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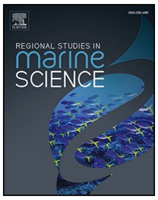

Green turtle foraging patterns revealed by seagrass meadow-centric time-lapse camera and drone surveys

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ABSTRACT

The recent repression of seagrass meadows threatens multiple ecosystem services. Seagrass overgrazing by herbivorous animals, such as green turtles (*Chelonia mydas*), may contribute to seagrass repression. Therefore, the foraging ecology of green turtles is important for understanding their interactions with seagrass meadows and assessing the sustainability of seagrass ecosystems. The diel cycle is a major driving factor of green turtle foraging patterns; however, tidal effects remain less well understood. This study aimed to clarify the influence of diel and tidal cycles on green turtle foraging in seagrass meadows by integrating time-lapse camera and drone surveys. Specifically, the timing and density of green turtle visits to a seagrass meadow on Ishigakijima Island, Yaeyama Islands, Japan, were investigated during 2023–2024. The presence or absence of green turtles in the time-lapse camera data indicated that the bimodal diel foraging activities peaked at 6:00–08:00 and 16:00–18:00. In addition, the green turtle observation probability in the time-lapse camera data and the density estimated from the drone surveys increased as the tide level increased. The results showed that more green turtles aggregated to forage in the seagrass meadow when access to seagrass was available during high tide. Furthermore, green turtle density tended to increase during these two years. The seagrass meadow-centric approach using time-lapse camera and drone surveys is set to complement individual-based biotelemetry and biologging techniques to reveal green turtle foraging ecology. This approach is also important for monitoring herbivores in seagrass meadows and considering their coexistence and conservation management.

1. Introduction

Seagrass meadows have been recognized for providing various ecosystem services, including carbon sequestration (Fourqurean et al., 2012; Duarte et al., 2013), coastal erosion mitigation (Christianen et al., 2013; Ondiviela et al., 2014), and nursery habitat provision for marine organisms (McDevitt-Irwin et al., 2016). Recently, a global decline in seagrass meadows has been attributed to various human activities, such as coastal development (Waycott et al., 2009). In addition, seagrass overgrazing by herbivorous animals has been identified as a major factor contributing to the collapse of seagrass meadows and degradation of their functionality (Carnell et al., 2020; Christianen et al., 2023). Understanding the interactions between seagrass meadows and herbivores is important for assessing their coexistence and the sustainability of seagrass meadows.

Green turtles (*Chelonia mydas*), which are known to graze on seagrass, have recently been reported to overgraze seagrass meadows in several regions globally (Christianen et al., 2014; Fourqurean et al., 2019; Gangal et al., 2021; Hsu et al., 2024). Although moderate seagrass grazing has been shown to enhance nutrient uptake and productivity within seagrass ecosystems (Jackson et al., 2001; Christianen et al., 2012), the recent increase in green turtle populations (Hays et al., 2024) has raised concerns regarding potential negative impacts on these habitats. The green turtle, which has been listed as Endangered on the International Union for the Conservation of Nature (IUCN) Red List since 2004, downlisted to Least Concern in October 2025 (Wallace and Broderick, 2025).

Understanding the interactions between seagrass meadows and green turtles necessitates an examination of green turtle foraging ecology, specifically in the timing and density of turtle visits to seagrass meadows. The diel cycle greatly impacts green turtle foraging patterns (Ogden et al., 1983; Taquet et al., 2006; Ballorain et al., 2013; Okuyama

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et al., 2013, 2025; Christiansen et al., 2017). However, the tidal effects are not well understood, although its importance in determining access to foraging sites and avoidance of shallow areas has been acknowledged (Brooks et al., 2009; Pillans et al., 2021). Even when diel foraging patterns have been observed, tidal effects cannot always be excluded, as Chambault et al. (2020) showed that the distance of green turtles to the shore varies with both the diel cycle and tide level. A comprehensive understanding of the diel and tidal foraging activities of green turtles in seagrass meadows is necessary to understand their interactions with seagrass meadows.

