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UNIVERSITY OF CALIFORNIA SANTA CRUZ

DIET, LIFE HISTORY, HABITAT, AND CONSERVATION OF IRRAWADDY DOLPHINS (ORCAELLA BREVIROSTRIS) IN THE GULF OF THAILAND

A dissertation submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Justine D. Jackson-Ricketts

March 2017

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Tyrus Miller Vice Provost and Dean of Graduate Studies Copyright © by

Justine D. Jackson-Ricketts

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Abstract

Diet, Life History, Habitat, and Conservation of Irrawaddy Dolphins (*Orcaella brevirostris*) in the Gulf of Thailand

by

Justine D. Jackson-Ricketts

The Irrawaddy dolphin (Orcaella brevirostris) is an imperiled Southeast Asian coastal and freshwater mammal species. Throughout their range, Irrawaddy dolphins face numerous anthropogenic threats including gillnet entanglement, habitat degradation, and boat disturbance (e.g. noise). Five subpopulations, four of which are freshwater, are classified as Critically Endangered on the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species and the species as a whole is classified as Vulnerable. It is thought that most subpopulations are small and declining. Little is known about this species' habitat preferences, life history, or movement. The subpopulation in the Gulf of Thailand is one that has yet to be evaluated and thus provides an ideal research subject to increase the body of knowledge on this rare and little-studies species. In Chapter 1, we analyzed stable isotopes of carbon and nitrogen using ANOVA and MANOVA to investigate regional subpopulation structure and ontogenetic patterns in the Gulf of Thailand and the Andaman Sea. We further used a mixing model (MixSIAR) to determine diet in two sites in the eastern Gulf of Thailand by comparing stable isotopes of dolphins to those of potential prey species. Limited age and sex structure was discovered. However, stable isotope ratios in Irrawaddy dolphins varied significantly by region (eastern Gulf, northern Gulf, western Gulf, Andaman Sea), suggesting distinct geographic groups. Mixing models revealed that the group within the eastern Gulf is primarily piscivorous, consuming mainly ponyfish, mackerel, gizzardshad, and scad, and secondarily crustacean-eating. Cephalopods make up a smaller proportion of the overall diet. Slight differences were found between the two study sites within the eastern

Gulf, suggesting weak sub-regional structure, perhaps driven by resource partitioning. In Chapter 2, we used a hurdle model to evaluate the habitat of Irrawaddy dolphins in the eastern Gulf of Thailand. We found that depth and temperature are significant predictors of dolphin presence and group size, respectively. Depth had a positive relationship with dolphin presence probability up to around 10.5 meters, at which the relationship became negative. Dolphin group size was significantly negatively correlated with temperature. We further identified two primary locations of dolphin occurrence probability (combined high presence and large group size probabilities), one large region in the center of the study area and a smaller region in the south. Finally, in Chapter 3, we used binomial and negative binomial GLMs to model fishing effort in three locations in the eastern Gulf of Thailand. We further compared these results to the results from Chapter 2 to determine where dolphins were more likely to encounter fishing vessels and gear.

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I feel it's a rite of passage for graduate students to knock desperately at Dr. Pete Raimondi's door and I feel a little guilty for perpetuating that tradition by advertising his seemingly perpetual availability. However, I would be remiss if I didn't thank him for letting me in and helping me with statistics when I felt truly overwhelmed. My statistics background was embarrassingly weak and he helped me make up that lost time and set me on the path towards the analyses I completed for this research. He is a truly fantastic resource for panicking graduate students.

None of this work would have been possible without the hard work of our multi-national field team, gracefully led by Chalatip Junchompoo of the Thai Department of Marine and Coastal Resources (DMCR). So many DMCR employees worked with us in the field, collecting data and watching for dolphins. Some even came back year after year to lend their experience and help us train the new recruits. I am so glad that I got to meet and work with them over the years and I am extremely grateful for their tireless work and their patience with my inability to

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ΧV

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times for you. Thank you for putting up with my moods and making sure I ate. I am lucky that I found you and luckier that you decided I was alright. I can't wait to start the next chapter of this life we're building together.

CHAPTER 1

Introduction

The Irrawaddy dolphin (Orcaella brevirostris) is an imperiled Southeast Asian coastal and freshwater mammal species. 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 areas (Smith and Jefferson 2002). Marine subpopulations of O. brevirostris are patchily distributed in the tropical and subtropical Indo-Pacific, while freshwater subpopulations inhabit the three largest Southeast Asian rivers: Ayeyarwady, Mahakam, and Mekong; and two lakes: Chilika in India and Songkhla in Thailand. It is unknown whether they move between fresh and saltwater or how they are able to survive in both environments (Leatherwood and Reeves 1994). Throughout this range, O. brevirostris face numerous anthropogenic threats including gillnet entanglement, habitat degradation, and boat disturbance (e.g. noise), but it is widely recognized that the greatest threat is entanglement in fishing gear (Smith et al. 2003, Smith et al. 2006, Beasley et al. 2007, Reeves et al. 2008, Minton et al. 2011). Until 2008, the International Union for the Conservation of Nature (IUCN) classified O. brevirostris as Data Deficient on their Red List of Threatened Species (Reeves et al. 2008), indicating there was not enough available information on the species to assess its extinction risk (IUCN 2013). In 2008, the IUCN changed its listing to Vulnerable over its entire range, meaning that it faces "a high risk of extinction in the wild" (IUCN 2013 page 10). Five subpopulations of O. brevirostris, only one of which inhabits a marine environment, have been listed as Critically Endangered, indicating "an extremely high risk of extinction in the wild" (Reeves et al. 2008, IUCN 2013 page 10). Several recognized subpopulations are not included in the Red List entry for O. brevirostris, indicating that they have not been evaluated and suggesting that they can still be considered Data Deficient. It is generally thought that most of these subpopulations are small and declining (Reeves et al. 2008).

More is known about freshwater subpopulation numbers, threats, and habitat preferences than about marine subpopulations (Smith et al. 2007, Reeves et al. 2008). O. brevirostris are known to inhabit high-salinity shallow areas of coastal habitats and deep, calm, pools in freshwater habitats. Such pools exhibit high biological productivity and are thought to be foraging areas in which calmer waters allow dolphins to maintain their position with little energy expenditure (Baird and Mounsouphom 1994, Smith and Hobbs 2002, Smith et al. 2006). They feed on low trophic level species, such as small fishes, crustaceans, and cephalopods, but most specific diet information is circumstantial (based upon fish remains found in the water near O. brevirostris individuals) and the only concrete prey evidence comes from stomach contents of one individual from a Laotian river (Baird and Mounsouphom 1997, Stacey and Leatherwood 1997, Stacey and Hvenegaard 2002), two individuals from the Mekong River (Marsh et al. 1989), one individual from Songhkla Lake (Adulyanukosol 1999), and one individual from the Gulf of Thailand (Ponnampalam et al. 2013). Coastal O. brevirostris rarely range farther offshore than a few kilometers, mainly remaining close to plumes of freshwater at river mouths. The farthest offshore they were seen in five years of survey off the eastern Gulf coast of Thailand was 11 km (Chapter 2). This close association with the coast makes marine subpopulations vulnerable to anthropogenic threats including increased boat traffic, overfishing of prey species, bycatch (especially in gillnets), and pollution (Smith et al. 2006, Reeves et al. 2008, Minton et al. 2011). Subpopulations of O. brevirostris in coastal and riverine habitats of Indonesia and the Mekong River actively avoid boats, decreasing available habitat (Stacey and Hvenegaard 2002, Kreb and Rahadi 2004). However, Smith et al. (2003) suggest that prey depletion due to fishing in the Mahakam River may cause O. brevirostris to approach boats to prey on fish caught in gillnets, presenting the danger of entanglement. In both the Mahakam and Mekong Rivers, over 80% of O. brevirostris mortality is attributed to gillnet entanglement (Smith et al. 2003, Beasley et al. 2007). Dams constructed upstream of dolphin habitat can lower water

levels and thus cause significant decreases in habitat area. Throughout Southeast Asia, deforestation and mining produce large amounts of sediment that can lead to shallower waters and decreased salinity as well as introducing chemicals into the water system (Reeves et al. 2008). Along the Andaman coast of Thailand, both illegal and legal fishing practices lead to incidental catch of marine mammal species (Hines et al. 2005). Limited conservation measures are in place, such as cultural prohibitions against harming or killing dolphins, wildlife conservation laws that include O. brevirostris, some fishing regulations, and some protected areas (Lekagul and McNeely 1977, Thein 1977, Hague 1982, Beasley and Davidson 2007, Smith et al. 2008, Sutaria 2009, Hashim and Jaaman 2011, Yanuar et al. 2011, Alava et al. 2012, Kreb et al. 2012, Ryan 2012, Duc 2013, Jutapruet 2013). In Thailand and Laos, for example, government regulations outlaw hunting, possessing and/or selling O. brevirostris body parts (Baird and Mounsouphom 1994, Smith and Beasley 2004). However, enforcement is weak in many places, and dangerous fishing practices (e.g. poison, dynamite, electrofishing, gillnets) are widespread (Baird and Mounsouphom 1994, Beasley and Davidson 2007, Kreb et al. 2007, Jutapruet 2013). More informed, directed conservation measures with consistent monitoring and enforcement are needed.

That *O. brevirostris* is listed as Vulnerable over its entire range and Critically Endangered over a fraction of its range suggests that conservation measures should be taken as soon as possible to prevent its extinction. Work in the Gulf of Thailand, an unevaluated subpopulation, uncovered a mass mortality event (fourteen deaths over a two-week period) (Hines et al. 2015), and research in Bangladesh (currently the largest known subpopulation) documented potentially unsustainable levels of anthropogenic mortality (Smith et al. 2005). These mortality rates highlight the need to evaluate all subpopulations for potential IUCN listing and conservation priority. Furthermore, each subpopulation's status will affect range-wide status. In order to establish successful conservation measures, a strong understanding of the biology of and threats to *O. brevirostris* is needed. Such information as diet and habitat preferences

in conjunction with the spatial distribution of anthropogenic threats, would help reduce human/endangered species conflict by informing the designation of biologically-relevant protected areas. To that end, I investigated the life history, subpopulation structure, diet, and habitat use of O. brevirostris in the Gulf of Thailand as well as anthropogenic use of the eastern Gulf and the overlap of fishing with dolphin habitat. The Gulf of Thailand lies between latitudes 5° 00' and 13° 30' N and longitudes 99° 00' and 106° 00' E, bordering Thailand, Cambodia, Malaysia, and Vietnam, has a total area of approximately 350,000 km², and a total Thai coastline of 1,878 km (Barbier et al. 2003, Cheevaporn and Menasveta 2003). Reaching a maximum depth of 84 meters and opening into the South China Sea (Cheevaporn and Menasveta 2003), it is comprised of three subsystems: the Inner Gulf at the extreme north, a shallow middle band that borders its east and west coasts, and the southern basin. A shallow sill at its extreme southern end limits water exchange with the South China Sea (Pauly and Chuenpagdee 2003). It has supported trawl fisheries since the early 1960s, mostly in the middle band area, and is home to numerous shrimp farms (Barbier 2003, Pauly and Chuenpagdee 2003). Squid, octopus, mackerel, scad, sardine, anchovy, tuna, crab, shrimp, threadfin bream, lizardfish, and bigeye are important fishery targets (Eiamsa-Ard and Amornchairojkul 1997).

To determine life history, subpopulation structure, and diet (**Chapter 2**), I conducted the first stable isotope analyses on *O. brevirostris*, using soft (muscle and skin) and hard (teeth) tissues from the Gulf of Thailand and the Andaman Sea. Such analyses can provide short-term (weeks to months) and long-term (years) temporal information, respectively, about diet variability and habitat use (Abend and Smith 1995, Walker and Macko 1999, Knoff et al. 2008). For life history and subpopulation structure, I compared stable isotopes between different regions of the Gulf of Thailand and the Andaman Sea. To determine diet, I compared stable isotopes in dolphin soft tissue to those in the soft tissues of potential prey

species. I discovered limited age and sex structure, but stable isotope ratios varied significantly by region, suggesting distinct geographic groups which may require distinct conservation strategies. I further discovered that the group of *O. brevirostris* within the eastern Gulf of Thailand is primarily piscivorous and secondarily crustacean-eating, consuming a smaller proportion of cephalopods. I found slight differences between two study sites within the eastern Gulf, suggesting resource partitioning within habitats.

I characterized habitat (**Chapter 3**) by building a species distribution model for the eastern Gulf of Thailand through the collation of *O. brevirostris* occurrence records with a suite of physical and biological environmental variables. Depth had a significant polynomial relationship with dolphin presence probability and temperature had a significant negative relationship with dolphin group size. I identified two primary locations of dolphin occurrence likelihood, which I recommend be considered for marine protected area establishment.

I investigated spatial intensity of anthropogenic use and impact severity, and correlation with environmental variables, in three areas in the eastern Gulf (**Chapter 4**) using density calculations and generalized linear models. I further created a spatial threat assessment showing where dolphins are most at risk of encountering hazardous human activities. Recorded densities of most types of fishing effort were similar between the three areas, with fixed fishing gear encountered in higher densities than boats. Temperature, salinity, chlorophyll-*a*, distance to coastline, turbidity, and year were important predictors of human use across study areas. Dolphin habitat, as determined in Chapter 3, overlapped areas of high presence probability and density of several types of human use. It is my hope that this information will be used to inform conservation within the Gulf of Thailand and beyond.

CHAPTER 2

Diet and Life History of Irrawaddy Dolphins (Orcaella brevirostris) in the Gulf of Thailand and the Andaman Sea

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Abstract

The Irrawaddy dolphin (Orcaella brevirostris) is a threatened, little-known cetacean found throughout Southeast Asia. The main threat to this species is entanglement in fishing gear. Information on this species' life history and ecology are needed to outline a feasible recovery strategy. For the first time for this species, skin and teeth from individuals in the Gulf of Thailand and the Andaman Sea were analyzed for stable carbon and nitrogen isotope ratios. In the eastern Gulf of Thailand, potential prey species were additionally collected to determine diet. Limited age and sex structure, possibly due to small sample size, was discovered. However, stable isotope ratios in Irrawaddy dolphins varied significantly by region (eastern Gulf, northern Gulf, western Gulf, Andaman Sea), suggesting distinct geographic groups which may require distinct conservation strategies. Mixing models revealed that the group within the eastern Gulf is primarily piscivorous, consuming mainly ponyfish, mackerel, gizzardshad, and scad, and secondarily crustacean-eating. Cephalopods make up a smaller proportion of the overall diet. However, slight differences were found between the two study sites within the eastern Gulf whereby animals from one site consumed more cephalopods than those from the other site, suggesting weak sub-regional structure, perhaps driven by resource partitioning. The results of this work can inform management strategies within the immediate study area and beyond by expanding our understanding of population structure and foraging habits.

2.1 Introduction

The Irrawaddy dolphin (Orcaella brevirostris) is a threatened, little-known species of cetacean found throughout Southeast Asia (Reeves et al. 2008). It is only one of three cetaceans (with the finless porpoise, Neophocaena phocaenoides, and the tucuxi, Sotalia fluviatilis) able to inhabit both marine and freshwater areas (Smith and Jefferson 2002), although the extent to which these animals move between fresh and saltwater or how they are able to survive in both environments is unclear (Leatherwood and Reeves 1994). Throughout their range, O. brevirostris has faced numerous anthropogenic threats including gillnet entanglement, habitat degradation, pollution, and boat disturbance (e.g. noise), but it is widely recognized that the greatest threat is entanglement in fishing gear (Smith et al. 2003, Smith et al. 2006, Beasley et al. 2007, Reeves et al. 2008, Minton et al. 2011). In 2008, the IUCN up-listed the species from Data Deficient to Vulnerable over its entire range, and five recognized subpopulations, only one of which inhabits an exclusively marine environment, have been listed as Critically Endangered (Reeves et al. 2008, IUCN 2013). However, several additional recognized subpopulations are not included in the Red List entry for O. brevirostris, indicating that they have not been evaluated and suggesting that they should be considered Data Deficient. It is generally thought that most of these subpopulations are small and declining (Reeves et al. 2008). Given the threatened status of this species and recognized anthropogenic impacts, much information is needed on its population structure, life history, diet, and habitat use as the first step in outlining a feasible recovery strategy. This study focuses on the life history and ecology of subpopulations of Irrawaddy dolphins in the Gulf of Thailand and the Andaman Sea that have yet to be evaluated (Figure 2.1).

Research on *O. brevirostris* has been limited and fragmented; prior studies have focused on either marine or freshwater habitats, but not both (Leatherwood and Reeves 1994, Reeves et al. 2008). Basic life history information on population ranges, habitat utilization, diet, and social structure is poorly documented. There is only one record, from Kuching Bay, Sarawak, Malaysia, based on photo identification mark-recapture, that indicated movement of one individual of approximately 40 kilometers around a peninsula (Minton et al. 2011, Peter 2012, Minton et al. 2013). Understanding Irrawaddy dolphin population dynamics can provide the basis to implement conservation strategies for this species, whether to focus on a small or large region, and how to address the bycatch issue. Such information can also aid future research efforts by providing a baseline for studying populations elsewhere.

Generally, Irrawaddy dolphins feed on small bony fish species, crustaceans, and cephalopods, but records are limited (Baird and Mounsouphom 1997, Stacey and Leatherwood 1997). Known prey in the Mekong River include various cyprinid (carp), silurid, pangasiid, and bagrid (catfish) species (Marsh et al. 1989, Baird and Mounsouphom 1997). Stomach contents of one male stranded in Songhkla Lake, Thailand, contained Puntius leiacanthus, a cyprinid species (Adulyanukosol 1999). A study by Smith et al. (2009) in the Ayeyarwady River of Myanmar found no overlap between fish species caught through cooperative fishing practices and known Irrawaddy dolphin prey from other locations and diet analyses were not conducted on the dolphins. However, fishermen did catch species in the same families as those known prey from the Mekong: Cyprinidae, Bagridae, and Siluridae (Smith et al. 2009). In the Gulf of Thailand, squid, octopus, mackerel, scad, sardine, anchovy, tuna, crab, shrimp, threadfin bream, lizardfish, and bigeye are important fisheries resources (Eiamsa-Ard and Amornchairojkul 1997). If Irrawaddy dolphins target the same species as humans, it is possible that prey depletion due to fishing could be an important contributing factor to range-wide population declines as dolphins could be forced to feed on suboptimal prey, likely affecting growth, reproduction, and survival (Smith et al. 2003, Hines et al. 2005, Smith et al. 2006, Beasley et al. 2007, Reeves et al. 2008, Minton et al. 2011). Understanding Irrawaddy dolphin diet is crucial to determine how their diet overlaps with fishery target species and to define areas in which they may be susceptible to overfishing of their prey and entanglement in fishing gear.

