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The population of Irrawaddy dolphins in Brunei Bay, Malaysia is currently under threat by anthropogenic activities. This study is aimed at contributing information on population size, group composition, spatial occurrence and habitat preferences of this dolphin species in the bay area. A total of 36 individuals (adults) of Irrawaddy dolphins were identified using dorsal fin photo match software (DARWIN) by undertaking 297.91 h of boat-based dedicated surveys (April 2013 – October 2015). By using the mark–recapture open-population parameterization, the estimated population size (adult) was 33 (95% CI = 28–39) with the apparent survival rate of 0.98 (0.89–0.99, SE = 0.01). Also, the recapture rate was 0.27 (0.14–0.45, SE = 0.07) and the estimated individual entry rate from super-population was 0.15 (0.10–0.22, SE = 0.03). The estimated entire population size was 41 (95% CI = 36–49) including calves. The observed mean group size was 6 (SE = 0.66, range 1–18). Two hotspots were identified for dolphin occurrences near Lawas and Labuan Island at a sighting rate of 2.8–12.3 km^{-2}. The dolphins were encountered in the bay over the entire year with no seasonal differences. The observation of dolphin calves in the groups are a positive indicator that the dolphins are breeding successfully in the Bay area and provide hope that the population will remain stable or increase in number. The dolphins showed habitat preferences of sea depths (2 to 9.99 m), surface water temperature (29 to 31.99°C), and coastline distance (1.5 to 4.49 km). This study provides the first detailed information about Irrawaddy dolphins in the Brunei Bay, Malaysia, and may serve as a baseline for future comparisons. It can help researchers, conservationists, local marine park managers and policy makers to propose effective conservation and management plans in the Brunei Bay area.

Delphinids (Delphinidae) represent one of the most social and complex groups of mammals, which have cognitive competencies present just in some mammal species (Whitehead et al. 2000). As top-level predators, they play a unique role in the structure and function of marine communities (Whitehead et al. 2000). They also have long life spans, late maturity, low reproduction rates and extended parental care (Taylor 2002). Therefore, they are incapable of enduring the increasing rates of anthropogenic mortality (Beasley 2007). These characteristics lead to slow rates of population growth and vulnerability to rapid population declines (Taylor 2002).

Population size is a vital aspect of the ecology of any species, and its estimation represents an indispensable component in the management of wildlife (Williams et al. 2002). For instance, the estimation of sustainable reduction of animal population levels necessitates the knowledge of the abundance and their variances (Wade 1998). In general, precise estimation of the cetacean population is difficult, costly and time-consuming (Taylor and Gerrodette 1993). The sampling design and environmental variability are crucial factors because they can affect our ability to estimate cetacean population sizes and trends of variation (Thompson et al. 2000). Careful survey plans and investigation of the assumptions are fundamental for reasonably accurate population estimates (Read et al. 2003).

Cetacean distribution is influenced by a list of environmental factors i.e. physico-chemical and climatological variables, biotic factors (competition and predation), and anthropogenic causes (fishing activities and boat traffic)

(MacLeod et al. 2004). Depending on the geographical area involved, interactions between these different aspects may vary (Jefferson et al. 1993). Fluctuations in temperature and salinity of different water bodies have an especially great impact on the distribution of cetaceans (Baumgartner and Mate 2005). In addition, cetacean distribution patterns are influenced by the seasons and time of the day due to seasonal abundance of resources, presence of other species and habitat structure (Daura-Jorge et al. 2005). Substantial social knowledge is essential for group members to recognize each other, distinguish their rank in the social hierarchy, form and uphold alliances, and engage in and interpret an extensive range of social behaviors (Herman 1991). Group size and composition can fluctuate depending on the species, location, prey availability, predation risk, age, gender and reproductive status of an individual in a group (Michaud 2005).

Among the diversity of habitats that are inhabited by dolphins in the marine environment, coastal areas are considered most vulnerable to anthropogenic activities (McIntyre 1999). Thus, some species of coastal dolphins are among the most threatened species of cetaceans (Parra 2005), and the Irrawaddy dolphin, *Orcaella brevirostris* (Owen in Gray, 1866) is one such example. Sir Richard Owen first described this species in 1866, based on a specimen found in 1852 in the harbor of Visakhapatnam on the east coast of India (Sinha 2004). Irrawaddy dolphins have been delineated as 'facultative' river cetaceans considering their adaptability to inhabit both marine and freshwater environments (Leatherwood and Reeves 1994). According to the International Union for Conservation of Nature (IUCN) Red List of Threatened species, they are categorized as Vulnerable (Reeves et al. 2008). In general, their population is decreasing (Reeves et al. 2008). Five subpopulations of Irrawaddy dolphin are already categorized as Critically Endangered in their habitats located in the Ayeyarwady River (Smith 2004), Mahakam River (Jefferson et al. 2008), Malampaya Sound (Smith and Beasley 2004a), Mekong River (Smith and Beasley 2004b) and Songkhla Lake (Smith and Beasley 2004c). Irrawaddy dolphins inhabit the shallow, near shore tropical and subtropical rivers, and in marine waters of the Indo-West Pacific (Dolar et al. 1997). These dolphins have been observed from Visakhapatnam to the deltas of Brahmaputra and Ganges Rivers in India (James et al. 1989). They have also been observed in coastal water bodies of Bangladesh, Brunei Darussalam, Cambodia, India, Indonesia, Lao People's Democratic Republic, Malaysia, Myanmar, Philippines, Singapore, Thailand and Vietnam (Pilleri and Gihr 1974, Perrin et al. 1995, Smith et al. 1997, Stacey and Leatherwood 1997, Parra 2005, Kreb et al. 2007, Reeves et al. 2008, Sutaria and Marsh 2011, Hines et al. 2015). Several studies on Irrawaddy dolphins were conducted already in Malaysia such as distribution and sighting rate estimated by Bali et al. (2008), Jaaman (2010) and Kuit et al. (2014); abundance estimated by Minton et al. (2013), Woan et al. (2013); acoustic studied by Hoffman et al. (2016); habitat characteristics and critical areas investigated by Peter et al. (2016); and behavioral observations by Kamaruzzan et al. (2011). However, the Irrawaddy dolphin population has not been studied yet in Brunei Bay and the dolphin population in the bay is under threat by several anthropogenic activities, i.e. accidental bycatch in fisheries (Jaaman et al. 2009), water quality and habitat degradation due to land clearing for coastal development (Long 2014), untreated domestic sewage from the catchment areas (Yau 1988), intense shipping and maritime activities (Eng 1992), and overfishing (Silvestre and Garces 2004). In order to contribute to the long-term conservation and management of this species, it was necessary to carry out an ecological assessment of the population in the Bay. To this aim, the present study was conducted to achieve the following specific objectives: 1) to estimate the population size of Irrawaddy dolphin in the Brunei Bay, Malaysia; 2) to quantify group size and composition (i.e. the presence and number of calves and adults); 3) to assess the spatial occurrence of Irrawaddy dolphins; 4) to assess the daytime (morning and afternoon) and seasonal occurrences of Irrawaddy dolphins; 5) to assess how habitat abiotic factors (sea depth, surface water temperature, salinity, turbidity and nearby coast distance) may impact the occurrence of Irrawaddy dolphins.

