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Habitat selection of freshwater-dependent cetaceans and the potential effects of declining freshwater flows and sea-level rise in waterways of the Sundarbans mangrove forest, Bangladesh

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ABSTRACT

1. Generalized additive models of sighting data for cetaceans collected during two surveys of waterways in the Sundarbans mangrove forest of Bangladesh indicated that Ganges River dolphin *Platanista gangetica gangetica* distribution was conditionally dependent ($P<0.05$) on low salinity, high turbidity, and moderate depth during both low and high freshwater flow; and Irrawaddy dolphin *Orcaella brevirostris* distribution was conditionally dependent ($P<0.05$) on low salinity during high freshwater flow, high and moderate depths during low and high freshwater flow, respectively; low and high-low extremes of turbidity during low and high freshwater flow, respectively; and high temperature and increasing numbers of large–small channel confluences during low freshwater flow.

2. According to sighting data collected over a 3-year period by the captains of three nature tourism vessels, there were significant differences between the actual and expected frequencies of Ganges River dolphin sightings and individuals according to various channel types (chi-square = 64.22, $P<0.0001$ and chi-square = 134.14, $P<0.0001$, respectively, df = 6) and of Irrawaddy dolphin sightings and individuals (chi-square = 15.28, $P=0.0182$, and chi-square = 29.42, $P<0.0001$, respectively, df = 6), with shared preferences for wide sinuous channels with at least two small confluences or one large confluence.

3. The dependency exhibited by both species for environmental characteristics associated with abundant freshwater flow, including low salinity and the availability of confluences, make them particularly vulnerable to habitat loss due to upstream water abstraction and sea-level rise.

4. Although the results of this study may not affect plans for construction in India of large-scale, inter-basin water transfer projects that will result in further declines in freshwater flows, or decisions within the international community about CO_2 emissions affecting global sea levels, they can be used to prioritize locations where protective measures could be employed to benefit the long-term conservation of both species.
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KEY WORDS: Ganges river dolphin (*Platanista gangetica*); habitat selection; Irrawaddy dolphin (*Orcaella brevirostris*); sea-level rise; Sundarbans; water development

INTRODUCTION

Declining freshwater flows profoundly threaten the world's riverine and estuarine biodiversity (Covich, 1993; Postel and Richter, 2003). Cetaceans living in these environments are especially at risk due to their particular environmental needs, including sufficient flow to allow movement between deep pools and the availability of hydraulic refuge from high velocity currents (Smith and Reeves, 2000). This study used generalized additive models (GAMs) and discriminant and chi-square statistics to investigate the potential effects of declining freshwater flows and sea-level rise on two small cetaceans: the Ganges River dolphin *Platanista gangetica gangetica* and Irrawaddy dolphin *Orcaella brevirostris* in waterways of the

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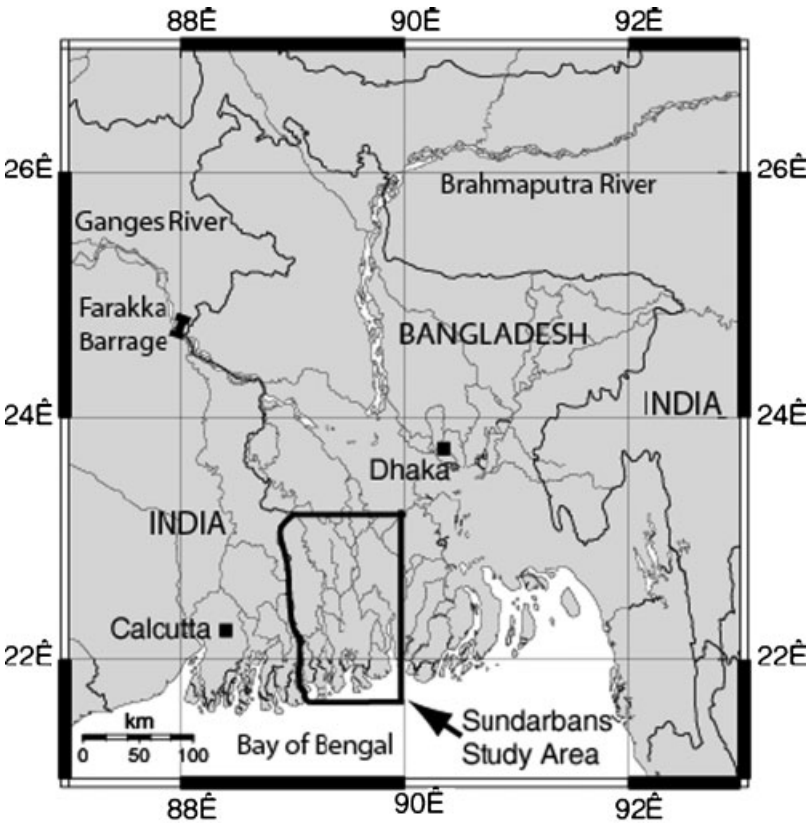

Figure 1. Map of Bangladesh showing the Sundarbans study area.

Sundarbans mangrove forest in Bangladesh (Figure 1). Information on the fine-scale distribution and habitat selection of these large, mobile, aquatic predators, which have dissimilar evolutionary histories and exhibit radically different anatomical and behavioural adaptations for surviving in riverine and estuarine environments, may provide important insights on the broader scale impacts of human-caused changes to the ecology of this dynamic river–sea interface.

The Ganges River dolphin, together with the Indus River dolphin *P.g. minor*, is a relict species of an evolutionarily rich but now monotypic superfamily Platanistoidea which occupies a near basal position in the Odontoceti suborder (Arnason and Gullberg, 1996; Cassens *et al*., 2000; Nikaido *et al*., 2001; Yang *et al*., 2002). This obligate freshwater species is among the most anomalous of cetaceans having adapted to a running water environment while it remained in the declining epicontinental seas of the Indo-Gangetic Basin during the Late Neogene (Hamilton *et al*., 2001). The Ganges River dolphin ranges from the upstream, fast-flowing, cool-water reaches of major Himalayan and peninsular tributaries of the Ganges–Brahmaputra–Meghna (GBM) river system to where these waters meet the sea in mangrove channels of the Sundarbans Delta in India and Bangladesh, and in the much smaller Karnaphuli–Sangu River system of southern Bangladesh. The range of the subspecies has declined since the 19th century when it was mapped by Anderson (1879) especially in the upstream reaches (Sinha *et al*., 2000; Smith *et al*., 2001). The diversity and scale of ongoing and projected threats led to its classification as 'endangered' according to IUCN Red List criteria (Smith *et al*., 2004a). Mark–recapture analyses of double concurrent counts made by independent teams during March 2002 of Ganges River dolphins in mangrove channels of the Sundarbans forest in Bangladesh generated an abundance estimate of 225 individuals (CV = 12.6%) by averaging Huggins conditional likelihood models that individually incorporated group size, sighting conditions and channel width as covariates (Smith *et al*., 2006).

The Irrawaddy dolphin is a member of the Delphinidae family, which is the largest and most diverse of the Order Cetacea (Rice, 1998). Members of this family occupy a large variety of ecological niches and the Irrawaddy dolphin is known as a facultative freshwater species because its range includes nearshore marine waters of the Indo-Pacific as well as three large rivers (Ayeyarwady of Myanmar, Mahakam of Indonesia and Mekong of Cambodia, Lao PDR and Vietnam) and two marine appended lakes (Songkhla of Thailand and Chilika of India). Recent investigations suggest that the marine distribution of the species in South and South-east Asia is generally limited to estuarine waters (Smith *et al*., 1997, 2004b, 2005), so a more accurate characterization of the species might be 'freshwater dependent'. Although Irrawaddy dolphins are classified by the IUCN as 'data deficient', five geographically isolated populations in Songkhla Lake, Malampaya Sound and the Mekong, Ayeyarwady, and Mahakam rivers are classified as 'critically endangered' according to IUCN Red List criteria (Smith and Beasley, 2004a, 2004b, 2004c; Smith, 2004; Kreb and Smith, 2000, respectively). Mark–recapture analyses of double concurrent counts of Irrawaddy dolphins made by independent teams during March 2002 in mangrove channels of the Sundarbans forest generated an abundance estimate of 451 individuals (CV = 9.6%) through averaging

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Huggins conditional likelihood models that individually incorporated the same covariates mentioned above for Ganges River dolphins (Smith *et al*., 2006).

The Sundarbans are the world's largest continuous mangrove forest encompassing almost 600 000 ha with about 30% composed of a complex network of tidal and fluvial waterways ranging from a few metres to a few kilometres wide and fed almost entirely by the GBM river system (Hussain and Karim, 1994). Although this river system is the world's third largest with an annual runoff of 1400 km^3 (Shiklomanov, 1993), the South Asian subcontinent through which it flows suffers from the lowest per-capita availability of fresh water worldwide (Asian Development Bank, 2003).

From west to east the largest rivers in the Bangladesh Sundarbans are the Raimangal, Bal, Sibsa, Passur and Sela Gang. The primary source of freshwater input to these distributaries is from the Gorai River, which is in turn a distributary of the Ganges diverging about 50 km downstream of the India-Bangladesh border and about 70 km upstream of its confluence with the Brahmaputra River. The far eastern portion of the Sundarbans also receives a relatively small amount of fresh water from the Baleswar River, which obtains most of its flow from the Ganges but from well below its confluence with the Brahmaputra. The Kobadek and Betna rivers are the only sources of fresh water in the far western portion of the Sundarbans. These rivers have been cut off from the Ganges, probably due to increased sedimentation caused by reduced discharges following construction of the Farakka Barrage in 1975, and are currently fed solely by local rainfall (IWM, 2003a).

