Indonesia	4–5 month		de Iongh et al. (1995)
Ellie Point, Australia	3–7 month	Dominance of pioneer seagrasses (HO) increased	Aragones and Marsh (2000)
Cardwell, Australia	3–8 month		Aragones and Marsh (2000)
Moreton Bay, Australia*	5–6 month	Dominance of pioneer seagrasses (HO) increased	Preen (1995)
Moreton Bay, Australia*	<12 months		Peterken and Conacher (1997)
Hawar Island, Bahrain*	4–6 months	Dominance of HS and HO increased relative to HU	This study

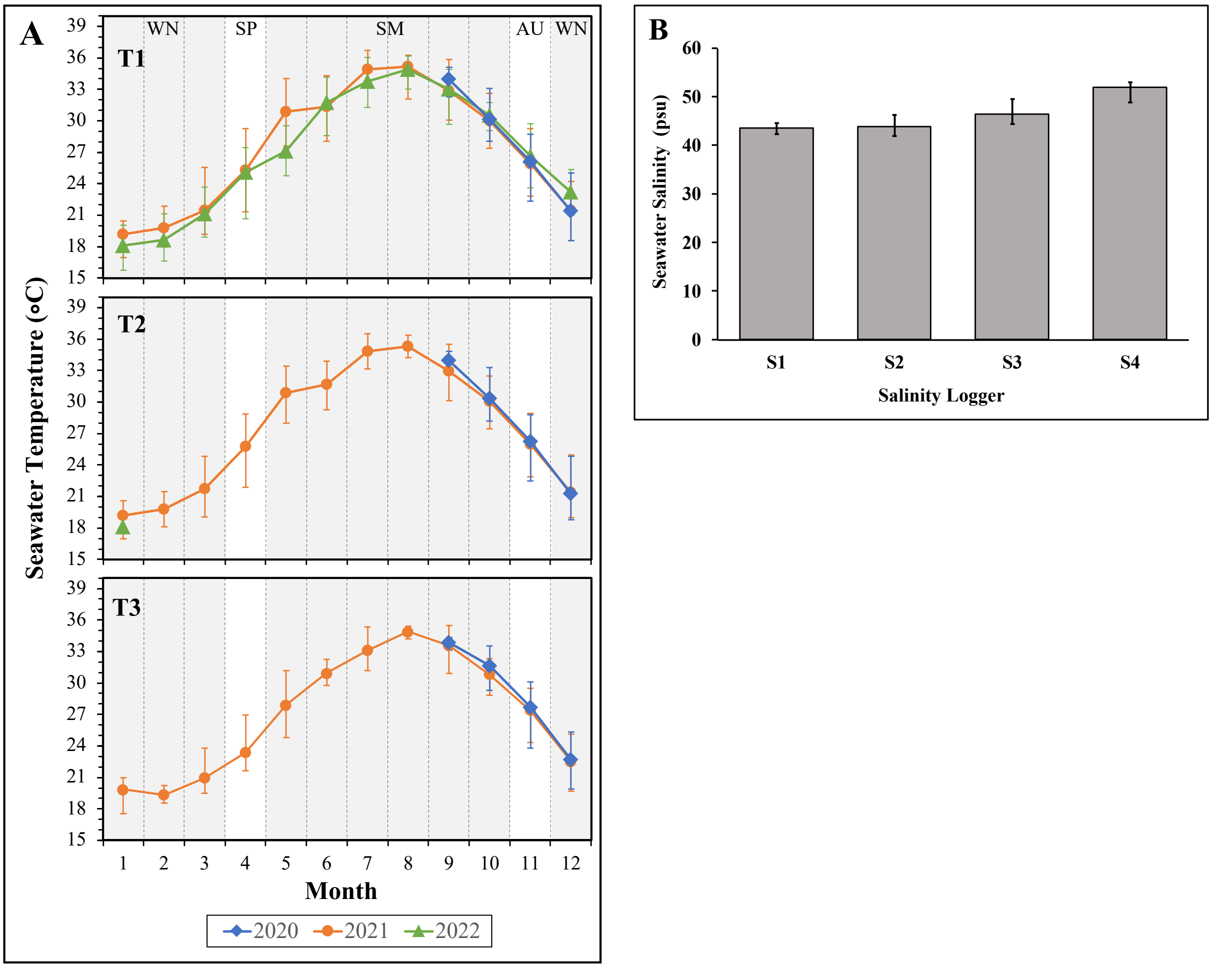

Figure S1. Spatial and temporal variations in seawater quality parameters: (A) temperature presented as monthly mean, minimum, and maximum; and (B) salinity presented as mean, minimum, and maximum values across monitoring sites. The temperature and salinity readings (*N*= 253,536 and 5,689, respectively) were measured by three and four *in situ* water quality loggers, respectively, deployed around Hawar Island (Bahrain) and configured to record a fix every 10 minutes (T= temperature logger number, S= salinity logger number, WN= winter, SP= spring transition period, SM= summer, AU= autumn transition period, bars= minimum and maximum values).

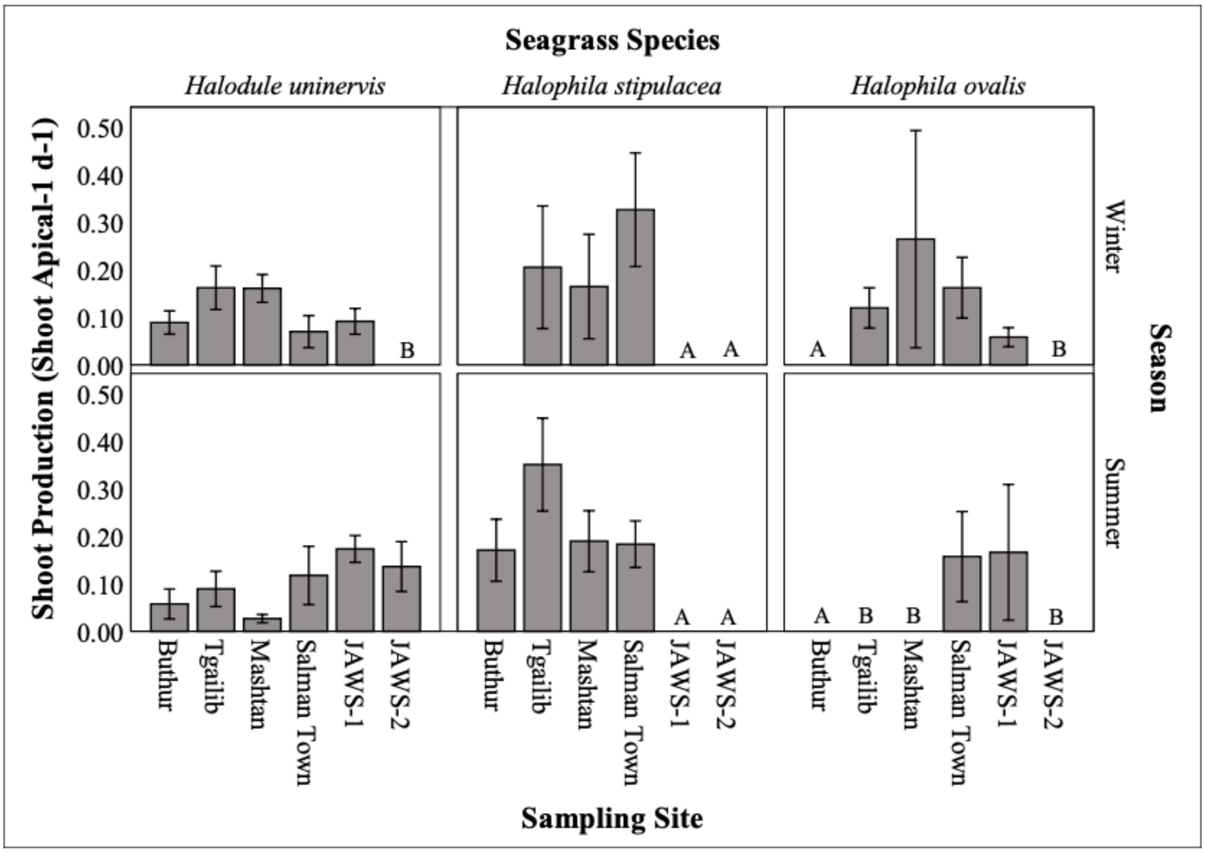

Figure S2. Seagrass shoot production rate per apical shoot (shoot apical^{-1} d^{-1}) measured through shoot tagging experiments for different seagrass species (*N*= 245) across seasons and experimental sites (*N*= 6) at Jabal Ali Wildlife Sanctuary, Dubai (JAWS-1 and JAWS-2) and around Hawar Island, Bahrain (Buthur, Tgailib, Mashtan, and Salman Town), (bar= standard error, A= species not present at a particular site, B= recovery of tagged shoots was not successful).