Material and methods

Study area

The study was conducted at the Malaysian side of Brunei Bay, which is important as a nursery, foraging and transient ground for sea turtles, dugongs and coastal cetaceans (Rajmani and Marsh 2010). About 30% of Brunei Bay is in Brunei territory, and 70% is in Malaysia, the joint domain of Sarawak, Sabah and Federal Territory of Labuan. The coastal and marine ecosystems in this bay comprise mangrove forests, seagrass beds, estuarine systems, mudflats and coral reefs (Bali 2005, Bujang et al. 2006, Jaaman et al. 2010). Also, this bay has a continental slope (Ahmad-Kamil et al. 2013), where the continental shelf is 50–70 km wide and underlained by 8–10 km of siliciclastic sediments (Straub et al. 2012). At a sea depth of ~200 m the continental shelf-slope break occurs, and the seabed descends steeply to reach the floor of the Borneo Trough at a sea depth of 2800 m (Straub and Mohrig 2009). According to Mohamed and Landner (1993), in Brunei Bay the water residence time (WRT) is two weeks, stratification occurs at approximately 6 m depth; due to a 2–3 ppt salinity difference, an upwelling is observed in the inshore waters. The sea surface temperature (SST) ranges from 24.60 to 32.02°C (Hee and Suratman 2016), and air average humidity throughout the year is 82% (Hogan 2011). Brunei Bay has a high quantity of fish resources (Joseph et al. 2016) and 54 species of fish mentioned by Mohamed and Landner (1993). Fishing is the second most important economic activity in the Bay (Department of Fisheries Sabah 2008). A total of 78 species of phytoplankton and 80 different soft bottom fauna species are reported in this Bay (Mohamed and Landner 1993). For its ecological uniqueness and economic significance, Brunei Bay is a high-priority area for research and conservation of marine organisms (Joseph et al. 2016).

Fieldwork

Line-transect boat surveys (Hiby and Hammond 1989, Beasley et al. 2013) were conducted in the Bay from April

2013 to October 2015 (Fig. 1). A 10 m long speedboat with 40 and 35 hp engines was used to survey the inner part of the Bay. The speed of the boat was approximately 12 km h^{-1}. The transect lines for each year were different to cover the whole Bay (Fig. 1). Transect lines were designed within the Malaysian territory. In the surveys, limitations were imposed by local marine security during crossings of borders in state waters and the international harbor in the bay. Surveys were conducted within 5 km from the coastline during four periods of the year (January, April, July and end of September or beginning of October). In Malaysia, the four periods are corresponding to the Northeast Monsoon (November–March) and Southwest Monsoon (May–September) with two transitional periods between the two monsoons, generally known as the Inter-Monsoon seasons (IMS), occurring in April and October (Malaysian Meteorological Department 2008). For each season, 10–12 days were dedicated to the survey (depending on sea conditions) with each covering the whole bay (except the Brunei part). Surveys were generally carried out between the 7:00 to 15:00 h range due to increasing winds in the afternoon. While the boat was moving along the transect line, there was a team of five observers; one observer located at the bow of the boat searched for dolphin groups ahead; two observers on each side of the boat made observations with the aid of 7 × 50 binoculars; and two additional observers maintained a constant search of the near area around the boat with the naked eye. Parra (2005) defined a school of dolphins as the case where a group of dolphins have relatively close spatial cohesion (i.e. the distance between individuals did not exceed 100 m). Once a group was encountered, the search effort stopped and the position of the boat was marked for site information and recorded with a marine handheld GPS receiver. An electronic compass barometer was used to collect information on weather and the Beaufort Sea state from the start of the transect line. This information was recorded again whenever conditions changed during the rest of the transect line. A depth meter was used to measure sea depth (m); a portable turbidity meter to measure turbidity (Nephelometric Turbidity Unit, NTU); YSI Multiprobe meter to measure sea surface temperature (°C) and surface water salinity (ppt). The survey boat would follow a dolphin or group by keeping a safe distance of 20 to 50 m from them, to identify species, assess group size and take photographs of the dorsal fins of the adults through two cameras. A calf was defined as a particularly smaller individual which is closely associated with another larger (adult) dolphin. The number of calves was counted in a group by the naked eyes, and they were not considered for this population estimation using mark–recapture photo-ID because calves are not born with marks in their dorsal fins

