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Habitat modeling of Irrawaddy dolphins (*Orcaella brevirostris*) in the Eastern Gulf of Thailand

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Abstract

Aim: The Irrawaddy dolphin (*Orcaella brevirostris*) is an endangered cetacean found throughout Southeast Asia. The main threat to this species is human encroachment, led by entanglement in fishing gear. Information on this data-poor species' ecology and habitat use is needed to effectively inform spatial management.

Location: We investigated the habitat of a previously unstudied group of Irrawaddy dolphins in the eastern Gulf of Thailand, between the villages of Laem Klat and Khlong Yai, in Trat Province. This location is important as government groups plan to establish a marine protected area.

Methods: We carried out boat-based visual line transect surveys with concurrent oceanographic measurements and used hurdle models to evaluate this species' patterns of habitat use in this area.

Results: Depth most strongly predicted dolphin presence, while temperature was a strong predictor of group size. The highest probability of dolphin presence occurred at around 10.0 m with an optimal depth range of 7.50 to 13.05 m. The greatest number of dolphins was predicted at 24.93°C with an optimal range between 24.93 and 25.31°C. Dolphins are most likely to occur in two primary locations, one large region in the center of the study area (11°54′18″N to 11°59′23″N) and a smaller region in the south (11°47′28″N to 11°49′59″N). Protections for this population will likely have the greatest chance of success in these two areas.

Main Conclusions: The results of this work can inform management strategies within the immediate study area by highlighting areas of high habitat use that should be considered for marine spatial planning measures, such as the creation of marine protected areas. Species distribution models for this species in Thailand can also assist conservation planning in other parts of the species' range by expanding our understanding of habitat preferences.

KEYWORDS

Gulf of Thailand, habitat, Irrawaddy dolphin, *Orcaella brevirostris*, spatial management, species distribution model

1 | INTRODUCTION

The Irrawaddy dolphin, *Orcaella brevirostris* (Figure 1), is an endangered marine and freshwater cetacean found in South and Southeast Asia. Marine populations are patchily distributed from coastal India and Bangladesh in the northeast through Myanmar, Thailand, Malaysia, Cambodia, Vietnam, the Philippines, and Indonesia. Freshwater subpopulations inhabit the three largest Southeast Asian rivers (Ayeyarwady, Mahakam, and Mekong) and two lagoons (Chilika in India and Songkhla in Thailand). The species is classified as Endangered by the International Union for the Conservation of Nature (IUCN) due to small subpopulations, declining ranges, and increasing anthropogenic threats (Minton et al., 2017). Five recognized subpopulations (IUCN, 2013), only one of which is exclusively marine, are considered Critically Endangered. Throughout their range, this species faces numerous anthropogenic threats including gillnet entanglement, habitat degradation, pollution, noise, and boat disturbance (Minton et al., 2017). For most subpopulations, the greatest threat is entanglement in fishing gear (Beasley et al., 2007; Minton, Peter, & Tuen, 2011; Reeves et al., 2008; Smith, Beasley, & Kreb, 2003; Smith, Braulik, Strindberg, Ahmed, & Mansur, 2006). Many related and coastal dolphin species (e.g., snubfin dolphin (*Orcaella heinsohnii*), Indo-Pacific humpback dolphin (*Sousa chinensis*)) experience similar entanglement threats (Bearzi, Fortuna, & Reeves, 2008; Bearzi et al., 2003; Karczmarski, 2000; Parra, Corkeron, & Marsh, 2006).

Marine protected areas (MPAs) that restrict fishing effort for gears with high potential impact can be a powerful tool for protecting important habitat of target species or biodiversity (e.g., Cañadas, Sagarminaga, De Stephanis, Urquiola, & Hammond, 2005; Hyrenbach, Forney, & Dayton, 2000; Kelleher, 1999). However, successful establishment of an effective MPA requires understanding the relationship between the population to be protected and its habitat as well as human uses and impacts (Cañadas et al., 2005, St. Martin & Hall-Arber, 2008). Statistically based habitat models can provide information on preferred habitats to identify areas critical for protection and future research (Bailey & Thompson, 2009).

FIGURE 1 Irrawaddy dolphins (*Orcaella brevirostris*) in the Gulf of Thailand

Little is known about Irrawaddy dolphin habitat preferences. It is one of only three cetaceans (with the finless porpoise, *Neophocaena phocaenoides*, and the tucuxi, *Sotalia fluviatilis*) able to inhabit both marine and freshwater (Smith & Jefferson, 2002). Most available data are collected from freshwater subpopulations (Baird & Beasley, 2005; Baird & Mounsouphom, 1994; Sahu, Kar, & Pattnaik, 1998; Smith & Hobbs, 2002; Smith & Jefferson, 2002; Smith et al., 2006; Smith, Shore, & Lopez, 2007; Stacey & Hvengaard, 2002; Sutaria, 2009; Pattnaik, Sutaria, Khan, & Behera, 2007; Reeves et al., 2008). In marine coastal areas, Irrawaddy dolphins are associated with warm (25°C), shallow (~6 m), and brackish to high-salinity (>20 ppt) waters near river mouths, rarely ranging more than a few kilometers offshore (Baird & Mounsouphom, 1994; Dolar, Perrin, Gaudiano, Yaptinchay, & Tan, 2002; Minton et al., 2013, 2011; Peter, Poh, Ngeian, Tuen, & Minton, 2016; Smith et al., 2006; Smith & Hobbs, 2002; Stacey, 1996; Sutaria, 2009). This suggests that they prefer shallow nearshore areas with high nutrient input and biological productivity, likely supporting prey resources (Dolar et al., 2002; Minton et al., 2013, 2011). However, a more detailed understanding of Irrawaddy dolphin habitat characteristics is needed to establish effective conservation measures. For this purpose, we use a species distribution modeling (SDM) approach in our study of a group of Irrawaddy dolphins offshore of Trat Province, Thailand.

SDMs relate records of species occurrence to environmental predictor variables (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Redfern et al., 2006), and have been used in studies of marine mammals (e.g., Bräger, Hararaway, & Manly, 2003, Goetz, Montgomery, Ver Hoef, Hobbs, & Johnson, 2012). Properly employed and tested SDMs can play an important role in conservation by helping to illuminate species' habitats, thus providing a framework for future research, information needed to predict species responses to environmental changes, and tools to develop effective management strategies (Bailey & Thompson, 2009; Brotons, Thuiller, Araújo, & Hirzel, 2004; Cañadas et al., 2005; Elith et al., 2006; Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Redfern et al., 2006). SDMs can also predict species occurrence in difficult-to-access or as-yet-unstudied locations and species' responses to environmental changes (Araújo, Pearson, Thuiller, & Erhard, 2005; Bailey & Thompson, 2009; Barry & Elith, 2006; Brotons et al., 2004; Elith et al., 2006; Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Morin & Thuiller, 2009). Extrapolating to unstudied areas carries risk often requiring validation, however, as species–environment relationships observed in one area may not be reflected in another (Manocci, Roberts, Miller, & Halpin, 2016).