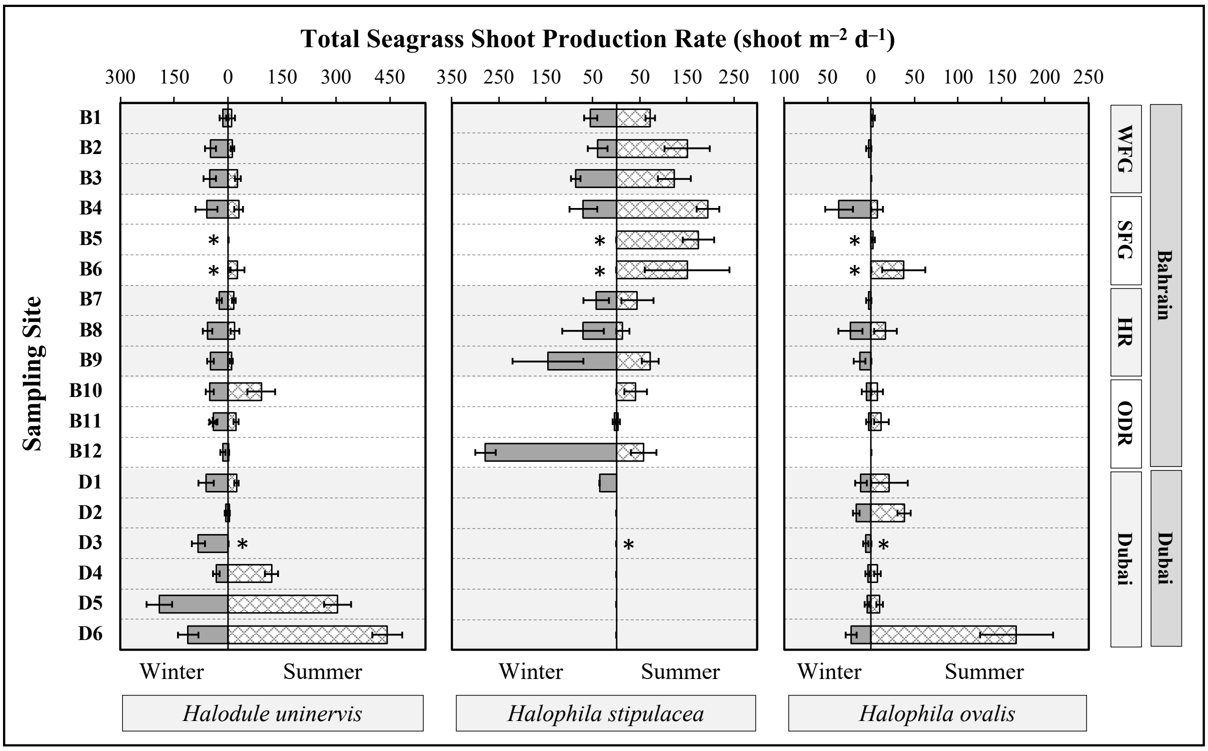

Figure S3. Spatial and temporal variations in relative shoot production rate (shoot m^{-2} d^{-1}) calculated for seagrass species across seasons and sampling sites at Jabal Ali Wildlife Sanctuary (Dubai) and around Hawar Island (Bahrain). Sampling sites are classified into key zones, including main large dugong group aggregation areas. Species and seasons are presented in different scales (B= sampling site around Hawar, D= sampling site at Jabal Ali Wildlife Sanctuary, WFG= winter feeding ground, SFG= summer feeding ground, HR= home range, ODR= overall distributional range of large dugong groups, bar= standard error, * = site not surveyed during a particular season).

11

Annex-2
Published Articles

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

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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

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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

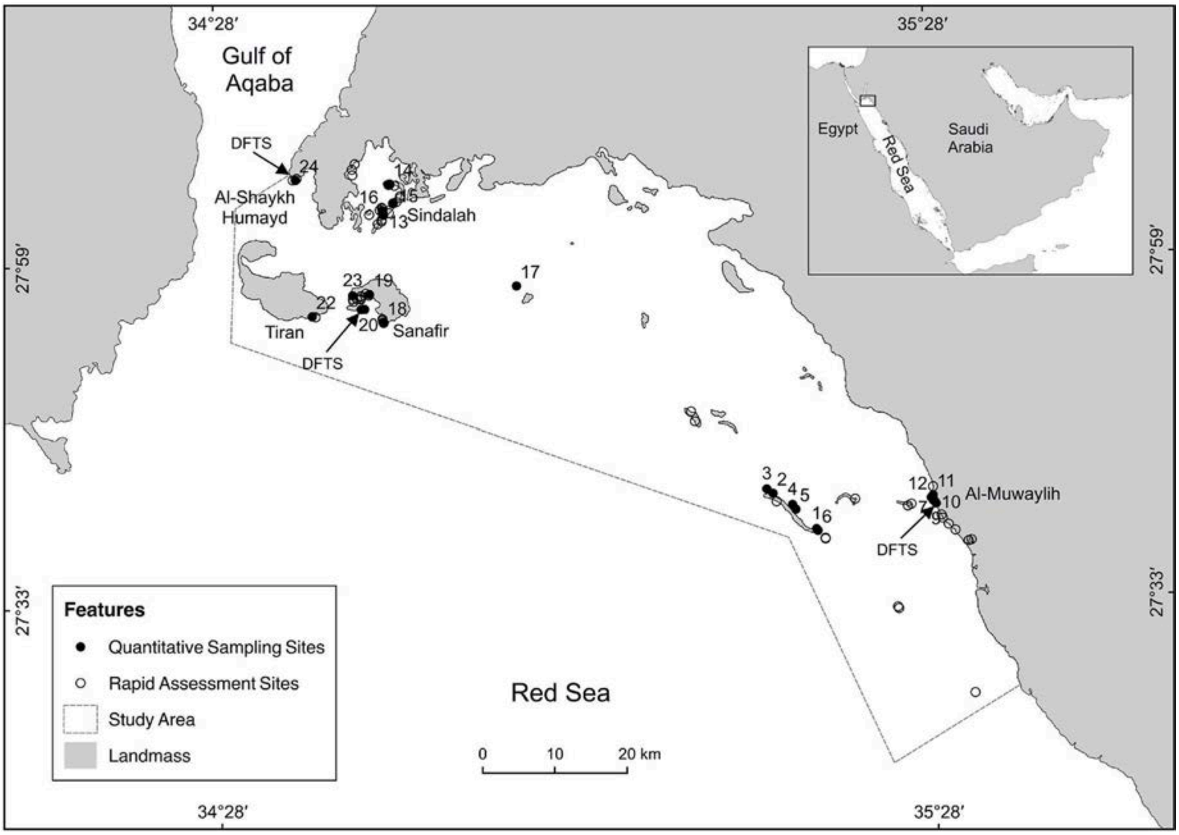

Fig. 1. Map of the study area showing the sampling sites quantitatively surveyed for the dugong feeding signs and seagrass meadow characteristics, dugong feeding trail measurement sites, and the initial rapid survey sites. The inset map shows the location of the study area in the Saudi Arabian northern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

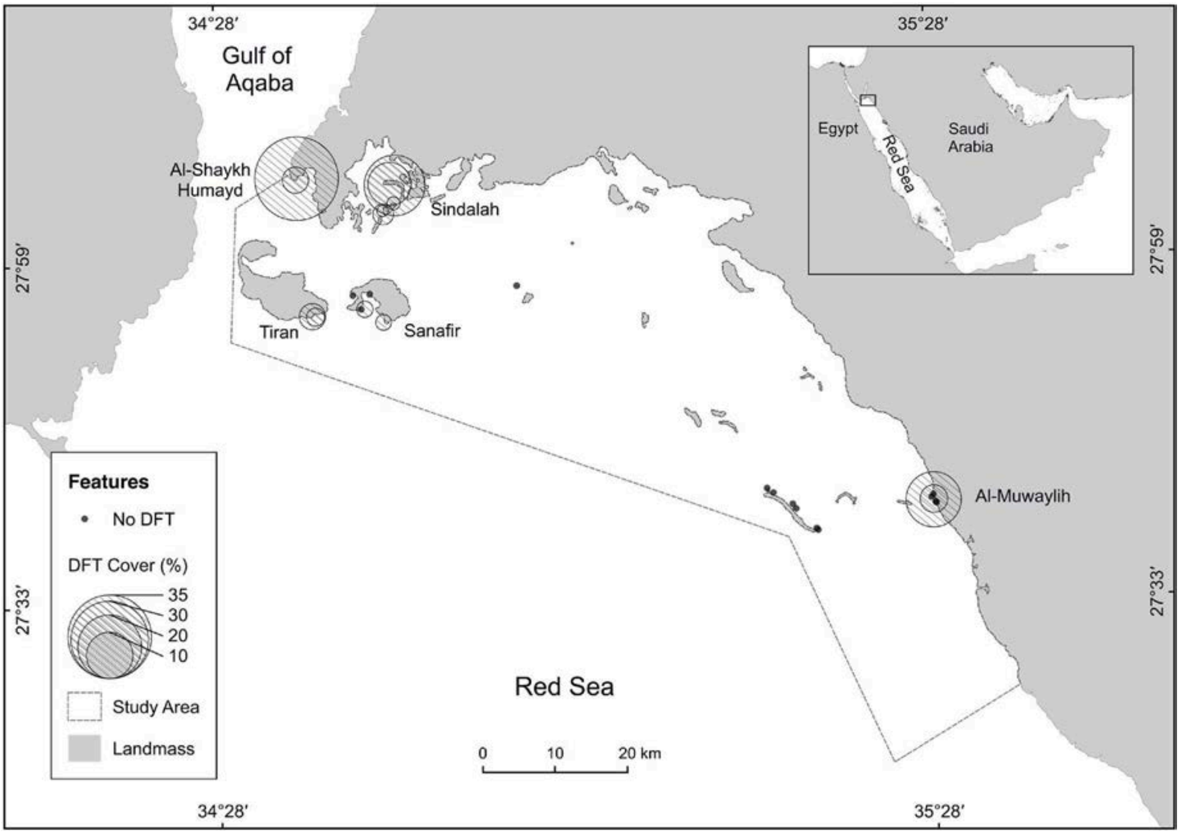

Fig. 2. Dugong feeding trail cover (%) across the study area superimposed on the sampling sites. The inset map shows the location of the study area in the north-eastern Red Sea (DFT = dugong feeding trail).