The Yaeyama Islands, located in the northwestern Pacific, serve as both nesting beaches (Okuyama et al., 2020, 2025) and foraging grounds for green turtles (Okuyama et al., 2013; Kameda et al., 2023). The increase in foraging green turtles (Kameda et al., 2023) and degradation of seagrass meadows, likely attributed to green turtle grazing (Inoue et al., 2021; Miyajima et al., 2025), have been documented in this region. Biotelemetry and biologging techniques (i.e., transmitters and data loggers) demonstrated that green turtles in Yaeyama exhibit bimodal foraging activities in seagrass meadows that peak at 05:00–09:00 and 17:00–19:00, with no significant tidal effects (Okuyama et al., 2013, 2025). These techniques have primarily focused on examining green turtle foraging behavior; however, tracking a limited number of turtles constrains the ability to elucidate specific seagrass meadow utilization. Seagrass meadow-centric information on green turtle movement and foraging is essential for comprehensively understanding the green turtle foraging ecology in seagrass meadows.

In this study, we aimed to investigate the timing and density of green turtle visits to a seagrass meadow on Ishigakijima Island, Yaeyama Islands, Japan, with particular focus on the influence of diel and tidal cycles. To accomplish this, we employed a seagrass meadow–centric approach that combined time-lapse cameras, which provided continuous daytime presence–absence data, with drone (unmanned aerial vehicle; UAV) surveys, which offered broader spatial coverage of turtle abundance and density. Specifically, we used time-lapse data to examine the effects of diel and tidal cycles on turtle presence, and drone data to assess the relationship between turtle density and tide level. By integrating these complementary methods, we sought to advance understanding of green turtle foraging ecology and provide a framework for monitoring herbivore–seagrass interactions to inform conservation management.

2. Materials and methods

2.1. Study site

The study concentrated on seagrass meadows at the mouth of the Fukido River, Ishigakijima Island, Yaeyama Islands, Japan (24.495°N, 124.225°E; Fig. 1). Ishigakijima Island serves as a major nesting site for green turtles in the Northwest Pacific (Okuyama et al., 2020), while the Fukido River mouth is recognized as a foraging ground for green turtles (Noguchi et al., 2025). Seagrasses are widely distributed in this area, with eight species identified: *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata*, *Enhalus acoroides, Syringodium isoetifolium, Halophila ovalis, Halodule uninervis*, and *H. pinifolia* (Biodiversity Center of Japan, Nature Conservation Bureau, Ministry of the Environment, 2024). However, the degradation of the large seagrass species *E. acoroides* is advancing because of intensive grazing by green turtles (Biodiversity Center of Japan, Nature Conservation Bureau, Ministry of the Environment, 2024).

2.2. Time-lapse camera survey

We installed three sets of time-lapse cameras (Brinno TLC300, Taiwan) in seagrass meadows (Fig. 1). The cameras were covered with waterproof cases and tied to concrete blocks as substrates. The cameras captured images every 10 s from July 13–18, 2023 (Summer 2023), September 29 to October 4, 2023 (Autumn 2023), February 14–21, 2024 (Winter 2024), August 5–12, 2024 (Summer 2024), and October 21–28, 2024 (Autumn 2024).

The green turtles were visually inspected in the collected images. Visual inspection commenced when the effects of camera settings, such as sand swirling, were assumed negligible and concluded when image capture ceased, likely due to low battery capacity or when algae attachment resulted in blurred images and complicated object detection. Because of the challenges in object identification at night, data from 05:30–19:30 were used. The presence or absence of green turtles was recorded in a binary format every 1 h.

2.3. Drone survey

Drone footage data were collected using a DJI Mavic 3 Pro (China) at the seagrass meadows during the following periods: July 4–14, 2023 (Summer 2023), October 24–29, 2023 (Autumn 2023), July 9–15, 2024 (Summer 2024), and October 22–26, 2024 (Autumn 2024). The DJI Fly App was utilized to collect nadir imagery (i.e., gimbal camera angle set

