Science of the Total Environment 934 (2024) 172776

Contents lists available at ScienceDirect

Science of the Total Environment

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

Identifying priority sites for whale shark ship collision management globally

Freya C. Womersley[a,b,c,*], Christoph A. Rohner[d], Kátya Abrantes[e], Pedro Afonso[f,g], Shin Arunrugstichai[h], Steffen S. Bach[i], Shir Bar[j], Adi Barash[j], Peter Barnes[k], Adam Barnett[e], Ginevra Boldrocchi[l], Noemie Buffat[m], Tom Canon[n], Clara Canovas Perez[o], Metavee Chuangcharoendee[p], Jesse E.M. Cochran[q], Rafael de la Parra[r], Stella Diamant[s], William Driggers[t], Christine L. Dudgeon[e,u], Mark V. Erdmann[v], Richard Fitzpatrick[e], Anna Flam[d], Jorge Fontes[f,g], Gemma Francis[k], Beatriz Eugenia Galvan[r], Rachel T. Graham[w], Sofia M. Green[x,y], Jonathan R. Green[x], Ya'ara Grosmark[j], Hector M. Guzman[z,aa], Royale S. Hardenstine[q], Maria Harvey[ab], Jessica Harvey-Carroll[o,ac], Abdi Wunanto Hasan[ad], Alex R. Hearn[x,y,aa], Jill M. Hendon[ae], Mochamad Iqbal Herwata Putra[ad], Mahardika Rizqi Himawan[af], Eric Hoffmayer[t], Jason Holmberg[ag], Hua Hsun Hsu[ah], Mohammed Y. Jaidah[i], Ashlee Jansen[ai], Christy Judd[aj], Baraka Kuguru[ak], Emily Lester[al], Bruno C.L. Macena[f,g], Kirsty Magson[am], Rossana Maguiño[an], Mabel Manjaji-Matsumoto[ao], Stacia D. Marcoux[ab], Travis Marcoux[ab], Jennifer McKinney[ap], Mark Meekan[aq], Alejandra Mendoza[an], Muhammad Moazzam[ar], Emily Monacella[m], Brad Norman[as,at], Cameron Perry[o,au,av], Simon Pierce[d,u], Clare Prebble[d], Dení Ramírez Macías[aw], Holly Raudino[k], Samantha Reynolds[as,at], David Robinson[i,ax], David Rowat[ay], Mudjekeewis D. Santos[az], Jennifer Schmidt[ba], Chad Scott[bb], Sian Tian See[ao], Abraham Sianipar[bc], Conrad W. Speed[bd], Ismail Syakurachman[ad], Julian A. Tyne[k], Kelly Waples[k], Chloe Winn[o], Ranny R. Yuneni[be], Irthisham Zareer[o], Gonzalo Araujo[b,bf]

[a] Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, UK
[b] Marine Research and Conservation Foundation, Somerset, UK
[c] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton, UK
[d] Marine Megafauna Foundation, West Palm Beach, FL 33411, USA
[e] Biopixel Oceans Foundation, Australia
[f] Institute of Marine Research - IMAR, Department of Oceanography and Fisheries, University of the Azores, 9900-140 Horta, Portugal
[g] Institute of Marine Sciences, OKEANOS, University of the Azores, 9900-140 Horta, Portugal
[h] Thai Marine Ecology Centre, Thailand
[i] Qatar Whale Shark Research Project, Doha, Qatar
[j] Sharks in Israel, Israel
[k] Department of Biodiversity, Conservation, and Attractions, WA Government, Australia
[l] University of Insubria, Italy
[m] New Heaven Reef Conservation Program, Thailand
[n] Protect What You Love, Australia
[o] Maldives Whale Shark Research Programme, Maldives
[p] Department of Marine and Coastal Resources, Thailand
[q] Red Sea Research Center, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia
[r] Ch'ooj Ajauil AC, Mexico
[s] Madagascar Whale Shark Project, Madagascar
[t] National Marine Fisheries Service, Southeast Fisheries Science Center, USA
[u] University of Sunshine Coast, School of Science, Technology and Engineering, Petrie, QLD, Australia
[v] Conservation International, USA

* Corresponding author at: Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, UK.
E-mail address: f.womersley@mba.ac.uk (F.C. Womersley).

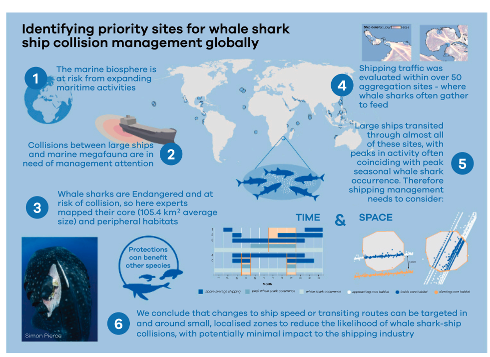
https://doi.org/10.1016/j.scitotenv.2024.172776
Received 13 February 2024; Received in revised form 21 April 2024; Accepted 23 April 2024
Available online 1 May 2024
0048-9697/

[w] MarAlliance, Cuidad del Saber, Panama City, Panama
[x] Galápagos Whale Shark Project, USA
[y] Galápagos Science Center, Universidad San Francisco de Quito, USFQ, School of Biological and Environmental Sciences, Diego de Robles sn y Pampite, Quito, Ecuador
[z] Smithsonian Tropical Research Institute, Panama
[aa] MigraMar, 2099 Westshore Rd, Bodega Bay, CA 94923, USA
[ab] Hawai'i Uncharted Research Collective, USA
[ac] Department of Biological and Environmental Sciences, University of Gothenburg, Medicinaregatan 18A, 413 90 Gothenburg, Sweden
[ad] Konservasi Indonesia, Indonesia
[ae] The University of Southern Mississippi, Center for Fisheries Research and Development, Ocean Springs, MS, USA
[af] University of Mataram, Indonesia
[ag] Wild Me, OR, USA
[ah] Coastal and Offshore Resources Research Center, Fisheries Research Institute, Council of Agriculture, Taiwan
[ai] Ash Karas Photography, Australia
[aj] University of Exeter, UK
[ak] Tanzania Fisheries Research Institute, United Republic of Tanzania
[al] University of Hawai'i, USA
[am] Thai Whale Sharks, Thailand
[an] EcOceanica, Peru
[ao] Borneo Marine Research Institute, University Malaysia Sabah, Malaysia
[ap] University of Southern Mississippi, USA
[aq] Oceans Institute, University of Western Australia, Perth, WA, Australia
[ar] WWF-Pakistan, Pakistan
[as] ECOCEAN Inc., Australia
[at] Murdoch University, Australia
[au] Georgia Aquarium, USA
[av] Georgia Institute of Technology, USA
[aw] Whale Shark Mexico, La Paz, BCS, Mexico
[ax] Sundive Research, NSW, Australia
[ay] Marine Conservation Society Seychelles, Seychelles
[az] National Fisheries Research and Development Institute, Quezon City, Philippines
[ba] Shark Research Institute, USA
[bb] Conservation Diver
[bc] Harry Butler Institute, Murdoch University, Australia
[bd] Australian Institute of Marine Science, Perth, WA, Australia
[be] WWF-Indonesia, Indonesia
[bf] Environmental Science Program, Department of Biological and Environmental Sciences, College of Arts and Sciences, Qatar University, Doha, Qatar

HIGHLIGHTS

- The marine biosphere is at risk from expanding maritime human activities.
- Collisions between large ships and marine megafauna are in need of management attention.
- Shipping was measured in over 50 global whale shark aggregation sites.
- Peaks in shipping activity often coincided with peak seasonal occurrences of whale sharks.
- Changes to ship speed or transiting routes can be targeted in small, localised zones.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Jay Gan

Keywords:
Marine megafauna
Endangered species
Collision threat
Spatial management
Socio-economic conflict

ABSTRACT

The expansion of the world's merchant fleet poses a great threat to the ocean's biodiversity. Collisions between ships and marine megafauna can have population-level consequences for vulnerable species. The Endangered whale shark (*Rhincodon typus*) shares a circumglobal distribution with this expanding fleet and tracking of movement pathways has shown that large vessel collisions pose a major threat to the species. However, it is not yet known whether they are also at risk within aggregation sites, where up to 400 individuals can gather to feed on seasonal bursts of planktonic productivity. These "constellation" sites are of significant ecological, socio-economic and cultural value. Here, through expert elicitation, we gathered information from most known constellation sites for this species across the world (>50 constellations and >13,000 individual whale sharks). We defined the spatial boundaries of these sites and their overlap with shipping traffic. Sites were then ranked based on relative levels of potential collision danger posed to whale sharks in the area. Our results showed that researchers and resource managers may underestimate the threat posed by large ship collisions due to a lack of direct evidence, such as injuries or witness accounts, which are available for other, sub-lethal threat categories. We found that constellations in the Arabian Sea and adjacent waters, the Gulf of Mexico, the Gulf of California, and Southeast and East Asia, had the greatest level of collision threat. We also identified 39 sites where peaks in shipping activity coincided with peak seasonal occurrences of whale sharks, sometimes across several months. Simulated collision mitigation options estimated potentially minimal impact to industry, as most whale shark core habitat areas were small. Given the threat posed by vessel collisions, a coordinated, multi-national approach to mitigation is needed within priority whale shark habitats to ensure collision protection for the species.

1. Introduction

The expansion of maritime trade routes and shipping infrastructure in response to globalisation is threatening the ocean's biodiversity (Duarte et al., 2021; Pirotta et al., 2019; Schoeman et al., 2020). The world's merchant fleet, including cargo, container ships and oil tankers, has doubled in size in just 16 years, and there are now >100,000 ships moving goods worldwide, accounting for over 80 % of world trade (UNCTAD, 2020). With this number expected to increase by as much as 1,200 % in the next 27 years (Sardain et al., 2019), understanding the current impacts of the shipping industry on marine biodiversity is paramount. Alongside other issues – such as anthropogenic noise (Duarte et al., 2021; Erbe et al., 2019; Malakoff, 2010), pollution (Wan et al., 2016), and invasive species transfer (Hulme, 2009; Saebi et al., 2020) – collisions between ships and wildlife are a growing concern (Schoeman et al., 2020). Ship collisions, also known as ship strikes, can occur when an animal crosses the bow of a moving vessel or is drawn toward the hull or propeller before there is time for either party to evade contact. These interactions can result in adverse effects on humans, wildlife, or both. Given the size and impact force of modern vessels, often the animal will be severely injured or will not survive (Pirotta et al., 2019; Schoeman et al., 2020). Although ship collisions can result in varying degrees of severity and impact (Schoeman et al., 2020), they can be a leading cause of mortality for some species. For example, alongside entanglement in fishing gear, ship strikes are the primary cause of human-induced mortality for the Critically Endangered North Atlantic right whale (*Eubalaena glacialis*) (Sharp et al., 2019). Other marine mammals, reptiles, and fishes are also impacted, with >75 species currently at risk of varied population-level consequences (Schoeman et al., 2020). Collision threats to marine mammals have received considerable research and conservation focus (Blondin et al., 2020; Conn and Silber, 2013; Hazen et al., 2017; Keen et al., 2019; Laist et al., 2001; McKenna et al., 2015). However, barriers to knowledge still exist for many species, preventing effective negotiation of solutions and long-term successful collision management strategies (Womersley et al., 2023).

