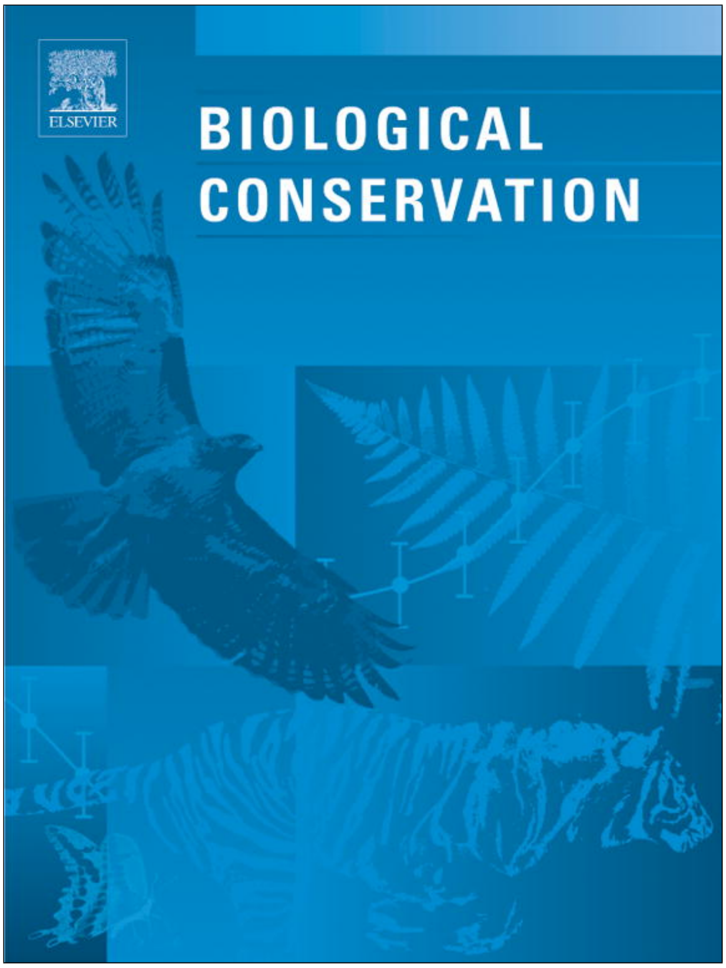
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An index of risk of co-occurrence between marine mammals and watercraft: Example of the Florida manatee

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ABSTRACT

Collisions between wildlife and vehicles represent a large source of mortality for many species. To implement effective protection zones, it is important to identify areas in which wildlife–vehicle collisions are likely to occur. We used statistical models to derive an index of risk of co-occurrence between manatees and boats. Our statistical models were used to predict the distribution of both manatees and boats, while accounting for observer-specific detection probabilities. Models used aerial survey data and we found that both environmental and temporal covariates influenced manatee and boat distributions. Moreover, the probability of detecting manatees varied substantially with the weather and among observers. To our knowledge, this is the first time that manatee distribution is modeled as a function of key environmental and seasonal covariates, while accounting for imperfect detection of manatees. We computed an index of risk of co-occurrence by multiplying the probability of manatee occupancy by the expected boat density and occupancy to identify areas where manatee–boat collisions are likely to occur. This analytical framework emphasizes the importance of accounting for imperfect detection, and how modeling distribution of both organisms and vehicles as a function of key covariates can help improve predictions of risk of collisions. Risk of collision metrics can then be used in designing protection zones.

1. Introduction

Wildlife–vehicle collisions can have a large effect on animal populations. Car collisions for terrestrial species have been well documented (Forman and Alexander, 1998) and are a large source of mortality for many mammals (Allen and McCullough, 1976; Gunson and Clevenger, 2003; Hell et al., 2005), birds (Hell et al., 2005), reptiles (Langen et al., 2009), amphibians (Puky, 2006; Langen et al., 2009) and insects (Rao and Girish, 2007). Many large marine animals, such as manatees (Aipanjiguly et al., 2003; Calleson and Kipp Frohlich, 2007), dugongs (Maitland et al., 2006), North Atlantic right whales (Kraus, 1990; Ward-Geiger et al., 2005; Fonnesbeck et al., 2008; Vanderlaan et al., 2008) and some dolphins (Wells and Scott, 1997; Stone and Yoshinaga, 2000), as well as green turtles (Hazel et al., 2007), suffer from strikes from both commercial and recreational watercraft. In the case of the Florida manatee (*Trichechus manatus latirostris*), collisions with boats are a primary source of mortality (Runge et al., 2007).

Protected areas with prohibited access or restrictions on vehicular speed can reduce wildlife–vehicle collisions and decrease their impact on wild animal populations (Allen and McCullough, 1976; Calleson and Kipp Frohlich, 2007; Hazel et al., 2007). It has been suggested that for manatees, boat speed limits in high-use areas tend to reduce the risk of deadly collisions by providing the boat operator and the manatee more time to avoid the collision, and by reducing the severity of injuries when a collision does occur (Calleson and Kipp Frohlich, 2007). Management policies regulating vehicle accesses and speeds can be controversial (e.g., because of the burden imposed on boaters, Aipanjiguly et al., 2003); therefore, to most effectively determine where to create protection zones, it is important to identify areas where wildlife and vehicles are most likely to collide.

One approach to identify areas with the highest risk of collisions has been to develop statistical models that use covariates to predict the distribution of the species of interest, and determine the risk of co-occurrence with the observed distribution of vehicles. For example, Fonnesbeck et al. (2008) developed a predictive model for whale distribution and used shipping traffic to evaluate the

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risk of vessel strikes under alternative routes. Here, we extend this approach by developing models using covariates for both manatees and boats to predict their distribution and compute the risk of co-occurrence between them, with the ultimate goal of improving the design of protection zones for wildlife. There are several benefits to modeling distribution of manatees and boats, instead of simply plotting observed locations of both. Firstly, scientific hypotheses about the effect of environmental covariates or habitat characteristics can be evaluated. This information can then be used to better identify areas of high risk by linking them to specific risk factors (e.g., presence of seagrass, or other important habitat characteristics). Secondly, this approach can be helpful in making predictions about areas that have not been surveyed, and thus help prioritize survey areas.

