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Research Article

Ecological dynamics and conservation challenges of sea turtle nesting habitats in Turtle Bay of Cilacap, Indonesia

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ABSTRACT

This study investigated the nesting ecology of sea turtles in Turtle Bay, Cilacap, Indonesia, focusing on environmental factors influencing the habitat suitability and nesting behaviours. The aim was to identify the key contributors, such as human activities, predator presence, and vegetation, that affect turtle nesting. Field surveys were conducted across the eight observation stations, analysing environmental parameters. Fishing was identified as the major ecological threat, with a significant impact score of 3, while demographic shifts, pollution, and human modifications were moderate influences, each scoring 2. Light reflection, although currently low (1.63), was noted as a potential future concern. Potential predatory species observed included *Ocypode kuhlii* and *Hippa adactyla*, in addition to domestic cats and dogs, which pose risks to sea turtle populations. Vegetation analyses showed that *Pandanus odorifer, Cocos nucifera*, and *Ipomoea pescaprae* were prevalent, with Sidaurip beach identified as the most suitable nesting area. This site exhibited low scores for pollution, light reflection, and human modification, despite high fishing activity. Additionally, high densities of *Cyperus rotundus, Pandanus odorifer,* and *Ipomoea pes-caprae* were recorded in Sidaurip beach. The findings highlight critical environmental factors that influence sea turtle nesting and provide evidence-based insights for enhancing conservation efforts.

Keywords: Anthropogenic, bay, conservation, ecology, nesting, turtle

INTRODUCTION

Marine turtles are considered migratory species with a complex life history. Their life history involves adult turtles migrating from foraging grounds (FGs) to distant breeding areas known as rookeries. Additionally, ontogenetic changes in marine turtles influence the distribution of juvenile turtles across various marine habitats (Jensen *et al.,* 2013). This research is particularly ground-breaking in the context of Turtle Bay of Cilacap, offering valuable scientific insights into the environmental factors influencing their presence. Building upon this, Pericic and Tanveer (2019) emphasized on the significance of evidence-based conservation, which may involve collecting and analysing the data on past conservation efforts. Such knowledge serves as a foundation for informing future decision-making in conservation activities.

The environmental disturbances directly or indirectly impacting Turtle Bay of Cilacap encompass predatory crabs, human activities such as fishing, poaching, pollution, habitat modification, light reflection, and noise. The majority of sampled stations are significantly affected by these factors, rendering them unsuitable for nesting. For instance, at Station 3 (Weluhan Wetan Beach), a deceased Hawksbill Sea turtle (*Eretmochelys imbricata*) was discovered. The station was marred by pollution, including plastics, as well as environmental degradation such as the excavation of holes and the lighting of fires around nesting sites by fishermen. Dharmawan (2020) demonstrated that turtles often mistake waste, particularly plastic waste, for jellyfish, exacerbating the impact of pollution on their habitat.

Due to the increasing tourism activities in Turtle Bay of Cilacap, numerous nesting stations witness vegetation loss owing to the construction of beach playgrounds and kiosks for residents. The significance of vegetation in nesting sites cannot be overstated, as highlighted by Keim (2007) and Susiarti and Rahayu (2010). These authors underscore the multi-functionality of *Pandanus* species beyond mere beach decoration. *Pandanus* serves as a natural coastal barrier, mitigating wave impact and preventing erosion and abrasion. Furthermore, vegetated beaches play a pivotal role as turtle nesting sites. The serrated leaves offer protection to turtle eggs against predators and create an environment conducive to maintaining optimal temperature and humidity for incubation process, ensuring the comfort of nesting turtles (Wiadnyana, 2003; Wiadnyana and Romantyo, 2012). Moreover, vegetation safeguards nesting sites against predators and deter them from being poached by fish farmers who harvest eggs for consumption or sale. Amid the Anthropocene era, turtles in Turtle Bay of Cilacap are already confronting extinction challenges.

