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Cover image: Adult female Bengal florican *Houbaropsis bengalensis* at the Angkor Centre for Conservation of Biodiversity, Cambodia (© Kees Groot)

Short Communication

Sandbanks revisited—Critical nesting habitat for the southern river terrapin *Batagur affinis edwardmolli* in the Sre Ambel river system, Cambodia

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The southern river terrapin *Batagur affinis edwardmolli*, known in Cambodia as the "Royal Turtle" (Andoeuk Luong) owing to an historical association with the royal family (Bourret, 1941), is a large (straight-line carapace length [SCL] up to 625 mm) aquatic turtle once common in rivers and estuaries of the Thai-Malay Peninsula (southern Thailand, Malaysia & Singapore), Sumatra, Cambodia and Vietnam (Moll *et al*., 2015). Populations of *B. affinis* throughout Southeast Asia are now either extinct (Thailand, Singapore & Vietnam) or greatly reduced (Sumatra, Malaysia & Cambodia) due to the chronic over-collection of eggs, direct killing for food, incidental take in fisheries gear, loss of critical sandbank nesting habitat and construction of hydropower dams (Moll *et al*., 2015). Consequently, *B. affinis* is now considered one of the 25-most endangered turtles in the world (Stanford *et al*., 2018) and ranked as Critically Endangered on the IUCN Red List (Horne *et al*., 2016; Rhodin *et al*., 2018).

In Cambodia, *B. affinis* historically occurred in the Mekong River, Tonle Sap Lake and rivers along the southwestern coast that flow into the Gulf of Thailand (Bourret, 1941; Platt *et al*., 2003, 2008; Moll *et al*., 2015). Other than two intact shells dredged from sediments in the Tonle Sap Lake, little is known about the *B. affinis* population in the Mekong River, which apparently went extinct in the early 1900s (Platt *et al*., 2008). *Batagur affinis* persisted longer in the rivers of southwestern Cambodia, although by the late 1990s these populations were also assumed to be extinct (Tana *et al*., 2000). Fears of extinction proved unfounded however, when a small population (<10 adult turtles; Çilingir *et al*., 2019) was rediscovered in the Sre Ambel river system (SARS) in 2001 (Platt *et al*., 2003). The SARS drains parts of Koh Kong, Kampot and Kampong Speu provinces, including the southwestern slopes of the Damrei and Cardamom mountains, before debouching into Kampong Som Bay (Platt *et al*., 2006).

Subsequent to the rediscovery, conservation efforts for *B. affinis* implemented by the Wildlife Conservation Society, Turtle Survival Alliance and Mandai Nature in collaboration with the Cambodia Fisheries Administration of the Ministry of Agriculture, Forestry & Fisheries largely focused on protecting critical sandbank nesting habitat, safeguarding nests, captive-breeding, and reintroduction of head-started turtles (Moll *et al*., 2015). At the time of writing (September 2025), 206 head-started *B. affinis* (125 females & 81 males, 4–7 years-old) have been released into the SARS (Som & Thorn, unpubl. data). Despite these measures, *B. affinis* in the SARS remains

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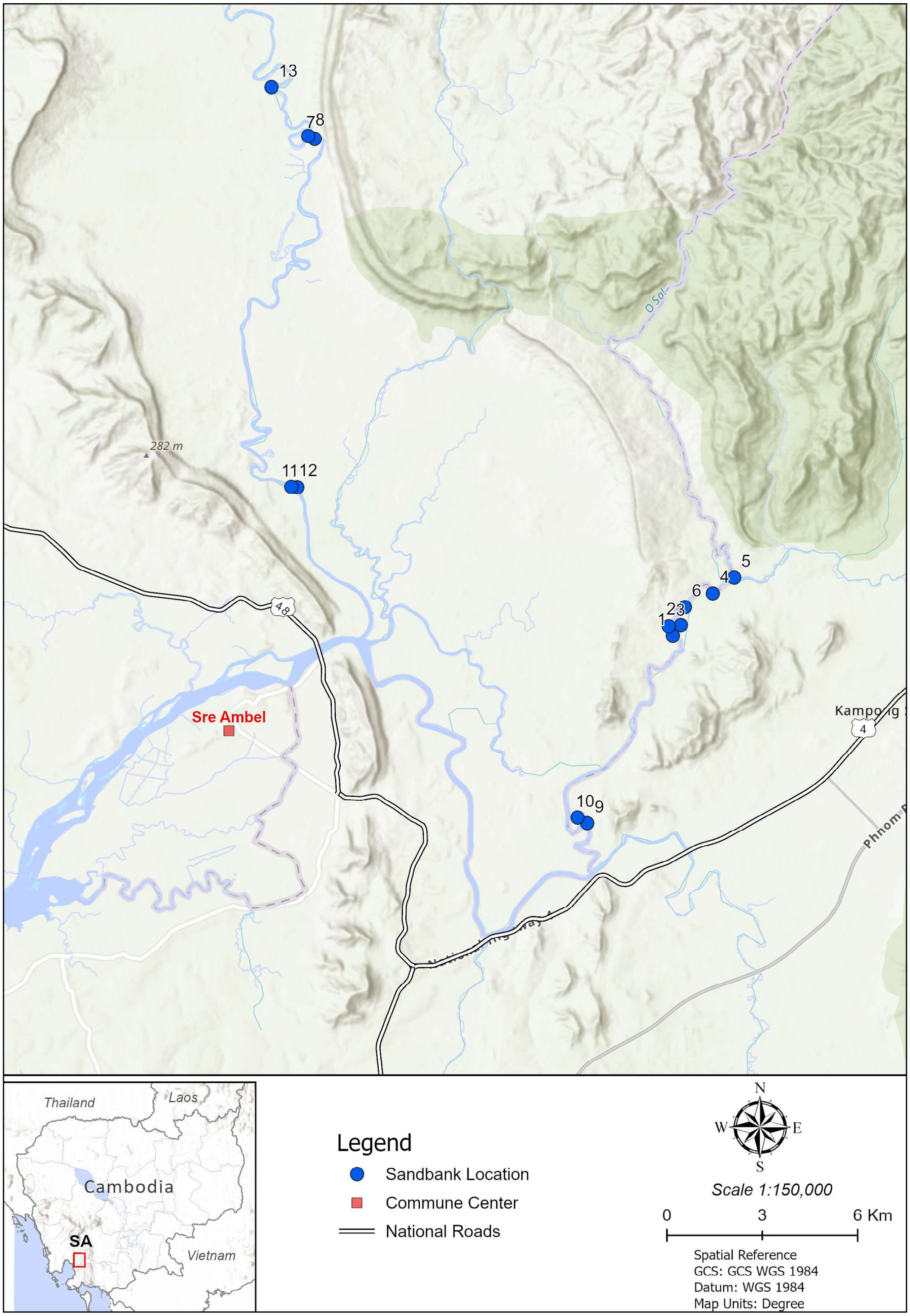

Fig. 1 Sre Ambel river system with locations of sandbanks used as nesting sites by the Critically Endangered *Batagur affinis*. Numbers correspond to sites listed in Table 1. Inset shows the location of Sre Ambel river system in Cambodia

Table 1 Sandbanks in the Sre Ambel river system used as nesting sites by *Batagur affinis*. Numbers correspond to locations shown in Fig. 1. Asterisks denote sandbanks not reported by Platt *et al*. (2003). Geographic coordinates in the table below were obtained in February 2025 (see text) and supersede those presented in Platt *et al*. (2003)

No.	Latitude (N)	Longitude (E)	Site Assessment / Notes
1	11.14039°	103.86993°	Sandbank now supports dense grass and woody vegetation with little exposed sand; unsuitable as turtle nesting habitat without removal of encroaching vegetation
2	11.14341°	103.87215°	Intact; remains suitable turtle nesting habitat
3	11.14310°	103.86870°	Sandbank with dense grass and scattered *Mimosa pigra*; in need of vegetation management to expose suitable nesting substrate
4	11.15239°	103.88120°	Sandbank destroyed by illegal sand-dredging in 2018; sand now being replenished by annual flooding
5	11.15686°	103.88719°	Partially destroyed by active sand-mining; human disturbance currently precludes turtle nesting
6	11.14860°	103.87330°	Grass and saplings on parts of beach, but abundant exposed sand; vegetation management is warranted to enhance nesting habitat
7	11.28102°	103.76874°	Small sandbank with dense grass; newly constructed recreational home adjacent to sandbank; human disturbance may deter future nesting
8	11.28178°	103.76690°	Exposed sand with scattered woody vegetation; vegetation management is warranted to enhance nesting habitat
9	11.80740°	103.84573°	Active nesting site; *B. affinis* clutches deposited most years from 2006 to present; known locally as Chheuteal Sandbank.
10	11.08901°	103.84293°	Exposed sand with woody vegetation; suitability as nesting habitat would be enhanced by vegetation management
11*	11.18421°	103.76380°	Low sandbank in pasture grazed by livestock; villagers excavating sand; clutch of *B. affinis* eggs recovered at this site in 2022
12*	11.18256°	103.76212°	Spoil deposit left by defunct sand dredging operations; two *B. affinis* clutches recovered at this site in 2020

imperilled by the destruction of critical nesting habitat from sand-mining, incidental take in fisheries gear, and illegal, albeit largely opportunistic capture for local consumption (Moll *et al*., 2015; Çilingir *et al*., 2019).

During the initial surveys conducted in 2001–2002, Platt *et al*. (2003)—working in collaboration with local villagers—identified 12 sandbanks along the Sre Ambel and Kampong Leu rivers (38–61 km upstream from Kampong Som Bay) used for nesting by *B. affinis*. These locations were well-known to local villagers, who collected turtle eggs for household consumption and sale in local markets (Platt *et al*., 2003). The sandbanks used for nesting by *B. affinis* consisted of unvegetated sand embankments elevated well-above the seasonal low-water level (Platt *et al*., 2003). Beginning in the mid-2000s, illegal and legal sand-mining became commonplace in the SARS and threatened to destroy these critical nesting sites (Som & Horne, 2017). A ministerial proclamation (Prakas No. 236) issued by the Ministry of Mines and Energy in 2017, banned sand-mining in the SARS (MME, 2017; Som, 2018). Nonetheless, industrial-scale sand extraction continued until at least June 2018 (Som, 2018), and small-scale sand-mining (legal and illegal) has occurred intermittently in the years since (Som & Thorn, unpubl. data).

Despite the importance of intact sandbanks for nesting, population recruitment, and ultimately the recovery of *B. affinis* in SARS, these critical habitats had not been assessed since the original surveys 23–24 years ago. This assessment was urgently needed to evaluate ongoing habitat protection measures and develop effective long-term conservation plans to restore *B. affinis* as a functional member of the Sre Ambel river ecosystem. To this end, we revisited the Sre Ambel and Kampong Leu rivers and attempted to relocate the sandbanks reported as *B. affinis* nesting sites by Platt *et al*. (2003). We aimed to determine if these sandbanks remained intact, and if so, qualitatively assess their suitability as nesting habitat for *B. affinis*.

Our survey was conducted from 18–20 February 2025 along the Sre Ambel and Kampong Leu rivers (Fig. 1). We used the previously published geographic coordinates (Table 1 in Platt *et al*., 2003) and copies of field notes and hand-drawn maps made during the original investigation by one of us (SGP) to relocate the sandbanks. On relocating each sandbank, we recorded a new set of coordinates using a hand-held GPS Unit (Garmin® 64S, accurate to within 5–10 m), evidence of anthropogenic disturbance (e.g., temporary and permanent dwellings, sand mining, and livestock grazing), and assessed the extent of any encroaching vegetation. We also recorded the coordinates of other sandbanks and spoil deposits used as nesting sites by *B. affinis* since 2004.

During our investigation we were able to relocate ten of the 12 nesting sandbanks reported by Platt *et al*. (2003) along the Sre Ambel and Kampong Leu rivers (Table 1, Fig. 1). We found inaccuracies in some of the geographic coordinates given by Platt *et al*. (2003), presumably resulting from limitations of the GPS technology available during the early 2000s. Despite erroneous coordinates, the hand-drawn maps and site descriptions in the original field notes allowed us to successfully relocate the sandbanks. We were unable to reach one sandbank on the upper reaches of the Kampong Leu River (Platt *et al*., 2003) due to a combination of low water levels and potential security threats posed by illegal sand-dredgers known to be operating in this area. Another sandbank along the Sre Ambel River (11.3275°N, 103.7288°E: Platt *et al*., 2003) no longer exists, having been removed during sand-dredging operations over ten years previously (see also Çilingir *et al*., 2019). Only one of the sandbanks reported by Platt *et al*. (2003) has been used for nesting by *B. affinis* (1–4 clutches/year) since the monitoring programme began in 2006 (Chheuteal Sandbank: Table 1, Fig. 2a). The sudden reduction in the number of sandbanks used by nesting turtles in 2006 and afterwards compared to 2001–02 no doubt reflects the rapid, catastrophic collapse of the *B. affinis* population that occurred in SARS during the early 2000s (Çilingir *et al*., 2019).

We found significant encroachment of grass and woody vegetation on six of the ten (60%) sandbanks located (Table 1, Fig. 2b). The presence of *Mimosa pigra* on one sandbank was particularly alarming because this invasive species is adapted to riverine habitats, tolerates flooding, and can aggressively overtake and eliminate other vegetation through allelopathy and direct competition (Welgama *et al*., 2022). Because *B. affinis* requires open, unvegetated, bare sand for nesting (Moll *et al*., 2015), encroaching vegetation could discourage or prevent the use of these sandbanks by nesting females in the future (Moll, 1997). Therefore, to maintain sandbanks in the SARS as suitable nesting substrates, the annual removal of grasses and woody vegetation should be undertaken prior to the nesting season (December–January) (Moll, 1997). Similar management practices are necessary to maintain nesting habitat for *B. affinis* in Malaysia where sandbanks are no longer scoured of vegetation by annual flooding because of hydrological changes stemming from upstream dam construction (Kalyar *et al*., 2007).

Since 2020, *B. affinis* have nested at two locations in the SARS not reported by Platt *et al*. (2003). The first location is a large pile of unvegetated sand immediately adjacent to the river, abandoned by a now-defunct dredging operation circa 2015 (Table 1, Fig. 2c). We recovered two *B. affinis* clutches (11 & 24 eggs) from this sandpile in 2020; both clutches were excavated and later reburied at the Chheuteal Sandbank to complete incubation (for methods see Som *et al*., 2015). The second location is a low-lying, riverside pasture (ca. 100 m downstream from the first location) where heavy grazing by water buffalo *Bubalus bubalis* exposed the deep sand substrate (Fig. 2d). We recovered a clutch of 15 *B. affinis* eggs from this site in 2022 and transferred these to Chheuteal Sandbank to complete incubation. To our knowledge, the clutches we recovered from the sandpile are the only confirmed report of *B. affinis* using an artificial substrate for nesting. This behaviour is not unexpected however, given that other turtles frequently use artificial islands and spoil deposits for nesting (Beaudry *et al*., 2010; Buhlmann & Osborn, 2011; Paterson *et al*., 2013). Our findings also raise the possibility that artificial nesting sites for *B. affinis* could be constructed along the river, perhaps using sand confiscated by government authorities from illegal dredging operations. However, given the high costs involved in the construction of new sandbanks, a more feasible approach would be to rigorously protect and manage existing sandbanks along the river.

Although most of the sandbanks identified by Platt *et al*. (2003) are no longer used for nesting by *B. affinis*, these sites should nonetheless be protected and managed in anticipation of future nesting by reintroduced turtles. To date, 125 female *B. affinis* have been reintroduced into the river and approximately 200 captive-bred hatchlings and juveniles are currently being head-started for eventual release. Because female *B. affinis* require 13–15 years to attain sexual maturity in captivity (Platt *et al*., 2023) and >20 years in the wild (Moll *et al*., 2015), reproduction among reintroduced turtles is unlikely to occur in the immediate future. Maintaining and protecting the existing sandbanks will ensure that sufficient nesting sites

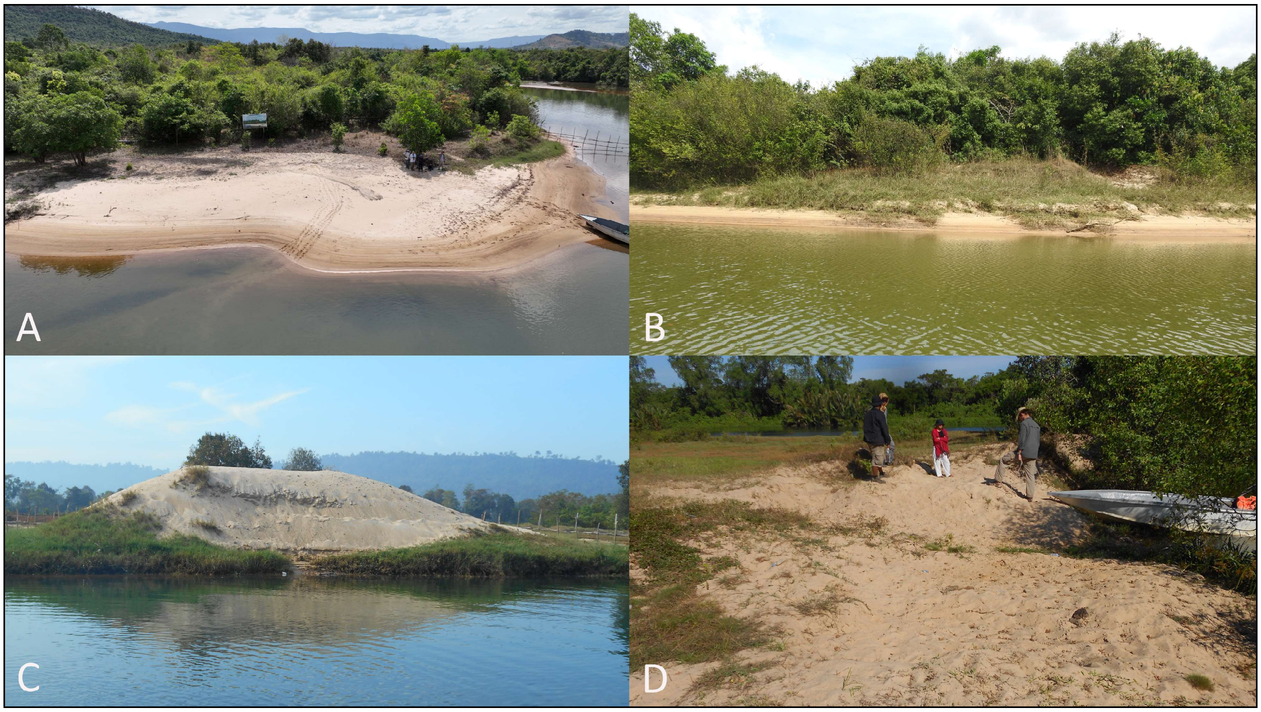

Fig. 2 A) Chheuteal Sandbank, an active nesting site where *Batagur affinis* clutches have been deposited during most years from 2006 to present, B) Sandbank with encroaching grass and woody vegetation, C) Spoil deposit left by defunct sand dredging operation and used as a nesting site by two *B. affinis* in 2020, D) Low sandbank in a heavily grazed livestock pasture where a clutch of *B. affinis* eggs was recovered in 2022

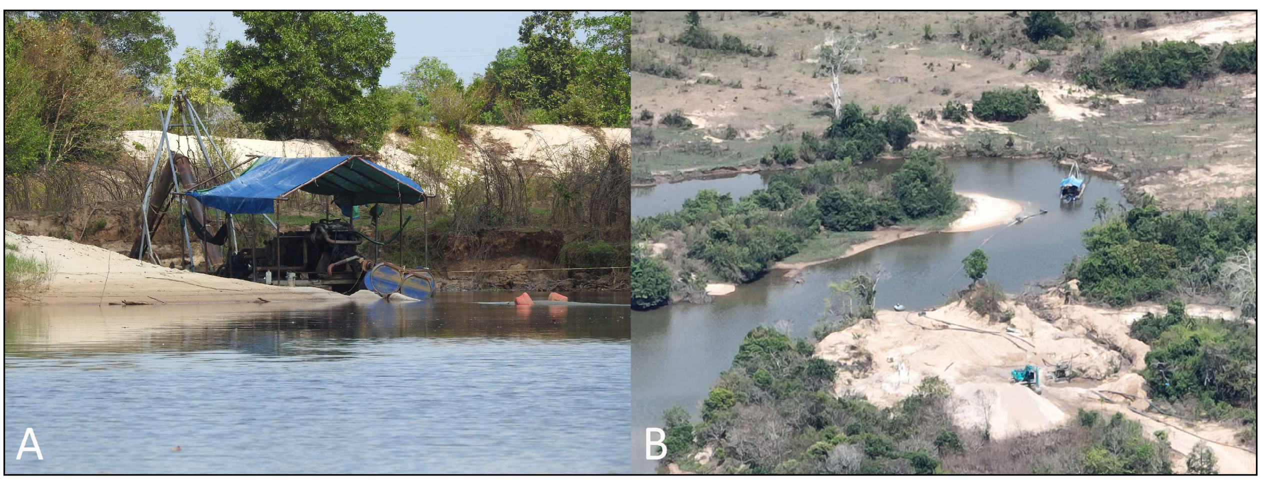

Fig. 3 Illegal sand dredging operation on the upper reaches of the Sre Ambel River (February 2025): A) Close-up of sand dredge, B) Aerial view showing environmental destruction caused by dredging

are available as reintroduced female turtles reach sexual maturity and begin to reproduce. Furthermore, existing sandbanks could also provide critical nesting habitat for other threatened turtles (e.g., *Amyda ornata* & *Pelochelys cantorii*) and perhaps shorebirds (e.g., Charadriidae).

The loss of only one sandbank to sand extraction operations during the 20+ years since the initial surveys (2001–2002) is encouraging and suggests that protective measures undertaken by the Ministry of Mines & Energy, Ministry of Agriculture, Forestry & Fisheries, Wildlife Conservation Society, Turtle Survival Alliance and Mandai Nature (Som, 2018) are at least partially effective in halting sandbank destruction. That said, we encountered illegal as well as legal sand extraction operations in the SARS during our survey in February 2025 (Fig. 3). Alongside threats posed by sand extraction to turtle nesting habitat, these operations also destroy benthic communities, negatively impact commercial and subsistence fisheries, lower river beds and alter water flows, modify flood regimes by increasing flood frequency and intensity, accelerate land loss from erosion, lower water quality, and damage infrastructure (Peduzzi, 2014; Jordan *et al*., 2019). Since the potential impacts of sand extraction obviously extend far beyond river turtle conservation, continued and intensified measures to enforce the 2017 ministerial proclamation are warranted in the SARS.

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Interactions between an Irrawaddy dolphin *Orcaella brevirostris* mother-calf pair and Indo-Pacific humpback dolphins *Sousa chinensis* in southern Cambodia

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របាយការណ៍អំពីការប៉ះទង្គិចគ្នារវាងថនិកសត្វរស់នៅក្នុងទឹកនៃលំដាប់បាឡែន (cetaceans) ដែលកើតមានជារឿយៗមានដូចជាភាពស្និតស្នាលដូចជាការថែទាំកូនជំនួសមេ (alloparental care) និងការឈ្លានពានរួមទាំងការប៉ះទង្គិចដល់ស្លាប់ផងដែរ។ អន្តរអំពើទាំងនេះមានភាពស្មុគស្មាញ ហើយអាចនាំឲ្យមានការបង្កើតក្រុមប្រភេទសត្វចម្រុះ ជាពិសេសចំពោះប្រភេទសត្វផ្សោតដែលមានរបាយភូមិសាស្ត្រដូចគ្នា (sympatric delphinids)។ នៅដែនទឹកតំបន់ឆ្នេរសមុទ្ររបស់ប្រទេសកម្ពុជា សត្វផ្សោតក្បាលត្រឡោក *Orcaella brevirostris* និងសត្វផ្សោតឃ្លាច *Sousa chinensis* រស់នៅក្នុងតំបន់ជាមួយគ្នា និងប្រឈមនឹងការគំរាមកំហែងស្រដៀងគ្នាដែលមានដូចជាការបាត់បង់ទីជម្រក និងការនេសាទបានដោយចៃដន្យ។ ក្នុងអំឡុងពេលនៃការសិក្សាស្រាវជ្រាវតាមទូក យើងបានសង្កេតឃើញអន្តរអំពើដ៏កម្ររវាងមេ-កូនសត្វផ្សោតក្បាលត្រឡោក និងក្រុមសត្វផ្សោតឃ្លាចចំនួនប្រាំពីរក្បាល (សត្វពេញវ័យប្រាំក្បាល សត្វជិតពេញវ័យមួយក្បាល និងសត្វវ័យជំទង់មួយក្បាល)។ ហេតុការណ៍នេះត្រូវបានកត់ត្រាដោយការថតរូប និងវីដេអូជ្រូនដែលអាចកំណត់អត្តសញ្ញាណឯកត្តៈសត្វផ្សោតឃ្លាចទាំងអស់។ អាកប្បកិរិយាស្រដៀងនឹងការថែរទាំកូនសត្វផ្សោតក្បាលត្រឡោកដោយសត្វផ្សោតឃ្លាច (alloparental care) ត្រូវបានសង្កេតឃើញជាលើកដំបូង។ ទោះបីជាអន្តរអំពើនេះនៅតែបន្ត ការឈ្លានពាននៅតែកើតឡើង ដូចជាការប៉ុនប៉ងបំបែកកូន និងការប៉ះទង្គិចគ្នា។ អាកប្បកិរិយាទាំងនេះមានលក្ខណៈប្រឆាំងគ្នា តែគ្មានភស្តុតាងបង្ហាញពីចេតនាសម្លាប់កូនសត្វផ្សោតឬរបួសធ្ងន់ធ្ងរនោះទេ។ អន្តរអំពើរវាងប្រភេទសត្វខុសៗគ្នាបែបនេះពិបាកបកស្រាយ និងនៅតែមានការយល់ដឹងតិចតួច ជាពិសេសនៅតំបន់ដែលមិនទាន់មានការសិក្សាច្រើន ដូចជាប្រទេសកម្ពុជា។ តាមការយល់ដឹងរបស់យើងនេះជាកំណត់ត្រាលើកដំបូងអំពីអន្តរអំពើរវាងប្រភេទសត្វទាំងពីរនៅក្នុងប្រទេសកម្ពុជា ហើយក៏ជាឯកសារលម្អិតនិងមានតិចបំផុតនៅលើពិភពលោកផងដែរ។ ការសិក្សាស្រាវជ្រាវបន្តមានសារៈសំខាន់ណាស់ ដើម្បីយល់ដឹងកាន់តែប្រសើរអំពីអាកប្បកិរិយា និងផ្សារភ្ជាប់វាជាមួយនឹងការអភិរក្សប្រភេទសត្វទាំងនេះ។

Abstract

Reports of interspecific encounters among cetaceans are common and range from affiliative behaviours such as allo-parental care to aggression, including lethal encounters. These interactions are complex and may lead to the formation of mixed-species groups, particularly among sympatric delphinids. In Cambodia's coastal waters, Irrawaddy

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dolphins *Orcaella brevirostris* and Indo-Pacific humpback dolphins *Sousa chinensis* share overlapping ranges and face similar threats, including habitat degradation and bycatch. During a boat-based survey, we observed a rare interaction between an Irrawaddy dolphin mother-calf pair and a group of seven Indo-Pacific humpback dolphins (five adults, one subadult and one juvenile). This event was documented through photography and drone footage, which allowed individual identification of all the humpback dolphins. Behaviours resembling alloparental care by the humpback dolphins toward the Irrawaddy calf were initially observed. As the interaction continued however, instances of aggression emerged, including calf separation attempts and physical contact. While these were agonistic, there was no evidence of infanticidal intent or serious harm. Interspecific interactions like these are difficult to interpret and remain poorly understood, particularly in understudied regions like Cambodia. To our knowledge, this is the first documentation of interactions between the two species in Cambodia and one of the few detailed accounts globally. Continued monitoring is essential to better understand these behaviours and their implications for conservation.

Keywords Agonistic interaction, alloparental care, Gulf of Thailand, mixed-species group

Introduction

Interspecific interactions between cetaceans have been widely reported and vary in character (Herzing *et al*., 2003; Syme *et al*., 2023; Bearzi, 2005; Maze-Foley & Mullin, 2006; Koper & Plön, 2016; Ramos *et al*., 2024). They can be mutually beneficial, offering advantages such as improved foraging efficiency, social benefits, or increased protection from predators for at least one species involved (Stensland *et al*., 2003). Alternatively, interactions can be neutral or negative, particularly in the case of competition for resources or space (Stensland *et al*., 2003). Interspecific interactions can be highly dynamic, involving direct behavioural exchanges and coordinated activities, or they may be passive associations (Stensland *et al*., 2003). Such groups can persist for varying temporal scales, from a few minutes to several years (Clua & Grosvalet, 2001; Stensland *et al*., 2003).

Interspecific alloparental care is defined as any behaviour by an individual towards non-descendant young that benefits the young (Woodroffe & Vincent, 1994). Although rarely observed (Conry *et al*., 2022), interspecific alloparental care has been documented for a few cetacean species (Conry *et al*. 2022; Würsig *et al*. 2023; Baumgartner *et al*., 2025), including the Indo-Pacific humpback dolphin *Sousa chinensis* (Karczmarski *et al*., 1997; Kamaruzzan & Jaaman, 2013; Wang *et al*., 2013) and the Indian Ocean humpback dolphin *Sousa plumbea* (Conry *et al*., 2022). Agonistic interactions often involve aggressive behaviours such as strikes delivered from the fluke and peduncle, bites or ramming with the rostrum, and sometimes involve calves or the attempted separation of mother-calf pairs (Crespo-Picazo *et al*., 2021; Ramos *et al*., 2024). Interspecific aggression can be unidirectional, with one species clearly initiating the agnostic interaction (Ramos *et al*., 2024), or multidirectional, where it is unclear which species is dominant or initiating the interaction (Cusick & Herzing, 2014). The drivers behind agonistic interactions can be complex and vary widely (Robinson, 2014) but may include competition over resources or space (Stensland *et al*., 2003; Cusick & Herzing, 2014), sexual aggression (Herzing & Elliser, 2013; Methion & Díaz López, 2021), infanticidal tendencies (Robinson, 2014; Estrade, 2017), or environmental disturbance (Elliser & Herzing, 2016). Additionally, factors such as habitat alteration, overexploitation, and land-use changes (among others) may reduce food and shelter, forcing more aggressive competition (Holbrook & Schmitt, 2002).

Although Indo-Pacific humpback dolphins (hereafter 'humpback dolphins') and Irrawaddy dolphins *Orcaella brevirostris* are sympatric and sometimes form mixed groups, records of persistent association between the species are rare. One such instance was documented in Malaysia, where an Irrawaddy dolphin calf repeatedly sought the company of a group of humpback dolphins (Kamaruzzan & Jaaman, 2013). Humpback dolphins are found in the Eastern Indian Ocean and throughout Southeast Asia (Jefferson & Smith, 2016), whereas Irrawaddy dolphins occur in waters across the Bay of Bengal to the Indonesian Archipelago (Fig. 1) (Krützen *et al*., 2018; Budi *et al*., 2024). Both species inhabit estuarine and brackish waters, with Irrawaddy dolphins also inhabiting rivers (Jutapruet *et al*., 2015; Huang *et al*., 2019). Both species occur in Cambodia (Beasley & Davidson, 2007) and are the focus of ongoing research by Marine Conservation Cambodia in the Kep and Kampot provinces.

There are no global population estimates for Irrawaddy dolphins or humpback dolphins. However, populations of both species are decreasing and experiencing severe anthropogenic fragmentation across their ranges (Jefferson *et al*., 2017), with Irrawaddy dolphins

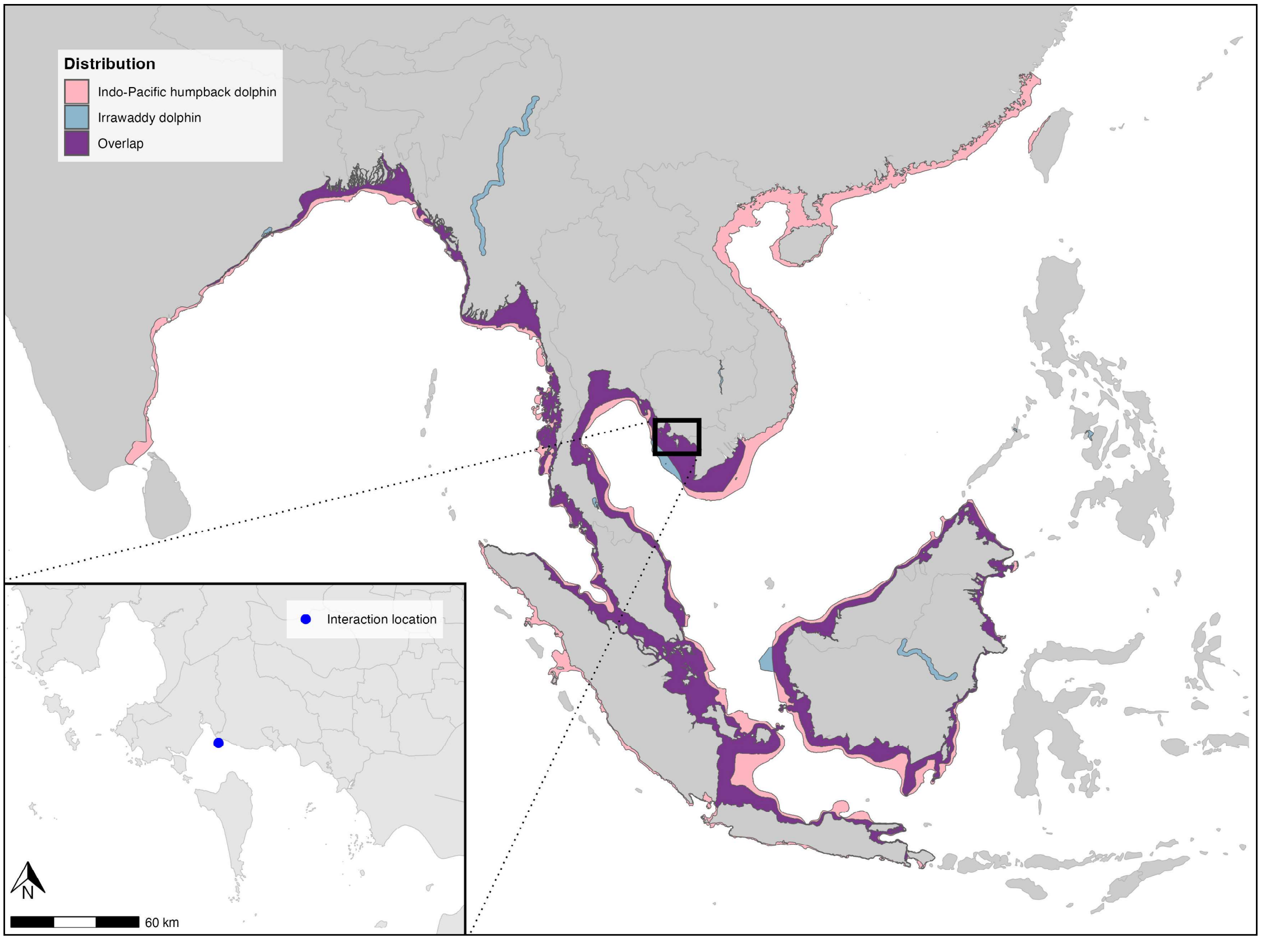

Fig. 1 Distribution of Indo-Pacific humpback dolphins and Irrawaddy dolphins (Jefferson *et al*., 2017; Minton *et al*., 2017), the black square marks the region presented in the inset, where the interaction was recorded

classified as Endangered (Minton *et al*., 2017) and humpback dolphins listed as Vulnerable (Jefferson *et al*., 2017). In Cambodia, gillnets and trawling have led to dolphin mortalities in Kep and Kampot provinces (Tubbs *et al*., 2019; Jones *et al*., 2022). In addition, extensive dredging and land reclamation are underway to construct an international shipping port in Preaek Tnaot, Kampot Province (B2B Cambodia, 2024), within the local range of humpback and Irrawaddy dolphins (MCC, unpubl. data).

Monitoring of marine mammal populations is an essential aspect of conservation management and especially important for understanding trends in fragmented and threatened populations, identifying critical habitats and sustainable fisheries management (Azzellino *et al*., 2017; Crespo-Picazo *et al*., 2021; Methion & Díaz López, 2021; Syme *et al*., 2024). To this end, boat-based surveys have been conducted in Kampot Province for two to three days each month between 0600–1000 and 1500–1800 hrs since July 2022, when weather conditions have allowed. This paper describes interspecific interactions observed during these surveys between an Irrawaddy dolphin mother and calf and a group of humpback dolphins.

