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Insights into the population demographics and residency patterns of photo-identified whale sharks *Rhincodon typus* in the Bird's Head Seascape, Indonesia

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The whale shark (*Rhincodon typus*) is an iconic species in the Bird's Head Seascape (BHS) in eastern Indonesia, yet little is known about its population and residency patterns across the region. This study documents the population demographics of this globally Endangered species from four key regions within the BHS: Cenderawasih Bay (CB), Kaimana (KA), Raja Ampat, and Fakfak. Using 13 years of photographic identification (photo-ID) data sourced from researchers and citizen scientists, we aim to provide a better understanding of population dynamics, residency patterns, and threats to the species. From September 2010 to October 2023, a total of 1,118 sightings of 268 different individuals were recorded, almost exclusively around lift-net fishing platforms (bagans). The population was strongly male-biased (8.8:1.0), with estimated total lengths ranging from 2 to 8 m, and most individuals in the 4–5 m size class, indicating a dominance of juvenile males. Over half (52.6%) of the individuals were re-sighted at least once, with one re-sighting span lasting 10.63 years. Most sightings (97.8%) were concentrated in CB (551 sightings, 159 individuals) and KA (542 sightings, 95 individuals). Only two individuals were seen in multiple regions, suggesting limited movement and potential habitat segregation. Lagged Identification Rates showed substantially higher residency in CB (77.1 days ± 34.4 SE) than in KA (37.8 days ± 9.7 SE). Scarring was recorded in 76.9% of individuals, with minor abrasions (47.4%) and fin nicks (39.9%) being the most common, followed by amputations (15.3%) and lacerations (14.2%). Only 2.4% of scars were likely inflicted by boat propellers, and only 3.4% of injuries were recorded as bites by predators. KA had a higher proportion of scarred sharks (83.7%) compared to CB (73.7%). The long-term presence and high re-sighting rates of juvenile whale sharks in CB and KA highlight their importance as key habitats within the BHS. While most sightings of whale sharks in the BHS occurred inside marine protected areas, the relatively high percentage of individuals with injuries apparently related to negative interactions with fisheries and tourism underscore the need for improved management to ensure the well-being of this fully protected species in Indonesia.

KEYWORDS

Papua, endangered species, population dynamics, marine megafauna, citizen science, conservation, elasmobranch

1 Introduction

A comprehensive understanding of the life history of threatened species, especially those that are wide ranging, is fundamental to effective conservation and management and for ensuring their long-term persistence (Nanglu et al., 2023). Investigating population demographics–such as size structure, sex ratio, and maturity status–can reveal population trends and identify vulnerable life stages (Norris, 2004), while residency patterns provide insights into how individuals use specific habitats over time (e.g., Setyawan et al., 2022b). These ecological parameters are critical for identifying essential habitats, informing spatial protection measures, and mitigating human impacts on the threatened species.

The whale shark, classified as Endangered on the International Union for the Conservation of Nature Red List and designated as Largely Depleted on the Green Status of Threatened Species, inhabits tropical and temperate waters across all three major ocean basins (Pierce and Norman, 2016; Pierce et al., 2021). Over the past five decades, global populations of whale sharks have declined significantly due to a range of anthropogenic threats, including entanglement in fishing gear, accidental bycatch in large net fisheries, and ship strikes (Pacoureau et al., 2021; Womersley et al., 2022). Despite its Endangered status, the species remains a significant contributor to economic revenue of many countries, generating millions of dollars through whale shark tourism (snorkeling and diving) at coastal locations across the tropics, including Ningaloo Reef (Australia), The Maldives, The Philippines, Yucatan Peninsula (Mexico), and Nosy Be (Madagascar) (Gallagher and Hammerschlag, 2011; Cagua et al., 2014; Huveneers et al., 2017; Lowe et al., 2019; Ziegler et al., 2021).

In Indonesia, whale sharks have been sighted sporadically across many regions (Supplementary Figure 1), and aggregations have been identified in the coastal waters of Talisayan (Kalimantan Timur Province), Probolinggo (Jawa Timur Province), Botubarani (Gorontalo Province), Saleh Bay in Sumbawa (Nusa Tenggara Barat Province), and Cenderawasih Bay and Kaimana (Papua Barat Province and Papua Tengah Province). At these locations, individual sharks are often sighted repeatedly, and can be present on a seasonal or year-round basis (Himawan et al., 2015; Kamal et al., 2016; Suruan et al., 2016; Farid et al., 2021). In 2006, a biodiversity survey of Cenderawasih Bay (Figure 1) recorded a remarkable interaction between bagan lift-net fisheries and a local aggregation of whale sharks (Meyers et al., 2020). A bagan is a traditional lift–net fishing platform that originated in South Sulawesi, Indonesia, and is used primarily to capture small pelagic fishes at night. The structure consists of a boat, a large wooden frame, and an expansive net suspended 10–20 m below the surface, with an array of lights suspended above the water to attract plankton and small fishes, which are then caught as the net is quickly winched to the surface (Salman et al., 2016). The large aggregations of plankton and bait fishes targeted by the technique in turn attract larger predators, including whale sharks, to the bagans (Meyers et al., 2020). Fishers reported regular year-round visits by whale sharks to feed on the baitfish brought to the surface by fishermen's lights above floating bagan platforms in nearshore water. This unique interaction, coupled with the predictable, year-round presence of these large animals, has catalyzed the development of a tourism industry offering snorkelers and divers in-water encounters with whale sharks, particularly in places such as Kwatisore, in the southern part of Cenderawasih Bay (Anna and Saputra, 2021).

The growing importance of whale sharks as a tourism attraction in Indonesia and the steady decline in their populations globally highlights the need for better information on the distribution, demography, and ecology of whale sharks in the region. Historically, whale sharks in Indonesian waters have faced limited hunting, with minimal interactions reported to fisheries agencies. However, in the early 2000s, there were a number of landings, particularly in Bali and Lombok, due to opportunistic or targeted fishing (White and Cavanagh, 2007). In 1996-1997, Taiwanese fishing fleets were reported to have captured over 100 individual whale sharks in the Lembeh Strait in North Sulawesi (Cochrane, 1997). Additionally, since 2010 at least 180 strandings of whale sharks have been recorded, primarily along the south coast of Java and the west coast of Sumatra – areas known for frequent cold-water upwellings where the whale sharks are attracted to these highly productive coastal areas and were likely exposed to net fisheries (Putra et al., in review[1]). However, perhaps the greatest threat to populations of whale sharks in both Indonesian waters and at global scales involves the risk of ship strikes (Speed et al., 2008; Womersley et al., 2022).

1 Putra, M. I. H., Wirasatriya, A., Asyraffauzan, H., Fahmi Syakurachman, I., Hasan, A. W., et al. Spatio-temporal patterns, trends, and oceanographic drivers of whale shark strandings in Indonesia. *Sci. Rep.* in review.

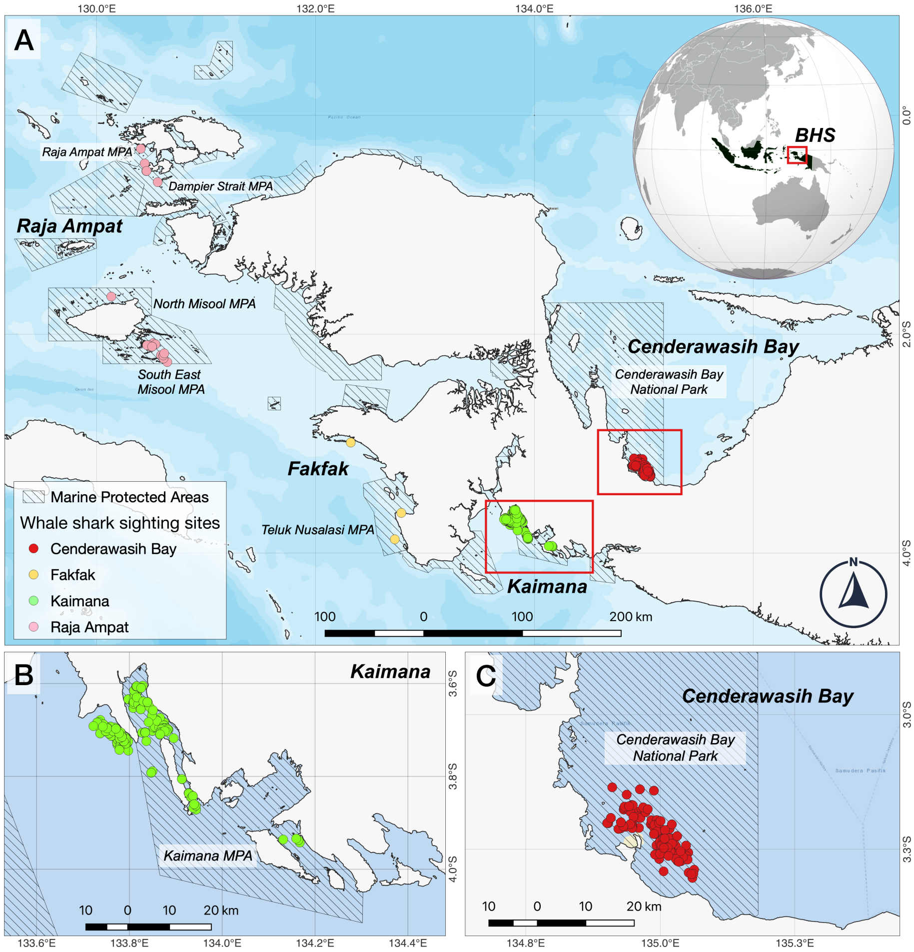

FIGURE 1
Distribution of whale sharks sighting sites in **(A)** the Bird's Head Seascape (BHS), **(B)** Kaimana, and **(C)** Cenderawasih Bay, eastern Indonesia, with locations of 26 marine protected areas (MPAs) network. Colored dots represent whale shark sighting sites in four regions (Cenderawasih Bay, Raja Ampat, Fakfak, and Kaimana) in the BHS.