We used sightings of Florida manatees recorded from aerial surveys flown in Collier County, Florida, USA, to construct an occupancy model (Royle and Kéry, 2007; Kéry, 2010). Similar surveys were conducted over the same area to record boat sightings and were used to construct abundance and occupancy models for boats (Martin et al., 2005; Kéry, 2010). We accounted for detection probability in the manatee occupancy model. Although survey designs that do not account for detection probability are cheaper, they can lead to an underestimation of the probability of occupancy and to spurious inference (Yoccoz et al., 2001; MacKenzie et al., 2002; Kéry, 2010).

Environmental features and conditions can play a large role in determining manatee distribution. Several studies (Axis-Arroyo et al., 1998; Jiménez, 2005; Olivera-Gómez and Mellink, 2005) have reported an effect of bathymetry on apparent occupancy (i.e., detection probability was not included) by manatees, and they indicated that manatees were more likely to be seen near seagrass, which is their main food resource. Axis-Arroyo et al. (1998) and Jiménez (2005) also found a positive relationship between manatee occupancy and water temperature. We quantified the effects of the environment by using environmental and temporal covariates in our manatee and boat models. We evaluated the influence of the environment on manatee and boat distribution, as well as its influence on manatee detection. We then calculated an index of risk of co-occurrence between manatees and boats to identify areas in which relative risk was high (Fonnesbeck et al., 2008; Vanderlaan et al., 2008). The information about risk of co-occurrence could ultimately be incorporated into a decision theoretical framework to help design manatee protection zones. Historically, manatee speed zones have been put in place with the expectation that it will likely be 10 years or more before the zones are re-evaluated. Therefore, in most cases, the establishment of speed zones can be viewed as a one time step decision process. Nevertheless, if zones need to be revised, our analytical framework would still be relevant but would likely require additional monitoring data.

2. Methods

2.1. Manatee distribution

2.1.1. Manatee aerial surveys

The Florida Fish and Wildlife Conservation Commission (FWC) conducted nine manatee aerial surveys (where GPS tracks were recorded) along the southwest coast of Collier County between July 2007 and May 2008 (Fig. 1). Flights were conducted from a high-winged Cessna 172 at an altitude of 250 m. Dual observers (two observers working independently to detect animals) recorded the location and the number of manatees they sighted within a 600-m distance from the right side of the aircraft (Pollock et al., 2006; Langtimm et al., 2011). In addition, information about survey conditions were recorded from the Automated Surface Observing Systems (ASOS) obtained from local airports. The plane followed a standardized path over the survey area, and a GPS was used to record the exact flight path. Data from nine of these surveys were used in the analyses because no GPS track was recorded for the other surveys. GPS tracks were necessary to rigorously evaluate the effects of key covariates on manatee distribution.

2.1.2. Manatee data analysis

Non-detection of the species of interest during a survey does not necessarily imply that the species is absent. An individual can go undetected by an observer because it is not available to be seen (e.g., a manatee resting on the bottom in turbid water); alternatively, an individual can be present and available to be detected by the observer, but for other reasons, is not observed (Pollock et al., 2006; Edwards et al., 2007; Fonnesbeck et al., 2009; Langtimm et al., 2011). Occupancy models can be used to estimate the probability of occurrence (ψ) of a species while accounting for detection probability (p) (MacKenzie et al., 2003, 2006). In the context of our study, ψ_{it} is the probability that site i is occupied by at least one manatee during survey t, whereas p_{it} is the probability that at least one manatee is detected at site i during survey t, given that it is present and available for detection. The input data to estimate ψ_{it} and p_{it} consist of vectors of 0s and 1s (or encounter histories) for each site, where 1 indicates that at least one manatee was detected and 0 indicates that no manatees were detected. If multiple visits are conducted, it is possible to simultaneously estimate ψ_{it} and p_{it}, in this case p_{it} also accounts for availability. The key assumption in estimating ψ_{it} and p_{it} is that the time between visits is sufficiently short to assume that the state of occupancy remains the same between visits (i.e., the site is assumed to be "closed"). Hereafter, we refer to these short visits as *passes,* and in our protocol the time between passes was less than 30 min. We also conducted multiple surveys at each site; the time between these surveys was more than 10 days (sites are not assumed to be "closed" among surveys). This protocol corresponds to a typical multiseason survey design (MacKenzie et al., 2006). Thus, repeat passes were used to estimate p_{it}, whereas repeat surveys were used to model ψ_{it} as a function of temporal covariates. Because this was a pilot study, there were not enough repeated passes to accurately estimate p_{it}; instead, we used observations from the first pass from both observers in lieu of observations from two different passes. This approach allowed us to estimate the probability of detection associated with each observer, given that manatees were available for detection. To create site encounter histories, we overlaid a grid (cell size, 1000 m $\times$ 1000 m) (Fig. 1) onto the survey area, defined each cell as a site, and assigned each cell a 1 if at least one manatee was detected by the observer at a site; otherwise 0 was assigned. For instance, for site i during survey t, the encounter history "01", meant that the first observer did not detect any manatees, and the second observer detected at least one manatee.

2.1.3. Manatee occupancy covariates

We modeled manatee occupancy as a function of key environmental covariates: bathymetry, distance to seagrass, distance to developed areas, and seasons.

