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First assessment of life history and spatial ecology of the endemic Raja Ampat epaulette shark (*Hemiscyllium freycineti*) in the Dampier Strait, Indonesia

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The Raja Ampat epaulette shark (*Hemiscyllium freycineti*) is an endemic species inhabiting shallow coastal habitats of the Raja Ampat Archipelago, Indonesia. Despite recent legal protection, information on its biology, population structure, and spatial ecology remains limited, constraining effective conservation. To address these gaps, a total of 64 nocturnal surveys (averaging 1.8–2.3 hours each) were conducted between February 2024 and April 2025 at six sites in the Dampier Strait region. Using photo-identification and passive integrated transponder tagging, 736 unique individuals were identified from 1,191 sightings, with most records from Arborek Island (n = 602). Of these, the population comprised 415 females and 321 males, resulting in a significantly female-biased sex ratio. Total length (TL) ranged from 19.4 to 75.0 cm (mean = 51.1 cm), and body mass ranged from 24 to 1,025 g (mean = 412.8 g). The length–weight relationships indicated negative allometric growth in both females (b = 2.91) and males (b = 2.81). Estimated length-at-maturity was 56.59 cm TL for females and 56.42 cm TL for males, with no significant difference between sexes. Relative density ranged from 333 to 2,462 individuals per km^2, representing the highest population density recorded globally for *Hemiscyllium*. A total of 256 individuals were resighted at least once, with resighting intervals extending up to 451 days. Immature individuals exhibited significantly higher growth rates than mature ones (7.8 vs 2.8 cm year^{-1}), while no sex-specific difference in growth was detected. The best-supported and biologically meaningful growth model, seasonally oscillating ELEFAN with simulated annealing, estimated an asymptotic length (L_∞) of 79.6 cm for all individuals, with a growth coefficient (K) of 0.747 year^{-1}. Growth showed pronounced seasonal oscillations (C = 0.915). Sharks were most frequently observed in seagrass meadows. Habitat use analyses revealed ontogenetic partitioning. Coral reefs appear to function as a nursery habitat with 69% immature sharks, while seagrass and sand habitats supported higher proportions of adults. Individuals were highly resident, showed no inter-site movement, and occupied small spatial ranges, with maximum net displacements of 475 m. Collectively, these findings provide the first demographic and spatial baseline for *H. freycineti* in Raja Ampat.

KEYWORDS

conservation, length-length relationships, length-weight relationships, natural history and growth rate, Papua, population dynamics, reproductive biology

1 Introduction

A comprehensive understanding of the life history and ecology of threatened species is critical for developing and implementing effective conservation strategies, as it provides detailed insights into reproductive behavior, population dynamics, and habitat requirements (1, 2). Such ecological knowledge allows researchers to identify critical factors driving species declines, enabling targeted, evidence-based conservation actions to mitigate specific threats (3, 4).

Hemiscyllium freycineti (Quoy & Gaimard, 1824), commonly known as the Raja Ampat epaulette shark (5; also referred to as the Indonesia speckled carpetshark in FishBase) is considered one of the most recently evolved shark species, having only diverged from its sibling species (*H. galei*) less than 2 million years ago (6). It is a small benthic shark that is endemic to the shallow coastal waters of the Raja Ampat archipelago and surrounding regions in Southwest Papua, Indonesia (6, 7). This species typically inhabits coral reefs, seagrass, and mangrove ecosystems up to 10 meters depth (5). It exhibits nocturnal and bottom-dwelling behavior, foraging at night across reef flats, seagrass meadows, and mangrove roots, preying primarily on benthic invertebrates such as snails, crabs, and worms (7). The species demonstrates a unique form of locomotion ("walking"), propelling itself across the substrate using its pectoral and pelvic fins in order to forage on benthic preys, though it is also able to swim (8). Nonetheless, it is believed to avoid deep water crossings, with depths of even 50–100 m between reefs likely to serve as a barrier to dispersal (8).

In 2021, *H. freycineti* was listed as Near Threatened (NT) on the IUCN Red List of Threatened Species, mainly due to its highly restricted size range and the various threats faced by the species (5). The number of individuals and overall population trend of this species are currently unknown. The population, however, is suspected to be declining due to various anthropogenic threats, particularly coastal development leading to habitat degradation and loss, limited but targeted fisheries for local consumption and potentially the ornamental fish trade, as well as climate change. In response to these concerns, the Indonesian government in early 2023 granted full legal protection to *H. freycineti* (along with the five other epaulette shark species occurring in Indonesian waters) through Ministerial Decree No. 23/2023 (9).

Despite this legal protection, fundamental gaps remain in our knowledge on the biology, ecology, and spatial distribution of *H. freycineti*, hampering the development of effective conservation management strategies. This is of particular concern, given that *H. freycineti* is a site-attached species with a highly restricted geographic range (7). With low population resilience and minimum population doubling time of 4.5–14 years (10), small populations can be especially vulnerable to localized disturbances (11). Without reliable baseline data, it is challenging to assess the population status, monitor population trends over time, or evaluate the effectiveness of current protective measures. This study aims to establish baseline population monitoring data for the *H. freycineti* population in the Dampier Strait region of Raja Ampat to inform long-term conservation planning, with several specific objectives: (1) quantify the demographic structure (size and sex distribution); (2) assess habitat preferences; and (3) examine and describe morphometric relationships and reproductive biology.

2 Methods

2.1 Study area

The Raja Ampat archipelago in eastern Indonesia represents the global epicentre of tropical marine biodiversity, with nearly 1,700 species of coral reef fishes documented to date (12). The region, protected by an extensive 2 million ha network of nine Marine Protected Areas (MPAs) (13), was highlighted with the designation of four Important Shark and Ray Areas (Dampier Strait, Southeast Misool, Northwest Waigeo, and the Northern Raja Ampat Corridor) by the IUCN in 2024, recognizing its importance for harbouring a range of critical habitats for multiple threatened elasmobranch species (14).

Our study was conducted exclusively within the Dampier Strait region in central Raja Ampat (Figure 1). For simplicity, we refer to the entire study area as the Dampier Strait region, although we note that the Saupapir site in the Fam Islands (western Dampier Strait)

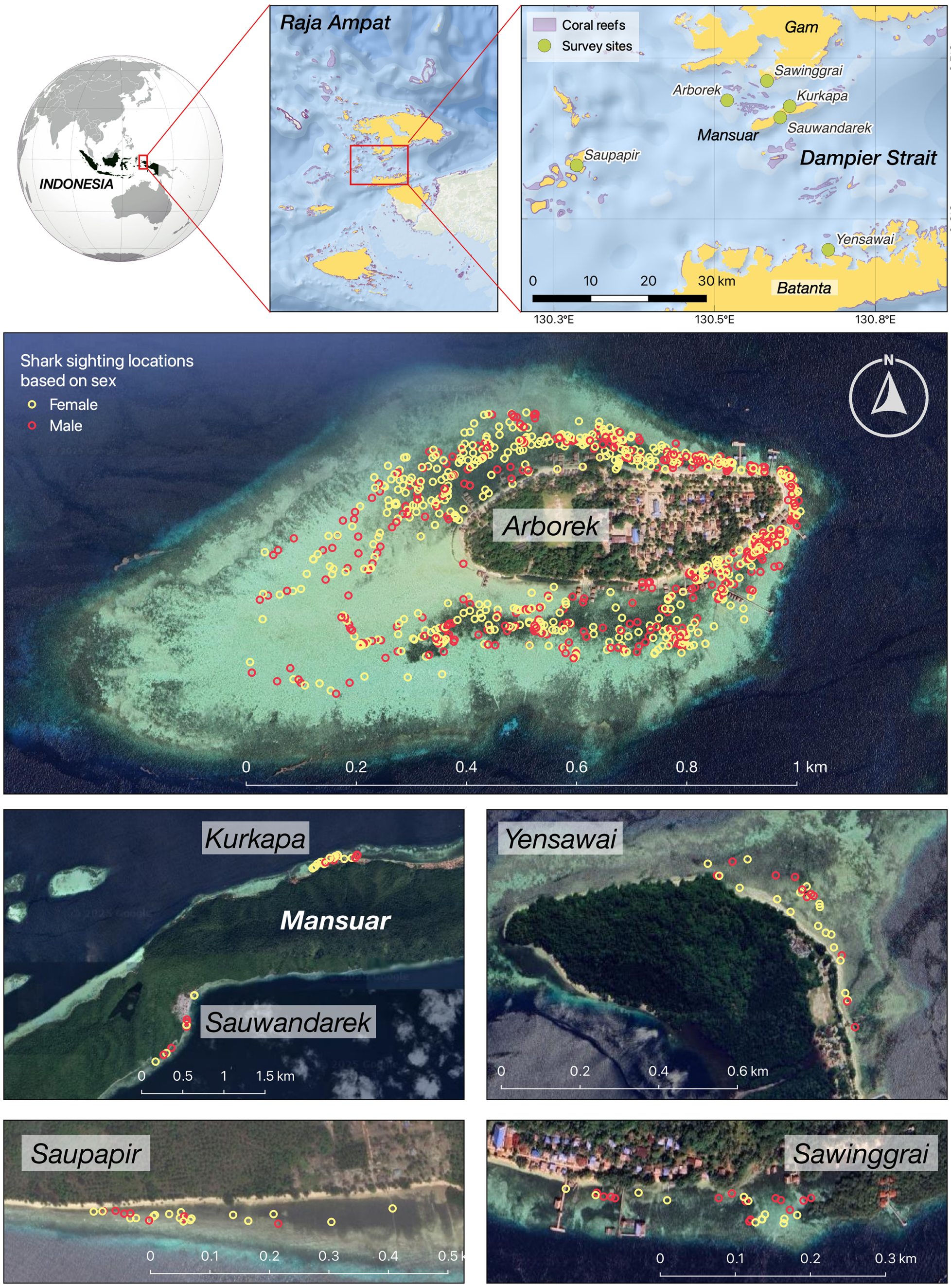

FIGURE 1
Survey sites and distribution of sightings locations of *H. freycineti* around Dampier Strait in central Raja Ampat between 4 February 2024 and 30 April 2025. Each ring represents a separate sighting of a unique individual shark. Females are shown in yellow and males in red. Google Satellite imagery via XYZ Tiles Basemap in QGIS 3.22.3-Białowieża.

falls under the Fam Islands MPA, while the remaining sites are within the Dampier Strait MPA. The Dampier Strait region is characterized by a complex underwater topography featuring fringing reefs, patch reefs, and submerged reefs. The region is strongly influenced by monsoon seasons: the northwest monsoon (November to April) brings warm, nutrient-poor waters, while the southeast monsoon (May to October) generates strong upwellings that increase primary productivity (15). It is also highly affected by Indonesian Through Flow that transport waters from the Pacific Ocean to the Indian Ocean (16). The region's average sea surface temperatures was 29.0 °C, with intertidal reef flats are frequently exposed to wide temperature swings of 7–8 °C (15).