Whale sharks spend long periods of daylight hours basking in surface waters, where they are vulnerable to being struck by fast moving vessels (Arrowsmith et al., 2021). Much of the presumed mortality from ship strikes is cryptic, as large vessels do not necessarily notice when a whale shark has been hit, and after death these sharks sink as they are negatively buoyant. Evidence that ship strike is a major threat to the species comes from both tracking studies (Womersley et al., 2024) and the prevalence of scarring on animals that survive encounters with vessels (Speed et al., 2008).

Here, we used a photo-identification approach (Meekan et al., 2006; Speed et al., 2007; Meenakshisundaram et al., 2021) to examine the ecology and residency of whale sharks at aggregation sites in eastern Indonesia. Our study focuses on whale sharks in the region of the Bird's Head Seascape (BHS), a global hotspot for tropical marine biodiversity and marine megafauna, and a region where there are important and valuable tourism industries that focus on whale sharks. Our work builds on the results of several previous studies that have examined whale shark populations within the BHS, providing insights into the population structure and demographics of sharks using photo-identification within Cenderawasih Bay (Himawan et al., 2015; Suruan et al., 2016; Tania et al., 2016). However, these studies, aside from having limited geographic coverage, were conducted over a relatively brief period spanning 5–6 years from 2010 to 2015. Addressing the need for an expanded temporal scope and a more comprehensive geographic range, the primary objectives of our study were to delineate and summarize fundamental demographic characteristics of the whale shark population across the entirety of the BHS. Leveraging an extensive ~13-year dataset spanning from 2010 to 2023 from our BHS whale shark photo ID database, we aim to provide a better understanding of population dynamics and threats to the species within the BHS.

2 Materials and methods

2.1 Study area

The Bird's Head Seascape (BHS) in eastern Indonesia (Figure 1) is renowned as the global epicenter of coral reef biodiversity (Allen and Erdmann, 2009; Veron et al., 2009) and is safeguarded by a network of 26 marine protected areas (MPAs) that cover an area of 52 million ha (Setyawan et al., 2022a). The seascape hosts a diverse range of megafauna, including cetaceans (Ender et al., 2014), manta rays (Beale et al., 2019; Setyawan et al., 2020), and whale sharks (Himawan et al., 2015; Tania et al., 2016; Meyers et al., 2020). Regions within the seascape include Cenderawasih Bay in the north-central part of the island of Papua, Raja Ampat in the northwestern tip of the BHS, Fakfak in the southwest of the BHS, and Kaimana in the south of the BHS (Figure 1). Both Cenderawasih Bay and Kaimana have been identified as Important Shark and Ray Areas (ISRAs) for whale sharks that serve as critical feeding habitats for this species (Jabado et al., 2024).

2.2 Data collection

Our database of whale shark sightings was gathered from two primary sources: field surveys and citizen science, including the Wildbook for Sharks platform – a visual database that collects photographic IDs of sharks. Our population monitoring program began in September 2010 in Cenderawasih Bay, with subsequent expansion to Kaimana in October 2013. The field work is ongoing, and the data set analyzed here spans the period between September 2010 and October 2023. In both locations, field surveys were conducted 2–4 times a year by researchers visiting bagans. Fewer field surveys occurred in Raja Ampat and Fakfak, due to both logistical constraints and a lower frequency of whale sharks present around bagans. During each survey, our research team spent 4–7 days in the area, capturing photographs and videos of whale sharks from both the left and right sides of each individual to obtain photo-ID data. For each of these animals, we also recorded the date and time of each encounter, GPS locations, sex and maturity status, injuries, and behavior. Sex of sharks was determined by the presence (male) or absence (female) of claspers. The total length (TL) of each whale shark that was sighted was estimated to the nearest meter. Additionally, the TL of individuals accidentally caught in bagan lift nets were measured using a tape measure while the animal was restrained in the net.

Supplementing field surveys, other sightings data of whale sharks were opportunistically sourced from citizen scientists, including tourists and tourism operators such as Kalilemon Homestay, the *True North* expedition vessel and *Coralia* liveaboard in Cenderawasih Bay and Triton Bay Divers in Kaimana. These tourism operators generously provided our research team with photo IDs of whale sharks encountered by both dive leaders and guests.

2.3 Whale shark photo ID database

Each whale shark exhibits a unique pattern of white spots and stripes on its dorsal surface (Meekan et al., 2006; Holmberg et al., 2009; Meenakshisundaram et al., 2021). This distinctiveness allows researchers to differentiate between individual whale sharks by analyzing patterns in a standard area of the dorsal-lateral surface of the shark located behind the fifth gill slit and above the pectoral fin (Figure 2D). Each ID photo/video collected through field surveys and citizen science was visually matched by authors of this study (Edy Setyawan, Abdy Hasan, and Abraham Sianipar) with other ID photos in our BHS whale shark ID catalogue to examine if the whale shark was a newly sighted or a re-sighted individual. Along with the photo ID images of whale sharks that have been identified, the associated metadata and observations recorded were entered into the BHS whale shark photo ID database using protocol and structure similar to the BHS manta ray photo ID database described by Setyawan et al. (2020).

2.4 Scarring and injuries

To better understand threats to BHS whale sharks, any scarring or injuries on a whale shark we encountered were photographed. Images were then classified by severity (i.e., major, minor) and assigned into one of seven categories: (1) lacerations, (2) nicks, (3) amputations, (4) abrasions, (5) blunt trauma, (6) bites, and (7) others (Speed et al., 2008; Lester et al., 2020). Major scars were those that were potentially life-threatening and included severe lacerations (penetrating the subdermal layer) to the head (e.g., eyes and mouth) or along the flank (e.g., gills) and dorsal surface, and complete or near-complete amputations to the pectoral, caudal, and dorsal fins. Minor scars were superficial and included abrasions and small nicks to the pectoral, caudal and dorsal fins (Speed et al., 2008). The position of the scarring and injuries on the body of the whale sharks were also recorded and categorized as head, first dorsal fin, second dorsal fin, caudal fin, pectoral fin, flank, dorsal surface, and ventral surface (Lester et al., 2020). The possible causes of scarring and injuries were also categorized as anthropogenic (e.g., boat strikes, fishing gear, rubbing on boats or bagans) and natural (e.g., predator attack).

2.5 Residency analysis

A maximum likelihood approach was used to assess the residency patterns of whale sharks. The Lagged Identification Rate (LIR), the probability of re-sighting an individual after a specified time lag (Whitehead, 2001), provides an estimate of how long an individual remains associated with a study area by examining the intervals between its sightings. A higher LIR over longer time lags suggests stronger site fidelity and longer residency times. The analysis was conducted using “Movement between areas” within the “Movement analyses” module in the program SOCPROG 2.9 (Whitehead, 2009). The analysis, requiring whale shark sighting data consisting of “Whale shark ID”, “Sighting date”, and “Region”, was separately conducted between our study region in the BHS using the “Whole study” approach within the “Lagged Identification Rate” module.

A total of eight models, comprising closed and open population models (Table 1), were fitted to the LIR data. These models, available as presets in SOCPROG 2.9, incorporated various demographic parameters such as emigration, reimmigration, and

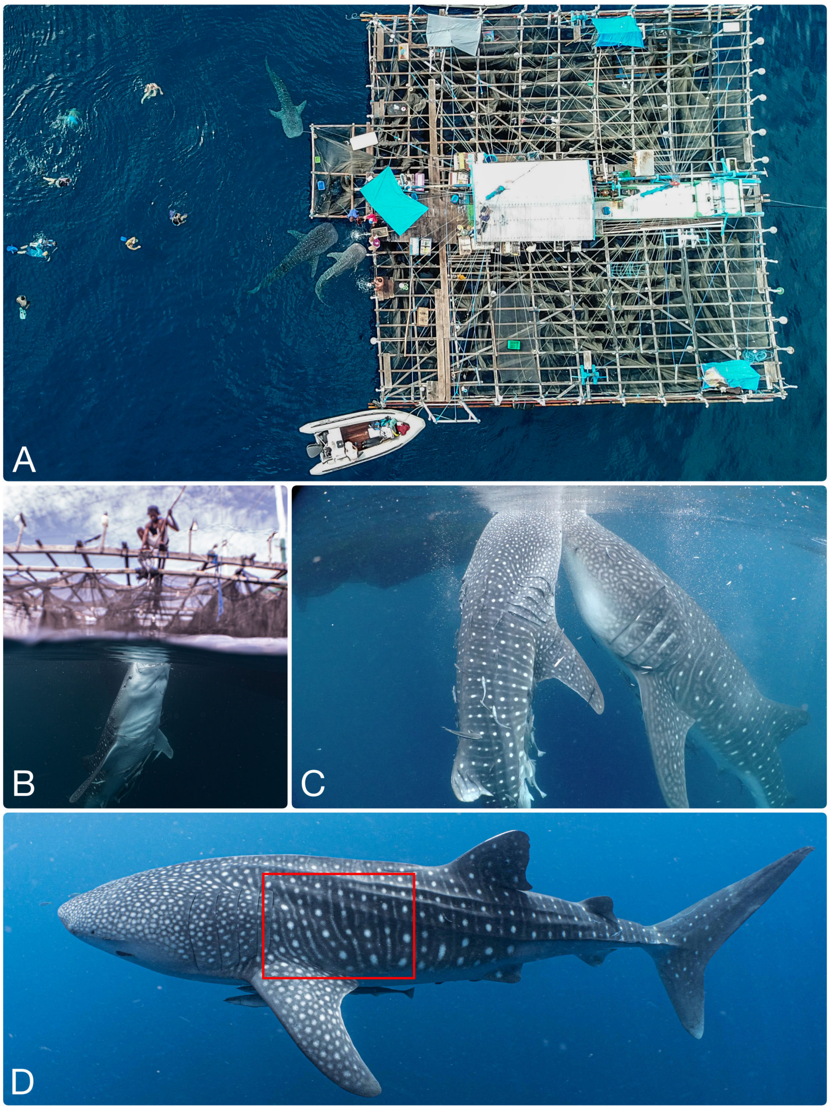

FIGURE 2
(A) Aggregation of whale sharks (*Rhincodon typus*) at a *bagan* captured by a drone in Cenderawasih Bay, Papua (©Mark Erdmann); **(B, C)** Stationary and vertical feeding behavior commonly observed during provisional feeding at bagans (©Abraham B. Sianipar); **(D)** A whale shark highlighting the area for identification behind its fifth gill slit and above the pectoral fin (©Abraham B. Sianipar).