Whale sharks (*Rhincodon typus*) have long been known to be at risk of ship strike with some of the first records of collisions documented in the early 1900s (Gudger, 1940; Womersley et al., 2022). They can make long-distance movements (1000s of kms, e.g. Hearn et al., 2021) throughout their circumtropical and warm temperate distribution and dive to great depths (>1900 m, e.g. Tyminski et al., 2015), but whale sharks spend almost half their time in surface waters – within range of ship hulls – and frequent coastal areas that are also heavily used by vessels (Womersley et al., 2022). Satellite tracks of >340 individuals recently revealed that >90 % of the horizontal space used by this species overlapped with large vessel activity, and that collisions might be more frequent than realised due to a lack of reporting mechanisms and potentially hidden cases of mortality (Womersley et al., 2022). During movements in both national waters (Exclusive Economic Zones, EEZs) and Areas Beyond National Jurisdiction (ABNJs), the study showed that tracked whale sharks regularly cross busy shipping routes where the risk of ship strike is greater (Womersley et al., 2022). With extensive overlap and potential for collisions to occur unnoticed globally, an important task for the conservation of this species now lies in identifying local areas of importance where management can be specifically targeted to reduce collisions. This is now a high priority given that their numbers are likely still declining (Pierce and Norman, 2016), even though targeted fishing (a key driver of past population declines; Rowat et al., 2021) has been prohibited in most countries.

Despite the wide coverage of the global fleet, when compared to other current threats to whale sharks – such as unintentional fisheries capture, climate change and plastic pollution – ship strikes are a relatively tractable problem. There are already several successful technologies, regulations, and schemes that have proved effective in reducing strikes for other species (e.g. spatial separation and speed reduction; see Schoeman et al., 2020 for a review of other collision mitigation strategies). However, these do not yet exist for whale sharks. One of the key challenges to their implementation is gathering robust data on where, when and how often ship strikes are occurring so mitigation can be targeted effectively (Womersley et al., 2023). Further, for management schemes to be successful in protecting the species while minimising disruption to the shipping industry, they should be based on accurate and localised information quantifying human activities within the same spatial and temporal scales as whale shark movements (Blondin et al., 2020). Such knowledge surrounding the location of high-collision-risk areas has led to protection for many vulnerable marine mammals (Schoeman et al., 2020). For example, moving a shipping route east in the Bay of Fundy, USA, to avoid important North Atlantic right whale habitats reduced the risk of vessels colliding with the animals by 90 % (Vanderlaan et al., 2008).

For whale sharks, the local information needed to inform these decisions is not yet available, nor have studies compiled these data globally to determine the location of – and relative levels of threat within – the most critical areas for this species. In addition, at broad scales collision threat is rarely analysed based on dynamic ship traffic within known important areas for species where seasonal occurrence of both animals and humans is incorporated. Such an approach would help account for the temporal variation in space use at the finer scales typical of many highly mobile marine species, including whale sharks (Hearn et al., 2021; Sequeira et al., 2019; Sequeira et al., 2018). Indeed, it has recently been argued that broad and thus coarse scales of spatial analysis or overly complex models can obscure local estimates of overlap and risk (Chaplin-Kramer et al., 2022; Harry and Braccini, 2021; Queiroz et al., 2021; Wyborn and Evans, 2021), highlighting the importance of fine-scale assessments to complement previous global analyses of whale shark collision risk (Womersley et al., 2022).

Although primarily solitary, whale sharks predictably aggregate at numerous sites globally, termed constellations (Norman et al., 2017; Rohner et al., 2021). This behaviour can assist in the creation of fine-scale local threat assessments, providing opportunity for evidence-based collision management (Rohner et al., 2020). Many of these sites are small, defined areas driven by prey availability (Robinson et al., 2013; Rohner et al., 2015; Rohner and Prebble, 2021) and consist of juvenile whale sharks between 3 and 9 m in length, with a significant bias toward males. Data suggests that adults – particularly females – are primarily oceanic, shifting habitat near the onset of maturity (Ramírez-Macías et al., 2017; Rohner et al., 2021). The habitat of neonates, females, and large mature whale sharks is poorly characterised at present (Rohner et al., 2021). However, protection measures focussed on constellation sites are likely the most tractable way to improve the whale shark's global conservation status (Pierce et al., 2021).

As pertinent to the mitigation of ship strikes, three key characteristics of whale shark constellations are: their predictability in space and time, the species' extensive use of surface waters at these sites, and the demographics of the individuals present. For example, hundreds of whale sharks gather off the Yucatán Peninsula, Mexico every year with predictable peaks in July and August (de la Parra Venegas et al., 2011).

At this site, over 400 individuals have been shown to aggregate in an area of approximately 18 km^2 to feed together on fish eggs that are floating at the water surface (de la Parra Venegas et al., 2011). With almost three times more juvenile males gathering here than females (de la Parra Venegas et al., 2011), collision mitigation targeted within known feeding areas at appropriate times of the year (i.e. peak shark occurrence) could help protect this particular demographic. Thus, to determine when and where to target measures a consolidated approach that brings together local insight from all known constellations is now needed. With no mitigation currently in place to limit large vessel collisions on whale sharks, addressing this issue presents an opportunity for conservation success for an Endangered marine megafauna species.

Here, we drew on the experience of a community of researchers to collect relevant information from all well-known whale shark constellation sites globally to i) qualitatively assess local threat and protection levels, ii) quantify local shipping activity patterns, and iii) identify opportunities for targeted ship strike management that can be relayed to decision makers. Since their aggregations are ecologically important for whale sharks, managing threats within these areas can have a disproportionately large positive impact on species recovery.

2. Materials and methods

2.1. Expert elicitation

A Google Form questionnaire was developed to elicit expert knowledge of each whale shark constellation site globally and to understand the local threats to the species in these areas. The online-based, semi-structured questionnaire was sent out to key researchers undertaking (or having undertaken) research at all known whale shark constellation sites globally. Over approximately two months in 2023, we received 40 individual form responses based on collaboration between >75 researchers.

Experts were asked to provide quantitative information on the number of whale shark encounters and individuals within the constellation as well as details on seasonal trends in sightings. This information was based on previous studies (Table S1) and ongoing research projects. To understand local trends or fluctuations in whale shark abundance, they were also asked whether whale shark numbers in their respective constellations were increasing, stable or decreasing, and whether this information was based on data or perception. In addition, they were asked to qualitatively provide details on their unique perception of threats based on local experience and knowledge and to share details on collision, or otherwise, focused policy and management mechanisms. Answers included a series of multiple-choice, option selection, ranked and descriptive structures (complete list of questions provided in Table S2).

To determine the location of constellation sites, experts were then asked to draw a boundary around the area where their surveys have encountered the most whale sharks (herein referred to as core habitat) and where they have encountered any whale sharks in the general area (herein referred to as buffer zone) via the online collaborative mapping platform SeaSketch (https://www.seasketch.org). SeaSketch is a platform where non-technical users can provide spatial inputs, and here experts were guided by land and sea floor depth base layers to delineate zones informed by their extensive whale shark location datasets (Table S1). To standardise for analyses, all core areas were cropped out of the buffer zone if they were drawn abutting or overlapping. Where separate core and buffer areas were submitted for a single constellation, these were numbered and analysed separately. In cases where no site location was submitted (n = 7), boundaries were drawn from the literature (Anderson et al., 2014; Araujo et al., 2014; Araujo et al., 2017; Guzmán et al., 2021; McCoy et al., 2018; Nelson and Eckert, 2007). In total, 107 areas (n = 57 core habitats, n = 50 buffer zones) were compiled from 26 countries and spatial data from almost all global constellations (n = 52 constellation sites) were combined in a worldwide analysis (Fig. 1a) with surveys dating back to 1991 (Fig. 1b).

2.2. Shipping traffic

Gridded shipping data were provided by Global Fishing Watch (GFW, https://globalfishingwatch.org) at a fixed 0.1 × 0.1° cell resolution scale, which equates to approximately 123 km^2 at the equator. Each cell provided the total count of uniquely identified vessels housing an Automatic Identification System (AIS) transmitter (vessels >300 gross tons as mandated by the International Maritime Organisation, IMO) within a ~123 km^2 area (one 0.1° resolution cell) for every month from 2017 through 2019. Monthly counts were gridded for nine vessel classes: 'bunker or tanker', 'bunker', 'cargo or reefer', 'cargo or tanker', 'cargo', 'container reefer', 'passenger', 'specialised reefer' and 'tanker' as per GFW (Fig. S1).

Here, we focus on large vessels in the above categories because they have an AIS transmitter allowing for global tracking of their movements, and because collisions with these ships are likely to be fatal for whale sharks (Womersley et al., 2022). Although smaller vessels (<300 gross tons) can also injure whale sharks (e.g. Harvey-Carroll et al., 2021; Penketh et al., 2020; Womersley et al., 2021), such vessels cannot yet be tracked at a global scale, so we explored the threat posed by small vessels purely on a qualitative basis (see Expert elicitation section).

To explore dynamic shipping activity within the most important areas for whale sharks, gridded vessel density maps were overlaid onto each constellation area and cropped to include only cells that fell within or intersected the sites' spatial boundary. Then, shipping density was summarised within each area individually. First, we summarised activity monthly using mean shipping data averaged between 2017 and 2019 for each month and then annually by taking the mean of all the 2017–2019 monthly aggregates. For each vessel class the minimum, maximum, and mean count of vessels within each constellation area was calculated at a 0.1° cell resolution scale. These metrics were also calculated for all vessel classes combined to reflect total vessel activity within important sites.

2.3. Collision threat quantification

To quantify levels of collision threat within important areas for whale sharks we explored shipping density on a relative basis (i.e. a comparison among sites) and did not measure absolute collision risk. Whether the threat of collision results in an actual collision event depends on animal-based factors such as whale shark avoidance behaviour or use of surface waters, and ship-based factors such as size and speed, which will influence the likelihood of a collision occurring (Schoeman et al., 2020). Here, because there is not yet information about how these factors can affect collision likelihood for whale sharks, our assessments are limited to measures of shark and ship co-occurrence, which we explored in detail. First, core habitats and buffer zones for each constellation were ranked from 1 (low) to 5 (high) by sorting the mean total shipping density within their boundaries into five quantiles to aid interpretation. This was defined as a site-specific 'danger rank', reflecting the relative localised threat of collision based on shipping activity within each site, where a higher vessel count served as a proxy for greater collision danger.