Bathymetry is believed to influence manatee distribution (Axis-Arroyo et al., 1998; Jiménez, 2005; Olivera-Gómez and Mellink, 2005). Using a GIS (ESRI ArcGIS version 9.3.1.), we partitioned bathymetric data (NOAA National Geophysical Data Center, U.S. Coastal Relief Model; http://www.ngdc.noaa.gov/mgg/coastal/crm.html) into 1-m depth bin categories. The mean depth value of each category was used in our models; tidal fluctuation was not taken into account, which has the potential to fluctuate up to 1 m from high tide to low tide in Southwest Florida. The bathymetric data that we used generally correspond to mean lower low

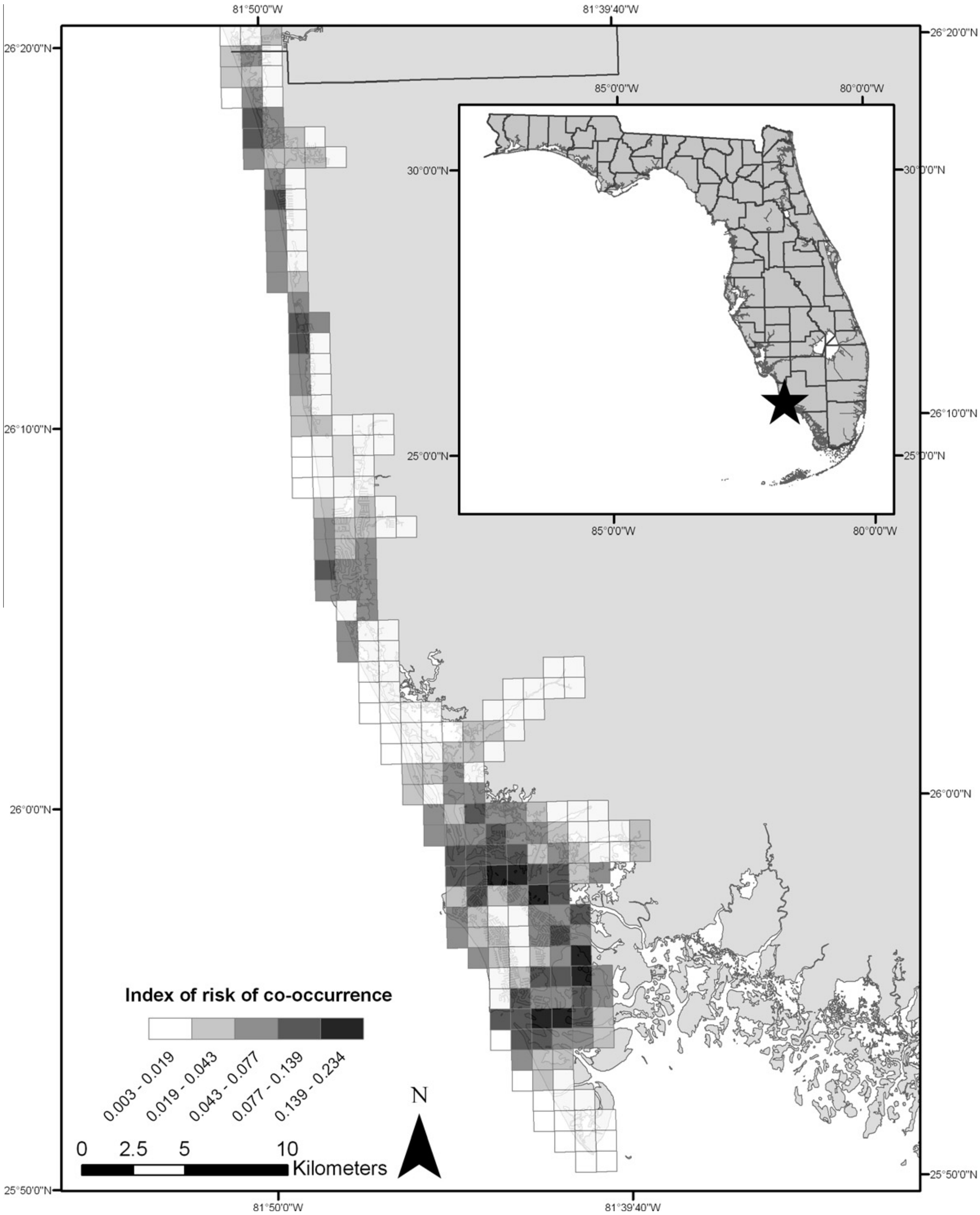

Fig. 1. Predicted index of risk of co-occurrence between manatees and boats reported on the study area (annual mean). Greater index values correspond to greater risk of co-occurrence (darker shades). Inset: map of the state of Florida; star indicates the location of surveys flown in Collier County. The risk of co-occurrence has been computed with the occupancy values for the boats.

water (MLLW), though some source data were in NAVD88. In the Coastal Relief Model (CRM), the bathymetry data are not established in a common vertical datum because the difference between the MLLW and NAVD88 is less than the vertical accuracy of the CRM, which should be considered to be no less than one meter. The depths used in our study area ranged from 0.5 m to 6.5 m (i.e., the deepest depth category was 6.00–6.99 m). When there were several depth categories within the same cell, we chose the depth that covered the largest area within that cell. Results related to the bathymetry covariates should be interpreted with caution for at least three reasons. First, the size of the cells was 1000 m $\times$ 1000 m, and depth can vary substantially within a cell. Secondly, the fact that we used a composite data source created from several datasets may have created additional noise. Thirdly, tide was not accounted for.

Manatees feed on seagrass; therefore, their distribution is likely to be influenced by this natural resource (Axis-Arroyo et al., 1998; Jiménez, 2005; Olivera-Gómez and Mellink, 2005). Seagrass bed locations were obtained from Collier County Environmental Services (http://www.colliergov.net/). Using a GIS, we calculated the distance from the midpoint of each cell (i.e., site) to the edge of the closest seagrass bed. The distances ranged from 0 m (i.e., the seagrass bed is in the cell) to 7031 m.

We hypothesized that manatees tend to avoid areas that have been extensively developed. To evaluate this covariate, we created polygons to distinguish developed areas from undeveloped areas (based on U.S. Geological Survey 2004 Digital Orthophoto Quarter Quads). We considered large tracts of land, such as parks or wetlands, which had minimal or no human development at the time of our survey, as undeveloped land. We calculated the distance to the closest developed land by calculating the distance from the midpoint of each cell to the nearest land classified as a developed area. Distances ranged from 0 m to 8474 m.