mortality, including permanent emigration from the study regions. Model fits were bootstrapped 100 times to generate standard errors (SE). The best-fitting model was determined based on the lowest quasi Akaike Information Criterion (QAIC) value, accounting for overdispersion in the sighting data (Whitehead, 2007). Finally, estimates for key parameters of the best-fit model were reported as mean ± standard error of mean (SE), along with 95% confidence intervals (CIs) presented as: lower CI – upper CI.

To understand the residency of whale sharks in the study region, we used LIR residency proportion (α_{LIR}), following Araujo et al. (2022). The α_{LIR}, derived from the LIR and used to estimate the proportion of time the whale sharks spent within the study area, was calculated by dividing a2 (mean time in study region) by a3 (mean time out of study region) from Model H in Table 1. This measure gives a more intuitive sense of how much time whale sharks remain in the area being monitored, making it particularly useful for understanding site–use patterns and assessing the ecological importance of the site for the population. To compare the residency of whale sharks in the BHS with those from other regions across the globe, we then calculated adjusted residency time (in days per year) using the following formula: (α_{LIR}*124.6)/1.97, as detailed in Araujo et al. (2022).

TABLE 1 Comparison of model parameters for Lagged Identification Rates (LIRs) of whale sharks in Cenderawasih Bay and Kaimana.

Model	Parameter descriptions	ΔQAIC	
		Cenderawasih Bay	Kaimana
A	Closed (1/a1 = N)	510.88	505.87
B	Closed (a1 = N)	510.88	505.87
C	Emigration/mortality (a1 = emigration rate; 1/a2 = N)	11.58	62.36
D	Emigration + reimmigration (a1 = emigration rate; a2/(a2 + a3) = proportion of population in study area at any time)	338.79	245.64
E	Emigration/mortality (a1 = N; a2 = mean residence time)	11.58	62.36
F	Emigration + reimmigration + mortality (a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate)	14.97	66.36
G	Emigration + reimmigration (a1 = N; a2 = mean time in study area; a3 = mean time out of study area)	13.58	245.64
H	Emigration + reimmigration + mortality (a1 = N; a2 = mean time in study area; a3 = mean time out of study area; a4 = mortality rate)	0.00	0.00

The parameters, as per Whitehead (2009) in SOCPROG 2.9, include tests from closed population models (A & B) to various combinations of emigration, reimmigration, and mortality (C–H). The displayed values represent the difference between the QAIC (quasi-Akaike information criterion) results obtained for each model and the smallest QAIC result.

3 Results

3.1 Whale shark aggregations and observation sites in the BHS

Whale shark sightings occurred in 327 sites spanning four regions in the BHS: Cenderawasih Bay (n = 111), Kaimana (n = 195), Raja Ampat (n = 18), and Fakfak (n = 3). Three of the 327 sighting sites lacked verified photo-IDs. GPS locations were not recorded for 136 of the 1,118 total sightings verified with photo-IDs. Of 327 sites where sightings occurred, 314 were considered "bagan aggregation sites" (defined here as a specific area where multiple bagans operate, creating localized hotspots that reliably attract whale sharks). Whale sharks were encountered around coral reefs or in open water in the remaining 13 sighting areas (Figure 1). Bagan aggregation sites were distributed across all regions but were predominantly concentrated in Cenderawasih Bay and Kaimana. Whale sharks were sighted at 37 different bagans in Kaimana and at one in Fakfak. Although the GPS locations of sightings were recorded, individual bagans in Cenderawasih Bay were not identified – though we estimate at least 30 different bagans operate at any given time in the Kwatisore region of Cenderawasih Bay, with whale sharks potentially encountered at all of them.

All sighting sites in Cenderawasih Bay were associated with bagans operating within the Cenderawasih Bay National Park. Similarly, all sighting sites in Kaimana were also associated with bagans, except for one in the Iris Strait. The majority of sighting sites were located within Kaimana MPA, although a number of sightings occurred near Kaimana City, where bagans operated beyond the boundaries of the MPA. In Raja Ampat, all sightings of whale sharks, including three sightings without verified ID photos (n = 25) occurred in the South East Misool, North Misool, Dampier Strait, and Raja Ampat MPAs (Figure 1), and 14 of these were associated with bagans. Of the three sightings in Fakfak, two were from coral reefs within the Teluk Nusalasi MPA, one was at a bagan situated outside of MPAs.

3.2 Individual sightings and BHS whale shark photo ID database

A total of 1,118 whale shark sightings verified with photo-IDs occurred in the BHS between September 2010 and October 2023, involving 268 individuals. Whale sharks occurred either individually or in aggregations of up to 12 individuals. The majority of sightings (97.8%) occurred in Cenderawasih Bay (551 sightings) and Kaimana (542 sightings). The rest of the sightings were recorded in Raja Ampat (22 sightings) and Fakfak (3 sightings). Whale shark were almost exclusively observed at bagans, except for 13 sightings distributed in Raja Ampat (n = 10 sightings), Fakfak (n = 2 sightings), and Kaimana (n = 1 sighting), where the whale sharks cruised along coral reefs and/or open seas.

The majority of sightings were obtained through field surveys conducted by our research team, with only 127 sightings (11.4%) contributed by citizen scientists. Typically, whale sharks were observed while feeding at bagans (Figure 2), where they targeted small baitfish including anchovies (Engraulidae), silversides (Atherinidae) and herrings and sprats (Clupeidae). Common behaviours observed at the bagans included: (1) horizontal feeding, involving forward swimming with an open mouth, either at the surface or in the water column, to engulf baitfish (this behavior was particularly common at night during bagan fishing operations, when the whale sharks would actively target the fish aggregated below bagan lights); (2) stationary vertical feeding, where a whale shark maintains a vertical position with its mouth towards the surface, actively gulping prey (this posture was often observed when tourist operators fed sharks to prolong their attendance at the surface so that they could be observed by snorkelers and divers; Figures 2B, C); and (3) direct suction of baitfish from the nets, often resulting in net damage.

Of the 268 individuals identified in the BHS, 52.6% were re-sighted at least once during the monitoring period. Among regions, the whale shark population in Kaimana had a higher rate of re-sightings (57.9%) than sharks in Cenderawasih Bay (52.8%) and Raja Ampat (16.7%). No re-sightings were recorded for whale sharks identified in Fakfak.

The longest time span between sightings of the same individual shark was 10.63 years; in this case a juvenile male (WS#0051, Supplementary Figure 2) was sighted four times at bagans in Cenderawasih Bay between February 2013 and October 2023. Additionally, another juvenile male shark was re-sighted 12 times over the decade between September 2013 and October 2023 in Cenderawasih Bay. In Kaimana, the longest span of re-sightings was 9.06 years for a juvenile male (WS#0133). The most frequently re-sighted individual was a juvenile male (WS#0191) which was recorded 34 times at bagans in Kaimana between December 2019 and December 2022.

Annually, the number of whale shark sightings in the BHS varied across years, with the highest number recorded in 2018 (n = 164 sightings), followed by 2022 (n = 161 sightings) (Figure 3). Within the two regions with the most sightings, Cenderawasih Bay recorded the highest number in 2018 (n = 152 sightings), with only one sighting in 2021 and none in 2020 and 2022. In Kaimana, the peak number of sightings occurred in 2022 (n = 159 sightings). Raja Ampat documented whale shark sightings annually from 2016 to 2022, while Fakfak recorded sightings only in 2019, 2022, and 2023. Importantly, only Raja Ampat had a consistent survey effort (citizen science observations by dive tourists) across years; the variation in sightings per year in Cenderawasih Bay, Kaimana and Fakfak were a direct result of highly variable survey effort across years and should not be interpreted as an indication of true variability in the presence of whale sharks across years in these regions.

There was similarly a non-uniform pattern of survey effort within the year in Cenderawasih Bay, Fakfak and Kaimana, although the cumulative number of sightings varied noticeably between months, particularly in Kaimana. In this region, most sightings occurred from February to April and November to December, with lower sightings from June to August during the southeast monsoon period, when rough seas prevent both tourism and often fishing activity so that survey effort was therefore minimal (Figure 4A). As such, it is impossible to ascertain from this data if whale sharks left the area or if they were present throughout the year, but were simply not observed during the southeast monsoon. In Cenderawasih Bay, which is largely protected from seasonal winds and remains calm throughout the year, individual sightings were broadly dispersed across months, confirming a year-round presence in the region.