Methods

Study area

Our observations of interspecific interactions between humpback dolphins and Irrawaddy dolphins occurred in the Preaek Tnaot Community Fishery (10.5725933°N, 103.936091°E). The community fishery is located on the eastern side of Veal Rinh Bay, Kampot Province (Fig. 1). Local waters are shallow (<11 m depth) and encompass diverse coastal habitats, including mangroves, coral reefs and seagrass meadows (FIA, 2022). The area receives substantial inputs from the Kampot River to the west and the Giang River to the east.

Data collection

Our observations occurred during boat-based surveys conducted as part of ongoing monitoring of marine mammals in the area. The occurrence and duration of surveys were dependent on weather conditions, particularly rain and wind.

Our categorisation of the maturity of Irrawaddy dolphins was based on their relative size (Jones *et al*., 2022), whereas humpback dolphin maturity was categorised based on pigmentation (Guo *et al*., 2020). Five crew members were required per survey: one boat captain and four observers aboard a nine-meter-long fishing boat with a single 13 horsepower outboard engine. Two observers searched for dolphins with binoculars (7 x 50 magnification) simultaneously, one scrutinising from 90° port to the bow and another from 90° starboard to the bow. Observers were rotated every ten minutes to reduce fatigue. When marine mammals were sighted, observations were recorded every five minutes. If individuals were not seen for over 20 minutes, a new observation began upon the next sighting. In addition, a Mavic 2 Pro drone (DJI, Shenzhen, China) was used to gather information on group composition and behaviour. The drone was operated 50–100 meters above sea level by an additional team member based on land.

Results

We observed a mixed-species group of dolphins on 11 March 2024 in the Preaek Tnaot Community Fishery. The group was observed from 0916 to 1025 hrs and comprised five adults, one subadult and one juvenile humpback dolphin, together with one adult and calf Irrawaddy dolphin. Following the sighting, a drone was flown directly over the group and 13 minutes and 44 seconds of video footage were recorded (MCC, 2025). The duration of drone observation was limited by battery life and the time taken to re-sight the group between battery changes. Selected images depicting major events are shown in Fig. 2 and Annex 1. Images taken from the boat during our observations facilitated identification of the humpback dolphins and the adult Irrawaddy dolphin via their dorsal fins (Fig. 3–6). No other dolphins were sighted during the observation.

Behaviour

For most of our observation, the Irrawaddy dolphin calf swam in the echelon position (i.e., alongside an adult dolphin, usually the mother, near her flank, to gain a hydrodynamic advantage while swimming) to one of the adult humpback dolphins or in the middle of the humpback dolphin group (Fig. 2a, 2c). The adult Irrawaddy dolphin, presumed to be the calf's mother, appeared to attempt to approach the calf but was repeatedly obstructed by the humpback dolphins (Fig. 2a, 2d). At 0928 hrs, one of humpback dolphins appeared to bite or attempt to bite the fluke of the adult Irrawaddy dolphin (Fig. 2b). Two minutes later, the Irrawaddy dolphin calf swam away from the dolphin group in the direction of our boat (Fig. 2e). The humpback and Irrawaddy dolphins stopped travelling, waited a moment in place, and then altered their course and pursued the calf. The humpback dolphins increased their speed and surrounded the calf. Within the group, two adult humpback dolphins then pushed the calf from underneath with their rostrums, launching it partially into the air (Fig. 2f). The group began diving at 0951 hrs, making interactions harder to discern and the dolphins were lost from sight at 1025 hrs. The following day, two of the adult humpback dolphins were re-sighted with the Irrawaddy dolphin adult and calf, however detailed observations could not be made due to challenging weather conditions. An additional two surveys were conducted on the following day however the individuals involved were not sighted again during these surveys.

One of the adult humpback dolphins in the interaction (known as "Big Mama") was re-sighted on 31 July 2024 with a new humpback dolphin calf (Fig. 7). Big Mama was sighted again on 27 January 2025 with her calf, surface-feeding close to a group of Irrawaddy dolphin but not particularly interacting with them. She was therefore likely heavily pregnant at the time of the interspecific interaction in March 2024.

Discussion

Existing literature on interactions between dolphin species mostly concerns bottlenose dolphins (Herzing & Elliser, 2013; Elliser & Herzing, 2015; Estrade, 2017; Crespo-Picazo *et al*., 2021; de Lima *et al*., 2021), with fewer studies involving other species (Kamaruzzan & Jaaman, 2013; Wang *et al*., 2013). Dolphin interactions can be especially difficult to interpret because many are observed from boats, potentially overlooking underwater behaviours. Our use of a drone to complement boat-based observations revealed aspects that would have otherwise remained unseen.

Even with drones, observations of wild dolphins are often fraught with uncertainties because events before and after the observation are unknown. For example, it is not clear if our humpback dolphins found the Irrawaddy dolphin adult and calf, or if the latter were part of a bigger group which separated due to the interaction. No

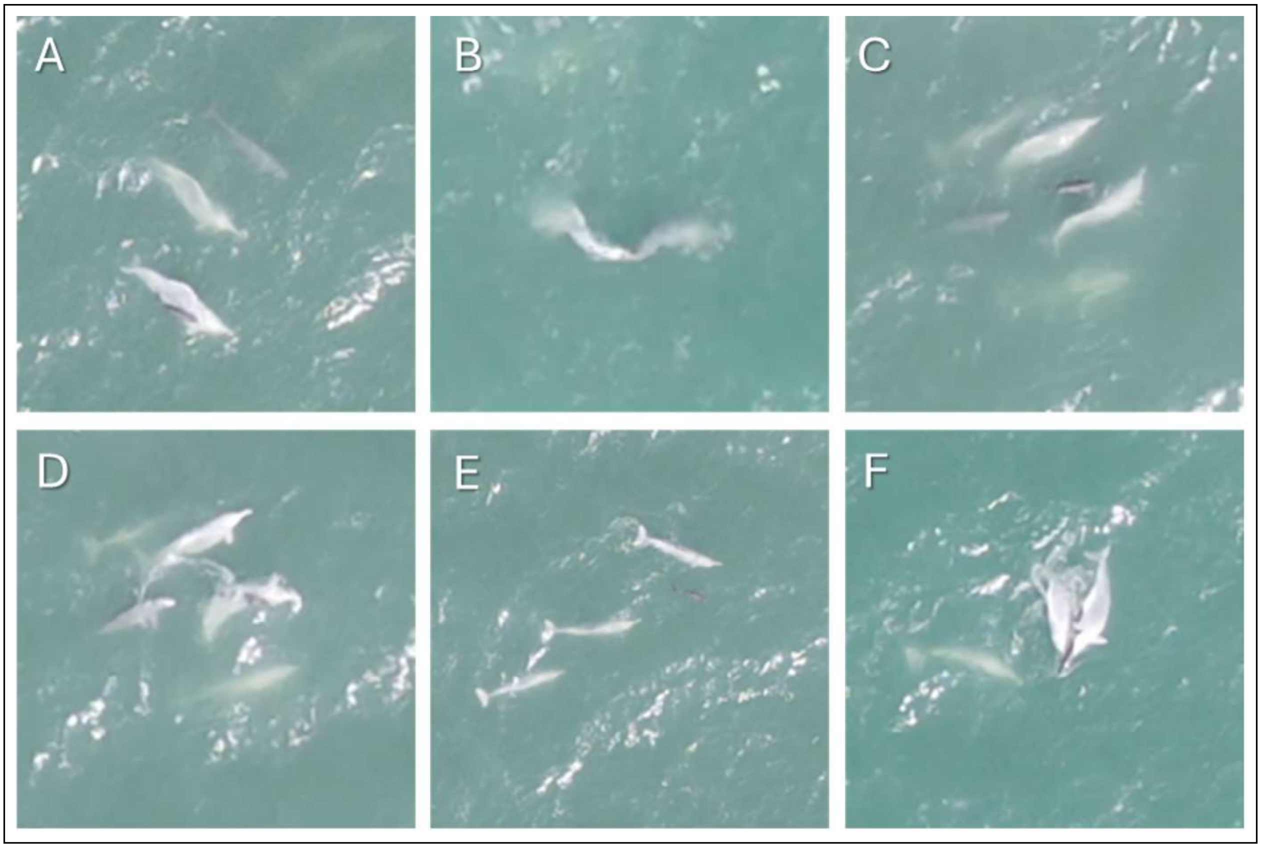

Fig. 2 Drone footage of interactions between Irrawaddy and Indo-Pacific humpback dolphins in March 2024. A) 0928 hrs—Two adult humpback dolphins are between the Irrawaddy dolphin mother and calf. The calf is being pushed up to the surface by the body of one of the adult humpback dolphins. B) The adult Irrawaddy dolphin moves to where the calf had been a few seconds earlier, then moves rapidly over the group, changing direction quickly. The former is followed by an adult humpback dolphin, possibly being bitten on the fluke. C) The adult Irrawaddy dolphin appears directly behind the calf, which is positioned in the middle of the humpback dolphins. D) The humpback dolphins are in a tight front formation, with two individuals flanking the calf on either side. The calf moves over the adult humpback dolphin and is once again separated from the adult Irrawaddy dolphin. E) 0930 hrs—The Irrawaddy dolphin calf swims away from the group and is swiftly chased by the humpback dolphins. F) Two of the humpback dolphins come together and push the calf with their rostrums, propelling the upper body of the calf out of the water (© Ronja Otterstedt & Vichith Kong)

other Irrawaddy dolphins were sighted and it is unclear how long the interaction might have occurred for before our observation. It is also unclear what happened after our observation and although additional surveys in the same area were undertaken in the following days, the group was not observed again.

Alloparental care

Interspecific alloparental care is rarely documented in the wild, including in dolphins (Conry *et al*., 2022). We observed apparent instances of this, such as a humpback dolphin pushing the Irrawaddy dolphin calf to the surface for air, and the calf swimming in echelon position with a humpback dolphin. Similar interactions were recorded in Malaysia where an Irrawaddy dolphin calf appeared to pursue a group of humpback dolphins (Kamaruzzan & Jaaman, 2013). Another instance was documented in China where a humpback dolphin assisted a finless porpoise *Neophocaena phocaenoides sunameri* calf, including three hours of herding the calf and pushing it up out of the water to breathe (Wang *et al*., 2013). Similar behaviours have been observed between orcas *Orcinus orca* and short-finned pilot whale *Globicephala melas* neonate calves, including the calves swimming in echelon position with orcas (Baumgartner *et al*., 2025). An Indian Ocean humpback dolphin mother with a calf has also been recorded with an Indo-Pacific

Fig. 3 Irrawaddy dolphin calf swimming with three adult Indo-Pacific humpback dolphins in March 2024 (© Rebecca Chambers)

Fig. 4 Three adult humpback dolphins with the Irrawaddy dolphin calf in March 2024 (© Rebecca Chambers)

Fig. 5 Adult humpback dolphin (Big Mama) with the Irrawaddy dolphin calf in March 2024 (© Phion Sopheanie)

Fig. 6 The adult Irrawaddy dolphin and presumed mother of the calf sighted in March 2024. Note damage to dorsal fin which does not appear fresh and several shallow rake marks (© Rebecca Chambers)

Fig. 7 Adult humpback dolphin (Big Mama) with a new humpback dolphin calf in July 2024 (© Phion Sopheanie)

bottlenose dolphin *Tursiops aduncus*. Approximately six years later, the same humpback dolphin was observed showing alloparental care towards a common dolphin *Delphinus delphis* calf (Conry *et al*., 2022).

It could be that certain individuals are more likely to exhibit alloparental care, or that other factors may influence such behaviour. Humpback dolphins typically exhibit a fission-fusion social structure, although Dungan *et al*. (2015) suggested associations may be stronger in populations experiencing high anthropogenic pressures in Taiwan, with a greater degree of alloparental care. It is possible that humpback dolphins in Kampot are more likely to exhibit these behaviours due to increasing pressures from coastal development and destructive fishing (Tubbs *et al*., 2019; Jones *et al*., 2022; B2B Cambodia, 2024), similar to the Taiwanese population. It is perhaps inevitable that Indo-Pacific humpback dolphins and Irrawaddy dolphins occasionally encounter one another due to overlap in their feeding or socialising areas (Kamaruzzan & Jaaman, 2013). We have witnessed groups of both species foraging in the same areas in Preaek Tnaot during other surveys, although no interactions have been observed between the two (MCC, unpubl. data).

Agonistic interactions

Although the humpback dolphins we observed appeared to assist the Irrawaddy dolphin calf, subsequent sightings and use of drone footage and photography revealed aggressive behaviours towards the calf and its presumed mother. These included an apparent bite or attempted bite to the adult Irrawaddy dolphin's fluke, repeated mother-calf separations, and two humpback dolphins using their rostrums to lift the calf into the air.

The dynamics and drivers of certain interspecific agonistic interactions, such as the separation of mother-calf pairs or aggression directed towards the calves of other species, remain poorly understood (Syme *et al*., 2021; Ramos *et al*., 2024). Calf-directed aggression has been documented in dolphins, including mother-calf separation, physical attacks such as ramming and biting, and infanticidal tendencies (Robinson, 2014; Estrade, 2017; Methion & Díaz López, 2021; Volker & Herzing, 2021; Ramos *et al*., 2024). Male dolphins are known to occasionally exhibit agonistic sexual behaviours towards other dolphin species, including separating mother–calf pairs or even killing a calf to gain sexual access to a female (Estrade, 2017). In the present case, the occurrence of a juvenile within the humpback dolphin group, together with the later sighting of Big Mama accompanied by a new humpback dolphin, suggests that at least two of the individuals were female. This raises the possibility that reproductive strategies were involved in the interaction, potentially including attempts to eliminate rival offspring to enhance reproductive success (Robinson, 2014). Given that Big Mama was presumably in the late stages of pregnancy during the March encounter, the intent to exclude or harm a competitor's calf could have been a contributing factor. However, overt aggression by the humpback dolphins toward the Irrawaddy mother–calf pair was rare, and no sustained effort was made to injure them in the manner typically observed in infanticidal events among dolphins (Robinson, 2014; Estrade, 2017).

In some documented agonistic events, dolphins have sustained serious injuries or even been killed, with deep rake marks and visible bleeding reported (Cusick & Herzing, 2014; Estrade, 2017; Crespo-Picazo *et al*., 2021). While photographic evidence showed that the adult Irrawaddy dolphin we observed had rake marks on her body (Fig. 6), there was no sign of fresh bleeding. The absence of severe visible injuries combined with the relatively infrequent aggressive behaviours observed suggests that while the interaction was agonistic (particularly the attempted separation of mother and calf), it did not appear to be intended to cause lethal harm to either individual.

Anthropogenic disturbance

Human activities in coastal regions, such as port construction and other infrastructure development, sea reclamation, overfishing and boat traffic can negatively impact marine mammals inhabiting these areas, potentially altering their habitat use and distributions (Karczmarski *et al*., 2017; Wu *et al*., 2017; Wang *et al*., 2024). Range shifts due to anthropogenic disturbance may increase the frequency of agonistic interactions between species, as species may experience increased competition for space or resources (Azzellino *et al*., 2017; Crespo-Picazo *et al*., 2021). While the drivers of the interactions we observed are difficult to determine, disturbance from human activities cannot be excluded (Azzellino *et al*., 2017) considering the construction and operation of a new international port close to the study area and high levels of fishing, including illegal and destructive practices such as bottom trawling (Beasley & Davidson, 2007; Tubbs *et al*., 2019; Hines *et al*., 2020; Verutes *et al*., 2021; Strong *et al*., 2023).

Agonistic interactions and possible alloparental care between humpback and Irrawaddy dolphins have never been reported for dolphin populations inhabiting coastal areas of Cambodia. Our use of drone technology enabled us to record and describe this seemingly rare event. Boat-based photography was also critical to confirm the presence of the adult Irrawaddy dolphin and identify the other dolphins in the interaction. These particularly allowed us to confirm the repeated attempted separation of mother and calf Irrawaddy dolphin, injuries sustained by the adult Irrawaddy dolphin and other agonistic behaviours. While not every behaviour and interaction can be unequivocally interpreted, our photographic and video documentation provides a permanent record of the event. It is hoped that this footage will provide opportunities for clarifying the nature and extent of these kinds of events. Continued monitoring is essential to better understand these behaviours and their implications for conservation of marine megafauna in Cambodia.

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Rebecca Chambers holds a BSc in Zoology (Bangor University, UK) and a MSc in Marine Conservation (University of Plymouth, UK). During her studies, she contributed to marine research and conservation initiatives, gaining hands-on experience with a diverse range of marine taxa, with a focus on marine mammals and elasmobranchs. Rebecca is currently the co-lead researcher and project lead for the Cambodian Marine Mammal Conservation Project. Her work centres on investigating the distribution, abundance, behaviour and conservation status of marine mammals in Cambodian coastal waters.

Sebastian Muñoz-Duque is a biologist with an MSc in Marine Biological Resources (Ghent University, Belgium). He serves as co-lead scientist at Marine Conservation Cambodia and focuses on fish diversity, abundance and passive acoustic monitoring in marine habitats. Since 2010, he has worked on research, consultancy and conservation projects for organizations including the Nature Conservancy, Lisbon University's Fish Bioacoustic Lab, and Universidad de Antioquia's Ichthyology Group. Sebastian regularly publishes peer-reviewed papers in leading journals such as *Aquatic Conservation*, *Global Ecology and Conservation*, Frontiers, *ICES Journal of Marine Science* and *Marine Environmental Research*, among others.

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Amy Jones is a PhD candidate at the Environmental Research Institute, University of the Highlands and Islands (Scotland). Her research explores the use of advanced remote-sensing technologies such as X-band marine radar to investigate the habitat associations of seabirds in tidally-driven marine environments. This work provides insights into the ecological impacts of marine renewable energy development. Amy has contributed to conservation initiatives focussed on Irrawaddy dolphins, sea turtles and marine habitats and published papers in journals such as *Chelonia Conservation and Biology* and the *ICES Journal of Marine Science*.

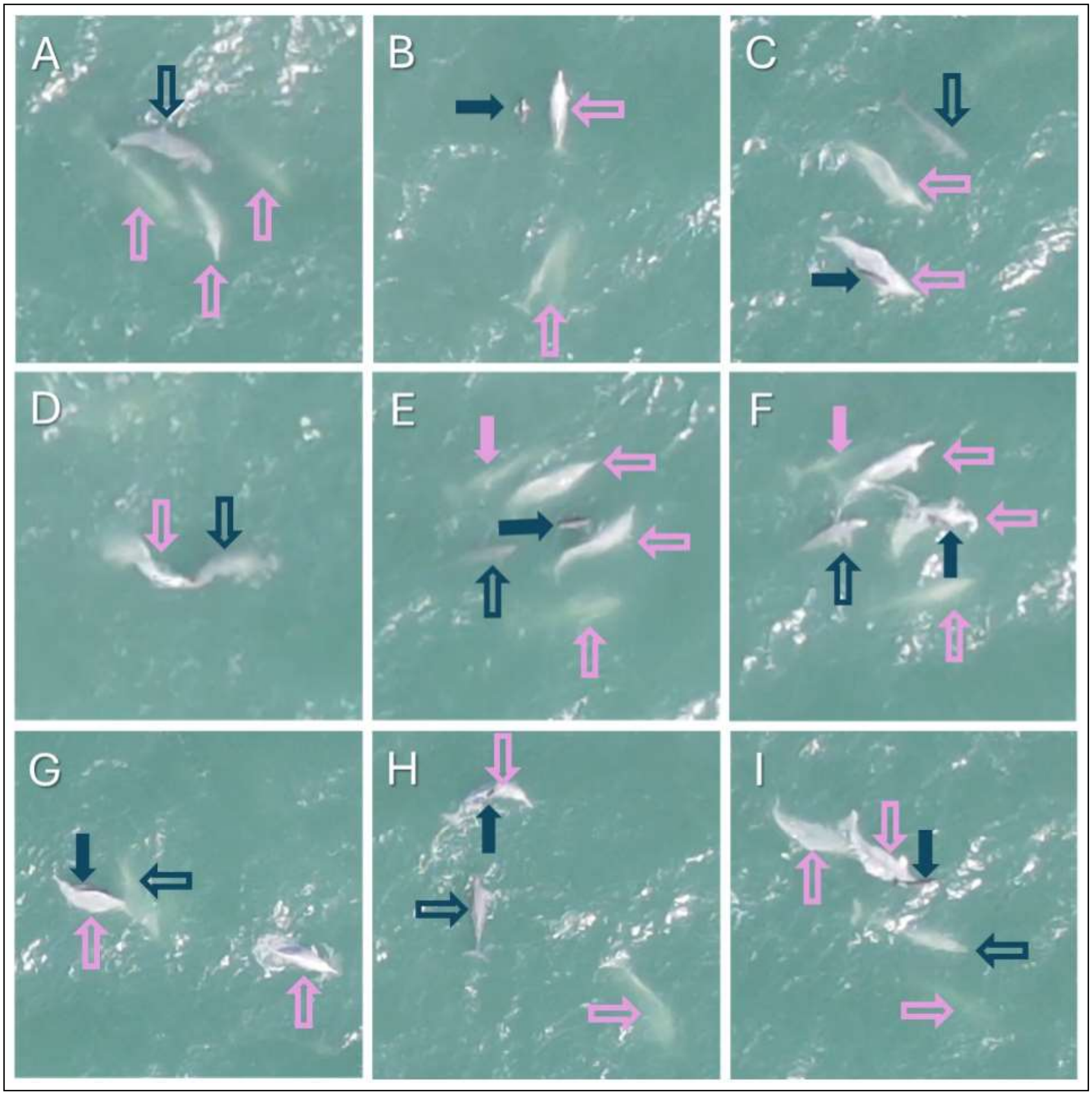
Annex 1 Screenshots from drone footage of interactions between Irrawaddy dolphin *Orcaella brevirostris* mother-calf pair and Indo-Pacific humpback dolphins *Sousa chinensis*

Adult Indo-Pacific humpback dolphin — Adult Irrawaddy dolphin

Juvenile Indo-Pacific humpback dolphin — Calf Irrawaddy dolphin

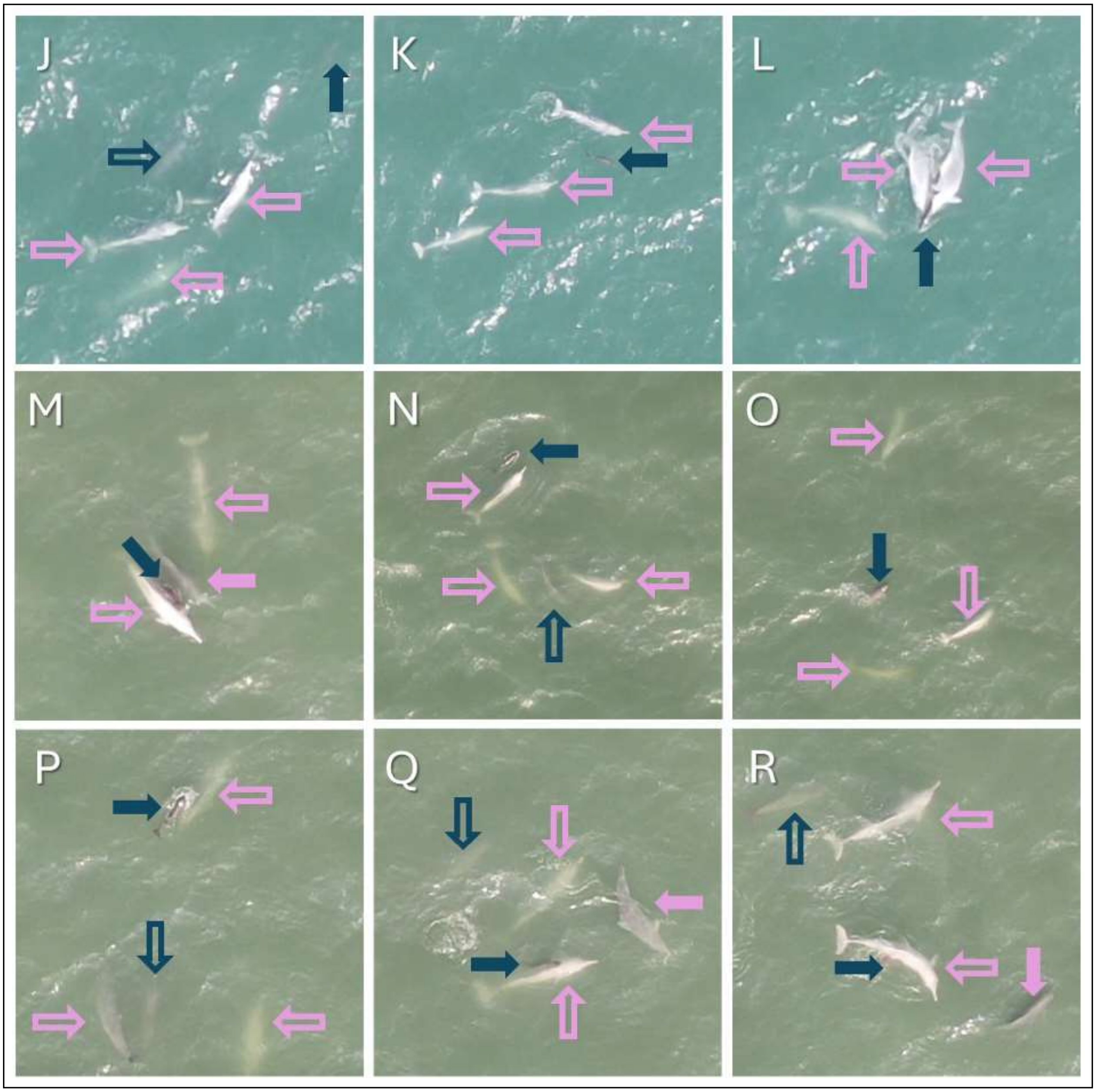
A) 0927 hrs—An adult Irrawaddy dolphin swimming with a group of Indo-Pacific humpback dolphin of mixed ages. The adult Irrawaddy dolphin can be seen swimming over the Indo-Pacific humpback dolphin and turning deliberately on several occasions. B) 0928 hrs—The Irrawaddy dolphin calf regularly swims in echelon position with the adult humpback dolphin. C) Two adult humpback dolphins are between the Irrawaddy dolphin mother and calf. D) The adult Irrawaddy dolphin moves to where the calf had been a few seconds earlier, then moves rapidly over the group, changing direction quickly and is followed by an adult humpback dolphin, possibly being bitten on the fluke.

Annex 1 cont'd



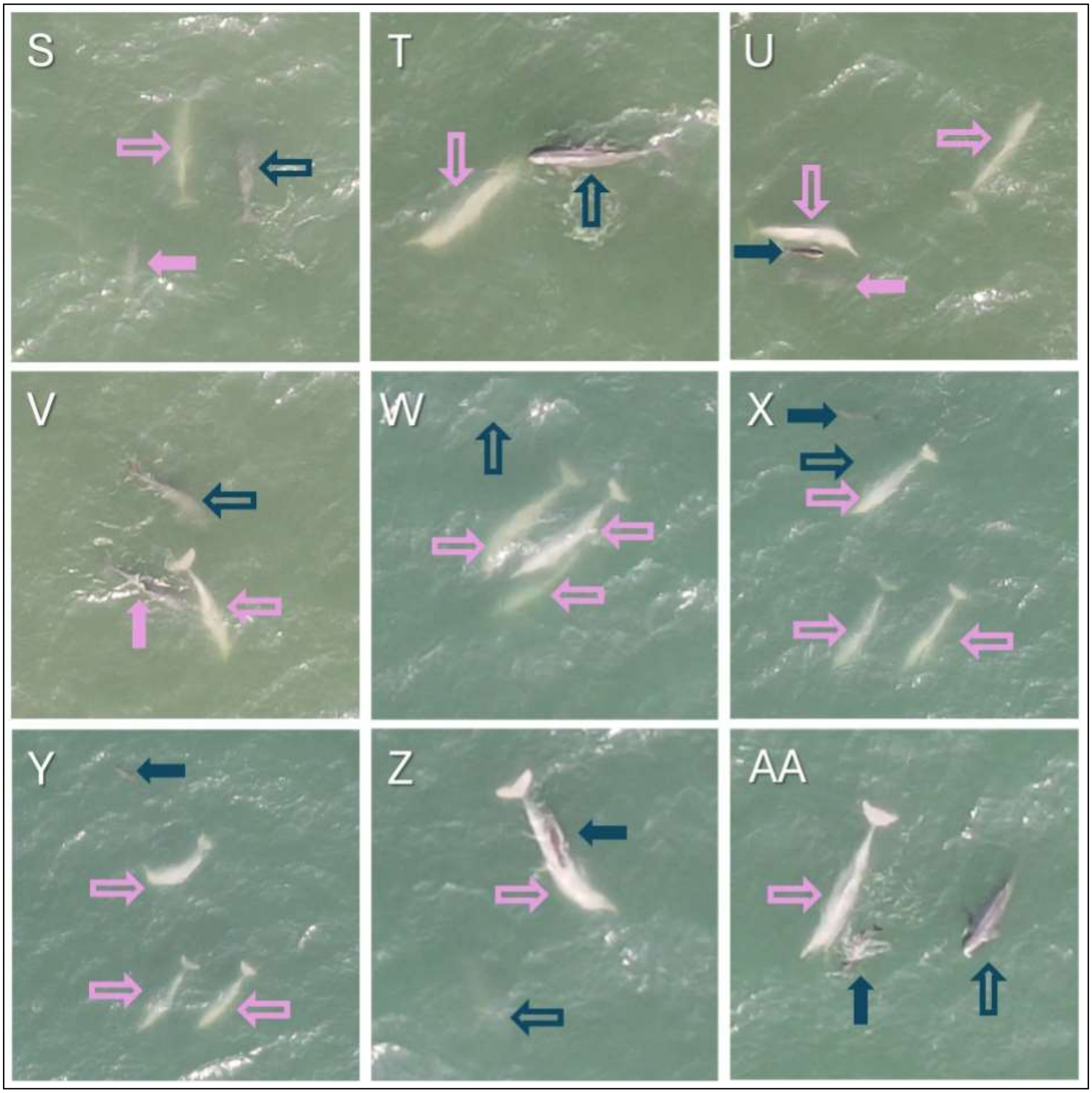
E) The adult Irrawaddy dolphin appears directly behind the calf, which is positioned in the middle of the humpback dolphin group. The humpback dolphin are in a tight front formation, with two individuals flanking the calf on either side. F) The calf goes over the humpback dolphin adult, so is once again separated from the adult Irrawaddy dolphin. G) 0929 hrs—The humpback dolphin uses its body to push the calf, turning it to face the opposite direction from which it was traveling (hereafter referred to as herding). The adult Irrawaddy dolphin is positioned underneath them. H) The adult Irrawaddy dolphin circles back around and heads directly toward the calf. I) 0930 hrs— Another humpback dolphin swims in and pushes the calf with its rostrum. J) The Irrawaddy dolphin calf attempts to swim away from the group. K) The Irrawaddy dolphin calf is swiftly chased by the humpback dolphins. L) Two humpback dolphins come together and push the calf with their rostrums, propelling the upper body of the calf out of the water. M) 0942 hrs—The Irrawaddy dolphin calf is flanked by an humpback dolphin adult and juvenile. The calf continues to be herded by

Annex 1 cont'd



the adult humpback dolphin while the Irrawaddy dolphin adult closely follows the group. N) 0943 hrs—As the adult Irrawaddy dolphin approaches the group, the adult humpback dolphin changes direction and herds the Irrawaddy dolphin calf on its left side in the opposite direction of travel. O) The remaining humpback dolphin and the adult Irrawaddy dolphin reduce their swim speed, rotate, and begin to follow the humpback dolphin adult and Irrawaddy dolphin calf. P) The Irrawaddy dolphin calf surfaces on the left side of the adult humpback dolphin. The pair are followed by the humpback dolphins and the Irrawaddy dolphin adult. The adult humpback dolphin displays continous herding behaviours towards the calf. Q) The juvenile humpback dolphin suddenly changes direction and rapidly swims away from the group and the adult Irrawaddy dolphin immediately becomes visible at the juvenile's original location. R) The adult humpback dolphin herds the Irrawaddy dolphin calf on its right side, turning away from the Irrawaddy dolphin adult and towards the juvenile humpback dolphin. S) The adult Irrawaddy dolphin follows the humpback dolphin

Annex 1 cont'd



adult and juvenile. These three individuals remain together, with minimal travel, for the following minute. No observations of the Irrawaddy dolphin calf are made. T) The adult Irrawaddy dolphin moves closer to the adult and juvenile humpback dolphin. The Irrawaddy dolphin crosses over the adult and interacts with its fluke. Shortly afterwards, both humpback dolphins change direction and begin to travel at speed. U) 0944 hrs—As the humpback dolphin adult and juvenile approach the larger group of humpback dolphins, the Irrawaddy dolphin calf reappears on the right side of the adult humpback dolphin. The adult Irrawaddy dolphin continues to follow the group. V) The adult humpback dolphin turns away from the adult Irrawaddy dolphin with the juvenile humpback dolphin and herds the Irrawaddy dolphin calf in the opposite direction. This sequence of pursuit from the adult Irrawaddy dolphin and herding from the adult humpback dolphin continues for several minutes. W) 0949 hrs—As the adult Irrawaddy dolphin adult continues to approach the Irrawaddy dolphin calf and adult humpback dolphin, two additional adult humpback dolphins flank

Annex 1 cont'd

the calf in a triangular formation. X) While the adult Irrawaddy dolphin is on the right side of the humpback dolphin group, the Irrawaddy dolphin calf swims over the Irrawaddy dolphin adult and changes direction, breaking away from the group. Y) 0950 hrs—The adult humpback dolphin slows and turns towards the calf, altering its direction. The adult remains in place and does not immediately pursue. Z) The adult humpback dolphin catches up with the Irrawaddy dolphin calf and herds this back in the original direction of travel. AA) The adult Irrawaddy dolphin remains close, making infrequent appearances at the surface. The trio continue to swim at speed with the adult humpback dolphin and Irrawaddy dolphin calf in front, and the adult Irrawaddy dolphin behind. These behaviours continue for the remainder of the observation (© Ronja Otterstedt & Vichith Kong).

Diversity, abundance and distribution of seagrasses in three community fisheries, Kampot Province, Cambodia

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មូលន័យសង្ខេប

ស្មៅសមុទ្របានផ្តល់នូវសេវាកម្មអេកូឡូស៊ីដ៏មានសារៈសំខាន់ចំពោះតំបន់ឆ្នេរនៅជុំវិញពិភពលោក ដោយវាដើរតួជាជម្រកសម្រាប់ការបន្តពូជ ព្រមទាំងរួមចំណែកក្នុងការការពារតំបន់ឆ្នេរ និងស្តុកកាបូន។ ទោះបីជា ប្រទេសកម្ពុជាជាប្រទេសដែលមានគម្របស្មៅសមុទ្រជាប់ចំណាត់ថ្នាក់ខ្ពស់ក្នុងចំណោមបណ្តាលប្រទេសនៃតំបន់អាស៊ីអាគ្នេយ៍ក៏ដោយ ប៉ុន្តែការស្រាវជ្រាវទៅលើស្មៅសមុទ្រនៅមានកម្រិតតិចតួច។ ទោះបីជាស្មៅសមុទ្រត្រូវបានរងការខូចខាត ដោយសារសកម្មភាពអភិវឌ្ឍន៍តំបន់ឆ្នេរ និងសកម្មភាពនេសាទខុសច្បាប់ជាប្រវត្តិសាស្ត្រ ស្មៅសមុទ្រដែលមានទំហំធំ និងចម្រុះប្រភេទមានវត្តមាននៅតំបន់ឆ្នេរខេត្តកំពត។ យើងបានធ្វើការវាយតម្លៃភាពចម្រុះនៃប្រភេទ ចំនួនឯកត្តៈ និងការកំណត់របាយស្មៅសមុទ្រនៅក្នុងដែនសហគមន៍នេសាទចំនួនបីក្នុងខេត្តកំពត រួមមានសហគមន៍នេសាទត្រពាំងរពៅ សហគមន៍នេសាទព្រែកត្នោត និងសហគមន៍នេសាទចង្ហោន។ ប្រភេទស្មៅសមុទ្រ និងភាគរយរបស់វាត្រូវបានកត់ត្រានៅក្នុងក្វាដ្រាតដែលបានដាក់នៅតំបន់ទឹកជោរនាច ដោយប្រើខ្សែម៉ែត្រដើម្បីកំណត់របាយស្មៅសមុទ្រនៅក្នុងតំបន់ទាំងនោះ។ ជាលទ្ធផលនៅក្នុងតំបន់ដែលបានសិក្សា ស្មៅសមុទ្រចំនួនប្រាំបីប្រភេទត្រូវបានកត់ត្រា ដែលគ្របដណ្តប់លើក្រឡាផ្ទៃចំនួន១,៨៨៨ហិកតា និងមានភាគរយជាមធ្យម២៨.២% នៅក្នុងដែនសហគមន៍នេសាទត្រពាំងរពៅ ៩៦.៥%នៅក្នុងដែនសហគមន៍នេសាទព្រែកត្នោត និងប្រមាណជា៩២.៥%នៅក្នុងដែនសហគមន៍នេសាទចង្ហោន។ ការរកឃើញនេះ បានគូសបញ្ជាក់ពីសារៈសំខាន់នៃអេកូឡូស៊ីជម្រកស្មៅសមុទ្រ និងផ្តល់នូវមូលដ្ឋានគ្រឹះសម្រាប់ការត្រួតពិនិត្យ និងការអភិរក្សដែនសហគមន៍នេសាទនៅក្នុងខេត្តកំពត។ ការអភិរក្សជម្រកស្មៅសមុទ្រមានសារៈសំខាន់ ដើម្បីទ្រទ្រង់ជីវៈចម្រុះ សេវាកម្មប្រព័ន្ធអេកូឡូស៊ី និងជីវភាពរស់នៅក្នុងតំបន់ ដោយផ្អែកលើវិស័យទេសចរណ៍ និងការនេសាទនៅតំបន់ឆ្នេរសមុទ្រនៃប្រទេសកម្ពុជា។

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Abstract

Seagrasses provide important ecosystem services in coastal regions worldwide, acting as nursery habitats and contributing to shoreline protection and carbon sequestration. Although Cambodia ranks highly among Southeast Asian countries for seagrass cover, research in the country has been limited. Large seagrass meadows with high species diversity historically occurred in coastal areas of Kampot Province, although these have been degraded by coastal development and illegal fishing practices. We evaluated the species diversity, abundance and distribution of seagrasses in three community fishery areas within the province (Trapang Ropov, Preaek Tnaot & Chang Houn). Species and percentage cover were recorded in quadrats placed along intertidal transect lines to determine the distribution of seagrasses in these areas. Eight seagrass species were recorded and seagrass meadows covered 1,488 ha within the study area, with an average cover of 28.2% in Trapang Ropov, 46.5% in Preaek Tnaot and 42.5% in Chang Houn. Our findings highlight the ecological significance of seagrass habitats and provide a baseline for monitoring and conservation of community fisheries in Kampot Province. Conservation of seagrass habitats is essential to sustain biodiversity, ecosystem services and local livelihoods based on tourism and fishing in coastal Cambodia.