Manatees tend to avoid cold water, as they get physiologically stressed at temperatures less than about 20 °C (Irvine, 1983), and seek warm water refuges when water temperature drops (Deutsch et al., 2003). Therefore, we included a "season" covariate to account for variations in manatee distribution due to temperature changes among seasons. This covariate consisted of two categories, warm-season: March to November (average temperature: 78.3 degree F [SD = 5.6]); and cold-season: December to February (68.3 degree F [SD = 3.6], temperatures were obtained from Naples [Collier County], FL, for the period of record from 6/1/2007 to 5/31/2008, internet source: http://www.sercc.com/cgi-bin/sercc/cliMAIN.pl?fl6078). Six surveys were conducted during the warm season, and three were conducted during the cold season. Although some warm water refuges are man-made sources (e.g., power plant), there was no such manatee refuges in our study area, neither natural ones (e.g., river).

A 600-m distance off the right side of the aircraft's path represented the area surveyed by the observers. The proportion of water area covered by the plane's path for each cell during each survey was included as a covariate.

2.1.4. Manatee detection covariates

We modeled the probability of manatee detection using covariates: bathymetry, wind speed, weather, and observer effect.

Pollock et al. (2006) showed that the probability of detecting manatees was negatively related to water depth (Pollock et al., 2006). Thus, we predicted a negative relationship between bathymetry and detection probability. The bathymetry covariate was the same as the one described in Section 2.1.3. The fact that some covariates could potentially affect occupancy and detection makes it especially important to account for imperfect detection when estimating occupancy (MacKenzie et al., 2006).

Wind speed can also negatively affect visibility. Wind speed in knots (kts) was recorded by the observers from the nearest ASOS during each survey. Speeds ranged from 5 kts to 10 kts. Weather conditions can affect water surface and overall visibility and can impede detection. For each survey, we assigned a number ranking to the overall weather conditions recorded by the observers during the survey: excellent: 4, very good: 3, good: 2 and fair: 1. If the weather rankings were different between observers, we used the mean of the two ranks.

Not all observers conducting surveys have the same skills to detect manatees from a plane, and their ability can affect manatee detection. Four observers participated in the surveys (two observers at a time surveying the entire study area during each survey), and we estimated detection probability for each observer by modeling it as a function of four groups (i.e., one group per observer, in a fixed effect model). The observers were then ranked based on the estimates from the model. A second approach was to create a continuous covariate that ranged from 1 to 4; each observer was assigned a value that corresponded to his/her rank based on the first approach to estimate detection probability. For instance, the observer with the lowest estimate of detection probability based on the first approach was assigned a value of 1, whereas the observer with the highest estimate was assigned a value of 4. The benefit of the second approach is that it required the estimation of only one coefficient parameter and one intercept parameter to account for the observer effect on detection, whereas treating the observer effect as four groups required the estimation of four parameters. Thus, the second approach allowed us to save degrees of freedom for evaluation of additional biological hypotheses. If more observers had been involved (e.g., 10) it would have been possible to treat the observer effect as a random effect. In the latter case, treating the observer effect as a random effect would be more efficient than using a fixed effect to account for variation in detection due to observers' skills in detecting manatees.

2.1.5. Manatee model

Detection and nondetection data for each cell i by observer j during the survey t was assumed to follow a Bernoulli distribution: $y_{ijt} \sim \text{Bernoulli}\,(z_{it} \times p_{ijt})$, where z_{it} is the state of occupancy in cell i during survey t and p_{ijt} is the detection probability by observer j. We defined the occupancy state as $z_{it} \sim \text{Bernoulli}\,(\psi_{it})$, where ψ_{it} is the occurrence probability (i.e., the probability that the site is occupied by at least one individual) (Kéry, 2010). We assumed both the occurrence and detection probabilities to be independent between individuals (Kéry, 2010).

The most general model (i.e., the model that included all the covariates considered in our study) was defined as:

$$\text{logit}(\psi_{it}) = \alpha_0 + \alpha_1 \times bat_i + \alpha_2 \times bat_i^2 + \alpha_3 \times dseag_i + \alpha_4 \times seas_t + \alpha_5 \times ddvlp_i + \alpha_6 \times area_{it}$$

$$\text{logit}(p_{ijt}) = \beta_0 + \beta_1 \times bat_i + \beta_2 \times weath_t + \beta_3 \times wind_t + \beta_4 \times obs_{jt}$$

where *bat*: bathymetry, *dseag*: distance to the closest seagrass bed, *seas*: season, *ddvlp*: distance to the closest developed land, *area*: water area covered by the plane's path, *weath*: weather, *wind*: wind speed, and *obs*: observer rank. The covariates (x_{it}) were standardized with the following formula:

$$\frac{x_{it} - \bar{x}}{sd(x_{it})}$$

where $\bar{x}$ is the mean of x_{it} and $sd(x_{it})$ is the standard deviation of x_i. We tested the relevance of the covariates we chose in our hypotheses with a model selection Bayesian method by adding indicator variables as parameters as described in Kuo and Mallick (1998). We calculated the probability of each of the models that we considered for our analysis given the data (i.e., the posterior probability). The model with the greatest posterior probability was the one that included the most relevant covariates. First, we ran this model selection method to choose the relevant covariates explaining detection probability (16 models tested); then, we tested the relevance of the covariates for the occupancy probability (64 models tested) (Lebreton et al., 1992). We also applied a Pearson correlation test to look at any possible correlation between covariates, but we considered only the correlations that were meaningful biologically. Parameters of the covariates for the best model selected (i.e., including only the relevant covariates) were estimated with a Bayesian approach. We also calculated the predicted estimates of ψ and its associated uncertainty.

2.2. Boat distribution

2.2.1. Boat aerial surveys

Mote Marine Laboratory collected counts of boats during nine surveys conducted in Collier County from December 2006 to November 2007 (seven surveys were conducted during our defined-warm period and two surveys were conducted during our defined-cold period). The surveys were mostly evenly spaced in time and covered most of the study area. More details about the survey method can be found in Gorzelany (2008). We used the same grid as for the manatee data, and overlaid the boat sighting data to calculate the number of boats seen per cell per survey. We removed all sightings of airboats, sailboats, kayaks, canoes and personal watercraft from our data set to focus primarily on boats most likely to cause serious injury or death to manatees. Although personal watercraft and airboats are less likely to cause injuries than other types of watercraft, they are subject to speed regulation and should probably be considered for management purposes.