Water is abstracted from the Ganges basin by an extensive network of at least 20 high dams and 21 low-gated dams (barrages) and lost to evaporation from reservoirs and open canals and seepage to recharge groundwater supplies that are generally declining due to intensive extraction by tube wells (Smith and Reeves, 2000; Smith *et al*., 2000). From the perspective of Ganges River dolphins, the most notable flow regulation structure is the Farakka Barrage which divides the overall metapopulation at its approximate geographical centre and diverts flow from the Ganges to the Hooghly River to reduce sedimentation in Calcutta Port (Sinha, 2000).

The problem of declining freshwater flow to the Sundarbans will become a much greater threat to dolphins and other aquatic fauna if plans proceed for a collection of large-scale, inter-basin water transfer projects which will involve additional dam construction and diversion of water from rivers within the GBM system. The paucity of technical details released by the National Water Development Agency in India makes it impossible to rigorously evaluate the environmental impacts of the plan but available information has generated much controversy (Ghosh *et al*., 2003; Patkar, 2004).

The proposed inter-basin linking plan has two components: (a) Himalayan Rivers and (b) Peninsula Rivers. The Sundarbans in Bangladesh will be affected by the Himalayan component, which aims to store 'excess' monsoon flows behind at least nine high dams in a series of storage reservoirs on major tributaries of the Ganges and Brahmaputra, and then link (1) upstream tributaries of the Ganges with the western rivers of peninsular India and (2) the Brahmaputra mainstem and its tributaries with the Ganges and then the Mahanadi River, which in turn would be connected to the Peninsula Rivers Component. The plan proposes to compensate for water abstracted from the Ganges above the Farakka Barrage through an inter-basin transfer from the Brahmaputra via a system of canals either linking the Manas, Sankosh and Teesta tributaries to the Ganges or via a more direct link from the Jogighopa and Teesta tributaries to the Ganges. Although no final decision has been taken to proceed with construction, feasibility studies are currently underway and it was anticipated in 2004 that, if built, the entire project would be finished by 2016 at an estimated cost of $US 120–200 Billion (Ghosh *et al*., 2003).

Salinity levels in the Sundarbans are determined primarily by physical forcing from freshwater flows and to a lesser degree by diurnal tides. After construction of the Farakka Barrage significant increases in salinity levels were documented in the Sundarbans. For instance in Mongla Port, located at the north-eastern edge of the mangrove forest, salinity increased during the dry season by almost 50% from pre- (1965–1974) to post-Farakka (1975–1992) periods during which time there was also a 46% decline in dry season flows in the Ganges River (percentages calculated from Tables 1 and 3 in Mirza, 1998a).

Increased sediment deposition due to reduced river discharges has led to the gradual drying up of distributaries that previously contributed to repelling salinity encroachment. Declines in the sediment carrying capacity of the Ganges in Bangladesh due to reduced freshwater discharge has increased deposition at the divergence of the Gorai River such that flows entering this river have been reduced even further than would be expected from declining discharge alone (Barua *et al*., 1995, Mirza, 1998a). Sedimentation has also been accelerated throughout the Sundarbans by flocculation (IWM, 2003a) — the synergy between sediment deposition and salinity caused when the repulsive forces of negatively charged ions is reduced as the proportion of positive ions increases thereby promoting the formation of flocs that settle on the channel bed at lower velocity flow than unbound particles (Van Rijn, 1993).

An additional contributing factor to ecological alteration in the Sundarbans is the effects of global climate change. According to simulation models reported by the Intergovernmental Panel on Climate Change (IPCC) average sea-surface temperature will increase by 1.1–6.4°C resulting in a globally averaged sea-level rise of 18–59 cm in 2090–2099

Table 1. Codes and criteria used to categorize 5-km segments along cruising routes of three nature tourism vessels operated by The Guide Tours Ltd in waterways of the Sundarbans mangrove forest in Bangladesh

Code	Criteria
S1	Narrow straight with no confluence
S2	Narrow straight with one or two small confluences
S3	Narrow straight with more than two small confluences or at least one large confluence
S4	Narrow sinuous with no confluences
S5	Narrow sinuous with one or two small confluences
S6	Narrow sinuous with more than two small confluences or at least one large confluence
S7	Wide straight with no confluence
S8	Wide straight with one or two small confluences
S9	Wide straight with more than two small confluences or at least one large confluence
S10	Wide sinuous with no confluences
S11	Wide sinuous with one or two small confluences
S12	Wide sinuous with more than two small confluences or at least one large confluence

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(IPCC, 2007a). However, these figures could potentially be much higher because the models used do not incorporate indirect factors such as carbon-cycle feedback. An alternative semi-empirical model estimated that sea levels could rise by as much as 1.4 m over the same period (Rahmstorf, 2007). Sea-level rise will cause similar effects as reduced freshwater supplies including increased salinity intrusion (IPCC, 2007b) and probably sedimentation. Exceeding critical sea-level thresholds can initiate non-linear and irreversible geomorphic and ecological processes in coastal systems (Burkett *et al.*, 2005).

METHODS

Dedicated surveys during the low and high water seasons

Habitat selection of Ganges River and Irrawaddy dolphins was investigated using data collected from visual boat-based surveys conducted over a broad spatial scale in waterways of the Sundarbans mangrove forest in Bangladesh during the pre-monsoon season (4–24 March 2002 — this was the same survey used to generate the abundance estimates for both species cited above) when freshwater flow was approaching its lowest and during the early post-monsoon season (18 September–2 October 2002) when freshwater flow was still relatively close to its peak. During these surveys, a team of three observers stood watch at all times while 'on-effort' (i.e. actively searching for dolphins and recording effort and sighting data), one stationed on both the port and starboard sides, searching with handheld 7×50 binoculars and naked eye from the beam to about 10° past the bow, and one in the centre searching by naked eye in about a 20° cone in front of the bow. Every 30 min and at the location of dolphin sightings the position was recorded with a Global Positioning System (GPS) and information taken on channel width, depth, salinity, temperature, and turbidity. Salinity and temperature measurements were taken with a TPS Model WP-84 conductivity–salinity–temperature meter (TPS Ltd. 4 Jamberoo St., Springwood, Brisbane, Australia 4127). Depth was measured with a Garmin 186 Sounder Garmin International Inc., 1200 East 151st Street, Olathe, Kansas 66062 USA connected to a 200 kHz, 20° transom-mounted transducer. Turbidity was measured with a LaMotte Model 2020 portable turbidity meter LaMotte Company, PO Box 329, 802 Washington Avenue, Chestertown, MD 21620, USA.

The transect lines followed during the 2002 surveys were divided into 5-km segments (which roughly corresponded to the 30 min interval when environmental data were collected) using the GIS program ArcView (ESRI Corporation, 2002). For each segment, values for salinity, depth, turbidity, temperature, mean channel width, sinuosity, the number of large and small convergences, and the number of individuals detected of each species were determined. Depth was recorded automatically at 100 m intervals along the vessel's course, which followed the approximate thalweg (pathway connecting the deepest points of successive cross-sections), and segment values were determined by averaging these data points. Temperature, salinity and turbidity were recorded at least once in each segment. When a segment contained more than one record, the values were averaged. Channel width, sinuosity and the number of confluences were determined using a detailed digital map of the Sundarbans generated from recent satellite images. Channel width was measured at the beginning, end and middle of the segment and averaged. If the segment was in open water at channel mouths, a width of 5000 m was assigned. Sinuosity was determined by dividing the channel length of each segment (i.e. 5 km) by the straight-line distance between the beginning and endpoints. A value of 1.0 represented a straight channel and higher values indicated greater sinuosity. When the searching path was located outside of a channel mouth, sinuosity did not apply so was given a value of 1. The number of confluences was also calculated for each segment according to three different types: a small channel ($\leqslant$400 m wide) converging with a large channel (>400 m wide), a small channel converging with a small channel, and a large channel converging with a large channel.

Generalized additive models (GAMs) were fitted to data collected during the low and high water seasons in the entire study area and within the extent of species occurrence (see definition in IUCN, 2001) to investigate relationships between dolphin numbers and environmental variables. A GAM comprises a sum of smooth functions of the covariates plus a conventional parametric component of the linear predictor (Hastie and Tibshirani, 1990). The GAMs have the form:

$$n_i = \exp\left\{\beta_0 + \sum_{j=1}^{q} f(z_{ij})\right\}$$

where n_i is the number of individual dolphins of either Ganges River or Irrawaddy dolphins detected in the ith segment during one of two surveys in 2002 (March or September–October), β_0 is the intercept, and $f(z_{ij})$ is a smooth function of the jth covariate z associated with the ith segment. A Poisson distribution was assumed.