Raja Ampat archipelago, especially the Dampier Strait region is subject to intensive and growing marine tourism (17). Key villages including Arborek and Sauwandarek serve as bases for ecotourism activities. The concentration of tourism has raised concerns about potential disturbance to marine species and habitat degradation. Additionally, coastal development (e.g., local homestays) and waste disposal from local villages and tourism operations pose emerging threats to water quality and reef health (18).

2.2 Shark surveys

Field surveys targeting *H. freycineti* were conducted during nighttime low tides from 4 February 2024 to 30 April 2025 at six sites across five islands in the Dampier Strait region in central Raja Ampat: Arborek Island; Sawinggrai on Gam Island; Kurkapa and Sauwandarek on Mansuar Island; Yensawai on Batanta Island; and Saupapir on Fam Island (Figure 1).

A total of 64 survey nights were conducted across all sites. Each survey began during the falling tide and lasted on average 1.8–2.3 hours, ending when the rising tide made the reef flat inaccessible. Sampling effort was not uniform across sites. Arborek received substantially greater effort (55 nights), mainly due to its accessibility and logistical support. The remaining sites were surveyed opportunistically during shorter visits, typically one or two nights per site. Consequently, comparisons among sites should be interpreted with consideration of these effort differences.

At each site, survey teams of five researchers waded through coastal waters less than 50 cm deep, continuously scanning for sharks with handheld and head torches. Surveys were opportunistic, with teams walking along accessible flat areas wherever water depth permitted. *Post-hoc* mapping of sighting locations revealed maximum search distances of up to 100 m from shore at most sites, but up to 500 m at Arborek due to the wider flat habitat at that location. Though *H. freycineti* is regularly found up to 10 m depth, and rarely to 20 m (8), past surveys have shown the greatest sighting rates in intertidal and shallow subtidal reef flat areas (Ronald Mambrasar, *pers. obs.*), so our surveys focused in these areas to maximize encounter rates with epaulette sharks. As such, search effort was not uniform across sites, and detection probabilities likely varied with habitat accessibility and search duration.

During each shark sighting, data on accompanying habitat and behavioural data were recorded. Habitat types were not predetermined but were defined collaboratively by the research team based on field observations, resulting in the following categories: seagrass, coral reef, sand, intertidal beach rock, rubble, and mangroves. Similarly, behavioural categories (feeding, cruising/swimming, mating, or resting) were established by team consensus. This team-based approach minimized individual observer bias, as all classifications were agreed upon collectively. Additionally, datetime stamps and GPS coordinates of each shark sighting were recorded using a handheld GPS unit.

2.3 Photographic identification, PIT tagging, and measurements

Upon detection, each individual shark was carefully approached and captured either by hand (using gloves) or with hand nets. Each shark was then placed on a styrofoam board for *in situ* examination. It was then photographed for individual identification using the spot pattern in the region between the posterior-most gill slit to just beneath the first dorsal fin, on both left and right sides (Figures 2A, B). These visually distinctive patterns were used to generate a photo-identification (photo-ID) catalogue following established protocols (19). The use of photo-ID in this study is supported within the genus *Hemiscyllium*. Although no formal assessment of long-term spot pattern stability exists for *H. freycineti*, recent work on another species within the same genus (*H. ocellatum*) demonstrated that adult individuals maintain consistent spot patterns over approximately two years and can be re-identified with high accuracy (86%) using AI models (20).

To provide an independent means of individual identification, a subset of sharks was additionally tagged with a Biomark APT12 passive integrated transponder (PIT) tag. We treated spot pattern stability as a working hypothesis and used concurrent PIT tagging to validate photo-ID assignments across repeated encounters. PIT tags were injected subcutaneously at the base of the first dorsal fin on the left side using a Biomark injection kit, and each tag's unique identification code was recorded prior to injection.

Each shark was then measured for its total length (TL; cm) using a meter tape and was then classified into 10 cm size classes (i.e., size class 1 = 10–19 cm TL, size class 2 = 20–29 cm TL, size class 3 = 30–39 cm TL, size class 4 = 40–49 cm TL, size class 5 = 50–59 cm TL, size class 6 = 60–69 cm TL, and size class 7 = 70–79 cm TL). Each shark was then weighed using a portable scale (to the nearest gram). The sex of each shark was determined by the presence (male) or absence (female) of claspers. The maturity status of each shark was assessed visually. Males were classified as mature individuals if their claspers extended beyond the pelvic fins and were already calcified, while shorter, soft, and uncalcified claspers were classified as immature (21). The inner clasper length (CL) of males was measured using a calliper (mm) from the origin of cloaca to the tip of right clasper. In females, maturity was determined by the presence of egg cases detected via gentle abdominal palpation along the lateral abdomen, a method successfully applied in small oviparous sharks including epaulette sharks (*H. ocellatum*) (22).

Life stage was classified using sex-specific criteria. Males were staged based on clasper development; adults had fully developed (calcified) claspers, and subadult males had claspers extending beyond the pelvic fins but remaining uncalcified. Female maturity was assessed operationally using body size: individuals with TL ≥56.7 cm (the smallest mature female recorded) were classified as adults. Juvenile females were operationally defined as individuals with TL of <50 cm, and subadult females were those with TL of 50.0–56.6 cm.

Overall, handling time out of water was limited to ~3–5 minutes. Individuals examined were released immediately to minimize stress. All procedures in this study followed a protocol approved by the Animal Care and Use Ethics Committee of the National Research and Innovation Agency (BRIN) under permit number 032/KE.02/SK/02/2024.

2.4 Epaulette shark density, movement, and residency

Epaulette shark density was calculated for all surveyed sites to provide a comparable measure of local abundance across the Dampier Strait. It was calculated by dividing the number of total unique individuals identified with the area of suitable habitats surveyed at each site (in km^2), not the total geographic area of each site. The surveyed area was defined *post-hoc* using GPS points

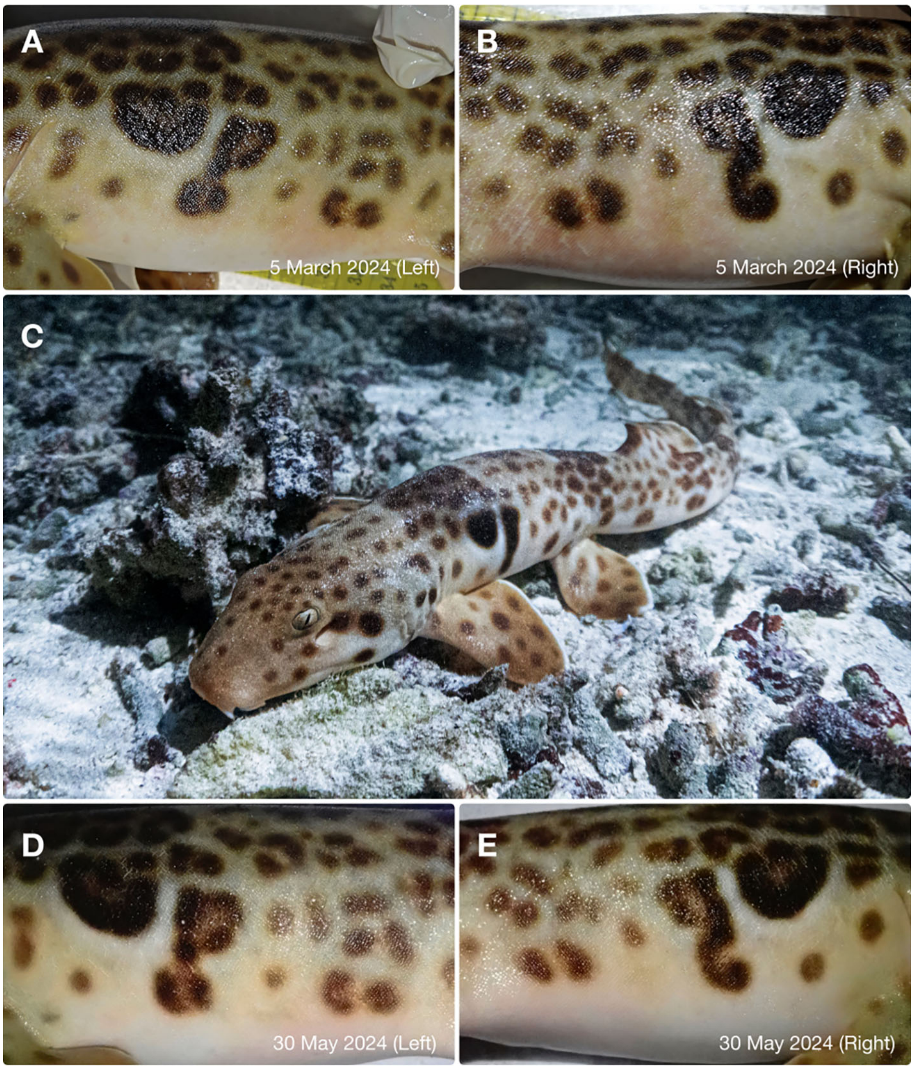

FIGURE 2
Right and left photo-identification of an individual *H. freycineti* that was sighted on 5 March 2024 **(A, B)** and 30 May 2024 **(D, E)** (©Edy Setyawan). **(C)** An individual of *H. freycineti* observed walking on substrate in Arborek (©Edy Setyawan).

recorded at the outermost extent of the search area. These waypoints were used to delineate a search polygon in QGIS 3.22.3-Białowieża, from which the area of suitable shallow habitat was calculated.