2.2.2. Boat density covariates

We modeled boat density as a function of several environmental covariates: distance to the shoreline and distance to the closest developed land; and temporal covariates: season. We also included the proportion of the cell's area that included water as a covariate. We calculated the distance from the midpoint of each cell to the closest shoreline. Distances to the shoreline ranged from 0 m to 2673 m.

2.2.3. Boat density model

We modeled boat distribution as a zero-inflated Poisson (ZIP) distribution because of the large number of zero counts in our data (i.e., sites unoccupied by boats) (Martin et al., 2005). We assumed perfect detection probability of boats (i.e., equal to 1) because boats are easily counted and detected from a plane flying at 250–300 m and surveys were recorded by a video camera. Counts of boats in each cell i during survey t was assumed to follow a ZIP distribution: $C_{it} \sim \text{Poisson}\,(z_{it} \times \lambda_{it})$. We defined the occupancy state of the site as $z_{it} \sim \text{Bernoulli}\,(\Omega_{it})$, where Ω_{it} is the probability that site i is occupied by at least one boat during survey t. The most general model to explain the number of boats per cell (parameter λ_{it}) was defined as:

$$\log(\lambda_{it}) = \gamma_0 + \gamma_1 \times dshor_i + \gamma_2 \times ddvlp_i + \gamma_3 \times seas_t + \gamma_4 \times area_i$$

where *dshor*: distance to the closest shoreline and *area*: proportion of water in the cell.

2.2.4. Boat occupancy model

As an alternative to the boat density model, we also developed a boat occupancy model. In this case, instead of modeling the number of boats per cell, we modeled the occupancy per cell, i.e., a cell that included at least one boat was considered occupied. Detection for boats was assumed to be equal to 1. The covariates tested for the occupancy model were the same as for the density.

2.3. Software and computational analyses

Both manatee and boat models were computed in program R (version 2.12.1) and estimated with WinBUGS (version 1.4) using the package R2WinBUGS. We used the Markov chain Monte Carlo (MCMC) simulation method, running three different chains, each of 15,500 iterations where the first 12,000 iterations were removed (burn-in). The initial values for the parameters were picked randomly from their priors, which were defined as uniform distributions (Kéry, 2010). We used the Brooks–Gelman–Rubin diagnostic (R-hat, Gelman et al., 2004), to assess the chains' convergence. We assessed the fit of the models with posterior predictive checks (Gelman et al., 2004; Kéry, 2010).

2.4. Index of risk of co-occurrence

2.4.1. Index based on the boat density model

We estimated an index of risk of co-occurrence between boats and manatees based on the co-occurrence of manatees and boats. This index was computed by multiplying the probability of manatee occupancy for each cell by the mean expected number of boats for these cells for the same season (Fonnesbeck et al., 2008; Vanderlaan et al., 2008). As an example, we computed the index of risk of co-occurrence for our study area as an average over a year. Using a GIS, we created a map showing the values of the index of risk of co-occurrence and identified where risk was greatest (Fonnesbeck et al., 2008; Vanderlaan et al., 2008). Our models can also be used for predictive purposes. For instance, given some information about relevant covariates for a particular site, one can estimate the probability of occurrence of manatees and the density of boats for that site, even if the site was not surveyed; however, the site would have to be part of the area of inference.

2.4.2. Index based on the boat occupancy model

This index was similar to the one described above, except that it was obtained by multiplying boat occupancy with manatee occupancy.

3. Results

3.1. Manatee model

The detection model that received the most support from the data assumed an effect from the weather, and from the observer identity on manatee detection (posterior probability was 0.60, Table A1). The MCMC chains for this model appeared to have reached convergence (R-hat < 1.1); and the posterior predictive check did not indicate lack of fit (Bayesian p value: 0.45). The distance to the closest seagrass bed, the distance to the closest developed land, the season, and the water area covered by the plane path were the covariates that received the most support from our data to explain manatee occupancy (posterior probability was 0.87, Table A2). Although, the distance to the closest seagrass bed was positively correlated with the distance to the closest developed land, the level of correlation was weak (Pearson's product-moment correlation test, $r = 0.13$, 95% CI (0.04–0.23)). Covariate parameter estimates for the best model are given in Table A3 with uncertainty (95% CI).

For the nine surveys, the average detection probability was 0.59, 95% CI (0.48–0.70) based on the MCMC approach, and the average estimate of occupancy probability was 0.10, 95% CI (0.06–0.17). The average estimate of the occupancy probability for the surveys conducted during the cold period was 0.05, 95% CI (0.03–0.09), and for surveys conducted during the warm period was 0.13, 95% CI (0.08–0.19).

By treating the four observers as four groups (as a fixed effect, using the first approach described in Section 2.1.4), the estimates of detection probabilities for the four observers were 0.43, 0.51, 0.75 and 0.79, whereas they were 0.44, 0.59, 0.73 and 0.83 when treating the observer effect as a continuous covariate (using the second approach; these values were obtained with our best model and by assigning a mean value of 0.5 to the weather covariate). Weather was an important variable affecting detection; this was in contrast with bathymetry and wind speed, which did not seem to affect detection probability. This could be the result of surveys being conducted on days with light wind and because Collier County contains mostly shallow areas, i.e. there was little variability in the values for these two covariates (e.g., mean depth:1.24 m, SD = 1.30 m).

3.2. Boat models

3.2.1. Boat density model

The model that included distance to shoreline, distance to the closest developed land and proportion of water in the site received the most support from the data (posterior probability was 0.86, Table B1). Parameter estimates of the covariates are available in Table B2. Based on the best model, the average number of boats expected per cell was 2.53, 95% CI (2.32–2.77). According to the parameter estimates of the covariates, boat density decreased with distance from the shoreline. Boat density also decreased with distance to the closest developed land. Our data did not provide supportive evidence of an effect of the season on boat density. The MCMC chains for the boat density model appeared to have reached convergence (R-hat < 1.1). However, the posterior predictive check provided significant evidence of lack of fit (Bayesian *p* value: 0.00). Thus, the results of the boat occupancy model should be interpreted with caution. As an alternative to the boat density model we also considered a boat occupancy model, for which there was no evidence of lack of fit.