The GAMs were fitted using the software R (R Development Core Team, 2004) with the multiple generalized cross-validation (mgcv) package (Wood, 2006). The mgcv package's unbiased risk estimator criterion (UBRE), which can be interpreted as an approximation of the Akaike's Information Criterion (AIC; Akaike, 1973), was used to guide model selection. Similar to the AIC, for a given data set, the UBRE score is minimized and smoothing parameters are chosen accordingly. The degrees of freedom for each smooth function in the model control the 'wiggliness' of that smooth term. The fewer the degrees of freedom, the less wiggly the smooth function, with the lower extreme of a straight line that has a degree of freedom of one. A tradeoff is required between the 'wiggliness' of a smooth function corresponding to a particular covariate which indicates overfitting and a lack of model fit. Overfitting reduces variance but generally leads to a biased model. Aside from the UBRE score other results considered during model selection include the proportion of the null deviance explained by the model, the adjusted r-squared for the model, and the approximate P-values for the null hypotheses that each smooth term is zero.

A discriminant analysis was also used to generate linear combinations of predictor environmental variables (depth, salinity, temperature and turbidity) that provided the best discrimination between the species. The functions generated from the sampled sightings were applied using a jackknife resampling procedure to new cases with measurements for the predictor variables of unknown group membership.

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Dolphin sightings from captains' logs

Results of the GAMs and discriminant analyses of variables related to channel morphology were evaluated using an additional data set from a cetacean sighting network established among captains of three nature tourism vessels operated by The Guide Tours Ltd from April 2002 to March 2005. After training, the captains routinely logged the geographic position, species identification and group size of all dolphin sightings on a simple data sheet developed in Bengali script. Entries were quality checked and registered at regular intervals in a computer spreadsheet. Routes were taken from the vessel track of the ship's GPS. Similar to the analysis of data from the dedicated surveys described above, the cruising routes were divided into 5-km segments using the GIS program ArcView. Each segment was then coded according to criteria related to channel width, sinuosity and the presence of large and small confluences (Table 1). Sinuosity and the numbers of large and small confluence were determined as described above. Straight and sinuous were defined as having sinuosity values of 1–1.5 and > 1.5, respectively.

The number of times each segment was surveyed during daylight hours was determined. These survey frequencies were then used to calculate the expected detection frequencies of Ganges River and Irrawaddy dolphins in each segment if they were distributed randomly among the different channel types according to:

$$(S_i/S_t) * D_t$$

where S_i = the number of times segment i was surveyed, S_t = the sum of the total number of times all individual segments were surveyed and D_t = the total number of dolphins observed during the study period. Chi-square statistics were then used to test for potential differences between the expected and actual frequencies of sightings and dolphin individuals recorded in each segment. Sighting biases, which undoubtedly resulted in missed detections, were assumed to be constant.

RESULTS

Dedicated surveys during low- and high-water seasons

For the low-water season survey, during 1561.5 km of search effort (Figure 2) 107 Irrawaddy dolphin groups were detected for a total of 236 individuals and 62 Ganges River dolphin groups for a total of 134 individuals (Figure 3). Encounter rates were 15.1 individuals per 100 km for Irrawaddy dolphins and 8.6 individuals per 100 km for Ganges River dolphins.

For the high-water season survey, during 743.2 km of search effort (Figure 4) 30 Irrawaddy dolphin groups were detected for a total of 52 individuals and 44 Ganges River dolphin groups for a total of 71 individuals (Figure 5). Encounter rates were 7.0 individuals per 100 km for Irrawaddy dolphins and 9.6 individuals per 100 km for Ganges River dolphins.

The low-water season survey included 240 channel segments of which 24.2% and 8.8% were occupied by Irrawaddy and Ganges River dolphins, respectively. The high-water season survey included 117 5-km channel segments of which 16.2% and 15.4% were occupied by Irrawaddy and Ganges River dolphins, respectively.

The GAMs indicated that during the low-water season within the entire study area Ganges River dolphin distribution was conditionally dependent on relatively low salinity and high temperature with a lesser but still significant dependence on high turbidity (Table 2; Figure 6). Within their extent of occurrence, Ganges River dolphin distribution was conditionally dependent on relatively low salinity,

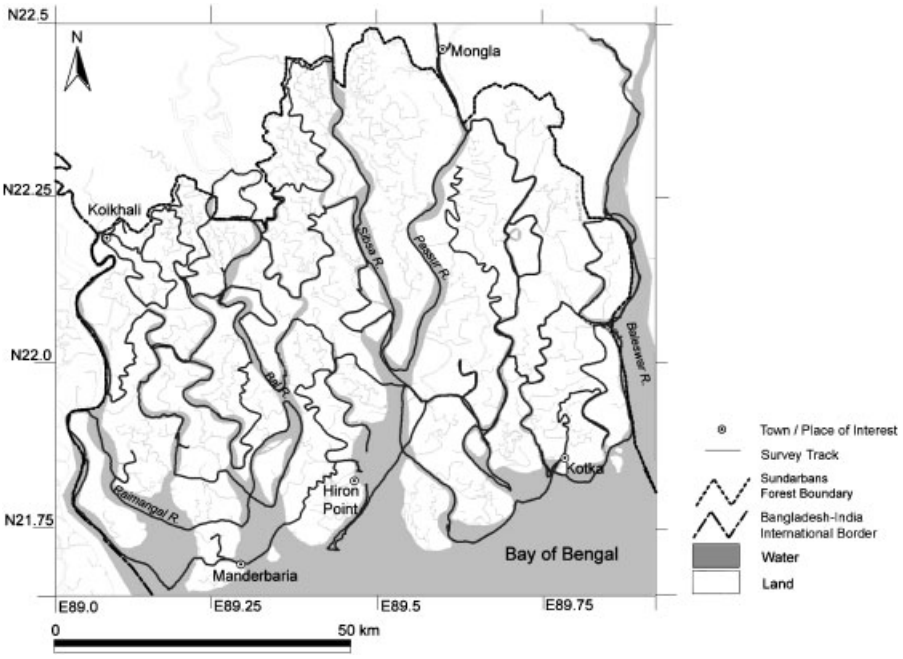

Figure 2. Map of the Sundarbans study area showing the tracklines followed during the low-water season survey in March 2002. Note that this map was derived from satellite imagery. It therefore shows numerous channels that do not contain water during the dry season and many others that are too small to support dolphins. The same comment applies to Figures 3–5.

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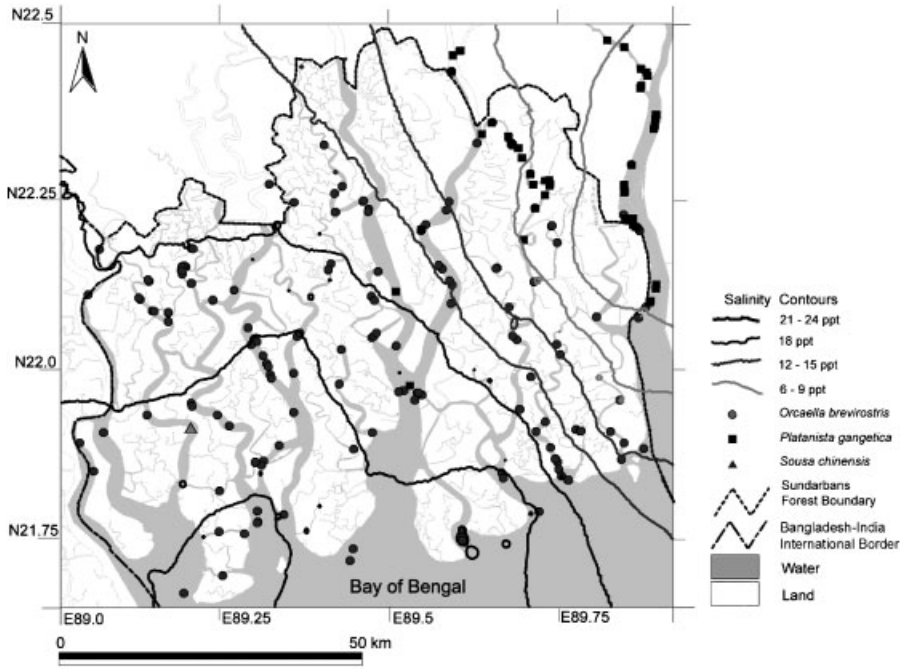

Figure 3. Dolphin sightings recorded during the low-water season survey in March 2002. Note the sighting of Indo-Pacific humpback dolphins *Sousa chinensis*, a coastal marine species, in the far west where salinity levels were especially high.

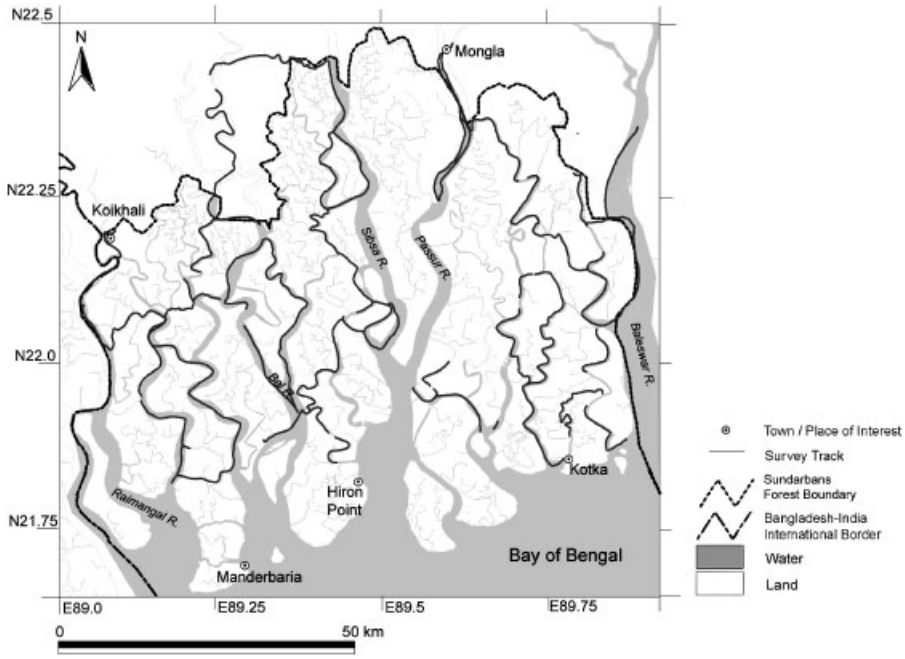

Figure 4. Map of the Sundarbans study area showing the tracklines followed during the high-water season survey in September–October.

moderate depth, high temperature and high turbidity (Table 2, Figure 7).