Here, for the first time for O. brevirostris, stable isotope analyses of soft (muscle and skin) and hard (teeth) tissues of Irrawaddy dolphins were used to provide short-term (weeks to months) and long-term (years) temporal information, respectively, about diet variability and habitat use (Abend and Smith 1995, Walker and Macko 1999, Knoff et al. 2008). Naturallyoccurring stable isotopes are used in ecology because organisms incorporate them into their soft tissues and biological minerals from consumed food, water, and gas (Peterson and Fry 1987, Wada et al. 1991, Hobson 1999, Rubenstein and Hobson 2004, Newsome et al. 2010). The elements most often used for ecological studies are carbon (¹³C) and nitrogen (¹⁵N) because they make up a large part of many organic materials and the relative mass differences between isotopes are large. Diet can be determined by comparing stable isotopes in predator tissue to potential prey tissues (Stenhouse and Baxter 1976, Hobson and Clark 1993, Hobson 1999). By analyzing the stable isotopic composition of teeth, which are metabolically inert once formed, target species movements and diet changes over a lifetime can be detected (Shell and Saupe 1993, Hobson 1999, Knoff et al. 2008). The level of variation within teeth can indicate whether individuals are generalist or specialist foragers (Hobson and Sease 1998, Walker and Macko 1999, Knoff et al. 2008), and describe movements due to differences in carbon and nitrogen isotope levels in different habitats (Peterson and Fry 1987, Hobson et al. 1994, Jennings et al. 1997, Bearhop et al. 1999, Hobson 1999, Newson et al. 2010, Ruiz-Cooley et al. 2012, Ruiz-Cooley and Gerrodette 2012). The main goals of this research are 1) to evaluate variability in feeding habits and foraging habitat use of O. brevirostris over their lifetimes, 2) to investigate differences between males and females, and 3) to determine O. brevirostris prey and their proportional contribution to diet composition in the Gulf of Thailand.

2.2 Methods

2.2.1 Field Methods

The Eastern Marine and Coastal Resources Research Center, a research station for the Thai Department of Marine and Coastal Resources, supplied a total of twenty-six dolphin teeth from the following sites: Khlong Yai (n=9), Mueang Trat (n=4), Chachengsao (n=1), Chumporn (n=1), Chonburi (n=1), Phetchaburi (n=1), Samutsakorn (n=1), Satun (n=1), Surattani (n=2), Trang (n=4), and an unrecorded location (n=1) (Table 2.1, Figure 2.1). In addition, we collected skin tissue samples from twenty-two independently stranded dolphins from two sites in Trat Province: Khlong Yai (n=17) and Mueang Trat (n=5) (Table 2.2, Figure 2.1). Stomach contents and foraging observations indicate that Irrawaddy dolphins consume small to medium sized cephalopods, crustaceans, and fish (Marsh et al. 1989, Baird and Mounsouphom 1997, Stacey and Leatherwood 1997, Ponnampalam et al. 2013). Therefore, we purchased species of those taxa from local fishermen in Ban Mai Rut, Trat, Thailand, for stable isotope analysis: two species of cephalopods with an average length of 13 to 24 cm, two species of crustaceans with an average length between 13 and 20 cm, and eight species of fish with average length of 9 to 17 cm (Figure 2.2, Table 2.3). We photographed and measured specimens to create a reference database of potential prey species. From the dorsal surface of each prey item, we took a muscle sample of weight 0.1 to 1.0 g for stable isotope analysis. We preserved all specimens in ethanol for transport to the United States (following Misarti et al. 2009, Huckstadt et al. 2012).

2.2.2 Laboratory Methods: Teeth

We soaked all twenty-six teeth in Milli Q water for approximately 24 hours to clean them, then sorted, measured, and photographed them. We mounted them to glass microscope slides with Crystal Bond. We selected the most complete, least worn, and longest teeth from each individual dolphin to be cut longitudinally in two equal halves, resulting in fifteen teeth. We drew guide lines along the center of the long axis of those fifteen whole teeth for cutting into two symmetric halves. We used a 4-mm diameter wafering blade on an Isomet 1000 saw to perform the cuts. Two were damaged and we did not use them for subsequent steps. We

remounted each tooth half so that the cut side faced up (one whole tooth per slide), and polished cut surfaces with three different grit levels of sandpaper (320, 600, and 1500 from coarse to fine). Using a New Wave Research micromill fitted with a 0.4 mm Brasseler drill bit, we extracted dentin from approximately 500-µm sampling lines (following the contours of the tooth and as close as possible to the lines indicating growth layer groups) measured using the micromill program (micrometer resolution) (Figure 2.3a). We determined the distance from each sampling line to the pulp cavity and tip. Unfortunately, given the small size of the teeth, we could not distinguish the growth layers. For the remaining set of thirteen teeth (eleven not cut in half plus the two that were damaged), we used a Brasseler hand-held drill to sample the cementum – the outermost, compressed layer of the tooth containing the same information as the dentin layers but a higher percentage of collagen (about 50%) (Perrin and Myrick 1980, Figure 2.3b). In this way, we obtained an average value for those thirteen teeth, which would be comparable to the averages calculated from the layers of the thirteen cut teeth. We weighed out one milligram of extracted dentin powder from each layer and the bulk cementum samples using a Sartorius CPA2P microbalance scale with a precision of 1µg. We placed each sample in tin capsules and arranged them in a 96-well sample plate for analysis on a Carlo Erba Elemental Analyzer coupled to a Thermo-Finnigan Delta Plus XP isotope ratio mass spectrometer in the UCSC stable isotope lab. We did not decalcify dentin samples, as is common in stable isotope studies of teeth, to reduce loss of material. Furthermore, decalcification has been proven unnecessary for bulk stable isotope analysis of modern odontocetes (Brault et al. 2014).

2.2.3 Laboratory Methods: Soft Tissues

We vortexed all soft tissue samples in Milli Q water for 30 seconds to remove ethanol. We then minced them using a scalpel and forceps and placed each sample into a new, labeled vial. We froze all samples at -20°C for approximately 72 hours, then freeze-dried them for approximately 12 hours. Lipid-rich tissues have a lower δ^{13} C value than lipid-poor tissues and

can confound δ^{13} C data (DeNiro and Epstein 1978, Tieszen et al. 1983, Howland et al. 2003, Newsome et al. 2010). Therefore, we extracted lipids from the prey and dolphin soft tissue in a Dionex ASE 200 Automated Solvent Extractor using petroleum ether (following the procedures of Dobush et al. 1985, Doucette et al. 2010, Kim and Koch 2012, Thermo Scientific 2012). We dried tissue samples by evaporation under a fume hood for 48 hours, then froze them at -20°C for a further 24 hours and freeze-dried them for a further 12 hours. We homogenized samples using the methods of Alexander et al. (2006). Briefly, we used a plastic vial holder melded to a reciprocating saw blade attachment. Each vial contained between two and four 3.2 mm chrome steel beads and we taped them into the vial holder attachment with electrical tape before agitating the samples for approximately 60 seconds. Finally, we weighed out approximately 1 mg of each powdered sample and standards in tin capsules and prepared a 96-well plate as for the tooth samples.

2.2.4 Analytical Methods

We examined isotopic variation in average tooth values of δ^{13} C and δ^{15} N in four different general locations: Eastern Gulf (specific sites: Khlong Yai and Mueang Trat), Northern Gulf (specific sites: Chonburi, Chachengsao, Samutsakorn, and Phetchaburi), Western Gulf (specific sites: Chumporn and Surattani), and Andaman Sea (specific sites: Trang and Satun), by sex (female, male, and unknown), and by the specific sites within the general locations using multivariate analysis of variance (MANOVA) with Pillai's Trace. We further assessed the variation within individual dolphins using within-subject ANOVA models with Bonferroni corrections on tooth layer values of δ^{13} C and δ^{15} N. Because we took samples approximately every 0.5mm starting at the pulp cavity (the most recent layer), we created a new variable, "age group", to assign values to relative age categories, with the outer 0.5mm considered age group 1 (youngest). As we could not discern layers due to the small size of the teeth, we considered each sample taken from the tooth (at 0.5mm intervals) as an age group. Therefore, these groups cannot be considered absolute age categories as layers

compress unevenly over an animal's lifetime (Newsome et al. 2009) and 0.5mm may not represent the same number of years in an older animal as in a younger animal. Prior to running MANOVA or ANOVA, the following assumptions must be met: each data point is independent of other data points, the dependent variables are approximately normally distributed within groups, there are linear relationships among all pairs of dependent variables, covariates, and variable-covariate pairs, there is homogeneity of variances, and (for MANOVA only) there is homogeneity of covariance matrices (French et al. 2008, Horn 2008). All average values are independent of one another and the point of a within-subject analysis is to assess the differences within individuals, precluding the independence assumption. We ran a Shapiro-Wilk multivariate normality test on δ^{13} C and δ^{15} N for the full dataset of all teeth, the dataset of average values, and the dataset of layer values using the package mvnormtest in R version 3.2.2 (Jarek 2015, R Core Team 2015). The full and layer datasets were normally distributed (W=0.97, p>0.05 and W=0.96, p>0.05, respectively). The averages dataset, however, was not (W=0.91, p<0.05). The test run by MANOVA and ANOVA is robust to non-normality in the absence of outliers (French et al. 2008), so we investigated dependent variables for the presence of outliers, considering any point more than three standard deviations from the mean in either δ^{13} C or δ^{15} N to be an outlier (the Zvalue test; Hodge and Austin 2004, Aggarwal 2013). We detected few outliers in any dataset (full, averages, or layers). Within the Northern Gulf samples, one layer value was an outlier at 3.35 standard deviations from the mean in δ^{15} N. Given that it was not an outlier within the individual or within its sex (male), we retained it. In addition, there were two outliers within the category "unknown collection year", one at 3.01 standard deviations from the mean in δ^{13} C and one at 3.02 standard deviations from the mean in δ^{15} N. For these values, given that the first was not an outlier within the individual or its sex (unknown), the second was not an outlier within its general location or sex (unknown), and that "unknown collection year" is not an appropriately unifying category, we kept these values. In order to test the linearity assumption, we plotted ANOVA residuals against observed isotope values by independent

variable for averages (specific site within each of the four regions, individual, general location (the four regions), and sex) and layers (specific site, individual, general location, sex, and age group). The variables "individual" and "specific site" showed slight nonlinear patterns in both datasets, indicating that the responses associated with those independent variables are not linear. We dropped the variable "individual" from the model. We further tested the variable "specific site" within each general location and found it to produce linear responses in the Eastern Gulf, Western Gulf, and Andaman Sea, but not within the Northern Gulf, so we removed it from the full model and investigated specific site differences within three of the general locations. We tested homogeneity of variances using Levene's Test for Homogeneity of Variances from the car package in R (Fox and Weisburg 2015, R Core Team 2015). All datasets were significantly homogenous in variance (all p-values >0.05). Finally, we used Box's M test from the **biotools** package in R (da Silva 2015, R Core Team 2015) to assess homogeneity of covariance matrices. Due to the high sensitivity of the test to non-normality. an alternative alpha level of 0.005 (Huberty & Petoskey 2000) is often used. In the average dataset, both sex (χ^2 (approx.) =14.24, df=6, p>0.01) and general location (χ^2 (approx.) =15.11, df=9, p>0.05) passed.

We ran two-way MANOVA tests with Pillai's trace on the averages dataset, testing for the effect of general location and sex. Where we found a significant effect of an explanatory variable, we examined the univariate results (with Bonferroni correction to reduce error rates) for each isotope to determine which (if either) was the driving factor of that effect. We further ran one-way MANOVAs on those variables that showed a significant effect. If the one-way MANOVAs were also significant, we made multiple pairwise comparisons with Bonferroni correction to determine which levels of that variable showed the greatest differences. We examined the effects of specific site and sex within the Eastern Gulf, specific site within the Western Gulf and Andaman Sea (in which dolphins of only one sex were collected), and sex within the Northern Gulf, following the same methods as for the full averages dataset.

For the layer dataset, we ran one-way, within-subject ANOVA tests with Bonferroni corrections using the variable "individual" as a grouping factor and "age group" as the within-subject independent variable. Where a significant effect was detected, we made multiple pairwise comparisons with Bonferroni corrections between age groups to determine which exhibited the largest differences. We ran the same tests within each general location.

To determine diet within the Eastern Gulf, we first accounted for fractionation between prey and dolphin tissues using trophic enrichment factors determined from other species. We chose two trophic enrichment factors. First, an average of values from several calculations across taxa (e.g. insects (Caut et al. 2009); aquatic fish, birds, snails, and mussels (Post 2002, Post et al. 2007, Caut et al. 2009); marine mammals (e.g. Hobson et al. 1996, Bode et al. 2003, Zhao et al. 2006, Caut et al. 2009, Alves-Stanley and Worthy 2010, Borrell et al. 2012), fish, birds, crustaceans, and cephalopods (DeNiro and Epstein 1978, Peterson and Fry 1987, Caut et al. 2009); and terrestrial mammals and birds), Δ15N = 3.22142857‰ and Δ13C = 0.9457143‰ (henceforth TEF1) (e.g. DeNiro & Epstein 1981, Minagawa & Wada 1984, France and Peters 1997, Newton 2010, Caut et al. 2011), and second, an average of values from several cetacean species, $\Delta 15N = 2.379\%$ and $\Delta 13C = 1.374\%$ (TEF2) (Caut et al. 2011, Fernandez et al. 2011, Borrell et al. 2012, Mendez-Fernandez et al. 2012, Browning et al. 2014). We plotted δ^{13} C (x-axis) and δ^{15} N (y-axis) in bivariate isotopic space for dolphins and each potential prey item with and without trophic enrichment factor corrections to examine the relationships between dolphins and potential prey. The potential prey species that fall closest to dolphins in isotopic space are most likely their actual prey as stable isotopes within prey are incorporated into the predator. Once fractionation is accounted for using the TEF values, the actual prey species isotopic signatures will be similar to those of the predator (Shoeninger and DeNiro 1984, Ambrose and DeNiro 1986, Schell et al. 1988, Gearing 1991, Hobson 1991, Rosing et al. 1998, Layman et al. 2007a, Ben-David and

Flaherty 2012). We plotted potential prey species over the convex hull of Irrawaddy dolphin isospace (Figure 2.4). We used the convex hull of Irrawaddy dolphin isospace as a measure of their dietary-habitat niche as diet and habitat biochemistry is integrated in animal tissues (Stenhouse and Baxter 1976, Peterson and Fry 1987, Wada et al. 1991, Hobson and Clark 1993, Schell and Saupe 1993, Hobson 1999, Rubenstein and Hobson 2004, Knoff et al. 2008, Newsome et al. 2010) and bulk stable isotope analysis cannot distinguish the effect of diet from baseline values (Ruiz-Cooley et al. 2012, 2014). The potential prey species that fall within the isotope niche of Irrawaddy dolphins would be the most likely true prey of this study group (Shoeninger and DeNiro 1984, Ambrose and DeNiro 1986, Schell et al. 1988, Gearing 1991, Hobson 1991, Rosing et al. 1998, Layman et al. 2007a, b, Ben-David and Flaherty 2012). Four species consistently fell outside of the convex hull: *S. latreille*, *S. sihama*, *O. ruber*, and *T. hamiltonii* and we therefore removed them from further analyses.

To group prey items, we employed hierarchical agglomerative clustering in R (R Core Team 2015). This method begins by considering each individual item as its own cluster, then merges the two most closely related clusters iteratively until all items are contained within one cluster ("Hierarchical Clustering"). We grouped prey items by stable isotope value and taxa (cephalopod, crustacean, or fish). The R stats function **hclust** can use multiple factors to group items. In order to appropriately group items, we visually inspected the dendrograms produced by the function. We considered species that were consistently grouped together early in the process to be distinct clusters.

We then used MixSIAR (Stock and Semmens 2013) to determine the relative contribution of each prey group and individual species to Irrawaddy diet overall in both sites (Khlong Yai and Mueang Trat, Trat Province) and compare diet between sites. Running MixSIAR on individual prey species allowed a more detailed exploration of trophic relationships. MixSIAR is a Bayesian mixing model jointly developed by the developers of the mixing models MixSIR and SIAR. We chose it because it combines elements of two previously developed mixing models and therefore is likely more robust than either of the original models alone.

2.3 Results

Overall, stable isotope time series from Irrawaddy teeth revealed moderate variability as a function of age group (Figure 2.5); some males exhibited higher variability than females over time. Within the 13 teeth, representing 10 animals, δ^{15} N generally changed by less than 2‰ and the overall value tended to decrease over an individual's lifetime, with two exceptions. One female from Chachengsao in the Northern Gulf exhibited nearly the same value initially as at the end of her life (Figure 2.5a), and one male from Samutsakorn Province in the Northern Gulf, in which the value decreased by almost 4‰ and then increased again to nearly the initial value (Figure 2.5b). The two female dolphins in this study exhibited a slight decrease in $\delta^{15}N$ (~1‰) between the first and second set of growth layers. (Figure 2.5a). The four males showed larger differences in δ^{15} N signature (~2‰, maximum ~4‰) that either leveled out after the first decrease or increased. Two males' signatures continued to decrease (Figure 2.5b). Average standard deviation of male δ^{15} N layer values was approximately twice that of females. The variability in δ^{13} C along teeth was similarly small, with most changes smaller than 2‰, but exhibited more variation in pattern. Both sexes show changes in δ^{13} C values over time, though as with δ^{15} N, the patterns differ. Average standard deviation of female δ^{13} C layer values was approximately twice that of males. One female exhibited a continuing decrease from birth on, with a total difference between first and last set of growth layers of approximately 4‰, while the other's δ^{13} C ratio decreased less than 1‰ and leveled out (Figure 2.5d). Half of the males studied exhibited a decrease of approximately 1.5‰ followed by an increase of about 1‰. The other half showed an increase of approximately 0.5% followed by a slight decrease. All males' final δ^{13} C ratios were within around 0.5‰ (Figure 2.5e).

The ANOVA using layer values revealed a significant within-subject effect of age group on both $\delta^{15}N$ and $\delta^{13}C$. Pairwise comparisons between each age group (individual as grouping factor), however, did not indicate any significant differences. In the Eastern Gulf, there was a significant effect of age group only on $\delta^{15}N$. There were no significant age group effects within the Northern Gulf or the Andaman Sea. Similar to the Eastern Gulf, there was a significant effect of age group on $\delta^{15}N$ in the Western Gulf (Table 2.4). To investigate the perceived sex differences, we also performed within-subject ANOVAs on females and males. However, we found no significant effects on either isotope.