Keywords Abundance, distribution, diversity, seagrass, community fisheries, Cambodia

Introduction

Seagrasses are marine angiosperms that provide vital ecosystem services in coastal regions worldwide (Duarte *et al*., 2008). Southeast Asia has the greatest diversity of seagrass species and habitat types globally (Fortes *et al*., 2018) and many coastal communities in the region depend on seagrass meadows for their livelihoods and food security (Unsworth *et al*., 2010). These meadows deliver essential services by sustaining marine fisheries and biodiversity, protecting coastlines and providing tourism opportunities (Ouk *et al*., 2010).

Cambodia ranks among the top countries in Southeast Asia for seagrass coverage and seagrass meadows accounted for over 6% of Cambodian waters in 2008 (Fortes *et al*., 2018). The shallow waters of the Kampot and Kep provinces historically supported some of the most extensive meadows in the region (UNEP, 2008; Supkong & Bourne, 2014). However, recent assessments suggest these declined significantly from an estimated 32,492 ha in 2008 to just 13,830 ha in 2023 across the kingdom's four coastal provinces (FiA, 2023a). Despite this, seagrass research remains limited in the country (Fortes *et al*., 2018).

The first largescale assessment of seagrasses in Kampot Province documented 12 species (Ouk *et al*., 2010), whereas a mapping survey in 2013 estimated seagrass coverage at 8,435.8 ha (Supkong & Bourne, 2014). More recent data indicate seagrass coverage has declined to 5,158 ha in Kampot and 6,399 ha in Kep province (FiA, 2023a). Seagrass meadows in Cambodia are threatened by land reclamation, pollution, coastal development (Supkong & Bourne, 2014) and illegal fishing practices such as trawling, gillnets, and motorised push nets (Cockerell *et al*., 2016). Seagrass meadows in Kampot Province particularly have been substantially degraded by industrial port development and associated land reclamation, alongside illegal bottom-trawling (WEA & MCC, 2020). These activities degrade water quality and clarity, thereby reducing the photosynthetic efficiency of the seagrass (Duarte, 2009; Duarte *et al*., 2008; Unsworth *et al*., 2024). The loss of seagrass meadows threatens the overall function of coastal ecosystems (Waycott *et al*., 2009) and compromises fisheries and food security (Unsworth *et al*., 2018). This is because seagrasses meadows provide shelter and nursery grounds for many marine species (Nordlund *et al*., 2018) and serve as a primary food source for macrograzers such as green sea turtles and dugongs and micrograzers such as sea urchins (Di Carlo & McKenzie, 2011).

Community Fisheries (CFIs) are a form of locally managed marine area in Cambodia which fall under the jurisdiction of the Ministry of Agriculture, Forestry and Fisheries (RGC, 2006). These are managed by groups of small-scale fishers who are granted co-management and resource use rights in their local fishing grounds, including delineation of boundaries and permissible fishing practices (RGC, 2007). Remaining seagrass beds in Kampot Province are largely confined to CFIs and particularly areas with passive anti-trawling measures such as submerged concrete blocks and demarcation poles (WEA & MCC, 2020). The aim of our study was to determine the diversity, abundance and distribution of seagrass in three CFIs in Kampot Province. These are located within a proposed Marine Fishery Management Area, a larger form of protected area in Cambodia which is co-managed by the CFIs and the Fisheries Administration under MAFF. Our assessment was undertaken to provide a baseline for monitoring the effectiveness of conservation interventions within the CFIs on seagrass diversity, abundance and distribution.

Methods

Study site

Our study was conducted between June and November 2021 in three adjacent CFIs in Kampot Province: Trapang Ropov (10°35′07.17″N, 103°55′39.04″E), Preaek Tnaot (10°34′58.26″N, 103°57′19.49″E) and Chang Houn (10°34′38.32″N, 103°58′43.16″E) (Fig. 1). Spanning a total area of 3,923 ha, the three CFIs were proposed in 2001 (FiA, 2021) and formally registered by MAFF in March 2011. We selected these areas for study due to their protection as CFI areas and location within a proposed Marine Fisheries Management Area. Additionally, the CFIs play an important role in protecting seagrass habitats and maintaining ecosystem diversity within the province.

Trapang Ropov CFI encompasses 1,251 ha and is situated between the Trapang Ropov and Preaek Tnaot rivers, where 315 ha of seagrass were previously recorded (FiA, 2011c). To the east of the Preaek Tnaot River, the Preaek Tnaot CFI spans 1,168 ha (FiA, 2011b). The Chang Houn CFI covers 1,504 ha, with 400 ha of seagrass previously documented (FiA, 2011a). These areas were evaluated Among seven CFIs in Kampot Province, these three were regarded as having high management effectiveness, institutional sustainability, committee performance and ecological impact (FiA, 2023a).

Data collection

The diversity and abundance of seagrasses in each CFI was assessed using the intertidal fixed transect sites methodology (McKenzie *et al*., 2003). Transects were located based on the distribution of seagrasses, areas of high species diversity, and site accessibility. Within each CFI, three 50 m transects spaced 25 m apart were established perpendicular to the shoreline in waters less than 1.5 m depth (McKenzie *et al*., 2001). Because seagrasses in the three CFIs occurred in intertidal and subtidal zones,

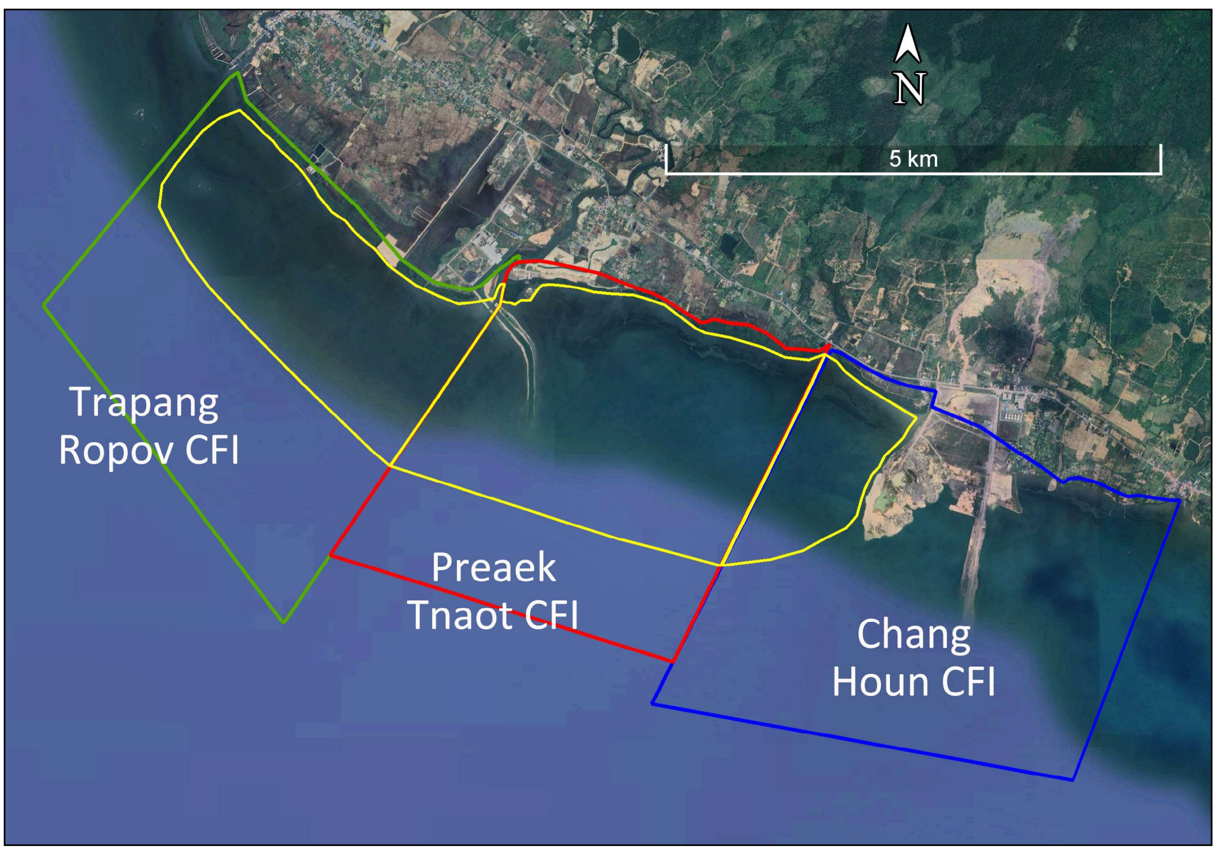

Fig. 1 Community fisheries (CFIs) and seagrass meadows (yellow boundary) studied in Kampot Province, Cambodia

our surveys required walking the transects during low tide and snorkelling in deeper sections.

Our survey area overlapped with previous studies (UNEP, 2008; Ouk *et al*., 2010) that mapped the extent of seagrasses along the Kampot coastline. We used a handheld GPS unit (GPSMAP 64s, Garmin, Kansas, USA) to locate and record the location of each transect, and surface marker buoys were dropped to mark the start and end of these. Transects were deployed via swimming or walking using a compass for orientation.

Three transects were surveyed in each CFI, giving a study total of nine transects. Quadrats (0.25 m^2) were placed at five metre intervals along each transect to identify seagrass species and estimate their percentage cover. The species identification and percentage cover calculation guidelines of McKenzie *et al*. (2003) were followed to ensure consistency. As potential indicators of environmental conditions such as nutrient enrichment, the percentage cover of benthic algae and epiphytic algae on seagrass leaves was also recorded. Water depth and substrate types were recorded for each quadrat.

The spatial distribution of seagrass in the three CFIs was documented using spot-checks undertaken along line transects spaced at 400 m intervals along the coastline. The presence or absence of seagrass was recorded at 200 m intervals along these transects, which extended offshore from shallow to deeper waters (McKenzie, 2003). This approach allowed the team to document seagrass distribution within the wider CFI areas, beyond the parts surveyed using quadrats.

Table 1 Seagrass species recorded in Community Fisheries in Kampot Province (x = present inside quadrats, + = present outside quadrats)

Species	Trapang Ropov	Preaek Tnaot	Chang Houn
Hydrocharitaceae			
Enhalus acoroides	x	x	x
Thalassia hemprichii	x	x	x
Halophila ovalis	+	+	+
Cymodocea serrulata	+	x	x
Cymodocea rotundata	x	x	x
Cymodoceaceae			
Halodule pinifolia	+	x	+
Halodule uninervis	+	x	x
Syringodium isoetifolium		x	x

Data analysis

Data were analysed in *R* software vrs. 4.4.0 (R CoreTeam, 2024). Species richness and relative abundance measures were used to quantify the seagrass flora at our study sites. Box and whisker plots were created using the *ggplot2* package and *geom_boxplot()* function (Barber, 2023) to visualise variations in seagrass species richness, percentage cover, and the relative abundance of benthic algae and epiphytic algae in the three CFIs. The Kruskal-Wallis test was employed to test for significant differences between the three CFIs, using *tidyverse* package (Borcard *et al*., 2011) in *R*. *ArcGIS* software (ERSI, California, USA) was used to map the distibution of seagrasses based on the data generated by spot-checks.

Results

Eight seagrass species arranged in two families (Hydrocharitaceae & Cymodoceaceae) were recorded in the Trapang Ropov, Preaek Tnaot and Chang Houn CFIs (Table 1). These included seven species documented within our quadrats, and one which was only observed outside of these (*Halophila ovalis*). All eight species were recorded in the Preaek Tnaot and Chang Houn CFIs, whereas only seven species were documented in the Trapang Ropov CFI (Table 1, Fig. 1).

Average species richness within the quadrats differed significantly between the three CFIs (Kruskal-Wallis, p=5.4^{e-06}) (Fig. 2). Preaek Tnaot had the highest species richness within the quadrats surveyed with seven species, followed by Chang Houn with six species. Only three species were observed within quadrats in Trapang Ropov. Mean cover of seagrass within quadrats was highest in Preaek Tnaot (46.5%), followed by Chang Houn (42.5%) and Trapang Ropov (28.2%). The relative abundance of seagrass differed significantly between CFI (Kruskal-Wallis, p=3.5^{e-07}) (Fig. 3).

The relative abundance of different seagrass species also varied by CFI (Fig. 4). In Trapang Ropov, *Thalassia hemprichii* was most abundant, alongside *Enhalus acoroides* and *Cymodocea rotundata*. In Chang Houn, *C. rotundata* was the dominant species, followed by *T. hemprichii* and *Cymodocea serrulata*. In Preaek Tnaot, *Syringodium isoetifolium* was the most abundant species followed by *T. hemprichii* and *C. rotundata*. Overall, *T. hemprichii* was most abundant across all three CFIs, followed by *C. rotundata*, *E. acoroides*, *S. isoetifolium*, *C. serrulata* and *Halodule uninervis*. The least common species was *H. pinifolia*.

Seagrass meadows covered a total of 1,488 ha across the three CFIs, with 544 ha in Trapang Ropov, 756 ha in

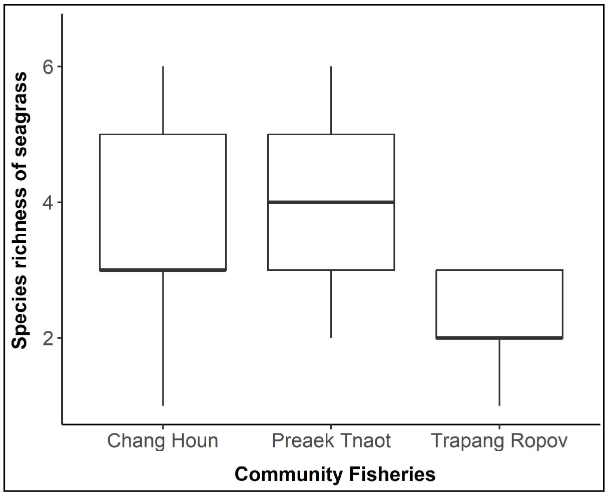

Fig. 2 Box and whisker plots of seagrass species richness in three community fisheries in Kampot Province

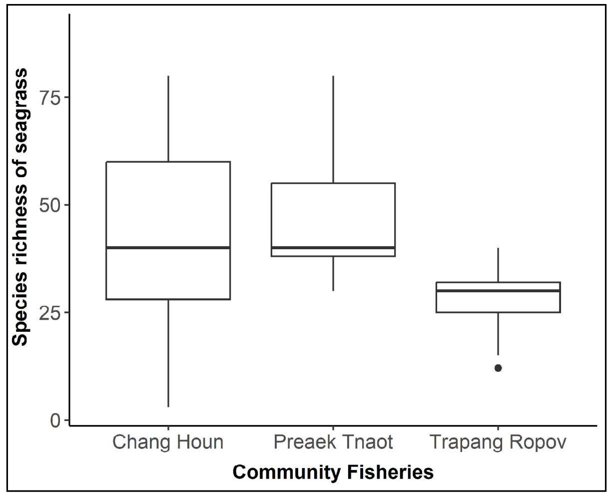

Fig. 3 Box and whisker plots showing relative abundance of seagrasses in three community fisheries in Kampot Province

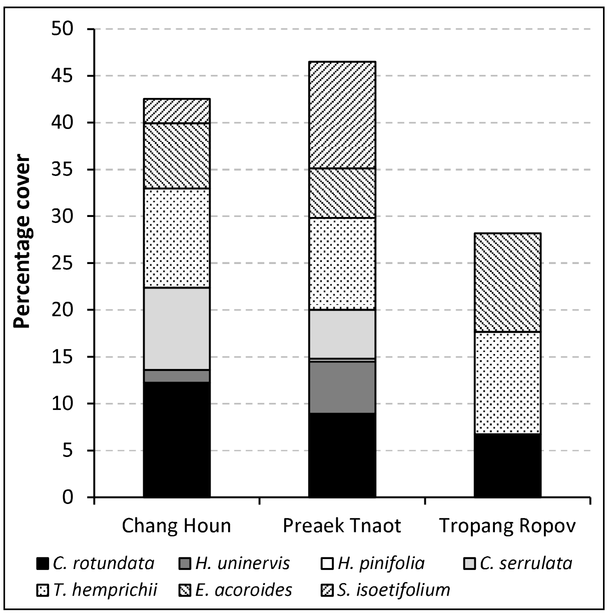

Fig. 4 Relative cover of seagrass species richness in three community fisheries in Kampot Province

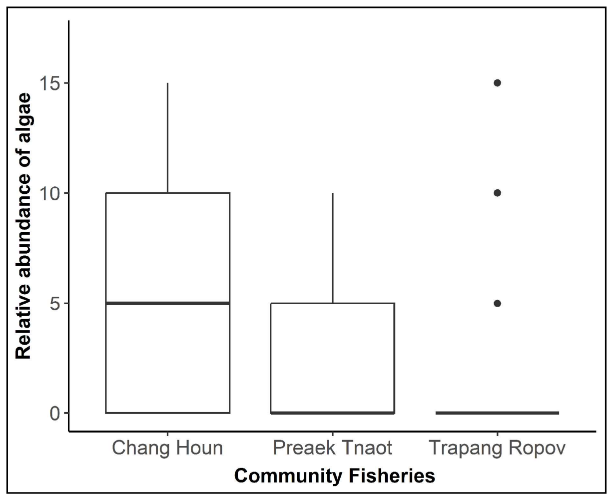

Fig. 5 Box and whisker plots showing relative abundance of benthic algae in three community fisheries in Kampot Province

Preaek Tnaot and 188 ha in Chang Houn (Fig. 1). Benthic algae were highest in Chang Houn and lowest in Trapang Ropov (Fig. 5). These differences were statistically significant (Kruskal-Wallis, p=0.00067). Epiphytic algae cover also differed significantly between the CFIs (Kruskal-Wallis, p=6.5^{e-05}), with the highest cover in Preaek Tnaot, followed by Chang Houn and Trapang Ropov (Fig. 6). Substrates across the three CFIs comprised coarse sand (42%), sand (30%), fine sand (21%) and rubble (7%).

Discussion

Our results provide a valuable baseline for monitoring efforts and may have implications for future conservation interventions in Kampot Province.

We recorded eight seagrass species, somewhat fewer than previously documented within the province. For instance, Ouk *et al*. (2010) recorded 12 species, whereas Supkong & Bourne (2014) documented 11 species, and FiA (2023a) recorded ten species. Higher species richness has also been recorded in Kep province by Reid *et al.* (2019) and Coals *et al*. (2019) who recorded nine and ten

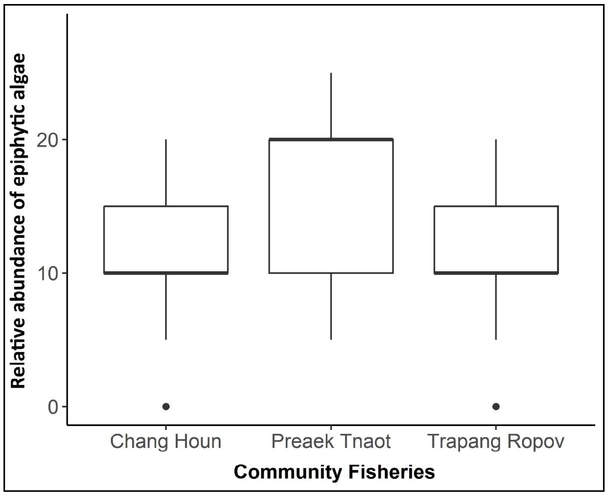

Fig. 6 Box and whisker plots showing relative abundance of epiphytic algae in three community fisheries in Kampot Province

species, respectively. The lower diversity we observed may be attributable to the relatively small area sampled in shallow intertidal zones (maximum depth of 1.5 m). Factoring in water depth, our results are closer to Ouk *et al*. (2010) who recorded six species in similarly shallow waters in Kampot province, including one species we did not observe: *Halophila decipiens*.

We recorded eight seagrass species in the Preaek Tnaot and Chang Houn CFIs, whereas seven were found in the Trapang Rapov CFI. Relative species richness in quadrats differed between these however, with the highest occurring in Preaek Tnaot (seven species) and lowest in Trapang Ropov (three species). Seagrasses primarily occurred in monospecific patches though some mixed-species patches were observed, particularly in the Trapang Ropov CFI. Future research could evaluate whether edge effects influence the species composition of seagrass meadows. For instance, Statton *et al*. (2015) found higher herbivory rates occurred at the edges of seagrass meadows compared to areas inside the meadows, with possible indirect effects on seagrass structure.

We found the dominant species in quadrats across the three CFIs were *T. hemprichii* and *C. rotundata*, whereas the least common was *H. pinifolia,* and *H. ovalis* was only observed outside of quadrats. This is consistent with other surveys in Kampot and Kep which identified *T. hemprichii* and *E. acoroides* as the dominant species (Coals *et al*., 2019; WEA & MCC, 2020) and *H. pinifolia* as the least common (Ouk *et al*., 2010). However, Supkong & Bourne (2014) found *H. pinifolia* was the third most dominant species within Kampot Province, suggesting it may be more abundant in other areas of the province. Similarly, Fauna & Flora (2024) found *H. pinifolia* was the dominant species in northern Koh Kong Province, further suggesting in-country variations in relative species abundances.

As long-leaved seagrasses, *E. acoroides* and *T. hemprichii* are well adapted to turbid waters in which their leaves can extend towards sunlight to maximise photosynthesis (Supkong & Bourne, 2014). These larger seagrass species outcompete smaller, opportunistic and pioneer species such as *H. ovalis*, *S. isoetifolium*, *H. uninervis* and *C. rotundata* (Moreira-Saporiti *et al*., 2021). Further, *T. hemprichii* can dominate intertidal zones due to its higher tolerance to air exposure (Lan *et al*., 2005). Following disturbance however, pioneer and faster-growing species such as *Halophila* spp. may outcompete slower-growing taxa such as *T. hemprichii* (WEA & MCC, 2020). The abundance of *E. acoroides* and *T. hemprichii* in our study sites may suggest the seagrass meadow in shallow areas of the three CFIs are relatively well protected from disturbance including illegal bottom-trawling. Conversely, the presence of eight species comprising a mix of fast- and slow-growing species, could indicate that persistent disturbance has maintained the multi-species meadow. As such, further studies are needed to understand the factors influencing the species composition of local seagrass assemblages.

The relative abundance of seagrasses was highest in Preaek Tnaot (46.5%), followed by Chang Houn (42.5%) and Trapang Ropov (28.2%). Based on Supkong & Bourne (2014) who considered coverage values of 25–50 % to indicate moderate seagrass health, the seagrass meadows of our three CFIs are moderately healthy. Similarly, Supkong & Bourne (2014) regarded seagrasses in an area overlapping with our study site (including intertidal zones extending from Trapang Ropov to Chang Houn CFI) as moderately healthy. Water depth influences seagrass abundance (Longstaff & Dennison, 1999; Ouk *et al*., 2010) and other studies have documented higher seagrass coverage in shallow, intertidal waters in Kampot Province (Fauna & Flora, 2024).

Benthic and epiphytic algae were most abundant in the Preaek Tnaot and Chang Houn CFIs. This is consistent with previous research showing a positive correlation between seagrass and algae abundance in the Kep Archipelago (Coals *et al*., 2019). Algae proliferation may be facilitated by the shallow, nutrient-rich and high-light conditions of our study site (Riegl *et al*., 2005). Water depth is crucial for understanding the distribution of macrophyte assemblages (Le Fur *et al*., 2018). When algal blooms occur, seagrass beds suffer directly from competition for resources and reduced living space (Han & Liu, 2014). Coastal pollution such as garbage, industrial waste and other anthropogenic pollutants can create excess nutrients that cause eutrophication and algal blooms (FiA, 2006).

Seagrasses meadows in the three CFIs encompassed 1,488 ha, comprising 544 ha in Trapang Ropov, 756 ha in Preaek Tnaot and 188 ha in Chang Houn. These data suggest seagrass cover within the CFIs has shifted since surveys in 2011 (FiA, 2011c). More specifically, our data suggest seagrass cover in Trapang Ropov increased by ca. 42% (from 315 ha: FiA, 2011c), whereas cover in Chang Houn declined 53% (from 400 ha: FiA, 2011a). The latter is primarily due to land reclamation for port development in the Chang Houn CFI (Fig. 4) and may also have been exacerbated by dredging activity, which can prevent seagrass growth by reducing water quality (Di Carlo & McKenzie, 2011). Water turbidity was evident throughout our study site, with sediments and algae accumulating on seagrass leaves, particularly near the development area in the Chang Houn CFI. Several studies have found trawling and coastal development increases sedimentation and reduces light penetration, thereby affecting seagrass (de Groot, 1984; Muhando & Rumisha, 2008; Sharma, 2009).

We found seagrasses in our CFIs occurred at water depths ranging from 0.5 m to 4 m. This is consistent with WEA & MCC (2020), who recorded them in water depths between 0.7 m and 3.8 m, with most present in water depths less than 2.6 m. Similarly, Fauna & Flora (2024) and FiA (2023a) found most seagrasses in Cambodia occurred in waters less than two metres depth, although Ouk *et al*. (2010) recorded seagrasses up to seven metres depth in Kampot. The absence of seagrass at depths greater than 4 m in our study could be the result of illegal bottom trawling which was observed in and around our sites. Similarly, WEA & MCC (2020) documented trawling vessels and their paths on the ocean floor during surveys in the three CFIs, where seagrass presence was largely confined to shallow waters inaccessible to trawling vessels and areas protected by concrete poles. Supkong & Bourne (2014) also identified destructive fishing practices including trawling as a primary threat to seagrass in Kampot Province.

Despite environmental pressures in the three CFIs, we found rich biodiversity within the seagrass beds including crabs, small fish, sea urchins, snails, oysters, and many other species. Seagrass provides an essential nursery and feeding habitat for a wide range of marine species (Chhoub *et al*., 2002; Hem *et al*., 2002; Di Carlo & McKenzie, 2011). Seagrass meadows are also vital to fisheries. Kaarlep (2014) found that 89% of economically valuable species caught by small-scale fishermen in Kampot Province are dependent on the seagrass ecosystem, including blue swimming crabs and several shrimp species. Further, habitat connectivity between seagrasses, coral reefs and mangroves increases fish diversity and abundance by increasing the availability of shelter and food provisioning (Unsworth *et al*., 2008). Consequently, maintaining connectivity is important for both marine biodiversity and local fisheries.

We recommend the adoption of management approaches that balance coastal development needs with seagrass protection in Kampot Province. These could include the formal establishment of a Marine Fisheries Management Area to enhance existing co-management efforts by the CFIs and Fisheries Administration. To the same end, rigorous environmental impact assessments should be undertaken prior to coastal development projects to mitigate negative effects on seagrass meadows. Additionally, specific planning is needed to designate areas for marine conservation and development. Tools for seagrass protection and monitoring may include research, designation of protected zones, community co-management, deployment of anti-trawling structures, and consideration of blue carbon stored in seagrass areas. Finally, we reiterate the important role that CFIs play in managing and safeguarding seagrass habitats in Cambodia. These promote marine conservation through sustainable practices and monitoring, ensuring the long-term viability of the ecosystem for future generations (Chea *et al*., 2014).

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A baseline assessment of fish and bivalve populations in the Kep Archipelago, Cambodia: insights for habitat recovery and sustainable management

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មូលន័យសង្ខេប

ប្រព័ន្ធអេកូឡូស៊ីសមុទ្រនៅតំបន់អាស៊ីអាគ្នេយ៍រងការគំរាមកំហែងកាន់តែកើនឡើងខ្លាំងពីការនេសាទខុសច្បាប់ ដែលមិនបានរាយការណ៍ និងគ្មានការគ្រប់គ្រង ជាពិសេសការនេសាទអូសអួននៅក្នុងសមុទ្រកម្ពុជា។ សកម្មភាពទាំងនេះនៅតែបន្តកើតមាន ទោះបីជាមានច្បាប់ការពារក៏ដោយ ដែលធ្វើឱ្យខូចដល់ជម្រក និងសេវាកម្មអេកូឡូស៊ីសំខាន់ៗ ដូចជាស្ថេរភាពឆ្នេរ និងការច្រោះទឹក។ យើងបានវាយតម្លៃជីវៈចម្រុះត្រី ប៉ុពុយឡាស្យុងសប្បីសត្វសំបកពីរ និងឌីណាមិចកករ (កំទេចកំទី) នៅជម្រកចំនួនបីប្រភេទរួមមាន វាលសប្បីសត្វសំបកពីរ ប្រអប់ជម្រកត្រីសិប្បនិម្មិត និងតំបន់រងការប៉ះពាល់។ ដោយប្រើការវិភាគពហុអថេរ (multivariate analyses) ជាលទ្ធផលបានបង្ហាញថា ទាំងជម្រកធម្មជាតិ និងជម្រកសិប្បនិម្មិតបង្កើនបរិមាណត្រី និងជីវៈចម្រុះ។ វាលសប្បីសត្វសំបកពីរមានទំនាក់ទំនងជាមួយនឹងតំហាយនៃកករក្នុងទឹក និងបង្កើនអត្រារស់រានមានជីវិតរបស់សប្បីសត្វសំបកពីរ ដែលបង្ហាញពីការរួមចំណែកដ៏មានសក្តានុពលដល់ការរក្សាស្ថេរភាពដីក្នុងតំបន់។ ប្រអប់ជម្រកត្រីសិប្បនិម្មិតបានបង្កើននូវភាពស្មុគស្មាញ និងអាចផ្តល់ជាជម្រកបណ្តោះអាសន្នសម្រាប់ត្រី ទោះបីជាវាមិនទាន់ប្រាកដថាអាចចូលរួមដល់ការស្តារឡើងវិញ ឬមានតួនាទីត្រឹមតែជាឧបករណ៍ប្រមូលផ្តុំត្រី។ ការសិក្សារបស់យើងនៅមានកម្រិតដោយសារការអនុវត្តបានចំនួនតិច និងពេលវេលានៃការសិក្សាមានកម្រិត ដែលបង្ហាញពីតម្រូវការសិក្សាតាមដានរយៈពេលវែង និងការស្ទង់មតិទូលំទូលាយជាងនេះ។ ទោះបីជាការសិក្សាស្រាវជ្រាវរបស់យើងមានការកំណត់ទាំងនេះក៏ដោយ ក៏លទ្ធផលនៃការសិក្សារបស់យើងបានផ្តល់នូវចំណេះដឹងអាចអនុវត្តបានអំពីមុខងារអន្តរទំនាក់ទំនងរវាងជម្រកបាតសមុទ្រ ជីវៈចម្រុះត្រី និងពពួកសប្បីសត្វសំបកពីរក្នុងប្រព័ន្ធអេកូឡូស៊ី។ លទ្ធផលនៃការសិក្សានេះបានបង្ហាញផងដែរពីសក្តានុពលនៃការស្តារជម្រកចម្រុះដោយរួមបញ្ចូលជម្រកពពួកសប្បីសត្វសំបកពីរ ប្រអប់ជម្រកត្រីសិប្បនិម្មិត និងជម្រកបាតសមុទ្រផ្សេងៗទៀតសម្រាប់ការអភិរក្សសមុទ្រ និងការគ្រប់គ្រងការនេសាទប្រកបដោយប្រសិទ្ធភាព និងការគ្រប់គ្រងនេសាទនៅក្នុងតំបន់ដែលមានទិន្នន័យមានកំណត់ដូចជាដែនសមុទ្រកម្ពុជាជាដើម។

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Abstract

Southeast Asia's marine ecosystems are increasingly threatened by illegal, unreported and unregulated fishing, particularly trawling in Cambodian waters. These activities persist despite legal protections, degrading habitats and undermining critical ecosystem services such as shoreline stabilisation and water filtration. We assessed fish biodiversity, bivalve populations and sediment dynamics across three habitat types: bivalve beds, fishery production structures and impacted sites. Using multivariate analyses, our findings reveal that natural and artificial reefs significantly enhance fish recruitment and biodiversity. Bivalve beds were associated with reduced sediment suspension and higher bivalve survival, suggesting potential contributions to local sediment stabilisation. Fishery production structures foster structural complexity and may provide short-term refuge for fishes, though it remains unclear whether they contribute to fisheries recovery or primarily function as fish aggregation devices. Our study is limited by low replication and restricted temporal coverage, highlighting the need for long-term monitoring and spatially broader surveys. Despite these constraints, our findings offer actionable insights into the interconnected roles of benthic habitats, fish and bivalves in ecosystem functioning. They also demonstrate the potential of multi-habitat restoration integrating bivalve beds, fishery production structures and other benthic systems for effective marine conservation and fisheries management in data-limited regions such as Cambodian waters.

Keywords artificial reefs, bivalve beds, Cambodia, ecosystem functioning, fish, habitat restoration, Kep Archipelago, marine conservation

Introduction

Cambodian fisheries are integral to national food security and economic stability, as they contribute over 80% of protein intake (FAO, 2018; Widjaja *et al*., 2023) and generate significant export revenue (ca. 75 million USD in 2019: Klinsukhon *et al*., 2022). However, increasing fishing pressures including illegal, unregulated, and unreported fishing and destructive practices such as electric trawling has led to habitat degradation, declining fish stocks and biodiversity loss (Rizvi & Singer, 2011; Song *et al*., 2020; Widjaja *et al*., 2023). These practices disrupt sediment stability, reduce habitat complexity and jeopardise ecosystem services, compounding challenges faced by conservation and sustainable fisheries management. Variations in habitat structure, driven by natural and artificial bivalve beds, can strongly influence fish assemblages, abundance and functional diversity (Carballeira Braña *et al*., 2021; Chow *et al*., 2021). Understanding these habitat-fish linkages is important for informing restoration efforts aimed at enhancing fisheries productivity and ecosystem resilience.

The marine ecosystems of the Kep Archipelago in Cambodia exemplify a complex interplay between habitat modifiers, habitat users, and the processes linking these. Bivalves, as key habitat modifiers (or ecosystem engineers, defined by Jones *et al*., (1994) as organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials), stabilise sediments, enhance water quality and create structural refuges (Gutiérrez *et al*., 2003; Coen *et al*., 2007; Grabowski *et al*., 2012). These functions foster favourable conditions for smaller (e.g., meiofauna: Coull, 1999) and larger organisms (e.g., fish assemblages: Nagelkerken *et al*., 2015). Fish, as habitat users, engage dynamically with these benthic environments, influencing community composition through predation, bioturbation (via foraging & burrowing) and nutrient inputs (Adámek & Maršálek, 2013; Nagelkerken *et al*., 2015; Shantz *et al*., 2015).