During the high-water season survey within the entire study area, Ganges River dolphin distribution was conditionally dependent on moderate depth and to a lesser extent on low salinity and high turbidity (Table 2, Figure 8). Within their extent of occurrence Ganges River dolphin distribution was conditionally dependent on relatively high turbidity and moderate depth (Table 2, Figure 9). Owing to the scarcity of data over the upper ranges of the covariate values the confidence intervals were much wider in these models than those selected for the March survey.

The GAMs indicated that during the low-water season in the entire study area Irrawaddy dolphin distribution was conditionally dependent on relatively high depth, high temperature and the availability of large–small confluences, with dependence on low turbidity to a lesser degree (Table 3, Figure 10). Within their extent of occurrence Irrawaddy dolphin

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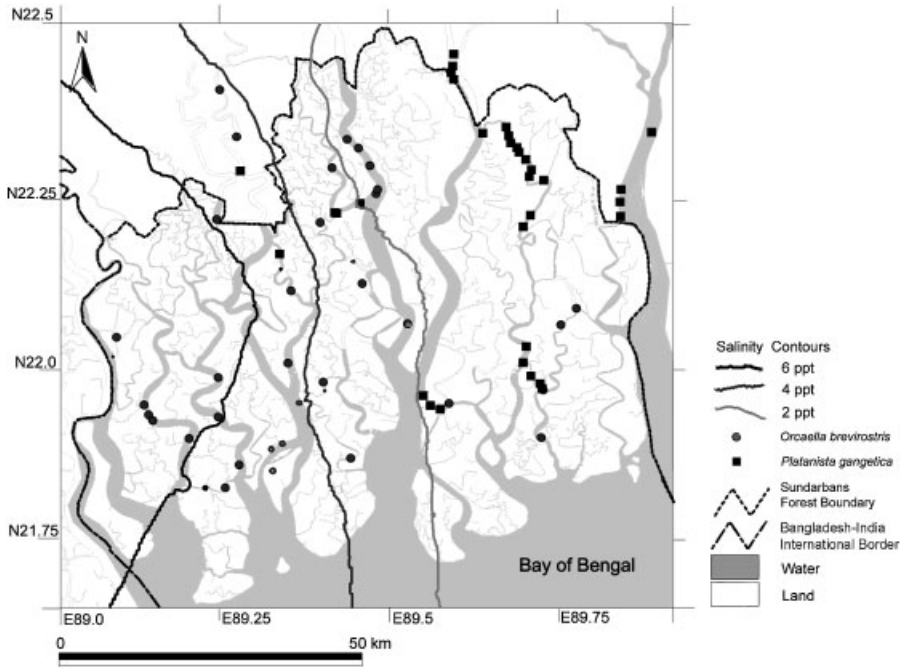

Figure 5. Dolphin sightings recorded during the high-water season survey in September–October 2002.

Table 2. Relative level (low, moderate and high), probability and maximum dependence (MD) of GAMs for depth (m), salinity (ppt), temperature (°C) and turbidity (NTUs) versus Ganges River dolphin distribution during low- and high-water seasons in the entire study area and extent of species occurrence during those seasons

	Depth			Salinity			Temperature			Turbidity		
Season/Area	Level	Prob.	MD	Level	Prob.	MD	Level	Prob.	MD	Level	Prob.	MD
Low-water												
Entire study area	NS	NS	NS	Low	2.22e−16	0	High	1.12e−14	↑ at 29	High	0.0336	→ 250; NAT
Extent of occurrence	Mod.	0.0001	8–18	Low	2.47e−05	→ 0	High	0.0003	↑ at 29	High	0.0011	↑ at 220
High-water												
Entire study area	Mod.	6.95e−06	9–20	Low	0.0019	→ 0	NS	NS	NS	High	0.0015	↑ at 800
Extent of occurrence	Mod.	0.0234	9–18	NS	NS	NS	NS	NS	NS	High	0.0035	↑ at 900

NS = non-significant ($P > 0.05$); → = approaching; ↑ = still rising; and NAT = no apparent trend due to increasing confidence intervals.

distribution was conditionally dependent on high depth, high temperature, the availability of large–small confluences and low turbidity to a lesser degree (Table 3, Figure 11).

During the high-water season survey within the entire study area Irrawaddy dolphin distribution was conditionally dependent on moderate depth, low salinity and extreme turbidity levels (Table 3, Figure 12). Within their extent of occurrence Irrawaddy dolphin distribution was conditionally dependent on extreme turbidity levels and to a lesser degree on low salinity (Table 3; Figure 13).

A one-way ANOVA of environmental data collected at the locations of dolphin sightings during the March 2002 survey rejected the null hypothesis of equality of means for salinity, turbidity and depth between the two species at $P < 0.05$ (df = 1, 165; Figure 14). A relatively low Wilks' lambda measurement and high absolute values of the standardized canonical discrimination coefficient and structure matrix (the latter measuring the pooled within-groups correlation between the discriminating variable and standardized canonical discriminant coefficient) pointed towards salinity (high and low for Irrawaddy and Ganges River dolphins, respectively) as the most important explanatory variable differentiating the species (Table 4). A chi-square test indicated that the discriminant model did better than random chance at separating the two species (chi-square = 139.4, $P < 0.0001$, df = 4) with the model correctly classifying 88.7% of the sightings to species and a cross-validation or jackknife resampling procedure correctly classifying 88.1%. The incorrect classifications reflected the small overlap in distribution of the two species. Due to significant departures from normality in the data set Mann-Whitney U tests were also used to test environmental variables individually and found differences in salinity and turbidity at $P < 0.0001$ and depth at $P = 0.0150$.

A one-way ANOVAs of sighting data from the high-water season survey rejected the null hypothesis of equality of means for salinity, turbidity and temperature between the two species at $P < 0.05$ (df = 1, 71; Figure 14). Similar to the analysis of sighting data from the low-water season surveys, a relatively low Wilks' lambda measurement and high absolute values of the standardized canonical discrimination coefficient and structure matrix pointed towards salinity (again, high and low for Irrawaddy and Ganges River dolphins, respectively) as the

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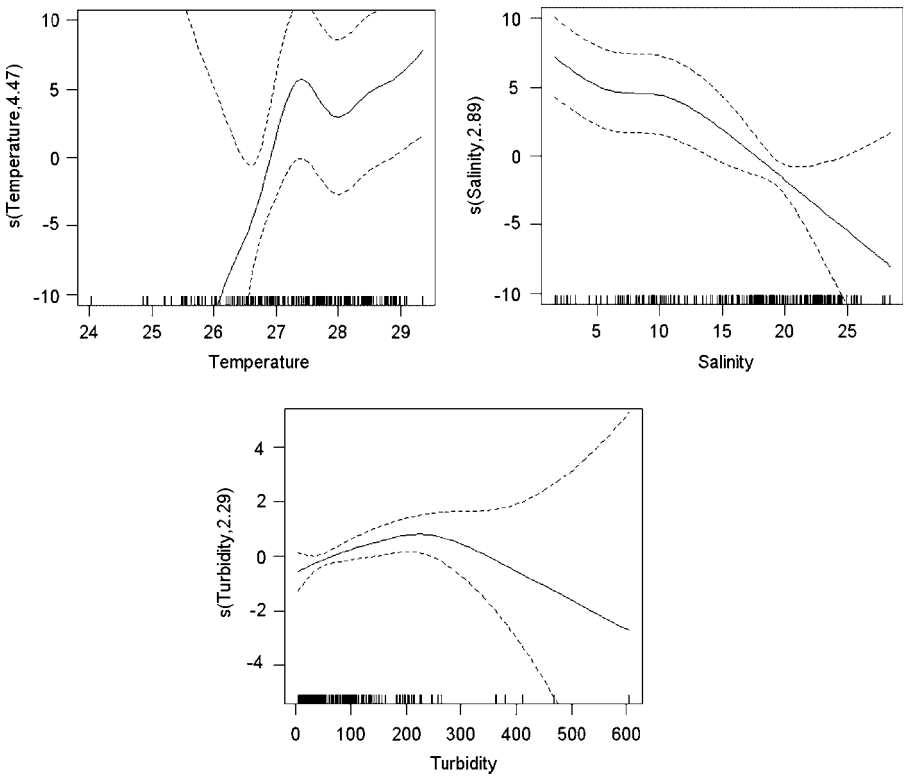

Figure 6. Estimated conditional dependence of Ganges river dolphin numbers on temperature, salinity and turbidity within the total study area during the low-water season. Estimates are solid lines and confidence intervals dashed lines with the covariate values for the observations shown as a rug plot along the bottom of each plot and the degrees of freedom given in the vertical axis heading (the same applies to Figures 7–13).

most important explanatory variable (Table 5). A chi-square test indicated that the discriminant model did better than random chance at separating the two species (chi-square = 41.7, $P = 0.000$, df = 4) with the model correctly classifying 84.9% of the sightings to species and a cross-validation or jackknife resampling procedure correctly classifying 82.2%. Mann-Whitney U tests found significant differences between species for salinity and turbidity at $P < 0.0001$.