Scatterplots of tooth stable isotope values exhibited high variability between Irrawaddy dolphins in the Eastern Gulf, Northern Gulf, Western Gulf, and Andaman Sea; average values from each of these geographic regions occupy distinct isospace with no overlap (Figure 2.6a). MANOVA results of all average tooth values indicated a significant main effect of general location. Univariate results showed that this result is driven primarily by the effect of δ^{13} C rather than δ^{15} N. There was no significant main effect of sex, nor any significant interaction effects. A one-way MANOVA also showed general location to have a significant effect on its own. Univariate results (with Bonferroni-corrected alpha level of 0.05/2=0.025) indicated a significant effect on both δ^{13} C and δ^{15} N (Table 2.5). Pairwise comparisons among general locations with a Bonferroni-corrected alpha level of 0.05/6=0.0083 revealed significant differences between the Eastern Gulf and all other general locations (Northern Gulf, driven by the effect on δ^{15} N; Western Gulf, driven by the effect on δ^{15} N; Andaman Sea with a significant effect on both δ^{13} C and δ^{15} N), and between the Western Gulf and the Andaman Sea, with no significant univariate results (Table 2.6). Dolphins from these regions seemed to further be divided along the coast as averaged values of teeth from the specific sites within these regions also showed differences (Figure 2.6b, Table 2.7). MANOVA results, however, found no significant effects of either sex or specific site within general locations. Similarly, scatterplots of skin stable isotope values from Mueang Trat and Khlong Yai (the two
sites within the Eastern Gulf) appeared different, with average stable isotope values approximately 1‰ different in δ^{15} N and 0.5‰ different in δ^{13} C. However, MANOVA results indicated no significant effects of location on skin stable isotope ratios between the two sites.

MixSIAR revealed that the group of Irrawaddy dolphins in Trat Province primarily consumes fish and shrimp, with a smaller proportion of the diet made up of cephalopods. Hierarchical agglomerative clustering yielded three potential prey groups:

- 1) R. kangurta, R. brachysoma, N. blochii, and A. kleinii (Fish group)
- 2) S. *inermis* and A. *aegina* (Cephalopod group)
- 3) *M. affinis* and *A. chacunda* (Mixed group)

We ran analyses on skin from both Mueang Trat and Khlong Yai combined (hereafter referred to as overall) and on each site separately. When using TEF1, the mixed prey group made up the majority of dolphin diet (~52-56%) followed by the fish group (between 35 and 40%), overall (both sites) and in Khlong Yai alone. All three groups made up nearly equal proportions of diet in Mueang Trat (fish ~36%, mixed ~34%, and cephalopod ~29%). When using TEF2, the fish group made up the majority of dolphin diet overall and in both regions separately, followed by the mixed prey group overall and in Khlong Yai and the cephalopod group in Mueang Trat. Overall and for Khlong Yai, the fish group made up approximately 67% of dolphin diet and the mixed prey group made up about 16-20%. In Mueang Trat, the fish group made up about 24% (Figure 2.7).

MixSIAR also identified the most important individual prey species in dolphin diet (Figure 2.8). When using TEF1, *M. affinis* made up the majority of dolphin diet overall and in Khlong Yai followed by *N. blochii*, which made up the majority of dolphin diet in Mueang Trat followed by

A. chacunda and *S. inermis*. The third most consumed species overall and in Khlong Yai was *A. chacunda*, and in Mueang Trat were *M. affinis* and *A. aegina*. This highlights the primary importance of fish in both areas and the difference between them with respect to cephalopods. Both *S. inermis* and *A. aegina* make up more of the diet in Mueang Trat than in Khlong Yai or overall. Overall and in both regions, dolphins consumed similar proportions of the top three species. When using TEF2, *N. blochii* was most consumed overall and by Mueang Trat dolphins and *R. brachysoma* was most consumed by Khlong Yai dolphins. The second most consumed species overall was *R. brachysoma*, in Mueang Trat was *A. kleinii*, and in Khlong Yai was *N. blochii*. The third most consumed species overall and in Khlong Yai was *R. kanagurta*, and in Mueang Trat was *S. inermis*. When using this TEF, the differences between the regions are less pronounced. While *S. inermis* was consumed more in Mueang Trat than Khlong Yai or overall, *A. aegina* was consumed in similar proportions throughout.

2.4 Discussion and Conclusions

We observed limited relative age or sex structure, perhaps constrained by sample size. Overall, the δ^{13} C difference between age groups one and three was nearly significant at p=0.006 (Bonferroni-corrected alpha level 0.0017) and the δ^{15} N difference between age groups one and two (p=0.004) and one and three (p=0.00176) were also close to significance. These age groups (1-3) have the largest sample size, and thus are better represented. Time series graphs show males and females exhibiting different isotopic patterns, and likely different lifetime foraging strategies as males' isotopic variability suggests a tendency to use distinct habitats or consume more heterogeneous prey items in comparison with females; the latter appearing rather to remain in the same habitat over their lifetime and/or use a narrower isotopic niche. The initial decreases observed in δ^{15} N for almost all individuals may represent the transition between suckling and foraging. Suckling animals are essentially consuming their mothers, and thus feeding at a high trophic level (Bocherens et al. 1995, Hobson and Sease 1998, Polischuk et al. 2001, Mendes et al. 2007, Newsome et al. 2010). However, within-subject ANOVAs by sex failed to reveal any significant differences by age group. This may be due to the small sample sizes in this study or confounding data arising from animals foraging while still suckling, which would exhibit intermediate ratios (Newsome et al. 2006, Newsome et al. 2010). A future study with a larger number of older and known-sex animals could reveal patterns more successfully. Such a study could provide a better understanding of lifetime foraging patterns and differences between males and females, which could further inform conservation in the Gulf of Thailand and beyond. If these ontogenetic isotopic changes represent shifting diets, habitats, or both, conservation measures could prioritize the diet and/or habitat of a certain maturity stage for females and males, such as a sensitive life history period (e.g. reproductive-age females and calves).

Despite the fact that we could not determine movement between fresh and saltwater with current data and other isotope markers are needed to investigate this aspect further, the range of δ^{13} C values detected within dolphin teeth (i.e. ~4‰) suggest little movement between the two habitats for foraging purposes. The expected general difference between freshwater and saltwater animals is approximately 7‰. Moreover, saltwater is enriched in ¹³C over freshwater (Peterson and Fry 1987, Bearhop et al. 1999, Newsome et al. 2010). The lowest value from the female that exhibited the 4‰ difference in δ^{13} C was at the end of the animal's life. That lower value was from the final set of growth layers the animal laid down, presumably when she was in saltwater, as that is the medium from which we recovered her body. Given these factors, a higher final isotope value would suggest a difference due to movement between fresh and saltwater. It is possible that due to the limitations posed by drill bit size, patterns exhibited within the samples taken were missed, though it is unlikely that they are larger than the differences that were detected. An additional isotope, such as δ^{18} O or δ^{34} S (Barros et al. 2010, Newsome et al. 2010), could have better elucidated habitat preferences as oxygen isotopes vary predictably with precipitation regimes (globally) and

seasons (locally) and marine ecosystems are heavily enriched in ³⁴S over terrestrial or freshwater ecosystems (Newton 2010).

That average stable isotope values from teeth in the four study regions were isotopically different suggests that dolphins from those areas maintain different diets and/or utilize distinct habitats with characteristic isotopic baseline (primary producer) values. Such baseline values, as the starting points for the food web, have a strong impact on the stable isotope signatures of consumers (DeNiro and Epstein 1978, 1981, Peterson and Fry 1987, Michener and Schell 1994, Hobson 1999, Vander Zanden and Rasmussen 1999, Clementz and Koch 2001, Post 2002, Newsome et al. 2012, Ruiz-Cooley et al. 2012). The carbon and nitrogen baseline values themselves are determined by several biogeochemical factors including temperature, ocean and atmospheric cycling leading to variable carbon and nitrogen concentrations, dissolved inorganic carbon, denitrification, dark CO₂ fixation (by chemoautotrophs), N₂ fixation, and differential lipid production by phytoplankton as well as other biological and physical processes resulting in enrichment or depletion of carbon and nitrogen (Smith and Morris 1980, Horrigan 1981, Rau et al. 1982, Goericke and Fry 1994, Takai et al. 2000, Ruiz-Cooley et al. 2012). In fact, as mentioned previously, δ^{13} C is used to distinguish habitat usage as it is known that some environments are enriched in ¹³C over others (Peterson and Fry 1987, Hobson et al. 1994, Jennings et al. 1997, Bearhop et al. 1999, Hobson 1999, Newsome et al. 2010). With the exception of the Northern and Western Gulf regions, which show overlap in isospace, the statistical differences between whole-tooth C and N stable isotope values for other regions and that they did not overlap in isospace indicate that these populations do not move among regions over their lifetimes. These data support the hypothesis that there are distinct geographic groups of Irrawaddy dolphins within the wider Gulf of Thailand population that do not share the same foraging habitat. Molecular, distribution, and species-habitat analyses are critical to further understand movement and genetic exchange among those regions to elucidate whether they represent subpopulations

(geographically distinct groups within the global population, IUCN 2013). This could have significant conservation implications and indicate that dolphins in different regions require specific and distinct conservation strategies.

That the Northern and Western Gulf regions lack a significant difference in average tooth stable isotope values suggests that they either represent one large subpopulation including dolphins from both areas or that they may share similar habitat biochemistry, diet, or both. The distance between Phetchaburi Province – the southernmost Northern Gulf location – and Chumporn – the northernmost Western Gulf location – is approximately 323 kilometers, lending more support to the idea that the habitat δ^{15} N and δ^{13} C baselines could be similar given that the greatest confirmed migration of this species is 40 kilometers (Minton et al. 2011, Peter 2012, Minton et al. 2013). In addition, the difference between the Northern and Western Gulf regions is greater in δ^{15} N than δ^{13} C, approximately 1.5‰ vs less than 1‰, perhaps indicating that the δ^{13} C biochemical baseline values in the two regions are alike and that differences in δ^{15} N indicate differences in diet. Habitat use and distribution research in each region could help elucidate this.

The regional isotope differences measured, and the lack of substructure in isotope signatures within regions suggest that the appropriate management unit for Irrawaddy dolphin conservation is at the regional level, and conservationists should plan targeted, potentially varied, protection measures tailored region by region.

Mixing model results indicate that, overall, the population of *O. brevirostris* in the Eastern Gulf of Thailand is primarily piscivorous, consuming mainly ponyfish, mackerel, gizzardshad, and scad. They also consume shrimp in high proportions, but appear not to feed as highly on cephalopods. These results may be due to the greater number of specimens collected from Khlong Yai, such that the results from this area drove the overall results and the influence of the Mueang Trat area samples was reduced. However, the apparent differences between samples from these areas is important, and may indicate that while the two groups likely mix (given the lack of geographic barriers and 63-kilometer separation between the regions), they are not feeding in the same habitats. Those in Mueang Trat appear to feed more heavily on cephalopods than those in Khlong Yai and overall (~18-24% vs ~7-14%). Mackerel, scad, and octopus are important fisheries targets in the Gulf of Thailand (Eiamsa-Ard and Amornchairojkul 1997), suggesting that there may be resource competition between dolphins and fisheries. We expected cephalopods to make up a larger proportion of the diet because Irrawaddy dolphins have been observed in or near patches of squid ink, once in the presence of squid tentacles, and twice directly following squid-circling behavior (Ponnampalam et al. 2013). However, squid species could not be obtained from local fishermen. The analysis only includes octopus and cuttlefish, which likely have different diet and habitat than squid species. For a complete analysis, it would be crucial to include species from the three main prey groups (cephalopods, crustaceans, and fish), with the addition of a squid species.

Considering the limitations previously discussed regarding prey items, from a conservation standpoint, the current MixSIAR results suggest that regulations to decrease bycatch should be introduced in small fish and shrimp fisheries, as these are the most common species eaten by Irrawaddy dolphins. A further recommendation would be bycatch mitigation measures in marbled octopus and spineless cuttlefish fisheries in Mueang Trat waters to reduce fishery interactions. This information can additionally be used to better describe not only *O. brevirostris* occurrence in the Gulf of Thailand and other locations (when the occurrence of these or closely related prey species is known), but can direct diet studies in other places where *O. brevirostris* is found.

2.5 Summary

This is the first dedicated diet and life history study conducted on O. brevirostris to date, and also the first study to use stable isotopes in this species' teeth to investigate lifetime feeding variability in addition to sexual and geographic variation. Although sample size of both dolphin material and prey was limited, we found distinct geographic variation in Irrawaddy dolphin stable isotope signatures among the regions studied, indicating strong potential subpopulation geographic separation. At the sub-regional level, we discovered little structure across most potential subpopulations. However, there may be some regions (e.g. Trat Province) where some sub-regional structure may exist. Limited sample size prohibited strong conclusions about sex and ontogenetic variation in foraging, but there is some evidence that animals feed in different locations or on different prey items at different life stages. Further investigation of this trend could lead to development of different conservation strategies for different life stages, or a means of targeting a specific, particularly vulnerable or crucial life stage for management. Finally, this work demonstrated that the group of Irrawaddy dolphins inhabiting the eastern Gulf of Thailand is primarily piscivorous and secondarily crustacean-eating. Cephalopods are consumed in the smallest proportions. Coastal bottlenose, common, and Hector's dolphins have all been found to eat mostly fish, including croaker, hake, pilchard, trevally, houndfish, and cod, often followed in the diet by cephalopods (Young and Cockroft 1994, Silva 1999, Blanco et al. 2001, Gannon and Waples 2004, Miller et al. 2012, Kiszka et al. 2014). Twenty species of odontocetes studied along the southern African coast between 1966 and 1990 fed mostly on hake and squid (Sekiguchi et al. 1992). Animals found in two specific sites within the eastern Gulf region likely do not forage in the same areas, as those in Mueang Trat consume more cephalopods than those in Khlong Yai. This suggests that different management strategies may be required for these two sites to protect important prey items for this dolphin species.

In addition to the implications these findings have for the Gulf of Thailand and Andaman Sea Irrawaddy dolphins, they can prove useful for research on other groups and subpopulations throughout the species' range. The geographic variation demonstrated in the Gulf of Thailand suggests that Irrawaddy dolphin groups may have small home ranges, which could affect management. As shown from the Eastern Gulf diet results, even animals in neighboring locations lacking geographic barriers forage on prey items in differing proportions. This may be a form of resource partitioning that could be taking place in other groups as well, demonstrating a diet flexibility that may be an asset to this species' continued existence. Because Irrawaddy dolphins exhibit ontogenetic variability, a management scheme could be adopted throughout the species' range once researchers determine if there is a specifically vulnerable or important life history stage that needs to be protected. Finally, the more precise diet information gleaned from this study can help inform fisheries management in other coastal areas where Irrawaddy dolphins are found. Not only has this study provided more data on a data-limited species and avenues for conservation of this species in the Gulf of Thailand and the Andaman Sea, but it has contributed to the baseline data that can be used to design surveys in other areas and can help inform conservation in coastal habitats throughout the species' range.

2.6 Tables

ID	Collection	Sex	Animal Length	Collection	Collection
	Year		(m)	Location	Site
T10U1	2010	U	1.6	Eastern Gulf	Mueang Trat
T11F1	2011	F	1.32	Northern Gulf	Chonburi
T11M1	2011	Μ	1.84	Northern Gulf	Phetchaburi
T11M2	2011	Μ	2.03	Northern Gulf	Samutsakorn
T11M3	2011	Μ	1.93	Western Gulf	Chumporn
T13F1	2013	F	2.2	Eastern Gulf	Khlong Yai
T13F2	2013	F	2.21	Eastern Gulf	Khlong Yai
T13M1	2013	Μ	2.12	Eastern Gulf	Khlong Yai
T13M2	2013	Μ	2.09	Eastern Gulf	Khlong Yai
T13M3	2013	Μ	na	Eastern Gulf	Khlong Yai
T13M4	2013	Μ	na	Eastern Gulf	Khlong Yai
T13M5	2013	Μ	2.18	Eastern Gulf	Khlong Yai
T13M6	2013	Μ	2.05	Eastern Gulf	Khlong Yai
T13M7	2013	Μ	2.21	Eastern Gulf	Khlong Yai
T13U1.1	2013	U	1.42	Eastern Gulf	Mueang Trat
T13U1.2	2013	U	1.42	Eastern Gulf	Mueang Trat
T13U2	2013	U	2.25	Eastern Gulf	Mueang Trat
T13F3	2013	F	1.86	Northern Gulf	Chachengsao
T13M8.1	2013	Μ	1.2	Western Gulf	Surattani
T13M8.2	2013	Μ	1.2	Western Gulf	Surattani
TYYU1.1	na	U	na	Andaman Sea	Trang
TYYU1.2	na	U	na	Andaman Sea	Trang
TYYU2	na	U	na	Andaman Sea	Trang
TYYU3	na	U	na	Andaman Sea	Trang
TYYU4	na	U	na	Andaman Sea	Satun
TYYU	na	U	na	na	na

Table 2.1: Tooth samples of *O. brevirostris* for stable isotope analysis.

Table 2.2: Skin samples f	rom O. brevirostris	used for stable isotope	analysis.

ID	Collection Year	Sex	Animal Length (m)	Collection Location
S08F1	2008	F	na	Khlong Yai
S09U1	2009	U	na	Khlong Yai
S09U2	2009	U	1.5	Khlong Yai
S10U1	2010	U	2	Mueang Trat
S11M1	2011	М	2.15	Khlong Yai
S12F1	2012	F	2.1	Khlong Yai
S12F2	2012	F	2.8	Khlong Yai
S12M1	2012	М	1.9	Khlong Yai
S13F1	2013	F	2.2	Khlong Yai
S13F2	2013	F	2.21	Khlong Yai
S13M1	2013	М	2.12	Khlong Yai
S13M2	2013	М	2.09	Khlong Yai
S13M3	2013	М	na	Khlong Yai
S13M4	2013	М	na	Khlong Yai
S13M5	2013	М	2.18	Khlong Yai
S13M6	2013	М	2.05	Khlong Yai

S13M7	2013	Μ	2.21	Khlong Yai
S13U1	2013	U	na	Khlong Yai
S13U2	2013	U	na	Mueang Trat
S13U3	2013	U	na	Mueang Trat
S13U4	2013	U	1.42	Mueang Trat
S13U5	2013	U	2.25	Mueang Trat

Table 2.3: Potential prey species for stable isotope analysis of *O. brevirostris* diet.

