SEASONAL AND SPATIAL PATTERNS OF AVIAN ASSEMBLAGES IN THE EASTERN TAIWAN STRAIT: IMPLICATIONS FOR OFFSHORE WIND FARM DEVELOPMENT

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ABSTRACT

Bai, M.-L., Huang, C.-H., & Lien, Y.-Y. (2025) Seasonal and spatial patterns of avian assemblages in the eastern Taiwan Strait: Implications for offshore wind farm development. *Marine Ornithology*, *53*(2), 383–392. http://doi.org/

The eastern Taiwan Strait, a region situated along the East Asian–Australasian Flyway and currently undergoing rapid offshore wind energy development, remains poorly studied with respect to its seabird assemblages. Through intensive vessel-based transect surveys conducted between 2014 and 2021, this study documented 22,187 birds from 105 species across 10 orders and 29 families. Migratory non-seabirds accounted for 55.2% of individuals and dominated the species richness, highlighting the region's importance for migratory pathways. Seabird density was relatively low, however, consistent with trends in other tropical regions, and this pattern may also reflect both environmental degradation and methodological differences in density estimation. Seasonal variations in bird density and species richness exhibited bimodal peaks in spring and autumn, driven by migration, while winter abundances reached seasonal lows, likely due to adverse wind conditions. Spatial analyses revealed that distance from the coast was the primary factor structuring bird assemblages. The coastal zone was dominated by waterfowl and gulls, while offshore zones, both deep and shallow, were characterized by procellariiforms and sulids. These findings establish an essential baseline for evaluating the impacts of offshore wind farms, underscoring the need to incorporate migratory bird populations into environmental assessments.

Key words: bird assemblage, seabird ecology, migratory birds, offshore wind farms, seasonal variation, environmental impact assessment

INTRODUCTION

Climate change and human activities are exerting profound impacts on marine ecosystems (Hoegh-Guldberg & Bruno, 2010). Seabirds, as upper-trophic level predators in marine environments, are widely recognized as valuable indicators of ocean health and ecosystem conditions (Parsons et al., 2008). Globally, seabirds are among the most threatened avian groups, with long-term population declines documented across many species and regions (Gibson et al., 2023; Paleczny et al., 2015; Rodríguez et al., 2019). Their reliance on both marine and terrestrial habitats exposes them to a wide range of threats, including bycatch and resource competition from commercial fisheries, marine pollution, invasive predators at breeding sites, habitat degradation, human disturbance, and global change (Dias et al., 2019).

The Taiwan Strait, a marine corridor bordering southeastern Asia, is characterized by intense human activity and high ecological pressure (Halpern et al., 2008) but represents one of the least studied regions globally regarding seabird ecology (Paleczny et al., 2015). Climate change and overexploitation have notably altered the region's fisheries in terms of yield and seasonality (Ho et al., 2016; Ju et al., 2020 *cf.* Kuo et al., 2023). More recently, the rapid expansion of offshore wind energy systems has introduced an additional potential stressor to seabirds. Offshore wind farms can pose varied impacts on marine ecosystems, with adverse effects on birds being widely documented (Galparsoro et al., 2022; Garthe et al., 2023; Peschko et al., 2020). Direct collisions with wind turbines can cause mortality. Compared to many terrestrial birds, most seabird species are long-lived and have relatively low reproductive rates. As such, increased adult mortality can lead to substantial population-level effects (Brabant et al., 2015; Hüppop et al., 2006).

Additionally, wind farms may displace seabirds from suitable foraging or roosting habitats. These disruptions, for locally breeding species, can result in lower provisioning rates for chicks and reduced reproductive success (Busch & Garthe, 2016; Peschko et al., 2020). Wind farms may also create physical barriers to movement, forcing birds to travel greater distances or at greater altitudes to avoid structures during migration or when commuting between nesting and foraging areas, thereby elevating energetic costs (Masden et al., 2010; Schwemmer et al., 2023). These potential impacts underscore an urgent need for comprehensive research to assess the effects of offshore wind energy systems on seabird populations and inform conservation strategies (Fauchald et al., 2024). Such evaluations must begin with the collection of baseline data on avian assemblages in proposed development areas to understand current conditions and detect potential changes over time.

In the eastern Taiwan Strait, research on seabirds to date has predominantly focused on the breeding biology of terns in colonies along coastal regions and on islets, leaving significant knowledge gaps concerning birds at sea—precisely where offshore wind projects are proposed. This study addresses this critical knowledge gap by presenting results from intensive vessel-based transect surveys that investigated avian assemblages in the eastern Taiwan Strait. The objectives were to (1) document the species composition of birds in the area, (2) examine seasonal patterns in species assemblages, and (3) analyze spatial variation in bird distribution. The study also extended its scope to include all avian fauna observed at sea in recognition of the potential impacts of offshore wind farms on migratory landbirds, in addition to seabirds.