Dolphin sightings from captains' logs

In total, 2477 Ganges River dolphins and 708 Irrawaddy dolphins were sighted by the captains of three nature tourism vessels in waterways of the Sundarbans. From the cruising routes, 131 5-km segments were delimited and classified according to channel width, sinuosity and the numbers of large and small confluences (see above). The sum of occasions each segment was transited resulted in a total of 5577 segment-samples. Three segment types: narrow straight with no confluence, narrow sinuous with one or two small confluences and wide sinuous with no confluences were not present in the study area, and these categories were therefore deleted from the analysis. Two additional segment types: narrow straight with one or two small confluences and narrow sinuous with no confluences were also deleted from the analysis because they were only transited on eight and four occasions, respectively, and observations of dolphins were less than five which meant that their inclusion would violate the sample size requirements of chi-square analysis (Zar, 1984). There was a great deal of variability in the number of times each of the remaining seven channel types were transited (mean = 795, SD = 815.6, range = 167–2625).

Significant differences were found between the actual and expected numbers of Ganges River dolphin sightings and individuals (chi-square = 64.22 and chi-square = 134.14, respectively, $P < 0.0001$, df = 6) and Irrawaddy dolphin sightings and individuals (chi-square = 15.28, $P = 0.0182$, and chi-square = 29.42, $P < 0.0000$, respectively, df = 6) according to channel type. The most favoured channel-type for both species was wide sinuous with more than two small confluences or at least one large confluence with deviations between observed and expected frequencies of occurrence equalling 51.2% and 57.0% for Ganges River dolphin sightings and individuals, respectively, and 18.9% and 20.0%, for Irrawaddy dolphin sightings and individuals, respectively. Both species also showed a preference for wide sinuous channels with one or two small confluences, but the deviations between the observed and expected frequencies were only 17.5% and 2.0% for Ganges River dolphin sightings and individuals, respectively, and 7.1% and 10.9%, for Irrawaddy dolphin sightings and individuals, respectively; only a single segment was categorized as this type, although it was surveyed 189 times. Wide straight channels with more than two small confluences or at least one large confluence were favoured by Irrawaddy dolphins with a percentage deviation of observed versus expected occurrence of 18.2% and 16.3% for sightings and individuals, respectively, but disfavoured by Ganges River dolphins with a percentage deviation of observed versus expected occurrence of −10.4% and −13.4%, respectively. Conversely, narrow straight channels with more than two small confluences or at least one large

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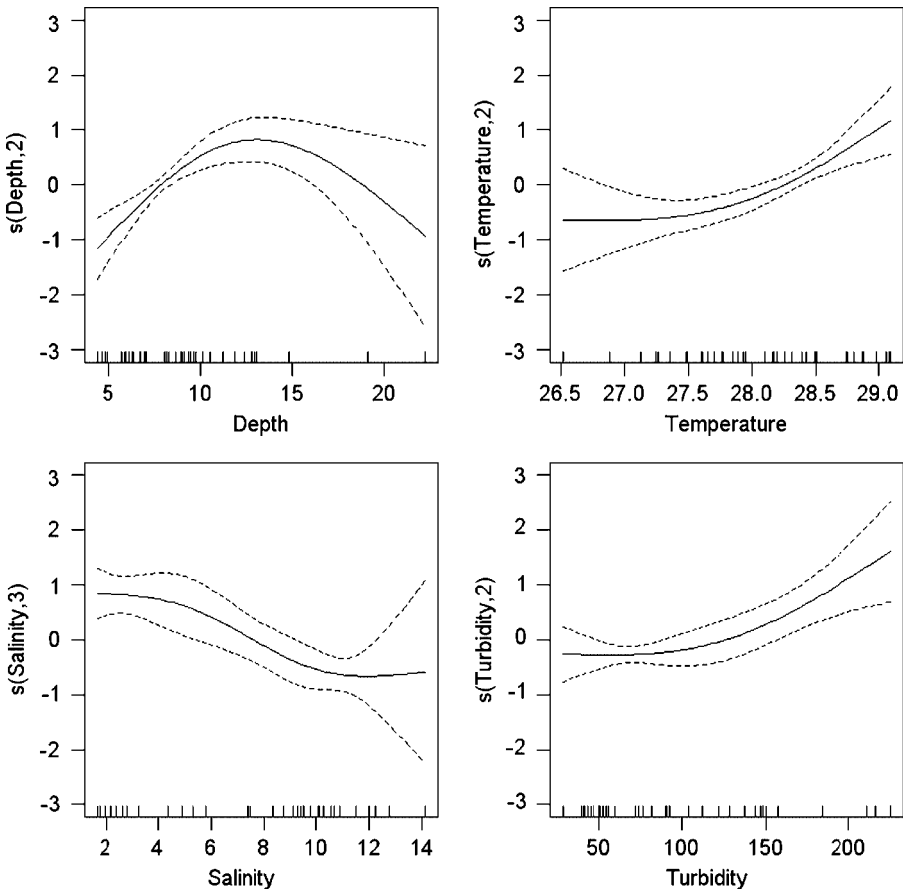

Figure 7. Estimated conditional dependence of Ganges River dolphin numbers on depth, temperature, salinity and turbidity within their extent of occurrence during the low-water season.

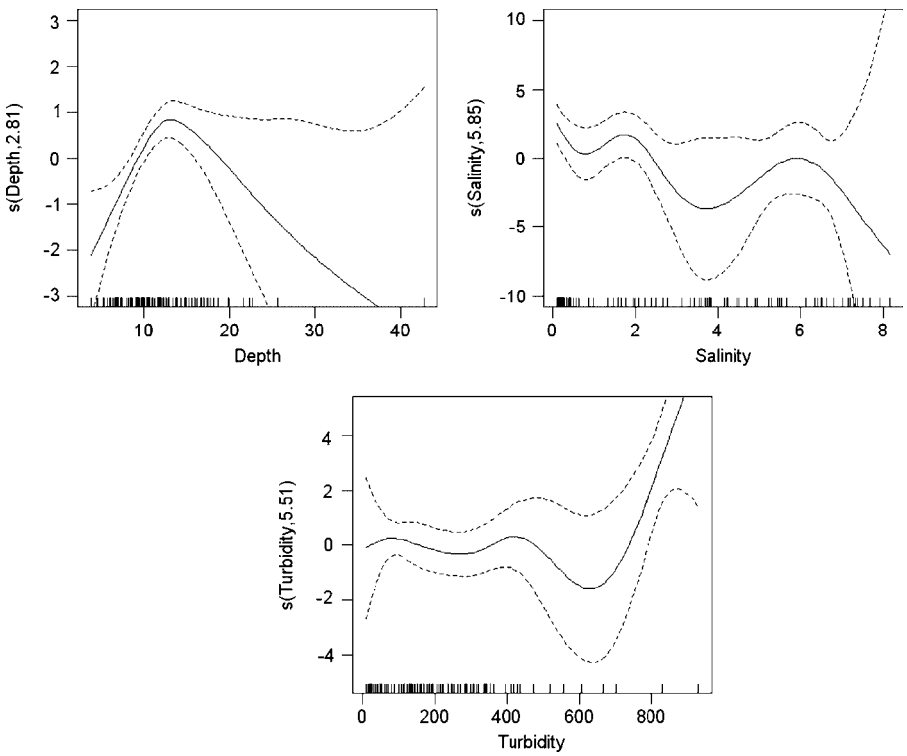

Figure 8. Estimated conditional dependence of Ganges River dolphin numbers on depth, salinity and turbidity within the entire study area during the high-water season.

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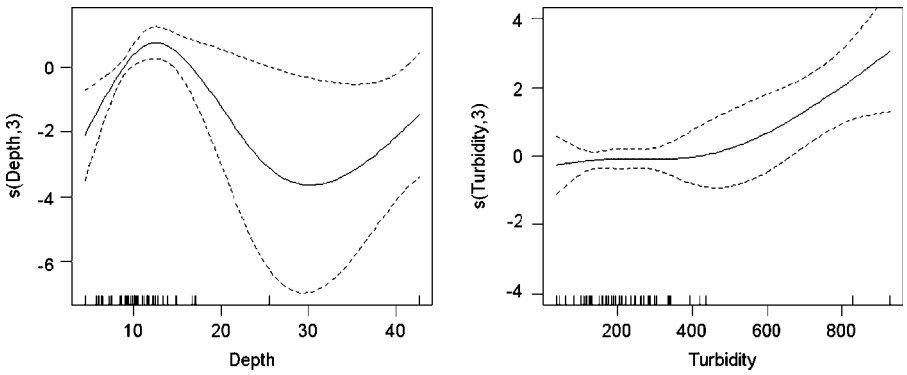

Figure 9. Estimated conditional dependence of Ganges River dolphin numbers on depth and turbidity within their extent of occurrence during the high-water season.