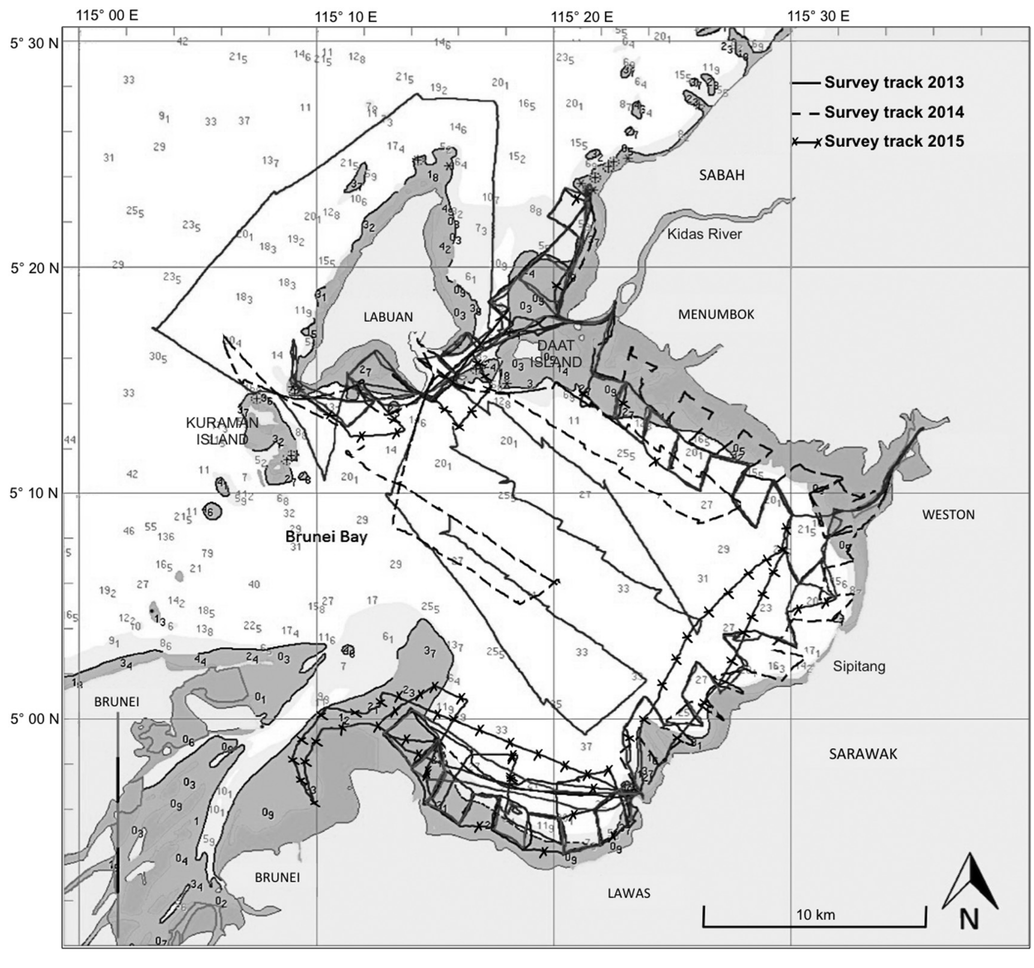

Figure 1. Map indicating survey transects lines for 2013–2015 survey years in the Brunei Bay, Malaysia. OpenCPN 4.2.0 (Windows 2016) was used to generate the map. Map modified from Mahmud et al. 2018.

(Ryan et al. 2011). The calves were observed to have grown in length by 59% (96 cm to 1.53 m) and 266% (12.3 to 45 kg) in weight during the first seven months (Tas'an et al. 1980), and they achieve their adult size in 4 to 6 years (Stacey and Arnold 1999).

Data analysis

Photo identification

Right side dorsal fin photographs of adult Irrawaddy dolphins were imported in Photos 1.5 for iOS 2015, a photograph-editing program. Images were organized by date, then cropped and sorted by putting rank (Q1–Q6) based on their quality (Gowans and Whitehead 2001). The highest quality considered as Q6 is when notches and niches of the dorsal fins were clearly visible and at a good focus (Towner et al. 2013). When the quality of photo-ID decreased the rank also decreased (Towner et al. 2013). Based on dorsal fin photographic assessment criteria of Gowans and Whitehead (2001), a total of 1078 photographs (right side of dorsal fin) of Q5, Q4 and Q3 were imported into DARWIN 2.22 for IOS 2011 dorsal fin ID software (Wilkin et al. 1998, Barata and Brooks 2005, Beirão et al. 2014) (Table 1). Well-marked (having nicks in dorsal fins) photographs were considered for analysis. Any unmarked photograph of dorsal fins was not considered for mark–recapture analysis. Each dorsal fin was traced with a fixed spacing of the points along the leading and trailing edges. After that, the dorsal fin was compared to the entire catalogues and obtained a rank based on the probability of the match. When fins matched, it meant that those fins were already in the catalogue with ID codes. Before considering a new fin the matching was confirmed by looking at fin outline and marks. Once a new fin was found, it was assigned to a unique ID code (first sighting date and time) and then added to the catalogue. From the surveys 106 photographs of left side dorsal fins were captured and not considered for the analysis.

Capture–recapture analysis

To assess the abundance, data from DARWIN was transferred to Microsoft Excel. Then Program MARK 8.1 was used to perform mark–recapture analyses of the individual sighting histories of identity (White and Burnham 1999, Kreb 2004, Smith et al. 2006, Sutaria and Marsh 2011, Minton et al. 2013). We had 11 encounter occasions from 2013–2015, and it was impossible to define secondary occasions. A close population model was not a plausible assumption here for several reasons i.e. mortality could occur over the survey period, the bay is open, and Irrawaddy dolphins were travelling to the bay area of Brunei part. In those cases, the open-population POPAN parameterization with Cormack–Jolly–Seber (CJS) model was used to estimate population parameters (Schwarz and Arnason 1996, 2009). The parameter ϕ refers to apparent survival rate, p is the probability of the observation, b is the probability that an individual from the super-population would enter the survey area between capture occasions, and N is the estimated population size (Schwarz and Arnason 1996). Super-population refers the sum of the observable (inside of study area) and unobservable (outside of study area) individuals (Kendall 2008). The subscripts **.** and t in model notation exemplify constant and time-dependent parameters respectively (Lebreton et al. 1992). Maximum likelihood models were used to estimate population parameters (Towner et al. 2013). For goodness-of-fit (GOF) tests of the CJS model, Program RELEASE was used for validating model assumptions (Burnham et al. 1987). Models were assembled for consolidations of time-dependence and consistency for each parameter, and the most suitable model was chosen using the small sample corrected Akaike information criterion (AIC_C) (Burnham and Anderson 1998). Based on the GOF results of TEST 2+ TEST 3 in RELEASE, a post hoc variance inflation factor ($\hat{C}$) could be calculated to conform for extra-binomial variation in the data resulting in a quasi-Akaike information criterion ($QAIC_C$).

Open capture–recapture models

To avoid initiating bias in estimates of abundance, survival, recapture and entrance probability using capture–recapture methods, it is necessary that model assumptions are met. In this study the open model (POPAN parameterization with CJS) model assumptions (Lebreton et al. 1992) were the following: 1) natural marks carried by dolphins during this study should not be lost or missed, 2) natural marks carried by all individuals should be accurately identified during recaptures, 3) individuals should be released quickly after being captured, 4) sampling sessions should be of shorter duration compared to total duration of the sampling period, 5) all live marked dolphins available on each sampling occasion should have equal capture probabilities, 6) survival probabilities, and 7) individual dolphins from super-population should have higher chance to enter the survey area between capture occasions. To validate the first assumption, strict quality controls were adopted during

Table 1. The scale applied during photographic assessment to determine the quality of Irrawaddy dolphins dorsal fin photos in Brunei Bay, based on the criteria by Gowans and Whitehead (2001).