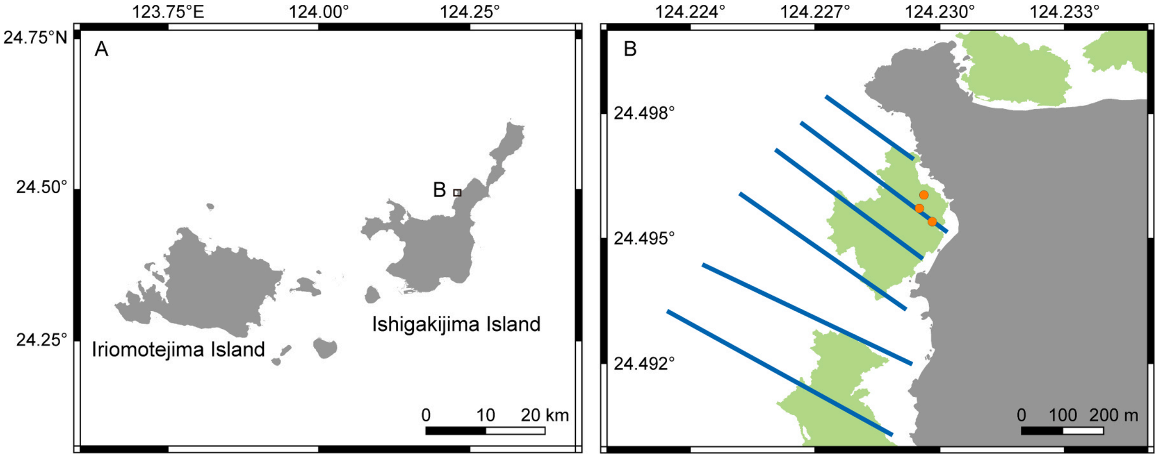

Fig. 1. (A) Map of the Yaeyama Islands, Japan, and (B) study site. Orange circles and blue lines represent time-lapse camera installation locations and drone flight routes, respectively. Green areas denote seagrass meadows identified through satellite imagery from 2018 to 2020, as estimated by the Biodiversity Center of Japan, Ministry of the Environment (data retrieved from http://gis.biodic.go.jp/webgis/ [accessed on September 22, 2025]). The map has been modified from Digital National Land Information (Okinawa Prefecture) available at https://nlftp.mlit.go.jp/ (accessed on July 9, 2025) using QGIS.

to −90°) along six predefined routes (260–630 m per route) (Fig. 1). Flight speed and height were established at 3 m/s and 30 m, respectively, encompassing a 42.23-m band along the routes (0.12 km^2 in total across six routes). The videos were recorded at a resolution of 3840 × 2160 pixels and frame rate of 59.94 fps. Surveys were conducted at 7–10 a.m. and 4–7 p.m., coinciding with the periods when green turtles commonly foraged in this area (Okuyama et al., 2013). Part of the video data was previously used in Noguchi et al. (2025).

The green turtles observed in each drone video (i.e., the route) were counted. Green turtle density was estimated by dividing the turtle counts by the area covered during each flight. Here, not all flights resulted in complete surveys of the six routes because of interruptions caused by sudden rain or obstacle detection; however, the subsequent analysis used data from drone flights that successfully completed all six routes.

2.4. *Data analysis*

Data was analyzed using R ver 4.3.2 (R Core Team, 2023).

Green turtle observation data from time-lapse cameras were utilized to model observation probability through generalized additive modeling (GAM), which assumed a binomial distribution using the mgcv package (Wood, 2017). Smoothers of tide level, hour of day, and their tensor-product interactions were included as explanatory variables. The tide level, indicated as deviations from the reference level, was sourced from the Japan Meteorological Agency. Seasons were also incorporated into the model as five categories (i.e., Summer 2023, Autumn 2023; Winter 2024; Summer 2024; and Autumn 2024). The difference among the three camera installation locations was treated as a random effect. According to Zuur et al. (2009), the importance of this random effect was first evaluated using models fitted by restricted maximum likelihood (REML). Then, the model fitted using maximum likelihood was selected based on the Akaike Information Criterion (AIC) with the MuMIn package ver 1.48.4. The selected model was refitted using REML. The green turtle observation probability in relation to explanatory variables was predicted based on the selected model with the packages gratia ver 0.10.0 and emmeans ver 1.10.6.

Data from drone flights were used to analyze the relationship between turtle abundance and tides, in addition to seasons, via generalized linear modeling (GLM). Turtle counts along all six routes served as response variables, whereas tide level and season (four categories: July 2023, October 2023, July 2024, and October 2024) function as explanatory variables. The negative binomial GLM was performed using the MASS package (Venables and Ripley, 2002) because of the occurrence of overdispersion in the Poisson GLM. The model was selected based on the AIC using the MuMIn package. Estimates based on the selected model in relation to the variables were performed using the emmeans package.

3. Results

For green turtle observation probability based on time-lapse camera data, the camera installation location effect was not supported (with the effect: AIC = 1142.7; without the effect: AIC = 1142.3); therefore, we evaluated the models without the random effect. The lowest AIC value was observed in the model with smoothers for tide level, hour of day, and seasons (Table 1). This model indicated that the probability of observation was higher during the morning (6–8 a.m.) and evening (4–6 p.m.) (Fig. 2). In addition, the observation probability increased as the tide level increased (Fig. 2).