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

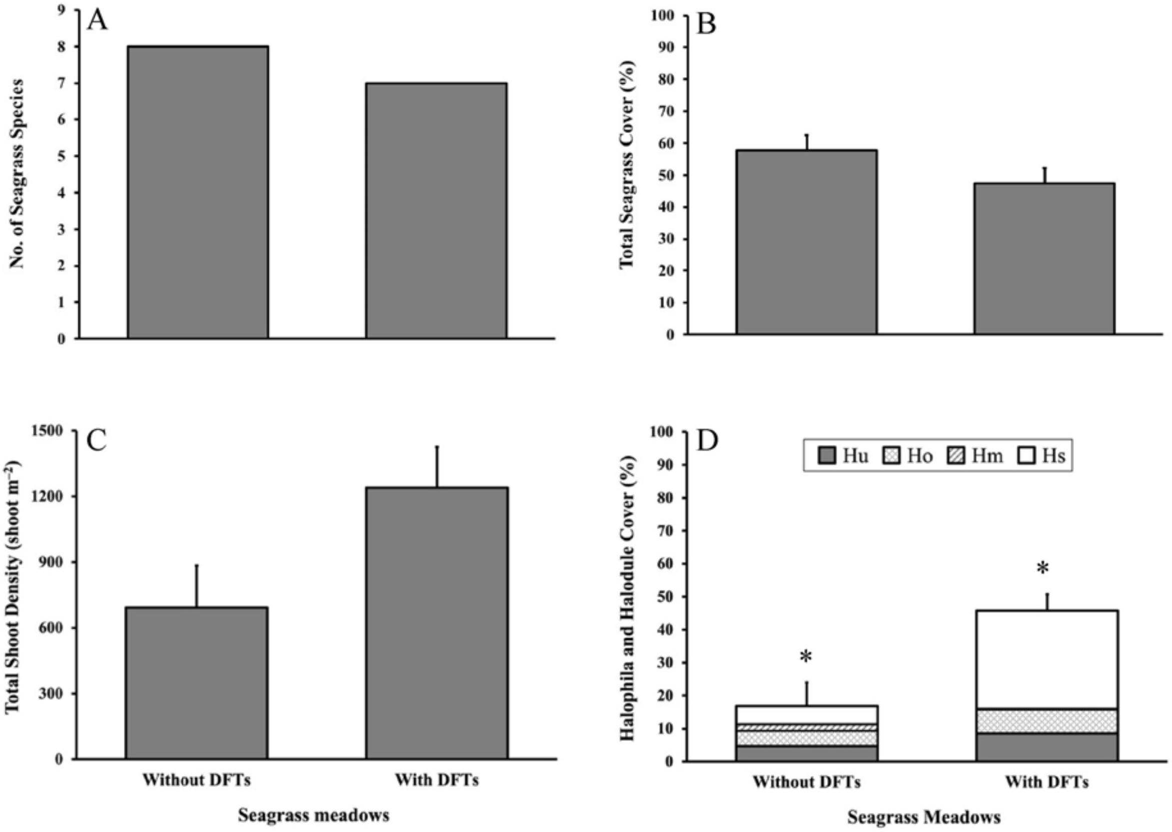

Fig. 3. Comparison between sites with and without dugong feeding trials based on a suite of seagrass diversity and abundance covariates: (A) number of seagrass species, (B) total seagrass cover (%), (C) total shoot density (shoot m^{-2}), and (D) combined cover (%) of *Halophila* and *Halodule* spp. (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

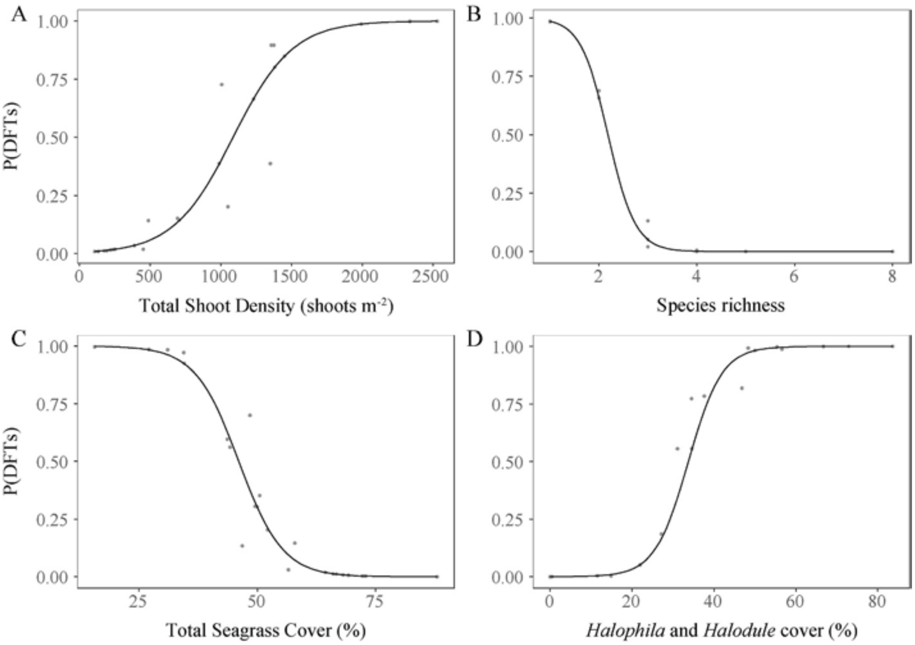

Fig. 4. Generalised Linear Model (GLM) output demonstrating the influence of selected biological factors on the dugong feeding trail detection probability (P (DFTs)) across the study area: (A) total shoot density (shoot m^{-2}), (B) species richness (i.e., total number of seagrass species), (C) total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

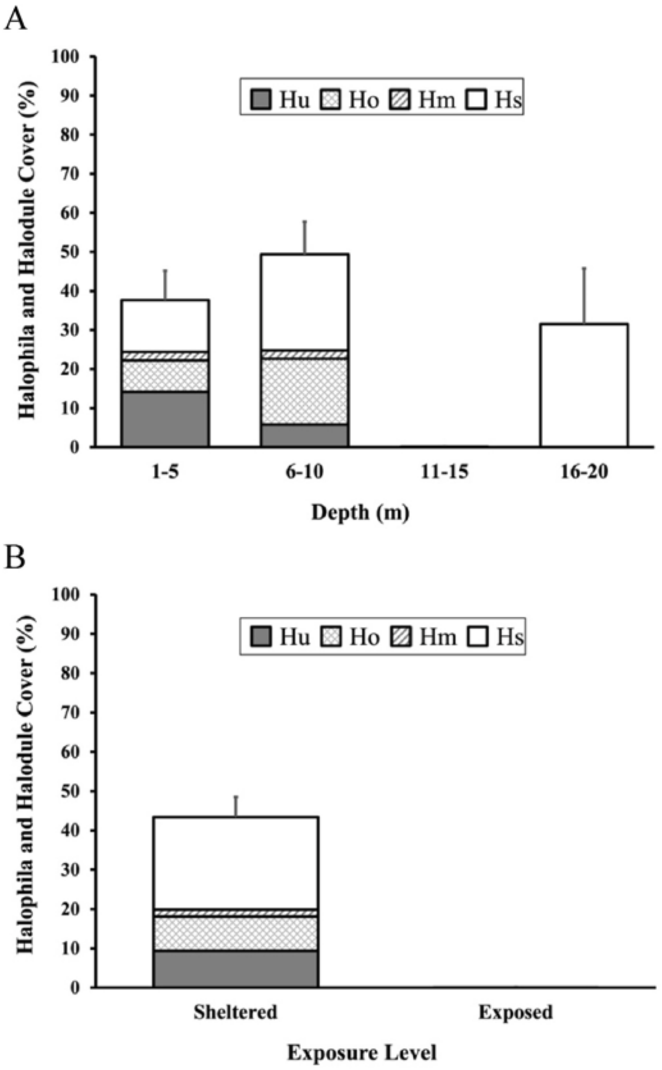

Fig. 5. Comparison among the sampling sites pinpointing the influence of key environmental factors on the combined cover (%) of seagrasses belonging to the genera *Halophila* and *Halodule*: (A) water depth (m), and (B) exposure to waves and currents (Hu = *Halodule uninervis*, Ho = *Halophila ovalis*,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

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RESEARCH ARTICLE

WILEY

Long-term persistence of large dugong groups in a conservation hotspot around Hawar Island, Kingdom of Bahrain

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Abstract

1. Predictable aggregations of large marine mammals are valuable conservation targets, but aggregated populations can also be exposed to site-level threats.
2. The globally vulnerable *Dugong dugon* has a wide distribution but is found in large numbers mainly in Australia and the Arabian Gulf. Though Australian dugong populations are well studied, much less is known of the dugongs in the Arabian Gulf.
3. The spatial and temporal persistence of dugongs around Bahrain, with a focus on large dugong groups (>50 dugongs), was determined using an occupancy modelling framework supported by historical records, structured interviews, citizen science network reports, and small-scale boat and unmanned aerial vehicle surveys.
4. Historical records and current distributional studies confirmed that large dugong groups have been reliably sighted around Hawar Island (Bahrain) since at least 1986, forming large, clumped groups that persist almost year round. The largest recorded so far in the world, these fluid groups (maximum of ~700 dugongs) account for ~60% of the dugongs found in Bahrain and ~12% of all dugongs in the Arabian Gulf.
5. The delineated occupancy core area of large dugong groups (~145 km^2) straddles the Bahrain–Qatar border, reflecting the transboundary nature of these groups.
6. Careful management of human-induced stressors (in particular, fishing, boating, and coastal development) combined with regular monitoring of Hawar Island's large dugong groups and their seagrass habitat is critical to safeguard this globally important population.
7. The effectiveness of any conservation management is predicated on strengthening cooperation among all range states in the Arabian Gulf. A key recommendation of this study is to establish a regional network of marine protected areas encompassing core aggregation sites for dugongs, particularly the

Hawar Islands in Bahrain, the north-western waters of Qatar, Marawah Island in the United Arab Emirates in addition to the shallow waters between Saudi Arabia, Qatar, and United Arab Emirates.

