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# On the Distribution, Behaviour and Seasonal Variation of Irrawaddy Dolphins (*Orcaella brevirostris*) in the Kep Archipelago, Cambodia

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**Abstract.** Irrawaddy dolphins (*Orcaella brevirostris*) are a globally Endangered cetacean species found in rivers, lakes, estuaries, and coastal waters across Southeast Asia. Whilst much attention has concentrated on understanding freshwater populations of the species, marine populations have received less research attention, with the majority of marine studies focusing on determining abundance and distribution. As part of The Cambodian Marine Mammal Conservation Project, the current study utilises a combination of year-long land and boat survey techniques to identify seasonal critical habitats for the species in Cambodia's Kep Archipelago, as well as fill knowledge gaps on the species' behavioural ecology, to contribute to the design of effective and tailored regional conservation strategies. Results showed Irrawaddy dolphins to be present in the Kep Archipelago in all seasons, with the highest encounter rates in Summer Monsoon (May–September) and Post-Monsoon (October–November) seasons, and the lowest encounter rates in Pre-Monsoon season (March–April). Juveniles were present in all seasons, suggesting the region represents an important nursing ground for the population. Foraging was the most commonly observed behaviour, with significant associations found between certain behavioural states and events, group sizes and seasons, group sizes and juvenile presence, and swim styles and juvenile presence.

**Key words.** Irrawaddy dolphin, critical habitat, behaviour, distribution, seasonality

## INTRODUCTION

To effectively manage a cetacean population for the purposes of conservation, it is vital to understand the behavioural ecology of the target species, as well as the distribution of the population's critical habitats (Lusseau & Higham, 2004; Taylor et al., 2005; Buchholz, 2007; Cañadas & Hammond, 2008; Ashe et al., 2010; Hoyt, 2012; Brakes & Dall, 2016). Critical habitats can be defined as specific geographic locations containing features essential for important life stages of a threatened species, such as regions used for foraging, nursing, resting, or breeding, hence they are important for the conservation of the species (U.S. Fish & Wildlife Service, 1973). As seasonality can affect the distribution and kind of usage of critical habitats (Wauters & Dhondt, 1992; Hanson & Defran, 1993; Northridge et al., 1995; Beasley, 2007; Sargeant et al., 2007; Miller & Baltz, 2010; Akkaya-Bas et al., 2018), an understanding of population-specific seasonality is also required to design successful conservation strategies (Ross et al., 2011; Hoyt, 2012).

Irrawaddy dolphins (*Orcaella brevirostris*) are an Endangered species of small cetacean, found in fragmented populations across Southeast Asia (Perrin et al., 1995; 1996; 2005; Hines et al., 2015a; 2015b; Minton et al., 2017; Mahmud et al., 2018). The species is unique, in that they inhabit both marine and freshwater environments, with marine populations often found in shallow, nearshore waters, associated with riverine input (Dolar et al., 2002; Smith, 2009; Minton et al., 2017). Their diet consists of small fish, crustaceans, and cephalopods, with some variation across populations (Baird & Mounsouphom, 1997; Stacey & Leatherwood, 1997; Jackson-Ricketts et al., 2018). Major threats to the species are fisheries bycatch and habitat degradation which are intensified by their proximity to land (Dolar et al., 2002; Smith & Jefferson, 2002; Reeves et al., 2003; Smith et al., 2004; Kannan et al., 2005; Perrin et al., 2005; Smith et al., 2008; Jaaman et al., 2009; Peter et al., 2016).

In recent years, a growing number of studies have focussed on marine populations of Irrawaddy dolphins. Whilst a small number of studies report behavioural observations (Minton et al., 2013; Ponnampalam et al., 2013), the majority of studies address abundance and distribution (Smith et al., 2008; Minton et al., 2011; Tongnunui et al., 2011; Ponnampalam, 2012; Teoh et al., 2013; Hines et al., 2015b), leaving large knowledge gaps on the species' behavioural ecology and seasonality.

In September 2017, the Non-Governmental Organisation Marine Conservation Cambodia launched The Cambodian Marine Mammal Conservation Project (CMMCP), which has

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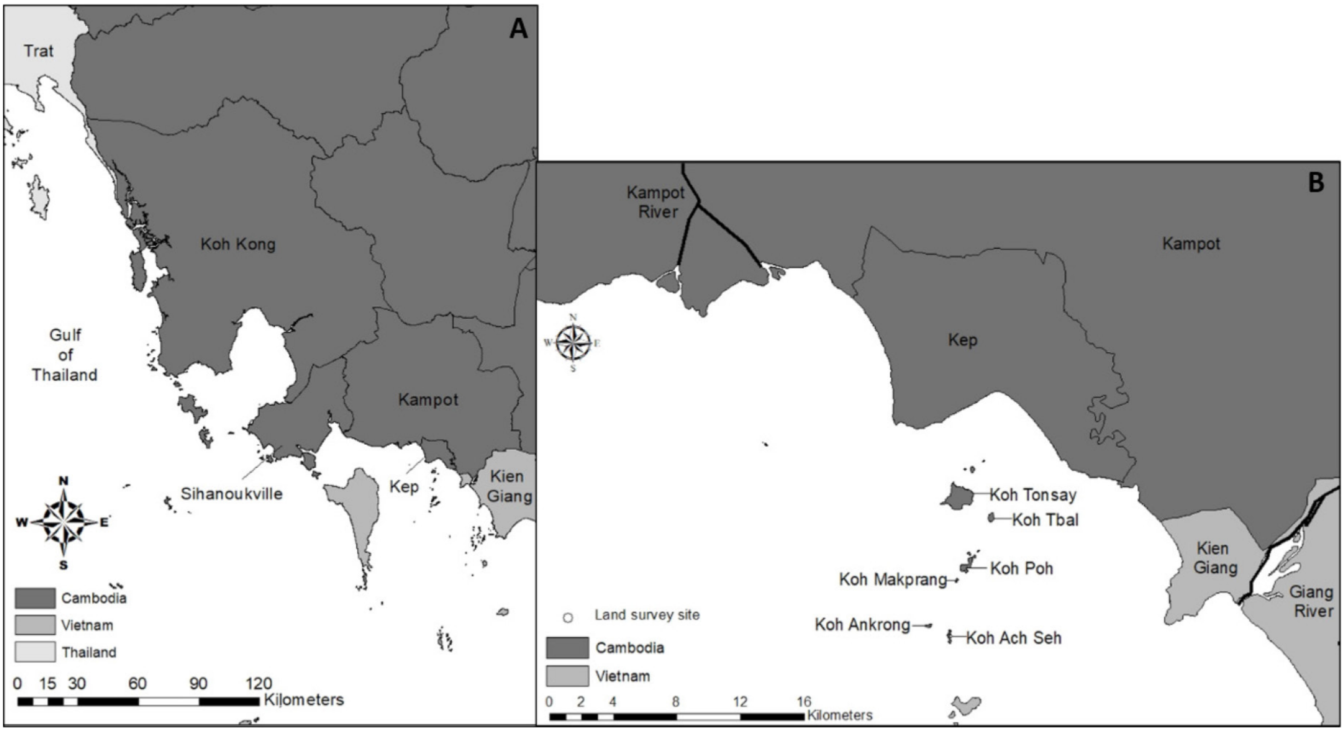


Fig. 1. A, the eastern coast of the Gulf of Thailand, showing the Cambodian coastal provinces and neighbouring Thai and Vietnamese Provinces; B, the study area, showing the waters of Kep and Kampot province, as well as the islands of the Kep Archipelago.

identified the presence of a population of Irrawaddy dolphins in Cambodia's Kep Province (Tubbs et al., 2019). As part of CMMCP's ongoing work, the current study uses year-long data to identify seasonal critical habitats for Irrawaddy dolphins, as well as fill knowledge gaps on the behavioural ecology of the species, in order to contribute towards effective and tailored regional conservation strategies.