Quality rating	Criteria	No. of well marked dorsal fin photos imported to DARWIN 2.22	No. of unmarked dorsal fin photos
Q1	very distant, poor focus and very little flank showing, fin not square on	NC	NC
Q2	very distant photograph with little flank showing	NC	NC
Q3	distant photograph with little flank showing	79	24
Q4	distant photograph with most of the flank showing	946	147
Q5	close with good representation of the flank	53	9
Q6	close photograph with most of the flank showing, well focused and exposed image, fin square on to camera	0	0

NC = not considered for the analysis.

data analysis and the only photo-ID images used to identify dolphins were high quality (Q3, Q4, Q5) with distinctive fins. Our current estimates were not produced using images of individuals with no marks so including them in future analysis might help to contextualize our current results. To validate the second assumption and minimize human errors in matching dorsal fins over the years, regular checks were conducted by only the most experienced researchers (SAJ or XZ). For the third assumption, dolphins were not physically removed during each photographic session but simply captured in a photo-identification image (Silva et al. 2009). The time spent photographing dolphins was much shorter in duration compared to the time spent searching for dolphins in between photographic sessions, so this assumption was respected. The fourth assumption was also met having sampling occasions of 10–12 days, which is much shorter of duration than the interval between occasions (three months). To verify the fifth, sixth and seventh assumptions were met using POPAN parameterization to estimate these parameters. Equal recapture probabilities were partially met because mixing between sampling periods occurred, with individuals observed leaving our study areas returning sometime later. However, movements outside of the bay (in the Brunei part) showed that some individuals have home ranges that extend beyond areas of our survey effort, making them unavailable for capture during this study. The assumption of equal survival probability was likely achieved in this study because no commercial or illegal hunting (of dolphins) occurred in Malaysian coastal shelf waters. The seventh assumption was partially met, where dolphins travelled to the Malaysian part from the bay of Brunei side, which could be attributed to foraging and socializing purposes.

Group composition

To investigate the group composition of Irrawaddy dolphins in relation to group size, the composition of groups was first calculated as percentages of adults and calves. The percentages of adults were then grouped into group sizes, i.e. small (1–5 individuals), medium (6–10 individuals) and large (11–20 individuals). For this purpose, the Kruskal–Wallis test was performed and a post hoc comparison Mann–Whitney pairwise test applied.

Distribution

The dolphins' spatial occurrence map and sighting density map were generated to locate hotspots for Irrawaddy dolphins using ArGIS 9 (ArcMap ver. 9.3) by importing all sighting GPS coordinates, to test if the Irrawaddy dolphins homogenously occurred in the Bay. To compare the mean number of sightings per hours of survey effort between morning and afternoon, the Mann–Whitney test was applied. Furthermore, to investigate if all groups of Irrawaddy dolphins had the same occurrence, the mean numbers of individuals were based on the seasons [IMS (April), SWM, IMS (October) and NEM] by performing the Kruskal–Wallis test and the post hoc comparison (Mann–Whitney pairwise test). This statistical test was performed by running PAST 3.04 for iOS 2014.

Habitat preference

To investigate if this dolphin population had preferences in terms of sea depth, surface water temperature, salinity, turbidity and distance from the coast, a chi-square test of conformity was performed using R ver. 3.1.3 for iOS 2014 to compare the number of individual occurrences in different ranges of abiotic factors. For this, all the abiotic factor parameters were stratified into bins of five units (e.g. 0.1–4.99 m, 5–9.99 m for depth; 27–27.99°C, 28–28.99°C for sea surface temperature; 0.1–4.99 ppt, 5–9.99 ppt for surface water salinity; 0NTU, 0.1–9.99NTU for turbidity; 0.1–1.49 km, 1.5–2.99 km for nearby coast distance from occurrence). The Euclidean distance function (ESRI 1996) was used to compute the shortest distance to the nearest shoreline from the sighting position. However, the survey effort was randomly distributed with respect to abiotic factors, the dolphins' sighting, and occurrences. For all statistic tests, $\alpha = 5\%$ were chosen as significance criterion.

Results

Survey effort and distance covered by the observers

A total of 3574.92 km of surveys were undertaken in 129 days from 2013 to 2015 in the Bay with a total survey effort of 297.91 hours. Survey effort was varied during the years and seasons due to different transect lines, which were followed for different years and changing sea state (Beaufort scale) (Table 2).

Population parameters estimation (capture–recapture)

A total of 36 individual adult Irrawaddy dolphins were photo-identified from 2013 to 2015. We tested eight CJS models with POPAN parameterization, where model $\{\phi_. \, p_t \, b\}$ did not converge. For the remaining seven models, model choice criteria and parameter estimates are shown in Table 3. On the basis of AIC_C scores, model $\{\phi_. \, p_t \, b_t\}$ (constant survival, time dependent probability of capture and probability of entry) was the most parsimonious, and the estimated population size (N) was 33 (95% confidence interval = 28–39, SE = 3) (Table 3). In addition, the estimated constant survival (ϕ-hat) was 0.98 (0.89–0.99, SE = 0.01), and the time dependent observation rate (p-hat) was 0.27 (0.14–0.45, SE = 0.07) (Table 4). The estimated time dependent individual entry rate from super-population (b-hat) was 0.15 (0.10–0.22, SE = 0.03) (Table 4). Based on the result of TEST 2 + TEST 3 in Program RELEASE (Table 5), a variance inflation factor of $\hat{C} = 0.83$ was estimated and applied, reflecting under-dispersion in the data (Cooch and White 2009). There was no violation of underlying open-population mark–recapture assumptions, and all TEST results indicated equal survival probabilities (SR) and seasonal migrations (SM) among photographically captured dolphins where no significant p-value was found in the TEST results (Table 5).

Entire population estimation

According to Jaaman (2010) following the Irrawaddy dolphins was sometimes very challenging because they are shy and evasive, often changing direction or swimming

Table 2. Conducted boat surveys for photographically identified Irrawaddy dolphins (adult and calf) with survey efforts from 2013–2015 in Brunei Bay. 11.10% of the observed animals were not amenable to photo-ID. Also, 12.02% of the sampled animals' photographs (Q3–Q5) were not amenable to mark–recapture analysis due to lack of the presence of a mark in their dorsal fins.