Here we examine habitat preferences of Irrawaddy dolphins in the eastern Gulf of Thailand, a subpopulation which remains unassessed by the IUCN and for which no formal habitat studies have been conducted. Local government groups are planning spatial protections for this species and need habitat and distribution information to make effective management decisions. We conducted standardized line transect surveys, collecting Irrawaddy dolphin occurrence data concurrently with data on physical and biological habitat characteristics. These data were used to develop

a SDM with three goals: 1) to determine the factors influencing suitable habitat in the study area, 2) to predict dolphin distributions for use in development of conservation measures (e.g., MPA development, boating/fishing restrictions, pollution mitigation efforts, reduced dolphin entanglement risk) in the Gulf of Thailand, and 3) to provide a model for predicting Irrawaddy dolphin presence for prioritizing future sampling efforts in less studied coastal subpopulations.

2 | METHODS

2.1 | Field methods

We carried out research primarily along the coast of the eastern Gulf of Thailand (Figure 2a) between the villages of Laem Klat and Khlong Yai, within Trat Province, Thailand. This subpopulation's abundance is estimated at 423 individuals, one of the largest for this species (Hines et al., 2015). In two field seasons, 2013 and 2014, we expanded the study area to cover offshore areas surrounding three islands off the coast of Trat—Koh Chang, Koh Mak, and Koh Kut (Figure 2b)—and waters along the coast of Chanthaburi Province (Figure 2c), respectively. From 2008 to 2009 and 2012 to 2014, we carried out line transect boat surveys for three to four weeks every January and February (into March in one year) and opportunistically for one week every other month. We surveyed from a 12-meter fishing boat, small inflatable motor boat, or 20-meter fishing boat (Table 1). We conducted all surveys, except for the April–May 2012 fieldwork, in the dry season during the northeasterly monsoon (see Hines et al., 2015 for details). The April–May 2012 environmental data fell within the range of values collected in other years, so we included it in the full dataset rather than modeling it separately. Total area surveyed was 552 km^2 in Trat Province, 2,127 km^2 around the islands, and 815 km^2 in Chanthaburi.

Environmental data were collected at time of sighting or at every 1-km^2 grid cell and included sea surface temperature, depth, salinity, turbidity, pH, and chlorophyll *a* (Table 1). All of these variables have been shown to inform marine mammal distribution models (Redfern et al., 2006; Torres, Read, & Halpin, 2008). These factors can limit dolphin distribution due to potential physiological constraints (e.g., temperature, salinity, and pH limits), prey availability (e.g., depth, chlorophyll *a*), and the influence of turbidity on visual capture ability and water quality. We included a binary variable indicating calf presence during a sighting as an independent variable to test whether calf presence influenced dolphin group size or presence.

2.2 | Analytical methods

We first measured distances to the coastline and river mouths for each environmental data point using ArcGIS (ESRI, 2014). We carried out all subsequent analyses in R version 2.13.1 (R Development Core Team, 2009–2013). We identified and removed outliers (points more than three standard deviations from the mean, according to the Z-value test) in each data category (e.g., sightings, depth, and salinity) (Aggarwal, 2013; Hodge & Austin, 2004). We binned turbidity and chlorophyll *a* into high, medium, and low categories using a Jenks natural breaks classification because variability was high between years, low within years, and non-normally distributed. We used a pair plot to initially explore the data and identify linear relationships. Next, we ran both Moran's I and Mantel tests to determine if sightings were spatially autocorrelated (Dray, Dufour, & Thioulouse, 2016; Paradis et al., 2015). Neither analysis found significant clustering of sightings ($p > 0.05$). We tested variables for collinearity using variance inflation factors (VIF) with a cutoff value of 3 (Naimi, 2015; Zuur, Ieno, Walker, Saveliev, & Smith, 2009), resulting in removal of the variable "distance to coastline." Frequency plots showed sightings data were highly zero-inflated and overdispersed (Figure 3a; mean = 0.78, variance = 4.91). We chose a hurdle model, which models data in two components. The zero component models data as binary with a binomial distribution (zeros vs. all nonzero counts) and the truncated count component models just nonzero counts using a Poisson, negative binomial, or geometric distribution (Hu, Pavlicova, & Nunes, 2011; Zeileis, Kleiber, & Jackman, 2008; Zuur et al., 2009). Hurdle models are an appropriate choice for this study given the nature of our data and their past use in modeling the distribution of marine mammals (e.g., Goetz et al., 2012; Gowan & Ortega-Ortiz, 2014; Ver Hoef & Jansen, 2007). The frequency curve for the sightings data (Figure 3a) closely resembles a negative binomial distribution with mean = 1 and dispersion parameter (k) = 0.1 (Zuur et al., 2009). Therefore, we analyzed our count data using a negative binomial distribution. This model family assumes that separate ecological processes influence presence/absence and number of individuals where the species is present (Zuur et al., 2009).

Hurdle models do not handle missing data well and *k*-fold cross validation failed on a model including all years and all variables. Due to uneven data collection across years and missing values caused by instrument error, data availability was uneven across years (Table 2). Therefore, we separated the data into five smaller datasets (Table 3). Four datasets included all data points for each year and thus left out variables with missing values. The fifth dataset held only points for which all variables were measured and was smaller than the prior four. Because there were no sightings around the islands or Chanthaburi, we left these data out of the analysis. We explore differences and potential reasons for this lack of sightings in the Discussion.

We fit the data to a suite of hurdle models (Jackman, Tahk, Zeileis, Maimone, & Fearon, 2015), first using all variables within each framework, then dropping terms sequentially and performing model selection tests and evaluations (detailed below) to determine which configuration of terms resulted in the best model. We used Akaike's information criterion (AIC) and *k*-fold cross validation (with 10 folds) (Alfons, 2012) to choose the best model within each framework (Johnson & Omland, 2004; Kadane & Lazar, 2003;