KEYWORDS

Arabian Gulf, conservation, fishing, GIS, grouping behaviour, historical data, marine mammals, memory recalls, seagrass

1 | INTRODUCTION

The tendency of many large marine mammals to gather in dense aggregations at predictable locations makes these sites hotspots for conservation (Nowacek et al., 2011; Brakes & Dall, 2016; di Sciara et al., 2016). At the same time, their high abundances and clumped distribution make these populations particularly vulnerable to human-induced stresses at their aggregation sites (Anderson, 1981; Laist & Reynolds, 2005; Schipper et al., 2008; Reeves, 2009; Reynolds & Marshall, 2012; Magera et al., 2013; Brakes & Dall, 2016). The globally Vulnerable dugong (*Dugong dugon*) (Marsh & Sobtzick, 2019) shows highly variable grouping behaviour (Preen, 1992; Hodgson, 2004; Marshall et al., 2018). Described as facultative herders (Preen, 1992), dugongs are usually found as solitary individuals, mother–calf pairs, or small groups (<10 dugongs), but they occasionally aggregate in large groups of several hundred (Anderson, 1981; Preen, 1992; Hodgson, 2004; Marsh, O'Shea & Reynolds, 2011; Marshall et al., 2018; Deutsch et al., 2022; Khamis et al., 2022; O'Shea et al., 2022).

Dugongs have experienced considerable reductions across their Indo-Pacific distributional range with reported regional extinctions dating back to the 18th century (Marsh, O'Shea & Reynolds, 2011; Aragones et al., 2012b; Marsh & Sobtzick, 2019). Yet, data on their population status and distribution are still scarce in many regions, even where they are known to be abundant (Marsh et al., 1999; Marsh et al., 2002; Marsh & Sobtzick, 2019; Khamis et al., 2022). Across their range, dugongs are threatened by incidental net entanglement, direct hunting, alteration and loss of their primary seagrass habitats, boat strikes, pollution, and climate change, pushing several geographically isolated populations to the edge of extinction (Marsh et al., 2002; Reynolds & Marshall, 2012; Aragones et al., 2012b; Marsh & Sobtzick, 2019; Marsh et al., 2022; Ponnampalam et al., 2022). For instance, the dugong population in China has recently been declared functionally extinct. In addition, dugongs in Japan and East Africa are Critically Endangered, and in New Caledonia they are considered Endangered (Marsh & Sobtzick, 2019; International Union for Conservation of Nature, 2022; Lin et al., 2022a; Lin et al., 2022b).

Their slow reproduction rate and long generation times impede the rapid recovery of depleted dugong populations (Anderson, 1981; Marsh et al., 1999; Marsh et al., 2002; Marsh & Kwan, 2008; Marsh, O'Shea & Reynolds, 2011). This makes areas where dugongs aggregate in large numbers of particular significance. On the one hand, they are ideal areas to conserve the population. On the other hand, anthropogenic stressors at these key sites can disproportionally affect a large number of breeding adults as well as calves. Therefore, identifying these aggregation sites and determining how dugongs use them over space and time are important conservation priorities (Hodgson, 2004; Preen et al., 2012). However, this is often not straightforward. Dugongs are characteristically wide-ranging and elusive animals (Marsh et al., 2002; Sheppard et al., 2006; Marsh, O'Shea & Reynolds, 2011), and obtaining reliable population estimates across extensive spatio-temporal scales can be a considerable challenge for conservation planners.

Despite its vast range, spanning around 44 countries and territories across the warm tropical and subtropical Indo-Pacific waters (Marsh & Sobtzick, 2019), large groups (co) of >100 dugongs have been reported in recent times predominantly from two broad regions: Australia (e.g. Moreton Bay, Cape York, and Shark Bay) and the Arabian Gulf (e.g. Bahrain, Qatar, and United Arab Emirates) (Preen, 1992; Marsh et al., 2002; Lanyon, 2003; Hodgson, 2004; Preen, 2004; Chilvers et al., 2005; Marshall et al., 2018). Slightly smaller groups of between 50 and 100 dugongs are more common and have been regularly sighted in Australia (e.g. Moreton Bay, Cape York, Shark Bay, Hervey Bay-Tin Can Bay, Cape Flattery–Princess Charlotte Bay, and Shoalwater Bay) and the Arabian Gulf (e.g. Bahrain, Qatar, and United Arab Emirates) (Preen, 1992; Preen & Marsh, 1995; Marsh et al., 2002; Hodgson, 2004; Preen, 2004; Sobtzick et al., 2017; O'Shea et al., 2022), but have also been encountered occasionally across a broader range, including New Caledonia (Cleguer, 2015), Thailand (Hines, Adulyanukosol & Duffus, 2005), and Mozambique (Findlay, Cockcroft & Guissamulo, 2011). Across this range, however, small groups of one or two dugongs are still frequently encountered (O'Shea et al., 2022).

The Arabian Gulf hosts one of the world's largest (∼5,800) dugong populations (Preen, 2004), second only to Australia (∼155,000 dugongs; Clark, Fischer & Hunter, 2021). The Arabian Gulf's population is considered the largest in the western and northern regions of the dugong's distributional range (Marsh et al., 2002; Preen, 2004; Hodgson, 2011; Preen et al., 2012). The population is spread over a wide area, and the key to maintaining and conserving the species is identifying hotspots of dugong use, especially those occupied by large groups (Preen, 2004; Preen et al., 2012). To date, however, the management of large dugong groups (LDGs) (>50 dugongs) and their primary habitats in the Arabian Gulf has been limited by sparse information. In 1986, Preen (1989) and Preen (2004) encountered exceptionally large groups totalling ~670 dugongs in the Arabian Gulf, south east of Bahrain, repeatedly cited as the largest ever reported in the world (Preen, 2004; Hodgson, 2011; Marsh, O'Shea & Reynolds, 2011; Preen et al., 2012; O'Shea et al., 2022). After this first record from over 35 years ago, reliable reports of LDGs in the Arabian Gulf are limited to a few sightings from Bahrain and United Arab Emirates (Preen, 2004; Hodgson, 2011; Preen et al., 2012; Environment Agency-Abu Dhabi, 2014). An exception was Marshall et al. (2018) who reported five LDGs in the north-western waters of Qatar near the Bahrain-Qatar border on surveys conducted in the winter of 2015. Given the current wide knowledge gaps, it is difficult to know where LDGs are reliably found in the Arabian Gulf, how persistent they are in these areas, and whether they form seasonally or use the area throughout the year. This baseline information is essential for effective spatial management of aggregating marine mammals such as dugongs.

In this study, current and past distribution of LDGs was evaluated around Bahrain and their persistence since their first encounter in 1986 was determined. For this, a set of complementary methods was used including historical records, structured interviews, citizen science network reports as well as small-scale boat and unmanned aerial vehicle (UAV) surveys. Consequently, current critical LDG areas around Bahrain were identified and a proactive conservation approach has been discussed with a focus on strengthening the role and utility of regional cooperation in managing this globally important dugong population and associated seagrass habitat.

2 | MATERIALS AND METHODS

2.1 | Study area

The study covered the territorial waters of the Kingdom of Bahrain (25°32′–27°9′ N; 50°20′–51°7′ E) that span over ~7,500 km^2 (Al-Zayani, Zainal & Choudhury, 2009). Bahrain is an archipelago comprising more than 36 islands and islets occupying a total landmass area of 778 km^2 (General Directorate of Statistics, 2017). The archipelago is situated in the Gulf of Bahrain, an inlet of the central southern coast of the Arabian Gulf whose southern part forms a shallow bay called Gulf of Salwa (Figure 1). The Gulf of Bahrain is recognized as an Important Marine Mammal Area (IMMA), named 'Gulf of Salwa IMMA' in recognition of its international importance for marine mammals, particularly dugongs (IUCN–Marine Mammal Protected Areas Task Force, 2021). An aerial survey carried out in 2006 indicated that Bahrain has a large population of 1,164 (95% confidence interval: 530, 1,798) dugongs with an average group size of 1.5 (±0.22 *SE*) dugongs (Hodgson, 2009; Preen et al., 2012). The shallow waters surrounding Hawar Island (hereinafter around Hawar) in the south-east of Bahrain have been consistently identified as one of the most important areas for the Arabian Gulf's dugong population (Preen, 2004; Hodgson, 2009; Preen et al., 2012). The area has the highest dugong density (0.59 km^{-2}) in Bahrain (Hodgson, 2009), and most LDG sightings in the Arabian Gulf have been reported from these shallows. These include the ~670 dugongs encountered by Preen (2004) on March 5, 1986, that was in fact composed of two nearby groups of ~570 and ~100 dugongs sighted around Fasht Mu'tarid, a small reef complex situated to the north-west of Hawar (Preen, 1989; Marsh et al., 2002). In addition, Bell (2001) sighted groups of ~55, ~150, and ~250 dugongs in 2000, and Preen et al. (2012) reported ~300 dugongs in 2005 around Hawar. Hodgson (2009) also encountered an LDG in 2006 comprising >50 dugongs off Fasht Jarim (~80 km from Hawar). In 2015, Marshall et al. (2018) identified five LDGs ranging from ~170 to 510 dugongs in Qatar to the east of the Bahrain–Qatar border.

2.2 | Compilation of past and present data on LDGs

Since the definition of a 'dugong herd' is problematic (Hodgson, 2004), we prefer to use the terms 'marine mammal group' as suggested by Acevedo-Gutierrez (2009) and 'scattered dugong group' as defined by Preen (1989) to describe the dugong groups around Bahrain. We consider a dugong group comprising >50 individuals with inter-dugong distance not exceeding 20 body lengths (mean dugong body length ~2.5 m; Hodgson, 2004) to be an 'LDG'. All LDG sightings obtained by various methods were categorized according to season, following the classification of Vousden (1995) of the temporal patterns of the marine environment around Bahrain: winter (December–March), spring transition period (April), summer (May–October), and autumn transition period (November). The sightings were then plotted with geographical information system (GIS) maps using the software Quantum Geographic Information System (QGIS; Version 3.18; QGIS Association).