Regarding movements, we quantified individual movements using three complementary metrics. First, cumulative distance travelled (in meters) was calculated as the sum of straight-line distances between consecutive sightings for each epaulette shark, representing the minimum distance moved across the resighting sequence. Second, net displacement (in meters) was calculated as the straight-line distance between the first and last recorded sighting locations of each individual. Third, movement efficiency index, which was calculated as the ratio of net displacement to cumulative distance travelled, providing an index of movement directionality, with values approaching zero indicating non-directional movement and values approaching one indicating increasingly straight, directional movement. Movement metrics were calculated only for individuals recorded on more than two occasions, allowing robust estimation of net displacement and movement efficiency.

2.5 Length-weight relationship

Length–weight relationship (LWR) describes how body mass scales with body length and provides insights into growth patterns and body condition. The LWRs were modelled using the power equation $W = aL^b$, where L is total length (TL, cm), W is body weight (g), and a and b are fitted parameters (23). The analysis was performed separately for females, males, and both sexes combined.

2.6 Length-at-maturity

Length-at-maturity (LM_{50}) is defined as the length at which a randomly chosen specimen has a 50% chance of being mature (23). The analysis included only data from the Arborek Island population. Sex-specific maturity ogives (curves) were estimated using logistic regression models relating binary maturity status (mature/immature) to total length. Models were fitted separately for females and males using bias-reduced logistic regression to mitigate potential issues associated with small sample size and (quasi-)separation. Bias reduction was implemented using the 'brglm2' R package (24), which applies a Jeffreys-prior penalty to obtain finite, bias-reduced parameter estimates (25).

Uncertainty in LM_{50} estimates was quantified using non-parametric bootstrap resampling (1,000 replicates), stratified by sex. For each bootstrap replicate, individuals were resampled with replacement, the maturity model was refitted, and the LM_{50} was computed. The 95% confidence intervals (CIs) for LM_{50} were calculated as the 2.5th and 97.5th percentiles of the bootstrap distributions. Differences in LM_{50} between sexes were assessed using the bootstrap distribution of the difference in LM_{50}, with statistical significance evaluated using percentile CIs and a two-sided bootstrap *p*-value.

2.7 Length frequency analysis

The growth parameters of *H. freycineti* were estimated using length–frequency analysis (LFA). Length–frequency distributions were constructed from surveys conducted in May, June, September, October, November 2024 and May 2025 at Arborek, providing a partial annual cycle of samples. Only data from Arborek were included in the LFA due to the more comprehensive and consistent survey effort at this site compared to other locations within the Dampier Strait. The growth parameters were estimated by fitting the von Bertalanffy Growth Function (VBGF) to the length–frequency data using the Electronic Length Frequency Analysis (ELEFAN) method (26), implemented in the 'TropFishR' R package (27).

The VBGF framework is widely applied in fisheries science and is particularly appropriate when age data are unavailable, as it enables growth parameter estimation directly from length–frequency distributions (26, 28). Length–frequency distributions were constructed using a 5-cm bin size. Growth parameters were estimated using two optimization routines available in TropFishR: ELEFAN with simulated annealing (ELEFAN_SA) and ELEFAN with a genetic algorithm (ELEFAN_GA) (27). For each optimization routine, both seasonal and non-seasonal formulations of the VBGF were fitted. The seasonal model incorporates periodic oscillations in growth, whereas the non-seasonal model assumes constant growth throughout the year.

Analyses were conducted on the fully pooled dataset as well as separately for females and males to systematically evaluate potential sexual growth dimorphism. An exploratory unpaired two-sample Wilcoxon test was applied to determine if growth rates significantly differed between sexes. The following growth parameters were estimated across all groupings: asymptotic length (L_{∞}), growth coefficient (K), time when length equals zero (t_{anchor}), amplitude of seasonal growth oscillation (C), time of the year when growth turns positive (t_s), and the growth performance index (ϕ'), calculated following Pauly and Munro (29). Among the candidate model formulations across the pooled and sex-specific datasets, the final optimal growth trajectory was selected by evaluating the highest goodness-of-fit score (Rn_{max}) in conjunction with biological realism.

2.8 Statistical analyses

All statistical analyses were performed using R version 4.5.3 (30). Sex ratios between males and females were tested for deviation from the expected 1:1 ratio using a chi-square (χ^2) goodness of fit test (31). Normality of the data was assessed using the Shapiro–Wilk test. Given that the assumptions of normality were violated, non-parametric tests were employed. Differences in total length and body mass between sexes were assessed using two-sample Wilcoxon rank-sum tests. Growth rates were compared between sexes and between maturity stages (immature vs. mature) using unpaired two-sample Wilcoxon rank-sum tests.

Binomial logistic regressions with logit link functions were used to examine the effects of habitat on shark sex and maturity status. A multinomial logistic regression from the 'nnet' R package (32) was fitted to examine the distribution of life stages across habitats. An additional binomial GLM tested the interaction between habitat and maturity on sex ratio. Type II analyses of deviance were used to assess overall effects. Predicted probabilities with 95% confidence intervals (CIs) were calculated using estimated marginal means from the 'emmeans' R package (33). Pairwise comparisons between habitats were adjusted for multiple comparisons using the Tukey method. Statistical significance was set at $\alpha = 0.05$.

3 Results

3.1 Epaulette shark surveys and sightings

A total of 64 surveys were conducted in the Dampier Strait between 4 February 2024 and 30 April 2025, totalling 8,774 minutes (~146 hours) of survey effort. The majority of surveys were undertaken at Arborek Island (n = 55), accounting for 7,681 minutes (~128 hours) of observations (Table 1). Overall, survey durations in Dampier Strait ranged from 23 to 380 minutes, with a mean (± SD) of 137 ± 66.7 minutes.

Over the study period, 1,191 sightings with *H. freycineti* were recorded, with Arborek contributing the highest number of sightings (n = 1,052; 88.3%). The number of shark sightings per survey ranged from 3 to 69 (mean ± SD = 19 ± 14), and the encounter rate varied from 1 to 27 individuals per hour (mean ± SD = 9 ± 5). Across 939 sightings of PIT-tagged individuals, representing 503 unique PIT tags, each PIT tag corresponded to a single photo-identified individual, and no PIT tag was ever associated with multiple photo IDs across repeated sightings. This high concordance supports the working assumption that spot patterns are stable and reliable for individual recognition over the duration of the study.

3.2 Temporal distribution and habitat use

The number of shark sightings varied by month, with the highest number recorded in October (n = 452; 38% of all sightings;

TABLE 1 Survey efforts and demographic structure of *H. freycineti* across six sites in the Dampier Strait from February 2024 to April 2025.

Site/region	N surveys	N survey hours	N sightings	N sharks	N (%) females	N (%) males	N (%) mature	N (%) juveniles	Search area (km^2)	Density (individuals per km^2)
Arborek	55	128	1,052 (88.3)	602 (81.8)	332 (55.1)	270 (44.9)	258 (57.1)	281 (46.7)	0.290	2,076
Kurkapa	2	4.2	36 (3.0)	36 (4.9)	27 (75.0)	9 (25.0)	19 (52.8)	11 (30.6)	0.032	1,125
Saupapir	2	3.6	27 (2.3)	26 (3.5)	17 (65.4)	9 (34.6)	10 (38.5)	15 (57.7)	0.025	1,040
Sauwandarek	1	2.2	10 (0.8)	10 (1.4)	5 (50.0)	5 (50.0)	8 (80.0)	2 (20.0)	0.030	333
Sawinggrai	2	4.4	36 (3.0)	32 (4.4)	16 (50.0)	16 (50.0)	13 (40.6)	17 (53.1)	0.013	2,462
Yensawai	2	3.8	30 (2.5)	30 (4.1)	18 (60.0)	12 (40.0)	12 (40.0)	16 (53.3)	0.042	714
Dampier Strait	64	146	1,191	736	415 (56.4)	321 (43.6)	320 (43.5)	342 (46.4)		

N surveys, total number of surveys during study period; N survey hours, total duration of surveys (in hours); N sightings, total number of shark sightings; N sharks, total number of different sharks identified; N (%) females, total number of females and its proportion; N (%) males, total number of males and its proportion; N (%) mature, total number of mature individuals and its proportion at first sightings; N (%) juveniles, total number of juveniles and its proportion at first sightings. Maturity and life stage status was assigned based on the first recorded sighting of each individual.

note that surveys were not conducted in the months of January, July and August) (Supplementary Figure 1). Temporally, though surveys were conducted throughout the nighttime hours (19:00 to 04:59), the cumulative number of sightings peaked around 23:00, during which 209 sightings (17.5%) were observed (Supplementary Figure 2). Spatially, most shark sightings occurred less than 150 m from shore, and less than 50 m from shore at Saupapir, Sawinggrai, Kurkapa, and Sauwandarek (Figure 1). On Arborek Island, shark sightings occurred all the way around the island, including very close to human habitation.