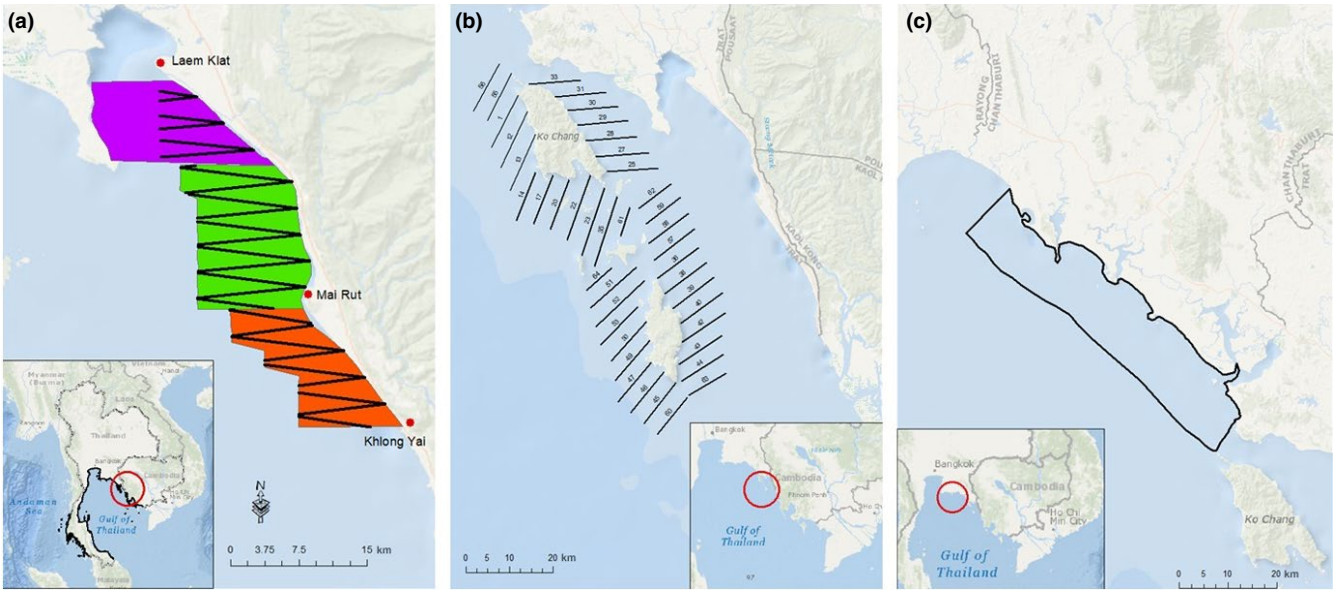

FIGURE 2 (a) Our study area off Trat Province in the eastern Gulf of Thailand including the zigzag transect lines followed for data collection with inset map showing its location in the wider Gulf of Thailand. (b) Expanded study area around the islands including parallel transect lines with inset map showing its relation to the other sites. (c) Chanthaburi study area with inset map showing its relation to the other sites

Kohavi, 1995; Redfern et al., 2006; Refaeilzadeh, Tang, & Liu, 2009; Zuur, Ieno, & Smith, 2007). We supplemented these criteria with a likelihood ratio test (Hothorn et al., 2015) to compare each reduced model to the full model within each framework (nested models), with a threshold of $p > 0.05$ (Johnson & Omland, 2004).

After choosing models from each framework, we evaluated each model component (presence/absence and count) using the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Franklin, 2009, Sing, Sander, Beerenwinkel, & Lengauer, 2015). We also calculated McFadden's pseudo-R^2 (ρ^2), a goodness-of-fit measure, as a method of model evaluation (McFadden, 1978). From these assessments, we chose a final set of models. To choose the final model, we ran all parameters as linear, except for depth and temperature, which were modeled using a quadratic (Figure 3b,c). After choosing the final model, we used the "predict" function in the PSCL package (version 1.4.9; Jackman et al., 2015) to obtain predicted probability, count, and overall fitted values from the model. We used these values to create an interpolated surface using an ordinary krige with a 3 × 3 smoother in ArcGIS (ESRI, 2014). We further determined optimal values of the significant variables identified by the models: We first set all environmental variables in the final model to their average values, then varied only the significant variables, using the "predict" function to make predictions for the relevant model part (zero or count). These optimal values were used to describe the preferred habitat of this species as well as to compare our results with temperature and depth preferences obtained in other parts of its range. To determine the areas most highly used by Irrawaddy dolphins along the Trat Province coast, we classified overall fitted values by Jenks natural breaks into five classes of dolphin occurrence likelihood (high probability of presence and large group size) in ArcGIS (ESRI, 2014).

3 | RESULTS

Dolphins were encountered in every part of the study area except around the islands or off the coast of Chanthaburi. The environment was similar in these regions, with the notable exceptions of depth and distance to river mouth (Table 4). Most observed groups were

TABLE 1 Dates, location, and duration of data collection as well as equipment used

Year	Area	Month(s)	Survey days	Depth	Temperature	Salinity	Turbidity	Chl *a*	pH
2008	Trat	February–March	18	Davis Instruments Portable Water Depth Sounder Gauge	YSI Model 30 Handheld Salinity, Conductivity, and Temperature System		Secchi disk	na	na
2009	Trat	January	17				LaMotte Model 2020 Turbidimeter		
2012	Trat	January	20						
	Trat	April–May	4						
2013	Islands	January	11		Eureka Environmental Manta 2 Water Quality Multiprobe				
	Trat	January–February	13						
2014	Chanthaburi	January	5	HawkEye Handheld Sonar System					Manta 2
	Trat	January	13						

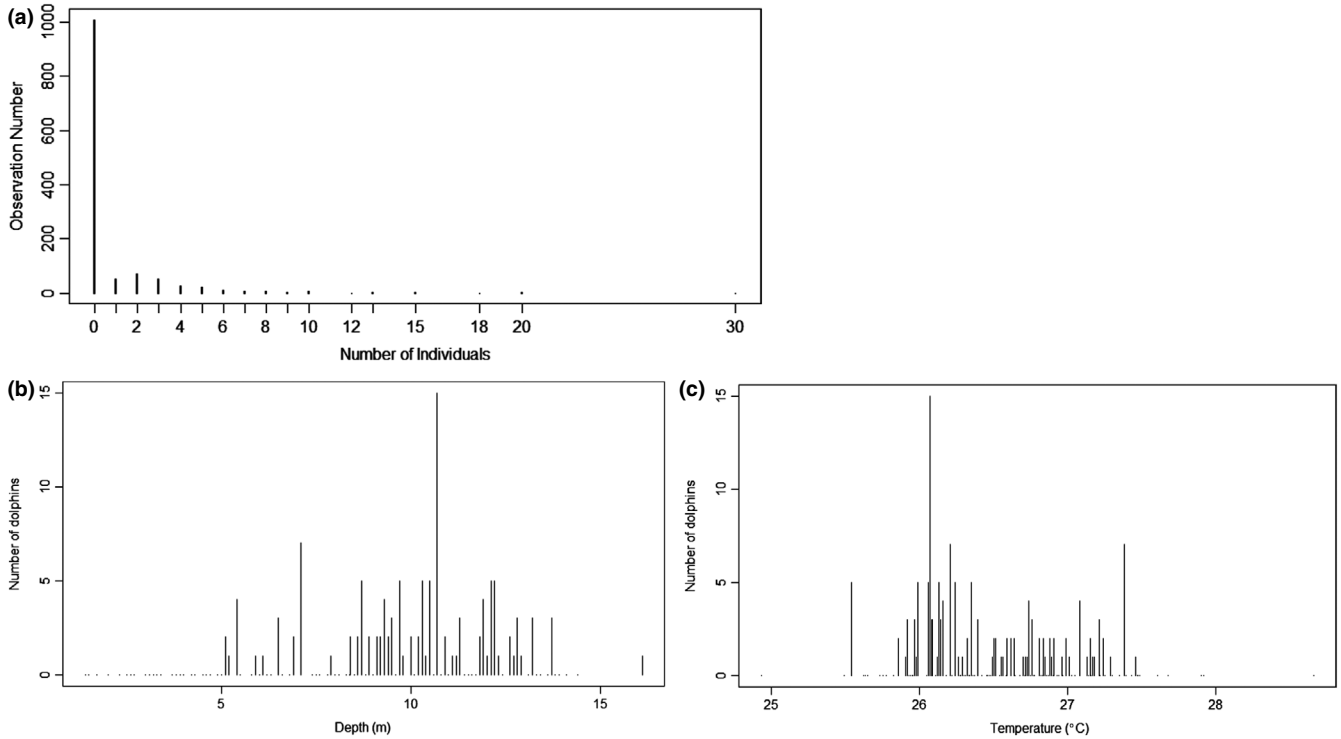

FIGURE 3 (a) Sightings frequency plot, showing the data to be highly zero-inflated, (b) histogram of dolphin sightings versus depth, (c) histogram of dolphin sightings versus temperature. Panels b) and c) are from the dataset used for the best model framework, showing that sightings appear concentrated at medium depths and temperatures

small (1–5 individuals), but a few large groups were observed in Laem Klat and Khlong Yai, and the largest were observed in Mai Rut (5–15 and 15–30 individuals, respectively; Figure 4). Average group size was 3.77 individuals (*SD* = 3.55, range = 1–30).