METHODS

Study area

The Taiwan Strait, an arm of the western Pacific Ocean, separates Taiwan from mainland Asia. It connects the East China Sea to the northeast and the South China Sea to the southwest, spanning approximately 300 km (Yu & Chou, 2001). It is predominantly shallow, with depths generally less than 200 m, except for its southeastern corner. Situated roughly in the middle of the East Asian–Australasian Flyway, the Taiwan Strait serves as a migratory corridor and navigational reference for many bird species flying over the region (Huang et al., 2021; Lisovski et al., 2016). Additionally, the uninhabited islets around the Penghu Archipelago and the eastern China coast host breeding colonies of several tern species, including the critically endangered Chinese Crested Tern *Thalasseus bernsteini* (Fan et al., 2011; Hung et al., 2019).

Our study site encompasses an area of approximately 10,185 km^2 in the northeastern Taiwan Strait (Fig. 1; 23.47°N–25.19°N, 119.57°E–121.27°E). The depth averages 45 m with a maximum of about 97 m, deeper in the northern part and shallower around the southern Chang-Yuen Ridge. The region experiences a subtropical monsoon climate, with prevailing southwest winds during the summer months and northeast winds in the winter. Seasonal changes in wind direction drive the movement of different water masses into the region (Hong et al., 2011). In summer, the warm, nutrient-poor South China Sea Water is the dominant water mass in the Taiwan Strait; whereas in winter, the cold, nutrient-rich Mixed China Coastal Water from the northeast and the warm, nutrient-poor Kuroshio Branch Water from the southwest converge in the area. These seasonal variations in water masses lead to fluctuations in oceanographic conditions, primary productivity, zooplankton assemblages, and fish communities (Ho et al., 2016; Hong et al., 2011; Tseng et al., 2020).

Abundant wind resources have made this region a prime site for offshore wind energy development (Cheng et al., 2020; Fang, 2014). The Taiwanese government has set a goal of achieving 5.7 GW of offshore wind power capacity by 2025, with most designated wind farm sites located within the study area (Bureau of Energy, 2015).

Survey methods

Vessel-based transect surveys were conducted between August 2014 and December 2021, before the commencement of large-scale wind farm construction in the region. Most surveys were initiated in response to proposed offshore wind farm developments and were carried out to fulfill environmental impact assessment requirements. As such, most designated project sites were included in the survey coverage, and survey effort was greater within these areas compared to surrounding waters. Surveys were conducted under favorable weather conditions (Beaufort sea state ≤ 4; visibility ≥ 3 km), with the vessel maintaining a speed of 8–10 knots (14.8–18.5 km/h). Due to safety and visibility requirements, surveys were only conducted during calm weather windows, which limited survey effort during the rougher winter months.

At least two experienced observers continuously scanned in all directions from opposite sides of the vessel, with an eye height of approximately 3–4 m above sea level. Given the generally low bird density in the Taiwan Strait, a continuous observation protocol without a predefined strip width was adopted, as recommended by the Ocean Conservation Administration of Taiwan (Yuan & Ding, 2021). This approach was considered more efficient in capturing sparse seabird encounters compared to the conventional 300-m strip with snapshot sampling. Observers recorded all birds detected,

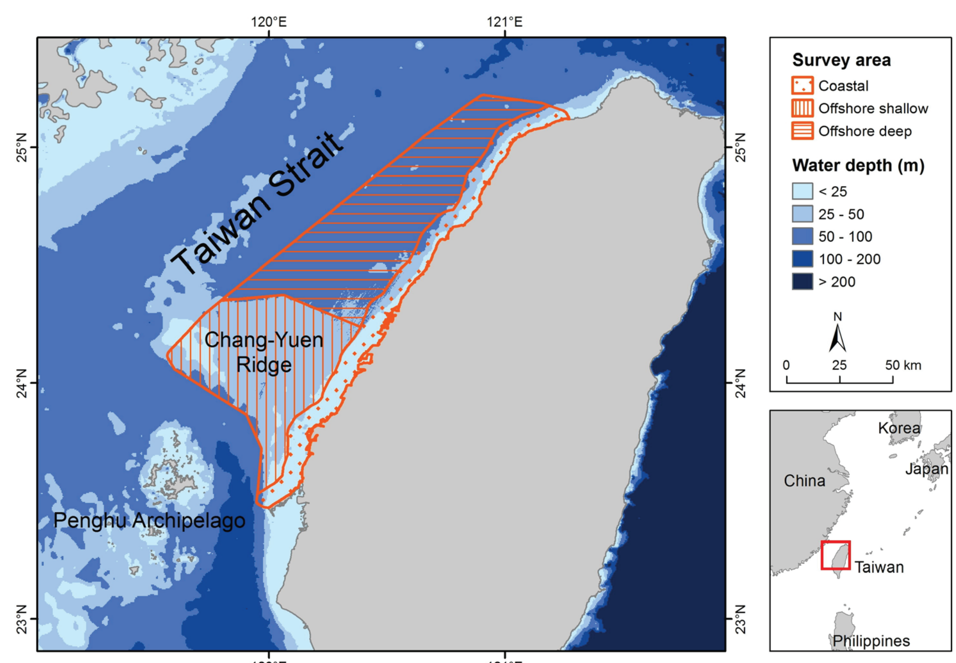

Fig. 1. Map of the study area in the eastern Taiwan Strait, showing the coastal zone (dotted pattern), offshore shallow zone (vertical stripes), and offshore deep zone (horizontal stripes).

