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Intensive grazing by green turtles depletes seagrass meadows and constrains turtle growth in Kume Island, Japan

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Conservation efforts have led to substantial recovery of green turtle (*Chelonia mydas*) populations globally, yet over- or intensive grazing by these megaherbivores is now degrading seagrass ecosystems. We assessed the impacts of turtle-driven grazing and its feedback on turtle nutritional status and growth at Kume Island, Japan, through a comprehensive study conducted between autumn 2023 and spring 2025. Our approach combined seagrass surveys, drone-based density estimation, capture–recapture studies, and stomach content analysis. The surveys revealed a 50.6% reduction in seagrass area since the 1990s, alongside a species shift from mid-sized, long-lived taxa (*Thalassia hemprichii*) to small, fast-growing species (*Halophila ovalis*). This species shift was consistent with changes observed in the turtles' diet composition. The foraging aggregation was dominated by immature turtles, with turtle densities reaching 452.6 individuals per km^2, among the highest reported. Body condition indices from 342 captured turtles revealed temporal fluctuations, with severe emaciation in autumn 2023 and spring 2025. The mean growth rate in straight carapace length was only 0.31 ± 1.57 cm/year, substantially lower than other foraging populations. Collectively, our findings demonstrate that intensive grazing by green turtles has fundamentally altered the structure of seagrass habitats, with direct negative feedbacks on turtle nutritional status and growth performance.

Keywords Ecosystem management, Herbivore–seagrass interactions, Isolated oceanic island, Overgrazing mitigation, Sea turtles

Intensive grazing resulting from the rapid population increase of large herbivores has been increasingly reported across a wide range of terrestrial taxa in recent years (e.g., cervids[1]; kangaroos[2]). In severe cases, overgrazing leads to pronounced shifts in vegetation structure and composition, soil erosion, and subsequent nutrient depletion, potentially driving ecosystems into alternative stable states characterized by persistently low productivity[1]. In environments with limited food resources, such as remote islands, overgrazing can cause ecosystem collapse, ultimately leading to food depletion and population crashes of the herbivores themselves (e.g., reindeer *Rangifer tarandus*[3]; sika deer *Cervus nippon*[4]. Similarly, in marine ecosystems, overgrazing by herbivores such as sea urchins and herbivorous fishes has caused widespread degradation of benthic habitats, often referred to as 'barrens'[5–7]. Sea urchins generally exhibit limited and context-dependent mobility, with movement behavior strongly influenced by food availability[8]. Under conditions of high-density grazing and resource depletion, food limitation has been shown to affect their growth rates and population structure, and may contribute to density-dependent feedbacks that stabilize overgrazed states[9]. In contrast, mobile herbivores may be able to leave depleted feeding sites and search for alternative foraging areas. Indeed, in species such as green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*), rotational feeding behavior, which is named cultivation grazing, has been suggested to prevent complete depletion of seagrass resources[10,11]. However, even for mobile herbivores, when their feeding habitats are located in submerged coastal feeding habitats (e.g. seagrass meadows) around isolated oceanic islands where movement to other regions is difficult, the availability of food resources is expected to be

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limited, similar to that on remote terrestrial islands. In such cases, individuals are likely to eventually leave the depleted feeding grounds and migrate to distant new habitats[12]. During this transition, continued foraging can progressively reduce local resource availability before individuals relocate. Nevertheless, little is known about how the trade-off between nutritional gain through foraging and resource depletion unfolds over time.

Following decades of concerted conservation efforts, populations of large marine herbivores, particularly green turtles, have increased in several regions worldwide[13–16]. Consequently, the IUCN Red List category for green turtles was downgraded from Endangered to Least Concern in 2025[17]. Green turtles are voracious herbivores, and their grazing pressure influences seagrass meadow structure (patch dynamics), productivity, and species composition[11,18,19]. Their population recovery has been accompanied by an increase in reports of seagrass meadows experiencing high grazing pressure at turtle foraging grounds across the globe, including the Lakshadweep Islands[20,21], Bermuda[22,23], Derawan Island[24,25], Iriomote Island[26], and Taiping Island[27]. Among these locations, the Lakshadweep Islands, Derawan Island, and Bermuda have experienced catastrophic seagrass meadow degradation due to intense grazing by green turtles[28]. Green turtles are capable of long-distance migrations; however, they also exhibit strong site fidelity to specific foraging grounds, repeatedly utilizing the same areas over extended periods[29–31]. This fidelity likely promotes the continuous use of particular feeding patches[23]. By engaging in cultivation grazing, turtles can prevent the complete depletion of food resources. Furthermore, such cultivation grazing has been reported to increase the nitrogen leaf content of certain seagrass species[11]. However, when sustained heavy grazing persists over long periods, it has been shown to reduce the biomass of long-lived, mid-sized seagrass species and consequently induce shifts in seagrass community composition from these species to fast-growing pioneer species[11,21]. Ultimately, the shoot densities of these pioneer species also decline, and turtles begin excavating rhizomes to consume the more nutritious belowground tissues. This process eventually results in the collapse of seagrass meadows, triggering turtle migrations to new foraging grounds[12]. Despite these observations, quantitative assessments of the impacts of near-collapse seagrass meadow conditions on the nutritional status and growth rates of green turtles remain limited.