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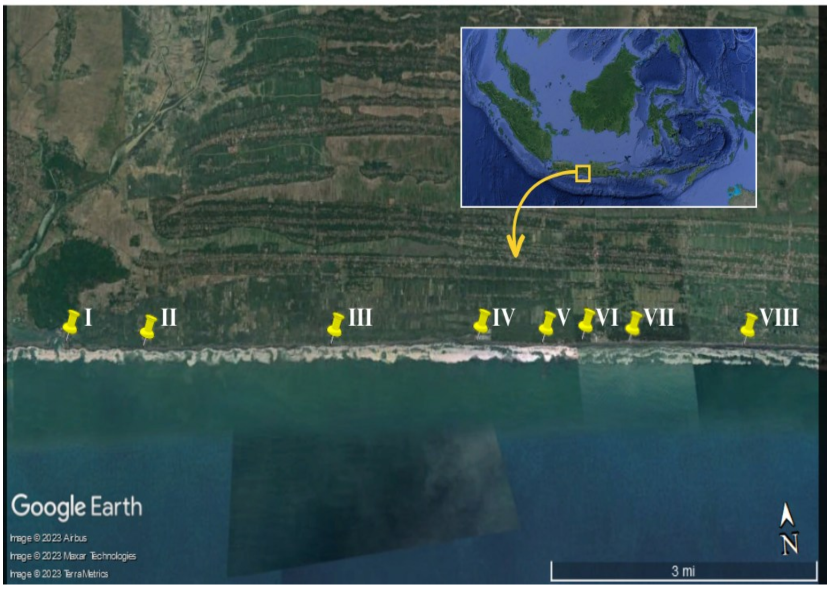
For instance, turtle landing tracks were discovered during the study, but no eggs were found. It is plausible that local residents, who may still be unaware of conservation efforts, are contributing to the frequent poaching of turtle eggs. Quiet and dimly lit beach conditions are optimal nesting habitats for green turtles and other sea turtle species (Dermawan, 2002; Panjaitan, 2012). This preference is attributed to the solitary and nocturnal nature of these organisms. Damanhuri *et al.* (2019) supported this notion by highlighting that the changes in coastal habitat conditions can alter the nesting patterns of turtles, primarily due to the disruptions in their ecological nesting habitat (Andriyono and Mubarak, 2011). Additionally, Mazaris *et al.* (2009) assessed coastal squeeze and its impact on sea turtle nesting. Their findings underscored the importance of understanding how habitat loss contributes to declining hatching rates, which is crucial for devising effective conservation strategies aimed at revitalizing sea turtle populations.

The Turtle Bay of Cilacap has undergone substantial modifications, resulting in many areas becoming unsuitable for turtle nesting. Therefore, it is crucial to conduct a comprehensive assessment of Turtle Bay to identify and safeguard suitable nesting areas. This proactive approach is vital to prevent further environmental degradation and to preserve the habitat for these essential umbrella species. Pericic and Tanveer (2019) have advocated evidence-based conservation practices as this approach involves collection and analysis of past conservation data to inform future decision-making, ensuring that conservation initiatives are built upon a foundation of knowledge and experience. Furthermore, Natih *et al.* (2021) have proposed various parameters that play a role in determining the suitability of turtle habitats. In this study, the parameters like human activities (including fishing, demographics, pollution, light reflection, and habitat modification), predatory crab species, and vegetation were subjected to scoring analysis. The objective of this analysis was to evaluate the suitability of the turtle nesting habitat in Turtle Bay of Cilacap, Indonesia.