Table 3. Relative level (low, moderate, high, and high/low extremes) probability and maximum dependence (MD) of GAMs for depth (m), salinity (ppt), temperature (°C) turbidity (NTUs) and number of large–small confluences versus Irrawaddy dolphin distribution during low- and high-water seasons in the entire study area and extent of species occurrence during those seasons

Season/Area	Depth			Salinity			Temperature			Turbidity			No. confluences		
	Level	Prob.	MD	Level	Prob.	MD	Level	Prob.	MD	Level	Prob.	MD	Level	Prob.	MD
Low-water															
Entire study area	High	6.09e−10	→ 24; NAT	NS	NS	NS	High	7.37e-06	↑ at 29	Low	0.0138	→ 0	High	1.94e−08	4
Extent of occurrence	High	3.35e−07	→ 25; NAT	NS	NS	NS	High	4.03e-05	↑ at 29	Low	0.0158	→ 0	High	5.89e−08	↑ at 3
High-water															
Entire study area	Mod.	7.56e−05	8–18	Low	4.49e−07	→	NS	NS	NS	High/low extremes	4.08e−05	↑ at 400/ → 0	NS	NS	NS
Extent of occurrence	NS	NS	NS	Low	0.0436	→	NS	NS	NS	High/low extremes	4.028e−05	↑ at 400/ → 0	NS	NS	NS

NS = non-significant ($P > 0.05$); → = approaching; ↑ = still rising; and NAT = no apparent further trend due to increasing confidence intervals.

confluence were favoured by Ganges River dolphins with deviations of observed versus expected occurrence of 10.5% and 12.7% for sightings and individuals, respectively, but disfavoured by Irrawaddy dolphins with deviations of observed versus expected occurrence of −32.5% and −38.3% for sightings and individuals, respectively (Table 6).

DISCUSSION

Encounter rates

Although less distance was covered during the high-water season survey than during the low-water season survey, the distribution of survey effort was roughly equal with the exception that it was not possible to survey quite as far south in the delta during the high-water season (see Figures 2 and 4). This implies that encounter rates for both species should be similar if their distribution was unchanged during the two survey periods. Two surveys provide an inadequate sample size for making statistical comparisons but the data do show apparent differences in the encounter rates of the two species during the low and high-water seasons. A higher encounter rate of Irrawaddy dolphins was recorded along the survey trackline during the low-water season (15.1 individuals per 100 km) when salinity levels were relatively high and turbidity levels relatively low, compared to the high-water season (7.0 individuals per 100 km) when, conversely, salinity was relatively low and turbidity was relatively high. The slightly higher encounter rates recorded for Ganges River dolphins during surveys conducted in the high-water season (9.5 individuals per 100 km) versus those conducted in the low-water season (8.6 individuals per 100 km) might be explained by random variation in sighting rates or the lack of survey coverage during the high-water season survey in the southern portion of the delta where, because of higher salinity levels, it might be expected that encounter rates for this obligate freshwater species would be lower.

Habitat selection

During both low- and high-water seasons Ganges River dolphins generally selected (with some exceptions — see above) channel segments characterized by low salinity, high turbidity and moderate depth. The results of the GAMs for Irrawaddy dolphins were less straightforward. Contrary to expectations based on differences between encounter rates recorded during low- and high-water seasons, Irrawaddy dolphins selected low salinity waters during the high-water season and there was very little support for dependence on salinity during the low-water season, as indicated by the high *P*-value of 0.9103 for this variable when it was included in the GAM. These results probably reflect the greater environmental plasticity of Irrawaddy dolphins compared with Ganges River

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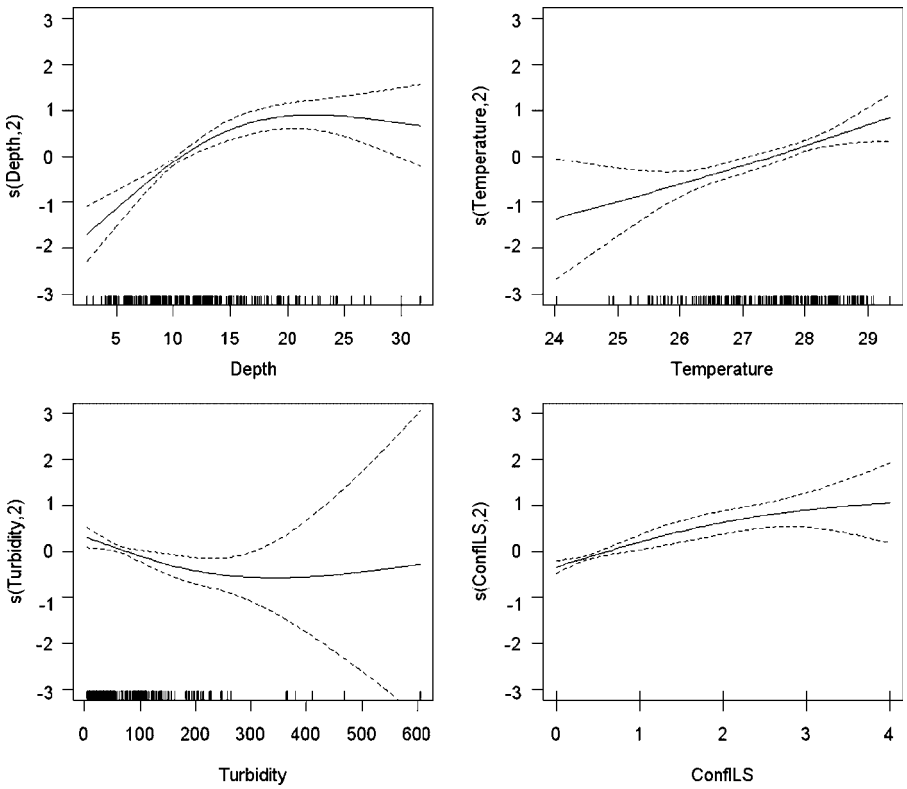

Figure 10. Estimated conditional dependence of Irrawaddy dolphin numbers on depth, temperature, turbidity and the number of large–small confluences within the entire study area during the low-water season.

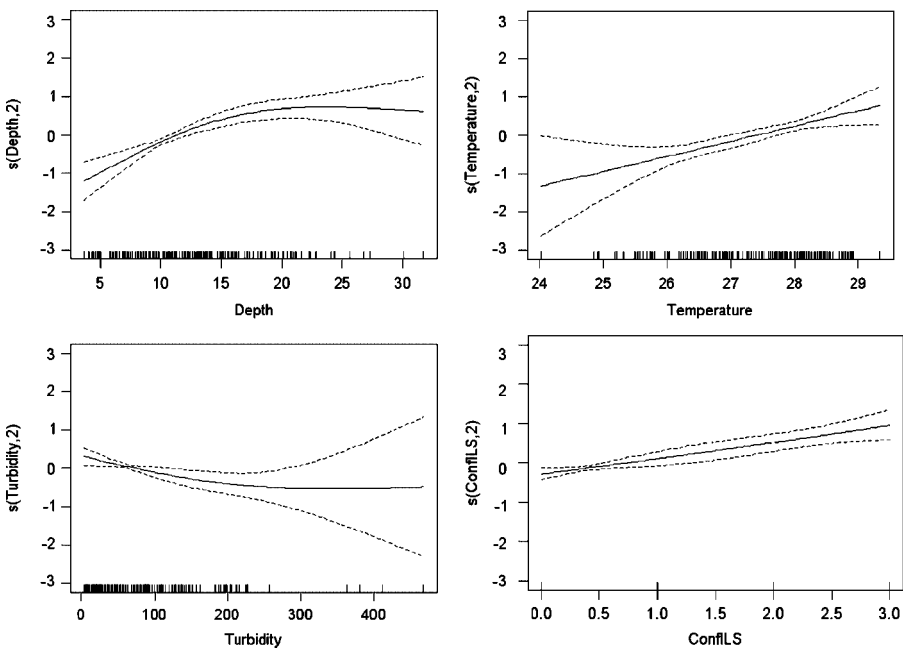

Figure 11. Estimated conditional dependence of Irrawaddy dolphin numbers on depth, temperature, turbidity and the number of large–small confluences within their extent of occurrence during the low-water season.

dolphins and suggest that limits to their upstream range might be constrained by interspecific competition rather than dependence on salinity. The fluvial distribution of Irrawaddy dolphins in three large rivers of Asia (see above) that are not inhabited by Ganges River dolphins provides circumstantial support for this explanation.