To examine the threat whale sharks face as they enter or leave the immediate constellation area (core habitat and buffer zones), we then calculated a 'peripheral zone' encircling each site at 100 km distance and analysed shipping activity in these surrounding waters. We used this peripheral danger rank to allow for whale sharks having to enter and leave the site through surrounding waters and to account for their high mobility (movements of approximately 20 km per day; Hearn et al., 2021, Womersley et al., 2022). Whale sharks are likely to travel through these peripheral areas regularly because their individual residency times within core habitats are often shorter than the duration of the seasons of peak occurrence according to the expert elicitation (Araujo et al., 2022). Here, mean total shipping density within the peripheral zone was also sorted into five quantiles, providing each site with a 'danger rank' from 1 to 5 to aid interpretation, representing the relative threat based on where

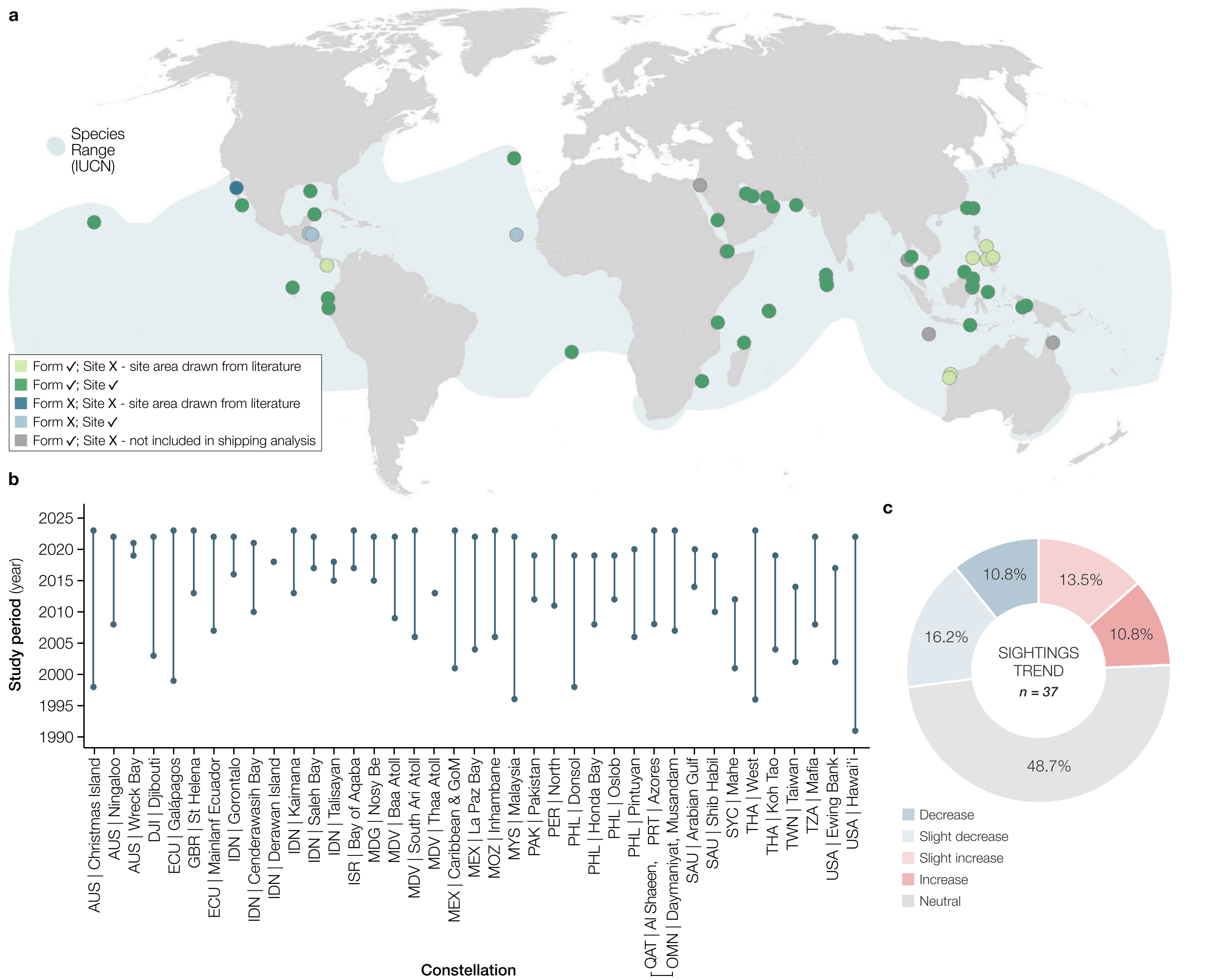


Fig. 1. **a**, Map showing global constellation sites coloured by data type submitted by experts or sought from the literature, where ticks in the legend mean associated information was provided by experts as opposed to crosses. The International Union for Conservation of Nature (IUCN) whale shark range is shown in blue. **b**, Duration of study periods in which experts collected data on whale sharks from each constellation. **c**, Sightings trend or inferred abundance trajectory of whale sharks at constellations, based on expert perception and data from each constellation coloured by status.

each site was positioned globally. Once again higher vessel count was interpreted as higher danger of collision. Peripheral danger ranks were compared to an individual shark derived collision risk index (CRI) based on whale shark movements (Womersley et al., 2022) using a Spearman's rank correlation. Here, mean CRI was calculated spatially by taking the mean of 0.25° resolution cells within the constellation peripheral zone.

Seasonal trends in shipping activity were explored by defining months as either high or low shipping times based on positive or negative differences from the annual average for each constellation. These months were then matched to seasonal whale shark occurrence based on information from the expert elicitation. The ship type posing the greatest threat was determined for each site from the highest mean count from the annual average.

2.4. Mitigation simulation

To explore potential mitigation strategies, a sample core habitat site was selected from within the northern Gulf of Mexico (Ewing Bank). Here, high-resolution vessel tracks for the year 2018 were downloaded from the National Oceanic and Atmospheric Administration (NOAA, https://coast.noaa.gov). Tracks were interpolated to contain one position per hour and filtered to include June through August (three core months of whale shark occurrence at Ewing Bank) before being explored in a speed reduction and rerouting simulation ($n = 6847$ unique vessels). Vessel speed was estimated based on the distance and time between each position and the one preceding it.

In total, 147 unique vessels passed through the Ewing Bank core habitat in June through August. For the vessel speed reduction simulation, positions where these vessels were travelling at speeds >50 m^{s-1} or the top 99th percentile were removed to trim potentially erroneous signals. In addition, if the number of rows where the vessel was considered stationary (travelling <0.01 m^{s-1}) was greater than a quarter of all positions or a vessel had fewer than 20 positions, it was removed. After filtering, total transit time and total distance travelled were calculated from the remaining positions. Speed reductions of 10 to 75 % at 1 % increments were then applied to all positions that fell within the core habitat area of whale sharks. A new total transit time including the speed reduction section was used to estimate the percentage increase from the original time.

For the rerouting analysis, the same subset of vessels was used ($n = 147$ unique vessels) with those that moved into and out of the core whale shark habitat being diverted. Here, the closest point around the perimeter from the original entry and exit was determined, and then the vessel was rerouted taking the shortest distance in space between the entry and exit points avoiding entering the area. Newly diverted positions were set to the average speed for the original locations moving through the area, including the positions prior to and post entry and exit, respectively. Averaged speeds and distances between diverted positions were used to estimate the new time for each, which was then applied to the rest of the track and incorporated into total time calculations to determine the percentage increase from the original.

2.5. Ethics statement

The expert questionnaire was voluntary and contained an opening paragraph explaining the purpose of the research. The questionnaire required participants to consent to sharing the information and knowledge as part of the process.

3. Results

3.1. Expert elicitation

Experts reported observations from 13,080 individual whale sharks within their constellations, representing ~64 % of all identified whale sharks in the global database (www.sharkbook.ai, n = 20,581 as of January 2024). Sites with a large number of individuals included Ningaloo Reef in Australia, the Mexican Caribbean, the Arabian/Persian Gulf, and southern Mozambique (Fig. 2b). Although more than half (55.0 %, n = 40 responses) of constellations reported that whale sharks can be seen throughout the year, only two locations (Hawai'i and the South Ari Atoll in the Maldives) did not have a defined peak season (i.e. consistent sightings across all months, Fig. S2a). On average, the peak season of whale shark occurrence had a duration of four months (n = 39 responses). For example, in Honda Bay, Philippines whale sharks are mostly seen from June to September, and in Coiba, Panama the peak season is from December to February (Fig. S2a). Some constellations had a short peak season of a single month, such as Shib Habil in the Red Sea or Saleh Bay in Indonesia, whereas others had longer peak seasons, including, for example, Baa Atoll in the Maldives with a six-month season (Fig. S2a). Core habitat zones were generally small, with a median area of 105.4 km^2 (Table S3). For example, the core zone for whale sharks in southern Mozambique was 144.2 km^2, and 98.1 km^2 in St. Helena. The smallest core zones were at two provisioning sites in Gorontalo (<0.1 km^2) and Oslob (0.1 km^2), and off Darwin Island in the Galápagos Archipelago (1.1 km^2). Experts perceived that the whale shark numbers in their constellations are mostly stable (48.7 % of responses, n = 37), with about equal responses for an increasing (24.3 %) or decreasing (27.0 %) trend in sightings (Fig. 1c).

Overall, 75.0 % (n = 36 responses) of experts thought that large vessels impacted whale sharks over the entire species range (not only inside their discrete constellation areas) (Fig. 2d). The constellations that listed large vessel collisions as their main concern within local waters included Ewing Bank situated in the northern Gulf of Mexico, the Seychelles, Wreck Bay and Ningaloo Reef in Australia, Donsol in the Philippines, and off the coast of mainland Ecuador. Although more than half of respondents (53.8 %, n = 39 responses) listed large vessel

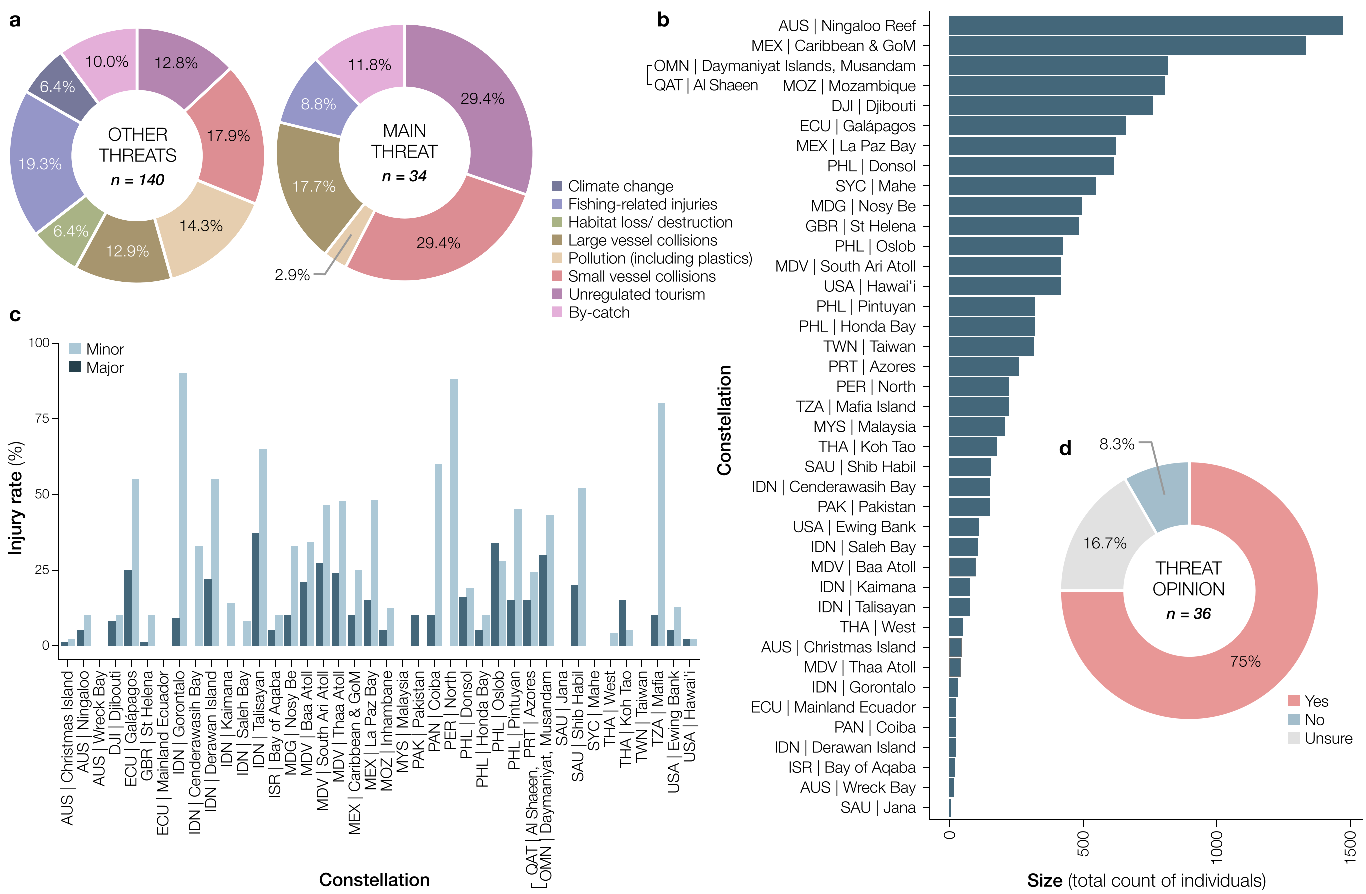


Fig. 2. **a**, Expert perception of any (left panel) or primary (right panel) threat to whale sharks within each constellation coloured by threat type. Experts were not asked to rank based on sources of mortality alone. **b**, Constellation size based on total count of uniquely identified whale sharks across the study periods in each constellation ordered by size. **c**, Injury and scarring rate given as a percentage of individuals recorded within each constellation across the entire study period coloured by type of affliction. For some sites, this value was an estimate. **d**, Expert opinion of the threat posed by large vessels to whale sharks across their entire range coloured by the answer to the question: '*Do you think vessel collisions affect whale shark populations in general?*'.