This study provides baseline data to support monitoring and management of benthic ecosystems under the Asian Development Bank's Sustainable Coastal and Fisheries Management project. This is intended to inform future restoration efforts across Cambodia's coastal provinces (ADB, 2024) and we provide a snapshot of fish assemblages and ecological patterns across bivalve beds, fisheries production structures and sites exposed to benthic trawling (impacted sites). This complements recent meiofaunal work (Gorra *et al*., 2025) and these habitat assessments indicate the roles of benthic structures in shaping fish assemblages and supporting habitat-associated communities. In addition, it is important to consider how fishing pressure varies across habitats and can influence fish assemblages. For example, bivalve beds experience daily exploitation through tube diving for invertebrates, spearfishing and gillnetting, which cause high bycatch and benthic disturbance. In contrast, fishery production structures tend to

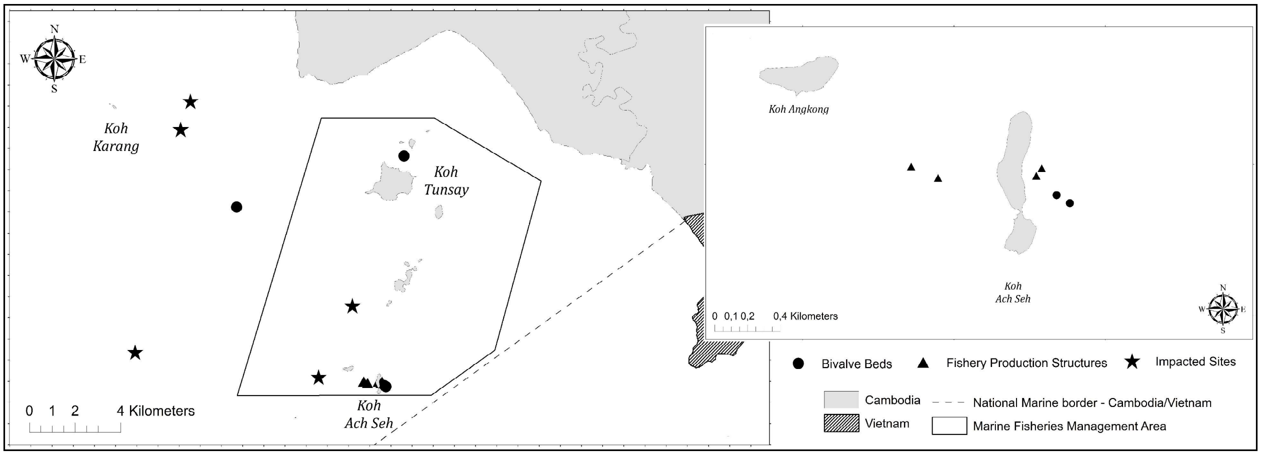

Fig. 1 Study area and sampling stations in the Kep Archipelago, Cambodia

be located in areas with less direct human disturbance and may act as *de fact*o refuges, with effects independent of habitat complexity on fish abundance and diversity. In providing largely missing baseline data, the work offers preliminary insights into the restoration potential of bivalve beds and artificial reefs for fishery recovery. To guide our study, we tested the null hypotheses that 1) fish assemblage structure did not differ between habitat types, and 2) functional traits of fish assemblages did not differ between natural and artificial habitats. The overall aim of our study was to support informed management practices, fostering resilience and recovery of marine ecosystems in the Kep Archipelago.

Methods

Study area

Fieldwork was undertaken around the Kep Archipelago over four weeks from 20 January to 24 February 2023. We focused on waters surrounding Koh Ach Seh (10.35736111°N, 104.32019444°E), where the average depth is approximately 4.5 metres (Marine Conservation Cambodia [MCC], unpubl. data). Survey stations were established across three subtidal habitats: bivalve beds (BB), impacted sites (IS) and fishery production structures (FPS), with priority given to sites near Koh Ach Seh to maximise logistical efficiency and proximity to areas of illegal fishing activity (Fig. 1).

Fishery production structures consisted of artificial structures approximately 2.5 m wide which comprised 3–4 stacked blocks (typically made of concrete, bamboo and metal) that have been deployed since 2018 as part of local restoration and enforcement efforts (Strong *et al.*, 2023). The structures vary in shape and size but generally resemble modular reef blocks or anti-trawling devices. Descriptions of these including site locations, depths and deployment years are given in Table 1.

Impacted sites comprised soft sediment areas with visible signs of benthic disturbance and structurally degraded habitat, likely due to repeated bottom-contact fishing activity. While historical data are limited, anecdotal evidence and proximity to bivalve beds suggest these areas may have previously supported more structured benthic communities (e.g, seagrass beds, bivalve aggregations, coral reefs). Station selection criteria and habitat characteristics are provided in Table 1.

Habitat surveys

We assessed the habitat characteristics of the three habitat types using scuba diving survey methods. Surveys were conducted in water depths of 2 to 11 m, with information on site depth and numbers of replicate transects provided in Table 1. At impacted sites and bivalve beds, bidirectional belt transects (20 m by 2 m) were laid out extending north and south from a central anchor point. At fishery production structures, transect designs were adapted to accommodate the structural complexity of artificial habitats (Annex 1). Habitat features were recorded at 1 m intervals along each transect (n=40 per station), including substrate type (e.g., sand, cobble, rock), benthic layer (e.g., seagrass & macroalgae), presence and density of bivalves, other encrusting and mobile invertebrates (Table 2), and measures of structural complexity (e.g., presence of crevices, holes, artificial structures).

In analysis, raw uniform point contact observations were retained and grouped into broader substrate categories to inform interpretation and allow for future

Table 1 Bivalve beds (BB), fishery production structures (FPS) and impacted sites (IS) sampled for fish and bivalve assemblages in the Kep Archipelago. 'NS' indicates 'no survey' as the site was used as a reference (sensor deployment/sediment sample collection only) or did not meet visibility requirements for survey

Site ID	Coordinates	Average Depth (m)	No of Transects	Remarks (FPS deployment year)
BB_01	10.44707 N, 104.33016 E	3.5	2	Mixed bivalve bed with light fishing activity observed
BB_02	10.35621 N, 104.32305 E	3	NS	Mix of seagrass and bivalve beds near Koh Ach Seh
BB_03	10.35665 N, 104.32232 E	2.2	2	Offshore of BB_02 (similar habitat)
BB_04	10.42693 N, 104.26429 E	6	2	Dense bivalve bed near Koh Pou
FPS_01	10.3576 N, 104.31579 E	5.3	2	Located west of Koh Ach Seh (2018)
FPS_02	10.35822 N, 104.31431 E	5.5	2	Located west Koh Ach Seh (2019)
FPS_03	10.35821 N, 104.32012 E	1.9	2	East of Koh Ach Seh (2017)
FPS_04	10.357772 N, 104.321137 E	1.9	2	Near coral reef east of Koh Ach Seh (2018)
FPS_05	10.357715 N, 104.321202 E	1.7	2	Prototype near coral reef east of Koh Ach Seh (2017)
IS_01	10.36976 N, 104.2244 E	5.1	2	Active trawling grounds with remnant patches of seagrass
IS_02	10.35996 N, 104.29659 E	5.8	2	Known fishing grounds
IS_03	10.38805 N, 104.3099 E	7.3	2	Fishing grounds nearby
IS_04	10.46854 N, 104.24616 E	5.6	2	Fishing ground near Koh Kron and channel (~10-15 vessels within 2 km radius)
IS_05	10.45751 N, 104.24229 E	10.9	NS	10m deep channel, near Kampot

analysis. Percentage cover of benthic layers (e.g., algae, seagrass) and substrate categories (e.g., bare sand/silt, sand/shell, structure, cobble, reef) were estimated across stations and summarised by habitat type (Table 2). These variables were used to explore associations between fish and bivalve assemblages. Differences in assemblage composition were tested using permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities, with 999 permutations (BB=3, FPS=5, IS=4). Similarity percentage (SIMPER) analyses were performed to identify the substrate or layer categories that contributed most to habitat differences. Finally, benthic data were compared with fish, bivalve, and invertebrate assemblages to explore potential habitat–fauna relationships, with stations containing zero values removed from analyses.

Bivalve surveys

We systematically counted, measured and identified bivalve morphospecies within six 0.25 m² quadrats spaced evenly along the same two 20 m transects (ca. 3.3 m apart: Fig. 2). Bivalves were primarily epifaunal, resting on or attached to the sediment surface or substrate. Although multiple bivalve morphospecies were recorded (and species recorded when possible), particular attention was given to oysters (Ostreidae) due to their relevance to local restoration efforts. Metrics included total bivalve density and oyster shell height, which was measured to the nearest 1 mm using callipers. Shell height was used as a proxy for individual age, contributing to baseline understanding of oyster demographics in each habitat (e.g., Powell *et al*., 1996; Baggett *et al*., 2015), physiological condition (e.g., health), because it can reflect environmental stress, growth rates and survival potential in oyster populations. Morphospecies identifications were based on personal observations, local knowledge (assisted by MCC staff, particularly Chhen Tai and Lor Samphors) and external sources such as *SeaLifeBase* (Palomares & Pauly, 2025) and the *World Register of Marine Species* (WoRMS, 2025).

Fish surveys & data processing

Twelve underwater fish surveys were conducted across the three habitat types to assess fish abundance and diversity. Underwater visibility was recorded during each dive and fish surveys were only conducted when horizontal visibility exceeded 1.5–2 m to ensure reliable identifications and counts. Sites with persistently poor

Table 2 Percentage cover of substrates and layer types at sites sampled in the Kep Archipelago. Size classes follow Wentworth (1922). Values represent average percentage cover [± standard error where applicable]

Substrate Category	Substrate Composition	Fishery Production Structures	Bivalve Beds	Impacted Sites
Bare sand (≤0.25 mm)	Fine	4 [4.0]	0 [0]	0 [0]
	Medium	15 [9.32]	15.8 [15.83]	10.6 [6.32]
	Coarse	6.5 [6.50]	0.8 [0.83]	0 [0]
Sand/shell mix (0.25–4 mm)	Fine	1 [1.0]	16.7 [9.39]	19.4 [13.55]
	Medium	1.5 [1.50]	1.7 [1.67]	1.9 [1.88]
	Coarse	21 [8.90]	26.7 [26.67]	0 [0]
Pebble mix (4–64 mm)	Fine	10.5 [6.54]	8.3 [8.33]	33.8 [19.72]
	Medium	2.5 [2.50]	10.8 [6.51]	34.4 [22.32]
	Medium coarse	1.5 [1.50]	13.3 [13.33]	0 [0]
	Coarse	13.5 [7.93]	5 [5.0]	0 [0]
Cobble/rock (65–256 mm)	Fine rock mix	0.5 [0.5]	0 [0]	0 [0]
	Medium rock mix	0 [0]	0.8 [0.83]	0 [0]
Reef/rock (≥256 mm)	Rock	0.5 [0.5]	0 [0]	0 [0]
Artificial reef (FPS)		22 [2.89]	0 [0]	0 [0]
Layer Type				
Algae		10 [4.26]	0 [0]	0 [0]
Bivalve cluster		0 [0]	7 [1.53]	0 [0]
Broken bivalve		0.5 [0.5]	1.7 [1.67]	0 [0]
Fish		0.5 [0.5]	0 [0]	0 [0]
Hard coral		2.5 [0.79]	5 [3.82]	0.8 [0.83]
Mobile invertebrate		4 [1.87]	3.3 [2.20]	0 [0]
Seagrass		0 [0]	12.5 [12.5]	1.7 [1.67]
Sessile invertebrate		22.5 [6.07]	30 [3.82]	4.2 [2.20]
Soft coral		2.5 [1.37]	2.5 [2.5]	0 [0]

visibility (e.g., IS_05, a channel) were excluded from the fish surveys. At each station, two transects measuring 20 m in length and 2 m in width were laid out in opposite directions to ensure replication and minimise the possibility of surveying the same fish twice. This helped to reduce spatial overlap and improve the representativeness of data collected.

Surveys were carried out using a standard visual census transect method, whereby a diver slowly swam along each transect line recording all species observed within the 2 m transect width. A GoPro BLACK 8 camera (GoPro, California, USA) was employed to document the entire transect, providing a permanent video record which was used to confirm species identifications and other observations in post-survey analysis. While fish behaviours such as schooling, feeding and habitat use (e.g., sheltering in crevices) were noted during the surveys, behavioural analyses were not performed as they were beyond the scope of our study. The survey protocols including transect layout, survey timing and data collection procedures are illustrated in Fig. 2.

Fish assemblage data were primarily derived from the video recordings which allowed us to quantify the species present and their abundance at each sampling station. Video processing was conducted using *GoPro Quik Studio* vrs. 11.15.1 (GoPro, California, USA). Non-overlapping frames were analysed to account for fish entering and exiting the field of view. Still images were then extracted from the footage to aid species identifications, which were undertaken by one co-author and local marine expert. Fish were identified to the lowest possible taxonomic level, with species being the primary goal.

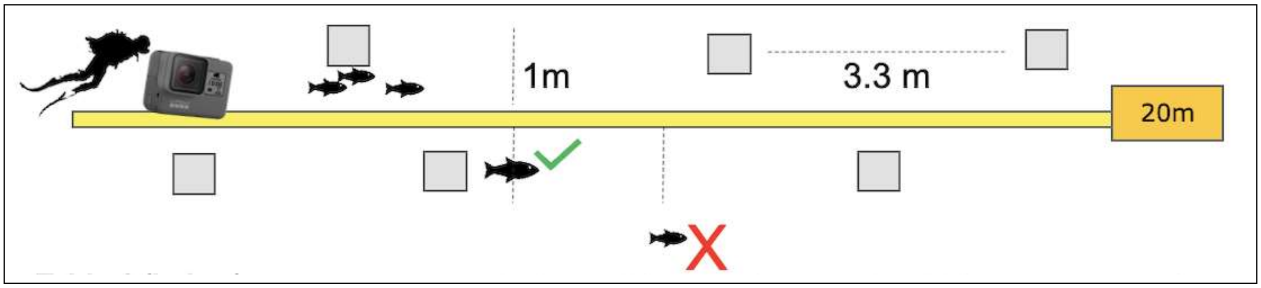

Fig. 2 Sampling design in the Kep Archipelago. Transects were 20m in length and included six 0.25 m² quadrats (grey squares) at ca. 3.3 m intervals. Species recorded within 1 m of the transect are indicated by check marks. Species beyond this boundary were excluded from the study and are depicted with an 'X'

Where species identification was not possible, genus or family names were used instead and Khmer names were provided where applicable. A diagnostic key was compiled to aid identification of fish and bivalves which is available from the corresponding author. Identifications were cross-checked using *FishBase* (www.fishbase.org), *Reeflex* (reeflex.net) and the *Reef Fish Identification—Tropical Pacific* field guide (Allen *et al*., 2005). Species names follow WoRMS (2025). Presence and absence of each taxon in each habitat type is provided in Annex 2.

Statistical analyses

All analyses were conducted in *RStudio* vrs. 2023.3.0.386 (R Core Team, 2023)] using the *Vegan* vrs. 2.6-4 package (Oksanen *et al*., 2022). Figures were produced using the *ggplot2* vrs. 3.4.0 package (Wickham *et al*., 2019).

Habitat surveys: Percentage cover of substrate types (n=40 points per station) and benthic layers (sample numbers varied by station) were estimated for all stations and habitats (mean). Differences in community composition were tested using PERMANOVA based on Bray-Curtis dissimilarities, which was undertaken using the adonis2 function in the *Vegan* package (Oksanen *et al*., 2022) with 999 permutations. When overall tests were significant, pairwise PERMANOVA were applied to identify which habitats differed. Because significant differences were detected among habitat layers, but not among substrate categories, subsequent analyses focused on habitat layer composition. To identify taxa and habitat variables contributing most to dissimilarities between habitats, SIMPER analysis was performed on substrate and layer data across all stations and habitats. The same analytical process (PERMANOVA > pairwise PERMANOVA > SIMPER) was applied to assemblage data for fish, bivalves and selected invertebrates.

Bivalve assemblages: Descriptive statistics were applied to assess bivalve density (individuals m-²) and shell height (mm) across the three habitat types. A one-way analysis of variance (ANOVA) was conducted to test the null hypotheses that 1) mean oyster density did not differ among the three habitat types, and (2) mean shell height did not differ between the three habitat types. Site means (BB n=4, FPS n=5 & IS n=5) were used as independent replicates. Shell height served as a proxy for bivalve age and condition, including growth rate and maturity (Ridgway *et al*., 2010).

The species composition and abundance of bivalves (and other sessile invertebrates) was analysed per quadrat. A species × sample (station) matrix was constructed using abundance counts, and samples with zero counts across all taxa (i.e., impacted sites) were excluded from analyses. Due to low representation of some habitats, analyses focused on the two most sampled habitats (BB n=3 & FPS n=5). Differences in assemblage composition between habitats were tested using the PERMANOVA > pairwise PERMANOVA > SIMPER analysis process, which was based on Bray–Curtis dissimilarities (999 permutations) and used only habitat as a predictor. Results from PERMANOVA and SIMPER were interpreted together to characterise habitat-specific differences in bivalve and broad invertebrate assemblages.

Fish assemblages: We analysed fish assemblage data obtained during transect surveys to test the null hypothesis that fish assemblage structure, diversity, and abundance did not differ among the three habitat types. Fish densities recorded during transects are provided in Table 3. Assemblage-level metrics including Shannon-Wiener diversity index (H': Shannon & Weaver, 1949), species richness (S) and Pielou's evenness (J': Pielou, 1966) were calculated from Hellinger-transformed counts to examine assemblage composition while minimising the influence of zero counts (e.g., from sites lacking fish observations) and very high counts of schooling species (e.g., damselfish). This transformation produces relative abundance data with reduced weight on highly abundant

Table 3 Oyster density, shell height and bivalve density recorded in bivalve beds (BB), fishery production structures (FPS) and impacted sites (IS) in the Kep Archipelago. Oyster counts are reported as individuals not measured*/individuals measured for shell height

Station ID	Mean oyster density (ind/ 0.25 m²) [SD]	Mean oyster shell height (mm) [SD]	Number of oysters	Raw density of bivalves (ind/0.25 m²) [SD]	Number of bivalves
BB_01	1.83 [2.53]	35.71 [26.24]	28	7.25 [25.05]	87
BB_03	1.83 [1.42]	48.5 17.80	75	7.92 [25.42]	95
BB_04	8.67 [7.56]	37 [26.96]	245*/44	22.50 [72.38]	270
BB	4.56 [5.78]	42.61 [23.20]	348*/147	12.56 [8.62]	452
FPS_01	0 [0]	-	0	0	0
FPS_02	0.09 [0.29]	29 [na]	1	1.33 [4.62]	16
FPS_03	2.17 [3.81]	45.15 [19.08]	27	2.25 [7.80]	27
FPS_04	0.67 [1.56]	27 [7.96]	10	0.83 [2.89]	10
FPS_05	0.92 [2.08]	62.30 [30.63]	27*/25	2.25 [7.80]	27
FPS	0.77 [2.21]	48.81 [26.21]	65*/63	1.33 [0.96]	80
IS_01	0	-	0	0	0
IS_02	0	-	0	0.33 [1.16]	1
IS_03	0	-	0	0	0
IS_04	0	-	0	0	0
IS	0	-	0	0.08 [0.58]	1

species, which makes it suitable for Euclidean-based ordination methods (e.g., principal component analysis) and improves the interpretability of assemblage composition patterns. We chose Hellinger transformation because our focus was to compare fish composition between habitats (rather than total abundance alone). Overall abundance patterns across habitats were examined separately using univariate analysis.

Assemblage differences across habitats were visualised using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity, where our null hypothesis that differences do not exist between habitats was tested using PERMANOVA. Principal component analysis and SIMPER were used to explore dominant trends in habitat use. Differences in fish abundance and species richness between habitats and stations were tested with ANOVA, followed by Tukey's honestly significant difference (HSD) post-hoc tests to clarify pairwise differences.

To examine patterns in fish species composition across stations and habitats, we first summed counts of each species per station to create a station × species matrix. Stations where no fish were observed were excluded from the analysis (i.e., IS_02, IS_03 & IS_04). We then tested whether fish assemblages varied with habitat type, total fish abundance and total bivalve abundance using a PERMANOVA (Bray–Curtis dissimilarity, 999 permutations). With the more detailed habitat data, species-level differences among sites were explored using SIMPER (Bray–Curtis dissimilarity) to identify which species contributed most to differences between stations and habitats.

Results

Habitat layers & substrates

The composition of benthic layers differed significantly between the three habitats (R^2=0.405, F=2.72, p=0.004), indicating that these are a strong driver of substrate and layer assemblages (Table 2). Pairwise tests revealed that FPS and IS habitats differed significantly (R^2=0.335, F= 3.02, p=0.02), whereas differences between BB and FPS habitats (p=0.073) and BB and IS habitats (p=0.1) were not significant. SIMPER analysis indicated that sessile invertebrates (p=0.043), algae (p=0.004) and mobile invertebrates (p=0.032) contributed most to differences between FPS and IS habitats. Bivalve clusters contributed most to differences between BB and FPS habitats (p=0.003) and BB and IS habitats (p=0.001), whereas layers such as sessile invertebrates and seagrass showed trends that were not statistically significant (Table 2).

Substrate composition showed weaker differences between habitats (PERMANOVA: R^2=0.36, F=1.99, p=0.115). Pairwise differences indicated that differences were driven largely by artificial reef structures in FPS habitats (=22% cover vs. 0% in BB and IS; p=0.015 & p=0.013, respectively) and by greater bare sand cover in IS compared to BB habitats (p=0.049). Sand and shell cover contributed to dissimilarities but did not differ significantly between habitats.

Bivalve assemblages

A total of 532 bivalves were identified based on local fisher knowledge and regional guidebooks and shell heights and densities were estimated for the five oyster morphospecies observed (Table 3). Three morphospecies were found in FPS and BB habitats, whereas two were exclusive to BB habitats. Presence–absence data for these are summarised in Annex 3.

Oyster density varied significantly between habitats (F=94.5, p<0.001). As no oysters were recorded in impacted sites, these were excluded from comparisons. Assumptions for ANOVA (normality and homogeneity of variances) were tested and met prior to analysis. Bivalve beds showed the highest mean density, with 18.24 (±23.12) individuals per m², while fisheries production structures had 3.08 (±8.84) individuals per m². Notably, FPS_03 exhibited the highest density among FPS stations, whereas BB_04, a dense mixed bivalve bed, supported the highest density across BB sites and overall (Fig. 3). Mean oyster shell heights were 42.61 mm (±23.20) in BB habitats and 48.81 mm (±26.21) in FPS habitats (F=5.477, p<0.001; Table 3). Mean bivalve shell heights were 46.6 mm (±37.4) in BB habitats and 60.6 (±27.5) in FPS habitats (F=6.303, p<0.001; Fig. 4, Table 3).

A simple PERMANOVA examining benthic layer and bivalve/invertebrate assemblages between BB and FPS habitats showed a significant effect of habitat on assemblage structure (R^2=0.34, F=3.15, p=0.023). Pairwise comparisons indicated that the strongest differences occurred between BB and FPS habitats (although impacted sites were excluded from analyses due to lack of observations). Similarity percentage analysis reflected this pattern, identifying an average Bray–Curtis dissimilarity of 34% between BB and FPS habitats. Species driving these differences included white clams (22%, p=0.001) and an unidentified mussel (20%, p=0.001) which were exclusive to BB habitats, alongside Indian rock oysters (11%, p=0.047), bicolour pen shells (7%, p=0.001) and penguin wing oysters (3%, p=0.001). These taxa collectively explained approximately 68% of the observed dissimilarity between the two habitats.

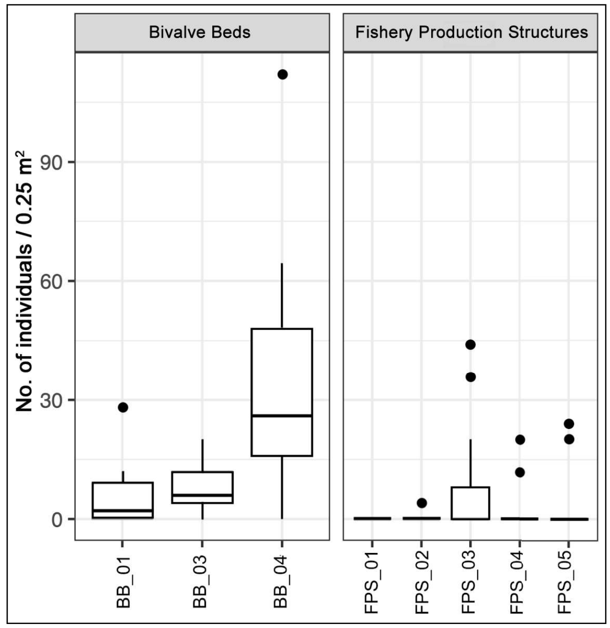

Fig. 3 Density of oysters in bivalve beds and fishery production structures sampled in the Kep Archipelago

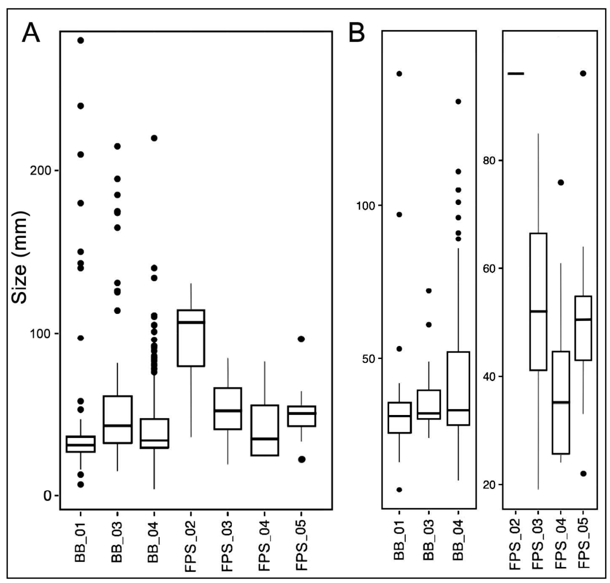

Fig. 4 Height of A) bivalve shells and B) oyster shells across bivalve beds (BB) and fishery production structures (FPS) sampled in the Kep Archipelago

Fish assemblages

A total of 849 fish were identified to the genus level (Annex 2). The highest abundance, diversity and evenness was observed in FPS habitats, followed by BB habitats and IS habitats (Fig. 5, Table 4). Total fish abundance differed significantly between habitat types (ANOVA, F=8.13, p<0.001), with FPS sites supporting nearly six times the fish density of BB sites and IS habitats exhibiting near absence. Fish diversity also differed between habitat types (F=2.593, p=0.05), with FPS habitats showing the highest diversity (H'=10.75), followed by BB habitats (H'=5.57) and IS habitats (H'=1.95) (*Table 4*). Multivariate analyses (PERMANOVA) were undertaken to assess assemblage structure across habitats. Damselfish (various species, including *Pomacentrus* spp.) were most abundant in FPS habitats, whereas paradise whiptails *Pentapodus paradiseus* (Günther, 1859) dominated BB and IS habitats. A list of species and families recorded during the study is provided in Annex 2.

Following significant ANOVAs, Tukey's HSD test revealed significantly higher mean fish abundance in FPS habitats (mean=152.8 ± 89.0) than IS habitats (mean=8.75 ±17.5; *p(adj)*=0.016), whereas BB habitats were intermediate (mean=16.7 ± 16.9). A FPS station (FPS_04) exhibited the highest richness (*p(adj)*<0.001) compared to all other stations), although this did not differ significantly from FPS_01, FPS_02 or FPS_03, which in turn did not differ from one another. Our PCA analysis, which summarised variance in the species abundance dataset, alongside SIMPER analysis on abundance, revealed two distinct assemblage types. This first was dominated by damselfish *Pomacentrus* spp. and *Neopomacentrus* sp. (primarily at FPS stations) and the second was characterised by paradise whiptails *P. paradiseus* and wrasse *Halichoeres* spp., which occurred at most BB stations and some IS stations. Our PCA also indicated the species responsible for most variation along the axes, with *Neopomacentrus* sp. and *P. paradiseus* driving separation along PC1 (39.1%) and PC2 (34.2%) axes (=74% of the cumulative variation: Fig. 6). Other species contributing variation to PC2 included whiteline cardinalfish *Ostorhinchus cavitensis* (Fowler, 1938) and wrasse *Halichoeres* sp. One outlier (IS_04) was identified due to the absence of fish observations. Impacted sites exhibited the greatest variability, with less diverse fish assemblages overall. Individual contributions of species were explored using SIMPER and all species in the *Neopomacentrus* genus were included in our analysis.

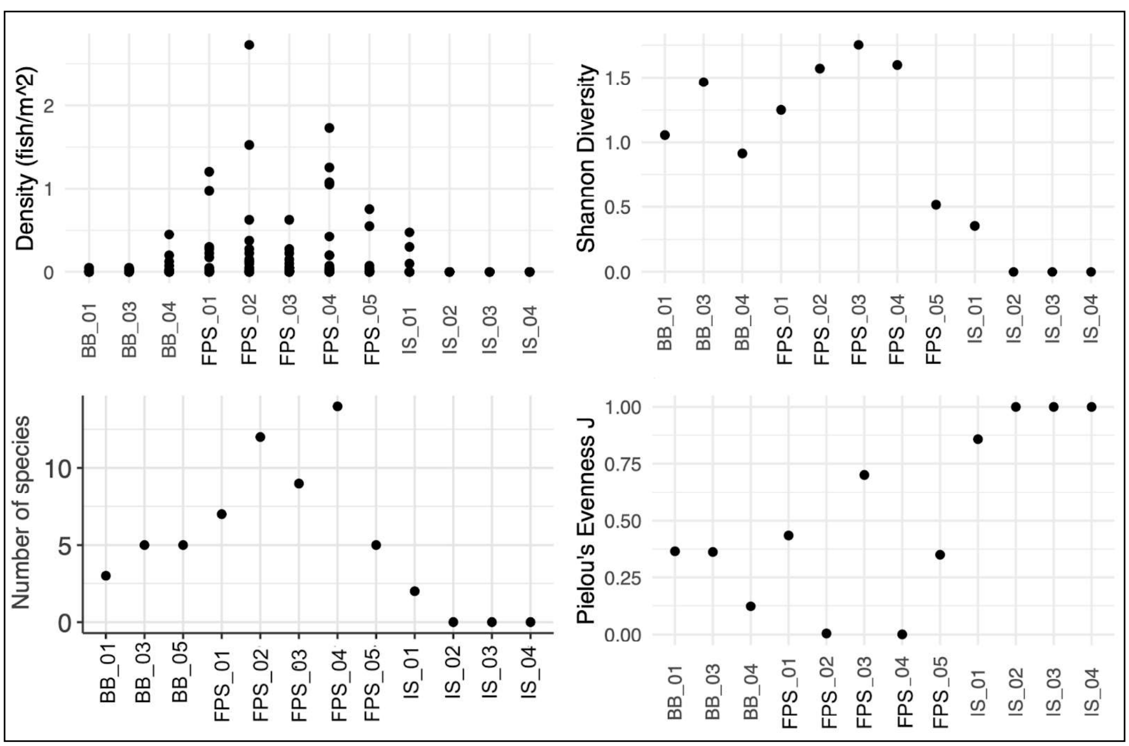

Fig. 5 Metrics for fish assemblages sampled in bivalve beds (BB), fishery production structures (FPS) and impacted sites (IS) in the Kep Archipelago

Table 4 Biodiversity metrics recorded for fish assemblages in bivalve beds (BB), fishery production structures (FPS) and impacted sites (IS) in the Kep Archipelago

Station	Alpha diversity	Gamma diversity	Beta diversity	Beta diversity (Shannon)	Pielou's evenness (J')	Mean density (ind/m²) [±SD]	Raw density (ind/m²) [±SD]	*n*
BB_01	3.5	5	0.53	4.47	0.35	0.08 [0.41]	0.125 [0.177]	5
BB_03	5.5	7	1.15	5.85	0.66	0.13 [0.46]	0.200 [0.000]	9
BB_04	5.0	7	0.78	6.22	0.48	0.6 [2.80]	0.900 [0.354]	36
BB	4.66	6.33	0.82	5.51	0.49	0.28 ±1.66	0.408 ±0.427	50
FPS_01	7.5	10	1.21	8.78	0.60	2.22 [8.74]	3.275 [2.934]	133
FPS_02	9.0	14	1.10	12.90	0.50	4.27 [17.47]	6.150 [0.465]	256
FPS_03	7.5	11	1.21	9.80	0.61	1.08 [3.99]	1.600 [1.980]	65
FPS_04	10.5	16	1.23	14.77	0.53	3.42 [13.02]	5.125 [1.874]	250
FPS_05	5.5	8	0.49	7.51	0.24	0.97 [5.10]	1.450 [0.071]	60
FPS	8	11.8	1.05	10.75	0.50	2.55 ±10.90	3.520 ±2.093	764
IS_01	3.5	4	0.23	3.77	0.17	0.58 [3.12]	0.875 [0.389]	35
IS_02	2.0	2	0	2.0	0	0 [na]	0.000 [0.000]	0
IS_03	2.0	2	0	2.0	0	0 [na]	0.000 [0.000]	0
IS_04	2.0	2	0	2.0	0	0 [na]	0.000 [0.000]	0
IS	1.9	2	0.05	1.95	0.04	0.15 ±3.12	0.219 ±0.438	35

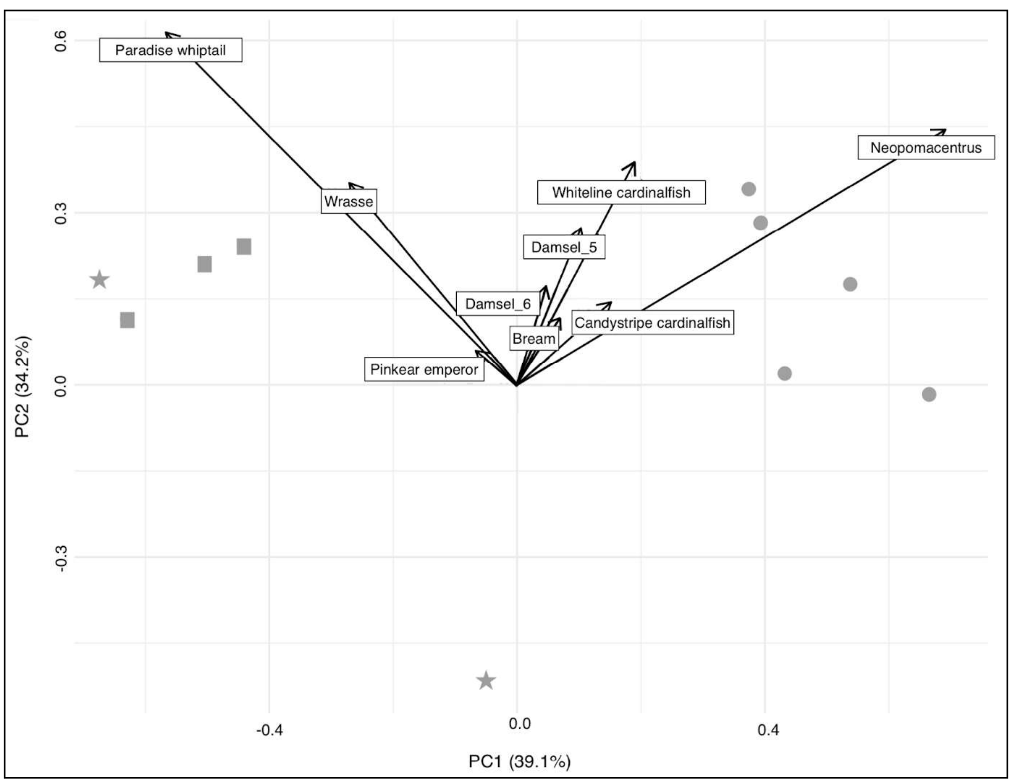

Fig. 6 Principal component analysis of fish assemblages recorded in bivalve beds (square symbols), fishery production structures (round symbols) and impacted sites (stars) in the Kep Archipelago

Table 5 Habitat features contributing most to differences between bivalve beds (BB), fishery production structures (FPS) and impacted sites (IS) in the Kep Archipelago. Variables include substrate and layer mean percent cover, fish, and bivalves. Contribution values are expressed as percentages of average dissimilarity. *** p<0.001, ** p<0.01, * p<0.05

Comparison (Substrate)	Global PERMANOVA	SIMPER	Main drivers	Notes
Overall	R^2≈0.288, F≈1.82, p=0.095 (substrate composition); R^2=0.36, F=1.99, p=0.115 (broad categories)			
FPS vs BB		p=0.015	FPS***, bare sand*, Rock***	Artificial reef more distinctive in FPS habitats (p=0.03), BB with more sand/shell (medium rock mix p=0.001) and pebble (Medium-coarse*)
FPS vs IS*		p=0.013	FPS***, pebble*	Artificial reef more distinctive in FPS (p=0.003); medium pebble mix (p=0.033)
BB vs IS		p=0.049	Bare sand***	Bare sand higher in IS; medium rock mix (p=0.001)
Overall	R^2≈0.405, F≈2.72, p=0.004		Macroalgae, seagrass	Significant differences among habitats
FPS vs BB	R^2=0.27, F=2.27, p=0.07		Algae (FPS), seagrass (BB); bivalve cluster**	*Neopomacentrus* spp. (47.5%, p=0.003) & *O. endekataenia* (92.8%, p=0.04); invertebrates***: white clam (22%), mussels (20%), Indian rock oyster (11%, p=0.047), bicolour penshell (7%) & penguin wing oyster (3%)
FPS vs IS*	R^2=0.34, F=3.02, p=0.02		Algae in FPS**, seagrass in IS, sessile invert*, mobile invert*	Seagrass only at IS_04 (5%)
BB vs IS	R^2=0.35, F=2.6, p=0.1		Bivalve cluster***, seagrass (BB), sessile invertebrate, turf algae (lower)	Bivalve clusters at BB only (5–10%); fish driver: *P. paradiseus* (79.8%, p=0.011)

Two distinct groupings of fish assemblages were evident on either side of the y-axis in our NMDS plot (Annex 4). The left cluster contained all BB sites (and IS_01) and was dominated by species such as pink emperor *Lethrinus lentjan*, silver sweetlips *Diagramma pictum*, wrasse *Halichoeres* sp., paradise whiptail *P. paradiseus*, sea bream *Gymnocranius* sp. and freckled goatfish *Upeneus tragula*. Conversely, the right cluster encompassed all FPS stations and was characterised by at least 16 fish species, many of which exhibit traits associated with coral reef assemblages, including shelter-seeking behaviour, territoriality and site fidelity. These include damselfish (Pomacentridae), cardinalfish (Apogonidae) and wrasse (Labridae). A PERMANOVA performed on Bray-Curtis dissimilarities of Hellinger-transformed fish count data revealed a highly significant difference in assemblage composition between habitats. Our SIMPER analysis revealed that FPS and BB habitats contributed most to assemblage separation (e.g., with *Neopomacentrus* spp. driving FPS variation and *P. paradiseus* dominating BB sites) when individual transects were used as replicates (F=7.0, R^2=0.40, p=0.001). When total fish abundance per station (i.e., pooled transects) was analysed, the significant differences among habitats remained (F=5.0, R^2=0.50, p=0.003).