3.2.2. Boat occupancy model

The model that included distance to shoreline and proportion of water in the site received the most support from the data (posterior probability was 0.95, Table C1). Parameter estimates of the covariates are available in Table C2. The data did not provide supportive evidence of an effect of the season and distance to developed areas on boat occupancy. The MCMC chains for this model appeared to have reached convergence (R-hat < 1.1); and the posterior predictive check did not indicate lack of fit (Bayesian *p* value: 0.34).

3.3. Index of risk of co-occurrence

3.3.1. Index based on boat density model

The mean annual value for the index of risk of co-occurrence between manatees and boats was 0.30 (SD = 0.35) with a minimum <0.01 and a maximum of 2.73. For the cold period, the mean value was 0.15 (SD = 0.19); for the warm period, the mean value was 0.35 (SD = 0.40). Because manatee occupancy was greater during the warm period, the risk of co-occurrence increased during that period. By mapping the mean values of the index of risk of co-occurrence calculated over a year (Fig. D1), we located where this risk was the greatest.

3.3.2. Index based on boat occupancy model

The map of mean annual values of the index of risk of co-occurrence based on the boat occupancy model (Fig. 1) looked similar to the one obtained based on the boat density model (Fig. D1). The mean annual value for the index of risk of co-occurrence between manatees and boats was 0.04 (SD = 0.04), with a minimum <0.01 and a maximum of 0.23. For the cold period, the mean value was 0.02 (SD = 0.02); for the warm period, the mean value was 0.04 (SD = 0.04).

4. Discussion

4.1. Manatee occupancy

Manatee occupancy models were used to estimate the effect of variables of interest but also to make predictions about the probability of manatee occupancy as a function of environmental and temporal covariates. Based on these analyses, distance to seagrass appeared to be an important environmental covariate that influenced the distribution of manatees. This was consistent with previous studies on this species, all of which found a positive relationship between manatee observations and presence of vegetation (Axis-Arroyo et al., 1998; Jiménez, 2005; Olivera-Gómez and Mellink, 2005). However, our study represents the first attempt to predict probability of occupancy of manatees as a function of seagrass availability while accounting for imperfect detection due to observer bias (Fig. 2).

There was some evidence of a negative relationship between distance to developed areas and manatee occupancy, which would suggest that manatees did not avoid developed areas. This relationship may be explained by the fact that the distance to the closest seagrass bed was positively correlated with the distance to the closest developed land (i.e., the seagrass is located near the developed areas for this specific study area), and as manatees are located close to the seagrass patches, they are also near the developed areas. Developed areas can also be a source of freshwater for manatees.

As predicted, manatees avoided our study area during the cold season. Collier County contains only a few warm water refuges, but these areas were not located in our study area and therefore were not covered in the surveys. Manatees may have been present at these refuges or may have left county waters during the cold periods.

We did not find an effect of bathymetry on manatee distribution, which may be explained by the lack of bathymetric variation in the areas that were surveyed. Although bathymetry appeared to be a useful covariate to consider *a priori*, our results related to this covariate should be interpreted with caution for several reasons. Firstly, the size of the cells was up to 1000 m $\times$ 1000 m, and depth can vary substantially within a cell; thus our approach of using the average depth category of the largest area within the cell would not capture potential variations. Secondly, the bathymetry information available was a composite of several data sources. Finally, variation in depth due to tides was not accounted for.

4.2. Accounting for manatee detection probability

It is possible to model occupancy while accounting for imperfect detection by following a robust design, for example, by conducting repeated visits or passes at each site (MacKenzie et al., 2003). These passes need to be close enough in time to meet the closure assumption at the site. With enough repeat passes, it is possible to estimate total detection probability, which includes

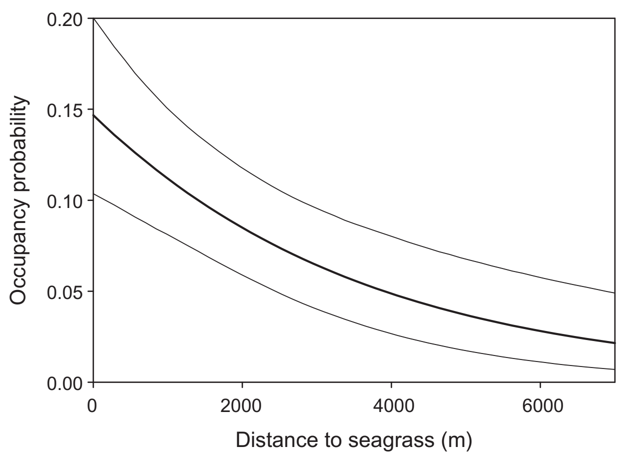

Fig. 2. Relationship between manatee occupancy probability and distance to the closest seagrass bed. The bold line represents the mean value of the relationship, and the two light lines represent the 95% CI.

the probability that manatees are available for detection, and the probability that observers will detect manatees given that manatees are available. Because our study did not include enough sites with repeated passes, we decomposed detection probability into its components and focused on observer-specific detection probabilities. Therefore, instead of using repeat passes, we treated the observations made simultaneously by the two observers as passes. Imperfect detection due to observer bias is a source of error that is specific to each individual observer. If an observer left the monitoring program (e.g., cannot conduct any more surveys), it would not be possible to know his/her contribution to total detectability, unless the study was specifically designed to estimate this source of error. This is in contrast to the probability of availability, which can be estimated from other sources of information (e.g., Pollock et al. (2006) used time-depth-recorder information to correct for probability of availability) and is less likely to change over time (e.g., manatees are likely to maintain the same rate of surfacing from year to year). Four observers participated in the surveys, and we showed that detection probability varied substantially among them (0.43–0.79). To improve the precision of our estimates, we included observer detection probabilities as a continuous covariate. The estimates of detection probabilities obtained with this approach were consistent with those obtained with a more complex model (e.g., 0.44–0.83). This second approach allowed us to focus on evaluating more interesting biological hypotheses (e.g., by reducing the number of parameters related to observers' detection and therefore being able to include more parameters related to occupancy in the model).