collisions as a threat to whale sharks in their constellations (Table S4), this concern was not regarded as a primary issue across constellations at a global scale, and only 13.5 % (n = 37 responses) ranked the threat as high (4) or very high (5). Experts stated that unregulated tourism (29.4 % of responses, n = 34) and small vessel collisions (29.4 %) were the leading threat to whale sharks within constellations (Fig. 2a, Table S4). Large vessel collisions followed and were mentioned in 17.7 % of responses, whereas bycatch (11.8 %) and fishing-related injuries (8.8 %) were mentioned less often. In addition, the most commonly mentioned types of vessels perceived to threaten whale sharks were small: tourist vessels (comprising 22.3 % of types mentioned, n = 130 and included in 77.8 % of responses, n = 37), recreational vessels (21.5 % of mentions, 75 % of responses), and artisanal fishing vessels (20.0 % of mentions, 69.4 % of responses)(Fig. S2b). With approximately 50 % (n = 40 responses) of respondents perceiving small vessel collisions as posing a high (4) or very high (5) threat within constellation sites (Fig. 3b, Table S4) and a mean of 12.5 % (n = 33 responses) of whale sharks having major injuries from vessel collisions (Fig. 2c, Table S5), these results suggest that experts are more aware of sub-lethal threats within constellation waters. Survivable whale shark injuries are most often obtained from small boats as collisions with larger vessels are likely to be fatal and 'cryptic' given the lack of direct evidence (Womersley et al., 2022). Unregulated tourism also has mostly sublethal impacts (Lester et al., 2020; Rowat et al., 2021), further indicating that experts perceive that whale sharks are at lower risk from direct mortality inside their constellations compared to these other threats.

Experts relayed that policy to manage collisions between ships and whale sharks is largely lacking within global whale shark constellations (Table S6). Some areas had policies focussed on managing vessels targeted at other species including Areas To Be Avoided (ATBA) in Ningaloo, Australia and Tubbataha Reefs, Philippines, which is designated as a Particularly Sensitive Sea Area (PSSA). In Indonesia, a framework to limit vessel speed and routes inside Marine Protected Areas (MPAs) and other important habitats exists, but it has not yet been applied to whale

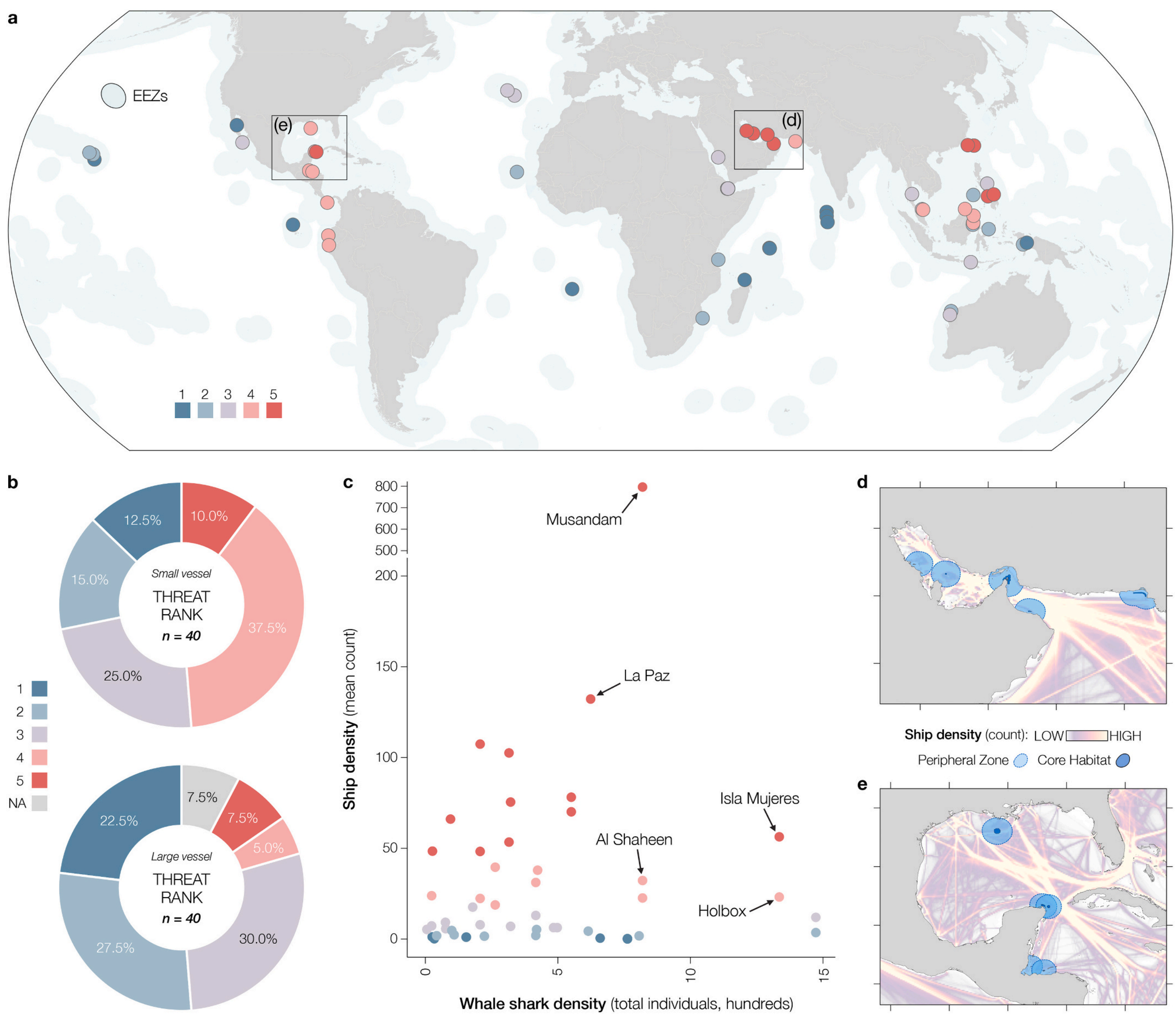


Fig. 3. **a**, Map showing global constellation sites coloured by quantified peripheral zone danger rank (1 = low, 5 = high). Countries Exclusive Economic Zones (EEZs) are shaded in blue. **b**, Expert perception of the threat posed by small (top panel) and large (bottom panel) vessels within each constellation coloured by a rank of 1–5. **c**, Ship and whale shark densities within each constellation coloured by quantified core habitat danger rank where several sites are highlighted as priorities for collision management. **d** and **e**, Map of Arabian/Persian Gulf and surrounding waters (**d**) and Gulf of Mexico (**e**) where five constellation sites (blue outlines) are shown in each overlaid with shipping density averaged for the years 2017–2019 where high (yellow) and low (purple) activity areas are displayed.

shark constellation sites. Other nations had recommendations targeted at protecting whale sharks from smaller vessels, such as in the Maldives, where a maximum speed of 10 knots is advised in all three aggregation areas for whale sharks. However, these limits are not enforced or monitored. Overall, our survey found that there are currently no mandatory or enforced management measures in place to safeguard whale sharks from large ship collisions in any of their constellation areas across the globe. In addition, experts listed a vaiery of other marine taxa potentially vulnerable to large vessel collisions within constellation waters (Table S5).

3.2. Shipping traffic

Movements of large vessels in all classes showed distinct patterns in the global ocean (Fig. S1). Most followed consistent routes across basins, as can be seen by cargo ships crossing the Indian Ocean between South Africa and Malaysia, for example, or passenger vessels crossing the Pacific between the Galápagos Islands and French Polynesia (Fig. S1). Others had more spread-out activities such as container reefers moving across the Atlantic Ocean between Europe and the Caribbean Sea (Fig. S1), and bunker vessels displayed the most seemingly random movements globally. Overall, cargo vessels were the most prevalent and container reefers the least, with maximum unique vessel counts within a ~123 km^2 cell of 13,949 and 95, respectively, per month, averaged from 2017 to 2019. Large vessels transited in all the constellation sites we examined, except for some core habitat areas in Djibouti; in this specific case, the location of the sites in narrow bays close to land meant they were obscured by the resolution of gridded shipping data.

3.3. Collision threat quantification

Many heavily-used shipping lanes passed through or close by to whale shark constellation sites worldwide (Fig. S1). To quantify potential collision threat posed by these activities, we first calculated a peripheral zone danger rank, from 1 (low) to 5 (high), based on the relative number of ships that transited through a 100 km radius around each whale shark core habitat. Constellations with the highest peripheral zone danger rank of 5 were located in the Arabian/Persian Gulf, the Gulf of Mexico, the Philippines, and Taiwan (Fig. 3a, Table S7). The least dangerous peripheral areas, with a danger rank of 1, were situated in waters surrounding remote islands (e.g. St Helena, Seychelles, Maldives, and the Galápagos Archipelago), or in secluded bays (e.g. Nosy Be, Madagascar and Cenderawasih Bay, Indonesia, Fig. 3a, Table S7). Although Djibouti had the only core whale shark habitat area without any large vessel traffic (Goubeth site), the peripheral zone was ranked as relatively dangerous (rank of 3) across all sites due to dense ship traffic passing in and out of the Red Sea through the Bab al-Mandab Strait. For sites with peripheral zones that overlapped with the spatial collision risk index (CRI) calculated in Womersley et al., 2022 ($n = 32$ peripheral zones), there was a positive correlation between CRI and our quantified danger rank ($rho = 0.76$, $p < 0.01$, Fig. S2c).