including taxonomic identity (to the lowest possible level), group size, and position.

Data analysis

The continuous survey protocol without a predefined strip width, while suitable for low-density environments, introduces potential biases in density estimation due to bird movement and imperfect detectability. To address these issues, Bai and Lien (2024) developed a correction approach tailored to this survey design. Simulations adapted from Glennie et al. (2015) were used to model how density estimates are affected by the speed of birds relative to the survey vessel. Based on the framework proposed by Spear et al. (1992), a speed-related correction factor was derived. Taxon-specific effective strip width (ESW) values were obtained from empirical data collected in the region. For each taxon, a corrected ESW was calculated by multiplying the empirical ESW by the corresponding correction factor. This allows bird density to be estimated using the common distance-sampling formulae, with the corrected ESW accounting for movement bias. Additional details of the correction procedure, including assumptions, simulation settings, and values of ESW and corrected ESW, are provided in Appendix 1 (available on the website).

To investigate density and phenology, birds were categorized into 12 taxonomic groups: waterfowl, waders, jaegers, gulls, terns, storm petrels, petrels, shearwaters, boobies, egrets/herons/spoonbills, raptors, and passerines. A minimum of 70 sightings was required for each group to ensure sufficient data for meaningful seasonal and spatial pattern analysis. Spatial variation in bird assemblages was examined by dividing the study area into three zones: (1) the coastal zone (within 10 km of the Taiwan coast), (2) the offshore shallow zone (the Chang-Yuen Ridge in the south), and (3) the offshore deep zone (in the north; Fig. 1). Detrended correspondence analysis (DCA) was applied to summarize variations in bird assemblages using monthly density data for each taxonomic group in each zone, pooled across years. DCA, an extension of correspondence analysis, removes the arch effect, a curvilinear distortion that can obscure ecological gradients, by segmenting and rescaling the first ordination axis (Hill & Gauch, 1980). It is widely used to summarize ecological gradients and assemblage changes. Analyses were conducted in R using the "vegan" package (Oksanen et al., 2025).

RESULTS

Overall species spectrum

Between August 2014 and December 2021, we conducted 51,025 km of on-effort surveys on 546 vessel-days, documenting 7,582 sightings totaling 22,187 birds. Of these, 16,108 individuals (72.6%) were identified to the species level, representing 105 species across 10 orders and 29 families (Appendix 2). Including individuals identified only to genus, family, or order level, 21,676 birds (97.7%) could be assigned to a taxonomic group with a corresponding corrected ESW and were included in the density analysis. Of these 21,676 individuals, 9,703 (44.8%) were seabirds representing 33 species, and 11,973 (55.2%) were migratory non-seabirds comprising 72 species, such as landbirds, waterfowl, and waders. The remaining 511 individuals, accounting for 2.3% of all 22,187 birds recorded, could not be reliably identified to a taxonomic level sufficient for assigning corrected ESW values and were excluded from density estimates.

Laridae was the most commonly observed family, accounting for 34% of all birds recorded, followed by Scolopacidae (16.5%) and Ardeidae (14.0%). The Red-necked Phalarope *Phalaropus lobatus* was the most abundant species (15.0%), followed by the Barn Swallow *Hirundo rustica* (11.7%), the Greater Crested Tern *Thalasseus bergii* (10.9%), and the Eastern Cattle Egret *Ardea coromanda* (10.2%). Most species were observed infrequently, with 26 species recorded from only a single sighting, primarily small migratory landbirds and waders (Appendix 2).

Seasonal variation

Monthly bird density in the region exhibited a bimodal pattern, peaking from March to May and again from August to October (Fig. 2). Species richness, measured as the total number of species observed per month, mirrored this trend, reaching a maximum of 55 species in April. In contrast, bird density and species richness were both markedly low from November to February.

Distinct seasonal patterns emerged across bird groups (Fig. 3). Terns were prevalent from spring through autumn, peaking in abundance in September, but were absent during winter. Conversely, gulls were observed primarily in winter and early spring. Other groups displayed bimodal abundance patterns corresponding to spring and autumn migrations, each characterized by unique timing and intensity. In spring, waterfowl and shearwaters reached peak abundance as early as February and March, while petrels and storm petrels were observed primarily from May onward. In autumn, waders and boobies peaked in August, while most shearwaters were recorded in October. Asymmetries in abundance were observed between the two migration seasons (spring and autumn) for several bird groups. Jaegers and shearwaters were more common in spring, whereas storm petrels and egrets were more abundant in autumn.