Data on time of day of sightings revealed that the majority occurred in the morning, peaking from 6 am to 10 am, with a gradual decrease until 2 pm. In Kaimana, the highest number of sightings was recorded at 8 am, whereas in Cenderawasih Bay, the peak in sightings occurred at 7 am (Figure 4B).

The discovery curve of whale shark sightings in both Kaimana and Cenderawasih Bay demonstrated a consistent upward trend in the number of newly identified individuals throughout the study period, with no apparent asymptote (Figure 5). The vast majority of re-sightings occurred in the same region where the sharks were initially sighted. Notably, WS#0101, first observed in January 2017 in Misool, southern Raja Ampat, exhibited consistent yearly re-sightings in the same area until November 2021, with no re-sightings reported from other regions.

Movements and re-sightings among regions were observed for two individuals within the BHS. A 5-m male whale shark (WS#0056) was sighted initially in Cenderawasih Bay in October 2013, and subsequently re-sighted in Kaimana in April 2017 before being observed twice in November 2017 back in Cenderawasih Bay. Another individual, also a 5-m male whale shark (WS#0086), was

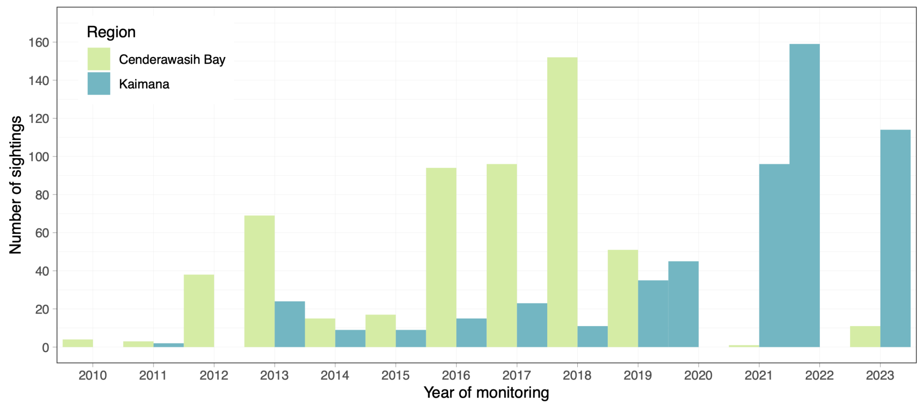

FIGURE 3
Individual whale sharks identified per year in Cenderawasih Bay and Kaimana. Note: sightings in 2023 were only recorded until October 2023.

first sighted in Cenderawasih Bay in October 2015. Subsequently, it was re-sighted nearly six years later in Misool, southern Raja Ampat, in March 2021, and finally re-sighted in Pulau Panjang (Fakfak) in August 2023, making it the sole individual documented in three regions within the BHS.

3.3 Demographic parameters derived from the BHS whale shark photo ID database

Of the 268 individuals we photographically identified in the BHS, 159 (59.3%) were recorded for the first time in Cenderawasih Bay, 95 (35.4%) in Kaimana, 12 (4.5%) in Raja Ampat, and only two in Fakfak. Sex was determined for 235 individuals, revealing that 89.8% (n = 211) were males, with 10.2% (n = 24) females, giving a significantly biased male to female sex ratio of 8.8:1.0 ($\chi^2 = 148.8$, df = 1, $p < 0.001$). Females were distributed across four regions: Kaimana (11 individuals), Cenderawasih Bay (6 individuals), Raja Ampat (5 individuals), and Fakfak (2 individuals). Among individuals for whom sex was determined in Cenderawasih Bay (n = 145) and Kaimana (n = 83), the proportion of males was slightly larger in the former (95.9%) than in the latter (86.7%) ($\chi^2 = 0.46353$, df = 1, $p < 0.496$). Of the 12 individuals first encountered in Raja Ampat, five were identified as females, while the sex of the remaining individuals could not be determined. Including WS#0086, a juvenile male initially sighted in Cenderawasih Bay and later resighted in both Raja Ampat and Fakfak, the total number of individuals recorded was 13 in Raja Ampat and three in Fakfak. Though Raja Ampat and Fakfak both had far fewer overall observations and individuals recorded than Cenderawasih Bay and Kaimana, these two regions

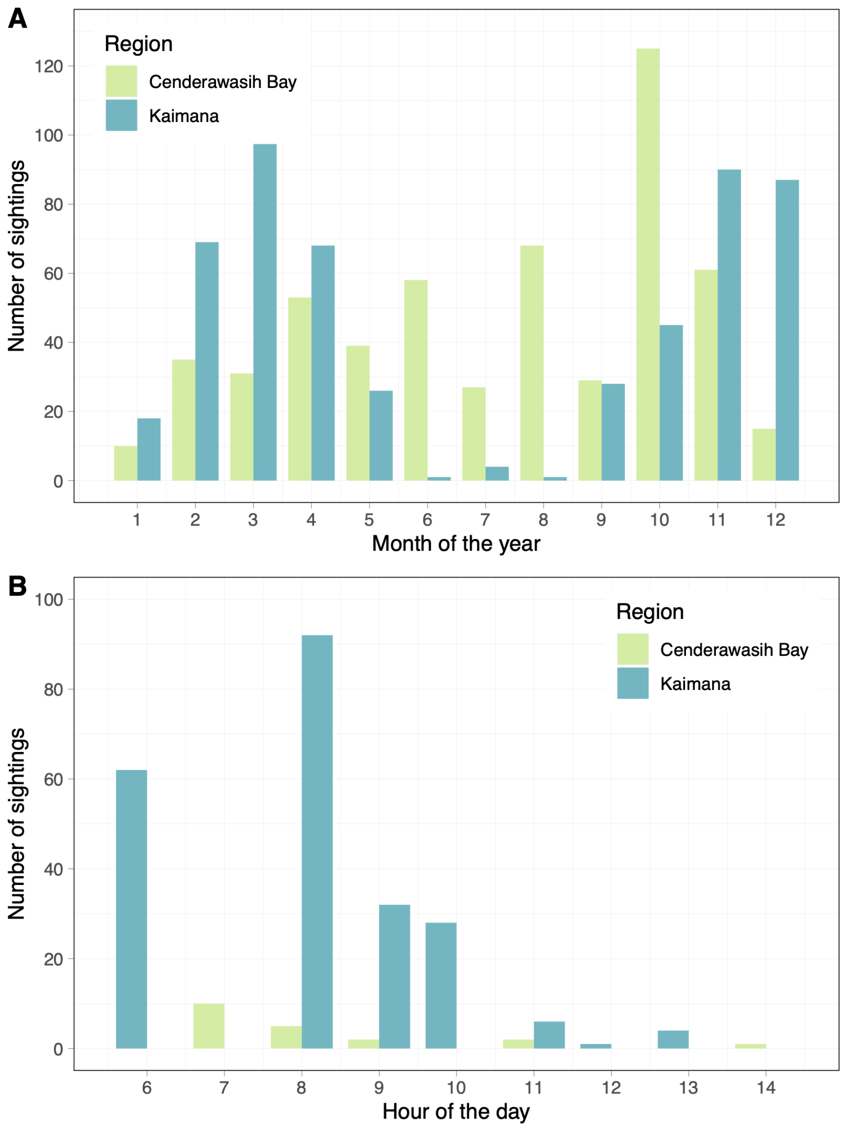

FIGURE 4
(A) Cumulative number of whale shark sightings for each month of the year; **(B)** cumulative number of whale shark sightings for each hour of the day (from 6 am to 2 pm) recorded between September 2010 and August 2023 in Cenderawasih Bay and Kaimana.

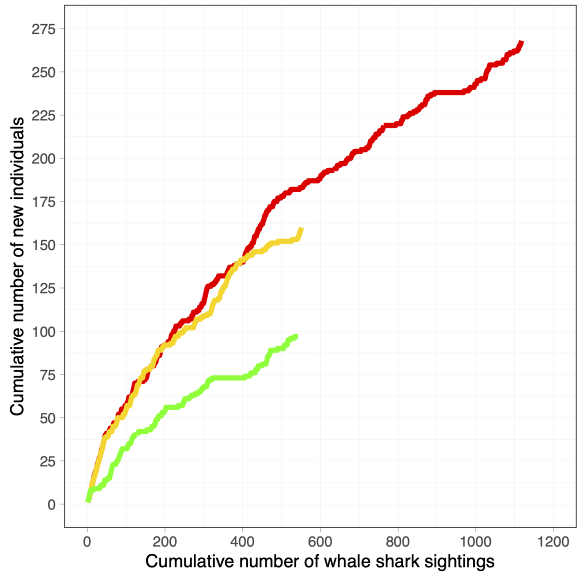

FIGURE 5
Discovery curves of whale sharks between September 2010 and October 2023 in the Bird's Head Seascape (red), Cenderawasih Bay (orange), and Kaimana (green).

showed a much higher percentage of females (83.3% in Raja Ampat and 66.7% in Fakfak), in sightings.

All sharks were sexually immature juveniles, as determined by observation of claspers in males (immature claspers do not extend beyond the pelvic fins and do not show calcification or "cauliflowering") and an assessment of body size in both males and females (all individuals were smaller than 9 m TL). Of the 203 individuals with sizes estimated visually, the TL of whale sharks ranged from 2 to 8 m (mean ± SD = 4.74 ± 1.15 m; Figure 6). Most individuals fell within the 4 and 5 m TL size classes, comprising 63.3% of sightings in Cenderawasih Bay and 65.7% in Kaimana. In Cenderawasih Bay, the mean estimated TL of whale sharks was 5.5 m (SD = 1.87) for males and 4.0 m (SD = 1.00) for females. A Mann-Whitney test revealed that there was no evidence ($p < 0.3192$) of a difference in the mean estimated TL between males and females in this region. In Kaimana, the mean estimated TL of whale sharks was 4.5 m (SD = 1.87) for males and 3.5 m (SD = 1.29) for females. A Mann-Whitney test revealed that there was evidence ($p < 0.0274$) of a difference in the mean estimated TL between males and females in this region. Additionally, the TL of 43 individuals measured with a tape ranged from 3.40 m to 7.51 m (mean ± SD = 5.35 ± 1.05).