MATERIALS AND METHODS

Research time and site

The study was conducted in Turtle Bay, Cilacap, Indonesia, across a designated area spanning SP1 to SP8, with each station covering a distance of 2 km (see Fig 1); Cilacap Beach, nestled in Cilacap Regency, Central Java, Indonesia, stretches along the Indian Ocean, offering a serene yet vital coastal landscape; geographically, it sits at about (−7.730°, 108.980°), surrounded by a mixture of sandy beaches and coastal hills; positioned roughly 200 km southwestern of Semarang and 300 km southeastern of Jakarta, the area is more than just a beautiful stretch of coastline; despite the growing industrial activity, the beach holds immense ecological value as a key nesting ground for sea turtles; this makes it a focal point for conservation efforts, where preserving the natural habitat becomes essential for the survival of these endangered species; Global Positioning Systems (GPS) were utilized to ascertain each station's research locations and coordinates; the sampling process involved monitoring during the nesting season at eight designated stations (SP1–SP8) with coordinates as follows: SP1 (−7.691°, 109.181°), SP2 (−7.691°, 109.191°), SP3 (−7.696°, 109.231°), SP4 (−7.692°, 109.244°), SP5 (−7.698°, 109.260°), SP6 (−7.698°, 109.261°), SP7 (−7.700°, 109.292°), SP8 (−7.700°, 109.287°). Environmental parameters associated with nesting were collected during the full moon and new moon phases of July, August, and September 2023 at eight observation stations within the Turtle Bay of Cilacap, Jawa Tengah (Indonesia) approximately covering an area of 16 km. *In situ* parameters, such as vegetation and the impact of human activities, were assessed directly in the field, while *ex situ* data were gathered for subsequent laboratory analysis.



Figuire 1. Map of research locations in Turtle Bay of Cilacap for data collection. The sites are i. Sodong Beach, ii. Srandil, iii. Welahan Wetan, iv. Widarapayung Kulon, v. Sidayu, vi. Widarapayung Wetan, vii. Sidaurip, and viii. Pagubugan

The sampling sites chosen for the study were coded as follows: SP1 = Sodong (7.69195˚S, 109.181622˚E), SP2 = Srandil (7.69195˚S, 109.191656˚E), SP3 = Welahan Wetan (7.696132˚S, 109.231723˚E), SP4 = Widarapayung Kulon (7.692683˚S, 109.244497˚E), SP5 = Sidayu (7.698763˚S, 109.260091˚E), SP6 = Widarapayung Wetan (7.698754˚S, 109.261489˚E), SP7 = Sidaurip (7.700976˚S, 109.292523˚E), and SP8 = Pagubugan (7.700794˚S, 109.287625˚E).

Data collection method

Vegetation sampling was conducted using a line-transect and quadrant method. A 50 m length was marked at each station, and along this line, 2.5 m x 2.5 m quadrants were established at every 10 m. Vegetation density was assessed by recording plant species at five points within each quadrant, and the average density was used to represent the overall vegetation at each site. The collected samples, along with photos, were later identified in the Botany Laboratory at the Faculty of Biology, Universitas Jenderal Soedirman, Indonesia.

Human activities were observed and documented through direct observation during both daytime (6 h) and nighttime (4 h), covering a total of 10 h day^{-1}. Photos were taken using a phone camera at regular 30 min intervals or when any human activity, such as fishing, recreational use, or infrastructure development, was observed. This documentation allowed researchers to assess the impact of these activities on the beach habitat.

The predatory crab species were collected using sample collection bottles filled with 70% ethanol. Hand gloves were worn to collect specimens around the beach, ensuring minimal disturbance to the surrounding ecosystem. The collected samples were subsequently identified in the Animal Taxonomy Laboratory in the Faculty of Biology, Universitas Jenderal Soedirman, Indonesia, using information from DecaNet (2024) and Ardika *et al.* (2015).

Data analysis

The analysis of field parameters utilized both qualitative and quantitative methods to comprehensively examine the research findings. Environmental data pertaining to human activities, vegetation distribution, and predatory crabs were systematically organized and presented in tables and narrative texts, ensuring a clear and structured approach.

Analysis of human activities

Human activities were observed and documented using direct observation methods, supplemented by photo documentation captured every 30 min using a phone camera. These observations were conducted during both daytime (6 h) and night-time (4 h), totalling 10 h monitoring per site daily. The data were analysed descriptively by assigning a score of 1 to 3 (low to high impact) for each activity. This scoring system allowed for a detailed assessment of the frequency and intensity of human activities across all the sites.