Spatial variation

Bird density in all zones followed the general seasonal pattern, with peaks in spring and autumn and very low densities in winter (Fig. 2). From June to September, bird density was highest in the coastal zone, peaking in September. Species richness in both the offshore shallow and deep zones displayed a bimodal pattern. In contrast, species richness in the coastal zone exhibited a less pronounced seasonal pattern, with relatively fewer species in spring and greater richness in summer.

The DCA ordination diagram, based on monthly density data for the 12 taxonomic groups, highlights variations in bird assemblages across both seasons and zones (Fig. 4). The first axis reflects primarily seasonal variation, with lower scores in summer and higher scores in winter. The gradient length of this axis is 3.5, indicating high species turnover across seasons. The second axis corresponds to distance from the coast, with coastal samples generally scoring lower and offshore zones higher. The positioning of monthly samples reveals an interaction between seasonal and spatial patterns. During summer months, samples from different zones cluster more closely, suggesting greater similarity in assemblages—likely due to the widespread occurrence of terns. In contrast, winter samples show greater separation among zones, with gulls and waterfowl more associated with the coastal zone and shearwaters more characteristic of offshore zones.

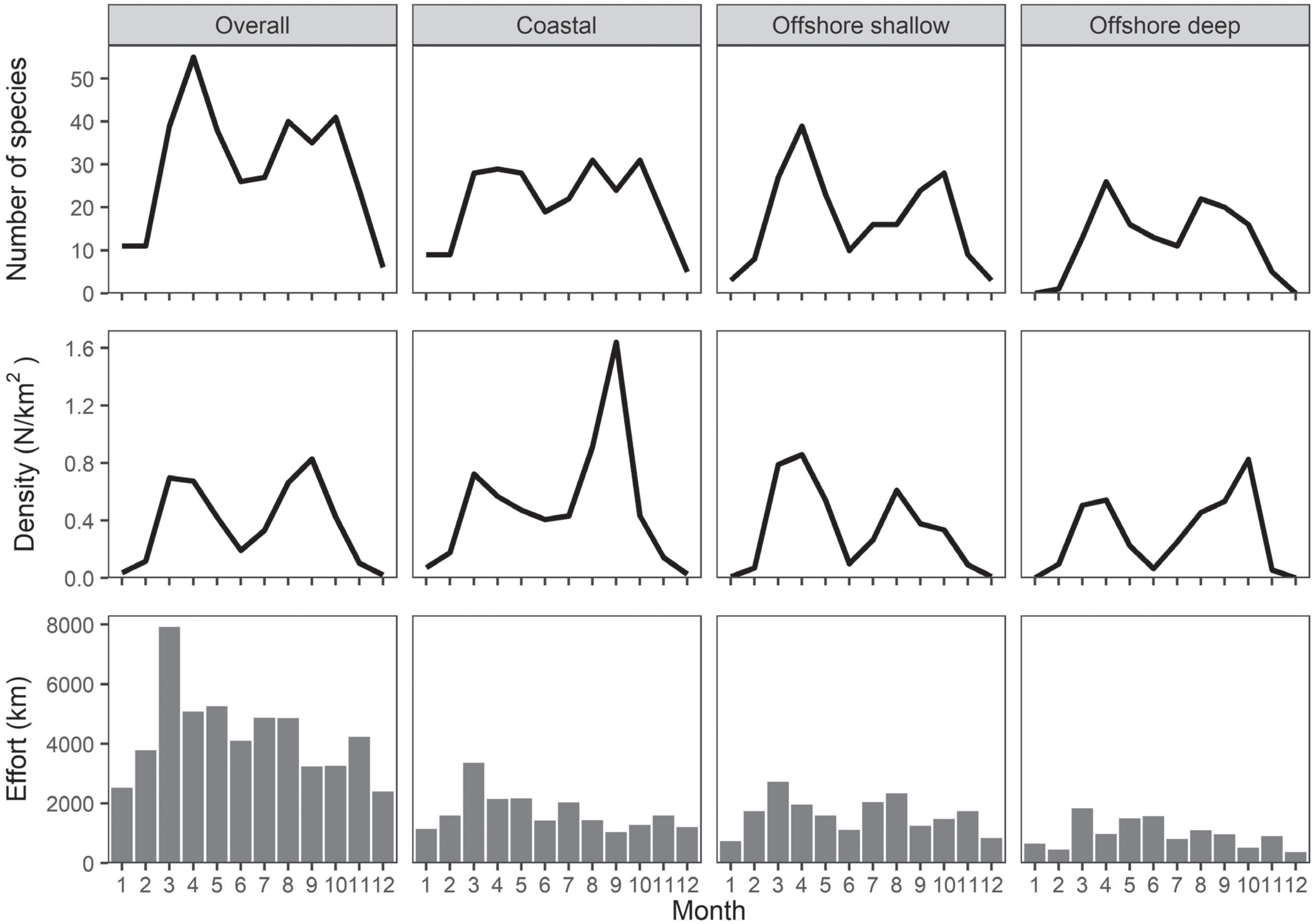

Fig. 2. Monthly variation in number of species, bird density (number of individuals/km^2), and survey effort (measured as total kilometers of on-effort transects) across marine zones in the eastern Taiwan Strait from 2014 to 2021. Columns represent the overall region, coastal zone, offshore shallow zone, and offshore deep zone, highlighting spatial and seasonal differences in avian abundance and diversity.

DISCUSSION

Species spectrum and density

Our study demonstrates that the eastern Taiwan Strait is used by a diverse array of birds throughout the year. Migratory non-seabirds were as prevalent as seabirds and dominated in terms of species richness. As many migrants travel at night or at altitudes beyond visual detection (Alerstam, 2009; Dokter et al., 2011), our visual surveys almost certainly captured only a fraction of the migration activity (Schneider et al., 2024). The high diversity and pronounced seasonal turnover we recorded are consistent with a major migratory corridor, underscoring the need to consider the potential impacts of offshore wind farms on migratory bird populations.