Our final chosen model was framework 4 with the quadratic depth term, containing data from 2014 only and including salinity, turbidity, calves, a quadratic depth term, and distance to river mouth in the zero component and temperature, turbidity, chlorophyll *a*, and pH in the count component (Table S3).

Both the first (linear)- and second (nonlinear)-order depth terms were significant predictors for the zero component ($p < 0.005$), while temperature was a significant predictor for the count component ($p < 0.005$) (Table S3). Predictions from the zero component (probabilities of dolphin presence) show a positive relationship with depth at 10.5 meters and below, with a negative relationship above 10.5 m (Figure 5a). Predictions from the count component (dolphin numbers) show a steady negative relationship with temperature, with multiple dolphins predicted at 25°C and almost none at around 28.6°C, the highest temperature recorded (Figure 5b).

Dry-season dolphin presence probability was greatest just off the coast from approximate latitudes 11°56′57′′N to 11°57′48′′N, between approximately 3.0 and 6.0 kilometers offshore (circled in green in Figure 6a). This small patch of high probability is surrounded by a larger patch of slightly lower probability extending to around 7.5 kilometers offshore between approximate latitudes 11°54′21′′N and 11°57′48′′N. Two other lower probability patches lie between 2.5 and 6.5 kilometers offshore from approximate latitudes 11°47′31′′N to 11°50′5′′N and between 5 and 12.5 kilometers offshore from approximate latitudes 12°0′30′′N to 12°3′28′′N, where water remains shallower farther offshore. The farthest offshore we encountered dolphins was 11.04 kilometers in the central section of the study area (11°55′12′′N, 102°40′12′′E). They are unlikely to be found in the shallowest nearshore waters between approximate latitudes 11°56′43′′N and 12°7′32′′N. These results are supported by a map of depth in the study area, showing that the areas of highest presence probability are in locations with mid-range depths (~5-10 m) (Figure 7a).

The largest dolphin group sizes were predicted in the central part of the study area, between approximately 1.0 and 5.0 kilometers offshore and approximate latitudes 11°55′28′′N and 11°59′10′′N, with a smaller patch at around 9.0 kilometers offshore between approximate latitudes 11°57′32′′N and 11°59′31′′N (Figure 6b). Two other areas with slightly lower predicted group sizes occur between approximate latitudes 11°47′29′′N and 11 °49′60′′N, around 3.0 to 7.0 kilometers offshore and nearshore from approximate latitudes 12°5′12′′N to 12°7′14′′N. However, given the low probability of dolphin occurrence in nearshore northern waters, this third area is unlikely to support large groups of dolphins. A map of temperature (the strongest predictor of dolphin group size) in the study area strongly supports model predictions (Figure 7b).

Optimal depths (dolphin presence probability > 0.50) are between 7.50 and 13.05 meters, with the highest probability of dolphin occurrence (0.6395) at around 10.0 meters. Optimal temperature

TABLE 2 Data availability in the Trat study area

Data	Total entries	Depth	Temperature	Salinity	Turbidity	Chl *a*	pH	Dist. to river mouth
February–March 2008	279	279	279	279	121	0	0	279
January 2009	218	218	218	218	218	0	0	218
January 2012	203	203	203	203	203	0	0	203
April–May 2012	35	35	35	35	35	0	0	35
January–February 2013	174	174	174	174	174	174	0	174
January–February 2014	185	185	185	185	185	185	185	185
TOTAL	1094	1094	1094	1094	936	359	185	1094

range (>5 dolphins predicted) is 24.93–25.31°C, with the highest number of dolphins (>7) predicted at 24.93°C. Above 26.99°C, <1 dolphin is predicted.

Overall fitted values suggest two small areas of both high probability of dolphin presence and large group size (>5 individuals) (Figure 6c). These are between approximately 3.0 and 6.0 kilometers offshore from approximate latitudes 11°56′6″N to 11°57′56″N and 2.5 and 7.5 kilometers offshore between approximate latitudes 11°47′27″N and 11°49′19″N.

Classification resulted in two areas of high dolphin occurrence likelihood. These surrounded the areas in Figure 6c, stretching from 11°54′18″N to 11°59′23″N in the middle of the study area, approximately 1.5 to 7.0 km offshore of Mai Rut, spanning longitudes 102°45′24″E to 102°42′18″E and from 11°47′28″N to 11°49′59″N offshore of Khlong Yai from 102°46′51″E to 102°49′4″E (Figure 8).

4 | DISCUSSION

4.1 | Dolphin–habitat relationships in the Gulf of Thailand

In the eastern Gulf of Thailand, dry-season dolphin presence was most strongly predicted by depth, while temperature strongly predicted group size. This indicates preference for relatively cool waters of intermediate depth. Geographically, this places Irrawaddy dolphins at 1.5 to 7.5 km from shore (Figure 6). Protected area planning with protective zoning based on these areas would likely have the greatest chance of protecting this population (Batisse, 1982; Day et al., 2012; Hooker, Whitehead, & Gowans, 1999; Hyrenbach et al., 2000; Kelleher, 1999; Lausche, 2011). Buffer zones could be formed surrounding the two areas, between approximate latitudes 11°51′34″N and 12°0′10″N, around 0.25 to 10.5 kilometers offshore of Mai Rut, and from approximate latitudes 11°47′28″N to 11°50′22″N, approximately 1.5 to 10.5 kilometers offshore of Khlong Yai (Figure 8) to protect animals traveling to and from core areas (Batisse, 1982; Day et al., 2012; Hooker et al., 1999; Hyrenbach et al., 2000; Kelleher, 1999; Lausche, 2011). Bycatch of cetaceans is high in the eastern Gulf of Thailand, with 12% of fishers interviewed reporting knowledge of cetacean bycatch. While willingness to change fishing gear is low (Teh, Teh, Hines, Junchompoo, & Lewison, 2015), Thai fishing communities consider marine conservation an important goal and are willing to work toward bycatch reduction (Teh et al., 2015). The Thai government is currently working to balance protection of dolphins with the needs of small-scale fishers. The Thai Department of Marine and Coastal Resources is currently working on creating the first MPA along the Trat Province coast, with an emphasis on conservation of Irrawaddy dolphins. Placing a zonal MPA (divided into zones of regulated use) that maximizes protection in the region where dolphins are most abundant could lead to significant bycatch reduction, although effective spatial protections for highly mobile species such as cetaceans can be difficult (Embling et al., 2009; Habtemariam & Fang, 2016).