Overall, the majority of shark sightings took place in seagrass meadows (n = 862, 72.4%), followed by coral reefs (n = 158, 13.3%), intertidal beach rock (n = 98, 8.2%), rubble (n = 32, 2.7%), mangrove (n = 23, 1.9%), and sand (n = 18, 1.5%). There was no significant effect of habitat on shark sex ratio (Type II deviance: $\chi^2 = 1.70$, df = 5, $p = 0.888$). Predicted probabilities of females ranged from 50.8% (95% CI: 38.8-62.6%) in intertidal beach rock habitats to 66.7% (95% CI: 37.6-86.9%) in mangrove habitats (Supplementary Figure 3). However, all 95% confidence intervals included 0.5, indicating that sex ratios did not deviate significantly from 1:1 in any habitat. Pairwise comparisons confirmed no significant differences between any habitat pairs after Tukey adjustment (all $p > 0.917$).

There was a marginally non-significant effect of habitat on the probability of shark immaturity (Type II deviance: $\chi^2 = 10.86$, df = 5, $p = 0.054$). Predicted probabilities of immature sharks were highest in coral reefs (69.4%, 95% CI: 58.9-78.3%), followed by intertidal beach rock (64.6%, 95% CI: 52.3-75.2%) and rubble (63.0%, 95% CI: 43.8-78.8%) habitats (Supplementary Figure 4). In contrast, seagrass habitats showed a more balanced composition (53.5% immature, 95% CI: 49.3-57.7%), while sand habitats had the lowest proportion of immature sharks (45.5%, 95% CI: 20.3-73.2%). Pairwise comparisons with Tukey adjustment revealed no statistically significant differences between any habitat pairs (all $p > 0.07$).

The multinomial logistic regression examining life stage (adult, juvenile, subadult) across habitats showed a marginally significant overall effect ($\chi^2 = 17.79$, df = 10, $p = 0.059$), consistent with the binomial GLM results. Coral reefs were dominated by juveniles (58.8%, 95% CI: 47.2-70.5%), followed by intertidal beach rock (60.0% juvenile) and rubble (55.6% juvenile) habitats. In contrast, seagrass habitats had a higher proportion of adults (46.5% adult, 95% CI: 41.8-51.1%), while sand habitats showed the highest adult proportion (54.5%). Subadults were the least represented life stage across all habitats, ranging from 4.6% (intertidal beach rock) to 18.2% (sand).

The interaction model testing whether the sex-maturity relationship varied by habitat revealed a significant main effect of maturity ($\chi^2 = 3.89$, df = 1, $p = 0.048$), but no significant effect of habitat ($\chi^2 = 1.45$, df = 5, $p = 0.919$) nor a habitat-maturity interaction ($\chi^2 = 7.51$, df = 5, $p = 0.185$). This indicates that while immature and mature sharks differ in sex ratio (with more females among mature individuals), this pattern is consistent across all habitat types.

Regarding behaviours during encounters, virtually all sightings (98%) involved sharks resting or remaining stationary on the substrate, and very few when they were cruising or walking on substrate.

3.3 Population demographics and resightings

Of the 1,191 shark sightings recorded, 736 unique individuals were identified using photo-ID across six survey sites: Arborek (n = 602; 88.3%), Kurkapa (n = 36; 3.0%), Saupapir (n = 26; 3.5%), Sauwandarek (n = 10; 1.3%), Sawinggrai (n = 32; 4.3%), and Yensawai (n = 30; 4.0%) (Figure 1; Table 1). All sharks were identified through photo-ID, and 503 individuals (68.3%) were also implanted with PIT tags.

Of the 736 individuals identified, 256 (34.8%) were resighted at least once during the study period. The highest number of sightings for a single individual was seven, and 18 individuals were sighted five or more times over the 14 months of the study. The longest resighting span (interval between first and last resighting) recorded for any individual was 451 days (1.24 years) (mean ± SD = 136 ± 113), observed in two sharks (Table 2). Only 10 sharks were resighted after one year. All resightings were site-specific, with no evidence of individual movement between sites, as determined by both photo-ID and PIT data.

3.4 Sex ratio and maturity status

The population appeared predominantly female, with 415 females (56.4%) and 321 males (43.6%) recorded, resulting in a female-to-male ratio of approximately 1.29:1. A chi-square goodness of fit test indicated strong evidence ($\chi^2 = 12.005$, $p = 0.0005$) of a difference in the numbers of females and males in the surveyed areas. In Arborek, the primary survey site, 602 individuals were identified, of which 332 were females (55.1%) and 270 were males (44.9%), yielding a female-to-male ratio of 1.23:1. There was also

TABLE 2 Summary of resighting histories for 20 epaulette sharks (*Hemiscyllium freycineti*) with the longest resighting spans, based on monitoring data collected across six sites in Dampier Strait from February 2024 to April 2025.

No.	Shark ID	Sex	Site at first sighting	First sighting date	Last sighting date	Total sightings	TL (cm) at first sighting	TL (cm) at last sighting	Resighting span (days)	Growth rate (cm year^{-1})
1	RA-HF-0032	F	Arborek	04/02/2024	30/04/2025	4	44.8	54.1	451	7.5
2	RA-HF-0035	F	Arborek	04/02/2024	30/04/2025	3	26.0	36.0	451	8.1
3	RA-HF-0039	M	Arborek	05/02/2024	30/04/2025	3	66.2	66.7	450	0.4
4	RA-HF-0068	F	Arborek	08/02/2024	28/04/2025	2	63.5	64.3	445	0.7
5	RA-HF-0056	F	Arborek	07/02/2024	23/04/2025	6	55.9	62.4	441	5.4
6	RA-HF-0075	F	Arborek	04/03/2024	30/04/2025	3	56.7	59.5	422	2.4
7	RA-HF-0080	F	Arborek	04/03/2024	30/04/2025	5	60.7	61.5	422	0.7
8	RA-HF-0096	F	Arborek	06/03/2024	29/04/2025	7	62.0	63.4	419	1.2
9	RA-HF-0090	F	Arborek	05/03/2024	27/04/2025	4	64.4	65.0	418	0.5
10	RA-HF-0106	M	Arborek	07/03/2024	28/04/2025	3	59.5	62.2	417	2.4
11	RA-HF-0124	M	Arborek	29/05/2024	30/04/2025	3	44.0	50.4	336	7.0
12	RA-HF-0125	F	Arborek	29/05/2024	30/04/2025	4	55.4	61.5	336	6.6
13	RA-HF-0127	M	Arborek	29/05/2024	30/04/2025	4	36.4	43.4	336	7.6
14	RA-HF-0141	F	Arborek	30/05/2024	27/04/2025	4	62.3	64.3	332	2.2
15	RA-HF-0171	F	Arborek	01/06/2024	29/04/2025	6	58.5	60.1	332	1.8
16	RA-HF-0175	F	Arborek	01/06/2024	28/04/2025	4	57.6	65.8	331	9.0
17	RA-HF-0123	M	Arborek	29/05/2024	23/04/2025	4	38.8	46.2	329	8.2
18	RA-HF-0033	M	Arborek	04/02/2024	05/11/2024	3	36.0	NA	275	NA
19	RA-HF-0058	M	Arborek	08/02/2024	29/10/2024	3	45.0	54.0	264	12.4
20	RA-HF-0029	M	Arborek	04/02/2024	21/10/2024	4	64.4	NA	260	NA

For each individual shark (Shark ID), the table reports sex, total length (TL) at first and last sightings, total number of sightings, site of first sighting, first and last sighting dates, resighting span (days between first and last sightings), and growth rate (cm year^{-1}).

strong evidence (χ^2 = 6.385, p = 0.011) of a difference at this site in the number of individuals between sexes. Of all individuals identified in Dampier Strait region, 320 individuals (43.5%) were sexually mature, and 416 individuals (56.5%) were immature. Of these immatures, 342 individuals (82.2%) were juveniles, and 74 (17.8%) were subadults (Table 1). Among the 415 females recorded, 63 (15.2%) were observed to be gravid, with egg cases detected.

3.5 Size distribution, length-weight relationships, length-at-maturity, and growth

The total length (TL) of *H. freycineti* individuals ranged from 19.4 to 75.0 cm (mean ± SD: 51.1 ± 12.1). The TL of males ranges from 22.0 to 75.0 cm, and similarly, the TL of females ranges from 19.4 to 70.2 cm. On average, females (mean ± SD: 51.8 ± 12.1 cm) were slightly larger in TL than males (mean ± SD: 50.3 ± 12.1 cm). A Wilcoxon rank-sum test further indicated moderate evidence (W = 68566, p = 0.036) that the median TL of females (55.4 cm) is different from that of males (53.0 cm). The most frequent size class for females was class 6 (60–69 cm) with 142 individuals, whereas males were most commonly found in size class 5 (50–59 cm) and 6 (60–69 cm) with 92 and 79 individuals, respectively (Supplementary Figure 5). Inner clasper length (CL) of all males varied from 9.0 to 73.8 mm (mean ± SD = 40.0 ± 23.7 mm), while the inner CL of mature males ranged from 54.9 to 73.8 mm (mean ± SD = 67.1 ± 3.8 mm). Individual shark body mass ranged from 24 to 1,025 grams (both by females), with a mean (± SD) of 413 ± 236 grams. The maximum body mass of males was only 975 grams. The average of the body mass of females was slightly higher (mean ± SD: 433 ± 243 grams) than males (mean ± SD: 386 ± 224 grams). The Wilcoxon rank-sum test indicated a strong evidence (W = 69930, p = 0.0094) that the median weight of females (444 grams) is different from that of males (383 grams).