Fish assemblage composition also varied significantly between habitat layers (PERMANOVA: R^2=0.435, F=4.60, p=0.002) and with total fish abundance (R^2=0.302, F=6.39, p=0.001), but was not significantly related to total bivalve abundance (R^2=0.073, F=1.55, p=0.141; Table 5). This indicates that habitat layers and fish density drive differences in assemblage structure, whereas bivalve abundance alone did not appear to exert a strong influence on fish assemblages. Specifically, SIMPER analysis showed that differences in fish assemblages between habitats were primarily driven by *Neopomacentrus* spp., *Ostorhinchus endekataenia* and *P. paradiseus*, which collectively explained 70–80% of the observed dissimilarity.

Discussion

Substrate composition & habitat differentiation

Substrate composition and benthic layer coverage differed markedly between the three habitat types and shaped the bivalve and broader faunal assemblages. Fishery production structures were unique in containing artificial reef structures (22%) that were mixed with sand/shell and pebble categories and provided complex, three-dimensional surfaces. This structural heterogeneity likely contributed to differences in the fish assemblages in the habitat (SIMPER: *Neopomacentrus* sp. 47.5%, *O. endekataenia* 92.8%), while also supporting smaller, less dense bivalve populations relative to bivalve beds. Bivalve beds were dominated by sand/shell (27%) and pebble mixes (up to 34%), coupled with dense bivalve clusters. These created favourable settlement surfaces and microhabitats for oysters and other sessile invertebrates. Layer composition reinforced these trends: macroalgae cover was greater in FPS habitats, whereas BB habitats supported more bivalve clusters and seagrass. This reflected substrate suitability and biological interactions. Conversely, impacted sites were primarily composed of sand/silt and minor shell–sand mixes, with very little coarse or structurally complex material and low layer coverage. While seagrasses were occasionally present, the predominance of unconsolidated fine sediments may help explain the absence of oysters and reduced faunal diversity in impacted sites. This would be consistent with studies showing that bivalve recruitment and persistence are limited in unstable or low-complexity substrates (Reise, 1985; Gutiérrez *et al*., 2003).

Similarity percentage analyses indicated that substrate and layer differences contributed to differences in assemblages between habitats. Among bivalves, the presence of white clams and unidentified mussels accounted for ca. 42% of the dissimilarity with FPS habitats, whereas Indian rock oysters *Saccostrea cucullata*, bicolour pen shells *Pinna bicolor* and penguin wing oysters *Pteria penguin* cumulatively contributed ca. 21%. Layer composition, including macroalgae in FPS and bivalve clusters in BB habitats, reinforced these habitat–fauna associations. These results collectively suggest that substrate type and benthic layer coverage are key drivers of assemblage structure, with artificial and structurally complex habitats supporting unique assemblages compared to natural bivalve beds or impacted sites.

Habitat complexity & fish assemblages

We found distinct habitat associations for both fish and bivalve assemblages across the three habitat types. Fish assemblages exhibited strong habitat preference, with FPS sites supporting higher species richness and overall abundance (Fig. 5, Table 4). These habitats were dominated by shelter-seeking reef fish such as damselfish (Pomacentridae) and sweetlips (Haemulidae), whereas BB habitats supported more open-environment and demersal foragers such as paradise whiptails (*P. paradiseus*), emperors (Lethrinidae), wrasses (Labridae), and sweetlips (Fig. 6, Annex 2). In contrast, impacted bare sand sites hosted a depauperate fish assemblage, indicating the importance of structural complexity in supporting diverse fish assemblages.

While quantitative rugosity measurements were not explicitly collected, BB and FPS habitats clearly had greater three-dimensional complexity compared to IS habitats dominated by sand. Given their vertical structure and clustered artificial reef units, FPS habitats likely had greater structural heterogeneity and complexity than BB habitats, albeit at more smaller scales. While localised, this complexity is ecologically significant, especially when units are deployed in sufficient numbers and proximity. This is because their combined presence may create corridors of connectivity between fragmented habitats (e.g., fringing reefs), similar to how seagrass meadows or BB habitats have traditionally served as functional linkages in disturbed areas such as trawled seascapes (Folpp *et al*., 2020). Previous studies have demonstrated that greater habitat complexity (e.g., rugosity, crevice volume, refuge size) supports higher fish diversity and abundance by providing food, shelter from predation, and increased opportunities for reproduction (Lazarus & Belmaker, 2021; Monfort *et al*., 2021; Flávio *et al*., 2023). As such, qualitative ranking of complexity across our habitat types would likely place FPS habitats highest, followed by BB and lastly IS habitats. We recommend future studies adopt photogrammetric or structure-from-motion techniques to quantify such metrics in the region (e.g., Monfort *et al*., 2021).

The fish assemblages we encountered reflected this gradient: FPS sites hosted a variety of reef-associated species with high commercial or ecological value—including snappers (Lutjanidae), jacks (Carangidae), and butterflyfish (Chaetodontidae), whereas BB sites supported demersal, benthic-foraging species adapted to less consolidated substrates. These groupings reflect different ecological functions: FPS habitats support refuge-seeking and potentially reef-dependent species, whereas BB habitats favour foragers contributing to benthic-pelagic trophic coupling and sediment bioturbation (Gutiérrez *et al*., 2003; Newell, 2004). However, contrasting levels of fishing pressure likely play a key role: while BB habitats are subject to daily exploitation, the deployment of FPS units restricts trawling and net fishing, thereby creating localised refuges or "fortress" zones that become less disturbed in over time (Haissoune, A., unpubl. data). This disparity may partly explain the greater abundance and diversity of commercially valuable species observed at FPS sites, independent of habitat complexity. Additionally, the mobile nature of pelagic schooling species (e.g., jacks, trevally, scads) and variable survey visibility may affect detectability, especially in the broader and more open areas characteristic of BB habitats. From a fisheries perspective, both habitats contribute valuable and complementary functions: FPS habitats support aggregations of reef-associated species, whereas BB habitats sustain benthic fish important for trophic connectivity and sediment health. This dual role demonstrates the value of incorporating artificial and natural structures into coastal restoration strategies. However, disentangling the effects of habitat structure and fishing pressure remains challenging. Carefully designed and enforced management measures—such as no-take zones or rotational closures—could help to decouple these factors in future studies and provide insights into their relative contributions to fish assemblage recovery. As marine protected areas continue to expand in the region, such approaches will be important to evaluate and optimise habitat restoration efforts.

Bivalve beds hosted a greater density and diversity of bivalve species compared to FPS sites. They also included several unique morphospecies, most of which appeared epifaunal based on field observations. However, bivalves at FPS sites were generally larger, possibly due to more stable conditions, lower predation pressure, and consistent recruitment over time (Gutiérrez *et al*., 2003; Bishop & Peterson, 2006; Ridgway *et al*., 2010; Karnauskas *et al*., 2017; Fig. 3–4). These differences may contribute to the variation in associated fish assemblages (Grabowski *et al*., 2012) and reinforce the role of natural and artificial complexity in shaping benthic and demersal assemblages. Given increasing use of artificial reefs in coastal restoration, there is a need to evaluate whether the structures influence the surrounding benthos positively or negatively (e.g., through altered sedimentation or competitive displacement). Future studies could consider whether coupling FPS deployments with naturally occurring BB and other habitats enhances biodiversity outcomes (e.g., as ecological corridors). Further, carefully designed FPS units could potentially serve as stabilising structures to facilitate seagrass or bivalve restoration and mitigate the hydrodynamic stresses (e.g., from tides & currents) that often hamper early establishment and seed retention in coastal restoration efforts. Such assessments could provide valuable insights before FPS are deployed more broadly within the region.

Long-term studies have shown that artificial reefs can attract and retain fish which support higher trophic levels including predatory fish (Richer, 2020; Strong *et al*., 2023; Marshall *et al*., 2025). This effect boosts fish density within the deployment site and may also benefit adjacent natural habitats through enhanced local fish production and spillover. This was observed by Folpp *et al*. (2020) in habitat-limited estuaries where artificial reefs supported higher fish abundances one to two years after their deployment. Previous research in the region also suggests that fish abundance and species richness can increase with structure age (Richer, 2020). This suggests benefits could potentially accrue in the long-term for fisheries and habitat restoration and future research could test this hypothesis by monitoring trends in fish recruitment, biomass and community turnover across FPS units of different ages. However, FPS are not ecological duplicates of natural coral reefs. While they can supplement habitats and offer localised benefits, natural reef systems should be prioritised for protection and restoration efforts because they provide a broader array of ecological functions and services. As such, FPS deployments should not act as a substitute for safeguarding natural coastal habitats. Using these to justify land reclamation or habitat loss could undermine ecological integrity and the coastal communities that depend on nearshore ecosystems for their livelihoods.

Influence of bivalve & fish assemblages on sediment characteristics

Bivalve and fish assemblages likely play complementary roles in shaping sediment conditions across habitats. Dense bivalve aggregations at BB sites contribute to sediment stability and organic matter retention through filtration, biodeposition and bioturbation, supporting benthic productivity and localised nutrient cycling (Gutiérrez *et al*., 2003; Newell, 2004). In contrast, FPS habitats are characterised by structural complexity and higher fish densities and may enhance organic enrichment through detrital deposition and faecal inputs (Cresson *et al*., 2014; Yang *et al*., 2019). These processes influence benthic functioning and distribution of associated invertebrates and highlight the importance of maintaining natural and artificial reef-like habitats to sustain benthic-pelagic linkages.

Conclusions

Our study provides baseline information on fish and bivalve assemblages in the Kep Archipelago and indicates the importance of habitat heterogeneity for sustaining biodiversity and ecosystem resilience. In demonstrating that natural bivalve beds and fishery production structures contribute to benthic-pelagic linkages and assemblage structure, our findings highlight the value of integrating habitat mosaics into coastal management. Conservation and restoration strategies should therefore combine the protection of natural habitats (including seagrass meadows, coral reefs and bivalve beds) with the deployment of fishery production structures. These should be complemented by long term monitoring of indicators for fish, bivalve and other benthic fauna to track changes in the ecosystem and guide future management of Cambodia's rapidly-developing coastal region.

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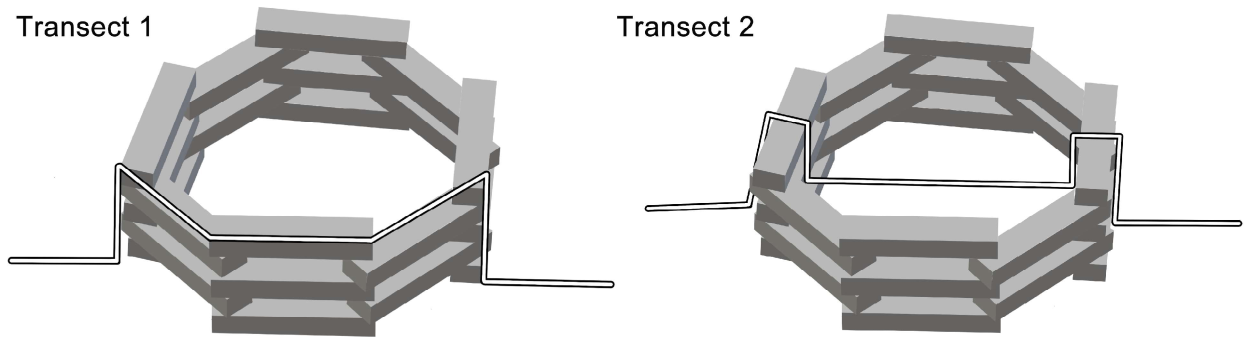
Annex 1 Sampling at fishery production structures in Kep Archipelago

Sampling was adapted to follow the 3-D contour of fishery production structures. Transect 1 (side view, left) followed the outer edge, while transect 2 (top view, right) crossed through the interior



Annex 2 Fish species recorded during study in Kep Archipelago

Common and Khmer names are based on MAFF (undated). Species of * commercial importance, ^{X} tourism importance

Family	**English / Scientific / Khmer Name** (where known)	Fishery Production Structures	Bivalve Beds	Impacted Sites
Ambassidae	Bald glassy / *Ambassis kopsii* / Trey kanchhanh chhras *	X		
Apogonidae	Candystripe cardinalfish / *Ostorhinchus endekataenia* / Trey ouert *^{X}	X		
	Whiteline cardinalfish / *Ostorhinchus cavitensis* / Trey kanchhanh chhras thmor *^{X}	X		
Carangidae	Jack / *Uraspis* sp. [unidentified] / Trey kam kouch *^{X}	X		
Chaetodontidae	Copperband butterflyfish / *Chelmon rostratus* / Trey meh om boa *^{X}	X		
Engraulidae	Indian anchovy / *Stolephorus indicus* / -	X		
Haemulidae	Silver sweetlips [juv.] / *Diagramma pictum* / Trey ka chi *		X	
Labridae	Wrasse / *Halichoeres* sp. [unidentified] / Trey sek ^{X}	X	X	X
Lethrinidae	Pinkear emperor / *Lethrinus lentjan* / Trey krorb knol		X	
	Sea bream / *Gymnocranius* sp. [unidentified] / -	X		
Lutjanidae	One-spot snapper / *Lutjanus monostigma* / Trey ang koeuy ouch muy *^{X}	X		
	Spanish flag snapper / *Lutjanus carponotatus* / Trey ang koeuy *^{X}	X		
Mullidae	Freckled goatfish / *Upeneus tragula* / Trey sek ^{X}		X	
Nemipteridae	Monogram monocle bream / *Scolopsis monogramma* / Trey an tak nu keo	X		
	Paradise whiptail / *Pentapodus paradiseus* / Trey ling lerm	X	X	X
Pempheridae	Sweeper / *Pempheris* sp. [unidentified] / -	X		
Pomacentridae	Bengal sergeant / *Abudefduf bengalensis* / Trey katang	X		
	Damselfish / *Neopomacentrus* sp. (possibly *N. azysron*) / - ^{X}	X	X	
	Damselfish [unidentified #1] / *Pomacentrus* sp. / - ^{X}	X		
	Damselfish [unidentified #2] / *Pomacentrus* sp. / - ^{X}	X		
	Damselfish [unidentified #3] / *Pomacentrus* sp. / - ^{X}	X		
	Damselfish [unidentified #4] / *Pomacentrus* sp. / - ^{X}	X		

Annex 2 cont'd

Family	**English / Scientific / Khmer Names** (where known)	Fishery Production Structures	Bivalve Beds	Impacted Sites
Pomacentridae	Damselfish [unidentified #5] / *Pomacentrus* sp. / - [X]	X	X	
	Damselfish [unidentified #6] / *Pomacentrus* sp. / - [X]	X	X	
Siganidae	Java rabbitfish / *Siganus javus* / Trey kantang thmor chhnout *	X		

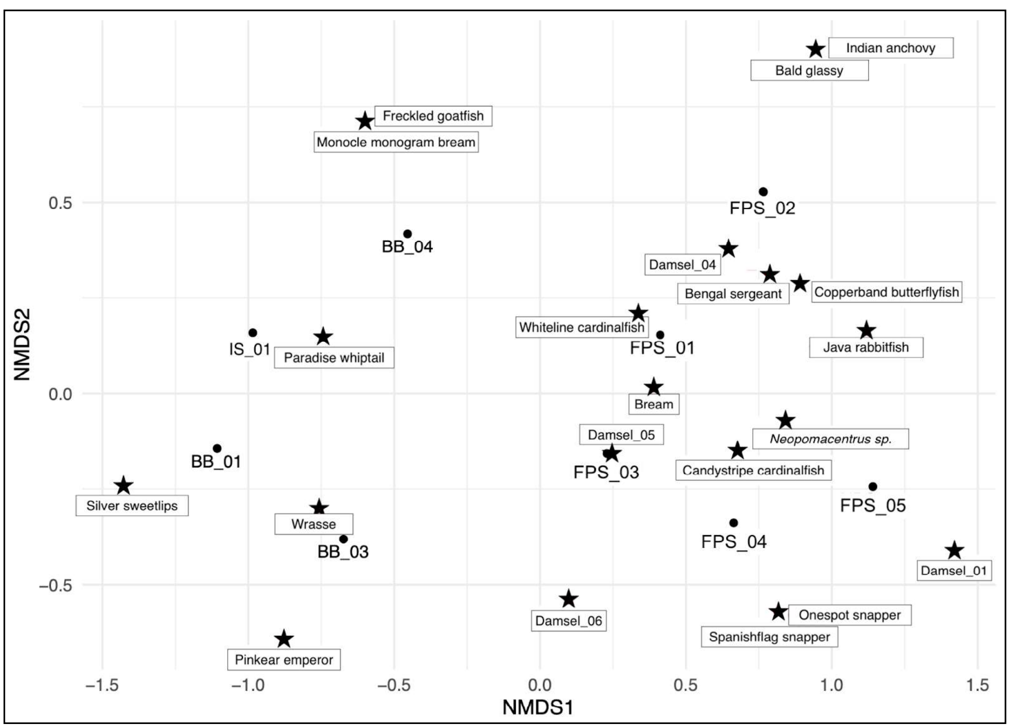
Annex 3 Oyster morphospecies recorded during study in Kep Archipelago

Asterisks indicate species of commercial importance

Common Name	**Scientific / Khmer Name** (where known)	Fishery Production Structures	Bivalve Beds	Impacted Sites
Rosy oyster	*Ostrea rosacea* (Deshayes, 1836) / -		X	
Penguin wing oyster*	*Pteria penguin* (Röding, 1798)) / Krum tra ses		X	
Indian rock oyster	*Saccostrea cucullata* (Gmelin, 1791)) / -	X		
Belcher's cupped oyster*	*Magallana belcheri* (G. B. Sowerby II, 1871) / -	X		
Imbricated oyster	*Hyotissa imbricata* (Lamarck,1819) / -	X		

Annex 4 NMDS plot of fish assemblages recorded in Kep Archipelago

Each point in graph below represents a fish assemblage from a single sampling site, whereas stars indicate individual fish species. Distances between points reflect dissimilarity in species composition based on Bray-Curtis distances



A novel baseline assessment of meiofauna in the Kep Archipelago, Cambodia: implications for sediment health and conservation planning

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មូលន័យសង្ខេប

ការនេសាទខុសច្បាប់ និងការបំផ្លិចបំផ្លាញភាវរស់ក៏ដូចជាទីជម្រកបានធ្វើឱ្យប៉ះពាល់យ៉ាងខ្លាំងដល់ប្រព័ន្ធអេកូឡូស៊ីសមុទ្រកម្ពុជា។ ដើម្បីបង្កើតមូលដ្ឋានសម្រាប់ការអនុវត្តលើការស្តារជម្រកឡើងវិញ យើងបានវាយតម្លៃភាពសម្បូរបែប និងសមាសភាពនៃសត្វល្អិតក្នុងដី (meiofauna) ជាសូចនាករសម្រាប់សិក្សាស្ថានភាពដីជម្រកបីប្រភេទ រួមមាន៖ វាលសប្បឹសត្វសំបកពីរ ជម្រកត្រីសិប្បនិម្មិត និងតំបន់រងផលប៉ះពាល់។ សត្វល្អិតក្នុងដីត្រូវបានកំណត់អត្តសញ្ញាណដល់កម្រិតចំណាត់ថ្នាក់ខ្ពស់ជាង ហើយការវិភាគពហុអថេរ (multivariate analyses) ត្រូវបានប្រើដើម្បីស្វែងយល់ពីគំរូរចនាសម្ព័ន្ធសហគមន៍សត្វល្អិតក្នុងដី អថេរបរិស្ថាន និងឌីណាមិចដី។ លទ្ធផលនៃការសិក្សារបស់យើងបង្ហាញថា ជម្រកសប្បឹសត្វសំបកពីរ និងជម្រកត្រីសិប្បនិម្មិតមានភាពចម្រុះជាង និងមានការប្រមូលផ្តុំដាច់ដោយឡែកនៃសត្វល្អិតក្នុងដីបើធៀបនឹងតំបន់រងផលប៉ះពាល់។ នេះបង្ហាញថាសត្វល្អិតក្នុងដីមានឥទ្ធិពលលើស្ថេរភាពបរិស្ថានកំទេចកំទីដីបាតសមុទ្រ។ ជម្រកសប្បឹសត្វសំបកពីរបានជួយជំរុញដល់លក្ខខណ្ឌដីបាតសមុទ្រឱ្យមានភាពអំណោយផល តាមរយៈការកាត់បន្ថយកករក្នុងផ្ទៃទឹក និងជួយឱ្យប្រសើរឡើងនូវប្រព័ន្ធអេកូឡូស៊ីស្រទាប់បាតសមុទ្រដោយពពួកវិស្វករអេកូឡូស៊ី មានដូចជាស្មៅសមុទ្រ និងពពួកសប្បឹសត្វសំបកពីរ។ ជម្រកត្រីសិប្បនិម្មិតអាចដើរតួជាជម្រកសុវត្ថិភាពសំខាន់រយៈពេលខ្លី និងអាចជាជំនួយដល់ការស្តារជម្រកឡើងវិញក្នុងដំណាក់កាលដំបូង។ លទ្ធផលនៃការសិក្សារបស់យើងបានផ្តល់នូវការយល់ដឹងអំពីសារៈសំខាន់ និងមុខងារនៃទីជម្រកទាំងនេះ ប៉ុន្តែទិន្នន័យរបស់យើងនៅមានកម្រិត និងការអនុវត្តមានចំនួនតិច។ ការស្រាវជ្រាវបន្ថែមគឺជាតម្រូវការចាំបាច់ដើម្បីបញ្ជាក់បន្ថែមលើលទ្ធផលរបស់យើង និងដើម្បីយល់ឱ្យកាន់តែច្បាស់ទៅលើការប្រែប្រួលរយៈពេលខ្លី។ ការសិក្សានេះបានផ្តល់នូវទិន្នន័យសត្វល្អិតក្នុងដីដំបូងបង្អស់ក្នុងដែនទឹកសមុទ្រកម្ពុជា ក៏ដូចជាទិន្នន័យមូលដ្ឋានថ្មីសម្រាប់ការសិក្សាតាមដាន និងការស្តារឡើងវិញនូវទីជម្រកប្រព័ន្ធអេកូឡូស៊ីបាតសមុទ្រនៃតំបន់ទាំងនេះ។

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Abstract

Illegal and destructive fishing practices have severely degraded marine ecosystems in Cambodia. To create a baseline for ongoing habitat restoration practices, we assessed meiofauna diversity and composition as a proxy for sediment condition across three habitat types: bivalve beds, fisheries production structures and impacted sites. Meiofauna were identified to higher taxonomic levels and multivariate analyses were applied to explore patterns in assemblage structure, environmental variables and sediment dynamics. Our results indicate that bivalve beds and fishery production structures support higher diversity and a distinct meiofauna assemblage compared to impacted sites and this suggests they have a stabilising effect on the sediment environment. Bivalve beds appear to foster favourable sediment conditions, likely through reduced resuspension and enhanced benthic–pelagic coupling by ecological engineers such as bivalves and seagrasses. Fishery production structures may function as short-term refugia, aiding in early-stage recovery. While our findings offer insights into the functional importance of these habitats, our dataset is limited spatially and by low replication. Further research is needed to confirm our results and better understand temporal variation. Nonetheless, the study provides the first information on meiofauna in Cambodian waters as well as novel baseline data for monitoring and rehabilitation of benthic ecosystems in these.

Keywords artificial reefs, bivalve beds, Cambodia, ecosystem functioning, habitat restoration, Kep Archipelago, marine conservation, meiofauna

Introduction

With an average depth of ≈50 m (Sok, 2022), Cambodian marine waters contain vulnerable and economically important habitats, including mangroves, seagrass meadows, coral reefs, bivalve beds and barren sands (UNEP, 2007; Strong *et al*., 2023). In recent decades, illegal, unreported and unregulated fishing, and particularly illegal beam trawling (Rizvi & Singer, 2011; Song *et al*., 2020; Widjaja *et al*., 2023), has caused extensive habitat degradation (Teh *et al*., 2017; FAO, 2018; Sala *et al*., 2018; Teoh *et al*., 2020; Ith *et al*., 2025). Climate change further exacerbates these threats (Agnew *et al*., 2009; IPCC, 2019; Sumaila & Tai, 2020).

Marine Fisheries Management Areas were established in the Kep Archipelago (Kep Province) to protect and restore local ecosystems in 2017. Artificial reefs known as fisheries production structures have been deployed to enhance habitat complexity and deter illegal trawling within these areas. Surveys between 2014–2018 indicated that these structures increase fish biodiversity and abundance significantly compared to surrounding areas (Reid *et al*., 2019; Richer, 2020; Strong *et al*., 2023), and support the recovery of seagrasses and other benthic habitats, with success rates of up to 50% in some regions (Reid *et al*., 2019). In providing hard substrates, fisheries production structures facilitate colonisation by bivalves and filter-feeding organisms and aid ecological restoration in a seascape otherwise dominated by degraded, barren sand (Marine Conservation Cambodia [MCC], unpubl. data).

Restoration efforts have increasingly prioritised degraded bivalve beds (particularly oyster-dominated habitats) due to their broad ecosystem benefits (Grabowski & Peterson, 2007). As ecosystem engineers (Dame *et al*., 2002; Yahya *et al*., 2020), oysters and other filter-feeding organisms transform bare substrates into three-dimensional, biodiverse ecosystems by providing shelter and nursery spaces, stabilising sediments, reducing erosion and mitigating eutrophication (Cressman, 2003; Coen *et al*., 2007; Grabowski *et al*., 2012; Coen & Humphries, 2017; Vaughn & Hoellein, 2018). Their filtration capacity improves water clarity and quality via nutrient sequestration and denitrification (Vaughn & Hoellein, 2018). These processes help prevent harmful algal blooms and maintain oxygenated sediments (Cressman, 2003; Coen & Humphries, 2017). This in turn promotes benthic productivity and supports food web functioning across multiple trophic levels (Newell *et al*., 2002; Shumway *et al*., 2003a; Seitz *et al*., 2014; Coen & Humphries, 2017; van der Schatte *et al*., 2020). Despite these benefits, baseline data on bivalve assemblages in Cambodian marine waters remain limited and this could hinder effective restoration planning.

Meiofauna are defined as organisms retained on a 38 μm sieve but passing through a 1 mm sieve (Fenchel, 1978). These are widely used as indicators of sediment condition and ecosystem functioning. Their assemblage structure reflects factors such as organic enrichment, sedimentation and oxygen availability (Danovaro *et al*., 2002; Giere, 2009; Balsamo *et al*., 2012; Yusal *et al*., 2017; Ridall & Ingles, 2021). Most meiofaunal taxa have short generation times, lack pelagic larval stages and live entirely within sediments. This makes them highly responsive to local environmental change (Fenchel, 1978; Giere, 2009). In feeding on deposited organic matter, meiofauna mediate benthic-pelagic coupling and link microbial processes to higher trophic levels (Schmid-Araya, 2002; Balsamo *et al*., 2012; Ridall & Ingles, 2021). Because they vary in their sensitivity to sedimentation rates (Nomaki *et al*., 2016), organic enrichment (Danovaro *et al*., 2002; Ingles *et al*., 2009), and hypoxia and/or anoxia (Moodley *et al*., 1997), the presence or absence of groups such as copepods and foraminifera and overall assemblage composition can indicate habitat stability and sediment health (Schratzberger & Warwick, 1998; Kennedy & Jacoby, 1999; Giere, 2009; Ridall & Ingles, 2021). Sediments thus archive processes occurring in overlying waters, such that meiofauna provide insights on how reef-like structures influence surrounding benthic habitats.

Despite their significance, meiofauna in Cambodian marine waters remain largely unstudied. Previous research has focused on the central Gulf of Thailand (Yeemin *et al*., 2013; Arnupapboon *et al*., 2019), coral reefs (Quan, 2020), or freshwater ecosystems such as the Tonle Sap Lake (Ohtaka *et al*., 2010), and Mekong River in Vietnam (Ngo *et al*., 2013). Study of meiofauna in Cambodian waters is required to bridge this knowledge gap, particularly in the light of planned increases to fishery production structures (ADB, 2024).

This study establishes a baseline for meiofauna inhabiting three habitats within the Kep Archipelago. Combined with a survey of fish and invertebrate assemblages (Gorra *et al*., 2025), our primary aim was to generate a snapshot of reef health using simple biodiversity and environmental metrics. To achieve this, we investigated three habitat types (trawled bare sand or impacted sites, bivalve beds, and fisheries production structures) and compared meiofauna diversity in relation to selected abiotic and biotic variables. We tested the following null hypotheses: 1) benthic meiofauna assemblages do not differ significantly across the three habitats, 2) sediment characteristics and other environmental variables do not vary between habitats, and 3) environmental variables do not influence meiofaunal differences across habitats. Our overall goal was to advance marine research in a data-deficient region by providing a baseline dataset and evaluating the potential of fisheries production structures to promote ecosystem recovery and sediment health.

Methods

Study area & site selection

Fieldwork was undertaken around the Kep Archipelago over four weeks from 20 January to 24 February 2023 (Fig. 1). We focused on waters surrounding Koh Ach Seh (10.35736111°N, 104.32019444°E), where the average depth is approximately 4.5 metres (MCC, unpubl. data).

Our survey focused on three subtidal habitats: bivalve beds (BB, n=4), impacted sites (IS, n=5), and fisheries production structures (FPS, n=5). The latter refer to small artificial installations approximately 2.5 m wide, which comprise 3–4 stacked concrete blocks. These were deployed by MCC as part of local restoration and enforcement efforts (Strong *et al*., 2023; Fig. 2) and their use has rapidly expanded in the area through a recent project (ADB, 2024), with potential effects on benthic communities that are poorly understood.

Sampling sites were chosen based on proximity to the Cambodian-Vietnamese border (an area frequented by illegal fishing vessels), logistical considerations and the need to standardise monitoring efforts for restoration projects (Fig. 1). The locations of sampling stations for bivalve beds and impacted sites were identified through reconnaissance dives, whereas locations for fishery production structures were provided by MCC. Bivalve beds were selected to represent filter-feeding communities dominated by oysters (including *Magallana belcheri*, *Saccostrea cucullata*, *Hyotissa imbricata*, *Ostrea rosacea* and *Pteria penguin*), mussels (*Perna* spp.) and mussel-like species (*Pinna* spp.). These were chosen to capture the ecological role of reef-forming bivalves (particularly oysters) due to their relevance to ongoing restoration and habitat recovery efforts. Coordinates and summary descriptions of sampling sites are provided in Annex 1.

Sampling methods

Abiotic surveys: We measured selected environmental variables in situ to support our ecological analyses. Divers recorded visibility, depth, temperature, substrate type and atmospheric conditions at all sampling stations (Annex 2). Salinity, light availability and granulometric size distribution were only measured at one station representative of each habitat type due to logistical and time constraints (Annex 3).

Two divers measured underwater visibility with a meter tape during each sampling session, based on the maximum distance at which they could see each other to the nearest 0.1 m. Water depth and temperature were estimated at all stations using a Suunto Novo dive computer

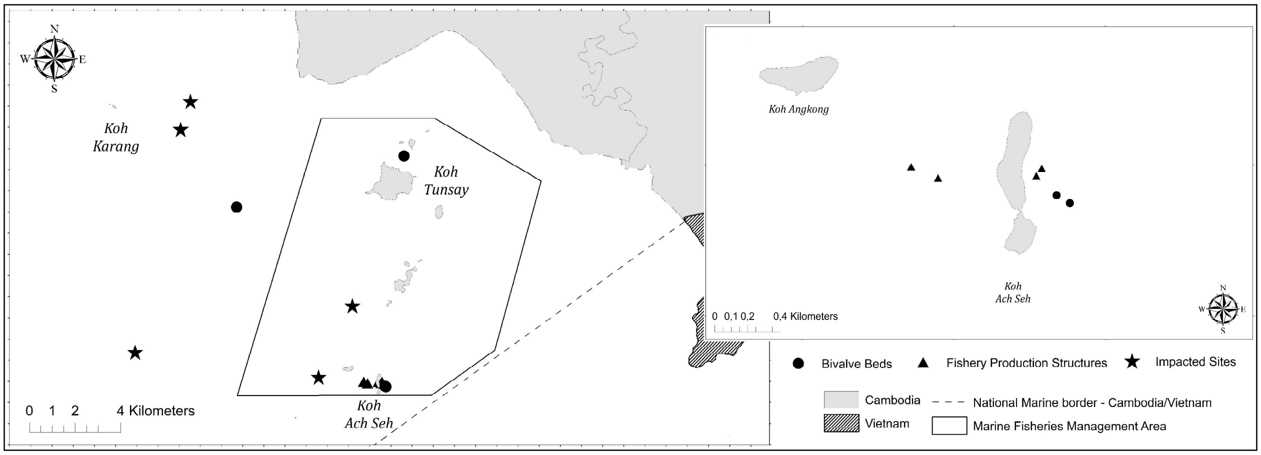

Fig. 1 Study area and sampling stations in the Kep Archipelago, Cambodia

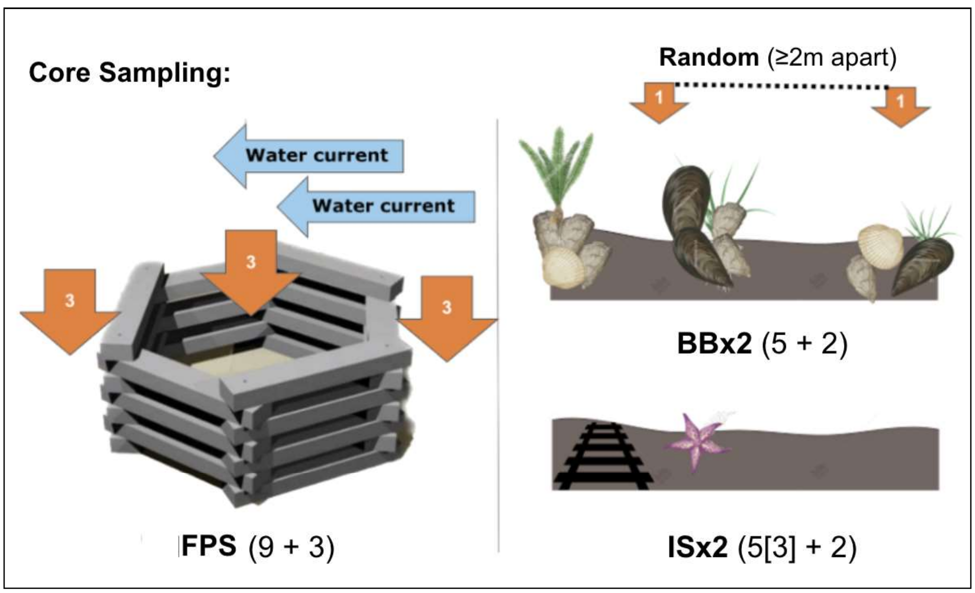

Fig. 2 Sampling strategy for sediment cores in the Kep Archipelago, Cambodia. Three to five randomly spaced cores (≥ 2m apart) were collected at bivalve beds (BB) and impacted sites (IS). Fisheries production structures (FPS) followed a modified design with three cores taken up-current, down-current, and inside the structure, plus a deeper (10 cm) core

(Suunto Oy, Vantaa, Finland) to 1(±2)°C resolution. Data collection was occasionally limited by boat availability and diving safety conditions. During accessible periods, sampling stations were equipped with a HOBO Pendant Temperature/Light 64k Data Logger (Li-COR, Nebraska, USA), which recorded temperatures and light levels every 10 minutes over 24 to 72 hour intervals, with ranges from -20 to 70°C (±0.53°C) and 0 to 320,000 lux, respectively. Two data loggers were deployed in each instance, one at the sediment surface and another unit one metre above the seabed. A reference sensor was mounted at the end of the MCC research pier (10.35768 N, 104.32122 E) to calibrate and verify logger performance during the study (Annex 2). These measurements helped account for possible variability in temperature and light measurements between stations. Average temperature and light availability data were retrieved from the loggers using *Onset* software vrs. 3.7.25 (HOBOware, Li-COR, Nebraska, USA).