Drone video data were collected from 53 flights (7–19 flights per season), 47 of which were successfully completed along all six routes. The average densities of green turtles were 74.6, 127.4, 122.9, and 134.0 turtles/km^2 in Summer 2023, Autumn 2023, Summer 2024, and Autumn 2024, respectively (Fig. 3 A). The GLM showed that the models incorporating tide level and seasons, as well as those including their interaction, exhibited similar AIC values (319.9 and 319.3, respectively; Table 2); therefore, the simpler model without the interaction was selected. The tide level demonstrated high explanatory power, indicating that more green turtles foraged in the seagrass meadow during high tide levels (Fig. 3B).

Table 1
Five models for green turtle observation probabilities ordered according to lowest AIC values.

Variables	df	AIC	ΔAIC
Hour, Tide, Season	11	1140.3	-
Hour, Tide, Season, (Hour, Tide)	15	1142.5	2.28
Hour, Tide, (Hour, Tide)	12	1153.1	12.88
Hour, Tide	7	1154.8	14.57
Tide, Season, (Hour, Tide)	8	1184.9	44.65

(Hour, Tide) indicates the interaction between the hour of the day and tide level. Bold font indicates the selected model.

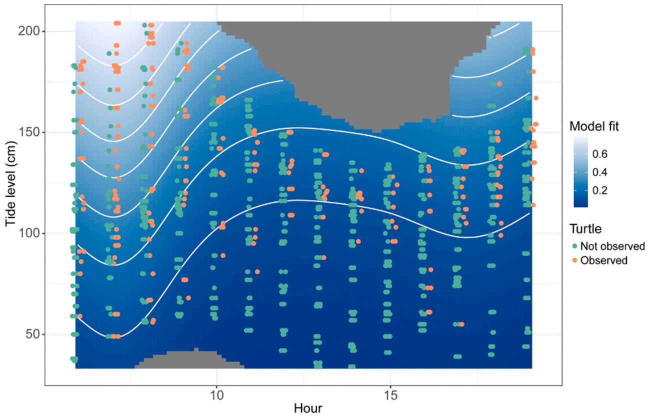

Fig. 2. Contour plot illustrating green turtle observation probability in relation to tide level and hour of day, as predicted by the selected model. Lighter color indicates a higher observation probability. Orange and green points indicate actual data of presence and absence of green turtles, respectively, in time-lapse camera data.

The selected models for green turtle observation probability from time-lapse camera data and green turtle density from drone data included the season as an explanatory variable. The estimated marginal means of both models indicated that the probability and density in Autumn 2024 were significantly higher than those observed in Summer 2023 ($t = 3.93$, $p < 0.001$; $z = 2.74$, $p = 0.031$) (Fig. 4). The observation probability tended to be higher in autumn than that in summer (Fig. 4A); however, the density tended to be higher in 2024 than that in 2023 (Fig. 4B).

4. Discussion

In coastal animals, rhythmic behavior interacts with both the diel cycle and tidal patterns (Krumme, 2009). Green turtles, recognized as coastal herbivores, typically display diel-foraging patterns (Taquet et al., 2006; Ballorain et al., 2013; Okuyama et al., 2013, 2025; Christiansen et al., 2017). Although the tide is considered important for green turtles in moving through channels and avoiding the shallowest areas during low tide (Brooks et al., 2009; Pillans et al., 2021; Mestre et al., 2025), the effects of tides on green turtle foraging behavior are not consistently clear (Okuyama et al., 2013, 2025; Webster et al., 2024). However, this study demonstrated that the green turtle observation probability and density increased with rising tide levels, thereby indicating that more green turtles aggregated for foraging in a seagrass meadow on Ishigakijima Island during high tide. The high probability and density of green turtle observations during high tide can be attributed to increased access to seagrass meadows, as indicated by Chambault et al. (2020).