3.4 Scarring, injuries, and mortality

A total of 206 individuals (76.9%) were observed with injuries or prominent scarring (Figure 7). Of these, 128 (62.1%) were observed with multiple types of scars. Eighty four percent (n = 173) of scars were classified as minor. Kaimana (83.7%) had a larger proportion of individuals with scars than Cenderawasih Bay (73.7%). Abrasion (47.4%) and nicks (39.9%) were the two most common scarring and injury types observed on the whale sharks, followed by amputation (15.3%) and laceration (14.2%) (Table 2). The scars and injuries of 34 individuals (12.7%) were classified as Others, which were predominantly scars from tagging (finmount satellite and/or spaghetti tags). The majority of the scarring and injuries were recorded on the first dorsal fin (55.6%), followed by flank (25.7%), pectoral fin (22.4%), and caudal fin (19.4%).

In terms of causes, of the 206 individuals recorded with injuries or scarring, 80.6% exhibited scars attributed to anthropogenic sources,

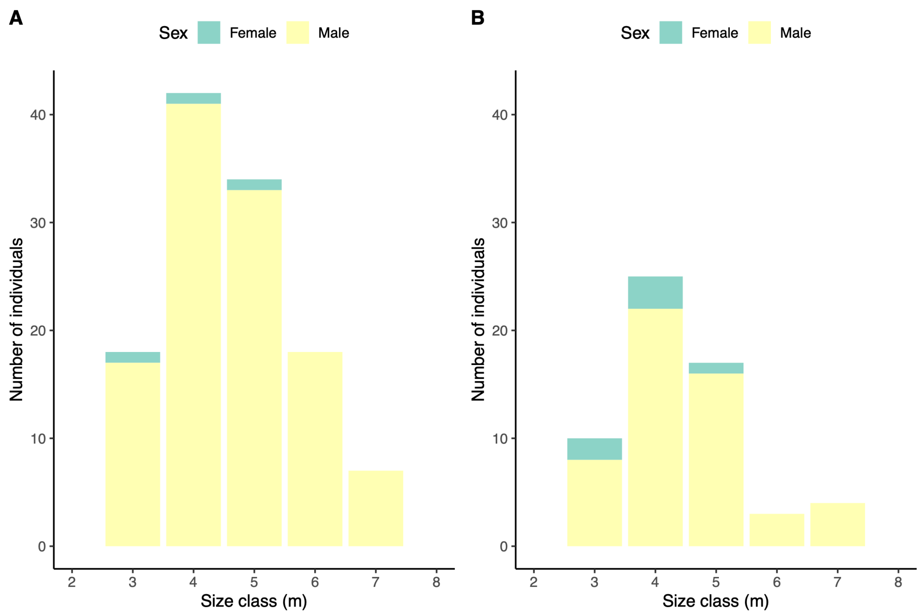

FIGURE 6
Size class distribution (in 1 m TL increments) of 203 whale sharks in **(A)** Cenderawasih Bay and **(B)** Kaimana.

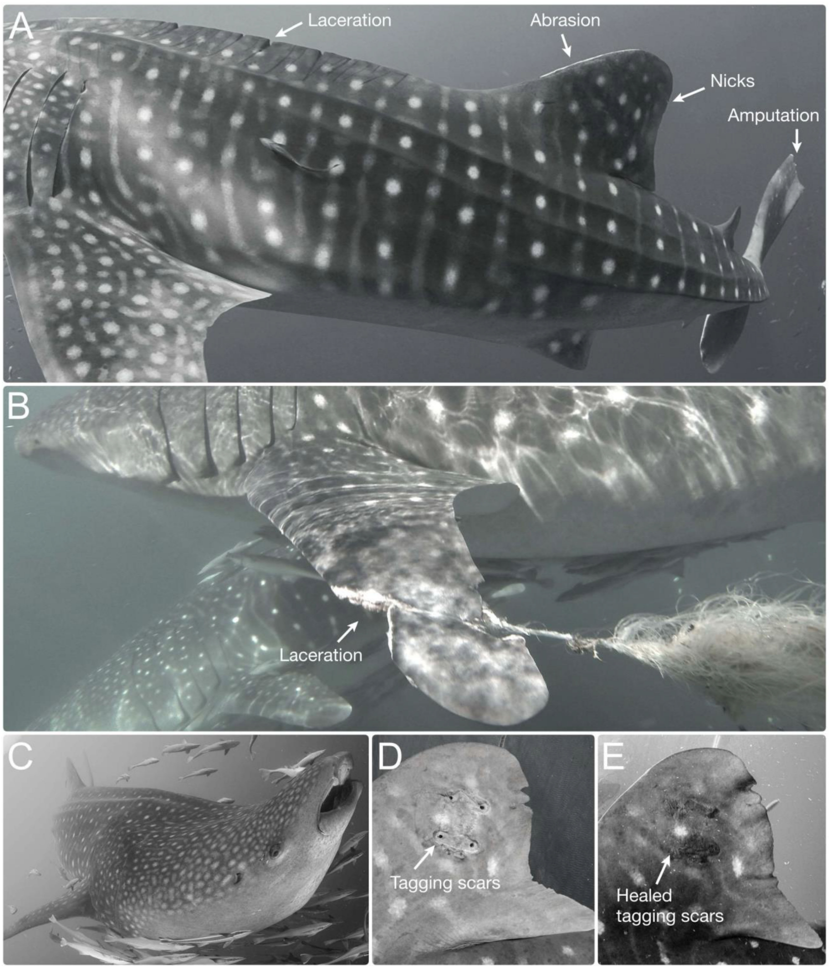

FIGURE 7
A depiction of the types of scarring recorded from whale sharks in the Bird's Head Seascape, Indonesia. These include **(A)** Abrasion (on the leading edge of first dorsal fin), Nicks (on the trailing edge of dorsal fin), Laceration (propeller-originated scars), Amputation (on the upper lobe of caudal fin) (see arrows); **(B)** Laceration (due to net entanglement); **(C)** Deformity (observed from an immature male whale shark, WS#0198, in Kaimana) (©Stevens Genkins); **(D)** Scars from fin-mount satellite tag deployment on WS#0052 (27 July 2017), and **(E)** Healed scars from fin-mounted satellite tag deployment on WS#0052 (1 November 2017).

while 58.3% showed evidence of scarring from natural causes. Additionally, 38.8% of these individuals displayed multiple injuries or scars resulting from both anthropogenic and natural sources. Of 206 individuals, only 2.4% of scarred and injured individuals were assessed to have been inflicted by boat propellers, 3.9% from predator attack, and 64% (n = 132) were caused by other anthropogenic sources (e.g., collisions with bagan fishing platforms and entanglement in fishing gear). A 5-m TL male whale shark (WS#0198) suffered from head deformation, with the anterior end bent upwards (Figure 7E). This shark was seen around a bagan in Kaimana on two different days in March 2020 and was not resighted again.

A single whale shark mortality in the BHS was recorded where an immature (6 m TL; WS#0081) whale shark was found dead on Wanggar Beach, Nabire, Cenderawasih Bay, on 25 September 2019. No signs of injuries were observed, and the whale shark was believed to have stranded itself while feeding too close to the beach. Prior to stranding, locals observed the whale shark chasing and feeding on baitfish nearshore to the beach. Four hours after the initial sighting by the locals, the whale shark was stranded on the beach and then died two hours later (Teluk Cenderawasih National Park, 2019).

3.5 Residency patterns and Lagged Identification Rates

Lagged Identification Rates (LIRs) were analysed using whale shark sighting data exclusively from Cenderawasih Bay and Kaimana, chosen for their reliable number of sightings during the study period. The analyses were conducted separately for these two regions, considering the differences in demographic parameters detailed in preceding sections. Model H, an open population model that incorporated emigration, re-immigration, and mortality, emerged as the most suitable for both Cenderawasih Bay and Kaimana (Table 1).

Briefly, the Lagged Identification Rates (LIRs) revealed a higher re-sighting probability for whale sharks in Kaimana compared to Cenderawasih Bay (Figure 8). In Cenderawasih Bay, the LIR exhibited an exponential decline. There was a slight increase after

TABLE 2 Types and number of individual whale shark injuries recorded between September 2010 and October 2023 in the BHS, eastern Indonesia.

Injury types	N individuals	Proportion (%) of all individuals
Abrasion	127	47.4
Nicks	107	39.9
Amputation	41	15.3
Laceration	38	14.2
Bites	9	3.4
Others	34	12.7

a mean of 381 days, suggesting that several whale sharks periodically return to Cenderawasih Bay after an absence of a year or more, before the LIR eventually declined to zero after approximately 4,300 days (~12 years) (Figure 8; Supplementary Table 1). In Kaimana, the LIR showed a rapid decrease from the first day until 94 days, followed by a significant increase after 376.8 days, indicating a stronger seasonal presence of whale sharks in Kaimana compared to Cenderawasih Bay, before eventually decreasing and reaching zero after a mean of approximately 4,300 days (~12 years).