Таха	Scientific Name	Common Name	#	Avg. Length (cm)
Cephalopod	Sepiella inermis	Spineless cuttlefish	5	13.16
Cephalopod	Amphioctopus aegina	Marbled octopus	5	23.72
Crustacean	Metapenaeus affinis	Jinga shrimp	5	13.40
Crustacean	Stomatopoda latreille	Mantis shrimp	2	19.95
Fish	Nuchequula blochii	Twoblotch ponyfish	5	9.43
Fish	Otolithes ruber	Tigertoothed croaker	5	17.40
Fish	Alepes kleinii	Golden scad	5	13.27
Fish	Rastrelliger kanagurta	Indian mackerel	2	15.50
Fish	Rastrelliger brachysoma	Short bodied mackerel	3	15.73
Fish	Anodontostora chacunda	Chacunda gizzardshad	5	13.16
Fish	Sillago sihama	Northern whiting	5	16.19
Fish	Thryssa hamiltonii	Hamilton's thryssa	5	13.28

Table 2.4: Results of within-subject ANOVA showing that stable isotope ratios change over time in *O. brevirostris* teeth.

Region	Isotope	df	F	р
Full study area	δ ¹⁵ N	5, 27	4.84	<0.01
Full study area	δ ¹³ C	5, 27	12.09	<0.001
E. Gulf	δ ¹⁵ N	3, 5	13.11	<0.01
W. Gulf	δ ¹⁵ N	3, 3	17.9	<0.025

Table 2.5: The effect of general location on stable isotopes in *O. brevirostris* teeth.

Model type	Isotope	Pillai	df	F	р	Sig. α	η²
MANOVA	δ^{13} C and δ^{15} N	0.64	2, 21	18.85	<0.001	0.05	0.64
ANOVA	δ ¹³ C	-	1, 22	31.49	<0.001	0.025	0.64
MANOVA	δ^{13} C and δ^{15} N	0.62	2, 23	19.05	<0.001	0.05	0.71
(one-way)							
ANOVA	δ ¹³ C	-	1, 24	32.25	<0.001	0.025	0.71
(one-way)	δ ¹⁵ N	-	1, 24	6.61	<0.025	0.025	0.71

Table 2.6: More	detailed look at the	e general location	s driving the pattern	is seen in the ful	I MANOVA
analyses.					

Pair	Model type	Isotope	Pillai	df	F	р	Sig. α
E. Gulf vs	MANOVA	δ ¹³ C and δ ¹⁵ N	0.86	2, 14	44.3	<0.001	0.0083
N. Guir	ANOVA	δ ¹⁵ Ν	-	1, 15	93.94	<0.001	0.0042
E. Gulf vs	MANOVA	δ ¹³ C and δ ¹⁵ N	0.64	2, 13	24.06	<0.001	0.0083
W. Gulf	ANOVA	$\delta^{15}N$	-	1, 14	50.78	<0.001	0.0042

E. Gulf vs	MANOVA	δ ¹³ C and δ ¹⁵ N	0.89	2, 15	13.39	<0.001	0.0083
Andaman		δ ¹³ C	-	1, 16	22.29	<0.001	0.0042
	ANOVA	δ ¹⁵ N	-	1, 16	22.11	<0.001	0.0042
W. Gulf	MANOVA	δ ¹³ C and	0.89	2, 5	20.12	<0.0083	0.0083
VS		δ ¹⁵ N					
Andaman							

 $\label{eq:2.7: Stable isotope value differences between specific sites within each geographic region.} \\ \underline{Location} & \overline{\delta^{13}C} \ difference} & \overline{\delta^{15}N} \ difference} \\ \end{array}$

Eastern Gulf						
Khlong Yai vs Mueang Trat	0.5‰	1‰				
Western Gulf						
Chomporn vs Surattani	0.1‰	2‰				
Northern Gulf						
Chachengsao vs Phetchaburi	0.6‰	0.2‰				
Phetchaburi vs Samutsakorn	0.3‰	2.2‰				
Chachengsao vs Samutsakorn	0.8‰	2.5‰				
Andaman Sea						
Trang vs Satun	0.3‰	1.5‰				

2.7 Figures



Figure 2.1: Gulf of Thailand with collection locations labeled.



Figure 2.2: Potential prey species from the Gulf of Thailand. All potential prey items are between 9 and 24 cm in length.



Figure 2.3: a) cut and drilled *O. brevirostris* tooth T13U1.2. A: tip of tooth, B: pulp cavity, C: base of tooth, D: drilled lines; b) *O. brevirostris* tooth T13M7.1 with cementum (smooth, outer layer) sampled. A: tip of tooth (very worn down, which makes it look misshapen), B: base of tooth, sampling site outlined in red.



Corrected Irrawaddy and Potential Prey SI Ratios with Average and SE (TEF: Cetacea Average)

b



Figure 2.4: Isospace plots of *O. brevirostris* soft tissue and potential prey results with convex hulls of Irrawaddy dolphin soft tissue results using a) TEF1 and b) TEF2, showing that four species (*S. latreille, S. sihama, O. ruber, and T. hamiltonii*) consistently fall outside of that convex hull.



Figure 2.5: δ 15N time series from a) female, b) male, and c) unknown sex, and δ 13C time series from d) female, e) male, and f) unknown sex dolphin teeth vs. age group, with collection locations labeled.



Figure 2.6: a) Isospace plot of *O. brevirostris* tooth results colored by general location, showing that the averaged values (with 95% CI) from each region occupy distinct areas in isospace, b) Isospace plot of the average and 95% CI of dolphin teeth by specific site, showing the possibility of distinct groups within each general location.



Figure 2.7: Results of *O. brevirostris* diet analysis using the fish, cephalopod, and mixed-taxa prey groups.



Figure 2.8: Results of *O. brevirostris* diet analysis using a reduced set of prey species. Green colors represent the fish group, pink colors represent the cephalopod group, and purple colors represent the mixed group. Note that when analyzing each species, the group percentages are not the same as those when analyzing by group.

CHAPTER 3

Habitat Modeling of Irrawaddy Dolphins (*Orcaella brevirostris*) in the Eastern Gulf of Thailand

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Abstract

The Irrawaddy dolphin (*Orcaella brevirostris*) is a threatened, little-known cetacean found throughout Southeast Asia. The main threat to this species is entanglement in fishing gear. Information on this species' ecology, and specifically habitat use, is needed to effectively inform management. We used hurdle models to evaluate this species' habitat in the eastern Gulf of Thailand, where it had yet to be studied. Depth was a significant predictor of dolphin presence, with a positive relationship up to around 10.5 meters, at which point the relationship becomes negative. Temperature was significantly negatively correlated with dolphin group size. We identified two primary locations of dolphin occurrence probability, one large region in the center of the study area and a smaller region in the south. The results of this work can inform management strategies within the immediate study area by outlining prime locations for marine protected areas. It can further assist conservation planning in other parts of the species' range by expanding our understanding of habitat preferences.

3.1 Introduction

The Irrawaddy dolphin, *Orcaella brevirostris*, is a threatened species of marine and freshwater cetacean found in south and southeast Asia. Marine populations are patchily distributed in waters from coastal India and Bangladesh in the northeast through Myanmar, Thailand, Malaysia, Cambodia, Vietnam, the Philippines, and Indonesia, while freshwater

subpopulations inhabit the three largest Southeast Asian rivers (the Ayeyarwady, the Mahakam, and the Mekong) and two lakes (Chilika in India and Songkhla in Thailand). It has been classified as Vulnerable by the International Union for the Conservation of Nature (IUCN) since 2008 (Reeves et al. 2008). Five recognized subpopulations (distinct groups within the global population (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 (Reeves et al. 2008). For most subpopulations, the greatest threat is entanglement in fishing gear (Smith et al. 2003, Smith et al. 2006, Beasley et al. 2007, Reeves et al. 2008, Minton et al. 2011). Many related and coastal dolphin species (e.g. snubfin dolphin (Orcaella heinsohnil), Indo-Pacific humpback dolphin (Sousa chinensis)) experience similar entanglement threats (Karczmarski 2000, Bearzi et al. 2003, Parra et al. 2006, Bearzi et al. 2008) and conservation measures have included restricted gillnet usage (Parra et al. 2006). A powerful tool for mitigating entanglement includes establishing a marine protected area (MPA), a delineated zone of the ocean designed to restrict fishing with high potential impact and thus protect important habitat of target species or biodiversity as a whole (e.g. Kelleher 1999, Hyrenbach et al. 2000, Cañadas et al. 2005). However, establishing a MPA requires an understanding of the relationship between the population to be protected and its habitat (Cañadas et al. 2005). Further, information on preferred habitats provides insight into areas critical for protection and future research (Bailey and Thompson 2009). A key step in this process is to develop a species distribution and habitat model.

Little is known about the habitat preferences of the Irrawaddy dolphin. 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 and Jefferson 2002), and most available information comes from studies conducted on freshwater subpopulations. These studies have shown that individuals are most often found in deep, calm, high-salinity, high-

productivity pools (Baird and Mounsouphom 1994, Smith and Hobbs 2002, Smith and Jefferson 2002, Stacey and Hvenegaard 2002, Smith et al. 2006, Smith et al. 2007, Reeves et al. 2008). In the Mekong River, Irrawaddy dolphins are most often observed in calm pool habitats at depths of 8 to 30 meters (Baird and Mounsouphom 1994, Baird and Beasley 2005). In Chilika Lagoon in India, dolphins are most often found in shallow waters (0.6-2.5m) between 18.8 and 34.5°C temperature, wide ranges of turbidity and salinity, and narrow pH (7.9-8.9) (Sahu et al. 1998, Pattnaik et al. 2007, Sutaria 2009). In studies conducted in saltwater coastal areas, Irrawaddy dolphin subpopulations have been found to remain in warm, shallow, and brackish to high salinity waters near river mouths, rarely ranging father offshore than a few kilometers (Baird and Mounsouphom 1994, Stacey 1996, Dolar et al. 2002, Smith and Hobbs 2002, Smith et al. 2006, Sutaria 2009, Minton et al. 2011). In Malampaya Sound, Philippines, Irrawaddy dolphins were most often found in depths of less than 6 meters, an average temperature of 30.2°C, average salinity of 28.3 ppt, and average turbidity of 2.2 NTU (Dolar et al 2002, Smith et al. 2004). In inshore waters of East Kalimantan, Indonesia, dolphins were encountered at an average depth of 6.9 meters (Kreb and Budiono 2005). Taken together, this suggests that coastal Irrawaddy dolphins prefer shallow nearshore areas with high nutrient input and high biological productivity, likely supporting important prey resources. However, a more detailed understanding of Irrawaddy dolphin habitat characteristics is needed for the establishment of effective conservation measures. For this purpose, we employ a species distribution model (SDM).

Species distribution models relate records of species occurrence to environmental predictor variables (Guisan and Thuiller 2005, Redfern 2006, Elith and Leathwick 2009). For example, Bräger et al. (2003) used a logistic regression model with a binary response variable to show the temperature, turbidity, and depth preferences of Hector's dolphins (*Cephalorhynchus hectori*) along the coast of New Zealand. Goetz et al. (2012) used a hurdle model to show that beluga whales (*Delphinapterus leucas*) in Cook Inlet, AK, prefer tidal flats and sandy

substrate in the summer. Panigada et al. (2008) used generalized additive models (GAMs) to elucidate the temperature, depth, bottom slope, and offshore preferences of fin whales (*Balaenoptera physalus*) and striped dolphins (*Stenella coeruleoalba*) in the Pelagos Sanctuary in the Western Mediterranean Sea. Assessments of model fit, prediction ability, and likelihood exist to evaluate discrepancies between model results and true phenomena to choose the model that best approximates the ecological reality (McFadden 1978, Kohavi 1995, Kadane and Lazar 2003, Johnson and Omland 2004, Redfern et al. 2006, Zuur et al. 2007, Franklin 2009, Refaeilzadeh et al. 2009). Properly employed and tested SDMs provide information about the type of habitat that can be predicted to be most highly used by a species (Redfern et al. 2006, Elith and Leathwick 2009) and can inform management decisions by identifying critical habitat for target species. They can also predict species responses to environmental changes (Brotons et al. 2004, Araújo et al. 2005, Guisan and Thuiller 2005, Barry and Elith 2006, Elith et al. 2006, Bailey and Thomspon 2009, Elith and Leathwick 2009).

Cetacean distributions are assumed to be nonrandom, driven primarily by prey distributions. Environmental variables collected to build the models serve as proxies for these prey distributions (Redfern et al. 2006, Torres et al. 2008). Environmental variables can be physiographic, such as depth, bottom slope, and distance from shore. They can also pertain to water quality, such as turbidity, sea surface temperature, and salinity, or be purely biological, such as chlorophyll-*a* concentration. These environmental variables are combined with sighting records for the species of interest, often using a geographical information system (GIS) (Stacey and Hvenengaard 2002, Panigada et al. 2008, Corkeron et al. 2011, Torres et al. 2008, Bailey and Thompson 2009). Marine SDMs can account for the threedimensional and dynamic complexities of marine systems and incorporate the responses of marine animals to the variability of marine environments (Bräger et al. 2003, Redfern et al.

2006). In addition, cetaceans are more likely to seek out new habitat than alter their behavior or life history strategies in response to changes in their environments. SDMs can help predict where these animals may go in the event of such changes (Redfern et al. 2006).

In this study, we examine the habitat preferences of Irrawaddy dolphins in the eastern Gulf of Thailand, a group on which no formal habitat studies have yet been conducted. Specifically, we collate Irrawaddy dolphin occurrence records with a range of physical and biological habitat characteristics to develop a species distribution model (SDM) to characterize and predict dolphin habitat with three goals: 1) determine the factors influencing suitable habitat in the study area, 2) predict dolphin distributions to use in the development of conservation measures (e.g. marine protected area (MPA) development, boating/fishing restrictions, pollution mitigation efforts, reduced dolphin entanglement risk) in the Gulf of Thailand, and 3) provide a model for predicting Irrawaddy dolphin presence in less studied coastal saltwater subpopulations.

3.2 Methods

3.2.1 Field Methods

We carried out this research primarily in the eastern Gulf of Thailand (Figure 3.1a), along the coast between the villages of Laem Klat and Khlong Yai, within Trat Province. This group's abundance has been estimated at 423 individuals, one of the largest abundance estimates 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 3.1b) - and waters along the coast of Chanthaburi Province (Figure 3.2), respectively. From 2008-2009 and 2012-2014, 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 from a 12-meter fishing boat or a small inflatable motor boat. For field work around the islands, we commissioned a 20-meter

fishing boat. Survey methods are described in detail in Hines et al. 2015. We collected the data for this research from Trat Province in February-March 2008 (18 total survey days), January 2009 (17 days), January 2012 (20 days), April-May 2012 (4 days), January-February 2013 (13 days), and January 2014 (13 days); the islands from January 2013 (11 days); and Chanthaburi Province from January 2014 (5 days). We conducted all surveys, with the exception of the April-May 2012 field work, in the dry season during the northeasterly monsoon. The April-May 2012 environmental data fell within the range of values collected in other years, and we thus included it in the full dataset rather than modelling it separately. Total survey area was 552 km² in Trat Province, 2,127 km² around the islands, and 815 km² in Chanthaburi.

We coded data via a unique identification number, location (latitude and longitude), and environmental data based on the time of a sighting or a 1-km² sampling area when a sighting point did not directly match an environmental data point. Environmental data collected included sea surface temperature, depth, salinity, turbidity, pH, and chlorophyll-a, which may influence species' distribution directly and indirectly through their prey resources (Guisan and Thuiller 2005). These factors can be considered limiting due to potential physiological constraints (e.g. temperature, salinity, and pH limits), prey availability (e.g. depth, chlorophylla), and the influence of turbidity on visual capture ability and water quality. We included a binary variable indicating whether calves were seen during a sighting as an independent variable to test whether the presence of calves had an effect on dolphin group size or presence. We also measured distances to the coastline and river mouths for each environmental data point using a GIS (ESRI 2014). In 2008, the first year of the study, we measured turbidity with a Secchi disk. In 2009 and 2012, we measured turbidity with a LaMotte Model 2020 Turbidimeter. In 2008, 2009, 2012, and 2013, we used a Davis Instruments Portable Water Depth Sounder Gauge. In 2014, we employed a HawkEye Handheld Sonar System to measure depth. In 2008, 2009, and 2012, we used a YSI Model

30 Handheld Salinity, Conductivity, and Temperature System to record sea surface temperature and salinity. In 2013 and 2014, we used the Eureka Environmental Manta 2 Water Quality Multiprobe to measure temperature, salinity, turbidity, and chlorophyll-*a*. In 2014, we expanded the multiprobe's use to record pH.

3.2.2 Data Organization Methods

We identified outliers as any point more than three standard deviations from the mean of each category (the Z-value test; Hodge and Austin 2004, Aggarwal 2013). We removed those outliers likely due to recording errors.

We binned turbidity and chlorophyll-*a* data 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.

3.2.3 Analytical Methods

We carried out all analyses in R version 2.13.1 (R Development Core Team 2009). We used a pair plot to initially explore the data and identify linear relationships. Next, we ran both a Moran's I test and a Mantel test to determine if sightings were spatially autocorrelated (Paradis et al. 2015, Dray et al. 2016). Both analyses found that there was no significant clustering of sightings (p>0.05). We checked independent variables for collinearity using variance inflation factors (VIF) with a cutoff value of 3 (Zuur et al. 2009, Naimi 2015), resulting in "distance to coastline" being removed. Frequency plots showed sightings data were highly zero-inflated and overdispersed (Figure 3.3a; mean = 0.78 and variance = 4.91). We chose a hurdle model, which models the data in two components. The zero component models the data as binary with a binomial distribution (zeros vs. all nonzero counts) and the truncated count component models just the nonzero counts using a Poisson, negative binomial, or geometric distribution (Zeileis et al. 2008, Zuur et al. 2009, Hu et al. 2011). This model family works under the assumption that separate ecological processes influence presence/absence and number of individuals where the species is present (Zuur et al. 2009). Hurdle models have previously been used as distribution models of marine mammals, including to examine the haulout patterns of harbor seals, wintering habitat of North Atlantic right whales, and summer habitat of belugas (Ver Hoef and Jansen 2007, Goetz et al. 2012, Gowan and Ortega-Ortiz 2014). The frequency curve for the sightings data (Figure 3.3a) closely resembles a negative binomial distribution with mean = 1 and dispersion parameter (k) = 0.1 (Zuur et al. 2009).

$$Var(Y) = \mu + \left(\frac{\mu^2}{k}\right)$$
$$4.91 = 0.78 + \left(\frac{0.78^2}{k}\right)$$
$$k = 0.15$$

We explored three distributions – negative binomial, Poisson, and zero-inflated negative binomial –and compared results from all three types.

Because there were no sightings around the islands or Chanthaburi, and this pattern could confound results, we left these data out of the analysis and explore the differences and potential reasons for this lack of sightings, and how it relates to model results, in the Discussion. Due to uneven data collection across years and missing values caused by instrument error, data availability was not even across years (Table 3.2). Hurdle models do not handle missing data well and *k*-fold cross validation failed on a model including all years and all variables. Therefore, we separated the data into five smaller datasets (Table 3.3). Four datasets included all points for the years included and thus did not include those variables that had missing values. The fifth dataset held only points with all variables.