The persistence of LDGs around Bahrain was assessed by combining historical records, structured interview surveys, and citizen science network reports together with opportunistic small-scale boat and UAV surveys. The field surveys and structured interviews were undertaken in accordance with the environmental permit RH/24/84/2019/AA and following the guidelines of the Research Ethics Committee of the University of Barcelona, who also approved the interview schedule. The identities of interviewed people were always kept anonymous.

To identify potential LDG core areas, LDG sightings recorded by all standardized aerial surveys undertaken thus far in Bahrain were inventoried: (a) March 1986 (Preen, 1989; Preen, 2004), (b) October 1986 (Preen, 1989; Preen, 2004), (c) October 2000 (Bell, 2001), and (d) October 2006 (Hodgson, 2009). These aerial surveys covered nearly all Bahraini waters up to the 10 m isobath marking the broad-scale distribution of dugongs in the Arabian Gulf, delineated by Preen (2004), with the exception of the 2000 survey that focused only on the waters around Hawar (Figure 1).

Owing to the paucity of historical records of dugongs, the persistence of the dugong population around Bahrain was assessed,

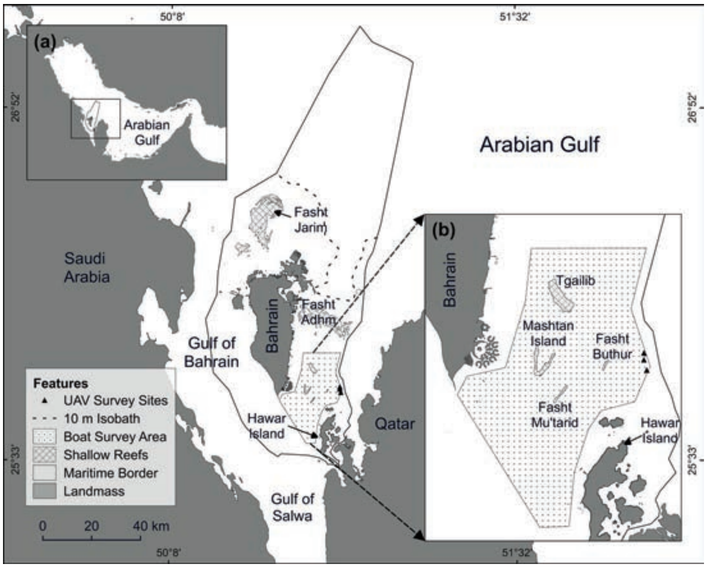

FIGURE 1 Map of the study area showing (a) the location of Bahrain in the Gulf of Bahrain and the larger context of the Arabian Gulf, and (b) major islands and shallow reef complexes (fashts), boat-based survey area, and large dugong groups (>50 dugongs) surveyed by unmanned aerial vehicles (UAVs). The dashed line represents the 10 m isobath marking the broad-scale distribution of dugongs in the Arabian Gulf delineated by Preen (2004).

with a focus on LDGs, through memory recalls. During 2020–2021, questionnaire-based structured interviews were conducted with local fishermen, tour boat operators, environmentalists, and researchers ($N = 97$). The interviewees were asked to specify important dugong areas and identify seasonal variations in dugong abundance. To obtain spatial data on dugong occurrence, knowledgeable key respondents ($n = 41$) were presented with a map of the region and requested to mark polygons representing the estimated spatial extent of all dugong sightings that they could remember encountering across all territorial waters of Bahrain. The informants were then asked to rank each polygon ($N = 149$) in terms of (a) time interval (1–3, 4–15, 16–30, and >30 years) and (b) size (1–10, 11–50, 51–100, 101–300, 301–500, and >500 dugongs) of the dugong group encountered. Sixteen key informants were chosen as members of a citizen science network and encouraged to report on all dugong sightings that they incidentally encountered across all Bahraini waters. Between October 2019 and February 2022, members of the citizen science network reported the location, timing, and group size (as the best estimated count of dugongs seen on water surface) of each dugong sighting.

A total of 61 LDG boat-based surveys were conducted between December 2019 and February 2022 around Hawar where LDGs had been reported by aerial surveys, structured interviews, and the citizen science network (Figure 1). During these trips, the boat travelled at 15–20 kn (27.8–37.0 km h^{-1}) while two observers scanned the surface, unaided or with 10 × 42 binoculars. Though this speed was not ideal for observing individual or paired dugongs, it allowed a large area to be covered in search of LDGs, which were the primary focus of these surveys. Although sightings of scattered dugongs were recorded whenever encountered, these records were not included in the analysis since spotting solitary or paired dugongs from a low platform in murky waters is challenging even at slower speeds.

Upon encountering a dugong group, the search was suspended and the boat slowly manoeuvred towards the animals, maintaining ~200 m from the group to minimize disturbance. The estimated geographical coordinates were then obtained with a Global Positioning System and the dugongs were observed more closely with binoculars. Since evaluating dugong abundance through boat-based surveys is challenging due to the elusive nature of dugongs and limited water visibility in their habitats (Hodgson, 2011; Aragones et al., 2012a; Keith-Diagne et al., 2022), three independent observers estimated the size of dugong groups encountered during boat surveys. First, the observers estimated the maximum number of dugongs seen on the surface using binoculars. Considering that the number of dugongs counted from a boat fluctuates over short time intervals due to the rapid changes in the predominant group behaviour (e.g. grazing or travelling), each observer continued to scan the dugong group for at least 5 min. After that, each observer estimated the group size, which was averaged across observers.

Three LDGs encountered on February 14, 15, and 16, 2021, were surveyed with two UAVs (DJI Mavic 2 Pro and DJI Inspire 2) equipped with high-resolution cameras mounted with wide-angle lenses and anti-glare polarizer filters. The UAVs were controlled from a speedboat and flown over the LDGs at a maximum height of 120 m. Still frames were then extracted from the UAV videos and carefully examined by three observers who obtained independent counts to estimate the average group size and calf proportions. The observers employed image-processing software (Adobe Photoshop) to mark (with a coloured dot) and count each shape with recognizable dugong features. The dugong group size and calf count and the proportion of the three LDGs surveyed were then averaged between observers.

Dugong group sizes were cross-verified by comparing overlapping UAV and boat-based dugong surveys on February 14, 15, and 16, 2021. This enabled an estimation to be made of the number of subsurface dugongs missed by boat-based observers at the time of counting. During all UAV flights, three observers in a nearby speedboat independently estimated the maximum number of dugongs seen near the water surface using binoculars as described earlier. On the February 15, 2021, survey, the percentage of individuals located within two dugong body lengths of nearest neighbours was also calculated. To identify habitats in key areas occupied by LDGs, six groups were observed until they moved away from their feeding spots (as indicated by their repetitive diving and the sediment plume generated by feeding; Hodgson, 2004; Marshall et al., 2018; Keith-Diagne et al., 2022) and then the benthos was visually examined by snorkelling or scuba.

2.3 | Current distribution of LDGs

The main distributional range of LDGs reported between 2019 to 2022 by the citizen science network and boat-based surveys was determined by computing kernel density estimate heatmaps using QGIS. The resultant heatmaps were then converted to percentage volume contours (PVCs) following the guidelines of MacLeod (2014) to identify where large groups were likely to occur 50% (50% PVC) and 95% (95% PVC) of the time. Shallow reef complexes (locally known as 'fashts'), marked on the habitat map produced by Al-Zayani, Zainal & Choudhury (2009), and islands were considered natural barriers and cropped from the resultant PVCs.

2.4 | Spatio-temporal trends of LDGs and dugong population

The persistence of LDGs over space and time around Bahrain was first determined visually by examining the GIS maps and observing any distinctive patterns in the spatial or temporal trends using the different methods included in the survey. These trends in persistence of LDGs were then compared with all dugongs around Bahrain to highlight any potential role of LDGs in maintaining the dugong population. To this end, a dynamic occupancy modelling framework (see Royle & Kéry, 2007) was used to estimate dugong occupancy (i.e. percentage of sites occupied), turnover (i.e. persistence), and colonization of all dugongs around Bahrain over time, based on the memory recall data reported by observers in the structured interviews, from >30 years ago to the time of data collection (i.e. 2021). It has to be noted that detectable changes in dugong occupancy, persistence, and/or colonization do not necessarily indicate corresponding changes (i.e. increase or decrease) in population size. A similar approach was also used by D'Souza et al. (2013) to estimate dugong occupancy and changes in distribution in India's Andaman and Nicobar Islands. Occupancy modelling allows for the probabilistic estimation of parameters related to species occurrence at specific sites conditional on the probability that all animals of the species may not be perfectly detected by observers. These surveys, conducted in a systematic spatial sampling framework, can prove helpful in estimating past distribution dynamics by addressing issues of imperfect detection inherent to available historical records or, in the case of this study, memory recalls. In this model, the probability of detection was estimated through spatial replicates represented by multiple informants in the same grid, who were providing memory recall information. Owing to the long intervals between the aerial surveys and the absence of any standardized dugong survey over the last 15 years, only data obtained through interviews (see earlier herein) were included in this analysis. First, the accuracy of the polygons marked by informants was verified by classifying them based on the time of sighting and dugong group size as already described herein. Then, polygons were overlaid on the historical dugong encounters recorded by corresponding aerial surveys undertaken in 1986 (Preen, 1989; Preen, 2004), 2000 (Bell, 2001) and 2006 (Hodgson, 2009) before the overlap percentage was calculated.