To estimate average salinity in practical salinity units (PSU), we collected two water samples from each station at depth. Salinity was measured using a hand refractometer (range: 0 to 53% ±0.2% at 20°C; ATAGO, Tokyo, Japan) which was calibrated with fresh water before each use. Three readings were taken for each sample, with the average taken as the recorded value. Duplicate sediment samples were collected using meiofauna perspex push cores (with a 3.6 cm inner diameter) for grain size analysis. Substrate types refer to the physical composition and cover of the seafloor at each sampling point. Categories included sand, silt, mud, shell hash, live bivalves, seagrass, macroalgae, rubble, and artificial structures (e.g., fishery production structures). These were recorded at 0.5 m intervals along a 40 m transect, following a modified version of Loya (1978).

Biotic surveys: We employed various scuba diving survey methods to assess meiofauna and habitat characteristics across the three habitats at depths ranging from 2 to 11 m (Annex 1). Perspex push cores (total n=28) were haphazardly collected at intervals of at least two metres within each station to document small-scale variation across all of the habitat types in Annex 1. Sampling methods for fisheries production structures were adapted to accommodate the three-dimensional structure of the artificial reefs and prevailing current direction (i.e., three cores from each position: centre, up & down-stream) (Fig. 2). The top 0–5 cm of each core was sliced in bulk (Higgins & Thiel, 1988), rinsed with filtered seawater (seawater sieved through a 32-μm mesh sieve three times in situ), and preserved in a 4% formalin-seawater buffer (1:3 vol:vol ratio) for subsequent processing at the University of Science and Technology in Hanoi, Vietnam. Photographic records of each core were taken, and the oxic layer depth was visually determined using a ruler, based on the average of three measurements per core. The layer was identified by the distinct darkening of the sediment, indicative of organic matter degradation and a drop in interstitial oxygen due to microbial activity.

Sample processing: Sample processing was partly conducted in the field (initial extraction by decanting meiofauna from sediments to reduce transport volume) and finalised at the Hanoi University of Science and Technology (Water-Environment-Oceanography laboratory), where meiofauna identification and grain size analysis was undertaken. Additional sediment cores (reserved for grain size analysis) were processed by slicing the top 0–5 cm of the bulk depth profile, followed by sun drying and storage in aluminium foil until further analysis could be conducted. Each sample was analysed using a Mastersizer 3000 laser-diffraction particle-size analyser (Malvern Panalytical, Massachusetts, USA) with approximately 10 g (dry weight) of the sample homogenised in 50 mL of deionised water. Triplicate subsample results were averaged and compared with the Wentworth (1922) grain size classification scale.

In the laboratory, sediment samples stored in formalin were homogenised in a generous volume of deionised water, which allowed for the resuspension of microscopic organisms and particulate matter. The remaining sediment was retained on a 40-μm mesh sieve, was preserved with formalin-acetic-acid, then stained with Rose Bengal dye to facilitate accurate counts and identification of meiofauna to higher taxonomic groups. Observations and identifications were conducted under an EMZ-13TR stereomicroscope (Mijitechno, California, USA) following Higgins & Thiel (1988) and Schmidt-Rhaesa (2020).

Statistical analyses

All analyses were conducted in *RStudi*o vrs. 2023.3.0.386 (R Core Team, 2023) using the *tidyverse* vrs. 2.0.0 (Wickham *et al*., 2019), *dplyr* vrs. 1.1.4 (Wickham *et al*., 2023), *vegan* vrs. 2.6 (Oksanen *et al*., 2022) and *car* vrs. 3.1-3 (Fox & Weisberg, 2019) packages. Figures were produced using *ggplot2* vrs 3.5.1 (Wickham, 2016).

Data including meiofauna abundances at higher taxonomic levels were analysed across factors including station, habitat, water depth and habitat characteristics using permutational multivariate analysis of variance (PERMANOVA). The homogeneity of dispersions among groups was assessed using permutation of multivariate dispersion (PERMDISP) and similarity percentage (SIMPER) was applied to identify the taxa contributing most to observed differences. Community structure was visualised using non-metric multidimensional scaling (NMDS). Univariate data such meiofauna abundances and diversity indices were compared using one-way analysis of variance (ANOVA) and assumptions of homoscedasticity and normality were checked. Alternative tests were employed where these assumptions were not met. Pairwise analyses were undertaken only when the main tests indicated significant differences.

Descriptive statistics were used to summarise environmental parameters. Comparisons between stations and habitats were performed using one-way ANOVAs, following checks for normality (Shapiro–Wilk) and homogeneity of variances (Levene's test). Distance-based Redundancy analysis (DbRDA) was used to evaluate the proportion of community structure variation explained by measured abiotic variables, with data transformed where necessary.

Meiofauna densities (individuals/10 cm^2) were fourth-root transformed and normalised before analyses. Diversity metrics (taxon richness, Pielou's Evenness J (Pielou, 1966), Simpson's (Simpson, 1949), Hill's Index (Hill, 1973) and Shannon-Wiener (Shannon & Weaver, 1949) were based on total abundances (except for Shannon Index, which was based on transformed data) and compared between habitats and stations using one-way ANOVAs. Tukey Honestly Significant Differences (HSD) post-hoc tests were applied where appropriate.

Multivariate community analyses were undertaken using Bray-Curtis dissimilarity matrices on the higher taxa density data (individuals/10cm^2). Differences between habitats were tested using PERMANOVA (factor: habitat; levels: BB, IS & FPS), which incorporated the hierarchical sampling design (cores as random replicates within stations and stations nested within habitats) to avoid pseudoreplication. When significant differences were detected, homogeneity of dispersion was evaluated with PERMDISP (factor: station, p=0.001). Community structure was visualised using NMDS, and where appropriate, SIMPER analysis was employed to determine the taxa shaping community patterns. Relative abundances were calculated from meiofauna higher taxa to account for differences in dominant taxa (e.g., nematodes) and used in SIMPER and NMDS visualisations.

Results

Abiotic surveys

Temperature and salinity ranged from 27 to 34°C and 30 to 34 PSU, with the lowest levels recorded for both parameters at BB_01 and the highest at IS_05 (Annex 2). Light intensity varied notably across sampling stations: IS_05 had the lowest values at both the sediment surface (12.6 ± 28.3 lx) and 1m (44.4 ±77.1 lx), whereas the highest levels were observed at IS_01 (sediment surface: 2483.7 ±4088.9 lx) and BB_02 (1 m: 6747.6 ±11312.9 lx). A sensor at IS_01 was knocked over, potentially skewing the 1 m light data. The results of measurements for all variables are provided in Annex 2.

Sediment characteristics also varied across habitats. Visual inspection of sediment cores revealed the shallowest oxic layer depths were at impacted sites, followed by fisheries production structures, with the deepest horizons at bivalve beds (reaching up to 3.71 cm at BB_02: Annex 3). Average oxic layer depths were 0 cm for impacted sites, 1.51 cm (±1.13) for fisheries production structures, and 3.41 cm (±0.79) for bivalve beds, with significant differences among habitats (ANOVA, factor habitat, F=14.03, p<0.001). Sediment grain size (0–5 cm sediment depth profile, with averages representing >90% of each sample) showed a complementary pattern: bivalve beds and fisheries production structures were characterised by medium grain sizes (0.25–0.5 mm), whereas impacted sites exhibited coarser material (0.5–1 mm), with significant variation across stations (ANOVA F=30.77, p<0.001). Sand-silt-pebble was the predominant substrate type across all 12 sampling stations, followed by silt and sand-shell, which collectively accounted for >50% of observations (Annex 2).

Oxic layer depths and sediment profiles also revealed evidence of bioturbation at bivalve beds, as indicated by the presence of bivalves in deeper layers (Annex 3). At fishery production structures, sediment included distinct pinkish-red clay and gravel, particularly in the central position, where high densities of testate amoebas (density=1,371 [±2,374] ind./cm², n=4,115) were exclusively observed.

Meiofauna assemblages

Twenty-four higher taxon groups were identified across the sampling sites, with a cumulative estimate of 39,200 meiofauna individuals. This study focuses on 17 of these taxa, primarily permanent meiofauna and bivalve larvae relevant to the study aims. Nematodes dominated meiofauna assemblages across the three habitats, comprising up to 60% at stations such as IS_05 and BB_01. Copepods and calcareous foraminifera were the second and third most abundant taxa respectively, with notable peaks at BB_02 (40.9% for foraminifera) and BB_01 (13.3% for copepods).

The highest densities of nematodes, copepods, and calcareous foraminifera were recorded at BB_01 (1,018 ±465.02 ind./10 cm^2), BB_01 (286 ±189.3 ind./10 cm^2), and BB_02 (410 ±289.05 ind./10 cm^2), respectively. The lowest densities were observed at BB_02 for nematodes (286 ±150.13 ind./10 cm^2), at IS_01 for copepods (105 ±44.59 ind./10 cm^2), and at BB_01 for calcareous foraminifera (143 ±172.82 ind./10 cm^2). Meiofauna densities across all stations are summarised in Table 1.

Fisheries production structures exhibited the highest relative abundance of higher meiofauna taxa with 46.88 (±0.82) ind./10 cm^2, whereas IS_05 had the lowest with 9.08 (±0.38) ind./10 cm^2 (PERMANOVA, (pseudo) F=2.4482, p<0.01, n(perm)=999; PERMDISP p>0.05; Fig. 3). Impacted sites contained the highest relative abundance of calcareous foraminifera (342.57 ±264.75 ind./10 cm^2), whereas bivalve beds hosted the greatest abundance of nematodes (651.66 ±505.03 ind./10 cm^2) and copepods (201.36 ±166.72 ind./10 cm^2) (Table 1). Fishery production structures ranked second for copepods and third for nematodes and calcareous foraminifera.

Table 1 Average density of permanent meiofauna across representative sampling sites in the Kep Archipelago. Values are given as individuals/10 cm² [standard deviation]

Taxa	Bivalve beds		Fisheries Production Structures	Impacted Sites	
	BB_01	**BB_02**	**FPS_01**	**IS_01**	**IS_05**
Amphipoda	0 [na]	2.6 [1.67]	0.5 [1.07]	0.5 [1.0]	8.5 [6.36]
Bivalvia	22.4 [21.96]	1.6 [1.52]	2.78 [4.29]	2.25 [1.26]	6.0 [0]
Cladocera	0 [na]	2 [2.35]	2.5 [5.24]	8.5 [5.80]	7.5 [0.71]
Copepoda	286.36 [189.30]	116.35 [92.98]	218.58 [109.64]	104.5 [44.59]	105.5 [16.26]
Cumacea	0.8 [0.84]	1.2 [1.30]	2 [2.39]	8.75 [5.38]	0.5 [0.71]
Foraminifera (P)	0.5 [1.0]	16.8 [12.54]	0.5 [1.27]	3.8 [8.50]	7 [2.65]
Foraminifera (C)	143.4 [172.82]	409.6 [289.05]	192.89 [137.45]	344 [271.04]	339 [1.41]
Gastrotricha	0 [na]	0.4 [0.55]	0.125 [0.35]	0.25 [0.5]	0 [na]
Halacaridae	0.2 [0.45]	1.8 [1.79]	0.56 [0.88]	7.25 [11.30]	0 [na]
Nauplii	10.8 [11.97]	39.8 [29.15]	34.3 [30.98]	11.0 [14.27]	12.33 [8.39]
Nematoda	1017.8 [465.02]	285.6 [150.13]	765.9 [811.94]	313 [191.86]	722.3 [227.78]
Ostracoda	52.6 [74.79]	49.4 [65.87]	80 [48.81]	117.0 [44.31]	37.0 [24.04]
Polychaeta	34.6 [17.02]	31.4 [10.14]	49.75 [22.86]	27.0 [23.34]	15.5 [4.95]
Rotifera	0 [na]	0.2 [0.45]	0.25 [0.71]	0 [na]	0 [na]
Tanaidacea	0 [na]	0 [na]	0.25 [0.71]	6.75 [5.56]	0.5 [0.71]
Tardigrada	0 [na]	12.4 [10.53]	0 [na]	0 [na]	0 [na]
Testate amoeba	0 [na]	0 [na]	1371 [2374.06]	0 [na]	0 [na]

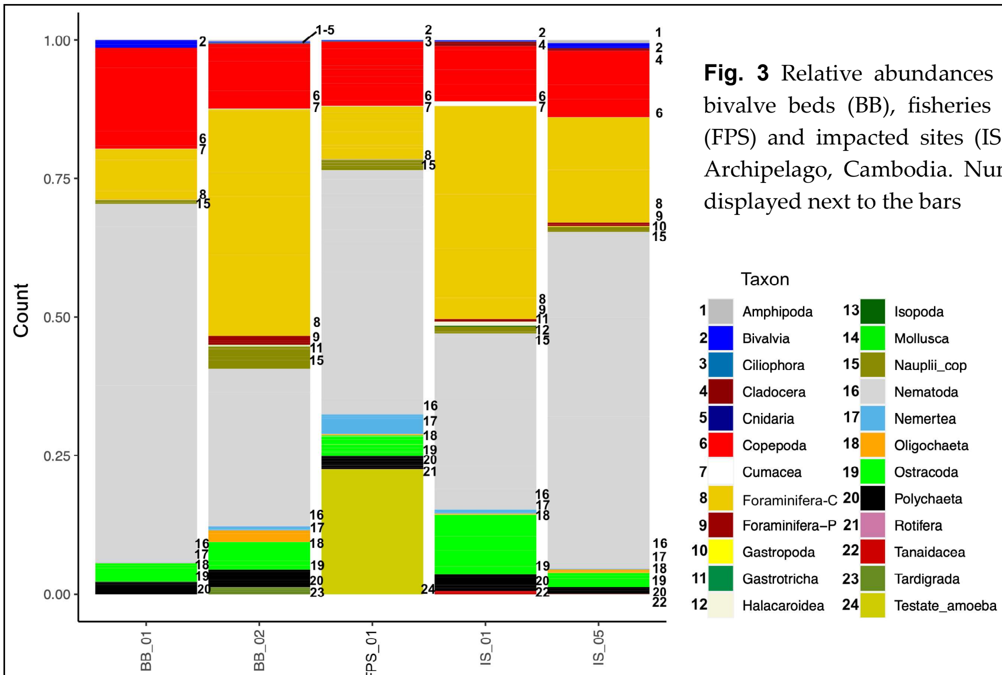

Fig. 3 Relative abundances of meiofauna taxa in bivalve beds (BB), fisheries production structures (FPS) and impacted sites (IS) sampled in the Kep Archipelago, Cambodia. Numeric taxon codes are displayed next to the bars

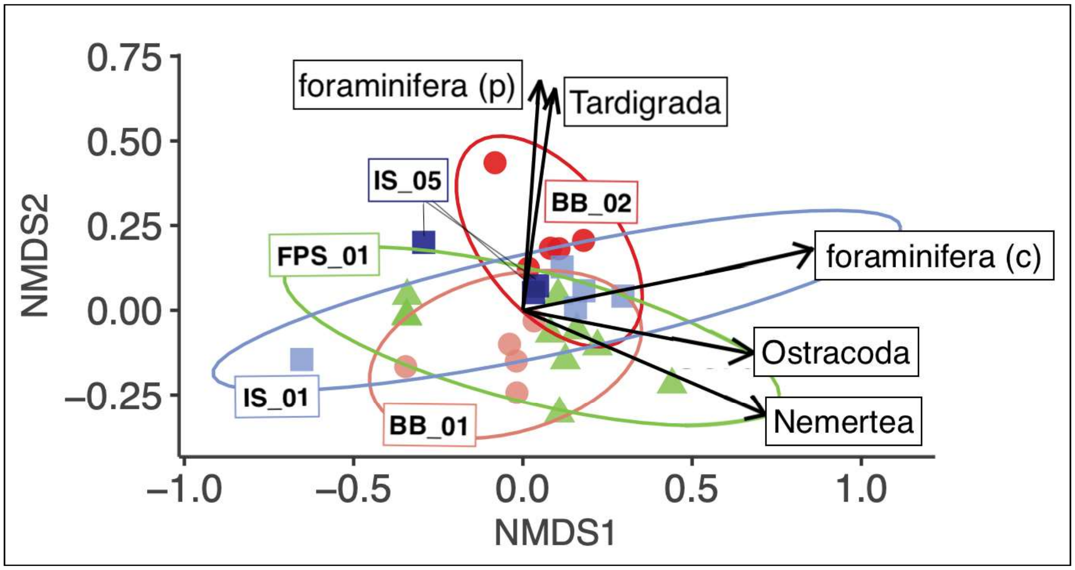

Fig. 4 Meiofauna composition based on non-metric multidimensional scaling. The ordination plot displays station groupings based on similarities in community composition, with station IDs labelled in bold (BB=bivalve beds, FPS=fisheries production structures & IS=impacted sites) and taxa contributing to group patterns shown in regular font

Table 2 Contrasts between bivalve beds (BB), fisheries production structures (FPS) and impacted sites (IS) based on SIMPER analyses, including the top three contributing taxa. Significance levels: * p<0.05, ** p<0.01, *** p<0.001

Taxa	Cumulative Contribution	Taxa	Cumulative Contribution	Taxa	Cumulative Contribution
Contrast: BB_01, BB_02 Dissimilarity: 34.8%		Contrast: BB_01, FPS_01 Dissimilarity: 30.9%		Contrast: BB_01, IS_01 Dissimilarity: 33.8%	
Tardigrada***	19.6	Bivalvia***	21.8	Nematoda***	23.8
Foraminifera(P)***	28.4	Oligochaeta*	43.0	Copepoda**	38.0
Oligochaeta**	44.0	Naupauli*	54.3	Tanaidacea**	62.5
Contrast: BB_01, IS_05 Dissimilarity: 28.9%		Contrast: BB_02, FPS_01 Dissimilarity: 34.1%		Contrast: IS_01, BB_02 Dissimilarity: 32.3%	
Amphipoda***	23.7	Tardigrada***	18.8	Tardigrada***	19.0
Foraminifera (P)*	33.0	Foraminifera (P)***	27.0	Foraminifera (P)**	27.5
Oligochaeta*	40.7	Amphipoda*	42.6	Tanaidacea*	43.4
Contrast: IS_05, BB_02 Dissimilarity: 27.3%		Contrast: IS_01, FPS_01 Dissimilarity: 33.6%		Contrast: IS_05, FPS_01 Dissimilarity: 32.3%	
Tardigrada*	21.0	Tanaidacea**	37.0	Amphipoda**	18.6
-	-	Halacaridae*	42.0	Foraminifera (P)*	26.0
-	-	-	-	Cnidaria*	94.7
Contrast: IS_05, IS_01 Dissimilarity: 32.6%					
Amphipoda**	34.7				
Halacaridae*	40.8				
Cumacea*	46.8				

Table 3 Shannon diversity and taxon richness values for bivalve beds (BB), fisheries production structures (FPS) and impacted sites (IS) sampled in the Kep Archipelago. Standard deviations are given in square brackets

Station	Core ID	Shannon Diversity	Taxon Richness	Ind./core	Station	Core ID	Shannon Diversity	Taxon Richness	Ind./core
BB_01	#001	1.95	10	1302	BB_02	#027	2.65	18	1332
	#002.2	2.30	14	2446		#028	2.59	17	901
	#003	2.04	11	1904		#029	2.63	18	1274
	#004	2.22	13	1588		#030	2.57	17	1140
	#005	1.91	10	625		#031	2.74	19	366
			11.6 [1.62]	7865				17.8 [0.75]	5013
FPS_01	#008	2.10	11	1358	FPS_01	#013	2.24	13	581
	#009	2.15	12	4173		#014	2.61	18	1667
	#010	2.26	13	734		#015	2.63	18	1241
	#011	2.34	14	1383		#016	2.51	16	581
	#012	2.36	14	5960		#019	2.21	12	677
								15 [2.34]	18355
IS_01	#020	2.55	16	519	IS_05	#034	2.56	17	1563
	#021	2.46	15	881		#035	2.44	15	1143
	#022	2.57	17	1341		#036	2.45	15	872
	#023	2.55	17	1633					
	#024	2.04	10	105					
			15 [2.61]	4479				15.7 [0.94]	3578

Table 4 Eveness and diversity indices for bivalve beds (BB), fisheries production structures (FPS) and impacted sites (IS) sampled in the Kep Archipelago

Station	Replicate Number	Mean Species Richness [SD]	Mean Pielou's Eveness (J)	Taxon Richness	Shannon Entropy Index	Simpson's Concentration Index
BB_01	5	11.6 [1.62]	0.416	9.6	2.70	2.05
BB_02	5	17.8 [0.75]	0.543	15.4	4.59	3.02
FPS_01	10	14.1 [2.34]	0.498	11.5	3.65	2.72
IS_01	5	15 [2.61]	0.617	12.6	4.84	3.73
IS_05	3	15.7 [0.94]	0.435	13.3	3.18	2.27

Meiofauna assemblages varied significantly between stations according to PERMANOVA and NMDS analyses (Fig. 4). The NMDS plot (stress=0.17) captured the primary patterns in meiofaunal assemblage structure, indicating a moderate fit. While some fine-scale relationships may not be fully resolved, the ordination reliably highlights broader ecological trends. Diagnostic metrics including a non-metric R^2 value of 0.97 and linear fit R^2 value of 0.878 supported the validity of our analysis in identifying habitat-driven differences. Permutational analyses of multivariate dispersions indicated that fisheries production strutures exhibited the highest within-site variability. This was likely due to our sampling of core positions within the centre of the semi-enclosed structures. Distinct patterns also emerged in the NMDS plot (Fig. 4), with four major groups identified based on taxa filtered using a significance threshold of p<0.001. Similarity of percentage analysis (n=36, p<0.05) identified

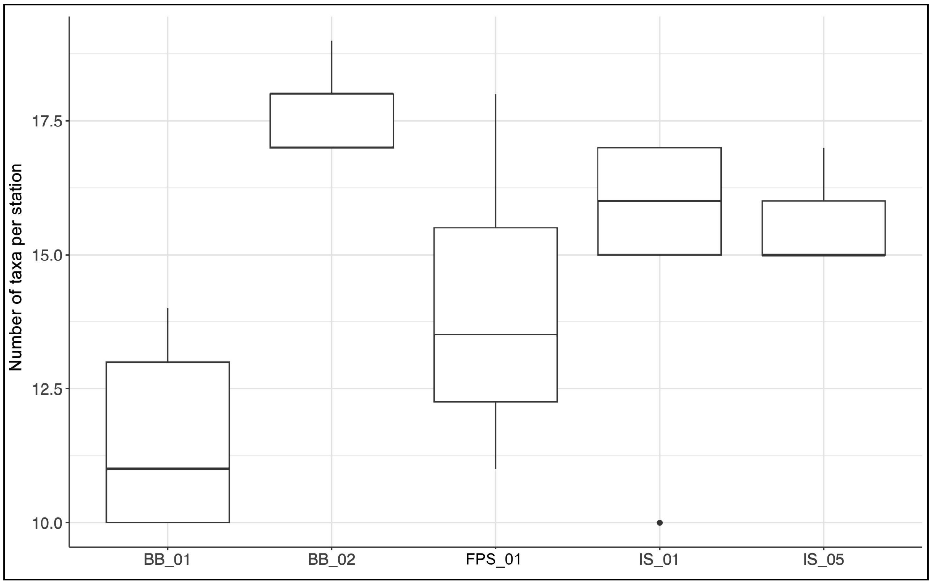

Fig. 5 Meiofauna taxon richness across sampling stations in bivalve beds (BB), fisheries production structures (FPS) and impacted sites (IS) in the Kep Archipelago

Tardigrada, Oligochaeta, bivalve larvae and Amphipoda as significant contributors to assemblage dissimilarity. The highest dissimilarity overall was observed in bivalve beds which ranged between 27% to 34% (Table 2).

Meiofauna assemblages varied at impacted sites and bivalve beds and this was reflected in differences between individual stations (e.g., BB_01 & BB_02). The highest within-habitat variation was observed in fisheries production structures (Fig. 4), again possibly due to our collection of cores in various positions within the semi-enclosed structures. Distinct dispersion patterns were apparent across stations in our NMDS plot (Fig. 4), which grouped meiofauna communities into three clusters. These groups were driven by taxa filtered with a significance threshold of $p<0.001$ (non-metric $R^2=0.97$, linear fit $R^2=0.878$). Calcareous foraminifera (86.5%), Nemertea (71.5%) and Ostracoda (68.8%) were the main contributors to NMDS1, while proteinaceous foraminifera (70.3%) and Tardigrada (68.6%) were influential along NMDS2. Bivalve beds aligned primarily along NMDS2, whereas fisheries production structures and impacted sites clustered along NMDS1.

Significant differences occurred in meiofauna taxon richness and Shannon diversity across stations (ANOVA, taxon richness, $F=5.499$, $p<0.01$; ANOVA, Shannon diversity, $F=7.323$, $p<0.001$; Fig. 5, Table 3). Tukey HSD tests indicated that taxon richness was highest at BB_02, whereas FPS_01 and IS_05 did not differ significantly. In contrast, BB_01 exhibited the lowest richness and was statistically distinct from all other stations. Shannon diversity followed a similar trend, with BB_02 showing the highest mean (2.64) and BB_01 the lowest (2.08). Intermediate diversity values were observed at IS_05 (2.48), IS_01 (2.44) and FPS_01 (2.34).

Mean Pielou's Evenness values were greatest at FPS_01 and lowest at BB_01, though evenness did not vary significantly across cores within stations (factor Core ID, $F=1.144$, $p=0.113$; Table 4). These results suggest that while certain habitats (e.g., BB_02) support greater diversity and richness, the relative abundance of taxa within cores at each station remained relatively stable.

The highest average Hill's Index values (based on raw count data) were recorded at BB_02 for taxon richness, at IS_01 for Shannon entropy index and Simpson's concentration index. The lowest values for all indices were recorded at BB_01. One-way analysis of variance revealed significant differences in Hill's indices among stations (taxon richness $F=5.088$, $p=0.00437$; Shannon entropy index $F=7.301$, $p=0.00059$; Simpson's concentration index $F=4.534$, $p=0.00757$). Tukey HSD post-hoc tests indicated that BB_02 and IS_01 typically exhibited higher diversity metrics than BB_01 (which was consistently lower in all indices). Additional details including replicate variations are provided in Table 4.

Environmental variables (including oxic layer depth, grain size, salinity, temperature & light availability) were examined to assess their influence on meiofauna variability. Permutational analysis of multivariate dispersions

Table 5 Outcomes of tests applied to examine the effects of abiotic variables measured in the Kep Archipelago

Variables	Test	Effect	Test statistic	*p* value	Remarks
Median grain size	1-way ANOVA	Between stations	*F*=30.77	2.51^{e-09}	Abiotic metrics differ between habitats and stations
Oxic layer depth	1-way ANOVA	Between habitats	*F*=14.03	0.0089	
Diversity	1-way ANOVA (richness, Shannon diversity)	Between habitats	*F*=5.499 (richness) *F*=7.323 (diversity)		Significant differences in meiofauna richness, and diversity, as well as relative abundances between assemblages. A pair-wise PERMDISP was insignificant. Similarly, assemblage variation was not sufficiently explained by environmental variables. More replicates are likely necessary
	PERMANOVA (relative abundances, nperm=999)	Between habitats	*(pseudo) F*=2.5	0.002 (Permdisp: >0.05)	
	DbRDA (squared-Bray distance)	inc. env variables	R^2=2.4482 Total inertia =0.43	>0.05	
Between-group differences	SIMPER (based on Bray-Curtis dissimilarity)	Between stations Driving taxa		0.05 0.001	- Most dissimilarity between BB_01 & BB_02 - Tardigrada, Oligochaete, Bivalvia (larvae) & Amphipoda drive between-site dissimilarity

showed no significant differences in dispersion among these. Likewise, DbRDA revealed no clear community structuring associated with the measured environmental parameters (Table 5). These results suggest that factors other than the measured variables likely account for the differences we observed in meiofauna assemblages.

Discussion

This study provides the first insight into meiofaunal assemblages in Cambodian waters and reveals how different habitat types (namely impacted sites, fisheries production structures & bivalve beds) influence benthic diversity and environmental stability. These habitats vary in structural complexity and ecosystem function and offer a natural gradient to examine how habitat characteristics influence meiofauna assemblages. In recent decades, the Kep Archipelago has experienced extensive degradation from coastal development and destructive practices such as bottom trawling (Jones *et al*., 2020; Tubbs *et al*., 2020; Strong *et al*., 2023), resulting in the loss of key ecosystem engineers such as oysters and other bivalves (Dudgeon *et al*., 2006; Gosling, 2008). Restoration of these benthic communities has become a priority for local stakeholders and regional management plans (FiA, 2021; MCC, unpubl. data).

Habitat complexity & ecosystem engineers

Oysters and other bivalves were once common in Cambodian waters (MCC, unpubl. data), contributing to sediment stability, organic matter cycling and biodiversity (Dudgeon *et al*., 2006; Gosling, 2008). Decades of bottom trawling have drastically reduced these populations (Jones *et al*., 2020; Strong *et al*., 2023), prompting initiatives to reintroduce bivalves and thereby recover lost ecosystem functions. As a result, fisheries production structures were deployed within the Marine Fisheries Management Area (Fig. 1) to enhance habitat complexity, deter illegal trawling, and promote recolonization by sessile fauna including bivalves (Strong *et al*., 2023).

We found that fisheries production structures and bivalve beds supported more stable conditions with lower sediment variation and a finer, more homogeneous grain composition (Annex 2–3). These patterns likely result from reduced sediment resuspension (Kaiser & Spencer, 1996; Hiddink *et al*., 2007) and increased benthic retention of organic matter. Fishery production structures also supported higher meiofaunal diversity, consistent with their role in facilitating the recruitment of sessile fauna (Reid *et al*., 2019; Strong *et al*., 2023; Gorra *et al*., 2025). The higher diversity and richness of meiofauna recorded at BB_02 may be attributable in part to the presence of seagrasses, since these enhance sediment stability, organic matter organic matter and habitat heterogeneity that favours colonisation (Danovaro *et al*., 2002). In stabilising sediments, creating microhabitats and enhancing benthic-pelagic coupling through bioturbation, leaf litter decomposition and organic matter retention (Lemmens *et al*., 1996; Larkum *et al*., 2006; Coen & Humphries, 2017; van der Schatte *et al*., 2020), these habitats provide conditions favourable for meiofauna. These processes can also lead to localised organic enrichment, which in turn can potentially lead to changes in meiofaunal composition depending on oxygen availability and microbial activity.

The increases we observed in sediment stability, habitat complexity and meiofaunal diversity around fisheries production structures align with ecological functions documented for artificial reefs. Artificial reefs enhance benthic-pelagic coupling in sediments by providing hard substrates for filter-feeders, as reflected by the presence of larger bivalves, and barnacle and bivalve recruits (Fivash *et al*., 2021; Natanzi *et al*., 2021; Jiang *et al*., 2022; Gorra *et al*., 2025). Further, elevated testate amoebae densities within fisheries production structures suggest microbial loop interactions (Luców *et al*., 2025) may be intensified and facilitate exchange between the water column and benthos (Wilkinson & Mitchell, 2010). Artificial reefs also influence sediment dynamics by stabilising substrates (Yang *et al*., 2019; Dai *et al*., 2025) and altering oxygen penetration, as reflected in a shallow oxic-anoxic front observed at these (Annex 3; Crain & Bertness, 2006; Seitz *et al*., 2014; Carrick & Forsythe, 2020). Consistent with findings from artificial and natural bivalve reefs, fisheries production structures appear to enhance local biodiversity and sediment-water interactions via water filtration by attached filter-feeders (Grabowski *et al*., 2012).

Environmental drivers

The composition and abundance of meiofauna in our study reflected differences in sediment stability, oxygenation and organic matter across habitats. In bivalve beds and fisheries production structures, finer and more stable sediments supported higher abundances of copepods and nematodes, groups typically associated with well-oxygenated microhabitats and active microphytobenthos (Danovaro *et al*., 2002). In contrast, impacted sites, which experience strong hydrodynamic disturbance and highsediment turnover from trawling, exhibited no distinct oxic layer and the highest light availability (Annex 3). These conditions likely maintain elevated oxygen penetration in the surface sediments but also limit organic matter retention, favouring opportunistic and disturbance-tolerant taxa such as calcareous foraminifera (Phleger & Soutar, 1973; Bongers & Bongers, 1998; Semprucci *et al*., 2017; Yusal *et al*., 2017). While fisheries production structures provide ecological benefits, their reduced water flow can promote the accumulation of fine sediments and organic matter (Dai *et al*., 2025). This sustains diverse meiofaunal assemblages but may also elevate hypoxia risk through microbial degradation (Yang *et al*., 2019). Elevated fish densities around the structures (Reid *et al*., 2019; Strong *et al*., 2023; Gorra *et al*., 2025) likely contribute to this enrichment via excretion. If so, appropriate design and placement of structures is important to maximise ecological benefits while mitigating hypoxic stress and material degradation (Yang *et al*., 2019; Melchers, 2020; Pratiwi *et al*., 2021; Higgins *et al*., 2022).

Our DbRDA based on environmental predictors did not reveal significant relationships. This was likely due to high within-group variation and the absence of clear separation in meiofauna assemblages across sites at the time of our study. Meiofauna typically exhibit high spatial and temporal variability in tropical shallow seas and this is influenced by seasonal change such as wet and dry seasons (Pinto & dos Santos, 2006). Other factors such as site location, proximity to the coast and human activities may also have an influence (Ith *et al*., 2025). Foraminifera populations, which are key consumers in microbial food webs in sediments (Lipps & Valentine, 1970), were dense at impacted sites. This suggests assemblages were supported by microphytobenthos and microbial biofilms, as indicated by coloured mats on sediment surfaces. Being tolerant of low-oxygen conditions, nematodes and foraminifera maintained high densities, even in less oxygenated sediments (Gupta & Machain-Castillo, 1993; Kitazume, 2018).

Recent work on Koh Seh coral reefs has revealed clear environmental gradients: the east is characterised by high sediment loads, elevated temperatures and pH, whereas the west has deeper waters with higher levels of dissolved oxygen and salinity (Ith *et al*., 2025). These gradients are likely to shape meiofauna assemblages. Oxygen and salinity sensitive taxa may thrive in the western conditions, whereas opportunistic or stress-tolerant taxa may dominate in the eastern conditions. Located east of Koh Seh Island, one of our sampling sites (BB_02) hosted a dense seagrass meadow and supported proteinaceous foraminifera and other low-oxygen taxa (Fig. 4, Table 1). This suggests habitat complexity combined with regulatory protection may help to maintain sediment stability and ecological resilience despite the elevated sediment stress observed in 2019 (Ith *et al*., 2025). In contrast, another sampling site (FPS_01) situated in west-like conditions, harboured a more diverse meiofaunal assemblage due to the combined effects of deeper water, improved oxygenation, and moderated sediment dynamics.

Spatial variability

Substantial within-habitat variation in meiofauna was observed at all sites, with the greatest microscale heterogeneity occuring in fisheries production structures (Fig. 3). The variation in these reflected differences in core collection locations within the semi-enclosed structures. Reduced water flow at the centre of these structures could limit bottom water renewal, promoting organic matter accumulation and elevated meiofauna densities (Table 1; Danovaro *et al*., 2002; Moccia *et al*., 2019). However, this feature was not measured as it was observed across structures given a buildup of finer sediments at specific locations within the structure and is a general consequence of artificial reefs (Dai *et al*., 2025). Shallow oxic layers may indicate enhanced microbial activity and oxygen consumption, creating conditions favourable for diverse assemblages (Balsamo *et al*., 2012). Pinkish sediment colouration corroborates the presence of bacterial communities thriving in the rich organic matter environments typical of artificial reefs (Cresson *et al*., 2014). High testate amoebae densities reflect adaptation to these microhabitats and reliance on bacterial food sources (Smirnov & Fenchel, 1996; Fenchel *et al*., 2012).