The present study was conducted at Kume Island, located in the central Ryukyu Archipelago, Japan (Fig. 1). The island is an isolated oceanic island with an area of approximately 60 km^2, with no other islands or landmasses within a 30 km radius. Previous surveys in the 1990s[32] reported abundant seagrass meadows in the inner reef areas along the southwestern and eastern coasts of the island (Fig. 1), consisting of species such as *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata*, *Syringodium isoetifolium*, *Halodule uninervis*/*pinifolia*, and *Halophila ovalis*, along with seaweed beds of *Sargassum polyporum*[32,33]. At present, however, a noticeable decline in seagrass meadows is visually evident in these areas. Moreover, according to local fishermen, the number of green turtles observed in the seagrass meadows has apparently increased. Furthermore, an increase has also been reported at nearby green turtle nesting sites[34,35].

This study aimed to quantitatively assess the current state of seagrass meadows and green turtle foraging populations at Kume Island, where seagrass decline due to turtle intensive grazing has been suspected. Furthermore, we investigated the effects of seagrass meadow degradation on the nutritional condition and growth rates of green turtles. To achieve these objectives, we conducted a comprehensive, multi-faceted study that included: (1) seagrass area assessment based on underwater surveys and machine learning analysis of aerial imagery; (2) estimation of green turtle population density using drone-based line transect surveys; (3) capture surveys to evaluate turtle size structure, nutritional status, and growth rates; and (4) stomach content analysis to examine dietary composition.

Results

Seagrass bed area, species composition, and morphology

Assessment of seagrass area based on underwater surveys and machine-learning analysis of aerial imagery revealed that the total seagrass bed area in both the eastern and western parts of Kume Island decreased from 0.867 km^2 in 1997–1998 to 0.439 km^2 in 2024, representing a 50.6% reduction (Fig. 1a). Although the total seagrass area remained similar between 2021 and 2024, species composition and dominant species changed markedly during this period (Tables 1, S1). Underwater seagrass surveys conducted at 37 locations in 2021, 117 locations in 2024, and 99 locations in 2025, together with visual assessments of aerial imagery at 51 locations, demonstrated that *Thalassia hemprichii* had disappeared from Eef Beach and Torishima by 2021, where it had previously been reported[31]. In contrast, *T. hemprichii* remained dominant at Oujima in 2021 (Table S1; Fig. S1). However, by 2024, nearly all *T. hemprichii* had also disappeared from Oujima (Table S1), with only small remnants observed around rocks and corals. In other areas (Maja, Gima, and Hatenohama), *T. hemprichii* was also rarely observed in 2024 (Table S1). Between 2021 and 2024, *Halophila ovalis* and *Halodule uninervis*/*pinifolia* became the dominant species, replacing *T. hemprichii* (Table 1, S1; Fig. 1b,c). In addition, the presence of *Cymodocea serrulata* and *Syringodium isoetifolium* was confirmed during other surveys conducted in 2021 (Fig. 1b), although these species were not observed within the quadrats. The kappa coefficient representing the accuracy of the aerial imagery analysis was 0.31 for Kume Island as a whole, indicating fair agreement between the seagrass meadow distribution maps and underwater survey data. In contrast, the kappa coefficient for the Maja seagrass bed was 0.58, indicating moderate agreement (Tables S2, S3, Figs. S2, S3).

To examine whether seagrass decline was caused by grazing by green turtles, turtle exclusion cages were installed in November 2024. One year after cage installation, seagrass coverage, biomass, and leaf length differed markedly between areas inside and outside the cages. Mean seagrass coverage within quadrats (± standard deviation [SD]) inside the cages was 78.0 ± 6.2% ($n = 5$), which was significantly higher than that outside the cages (6.2 ± 3.8%, $n = 5$) (Table S4; Figs. S4, S5). In addition, mean seagrass dry weight (DW ± SD) inside the cages was 33.6 ± 9.3 g DW m^{-2} ($n = 5$) for aboveground biomass and 71.1 ± 30.9 g DW m^{-2} ($n = 5$) for belowground biomass. In contrast, outside the cages, mean DW was 3.3 ± 1.4 g DW m^{-2} ($n = 5$) for aboveground biomass and 4.4 ± 2.2 g DW m^{-2} ($n = 5$) for belowground biomass (Table S5). Both above- and belowground biomasses were