The territorial waters of Bahrain, confined within the Gulf of Bahrain, were partitioned into 2 × 2 nmi^2 ($\sim 3.70 \times 3.70\ \text{km}^2$) grid cells ($N = 490$). From the 490 grids sampled, a reconfigured dataset of 151 grid cells, with three or four spatial replicates each based on proximate grids, was used across the four time intervals of memory recalls reported by interviewed informants. The northernmost waters of Bahrain were not included in the modelling as they are further offshore than the 10 m isobath cut-off, as detailed earlier herein. The data on dugong occurrence reported by memory recalls were assigned in a 1/0 format to the 151 grids. Reports of confirmed dugong sightings were assigned '1' and reports of not having seen dugongs were assigned '0' from all interviewees for that particular grid. These data represented detections and non-detections, and not true presence or absence of dugongs, as the reported sightings were conditional on (a) the interviewee's probability of encountering a dugong and correctly reporting it, (b) the interviewee's ability to accurately recall past sightings, and (c) internal consistency in reporting sightings for the four time-periods for which information was requested. Clearly, some of these detections are likely to be imperfect. It is also reasonable to expect that recent detections would have a lower uncertainty than past detections. All these caveats and assumptions lent themselves to an occupancy modelling approach. The model was run in the R software (R Core Team, 2020), using the packages 'rjags' and 'jagsUI', through the Bayesian statistical programming module JAGS (Plummer, 2014). For each model, 10,000 Markov chain Monte Carlo iterations were run in three chains and a burn-in time of 5,000 interactions was used. All model parameter estimates were checked for convergence, and their Bayesian credible intervals (95%) were reported.

2.5 | Potential transboundary movements of LDGs

To highlight likely transboundary movements of LDGs in the Arabian Gulf, LDG sightings recorded during this study that are <2 km from the maritime border of Bahrain were examined. In addition, the interval distances between the LDGs in Bahrain and those recorded earlier in Qatar (Marshall et al., 2018) and United Arab Emirates (Preen, 1989; Preen, 2004) were estimated and compared with the dugong movement ranges defined by earlier studies (e.g. Sheppard et al., 2006; Deutsch et al., 2022).

3 | RESULTS

3.1 | Current distribution of LDGs

Based on data from boat-based surveys and the citizen science network between 2019 and 2022, a number of LDGs were identified around Hawar (Figure 2a). Kernel density estimate heatmaps indicated that LDGs were distributed over 490 km^2 of the shallow waters surrounding Hawar (i.e. distributional range). These shallows encompassed an LDG occupancy area (144.6 km^2) that is composed of three PVCs indicating where LDGs spend 50% and 95% of their time. Two 50% PVCs were located to the west and north of Hawar, one around Fasht Mu'tarid of 7.9 km^2 and another off Fasht Buthur of 38.3 km^2 (~1% of the latter straddles the Bahrain–Qatar border). The longitudinal axis of the 50% PVCs around Fasht Mu'tarid measured 6.8 km and around Fasht Buthur measured 8.1 km. The linear nearest interval distance between the edges of the two 50% PVCs was 5.2 km. The 95% PVC occupied 98.4 km^2 off the western and northern coasts of Hawar, with 5.4% of its total area extending eastwards beyond the Bahrain–Qatar border. In addition, the distribution of the LDGs shows distinct spatial separation between winter and summer feeding grounds as described in the following (Figure 2b).

3.2 | Temporal and spatial trends of LDGs

Structured interviews showed a clear persistence of LDGs around Bahrain over the last three decades. A total of 35% of all respondents reported that they had encountered LDGs during their lifetime, although the size of the largest groups they sighted varied considerably (size category: 51–100 dugongs [32%], 101–300 dugongs [27%], 301–500 dugongs [19%] and >500 dugongs [22%]; maximum: 1,000 dugongs). The informants outlined a total of 25 polygons representing LDG sightings; these spanned all time intervals apart from the >30 years. The persistence of these groups in the shallow waters around Hawar was also confirmed by citizen science network reports and boat-based surveys, recording a total of 149 dugong groups, of which 64 (43%) were LDGs. The historical aerial survey records further confirmed that LDGs persisted over the period 1986–2000 within the same core areas they currently occupy (Figure 3). In addition to Hawar, both structured interviews and aerial survey records reported LDG sightings ($n = 3$) off Fasht Jarim.

Of the interviewed respondents that recorded LDGs, 27% encountered large groups in both summer and winter and 46% and 27% sighted them either in summer or winter respectively (Figure 4). The citizen science network and boat surveys provided further insight into the seasonal patterns of LDGs. The large groups around Hawar were persistently recorded in each of the 12 calendar months with the exception of April and May, although logistical constraints prevented adequate sampling of the region in April. Additionally, distinctive seasonal patterns were detected in the distribution of these groups around Hawar. In warm months (June–October), LDGs were mostly found in the 50% PVC around Fasht Mu'tarid, where they continued to be sighted until October or November. Later, most LDG sightings were encountered in the 50% PVC around Fasht Buthur, where they persisted throughout the cold winter months (December–March; Figure 2b). Occasionally, however, LDGs moved to the winter ground before the end of summer, leading to a slight overlap between the two areas. On all boat surveys, LDGs were sighted either at summer (i.e. around Fasht Mu'tarid) or winter (i.e. around Fasht Buthur) feeding grounds, except for two occasions in September when two LDGs were observed concurrently at both feeding grounds.

3.3 | Dugong baseline occupancy and changes in spatial distribution

Structured interviews showed that dugongs were unevenly distributed across the waters of Bahrain with dugong sightings (marked as polygons on maps by respondents) highly clustered around Hawar. Two other dugong core areas were recognized around Fasht Jarim and off the south-western coast. Additionally, the respondents reported a number of dugong sightings beyond the 10 m isobath across all time intervals apart from >30 years. Historical dugong sighting records ($N = 89$) reported from the 1986 and 2006 standardized aerial surveys ($N = 3$) confirmed these spatial trends with 59% of all encounters around Hawar; Fasht Jarim and the south-western coast accounted for 13% and 9% of encounters

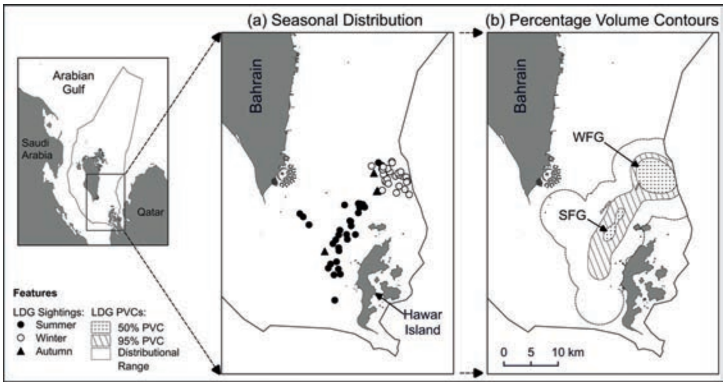

FIGURE 2 Spatio-temporal patterns of large dugong groups (LDGs; >50 dugongs) recorded during 2019–2022 through boat-based surveys and citizen science network: (a) large dugong group sightings classified by season, and (b) spatial extent of the overall distributional range as well as 50 and 95 percentage volume contours (50% and 95% PVC respectively) of large dugong groups. SFG: summer feeding ground; WFG: winter feeding ground.

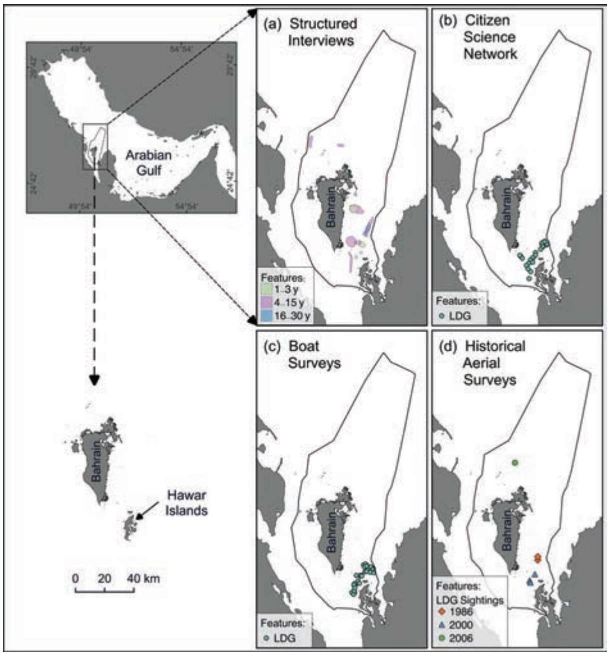

FIGURE 3 Large dugong group (>50 dugongs) sightings recorded by multiple methods: (a) memory recalls obtained through structured interviews (classified according to time intervals: 1–3, 4–15, and 16–30 years), (b) 2019–2022 citizen science network reports, (c) 2019–2022 boat-based surveys, and (d) historical records from 1986 (Preen, 1989; Preen, 2004), 2000 (Bell, 2001), and 2006 (Hodgson, 2009) aerial surveys. LDG: large dugong group; y: years.

FIGURE 4 An aerial photograph of a large dugong group (>50 dugongs) encountered in summer (October 4, 2021) to the north of Hawar Island, Bahrain, indicating the difficulty associated with accurately estimating the group size of large dugong groups. (Photograph courtesy of Janez Lotric, Diplomatic Protocol Communications).

respectively. Confirming the general agreement between the two methods, the memory recall polygons of the corresponding time intervals overlapped with the 1986, 2000, and 2006 aerial survey sightings by 46%, 75%, and 73% respectively (Figure 5).

The occupancy model indicated baseline occupancy (>30 years) of the dugong population around Bahrain at 32% of the total 151 grid cells. In addition, high persistence probability (∼95%) of dugongs was detected across the four time intervals. Colonization probability increased over time, with 35% of unoccupied sites recently occupied by dugongs. This increased overall dugong occupancy in 2021 to 55% (i.e. by nearly 23% from the baseline). Detection probability was estimated at 63% based on the memory recalls of interviewed respondents. Table 1 presents the parameter estimates and Bayesian credible intervals from the final selected model.