Boat surveys		No. of dolphins				Survey efforts (h) under different Beaufort sea states from 2013–2015				
Year	Seasons	Observed	Captured photographically	Captured photographically with well-marked dorsal fins (nicks)	Newly identified (adult)	B0	B1	B2	B3	Total effort
2013	inter-monsoon (April)	10	8	0	0					
	south-west monsoon	56	52	48	12	23.37	44.43	8.05	8.98	84.83
	inter-monsoon (October)	1	1	1	0					
2014	north-east monsoon	47	42	38	11					
	inter-monsoon (April)	16	14	12	2	48.88	72.03	8.0	10.57	139.48
	south-west monsoon	4	4	2	1					
	inter-monsoon (October)	43	39	36	8					
2015	north-east monsoon	21	19	17	2					
	inter-monsoon (April)	39	35	33	0	20.4	32.87	11.75	8.58	73.60
	south-west monsoon	17	14	12	0					
	inter-monsoon (October)	33	30	28	0					

away when the survey boat approached them. In Brunei Bay, 11.10% of the observed animals were not amenable to photo-ID due to several reasons: (a) sometimes dolphins were disappeared completely from water surface before capturing their dorsal fin photos due to the boat approaching, (b) poor quality dorsal fin photos (Q2, Q1) were taken due to bad weather conditions (Beaufort sea state 4). Also, 12.02% of the sampled animals' photographs (Q3-Q5) were not amenable to mark–recapture analysis due to lack of the presence of a mark in their dorsal fins. Hence the population was estimated for the 0.88 proportion that was well marked. Dividing the estimate (N) by this proportion yielded a result of 38 as an estimate of the adult population. Applying the same on 95% CI (confidence interval) gave a result of 38 (95% CI = 32–44) for the adult population. Also, once we included calves using the same approach we got an estimate of 41 (95% CI = 36–49) for the entire population including calves.

Group size and composition

A total of 47 dolphin groups were encountered during the survey period. Groups of Irrawaddy dolphins varied in size from 1 to 18 animals, with a mean of 6 (SE = 0.66). In the group composition we had observed zero to one calf in small and medium-sized groups, and one to two calves in large size groups. The mean proportion of adults and calves in the group were 91.25% ± 1.84% and 8.75% ± 1.84% respectively. No statistically significant differences were observed comparing the group composition under different group sizes. However, the observations of Irrawaddy dolphin calves in the groups are a positive indicator that the dolphins are breeding successfully in the bay area and provide hope that the population will remain stable or increase in numbers.

Distribution

The survey team encountered 47 dolphin groups at 36 GPS locations (sightings). Dolphins were encountered more than once near the GPS locations of Lawas and Labuan Island. Dolphins did not occur homogeneously in the Brunei Bay, Malaysian waters. Two hotspots were identified there, one near Lawas and the other near Labuan Island. The number of sightings (sighting rate 2.8–12.3 km^{-2}) (Fig. 2a) and the number of individuals' occurrence was higher in both areas (Fig. 2b). However, there were no significant differences between seasons by comparing the mean number of sightings per hours of survey effort. Also, no significant differences were found between seasons by comparing the mean number of individuals' occurrence. Regarding daytime occurrence, there were 30 sightings in the morning and six in the afternoon. No statistically significant differences were found by comparing the mean number of sightings per hours of survey effort between morning and afternoon. Survey efforts were higher in the morning than the afternoon, with 217.93 hours in the morning and 79.98 in the afternoon. Comparing the mean number of individ-

Table 3. Model choice criteria and abundance estimates (N) tested in the mark–recapture analysis of Irrawaddy dolphins in the Brunei Bay, Malaysia (2013–2015), using the open-population POPAN parameterization in Program MARK.

Model	AIC_C	ΔAIC_C	AIC_C weight	Model likelihood	Parameters	Deviance	n	n with 95% confidence interval Lower	Upper	SE for n
$\phi_{.}\, p_t\, b_t$	351.31	0	0.99997	1.00	13	69.86	33	28	39	3
$\phi_t\, p_t\, b_t$	372.34	21.02	0.00003	0	22	66.91	32	27	37	3
$\phi_{.}\, p_{.}\, b_t$	379.48	28.16	0	0	5	116.55	33	28	38	3
$\phi_t\, p_{.}\, b_t$	394.64	44.33	0	0	13	114.18	32	27	38	3
$\phi_t\, p_t\, b_{.}$	536.09	184.77	0	0	19	239.07	46	39	55	4
$\phi_{.}\, p_{.}\, b_{.}$	17284.08	16932.77	0	0	3	17025.43	93	48	181	33
$\phi_t\, p_{.}\, b_{.}$	17322.49	16971.19	0	0	10	17048.26	80	79	81	1

ϕ = apparent survival; p = probability of the observation; b = probability that an individual from the super-population enters the survey area; **.** = constant parameter; t = time-dependent parameter; AIC_C = Akaike information criterion for small sample bias; n = estimated population size; SE = standard error.
Model {$\phi_{.}\, p_t\, b_{.}$} did not converge.

uals per group, adults per group and calves per group, there were no significant differences observed between seasons.

Habitat preference

In the current study, the range of sea depth was 2 to 30.4m during the dolphins' encounters. Statistically significant differences ($\chi^2 = 40.26$, df = 5, p-value < 0.001) were observed for dolphin occurrences under different depth categories. Numbers of encounters and occurrences were higher between 2 to 9.99 m depths (Table 6). The range of surface water temperatures during the survey periods was 28 to 32°C and significant differences were observed for individual occurrences under different water temperature ranges ($\chi^2 = 12.67$, df = 5, p-value = 0.03). The highest number of encounters occurred between 29 to 31.99°C (Table 6). The range of surface water salinity was 0.27 to 27.42 ppt during the encounter period. There were no statistically significant differences observed for individual occurrences under different categories of salinity (Table 6). No significant differences were found statistically under different turbidity ranges (Table 6). Also, no encounters happened when nearby coastline distance was < 1 km and > 7 km, and maximum occurrences were from 1.5 to 4.49 km. A statistically significant difference of occurrence was found at different coastline distances from dolphins' occurrences ($\chi^2 = 27.23$, df = 4, p-value < 0.001) (Table 6).

Discussion

Photo-identification was validated as an indispensable tool in the evaluation of population size, occurrence, social organization, distribution and migration patterns of many species of cetaceans since 1970 (Hammond et al. 1990, Whitehead et al. 2000). Irrawaddy dolphins are elusive and display unobtrusive behavior at the water surface; during a slow rolling dive only the upper-most dorsal surface of the animal becomes visible (Smith 2009). The absence of distinctive marks, cryptic surfacing and research vessel avoidance by the dolphins are the main problems for the photo identification techniques (Smith et al. 2004), so higher effort is needed for their photo-identification (Lloze 1973, Dhandapani 1992, Kreb 1999). Similar problems had occurred for our survey team in the Brunei Bay. In this case, the computer program DARWIN was used and found suitable for dorsal fin matching (based on fin shape and outline) and cataloging, but this program also had infrequent considerable errors to rank fins. This flaw was considered as minor when compared to the naked eye matching (Towner et al. 2013).