Seabird abundance is generally higher in the cooler, more productive Arctic and sub-Arctic ocean waters than in warmer, less-productive tropical and subtropical waters (Ainley & Boekelheide, 1983; Hyrenbach et al., 2007). Even among low-latitude regions, however, the eastern Taiwan Strait exhibited some of the lowest seabird densities reported. In the eastern South Pacific Ocean, Ainley and Boekelheide (1983) recorded seabird densities of 4.2 and 3.4 birds/km^2 in subtropical and tropical zones, respectively. In French Polynesia, Vanderwerf et al. (2006) reported 4.1 birds/km^2 in tropical waters. In the Indian Ocean, Hyrenbach et al. (2007) reported 2.4 birds/km^2 in the subtropical zone. In contrast, our estimates for the Taiwan Strait were markedly lower.

Part of this discrepancy probably stems from methodological differences (Spear et al., 2004). In vessel-based seabird surveys, distance-related detectability and the relative movement of flying birds are major causes of density bias (Camphuysen et al., 2004; Spear et al., 1992). Most studies adopted a fixed 300-m strip and a high eye height to maximize detection probabilities. However, many studies did not apply snapshot sampling or other adjustments to account for animal movement. If observers count birds continuously during strip-transect survey, densities can be inflated by up to three-fold when birds fly at twice the vessel speed (Spear et al., 1992). In our study, we used small vessels with limited eye height, and therefore we adopted distance-sampling analysis to account for incomplete detection. We also applied taxon-specific correction factors derived from simulation to account for animal movement (Appendix 1; Bai & Lien, 2024). Although the simulations assume straight-line, constant-speed flight in random directions, a recognized simplification, the approach substantially reduces movement bias (Glennie et al., 2015). Applying such corrections lowered raw density values by a factor of 2.4–3.9 (Table A1 in Appendix 1), which may partly explain why our estimates are lower than many uncorrected literature values.