To identify the threat level from large vessels within each constellation site, we then calculated the local danger rank based on the number of ships that transited through the core habitat area. The most dangerous constellation areas for whale sharks globally were off the mainland of Ecuador, Isla Mujeres and La Paz in Mexico, Ewing Bank in the northern Gulf of Mexico, Kota Kinabalu and Redang Island in Malaysia, Pintuyan in the Philippines, Musandam in Oman, and around the Seychelles and Taiwan (Table S7). Many of these sites had areas within the constellation with over 1.0 vessel per km^2 in the core habitat where the greatest number of whale sharks are sighted. In most cases, buffer zones (that is, any areas where experts have seen whale sharks during their surveys) were ranked similarly to their associated core areas (Table S8). However, there were some instances where the core habitat was less dangerous. For example, the core habitat in Pakistan was ranked as relatively safe (rank of 2) with an average of 1.5 vessels per cell within the area monthly. This site is positioned close to a busy shipping route that passes by the core habitat but transits straight through the buffer zone, which was ranked relatively dangerous (4), with 44.3 vessels per cell, on average. This route also passed through the 100 km peripheral zone surrounding the core habitat suggesting the whale sharks are exposed to threat from vessels when entering or leaving the core constellation site. Conversely, we identified some sites with a higher danger rank inside the core habitat than in the buffer area or 100 km peripheral zone. It is important to note that both indices are relative to the ship traffic elsewhere in the same zone, so this does not necessarily mean that there were more ships in the core area than in the peripheral zone, although this was often the case. For example, aggregations in the Seychelles had a high danger rank (5) inside the whale shark area, and a low danger rank (1) in the 100 km peripheral area surrounding it. Here, local traffic of large vessels within the core habitat is the primary concern as opposed to close by shipping routes, as is the case with Pakistan. Other areas with a similar trend included St Helena, La Paz in Mexico, Nosy Be in Madagascar, and Boa Vista in Cape Verde (Table S7). Sites with such discrepancies are likely to provide benefit to whale sharks in their larger region if measures are implemented to reduce ship collisions within a relatively small, localised area.

Among areas with a high relative collision threat, several had no safe waters within their spatial extent, with a minimum of 25 vessels per ~123 km^2 grid cell (Table S7). These included Isla Mujeres in Mexico, mainland Ecuador and Redang Island in Malaysia, showing that in these locations, vessels are spread across the entire whale shark core habitat where most encounters occur. The highest ship density recorded from all vessel classes combined and all core constellation habitats was off the coast of Musandam, Oman, where an average of 788.0 ships were present monthly (Fig. 4b); >400 of these were tanker vessels. The maximum density in one ~123 km^2 area was over 2400 vessels per month (Table S7). Nine other core zones of whale shark constellations had particularly high densities of ship traffic, with a mean of >50 vessels per month (Fig. 4b, Table S7). For example, in La Paz, Mexico, >100 passenger vessels passed through the core zone of the constellation monthly, with a comparatively low number of cargo vessels (<10). Off the west coast of Taiwan, >100 vessels were recorded as the monthly average, with peak areas having >300 vessels transiting through ~123 km^2 in the core whale shark habitat. Other sites with high vessel traffic were in the Seychelles, Pintuyan (Philippines), Isla Mujeres (Mexico), and Kota Kinabalu (Malaysia) (Table S7). There were also sites with low relative collision threat where maximum vessel densities per cell were below a single vessel present within the site per month. Most of these safe constellations had a particularly small area, often comprising only ~2 grid cells, such as Gorontalo in Indonesia and Darwin Island in the Galápagos (Table S7).

Although we show that large vessels pose a threat to whale sharks in all constellations around the globe, some sites require the most urgent action to reduce the threats posed by shipping. These sites are characterised by high numbers of whale sharks using an area with high monthly shipping activity during the same time frame (Fig. 3c). Constellations that stand out as requiring urgent mitigation measures within the core habitat include Holbox, Isla Mujeres, and La Paz in Mexico, Musandam in Oman and Al Shaheen in Qatar. For example, Isla Mujeres has ~1335 individual whale sharks using the area and 56.3 ships (per ~123 km^2) passing through the core habitat monthly (54.0 passing through the buffer zone). Targeted measures should be considered a priority for these areas with high concurrent ship and shark densities, especially those with a high danger rank in the peripheral zone (Table S7), including Isla Mujeres, Mexico and Musandam, Oman (Fig. 3c, d, e).

In many cases, expert perception of the local threat posed by large vessels within their constellation matched our quantified relative local danger rank (Table S4, Table S7). Some areas underestimated the threat, such as Taiwan and La Paz in Mexico, both of which had a high quantified danger rank. Others overestimated the threat posed by large vessels within the constellations, such as Shib Habil in Saudi Arabia or

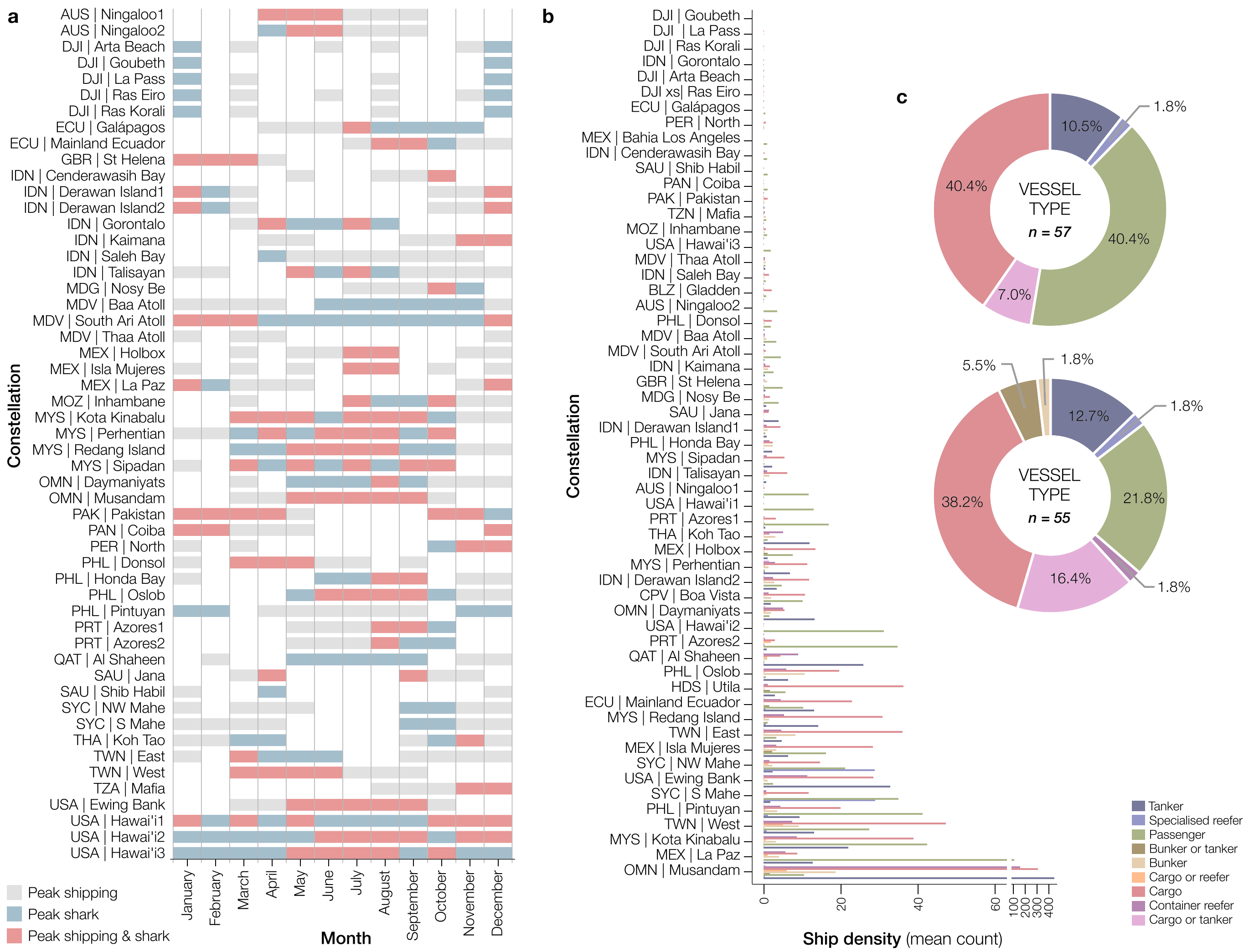


Fig. 4. **a**, Seasonal variation in ship and whale shark density within each constellation core habitat area coloured by level of co-occurrence where grey represents peak shipping activity (levels greater than annual mean), blue represents the peak whale shark occurrence season and red represents months when these two groups co-occur. **b**, Ship density within each constellation core habitat coloured by vessel type and ordered by mean number of ships within each site per month (average month from 2017 to 2019). **c**, Vessel type posing the greatest (left panel) and second greatest (right panel) threat within each constellation based on the mean count of vessels within the core habitat area coloured by vessel type.

Ningaloo Reef in Australia. Some of these sites also reported a high level of vessel-inflicted scars and injuries on the sharks, potentially influencing expert perception (Fig. 2c). In these cases, sharks could be attaining injuries elsewhere in their range before arriving at the constellation or be at risk of small vessel collisions more locally. We could not include whale shark behaviour in the quantitative analyses, due to limited data on the subject, but local experts regularly observe whale sharks displaying minimal avoidance from approaching ships and thus may perceive the danger as higher than the number of ships would infer.

Shipping density was not consistent throughout the year, and 39 constellation core habitats had above-average vessel activity in months that were also peak whale shark occurrence seasons (Fig. 4a). For example, the peak whale shark season in Coiba, Panama, was from December to February, which overlaps with above average ship traffic in the core habitat. Peak overlap was often driven by a single class of vessels being present seasonally in the area. Overall, whale sharks in core constellation habitats were most at threat from cargo (40.4 %, n = 57, Fig. 4c) and passenger (40.4 %) vessels. Other minor categories included tanker (10.5 %), cargo or tanker (7.0 %), and specialised reefer (1.8 %, Fig. 4c). Sites where passenger vessels posed the greatest threat included the Galápagos Islands, St. Helena, Azores, and Hawai'i, among others (Table S7). These whale shark areas tended to be located along heavily-used transit routes, with passenger vessels having the least spread and highest density gradients among the different types of vessels (Fig. S1). Sites where cargo and tanker vessels posed the greatest threat included off the coast of mainland Ecuador, Holbox (Mexico), and Ewing Bank in the Northern Gulf of Mexico, among others (Table S7). These key whale shark sites were located within important maritime trade routes with frequent cargo and tanker traffic (Fig. S1).

3.4. Mitigation simulation

Following the track filtering steps, 147 unique vessels passed through the Ewing Bank core whale shark habitat situated in the northern Gulf of Mexico from June to August in 2018 (Fig. 5a, b). Positions associated with each unique vessel were run through a speed reduction and re-routing mitigation simulation. For the speed simulation, reductions of 75 % within the core habitat area resulted in an approximate 5.0 % increase in total transit time on average, and 69.6 additional transiting hours averaged across each unique vessel in 2018 (Fig. 5c). Cases where simulated speed reductions resulted in vast increases in transit time skewed this result and included vessels that remained within the zone for extended time periods (e.g. Fig. 5d). When