Fishery production structure appear to promote recolonization and microbial activity that supports sediment nutrient cycling and potentially facilitates recruitment of bivalves and seagrass (Reid *et al*., 2019). However, the long-term contribution of these processes to habitat restoration has yet to be determined. Local hydrodynamics and sediment characteristics in the study region (Ith *et al*., 2025) indicate the importance of careful placement of fisheries production structures. They also suggest optimising design to balance organic matter retention with water exchange could enhance their function in promoting habitat regeneration in degraded benthic environments.

We found the composition of meiofauna varied across habitats. For example, SIMPER analysis revealed that tardigrades and bivalves contributed strongly to differences within bivalve beds (with tardigrades particularly abundant at BB_02) (Fig. 5; Table 2). Nematodes were prevalent in fisheries production structures (and BB_01 & IS_05; Table 2) and have diverse feeding behaviours in preying on tardigrades, protists and microalgae. This reflects their role in sedimentary trophic dynamics (Bartsch, 2004; Moens *et al*., 2005; Schmid-Araya *et al*., 2016). Oligochaetes dominated one bivalve bed (BB_01) whereas amphipods and testate amoebae characterised a fisheries production structure (FPS_01), with the latter unique to these structure in thriving in low-oxygen and organic rich sediments (Fig. 3, 5; Annex 3; Smirnov & Fenchel, 1996; Wu *et al*., 2023). Reduced flow at fisheries production structures also influenced sediment grain size and composition, concentrating finer particles at the centre (i.e., clay) and coarser grains at the periphery (Annex 3; Levin & Paine, 1974; Ambrose & Anderson, 1990). While organic matter accumulation enhances microbial productivity and meiofaunal diversity, excessive enrichment could induce hypoxia, potentially affecting larger benthic organisms (Levin *et al*., 2009). Design modifications that improve water exchange while maintaining OM retention may optimise FPS effectiveness for restoration.

At impacted sites such as IS_01, Halacaridae and Tanaidacea dominated in preferring silty to gravelly sediments with high resuspension, which are often linked to trawling (Blazewicz-Paszkowycz *et al*., 2012). Cumacea and amphipods were most abundant at IS_05, probably due to lower disturbance and greater depths providing a more stable habitat (Barnard, 1976; Gerken, 2016; Annex 2). Proteinaceous foraminifera were most prominent at BB_02 and IS_05, followed by IS_01, and were least abundant compared to BB_01 and fisheries production structures (Fig. 3, 5; Annex 3; Table 4). These thrive in low-oxygen sediments with rich organic matter where microbial biofilms and detritus are abundant (Bernhard & Reimers, 1991; Levin *et al*., 2009). Calcareous foraminifera exhibited more consistent densities across stations, suggesting a broader tolerance to sediment and oxygen variability.

Future directions

Bivalves are important ecosystem engineers that enhance habitat complexity, stabilise sediments, and improve sediment and water quality (Grabowski *et al*., 2012; Norkko *et al*., 2013). Our results confirm that bivalves support resilience by cycling nutrients, mitigating hypoxia and promoting benthic-pelagic coupling (Cressman, 2003; Coen & Humphries, 2017). High oyster abundance at BB_02 coincided with deeper oxic layers and greater visibility (Annex 2–3), whereas organic matter accumulation in fisheries production structures suggests that restricted hydrodynamics rather than biogenic activity may drive retention of the latter. While oysters improve sediments through filtration and bioturbation, fisheries production stuctures may foster organic matter due to limited water exchange (Dai *et al*., 2025). These contrasts highlight the need to refine structural design to better emulate bivalve functions or even to combine both approaches to optimise restoration outcomes.

Bivalves maximise filtration in shallow habitats, particularly during algal blooms, funnelling organic matter to sediments in more refractory forms (Newell, 2004; Pomeroy *et al*., 2007; Gobler *et al*., 2022). This was reflected in deeper oxic layers at BB_02, dense seagrass and oyster clustering (Gorra *et al*., 2025), high water clarity (Annex 2) and greater meiofauna richness and diversity (Annex 3; Fig. 5; Table 3). In contrast, BB_01 had fewer oysters and sparse seagrass (Gorra *et al*., 2005), coupled with shallower oxic layers, lower visibility and reduced diversity (Fig. 5; Annex 2–3). Selective filtration by oysters, including rejection of particles as pseudofaeces (Hawkins *et al*., 1996), is important to sustain tropical marine ecosystems and mitigate harmful algal blooms (Shumway *et al*., 2003b; Galimany *et al*., 2021). The severe bloom in Kep in 2016–2017 caused widespread marine die-offs and underscores the urgency of protecting bivalve beds to safeguard sediment and meiofauna health. While the relationship between oxygen penetration and microbial activity is complex in involving both oxygen-consuming and anaerobic bacterial processes (Aller, 1982), these influence sediment redox dynamics and consequently meiofauna. Future studies should include direct measurements of oxygen and organic matter alongside other abiotic parameters to better quantify the role of sediment biogeochemistry in structuring meiofaunal assemblages.

In conclusion, this study reveals how habitat types shape benthic diversity. Natural bivalve beds stabilise sediments, cycle nutrients, and support diversity, whereas fisheries production structures increase habitat complexity and provide surfaces for sessile fauna. The patchy distribution of meiofauna reflects fine-scale variations in oxygen, organic matter and sediment characteristics. This underscores their utility as bioindicators of ecosystem health, while also highlighting their limitations and the need for improved spatial and temporal replication. Protecting natural bivalve beds and refining the design of fisheries production structures will be important for optimise restoration efforts. Future research should monitor meiofaunal taxa, sediment processes, and seasonal dynamics. Coupling structural interventions with regulatory protection under the Marine Fisheries Management Area may sustain biodiversity, fisheries, and resilience against stresses such as hypoxia and harmful algal blooms, supporting ecosystem recovery in Cambodian waters.

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Annex 1 Sampling stations in the Kep Archipelago

Bivalve beds (BB), fishery production structures (FPS) and impacted sites (IS) sampled for meiofauna in the Kep Archipelago. Asterisks indicate representative stations for meiofaunal diversity

Site ID	Coordinates	Average Depth (m)	Remarks (FPS deployment year)
BB_01*	10.44707 N, 104.33016 E	3.5	Mixed bivalve bed with light fishing activity observed
BB_02*	10.35621 N, 104.32305 E	3	Mix of seagrass and bivalve beds near Koh Ach Seh
BB_03	10.35665 N, 104.32232 E	2.2	Offshore of BB_02 (similar habitat)
BB_04	10.42693 N, 104.26429 E	6	Dense bivalve bed near Koh Pou
FPS_01	10.3576 N, 104.31579 E	5.3	Located west of Koh Ach Seh (2018)
FPS_02	10.35822 N, 104.31431 E	5.5	Located west Koh Ach Seh (2019)
FPS_03	10.35821 N, 104.32012 E	1.9	East of Koh Ach Seh (2017)
FPS_04	10.357772 N, 104.321137 E	1.9	Near coral reef east of Koh Ach Seh (2018)
FPS_05	10.357715 N, 104.321202 E	1.7	Prototype near coral reef east of Koh Ach Seh (2017)
IS_01*	10.36976 N, 104.2244 E	5.1	Active trawling grounds with remnant patches of seagrass
IS_02	10.35996 N, 104.29659 E	5.8	Known fishing grounds
IS_03	10.38805 N, 104.3099 E	7.3	Fishing grounds nearby
IS_04	10.46854 N, 104.24616 E	5.6	Fishing ground near Koh Kron and channel (~10-15 vessels within 2 km radius)
IS_05*	10.45751 N, 104.24229 E	10.9	10m deep channel, near Kampot

Annex 2 Environmental variables at sampling stations in the Kep Archipelago

Abiotic parameteres recorded in bivalve beds (BB), fishery production structures (FPS) and impacted sites (IS) in the Kep Archipelago, with representative stations * measured at 0 and 1 m depth

Station	Depth (m)	Visibility (m)	Temp (°C)	Salinity (PSU)	Light (mean lux)		Temp (°)		Dominant substrate
					Sediment Surface [SD]	1 m [SD]	Sediment Surface [SD]	1 m [SD]	
BB_01*	3.5	3.5	27	30	526.6 [889.12]	353.3 [527.47]	28 [0.38]	28 [0.39]	Silt
BB_02*	3	4.3	29	32	2166.3 [156.73]	6747.6 [11312.89]	28.9 [0.25]	29.1 [0.43]	No survey
BB_03	2.2	2.5	30		-	-	-	-	Sand/shell
BB_04	6	6	30		-	-	-	-	Sand/Shell/Silt/ Pebble
FPS_01	5.3	1.5	31	32	545. 4 [896.35]	1911.4 [2969.69]	28 [0.42]	28 [0.43]	Silt
FPS_02	5.5	2	29		-	-	-	-	ST
FPS_03	1.9	2.5	30		-	-	-	-	Sand/shell
FPS_04	1.9	3	30		-	-	-	-	Sand/shell
FPS_05	1.7	2.5	29		-	-	-	-	Sand/shell
IS_01*	5.1	4	32	32	2483.7 [4088.90]	1854.9 [3265.21]	27.8 [0.28]	27.81 [0.28]	
IS_02	5.8		33		-	-	-	-	Sand/Silt/Pebble
IS_03	7.3	2.6	31		-	-	-	-	Sand/Silt/Pebble
IS_04	5.6	4	31		-	-	-	-	Sand/silt
IS_05*	10.9	2	29	34	12.6 [27.28]	44.4 [77.14]	28.9 [0.11]	28.9 [0.13]	No survey
Control					43262.5 [64221.92]		29.5 [4.76]		

Annex 3 Sediment characteristics at sampling stations in Kep Archipelago

Values are given as mean [standard deviation] for bivalve beds (BB), fisheries production structures (FPS) and impacted sites (IS). The mean oxic layer depth excludes the adjacent sample collected at FPS_01

Sampling Station	Average oxic layer depth (cm) [SD]	Number of cores	Median grain size (DX90 µm) [SD]	Wentworth (1922) grain size classification
BB_01	3.11 [0.50]	7	136.22 [45.02]	Fine to medium sand
BB_02	3.71 [0.95]	7	619.67 [60.26]	Coarse sand
BB	3.41 [0.79]	14	377.94 [257.52]	Medium sand
FPS_in	1.78 [1.32]	4	644.33 [243.82]	Coarse sand
FPS_up	1.33 [1.04]	3	-	-
FPS_down	1.30 [1.17]	4	-	-
FPS_adjacent	3 [na]	1	347.30 [8.14]	Medium sand
FPS_01	1.51 [1.13]	12	495.83 [224.20]	Medium sand
IS_01	0 [na]	7	1035.67 [280.54]	Very coarse sand

Annex 3 cont'd

Sampling Station	Average oxic layer depth (cm) [SD]	Number of cores	Median grain size (DX90 μm) [SD]	Wentworth (1922) grain size classification
IS_05	0 [na]	5	143.67 [42.19]	Fine sand
IS	0	12	589.67 [503.57]	Coarse sand

Ex-situ management of Cambodia’s birds: an assessment of priorities

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មូលន័យសង្ខេប

វង្វាយតម្លៃអាទិភាពជំហានដំបូងនៃប្រភេទសត្វស្លាបក្នុងប្រទេសកម្ពុជាបានកំណត់សត្វស្លាបចំនួន៥ប្រភេទ ដែលមានអាទិភាពខ្ពស់ក្នុងការគ្រប់គ្រងក្រៅជម្រកធម្មជាតិ (ex-situ) ជាផ្នែកមួយដ៏សំខាន់នៃផែនការការពារប្រភេទសត្វទាំងនោះពីការផុតពូជជាសាកល។ ការគ្រប់គ្រងក្រៅជម្រកធម្មជាតិនៃសត្វស្លាបចំនួនបីប្រភេទក្នុងចំណោមសត្វស្លាបដែលមានអាទិភាពខ្ពស់ទាំងនេះ (សត្វខ្សឹប *Houbaropsis bengalensis* សត្វត្រយ៉ងយក្ស *Thaumatibis gigantea* និងសត្វត្រយ៉ងចំកំកស *Pseudibis davisoni*) បានធ្វើនៅមជ្ឈមណ្ឌលអង្គរសម្រាប់អភិរក្សជីវៈចម្រុះ (ACCB)។ សកម្មភាពគ្រប់គ្រងក្រៅជម្រកធម្មជាតិនៅមិនទាន់ចាប់ផ្តើមនៅឡើយទេចំពោះប្រភេទអាទិភាពខ្ពស់២ផ្សេងទៀត (សត្វទាព្រៃស្លាបស *Asarcornis scutulata* និងសត្វពពូលទឹក *Heliopais personatus*)។ បើសិនជាសកម្មភាពទាំងនេះមិនត្រូវបានអនុវត្តក្នុងពេលវេលាសមស្របណាមួយទេ នោះវាមានលទ្ធភាពខ្ពស់ដែលប្រភេទទាំងនេះនឹងរងការផុតពូជ។ សត្វស្លាបចំនួន៥ប្រភេទទៀត (សត្វទទាទ្រូងលឿង *Arborophila davidi* សត្វចាំត្រពាំង *Carpococcyx renauldi* សត្វត្រដក់ធំ *Leptoptilos dubius* សត្វនាលស *Mycteria cinerea* និងសត្វស្ទាំងតូចចុងខ្នងស *Neohierax insignis*) ត្រូវបានកំណត់ជាប្រភេទអាទិភាពមធ្យម ដែលក្នុងនោះសកម្មភាពគ្រប់គ្រងសត្វត្រដក់ធំបាននិងកំពុងដំណើរការនៅ ACCB។ ប្រភេទសត្វស្លាប អាទិភាពកម្រិតមធ្យមដ៏ទៃទៀតគួរតែត្រូវបានត្រួតពិនិត្យ និងវាយតម្លៃឡើងវិញជាប្រចាំ ទើបធ្វើអោយការគ្រប់គ្រងក្រៅជម្រកធម្មជាតិអាចផ្តួចផ្តើមទៅបានបើសិនជាចាំបាច់។

Abstract

A rapid first-cut priority assessment of Cambodia’s bird species identified five high-priority species for which ex-situ management is a critical component of plans to prevent their global extinction. The ex-situ management of three of these high-priority species (Bengal florican *Houbaropsis bengalensis*, giant ibis *Thaumatibis gigantea* & white-shouldered ibis *Pseudibis davisoni*) has already begun at the Angkor Centre for Conservation of Biodiversity (ACCB). For the two remaining high-priority species (white-winged duck *Asarcornis scutulata* & masked finfoot *Heliopais personatus*), ex-situ management activities have yet to begin. If such activities are not pursued in a timely manner, there is a significantly higher chance that these species will go extinct. A further five species (orange-necked partridge *Arborophila davidi*, coral-billed ground-cuckoo *Carpococcyx renauldi*, greater adjutant *Leptoptilos dubius*, milky stork *Mycteria cinerea* & white-rumped pygmy-falcon *Neohierax insignis*) were identified as medium-priority, with ex-situ management activities for

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greater adjutant having already begun at the ACCB. The other medium-priority species should be monitored and reassessed on a regular basis so that ex-situ management can be initiated if deemed necessary.

Keywords birds, breeding, Cambodia, conservation prioritisation, ex-situ, management, reintroduction, threatened

Introduction

Ex-situ management is increasingly used as a tool to prevent extinctions of species. It has also facilitated reintroduction and reinforcement efforts of populations to wild or semi-wild states. Ex-situ management has historically focused on large, charismatic species in developed countries, and smaller species that are restricted to islands where invasive species are an important threat. However, ex-situ management is increasingly seen as an important component of conservation of a broad range of continental species that are primarily threatened by habitat loss and fragmentation, compounded by unsustainable levels of exploitation. At the same time as the threat status of an increasing number of the world's species worsens, improvements in animal husbandry make it possible to keep and breed a greater variety of species under human care than ever before. If the end goal of ex-situ management is prevention of extinction and re-establishment of wild populations, it is of critical importance that it be coupled with a parallel process of protection of habitats, and ideally, remnant wild populations. Reintroductions and population reinforcement efforts usually fail when the processes that caused declines and/or extinction of wild populations are not removed prior to reintroduction or population reinforcement. In addition, the detailed practicalities of ex-situ management, particularly when a species is little known, are often challenging, as documented for example by Collar (2020).

Ex-situ management of species is typically more financially costly than in-situ conservation, and in some cases, it can increase the extinction risk of wild populations through removal of individuals. It is sometimes unsuccessful, particularly if the number of founders is low. Some of these costs and risks can be reduced or mitigated by establishing ex-situ populations before a species reaches a point where wild populations are extremely small and imperilled. Achieving this requires decisions about whether to initiate ex-situ management before wild populations reach extremely low levels. Not deciding whether to proceed with ex-situ management is the same as deciding not to proceed with ex-situ management; slow or absent decision making on ex-situ management has been cited as a causal factor in the extinction of several taxa. In that context, the IUCN have developed a five-step process for evaluating whether to embark on ex-situ management for a given species (IUCN/SSC, 2014). However, the process itself is time-consuming and there are a vast number of species that could at least be considered as candidates for ex-situ management. In this analysis of Cambodia's birds, we aim for a complementary, simpler and more time efficient process, which can eliminate from consideration species that are not priorities for ex-situ management and produce a list of species that might be. To this end, we document the results of a rapid first-cut priority assessment of the need for ex-situ management for bird species in Cambodia. We also aim to identify species for which Cambodia could make a significant contribution to their global conservation through ex-situ management.

Methods

Rather than evaluate all of the c. 640 bird species documented in Cambodia (Tan *et al.* 2023), we aimed to rapidly rank species as either high, medium, or low priority for ex-situ management in Cambodia. We restricted our analysis to globally threatened (Critically Endangered [CR], Endangered [EN], Vulnerable [VU]) or Near Threatened (NT) bird species that breed in Cambodia (IUCN, 2025). Non-threatened (IUCN Least Concern) bird species were assumed to have healthy global wild populations and therefore not require ex-situ management, even if (in some cases) the populations of those species in Cambodia are very small and/or highly threatened. We adhered to this principle even if the subspecies occurring in Cambodia would likely be considered globally threatened if evaluated against IUCN Red List criteria. Globally threatened and near threatened species that only visit Cambodia as non-breeders were not considered potential priorities for ex-situ management in Cambodia and so are not evaluated here. Species that are considered extinct in Cambodia (namely Indian skimmer *Rynchops albicollis* and black-bellied tern *Sterna acuticauda*) were not assessed because owing to an absence of a wild population, it is now impossible for Cambodia to contribute to their conservation through ex-situ management.

Our assessment aimed to divide species into the following three categories which corresponded with their priority for ex-situ management in Cambodia:

- High Priority: Immediately begin or continue ex-situ management
- Medium Priority: Monitor wild populations and regularly re-assess whether to begin or continue ex-situ management
- Low Priority: Do not begin or consider discontinuing ex-situ management

To allocate species to one of the three categories, we considered the following criteria for each species (in descending order of importance):

i. Global IUCN threat status: species with a higher global threat status (CR or EN) were considered higher priorities, and those with a lower global threat status (NT) a lower priority.

ii. Relative importance of the Cambodian population in the context of the global status of the species: species for which Cambodia has a higher relative percentage of the global population were considered higher priorities.

iii. Risk of loss of the Cambodian population if ex-situ management was not initiated/continued: species for which the Cambodian population is likely to be lost in the short or medium term were considered higher priorities because if the opportunity to begin ex-situ management is not taken in the short term then the opportunity may otherwise be lost forever.

iv. Number of individuals in ex-situ facilities worldwide: species for which there are significant ex-situ populations in other countries were considered a lower priority because there is no need to duplicate such holdings in Cambodia.

Global IUCN threat and status data were obtained from BirdLife International (2025), supplemented by Billerman *et al*. (2025). Cambodian status was based on Goes (2013), supplemented by data from eBird (2025) and personal knowledge. Numbers in ex-situ holdings worldwide by Species360 members were obtained from the Species360 Zoological Information Management System (Species360, 2025). The initial assessment was conducted qualitatively by three people: S.M., M.M. and C.P., and then supplemented by further consultation with C.G. and R.T.

In general, a species was considered an ex-situ management priority in Cambodia if it was judged to be at a high risk of global extinction with a significant proportion of the wild global population found in Cambodia, and no global ex-situ population. It was then believed that ex-situ management in Cambodia could make a significant contribution to preventing the global extinction of the species, particularly for species where the wild Cambodian population may no longer be viable. Species at a high risk of global extinction with a small proportion of their global population in Cambodia were assessed as being of a lower priority for ex-situ conservation in Cambodia because ex-situ conservation might better be initiated elsewhere, and species at a high risk of global extinction with a significant proportion of the global wild population found in Cambodia but already a large ex-situ population outside Cambodia were considered lower priorities than those with no such ex-situ population globally.

Results

A total of 48 bird species were assessed (Table 1). Of these, five were considered high priorities for ex-situ management in Cambodia, five were considered medium priority, and the remaining 38 were considered low priority. Table 1 details the species assessed and summarizes the outcomes of the meeting, given the information available to participants. This section is followed by detailed discussion for each species (or group of similar species) that justify the decisions taken, identify information gaps, and list the priorities for action. Species names and systematic order follow BirdLife International (2025).

Species accounts

Orange-necked partridge *Arborophila davidi* NT — Medium Priority

Orange-necked partridge has a very small global range in southern Vietnam and eastern Cambodia, within which it is restricted to broadleaf evergreen and semi-evergreen forest dominated by large-stem bamboo on slopes at elevations between 130 m and 250 m asl (McGowan *et al*., 2020). It is likely to be elevated to a higher threat category owing to ongoing declines caused by habitat loss and hunting. Declines have been particularly severe in Cambodia, but where present it might be locally common because partridges have high reproductive rates that buffer populations from high trapping pressure (Brickle *et al*., 2008). It is not held ex-situ in Species360 member facilities, and while there is considerable experience globally in the ex-situ management of *Arborophila* partridges, the specific husbandry issues around orange-necked partridge are unknown. The priority actions are locating a wild population from which to source founders and investigating husbandry requirements for similar species so that thorough plans can be made to establish an insurance population. A survey should be conducted of suitable habitat in Keo

Table 1 Summary of the 48 bird species assessed and their ex-situ management priority in Cambodia. Number of individuals held at the Angkor Centre for Conservation of Biodiversity (ACCB), presented as male.female.unknown

English & Scientific name	IUCN threat status	Global status	Cambodia status	Importance of Cambodian population	Risk of loss of Cambodian population	No. at ACCB	Holdings by Species360 members	Ex-situ management priority in Cambodia
Orange-necked partridge *Arborophila davidi*	NT	Tiny range, specialized habitat	Population & distribution greatly reduced	Low/Medium	High	0	0	Medium
Green peafowl *Pavo muticus*	EN	Locally common on Java & mainland SE Asia	Widespread & locally common	Medium	Low	3.0.7	142	Low
Germain's peacock-pheasant *Polyplectron germaini*	VU	Locally common in eastern Cambodia & southern Vietnam	Localized but fairly common	Medium	Low	0	13	Low
White-winged duck *Asarcornis scutulata*	CR	Rare and localized in India, Myanmar & Sumatra (Indonesia)	<50 mature individuals	Medium	High	0	171	High
Pale-capped pigeon *Columba punicea*	VU	Scarce but widespread in SE Asia & India	Rare & localised	Low	Low	0	2	Probably Low
Nicobar pigeon *Caloenas nicobarica*	NT	Scarce but widespread on islands from Indian Ocean to the Pacific	Rare & localised on remote offshore islands	Low	Medium	0	2187	Low
Ashy-headed green pigeon *Treron phayrei*	NT	Widespread in SE Asia	Fairly common in suitable habitat	Medium	Low	0	0	Low
Green imperial-pigeon *Ducula aenea*	NT	Widespread in tropical Asia	Fairly common in suitable habitat	Low	Low	0	145	Low
Coral-billed ground-cuckoo *Carpococcyx renauldi*	EN	Local & scarce in Thailand & Indochina	Uncommon	Medium	Medium	0	0	Medium
Masked finfoot *Heliopais personatus*	CR	Rare & localised	Few in Northern Plains, probably a few in Tonle Sap & Cardamoms	High	High	0	0	High
Sarus crane *Grus antigone*	VU	Widespread in South Asia	Most birds breed in northern plains, smaller numbers in east	Low	High	0.1.1	214	Low
Bengal florican *Houbaropsis bengalensis*	CR	Locally uncommon in South Asia & Cambodia	Rare, localized & in rapid decline	High	High	7.8.3	18	High

Table 1 Cont'd

English & Scientific name	**IUCN threat status**	**Global status**	**Cambodia status**	**Importance of Cambodian population**	**Risk of loss of Cambodian population**	**No. at ACCB**	**Holdings by Species360 members**	**Ex-situ management priority in Cambodia**
Greater adjutant *Leptoptilos dubius*	NT	Extremely localized in South Asia & Cambodia	Only breeds at Prek Toal in the Tonle Sap Lake	High	Medium	4.3	14	Medium
Lesser adjutant *Leptoptilos javanicus*	NT	Widespread but rare & little sign of breeding in many places	Widespread & locally common	High	Medium	5.1	111	Low
Milky stork *Mycteria cinerea*	EN	Rare, local, & declining in Java, Cambodia & Sumatra	Rare and local breeder in Prek Toal & coastal area	Low	Medium	0	133	Medium
Asian woolyneck *Ciconia episcopus*	NT	Widespread & fairly common in South Asia, uncommon & declining in SE Asia	Uncommon or fairly common breeder in forested areas	Low	Medium	2.0	68	Low
Black-necked stork *Ephippiorhynchus asiaticus*	NT	Fairly common in northern Australia; Asian population <1,000 birds, mostly in India	Very rare, possibly fewer than 10 pairs	Low	High	0	38	Low
White-shouldered ibis *Pseudibis davisoni*	CR	Almost entire global population is in Cambodia; very few in Kalimantan	c.1,000–1,500 mature individuals in decid-uous & riverine forest	High	High	6.11.4	21	High
Giant ibis *Thaumatibis gigantea*	CR	Now only or almost only in Cambodia	c.200 mature individuals	High	High	3.1	4	High
Spot-billed pelican *Pelecanus philippensis*	NT	Widespread & fairly common in South Asia, uncommon in SE Asia	Breeds only around the Tonle Sap Lake	Low	Low	0	174	Low
Great thick-knee *Esacus recurvirostris*	NT	Widespread & fairly common in South Asia, rare & local in SE Asia	Tiny population breeds on the islands in the upper Mekong and major tributaries	Low	High	0	0	Low
Malay plover *Charadrius peronii*	NT	Widespread & uncommon in SE Asia	Rare coastal breeder	Low	High	0	0	Low

Table 1 Cont'd

English & Scientific name	IUCN threat status	Global status	Cambodia status	Importance of Cambodian population	Risk of loss of Cambodian population	No. at ACCB	Holdings by Species360 members	Ex-situ management priority in Cambodia
River lapwing *Vanellus duvaucelii*	NT	Widespread & fairly common in South Asia, rare & local & SE Asia	Small population breeds on the islands in the upper Mekong & major tributaries	Low	High	0	0	Low
River tern *Sterna aurantia*	VU	Widespread & fairly common in South Asia, rare & local in Southeast Asia	Small population breeds on the islands in the upper Mekong & major tributaries	Low	High	0	0	Low
Red-headed vulture *Sarcogyps calvus*	CR	Widespread & uncommon in South Asia, rare & local in SE Asia	5–20 pairs in northern & eastern plains	Low	High	0	17	Low
White-rumped vulture *Gyps bengalensis*	CR	Locally common in South Asia, rare & local in SE Asia	No known nest sites in Cambodia, probably fewer than 30 pairs	Low	High	0	4	Low
Slender-billed vulture *Gyps tenuirostris*	CR	Local & uncommon in South Asia, rare & local in SE Asia	10–20 pairs in Siem Pang	Low	High	0	0	Low
Mountain hawk-eagle *Nisaetus nipalensis*	NT	Widespread & uncommon in mainland Asia	Uncommon & restricted to montane areas	Low	Low	0	9	Low
Rufous-bellied eagle *Lophotriorchis kienerii*	NT	Widespread & uncommon in mainland Asia	Uncommon	Low	Low	0	0	Low
Indian spotted eagle *Clanga hastata*	VU	Widespread & uncommon in India, rare & local in SE Asia	Very rare & seemingly in decline	Low	High	0	0	Low
Lesser fish-eagle *Icthyophaga humilis*	NT	Widespread & uncommon in SE Asia	Rare & localized	Low	High	0	0	Low
Grey-headed fish-eagle *Icthyophaga ichthyaetus*	NT	Widespread & uncommon in South & SE Asia	Very locally common in Prek Toal (Tonle Sap) & parts of the northern plains	Low	Medium	1	1	Low

Table 1 Cont'd

English & Scientific name	IUCN threat status	Global status	Cambodia status	Importance of Cambodian population	Risk of loss of Cambodian population	No. at ACCB	Holdings by Species360 members	Ex-situ management priority in Cambodia
Great hornbill *Buceros bicornis*	VU	Fairly common & widespread in South & SE Asia	Moderately common in evergreen forest	Low	Low	0	166	Low
Austen's brown hornbill *Anorrhinus austeni*	NT	Uncommon & localized in hill forest	Rare and very localized in hill forest	Low	Medium	0	0	Low
Wreathed hornbill *Rhyticeros undulatus*	VU	Fairly common & widespread in SE Asia	Moderately common in evergreen forest	Low	Low	0	138	Low
Red-collared woodpecker *Picus rabieri*	NT	Locally common in Indochina & China	Uncommon in extreme north-east	Low	Low	0	0	Low
Great slaty-woodpecker *Mulleripicus pulverulentus*	VU	Uncommon to fairly common in SE Asia	Uncommon to fairly common in forest areas	Low/Medium	Low	0	1	Low
White-rumped pygmy-falcon *Neohierax insignis*	NT	Uncommon & local in SE Asia	Uncommon in deciduous forest	Medium	Medium	0	0	Medium
Grey-headed parakeet *Himalayapsitta finschii*	NT	Uncommon & local in SE Asia	Rare to locally fairly common in mixed deciduous forest	Low	Low	0	0	Low
Blossom-headed parakeet *Himalayapsitta roseata*	NT	Uncommon in SE Asia	Fairly common in deciduous forest	Medium	Low	0	0	Low
Red-breasted parakeet *Psittacula alexandri*	NT	Common in South & SE Asia	Common in forest	Low	Low	0	59	Low
Alexandrine parakeet *Palaeornis eupatria*	NT	Fairly common in South Asia, uncommon in SE Asia	Uncommon in deciduous forest	Low	Low	4.1	367	Low
Cambodian tailorbird *Orthotomus chaktomuk*	NT	Common in suitable habitat in restricted range in Cambodia	Endemic; localized, but common to abundant where it occurs	High	Low	0	0	Low
Black-headed parrotbill *Paradoxornis margaritae*	VU	Uncommon in submontane forest in Da Lat Plateau	Marginal occurrence in the north-east	Low	Medium	0	0	Low
Chinese grass-babbler *Graminicola striatus*	NT	Widespread & locally common in southern China, highly localized in SE Asia	Known from one site in the Tonle Sap floodplain, where fairly common	Low	High	0	0	Low

Table 1 Cont'd

English & Scientific name	IUCN threat status	Global status	Cambodia status	Importance of Cambodian population	Risk of loss of Cambodian population	No. at ACCB	Holdings by Species360 members	Ex-situ management priority in Cambodia
Cambodian laughingthrush *Garrulax ferrarius*	NT	Restricted to montane forest in the Cardamom Mountains	Endemic; localized but fairly common in suitable habitat	High	Low	0	0	Low
Asian golden weaver *Ploceus hypoxanthus*	NT	Widespread & fairly common in SE Asia	Widespread & fairly common	Medium	Low	0	4	Low
Mekong wagtail *Motacilla samveasnae*	NT	Restricted range on the Mekong River & major tributaries; locally common where it occurs	Locally common within small range & narrow habitat requirements	High	Medium	0	0	Low

Seima Wildlife Sanctuary (the only known location that still supports the species in Cambodia) to verify the persistence of a population from which founders could be sourced. Locally used methods of partridge capture could be modified to enable birds to be caught alive and undamaged to establish an ex-situ population at the Angkor Centre for Conservation of Biodiversity (ACCB).

Green peafowl *Pavo muticus* EN — Low Priority

Green peafowl is thought to be undergoing a moderately rapid decline in Cambodia, which supports most of the global population (Goes, 2013). However, it is a fast breeder and persists in heavily degraded habitat, so it is unlikely to go extinct in the country, although important populations should be monitored. *Pavo muticus imperator*, the subspecies endemic to Indochina and Thailand, is thought to be poorly represented in ex-situ facilities outside of its native range. The genetic structure of wild populations is poorly understood, although a recent study including birds from Cambodia, Thailand and China suggests that these populations have a low level of genomic diversity and a high level of inbreeding (Feng *et al.*, 2021). Moreover, the origin of many ex-situ populations is unclear, and the purity of subspecies has likely not been maintained in many. Two subspecies of green peafowl are present in the European Association of Zoos and Aquaria (Dams *et al.*, 2023) population, along with confirmed presence of hybrids between *P. m. muticus* and *P. m. imperator*, as well as crossbreeds with Indian peafowl *P. cristatus*. The ACCB occasionally receives confiscated green peafowl, these are usually male and are typically too tame for release to the wild. The mortality rate of rescued peafowl is high due to the species being extremely prone to capture myopathy. The ACCB has successfully undertaken hard release of captive-bred green peafowl at Siem Pang Wildlife Sanctuary and Phnom Tnout Wildlife Sanctuary. Other areas such as Changkran Roy in Siem Reap or Prey Veng in Kulen Promtep Wildlife Sanctuary could also be considered, where they would be safe from hunting even if relatively tame and would increase the appeal of the sites to visiting nature-lovers and photographers.

Germain's peacock-pheasant *Polyplectron germaini* VU — Low Priority

The species is still fairly common within its restricted range and therefore a low priority for ex-situ management.

White-winged duck *Asarcornis scutulata* CR — High Priority

Cambodia supports a small population of white-winged ducks, probably totalling fewer than 50 individuals. However, this population is of high importance in a regional context. The species is probably extinct or almost so in Laos and Vietnam and is known from just two sites in Thailand, one of which comprises only released birds (BirdLife International, 2024a). Its global stronghold is north-west Myanmar and north-east India, where a few hundred individuals are estimated to remain. Small numbers persist in southern Sumatra (Indonesia) and its status elsewhere on the island is unclear (Carboneras & Kirwan, 2020; BirdLife International, 2024a). The only Cambodian records in the past ten years are from Chhaeb-Preah Roka Wildlife Sanctuary and Kulen Promtep Wildlife Sanctuary in the northern plains of Preah Vihear Province, where fewer than 20 birds are thought to be present (Mao K., in litt. January 2020), and one sighting of a bird photographed in the Mekong Ramsar site in Stung Treng Province in March 2013. It is now absent from protected areas in Stung Treng Province and has not been recorded in Mondulkiri Province for over 15 years. The species was reported from remote parts of Cardamom Mountains in the early 2000s but has not been searched for since (Goes, 2013).

There is an ex-situ population of white-winged ducks, notably in Europe, where they have been bred at a number of facilities (Petry & Davoigneau, 2025). However, all these birds are believed to be derived from very few founders from Assam (north-east India) in the late 1960s and 1970s (Mackenzie & Kear, 1976; Green, 1993). Captive birds (from northeast India) are highly differentiated genetically from wild birds sampled in Sumatra, Indonesia (Bolton *et al*., 2025), but the genetic structure of wild white-winged ducks across the rest of their range is unknown, as is the origin and genetic structure of the released population in Thailand. The success of ex-situ breeding programmes in both Europe and the US has declined significantly due to the species' high susceptibility to *Mycobacterium avium*, avian tuberculosis (Petry & Davoigneau, 2025). This infection results in the premature mortality of over 80% of birds, with birds with higher levels of inbreeding succumbing earlier to infections, suggesting inbreeding depression (Bolton *et al*., 2025). There is a critical need to determine the genetic structure of wild white-winged ducks across their distribution and determine in this context if the Cambodian birds constitute the last vestige of an evolutionary significant unit.

If this were the case it would significantly increase the importance of the Cambodian population and it would then be imperative to establish an ex-situ insurance population. Even if there were no unique genetic contribution, establishing a new ex-situ population separate from the ailing global one, in its own range, climate and habitat (all rather different from Assam) is sufficient justification. Given the rapid decline in sightings in the only two areas of the northern plains that still support populations of white-winged ducks and the destruction of the only known nesting tree in 2021, it might be prudent to try and capture all remaining birds regardless, before the species becomes extinct in the wild in Cambodia. Alternatively, based on an assumption that white-winged duck is limited by availability of nest sites, nest boxes could be installed at suitable sites in the northern plains. If the ducks begin to nest in these boxes, this would also facilitate easy access to eggs for use in an ex-situ breeding programme. The population of white-winged ducks in the northern plains should also be quantified through evaluation of images (the pattern of black and white feathering on the head of a white-winged duck being individually unique).