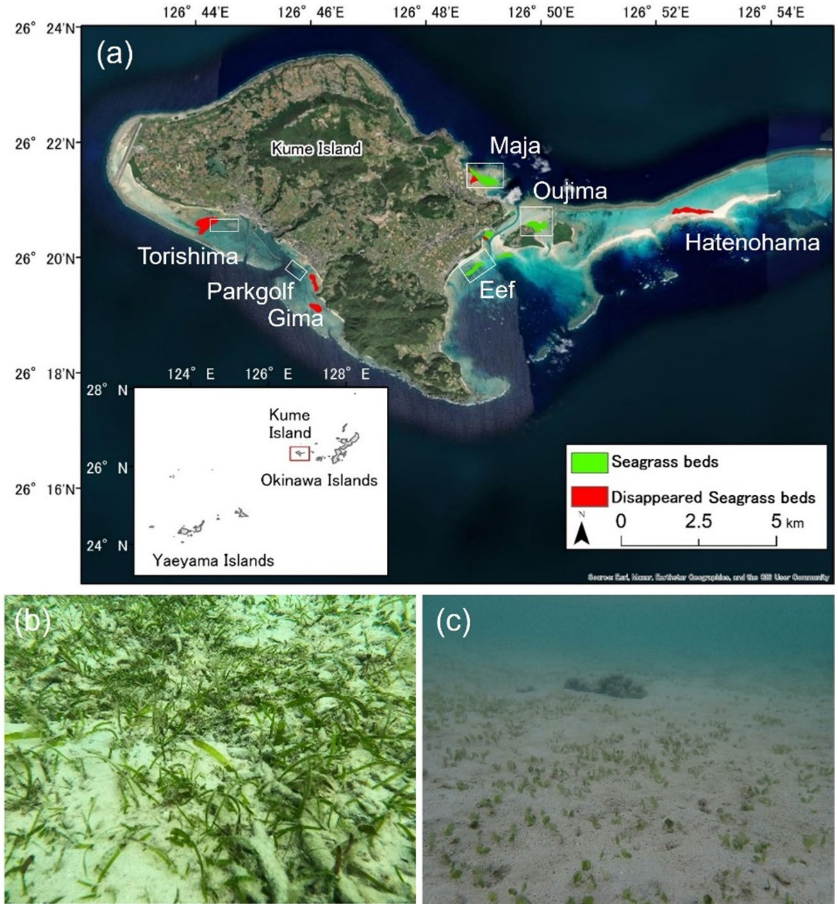

Fig. 1. (**a**) Map of Kume Island. The areas outlined by white rectangles indicate the survey sites for the capture survey and/or drone-based population density surveys. For details of the drone transect lines, see Fig. S6. Green areas represent seagrass meadows confirmed in 2024, while red areas indicate regions where seagrass meadows were present in 1997 but had disappeared by 2024. Satellite image sources: Esri, Maxar, Earthstar Geographics, and the GIS User Community. Changes in seagrass species composition at Eef area on the eastern side of Kume Island: (**b**) dense seagrass dominated by *Halodule uninervis/pinifolia*, *Thalassia hemprichii*, *Cymodocea serrulata*, and *Syringodium isoetifolium* in October 2021, and (**c**) sparse seagrass dominated by *Halophila ovalis* in November 2024.Note: This photograph shows an area where *H. ovalis* was relatively abundant and does not represent seagrass meadow conditions across Kume Island as a whole.

Year	Seagrass area (km^2)	Species occurrence	Dominant species	References
1992	N/A	Th, Cs, Cr, Si, Ho, Hu/p, Zj	Th, Cs, Si	[31]
1997–1998	0.867	N/A	N/A	[32]
October 2021	0.439	Th, Cs, Hu/p, Si, Ho	Th, Ho, Hu/p	This study
November 2024	0.439	Th, Ho, Hu/p	Ho, Hu/p	This study
August 2025	N/A	Th, Ho, Hu/p	Ho, Hu/p	This study

Table 1. Changes in Seagrass area and species composition in the coastal area of Kume Island. Th (*Thalassia hemprichii*), Cs (*Cymodocea serrulata*), Cr (*Cymodocea rotundata*), Si (*Syringodium isoetifolium*), Ho (*Halophila ovalis*), Hu/p (*Halodule uninervis/pinifolia*), Zj (*Zostera japonica*)

significantly greater inside the cages than outside (Table S5), indicating substantial seagrass recovery within 1 year following cage installation. Furthermore, mean leaf length (± SD) of *Thalassia hemprichii* was 109 ± 26 mm ($n = 6$) inside the cage (Cage 5), compared with 24 ± 12 mm ($n = 6$) outside the cage, where *T. hemprichii* was only sparsely observed (Table S5). Similarly, mean leaf length of *Halophila ovalis* was 14.8 ± 0.5 mm ($n = 6$) inside the cage and 11.9 ± 1.3 mm ($n = 6$) outside the cage, while *Halodule uninervis/pinifolia* exhibited mean leaf lengths of 82.9 ± 12.2 mm ($n = 6$) inside the cages and 46.0 ± 10.7 mm ($n = 6$) outside the cages (Table S6). Leaf lengths of all three species were significantly greater inside the cages than outside (Table S6).

Site	Area (km^2)	Density (turtles/km^2)		
		Autumn 2023	Summer 2024	Autumn 2024
Maja	0.1779	452.6	334.9	406.4
Oujima	0.2385	256.4	185.1	277.9
Eef	0.0848	179.6	121.3	194.6
Parkgolf	0.0344	190.0	100.7	201.1

Table 2. Average green turtle density at four sites in Kume Island.

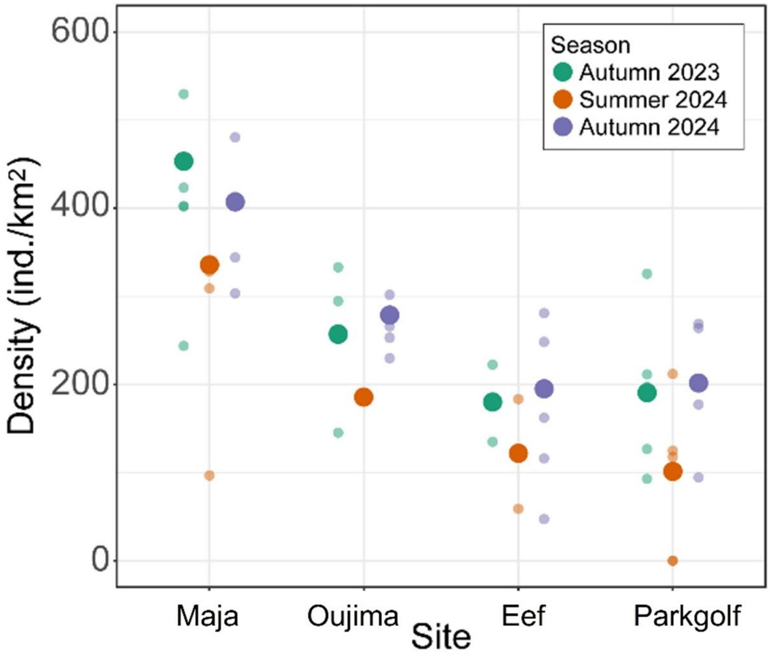

Fig. 2. Estimated population densities of green turtles foraging in four areas of seagrass meadows in Kume Island. Large circles indicate overall means of each season, whereas small circles indicate densities estimated for each flight.