We fit the data to a suite of zero-inflated models (Jackman et al. 2015), using every combination of variables within each framework for the three model types. This produced 699 total models. 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. Models with lower AIC values (lower variance) provide a better fit to the collected data (Kadane and Lazar 2003, Johnson and Omland 2004, Redfern et al. 2006). *K*-fold cross validation splits the data into *k* subsets (folds) and leaves one out of the model in turn, testing the model on the last fold, and repeats this process a specified number of times (Kohavi 1995, Zuur et al. 2007, Refaeilzadeh et al. 2009), returning an estimate of the prediction error of the model. Lower values indicate a better model (Alfons 2012). We supplemented these model selection criteria with a likelihood ratio test (Hothorn et al. 2015) to compare each reduced model to the full model within each framework (nested models). This test finds the ratio between the negative log likelihoods of the reduced and full models. Nonsignificance (p>0.05) indicates that the null hypothesis - that the difference observed in the full model is due to chance alone - cannot be rejected and thus the reduced model is sufficient (Johnson and Omland 2004).

After choosing one model with each link function/family (negative binomial hurdle, Poisson hurdle, and zero inflated negative binomial) and the same subset of variables, we evaluated each model component (presence/absence and count) using the area under the curve (AUC) of the receiver operating characteristic (ROC) plot, a plot of the false-positive (*x*-axis) to true-positive (*y*-axis) rate based on the values predicted by the model (Franklin 2009, Sing et al. 2015). AUC values range from 0 to 1, with values of 0.5 considered no better than random (Franklin 2009). We also calculated McFadden's pseudo-R² (ρ^2) as a method of model evaluation. This is a goodness-of-fit measure that is found thus:

$$\rho^2 = 1 - \left(\frac{L1}{L0}\right)$$

where $L1 = (-2) * \log likelihood from full model$

and $L0 = (-2) * \log likelihood from null model$

Values of 0.2-0.4 are considered representative of an excellent model fit (McFadden 1978).

Depth and temperature appeared to show a concave form in relation to sightings (Figures 3.3b, c). Therefore, after model selection, we re-ran the full chosen models with depth and temperature as quadratic, rather than linear, functions. We dropped terms from each model sequentially and performed model selection tests and evaluations as above to determine which configuration of terms resulted in the best model.

After choosing the final best model, we determined the optimal values of the significant predictors. We first set all predictors to their average values, then varied only the predictor of interest and determined predictions for the relevant model part.

We obtained predicted probability, count, and overall fitted values from the model and mapped them using ordinary kriging and a 3x3 smoother in a GIS (ESRI 2014) for both occurrence and group size. In order to determine the best locations for protected area designation, we classified overall fitted values by Jenks natural breaks into five classes of dolphin occurrence likelihood in a GIS (ESRI 2014).

3.3 Results

We did not observe dolphins around the islands or off the coast of Chanthaburi, but the environment was similar, with the notable exceptions of depth and distance to river mouth (Table 3.1). We observed the largest groups off the coast of Mai Rut, the next largest concentrated near Laem Klat, and a few large groups off Khlong Yai, with smaller groups observed throughout the Trat study area. Figure 3.4 shows the sightings data used for each model. Average group size was 3.77 individuals (SD = 3.55, range = 1-30). Initial model

selection showed that the full zero-inflated negative binomial framework 3 model (seven variables) best modeled the zero component (ρ^2 =0.08) and that a negative binomial hurdle model using four variables from framework 4 best modeled the count component (ρ^2 =0.10) (Table 3.4).

The framework 3 hurdle model including depth as a quadratic performed slightly better than the zero-inflated negative binomial model (AIC: 767.26 vs 769.27). Therefore, we retained the hurdle model for all subsequent tests. Model selection results are presented in Table 3.5. The best model chosen from framework 3 with the addition of the quadratic depth term included all seven variables for the zero component and all but depth in the count component. The best model chosen from framework 4 with the addition of the quadratic depth and temperature terms included five variables in the zero component (temperature, pH, and chlorophyll-*a* removed) and four variables in the count component (depth, distance to river mouth, salinity, and calves removed). However, the second-order temperature term was not significant (p=0.519), so we chose the model with the same variables in each component without the quadratic temperature term, which also had a better AUC value for the zero component than the framework 3 model. We therefore chose this model, 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, as the final model.

Both the first- and second-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 3.6). Predictions from the zero component of the model (probabilities of dolphin presence) show a positive relationship with depth until around 10.5 meters, at which point the relationship becomes negative (Figure 3.5a). Predictions from the count component (dolphin numbers) show a steady negative relationship with temperature, with almost no

dolphins predicted at around 28.6°C (Figure 3.5b). Full model fitted values show the same functional relationships (Figure 3.5c, d).

Dolphin presence probability was greatest just off the coast from approximate latitudes 11°56'57.358"N to 11°57'48.131"N, between approximately 3 and 6 kilometers offshore (Figure 3.6a). This small patch of high probability is surrounded by a larger patch of slightly lower probability that extends to around 7.5 kilometers offshore and lies between approximate latitudes 11°54'21.016"N and 11°57'48.131"N. Two other lower probability patches lie between 2.5 and 6.5 kilometers offshore from approximate latitudes 11°50'4.828"N and between 5 and 12.5 kilometers offshore from approximate latitudes 12°0'29.931"N to 12°3'28.241"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°56'42.806"N and 12°7'32.03"N. These results are supported by a map of depth in the study area, showing that the areas of highest occurrence probability are in locations with mid-range depths (Figure 3.7a).

The largest dolphin group sizes were predicted in the central portion of the study area, between approximately 1 and 5 kilometers offshore and approximate latitudes 11°55'28.24"N and 11°59'9.906"N, with a smaller patch at around 9 kilometers offshore between approximate latitudes 11°57'31.967"N and 11°59'30.523"N (Figure 3.6b). Two other areas with slightly lower predicted group sizes occur between approximate latitudes 11°47'28.652"N and 11°49'59.945"N, around 3 to 7 kilometers offshore and nearshore from approximate latitudes 12°5'12.366"N to 12°7'14.301"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 in the study area strongly supports the model predictions (Figure 3.7b).

Overall fitted values from the model suggest two small areas of both high probability of dolphin presence and large group size (Figure 3.6c). These are between approximately 3 and 6 kilometers offshore from approximate latitudes 11°56'6.047"N to 11°57'56.023"N and 2.5 and 7.5 kilometers offshore between approximate latitudes 11°47'26.933"N and 11°49'18.686"N. Classification resulted in two areas of high dolphin occurrence likelihood. These surrounded the areas in Figure 3.6c, stretching from 11°54'17.823"N to 11°59'23.166"N in the middle of the study area, approximately 1.5 to 7 km offshore of Mai Rut, spanning longitudes 102°45'24.773"E to 102°42'18.378"E and from 11°47'28.429"N to 11°49'59.055"N offshore of Khlong Yai from 102°46'51.469"E to 102°49'3.679"E (Figure 3.8).

The optimal depths (those at which dolphins are most likely to be encountered) are between 7.5 and 13.05 meters, with the highest probability of dolphin occurrence at around 10 meters (Table 3.7). The optimal temperature range for Irrawaddy dolphins is 24.93-25.31°C, with the highest number of dolphins predicted at 24.93°C (Table 3.8). Because this is the lowest temperature in the dataset, however, the relationship with lower temperatures would be an extrapolation.

3.4 Discussion

3.4.1 Dolphin-habitat relationships in the Gulf of Thailand

In the eastern Gulf of Thailand, dolphin presence was most strongly predicted by depth, while temperature was a strong predictor of group size. Together, this indicates a preference for relatively cool waters of intermediate depth. Geographically, this places Irrawaddy dolphins at intermediate distances from shore (Figure 3.6). Thus, while effective spatial protections for highly mobile species such as cetaceans are difficult to establish (Embling et al. 2009), the two regions that have the greatest predicted dolphin occurrence, shown in red areas in Figure 3.8, represent the most effective sites for a marine protected area (MPA), as they would have the greatest chance of protecting this population (Batisse 1982, Hooker et al. 1999, Kelleher 1999, Hyrenbach et al. 2000, Lausche 2011, Day et al. 2012). Further buffer zones could be formed surrounding the two areas, between approximate latitudes 11°51'34.51"N and 12°0'9.807"N, around 0.25 to 10.5 kilometers offshore, and from approximate latitudes 11°47'28.429"N to 11°50'22.39"N, approximately 1.5 to 10.5 kilometers offshore (Figure 3.8) to protect animals traveling to and from the core areas (Batisse 1982, Hooker et al. 1999, Kelleher 1999, Hyrenbach et al. 2000, Lausche 2011, Day et al. 2012). Bycatch of cetaceans is somewhat greater in the eastern Gulf of Thailand compared to other subpopulations, with 12% of fishers reporting cetacean bycatch (compared with 6% in Sabah, Malaysia) and willingness to change fishing gear is low. Thai fishing communities, however, consider marine conservation to be an important goal and have shown willingness to work towards bycatch reduction (Teh et al. 2015). Placing a MPA in the region where the dolphins are most abundant would likely lead to a significant reduction in bycatch. The Thai Department of Marine and Coastal Resources is currently working on creating the first MPA along the coast of Trat Province, with an emphasis on the conservation of Irrawaddy dolphins, and our research will help inform these efforts (E. Hines pers comm).

3.4.2 Comparison with other locations

Prior studies on Irrawaddy dolphin distribution and habitat have been informal, based upon the average environmental variables at locations of dolphin sightings, with the exception of work conducted in Kuching Bay, Sarawak, Malaysia (Minton et al. 2013, Peter et al. 2016). Marine Irrawaddy dolphin habitat criteria has been assessed in bay, delta, estuary, and coastal areas of seven countries: Bangladesh, Cambodia, Indonesia, Malaysia, Myanmar, the Philippines, and now Thailand (Table 3.9). 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, narrow temperature ranges, narrow turbidity ranges, moderate salinity ranges, and somewhat basic pH (Dolar et al. 2002, Smith et al. 2004, Kreb and Budiono 2005, Beasley and Davidson 2007, Minton et al. 2011, Yanuar et al. 2011, Ponnampalam 2012, 2013, Ponnampalam et al. 2014).

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 dolphins prefer nearshore, somewhat brackish and turbid waters of widely varying depths (Kreb and Rahadi 2004, Kreb and Budiono 2005, Minton et al. 2013, Peter et al. 2016). Average depth of dolphin sightings was deeper than our predicted optimal depth (Kreb and Rahadi 2004, Kreb and Budiono 2005), 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.

In the outer Sundarbans Delta of Bangladesh and deltas of East Kalimantan, Indonesia, dolphin observations occurred in habitats of narrow depth and temperature ranges, but wide turbidity and salinity ranges (Kreb and Budiono 2005, Smith et al. 2005). Average depths were lower than those we identified for the Gulf of Thailand. Temperatures at which dolphins were found were generally lower than those determined to be optimal in the Gulf of Thailand with the average temperature of dolphin sightings in the Sundarbans Delta 1.2°C lower than this study's optimal.

3.4.3 Potential reasons for absence in the islands and Chanthaburi

We did not record any sightings in the islands or Chanthaburi, but we can compare environmental measures between these areas and Trat. As Table 3.1 shows, the average values of the environmental variables are mostly similar. For temperature (Table 3.10), chlorophyll-*a*, and salinity, the values from Trat fall in between the values of the other two areas, while depth (Table 3.11), turbidity, and distance to river mouth are lower in Trat than in either of the other areas and pH in Trat is lower than that in Chanthaburi. The biggest differences are in depth (of which Trat has the lowest value – almost half that of the islands – followed closely by Chanthaburi) and distance to river mouth. Additional unmeasured variables, in conjunction with depth, could be affecting the sighting probabilities in the islands and Chanthaburi. Chanthaburi is a more developed region than Trat, with more fishing and industrial activity, which could potentially have a negative effect on dolphin presence. Distance to river mouth is considered a reliable indicator for this species in other systems (Morzer Bruyns 1966, Marsh et al. 1989, Baird and Mounsouphom 1994, Stacey 1996, Dolar et al. 2002, Smith and Hobbs 2002, Smith et al. 2006, Sutaria 2009, Minton et al. 2011). In this work, it was very different between study areas (Table 3.12). 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 rivers are sources of nutrients to coastal waters and that areas of fresh and salt water mixing are highly productive (Hobbie 2000, McClusky and Elliott 2006, Rossi-Santos et al. 2006).

3.4.4 Model caveats and next steps

Using models to guide management decisions requires some assessment of the uncertainties involved. Of concern are low AUC and p^2 values (Table 3.5), even after repeated model improvements. Such universally low values found in multiple iterative tests could be due to missing covariates. Upwelling, currents, fronts, and prey distributions have all been utilized in other SDMs (Hyrenbach et al. 2000, Torres et al. 2008). Their collection could perhaps make possible a more detailed model, but satellite imagery at such a fine scale is only just becoming available. Furthermore, data on human use, specifically fishing effort, could provide an additional limiting factor for dolphin distribution. However, given the paucity of data for this species, our data provides the first model that can be used to develop

conservation options for this group of Irrawaddy dolphins, and can be directly used in the study area as a guideline for MPA designation.

These results can also be applied 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 (Chasen 1940, Morzer Bruyns 1966, Pilleri and Gihr 1974, Ratnam 1982, Dolar et al. 1997, Adulyanukosol 1999, Anderson and Kinze 1999, Jaaman 2000, Perrin et al. 2005, Ponnampalam 2012, Hines et al. 2014). Our results can be used to optimize exploratory surveys in these 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 (Wenger & Olden 2012, Manocci et al. 2016). The methods we employed can further be used as a template for study designs in these other locations.

Our understanding of this species would greatly benefit from the development of additional species distribution models for the bays, deltas, and coastal areas where surveys have been undertaken in the past. Additional models can both inform key predictor variables as well as provide insight on variability in habitat preferences across the species' range. SDMs can play an important role in Irrawaddy dolphin conservation by helping to illuminate the habitat of this species, thus providing a framework for future research, information needed to predict species responses to changes in habitat ecology and develop effective management strategies (Brotons et al. 2004, Cañadas et al. 2005, Guisan and Thuiller 2005, Elith et al. 2006, Redfern 2006, Bailey and Thompson 2009, Elith and Leathwick 2009).

3.5 Tables

Table 3.1: Mean of environmental variables in each study area.

	Trat	Islands	Chanthaburi
Average temperature (°C)	28.73	29.3	27.83
Average chlorophyll <i>a</i>	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

Table 3.2: Data availability for each time period and location.

Total entries	Depth	Temperature	Salinity	Turbidity	Chl a	рН	Dist. to river mouth
279	279	279	279	121	0	0	279
218	218	218	218	218	0	0	218
203	203	203	203	203	0	0	203
35	35	35	35	35	0	0	35
174	174	174	174	174	174	0	174
185	185	185	185	185	185	185	185
1094	1094	1094	1094	936	359	185	1094
	Total entries 279 218 203 35 174 185 1094	Total entries Depth 279 279 218 218 203 203 35 35 174 174 185 185 1094 1094	Total entriesDepthTemperature279279279218218218203203203353535174174174185185185109410941094	Total entriesDepthTemperatureSalinity279279279279218218218218203203203203353535351741741741741851851851851094109410941094	Total entries Depth Temperature Salinity Turbidity 279 279 279 279 121 218 218 218 218 218 203 203 203 203 203 35 35 35 35 35 174 174 174 174 174 185 185 185 185 185 1094 1094 1094 1094 936	Total entries Depth Temperature Salinity Turbidity Chl a 279 279 279 279 121 0 218 218 218 218 218 0 203 203 203 203 203 0 35 35 35 35 0 174 174 174 174 174 185 185 185 185 185 1094 1094 1094 1094 936 359	Total entries Depth Temperature Salinity Turbidity Chl a pH 279 279 279 279 121 0 0 218 218 218 218 218 0 0 203 203 203 203 203 0 0 35 35 35 35 35 0 0 174 174 174 174 174 0 185 185 185 185 185 185 185 1094 1094 1094 1094 936 359 185

Table 3.3: Model frame	works organized in orde	er to maximize data	a used in the models.	Framework 5 is
reduced such that it only	y contains entries with a	all variables.		

Model Framework	Variables	Data
1	 Depth Temperature Salinity Distance to river mouth Calves Year 	 2008 2009 January 2012 April-May 2012 Coast 2013 Coast 2014
2	 Depth Temperature Salinity Turbidity Distance to river mouth Calves Year 	 2009 January 2012 April-May 2012 Coast 2013 Coast 2014
3	 Depth Temperature Salinity Turbidity Chlorophyll <i>a</i> Distance to river mouth Calves 	Coast 2013Coast 2014
4	Depth	• Coast 2014

 Tem 	perature
-------------------------	----------

- Salinity •
- •
- Turbidity Chlorophyll a •
- pН •
- Distance to river mouth •
- Calves •
- Depth •
- . Temperature •
- Salinity •
- Turbidity ٠

Calves

- Distance to river mouth •
- April-May 2012 Coast 2013 •

•

•

•

•

Year •

•

5

Coast 2014 •

2008

2009

January 2012

Table 3.4: Model selection results, giving the criteria from the best models of each type from each
framework. Single asterisks indicate the best AUC score for that framework. Double asterisks indicate
the best overall AUC scores.

Framework	No. of variables	AIC	CV	LR test	AUC
1					
Negative binomial hurdle	5	2200.07	2.22	p>>0.05	Zero: 0.644 Count: 0.632
Poisson hurdle	5	2391.68	2.22	p>0.05	Zero: 0.649* Count: 0.630
Zero-inflated negative binomial	5	2207.99	2.23	p>0.05	Zero: 0.645 Count: 0.633*
2					
Negative binomial hurdle	4	1743.83	2.38	p>>0.05	Zero: 0.562 Count: 0.5251
Poisson hurdle	4	1932.64	2.39	p>>0.05	Zero: 0.569* Count: 0.522
Zero-inflated negative binomial	4	1752.73	2.39	p>>0.05	Zero: 0.561 Count: 0.5255*
3					
Negative binomial hurdle	3	779.38	1.76	p>0.05	Zero: 0.672 Count: 0.635*
Poisson hurdle	6	805.99	1.75	p>>0.05	Zero: 0.674 Count: 0.632
Zero-inflated negative binomial	7	786.98	1.79	NA: full model	Zero: 0.679** Count: 0.640
4					
Negative binomial hurdle	4	425.35	1.82	p>>0.05	Zero: 0.631 Count: 0.681**
Poisson hurdle	4	438.62	1.76	p>>0.05	Zero: 0.648* Count: 0.665
Zero-inflated negative binomial	1	426.87	1.73	p>0.05	Zero: 0.638 Count: 0.532
5					
Negative binomial hurdle	4	1902.35	2.28	p>>0.05	Zero: 0.649 Count: 0.658
Poisson hurdle	4	2093.73	2.28	p>>0.05	Zero: 0.652* Count: 0.658
Zero-inflated negative binomial	4	1910.65	2.28	p>>0.05	Zero: 0.650 Count: 0.659*
Table 3.5: Model selection results of models with quadratic terms. The framework 4 model actually had a higher AUC for the zero component than the framework 3 model. Although the AUC was higher for the count component of the first framework 4, the second-order temperature term was not significant.