Pale-capped pigeon *Columba punicea* VU, Nicobar pigeon *Caloenas nicobarica* NT, ashy-headed green pigeon *Treron phayrei* NT & green imperial-pigeon *Ducula aenea* NT — Low Priority

These four pigeon species are in little danger of global extinction and are therefore of low priority for ex-situ management.

Coral-billed ground-cuckoo *Carpococcyx renauldi* EN — Medium Priority

Cambodia is likely to support a significant proportion of the global population of coral-billed ground-cuckoo, which was up-listed to Endangered in 2024 due to ongoing declines across its limited range in Cambodia, Laos, Thailand, and Viet Nam (BirdLife International, 2024b). The species is nowhere secure, and widespread snaring might threaten its existence in Cambodia. Wild populations should be monitored using existing and targeted camera-trap and passive acoustic monitoring programs. The species has been successfully bred ex-situ in Europe and North America (Atkinson, 1982; Poprasert & Pierce, 2010; Payne & de Juana, 2020), but is apparently no longer held in any Species360 member collections (Species360, 2025). Early ex-situ efforts indicate that individuals can adapt well when appropriately managed, but that historical challenges, particularly diet-related kidney and gout-like issues, likely contributed to limited long-term success. Improved husbandry knowledge, including the need for an insect-based diet, careful pair management, and provision of robust, sheltered nest baskets, suggests that the feasibility of renewed ex-situ management should be reassessed considering modern best practices (S. Bruslund, in litt. November 2025). These lessons learned should be evaluated to determine their applicability to a potential conservation breeding programme at the ACCB.

Masked finfoot *Heliopais personatus* CR — High Priority

Masked finfoots have disappeared from almost their entire former range in Southeast Asia. They are in danger of global extinction in part through the potential impacts of sea-level rise which are predicted to imperil the population that remains in the Bangladeshi Sundarbans. Cambodia might support the second largest population worldwide, but it is now extremely localized and only regularly recorded from the Memey River and its tributaries in Kulen Promtep Wildlife Sanctuary, where optimistically a few tens of birds might remain (Chowdhury *et al*., 2020). The entire Memey river system is subject to intensive small-scale fishing using traps, baited hooks, and gill-nets, and unless this can be successfully addressed (it would be extremely challenging), extinction in the wild in Cambodia appears likely.

There is an urgent need to pursue options for developing an ex-situ management programme for masked finfoots. This would be an immense challenge given there is no experience globally of ex-situ management of masked finfoot or of either of its closest relatives African finfoot *Podica senegalensis* or Sungrebe *Heliornis fulica*. However, the only published account documenting African finfoot husbandry (Tanner, 1948) concludes "perhaps Finfoots are outside the scope of aviculturists, but one never knows, one or two may arrive. I feel sure from my experience that they will thrive, given the same treatment as small Waders, especially in a marshy aviary in the summer". Were this endeavour to be undertaken, it would need to be of a similar scale to that launched for spoon-billed sandpiper *Calidris pygmaea* (Lee *et al*., 2015). While the establishment of an ex-situ population of masked finfoot would be prudent, removing birds from the wild is likely to contribute to the further decline of the remaining in-situ population. However, if the significant challenges (above) could be overcome, the threat of global extinction is such that it would be potentially a lower risk to accept the contribution to the inevitable decline of the wild population that securing founders would involve.

To inform these decisions, consultations should be undertaken including conservationists from range countries and ex-situ facilities including the ACCB and their associated zoos, Bronx Zoo, WWT Slimbridge, UK and Mandai Nature, Singapore. At the same time, it would be prudent to conduct surveys of suitable habitat in the Cardamom Mountains, where the species was last recorded in 2014, and also of the Sre Ambel River, Koh Kong Province, where habitat is suitable although the species has never been recorded. This should include using both camera-traps and passive acoustic monitoring, the latter having recently been piloted successfully in the northern plains of Cambodia (Auda, 2025). Finally, any birds accidentally taken in fishing gear should be taken to the ACCB.

Sarus crane *Grus antigone* VU — Low Priority

Sarus cranes are in little danger of global extinction, but the subspecies that occurs in Southeast Asia—*Grus antigone sharpii* "eastern sarus crane"– has experienced a rapid decline in range and population. This is now restricted to Myanmar, where there are a few hundred pairs, Cambodia, where there are probably fewer than one hundred pairs, and Thailand, where it went extinct but has since been reintroduced in Buriram Province (Archibald *et al*., 2020). In Cambodia, sarus cranes only breed in grasslands (veals) in deciduous forest, in contrast to the rest of their distribution where they breed in rice paddies. This is evidently a result of human exploitation of waterbirds and their nests in rice paddies and any other easily accessible habitat. Cambodia's sarus crane population has undergone a rapid decline that is correlated with the opening of remote areas of lowland Cambodia for logging during the past decade and the incursion of people who have since settled in those areas, usually in areas that are more suitable for agriculture (such as grasslands). The 2024 Cambodia census recorded a peak count of 214 sarus cranes, reflecting a 37% increase from the 2022 total of 156 individuals (Ny *et al*., 2025). While this may suggest that the sharp decline observed in the Cambodia-Vietnam sarus crane population since 2014 is slowing or stabilizing, projections still indicate that the species is at risk of becoming extinct as a breeding species in Cambodia within the next two decades.

Ex-situ husbandry of sarus cranes is well understood and technically relatively straightforward. Taking eggs from the wild should begin as soon as possible if ex-situ management is desired. It would likely accelerate the decline in the wild population, although this may be of little consequence if the population is already doomed. However, there is uncertainty regarding the need for ex-situ management of sarus cranes in Cambodia. At the species level, sarus cranes are secure in India. Eastern sarus crane is well-represented in ex-situ facilities in Thailand and in 1997, the Nakhon Ratchasima Zoo in Thailand initiated an ex-situ breeding and rewilding programme. As of 2024, 174 cranes have been released into the wild, with over 100 surviving and over 50 chicks born in natural habitats (MBF, 2025). In addition, in April 2025, six juvenile sarus cranes from this ex-situ breeding programme were transferred to Saigon Zoo in Vietnam, with plans for their release into Tram Chim National Park in the Mekong Delta near the Cambodia-Vietnam border (ICF, 2025). There is a need to better understand current ex-situ breeding and reintroduction programs and use this information to evaluate the efficacy and potential of developing a similar programme in Cambodia in future.

Bengal florican *Houbaropsis bengalensis* CR — High Priority

The Southeast Asian subspecies of Bengal florican—*Houbaropsis bengalensis blandini*— is now endemic to Cambodia, where the population is very small and in rapid decline (Mahood *et al*., 2020). Ex-situ management of Bengal floricans began in Cambodia in 2019 following an extensive evaluation of the pros and cons, which is detailed in Mahood *et al*. (2021).

Since its establishment, the ACCB ex-situ management programme has achieved several milestones. Founders, rescued individuals and sustainably collected eggs, from three Bengal Florican Conservation Areas at the northern Tonle Sap floodplain have adapted well to management under human care. The first breeding attempt occurred in 2023, although the egg embryo did not survive, followed by further courtship observations in subsequent years. The current ex-situ population at the ACCB is 18 individuals, comprising seven males, eight females and three juvenile unsexed birds.

A recent genetic study revealed low genetic diversity within the Cambodian population of floricans (Ball *et al*., 2025). Analysis of 22 individual samples identified only 629 single nucleotide polymorphisms (SNPs) and a single mitochondrial haplotype, though the ex-situ population appears representative of the wider in-situ population. Some individuals within the insurance population at the ACCB are closely related, highlighting the need for careful breeding management. The study also identified 68 SNP markers, which provide a foundation for developing assays to monitor wild populations using feathers or other non-invasive samples. These findings emphasize the urgent need to introduce additional founders to the breeding programme to increase genetic diversity and safeguard its long-term viability. Other recommendations from this study include conducting whole-genome sequencing to better assess inbreeding risk, and exploring the genetic relationship with *H. b. bengalensis* of India and Nepal as a potential avenue for genetic rescue.

In addition to genetic analyses, the ACCB has also generated the first haematological and biochemical reference values for the species under human care (Blümm Rexach *et al*., in prep.). This will provide an essential diagnostic baseline for veterinary monitoring and future health assessments.

Greater adjutant *Leptoptilos dubius* NT — Medium Priority

The persistence of greater adjutants in the wild is largely due to intensive community-based conservation. Following a massive contraction in its population and distribution, the species is probably now increasing throughout its range. Nesting colonies in Assam (India) are only found in a small number of villages, where the passion and drive of Purnima Devi Barman has persuaded local women to protect them (Barman *et al*., 2020). Following the loss of a colony in Kulen Promtep Wildlife Sanctuary in 2013, the only location in Southeast Asia where the species breeds is Prek Toal Ramsar Site in the Tonle Sap Lake. The number of pairs in Prek Toal increased from 56 in 2004 to 394 in 2022 (Sun *et al*., in prep.), but these are still dependent on protection from local community and Provincial Department of Environment rangers and are extremely vulnerable to events that could impact the entire colony, such as highly pathogenic avian influenza (BirdLife International, 2023a).

Greater adjutants have been successfully bred at Assam Zoo. As stork species often require parenting experience before becoming effective breeders, a patient, long-term approach is essential. It would be an insurmountable logistical challenge to take eggs or chicks from the nests in Prek Toal because they nest among many other waterbirds in a vast mixed colony. The current population at the ACCB was established from confiscated birds and the first two captive-bred, parent-reared greater adjutants hatched at ACCB during the 2024/2025 breeding season were successfully soft released in October 2025. This pilot release aims to assess the feasibility of augmentation translocation of the captive-bred individuals. Post-release monitoring of movement-patterns and survival will be critical in evaluating the success and future potential of this approach.

Lesser adjutant *Leptoptilos javanicus* NT — Low Priority

Although widespread, lesser adjutants are nonetheless nowhere common and probably suffer from low breeding success owing to hunting and taking of eggs and chicks throughout most of their global range. However, it is a low priority for ex-situ management in Cambodia because the wild population remains large and the species' large range buffers it against local declines.

The Bronx Zoo has long held a small population of lesser adjutants. Breeding this species at the Bronx Zoo would be beneficial to the global ex-situ population of the species, so we recommend that the possibility of sending confiscated Cambodian lesser adjutants or captive laid eggs to New York be investigated.

Milky stork *Mycteria cinerea* EN — Medium Priority

Outside Cambodia, milky stork currently breeds only in Sumatra and Java (Indonesia), where there are at most a few thousand pairs and the species is declining (Elliot *et al*., 2020a; BirdLife International, 2023b). The status of milky stork in Cambodia is poorly known. Fewer than ten pairs are recorded annually at Prek Toal, where mixed pairs with painted storks *Mycteria leucocephala* have also been regularly recorded. It is possible that a separate population also breeds in Cambodia's coastal mangroves.

A reintroduction programme begun in 1998 with captive-bred birds in Malaysia has met with limited success (Ahmad Ismail & Faid Rahman, 2016). In addition, two recent studies of regional ex-situ populations of the species have demonstrated extensive hybridization with painted storks (Baveja *et al*., 2019; Kaminsin *et al*., 2023). We recommend surveys of coastal nesting areas at the right time of year, using drones to locate nests. Based on the results of the surveys, it might be prudent to investigate taking eggs from such nests to begin an ex-situ management programme at the ACCB. As with greater adjutants, collection of eggs or chicks from nests in Prek Toal would pose an insurmountable logistical challenge.

Asian woolyneck *Ciconia episcopus* NT — Low Priority

This species is in little danger of global extinction due to a widespread, large population, primarily in India, and is therefore of low priority for ex-situ management.

Black-necked stork *Ephippiorhynchus asiaticus* NT — Low Priority

Black-necked storks remain abundant in northern Australia. However, the nominate subspecies in South Asia and Cambodia now numbers less than 1,000 birds (Elliot *et al*., 2020b). Black-necked storks occur throughout the deciduous forest of Cambodia, but it is the rarest of the large waterbirds, with a population that may be fewer than ten pairs. The populations in Australia and those remaining in South Asia make black-necked storks a low priority for ex-situ management in Cambodia. All five birds in human care in Cambodia are currently held at the Phnom Tamao Wildlife Rescue Centre, where the first recorded breeding success occurred in 2022.

Giant ibis *Thaumatibis gigantea* CR & white-shouldered ibis *Pseudibis davisoni* CR — High Priority

These two Critically Endangered ibis species are treated together owing to similarities in their distribution, status, threats, ex-situ situation and our recommended actions.

Giant ibises are effectively extinct outside Cambodia, where the population is approximately 200 mature individuals. The species is declining rapidly as a result of habitat loss and the logging of nest trees; extinction in the wild is highly likely (BirdLife International, 2018; Matheu *et al*., 2020). The species has an apparent preference for remote deciduous dipterocarp forest, where it occurs at extremely low density (less than one bird per 1,000 ha) and is typically solitary or encountered in pairs (Keo, 2008), although this may be an artifact of its extinction from more favourable habitats. For instance, almost 100 years ago, Jean Delacour reported flocks of giant ibis in Kampong Thom (Delacour, 1929), an area with semi-evergreen forest and extensive wetlands. Globally, only three individuals (two adults and one subadult, unsexed) are currently held in human care, all of which are at the ACCB. Since 2011, the ACCB has rescued 11 individuals. While healthy giant ibises adapt relatively well to captivity, their survival depends heavily on their condition at the time of rescue, as well as the quality of temporary housing, transport conditions, and the duration of transit.

Almost the entire global population of white-shouldered ibises occurs in Cambodia and a national census in 2023 led to a minimum population estimate of 752 individuals, based on the maximum recorded count (CIWG, 2024). The total population is unknown, but unlikely to exceed 1,000 mature individuals. However, white-shouldered ibises are possibly more at risk than giant ibises because they are frequently found in habitats used by people, including rice fields in forested areas and riparian forests along the Mekong River and its major tributaries. They are also absent from large areas of deciduous dipterocarp forest (e.g., Chhaeb-Preah Roka Wildlife Sanctuary), which are likely to be marginal habitat for the species. Very small numbers may persist in the Tonle Sap floodplain where it was formerly abundant. Sixteen individuals are kept at the ACCB, derived from rescued birds and breeding successfully under human care.

Despite considerable efforts, both species continue to decline outside protected areas. Successful in-situ conservation in Cambodia is critical to the persistence of giant and white-shouldered ibises in the wild. No significant wild or ex-situ populations exist outside Cambodia, so the hopes for establishing ex-situ populations of either species rest primarily with Cambodia. There are many examples of successful ex-situ breeding (and reintroduction) of ibis species from across the world, for example northern bald ibis *Geronticus eremita* (Böhm *et al*., 2021) and Asian crested ibis *Nipponia nippon* in China (Yu *et al*., 2009; Wang *et al*., 2017) and Japan (Okahisa & Nagata, 2022). There is, therefore, considerable global ex-situ husbandry experience relevant to conservation breeding of ibises, although perhaps not specifically for a more solitary species such as giant ibises.

We recommend establishing an ex-situ breeding programme for giant ibis and continuing the white-shouldered ibis programme at the ACCB. Additional dedicated facilities will need to be built and all rescued birds should be kept and integrated into the breeding programme. To support the management of breeding pairs, in-country DNA sexing capacity has already been established in collaboration with Institut Pasteur du Cambodge, using their mobile field-deployable molecular laboratory (Fomsgaard *et al*., in prep.). Successful breeding of white-shouldered ibises began during the 2022/2023 breeding season. Breeding and parent-rearing have successfully continued since then, with a total of eight chicks raised to date between two pairs (Groot *et al*., 2024). Plans are underway to conduct a pilot soft-release study of captive-bred white-shouldered ibises, ensuring post-release monitoring to evaluate the viability of the ex-situ programme in supporting population recovery. For giant ibises, plans should be considered to harvest eggs from wild nests at a rate that is unlikely to jeopardize the persistence of well-protected populations, at a time when such populations persist at a size that can sustain the offtake. This will be challenging given its preference for locating nests at the end of high branches. Considering the considerable in-region expertise in ex-situ breeding and reintroduction of Asian crested ibis, the potential for collaborating with relevant institutions in China or Japan should be considered.

Spot-billed pelican *Pelecanus philippensis* NT & great thick-knee *Esacus recurvirostris* NT — Low Priority

Although these species face a considerable danger of extinction in Cambodia, they are in little danger of global extinction due to large populations in India. They are therefore of low priority for ex-situ management.

Malay plover *Charadrius peronii* NT — Low Priority

This species is in little danger of global extinction as a large population exists across Southeast Asia. It is therefore of low priority for ex-situ management.

River lapwing *Vanellus duvaucelii* NT & river tern *Sterna aurantia* VU — Low Priority

Although at considerable danger of extinction in Cambodia (Claassen, 2018), these species are in little danger of global extinction due to large populations in India. They are therefore of low priority for ex-situ management.

Red-headed vulture *Sarcogyps calvus* CR, white-rumped vulture *Gyps bengalensis* CR & slender-billed vulture *Gyps tenuirostris* CR — Low Priority

Cambodia supports relict populations of Asia's three Critically Endangered vulture species. Once abundant across South and Southeast Asia, vultures have declined precipitously in recent decades. In Southeast Asia, a lack of food and wildlife hunting caused the decline, and a few hundred birds now remain in each of Cambodia and Myanmar (Clements *et al*., 2012). In South Asia, declines were caused by use of the veterinary drug diclofenac, and vultures are widespread, but rare. Cambodian populations of all three vulture species are very small and continue to decline. Almost all the remaining white-rumped and slender-billed vultures, which numbered 78 and 48 respectively in 2024, occur in the Siem Pang and Chhaeb-Preah Roka wildlife sanctuaries. The population of red-headed vultures is 14, spread across Cambodia's deciduous forests in the north and east. A small number of accidental poisoning events could wipe out most of the remaining birds (Legrand *et al*., 2025). As of the end of 2023, ten vultures were being tracked via GPS/GSM transmitters (comprising six white-rumped vultures, two red-headed vultures & two slender-billed vultures), in support of ongoing efforts to monitor their movements and habitat use. All known nests of slender-billed vultures are in Siem Pang Wildlife Sanctuary, whereas following the logging of all known nest trees in 2012–14, nesting of white-rumped vultures has only been confirmed once in Cambodia since 2013. In 2020 however, a colony of white-rumped vultures was discovered in Champasak Province (Laos), just across the border from Siem Pang (Legrand *et al*., 2024). Fifteen nests were recorded in 2023, including 12 which were active. To support breeding success and reduce potential limitation of nest sites, a pilot study installing artificial nesting platforms was conducted in Siem Pang. During the 2021–2022 and 2022–2023 breeding seasons, a pair of slender-billed vultures successfully nested on these platforms, demonstrating their potential for aiding conservation of the species (Legrand *et al*., 2024).

An ex-situ breeding programme for white-rumped and slender-billed vultures is underway in India and a small ex-situ breeding programme for red-headed vultures exists in Thailand. Replicating these initiatives for any of the species in Cambodia would be extremely costly and hampered by an inability to source eggs. Although vultures may become extinct in Cambodia without ex-situ management, they are unlikely to go extinct globally and so ex-situ management in Cambodia would do little for the global conservation of any of the vulture species. We recommend rehabilitation and release of any vultures received by the ACCB into suitable habitat. There is also a need to attempt to maintain wild populations by supplementary feeding and devote greater effort towards nest searching and protection. Further construction of nest platforms near to vulture restaurant sites should also be pursued.

Mountain hawk-eagle *Nisaetus nipalensis* NT & rufous-bellied eagle *Lophotriorchis kienerii* NT — Low Priority

These two species are widespread in hill forests in South and Southeast Asia and at little risk of global extinction. They are therefore of low priority for ex-situ management.

Indian spotted eagle *Clanga hastata* VU — Low Priority

Indian spotted eagles are widespread and uncommon in India, where population trends are obscured by identification difficulty. It is extremely poorly known in Southeast Asia, where it is known only from Myanmar (few records) and Cambodia. The population in Cambodia is evidently very small; it is primarily found in deciduous forest where it is sparsely distributed (Handschuh *et al*., 2011). There is anecdotal evidence of a decline, because birds are seen less frequently than in the recent past at well-watched sites and known pairs have disappeared even in areas where extensive forest remains (e.g., the northern plains). This suggests that the species has been impacted by loss of nesting trees due to illegal logging or selective capture of chicks for the expanding raptor trade. Despite the risk that Indian spotted eagles will be lost from Cambodia, in a global conservation context there is little reason to start a programme of ex-situ management at the ACCB because the population in India is still thought to be fairly large (del Hoyo *et al*., 2020).

Lesser fish-eagle *Icthyophaga humilis* NT — Low Priority

Scarce and localized in Cambodia (Goes, 2013), this species is widespread in South and Southeast Asia, but is believed to be in decline across most of its range (BirdLife International, 2024c). It is not a priority for ex-situ management in Cambodia.

Grey-headed fish-eagle *Icthyophaga ichthyaetus* NT — Low Priority

This species remains fairly common very locally in Cambodia (Tingay *et al*., 2006). It is widespread, particularly in South Asia (Clark *et al*., 2023), and is a low priority for ex-situ management in Cambodia.

Great hornbill *Buceros bicornis* VU, Austen's brown hornbill *Anorrhinus austeni* NT & wreathed hornbill *Rhyticeros undulatus* VU — Low Priority

All of Cambodia's hornbill species are likely to be experiencing a slow decline, due to logging of large trees suited for nesting and the associated collection of fledglings for the local pet trade. There are interesting differences in abundance and distribution between the species, with great hornbills occurring at similar abundance in the Cardamom Mountains and eastern plains, wreathed hornbills extremely scarce in the eastern plains but fairly common in the Cardamom Mountains (Tan, 2004; Goes, 2013), and Austen's brown hornbill presently known only from the eastern edge of the Cardamoms on Phnom Aural and Kirirom, and from Virachey, but apparently absent elsewhere in the Cardamoms and Phnom Bokor. However, all three species are relatively widespread globally and better protected in other countries. Ex-situ management of hornbills in Cambodia is therefore not recommended.

Red-collared woodpecker *Picus rabieri* NT — Low Priority

This species occurs only marginally in Cambodia, is significantly more widespread in neighboring countries, and is not a priority for ex-situ management.

Great slaty woodpecker *Mulleripicus pulverlentus* VU — Low Priority

This species occurs throughout forested parts of Cambodia and is potentially vulnerable to habitat loss as a result. However, large populations persist both in Cambodia and elsewhere in Southeast Asia, so it is not a priority for ex-situ management.

White-rumped pygmy-falcon *Neohierax insignis* NT— Medium Priority

This is a scarce inhabitant of deciduous forest, which is still widespread in Cambodia and it is also found in Myanmar and locally in Thailand (Clark *et al*., 2022). It is increasingly targeted by trappers for the pet trade and there is a need to monitor trade in the species and quantify trends in wild populations. At the same time, it would be prudent to investigate the husbandry requirements of similar small raptors to evaluate the ease of keeping and breeding the species. Any individuals confiscated from trade should be kept at the ACCB to learn more about its ex-situ management, which is likely to be lower cost and less demanding on space than larger raptors.

Grey-headed parakeet *Himalayapsitta finschii* NT, blossom-headed parakeet *Himalayapsitta roseata* NT, red-breasted parakeet *Psittacula alexandri* NT & Alexandrine parakeet *Palaeornis eupatria* NT — Low Priority

These species have relatively large populations either nationally, regionally, or globally, and are therefore of low priority for ex-situ management.

Cambodian tailorbird *Orthotomus chaktomuk* NT — Low Priority

This species is abundant where suitable habitat persists within its tiny global range (Mahood *et al*., 2013). It is therefore a low priority for ex-situ management.

Black-headed parrotbill *Paradoxornis margaritae* VU — Low Priority

This species occurs only marginally in Cambodia and is therefore a low priority for ex-situ management.

Chinese grass-babbler *Graminicola striatus* NT — Low Priority

This species is highly localized in Cambodia and at risk of extinction if habitat loss continues at the one site where it is known to occur (Eaton *et al*., 2014). However, it is fairly common at a number of sites in southern China and at low risk of global extinction (Zheng *et al*., 2021), so it is a low priority for ex-situ management in Cambodia.

Cambodian laughingthrush *Garrulax ferrarius* NT — Low Priority

Globally, this species is restricted to higher elevations in the Cardamom Mountains in southwest Cambodia (Goes, 2013). It is under no immediate threat. Were it to be targeted by bird trappers, as laughingthrushes are in other countries, its small, fragmented, population would put it at a high risk of extinction. Currently, it is a low priority for ex-situ management, but trade trends should be monitored in case this requires re-evaluation.

Asian golden weaver *Ploceus hypoxanthus* NT — Low Priority

This species is widespread and common in lowland wetland and non-forested areas of Cambodia. It is a low priority for ex-situ management.

Mekong wagtail *Motacilla samveasnae* NT — Low Priority

The Mekong wagtail has a tiny linear distribution along a part of the Mekong River and its major tributaries. The main threat to species alteration of habitats caused by construction of hydropower dams and subsequent changes in upstream and downstream vegetation. However, it is not known how or even if Mekong wagtail will be impacted by these changes (Duckworth *et al*., 2001). A priority is to evaluate the changes in Mekong wagtail populations upstream and downstream of major dams that have already been constructed. One location where this could be investigated is downstream of the Lower Sesan 2 dam, where there was previously a significant population. If it were found that dam-induced vegetational changes have major negative impacts on Mekong wagtail populations, then it might be prudent to establish an ex-situ population if a dam proposed for the mainstream Mekong is constructed. Currently however, the species is a low priority for ex-situ management.

Discussion

A well-designed ex-situ management programme that focuses on the five highest priority bird species we identify (white-winged duck, masked finfoot, Bengal florican, white-shouldered ibis & giant ibis) will be a critical component of plans to prevent the global extinction of these species. It also aligns with the most recent *Cambodian National Biodiversity Strategy and Action Plan* (MoE, 2016), specifically Theme 3: Ex-situ Conservation, Strategic Objective 2: "Recover species and populations. Reintroduction of captive-bred species to re-establish populations of endangered or rare plants and animals in the original habitat is necessary".

If ex-situ management programmes are not begun in a timely manner, there is a significantly higher chance that these species will go extinct. The ex-situ management of three of these high-priority species (Bengal florican, giant ibis & white-shouldered ibis) has already begun at the ACCB. For the two other high-priority species (white-winged duck & masked finfoot), ex-situ management activities have yet to begin.

We identify five additional species (orange-necked partridge, coral-billed ground-cuckoo, greater adjutant, milky stork and white-rumped pygmy-falcon) as being of medium-priority, with ex-situ management activities having begun for one of them (greater adjutant) at the ACCB. The remaining medium-priority species should be monitored and reassessed on a regular basis so that ex-situ management can be initiated in a timely fashion if deemed necessary.

For low priority species we have identified, management of any confiscated individuals should follow IUCN (2019). Whenever possible we recommend such individuals should be released at the earliest opportunity into suitable habitats within their known range, because although not currently a priority for ex-situ management these species are globally threatened.

The recommendations prioritised in our analysis will require significant investments in time, expertise, facilities and, perhaps most importantly, funding. This is particularly challenging in the case of masked finfoot whose husbandry issues are unknown and the potential for founder stock is very low. As the ongoing reintroduction of Vietnam pheasants *Lophura edwardsi* in neighbouring Vietnam demonstrates, such programmes are long, complicated and expensive, and even more so if action is only taken after a species is already extinct in the wild (Collar *et al*., 2024).

In conclusion, our analysis demonstrates the applicability of our process for rapid assessment of ex-situ management priorities for Cambodia's birds. We believe the same methodology could be piloted for other taxonomic groups, e.g. chelonians, including in other locations. Where additional data is available, additional factors such as risk of regional extinction could also be fully incorporated and weighted differently, which might lead to different conclusions in marginal cases.

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Short Communication

Blue-eared kingfishers in a town garden, Takeo and a review of further non-forest records in Cambodia

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Blue-eared kingfishers *Alcedo meninting* are widely distributed in South and Southeast Asia, from parts of India to the Philippines and from southern China to Indonesia (Birdlife International, 2020). Six subspecies are recognised, with *A. m. coltarti* the only form occurring in Indochina (Woodall, 2020). This is a resident and rather shy species which inhabits streams, creeks, channels and estuaries in evergreen and semi-evergreen forests up to 1,000 m, as well as mangroves. It is also occasionally seen in tree plantations (Woodall, 2020).

In Cambodia, the species is considered an uncommon resident of streams in semi-evergreen and hill evergreen forests from lowlands up to 1,400 m and is mainly present in the hilly southwest of the country (Goes, 2013). We describe the unusual occurrence and long-term presence of several individuals in a garden in Takeo Provincial town, southeast Cambodia during 2012–2013. We also review additional records of the species outside of forest areas in Cambodia.

Takeo town is a provincial capital located 75 km south of Phnom Penh. Rice fields and wetlands cover most of the province, and nearly all the south-eastern region of Cambodia. Forests persist in isolated patches of dry secondary growth, acacia plantations and pagoda groves. Most inhabitants of Takeo town live in Khmer-style houses with garden groves, which often include a pond. A large marsh-like reservoir borders the town centre and during the rainy season, surrounding rice fields become inundated and border the outskirts of town (Fig. 1). The closest area of substantial semi-evergreen forest lies 80 km to the west, at the edge of Bokor National Park (Kampot Province). This is also the nearest site where blue-eared kingfishers had then been recorded in Cambodia (Goes, 2013). Our observations took place in the garden of a house (Fig. 2) located on the eastern edge of town where the gardens of many residential properties are shaded by fruit trees and include ponds.

In January 2012, R.O. noticed a blue-eared kingfisher chasing a female common kingfisher *Alcedo atthis* through his garden and sometimes fishing in the garden pond. On 26 January, he built a hide by the pond and photographed the bird (an adult male) the next morning (Fig. 3). During the following months, the same individual (bird 1) was regularly observed and photographed around the pond where it roosted almost every night. From 4 April, a second bird and then a third appeared. The former had a black bill with a red base (bird 2), whereas the latter had a fully red lower mandible (bird 3) (Fig. 4). These features indicate that these were adult females (D. Wells, in litt.), with 'bird 3' possibly being younger as the extent of red might be age-related (W. Duckworth, in litt.). The female birds repeatedly roosted at the pond, first individually until 6 May, then together on several occasions until 23 May. The male was still present during this period.

During R.O.'s absence in July, the house guard noted blue-eared kingfisher(s) roosting near the garden pond almost daily. On 29 July however, he found one sick bird along the nearby road. Despite care, the bird died soon afterwards. The guard confidently claimed that the bird was the individual with the red base to its bill (bird 2).

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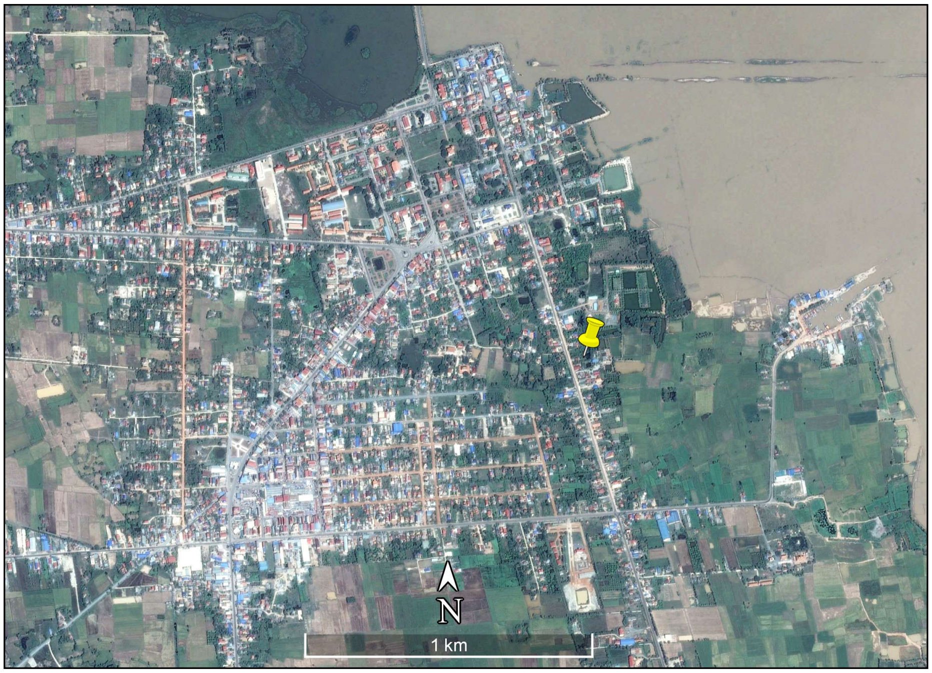

Fig. 1 Remote sensing image of Takeo town in December 2013, including the location of the blue-eared kingfisher observations (yellow pin) (GoogleEarth)

Fig. 2 Garden pond in Takeo town where blue-eared kingfishers were observed

Fig. 3 Male blue-eared kingfisher at the garden pond, 24 February 2012

The other female (bird 3) was not seen again, although the adult male (bird 1) continued to roost almost daily at the pond until mid-September, and subsequently visited the pond during the daytime to fish until 23 October. Not long afterwards, the male flew into one of the house windows and was found dead nearby on 3 November (Fig. 5). In 2013, blue-eared kingfishers periodically reappeared in the Takeo garden: a female similar to 'bird 2' perched by the pond on 30 May and was regularly seen up to 15 June. A male (bird 4) was also noted intermittently from 6–7 September until the end of the month. Towards the end of December, a second blue-eared kingfisher collided with a house window, although this time the bird eventually recovered. Following this event, blue-eared kingfishers were no longer observed.

At the time of these observations, there were no other records of blue-eared kingfishers outside of large tracts of

Fig. 4 Duo of female blue-eared kingfishers that roosted at the garden pond in Takeo town in April–May 2012

dense forest habitat in Cambodia. As such, these were the only records from the central Tonle Sap-Mekong floodplain published in Goes (2013), who extensively reviewed literature, including field survey reports, trip reports and unpublished sightings from resident or visiting birdwatchers and local guides. From 2016 onwards however, the use of the eBird platform became popular as the main platform for documenting bird observations.

We extracted records of blue-eared kingfishers documented outside of forest habitats from the eBird database and assessed their reliability by contacting the observers. Where observers could not be contacted or failed to reply, we assumed their records were erroneous and rejected them, except in instances where they: i) acknowledged the unusual occurrence of the species, and/or, ii) documented the correct identification features for the species. Irrespectively, we assumed that all identifications outside of the wintering period for common kingfisher in Cambodia (typically September to April, although records extend to early May and returnees might occur as early as mid-July) were correct (Goes, 2013).

This collation yielded 44 records of blue-eared kingfishers outside of forest areas in Cambodia as of 2022. These were distributed across 23 sites in all but one region of the country. Nine of these records were discarded, resulting in 35 reliable or confirmed records.

Fig. 5 Dead male blue-eared kingfisher found on 3 November 2012, after a collision with a house window

These mostly stemmed from long-term resident birdwatchers as well as from one Cambodian bird photographer. All but four locations of the confirmed records were in the Phnom Penh area, reflecting the distribution of most resident birdwatchers. The other locations included one site in Siem Reap Province (one winter record), one in Kampong Thom Province (five records) and two in Kampong Speu Province (three records), the latter all being summer records by a single observer. Overall, a slight majority of the records were in April–August, when the common kingfisher is absent or rarely present. The records were from pagoda groves, open countryside and floodplain scrub usually near a pond or stream, and once along a major river.

Recent field guides do not mention that *A. m. coltarti* undertakes seasonal movements, or include 'gardens' or 'parks' as occasional habitats in mainland South-east Asia (Robson, 2008; Craik & Lê, 2018; Treesucon & Limparungpatthanakij, 2018; CBGA, 2019), although the species occurs in a wider variety of habitats in other parts of its range (Rasmussen & Anderton, 2012; Eaton *et al*., 2021). Experts also confirmed that to their knowledge it is absent outside of its usual forest habitats in Indochina and non-peninsular Thailand (W. Duckworth & P. Round, in litt.).

The presence of several blue-eared kingfishers in a town garden over an extended period including the dry and wet seasons is noteworthy. Despite numerous recent records in open countryside and human-modified landscapes throughout the central floodplain of Cambodia, very few involve more than one bird and occurrence has not been noted for longer than a few months at any site, although this might be due to observer effort. The reasons for these widespread records of blue-eared kingfishers outside forest areas remain unclear. As such, it is unknown if the records reflect a recent change in status for the species as a non-breeding visitor to garden groves and similar habitats, or were simply overlooked in the past due to its secretive behaviour and similarity to common kingfisher. It is also the case that observation effort increased over the same period in Cambodia due to greater numbers of birdwatchers and photographers, which at least partly contributed to the new pattern of records.

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