Population densities of green turtles foraging in seagrass meadows

Drone-based line transect surveys revealed that green turtle density varied among sites and seasons, with the highest mean density observed at Maja (Fig. S6) (334.9–452.6 turtles/km^2; Table 2). Moderate densities were recorded at Oujima adjacent to Maja (185.1–277.9 turtles/km^2), while lower densities were found at Eef beach and Parkgolf (100.7–201.1 turtles/km^2; Table 2). Across all sites, turtle density tended to peak in autumn and was comparatively low during summer 2024 (Fig. 2).

Turtle size, body condition and growth rate

In total, 394 turtles were captured, including 347 individuals captured once, 43 recaptured twice, three recaptured three times, and one recaptured four times. The mean straight carapace length (SCL ± SD) of turtles captured for the first time was 54.6 ± 11.5 cm, ranging from 37.6 to 101.6 cm ($n = 347$; Fig. 3). For the 342 turtles for which body weight (BW) was recorded, the mean body condition index (BCI ± SD) was 1.22 ± 0.16, with values ranging from 0.67 to 2.05. BCI differed significantly among survey periods (one-way ANOVA, $F_{4,337} = 6.1$, $P < 0.001$; Fig. 4). The mean BCI was lowest in autumn 2023, recovered between winter and autumn 2024, and declined again in spring 2025 (Fig. 4). For turtles recaptured more than twice with an interval exceeding 180 days, the mean initial SCL (± SD) of the recaptured turtles ($n = 20$) was 55.1 ± 12.6 cm. Their mean growth rates in SCL ($n = 20$) and BW ($n = 16$) were 0.31 ± 1.57 cm/year and 0.67 ± 2.05 kg/year, respectively.

Stomach contents

The volume of entire stomach contents from 12 green turtles ranged from 6.9 ml to 270.4 ml, as the measurement from one individual was unavailable (Table S7). The dry weight of the sorted contents from 13 turtles ranged from 0.8 g to 30.8 g (Table S7). The diet comprised two species of mid-sized seagrasses (*Thalassia hemprichii*, *Cymodocea rotundata*), two species of small, fast-growing seagrasses (*Halophila ovalis*, *Halodule uninervis/pinifolia*), 11 species or genera of red algae (*Laurencia* spp., *Digenea simplex*, *Ceratodictyon spongiosum*, etc.), four species of brown algae (*Sargassum polyporum*, etc.), two species of green algae (*Dictyosphaeria cavernosa*,

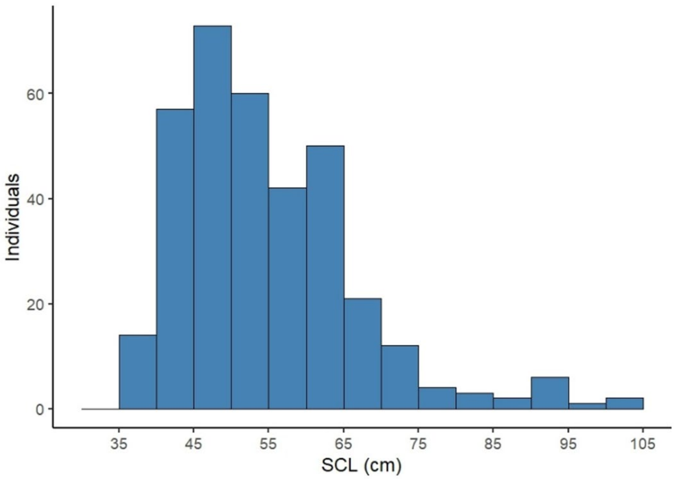

Fig. 3. Histogram of straight carapace length (SCL) of green turtles captured at the first time ($n = 347$) in seagrass meadows of Kume Island.

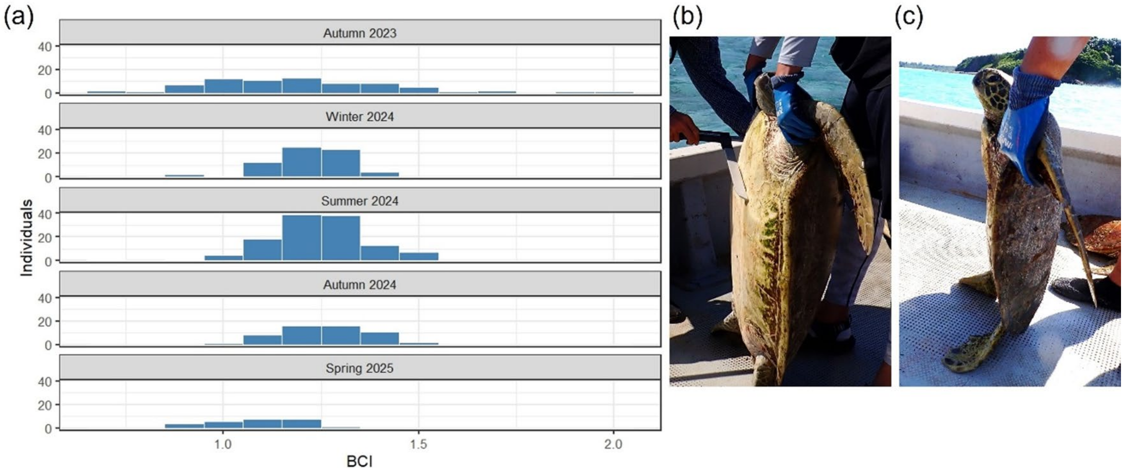

Fig. 4. (**a**) Temporal variation in body condition index (BCI) values of green turtles captured in seagrass meadows of Kume Island. Photographs show representative individuals with BCI values of (**b**) 1.4 and (**c**) 0.67.