Framework	Vars: zero model	Vars: count model	AIC	cv	LR test	AUC	ρ²
3 quadratic depth	7	6	765.54	1.73	p>0.05	Zero: 0.724 Count: 0.619	0.11
4 quadratic depth and temp	5	4	418.06	1.70	p>0.05	Zero: 0.733 Count: 0.759*	0.13
4** quadratic depth	5	4	416.48	1.71	p>0.05	Zero: 0.737* Count: 0.746	0.13

Table 3.6: Results of the chosen model, showing a significant polynomial relationship between dolphin presence and depth and a significant negative relationship between group size and temperature.

•	Variable	Estimate	Std. Error	Z value	p value
	Intercept	-51.27	38.02	-1.35	0.177
	Salinity	1.50	1.16	1.30	0.194
Zara	Turbidity	1.39	0.72	1.93	0.053
Zeio	Calves	17.20	1476.85	0.01	0.991
component	1 st order depth	14.11	3.89	3.62	0.0003***
	2 nd order depth	-11.82	3.78	-3.12	0.002**
	Distance to river mouth	-0.08	0.06	-1.40	-1.35 0.177 1.30 0.194 1.93 0.053 0.01 0.991 3.62 0.0003*** -3.12 0.002** -1.40 0.163 3.08 0.002** -2.86 0.004** 1.61 0.107 -1.04 0.301 -1.16 0.247
	Intercept	30.90	10.03	3.08	0.002**
Count	Temperature	-0.95	0.33	-2.86	0.004**
component	Turbidity	0.53	0.33	1.61	0.107
component	Chlorophyll a	-0.20	0.20	-1.04	0.301
	рН	-0.68	0.58	-1.16	0.247

Table 3.7: Predictions of probability of dolphin presence at three different depths.

Depth (m)	Predicted Probability
7.5	0.5005
10	0.6395
13.05	0.5009

Table 3.8: Predictions of number of dolphins at three different temperatures.

Temperature (°C)	Predicted Number
24.93	7.207
25.31	5.015
26.99	1.009

	Sound, Philippines Gulf of Thailand*	Archipelago, Myanmar Malampaya	Kuching Bay, Malaysia* Mercui	Sarawak, Malaysia	Perak, Malaysia	Balikpapan Bay, Indonesia	Mahakam Delta, Indonesia	East Kalimantan, Indonesia	East Kalimantan, Indonesia	East Kalimantan, Indonesia	Cambodia	Sundarbans, Bangladesh	Area
Coastal	Coastal	Offshore	Bay	Coastal	Coastal and Estuary	Bay	Delta	Delta	Coastal	Bay	Coastal	Delta: outer	Habitat Type
Range: 7.5-	Mean: 6.5 Range: 1.5-15.1 Optimal: ∼10	18.8	na	Mean: 3.3 Range: 2-5.4	Mean: 5.57 Range: 0.9-14.4	Mean: 14.5 Range: 2-30	Mean: 5.6 Range: 3-10	Mean: 5.6 Range: 3-10	Mean: 6.9 Range: 2-23	Mean: 14.3 Range: 2.5-30	Mean: 8 Range: 1.6-16.7	Mean: 7.5 Range: 2.7-16	Depth (m)
Range: 24.93-	Mean: 30.2 Range: 27-32.5 Optimal: 24.93	30.2	na	na	Mean: 29.71 Range: 26.7-31.2	na	na	na	na	na	na	Mean: 23.7 Range: 21.8-25.4	Temperature (°C)
na	Mean: 2.2 NTU Range: 0-9.6	4 NTU	na	na	na	Mean: 170 cm	na	na	na	na	na	Mean: 295 NTU Range: 8.5-3079	Turbidity
na	Mean: 28.3 Range: 14-34	31.8	Optimal: 28- 30.99	na	Mean: 29.61 Range: 19.97-34.52	na	Mean: 12 Range: 4.6- 19.3	na	na	na	na	Mean: 16.1 Range: 7-34	Salinity (ppt)
na	na	na	na	na	Mean: 8.16 Range: 6.46- 10.6	na	na	na	na	na	na	na	рН
na	na	na	na	Mean: 1.38	na	na	na	na	na	na	na	na	Distance to coast (km)
na	na	na	≤6	Mean: 3.53	na	na	na	na	na	na	na	na	Distance to river mouth (km)
This study	Dolar et al. 2002, Smith et al. 2004	Smith et al. 2005	Minton et al. 2013, Peter et al. 2016	Minton et al. 2011	Ponnampalam 2012, 2013, Ponnampalam et al. 2014	Kreb and Rahadi 2004	Kreb and Budiono 2005a	Kreb and Budiono 2005a	Kreb and Budiono 2005a	Kreb and Budiono 2005a	Beasley and Davidson 2007	Smith et al. 2005	Reference

Table 3.9 (facing page): Existing habitat data, this study included as the last entry. *Studies in which habitat was determined statistically.

Table 3.10: Temperature records from all study areas within and outside of the range in which at least one dolphin is predicted by the model.

Data	Entries in range	Entries out of range
Islands	0	137
Chanthaburi	8	30
All Trat	230	864
Trat 2014	146	40

Table 3.11: Depth records from all study areas within and outside of the optimal range identified by the model.

Data	Entries in range	Entries out of range
Islands	23	114
Chanthaburi	10	26
All Trat	625	469
Trat 2014	103	82

Table 3.12: Average, minimum, and maximum values of distance to river mouth in each area, which may have contributed to the difference in dolphin sightings.

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

3.6: Figures



Figure 3.1: a) Our study area off Trat Province in the eastern Gulf of Thailand including the zig-zag transect lines followed for data collection. b) Expanded study area around the islands including parallel transect lines (Figure credit: Ellen Hines).



Figure 3.2: Chanthaburi study area, with inset map showing its relation to the other study sites.



Figure 3.3: a) Sightings frequency plot, showing the data to be highly zero-inflated, b) histogram of dolphin sightings vs. depth, c) histogram of dolphin sightings vs. temperature. Panels b) and c) from dataset used for best model framework, showing that sightings appear concentrated at medium depths and temperatures.



Figure 3.4: Sightings data used for the five hurdle models. Largest groups are a lighter blue and were all observed off the coast of Mai Rut.



Figure 3.5: Scatterplots with lowess lines showing a) a positive relationship between predicted probability of dolphin presence and depth until around 10.5 meters, at which point the relationship becomes negative, b) a negative relationship between predicted dolphin number and temperature, c) the relationship between model fitted values and depth, and d) the relationship between model fitted values and temperature.



Figure 3.6: a) Predicted probability of dolphin occurrence, including three somewhat 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 likelihood of dolphin occurrence and large group size. We employed kriging and a 3x3 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 3.7: Maps of a) depth in the study area with point values of presence probability, showing that areas of high predicted dolphin presence probability coincide with areas of medium depth, 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. We applied kriging and a 3x3 smoother to the raw data, so the ranges of depths and temperatures depicted are smaller than the recorded ranges (1.4-16.1 m and 24.93-28.66°C, respectively).



Figure 3.8: 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.

CHAPTER 4

Human Use of the Eastern Gulf of Thailand and Implications for Irrawaddy Dolphin (*Orcaella brevirostris*) Conservatoin

JD Jackson-Ricketts, T Whitty, EL Hazen, C Junchompoo, EM Hines

Abstract

The Irrawaddy dolphin (*Orcaella brevirostris*) is a threatened, little-known cetacean found throughout Southeast Asia. The main threat to this species is entanglement in fishing gear. Information on potentially threatening human use where this species occurs is needed to effectively inform management. Specifically, data on areas with the potential for cumulative impacts are necessary for ecosystem-based management through marine spatial planning. We used density calculations and two-part generalized linear models to investigate human use in three areas of the eastern Gulf of Thailand and its overlap with dolphin high use areas. Recorded densities of most types of fishing effort were similar between the three areas, with fixed fishing gear found in higher densities than boats. Temperature, salinity, chlorophyll *a*, distance to coastline, turbidity, and year were important predictors of human use across all study areas. In Trat Province, where dolphins are found, their habitat overlapped areas of high presence probability and density of several types of human use. We recommend fishing regulations within Trat to shift fishing effort outside of dolphin high use areas. Our hope is that this work can serve as a basis for future such efforts and management strategies in other parts of *O. brevirostris* range.

4.1 Introduction

Human activities have caused dramatic changes to global ecosystem function, often surpassing natural processes (Steffen et al. 2011, Goudie 2013). Between 1955 and 2005,

humans altered ecosystems more rapidly and pervasively than in any comparable span of time in human history (World Resources Institute 2005). Adverse impacts of anthropogenic activities on ocean ecosystems include overfishing, loss and destruction of habitat, pollution, climate change, and cumulative effects of these and others (Collie et al. 2000, Chuenpagdee et al. 2003, Ban and Alder 2008, Douvere 2008, Halpern et al. 2009, Ban et al. 2010). Management that focuses on the impacts of one threat without taking into account the effects of others is ineffective as simultaneous human activities lead to multiple effects on individual species and whole communities (Halpern et al. 2009, Gregory et al. 2013). Ecosystem-based management focuses on the functional relationships and processes within ecosystems as well as the distribution of benefits from ecosystem services to the wider community (Douvere 2008, Halpern et al. 2008, Lester et al. 2013). It follows an adaptive management strategy that responds to changes in the ecosystem with changes in management actions (Douvere 2008, St. Martin and Hall-Arber 2008, Borgström et al. 2015). Ecosystem-based management further implements regulations at multiple scales and requires cooperation in multiple sectors of government from federal to local. In marine and terrestrial environments, there are both human-human and human-environment conflicts, but it is more difficult to protect and manage vulnerable areas, species, and environments (and delineate different environments) in the marine realm (Douvere 2008, St. Martin and Hall-Arber 2008, Aswani et al. 2012, Berkes 2012). Marine spatial planning, however, presents an avenue for more comprehensively managing marine ecosystems that can handle the complexity of ecosystembased management (Douvere 2008, Halpern et al. 2008, St. Martin and Hall-Arber 2008, Berkes 2012, Lester et al. 2013). The goal of marine spatial planning is to institute a more logical organization and use of space in marine environments as well as the interactions among different uses by guiding human behavior and activities. Built into this strategy is the understanding that the ocean is a conglomeration of heterogeneous ecosystems and services. By facilitating the integration of spatial data collection methods such as remote sensing and animal tracking, it allows more comprehensive mapping of species habitats and

human uses, thereby making potential sources of conflict between humans and the environment more visible (Douvere 2008, St. Martin and Hall-Arber 2008, Halpern et al. 2012, White et al. 2012, Lester et al. 2013, Maxwell et al. 2013). Marine spatial planning promotes the consideration of alternate ecosystem-based management scenarios and engages multiple managers. The Great Barrier Reef, Wadden Sea, Florida Keys, Channel Islands, and Eastern Scotian Shelf are just some of the places where this program has been successfully implemented (Douvere 2008). For such successes to be possible, researchers and decisionmakers must understand both how humans use marine environments, consumptive and nonconsumptive practices, and the relationship between human activities and ecological impacts (St. Martin and Hall-Arber 2008, Selkoe et al. 2009, Eastern Research Group 2010, White et al. 2012). Thus, they can characterize threats and identify potential conflicts. To evaluate the conflicts or, conversely, the compatibility between humans and the environment, researchers need to assess the spatial distribution of all human impacts more than simply the oft-collected fisheries catch statistics (Halpern et al. 2008, St. Martin and Hall-Arber 2008, Stewart et al. 2010, Halpern et al. 2012, White et al. 2012). To properly evaluate the impacts of such changes to habitats, fish stocks, and non-target species, areas of intense human use need to be delineated in space and time (Stewart et al. 2010). While analyzing cumulative effects can be challenging, studies of individual stressors can be used to predict where cumulative effects are likely to occur and can aid in beginning to develop effective mitigation measures (Ban et al. 2010).

Irrawaddy dolphins (*Orcaella brevirostris*) are a threatened species of marine and freshwater cetacean found in south and southeast Asia (Reeves et al. 2008). The most significant danger throughout this species' range is incidental bycatch in fishing gear (Smith et al. 2003, Smith et al. 2006, Beasley et al. 2007, Reeves et al. 2008, Minton et al. 2011). To assess the potential dangers to this species in a marine environment, we examined human use in three areas along the Thai eastern Gulf of Thailand: the coast of Trat Province, nearby islands

offshore of Trat, and along the coast of Chanthaburi Province (Figure 4.1). For this research, we use the term human use to include boats on the water and fixed gear indicated at the surface by markers (i.e. buoys, flags, or poles). Data on the type and distribution of human use in the study areas were collected concurrently during a boat-based line transect abundance survey (Hines et al. 2015). This work builds upon prior work by Stewart et al. (2010), who assessed fishing effort in southeast Asia and five other regions and follows research by Briscoe et al. (2014), who compared overlap of dugong habitat with fishing effort in Sabah, Malaysia. The objectives were to characterize human use using the proxies of gear and vessel occurrence, to classify the threat levels of anthropogenic activities, assess the relative spatial intensity of those activities, model correlations between environment and human use, and finally to create a spatial threat assessment showing where dolphins are most at risk of encountering hazardous human activities.

4.2 Methods

4.2.1 Field Methods

Field methods and study area are described in detail in Hines et al. (2015) and Chapter 3. We collected boat and fixed gear data continuously during line transect surveys for Irrawaddy dolphins in 2008, 2009, 2012, 2013, and 2014. We followed zig-zag transect lines along the Trat Province coast (Strindberg and Buckland 2004), and parallel transect lines around the islands and along the Chanthaburi coast. Boats and fixed gear were identified through binoculars when unidentifiable with the naked eye. For this research, we used data collected from Trat Province in February-March 2008 (18 total survey days), January 2009 (17 days), January 2012 (20 days), April-May 2012 (4 days), January-February 2013 (13 days), and January 2014 (13 days); the islands from January 2013 (11 days); and Chanthaburi Province from January 2014 (5 days). We conducted all surveys, except that in April-May 2012, in the dry season during the northeasterly monsoon. The April-May 2012 environmental and human use data fell within the range of values collected in other years, and we thus included it in the

full dataset rather than modeling it separately. Total survey area was 552 km² in Trat Province, 2,127 km² around the islands, and 815 km² in Chanthaburi.

We coded data via a unique identification number, location (latitude and longitude), and environmental data. Boat data included size (small, medium, large), category (fishing, transport, military, tourism/recreation, other), type (commercial fishing, small scale fishing, indeterminate fishing, cargo, tug, military, ferry, tourist, other), subtype (purse seine, trawl, gillnet, squid jigger (commercial), surrounding net, longtail, squid (small-scale), barge, speedboat, sailboat, dive boat, other), impact (determined from literature review), and gear. We assigned categories and types based on designations made by the Eastern Research Group (2010) for the National Oceanic and Atmospheric Administration's review of human use mapping and consultation with collaborating researchers from the Thai Department of Marine and Coastal Resources. We identified fixed gear to category (fishing, nonconsumptive), type (bamboo pole, bamboo trap, fish corral, line, pole, buoy), impact, and number. Prior to 2013, no data were recorded for boat type and prior to 2012, no fixed gear data were recorded. When vessel or fixed gear type could not be determined or metadata were not collected, we classified type as "indeterminate".

Environmental data and collection methods were the same as for Chapter 3, with the addition of distance to nearest port town (Laem Klat, Mai Rut, Khlong Yai) measured for each point in Trat Province. Khlong Yai is a larger, more commercial port than either Laem Klat or Mai Rut, and Mai Rut is in turn larger than Laem Klat. Outlier detection and management is described in Chapter 3. We binned turbidity and chlorophyll-*a* data as in Chapter 3.

4.2.2 Impact Designation

We classified the impact of each human use as high, medium, or low. High impact human uses included bottom trawls, bottom gillnets, dredges, midwater gillnets, medium to large

commercial fishing boats, and surrounding nets (Chuenpagdee et al. 2003, Hashim and Jaaman 2011, Whitty 2014). Medium impact uses included pots, traps, pelagic and bottom longlines, recreational motor boats, small-scale cast nets, midwater trawls, seine nets, navigational buoys, and indeterminate buoys (Chuenpagdee et al. 2003, Kreb and Rahadi 2004, Hashim and Jaaman 2011, Whitty 2014). Low impact uses included hook and line fishing, shipping vessels, cruise ships, sailboats, military vessels, and squid jiggers (Blezard and Burgess 1999, US EPA 2001, Cheevaporn and Menasveeta 2003, Hampton et al. 2003, Stevens and Ekermo 2003, Kreb and Rahadi 2004, Buck 2007, Ban and Alder 2008, Hashim and Jaaman 2011, Whitty 2014).

4.2.3 Analytical Methods - Density

To characterize the spatial intensity of human uses of the Gulf of Thailand, we determined the density of each human use type in each study area in each year. In a GIS, we created raster datasets of each human use category with 1 km² cell size and determined the number of boats or fixed gear in each cell. Boat and fixed gear type could not be reliably determined beyond 1 km in the field, and Moran's I tests run on resulting model residuals showed low spatial autocorrelation. Because effort was uneven between study areas, we then weighted density by effort (i.e. how many times our research vessel occupied the cell).

4.2.4 Analytical Methods – Environmental Drivers

We only analyzed datasets that contained sufficient data to perform statistics (Table 4.1). For example, we removed non-consumptive boats due to insufficient data, but they remain in the impact categories. We further considered navigational buoys to be uninformative on their own and only analyzed them as part of medium impact fixed gear. We pooled Trat data because they were collected each year and such time series could indicate overall drivers across years. The year was retained as an independent variable for these datasets. We used pair plots to explore the data in R version 2.13.1 (R Development Core Team 2009). The pair

plots identified multicollinearity between some independent variables, which may confound model results. To reduce multicollinearity, we used variance inflation factors as in Chapter 3. This resulted in different variables being removed for different datasets (Tables 4.2, 4.3). We created frequency plots in R, showing that most human use data were zero-inflated. In addition, some datasets were overdispersed (Zuur et al. 2009, Chapter 3). We performed a Shapiro-Wilk normality test in R, which calculates a W statistic. The null hypothesis, that the data came from a normal distribution, is rejected if significance is p<0.05 (Royston 1982). The test indicated that none of the human use datasets were normally-distributed. Thus, given the small sample sizes, we used non-parametric tests rather than transformations, which are a common means of managing non-normality. We assessed spatial autocorrelation as in Chapter 3, and found it to occur in some datasets.