3.4 | Additional observations on LDG dynamics and habitat

Of all boat surveys with successful LDG sightings ($n = 54$), a single group was most frequently encountered during the survey (83%). On occasions, however, two (15%) and rarely three (2%) groups were observed. When two or more groups were found, the inter-group distance ranged between 0.2 and 2 km, with a single instance of 17.2 km between sightings. As confirmed by in-water observations, LDGs were found in extensive seagrass areas. These include the three groups surveyed by UAVs on February 14, 15, and 16, 2021, that were located at 3–4.5 m deep seagrass meadows in the winter feeding ground. Independent counts of the UAV footage estimated the average size of these LDGs as 181 (±4 *SD*), 696 (±5 *SD*), and 648 (±8 *SD*)

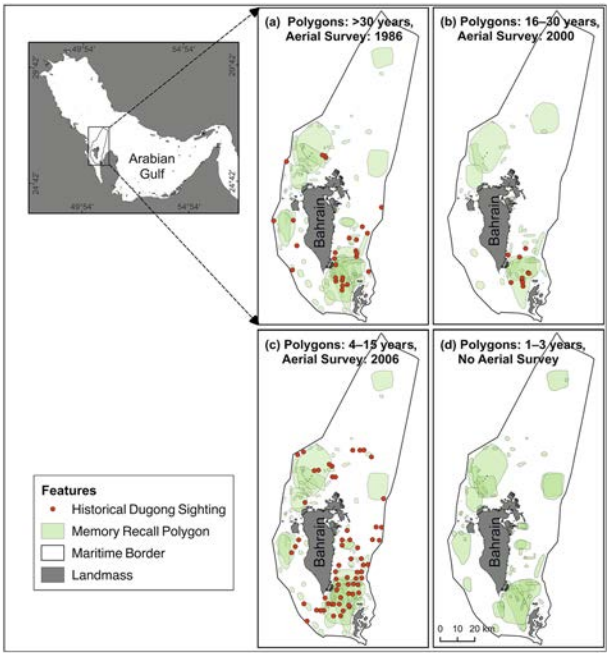

FIGURE 5 Historical dugong occurrence records presented as memory recall polygons (delineated by informants interviewed in 2020–2021), classified according to time intervals: (a) >30 years, (b) 16–30 years, (c) 4–15 years, and (d) 1–3 years. The maps are overlaid with dugong sightings recorded during the 1986 (Preen, 1989; Preen, 2004), 2000 (Bell, 2001), and 2006 (Hodgson, 2009) aerial surveys. There was no aerial survey conducted during the 1–3 years interval. Unlike the 1986 and 2006 surveys, the 2000 aerial survey covered only the south-east of Bahrain.

TABLE 1 Estimates of occupancy model parameters, with standard deviation and Bayesian credible intervals (95% of posterior distribution of probabilities) from one of the best models explaining dugong occurrence around Bahrain across four time intervals (1–3, 4–15, 16–30, and >30 years) based on memory recall data obtained through structured interviews undertaken in 2020–2021. The credible intervals or posterior distributions of effect sizes do not include zero, indicating a significant effect.

State parameters	Notation	Parameter mean (±*SD*)	Credible interval (2.5%)	Credible interval (97.5%)
Pr(occupancy)	ψ	0.315 (±0.063)	0.20	0.44
Pr(persistence)	ϕ	0.96 (±0.013)	0.94	0.99
Pr(colonization)	γ	0.36 (±0.04)	0.30	0.44
Pr(detection)	p	0.63 (±0.02)	0.58	0.66

dugongs respectively. In addition to their exceptional sizes, LDGs appeared in the aerial footage densely clumped particularly when the groups were grazing or fleeing from approaching boats. For instance, ~91% of dugongs in the group sighted on February 15, 2021, were less than two body lengths from their nearest neighbour. The aerial footage further revealed that dugongs often arranged themselves in multiple layers in the water column despite the limited depth. In most cases, the clumped groups occupied an area <0.5 km^2. The sea floor was visible in the captured aerial footage in only parts of the surveyed area, but it was mostly not visible at the spots occupied by the groups possibly due to the sediment clouds generated by their mass grazing (Figure 4). Hence, the size of these LDGs may be larger than estimated, particularly when surveyed from a boat. In essence, comparing boat and UAV counts estimated on February 14, 15, and 16, 2021, indicated that boat counts were found to underestimate those of the UAV flights by 2.66, 5.15, and 4.47 times respectively. A total of 11 (±1 *SD*; 6.1%), 45 (±2 *SD*; 6.4%), and 39 (±1 *SD*; 6.0%) calves were counted within the LDGs surveyed on February 14, 15, and 16, 2021, respectively. Further examination of the UAV footage showed that mother–calf pairs were occasionally difficult to recognize in extracted still images due to the murky waters and the elusive behaviour of calves, suggesting that the calf proportions could be underestimated. Given that clumped LDGs typically occupied an area of <0.5 km^2, the density of dugong calves (i.e. number of calves per unit area) within the foraging area of the LDG was approximately 11–45 calves per 0.5 km^2.

Structured interviews and boat-based surveys showed that many LDGs encountered in cold winter months were in close proximity to the Bahrain–Qatar border and <2 km from the large groups sighted in Qatar by Marshall et al. (2018). Similarly, interviewees marked LDG sightings off Fasht Jarim, <1 km from the Bahrain–Saudi border (Figure 3). At a larger scale, Hawar's LDGs were ~430 km from the dugong core area around Murawah Island in the United Arab Emirates (Figure 6).

4 | DISCUSSION

Hawar Island is a globally significant hotspot for dugong conservation, with some of the largest, most persistent and actively reproducing groups of dugongs recorded across its Indo-Pacific range. Combining data from historical and current distributional studies using a mix of approaches, this study confirms that LDGs, measuring in the hundreds, have used Hawar's shallow seagrass meadows for at least the last four decades. The models suggest that the occupancy range of the dugong population around Bahrain may be expanding in recent years, although LDGs are still mostly restricted to the relatively small core occupancy area around Hawar.

In the field, the groups encountered on February 15 and 16, 2021, outnumber all earlier reports from this region (Preen, 1989; Preen, 2004; Marshall et al., 2018) as well as from Australia

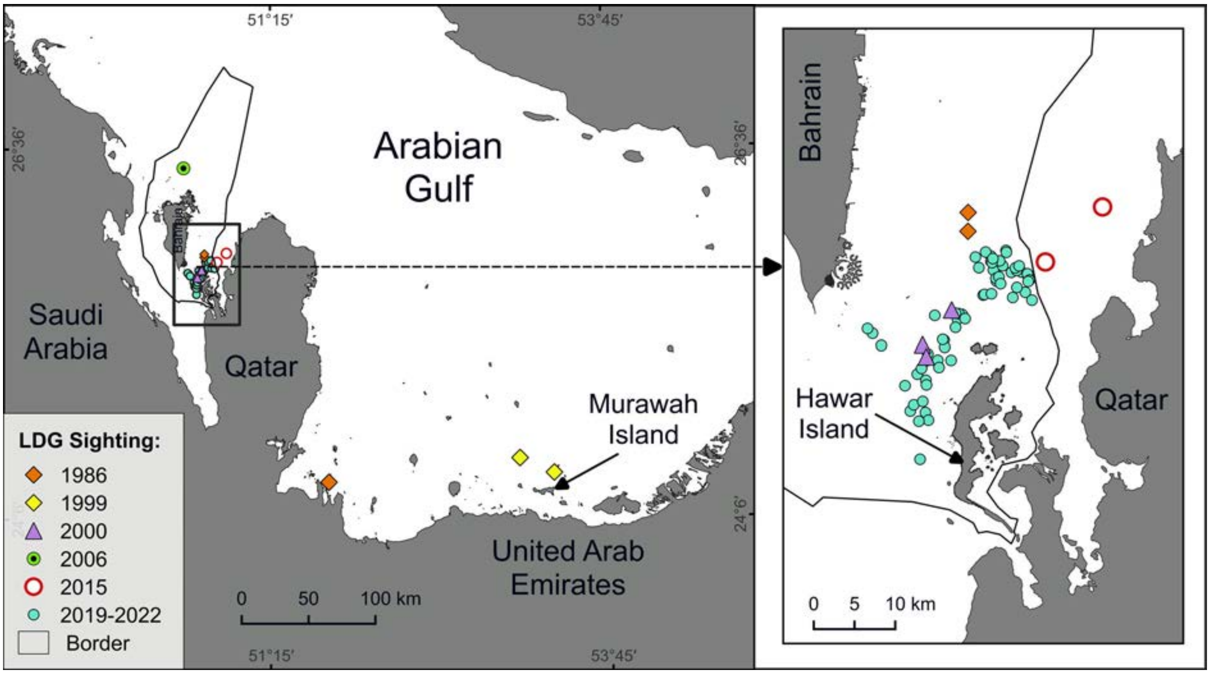

FIGURE 6 Historical and recent large dugong group (>50 dugongs) sightings in the Arabian Gulf, recorded by aerial and boat surveys and citizen science network in 1986 (Preen, 1989; Preen, 2004), 1999 (Preen, 2004), 2000 (Bell, 2001), 2006 (Hodgson, 2009), 2015 (Marshall et al., 2018), and 2019–2022 (this study), indicating their likely transboundary movements. The inset map shows the proximity of the large dugong groups reported in both Bahrain and Qatar to the Bahrain–Qatar border. Arrows indicate the location of Murawah Island (United Arab Emirates) and Hawar Island (Bahrain), the most important core dugong areas in the Arabian Gulf.