etc.), animal matter (gelatinous organisms and eggs), and plastic debris (fragments of plastic bags and strings) (Table S7). Seagrasses and red algae were the primary dietary components, accounting for 44.7% and 43.1% of the total dry weight across all individuals (Table S7). Moreover, the frequencies of occurrence (FO) of them occupied 76.9% and 92.3%, whereas those of brown and green algae were 7.7% and 15.4%, respectively (Table S7). Animal matter and plastic debris accounted for only 1.3% and 0.9% of the mean dry weight proportion, respectively, and their FO were 46.2% and 15.4%, respectively. Some turtles exhibited dietary specialization: in certain individuals, seagrasses comprised over 80% of stomach contents by weight, whereas others consumed predominantly red algae with no seagrass present (Table S7). Temporal analysis showed that mid-sized seagrasses accounted for 32.6% of diet dry weight in autumn 2023, but their contribution declined to approximately 1% after summer 2024 (Fig. 5, Table S8). The dry weight proportions of major dietary items differed significantly among sampling periods ($\chi^2 = 148.1$, $P < 0.001$).

Discussion

Our study suggests that the disappearance of mid-sized seagrass species around Kume Island began around 2018, although these species persisted with some biomass until approximately 2021. Our turtle exclusion cage experiment clearly demonstrated that the degradation of seagrass meadows around Kume Island was caused by intensive grazing by green turtles. In nearby areas of the Ryukyu Archipelago, severe depletion of seagrass meadows was first documented in 2009 at Iriomote Island, part of the Yaeyama Islands located 360 km southwest of Kume Island (Fig. 1)[26,36]. Furthermore, at Kuro Island, also in the Yaeyama Islands, the foraging population of green turtles approximately tripled between 2010 and 2020[37]. These findings imply that by around 2009, green

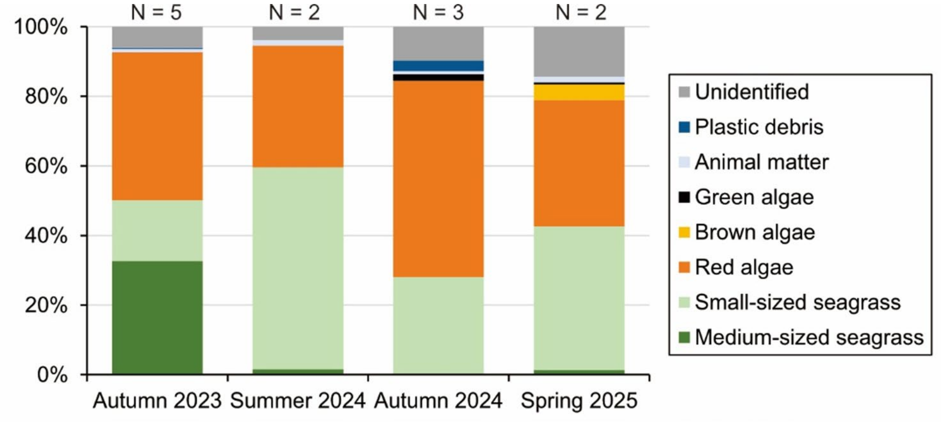

Fig. 5. Temporal changes in the major dietary components of green turtles, shown as the proportion of dry weight around Kume Island. The numbers above the bars indicate the number of sea turtles surveyed during each period.

turtle densities around the Yaeyama Islands had already reached levels capable of inducing intensive grazing. As turtle populations continued to grow, grazing impacts may have progressively expanded northward along the Ryukyu Archipelago from Iriomote Island to Kume Island after 2010, mirroring patterns observed in the Lakshadweep Archipelago, India, where overgrazing sequentially caused widespread seagrass meadow collapse across five atolls[21]. The Ryukyu Archipelago and the Lakshadweep Archipelago share the common feature of consisting of isolated oceanic islands. In such island systems, available food resources—particularly seagrass patches—are spatially limited and fragmented, rendering them more susceptible to depletion under intense grazing pressure. Consequently, these environments are prone to sequential overgrazing, in which grazing impacts progressively expand across spatially discrete habitats, as observed in the Lakshadweep Archipelago[21].

Our turtle exclusion cage experiment demonstrated substantial recovery of seagrass, including the medium-sized species *T. hemprichii*, within one year after installation, as evidenced by increases in percent cover, biomass, and leaf length, despite potential reductions in light availability and water flow caused by algal growth on the mesh cages (Fig. S5). Our results further indicate that the near absence of *T. hemprichii* outside the cages reflects grazing rates by green turtles that exceed the recovery capacity of this species, ultimately leading to its local disappearance. In contrast, the persistence of small-sized species such as *H. ovalis* and *H. uninervis/pinifolia* under high green turtle densities likely reflects their role as pioneer species with rapid growth and recovery rates[11,21].

The kappa coefficients for estimating seagrass meadow area using aerial image analysis were relatively low for both Kume Island as a whole and the Maja seagrass meadow. This outcome is likely attributable to the fact that, by the time of image acquisition in 2024, most seagrass meadows had already transitioned to low-coverage states dominated by small-sized species. Such meadows are difficult to reliably distinguish using aerial imagery, which likely reduced classification accuracy and resulted in only fair agreement. Nevertheless, based on ground-truth underwater survey data and visual interpretation of the aerial images, there is little doubt that seagrass meadow area around Kume Island has declined markedly compared with past conditions.