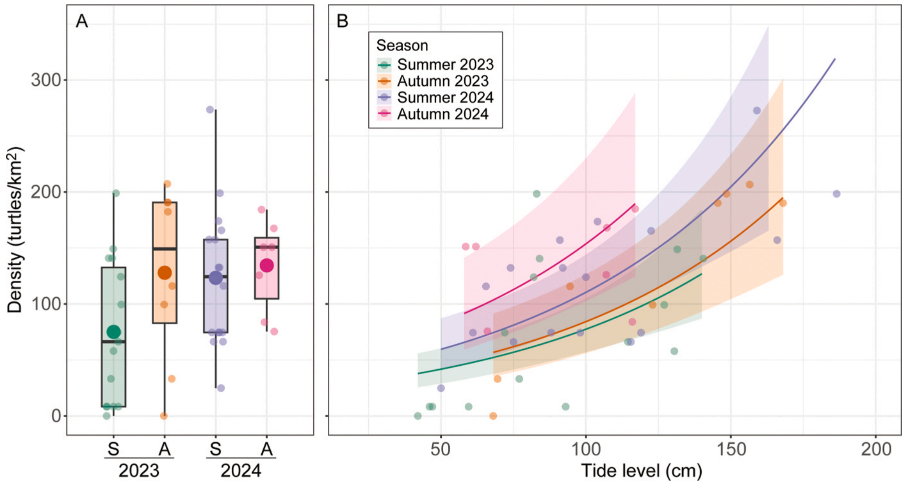

Fig. 3. (A) Boxplots illustrating green turtle density observed across four seasons, with large circles representing the average and small circles indicating raw data for each drone flight; (B) Green turtle density in relation to tide level. Lines and shades indicate estimates and 95% confidence intervals of the selected model.

Table 2

Models for green turtle density ordered according to lowest AIC values.

Variables	df	AIC	ΔAIC
Tide, Season, (Tide, Season)	9	319.3	-
Tide, Season	6	319.9	0.61
Tide	3	322.0	2.77
(Null)	2	336.4	17.10
Season	5	337.1	17.84

(Tide, Season) indicates the interaction between tide level and season. (Null) indicates a null model that includes solely the intercept term. Bold font indicates the selected model.

In addition to the effect of tide level, the diel cycle of green turtle foraging was also supported in this study. The relatively high observation probability in the seagrass meadow during the morning and evening was consistent with the bimodal foraging pattern reported in previous studies (Ogden et al., 1983; Okuyama et al., 2013, 2025). In fact, when the tide level was 50–80 cm, green turtles were occasionally observed in the seagrass meadow during the morning and evening, despite their absence during daytime. This indicated active foraging in the morning and evening. In green turtles, shallower dives during the daytime compared to those at nighttime are typically interpreted as indicative of diurnal foraging or active behavior (Hazel et al., 2009; Ballorain et al., 2013). Even shallower dives at dawn and dusk (Hazel et al., 2009) may reflect active foraging during these periods, as observed in the present study.

Recent investigations into the foraging behavior of wild green turtles have primarily utilized biotelemetry and biologging techniques. These techniques enable continuous tracking of green turtle behavior over extended periods; however, tracking a relatively small number of turtles limits a comprehensive understanding of seagrass meadow utilization by green turtles. Instead, time-lapse cameras and drones were employed for seagrass meadow-centric green turtle surveys in this study. Drone surveys have recently become an effective methodology for monitoring coastal animals, including sea turtles (Hsu et al., 2024; Yamaguchi et al., 2024; Noguchi et al., 2025), dugongs (Hodgson et al., 2013; Yamato et al., 2024), and sharks (Colefax et al., 2019). Camera traps, which include both time-lapse recordings and motion-triggered recordings, have been widely used to study terrestrial mammals and birds (Burton et al., 2015; Leorna and Brinkman, 2024). Implementing triggering systems for aquatic animals presents a technical challenge (Lahoz-Monfort and Magrath, 2021); however, time-lapse recordings offer valuable insights into green turtle foraging behavior.

Although this study supports the effects of tide level and diel cycle on green turtle foraging on Ishigakijima Island, green turtle foraging