(Preen, 1992; Lanyon, 2003), making them the largest ever documented in recent times. These findings, however, should be interpreted with caution considering the difficulties associated with accurately estimating the group size of LDGs (see later). As with the LDGs reported in Australia, these groups tended to be highly clumped and group size extremely fluid, often breaking up into subgroups several kilometres apart that occasionally joined again (Anderson, 1981; Preen, 1989; Preen, 1992; Preen, 2004; Hodgson & Marsh, 2007; Marsh, O'Shea & Reynolds, 2011; Marshall et al., 2018). This characteristic fission and fusion behaviour is common across aggregating species from birds to baboons, and it is also seen in many marine mammal groups (Marsh, f & Reynolds, 2011; Tsai & Mann, 2013; Zuluaga, 2013; Díaz López et al., 2018; O'Shea et al., 2022). It is likely that when dugongs were much more abundant in other parts of the Indo-Pacific, large groups were more common and that the LDGs of the Arabian Gulf and Australia, measuring in the hundreds, may be relicts of a once widespread grouping strategy (see Preen, 1992; Hodgson, 2004). Why dugongs still gather in such large numbers at only certain localities remains a matter of some conjecture (Preen, 1992; Marsh et al., 2002; Marshall et al., 2018; O'Shea et al., 2022). Several factors have been examined to explain dugong grouping behaviour, including population density thresholds, thermoregulation, calf nursing, predatory defence, grazing efficiency, extreme weather conditions, and social interactions (Anderson, 1981; Preen, 1992; Anderson, 1998; Hodgson, 2004; Holley, 2006; Cleguer, 2015). Which of these factors play a role in Hawar's LDGs would require detailed, context-specific studies on environmental, population, and behavioural triggers. Whatever factors determine this grouping behaviour, it likely plays important social functions, including cultural transmission and information sharing about resource distributions and reproduction.

The calf proportions of the studied LDGs are lower than earlier LDG reports from this region (15.7%; Preen, 2004) but comparable to proportions reported in the LDGs of Qatar (5.4–9.9%; Marshall et al., 2018). For most reported LDGs, calf proportions tend to fall within average values reported across dugong populations (Preen, 1992; Hodgson, 2004): United Arab Emirates (7.46–8.4%; Das, 2007), Red Sea (1.4–14.9%; Preen, 1989; Preen, 1992), Hervey Bay (1.5–22.1%; Sobtzick et al., 2017), and New Caledonia (4.7–18.0%; Cleguer et al., 2017). In terms of calf density, however, it was remarkably high in Hawar's LDGs (45 calves occupying <0.5 km^2), conforming with earlier reports from nearby Qatar (51 calves in <1 km^2; Marshall et al., 2018). These results suggest that persistent aggregation sites of LDGs across their range possibly represent important calf birthing and/or rearing grounds. This is further supported by the multi-decadal persistence of mother–calf pairs around Hawar, which is a positive sign that the population is likely reproductively healthy given their slow rate of reproduction and the vulnerability of orphaned calves (Anderson, 1981; Preen, 1992; Marsh et al., 1999; Marsh & Kwan, 2008).

Another remarkable feature of Hawar's LDGs is their persistence in space and time. The core area of dugong occupancy around Hawar has had consistent reports of LDGs for >35 years, indicating that these shallow waters are a traditional grouping location for the population. Considering the difficulties inherent in estimating the group size of LDGs (see later), the persistence of sizeable LDGs of almost the same number (~700 dugongs; Preen, 2004; this study) around Hawar for over three decades further underscores the significance of this area for dugong conservation. The multidecadal persistence of LDGs also lends support to the global importance of the Gulf of Salwa IMMA for dugongs (Knight, Seddon & Al-Midfa, 2011; IUCN–Marine Mammal Protected Areas Task Force, 2021).

Of all historical LDG records in Bahrain (Bell, 2001; Preen, 2004; Hodgson, 2009), 67% were in summer, supporting our findings that dugongs aggregate around Hawar not just in winter, as was previously thought (Preen, 1989; Preen, 2004; Preen et al., 2012; Marshall et al., 2018). To our knowledge, Hawar is second only to Moreton Bay in harbouring groups of >100 dugongs year round (Preen, 1992; Hodgson, 2004; Chilvers et al., 2005; O'Shea et al., 2022). That said, these fluid groups do show distinctive seasonal movements, but at a highly reduced scale, shifting between distinct but slightly overlapping summer and winter feeding grounds. Highlighting the importance of socially transmitted information (Anderson, 1981; O'Shea et al., 2022), these results add to the evidence from Moreton Bay where large groups repeatedly use the same feeding grounds (Anderson, 1981; Lanyon, 2003) in a systematic manner following predictable seasonal movement routes (Hodgson, 2004). Without more detailed studies on seagrass nutrient contents and temporal patterns of seagrass availability, it is difficult to speculate on the reasons for this seasonal movement. However, these small-scale migrations have important consequences for managing these LDGs. The encounter of LDGs at winter feeding grounds during November–March conforms with the results of Marshall et al. (2018), who reported that LDGs start arriving in the nearby Qatari waters in November and persist until February. These consistent reports highlight the transboundary nature of LDGs and underscore the role of seasonality in shaping their spatial distribution and, hence, the larger Arabian Gulf's population (Preen, 2004; Marshall et al., 2018).

The year-round persistence of LDGs around Hawar enabled the mapping of a well-delineated hotspot where hundreds of dugongs spend their summers and winters in large groups. While this allows managers to focus management efforts on a relatively small and well-defined hotspot for conservation, it also increases the vulnerability of the dugong population to site-level threats. Owing to their exceptionally large size, clumped distribution, and high calf density, any significant human-induced stressors to LDGs and/or their primary aggregation sites will have disproportionate impacts on the entire dugong population. Given the global significance of this population, there is a need to urgently put in place a series of management actions with a focus on restricting the use of gillnets and imposing boat speed limits across the LDG occupancy area, since bycatch has been identified as a major source of dugong mortality in the Arabian Gulf (Hodgson, 2009; Knight, Seddon & Al-Midfa, 2011; Environment Agency-Abu Dhabi, 2014; Abdulqader et al., 2017). Also, it is crucial to safeguard the extensive seagrass beds around Hawar from the impacts of accelerating coastal development in the south of Bahrain.

Establishing and maintaining a continuous monitoring programme is a priority to identify any decline in dugong populations or degradation in seagrass habitats at early stages, allowing timely conservation interventions. In all this, it is vital that local communities are made partners in dugong conservation, to ensure that small-scale fishing can sustainably thrive alongside LDGs. There is little doubt that these LDGs cross international jurisdictional boundaries, and hence establishing a regional network of marine protected areas spanning all the Arabian Gulf's range states is crucial to achieving the effective protection of these groups and the larger dugong population. This network should encompass confirmed and potential core dugong aggregation sites, including Murawah Island and Al Yasat Island in the United Arab Emirates, Hawar Island, Fasht Buthur, and Fasht Jarim in Bahrain, the north-western waters of Qatar in addition to the shallow waters between Saudi Arabia, Qatar, and United Arab Emirates. Of these, only the first three have been officially designated as marine protected areas. The network could be established progressively with the first series of core zones encompassing the designated protected areas (42%), followed by Fasht Buthur and the north-western waters of Qatar (29%). The addition of Fasht Jarim and the shallow waters between Saudi Arabia, Qatar, and United Arab Emirates would expand the network by a further 29%. In addition to these core zones, the regional network should promote ecological connectivity by imposing a similar array of interventions on LDG migration corridors and key habitats interconnected with seagrass, particularly coral reefs and islands.

This multidisciplinary study has confirmed the persistence of LDGs around Hawar and defined their core occupancy area using cost-effective methods supported by UAV surveys. In interpreting these results, it is important to consider a few important caveats. Given the chosen boat speed, it is possible that some dugong groups may have been missed. In addition, an important source of information was the structured interviews with key informants, and the possibility of inaccurate recollections of encounters due to failing memories cannot be discounted. Despite their large numbers, clumped dugong groups are often difficult to observe from the air (Preen, 1989; Pollock et al., 2006; Cleguer, 2015; Cleguer et al., 2021; Trotzuk et al., 2022). This is even more complex for boat-based surveys that depend on surfacing individuals; dugongs resting or feeding underwater make accurately estimating group size a real challenge. Given this difficulty it is possible that LDGs could be more common across the dugong global range than currently reported. Despite these caveats, by using multiple approaches, these results are considered to be robust and signify the high conservation importance of this region. It is hoped that the enhanced knowledge on the Arabian Gulf's LDGs from ongoing research in Bahrain, Qatar, and United Arab Emirates will inform evidence-based conservation management.

What is remarkable about dugong groups is just how variable they are in size, from solitary or paired individuals to mega-aggregations of hundreds of dugongs. A complex set of trade-offs and life-history characters underlie this variability (Anderson, 1981; Preen, 1995; Hodgson, 2004; Zeh et al., 2018). This variable grouping behaviour may possibly contract across the dugong's range as accidental bycatch, hunting, seagrass meadow loss, and boat strikes combine to see fragmentation and decline of local populations. What makes the Hawar's LDGs so vital is that they represent an important part of the suite of dugong behaviours across its range. Conserving the LDGs around Hawar should be a global priority to preserve the population of the Arabian Gulf and maintain the remarkable behavioural flexibility this species can show across its range.

Given the LDGs encountered during this study, and assuming that the population sizes reported by Hodgson (2009) and Preen (2004) have not changed substantially over time, it is estimated that ~12% of all dugongs in the Arabian Gulf (equating to ~60% in Bahrain) may aggregate, forming large groups around Hawar. As speculated earlier by Preen (2004), the interval distance between Hawar and Murawah islands is within the large-scale dugong movement range (Sheppard et al., 2006; Deutsch et al., 2022), suggesting possible contributions of regional migration to the formation of Hawar's LDGs. The extension of the LDG occupancy area beyond the Bahrain–Qatar border further highlights the transboundary nature of the LDGs around Hawar. These reports underscore the significance of LDGs in maintaining sizeable dugong populations, a primary consideration for any dugong conservation or management strategies in the Arabian Gulf (Knight, Seddon & Al-Midfa, 2011; Preen et al., 2012). For this globally important population to persist, therefore, the LDGs and their core aggregation sites and migration corridors should be effectively conserved through an evidence-based regional conservation plan. Establishing a regional network of marine protected areas and effectively engaging local communities are critical steps in maintaining the LDGs in their northern distributional limits.

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CONFLICT OF INTEREST STATEMENT

The authors have declared no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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