4.2 | Comparison with other locations

Prior studies on Irrawaddy dolphin distribution and habitat have been informal, based upon average environmental variables at dolphin sighting locations, with the exception of work conducted in Kuching Bay, Sarawak, Malaysia (Minton et al., 2013; Peter et al., 2016). Marine Irrawaddy dolphin habitat has been assessed in bay, delta, estuary, and coastal areas of Bangladesh, Cambodia, Indonesia, Malaysia, Myanmar, the Philippines, and now Thailand (Table S4). Comparisons between our site and other locations can help managers make inferences about potential reasons for absence in some areas while building a more complete picture of Irrawaddy dolphin habitat. While this study confirms the general trends detected in other study areas, there are a few aspects in which our results differ from those of other studies. In coastal areas of Cambodia, Indonesia, Malaysia, and the Philippines, dolphins were encountered within a few kilometers of the coast and river mouths, in relatively wide depth ranges (13.32m average spread, 21m maximum), narrow temperature ranges (average range 5°C), narrow turbidity ranges, moderate salinity ranges (average range 17.28 ppt), and somewhat basic pH (Table S4) (Beasley & Davidson, 2007; Dolar et al., 2002; Kreb & Budiono, 2005; Minton et al., 2011; Ponnampalam, 2012, 2013; Ponnampalam, Kuit, & Chong, 2014; Smith et al., 2004; Yanuar et al.,

TABLE 3 Model frameworks organized in order to maximize data used in the models. Framework 5 is reduced such that it only contains entries with all variables

Model framework	Variables	Data
1	Depth	2008
	Temperature	2009
	Salinity	January 2012
	Distance to river mouth	April–May 2012
	Calves	January–February 2013
	Year	January–February 2014
2	Depth	2009
	Temperature	January 2012
	Salinity	April–May 2012
	Turbidity	January–February 2013
	Distance to river mouth	January–February 2014
	Calves	
	Year	
3	Depth	January–February 2013
	Temperature	January–February 2014
	Salinity	
	Turbidity	
	Chlorophyll *a*	
	Distance to river mouth	
	Calves	
4	Depth	January–February 2014
	Temperature	
	Salinity	
	Turbidity	
	Chlorophyll *a*	
	pH	
	Distance to river mouth	
	Calves	
5	Depth	2008
	Temperature	2009
	Salinity	January 2012
	Turbidity	April–May 2012
	Distance to river mouth	January–February 2013
	Calves	January–February 2014
	Year	

2011). Our depth and temperature ranges were narrower than those found in other studies (5.55 m and 2.06°C, respectively). This may be due to more uniform conditions, narrower dolphin preference in this region, or a combination of factors that our model was unable to address.

In bays of East Kalimantan, Indonesia, and Sarawak, Malaysia, a combination of anecdotal sightings reports and statistical methods (Kruskal–Wallis U tests, Fisher's exact test), indicated that

TABLE 4 Mean of environmental variables in each study area

	Trat	Islands	Chanthaburi
Average temperature (°C)	28.73	29.3	27.83
Average chlorophyll *a*	1.62	1.74	1.48
Average salinity (ppt)	31.2	29.93	32.88
Average depth (m)	8.22	16.42	9.68
Average turbidity	1.64	2	1.95
Average pH	7.89	na	8.14
Average distance to river mouth (km)	7.58	26.62	10.58

dolphins prefer nearshore, somewhat brackish and turbid waters of widely varying depths (Table S4) (Kreb & Budiono, 2005; Kreb & Rahadi, 2004; Minton et al., 2013; Peter et al., 2016). Average depth of dolphin sightings was deeper than our predicted optimal depth (Kreb & Budiono, 2005; Kreb & Rahadi, 2004), suggesting that a different variable, likely salinity (Minton et al., 2013; Peter et al., 2016), is a stronger driver in this habitat than in the Gulf of Thailand (Table S4).

In the outer Sundarbans Delta of Bangladesh and deltas of East Kalimantan, Indonesia, dolphin observations occurred in narrow depth (average spread 9.1 m) and temperature ranges (3.6°C), but wide turbidity and salinity ranges (Table S4) (Kreb & Budiono, 2005, Smith et al., 2005). Average depths were shallower than identified for the Gulf of Thailand (average 6.23m). Temperatures at which dolphins were found were generally lower than those optimal in the Gulf of Thailand (average 23.7°C). This may be due to habitat availability (e.g., no temperatures below 24.93°C were recorded in any region of our study area) or the interaction of factors that were not discernible to our model.

4.3 | Potential reasons for absence in the islands and Chanthaburi

We did not see dolphins in the islands or Chanthaburi, but we can compare environmental measures between these areas and Trat. As Table 4 shows, average values of environmental variables are mostly similar. For temperature (Table 5), chlorophyll *a*, and salinity, Trat values fall between the values of the other two areas. The Trat study area is, however, characterized by much lower depths (Table 5), turbidity, and distances to river mouth than the other areas (Table 4) and is much less developed than Chanthaburi, with lower levels of fishing activity and industrial development. River mouths were less prevalent in the islands and Chanthaburi, resulting in sampling locations much farther from river mouths in those areas (average: 26.62 km and 10.58 km, respectively) than in Trat (average: 7.58 km) (Table 6). In Trat, sightings did not occur more than 14.17 kilometers from a river mouth. The potential importance of proximity to river mouths is supported by the fact that distance to river mouth is considered a reliable indicator for this species in other systems (Baird & Mounsouphom, 1994; Dolar et al., 2002; Marsh, Lloze, Heinsohn, & Kasuya, 1989; Minton