4.3. Boat models and index of risk of co-occurrence

We computed two indices of risk of co-occurrences. The first one was obtained by multiplying the probability of manatee occupancy by the expected boat density at each site, whereas the second was derived by multiplying probability of manatee occupancy by the probability of boat occupancy. Modeling boat density and occupancy allowed us to evaluate hypotheses about potential factors that drive these variables. The boat density model that appear to be best supported by the data included distance to shoreline, distance to the closest developed land and proportion of water in the site, whereas the boat occupancy model with the most support from the data only included distance to shoreline and proportion of water in the site. We note that there was evidence of lack of fit for the boat density model, which was evaluated with a posterior predictive check. Therefore, the results for the boat density model and associated risk of co-occurrence should be interpreted with caution. In contrast, there was no evidence of lack of fit for the boat occupancy model, thus in our case the index of risk of co-occurrence based on the boat occupancy model appears more reliable. Interestingly, the risk maps obtained from both models looked similar (Figs. 1 and D1). These indices of manatee–boat co-occurrence could be viewed as surrogates of risk of collision, indeed, as the index value increases, the risk of collision between boats and manatees should increase (Fonnesbeck et al., 2008; Vanderlaan et al., 2008). One of the limitations of our indices is that they are based on manatee occupancy (i.e., whether a cell is occupied) rather than manatee density (i.e., number of manatees per cell); therefore the index of collision for an occupied cell would be the same no matter how many manatees were present in the cell. This, of course, is also a limitation of the index of risk of co-occurrence based on the boat occupancy model. Note, however, that several studies have indicated a positive relationship between occupancy and density (e.g., MacKenzie et al., 2006); in fact, as noted earlier, the risk maps based on the boat occupancy and boat density models are similar (Figs. 1 and D1). In addition, this index does not account for increased risk due to the three-dimensional configuration of the areas, the behavior of manatees (foraging/resting or moving), or the boat (anchored or moving). For instance, risks of collisions may increase in narrow and shallow canals; in addition, the surfacing behavior of manatees may vary, depending on habitat type. Thus, it would be worth considering these factors to improve our index. Nonetheless, our index should be useful in the design of manatee protection zones. Identifying areas where the risk of collisions is high is important for improving the design of such protection zones. The data analyzed for this study were part of a pilot study. Because this study design is relatively new, the data set available is limited, and therefore, the results should be interpreted with caution when considering management applications. Nevertheless, the reliability of the models and the relevance to management will increase as more aerial survey data on boats and manatees become available. Indeed, the integrated Bayesian approach that we have described can readily integrate new information in order to improve the performance of our models.

4.4. Future studies

Our work provides insights on how to improve the design of future aerial surveys and analyses to predict risk of collisions. First, focusing on manatee density (i.e., accounting for the number of manatees per site), rather than manatee occupancy could improve the quality of the index. N-mixture models could be considered for these types of analyses, although non-independence of detection remains a problem for the application of these models to aerial survey data for manatees (Martin et al., 2011). Second, estimates of occupancy or densities of manatees should also account for probability of availability, not just the probability of imperfect detection due to observers. Repeat passes could be used to account for this source of variation, but there is a trade-off between spatial extent of area covered, the number of passes, and cost. By collecting covariates affecting the probability of availability (e.g., turbidity, which were not available for the current study), we should be able to account for probability of availability from other sources of data without necessarily increasing the number of passes. For instance, FWC is testing a methodology for estimating statewide abundance of manatees, and during these surveys, multiple passes are conducted at each site, and turbidity is recorded. It will be possible to construct a model that will integrate the relationship between turbidity and probability of availability elucidated in these surveys into the analyses of the surveys that we present in this study (i.e., with a double-observer protocol, but without repeat passes). An alternative is to use artificial manatee models and to obtain dive profiles of manatees with time depth recorders to determine zones of detectability under ranges of conditions (e.g., depth, turbidity) encountered during aerial surveys (Pollock et al., 2006). Note that in both cases, a double-observer protocol is still necessary for these types of surveys to decompose the probability of detection into the probability of availability of the individual and the probability of detection due to the observer. Collecting boat and manatee data simultaneously with two planes (e.g., one dedicated to boat observations and the other to manatee observations) could potentially improve the index of risk of co-occurrence. On the other hand, having the same observer collect information on boats and manatees at the same time could be distracting and would probably reduce detection of manatees. In any case, the approach that we described does not require the information on boats and manatees to be collected simultaneously. Finally, future development of index of co-occurrence could also consider the spatial configuration (e.g., narrow passes versus wide-open water; shallow and deep areas); boat types (e.g., size), boat speed, manatee and boater behavior. These improvements over traditional surveys come with an added cost, but not properly accounting for important sources of errors in monitoring data can lead to spurious inference (Yoccoz et al., 2001; MacKenzie et al., 2002; Kéry, 2010).

5. Conclusion

Despite some limitations and the potential for improvement, our study provides the first model for predicting an index of risk of co-occurrence between manatees and boats based on aerial survey data while accounting for detection probabilities due to observers. The analytical framework will also be useful in the design of aerial surveys that aim to predict risk of co-occurrence in other systems and for other species when detection is not perfect. This approach could be applied to estimate wildlife–vehicle co-occurrence risk for other systems (including terrestrial systems, especially for species surveyed by air), and help in the design of protection zones.

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Appendix A

See Tables A1–A3.

Appendix B

See Tables B1 and B2.

Table A1
Posterior probability for models tested with different covariate combinations to explain the manatee detection probability. The estimates were made by the model selection Bayesian method. The other 12 models (16 models were tested) are not shown in the table, because their probability was <0.001.

Model tested	Posterior probability
Weather + Observer identity	0.60
Weather + Observer identity + Bathymetry	0.34
Weather + Observer identity + Wind speed	0.05
Weather + Observer identity + Bathymetry + Wind speed	0.01

Table A2
Posterior probability for models tested with different covariate combinations to explain the manatee occupancy probability. The estimates were made by the model selection Bayesian method. The other 60 models (64 models were tested) are not shown in the table because their probability was <0.001.

Model tested	Posterior probability
Distance to seagrass + Distance to developed land + Season + Water area covered	0.87
Distance to seagrass + Distance to developed land + Season + Water area covered + Bathymetry	0.09
Distance to developed land + Season + Water area covered	0.02
Distance to seagrass + Season + Water area covered	0.02

Table A3
Parameter estimates from WinBUGS for the relevant covariates explaining the occupancy probability and the detection probability of manatees.