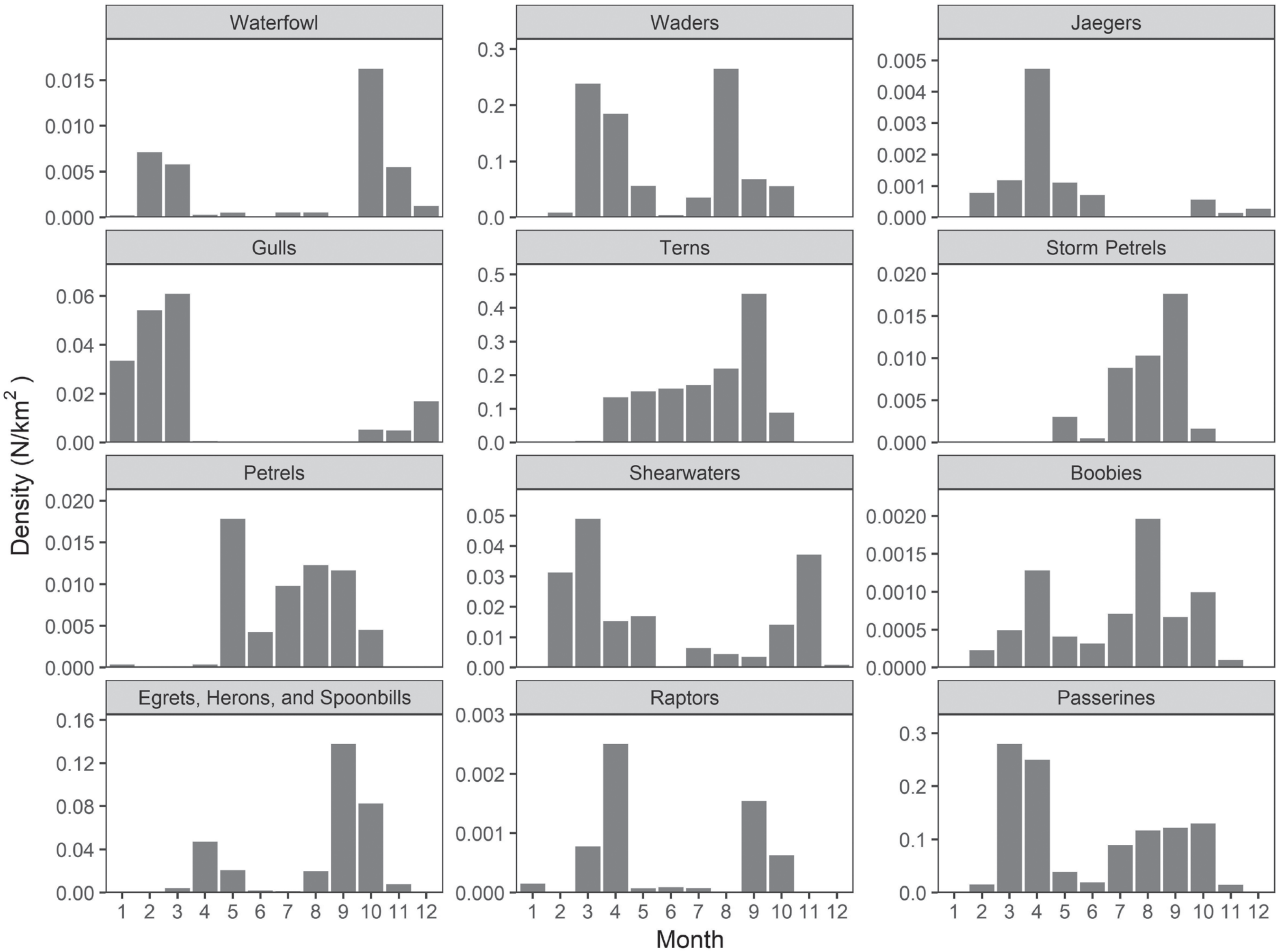

Fig. 3. Monthly variation in the density (number of individuals/km^2) of different bird groups observed in the eastern Taiwan Strait, 2014–2021. Each panel represents a specific bird group, highlighting seasonal patterns in their occurrence.

Environmental degradation is likely another potential cause for the observed low seabird densities. The region has experienced intense fishing activity, ranking among the highest globally (Kroodsma et al., 2018; Swartz et al., 2010). Of the 16 commercial fish stocks assessed, 10 stocks have collapsed, five are overfished, and only one stock remains in healthy condition (Ju et al., 2020 *cf.* Kuo et al., 2023). Reduced prey availability, together with direct human disturbance, has coincided with the loss of several breeding seabird colonies (Severinghaus et al., 2017). The Short-tailed Albatross *Phoebastria albatrus*, once a common breeder in the Penghu Archipelago, disappeared by the 1930s (Hachisuka & Udagawa, 1951). Likewise, breeding colonies of the Greater Crested Tern on Keelung Islet and Craig Island vanished in the mid-20th century (Severinghaus et al., 2017). These patterns indicate that human exploitation has adversely influenced seabird abundance and shaped the assemblage observed during our study period.

Seasonal variation

Both bird density and species richness in the eastern Taiwan Strait exhibited pronounced seasonal fluctuations, peaking during spring and autumn migrations and falling sharply in winter. Bird density in September, the month with the most abundant birds observed, was 40 times greater than in December, the month with the fewest observations. Even after migratory non-seabirds were excluded, seabird density in winter remained notably low compared to other seasons. Although the Taiwan Strait lies within the non-breeding range of several tropical and subtropical seabirds, these species were rarely recorded in winter in the study area.