No historical data for the abundance of Irrawaddy dolphin exist in the Brunei Bay population. In the current study, the estimated entire population size was 41 (95%; CI = 36–49), which is comparatively higher than Songkhla Lake population but lower than the population of Sundarban Mangrove Forest, Kuching Bay, Bangpakong Estuary, Balikpapan Bay, Coastal water bodies of Bangladesh, Chilika Lake, Banten

Table 4. Model with estimated survival rate, observation rate, and individual entry rate from super-population in the mark–recapture analysis for right side fins of Irrawaddy dolphins in the Brunei Bay, Malaysia (2013–2015), using the open-population POPAN parameterization in Program MARK.

Model	ϕ-hat	ϕ-hat with 95% confidence interval Lower	Upper	SE for ϕ-hat	p-hat	p-hat with 95% confidence interval Lower	Upper	SE for p-hat	b-hat	b-hat with 95% confidence interval Lower	Upper	SE for b-hat
$\phi_{.}\, p_t\, b_t$	0.98	0.89	0.99	0.01	0.27	0.14	0.45	0.07	0.15	0.10	0.22	0.03
$\phi_t\, p_t\, b_t$	0.94	0.63	0.98	0.07	0.28	0.15	0.46	0.08	<0.001	<0.001	<0.001	<0.001
$\phi_{.}\, p_{.}\, b_t$	0.98	0.90	0.99	0.01	0.48	0.41	0.56	0.04	<0.001	<0.001	<0.001	<0.001
$\phi_t\, p_{.}\, b_t$	0.90	0.55	0.98	0.09	0.49	0.42	0.56	0.03	<0.001	<0.001	<0.001	<0.001
$\phi_t\, p_t\, b_{.}$	0.99	0.98	1.00	<0.001	0.26	0.15	0.41	0.07	<0.001	<0.001	<0.001	<0.001
$\phi_{.}\, p_{.}\, b_{.}$	0.96	0.92	0.98	0.01	0.61	0.58	0.64	0.02	1.00	0	1.00	1.00
$\phi_t\, p_{.}\, b_{.}$	0.90	0.90	0.91	<0.001	0.61	0.60	0.61	<0.001	0.99	<0.001	1.00	<0.001

ϕ-hat = survival rate; p-hat = observation rate; b-hat = individual entry rate from super-population; SE = standard error.

Table 5. Goodness-of-fit results (program RELEASE) for the fully time-dependent/Cormack–Jolly–Seber model tested in mark–recapture analysis of individual sighting histories of Irrawaddy dolphins in the Brunei Bay, Malaysia (2013–2015), using open-population POPAN parameterization (program MARK).

Test	χ^2	df	p-level	$\hat{C}$
2	10.5886	8	0.2261	
3	0.9804	6	0.9863	
3.SR	0.6816	3	0.8775	
3.SM	0.2988	3	0.9603	
2+3	11.5690	14	0.6409	0.83

$\hat{C}$ = variance inflation factor; SR = survival rate; SM = seasonal migration; df = degrees of freedom.

Bay, Cowie Bay and Malampaya sound (Table 7). The estimated mean group size and group size range of Irrawaddy dolphins are similar to the findings of Parra (2005) and Dolar et al. (1997), but higher than Smith et al. (2006) and Kreb and Budiono (2005a) (Table 8).

Out of 36 sightings of the dolphins, most of the encounters happened near the Lawas area and Labuan Island. One of the possible reasons could be fish availability in these areas. In fact, during the survey period the survey team observed higher numbers of fishing trawlers near these areas compare to the other sides of the bay. Dolphins have a greater risk of injury and mortality through the entanglement in the trawlers' fishing nets. According to Read (2008), fishing-related mortality of small cetaceans is considered the most severe and immediate threat worldwide. Based on DOF Sabah (2008), Brunei Bay is one of the major prawn trawling grounds of Sabah. Fishing time in the bay varies and is often determined by weather (Matsumoto 2007). In the Brunei Bay, Matsumoto (2007) identified 106 species of fishes, crustaceans, bivalves, gastropods and cephalopods, including