## MATERIAL AND METHODS

**Study area.** Cambodia's Kep Archipelago is situated in the coastal waters of Kep Province (Fig. 1). The archipelago is comprised of 13 islands, stretching from the coastline to 13 km offshore. The waters are shallow, not surpassing depths of 12 m, and support fringing coral reef, mangrove, and seagrass habitats. The region receives riverine input from two sources, Kampot river to the north-west and Giang river in Vietnam to the east. In addition, the archipelago is situated within a Marine Fisheries Management Area (Cambodia's equivalent of a Marine Protected Area; Ministry of Agriculture, Forestry and Fisheries, 2018), as well as an Important Marine Mammal Area (Marine Mammal Protected Area Taskforce, 2019).

**Boat surveys.** Between the 5 October 2017 and 6 September 2018, 29 boat survey days were undertaken in the Kep Archipelago (average of 2.5 surveys days/month ± SD 1.24). Survey days lasted for between three and five hours, during a Beaufort Sea state ≤ 3, following one of two pre-determined tracklines. Track one followed a circular route to pass all islands of the Kep Archipelago, whilst track two was determined by logistical constraints and travelled east from Koh [=Island] Ach Seh towards Kampot province and back (Fig. 2). Surveys were conducted on a converted pair trawling boat with a 200HP inboard engine and a viewing platform 3.8 m above sea level. The boat travelled at a speed of 4 knots, with boat tracklines recorded using a Garmin 64s GPS. Five surveyors were present during each survey, three observers scanned the sea with Bushnell 8×42 binoculars in search of cetaceans while two observers were on rest shifts. Observers rotated roles every 10 minutes to avoid fatigue effects.

**Land surveys.** Between the 2 October 2017 and 14 September 2018, 95 land surveys took place (average of 7.9 surveys/month ± SD 2.27) from a specified observation platform, 21 m above sea level, with views of the study area (Fig. 1). Surveys lasted for a minimum of three hours during a Beaufort Sea state ≤ 3. Four surveyors were present during each survey, two observers scanned the sea with 8×42 Bushnell binoculars while two observers were on rest shifts. Observers rotated roles every 15 minutes to avoid fatigue effects.

**Data collection.** For both survey techniques, a cetacean "group" was defined as a set of individuals with coordinated behavior over a period of several minutes, derived from Connor et al.'s (1998) definition of a "school". Upon a cetacean group sighting, a group number was assigned, time recorded, and five-minute interval sampling used, as in Affinito et al. (2018), to record: species; group size; presence of juveniles, with juveniles being identified by their size; behavioural state, determined using the scan number as in Altmann (1974; Table 2); the frequency and type of behavioural events, defined as 'a series of body movements that could be unambiguously identified as a unit' by Lusseau (2006; Table 2); and swim style, defined as the spatial structure and formation pattern of the group, derived

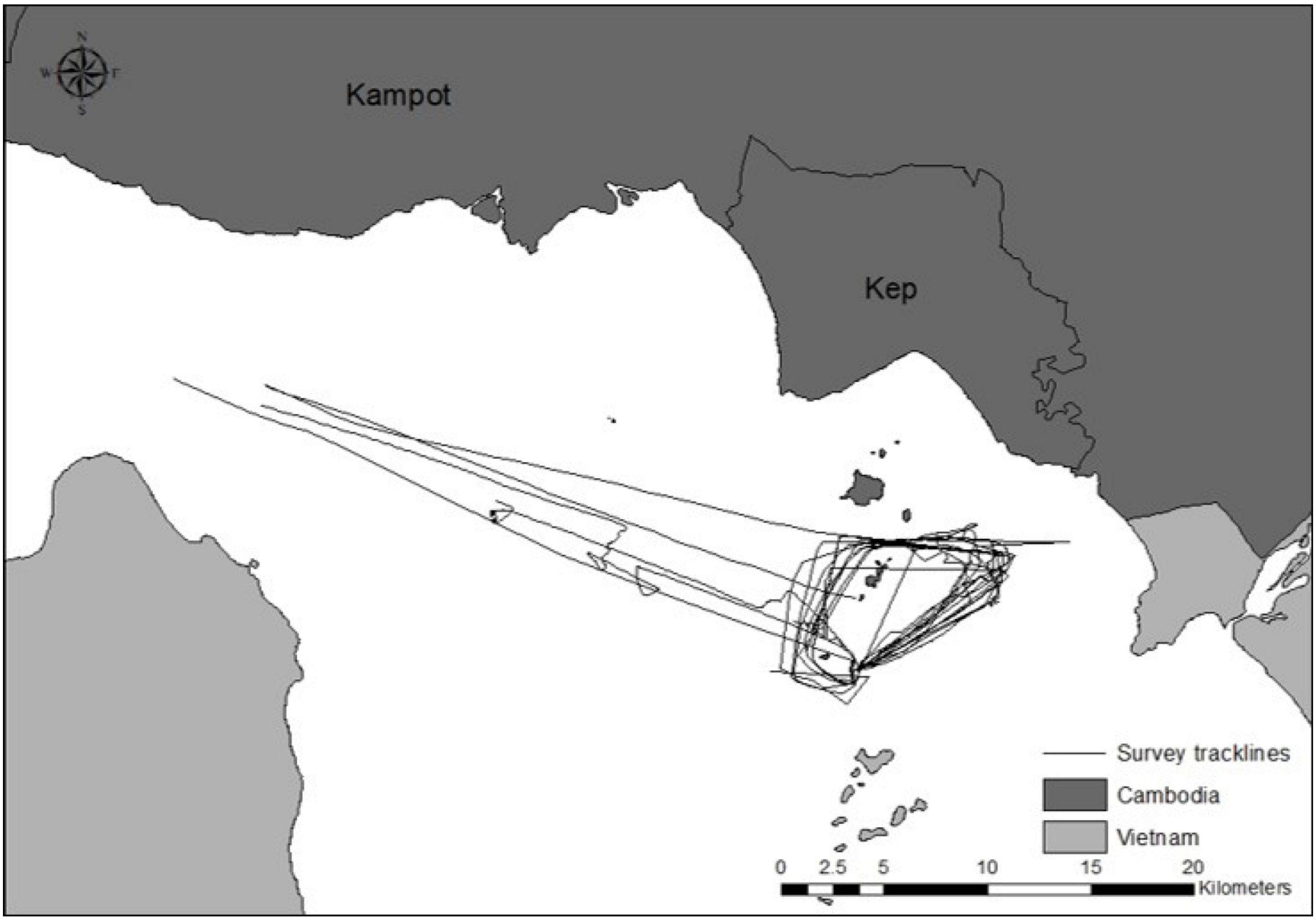


Fig. 2. Boat tracklines followed between 5 October 2017 and 6 September 2018.

from Akkaya-Bas et al.'s (2017) definition (Table 2). The behavioural states and swim styles represent an exhaustive list of all possible Irrawaddy dolphin states and swim styles, adapted from those used by Lusseau (2003, 2006), Parra (2006), and Akkaya-Bas et al. (2017). Whereas the events used were only a selection of possible events, adapted from Lusseau (2003) and Akkaya-Bas et al. (2017). Groups were followed until they were either no longer visible or until a negative reaction to the research vessel was exhibited by the group for over 10 minutes, characterised by the groups swimming away from the vessel. During boat surveys, additional data on the distance of the group from the research vessel and the angle of the group from north were also collected at each sampling interval, with the research vessel aiming to keep a minimum distance of 30 m from the dolphin group.