Stomach content analysis revealed that since summer 2024, green turtles have shifted their primary diet from mid-sized, long-lived seagrass species to small, fast-growing species. This dietary shift coincided with changes in species composition observed in seagrass meadow surveys. Indeed, drone observations conducted in 2024 confirmed active foraging in areas dominated by *H. ovalis* and *H. uninervis/pinifolia*. These small-sized species outside the cages exhibited shorter leaf lengths than those inside the cages, where grazing pressure was absent (Tables S5, S6), suggesting that even these fast-growing species were subjected to intensive and continuous grazing by turtles. Similar shifts in seagrass species composition have been reported in other regions, including the Lakshadweep Archipelago and Derawan Island[11,21,38,39]. Such compositional changes and the associated loss of seagrass species diversity are known to weaken ecosystem functions[21].

Our drone surveys indicate that green turtle densities in the seagrass meadows of Kume Island exceeded 300 individuals km^{-2} at the densest site. Green turtle densities in Kume Island were lower than those reported from severely degraded meadows, such as those in Derawan Island[25] and the Lakshadweep Islands[21] (Table 3). Although very high densities have been reported in studies surveying limited areas[27,40,41], the densities observed in this study were comparable to those reported from Taiping Island—where intensive seagrass grazing has been documented—when relatively large areas were monitored[27] (Table 3). Although direct comparisons are constrained by differences in methodology, geography, and survey area size, green turtle densities in Kume Island appear to be sufficiently high to cause intensive grazing of seagrass meadows. When our drone surveys began, mid-sized seagrass species had already disappeared from Kume Island (Tables 1, S1). Considering the previously reported relationship between turtle density and seagrass cover during degradation phases[21], it is plausible that turtle densities around Kume Island were even higher several years prior to our observations. Turtle density declined across all four survey sites during summer 2024 but subsequently recovered in autumn. This temporary decline may have resulted from reduced detectability due to strong winds and waves associated

Location	Area (km^2)	Density (turtles/km^2)		Year	Method	References
		Range	Average			
Kuro Island, Yaeyama Islands	0.063	234.4, 246.2		2021–2022	Drone	69
Taiping Island, South China Sea	0.16–0.19	381–681		2019	Drone	26
	0.035–0.040	1543–1775*		2019	Drone	26
Derawan Island, Indonesia			1540–2060	2008–2011	Boat	24
Lakshadweep Islands, Indian Ocean		1114, 2334*		2007, 2013	Boat	20
		4–520		2014–2020	Boat	20
Key West, Florida, USA	14.6–35.7		3.8 (1.8–8.0) (min)	2003–2012	Boat	70
			58.5 (33.0–103.8) (max)**			
	30		72.5 (61.2–85.8) (juveniles)	2006–2018	Boat	71
			47.3 (38.3–58.5) (adults) **			
Mayotte Island, Western Indian Ocean	0.11–1.60	13–297		2002	Paramotor	39
	0.011		2390 ± 100 (SD)	2004–2005	Snorkeling	72
Marsa Abu Dabbab, Red Sea	0.026–0.052		59.3 ± 47.1 (SE) (min)	2011–2012	Snorkeling	40
			257.2 ± 49.2 (SE) (max)			
Arraial do Cabo, Brazil	0.014		1000 ± 1400	2019	Underwater scooter	73
Guam,	2.58–15.70	0.03–2.08		2008–2012	Aircraft	74
Marianas Islands						

Table 3. Comparisons of population densities of green turtles in the foraging grounds, ranges of point estimates or averages across multiple surveys in years or sites, reported from previous studies. *High densities in the limited years or areas are shown in the different rows. **Density estimation (95% confidence intervals) in which detection probability was considered in distance sampling methods.

with a typhoon shortly before the summer surveys. Given current data limitations, long-term monitoring is essential to assess seasonal and interannual variation.

A global meta-analysis of body condition indices (BCI) in foraging green turtles identified 1.2 as a reliable threshold for adequate nutritional status in both juvenile and adult green turtles[42]. Compared to BCI values reported from other foraging populations[43–46], turtles at Kume Island exhibited significantly lower BCI, indicative of severe emaciation, particularly during surveys in November 2023 and March 2025. The combination of high turtle density, degraded seagrass meadows, and species compositional shifts strongly suggests that this emaciation is a consequence of self-induced intensive grazing. BCI values showed temporary recovery during three surveys conducted in 2024. Although these capture surveys were not directly coupled with drone and seagrass surveys, and thus detailed interpretation remains limited, it is possible that temporary reductions in turtle density increased food availability per individual in 2024.

Our capture-recapture survey clearly indicate that green turtles around Kume Island exhibit restricted growth under conditions of reduced seagrass biomass and a dietary shift toward smaller seagrass species, although potential measurement errors in SCL and body weight (BW) cannot be excluded because the data were collected from a boat. Green turtle growth rates are known to be size-dependent, with particularly rapid growth occurring during the small juvenile stage[43,44,47]. Our results show that most turtles inhabiting the seagrass meadows around Kume Island are small juveniles, with a peak in SCL at the 45–50 cm size class (Fig. 3). Despite the dominance of small juveniles that are typically expected to exhibit rapid growth, their growth rates were notably low. Such extremely low growth rates contrast sharply with those reported from the Yaeyama Islands, where mean annual growth in SCL reaches 2.24 cm/year[48], even though the size composition[48] and diet composition[49] of green turtles in both regions are highly similar. Moreover, green turtles that primarily feed on seagrasses exhibit higher growth rates than those that feed mainly on algae or have mixed seagrass–algae diets[50]. Among previous studies reporting relatively slow growth in green turtles that predominantly consume macroalgae, growth rates for individuals within a comprehensive size class (40–70 cm) ranged from 2.8 to 3.0 cm/year in CCL[51], 1.33 to 2.13 cm/year[52], and 1.0 to 1.4 cm/year in SCL[53]. Even relative to these populations, turtles around Kume Island exhibited lower growth rates. Furthermore, their growth rates were comparable to—or even lower than—those reported for green turtles in the Galápagos Islands, which show the slowest known growth rates (0.03–1.6 cm/year in SCL and − 0.8 to 5.9 kg/year in BW[54]). Growth is also influenced by aggregation density through intraspecific competition[43] and by food resource availability[55,56]. Together, our findings indicate that substantial reductions in available food—driven by declining seagrass biomass in combination with high turtle densities—have led to emaciation and stunted somatic growth in green turtles around Kume Island.