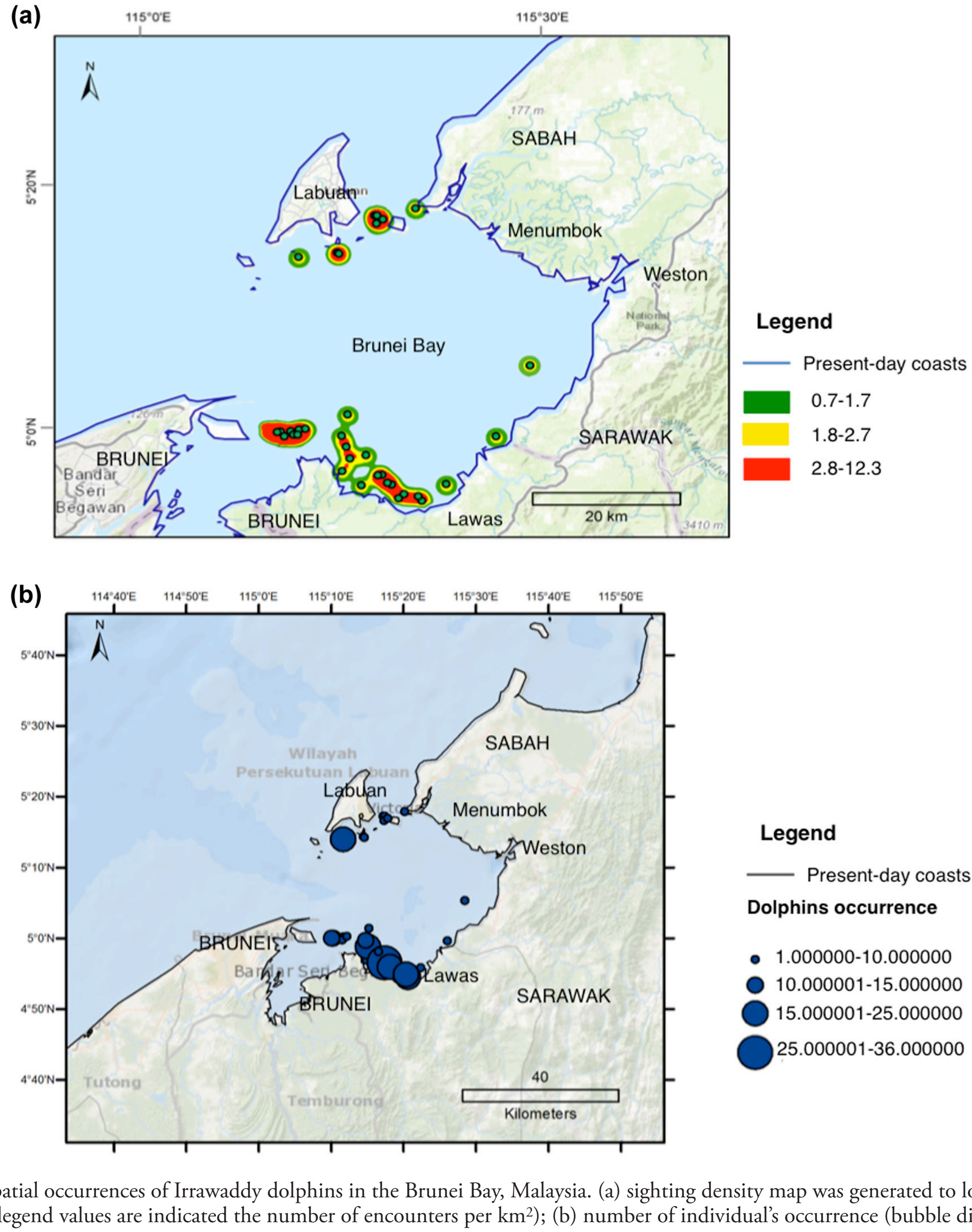

Figure 2. Spatial occurrences of Irrawaddy dolphins in the Brunei Bay, Malaysia. (a) sighting density map was generated to locate hotspots in the bay (legend values are indicated the number of encounters per km²); (b) number of individual's occurrence (bubble diagram).

Table 6. Comparison of the number of individual occurrences and sightings under different abiotic factors range in the Brunei Bay, Malaysia (χ^2-test).

Abiotic factors	Parameters range	No. of individual occurrence	No. of sightings	χ^2-test for given probabilities		
				χ^2 value	df	*p*-value
Sea depth (m)	0.1–4.99	64	11			
	5–9.99	74	9			
	10–14.99	70	7			
	15–19.99	53	4	40.26	5	< 0.001
	25–29.99	11	4			
	30–34.99	10	1			
Surface water temperature (SWT) (°C)	27–27.99	2	1			
	28–28.99	12	1			
	29–29.99	102	13	12.67	5	0.03
	30–30.99	102	13			
	31–31.99	62	7			
	32–32.99	2	1			
Surface water salinity (SWS) (ppt)	0.1–4.99	26	3			
	10–14.99	10	3	8.80	4	0.06
	15–19.99	15	2			
	20–24.99	79	9			
	25–29.99	152	19			
Turbidity (NTU)	0	57	8			
	0.1–9.99	152	19			
	10–19.99	51	6	0.66	3	0.88
	30–39.99	22	3			
Nearby coastline distance from occurrence (NCDFO) (km)	0.1–1.49	40	6			
	1.5–2.99	98	9			
	3–4.49	110	13	27.23	4	< 0.001
	4.5–5.99	33	7			
	6–7.49	1	1			

For 20–24.99 m depth, 5–9.99 ppt salinity and 20–29.99 NTU turbidity ranges, we did not encounter any dolphins.

12 families of fishes and three families of cephalopods with a total of 29 species that are preferred by Irrawaddy dolphins as prey (Heinsohn 1979, Marsh et al. 1989). There were no dolphin occurrences in the east of the Brunei Bay, near Weston and Menumbok. The probable cause for this may be the presence of a developed industrial (offshore oil platform), mega coastal development projects and an international harbor (busy water traffics) in those areas. These infrastructures may have disturbed and chased out Irrawaddy dolphins from the areas as in Banten Bay, Indonesia (Khalifa et al. 2014), but more study is needed to determine that. Furthermore, this dolphin species exhibits high sensi-

Table 7. Estimated population sizes of Irrawaddy dolphins in different areas. CI = confidence interval; CV = coefficient of variance; SE = standard error; NA = not available.

Countries	Places	Estimated population size	Size of the study area (km²)	Reference(s)
Australia	Bowling Green Bay	3	NA	Parra and Corkeron 2001
Australia	Cleveland Bay, northeast Queensland	67 (95 % CI = 51-88)	NA	Parra 2005
Bangladesh	Coastal water bodies of Bangladesh	5383 (CV = 40 %)	47150	Smith et al. 2005
Bangladesh	Sundarbans mangrove forest	451 (CV = 9.6 %)	1756	Smith et al. 2006
Cambodia	Mekong River	40	NA	Baird and Beasley 2005
Cambodia, LAO PDR, Vietnam	Mekong River	125 (95% CI = 114–152)	NA	Beasley et al. 2007
India	Chilika Lake	109 (CV = 7 %)	1165	Sutaria and Marsh 2011
Indonesia	Mahakam River	70 (CV = 10 %)	NA	Kreb et al. 2007
Indonesia	Banten Bay	10–15	150	Khalifa et al. 2014
Indonesia	Balikpapan Bay	67 (59–74)	120	Kreb 2008
Malaysia	Kuching Bay, Sarawak	149 (CV = 28 %)	ca. 520	Minton et al. 2013
Malaysia	Cowie Bay, Sabah	31 (SE = 1.8508)	500	Woan et al. 2013
Malaysia	Brunei Bay, Malaysia	41 (95 % CI = 36–49)	ca.1690	this study
Myanmar	Ayeyarwady River	58–72	NA	Smith et al. 2007
Philippines	Malampaya Sound	77 (CV = 27.4 %)	2001.15	Smith et al. 2004
Thailand	Songkhla Lake	1–15	1040	Kittiwattanawong et al. 2007
Thailand	Eastern Gulf Coast of Thailand	423	NA	Hines et al. 2015
Thailand	Trait Bay, Trait province	171 (SE = 73.18)	NA	Junchompoo et al. 2014
Thailand	Bangpakong Estuary	20–5	135	Tongnunui et al. 2011

Table 8. Estimated group sizes of Irrawaddy dolphins in different areas. SE = standard error; SD = standard deviation.