**Opportunistic sightings.** Between October 2017 and September 2018, the research team resided on Koh Ach Seh (Fig. 1). If dolphins were sighted opportunistically (off-effort) from the island, or during boat trips between the island and the mainland, the same data were collected as described above.

**Data processing and analysis.** Boat survey tracks were transferred to Google Earth, extracted to Microsoft Excel, and uploaded to Esri® ArcGIS™ for visual display. To investigate the seasonality of behavioural ecology and distribution, the year was split into four seasons as follows, based on rainfall research conducted between 2010 and 2015 (Tsujimoto et al., 2018): Post-Monsoon (October – November), Dry (December – February), Pre-Monsoon (March – April), and Summer Monsoon (May – September). Encounter rates for land and boat surveys were calculated separately, based on the total number of hours on effort searching for dolphins and the number of groups seen, therefore excluding data collected from opportunistic sightings.

Critical habitat maps for each season and each behaviour observed were produced from dolphin sighting locations attained during boat surveys. To produce maps, dolphin group coordinates were calculated using the GPS location of the research vessel, the angle of the dolphins from north, and the distance of the dolphins from the research vessel. Dolphin locations were uploaded as point data to Esri® ArcGIS™ and subsequently transformed into line data. Line data were used to produce kernel density maps, weighted by group size. The output cell size was set to 75, and the search radius set to 750. Kernel density was chosen as it is considered a common tool to estimate ecological distribution (Silverman, 1986; Worton, 1989; Hastie et al., 2004; Sprogis et al., 2016).

Statistical analysis was carried out in R Studio (version 1.1463, RStudio Team, 2015). Observations from on-effort surveys and opportunistic sightings were included in the

Table 1. Ethogram defining behavioural states, behavioural events, and swim styles used in the current study, adapted from Lusseau (2003, 2006), Parra (2006), and Akkaya-Baş et al. (2015).

| **Behavioural State** | |
|---|---|
| Surface-Feeding (SU-FE) | Individuals show active, rapid directional changes just under the surface. Splashes may be present. |
| Diving (DV) | Individuals disappear from surface for between 30 seconds and several minutes. Individuals show no obvious progressional movement and resurface within 100 m from where they disappeared. |
| Travel-Diving (TR-DV) | Individuals disappear from surface for between 30 seconds and several minutes. Individuals make progressional movement, reappear at distance from their starting location. |
| Travelling (TR) | Individuals move with a constant speed in a certain direction, with a diving interval of 3–5 seconds. |
| Travel-Fast (TR-F) | Individuals swim rapidly through the surface of the water, rarely disappearing under the surface. |
| Socialising (SOC) | Individuals show various interactive behaviours and create body contact with each other. |
| Resting (RE) | Individuals are drifting at the surface, disappearing and reappearing in the same location. |
| Milling (MI) | The group shows no net movement, individuals are surfacing facing different directions, the group often changes direction. Dive intervals are variable but short. |
| **Behavioural event** | |
| Breaching (BR) | Individual leaps partly out of the water and lets its body slap the water surface as it falls. |
| Tail Slap (TS) | Individual slaps its fluke on the water surface. |
| Fluke Up (FU) | Individual raises only its tail fluke above the water surface. |
| Spy Hopping (SH) | Individual raises only its head above the water surface. |
| Full Leap (FL) | Individual leaps its complete body above the water surface. |
| Belly Up (BU) | Individual turns upside down with the ventral side facing up. |
| **Swim style** | |
| Front (FR) | Individuals swim in a line, side by side. The line can be straight or offset. |
| Line (LI) | Individuals swim in a line, head to tail. The line can be straight or offset. |
| Cluster (CL) | Individuals are clustered with no directional movement. |
| Spread (SP) | The group is spread out, individuals do not swim close to each other. |
| Team (TE) | The group is split up into smaller independent teams. |
| Kettle (KE) | Individuals are clustered at the surface and water appears to be boiling like a kettle. Splashes may be present. |
| Circular Diving (CD) | Individuals create a circular formation by appearing in turns at the surface after each other. |
| Alone (AL) | One single individual is present. |

statistical analysis, with the boat and land data kept separate. Group sizes were clustered into categories, then assigned numbers for analysis (presented in brackets): Small, 1–3 individuals (1); Medium, 4–8 individuals (2); and Large, ≥ 9 individuals (3). Behavioural states were grouped for analysis and assigned numbers: Diving and Surface-Feeding were grouped as Foraging behaviour (1), Travelling, Travel-Diving and Travel-Fast became Travelling (2), while Socialising (3), Milling (4), Resting (5) and Undetermined (0) were grouped separately. Behavioural events, swim styles, and seasons were assigned respectively as follows: Fluke Up (1), Tail Slap (2), Breaching (3), Full Leap (4), Spy Hopping (5), Belly Up (6); Alone (1), Varied (2), Cluster (3), Spread (4), Line (5), Front (6), Teams (7), Kettle (8), Circular Dives (9); Post-Monsoon (1), Dry Season (2), Pre-Monsoon (3), Summer Monsoon (4).

All data were tested for normality by visually checking histograms, dotcharts, qqnorm and qqline plots, and finally by statistically testing using the Shapiro Wilks test. None of the data were normally distributed so a Generalized Linear Model (GLM) was used to test for statistical significance and associations between variables. All variables were treated as Gaussian family. Multiple four-way models were tested comparing behavioural state, behavioural event, group size, and swim style, with the Akaike's Information Criteria (AIC) values checked on outcome. Depending on the order in which the variables were entered into the R code, the

Table 2. Irrawaddy dolphin encounter rates over each season, from land and boat surveys.

| Season | Total time spent surveying (hh:mm:ss) | Total number groups seen | Encounter rate per hour on effort |
|---|---|---|---|
| **Boat** | | | |
| Pre-Monsoon | 5:30:00 | 1 | 0.182 |
| Monsoon | 31:24:00 | 23 | 0.732 |
| Post-Monsoon | 15:57:00 | 5 | 0.313 |
| Dry | 21:50:00 | 11 | 0.504 |
| Total | 74:41:00 | 40 | — |
| Average | — | — | 0.433 |
| **Land** | | | |
| Pre-Monsoon | 34:58:00 | 0 | 0.000 |
| Monsoon | 99:44:00 | 17 | 0.170 |
| Post-Monsoon | 30:50:00 | 6 | 0.195 |
| Dry | 58:22:00 | 4 | 0.069 |
| Total | 223:54:00 | 27 | — |
| Average | — | — | 0.108 |

model with the lowest AIC score was chosen as the best fit (Boat, GLM(formula=Boat$Group.Size~Boat$Swim.Style*Boat$Event*Boat$State)AIC=306.49; Land, GLM (formula=Land$Group.Size~Land$Swim.Style*Land$State*Land$Event)AIC=132.18). Monsoon season and juvenile presence were individually compared in separate models with behavioural state, swim style, and group size.