Given that all the data were non-normal, some were zero-inflated, some were overdispersed, and some showed spatial autocorrelation, we used a generalized linear modelling (GLM) approach with backwards variable selection, creating one model for presence and absence, and a second model for the weighted densities calculated above. GLMs are used for non-normally distributed data, can handle extreme values of dependent variables, and have a mechanism for addressing spatial autocorrelation (Zuur et al. 2009). They have been employed in many species distribution studies and were used to investigate the relationship of fishing effort (density) to socioeconomic (e.g human population size) and physical (e.g. coastline length) variables in coastal areas (Guisan et al. 2002, Stewart et al. 2010). If residual spatial autocorrelation remains after employing a GLM, a generalized linear mixed model (GLMM) is then run to take that residual spatial autocorrelation into account (Dormann et al. 2007). Dobbie and Welsh (2001) created a two-part generalized estimating equation model to handle spatially autocorrelated zero-inflated count data for their study on Noisy Friarbirds (*Philemon corniculatus*) in Canberra while Lyashevska and colleagues (2016) created a two-part Poisson mixture model to map species prevalence and intensity in the

Wadden Sea. For each dataset, we ran six models: three with a binomial distribution (presence/absence) and three with a negative binomial distribution with log link (density x 100 and rounded as GLMs must include integers). We included latitude and longitude in some models to account for spatial autocorrelation and compared models with and without coordinates (Lobo and Martín-Piera 2002, Matsui et al. 2004, Cresswell et al. 2009, Dormann 2009, Jácome-Flores et al. 2015, Maurice et al. 2016). The inclusion of geographic variables serves to model the spatial dependence of variables and thereby reduce residual spatial autocorrelation (Franklin 1998, Miller et al. 2007, Dormann 2009). One model of each distribution included latitude and longitude as independent variables throughout (even when not significant), one included latitude and longitude treated as all other variables (dropped when not significant), and one did not include latitude and longitude. We created Moran's I correlograms in R using the package **ncf** for raw presence/absence and density as well as residuals from each model to determine how well each model type handled the spatial autocorrelation (Zuur et al. 2009, Bjornstad 2016). If residual spatial autocorrelation was low, as indicated by the center line of the correlogram remaining near the zero line (Zuur et al. 2009), we considered the model acceptable and did not run a follow-up GLMM. We performed model selection as in Chapter 3, replacing the likelihood ratio test with ΔAIC .

After choosing the final best models, we interpolated the fitted values using kriging in a GIS (ESRI 2016) to create an overall spatial representation of human use in the study areas. Finally, using results from Chapter 3, we investigated the overlap of human use and dolphin habitat use to determine where dolphins are most likely to encounter human activity and specifically, types of human activity that pose a threat to the animals.

4.3 Results

4.3.1 Density

Density results are presented in Table 4.4. Boat categories were not identified between 2008 and 2012, but overall boat density in Trat declined over that time, with maximum predicted density falling from 24.9 to 11 boats/km²/unit effort. Starting in 2013, boats were identified to the lowest level possible. Overall fishing boat density across study areas ranged from 0.05 to 3 boats per km² per unit effort, with the highest densities observed in the islands and Chanthaburi. Commercial fishing boats were observed at densities between 0.04 and 3 boats per km² per unit effort and small-scale fishing boats at densities between 0.05 and 3 boats per km² per unit effort. Low impact boat densities across study areas ranged from 0.02 to 3 boats per km² per unit effort, with the highest densities observed around the islands. Medium impact boats were observed at densities between 0.05 and 3 boats per km² per unit effort, highest in the islands and Chanthaburi. High impact boat densities ranged from 0.07 to 2 boats per km² per unit effort, with higher densities in Trat and Chanthaburi. Fishing effort in all study areas was primarily commercial in nature, with densities of commercial fishing boats in the islands, Trat in 2013, and Chanthaburi twice those of Trat in 2014. Small-scale fishing boat density mirrored all fishing in Chanthaburi and was higher than in the islands or Trat. Fishing boats were distributed fairly evenly throughout the island study area, primarily in the southern portion of the Chanthaburi study area, and nearshore in Trat.

Fixed gear was universally found at higher densities than boats. Fixed fishing gear covered much of the Trat study area and was found in high densities in all study areas, ranging from 0.07 to 30 markers per km² per unit effort, with the highest densities observed off the northwest coast of Koh Chang in the islands study area. Medium impact fixed gear ranged from 0.06 to 18.67 markers per km² per unit effort across study areas, with the highest densities off the west coasts of all three islands. High impact fixed gear densities were between 0.17 and 0.5 markers per km² per unit effort and only observed in Trat in 2012 and the islands.

4.3.2 Environmental models and overlap with dolphin habitat

Correlograms indicated that residual spatial autocorrelation was low in all GLMs, precluding the need for GLMMs. Predictive power as measured by *k*-fold cross-validation was poor for the negative binomial models (density), which also had higher AIC values than binomial (presence/absence) models. AUC values were comparable, and in some cases superior, to those for binomial models, suggesting that while negative binomial models were poor predictors for unknown values, they fit the given data well. ρ^2 values were overall low. Within model sets (e.g. binomial models for Trat 2013 fishing boats), however, values of all model selection criteria were within the same order of magnitude, making them effective means of comparison.

Model results for boats in the islands and Chanthaburi are reported in Table 4.5. Of 22 models, distance to river mouth was a significant predictor in the most models (n=6), having a universally negative effect and emerging as important more in Chanthaburi than the islands. It predicted all types of fishing and medium impact boats. Distance to coastline was the second most important predictor, having a significant, primarily negative, effect in 3 models. Temperature, salinity, and chlorophyll *a* were significant in 2 models each, temperature with a universally positive relationship to boat density in the islands, salinity having a positive relationship with commercial fishing boat density and a negative relationship with small-scale fishing boat density, and chlorophyll *a* significant in one model each, depth showing a negative relationship with high impact boat density in the islands and turbidity having a positive effect on fishing boat presence, also in the islands. Latitude and longitude were significant in 6 and 4 models, respectively, highlighting the importance of accounting for spatial autocorrelation in this manner.

Around the islands, overall and small-scale fishing was most likely to occur in the greatest densities in the north. Commercial fishing boats were additionally predicted in the south, just off the coast of Koh Kut, with an area of high predicted density located centrally (Figure 4.2). Similar densities of low and medium impact boats were predicted in much the same areas, though with low impact boats predicted to occur off the west of Koh Chang and medium impact off the east. High impact boats were predicted to occur with low impact boats west of Koh Chang in lower densities than low or medium impact boats (Figure 4.3). Within Chanthaburi, fishing boats were predicted to occur throughout much of the study area, but to be found in the highest densities in the south (Figure 4.4a, b). Small-scale fishing boats had a slightly higher probability of presence than commercial fishing boats, and these two types of fishing were predicted to occur in different areas (Figure 4.4c, e). Small-scale fishing was predicted more likely to occur in the north, while commercial fishing was more likely to occur offshore in the south. Predicted medium and high impact boat densities were similar in Chanthaburi, with the highest densities 1.61 and 1.41 per km², respectively (Figure 4.5b, d).

Results of fixed fishing gear models for the islands and Chanthaburi are reported in Table 4.6. Of the four chosen models, temperature and turbidity were the most important predictors, each significant in two models, with a positive effect on presence and a negative effect on density. Chlorophyll *a* and distance to coastline were significant in one model each, chlorophyll *a* having a positive relationship with fixed fishing gear density and distance to coastline a negative relationship with presence in the islands. Latitude and longitude were significant in three and two models, respectively.

Fixed fishing gear was most likely to occur in the northern portion of the islands study area, around Koh Chang, with the greatest densities of fixed fishing gear predicted in the northeast, near the mainland village of Laem Ngop (Figure 4.6). Fixed fishing gear was predicted to

occur throughout the Chanthaburi study area, with the highest densities predicted nearshore in the north (Figure 4.7).

We did not encounter dolphins around the islands or in waters off Chanthaburi Province. However, a hurdle model run on dolphin occurrence and group size data in Trat predicted two core areas of high dolphin occurrence likelihood within larger peripheral areas of slightly lower likelihood (Figure 4.8). The core areas lay between approximately 1.5 and 7 km offshore from approximate latitudes 11°54'17.823"N to 11°59'23.166"N and 3.5 to 9.5 km offshore between approximate latitudes 11°47'28.429"N to 11°49'59.055"N. The peripheral zones were located between approximate latitudes 11°51'34.51"N and 12°0'9.807"N, around 0.25 to 10.5 kilometers offshore, and from approximate latitudes 11°47'28.429"N to 11°50'22.39"N, approximately 1.5 to 10.5 kilometers offshore (Chapter 3).

Results of Trat models are reported in Table 4.7. Across the 10 boat models, salinity and distance to nearest port were the most important predictors, significant in 5 models each. Salinity had a primarily positive effect, while distance to nearest port was universally negatively correlated with presence and density. Temperature followed, significant in four models with a universally positive relationship. Chlorophyll *a* and year were both significant in three models, chlorophyll *a* having a primarily positive effect and year a mainly negative effect. Distance to coastline was significantly positively correlated with density in two models. Depth and turbidity were only significant in one model each, both positively related to boat presence. Latitude and longitude were significant in six and four models, respectively.

All types of fishing boat had a high probability of occurrence over a majority of the Trat study area (Figure 4.9). Maximum presence probability of small-scale fishing boats was the highest of all presence predictions at 0.91 (Figure 4.9e), followed by all fishing boats (Figure 4.9a), medium impact boats (Figure 4.10a), and commercial fishing boats (Figure 4.9c). High impact boats had the lowest maximum presence probability at 0.22 (Figure 4.10c). Maximum predicted density of fishing boats was highest at 0.70 (Figure 4.9b), followed by high impact boats (Figure 4.10d) and medium impact boats (Figure 4.10b). Commercial and small-scale fishing boats were lowest, at 0.47 and 0.46, respectively (Figure 4.9d, f).

The variables showing significant relationships with fixed fishing gear were each only significant in one model (Table 4.7). Salinity was negatively correlated with fixed fishing gear presence, turbidity positively correlated with density, distance to coastline negatively correlated with density, and year positively correlated with presence. The remaining variables, temperature, depth, chlorophyll *a*, pH, and distance to nearest port were not significant in any models.

Fixed fishing gear was predicted to occur throughout most of the study area, with a small area of very low probability off Laem Klat (Figure 4.11a). The highest densities were predicted in nearshore areas between Laem Klat and Mai Rut (Figure 4.11b).

Predicted dolphin habitat (both core and peripheral areas) overlapped with areas of high fishing boat presence probability (Figure 4.9a), moderate fishing boat density (Figure 4.9b), commercial fishing boat presence probability (Figure 4.9c), low to moderate commercial fishing boat density (Figure 4.9d), and high and moderate small-scale fishing (Figure 4.9e, f). Dolphin habitat was found in the same areas as high to moderate medium impact boat presence probability (Figure 4.10a) and density (Figure 4.10b) and high impact boat presence probability (Figure 4.10c), and high and low high impact boat density (Figure 4.10d). Additionally, predicted dolphin habitat overlapped areas of high to moderate fixed fishing gear presence probability (Figure 4.11a) and low fixed fishing gear density (Figure 4.11b),

4.4 Discussion and Conclusions

This study provides a spatial measure of fishing effort (both presence and density) at a regional scale that can be used for fisheries management and conservation, specifically mitigating bycatch risk. The work showed, through density mapping and generalized linear modelling, that Thai waters of Trat Province, Chanthaburi Province, and the islands of Koh Chang, Koh Mak, and Koh Kut are heavily fished. GLMs indicated that presence probability of most human uses is mainly influenced by year, salinity, and turbidity, while density is more influenced by temperature, chlorophyll *a*, salinity, and distance to coastline. Dolphin presence in Trat over the five survey years, as determined by a hurdle model in a prior study, was significantly correlated with depth, showing a positive relationship up to a depth of around 10.5 meters, after which the relationship became negative. Dolphin group size showed a negative relationship with temperature (Chapter 3). Human use mainly correlated positively with depth and temperature, suggesting that dolphins may be at higher risk for encountering boats or fixed gear at intermediate depths (e.g. 7-10 m), but might not co-occur with those more strongly associated with higher temperatures.

Offshore, around the islands of Koh Chang, Koh Mak, and Koh Kut, fishing was sparsely distributed, but highly concentrated. Model predictions suggest that most fishing occurs in the north, near the mainland coast of Laem Ngop, with some commercial fishing taking place more centrally. Chanthaburi Province displays fishing patterns somewhere between the other two study areas, with three clusters of fishing effort, two denser than the third. GLM results indicated high probability of fishing in the north of Chanthaburi, with higher densities of boats, likely found near river mouths, occurring in the south. Recorded fishing effort was similarly dense in all three study areas, but Trat Province is the only one where dolphins were regularly found. Given that the greatest threat to Irrawaddy dolphins is bycatch in fishing gear (Smith et al. 2003, Beasley et al. 2007, Hines et al. 2015), protected areas are most needed in Trat Province over the other study areas. It is further postulated that the range of the Trat

Province dolphin group extends south into Cambodia. The governments of Thailand and Cambodia are beginning to plan a transboundary marine protected area (Hines et al. 2015), which we hope will be informed by the results of this research.

In Trat, high fishing boat densities nearshore in the south are likely due to the location of Khlong Yai, a major port at the extreme southern end of the study area. GLM results predicted similar densities of commercial and small-scale fishing boats and a higher probability of small-scale fishing boat presence. A recent interview survey in Trat indicated that commercial fishing has decreased in the area due to increased fuel costs and decreased catch (Whitty 2014), which could be responsible for the lower probability of commercial fishing boat presence and the significant negative relationship between year and commercial fishing boat presence. GLM results further showed a negative relationship of presence of fishing boats overall with year and a positive relationship between presence of small-scale fishing boats and year, and predicted greater densities of commercial and small-scale fishing boats in the islands and Chanthaburi than Trat. This pattern could indicate that dolphins were driven out of these areas by high boat traffic, a hypothesis supported by the fact that Chanthaburi at least was historically considered a location of high dolphin abundance (Stacey 1996, Anderson and Kinze 1999). However, there is no historical information about dolphin occurrence in the waters surrounding the islands.

Recorded densities of boats of all impact levels were lowest in Trat waters, but we recorded similar and high densities of fixed gears in all study areas. The high densities of medium impact fixed gears (up to 18.67 markers per square kilometer per unit effort in the islands) present an entanglement danger to Irrawaddy dolphins in the region. High impact fixed gears were virtually absent from the Gulf of Thailand. However, because some indeterminate fixed gears are likely some form of fishing gear, a subset of these may be high impact. Specific fixed gear types (e.g. longlines, pots, traps) were difficult to identify from surface markers.

Therefore, some of the impact designations may be over- or under-estimates of the actual threat level.

Fixed fishing gear is moderately to highly likely to overlap with dolphin high use areas. Furthermore, fixed fishing gear presence was positively correlated with year, suggesting that they are increasing. Such potential cumulative impacts present a clear bycatch risk. In addition, O. brevirostris in Trat feed on fishery target species, making competition for food resources another likely conflict between humans and dolphins (Chapter 2). Predicted densities of fishing boats were generally moderate (<1 per square km and, in the case of commercial and small-scale boats separately, <0.5) in dolphin high use areas, suggesting that perhaps dolphin protected areas in those high use regions would be met with little resistance from fishers. Despite the high probability of their presence within dolphin areas, fishing boats appear to be concentrated primarily outside. Only minor movement (based on the predicted density maps), inshore for commercial vessels or offshore for small-scale fishing boats, would place them fully outside. Furthermore, despite their documented increase over time, dolphins are likely to encounter some of the lowest densities of fixed fishing gear. Thus, marine protected areas established around the dolphin high use zones would have likely low impact on fishers in the region. A recent study on the effect of marine protected areas on fisher cooperation and conflict in Baja California, Mexico, showed that both cooperation and conflict was increased in communities with marine protected areas over those without, indicating that conflict did not appear to negatively affect cooperation. Even non-fishers were shown to exhibit more cooperation in MPA communities than non-MPA communities (Basurto et al. 2016). The changes suggested by model results for vessel-based fishing in Trat, that commercial fishers move inshore and small-scale fishers move offshore, may further decrease conflict between these two groups. However, commercial fishers are restricted by regulations mandating that they cannot operate within 3 km of the coast in most areas (FAO 2016), likely precluding an inshore shift. A more significant southern shift may

mitigate the conflict between a dolphin protected area and current commercial fishing regulations (a northern shift would place them in an area of both low dolphin and low boat density, which, while attractive on the surface, likely means the area contains poor fishing grounds). Relocating fixed fishing gear, however, may cause increased conflict with little offset through cooperation, given the high densities already encountered along the coast. However, encouraging fishers and government to work together could help alleviate these issues. In Baja California, Mexico, for example, nongovernmental organizations coordinated trust-building exercises for local stakeholders (Basurto et al. 2016), an activity which could be implemented within Trat to help fishers and government better communicate and work together toward an economically-sound conservation solution that both protects dolphins and prevents local fishers from losing their livelihoods. Toward this end, a non-governmental organization has been established in Mai Rut to raise awareness about local cetaceans and the threat they face from bycatch (E. Hines pers. comm.). Further, a self-monitoring system could be implemented whereby fishers record data about catch and bycatch after designation of MPAs (and where those catches took place), thus providing feedback on MPA effectiveness and effects on fisheries. This would provide fishers with a sense of participation and ensure that their interests and concerns are taken into account (St. Martin and Hall-Arber 2008). The MPA would need to be closely monitored and re-evaluated at established intervals to determine its effectiveness and whether strategies would need to be changed to adapt to the changing environment, dolphin movements, or anthropogenic effects (Hyrenbach et al. 2000, Douvere 2008).

This study's conclusions are limited by ability to identify types of human use. Seasonal changes in human use also could not be observed under the study design, precluding the elucidation of fine-scale variability. Despite these limitations, however, this is the first detailed study on regional human use within the Gulf of Thailand and its relationship with *O*.

brevirostris. We believe this research to be an invaluable first step towards cumulative impact assessment and marine spatial planning within the Gulf of Thailand and beyond.