Our comprehensive studies provide clear evidence that intensive grazing by green turtles has substantially altered the structure and species composition of seagrass meadows around Kume Island. The degradation of these meadows threatens associated fish and invertebrate communities and undermines key ecosystem services[21,57]. Indeed, Kume Island has experienced sharp declines in fish catches of seagrass-associated species such as emperor breams (*Lethrinus* spp.) and the collapse of the harvest of mozuku seaweed (*Cladosiphon okamuranus*), a commercially important species that requires seagrass substrates for settlement. Estimated economic losses to fisheries are approximately 200 to 500 million yen annually (Kume Island Fisheries Cooperative Association, personal communication). Exclusion cages have proven effective in protecting seagrasses from turtle grazing in Kume Island as well as other regions[19,25,27,58]. However, on Kume Island, where most seagrass species have already disappeared, little remains to be protected, rendering such measures ineffective. While the need for population management of green turtles within the framework of wildlife management has been highlighted[21,59], legal constraints associated with their endangered status and potential public opposition make implementation extremely challenging. Therefore, developing techniques for large-scale seagrass seedling production and habitat restoration[60] will be critical to promoting the coexistence of green turtles and seagrass ecosystems.

Methods

Seagrass survey

To assess historical trends in seagrass meadow areas around Kume Island, we utilized seagrass distribution data from the 5th National Survey on the Natural Environment of Japan conducted in 1997–1998[33]. Because this survey did not include information on species composition, we referred to additional surveys conducted during the same decade[32]. In the Okinawan waters, including the study area, a hybrid between *Halodule uninervis* and *H. pinifolia* has been reported[61]. As these two species and their hybrid are difficult to distinguish based on external morphology, they were treated collectively as *H. uninervis/pinifolia* in this study. Follow-up underwater seagrass surveys were conducted at Eef and Torishima in 2021, Eef, Torishima, Oujima, Maja, Gima and Hatenohama in 2024 and Oujima and Maja in 2025 at the same sites where seagrass meadows had been identified in the 1997–1998 survey (Fig. 1). During these surveys, species composition and percent cover were assessed using 50-cm quadrats at 253 locations across 2021, 2024 and 2025 (Table S1). To complement the limited number of underwater survey data collected in 2021, aerial imagery acquired at Maja for seagrass area estimation (see below) was also used to confirm the presence or absence of medium-sized seagrass species in that year. Medium-sized species can be distinguished based on their morphological characteristics, whereas species-level identification of small-sized seagrasses is difficult using aerial imagery (Fig. S1).

To further estimate the spatial extent of seagrass meadows, aerial imagery covering the entire seagrass meadow area around Kume Island was acquired in both 2021 and 2024 using a drone (DJI Air 2 S, DJI Technology Co., Ltd.) with a still image resolution of 5472 × 3648 pixels, flown at altitudes of 50–100 m. These images were analyzed using a supervised image classification approach implemented in ArcGIS version 10.8.2 with the Spatial Analyst extension (ESRI, Redlands, CA). Presence–absence data on seagrass obtained from underwater surveys at 154 locations in 2021 and 2024 (Table S1) were used as training data for the classification. In this study, areas with greater than 5% seagrass cover were defined as seagrass beds[62]. Seagrass distribution and species composition derived from the 2021 and 2024 surveys were compared with those reported in the 1990s[32,33].

The accuracy of the aerial imagery analysis was evaluated using presence–absence data from underwater surveys conducted at a total of 243 locations, including 154 locations surveyed in 2021 and 2024 and an additional 99 locations surveyed in 2025 (Table S1). Agreement between the aerial imagery classification results and the underwater survey data was assessed by calculating the kappa coefficient[63]. A kappa coefficient of 0 indicates agreement equivalent to that expected by chance, whereas positive values indicate agreement greater than chance, with a maximum value of 1. Kappa values were interpreted as follows: 0.00, poor agreement; 0.00–0.20, slight agreement; 0.21–0.40, fair agreement; 0.41–0.60, moderate agreement; 0.61–0.80, substantial agreement; and 0.81–1.00, almost perfect agreement[64]. This evaluation was conducted for seagrass meadows around Kume Island, including the Maja site, where seagrass remains in relatively good condition owing to the presence of rocky reef topography.

To examine whether the decline of seagrass meadows observed around Kume Island is attributable to grazing by green turtles, five turtle exclusion cages were installed in November 2024. Each cage measured 3.0 m in length, 1.5 m in width, and 0.6 m in height, and was constructed of wire mesh with a grid size of 10 cm (Fig. S5). The cages were installed at sites where *T. hemprichii* was only sparsely present. One year after installation, in November 2025, percent cover was quantified and seagrass samples were collected using 20-cm quadrats both inside each cage and at a distance of 1 m outside the cages (Figs. S4, S5). Seagrass biomass sampled within the quadrat area (0.04 m^2) was converted to biomass per square meter (1 m^2). In addition, for Cage 5—where *T. hemprichii* was present both inside and outside the cage (Table S5)—six quadrats were established inside and outside the cage, respectively, and leaf lengths of *T. hemprichii*, *H. ovalis*, and *H. uninervis/pinifolia* were measured both inside and outside the cage.