## RESULTS

**Sightings and encounter rates.** During 29 boat survey days (74 hours 41 minutes), 40 groups of Irrawaddy dolphins were sighted, with an average group size of 5.83 (smallest group size 1, largest group size 14). During 95 land survey days (233 hours 54 minutes), 27 groups of Irrawaddy dolphins were sighted, with an average group size of 4 (smallest group size 1, largest group size 10). Through a combination of land and boat surveys, as well as opportunistic sightings, Irrawaddy dolphins were sighted in all four seasons. No other cetacean species were sighted during surveys.

Average encounter rates for land and boat surveys, as well as seasonal encounter rates, are presented in Table 3. The average Irrawaddy dolphin encounter rate during boat surveys, over all seasons, was 0.433 groups per hour on effort, with the highest encounter rate observed in Summer Monsoon season (0.732 groups per hour on effort), and the lowest observed in Pre-Monsoon season (0.182 groups per hour on effort). During land surveys, the average Irrawaddy encounter rate over all seasons was 0.108 groups per hour on effort, with the highest encounter rate observed in Post-Monsoon season (0.195 groups per hour on effort), closely followed by Summer Monsoon season (0.17 groups per hour on effort), with the lowest encounter rate in Pre-Monsoon season (0.00 groups per hour on effort).

Table 3. P-values from generalised linear models comparing Independent variables (Behavioural state, Monsoon Season, Juvenile Presence) to explanatory variables for both boat and land survey data. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

| Behavioural State | Land | Boat |
|---|---|---|
| Behavioural event | 0.0117* | 0.229 |
| Swim style | 0.228 | 0.423 |
| Group size | 0.992 | 0.274 |
| **Monsoon season** | **Land** | **Boat** |
| Behavioural state | 0.441 | 0.105 |
| Group size | 0.00601** | 0.073 |
| Juvenile presence | 0.585 | 0.669 |
| **Juvenile presence** | **Land** | **Boat** |
| Behavioural state | 0.203 | 0.783 |
| Swim style | 0.00106** | 0.00181** |
| Group size | 0.0116* | 0.806 |

**Distribution and critical habitat preferences.** Using data from boat observations, there were 65 accounts of Foraging behaviour, 59 accounts of Travelling, 8 accounts of Resting, 7 accounts of Socialising, and 1 account of Milling. Using data from land observations, there were 43 accounts of Foraging behaviour, 18 accounts of Travelling, 5 accounts of Resting, and 5 accounts of Socialising.

In Post-Monsoon season, the highest Foraging densities were observed during boat surveys, within a 2 km range of the central islands of the Archipelago: Koh Tbal, Koh Poh, and Koh Makprang (Fig. 3). In Dry season, the highest Foraging density was observed further south, near Koh Ankrong, as well as between Koh Tbal and Koh Poh, with density distribution stretching 8 km eastwards, away from the archipelago (Fig. 3). Density maps could not be produced for Foraging behaviour in Pre-Monsoon season due to a lack

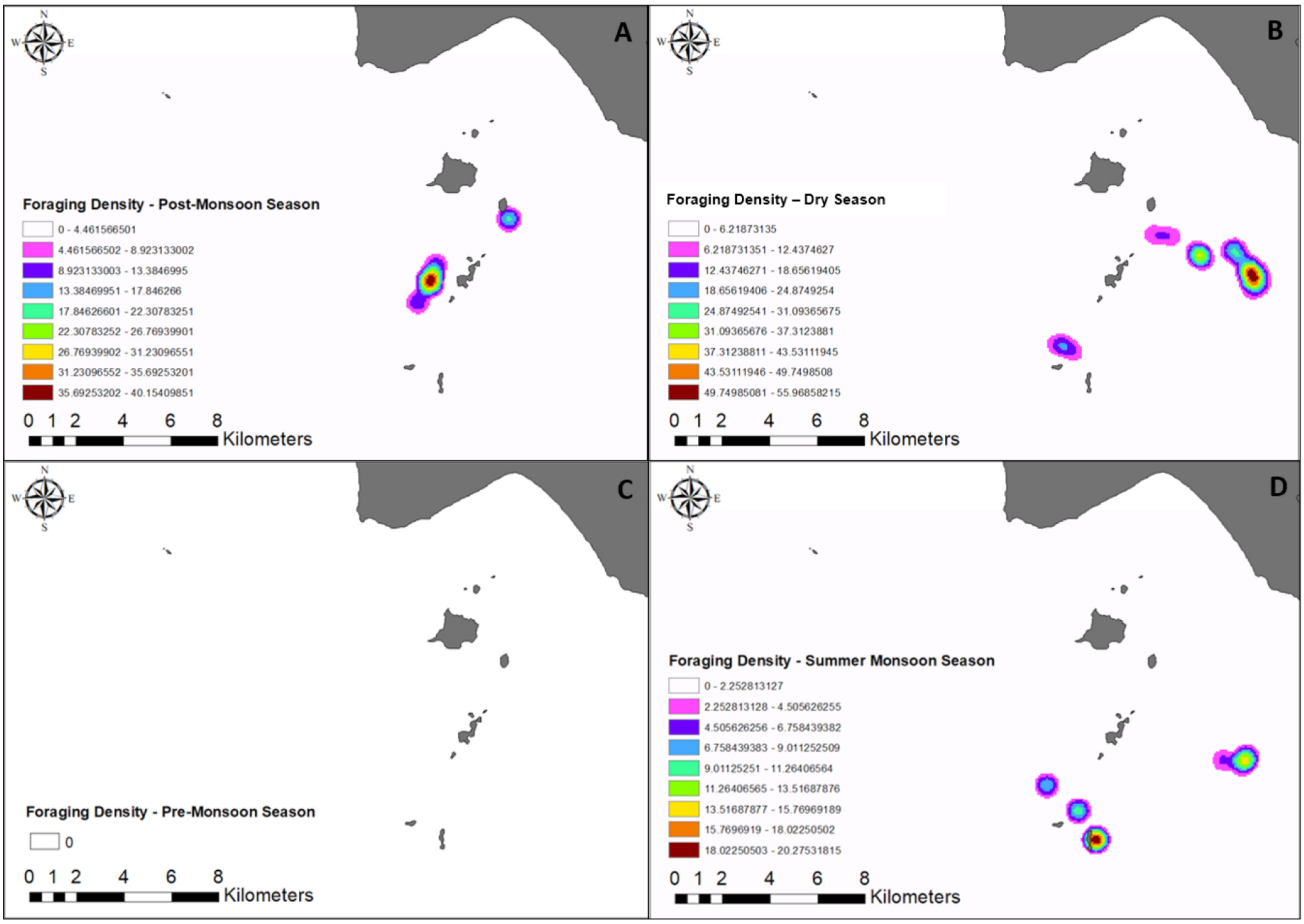


Fig. 3. Kernel densities of Irrawaddy dolphin Foraging behaviour in the Kep and Kampot region in Post-Monsoon (A), Dry (B), Pre-Monsoon (C), and Summer Monsoon (D) seasons.

of observations. In Summer Monsoon season, the highest Foraging densities were found in the southern and central archipelago, in the nearshore waters of Koh Ach Seh and Koh Ankrong, as well as ca. 5 km east of Koh Makprang (Fig. 3).