The constant a and exponent b, calculated as part of the LWR, varied between sexes. For females, the estimated constant a was 0.0038 (95% CI: 0.0032, 0.0046) and the exponent b was 2.91 (95% CI: 2.87, 2.96) (Figure 3A). For males, the estimated constant a was 0.0057 (95% CI: 0.0045, 0.0072) and the exponent b was 2.81 (95% CI: 2.75, 2.87). For all individuals combined (both sexes), the estimated constant a was 0.0045 (95% CI: 0.0039, 0.0052) and the exponent b was 2.87 (95% CI: 2.83, 2.91). Regarding the length-at-maturity of sharks in Arborek, the estimated length-at-maturity (LM_{50}) for females was 56.59 cm TL (95% CI: 56.34, 56.88), while for males was 56.42 cm TL (95% CI: 55.81, 57.01) (Figure 4). The difference in length-at-maturity was not significant (p = 0.636), indicating that males and females reach maturity at similar lengths. Additionally, the smallest mature male measured 54.6 cm TL, while the smallest gravid female carrying egg cases was 56.7 cm TL.

The maximum observed growth rate was 16.7 cm year^{-1}, with a mean growth rate of 5.3 ± 4.6 cm year^{-1} across individuals. Growth rates differed significantly between maturity stages, with immature individuals exhibiting significantly higher growth rates (7.8 ± 4.7 cm year^{-1}) than mature individuals (2.8 ± 2.8 cm year^{-1}; unpaired two-sample Wilcoxon test: W = 4295.5, p < 0.001). In contrast, growth rates did not differ between sexes (females: 5.1 ± 4.4 cm year^{-1}; males: 5.6 ± 4.8 cm year^{-1}; unpaired two-sample Wilcoxon test: W = 2567.5, p = 0.616).

Length–frequency analysis of *H. freycineti* (N = 722) using the seasonal ELEFAN_SA routine yielded an asymptotic length (L_∞) of 79.6 cm, a growth coefficient (K) of 0.747 year^{-1}, and a growth performance index (ϕ') of 3.675 (Rn_{max} = 0.583; Table 3). This model estimated an annual growth oscillation amplitude (C) of 0.915, a time of the year when growth turns positive (t_s) of 0.009, and a time when length equals zero (t_{anchor}) of 0.471. In comparison, the pooled non-seasonal ELEFAN_SA model achieved a marginally higher fit score (Rn_{max} = 0.586) but produced divergent parameters (L_∞ = 67.8 cm, K = 0.998 year^{-1}), while both seasonal and non-seasonal configurations optimized via the genetic algorithm (ELEFAN_GA) resulted in lower goodness-of-fit values (Rn_{max} = 0.487 and Rn_{max} = 0.460, respectively).

When segregated by sex, seasonal ELEFAN_SA models captured a pattern of male-biased size dimorphism. The female model (N = 405, Rn_{max} = 0.861) converged on a lower asymptotic length and faster growth (L_∞ = 71.1 cm), K = 0.670 year^{-1}), whereas the male model (N = 317, Rn_{max} = 0.520) favoured a higher asymptotic length and slower growth (L_∞= 93.3 cm, K = 0.302 year^{-1}).

3.6 Epaulette shark density

Relative density varied markedly among locations, ranging from 333 to 2,462 individuals per km² (Table 1). Sawinggrai, on Gam Island, exhibited the highest relative density, with 2,462 individuals per km², despite having the smallest surveyed area (0.013 km²). In contrast, Arborek, where the majority of epaulette shark encounters were recorded and survey coverage was most extensive, ranked second, with a relative density of 2,124 individuals per km², based on an estimated search area of 0.29 km² on shallow reef-flat habitat surveyed. Among all sites, Sauwandarek had the lowest relative shark density, at 333 individuals per km². Across sites, mean shark density was 1,300 ± 825 individuals per km², highlighting substantial spatial heterogeneity in local abundance.

3.7 Epaulette shark residency and movements

No movement of *H. freycineti* between six sites was recorded during the 14 month survey period in Dampier Strait region. Across all individuals sighted more than twice (n = 122), cumulative distance travelled ranged from 14.3 to 804.3 m (mean ± SD = 168.2 ± 134.4), whereas net displacement ranged from 4.3 to 474.5 m (mean ± SD = 63.2 ± 66.2). Cumulative distance travelled increased with net displacement across individuals. Most sharks, however, exhibited net displacement values substantially lower than cumulative distance travelled, as indicated by points falling below the 1:1 line (Figure 5). This pattern was consistent across both sexes, with extensive overlap between males and females throughout the observed range of movement distances. In general, individuals with cumulative distances of up to approximately 400 m exhibited relatively low net displacement (<200 m). Additionally, individuals with low cumulative movement showed correspondingly low net displacement.

Movement efficiency index ranged from 0.03 to 0.99 (mean ± SD = 0.44 ± 0.28) with most individuals exhibit low to moderate

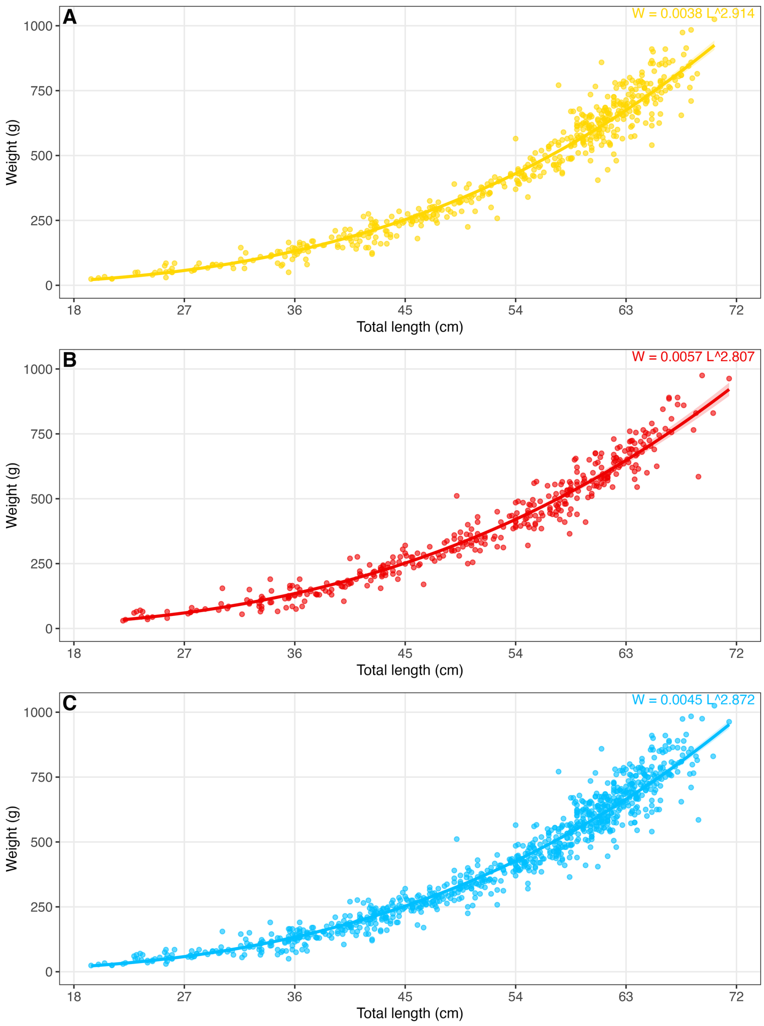

FIGURE 3
Sex-specific and pooled length–weight relationships for *H. freycineti* based on log–log linear regression. **(A)** Females (in yellow), **(B)** Males (in red), and **(C)** Pooled dataset (both sexes combined, in blue). Points represent individual observations, solid lines show fitted mean relationships, and shaded bands indicate 95% CIs.

efficiency index values, indicating that cumulative movement generally results in limited net displacement. This pattern is evident across both sexes, with substantial overlap between males and females and no clear sex-specific separation. High movement efficiency values (approaching 1; blue dashed line) occur almost exclusively at low cumulative distances, indicating short, relatively straight movements over limited spatial scales. As cumulative distance travelled increases, movement efficiency generally declines, with most individuals showing efficiency values below 0.5.

4 Discussion

4.1 Baseline ecology and validation of individual-based monitoring

This study provides the first comprehensive baseline of demographic structure, reproductive biology, spatial ecology, and habitat use of the endemic Raja Ampat epaulette shark *Hemiscyllium freycineti*. The consistency of individual identifications through photo-ID across repeated encounters supports the use of spot patterns for tracking individuals at seasonal to interannual timescales. Although lifetime pattern stability has not been formally tested for this species, concordant resightings and evidence from multiple individuals (20) suggest that adult spot patterning is sufficiently stable for demographic and movement analyses for this species. This reliability underpins key inferences from this study, including strong site fidelity, limited spatial displacement, and residency within shallow reef habitats. Photo-ID therefore represents a practical, non-invasive tool for long-term monitoring of small benthic sharks, while highlighting the need for future studies to explicitly assess ontogenetic pattern change, particularly in juveniles.