Winter food scarcity does not appear to explain the pattern. Due to the southward flow of nutrient-rich Mixed China Coastal Water, productivity in the Taiwan Strait is higher in winter than in summer (Hong et al., 2011). Fish surveys with various gears also generally suggest greater fish abundance in winter compared to other seasons (Chen et al., 2014; Hsiao et al., 2017; Lee et al., 2018). Additionally, bottlenose dolphins *Tursiops* spp. were more common in the region during winter months (Bai et al., 2025). We suggest that strong winter winds may be a likely reason for the low seabird density. In the study area, wind speeds of 12 to 25 m/s are common during winter (Cheng et al., 2020; Shimada et al., 2016). Such strong winds can significantly affect avian flight performance and greatly increase the energetic cost of flight (Gabrielsen et al., 1987; Spear & Ainley, 1997). Similar relationships between wind exposure and seabird distribution have been documented elsewhere (Garthe et al., 2009). Although many seabirds are capable of flying in strong

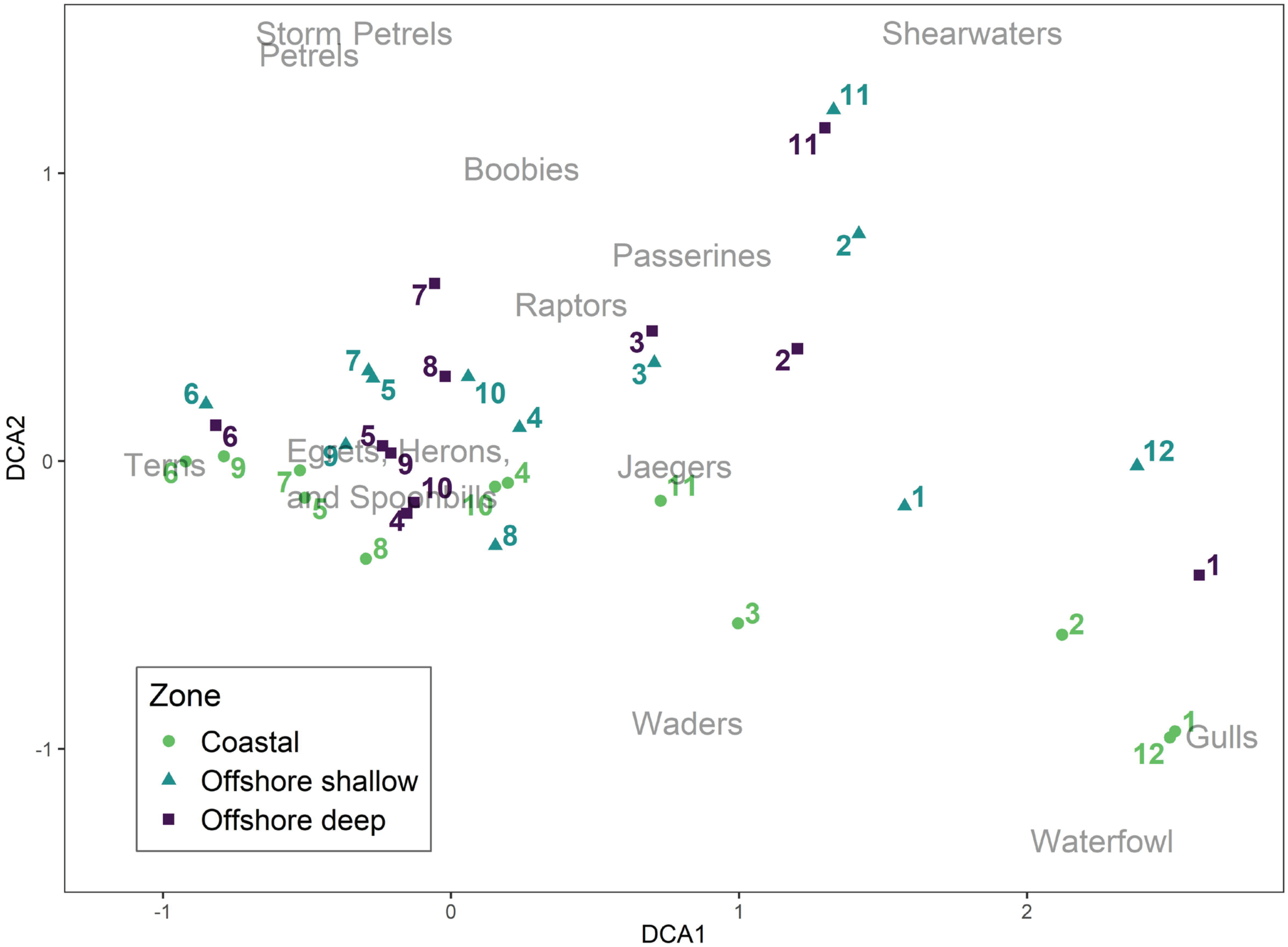

Fig. 4. Detrended correspondence analysis (DCA) plot showing bird assemblages across coastal, offshore shallow, and offshore deep zones in the eastern Taiwan Strait. Each point represents the bird assemblage for a specific month in a given zone. Numbers indicate months (from 1 = January to 12 = December), while the shapes and colors of the points denote the respective zones. Bird groups are labeled based on their species scores. The first axis (DCA1) reflects primarily seasonal variation, whereas the second axis (DCA2) represents the gradient of distance from the coast. The position of each bird group reflects its spatial and temporal occurrence. For example, terns occurred in summer across both coastal and offshore zones, while gulls were more common in winter and preferred coastal areas. Assemblages across zones were more similar in summer, mainly due to the widespread presence of terns. In contrast, separation among zones was greater in winter months, reflecting species-specific preferences for different habitats.

winds, the energetic cost of sustained high winds may outweigh the benefits of otherwise favorable foraging conditions, causing most seabirds to avoid the region in winter.