In Post-Monsoon season, the highest Travelling density was observed between Koh Tbal and Koh Poh, in the central archipelago (Fig. 4). In Dry season, the highest Travelling densities were observed east of Koh Tbal and Koh Poh, as well as in the southern archipelago, near Koh Ankrong (Fig. 4). Density maps could not be produced for Travelling behaviour in Pre-Monsoon season due to a lack of observations. In Summer Monsoon season, Travelling was seen in the southern archipelago, north of Koh Ach Seh and Koh Ankrong, as well as ca. 10 km west of the archipelago (Fig. 4).

Due to the low amounts of data on Resting and Socialising, maps were not produced for these behaviours, as they would not have been representative.

**Behavioural ecology.** All behavioural states (Foraging, Travelling, Socialising, Milling, and Resting) were observed during boat surveys. Behavioural events of Fluke Up, Tail Slap, Breaching, Full Leap, and Spy Hopping were recorded, however, no Belly Up events were recorded. Swim styles of Alone, Varied, Cluster, Spread, Line, Front, Team, and Kettle were observed, however no Circular Diving was observed. Small, Medium, and Large group sizes were observed. Using data from boat surveys, there was no significant association observed between behavioural states, behavioural events, swim styles, and group sizes (GLM; behavioural state–behavioural event p=0.229; behavioural state–swim style, p=0.423; behavioural state–group size, p=0.274, Null deviance: 146.87 on 141 degrees of freedom; Fig. 5; Table 3), suggesting any variation occurred by chance. When dolphins were Resting, no behavioural events were seen. Clustered swim styles were only observed when the dolphins were Milling (Fig. 5). During Milling and Resting behaviours, groups were most commonly of Medium or Large sizes, with groups of all sizes observed Socialising (Fig. 5).

Based on boat survey data, juvenile presence could be explained by swim style (GLM, p=0.00181, Null deviance: 263.26 on 86 degrees of freedom), but not by behavioural state (GLM, p=0.105, Null deviance: 9.6250 on 87 degrees of freedom) or group size (GLM, p=0.806, Null deviance: 51.577 on 141 degrees of freedom; Table 3), with juveniles most commonly seen during Varied, Spread, Team, and Kettle swim styles.

During land surveys, behavioural states of Foraging, Travelling, Socialising, and Resting were observed, however

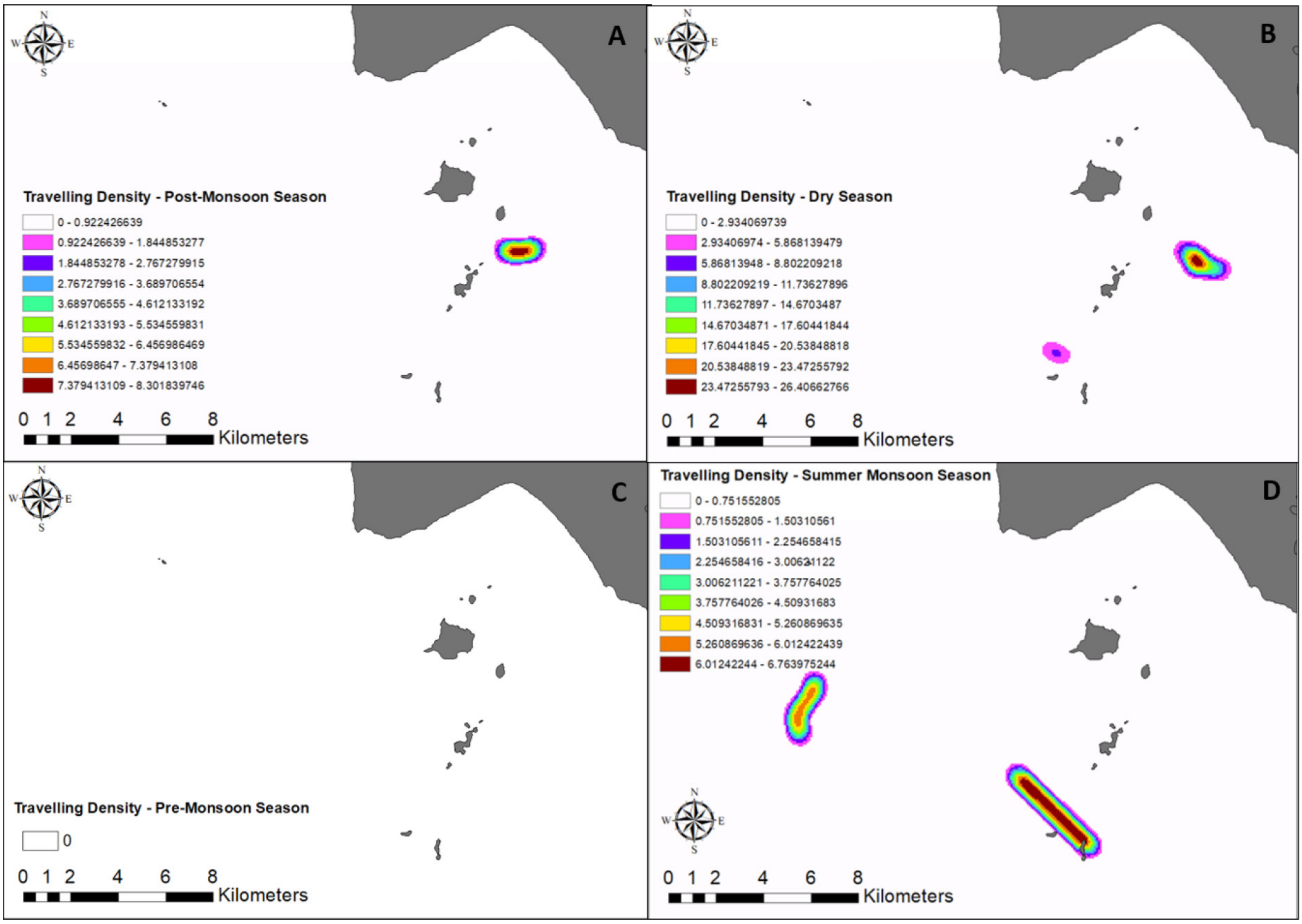


Fig. 4. Kernel densities of Irrawaddy dolphin Travelling behaviour in the Kep and Kampot region in Post-Monsoon (A), Dry (B), Pre-Monsoon (C), and Summer Monsoon (D) seasons.