4.2 Population density and habitat quality

Our findings indicate that *H. freycineti* is locally abundant in the Dampier Strait region during the study period (February 2024 – April 2025), particularly around Arborek Island and Sawinggrai on

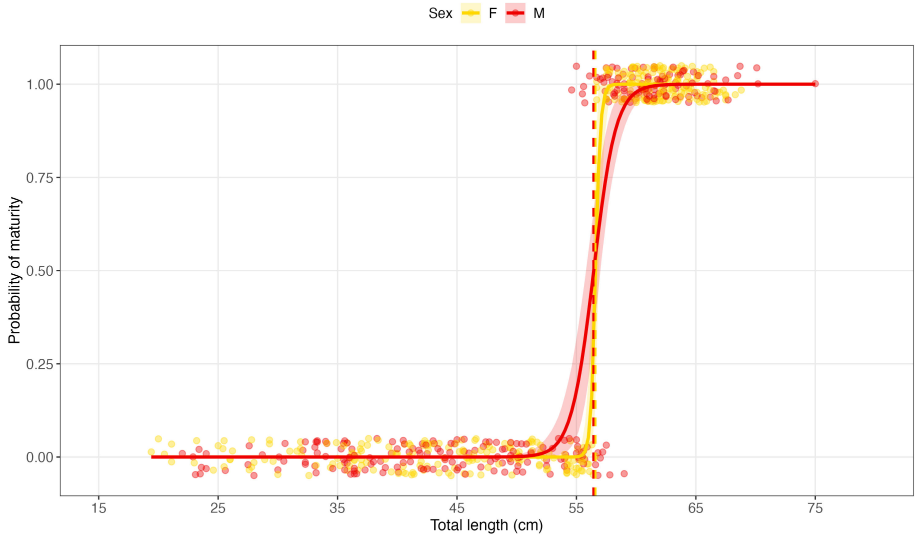

FIGURE 4
Sex-specific maturity ogives (curves) estimated from logistic regression of maturity status against total length. Points represent individual observations (jittered for clarity). Solid lines show the median predicted probability of maturity for females (yellow) and males (red) derived from non-parametric bootstrap resampling, and shaded ribbons represent 95% bootstrap confidence intervals based on empirical quantiles of predicted maturity probability at each length. Dashed vertical lines indicate the median length-at-maturity (LM_{50}) for females and males, estimated from the bootstrap distribution.

southern Gam Island, where relative densities within the surveyed suitable habitats exceeded 2,000 individuals per km². These values are substantially higher than previous estimates reported for the species elsewhere, including densities of approximately 200 individuals per km² estimated in recent Red List assessments (5). High densities observed within relatively small survey areas suggest strong local aggregation and potentially high habitat suitability at fine spatial scales. These patterns are unlikely to be explained solely by the areal extent of suitable habitat. Although Sawinggrai and Arborek contain habitat types similar to those present at nearby islands such as Mansuar and Fam, the shark densities at these sites were markedly higher. This suggests that fine-scale differences in habitat quality, such as the availability of refuge structures including crevices, coral rubble, and complex seagrass as well as reef rugosity, may enhance suitability for *H. freycineti* by increasing shelter availability and reducing predation risk. However, because we did not collect quantitative habitat data, these hypotheses remain untested. Many reef sharks, including epaulette sharks, are considered as small meso-predators that function as both predators and prey (34). Site-specific differences in disturbance levels, human activity, and predator assemblages may further contribute to observed spatial variation in density. Targeted habitat assessments

TABLE 3 **Estimated growth parameters and goodness-of-fit scores (Rn_{max}) derived from seasonal and non-seasonal formulations of the von Bertalanffy Growth Function (VBGF) optimized via ELEFAN_SA (simulated annealing) and ELEFAN_GA (genetic algorithm).**

VBGF models	Sex	Sample size (N)	L_∞	K	t_{anchor}	C	t_s	ϕ'	Rn_{max}
ELEFAN_SA (Seasonal)	Both	722	79.6	0.747	0.471	0.915	0.009	3.675	0.583
	Female	405	71.1	0.670	0.484	0.990	0.642	3.529	0.861
	Male	317	93.3	0.302	0.113	0.659	0.996	3.420	0.520
ELEFAN_SA (Non-Seasonal)	Both	722	67.8	0.998	0.662	NA	NA	3.662	0.586
	Female	405	78.6	0.463	0.065	N/A	N/A	3.457	0.623
	Male	317	95.7	0.150	0.025	N/A	N/A	3.138	0.439
ELEFAN_GA (Seasonal)	Both	722	68.8	0.871	0.511	0.469	0.313	3.615	0.487
	Female	405	68.9	0.779	0.503	0.536	0.471	3.569	0.801
	Male	317	82.1	0.267	0.628	0.336	0.829	3.254	0.368
ELEFAN_GA (Non-Seasonal)	Both	722	67.3	0.899	0.592	N/A	N/A	3.610	0.460
	Female	405	72.6	0.617	0.355	N/A	N/A	3.512	0.580
	Male	317	85.3	0.374	0.291	N/A	N/A	3.435	0.351

Results are presented for females, males, and the pooled dataset of the Raja Ampat walking shark (*Hemiscyllium freycineti*) based on length–frequency data collected in Arborek, Dampier Strait, from May 2024 to April 2025. The reported growth parameters include asymptotic length (L_∞), growth coefficient (K), theoretical age at zero length (t_{anchor}), amplitude seasonal growth oscillations (C), the time between $t = 0$ and the start of a sinusoidal growth oscillation (t_s), growth performance index (ϕ').

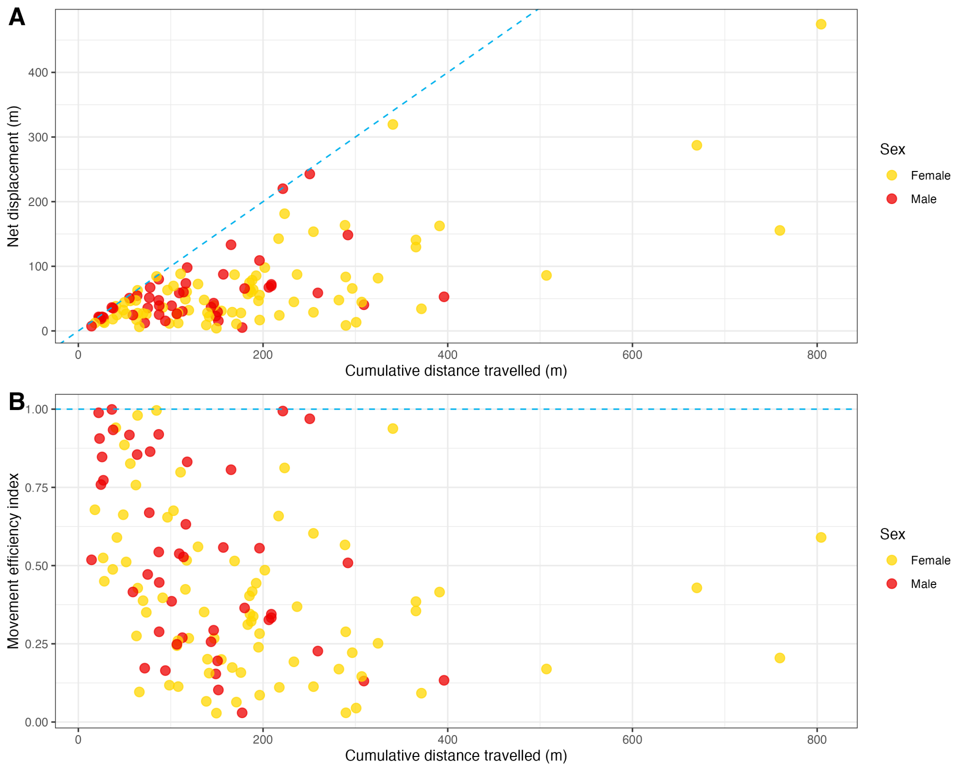

FIGURE 5
Movement metrics of resighted Raja Ampat epaulette sharks (*H. freycineti*). **(A)** Net displacement (metres) plotted against cumulative distance travelled (metres). The dashed blue line indicates a 1:1 relationship, where net displacement equals cumulative distance travelled. **(B)** Movement efficiency index, plotted against cumulative distance travelled (metres). In both panels, points represent individual sharks and are coloured by sex.

measuring rugosity, refuge availability, and benthic composition are necessary to determine which specific habitat features drive the observed spatial variation in density.

It remains unclear whether the high densities recorded at Arborek and Sawinggrai are broadly representative of *H. freycineti* populations across Raja Ampat or reflect localized hotspots. Survey effort was uneven among sites, with Arborek receiving substantially greater coverage than other locations, and the small search area at Sawinggrai likely inflating density estimates. Lower densities at the remaining sites suggest considerable spatial heterogeneity in local abundance, a finding which is further underscored by comparison to other recent studies of epaulette sharks in the region. For instance, a study by Widiarto et al. (35) on *H. freycineti* in Misool in southern Raja Ampat uncovered only 62 individuals from three days of surveys at four sites, with a density of 5.3 individuals per hectare, which equates to 530 individuals per km^2. Moreover, a study of the closely-related species *H. halmahera* in Kao Bay, Halmahera found a total of 604 individuals between March 2017 and February 2018 from four sites (36), although the surveys were done via night dives, making it difficult to directly compare their results to ours. A similar study via night dives was also done on *H. galei* at two sites in Doreri Bay, West Papua estimated abundance of 13.33 individuals per hectares and 8.88 individual per hectares, which equate 1,333 individuals per km^2 and 888 individuals per km^2 (37). A study of the congener *H. henryi* in Triton Bay, Kaimana, encountered only 6 individuals from 3 different survey sites, with a density of 2.4 individuals per hectare (240 individuals per km^2) (38). Finally, a study on *H. ocellatum* on Heron Island Reef, Great Barrier Reef, Australia, encountered a total of 496 individuals in 0.25 km^2, which equates to 1,984 individuals per km^2 (39). This density is slightly lower than that of *H. freycineti* in Arborek, but substantially lower than that *H. freycineti* in Sawinggrai in our study.