Analysis of vegetation samples

The vegetation data were collected using the line-transect and quadrant method. The average density of each plant species was calculated for each site, with results presented in tabular format. This analysis highlighted variations in vegetation distribution, focusing on how different species' densities might influence the turtle nesting habitat.

Predatory crab analysis

Two common predatory crabs, *Ocypode kuhlii* and *Hippa adactyla,* were identified across the study area. Their presence was recorded during site observations, and the abundance of these species was evaluated qualitatively. Descriptive analysis was used to understand their potential impact on turtle nests, particularly in terms of predation risk at the nesting sites.

Comprehensive environmental assessment

By combining human activities, vegetation, and predatory crab data, a thorough assessment of the environmental conditions within Turtle Bay of Cilacap was conducted. This integrated approach allowed an understanding of how human influence and ecological factors, such as crab predation and vegetation patterns, affect the suitability of turtle nesting sites.

RESULTS AND DISCUSSION

A comprehensive evaluation of sea turtle's nesting ecology was conducted in the Turtle Bay of Cilacap (Indonesia) so as to identify environmental cues conducive for sea turtles to come ashore and lay their eggs. This study holds significance, as the suitability of the ecosystem plays a crucial role in determining the success of turtle nesting and hatching. Since deteriorating environmental conditions has led the turtles to desert many expansive beaches (Kasenda *et al*., 2013), the Turtle Bay of Cilacap was selected as a focal point for studying the overall impact of environmental conditions on turtle nesting. This study involved factors like human activities, vegetation, and the presence of predatory species.

Table 1. Vegetation density* across sampling points (SP1–SP8) (m)

Plant species 10 m^{-1}	SP1	SP2	SP3	SP4	SP5	SP6	SP7	SP8
Ipomoea pes-caprae	9.6	11.2	1.8	2.8	3.0	2.6	15.0	7.0
Casuarina equisetifolia	2.0	3.2	0.2	4.8	0.2	1.6	4.6	2.0
Cocos nucifera	3.6	5.0	8.2	4.6	7.8	3.6	10.2	6.8
Pandanus odorifer	5.0	1.4	-	5.4	0.6	-	16.2	0.4
Cyperus rotundus	11.0	14.2	-	17.6	9.4	11.0	21.6	11.5
Pennisetum purpureum	3.6	-	1.8	2.4	-	-	-	1.6
Melanthera biflora	4.4	-	-	-	-	-	-	-
Chaptalia exscapa	0.6	-	-	-	-	-	-	-
Calophyllum inophyllum	-	-	-	0.4	-	-	-	-

SP1: Sodong Beach, SP2: Srandil, SP3: Welahan Wetan, SP4: Widarapayung Kulon; SP5: Sidayu, SP6: Widarapayung Wetan, SP7: Sidaurip, SP8: Pagubugan, SP "Sampling Point". *Vegetation density (measured as the number of individual plants per square meter) for various plant species at each of the eight sampling sites (SP1-SP8). Vegetation was sampled using a line-transect method with quadrants set at 10-meter intervals along a 50-m line.

Vegetation sampling

The vegetation identified at the sampling locations within Turtle Bay of Cilacap is given in Table 1. The beaches exhibited varying combinations of plant species in different proportions, with certain species like *Melanthera biflora, Chaptalia exscapa* and *Calophyllum inophyllum* present in SP1 and SP2 only. Plant density data was meticulously analysed to assess how vegetation cover influences the nesting behaviours of sea turtles in the area. This analysis sheds light on the importance of vegetation in providing suitable nesting habitats for sea turtles and underscores the need for conservation efforts to preserve these critical ecosystems.

Vegetation plays a crucial role in providing suitable nesting habitats for sea turtles. Rubio (2009) highlighted the significance of coastal vegetation, particularly dense tree cover, in promoting the stability of sea turtle nesting populations.