no Milling behaviour was observed. Behavioural events of Fluke Up, Tail Slap, Breaching, Full Leap, and Spy Hopping were recorded, however no Belly Up events were recorded. Swim styles of Alone, Varied, Cluster, Spread, Line, Front, Team, and Kettle were observed, but no Circular Diving was observed. Small, Medium, and Large group sizes were observed. Using data from land surveys, the likelihood of seeing certain behavioural events could be statistically explained by the presence of certain behavioural states (GLM, p=0.0117, Null deviance: 33.105 on 75 degrees of freedom). Fluke Up, Tail Slap, Breaching, Full Leap, and Spy Hopping events were observed during Foraging behaviours (Fig. 6). The only behavioural event observed with Travelling and Resting behaviour was Fluke Up, and the only events observed with Socialising behaviour were Fluke Up and Tail Slap (Fig. 6). The variation in swim styles and group sizes observed could not be statistically explained by behavioural state (GLM, state–swim style, p=0.228; state–group size, p=0.992; Null deviance: 33.105 on 75 degrees of freedom; Table 1), suggesting all variation had occurred by chance, however when the dolphins were observed Socialising, they were never in a Clustered or Varied swim style (Fig. 6). No Large group sizes were observed during Socialising or Resting Behaviours, but during Foraging and Travelling behaviours all group sizes were observed, with Large group sizes being the least common (Fig. 6).

During land surveys, swim style could also explain the variation in juvenile presence (GLM, p=0.00106, Null deviance: 94.625 on 23 degrees of freedom), with juveniles most commonly seen during Cluster, Spread, and Line swim styles. Group size also influenced juvenile presence, with juveniles most likely to be seen in Medium and Large groups (GLM, p=0.0116, Null deviance: 20.776 on 75 degrees of freedom). However, behavioural state could not significantly explain any variation in juvenile presence (Table 3).

**Seasonality.** Based on observations from boat surveys, there was no variation in behavioural states or group sizes with season, with all behaviours and group sizes having the same likelihood of occurrence in all seasons (GLM; behavioural state, p=0.105, Null deviance: 138.94 on 144 degrees of freedom; group size, p=0.073, Null deviance: 137.97 on 141 degrees of freedom; Fig. 7; Table 3). Groups of all sizes were observed in all seasons, except for Large groups which were not observed in Pre-Monsoon season (Fig. 7). Post-Monsoon season was the only season with all behaviours observed.

Based on observations from land surveys, no variation in behavioural states was observed with season (GLM, p=0.441, Null deviance: 33.988 on 79 degrees of freedom; Table 3). Foraging behaviour was observed in all seasons. In Dry season, Foraging was the only behaviour observed,

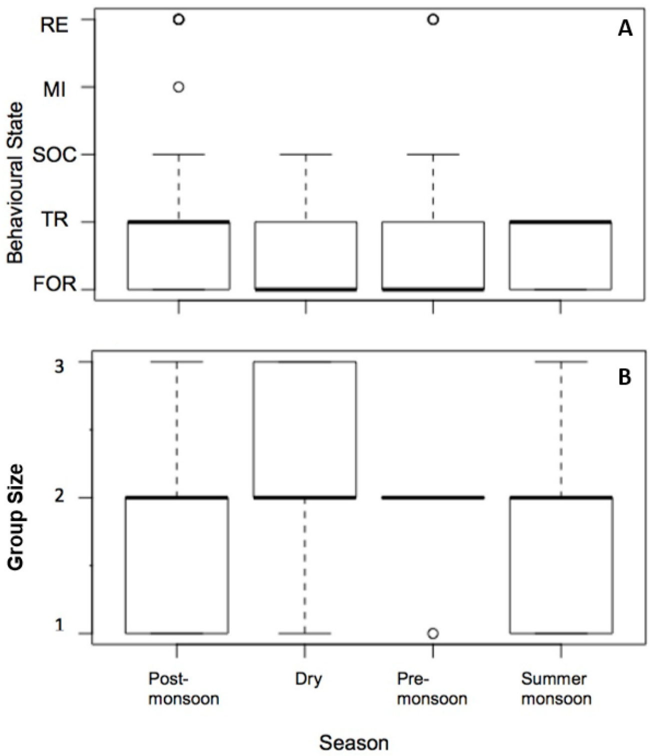


Fig. 5. Boxplots showing which: **A**, Behavioural Events (FU, Fluke Up; TS, Tail Slap; BR, Breaching; FL, Full Leap; SH, Spy Hopping); **B**, Swim Styles (KE, Kettle; TE, Team; FR, Front; LI, Line; SP, Spread; CL, Cluster; VA, Varied; AL, Alone); and **C**, Group Sizes (1, Small; 2, Medium; 3, Large) were seen with certain Behavioural States (RE, Resting; MI, Milling; SOC, Socialising; TR, Travelling; FOR, Foraging). All data shown from boat survey observations.

with one outlying occurrence of Socialising behaviour. In Summer Monsoon season, no Milling or Resting behaviours were observed. In Post-Monsoon season, all behaviours were observed (Fig. 8). Season could explain the differences in group sizes (GLM, p=0.00601, Null deviance: 32.947 on 75 degrees of freedom; Table 3). Large group sizes were only observed from land surveys in Post-Monsoon season, with Dry season supporting more Medium sized groups and Summer Monsoon supporting more Small groups (Fig. 8). Post-Monsoon season was the only season with all behaviours observed.

Season could not explain the variation seen in juvenile presence (GLM, boat, p=0.669, Null deviance: 53.034 on 144 degrees of freedom; land, p=0.585, Null deviance: 21.550 on 79 degrees of freedom), with juveniles present year-round.

## DISCUSSION

**Species occurrence and seasonality.** Irrawaddy dolphins were sighted in the Kep Archipelago in all seasons, suggesting the population are year-round residents. The average encounter rate during boat-based surveys was 0.433 groups per hour on effort searching (Table 2). Minton et al. (2011; 2013) conducted boat surveys for cetaceans at four Malaysian sites, presenting Irrawaddy encounter rates of 0.288 for Kuching, 0.192 for Similajau, 0.197 for Miri, and 0.196 for Sarawak. A population size estimate of 208 (CV 29.1%, 95% CI 118–364) was attained for the Sarawak population, using DISTANCE sampling. The differences in encounter rates between the Malaysian population and Kep's population, and estimated population size for the Sarawak population could suggest that there is a higher abundance of Irrawaddy dolphins in Kep. This difference could also be explained by differences in Irrawaddy dolphin ranges across the study sites. An investigation into population ranges of Kep's population is therefore suggested.