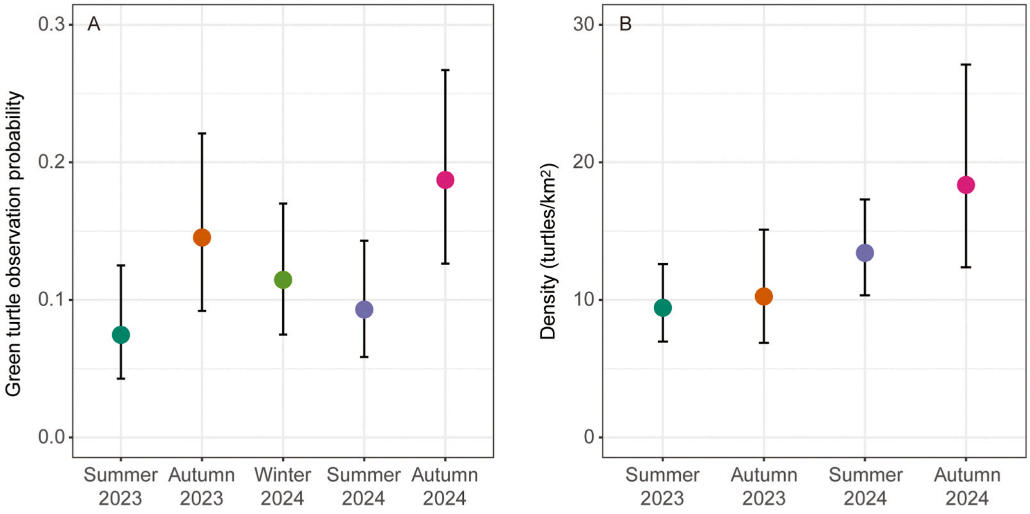

Fig. 4. Differences in (A) green turtle observation probability and (B) green turtle density among seasons evaluated as estimated marginal means of selected models. Bars indicate 95% confidence intervals.

behavior can vary geographically and individually (Heithaus et al., 2007; Chambault et al., 2020). Movement through tidal channels is crucial for accessing foraging areas in Baja California, Mexico; however, the diel cycle of activity is not clear (Brooks et al., 2009). The seagrass meadow surveyed in this study was accessible without traversing channels, suggesting that diel foraging patterns were not restricted. The habitat preferences of green turtles depend on individual body conditions and associated risk factors, indicating that those in suboptimal conditions tend to take greater risks in pursuit of high-quality food (Heithaus et al., 2007).

Seagrass overgrazing by green turtles, probably due to population recovery, has recently been reported across multiple seagrass meadows (Christianen et al., 2014; Fourqurean et al., 2019; Gangal et al., 2021; Hsu et al., 2024). In severe cases, green turtle density exceeds 1000 turtles/km^2 (Christianen et al., 2014; Gangal et al., 2021). The density in this study (74.6–134.0 turtles/km^2 on average) was moderate and comparable to that of other foraging aggregates (Roos et al., 2005; Mancini et al., 2015; Yamaguchi et al., 2024). However, as the diel cycle and tide level may influence green turtle foraging patterns, the time and tidal conditions of density estimation are critical for accurately estimating and comparing its abundance. Given the observed seagrass repression in the Yaeyama Islands (Inoue et al., 2021) and nearby Taiwan (Hsu et al., 2024), the seagrass meadows on Ishigakijima Island may be similarly at risk.

Relatively high green turtle observation probability and density were estimated in Autumn 2024, particularly in comparison to those of Summer 2023. This may be attributed to an increasing trend in the abundance of foraging green turtles on Ishigakijima Island, as indicated by density estimates derived from drone data. However, seasonal effects may also influence the foraging behavior of green turtles, as suggested by the lower observation probability in summer compared with that in autumn in time-lapse camera data. Adult turtles may leave foraging areas for reproduction in the summer (Joseph et al., 2023). Consequently, the observation probability in relatively shallow areas near time-lapse cameras decreases in summer, although small turtles tend to use shallower areas than those used by large turtles (Hazel et al., 2009). Nonetheless, continuous monitoring is important to elucidate seasonal effects and trends in abundance.

In summary, this study demonstrates that green turtle foraging in Ishigakijima seagrass meadows is shaped by both tide level and diel cycle, with higher densities observed during high tide and crepuscular periods. Conducting nighttime surveys presented challenges in this study; however, by combining time-lapse cameras and drone surveys, we introduced a seagrass meadow-centric monitoring framework that complements individual-based telemetry and provides population-level insights into turtle–seagrass interactions. For managers, these findings underscore the importance of accounting for tidal stage and time of day when estimating turtle abundance, as survey timing can strongly influence density estimates. Incorporating such considerations into monitoring programs will improve the accuracy of population assessments and support conservation strategies that balance turtle population recovery with the long-term resilience of seagrass ecosystems.

CRediT authorship contribution statement

Naoya Noguchi: Investigation. **Haruki Murai:** Formal analysis. **Iwao Tanita:** Writing – review & editing, Investigation. **Junichi Okuyama:** Writing – review & editing, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Hideaki Nishizawa:** Writing – original draft, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of Competing Interest

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

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Data availability

Data will be made available on request.

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