Because density estimates in our study were derived from encounter-based surveys, they should be interpreted as relative measures influenced by site-specific sampling effort and detection probability. Nevertheless, density provides a more informative and comparable metric than raw encounter numbers and establishes an essential baseline for future monitoring of population trends and spatial dynamics.

4.3 Life history traits, length-at-maturity, and growth

The TL range observed in this study (19.4–75.0 cm) is consistent with values reported for other *Hemiscyllium* species across the Indo-Pacific (Table 4). Previous studies documented TL ranges of 20.0–70.0 cm for *H. freycineti* in Misool (35), 16.9–79.0 cm for *H. halmahera* in Kao Bay (mean = 56.7 cm; 36), 55.0–88.0 cm for *H. henryi* at Triton Bay, Kaimana (38), and 28.5–75.0 cm for *H. ocellatum* at Heron Island Reef, eastern Australia (39). The largest individual reported in a published studies are an 88 cm (38) and an 81.5 cm TL (7) *H. henryi*, both from Triton Bay, West Papua. In addition, an 87 cm TL female *H. freycineti* was recorded at Magic

TABLE 4 Total length range and maximum total length (cm) of *Hemiscyllium* species in the Indo-Pacific reported in published studies.

Species	Total length range (cm)	Maximum total length (cm)	Locations	Studies
H. freycineti	19.4–75.9	75.9	Dampier Strait, Raja Ampat	This current study
H. freycineti	20.0–70.0	70.0	Misool, Raja Ampat	Widiarto et al. (35)
H. freycineti	–	87.0	Misool, Raja Ampat	Erdmann and Ichida, *unpubl. data*.
H. halmahera	16.9–79.0	79.0	Kao Bay, Halmahera	Jutan et al. (36)
H. henryi	55.0–88.0	88.0	Triton Bay, Kaimana	Prehadi et al. (38)
H. henryi	–	81.5	Triton Bay, Kaimana	Allen et al. (7)
H. ocellatum	28.5–75.0	75.0	Heron Island Reef, eastern Australia	Heupel and Bennet (39)

Mountain, southeast Misool, in 2023 (M.V. Erdmann & N. Ichida, *unpubl. data*), suggesting that maximum size in this species may be slightly larger than previously documented.

Sex-specific growth patterns observed in this study indicate negative allometry in both female and male epaulette sharks ($b < 3$), with females exhibiting slightly higher *b* values than males. The *b* coefficient of *H. freycineti* estimated in our study (2.91 for females and 2.81 for males) were similar to reports from other species of carpet sharks Orectobliformes: nurse shark *Ginglymostoma cirratum* (b = 2.91) (40), brown-banded bamboo shark *Chiloscyllium punctatum* (b = 2.81–3.21) (41), and epaulette shark *Hemiscyllium ocellatum* (b = 2.80) (42). By contrast, a *b* coefficient of 3.43 reported for the Triton epaulette shark *H. henryi* (38) was significantly higher than those estimated in our study, though this study examined only six specimens in deriving that figure. Conversely, a much lower *b* value (2.34) was documented for *H. galei* in Doreri Bay (37), although that study was likewise based on only six individuals. These discrepancies likely reflect differences in sample size, size range, or local environmental conditions rather than true biological divergence among species. Such sensitivity to sampling design is well documented in length-weight relationship studies (42).

Negative allometric growth is commonly reported in sharks and reflects changes in body shape, energy allocation, and ecological demands as individuals increase in size (e.g., 43). The relatively higher allometric coefficient in females is consistent with reproductive allocation theory, whereby females allocate proportionally more energy to somatic mass accumulation associated with gonadal development and egg production (44, 45). In contrast, lower relative mass gain in males may reflect alternative energetic strategies, including greater investment in movement, mate-searching behaviour, or other reproductive activities rather than somatic growth (46–48). Such sex-specific differences in growth allometry likely arise from a combination of reproductive roles, behavioural ecology, and habitat use, and are consistent with patterns documented across a range of elasmobranch species (e.g., 49, 50).

Estimated length-at-maturity (LM_{50}) for *H. freycineti* in this study was remarkably similar between sexes, at 56.59 cm TL for females and 56.42 cm TL for males. These values closely align with published maturity estimates for other species within the same genus. Heupel et al. (51) report that male *H. ocellatum* in eastern Australia mature at approximately 55–60 cm TL, while females reach maturity around 55 cm TL. Similarly, Allen et al. (7) reported rapid male maturation in *H. henryi* and *H. galei* within the 55–60 cm TL range, based on clasper development. Although VanderWright et al. (11) suggested a broader maturity range (48–68 cm TL) across the genus, our results and those of previous studies indicate that length-at-maturity may be more tightly constrained, clustering around 55–60 cm TL. Collectively, these findings suggest that *Hemiscyllium* species share broadly conserved life-history strategies characterized by small adult body size and relatively early maturity (11). While early maturation may confer some reproductive resilience, the combination of strong site fidelity, restricted spatial distribution, and habitat specialization likely increases vulnerability to localized disturbances (11). Accurate estimates of length-at-maturity are therefore essential for informing species-specific management measures and ensuring that mature individuals and reproductive output are adequately protected.

The absence of sex-specific differences in overall growth rates suggests that length-frequency analysis using pooled dataset is more preferable to sex-separate analyses. Between the two models fitted to the pooled dataset (seasonal and non-seasonal ELEFAN_SA), the seasonal formulation was more biologically meaningful as the non-seasonal ELEFAN_SA produced a K of 0.998 year^{-1}, which is unrealistically high for an elasmobranch. The seasonally oscillating ELEFAN_SA for the pooled dataset estimated an asymptotic length (L_∞) of 79.6 cm, which is slightly shorter than that reported for *H. halmahera* in Kao Bay, Halmahera (36) with 81.25 cm.

The maximum total length observed in our Dampier Strait sample (75 cm) is smaller than the largest recorded individual for the species (87 cm; a female recorded at Magic Mountain, Misool, in 2023). However, given the strong site attachment and limited dispersal capacity of *Hemiscyllium* species (7; this study), these two localities (~200 km apart) very likely represent separate populations. Our growth parameter estimates should therefore be interpreted as applying to the Dampier Strait region population specifically. Within this population, the seasonal growth coefficient (K = 0.747 year^{-1}) falls into the category of fast-growing sharks where $K > 0.2$ (52). Such rapid growth is consistent with patterns reported for *H. halmahera* with 0.51 year^{-1} (36) and confamilial species within the genus *Chiloscyllium* (53) and may reflect adaptations to shallow, productive reef environments where early attainment of larger body size can enhance survival and reproductive output.

The growth performance index (ϕ' = 3.675) is comparable with those from other small-bodied benthic sharks. For example, the whitespotted bamboo shark (*C. plagiosum*; Orectolobiformes) has published VBGF parameters (e.g., L_∞ = 95.9 cm, K = 0.205 for females; L_∞ = 100.9 cm, K = 0.198 for males), which correspond to ϕ' values of 3.275 - 3.304 when calculated from those parameters. The high value of growth performance index on *H. freycineti* in Arborek indicates faster somatic growth and earlier attainment of large body size, which may shorten generation time and enhance population productivity relative to more slowly growing elasmobranchs (54).

Although the seasonal model indicated pronounced variability in growth, incomplete monthly sampling limited our ability to precisely determine the timing of growth minima, the specific time of year when growth slows the most. Nevertheless, the estimates of L_∞, K, and ϕ' are considered robust, as these parameters are primarily driven by the overall size-frequency distribution rather than fine-scale temporal resolution.

4.4 Spatial ecology, habitat use, and movement patterns

Coral reefs appear to serve as a primary nursery habitat for *H. freycineti*, characterised by a predominance of juvenile sharks and a low proportion of mature sharks. The high abundance of juvenile sharks in coral reefs aligns with the nursery habitat definition proposed by Heupel et al. (55), which requires that a habitat contributes disproportionately to juvenile survival, growth, or recruitment. Coral reefs likely provide structural complexity that offers protection from predators and abundant foraging opportunities for small-bodied juvenile sharks (56). The low proportion of subadults in these habitats suggests that as sharks mature, they may shift to other habitats. In contrast to coral reefs, seagrass and sand habitats contained higher proportions of mature sharks (46.5% and 54.5%, respectively). This pattern suggests ontogenetic habitat partitioning, where juveniles concentrate in structurally complex reef habitats, while adults utilize more open habitats such as seagrass beds and sand flats. Similar ontogenetic shifts have been documented in other elasmobranch species, including blacktip reef sharks (*Carcharhinus melanopterus*) (57), lemon shark (*Negaprion brevirostris*) (58), and several Dasyatids (59).

The absence of habitat-specific sex segregation indicates that males and females use all habitat types equally. This contrasts with some shark species where females segregate to nursery areas or males show differential habitat use (60). However, the significant effect of maturity on sex ratio suggests that more females are present among mature individuals, potentially reflecting sex-specific growth rates, survival, or movement patterns. The lack of habitat-maturity interaction indicates this pattern is consistent across all habitats.