The estimated number of individuals at one time (a1) in Cenderawasih Bay (25.9 individuals ± 2.96 SE; 95% CI: 21.00 – 29.89) was significantly higher than in Kaimana (10.2 individuals ± 1.93 SE; 95% CI: 8.33 – 15.20) on any given day (Table 3). Regarding residency patterns, whale sharks exhibited longer stays in Cenderawasih Bay (77.1 days ± 34.37 SE; 95% CI: 10.13 – 132.37) compared to Kaimana (37.8 days ± 9.67 SE; 95% CI: 19.93 – 57.75), as shown by mean residency time in study area (a2). Conversely, the residence time outside the study region was shorter in Cenderawasih Bay (41.1 days ± 20.15 SE; 95% CI: 7.86 – 79.31) than in Kaimana (56.5 days ± 24.19 SE; 95% CI: 12.95 – 102.45), as shown by mean time outside study area (a3). The LIR residency proportion (α_{LIR}) of population in Cenderawasih Bay (1.88) was substantially higher than that in Kaimana (0.67). Furthermore, the adjusted residency for Cenderawasih Bay (118.91 days per year) was nearly triple that for Kaimana (42.38 days per year). As for mortality rates (accounting for death and/or permanent emigration), both regions exhibited negligible values: Cenderawasih Bay displayed a mortality rate of 0.000775 ± 0.00012327 SE (95% CI: 0.00057174 – 0.0010136), while Kaimana showed a rate of 0.00074705 ± 0.00023455 SE (95% CI: 0.0004017 – 0.001298).

4 Discussion

4.1 Whale shark aggregations and their association with bagans

Whale shark aggregations in Cenderawasih Bay and Kaimana were strongly associated with the bagan lift net fishery, which target the same baitfish that the whale sharks preferentially feed upon, creating competition in these highly productive habitats (Meyers et al., 2020). Monitoring whale sharks around bagans offers several advantages, including a predictable study location, opportunities to observe interactions between whale sharks and tourists engaged in whale shark tourism, and the ability to monitor cetaceans that interact with whale shark food provisioning (Putra et al., 2025a).

The interaction between whale sharks and bagans can also be found in other regions in central Indonesia, including Saleh Bay (Nusa Tenggara Barat) and Talisayan (Kalimantan Timur) (Himawan et al., 2016), where their aggregations appear to be year-round in the former (Farid et al., 2021), but seasonal in the latter region (Sianipar, 2022). In some other regions in Indonesia, like Probolinggo (Jawa Timur), whale shark aggregations are not associated with bagans and their presence in the area appears to be seasonal between late December to March, taking advantage of high densities of prey during this period (Kamal et al., 2016). Whale shark aggregations not associated with bagans are also found in Botubarani, Gorontalo, where whale sharks are associated with the presence of baitfish and provisional feeding of shrimp carapaces (from a nearby shrimp processing plant) by small boats in whale shark tourism activities (Handoko et al., 2018; Yasir et al., 2024b). In other countries such as Mexico, whale sharks in Bahía de La Paz, southern Gulf of California, aggregate seasonally, with spatial segregation observed between adults (larger than 9 m in TL) and juveniles (less than 6 m in TL) (Ketchum et al., 2013). Seasonal aggregations of whale sharks are also found in Donsol (Philippines) (McCoy et al., 2018) and Ningaloo Reef (Australia) (Wilson et al., 2001). In the Maldives, whale shark aggregations occur year round in South Ari Atoll (Harvey-Carroll et al., 2021).

In comparison to other well-studied whale shark aggregations around the world, Cenderawasih Bay and Kaimana are perhaps best classified as medium-sized aggregations (see Table 4 for a comparison). Though numbers of whale sharks recorded in our study of the BHS were larger than studies from, e.g., Honduras, the Gulf of Thailand and Tanzania, the maximum aggregation sizes recorded in Cenderawasih and Kaimana were much smaller than those observed off Holbox Island in the Yucatan Peninsula of Mexico, where in 2009, approximately 420 individual whale sharks were observed within an 18 km^2 area, feeding on dense patches of little tunny *Euthynnus alletteratus* eggs (de la Parra Venegas et al., 2011).

4.2 Re-sighting rates, residency, and site fidelity

The resighting rates of photo-identified individual whale sharks in Cenderawasih Bay (52.8%) and Kaimana (57.9%) were relatively similar to those in Donsol and Southern Leyte in The Philippines (53% and 56.5%, respectively; Table 4) (Araujo et al., 2016; McCoy et al., 2018), but were smaller than those in Saleh Bay (77%; Nusa Tenggara Barat – Indonesia) (Putra et al., 2025b), Praia do Tofo (Mozambique; 72%), and Mafia Island (Tanzania; 96%) (Rohner et al., 2015). Other regions report significantly lower resighting rates of photo-identified individuals, with less than 30% of individuals re-

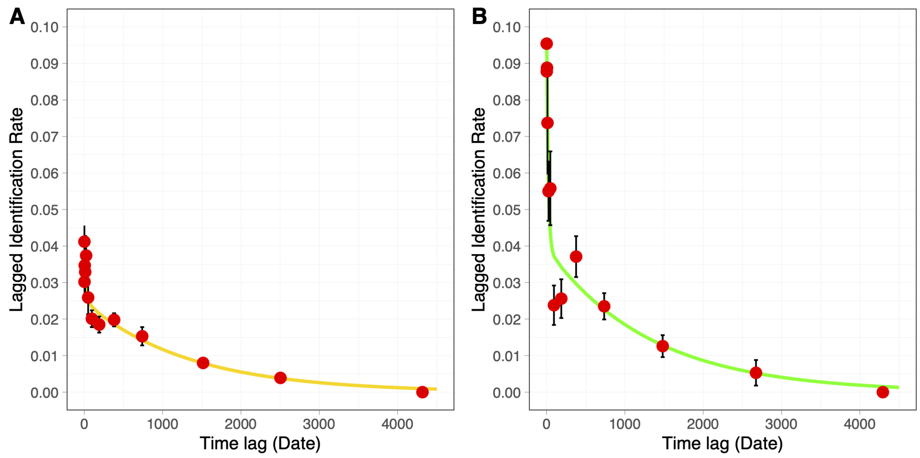

FIGURE 8
Lagged Identification Rates (LIR) for whale sharks for **(A)** Cenderawasih Bay and **(B)** Kaimana. The observed LIR values (± SE, in red) represent the likelihood of resighting the same individual after a given time interval. The fitted lines, yellow for Cenderawasih Bay and green for Kaimana, are based on the most parsimonious maximum likelihood model incorporating emigration, re-immigration, and mortality. Together, these results provide insights into the residency patterns and site fidelity of whale sharks within the two aggregation areas.

encountered. These regions include Nosy Be (Madagascar; 28.0%), Gulf of Thailand (23.0%), Utila (Honduras; 22.0%), Seychelles (17.8%), Galapagos Island (Ecuador; 14.6%), and Holbox Island (Mexico; 13.1%) (Rowat et al., 2009; Ramírez-Macías et al., 2012a; Fox et al., 2013; Acuña-Marrero et al., 2015; Diamant et al., 2021; Magson et al., 2022) (Table 4).

The maximum likelihood analyses exhibited different residency patterns between populations in Cenderawasih Bay and Kaimana located on the opposite sides of the BHS. Whale sharks in Cenderawasih Bay were estimated to have longer residencies compared to those in Kaimana. It is likely that the large, shallow, and enclosed Cenderawasih Bay provides a sufficient year-round source of food for the juvenile whale sharks within the bay. The bay is surrounded by mangrove forest and large river outlets that continuously provide nutrients that enrich water productivity (Sianipar, 2022), resulting in abundant plankton and baitfish aggregations that likely satisfy the energy demands for juvenile whale sharks to grow (Norman et al., 2017). Furthermore, although photo ID surveys were restricted to areas within the National Park in the southwestern part of Cenderawasih Bay, satellite tagged individuals were also recorded moving into the eastern areas of the bay (Meyers et al., 2020).

TABLE 3 Model H outputs and residency parameters for whale sharks in Cenderawasih Bay and Kaimana based on Lagged Identification Rate analyses, which include the estimated number of individual whale sharks at one time (a1), the mean time in the study area (a2) in days, the mean time outside the study area (a3) in days, LIR residency proportion (α_{LIR}) of population, adjusted residency in days per year, and mortality.

Residency parameters	Cenderawasih Bay	Kaimana
a1	25.9 ± 2.96 (21.00 – 29.89)	10.2 ± 1.93 (8.33 – 15.20)
a2	77.1 ± 34.37 (10.13 – 132.37)	37.8 ± 9.67 (19.93 – 57.75)
a3	41.1 ± 20.15 (7.86 – 79.31)	56.5 ± 24.19 (12.95 – 102.45)
α_{LIR}	1.88	0.76
Adjusted Residency	118.91	42.38
a4	0.000775 ± 0.00012327 (0.00057174 – 0.0010136)	0.00074705 ± 0.00023455 (0.0004017 – 0.001298)

All parameters are reported in the following format: estimates ± SE (95% CI), except for α_{LIR} and adjusted residency of which only the estimates were reported.

Similar to Cenderawasih Bay, the aggregation sites in Kaimana are located inshore, but the region is geographically smaller and is situated along the edge of a deep basin in the eastern Banda Arc. Kaimana, along with southern Papua, is exposed to the southeast monsoon that occurs between June and September. This southeast monsoon, characterized by persistent strong winds, drives more frequent and intense upwelling events, particularly off the continental shelf edge, leading to increased primary productivity in the region (Gordon, 2005). It is likely that during this period, the whale sharks move from the Kaimana area to forage in high productivity areas in the Seram Sea – a phenomenon also recorded for oceanic manta rays during the southeast monsoon (Beale et al., 2019) – before returning to Kaimana waters. This hypothesis is supported by the low number of whale shark sightings recorded in Kaimana between June and August (Figure 3), although reduced survey effort due to rough sea conditions during this season may also have contributed to the lower detection rates at this time.