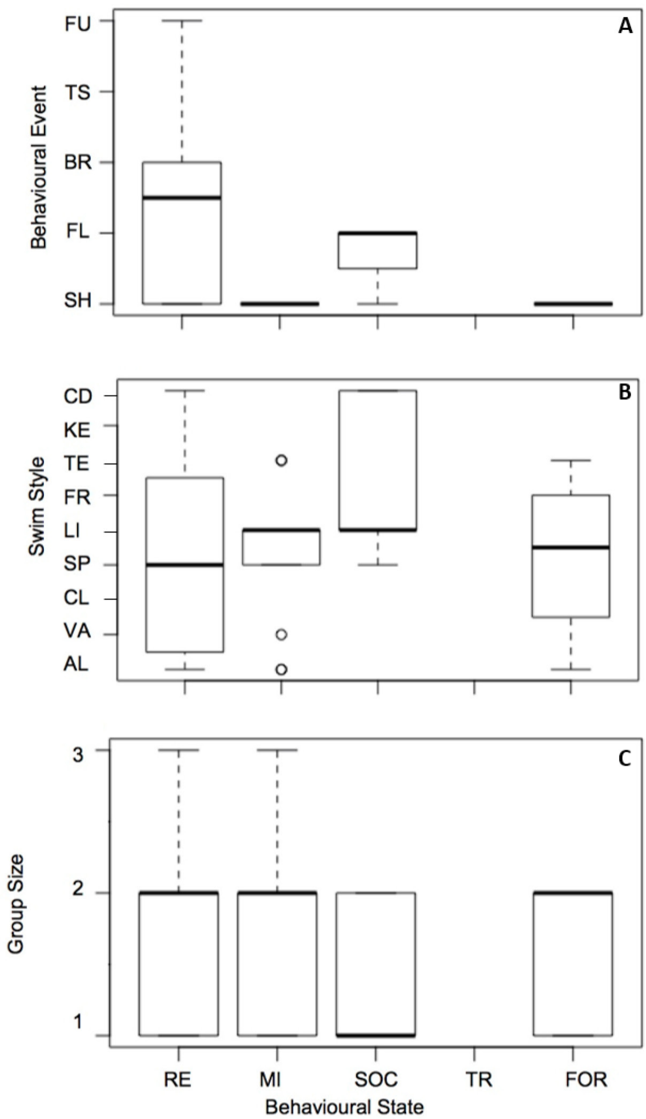


Fig. 6. Boxplots showing which: **A**, Behavioural Events (FU, Fluke Up; TS, Tail Slap; BR, Breaching; FL, Full Leap; SH, Spy Hopping); **B**, Swim Styles (KE, Kettle; TE, Team; FR, Front; LI, Line; SP, Spread; CL, Cluster; VA, Varied; AL, Alone); and **C**, Group Sizes (1, Small; 2, Medium; 3, Large) were seen with certain Behavioural States (RE, Resting; MI, Milling; SOC, Socialising; TR, Travelling; FOR, Foraging). All data shown from land survey observations.

Dedicated boat and land surveys revealed the lowest encounter rates were observed in Pre-Monsoon season (0.00 groups per hour on effort; 0.00 groups per hour on effort; Table 2), suggesting this is a regional "low-season" for the species. The highest encounter rates were observed in

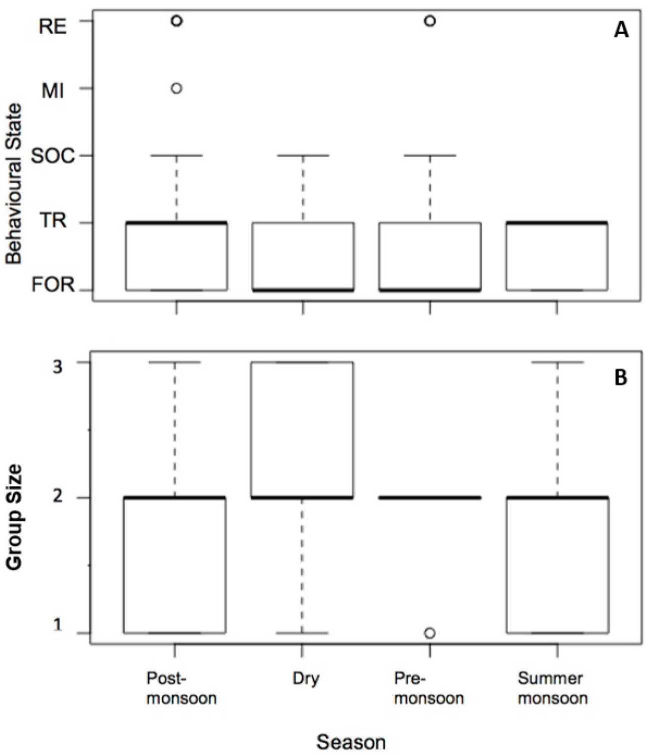


Fig. 7. Boxplots showing which: **A**, Behavioural States (RE, Resting; MI, Milling; SOC, Socialising; TR, Travelling; FOR, Foraging); and **B**, Group Sizes (1, Small; 2, Medium; 3, Large) were seen in each monsoon season based upon boat survey observational data.

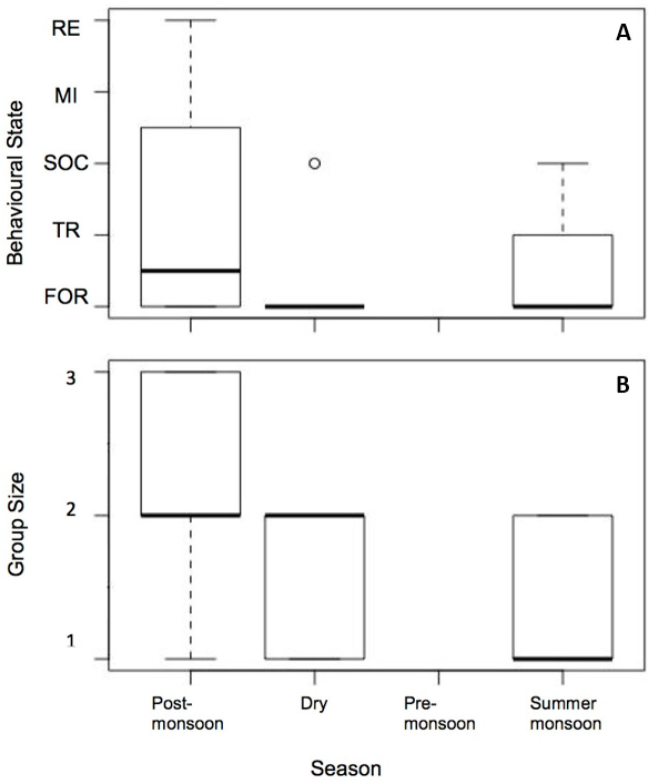


Fig. 8. Boxplots showing which: **A**, Behavioural States (RE, Resting; MI, Milling; SOC, Socialising; TR, Travelling; FOR, Foraging); and **B**, Group Sizes (1, Small; 2, Medium; 3, Large) were seen in each monsoon season based upon land survey observational data.

Summer Monsoon season for boat surveys and Post-Monsoon season for land surveys (Table 2). Seasonal differences in distribution have been reported for the freshwater population of Irrawaddy dolphins in the Mekong river (Beasley, 2007), however where the seasonality of marine populations have been studied, such as those in Sarawak, Malaysia, no seasonal variation has been observed (Minton et al., 2013). Minton et al. (2013)'s Sarawak study did, however, use different seasons (March to May, June to August, September to November) from the current study, which could account for these differences. Discrepancies between land and boat encounter rates during the current study could be explained by the study areas of the land and boat surveys comparatively. The boat surveys covered the northern, central, and southern sections of the archipelago, whereas land surveys only covered the south-east and east portion of the archipelago (Fig. 1). Thus, highlighting a limitation of our land surveys, in that data collected is only representative of a portion of the Kep Archipelago.