The areas investigated in this study were identified as areas of high fishing effort in southeast Asia by Stewart et al. (2010), who compiled FAO country profiles, publications, and reports on coastal fisheries in southeast Asia and five other regions. Using the metric boat-meters (boat number*boat length), they calculated fishing effort as boat-meters per km² in different countries throughout each region. The current study builds upon their effort by providing more detailed regional fishing effort data and thus showing finer-scale spatial variation. Furthermore, their study indicated that population size has a positive relationship with fishing boat density. Socioeconomic data could potentially be used in Thailand to predict relative fishing effort in other coastal Gulf provinces based upon our results for Trat Province, helping to determine which regions are more heavily affected by human use (Teh et al. 2015).

The results of this study indicate that small changes in human use, as detailed above, are needed to protect dolphins and that there is potential for decreased conflict between commercial and small-scale fishing, given the above suggestion that they move in opposite directions to avoid the dolphin high use areas. This suggests that the waters of Trat, Thailand, are a strong candidate for effective ecosystem-based management through marine spatial planning.

4.5 Tables

Year	Area	Class	Category	Туре	Analysis
2008	Trat	Boat	Indeterminate	na	Density
2009	Trat	Boat	Indeterminate	na	Density
		Boat	Indeterminate	na	Density
2012	Trot		Fishing	na	Density
	ITal	BoatIndeterminateBoatIndeterminateBoatIndeterminateFixed gearFishingMedium impactHigh impactHigh impactEishingBoatLow impactBoatMedium impactBoatHigh impactBoatFishingBoatLow impactHigh impactHigh impactFixed gearFishingBoatLow impactBoatLow impactHigh impactHigh impactFixed gearFishingFixed gearFishingBoatFishingBoatLow impactHigh impactHigh impactHigh impactHigh impactHigh impactHigh impactHigh impactFishingBoatFishingBoatFishingBoatFishingFishingMedium impactHigh impactHigh impactHigh impactHigh impactFixed gearFishingBoatFishingFishingMedium impactHigh impactHigh impactHigh impactFishingBoatFishingFishingMedium impactHigh impactFishingBoatFishingFishingMedium impactHigh impactFishingHigh impactFishingFishingFishingFishingFishingFishingFishingFishingFishingFishingFi	na	Density	
			CategoryTypeFinalIndeterminatenaDensitIndeterminatenaDensitIndeterminatenaDensitFishingnaDensitHigh impactnaDensitHigh impactnaDensitHigh impactnaDensitGLMSmall-scaleDensitCommercialDensitMedium impactnaDensitLow impactnaDensitHigh impactnaDensitHigh impactnaDensitHigh impactnaDensitFishingnaDensitFishingnaDensitMedium impactnaDensitFishingnaDensitMedium impactnaDensitHigh impactnaDensitMedium impactnaDensitMedium impactnaDensitHigh impactnaDensitHigh impactnaDensitGLMSmall-scaleDensitMedium impactnaDensitMedium impactnaDensit <td>Density</td>	Density	
			.	na	Density
					GLM
			Fishing	Commercial	Density GLM
		Deet		Small-scale	Density GLM
	Islands	Boat	Low impact	na	Density GLM
			Medium impact	na	Density GLM
2013			High impact	na	Density GLM
		Fixed gear	Fishing	na	Density GLM
			Medium impact	na	Density
				na	Density
			Fishing	Commercial	Density
		Boat		Small-scale	Density
	Trat	Doat	Low impact	na	Density
	mat		Medium impact	na	Density
			High impact	na	Density
		Fixed dear	Fishing	na	Density
		· med gedi	Medium impact	na	Density
				na	Density GLM
			Fishing	Commercial	Density GLM
		Boat		Small-scale	Density GLM
	Chanthaburi		Low impact	na	Density
	•		Medium impact	na	Density GLM
2014			High impact	na	Density GLM
2014		Fixed gear	Fishing	na	Density GLM
			Medium impact	na	Density
				na	Density
			Fishing	Commercial	Density
		Boat		Small-scale	Density
	Trat	2.54	Low impact	na	Density
			Medium impact	na	Density
			High impact	na	Density
		Fixed dear	Fishing	na	Density
			Medium impact	na	Density
2012-2014	Trat	Fixed gear	Fishing	na	GLM

Table 4.1: Data used for this study and the analysis for which each dataset was used.

			na	GLM
		Fishing	Commercial	GLM
2013-2014	Boat		Small-scale	GLM
		Medium impact	na	GLM
		High impact	na	GLM

	2014							2013 2014					
	Chanthaburi								Islands				Area
Fixed gear			Boat			Fixed gear			Doar				Class
Fishing	High impact	Medium impact		Fishing		Fishing	High impact	Medium impact	Low impact		Fishing		Category
na	na	na	Small-scale	Commercial	na	na	na	na	na	Small-scale	Commercial	na	Туре
×		×			×	×		×	×	×	×	×	Temp
							×						Depth
			×	×		×	×	×	×	×	×	×	Salinity
×		×			×	×					×	×	Turbidity
×	×	×	×	×	×	×	×	×	×		×	×	Chl a
×	×			×	×	×	×	×	×	×	×	×	Dist coast
	×	×	×		×		×	×	×	×	×	×	Dist river

Table 4.2: Islands and Chanthaburi datasets used for GLMs and variables included (Xs indicate variables retained after VIF calculations).

Class	Category	Туре	Year	Temp	Depth	Salinity	Turbidity	Chl a	Dist coast	Dist port
Boat		na	Х	Х	Х	Х	Х	Х	Х	Х
	Fishing	Commercial	Х	Х	Х	Х	Х	Х		Х
	_	Small-scale	Х	Х	Х	Х	Х	Х	Х	Х
	Medium impact	na	Х	Х	Х	Х	х	Х	Х	х
	High impact	na	Х	Х	Х	Х	Х	Х	Х	
Fixed gear	Fishing	na	Х	Х	Х	Х	Х	Х	х	Х

Table 4.3: Datasets from Trat only (boats: 2013-2014; fixed gear: 2012-2014) used for GLMs and variables included.

Table 4.4: Density res	sults for humar	n use categories.	Density units are	boats or mar	kers per s	quare km
per unit effort.						

Year	Area Class Category		Туре	Minimum	Maximum		
					Density	Density	
2008	Trat	Boat	Indeterminate	na	0.10	24.90	
2009 Trat Boat Indeterminate				na	0.16	14.00	
		Boat	Indeterminate	na	0.22	11.00	
2012	Trot	Fived	Fishing	na	0.19	16.50	
	Trat	rixeu	Medium impact	na	0.06	16.50	
		year	High impact	na	0.17	0.50	
				na	0.16	3.00	
			Fishing	Commercial	0.16	3.00	
		Poot		Small-scale	0.20	2.00	
		Boat	Low impact	na	0.33	3.00	
	Islands		Medium impact na 0.16		0.16	3.00	
			High impact na 0		0.25	1.00	
		Fixed	Fishing	na	0.24	30	
		Fixed	Medium impact	t na 0.22		18.67	
2013		year	High impact	na	0.50	0.50	
	Trat	Boat		na	0.05	3.00	
			Fishing	Commercial	0.06	3.00	
				Small-scale	0.05	1.50	
			Low impact	na	0.25	0.50	
			Medium impact	na	0.05	3.00	
			High impact	na	0.07	2.00	
		Fixed	Fishing	na	0.11	14.33	
		gear	Medium impact	na	0.23	14.86	
2014	Chanthaburi	Boat		na	0.14	3.00	
			Fishing	Commercial	0.20	3.00	
				Small-scale	0.14	3.00	
			Low impact	na	0.33	2.00	
			Medium impact	na	0.11	3.00	
			High impact	na	0.20	3.00	
		Fixed	Fishing	na	0.22	14.00	
		gear	Medium impact	na	0.22	14.00	
		Boat		na	0.05	2.00	
			Fishing	Commercial	0.04	1.50	
	Trat			Small-scale	0.05	1.00	
			Low impact	na	0.02	1.00	
			Medium impact	na	0.05	1.66	
			High impact	na	0.07	1.00	
		Fixed	Fishing	na	0.07	17.00	
		gear	Medium impact	na	0.07	17.00	

2014	2013	Year
Chanthaburi	Islands	Area
Presence Density	Presence Density	GLM
Medium impact High impact Fishing Small-scale Fishing Medium impact High impact Small-scale Fishing Small-scale Fishing Medium impact	Small-scale Fishing Low impact Medium impact High impact Fishing Commercial Fishing Small-scale Fishing Low impact	Type Fishing
	+ +	Temp
1		Depth
	+	Salinity
		Turbidity +
		ChI a
· +		Dist coast Dist river
594.33 113.30 36.22 41.87 34.58 31.86 38.00 168.54 139.51 91.26 134.39 108.73	100.78 116.75 183.59 74.42 453.69 331.65 203.71 217.91	AIC 149.25
7.03 3.45 5.05 2.00 3.09 2.99 2.99 2.99 7.43 7.43 7.43 7.43 3.19 3.31	5.91 5.72 5.19 5.19 9.17 4.88	ΔΑΙC 4.17
0.001 0.08 0.14 0.15 0.30 0.04 0.04 0.04 0.08 0.08 0.08 0.08	0.04 0.05 0.05 0.01	0.07 0.07
107.40 64.76 1.12 1.40 2.31 0.68 1.96 1.96 1.96 108.20 108.20 108.20 108.20 107.49	1.33 2.71 2.10 1.28 1.28 3.53 3.53 3.53 96.92 96.92 96.30	1.26
$\begin{array}{c} 0.97\\ 0.97\\ 0.73\\ 0.76\\ 0.86\\ 0.86\\ 0.83\\ 0.99\\ 0.93\\ 0.99\\ 0.99\\ 0.99\end{array}$	0.79 0.766 0.77 0.77 0.77 0.77 0.77 0.77	AUC

Table 4.5: Boat GLM results for the islands and Chanthaburi. Significant variables in each model indicated with the sign of their correlation.

Table 4.6: Islands and Chanthaburi fixed gear GLM r	esults. Significant variables in each model
indicated with the sign of their correlation.	

Year	Area	GLM	Туре	Temp	Turbidity	Chl a	Dist coast	AIC	ΔΑΙϹ	ρ²	cv	AUC
2013	امعمام	Presence	Fishing	+	+		-	99.28	2.40	0.38	3.04	0.89
	Islands	Density	Fishing	-		+		470.25	1.99	0.05	647.20	0.80
2014 0	Chanthaburi	Presence	Fishing					22.43	1.57	0.49	9.05	0.91
		Density	Fishing		-			384.47	2.39	0.02	458.51	0.67
i ven Seai	Eived moor	Boat										Class
------------	------------	-------------	---------------	---------------------	---------------------------	---------	-------------	---------------	---------------------	---------------------------	---------	------------
Density	Presence			Density					Presence			GLM
Fishing	Fishing	High Impact	Medium Impact	Small-scale Fishing	Commercial Fishing	Fishing	High Impact	Medium Impact	Small-scale Fishing	Commercial Fishing	Fishing	Туре
		+	+			+				+		Temp
							+					Depth
	ı		+		ı	+				+	+	Salinity
+								+				Turbidity
				+			+					Chl a
ı			+			+						Dist coast
												Dist port
	+								+	,		Year
5320.4	422.04	262.26	1934.8	1371.00	1184.00	2151.10	175.97	390.15	356.03	348.01	387.06	AIC
4.90	з.8	6.12	7.2	4.20	8.10	5.80	6.55	2.15	8.68	2.28	4.40	ΔΑΙC
0.01	0.45	0.08	0.03	0.03	0.004	0.03	0.09	0.08	0.16	0.11	0.06	ρ
363.05	2.11	51.44	54.66	37.42	54.97	58.19	2.76	0.86	1.27	1.36	0.82	S
0.68	0.89	0.67	0.73	0.65	0.55	0.69	0.71	0.69	0.77	0.73	0.67	AUC

Table 4.7: Trat GLM results. Significant variables in each model indicated by the sign of their correlation.

4.6 Figures



Figure 4.1: Study areas in the Gulf of Thailand.



Figure 4.2: Predicted a) presence probability and b) density of fishing boats, c) presence probability and d) density of commercial fishing boats, and e) presence probability and f) density of small-scale fishing boats around the islands in 2013.



Figure 4.3: Predicted a) presence probability and b) density of low impact boats, c) presence probability and d) density of medium impact boats, and e) presence probability and f) density of high impact boats around the islands in 2013.



Figure 4.4: Predicted a) presence probability and b) density of fishing boats, c) presence probability and d) density of commercial fishing boats, and e) presence probability and f) density of small-scale fishing boats in Chanthaburi in 2014.



Figure 4.5: Predicted a) presence probability and b) density of medium impact boats and c) presence probability and d) density of high impact boats in Chanthaburi in 2014.



Figure 4.6: Predicted a) presence probability and b) density of fixed fishing gear around the islands in 2013.



Figure 4.7: Predicted a) presence probability and b) density of fixed fishing gear in Chanthaburi in 2014.



Figure 4.8: Predicted areas of high dolphin occurrence probability, designated using Jenks natural breaks classification in a GIS, in Trat in red. Orange areas surrounding the red areas are potential buffer zones.



Figure 4.9: Predicted a) presence probability and b) density of fishing boats, c) presence probability and d) density of commercial fishing boats and e) presence probability and f) density of small-scale fishing boats in Trat; areas of highest dolphin occurrence likelihood outlined in purple; potential buffer zones outlined in blue.



Figure 4.10: Predicted a) presence probability and b) density of medium impact boats and c) presence probability and d) density of high impact boats in Trat; areas of highest dolphin occurrence likelihood outlined in purple; potential buffer zones outlined in blue.



Figure 4.11: Predicted a) presence probability and b) density of fixed fishing gear in Trat; areas of highest dolphin occurrence likelihood outlined in purple; potential buffer zones outlined in blue.

CHAPTER 5

Synthesis

I initially undertook this work knowing almost nothing about Irrawaddy dolphins. I was invited into a large, multinational project aimed at contributing to the small but growing body of knowledge on this rare species with the ultimate goal of preventing its extinction. Basic information about Irrawaddy dolphins, such as habitat and diet preferences, which would aid in such management efforts as predicting their response to environmental changes and reducing conflict with humans by facilitating the designation of biologically-relevant protected areas (among others), is lacking. Only five recognized subpopulations, occupying small portions of their global range, are known well enough for IUCN listing. The species as a whole is considered Vulnerable. However, subpopulation delineation is difficult, especially in the marine realm, and the majority of recognized subpopulations are Critically Endangered. This suggests that many of the regional groups that cannot yet be considered subpopulations due to lack of population structure data may be highly threatened. The invitation was first extended for me to create a habitat model for the group in the eastern Gulf of Thailand, on which data had been collected for two prior years. In my background research, I discovered that their diet was poorly understood, especially that of marine populations. Through discussions with colleagues and committee members, I settled on incorporating a further basic stable isotope diet study with the addition of teeth to help elucidate lifetime foraging variations and thus a piece of their life history. That teeth from around the Gulf of Thailand and even the Andaman Sea were available was fortuitous. The human use study emerged during further discussion as a natural extension of the habitat model and a managementrelevant piece of the overall project. Thus, my part of this work was poised to answer three basic, yet crucial, questions about this poorly understood, threatened species:

1) What do they eat?

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- 2) Where do they live?
- 3) How and how often do they interact with humans?

While I completed my part, others were answering questions about population size, population dynamics, and behavior.

The first data chapter (Chapter 2) gave me more information than I had expected. That there were significant differences between dolphins in several regions around the Gulf of Thailand suggests at least two, likely three, subpopulations within the Gulf. Genetic studies could confirm this possibility. If true, it indicates more than previously known about Irrawaddy dolphin home ranges, which can be applied to other areas, and provides critical information for management within the Gulf of Thailand. The difference between the Gulf of Thailand and the Andaman Sea regions was not a surprise given the evident geographical barrier to mixing.

The second data chapter (Chapter 3) helped us understand what influenced dolphin occurrence in one Gulf region. If dolphin home ranges are in fact larger than suggested by Chapter 2, the results of Chapter 3 may help explain the subpopulation structure discovered in Chapter 2 if the regions are separated by stretches of unsuitable habitat. Expanded habitat studies could help elucidate this. Given their current absence in Chanthaburi despite recorded past presence and habitat similarity (relative to the islands), however, anthropogenic effects may also be contributing to the isolation of these potential subpopulations. The further dietary differences between sites within the eastern Gulf discovered in Chapter 2 were also unexpected. The fact that no significant differences were discovered in average tooth or skin values suggests this is not indicative of further division, but perhaps represents social dynamics via resource partitioning. The work my colleagues are conducting on population dynamics and behavior can perhaps provide insight into the reasons for this difference. Finally, the third data chapter (Chapter 4) builds upon the results of Chapter 3 to present a spatial representation of threats to dolphins and how vulnerable the dolphins are to these threats. Fishing effort is widespread in all three study areas and overlaps with dolphin high use areas in Trat Province. This result is unsurprising given that bycatch is reported in Trat Province. However, knowing where that bycatch is most likely to occur can directly help conservation efforts. A mutually beneficial solution must be devised whereby the risk to dolphins is reduced without destroying the livelihoods of fishers. One such possibility is a reward system in which fishers who work to reduce bycatch in their own operations are given special permits to fish within MPA boundaries, thus providing an incentive for safe fishing practices. Such a system would need regular evaluations to ensure that fishers continued using safe practices after permit achievement. There are undoubtedly a range of other options, but given my lack of social science background or an understanding of Thai government organization, I leave their elucidation to the experts.

The Thai government is currently working towards a MPA in Trat and in talks with the Cambodian government to develop a transboundary MPA system to address potential connectivity with the dolphins studied just across the border in Cambodia. It is my hope that this work will be used in these endeavors as biologically-relevant MPAs will be the most effective. In addition to the potential for conservation of the target species, Irrawaddy dolphins share the eastern Gulf of Thailand with two other threatened cetaceans, the Indo-Pacific humpback dolphin (*Sousa chinensis*) and the Indo-Pacific finless porpoise (*Neophocaena phocaenoides*). The Irrawaddy dolphin could perhaps serve as an umbrella species for the eastern Gulf region, conferring protections to other species. The finless porpoise is especially cryptic and thus likely more difficult to study than the Irrawaddy dolphin. I further hope to see the results of this work applied throughout Irrawaddy dolphin range to help understand their populations, serve as baseline information for new studies, and inform future conservation

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measures. Additional to the utility of this research to other Irrawaddy dolphin populations, the methods employed here can serve as a template for other threatened, little-known species. The same types of information as collected in the overall project of which my work is only part (e.g. population, habitat, diet, threats, behavior) are needed across species. A study that can answer all of these questions simultaneously with cooperation and open communication between colleagues can only be an asset to threatened species management.

I began this project knowing only that this species existed and learned that very little information was known by anybody, the unknown being methodically chipped away by dedicated researchers around the world. Now I contribute my findings to this compilation in the hopes that they provide aid to current and future work on a species I have come to regard as fascinating and that is in need of immediate conservation in many parts of its range.

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