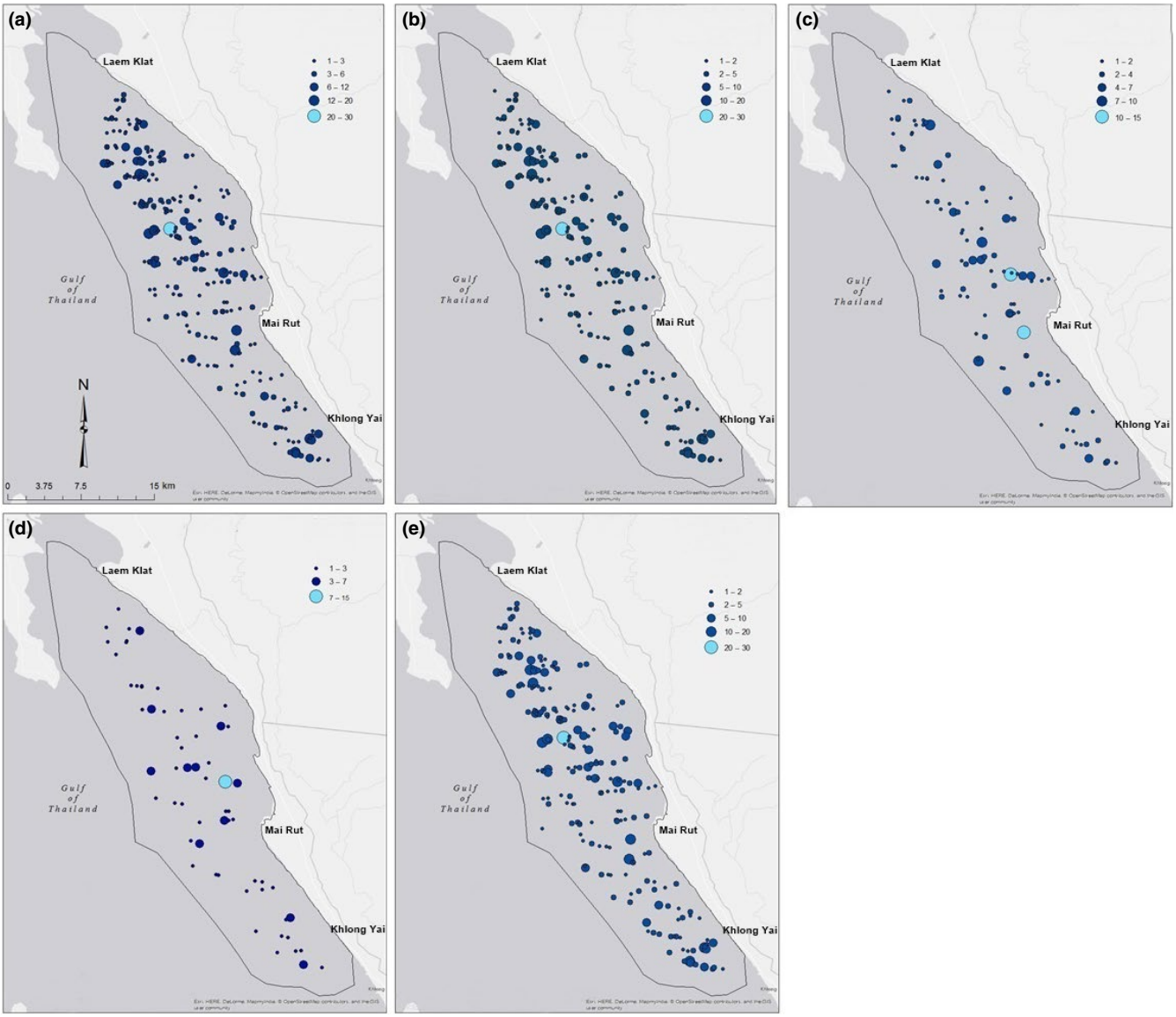

FIGURE 4 Sightings data used for the five hurdle models. (a) Model 1 data, which include sightings from between 2008 and 2014. (b) Model 2 data, which include sightings from between 2009 and 2014. (c) Model 3 data, which include sightings from between 2013 and 2014. (d) Model 4 data, which include sightings from 2014. (e) Model 5 data, which include sightings from between 2008 and 2014, only containing entries which included all variables. Largest groups are a lighter blue and were all observed off the coast near the town of Mai Rut

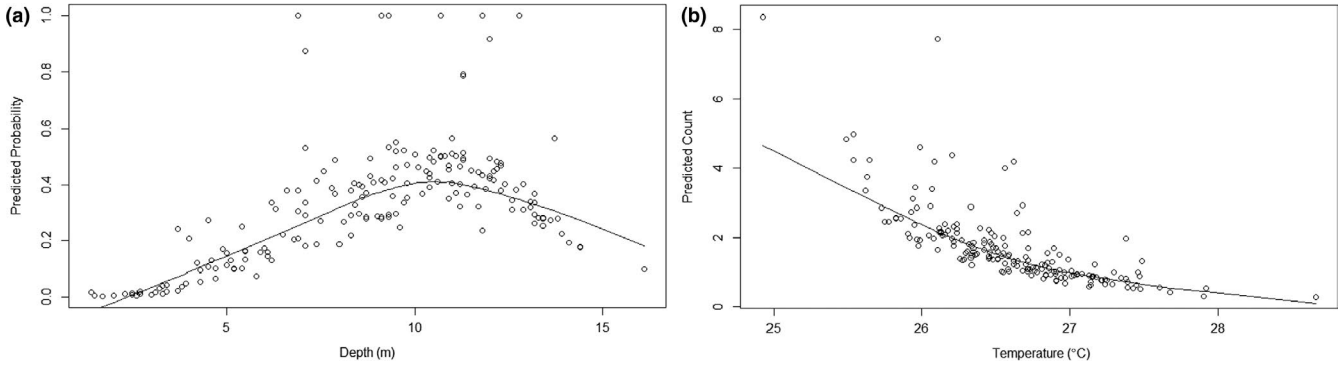

FIGURE 5 Scatterplots with lowess lines showing (a) a positive relationship between predicted probability of dolphin occurrence and depth until around 11 meters, at which point the relationship becomes negative, and (b) a negative relationship between predicted dolphin number and temperature

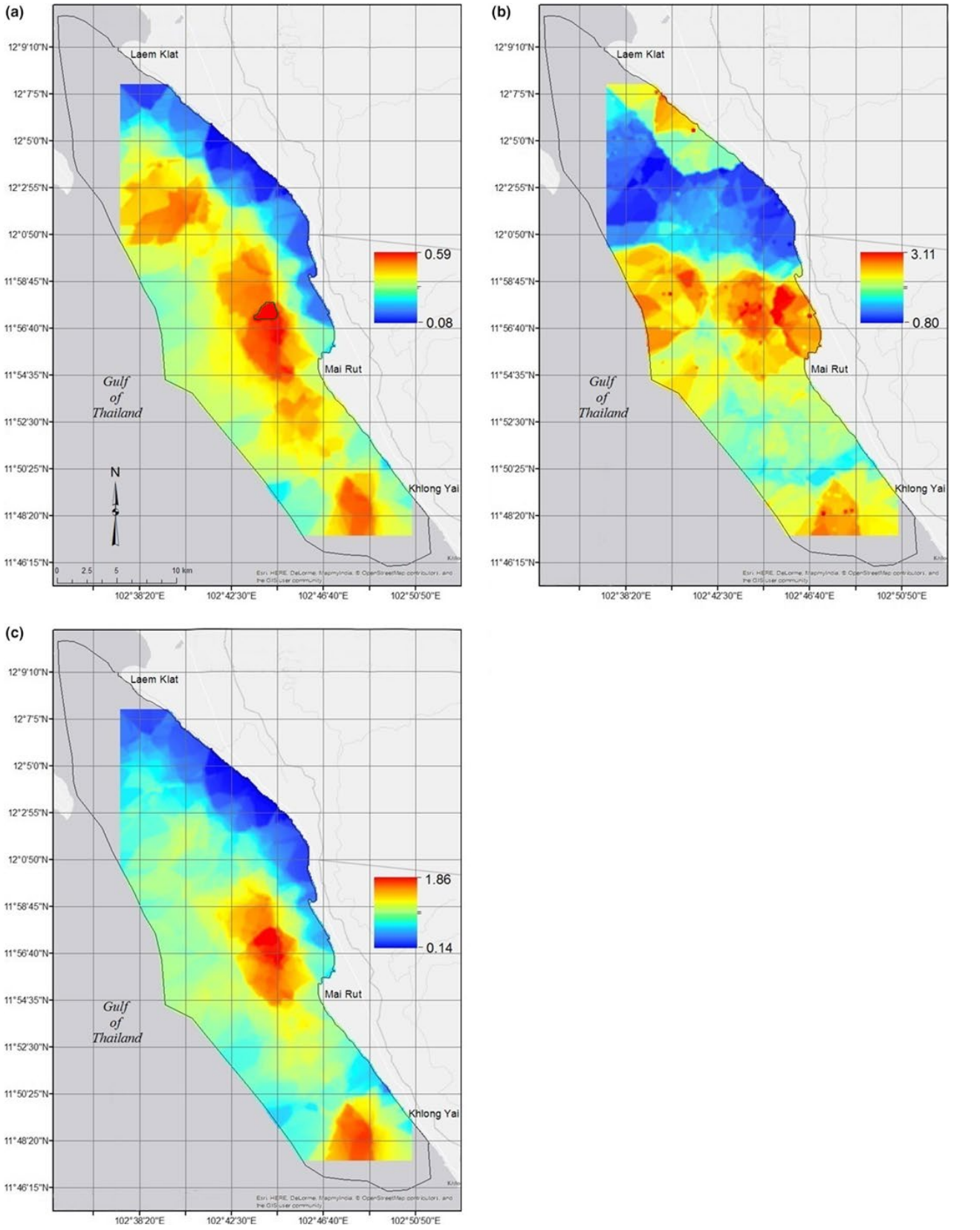

FIGURE 6 (a) Predicted probability of dolphin occurrence, indicating three distinct areas of high probability, (b) predicted dolphin counts, showing one major area of dolphin congregation and two minor areas, one of which is likely to support large groups, given the probability results shown in a, and (c) fitted model predictions, clearly showing two distinct areas of high probability of dolphin presence and large group size (together dolphin occurrence likelihood). We employed kriging and a 3 × 3 smoother to the data, so the ranges are smaller than those predicted by the model (0.004–1 for probability, 0.29–8.36 for counts, and 0.01–4.16 for fitted predictions)