The following species were observed:

Ipomoea pes-caprae: It was found in significant densities, with values ranging from 1.8 at SP3 to 15 at SP7, indicating a strong presence at several locations, particularly SP2 and SP7.

Casuarina equisetifolia: It showed variable density, with a maximum of 4.8 at SP4 and a minimum of 0.2 at SP3 and SP5, suggesting it to be less prevalent in some areas.

Cocos nucifera: It was recorded in densities ranging from 3.6 to 10.2, peaking at SP7, showcasing its presence across multiple sites.

Pandanus odorifer: It was notably abundant at SP7 (16.2), but absent at SP3, highlighting its localized distribution.

Cyperus rotundus, *Pennisetum purpureum*, *Melanthera biflora*, *Chaptalia exscapa*, and *Calophyllum inophyllum*: These species had varied densities across the sampling sites, contributing to the overall vegetation complexity.

Bustard (1972) emphasized that vegetation significantly influences environmental factors such as humidity, temperature, and sand stability, creating a conducive environment for nest excavation and enhanced that *Pandanus* sp., is the preferred vegetation for *Chelonia* sp., spawning, indicating its importance in providing suitable nesting habitats for sea turtles. This finding aligns with the observations of Diamond (1976), Horrocks and Scott (1991), Kamel and Mrosovsky (2005), and Ditmer and Stapleton (2012), who noted that hawksbill sea turtles tend to nest on or near vegetation. Considering the high density of *Pandanus odorifer* observed at location SP7 (16.2) alongside other plant species, this site is likely conducive for nesting by both green turtles and hawksbill turtles.

Dewi (2016) suggested that *Pandanus* vegetation benefits *Chelonia mydas* due to its root system's capacity to enhance moisture levels and provide sand stability without impeding nest excavation. Additionally, vegetated beaches offer essential protection for nesting turtles and their eggs against predators and potential poaching by fishermen. It is evident that laying eggs on open, un-vegetated beaches increases the risk of predation by wild animals (Leighton *et al*., 2010). The diversity and density of vegetation across the sampling sites underscore the critical role these plants play in supporting the healthy sea turtle nesting populations.

Impact of human activities sampling

***Photo documentation**:* Photos were taken after every 30 min throughout the observation period (10 h daily, with 6 h during the day and 4 h at night). These photos were reviewed by the researchers to document and quantify the changes in human activities and environmental conditions at each site. Activities like fishing, demographic presence, pollution, light reflection, and habitat modification were captured in the photos and carefully analysed. Based on this visual evidence, researchers assigned scores to each parameter at every site, reflecting the frequency and intensity of human impacts. For example, the sites with frequent fishing activity or significant habitat modifications received higher scores, while those with minimal activities were scored lower, which was compiled in Excel format. The scores in Table 2 represent the cumulative result of this detailed photo review, ensuring that each site's human activity impact is accurately reflected.

Table 2. Detailed assessment of the impact of human activities on the sampling points*

Parameters	**SP1**	**SP2**	**SP3**	**SP4**	**SP5**	**SP6**	**SP7**	**SP8**	**Overall mean**
Fishing	2	2	3	3	3	3	3	3	2.75
Demographics	2	2	2	2	3	3	2	2	2.25
Pollution	3	3	3	2	2	2	1	1	2.13
Light reflection	2	1	1	3	2	2	1	1	1.63
Habitat modification	2	2	2	3	3	3	1	2	2.25

*SP1: Sodong Beach, SP2: Srandil, SP3: Welahan Wetan, SP4: Widarapayung Kulon; SP5: Sidayu, SP6: Widarapayung Wetan, SP7: Sidaurip, and SP8: Pagubugan; Formula: Average = Number of values/ sums of all values.
Activity level scoring: Score of 1: Low impact**;** 2: Moderate impact**;** and 3: High impact

Table 2 presents a comprehensive evaluation of the impact of five human activity parameters - fishing, demographics, pollution, light reflection, and habitat modification - across eight sampling points (SP1-SP8). The scores (ranging from 1 to 3) reflect the frequency and intensity of these activities, based on observations and photographic documentation conducted at each site. A score of 1 indicated minimal activity, 2 as moderate activity, and 3 as high activity. The average score for each parameter across all sites provides an overall indication of the human impact on the study area.