The seasonal variation in encounter rates could be explained by variations in freshwater input due to seasonal variations in rainfall. Marine populations of Irrawaddy dolphins reside close to river mouths (Smith et al., 2008; Peter et al., 2016; Mahmud et al., 2018), which could indicate a reliance upon lower salinity waters. Fury & Harrison (2011) carried out a study testing the effects of water quality on dolphin occupancy of estuaries and found that during flood events, i.e., wet season, equivalent to Summer Monsoon season in the current study, dolphins moved further away from the river mouths. Pre-Monsoon had the lowest encounter rates and could be expected to be the season with the lowest freshwater input, due to the lag-time of the low amounts of rainfall during Dry season. As freshwater discharge varies seasonally, so does temperature and the associated turbidity and salinity levels, as well as prey distribution (Quiñones & Montes, 2001; Jung & Houde, 2003; Lloret et al., 2004; Smith et al., 2004; Smith et al., 2006; Coscarella et al., 2010; Minton et al., 2013; Palmer et al., 2014; Wang et al., 2016). For other species of small coastal cetacean, such as the Indo-Pacific Humpback dolphin in Xiamen Bay, China, it is hypothesised that distributional changes throughout the seasons are related to changes in prey availability (Wang et al., 2016). Here, smaller groups are seen further from the coast in the wet season, when prey are more dispersed, and aggregated closer to the coast in the dry season when resources are more concentrated (Wang et al., 2016). Differences in seasonality could therefore be attributed to prey distribution. Squid, which have seasonal variability in abundance due to their mating and spawning cycles (Nabhitabhata et al., 2005), have been shown to be a favoured prey species for the Irrawaddy dolphin (Stacey & Arnold, 1999; Minton et al., 2011; Ponnampalam et al., 2013). A final suggested explanation for variations in encounter rates is water temperature. For Irrawaddy dolphins (Smith et al., 2006), as well as bottlenose dolphins (Vermeulen et al., 2015) and Commerson's dolphins (Coscarella et al., 2010), seasonal movements were found to be associated with water temperature. Therefore, it is suggested that seasonal water temperatures of the Kep and Kampot regions should be researched.

**Critical habitats and seasonality.** Data collected during this study suggests that the Kep Archipelago represents a critical habitat for a population of coastal Irrawaddy dolphins. Juveniles were present throughout all seasons, suggesting the region acts as a critical nursing ground. Protecting nursing grounds is pertinent to the conservation of small cetaceans, as young life stages are particularly vulnerable to species threats (Ross et al., 2011).

Behavioural maps suggest the region is used as a foraging and travelling ground, with habitats changing locations marginally with season (Figs. 3, 4). The increased southerly distribution of Foraging behaviour in the Summer Monsoon season could be attributed to fluctuating freshwater input and associated salinity levels (Tsujimoto et al., 2018), meaning that when there is increased freshwater input, the dolphins expand their distribution further offshore. When looking at behavioural distribution maps, it is important to consider that the locations of the two behaviours were often overlapping. This could be explained by a bias introduced to the data collection methods through the research vessel altering the dolphin's behaviour. Vessel reactions have been shown to occur in other populations of Irrawaddy dolphins in Malaysia and Indonesia (Kreb & Rahadi, 2004; Hashim & Jaaman, 2011).

Socialising behaviour was rarely observed during the current study. For this reason, neither a breeding season, nor a breeding habitat could be determined. However, land data showed that Large group sizes were associated with Post-Monsoon season (GLM, $p=0.00601$; Null deviance: 32.947 on 75 degrees of freedom), with Large group sizes often associated with socialising behaviour for small cetacean species, including Irrawaddy dolphins (Bearzi et al., 1997; Azevedo et al., 2005; Quick & Janik, 2008; Ponnampalam et al., 2013; Akkaya-Bas et al., 2018).

**Behavioural ecology.** Although links between certain behavioural states, behavioural events, swim styles, and group sizes were observed, only certain relationships proved significant. Four of the five relationships that proved significant were from land survey data. This could be a result of land surveys using more passive observation methods than boat surveys.

The current study reports that by using data collected from land surveys, certain behavioural events were found to be linked to certain states. Foraging was found to be associated with the most events. The events presented included Fluke Up, with it likely that this behaviour was used to give the dolphins extra force on a dive bout (Lusseau, 2006), and Tail Slaps, which were likely used as a way to either stun fish or communicate with other members of the group (Connor et al., 2000). Lusseau (2006) carried out a similar study on bottlenose dolphins in New Zealand's Doubtful Sound, reporting that 'tail out dives' and 'tail stock dives' (equivalent to our definition of Fluke Up) were associated with diving (equivalent to our definition of Foraging behaviour). Tail slaps were not found to be associated with diving in the Doubtful Sound, however it was suggested that this could be due to the waters being deep (> 200 m), meaning slaps would not be efficient at stunning fish. Another similar study on the Guiana dolphins of Ilha Grande Bay, Brazil, showed that tail-out dives (equivalent to our definition of Fluke Up) were mostly observed during feeding, signifying the capturing of demersal prey in a shallow sandy/muddy bottom (Tardin et al., 2014). The tail-out dives, or Fluke Up events, indicate that the dolphins may spend longer underwater, increasing their chances of catching demersal prey (Tardin et al., 2014). The waters of Kep and Kampot are shallow, with a sandy/muddy bottom, so it could explain why Fluke-up and Tail Slap events were associated with Foraging in the current study.

Land survey data revealed that juveniles were more commonly found in Medium and Large group sizes, than in Small group sizes (GLM, $p=0.0116$, Null deviance: 20.776 on 75 degrees of freedom). This may be due to larger group sizes providing juveniles with increased protection and learning opportunities, as well as providing more opportunities for calf assistance (Cliff & Dudley, 1992; Vermeulen et al., 2015).

**Conservation significance.** This study provides important initial information on the behavioural ecology, critical habitats, and seasonality of Irrawaddy dolphins in Cambodia's Kep Archipelago. It is also the first study of its kind to provide insight into the relationships between behavioural states and behavioural events for Irrawaddy dolphins. Given the species' conservation status and the threats present in the Kep Archipelago, the study highlights an urgent need to protect regional important habitats for the species (Thompson et al., 2000; Dolar et al., 2002; Smith & Jefferson, 2002; Reeves et al., 2003; Smith et al., 2004; Kannan et al., 2005; Perrin et al., 2005; Smith et al., 2008; Jaaman et al., 2009; Ross et al., 2011; Peter et al., 2016; Minton et al., 2017; Tubbs et al., in press). To support the development of such protection, it is highly recommended that additional research be carried out to: (i) produce rigorous abundance estimates for the population; and (ii) utilise social science techniques to understand the dimensions of threats.

Researchers will work closely with government authorities, fishing communities, and relevant stakeholders to apply findings of seasonal distribution to the development of appropriate conservation measures for the regional population. Additionally, the authors recommend long-term monitoring in the study region to detect changes in distribution over time, as well as an expanded survey area to define the full extent of the population's range. Finally, as the study site is located near the Cambodian-Vietnamese border region, collaboration between scientists from both countries is recommended to determine movement and habitat use across borders.

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