The outwardly confusing result of dependence on extreme turbidity levels during the high-water season points towards a possible explanation where a portion of the population within the mangrove forest moves upstream into channels that were either not occupied by Ganges River dolphins or where there is sufficient prey to avoid competition during the post-monsoon

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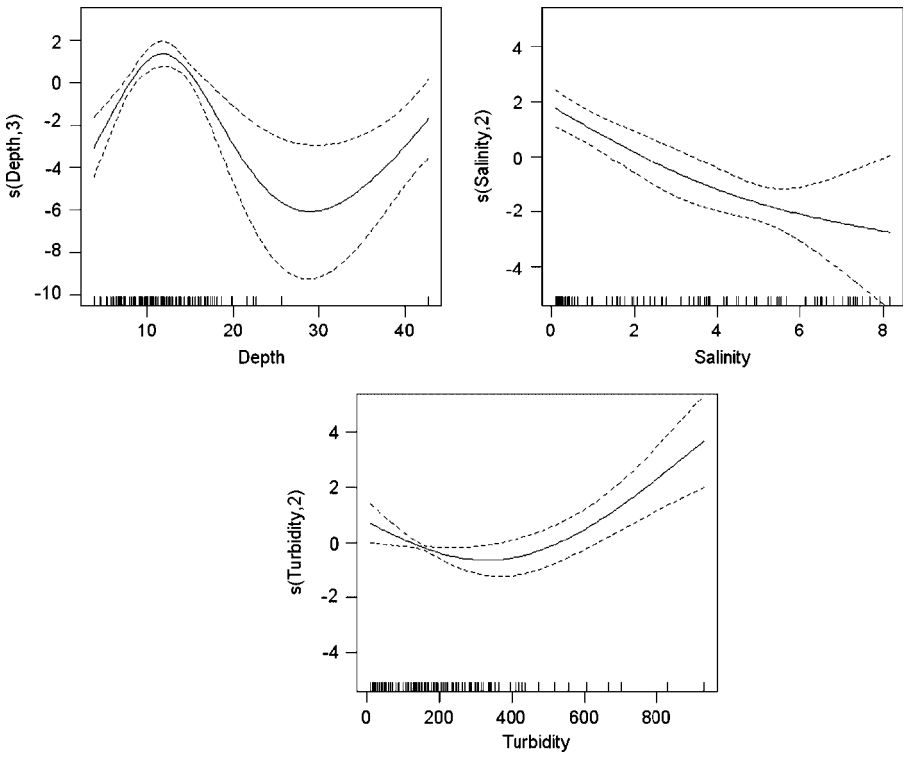

Figure 12. Estimated conditional dependence of Irrawaddy dolphin numbers on depth, salinity, and turbidity within the entire study area during the high-water season.

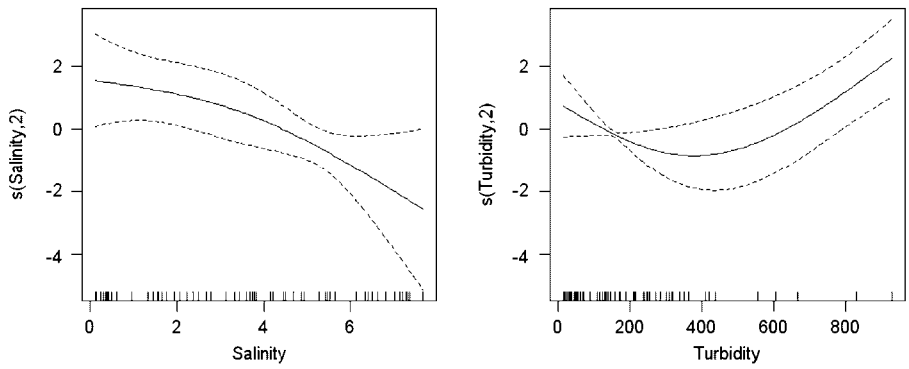

Figure 13. Estimated conditional dependence of Irrawaddy dolphin numbers on salinity and turbidity within the extent of their occurrence during the high-water season.

Table 4. Results of the discriminant analyses of environmental data collected during the low-water season survey at the locations of dolphin sightings showing the F-values of the ANOVAs (df = 1, 165), significance of the F-values, Wilks' Lamda values, standardized canonical discriminant coefficients and structure matrix values

Environmental variable	F-value of ANOVA	Significance of F-value	Wilks' Lambda value	Standardized canonical discriminant coefficient	Structure matrix value
Salinity	214.630	0.000	0.435	1.001	0.981
Turbidity	8.660	0.004	0.950	0.001	−0.197
Depth	5.330	0.022	0.969	0.052	0.155
Temperature	0.658	0.419	0.996	0.189	0.054

season when there is a burst of floodplain fish and crustacean productivity. According to this explanation, the other portion of the Irrawaddy dolphin population remains in less turbid, higher salinity channels close to open water where, during the dry season, about 92% of the population in Bangladesh resides (percentages calculated from abundance estimates for the outer delta (5383 individuals, CV = 39.5; Smith *et al.*, 2005) and waterways of the mangrove forest (451 individuals; CV = 9.6%; Smith *et al.*, 2006)).

Because turbidity exhibits greater spatial variation than salinity, the extremes of this variable may have shown up in the GAMs, while salinity exhibited only a minor decreasing trend

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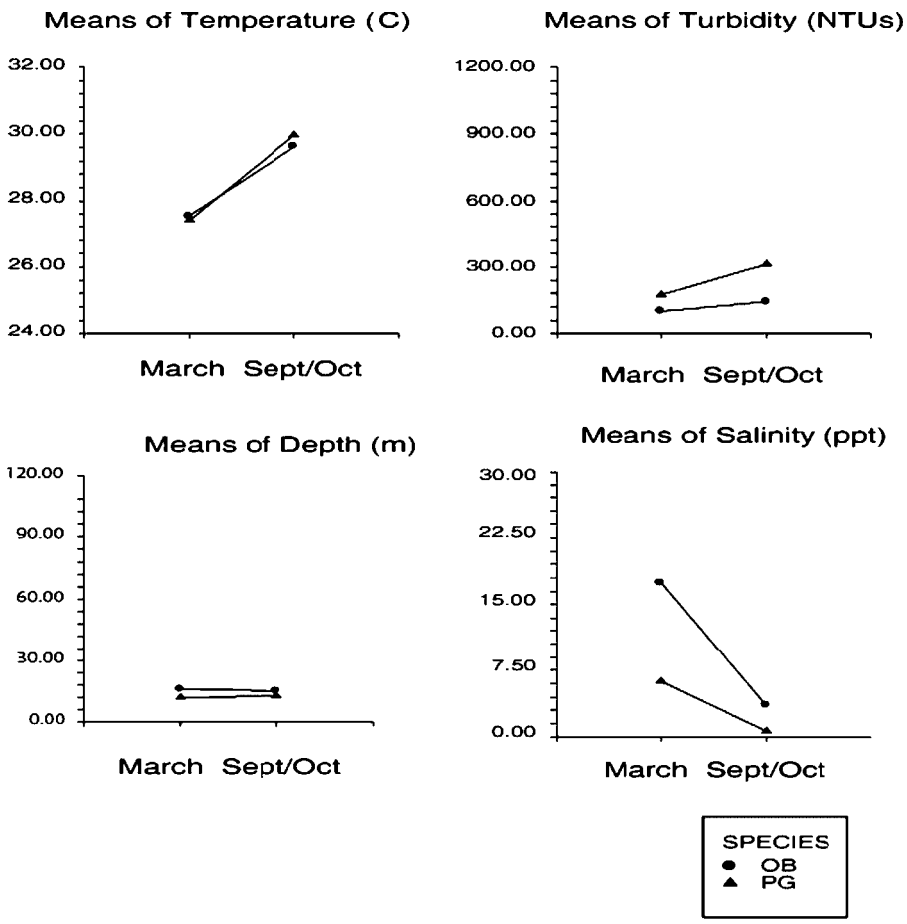

Figure 14. Means of temperature, turbidity, depth, and salinity recorded for Irrawaddy dolphin (OB) and Ganges River dolphin (PG) sightings recorded during surveys in the low-water season (March) and high-water season (Sept/Oct).

Table 5. Results of the discriminant analyses of environmental data collected during the high-water season survey at the locations of dolphin sightings showing the F-values of the ANOVAs (df = 1, 71), significance of the F-values, Wilks' Lamda values, standardized canonical discriminant coefficients and structure matrix values

Environmental variable	F-value of ANOVA	Significance of F-value	Wilks' Lambda value	Standardized canonical discriminant coefficient	Structure matrix value
Salinity	40.290	0.000	0.638	−0.687	−0.826
Turbidity	10.160	0.002	0.875	0.527	0.415
Depth	2.921	0.092	0.960	−0.169	−0.222
Temperature	5.766	0.019	0.925	0.564	0.313

Table 6. Summary of the number of segments and segment-surveys according to channel type (see Table 1), and the number of observed (O) and expected (E) Ganges River dolphin (PG) and Irrawaddy dolphin (OB) sightings (S) and individuals (I), and the percentage deviation (% Dev.) between observed and expected from data collected by captains of nature tourism vessels in the Sundarbans mangrove forest between April 2002 and March 2005

Channel type	Number of segments	Number of segment surveys	PG S-O	PG S-E	% Dev. PG S	PG I-O	PG I-E	% Dev. PG I	OB S-O	OB S-E	% Dev. OB S	OB I-O	OB I-E	% Dev. OB I
S3	24	1229	269	244	10.5	546	485	12.7	55	73	−32.5	106	147	−38.3
S6	7	336	53	67	−25.6	132	132	−0.4	16	20	−24.5	38	40	−5.5
S7	8	167	3	33	1002.9	7	66	−840.7	8	10	−23.7	20	20	0.4
S8	12	567	127	112	13.0	240	224	7.4	23	34	−46.1	46	68	−47.0
S9	65	2625	471	520	−10.4	913	1035	−13.4	184	156	18.2	364	313	16.3
S11	1	189	44	37	17.5	76	75	2.0	12	11	7.1	25	23	10.9
S12	9	454	136	90	51.2	281	179	57.0	32	27	18.9	65	54	20.0

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relative to increasing dependence. Direct comparisons of the two species in discriminant and non-parametric analyses showed that regardless of dependency, there were significant differences between them for salinity and turbidity during both low- and high-water seasons.