Drone survey for green turtles

The population density of grazing green turtles at four seagrass meadow sites (Maja, Oujima, Eef, Parkgolf; Figs. 1, S6) around Kume Island was assessed using drones (DJI Mavic 3 Pro, DJI Technology Co., Ltd.). Flights were controlled via the DJI Fly App, with drones flown along predefined transect lines (200 to 725 m per line; Fig. S6) while recording nadir-view videos (gimbal angle − 90°). Surveys were conducted in three seasons: Autumn 2023 (October 30 to November 4), Summer 2024 (July 22 to 28), and Autumn 2024 (November 3 to 8). At each site, 2–5 drone flights were conducted per season. Videos were recorded at 3840 × 2160 pixels, 59.94 fps. Flight speed and altitude were set to 3 m/s and 30 m, though some flights began at 10 m altitude, corresponding to ~ 40 m above sea level. Drone surveys were conducted between 7:00–10:00 a.m. and 4:00–7:00 p.m., coinciding with peak foraging times for green turtles[29]. Some of the video data were previously analyzed in Noguchi et al.[65].

Turtles observed along transects were counted. To differentiate turtles from similarly sized coral bommies, videos recorded along the same transects on different days were compared. Stationary objects observed consistently were classified as non-turtles. Although drones were flown at constant altitudes, sea surface height varied across flights; therefore, coral bommies or rocks on the transect lines were used as reference objects to correct height and calculate accurate survey areas from video imagery. Turtle densities at each site were calculated by dividing turtle counts by the corrected survey area. Because not all flights resulted in completion of all the transect lines when it suddenly rained or obstacles were detected, the seasonal mean turtle density for each site was calculated by the two steps: (1) calculating mean density on each transect line, and (2) averaging mean density across all the transect lines.

Capture survey

Capture surveys were conducted during five periods: October 31–November 2, 2023 (Autumn 2023); February 26–28, 2024 (Winter 2024); July 28–30, 2024 (Summer 2024); November 4–6, 2024 (Autumn 2024); and March 21, 2025 (Spring 2025). Surveys were conducted in seagrass meadows, which were largely degraded, in the eastern (Oujima and Maja; Fig. 1) and southwestern (Torishima; Fig. 1) parts of Kume Island. Green turtles were captured either by hand, with a person jumping from a boat (rodeo method)[66], or using a gaff with a modified tip to prevent deep penetration to hook the turtle from the boat, after which they were brought aboard manually by grabbing their flippers. Straight carapace length (SCL, cm) and body weight (BW, kg) were measured on board, and turtles were tagged with PIT and Inconel tags before release. For turtles with BW measurements, the Body Condition Index ($BCI = BW/SCL^3 \times 10{,}000$) was calculated to assess nutritional status[43].

Growth rates (cm/year or kg/year) were calculated for individuals captured more than once by dividing the difference in SCL or BW between capture events by the time interval (in years). Growth data from seven turtles, which were bycaught or stranded and later tagged and released after 2000, were also included. Due to potential measurement errors from onboard data collection, only individuals with a minimum interval of 180 days between captures were included in the growth analysis.

Stomach content analysis

Stomach contents were obtained from 13 green turtles either stranded on beaches or legally caught for food use, with permission from the Fisheries Adjustment Commission of Okinawa Prefecture. SCL ranged from 37.6 to 100.3 cm. Stomachs were removed and cryogenically stored. The stomach contents were rinsed with seawater, and food volume was measured using the volume displacement method[67]. However, the measurement from one turtle was unavailable due to an analytical error. Afterward, they were dried in a 60 °C oven for at least three days. When possible, all contents were sorted; for large volumes, material was spread in a tray, and a random subsample (at least 1/20 of the area) was sorted. Diet items were identified to the lowest taxonomic level possible using a light microscope. Items that were too fragmented or digested to allow identification were classified as "unidentified." The dry weight of each dietary component was recorded, and its proportion relative to the total dry weight was calculated. In addition, the ingested food contents were analyzed using the index of frequency of occurrence (FO), which was calculated as the number of samples containing each food item divided by the total number of samples[68].

Stomach content data were categorized by date of capture or stranding into four periods: Autumn 2023 ($n = 5$), Summer 2024 ($n = 2$), Autumn 2024 ($n = 3$), and Spring 2025 ($n = 3$) (Tables S7, S8). Diet items were grouped into the following categories: small-sized seagrass, medium-sized seagrass, red algae, brown algae, green algae, animal matter, plastic debris, and unidentified material. The percentage dry weight of each category was calculated for each period. Temporal changes in diet composition were analyzed using chi-square tests.

Ethics statement

The study was conducted in accordance with the ARRIVE guidelines. All procedures involving turtle handling, including capture methods, were performed under special permits issued by the Fisheries Adjustment Commission of Okinawa Prefecture (Permit Nos. 5–8, 6-k8) and Okinawa Prefecture (Permit No. 6–42). The research protocol was also approved by the Animal Experimentation Committees of the Fisheries Technology Institute, Japan Fisheries Research and Education Agency (Approval Nos. YA2023-03, YA2024-02).

Data availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Author contributions

J.O., H.N., and K.S. contributed to conceptualization, investigation, data curation, data analysis, visualization, and writing of the original draft. H.S. and N.Y. contributed to investigation, data curation, data analysis, visualization, and writing of the original draft. H.M. contributed to investigation, data curation, and data analysis. Y.T., S.S., and M.T. contributed to investigation. All authors reviewed and edited the manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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