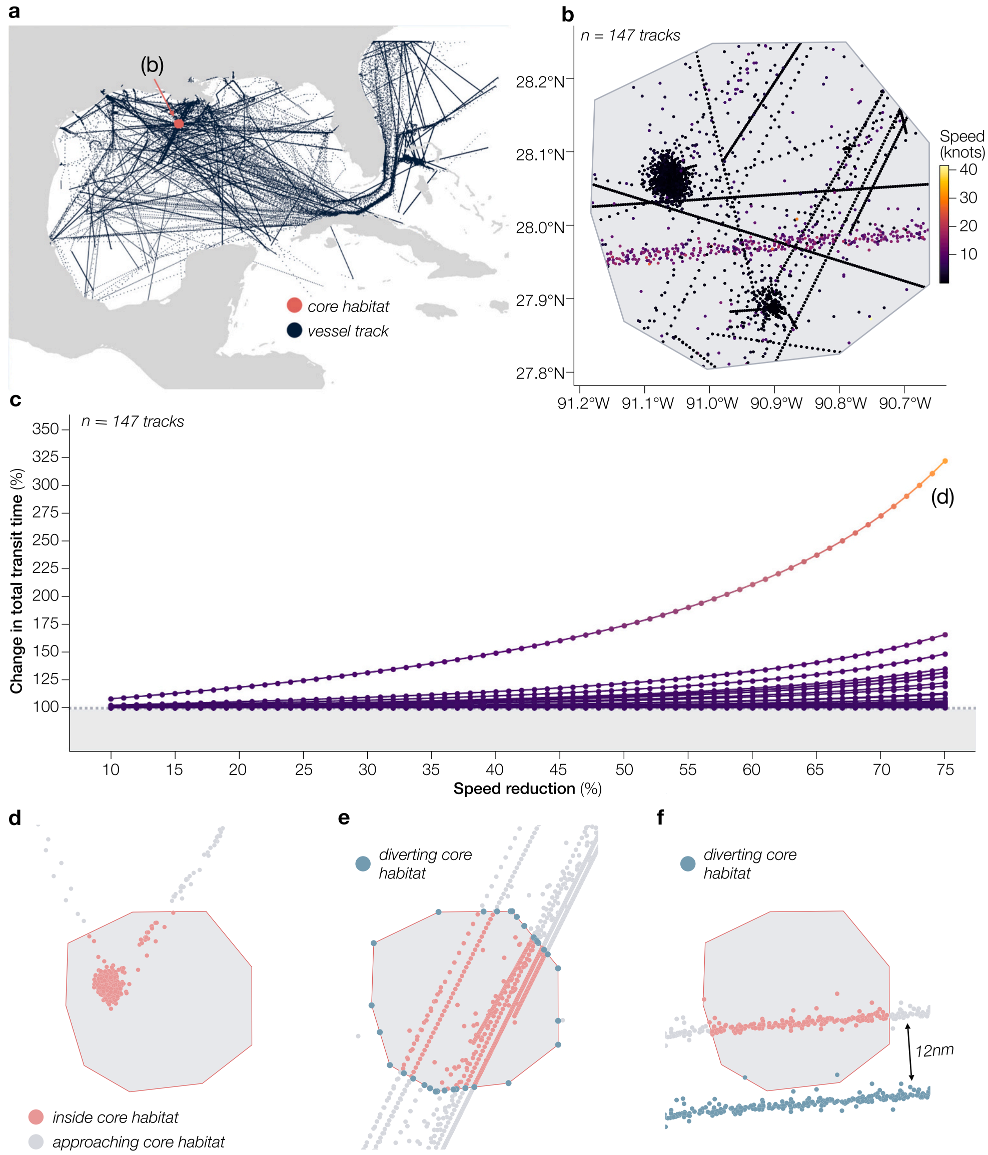


Fig. 5. **a**, Map of vessel tracks from June to August within the Gulf of Mexico in 2018 (dark blue) which move through the Ewing Bank core whale shark habitat (red). **b**, Tracks passing though the Ewing Bank core whale shark habitat coloured by low (black) and high (yellow) travelling speeds (knots) within the area. **c**, Change in total transit time of vessels passing through the Ewing Bank core habitat area where speed reductions from 10 to 75 % were applied when within the core habitat. **d**, Example track of a vessel that experienced total transit time increases >300 % due to a considerable portion of the track occurring inside the core habitat (red) where speed limits were applied. **e**, Example of track diversions around the core habitat area (blue) instead of through (red). **f**, Example of shipping lane diversion where a lane was defined by selecting vessels transiting through the core habitat areas at >15 knots (**b**) and moved south by 12 nautical miles (nm, blue) to avoid the area.

vessels were re-routed entirely around the core whale shark habitat, transiting at the same average speeds as they originally moved through the area resulted in an approximate 0.5 % increase in total transiting time and a 1.1 % increase in total distance travelled on average, with the maximum reroute approximately 26 km (84 km being half the perimeter of the area minus the maximum distance across, 58 km). The average extra time per unique vessel was 2.4 h (Fig. 5e). For vessels travelling through the area at speeds >15 knots (7.7 m^{s-1}, Fig. 5b) and considered to be using a fixed transit route used by multiple vessels, we found that a shift of approximately 12 nautical miles (nm) due south would be required to avoid the core whale shark habitat area entirely (Fig. 5f).

4. Discussion

4.1. Estimating threat within constellations

We gathered information from experts based at most of the known global whale shark constellations. Overall, the number of encounters within sites was temporally stable, and where a trend was seen, there were a near equal number of sites with increasing or decreasing sightings. Experts rated local threats, vessel injury rates, and the threat posed by small and large vessels based on their in-water observations over many years of whale shark research. Overall, experts were concerned about the threat posed by large vessels within constellations, but some feel that other threats are more pertinent. For example, unregulated tourism and small vessel collisions were frequently mentioned as a concern within coastal constellations, likely because injuries and scars from smaller boats are more visible to observers, and conflict with tourism operations can be directly witnessed. Although these threats are more detectable to researchers, whale sharks are known to heal from injuries (Womersley et al., 2021), and the high percentage of returning individuals suggests that these local threats do not keep them from occupying constellation areas (Araujo et al., 2022). The impacts of these activities are more likely to be sub-lethal, negatively influencing individual fitness, foraging efficiency (Barry et al., 2023) or altering diving activities (Araujo et al., 2020), among other impacts. As such, whale sharks would benefit from improved management of small vessel traffic and tourism operations within constellation sites.

Population-level impacts of unregulated tourism and small vessel collisions are difficult to gauge at present, although evidence from some sites supports that survival rates between scarred and non-scared individuals are virtually the same (Lester et al., 2020; Speed et al., 2008) or even higher for scared individuals (Harvey-Carroll et al., 2021). Collisions with large vessels, however, are likely to be fatal (Womersley et al., 2022), removing individuals from the population entirely and, because whale sharks are slightly negatively buoyant, their bodies sink so that evidence of fatal collisions is scarce. As a result, local experts are unlikely to observe or gather evidence of this threat within their site, as was apparent in the survey, though the majority appreciate that large vessel collisions may influence populations globally. This underestimation is concerning and highlights the importance of studies that quantify collision related threats where direct evidence is lacking. In addition, it emphasises the need to improve on both collision monitoring and mitigation frameworks (Womersley et al., 2023).

Our quantitative analyses of shipping traffic within core whale shark habitats, buffer zones, and the peripheral areas surrounding them, showed that the threat from large vessels can indeed be underestimated, with large vessels transiting through almost all the constellation sites we examined. We found that some sites had the maximum core habitat and peripheral zone danger rank, and high numbers of individual whale sharks identified, prioritising their waters as in urgent need of conservation attention. Although we could signpost toward sites of concern, our study could not quantify absolute collision risk. In fact, variation in the actual likelihood of collision within each constellation is still an open question and requires data that were beyond the scope of our study. For example, whale sharks alter their fine-scale depth use depending on several factors such as physiological/metabolic requirements (Thums et al., 2013), prey distribution (Gleiss et al., 2013), human presence (Barry et al., 2023), or environmental cues (Arrowsmith et al., 2021). Collisions only pose a risk when individuals are at the surface, usually in waters shallower than 20 m. So, understanding vertical movements of whale sharks within constellations is crucial and will likely vary between and within sites on a diel and seasonal cycle. Future research should aim to explore drivers of vertical habitat use in sufficient detail so that this dimension can be included in future threat quantification studies. Similarly, we could not explore how whale sharks may respond to vessels within each constellation. Although past research suggests they are unlikely to avoid oncoming ships (Womersley et al., 2022), more work is required to solidify these observations using high-resolution shark and ship tracking, targeted within the high collision-threat areas we have identified here.

4.2. Management suggestions

Our expert survey revealed that no mandatory or enforced management measures are currently in place to safeguard whale sharks from large ship collisions in any of the constellation sites we reviewed. Their small spatial extent and the relatively short peak seasons of whale shark occurrence within these known areas can allow for tailored management measures inside their boundaries, potentially minimising disruption to the shipping industry while maximising conservation benefit. For example, we simulated the impact of speed reductions applied to ships moving within the Ewing Bank core habitat in the northern Gulf of Mexico. Our estimates are conservative because a 75 % reduction in speed may result in ships travelling more slowly than required to reduce collision frequency or likelihood of lethal collisions for whale sharks. The area of the Ewing Bank site is also over ten times the average constellation area. Speed reduction models explored for North Atlantic right whales found that collision risk dropped by 90 % when ships travelled at 10 knots or less (Conn and Silber, 2013), and for other species, speeds of 10 knots reduced the probability of lethality by 57 % compared to 29 % at 12 knots (Wiley et al., 2011). Vessel classes explored in our analyses frequently travel faster than 10 knots on average (Wood, 2021), but for whale sharks, it is not yet known what speed is optimal to balance industry disruption with conservation benefit. By permuting percentage reductions in speed instead of absolute speed, here we provide proof of concept that speed limits can result in potentially small changes in industry operating times. More research is needed in this area, specifically studies that focus on potential whale shark ship evasion rates or response times at different vessel transiting speeds or while the animal is engaging in feeding activities, for example. With improved information on these metrics, future mitigation simulations can incorporate absolute speeds into estimates on a site-by-site basis to ensure shipping industry disruption is minimised alongside conservation benefit for whale sharks.

Using marine mammal collision management as a model until we have improved data for whale sharks, speed reductions to 10 knots within core habitats could be a viable option. One of the benefits of speed reductions is that they can be temporally restricted to apply only during whale shark peak seasons. Given their small size and the high predictability in the timing and location of whale shark aggregation sites, there is potential for voluntary speed reductions to have high levels of engagement due to a potenially low overall impact on shipping operations, although in some cases mandatory regulations have higher levels of compliance (Allen et al., 2007). An additional important benefit of speed reductions is that regulations can also apply to small vessels, which can operate at higher speeds and likely have sub-lethal impacts on the species. Experts reported that small vessel collisions are a significant concern within constellations on a global level, and scarring/injury data further support this as an important threat to whale sharks (Harvey-Carroll et al., 2021; Lester et al., 2020; Penketh et al., 2020; Speed et al., 2008; Womersley et al., 2021). Monitoring compliance of smaller ships without AIS transmitters or similar equipment will be challenging, but voluntary compliance, at least among tourist vessels, is likely to be high based on current engagement levels and the high eco-tourism value of the species (Ziegler and Dearden, 2021). Measures at sites such as Ningaloo Reef where remote monitoring of tourism vessels has been used to explore impacts of the industry could be trialled at other constellations (Lester et al., 2019).

We also simulated the impact of re-routing vessels around the perimeter of the Ewing Bank core whale shark habitat, which resulted in a slight increase in total transit time. Spatially separating ships from whale sharks is the most direct way to reduce the risk of collision. Our polygons of core habitats and buffer zones for each constellation area, drawn by local experts, provide an excellent blueprint for where spatial separations are needed for this species. In addition, our results suggest that – given the small area of most constellations – routes around them will not be much further than through them in most cases. For example, transiting through the core habitat zone of the Holbox aggregation in Mexico covers a distance of ~26.5 km. A container ship travelling at 24 knots takes 36 min to transit the area. Re-routing this transit around the core whale shark zone would add 14.1 km in distance for a total transit time of 55 min. Continuing the example to include speed reduction, a direct transit through the core zone would take 86 min at a speed of 10 knots, or 107 min at a speed of 8 knots. These simple area-based calculations and our dedicated mitigation simulation suggest that re-routing will often be more cost-effective than speed reduction in that the increase in transit time is lower, at least for fast vessels such as container ships. Here, we found that movements of as little as 12 nm (22.2 km) south of a core whale shark habitat could mean fast transiting ships avoid the site entirely. Ship re-routing was recently implemented off the southern coast of Sri Lanka, where the Mediterranean Shipping Company (MSC) re-routed their vessels by shifting a Traffic Separation Scheme (TSS) approximately 15 nm south to avoid core blue whale (*Balaenoptera musculus*) habitat based on guidance provided by a range of stakeholders (MSC, 2023).