The restricted distribution and habitat specificity observed in this study are consistent with previous descriptions of *H. freycineti* as a shallow-water, site-attached species closely associated with seagrass beds, mangroves, and adjacent coral reefs (5, 7, 35). High site fidelity and limited movements within sites indicate that individuals occupy small spatial ranges and rely heavily on localized habitats. Movement analyses further revealed low net displacement relative to cumulative distance travelled, likely indicating repeated, non-directional movements within restricted areas rather than sustained directional dispersal. These patterns were consistent across sexes, suggesting broadly similar space-use strategies. The strong site fidelity and limited movements of these sharks contribute to reproductive success of individuals (61) that may explain their high densities at certain sites. These characteristics support the notion that epaulette sharks as reef residents were reef-specialists that spend most of their time at a single reef and/or have limited movement between reef habitats nearby (62).

Such localized movement behaviour likely reflects reliance on fine-scale habitat features for shelter and foraging and may contribute to the high densities observed at certain sites. However, strong site fidelity and limited dispersal also increase vulnerability to localized disturbances, emphasizing the importance of protecting nearshore intertidal habitats where sharks are most frequently encountered (11).

4.5 Conservation implications and management recommendations

Together, our findings provide critical baseline data and information to support the implementation of conservation efforts (e.g., Ministerial Decree No. 30/2023) to protect the species (9). Although no immediate threats were documented during this study, intensified human activity in shallow coastal areas, rapid coastal development associated with a growing tourism industry, habitat degradation, and coastal pollution pose potential risks to this highly site-attached species. The combination of restricted range and high residency of *H. freycineti* on shallow coastal habitats highlight the species' vulnerability to localized anthropogenic pressures.

Climate change, particularly rising sea temperatures, represents an additional threat to *H. freycineti* in Raja Ampat. As a shallow-water benthic species inhabiting coastal habitats (<10 m depth) (5), this species is potentially highly susceptible to marine heatwaves (63). Globally, all shark species are projected to be affected by climate change regardless of emission scenario, with effects expected over the short term (64). Studies on the congeneric epaulette shark *H. ocellatum* have shown that juveniles acclimated to 32 °C (predicted end-of-century summer temperatures) exhibit significantly decreased growth rates and 100% mortality compared to 33% mortality at 28 °C (65). Furthermore, *H. ocellatum* body temperatures on reef flats mirror environmental temperatures (15-34 °C), and the species' preferred temperature under controlled conditions is only 20.7 ± 1.5 °C (66), suggesting limited capacity for behavioural thermoregulation. Given the strong site attachment documented in our study, *H. freycineti* may be unable to move to cooler waters as temperatures rise, potentially leading to thermal stress and reduced fitness. Future research should prioritize investigating the thermal tolerance of *H. freycineti* to projected warming scenarios.

At the same time, the high local abundance and visibility of *H. freycineti* (8) present opportunities for sustainable, non-extractive ecotourism, such as guided night observations (67), which could generate local economic benefits while promoting conservation awareness. When integrated with community-based monitoring and citizen science initiatives, such approaches may strengthen long-term conservation outcomes. Ultimately, effective protection of *H. freycineti* will require the integration of species-level legal protection with habitat management, long-term monitoring, adaptive conservation strategies, and consideration of climate change impacts on both the species and its shallow coastal habitats.

4.6 Future research directions

Our study revealed important knowledge gaps, particularly those related to spatial movements, threats to populations, population connectivity, reproductive physiology, and life stage or maturity definition – common key research questions and critical questions in reef shark science (62). Specific studies required to address these research gaps include long-term monitoring, expanding survey efforts to the broader region, genetic connectivity analyses, habitat modelling, environmental DNA (eDNA) surveys, as well as trophic and reproductive studies.

Long-term monitoring is essential for assessing growth rates and population trends, ideally through mark-recapture techniques (e.g., 68) via the use of PIT tags combined with photo-IDs, which can improve individual recognition efficiency (69). Our study focused on the *H. freycineti* population in the Dampier Strait region and surveys beyond Arborek Island were constrained by limited duration and logistical challenges. To better understand population dynamics, future efforts should encompass the broader region, including the northern and southern Waigeo coasts, southern Raja Ampat (Misool and Kofiau), and Pulau Dua (northern Papuan coast). The use of eDNA offers a promising approach for detecting epaulette shark presence in areas within known or suspected *Hemiscyllium* species' ranges. The use of eDNA has proven effective in identifying elusive species such as sawfishes (*Pristidae*) (70, 71). The use of habitat modelling could further predict important habitats of this species (e.g., 72). Genetic studies are required to assess population connectivity across the species' range, which is likely to be limited given the limited mobility of *H. freycineti* and indeed all epaulette sharks (6). Examination of other small benthic shark species suggests population connectivity is often limited in this guild; for instance, mitochondrial DNA analysis revealed small-scale population structure in the California Horn Shark (*Heterodontus francisci*) (73).

Incorporating technological advancements would be beneficial to improving understanding of fine scale spatial movements, physiological states, and habitat preferences, which are essential for robust conservation actions. For instance, passive acoustic telemetry could provide insights into site fidelity, habitat use, and fine-scale horizontal movements (e.g., 74, 75). The use of biologgers (e.g., 76) could help revealing depth and temperature preferences of *H. freycineti*, as well as their diel activity patterns. Determining female reproductive maturity was hampered by the inability to visually confirm yolk eggs, though egg cases were detected via gentle palpation. Non-invasive ultrasonography could enhance accuracy, as demonstrated in oviparous catsharks (e.g., 77, 78), and hormonal profiling could further elucidate reproductive status (51).

4.7 Limitations

Despite providing important baseline data on *H. freycineti* in Raja Ampat, our study has several limitations. Firstly, our survey effort was unevenly distributed across sites, with the majority of surveys concentrated at Arborek Island. This strongly limits robust site-level comparisons, though we believe the intensive survey effort at Arborek was invaluable in providing the large datasets we were able to analyze for this paper. Secondly, surveys were restricted to shallow intertidal habitats and were undertaken during low tides (≤50 cm depth) at all sites, potentially overlooking deeper habitats such as reef slopes, where *H. freycineti* has been observed sheltering beneath coral structures during daytime dives and nocturnal observations. Therefore, our findings likely underestimate the species' true habitat range and abundance, introducing a sampling bias. Although we have no reason to believe so, it is also possible that males may prefer deeper habitats, which would help explain the significantly female-skewed sex ratio we found of 1.29:1. Finally, our visual method for assessing maturity, especially for females, provides limited accuracy, which necessarily limits our understanding of the reproductive biology of *H. freycineti*. In our study, maturity category of females was determined only based on the presence or absence of egg cases. This may not accurately enough to define the female maturity level. The maturity stages of females Hemiscyllidae species are determined not only from the presence of egg cases but also from condition of the ovary, oviducal glands, and uteri (79).

5 Conclusions

This study provides the first comprehensive insights into the life history (biology, demographic structure, growth) and habitat uses of the endemic Raja Ampat epaulette shark *Hemiscyllium freycineti* in the Dampier Strait region, Raja Ampat. By integrating nocturnal field surveys, photo-identification, PIT tagging, morphometrics, and reproductive assessments, we establish a robust biological and ecological baseline for a previously understudied shark species. Our findings reveal exceptionally high local abundance, a significantly female-biased sex ratio, strong site residency, limited spatial movements, and a distribution confined to shallow mangrove, seagrass, and coral reef habitats. Importantly, coral reefs appear to function as nursery habitat, with juveniles predominating in reefs while adults occupy seagrass and sand habitats, a pattern of ontogenetic habitat partitioning that highlights the importance of coral reefs for recruitment. Seasonal growth patterns and clear ontogenetic differences in growth rates further highlight a life history characterized by relatively fast growth, early maturity, and strong site residency. Given the absence of prior demographic and spatial data, these results provide critical benchmarks for population monitoring, site-based management, and the effective implementation of existing legal protection for *H. freycineti* in Raja Ampat.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was approved by the Animal Care and Use Ethics Committee of the National Research and Innovation Agency (BRIN) under permit number 032/KE.02/SK/02/2024 issued to Mochamad Iqbal Herwata Putra. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

ES: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. RM: Investigation, Writing – review & editing. AWH: Investigation, Project administration, Writing – review & editing. OA: Investigation, Writing – review & editing. IM: Investigation, Writing – review & editing. NS: Investigation, Writing – review & editing. AU: Investigation, Writing – review & editing. LM: Investigation, Writing – review & editing. DM: Investigation, Writing – review & editing. HB: Investigation, Writing – review & editing. NM: Investigation, Writing – review & editing. UM: Investigation, Writing – review & editing. OM: Investigation, Writing – review & editing. DO: Investigation, Writing – review & editing. WM: Investigation, Writing – review & editing. GS: Investigation, Writing – review & editing. LR: Investigation, Writing – review & editing. PM: Investigation, Writing – review & editing. ES: Investigation, Writing – review & editing. MI: Data curation, Validation, Writing – review & editing. DAP: Writing – review & editing, Investigation. AS: Writing – review & editing. F: Investigation, Writing – review & editing. MIHP: Investigation, Data curation, Funding acquisition, Project administration, Writing – review & editing. MVE: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was used in the creation of this manuscript. The author(s) declare that Generative AI (ChatGPT GPT-4.5) and DeepSeek were used to refine and edit the original draft of the manuscript.

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The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frish.2026.1820382/full#supplementary-material

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