In comparison with populations in other regions, the residency time (a2 in Model H) of whale sharks in the BHS, especially Cenderawasih Bay (77.1 days) was higher than that in other regions, such as Al Lith (the Red Sea; 16.8 days), Al Shaheen (Qatar; 22.1 days), Bahia de La Paz (65.9 days), and Bahia de Los Angeles (Mexico; 19.9 days) (Araujo et al., 2022). The residency time of whale sharks in Kaimana (37.8 days) was similar to that in Donsol (Philippines; 33.3 days), Gulf of Tadjoura (Djibouti; 34.1 days), and South Ari Atoll (Maldives; 38.9 days) (Araujo et al., 2022).

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TABLE 4 Summary of whale shark populations across different regions, including location/country, the number of individuals (N individuals), survey period, percentage of male individuals in the population (% male) based only from sexed individuals, and re-sighting rate (%).

No.	Location/country	N individuals	Survey period	% male	Re-sighting rate (%)	References
1	Praia do Tofo - Southern Mozambique	664	2005–2015	71.7	-	Prebble et al. (2018)
2	Donsol – The Philippines	479	2007–2016	87.8	53.0	McCoy et al. (2018)
3	Al Shaheen - Qatar	437	2007–2015	68.9	-	Prebble et al. (2018)
4	Nosy Be - Madagascar	408	2015–2019	81.9	28.0	Diamant et al. (2021)
5	Seychelles	360	2001–2007	-	17.8	Rowat et al. (2009)
6	Holbox Island - Mexico	350	2005–2008	70.9	13.1	Ramírez-Macías et al. (2012a)
7	Al Shaheen - Qatar	341	2011–2014	68.7	41.0	Robinson et al. (2016)
8	St Helena Island - British Overseas Territory	277	2013–2019	54.2	35.0	Perry et al. (2020)
9	Ningaloo Reef - Australia	184	1992–2004	82.5	32.6	Meekan et al. (2006)
10	Gulf of Thailand - Thailand	178	2004–2019	31.3	23.0	Magson et al. (2022)
11	Cenderawasih Bay - Indonesia	145	2010–2023	95.9	52.8	Current study
12	Red Sea - Saudi Arabia	136	2010–2015	47.2	39.7	Cochran et al. (2016)
13	Bahia de Los Angeles - Mexico	129	2003–2009	68.5	49.6	Ramírez-Macías et al. (2012b)
14	Mafia Island - Tanzania	129	2006–2015	86.5	–	Prebble et al. (2018)
15	Bahia de La Paz - Mexico	125	2003–2009	69.0	48.8	Ramírez-Macías et al. (2012b)
16	Praia do Tofo - Southern Mozambique	123	2010–2013	75.7	72.0	Rohner et al. (2015)
17	South Ari Atoll - The Maldives	100	2014–2019	95.7	-	Harvey-Carroll et al. (2021)
18	Utila - Honduras	95	2001–2011	65.1	22.0	Fox et al. (2013)
19	Southern Leyte – The Philippines	93	2013–2014	80.6	56.5	Araujo et al. (2016)
20	Kaimana - Indonesia	83	2013–2023	86.7	57.9	Current study
21	Galapagos Island - Ecuador	82	2011–2013	1.2	14.6	Acuña-Marrero et al. (2015)
22	Mafia Island - Tanzania	56	2012–2013	87.5	96.0	Rohner et al. (2015)

Data rows are arranged from largest to smallest number of individuals (N) recorded.

The LIR residency proportion (α_{LIR}) in Cenderawasih Bay (1.88) was much higher than that of Kaimana (0.67). Among five regions with α_{LIR} values greater than 1 – Belize (1.10), Gulf of Tadjoura (1.01), Mafia Island (1.25), Oslob (1.97), and South Ari Atoll (1.62), as reported by Araujo et al. (2022), only Oslob exhibited a higher residency proportion than Cenderawasih Bay. Similarly, of the 25 regions analyzed by Araujo et al. (2022), only the whale shark population in Oslob (124.6 days/year) showed a slightly higher adjusted residency time than that in Cenderawasih Bay (118.9 days/year).

Feeding of whale sharks by tourism operators in other areas such as Oslob in the Philippines has been shown to alter the behavior of some individuals, making them more tolerant of human interactions and less likely to exhibit avoidance behaviors (Schleimer et al., 2015). This conditioning encourages prolonged site fidelity and elevates the probability of resighting, resulting in a "trap–happy" response that can bias mark–recapture or photo–ID data (Reinhardt and Hrodey, 2019). As a result, the apparent high residency and strong site fidelity inferred from our data might be overestimated, because tourism provisioning of food could encourage repeated visits and extended residency at specific locations. Importantly, however, food provisioning in Cenderawasih Bay and Kaimana is seemingly much lower than that reported for Oslob, where provisioning happens year-round (Schleimer et al., 2015). In Cenderawasih Bay and Kaimana, our observations suggest that food provisioning by tourism operators happens no more than 60–100 days per year.

4.3 Population demographics

The number of photo-identified individuals in three regions of the BHS – Cenderawasih Bay (n = 159 individuals), Kaimana (n = 95 individuals), and Raja Ampat (n = 12 individuals) – is comparable to other Indonesian regions including Saleh Bay (n = 105 individuals) (Putra et al., 2025b) and Talisayan – Kalimantan Timur (n = 80) (Araujo et al., 2022), where the sightings of whale sharks are also primarily associated with bagans. In contrast to

Botubarani – Gorontalo, where 38 individual whale sharks have been identified (Yasir et al., 2024b) and sightings are not associated with bagans, the number of identified individuals in bagan-associated sites is notably higher. This suggests that the presence of bagans and associated food provisioning may influence whale sharks to aggregate around these platforms, while also providing relatively easier access for monitoring efforts.

Compared to other countries, the number of individual whale sharks recorded in the BHS was smaller than those in Praia do Tofo, Southern Mozambique (n = 664), Donsol, Philippines (n = 479), Nosy Be, Madagascar (n = 408), Seychelles (n = 360), Holbox Island, Mexico (n = 350), and St Helena Island, British Overseas Territory (n = 277) (Table 4). However, the number of individuals recorded in the BHS was higher than that for Ningaloo Reef, Australia (Meekan et al., 2006), Gulf of Thailand, Thailand (Magson et al., 2022), Red Sea, Saudi Arabia (Cochran et al., 2016), Bahia de Los Angeles and Bahia de La Paz, Mexico (Ramírez-Macías et al., 2012b), Mafia Island, Tanzania (Prebble et al., 2018), South Ari Atoll, Maldives (Harvey-Carroll et al., 2021), Utila, Honduras (Fox et al., 2013), and Galapagos Islands, Ecuador (Acuña-Marrero et al., 2015).

All whale sharks identified in the BHS were immature, ranging from 3–8 m TL, and were predominantly males, which is similar to the results of studies from coastal whale shark aggregation sites across the world (Dove and Pierce, 2021). This is different from the whale shark population recorded in Shib Habil (the Red Sea) (Cochran et al., 2016) where the number of males and females was nearly equal, and those in St. Helena (Atlantic Ocean) (Perry et al., 2020) and the Galapagos Islands, Ecuador (Acuña-Marrero et al., 2015) where the populations were dominated by adult females. The proportions of males in Cenderawasih Bay and Kaimana are among the highest recorded when compared to 20 other regions (Table 4). Globally, the highest proportion of males was found in South Ari Atoll (95.7%; 100 individuals) (Harvey-Carroll et al., 2021) and the lowest was found in the Galapagos Islands (1.2%, 82 individuals) (Acuña-Marrero et al., 2015). In areas where whale sharks aggregate inshore, it appears that the populations are dominated by immature males like those in The Philippines (Araujo et al., 2014). Conversely, aggregation sites located offshore or near oceanic islands appear to be dominated by adult females like those in the Gulf of California (Ketchum et al., 2013) and Galapagos. Importantly, in the BHS, the two regions where whale sharks were predominantly single individuals not aggregated to feed at bagans (Raja Ampat and Fakfak) displayed sex ratios much closer to parity (41.6% females in Raja Ampat and 60% females in Fakfak). This observation, though based on far fewer numbers of individuals, would seem to suggest that immature females may actively avoid "brat pack" inshore aggregations of young males.

The marked differences in male-to-female sex rations among whale shark aggregation sites are likely driven by life-history and behavioral traits. In shallow, productive coastal areas (e.g., Cenderawasih Bay and Kaimana), aggregations are dominated by immature males, suggesting these habitats may serve as nursery or foraging grounds where younger males can optimize feeding strategies and minimize predation risk while growing. It is not clear why young females do not also utilize these coastal foraging grounds in significant numbers, though perhaps they are less gregarious and may be avoiding the aggregated males for as-yet-undetermined behavioral reasons. In contrast, offshore or oceanic habitats (e.g., Galapagos, St. Helena, Yucatán Peninsula) tend to be dominated by adult females, potentially related to reproductive activity or access to deep-water prey (Dove and Pierce, 2021). Such sex- and size-structuring is not unique to whale sharks and is observed in many other migratory elasmobranchs, including hammerhead and reef sharks, where adult females segregate from males spatially and temporally (Dove and Pierce, 2021). This partitioning is thought to reduce intraspecific competition and optimize survival and reproductive success across life stages.

Based on model H, the estimated number of individuals present on any given day in both Cenderawasih Bay and Kaimana (25.9 and 10.2, respectively) was relatively low compared to other regions. By contrast, the Yucatan Peninsula in Mexico (Ramírez-Macías et al., 2012b), Al Shaheen in Qatar (Robinson et al., 2016), and St. Helena in the Atlantic Ocean (Perry et al., 2020) reported the highest daily estimates, each exceeding 100 individuals.