Other mitigation measures such as including observers on board vessels or implementing new technologies to detect whale sharks should be explored (Womersley et al., 2023), as should those that aim to track vessel movements at finer scales, such as Vessel Monitoring Systems (VMS). Support for these requires increased awareness and education surrounding the issue as well as improved data on where the species is exposed to the threat of collision. Along with our results identifying constellation sites where threat is greater, we suggest that a centralised collision recording framework can help pinpoint where collisions are occurring. This could not only help validate collision risk and threat quantification studies but also further target management enabling adaptive approaches to the issue moving forward. This will be especially important for climate change adaptation and planning, which may see whale shark constellations shift as local oceanography changes in future. The species may move into new areas where shipping density is higher requiring adaptive approaches to management where on-the-ground monitoring will be invaluable. Further collaborative research is needed to explore these hypotheses, modelling both whale shark movements and the location of constellation sites in the future to predict how the species may interact with human threats in years to come. It is also important to continue to gather information on less well-known sites, such as Wreck Bay in Australia, as sharks gathering in locations not spatially reviewed here are subjected to unknown levels of threat from collisions.

5. Conclusions

The scale of global shipping and the almost ubiquitous overlap of at least some large vessel traffic with whale shark constellations, underlines the magnitude of the threat the shipping industry poses. Here, we show that whale sharks are not only threatened by ship collision during their long-distance movements, when they can pass through shipping lanes and heavily-used vessel areas (Womersley et al., 2022), but also when they spend time within small, localised aggregation sites. Our findings highlight the need for a combination of targeted measures within these constellation areas to reduce the risk of vessel collisions and suggest that these have the potential to substantially improve the conservation status of Endangered whale sharks.

Protecting whale sharks from large ship collisions requires global cooperation and a multifaceted approach that combines regulatory measures, technological innovations, education, collaborative research, and a balance between conservation and the goals of the shipping industry. Awareness surrounding marine megafauna collisions is increasing, and although progress is slow, measures to reduce ship strikes for other marine megafauna are being implemented (Schoeman et al., 2020; Womersley et al., 2023), indicating that the shipping industry is amenable to the issue. Governments should engage with the industry to develop ways to protect this species. For example, in 2024 a resolution was adopted by the Convention on the Conservation of Migratory Species of Wild Animals (CMS), aimed at "reducing the risks of vessel strikes for marine megafauna – including specific guidance for Whale Sharks" (UNEP/CMS/Resolution 14.5) (CMS, 2024) following Araujo et al. (2023). This resolution is in line with Article III(4) of CMS (given the whale shark's listing on Appendix I of the convention), The Memorandum of Understanding on the Conservation of Migratory Sharks (Sharks MOU, given the species' listing on Annex 1 of the agreement), and Target 3 of the Global Biodiversity Framework 30 by 30. The resolution is the first of its kind for sharks, and should provide a roadmap for industry, governments and other stakeholders to take action for the conservation of the species, as well as supporting regulations for other at-risk marine megafauna. By implementing the management strategies suggested therein, we could pave the way for coexistence between this ecologically and culturally important species and the shipping industry, ensuring a sustainable future for both humans and whale sharks.

CRediT authorship contribution statement

Freya C. Womersley: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Conceptualization. **Christoph A. Rohner:** Writing – review & editing, Project administration, Methodology. **Kátya Abrantes:** Writing – review & editing. **Pedro Afonso:** Writing – review & editing. **Shin Arunrugstichai:** Writing – review & editing. **Steffen S. Bach:** Writing – review & editing. **Shir Bar:** Writing – review & editing. **Adi Barash:** Writing – review & editing. **Peter Barnes:** Writing – review & editing. **Adam Barnett:** Writing – review & editing. **Ginevra Boldrocchi:** Writing – review & editing. **Noemie Buffat:** Writing – review & editing. **Tom Canon:** Writing – review & editing. **Clara Canovas Perez:** Writing – review & editing. **Metavee Chuangcharoendee:** Writing – review & editing. **Jesse E.M. Cochran:** Writing – review & editing. **Rafael de la Parra:** Writing – review & editing. **Stella Diamant:** Writing – review & editing. **William Driggers:** Writing – review & editing. **Mark V. Erdmann:** Writing – review & editing. **Richard Fitzpatrick:** Writing – review & editing. **Anna Flam:** Writing – review & editing. **Jorge Fontes:** Writing – review & editing. **Gemma Francis:** Writing – review & editing. **Beatriz Eugenia Galvan:** Writing – review & editing. **Rachel Graham:** Writing – review & editing. **Sofia M. Green:** Writing – review & editing. **Jonathan R. Green:** Writing – review & editing. **Ya'ara Grosmark:** Writing – review & editing. **Hector M. Guzman:** Writing – review & editing. **Royale S. Hardenstine:** Writing – review & editing. **Maria Harvey:** Writing – review & editing. **Jessica Harvey-Carroll:** Writing – review & editing. **Abdi Wunanto Hasan:** Writing – review & editing. **Alex R. Hearn:** Writing – review & editing. **Jill M. Hendon:** Writing – review & editing. **Mochamad Iqbal Herwata Putra:** Writing – review & editing. **Mahardika Rizqi Himawan:** Writing – review & editing. **Eric Hoffmayer:** Writing – review & editing. **Jason Holmberg:** Writing – review & editing. **Hua Hsun Hsu:** Writing – review & editing. **Mohammed Y. Jaidah:** Writing – review & editing. **Ashlee Jansen:** Writing – review & editing. **Christy Judd:** Writing – review & editing. **Baraka Kuguru:** Writing – review & editing. **Emily Lester:** Writing – review & editing. **Bruno C.L. Macena:** Writing – review & editing. **Kirsty Magson:** Writing – review & editing. **Rossana Maguiño:** Writing – review & editing. **Mabel Manjaji-Matsumoto:** Writing – review & editing. **Stacia D. Marcoux:** Writing – review & editing. **Travis Marcoux:** Writing – review & editing. **Mark Meekan:** Writing – review & editing. **Alejandra Mendoza:** Writing – review & editing. **Muhammad Moazzam:** Writing – review & editing. **Emily Monacella:** Writing – review & editing. **Brad Norman:** Writing – review & editing. **Cameron Perry:** Writing – review & editing. **Simon Pierce:** Writing – review & editing. **Clare Prebble:** Writing – review & editing. **Dení Ramírez Macías:** Writing – review & editing. **Holly Raudino:** Writing – review & editing. **Samantha Reynolds:** Writing – review & editing. **David Rowat:** Writing – review & editing. **Mudjekeewis D. Santos:** Writing – review & editing. **Jennifer Schmidt:** Writing – review & editing. **Chad Scott:** Writing – review & editing. **Sian Tian See:** Writing – review & editing. **Abraham Sianipar:** Writing – review & editing. **Conrad W. Speed:** Writing – review & editing. **Ismail Syakurachman:** Writing – review & editing. **Julian A. Tyne:** Writing – review & editing. **Kelly Waples:** Writing – review & editing. **Chloe Winn:** Writing – review & editing. **Ranny R. Yuneni:** Writing – review & editing. **Irthisham Zareer:** Writing – review & editing. **Gonzalo Araujo:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request to the corresponding author.

Acknowledgements

This study builds on the report "Limiting global ship strikes on whale sharks: Understanding an increasing threat to the world's largest fish" (UNEP/CMS/COP14/Inf.27.2.3) that was prepared for the Convention on the Conservation of Migratory Species of Wild Animals (CMS) with funding from the German Federal Ministry of Environment, Nature Conservation, Nuclear Safety and Consumer Protection, and partial funding from the Marine Research and Conservation Foundation. FCW was also supported by the UK Natural Environment Research Council (NERC INSPIRE DTP NE/S007210/1). We would like to express our special thanks to Andrea Pauly (CMS) for her continuous support during the project. We would also like to acknowledge the collaborative work of the 69 scientists from 18 countries as part of the GSMP (www.globalsharkmovement.org) whale shark tracking sub-project which revealed the global extent of ship strike risk to whale sharks including potential mortality taking place and identifying the specific need for collision mitigation policy (https://doi.org/10.1073/pnas.2117440119). Thanks also for the shipping data contributions from Global Fishing Watch (https://globalfishingwatch.org) and for software permissions and guidance from SeaSketch (https://www.seasketch.org).

Appendix A. Supplementary information

Supplementary information related to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.172776.