The adverse impacts of environmental disturbances in Turtle Bay of Cilacap have prompted the relocation of turtle eggs to the Sodong Beach Conservation

Area (*Penyu Konservasi*), where conditions are more conducive for incubation and hatching. This proactive measure aims to mitigate the threats posed by human activities and habitat degradation on sea turtle populations. Tripathy and Rajasekhar (2009) also identified similar challenges faced by sea turtles in India due to the changes in coastal land use, underscoring the global significance of addressing these issues. Additionally, the warning of Zamani (1996) about the detrimental effects of coastal development and construction on turtle populations serves as a poignant reminder of the urgency to enact conservation strategies to safeguard these vulnerable species.

Direct observations, as reflected in Table 2, affirm the significant impact of human activities on all beaches within the study area. Noteworthy is the severe disturbance caused by fishing (2.75 score), demographic factors (2.25 score), habitat modification (2.25 score) and pollution (2.13 score), all indicating moderate to high impacts. In line with this, sampling sites SP3, SP4, SP5, SP6, SP7, and SP8 were highly influenced by fishing (score of 3, indicating high significance), while SP5 and SP6 experienced high demographic impacts (score of 3) which may primarily be attributed to high levels of tourism and industrialization in these regions (see Fig 2). SP1 and SP2 are still moderately impacted (score of 2) by these three ecological factors, while SP3, SP4, and SP7 show moderate scores of 2 in either demographics, habitat modification, or both, indicating a moderate impact in those areas. Conversely, pollution levels are another significant environmental impact, with an average pollution score of 2.13, indicating a moderate level. SP1, SP2, and SP3 exhibit significant pollution with a score of 3, while SP4, SP5, and SP6 scored 2, indicating moderate pollution. SP7 and SP8 have a low impact from pollution (score of 1).

Light penetration is another major ecological challenge in the study area. The average score for light reflection was 1.63 (Table 2). Light penetration varied across the surveyed stations, with SP4 scoring a significant 3; SP1, SP5, and SP6 scoring 2, while SP2, SP3, SP7, and SP8 scored 1. An important contributing factor to light pollution observed at SP2, SP3, SP7, and SP8 was the use of torchlights by residents gathering early in the morning to tap sap from coconut trees. It was noted that beaches with a high density of *Cocos nucifera* experience increased torchlight usage during nesting period. Some of the stations that scored 3 and 2 were disturbed by streetlights.

Nonetheless, significant disturbances persisted across all the beaches due to the fishermen and their activities, albeit with relatively higher impacts observed in SP3 to SP8. Fishermen are significant sources of noise pollution, contributing to habitat degradation. Sea turtles exhibit a preference for quiet environments when emerging from water for spawning, and noise generated by motorbikes can prompt turtles to migrate to quieter beaches for nesting. Moreover, SP1, SP2, and SP3 display elevated pollution levels, marked by the presence of plastics, decaying bamboo wood, fishnets, and wood logs. Fujisaki (2016) notes that beaches littered with debris are unsuitable for turtle nesting. Alongside disturbances caused by fishermen, activities like digging holes (observed at depths of 34 cm and widths of 70 cm) along the beach and setting fish traps pose additional risks to nesting turtles. These sensitive creatures may adjust their nesting locations in response to such environmental disruptions.

While green and hawksbill turtles tend to favour nesting beaches with vegetation, as highlighted by Budiantoro *et al.* (2019) and Whitemore and Dutton (1985), respectively, olive ridley and leatherback turtles show a preference for open coastal areas. This underscores the importance of protecting nesting areas against human activities (Fig. 2 illustrates their impact).