All taxa exhibited strong seasonal abundance patterns, with no year-round residents in the study area. Terns were primarily summer visitors, with breeding colonies of the Greater Crested Tern, Bridled Tern *Onychoprion anaethetus*, Roseate Tern *Sterna dougallii*, Black-naped Tern *S. sumatrana*, Brown Noddy *Anous stolidus*, and Little Tern *Sternula albifrons* established in the Penghu Archipelago. Other tern species, including the Common Tern *Sterna hirundo*, Whiskered Tern *Chlidonias hybrida*, and White-winged Tern *C. leucopterus*, bred primarily in coastal and inland temperate Asia, passing through the Taiwan Strait only during migration. Gulls were winter visitors, represented mainly by the Black-tailed Gull *Larus crassirostris* and the Vega Gull *L. vegae* / Mongolian Gull *L. mongolicus* / Lesser Black-backed Gull *L. fuscus* complex. A peak density of gulls in March indicated the northward migration of individuals that overwintered farther south. Jaegers, storm petrels, petrels, shearwaters, and boobies exhibited bimodal patterns in their seasonal abundances. Procellariiforms and sulids could occasionally be observed throughout summer. However, apart from a few Streaked Shearwaters *Calonectris leucomelas* breeding sporadically on Craig Island north of the study area, they did not breed in Taiwan waters. Individuals observed in summer could be non-breeders or pre-breeders, or breeders undertaking long foraging trips, a common behavior among procellariiforms (Hedd et al., 2018; Rotger et al., 2020).

Asymmetric abundance between spring and autumn migration was observed in several bird groups. Jaegers and several procellariiform species are known to use different migratory routes in spring and autumn (Gilg et al., 2013; Hedd et al., 2012), presumably as an adaptation to meteorological conditions (González-Solís et al., 2009). Terns often exhibit rapid and direct movement in spring to arrive at breeding grounds earlier, while employing a fly-and-forage strategy with more stopovers in autumn to refuel (Hromádková et al., 2020; Yu et al., 2022). Thus, seasonal variations in the bird assemblages in the Taiwan Strait reflect interactions between local environmental factors, large-scale meteorological conditions, and avian breeding cycles.

Spatial variation

Bird assemblages in the eastern Taiwan Strait varied with proximity to the coast, and this cross-shelf variation was further shaped by seasonal dynamics. During summer months, bird assemblages across coastal and offshore zones were relatively more similar, largely due to the widespread presence of terns, which were abundant and broadly distributed across all zones. In contrast, stronger spatial segregation emerged during migratory periods and winter. Waterfowl, waders, and gulls were characteristic of the coastal zone. Waterfowl and waders often follow coastal migration routes for navigational cues and access to stopover sites (Kölzsch et al., 2016; Yamaguchi et al., 2008). Most gull species prefer to forage in nearshore environments (Kubetzki & Garthe, 2003; O'Hanlon et al., 2022). Procellariiform birds and boobies were typical of offshore zones. Relying primarily on pelagic or mesopelagic prey, these birds generally prefer open waters where such food resources are more abundant (Correia et al., 2021; Dias et al., 2016).

The environmental gradient associated with distance from the coast or water depth is a key factor structuring many marine bird assemblages (Goyert et al., 2016; Michael et al., 2023). Since distance from the coast and water depth are often highly correlated, differentiating their relative influence can be challenging. In the eastern Taiwan Strait, the Chang-Yuen Ridge decouples these two variables, allowing us to identify distance from the coast as the primary factor shaping spatial patterns of bird assemblages in this region.

CONCLUSION

Our study provides a baseline understanding of the bird assemblage in the eastern Taiwan Strait, offering critical information for site selection and monitoring of the impacts of offshore wind farms. The significant presence of migratory non-seabirds highlights the need to incorporate these species into environmental assessments to fully evaluate the potential effects of wind farm developments. The pronounced and diverse seasonal fluctuations observed in each bird group underscore the interconnected nature of the eastern Taiwan Strait with distant ecosystems—jaegers linked to the Arctic, waders to Australia, and procellariiform birds to the vast Pacific Basin. Consequently, environmental and anthropogenic stressors in the Taiwan Strait have the potential to affect avian populations across extensive geographical scales.

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AUTHOR CONTRIBUTIONS

YYL conceived the study and was in charge of overall direction and planning. CHH coordinated the field work and curated the data. MLB performed data analysis and wrote the manuscript with input from all authors.

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