Covariate	Parameter estimate	95% CI
Weather	0.85	[0.48; 1.20]
Observer identity	0.57	[0.29; 0.85]
Distance to seagrass	−0.49	[−0.76; −0.25]
Distance to developed land	−0.55	[−0.87; −0.28]
Season	0.91	[0.47; 1.37]
Water area covered	0.70	[0.38; 1.04]

Table B1
Posterior probability for models tested with different covariate combinations to explain the expected boat density. The estimates were made by the model selection Bayesian method. The other 14 models (16 models were tested) are not shown in the table as their probability was <0.001.

Model tested	Posterior probability
Distance to shoreline + Distance to developed land + Water area covered	0.86
Distance to shoreline + Distance to developed land + Water area covered + Seasons	0.14

Table B2
Parameter estimates from WinBUGS for the relevant covariates explaining the expected boat density.

Covariate	Parameter estimate	95% CI
Distance to shoreline	−1.07	[−1.23; −0.91]
Distance to developed land	−0.10	[−0.14; −0.07]
Water area	0.91	[0.84; 0.98]

Table C1
Posterior probability for models tested with different covariate combinations to explain the expected boat occupancy. The estimates were made by the model selection Bayesian method. The other 13 models (16 models were tested) are not shown in the table as their probability was <0.001.

Model tested	Posterior probability
Distance to shoreline + Water area covered	0.95
Distance to shoreline + Water area covered + Season	0.02
Distance to shoreline + Water area covered + Distance to developed land	0.02

Table C2
Parameter estimates from WinBUGS for the relevant covariates explaining the boat occupancy probability.

Covariate	Parameter estimate	95% CI
Distance to shoreline	−7.02	[−8.30; −5.83]
Water area covered	3.39	[3.00; 3.78]

Appendix C

See Tables C1 and C2.

Appendix D

See Fig. D1.

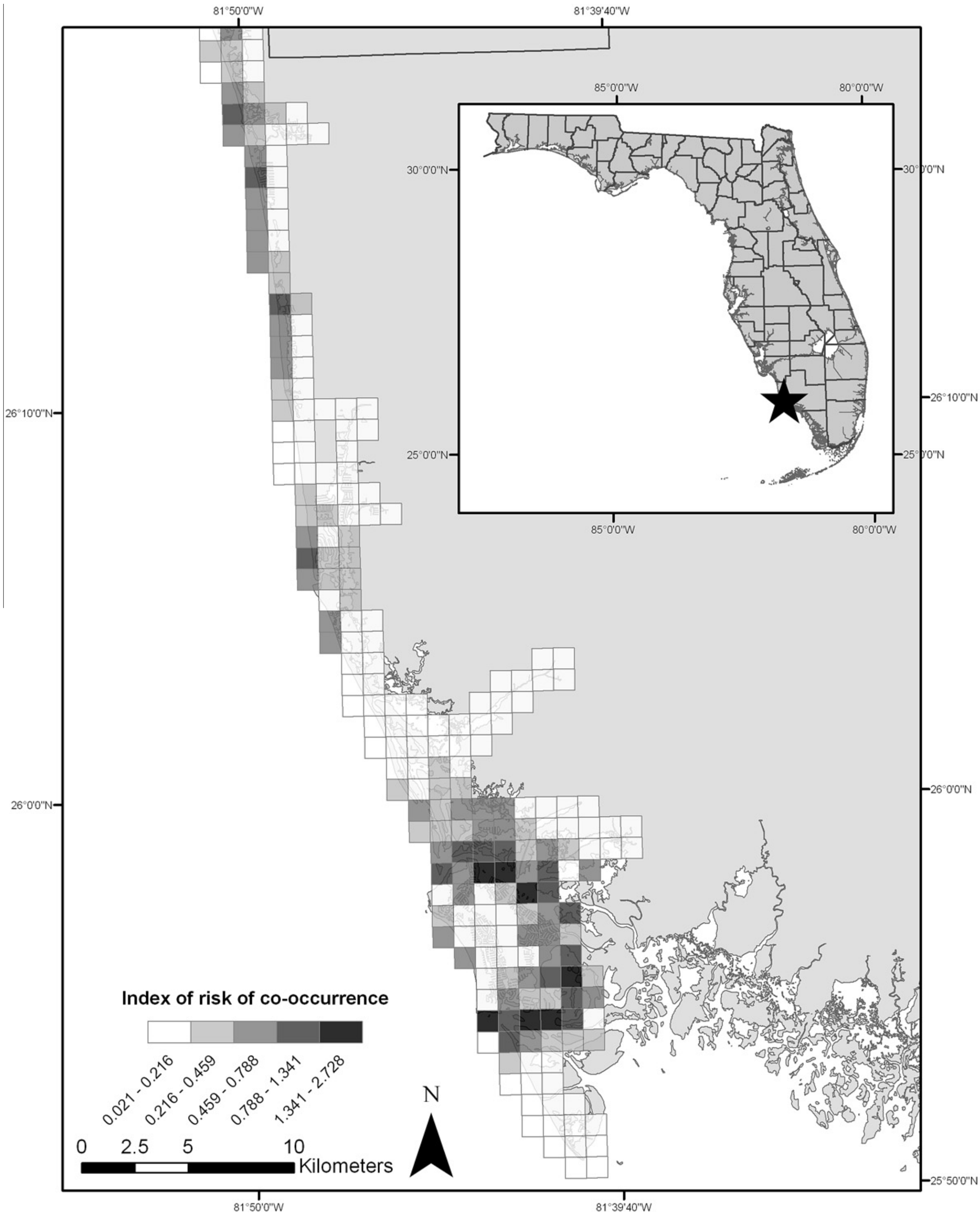

Fig. D1. Predicted index of risk of co-occurrence between manatees and boats reported on the study area (annual mean). Greater index values correspond to greater risk of co-occurrence (darker shades). Inset: map of the state of Florida; star indicates the location of surveys flown in Collier County. The risk of co-occurrence has been computed with the density values for the boats.

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