4.4 Scarring, injuries, and mortality

Most of the scars and injuries observed on whale sharks in the BHS were minor, such as small abrasions or nicks, and were unlikely to pose a serious threat to the health of these individuals. Most abrasions were likely caused by contact with bagans, particularly along the leading edge of the dorsal fin due to rubbing against the structure. More severe injuries, including fin amputations, were likely the result of fishing gear entanglement, predator attacks, or other unknown human-related causes. Compared to other regions, the proportion of injured individuals in the BHS (76.9%) was lower than in Cebu, Philippines (98.4%) (Penketh et al., 2021), similar to Botubarani, Central Indonesia (74.0%) (Yasir et al., 2024a), but higher than in Seychelles (67.0%) (Speed et al., 2008), Shib Habil – The Red Sea (57.0%) (Cochran et al., 2016), and Ningaloo Reef (38.8%) (Lester et al., 2020).

Food provisioning associated with whale shark tourism likely increases interactions between whale sharks and human activities – particularly with bagans and boats, a scenario unique to Indonesia. This has led to a higher proportion of individuals showing minor injuries, especially abrasions. In contrast, injuries caused by boat strikes – especially propeller scars – are less common here than in other countries. The rate of boat strike injuries in the BHS (2.4%) is similar to that in Ningaloo Reef (3.6%) (Lester et al., 2020), and much lower than reported rates in Cebu (47%) (Araujo et al., 2014), Donsol (19%) (McCoy et al., 2018), Shib Habil (15%) (Cochran et al., 2016), and Holbox Island (up to 33%) (Ramírez-Macías et al., 2012a). Similarly, the proportion of injuries attributed to predator attacks in the BHS (3.9%) is considerably lower than those reported in the Seychelles (27%) (Speed et al., 2008), Botubarani (12%) (Yasir et al., 2024a), but close to Ningaloo Reef (4.8%) (Lester et al., 2020). The relatively low proportion of injuries from predators in the BHS might be due to the loss of apex predators in eastern Indonesian waters due to overharvesting of sharks, as Indonesia is well-known to have the largest shark fishing industry in the world (Prasetyo et al., 2021).

4.5 Conservation and management implication

Our findings on whale shark residency and population structure in the BHS, particularly in Cenderawasih Bay and Kaimana, highlight the potential for developing and better managing whale shark tourism in these regions. Given that the majority of the whale shark sightings occurred at bagans, and that whale shark tourism associated with these platforms is likely to continue growing, the risk of injuries from bagans and boats is expected to increase. To mitigate this risk, it is critical to improve the structural design of bagans, especially along edges that have a higher potential for friction-related injuries. Additionally, all boating activities near bagans should strictly adhere to the established codes of conduct for whale shark watching tourism in Cenderawasih Bay (Balai Taman Nasional Teluk Cenderawasih, 2020) and Kaimana.

In addition to managing tourism impacts associated with bagans and boating activities, addressing the growing concern of whale shark strandings is essential for the long-term conservation of the species in the region. Whale shark stranding events appear to be a common and recurring phenomenon in Indonesia (Putra et al., in review). Further research is needed to understand the drivers behind these strandings. Equally important is the implementation of mitigation measures and the widespread dissemination and application of the national code of conduct (CoC) established in mid 2024 for responding to stranded whale sharks (Ministry of Marine Affairs and Fisheries, 2024).

4.6 Future directions

Our study offers a comprehensive overview of whale shark demographics and residency patterns in the Bird's Head Seascape (BHS), eastern Indonesia. However, it also highlights critical knowledge gaps, particularly with respect to population size and spatial movement ecology. To address this gap in our understanding of BHS whale shark population size, expanding photo-identification (photo ID) efforts is essential. Although our data suggest possible seasonal patterns in whale shark presence, conducting frequent and large-scale monitoring to confirm this is resource-intensive and unlikely to be achievable in the near future. To maximize efficiency, we recommend focusing standardized monitoring efforts in the two main aggregation sites: Cenderawasih Bay and Kaimana. Collaborating with tourism operators to promote citizen science initiatives could greatly enhance data collection. Although current contributions from citizen scientists are quite limited compared to the data compiled from intensive field surveys by trained scientists in the BHS, it has the potential to document transboundary movements of whale sharks such as between Taiwan and The Philippines (Araujo et al., 2016). Increasing citizen engagement could improve photo ID data in under-surveyed regions like Raja Ampat and Fakfak and encourage reporting of past sightings across the BHS. The use of citizen science data has emerged as an increasingly valuable approach in shark research (e.g., Marcoux et al., 2023), providing critical information on a wide range of elasmobranch species, particularly in understudied and data–deficient regions (e.g., Ozaki et al., 2024).

A key step forward would be consolidating existing photo ID datasets, currently held by various research groups and agencies, including Cenderawasih Bay National Park and UNIPA (State University of Papua). Creating a unified database would lay the groundwork for more advanced analyses, such as open population models (e.g., POPAN), which allow for robust estimates of population size, survival, and demographic shifts over time. These models can also help assess the influence of environmental drivers like El Niño on whale shark populations (e.g., Beale et al., 2019; Harvey-Carroll et al., 2021; Setyawan et al., 2022c).

Genetic studies would further strengthen our understanding of population dynamics in the BHS. Trends in genetic diversity can indicate population stability or decline, as shown in whale shark populations in Australia and the Red Sea (Vignaud et al., 2014; Hardenstine et al., 2022). Combining genetic analyses with mark-recapture data, an approach successfully used for white sharks (*Carcharodon carcharias*) (Andreotti et al., 2016) and reef manta rays (*Mobula alfredi*) (Whitney et al., 2023), could also help estimate effective population size and inform long-term conservation strategies.

Exploring the feeding ecology of juvenile whale sharks, particularly their association with bagans, is another important research avenue. Little is known about the full diet of juvenile whale sharks, particularly whether it includes large zooplankton or other prey from coastal or benthic habitats (Whitehead and Gayford, 2023). Stable isotope analysis, as used by Borrell et al. (2011) and Whitehead et al. (2020), could provide valuable insights into their trophic ecology and ecological role in the BHS.

Understanding spatial movements and habitat use is also crucial. It remains challenging to describe spatial movement patterns from the repeated sightings based solely on photo-ID data, and it remains unclear if the individuals that were observed multiple times were observed during their broader migratory movements or if they returned because of attractions to individual sites in the regions. From 2014 to 2023, a total of 58 satellite tags – including SPLASH10, miniPAT, and multi-sensor tags – have been deployed on whale sharks in Cenderawasih Bay, Kaimana, and Raja Ampat. While some data have been published (e.g. Meyers et al., 2020; Sianipar, 2022), many analyses are ongoing. Future studies should build on this effort to examine seasonal movement patterns, environmental drivers of habitat use, and regional differences in residency. Pairing satellite telemetry with passive acoustic telemetry could offer finer-scale insights into site fidelity, especially around bagans, and provide science-based recommendations for tourism management.

Finally, to ensure that whale shark tourism is sustainable and beneficial for conservation, studies evaluating the impacts of tourism activities and supplemental feeding are needed. Economic valuations of whale shark tourism, particularly in Kaimana and Cenderawasih Bay, would also help assess the effectiveness of current conservation measures and support evidence-based policy and management decisions. The use of biologgers equipped with accelerometers would also be useful to understand the fine-scale movement ecology and potential influence of interactions with tourists at bagans on their energetic costs (e.g., Barry et al., 2023).

5 Conclusions

Whale sharks inhabit the rich marine ecosystems of the BHS in eastern Indonesia, where they form unique associations with bagans, creating a rare interaction between these gentle giants and local fishers. Juvenile and immature male whale sharks, ranging from 2 to 8 meters in length, are commonly found in key aggregation sites, particularly in Cenderawasih Bay and Kaimana. These relatively small populations show strong residency, with whale sharks present year-round in Cenderawasih Bay and seasonally in Kaimana. Over 13 years of monitoring, most sightings have come from these two regions. However, there is limited movement of identified individuals across the four monitored areas, suggesting habitat segregation – especially between Cenderawasih Bay and Kaimana. High re-sighting rates and long sighting spans indicate strong site fidelity and repeated use of key foraging habitats. Overall, our findings highlight the importance of the BHS as a critical habitat where juvenile whale sharks can feed, grow, and reduce mortality risk before migrating to other areas. Protecting these habitats and managing the human interactions (e.g., the unique bagan and whale shark interactions) can help ensure that more individuals survive to reach reproductive maturity and contribute to the recovery of declining populations across the Indo-Pacific.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by the Cenderawasih Bay National Park Authority (BBTNTC): SIMAKSI SI.18/BBTNTC-2/TEK/2015, SIMAKSI SI.46/BBTNTC-2/TEK/2015, SIMAKSI SI.05/BBTNTC-2/TEK/2016 issued to Abraham Sianipar. All field surveys were undertaken according to the ethical procedures for care and use of animals of the Ministry of Environment and Forestry as approved in those permit applications. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

ES: Conceptualization, Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. AH: Investigation, Writing – review & editing, Data curation, Validation. YM: Investigation, Writing – review & editing, Data curation, Validation. AS: Investigation, Project administration, Writing – review & editing. RM: Investigation, Writing – review & editing. MM: Writing – review & editing. BG: Writing – review & editing. BD: Writing – review & editing. MP: Investigation, Writing – review & editing, Project administration, Supervision. ME: Investigation, Writing – review & editing, Conceptualization, Funding acquisition, Project administration, Supervision.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The author(s) declare that Generative AI was used in the creation of this manuscript. ChatGPT GPT-4o was used to refine and edit the original draft of the manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1607027/full#supplementary-material

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