References

Allen, S., Smith, H., Waples, K., Harcourt, R., 2007. The voluntary code of conduct for dolphin watching in Port Stephens, Australia: is self-regulation an effective management tool? J. Cetacean Res. Manag. 9, 159–166.
Anderson, D.J., Kobryn, H.T., Norman, B.M., Bejder, L., Tyne, J.A., Loneragan, N.R., 2014. Spatial and temporal patterns of nature-based tourism interactions with whale sharks (Rhincodon typus) at Ningaloo Reef, Western Australia. Estuar. Coast. Shelf Sci. 148, 109–119.
Araujo, G., Lucey, A., Labaja, J., So, C.L., Snow, S., Ponzo, A., 2014. Population structure and residency patterns of whale sharks, Rhincodon typus, at a provisioning site in Cebu, Philippines. PeerJ 2, e543.
Araujo, G., Snow, S., So, C.L., Labaja, J., Murray, R., Colucci, A., et al., 2017. Population structure, residency patterns and movements of whale sharks in Southern Leyte, Philippines: results from dedicated photo-ID and citizen science. Aquat. Conserv. Mar. Freshwat. Ecosyst. 27, 237–252.
Araujo, G., Labaja, J., Snow, S., Huveneers, C., Ponzo, A., 2020. Changes in diving behaviour and habitat use of provisioned whale sharks: implications for management. Sci. Rep. 10, 1–12.
Araujo, G., Agustines, A., Bach, S.S., Cochran, J.E.M., Edl, Parra-Galván, Rdl, Parra-Venegas, et al., 2022. Improving sightings-derived residency estimation for whale shark aggregations: a novel metric applied to a global data set. Front. Mar. Sci. 9.
Araujo, G., Rohner, C.A., Womersley, F.C., 2023. Limiting global ship strike on whale sharks: Understanding an increasing threat to the world's largest fish, prepared for The Convention on the Conservation of Migratory Species of Wild Animals (CMS).
Arrowsmith, L.M., Sequeira, A.M.M., Pattiaratchi, C.B., Meekan, M.G., 2021. Water temperature is a key driver of horizontal and vertical movements of an ocean giant, the whale shark Rhincodon typus. Mar. Ecol. Prog. Ser. 679, 101–114.
Barry, C., Legaspi, C., Clarke, T.M., Araujo, G., Bradshaw, C.J.A., Gleiss, A.C., et al., 2023. Estimating the energetic cost of whale shark tourism. Biol. Conserv. 284, 110164.
Blondin, H., Abrahms, B., Crowder, L.B., Hazen, E.L., 2020. Combining high temporal resolution whale distribution and vessel tracking data improves estimates of ship strike risk. Biol. Conserv. 250, 108757.
Chaplin-Kramer, R., Brauman, K.A., Cavender-Bares, J., Díaz, S., Duarte, G.T., Enquist, B. J., et al., 2022. Conservation needs to integrate knowledge across scales. Nat. Ecol. Evol. 6, 118–119.
CMS, 2024. Resolution 14.5 Reducing the risk of vessel strikes for marine megafauna, including specific mention for Whale Sharks. In: Convention on the Conservation of Migratory Species of Wild Animals (CMS) 14th Meeting of the Parties (COP14).
Conn, P.B., Silber, G.K., 2013. Vessel speed restrictions reduce risk of collision-related mortality for North Atlantic right whales. Ecosphere 4 (4), 1–16.
de la Parra Venegas, R., Hueter, R., Cano, J.G., Tyminski, J., Remolina, J.G., Maslanka, M., et al., 2011. An unprecedented aggregation of whale sharks, Rhincodon typus, in Mexican coastal waters of the Caribbean Sea. PLoS ONE 6, e18994.
Duarte, C.M., Chapuis, L., Collin, S.P., Costa, D.P., Devassy, R.P., Eguiluz, V.M., et al., 2021. The soundscape of the Anthropocene ocean. Science 371, eaba4658.
Erbe, C., Marley, S.A., Schoeman, R.P., Smith, J.N., Trigg, L.E., Embling, C.B., 2019. The effects of ship noise on marine mammals—a review. Front. Mar. Sci. 6.
Gleiss, A.C., Wright, S., Liebsch, N., Wilson, R.P., Norman, B., 2013. Contrasting diel patterns in vertical movement and locomotor activity of whale sharks at Ningaloo Reef. Mar. Biol. 160, 2981–2992.
Gudger, E.W., 1940. Whale Sharks Rammed by Ocean Vessels: How These Sluggish Leviathans Aid in Their Own Destruction. N. Engl. Nat. 7, 1–10.
Guzmán, H.M., Beaver, C.E., Díaz-Ferguson, E., 2021. Novel insights into the genetic population connectivity of transient whale sharks (Rhincodon typus) in Pacific Panama provide crucial data for conservation efforts. Front. Mar. Sci. 8.
Harry, A.V., Braccini, J.M., 2021. Caution over the use of ecological big data for conservation. Nature 595, E17–E19.
Harvey-Carroll, J., Stewart, J.D., Carroll, D., Mohamed, B., Shameel, I., Zareer, I.H., et al., 2021. The impact of injury on apparent survival of whale sharks (Rhincodon typus) in South Ari Atoll Marine Protected Area, Maldives. Sci. Rep. 11, 937.
Hazen, E.L., Palacios, D.M., Forney, K.A., Howell, E.A., Becker, E., Hoover, A.L., et al., 2017. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. J. Appl. Ecol. 54, 1415–1428.
Hearn, A.R., Green, J.R., Peñaherrera-Palma, C., Reynolds, S., Rohner, C.A., Román, M., et al., 2021. Whale shark movements and migrations. In: Whale Sharks: Biology, Ecology, and Conservation. CRC Press.
Hulme, P.E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. J. Appl. Ecol. 46, 10–18.
Keen, E.M., Scales, K.L., Rone, B.K., Hazen, E.L., Falcone, E.A., Schorr, G.S., 2019. Night and day: diel differences in ship strike risk for fin whales (Balaenoptera physalus) in the California current system. Front. Mar. Sci. 6.
Laist, D.W., Knowlton, A.R., Mead, J.G., Collet, A.S., Podesta, M., 2001. Collisions between ships and whales. Mar. Mamm. Sci. 17, 35–75.
Lester, E., Speed, C., Rob, D., Barnes, P., Waples, K., Raudino, H., 2019. Using an electronic monitoring system and photo identification to understand effects of tourism encounters on whale sharks in Ningaloo Marine Park. Tour. Mar. Environ. 14, 121–131.
Lester, E., Meekan, M.G., Barnes, P., Raudino, H., Rob, D., Waples, K., et al., 2020. Multi-year patterns in scarring, survival and residency of whale sharks in Ningaloo Marine Park, Western Australia. Mar. Ecol. Prog. Ser. 634, 115–125.
Malakoff, D., 2010. A push for quieter ships. Science 328, 1502–1503.
McCoy, E., Burce, R., David, D., Aca, E.Q., Hardy, J., Labaja, J., et al., 2018. Long-term photo-identification reveals the population dynamics and strong site fidelity of adult whale sharks to the coastal waters of Donsol, Philippines. Front. Mar. Sci. 5.
McKenna, M.F., Calambokidis, J., Oleson, E.M., Laist, D.W., Goldbogen, J.A., 2015. Simultaneous tracking of blue whales and large ships demonstrates limited behavioral responses for avoiding collision. Endanger. Species Res. 27, 219–232.
MSC, 2023. MSC Adjusts Course Around Sri Lanka to Protect Blue Whales. MSC.
Nelson, J.D., Eckert, S.A., 2007. Foraging ecology of whale sharks (Rhincodon typus) within Bahía de Los Angeles, Baja California Norte, México. Fish. Res. 84, 47–64.
Norman, B.M., Holmberg, J.A., Arzoumanian, Z., Reynolds, S.D., Wilson, R.P., Rob, D., et al., 2017. Undersea constellations: the global biology of an endangered marine megavertebrate further informed through citizen science. BioScience 67, 1029–1043.
Penketh, L., Schleimer, A., Labaja, J., Snow, S., Ponzo, A., Araujo, G., 2020. Scarring patterns of whale sharks, *Rhincodon typus*, at a provisioning site in the Philippines. Aquat. Conserv. Mar. Freshwat. Ecosyst. 31 (1), 99–111.
Pierce, S.J., Norman, B., 2016. *Rhincodon typus*. The IUCN Red List of Threatened Species 2016. e.T19488A2365291.
Pierce, S.J., Grace, M.K., Araujo, G., 2021. Conservation of whale sharks. In: Whale Sharks: Biology, Ecology, and Conservation. CRC Press.
Pirotta, V., Grech, A., Jonsen, I.D., Laurance, W.F., Harcourt, R.G., 2019. Consequences of global shipping traffic for marine giants. Front. Ecol. Environ. 17, 39–47.
Queiroz, N., Humphries, N.E., Couto, A., Vedor, M., da Costa, I., Sequeira, A.M.M., et al., 2021. Reply to: caution over the use of ecological big data for conservation. Nature 595, 20–28.
Ramírez-Macías, D., Queiroz, N., Pierce, S.J., Humphries, N.E., Sims, D.W., Brunnschweiler, J.M., 2017. Oceanic adults, coastal juveniles: tracking the habitat use of whale sharks off the Pacific coast of Mexico. PeerJ 5, e3271.
Robinson, D.P., Jaidah, M.Y., Jabado, R.W., Lee-Brooks, K., Nour El-Din, N.M., Malki, A. A.A., et al., 2013. Whale sharks, Rhincodon typus, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. PLoS ONE 8, e58255.
Rohner, C.A., Prebble, C.E., 2021. Whale shark foraging, feeding, and diet. In: Whale Sharks: Biology, Ecology, and Conservation. CRC Press.
Rohner, C.A., Armstrong, A.J., Pierce, S.J., Prebble, C.E., Cagua, E.F., Cochran, J.E., et al., 2015. Whale sharks target dense prey patches of sergestid shrimp off Tanzania. J. Plankton Res. 37, 352–362.

Rohner, C.A., Cochran, J.E., Cagua, E.F., Prebble, C.E., Venables, S.K., Berumen, M.L., et al., 2020. No place like home? High residency and predictable seasonal movement of whale sharks off Tanzania. Front. Mar. Sci. 7, 423.
Rohner, C.A., Norman, B., Araujo, G., Holmberg, J., Pierce, S.J., 2021. Population ecology of whale sharks. In: Whale Sharks: Biology, Ecology, and Conservation. CRC Press.
Rowat, D., Womersley, F., Norman, B.M., Pierce, S.J., 2021. Global threats to whale sharks. In: Whale Sharks Biology, Ecology, and Conservation. CRC Press.
Saebi, M., Xu, J., Curasi, S.R., Grey, E.K., Chawla, N.V., Lodge, D.M., 2020. Network analysis of ballast-mediated species transfer reveals important introduction and dispersal patterns in the Arctic. Sci. Rep. 10, 19558.
Sardain, A., Sardain, E., Leung, B., 2019. Global forecasts of shipping traffic and biological invasions to 2050. Nat. Sustain. 2, 274–282.
Schoeman, R.P., Patterson-Abrolat, C., Plön, S., 2020. A global review of vessel collisions with marine animals. Front. Mar. Sci. 7.
Sequeira, A.M.M., Rodriguez, J.P., Eguiluz, V.M., Harcourt, R., Hindell, M., Sims, D.W., et al., 2018. Convergence of marine megafauna movement patterns in coastal and open oceans. Proc. Natl. Acad. Sci. U. S. A. 115, 3072–3077.
Sequeira, A.M.M., Hays, G.C., Sims, D.W., Eguíluz, V.M., Rodríguez, J.P., Heupel, M.R., et al., 2019. Overhauling Ocean spatial planning to improve marine megafauna conservation. Front. Mar. Sci. 6.
Sharp, S.M., McLellan, W.A., Rotstein, D.S., Costidis, A.M., Barco, S.G., Durham, K., et al., 2019. Gross and histopathologic diagnoses from North Atlantic right whale Eubalaena glacialis mortalities between 2003 and 2018. Dis. Aquat. Org. 135, 1–31.
Speed, C.W., Meekan, M.G., Rowat, D., Pierce, S.J., Marshall, A.D., Bradshaw, C.J.A., 2008. Scarring patterns and relative mortality rates of Indian Ocean whale sharks. J. Fish Biol. 72, 1488–1503.
Thums, M., Meekan, M., Stevens, J., Wilson, S., Polovina, J., 2013. Evidence for behavioural thermoregulation by the world's largest fish. J. R. Soc. Interface 10, 20120477.
Tyminski, J.P., De La Parra-Venegas, R., González Cano, J., Hueter, R.E., 2015. Vertical Movements and Patterns in Diving Behavior of Whale Sharks as Revealed by Pop-up Satellite Tags in the Eastern Gulf of Mexico, 10 e0142156.
UNCTAD, 2020. Review of Maritime Transport 2020.
Vanderlaan, A.S., Taggart, C.T., Serdynska, A.R., Kenney, R.D., Brown, M.W., 2008. Reducing the risk of lethal encounters: vessels and right whales in the Bay of Fundy and on the Scotian Shelf. Endanger. Species Res. 4, 283–297.
Wan, Z., Zhu, M., Chen, S., Sperling, D., 2016. Pollution: three steps to a green shipping industry. Nature 530, 275–277.
Wiley, D.N., Thompson, M., Pace, R.M., Levenson, J., 2011. Modeling speed restrictions to mitigate lethal collisions between ships and whales in the Stellwagen Bank National Marine Sanctuary, USA. Biol. Conserv. 144, 2377–2381.
Womersley, F., Hancock, J., Perry, C.T., Rowat, D., 2021. Wound-healing capabilities of whale sharks (Rhincodon typus) and implications for conservation management. Conserv. Physiol 9 (1), coaa120.
Womersley, F.C., Humphries, N.E., Queiroz, N., Vedor, M., Id, Costa, Furtado, M., et al., 2022. Global collision-risk hotspots of marine traffic and the world's largest fish, the whale shark. Proc. Natl. Acad. Sci. 119, e2117440119.
Womersley, F.C., Loveridge, A., Sims, D.W., 2023. Four steps to curb 'ocean roadkill'. Nature 621, 34–38.
Wood, A., 2023. Vessels shun 'go slow' amid turbulent 2020 market conditions. Accessed 21-02-2024.
Wyborn, C., Evans, M.C., 2021. Conservation needs to break free from global priority mapping. Nat. Ecol. Evol. 5, 1322–1324.
Ziegler, J., Dearden, P., 2021. Whale shark tourism as an incentive-based conservation approach. In: Whale Sharks: Biology, Ecology, and Conservation. CRC Press.