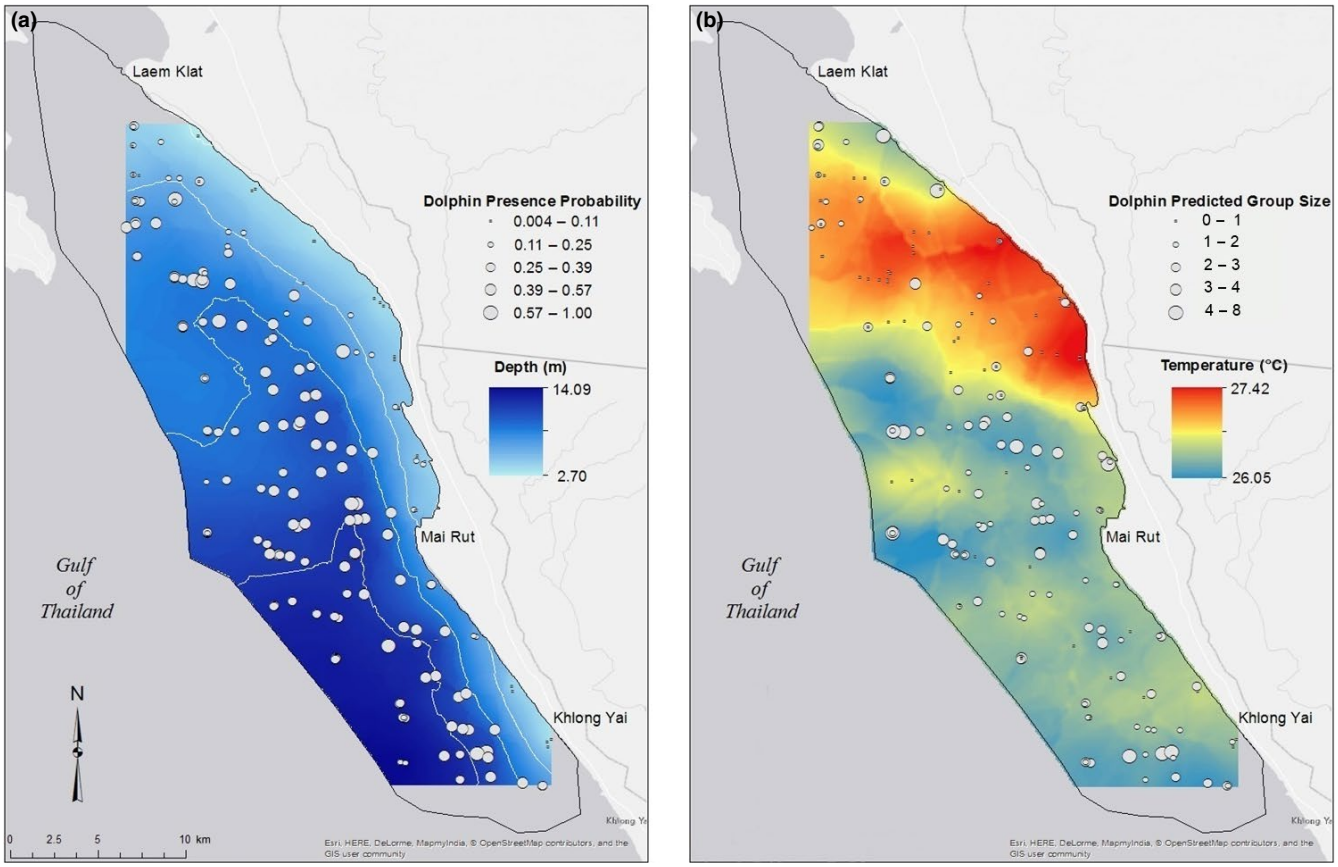

FIGURE 7 Maps of (a) depth in the study area with point values of presence probability, showing that areas of high predicted dolphin occurrence probability coincide with areas of medium depth (1.4–16.1 m), and (b) temperature in the study area with point values of predicted group size, indicating that higher numbers of dolphins are most likely found in lower temperature areas. I applied kriging and a 3 × 3 smoother to the raw data in order to obtain a smooth surface. These calculations resulted in ranges of depths and temperatures that were smaller than the recorded ranges (1.4–16.1 m and 24.93–28.66°C, respectively)

et al., 2011; Mörzer Bruyns, 1966; Smith & Hobbs, 2002; Smith et al., 2006; Stacey, 1996; Sutaria, 2009). The Trat data may not have been collected far enough from river mouths to be a significant variable in our model. Thus, we may not have recorded a sufficient range of distance to river mouth to properly test the importance of this variable. Trat may represent the ideal habitat for this species, with its access to nutrient-rich river effluence, given its importance to other small, coastal cetaceans (Hobbie, 2000; McClusky & Elliott, 2006; Rossi-Santos, Wedekin, & Sousa-Lima, 2006). Anecdotal evidence suggests that Irrawaddy dolphins were present in Chanthaburi in the past (C. Junchompoo pers. comm.). If we accept these reports, then an alternative explanation for their absence is overfishing in the Gulf of Thailand, for which there is ample evidence (Ahmed, Boonchuwongse, & Dechboon, 2007; Christenson, 1998; Pauly & Chuenpagdee, 2003; Suvapepun, 1991). In addition, Chanthaburi Province and nearby Rayong Province are hubs of industry in the Gulf, part of Thailand's Eastern Seaboard Development Program (Thailand Government Public Relations Department, 2016). Fishing pressure and industrial development have well-documented negative effects on marine populations through pollution, defaunation, and other means (e.g., Gimpel, 1976; Goudie, 2013; Constant, Nourry, & Seegmuller, 2014; D'Souza & Peretiatko, 2002; Kalavrouziotis, 2016; Maojun, Jie, Xuechun, & Jin, 2011; McCauley et al., 2015; Nriagu, 1996; Solomon & Palanisami, 2016; Stocker, 2016; Wang, Xu, Sun, Liu, & Li, 2013). Either influence category presented (environmental differences, human encroachment) could explain their absence, but the two need not be mutually exclusive.