Potential biases of the habitat selection models

The covariates most often selected by the GAMs were based on empirical measurements made during the survey (i.e. salinity, temperature, depth, and turbidity) rather than derived from GIS techniques (i.e. sinuosity, channel width, and the numbers of large and small confluences). This may indicate problems with accuracy of the covariates obtained by means of GIS measurements from satellite maps or scale issues related to intrinsic differences between the two covariate groups – the former based on water quality gradients operating on an estuary-wide scale and the latter on local geomorphic features that may elicit fine-scale dependencies within wider-ranging water quality gradients.

Results of the chi-square analyses, which used the same GIS techniques as the GAMs for deriving channel morphology variables, supported the scale-difference explanation, with preferences exhibited by both species for wide sinuous channels with more than two small confluences or at least one large confluence and wide sinuous channels with one or two small confluences. The preference of Irrawaddy dolphins but aversion of Ganges River dolphins for wide straight channels with more than two small confluences or at least one large confluence, and preference of Ganges River dolphins but aversion of Irrawaddy dolphins for narrow straight channels with more than two small confluences or at least one large confluence can probably be explained by the great availability of these different channel types within the respective broader scale distribution of each species as determined by salinity, depth, temperature and turbidity dependencies indicated by the GAM models.

The habitat selection analyses made no assumption that all dolphins were detected during dedicated surveys or nature tourism cruises. However, the GAMs and chi-squared models did assume that potential sighting biases were independent of the physical variables included in the analyses. Imperfect detection of a species can result in severely biased habitat models if detection probabilities are correlated with habitat features (Gu and Swihart, 2004; MacKenzie, 2006). The covariate included in the habitat selection analyses most likely to have affected the detection (sighting) of dolphin groups was channel width; however, using information derived from double concurrent counts made by independent observer teams during the March 2002 survey, Smith *et al.* (2006) found no significant differences (Mann–Whitney U test $P > 0.05$) in sighting frequencies of Irrawaddy and Ganges River dolphins according to channel width. This probably reflects the relatively close proximity to the shore generally maintained by both species regardless of channel width.

Declining freshwater flows

Surface water in the Ganges River is diverted by engineering structures (e.g. dams and barrages) and reduced by losses to groundwater accelerated by subsurface extraction. If built, the Indian Rivers Interlinking Project will cause further declines in freshwater flow reaching the Sundarbans. Plans to supplement dry-season flow in the Ganges with water from the Brahmaputra River basin are unrealistic and conflict with other ongoing water development projects. For instance at 75% dependability, the annual flow available for planned canals linking the Manas, Sankosh and Teesta tributaries to the Ganges, after withdrawals from the Teesta Barrage which is currently under construction, will be about 28 billion m^3 $year^{-1}$ while projected removals from the Ganges are about 49 billion m^3 $year^{-1}$ (Basu, 2003). Freshwater withdrawals of this magnitude will undoubtedly cause major ecological changes in the Bangladesh Sundarbans including the reduction of available habitat for freshwater dependent cetaceans.

Global climate change and sea-level rise

The effects of climate change will exacerbate those problems related to declining freshwater flows and must be taken into account when considering freshwater flows necessary to maintain cetacean populations in waterways of the Sundarbans mangrove forest. A 10–45 cm sea-level rise was predicted to cause inundation of about 15% or 750 km^2 of the total land mass of the Sundarbans (Mirza, 1998b), and a rise of 50 cm would cause salinity to increase by about 2 ppt during the dry season in the far west with an increasing extent of sea water intrusion until a maximum is reached in the Passur and Sibsa channels (IWM, 2003b) — which is prime habitat for Irrawaddy and Ganges River dolphins.

Predicted effects of declining freshwater flows and sea-level rise

The results of this study demonstrate the complex habitat selection behaviour exhibited by two apex predators in a dynamic aquatic environment and the importance of understanding these processes for effective conservation management. The results also allow for some tentative predictions to be made on the distributional responses of both species to projected declines in freshwater flow and sea-level rise.

Owing to their obligate dependency on freshwater flow, Ganges River dolphins would be expected to be more affected by seawater incursion than Irrawaddy dolphins. Salinity is probably the dominant factor affecting the downstream distribution of these riverine specialists, but turbidity may also play an important role. Although the retinas of the Ganges River dolphin have light-gathering receptors, their extremely small eyes lack a crystalline lens (Herald *et al.*, 1969). Their poor vision, however, is compensated by exceptional echolocation abilities (Pilleri *et al.*, 1976), which make them particularly adapted to living in an extremely turbid environment. Other anatomical features such as unfused cervical vertebrates and large, highly flexible pectoral fins make the species highly manoeuverable and well suited to preying on riverine fishes and crustaceans (Smith, 2002).

Although the GAMs did not generally indicate dependence on confluences, the chi-square model that included a much larger sample size revealed a significant dependency on these features, which is consistent with observations in the field. Reduced discharge in alluvial rivers can result in channel

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narrowing and bed aggradation. In the mouth of the Mrigamari River, a distributary of the Passur River where relatively high concentrations of Ganges River dolphins were observed during the low-water season survey (Smith *et al.*, 2006), a substantial decline in channel width was recorded in 1995–2000. If current depositional trends continue, the Mirgamari River and the upper reaches of the Sela Gang River may soon become dewatered (IWM, 2003c). Increasing sedimentation, salinity and possibly decreasing turbidity due to reduced river discharges and sea-level rise can be expected to result in the loss of fluvial habitat for Ganges River dolphins in the downstream portions of their current range.

The potential effects of declining freshwater flows and sea-level rise on Irrawaddy dolphins were less clear. This species appears to be opportunistic in its ability to take advantage of the benefits of fluvial environments. It would therefore be tempting to hypothesize that the response of Irrawaddy dolphins to a decline in the range of Ganges River dolphins would be to correspondingly extend their range upstream. However, during the low-water season, their dependence on greater depths (of the thalweg) and wide sinuous channels with large and small confluences (which are primarily available in the downstream portion of the delta) suggests that the situation may not be so straightforward. Although the species may occupy a wide range of habitat in terms of salinity and turbidity, it also exhibited more localized dependencies related to the availability of confluences. This makes the species particularly susceptible to potential habitat loss due to sediment deposition at confluences and may limit their dispersal farther upstream in response to a possible release from competition with Ganges River dolphins that are likely to vacate these waters with increasing salinity. Declining freshwater flows may also affect habitat availability for Irrawaddy dolphins in the open waters of the delta where Smith *et al.* (2005) found that salinity was the most important water quality variable separating the near- and off-shore distribution of Irrawaddy dolphins and finless porpoises *Neophocaena phocaenoides*, respectively. A potential scenario in these waters might be for the offshore range of Irrawaddy dolphins to shrink while the potential for new habitat to become available upstream with increasing salinity could be lost due to a decline in the availability of large and small confluences.

Physical parameters as proxies for biological resources

Physical processes dramatically affect the ecology of estuaries with interactions occurring at broad temporal and spatial scales and affecting multiple trophic levels. Understanding the connections between physical and ecological processes is vital for distinguishing between natural environmental variation and anthropogenic impacts (Geyer *et al.*, 2000). The dependencies on physical variables indicated by the GAMs and chi-square analyses probably play a direct role in determining the suitability of aquatic habitat in the mangrove forest for Ganges River and Irrawaddy dolphins. For instance, counter-currents induced by confluences provide hydraulic refuge from fluvial and tidal currents (Smith *et al.*, 2006), and Ganges River dolphins are probably physiologically intolerant to high salinity conditions due to osmoregulation challenges; the species is unique among odontocete cetaceans in having a relatively primitive and unlobulated kidney (Smith, 2002). However, the observed dependencies on physical parameters may also be proxies associated with biological resources (i.e. dolphin prey and the assemblage of lower trophic-level organisms upon which the prey depends) that are key drivers for the habitat selected by the dolphins. Smith *et al.* (2004b) reported that high salinity conditions in Malampaya Sound, Philippines, did not appear to have direct adverse effects on Irrawaddy dolphins during the dry season when the population remained close to river mouths that provide substantial freshwater input to the inner Sound during the wet season. The authors interpreted this to mean that the affinity of the species for low salinity waters was likely due to ecological preferences rather than physiological intolerance to high-salinity conditions.

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

It would probably be unrealistic to suggest that concerns about dolphin habitat in Bangladesh could affect decisions about the construction and management of a water development 'mega-project' upstream in India, or decisions among global nations about CO_2 emissions affecting world sea levels. However, the results of this study can be used for incorporating knowledge about habitat selection and the potential effects of declining freshwater flows and sea-level rise into the design of a protected area network for freshwater-dependent cetaceans inside the mangrove forest.

Dolphin sighting data collected during dedicated surveys and nature tourism cruises are currently being used to investigate seasonal occupancy patterns and identify high-density hotspots for focal conservation attention. The strong dependency of both species on estuarine attributes associated with freshwater flow, including low salinity and the availability of large and small confluences, will be used as part of the prioritization process for identifying the locations and configurations of waterways where special protective measures could be employed. Priorities for future research also include investigating how the distribution of dolphins within the mangrove waterways relates to other biodiversity elements and whether or not site-based protection of freshwater cetaceans could result in spin-off benefits for other aquatic taxa, especially fish and crustacean communities that are of vital importance to the livelihoods and nutritional health of a large and growing human population.

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