Countries	Places	Mean group size	Group size range	Reference(s)
Australia	Cleveland Bay	5.35 (SE= 0.35)	1–15	Parra 2005
Bangladesh	Sundarbans Mangrove forest	2.30 (SD = 1.36)	1–6	Smith et al. 2006
Indonesia	Mahakam River	4.4 (SD = 2.2)	1–10	Kreb and Budiono 2005a
Indonesia	Malampaya Sound	5.26 (SE = 1.06)	1–15	Dolar et al. 1997
Malaysia	Brunei Bay	6 (SE = 0.66)	1–18	this study

tivity to noise pollution, i.e. roaring sound of the speedboat and ship engines, excessive ship and boat traffic and coastal construction works (Stacey and Hvenegaard 2002, Hashim and Jaaman 2011). Noise likely distracts them because most of the dolphin activities are depending on sound perception and biosonar (Van Parijs et al. 2000, Hoffman et al. 2016). However, the dolphins show an adaptive behavior to the negative stimuli by doing deep diving, short time surfacing for breathing (Stacey and Hvenegaard 2002) and changing the travelling direction (Kreb et al. 2012).

Seasonally, the mean number of sightings did not vary significantly between seasons nor did the mean number of individuals per group vary between seasons. These results may indicate that Irrawaddy dolphins inhabit in Brunei Bay the whole year, with no seasonal differences. Similar results have been observed in Cleveland Bay, Australia (Parra 2005), as well as in Banten Bay, Indonesia for Irrawaddy dolphins (Khalifa et al. 2014). Considering daytime, the number of sightings was higher in the morning compared to the afternoon but not significantly. The factor behind this was the bad weather conditions (wind, swell and higher Beaufort level) in the afternoon, which resulted in less survey effort compared to the morning. In general, the swell of Beaufort Sea state 4 decreases the ability to sight dolphins at a distance which creates a bias. This dolphin occurs most often from medium to low water level (Smith et al. 2004). In this study, surveys have been done in the high tide time. Beasley (2007) also noticed a higher occurrence of dolphins in the slow current.

In Brunei Bay, Malaysia, Irrawaddy dolphins showed habitat preferences (e.g. 2 to 19.99 m sea depths, 29 to 31.99°C surface water temperature, and 1.5 to 4.49 km coastline distance), and the numbers of encounters were significantly different at different ranges of some abiotic factors. Dolar et al. (2002) mentioned that the distribution of Irrawaddy dolphins was restricted to sea depths of $\leq$ 15 m in Malampaya Sound, Indonesia. In the East Kalimantan, this dolphin occurred at sea depths of 5–14 m (Kreb and Budiono 2005b). In Banten Bay, Indonesia, Khalifa et al. (2014) observed this dolphin at sea depths of 1–9 m. In Cleveland Bay, Australia they occurred at water depths of $<$ 15 m depth (Parra 2005). Geographically Brunei Bay is in the tropical region and air temperature does not fluctuate much. Seasons do not change the surface water temperature much in the Bay. Peter et al. (2016) observed Irrawaddy dolphins with a mean sea surface temperature of 30.42 ± 0.61°C in Kuching Bay, Sarawak, and our result is similar to this. Smith et al. (2004) found that the dolphins prefer low salinity conditions, and in the waterways of Sundarbans Mangrove Forest of Bangladesh the occurrence of dolphins were dramatically decreased in high salinity areas (Smith et al. 2006). In Malaysian Kuching Bay, Peter et al. (2016) also found habitat preference of this dolphin for lower water salinity. In Brunei Bay water salinity is variable because there are eight river mouths entering the bay, which also bring sediments from upstream, often increasing turbidity (Howes and NWPO 1986). Also in Brunei Bay, the occurrence of dolphins was lower in high turbid waters, which is an opposite finding compared to those of other researchers (Stacey and Arnold 1999, Smith et al. 2004). Other studies linked Irrawaddy dolphins to shallow areas close to river mouths and changing tidal states, features which are likely to be associated with higher levels of turbidity (Dolar et al. 2002, 2006, Peter et al. 2016). In Cleveland Bay, Australia, 50% of the sightings of Irrawaddy dolphins were within 15 km of the coast (Parra 2005). Also, Parra et al. (2002) observed this dolphin on the east coast of Queensland within 10 km of the nearest land. These findings for nearby coastline distance from dolphins' occurrence are similar to our result in the Brunei Bay.

The present study provides the first detailed information about population abundance, spatial occurrence and habitat preferences of Irrawaddy dolphins in the Brunei Bay. This study may serve as an important baseline for future comparisons and will help researchers, conservationists, local marine park managers and policy makers in developing effective conservation and management plans for the area. Additionally, the current estimated data should also be added to inform the IUCN Red List of Threatened Species Criteria (IUCN 2012a, b), so that status assessment of Irrawaddy dolphin population in Brunei Bay could be performed. In the future, population genetics can be studied, which will help to obtain

Table 9. Marine mammals observed in the Brunei Bay, Malaysia, during the survey period (2013–2015) with IUCN Red List status. No. = number; IUCN = International Union for Conservation of Nature. Table modified from Mahmud et al. 2018.

Serial no.	English name	Scientific name	IUCN (2015) Red List Status
01	Indo-Pacific bottlenose dolphin	*Tursiops aduncus* (Ehrenberg, 1833)	data deficient
02	Indo-Pacific finless porpoise	*Neophocaena phocaenoides* (G. Cuvier, 1829)	Vulnerable
03	Indo-Pacific humpbacked dolphin	*Sousa chinensis* (Osbeck, 1765)	Near Threatened
04	Irrawaddy dolphin	*Orcaella brevirostris* (Owen in Gray, 1866)	Vulnerable
05	Killer whale	*Orcinus orca* (Linnaeus, 1758)	data deficient
06	Dugong	*Dugong dugon* (Müller, 1776)	Vulnerable

more information about the Irrawaddy dolphin population in the bay. Furthermore, a long-term research program is needed where the research team can continue (at least seasonally) to monitor the dolphins and develop a complete knowledge of the population status and trends of Irrawaddy dolphins in the bay. This bay is not only a good habitat for Irrawaddy dolphins, but also for other marine mammals (Table 9), so a long-term conservation plan and management are necessary to reduce the anthropogenic activities in the bay. For this, there are several strategies the state governments can consider:

- local governments can announce the Lawas area and Labuan Island as a Marine Protected Areas (MPA). However, conflict between bordering state and country waters may challenge this.
- Reduction of fishery activities near Lawas area and Labuan Island could be enforced.
- Speed limits for boats and ships, and specified water routes could be implemented.
- Focus group discussions with local fisherman communities could be developed to create awareness about the importance of marine mammals.

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