4.4 | Model caveats and next steps

Using models to guide management decisions requires some assessment of uncertainties. Of concern are low AUC and ρ^2 values (Table S2), even after repeated model improvements. Such universally low values in multiple iterative tests could be due to missing covariates. Other variables such as prey distributions have been utilized in other SDMs; however, collecting prey data at appropriate scales for modeling efforts is quite difficult (Becker et al., 2016; Hazen & Johnston, 2010; Hyrenbach et al., 2000; Torres et al., 2008). Collection of additional covariates such as finer-resolution bathymetry data could perhaps allow a more detailed model, but bathymetric data at such a fine scale are less commonly available. Data on human use, specifically fishing effort, could provide an additional limiting factor for dolphin distribution given the

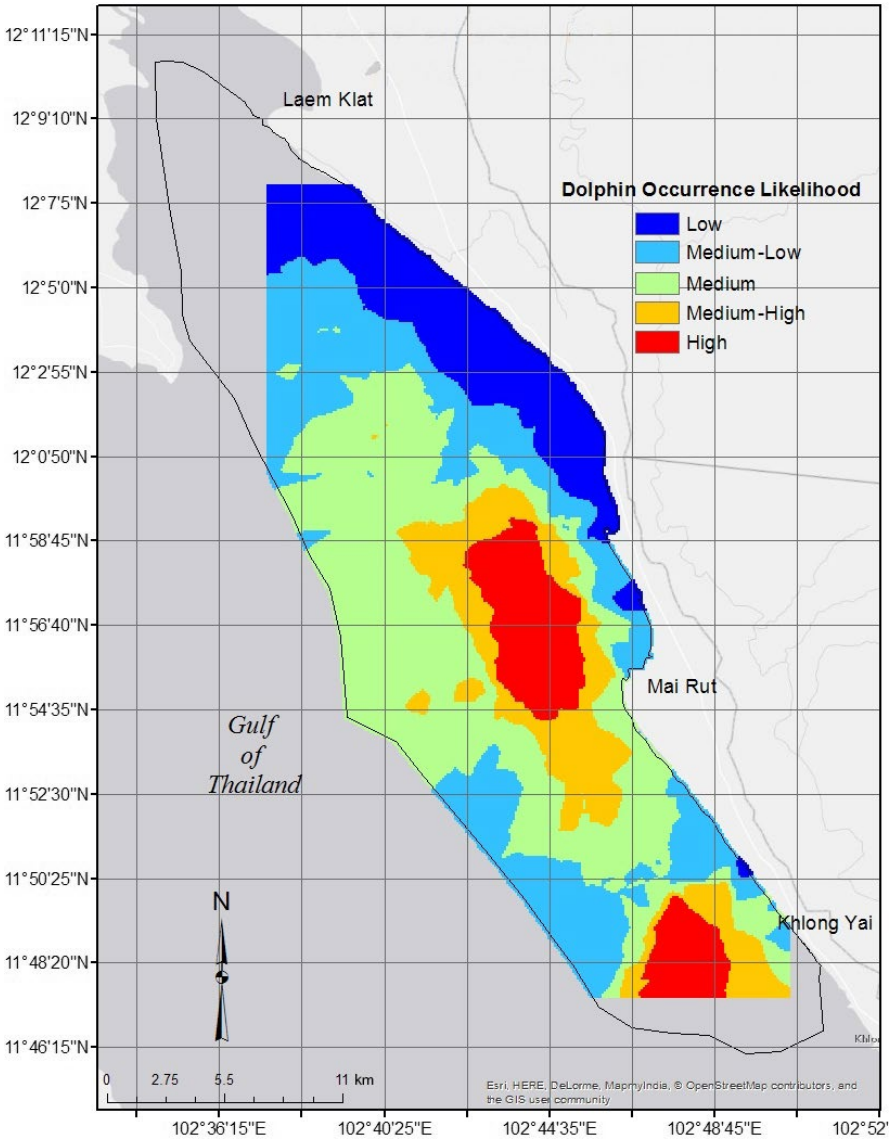

FIGURE 8 Map of dolphin occurrence likelihood. Red indicates areas of highest dolphin occurrence likelihood that, if protected, would preserve the greatest number of dolphins. Orange indicates potential buffer zones surrounding the high likelihood areas

observed absences near the islands and Chanthaburi. Such data for our field sites have been collected and analyzed (Jackson-Ricketts, 2017). However, given the paucity of data for this species, this is the first SDM that can be used to inform conservation options for this population of Irrawaddy dolphins.

TABLE 5 Temperature and depth records from all study areas within and outside of the optimal ranges identified by the model

Data	Variable	Entries in range	Entries out of range
Islands	Temperature	0	137
	Depth	23	114
Chanthaburi	Temperature	8	30
	Depth	10	26
All Trat	Temperature	230	864
	Depth	625	469
Trat 2014	Temperature	146	40
	Depth	103	82

These results can also be extended to other Irrawaddy dolphin populations where no habitat data exist. Such locations are spread across South and Southeast Asia, in Brunei, Cambodia, India, Indonesia, Malaysia, the Philippines, Singapore, and Thailand (Adulyanukosol, 1999; Anderson & Kinze, 1999; Chasen, 1940; Dolar et al., 1997; Hines, Junchompoo, Ilangakoon, Ponnampalam, & Jackson-Ricketts, 2014; Jaaman, 2000; Mörzer Bruyns, 1966; Perrin et al., 2005; Ponnampalam, 2012; Pilleri & Gihr, 1974; Ratnam, 1982). Our results can be used to optimize exploratory surveys in poorly understood areas to determine if the species is present, with the understanding that extrapolation to unstudied areas is only as accurate as the relationships between species and habitat variables are similar (Manocci et al., 2016; Wenger & Olden, 2012).

Our understanding of this species would greatly benefit from development of additional species distribution models for the bays, deltas, and coastal areas where this species is known to occur. Additional models can inform key predictor variables and provide insight on variability in habitat preferences across the species' range.

TABLE 6 Average, minimum, and maximum values of distance to river mouth in each area

Variable	Area	Average	Minimum	Maximum
Distance to river mouth (km)	Trat	7.58	0.65	15.34
	Islands	26.62	4.18	47.7
	Chanthaburi	10.58	2.79	17.21

In addition, models can provide aid in the form of preliminary information on sympatric species. Indo-Pacific humpback dolphins (*Sousa chinensis*) and Indo-Pacific finless porpoises (*Neophocaena phocaenoides*) share habitat with Irrawaddy dolphins along the Trat Province coast (Hines et al., 2015). Any form of spatial management undertaken in this area must account for these species, ensuring that spatial management for Irrawaddy dolphins considers the needs of these other cetaceans.

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AUTHORS CONTRIBUTIONS

J. Jackson-Ricketts, C. Junchompoo, E. Hines, L. Ponnampalam, A. Ilangakoon, and S. Monanunsap collected the data used in this manuscript. J. Jackson-Ricketts, E. Hines, and E. Hazen chose and performed the statistical analyses. J. Jackson-Ricketts and E. Hines obtained funding. J. Jackson-Ricketts wrote the manuscript with input from C. Junchompoo, E. Hines, E. Hazen, L. Ponnampalam, and A. Ilangakoon. C. Junchompoo, E. Hines, and S. Monanunsap acted as principal investigators for a larger project of which this manuscript is one part.

DATA AVAILABILITY STATEMENT

Data underlying this article will be available on Dryad, with https://doi.org/10.5061/dryad.r2280gb94.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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