A	B	C

Figure 2. a) Habitat modification in SP5, b) Dead Hawksbill turtle recovered in SP3, c) Fishing activities and pollution in the study area

Predatory crabs: Ocypode kuhlii and Hippa adactyla

Assessing the impact of predators on the sea turtle population in Turtle Bay of Cilacap is crucial. According to Marco *et al.* (2015), many sea turtle populations face extinction due to nest predation, a significant natural threat. Predators, such as crabs, continuously seek food, and when their population exceeds that of their prey, as observed in Turtle Bay of Cilacap, they pose a substantial risk to the survival of sea turtle nests (Barton and Rot, 2008; Leighton *et al.,* 2010).

The suspected predator crab species that may prey on sea turtles in Turtle Bay of Cilacap, include *Ocypode Kuhlii* De-Haan and *Hippa adactyla* F. The presence of these crabs poses a significant threat to the turtle species in the study area. According to Marco *et al.* (2015), Ghost crabs (*Ocypode* spp.) are among the largest and most conspicuous invertebrates found on ocean-exposed sandy beaches worldwide. They demonstrate remarkable adaptability, occupying various trophic roles such as scavengers, employing diverse feeding strategies, and consuming a wide range of prey (Lucrezi and Schlader, 2014). However, despite several studies focusing on the predation of Ghost crabs on turtle nests, there is still a need for more information about the patterns and behaviours of these decapods during nest predation. Lucrezi and Schlader (2014) compiled data on Ghost crab predation rates on sea turtle nests, eggs, and hatchlings, primarily centred on *Ocypode quadrata*, a species found in the USA and French Guiana. Nonetheless, *Ocypode cursor* L., 1755, has been documented preying on turtle nests along the Western African coast and in the Eastern Mediterranean (Smith *et al.,* 1996; Strachan *et al.,* 1999; Aheto *et al.,* 2011).

In addition to predatory crabs, domestic cats (*Felis* spp.) and dogs (*Canis* spp.) were observed near Turtle Bay of Cilacap during early morning when turtles nest and throughout the day. Phillot (2020) noted that most cats preying on turtle hatchlings are not domestic pets but are rather classified as feral, stray, or free-roaming cats in various countries. Seabrook (1989) documented the instances of feral cats (*Felis catus*) preying on hatchlings, including green turtles (*Chelonia mydas*) on Aldabra Atoll in Seychelles and loggerhead turtles (*Caretta caretta*) at Turtle Bay on Dirk Hartog Island in Western Australia (Hilmer *et al.,* 2010). Turkecan (2014) has reported that feral cats in Beymelek (Turkey) destroyed loggerhead turtle eggs. Further research is warranted to determine whether the crabs, cats, and dogs in Turtle Bay of Cilacap prey on nesting turtles, their eggs, and juveniles and gather additional data on predator-prey behaviour and its impact on sea turtles.

CONCLUSION

This study provides valuable insights into the nesting ecology of sea turtles in Turtle Bay, Cilacap (Indonesia), emphasizing the threats posed by human activities and predation. Despite these challenges, Sidaurip Beach offers a suitable nesting site due to its favorable conditions. These findings highlight the need for evidence-based conservation practices to protect sea turtle habitats in the region. However, further research is needed to fully understand predator-prey dynamics and their impact on sea turtles. These findings underscore the importance of evidence-based conservation practices for the preservation of sea turtle habitats in Turtle Bay.

Recommendation: Given the critical role of Cilacap Beach as a nesting habitat for sea turtles, it is recommended that conservation efforts be intensified through strict protection of nesting sites, regulation of industrial activities near the coastline, and community-based awareness programs. Regular monitoring and collaboration with local stakeholders will be vital to ensure long-term sustainability and protection of this ecologically significant area.

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Data Availability

All data generated or analysed during this study are included in the manuscript and its supplementary information files. No additional data is available beyond what is provided in this submission.

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