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River dolphin distribution in regulated river systems: implications for dry-season flow regimes in the Gangetic basin

SUNIL CHOUDHARY[a,b], SUSHANT DEY[a], SUBHASHISH DEY[a], VIVEKSHEEL SAGAR[c], TARUN NAIR[d,e] and NACHIKET KELKAR[a,f,*]

[a]*Vikramshila Biodiversity Research and Education Centre, T.M. Bhagalpur University, Bhagalpur 812007, India*
[b]*P.G. Department of Botany, T.M. Bhagalpur University, Bhagalpur – 812007, India*
[c]*Freshwater & Wetlands Division, WWF-India, Lodi Estate, New Delhi-110003, India*
[d]*Post-graduate Program in Wildlife Biology and Conservation, Wildlife Conservation Society-India Program, Centre for Wildlife Sciences, National Centre for Biological Sciences – TIFR, GKVK Campus, Bangalore 560065*
[e]*Gharial Conservation Alliance, Centre for Herpetology, Madras Crocodile Bank Trust, P.O. Box 4, Mamallapuram, Chennai 603 104, Tamil Nadu, India*
[f]*Nature Conservation Foundation, 3076/5, IV Cross, Gokulam Park, Mysore 570002, India*

ABSTRACT

1. River flow regulation and fragmentation is a global threat to freshwater biodiversity, ecosystem processes, and associated human activities. Large dams in the Ganges river basin of the Indian subcontinent have severely altered natural flow regimes, particularly in the low-flow dry season. Altered flows could have negative impacts on endangered species such as the Ganges river dolphin *Platanista gangetica*.

2. Habitat use by river dolphins was investigated in relation to river channel depth and morphology, over 332 km of the flow-regulated Gandak River in India. Dolphin distribution patterns were compared across multiple spatial scales in the Gandak, Kosi, Chambal, Sone Rivers and the upper and lower sections of the Ganges main stem.

3. Dolphin presence was recorded in 40% of segments in the Gandak river, with a best count of 257 (range 250–267) and average individual encounter rates at 0.75 dolphins km^{-1} (SD 0.89). Bayesian zero-inflated spatial models showed that river dolphin abundance was positively influenced by river depth, presence of meanders and corresponded closely with gillnet fishing. Minimum mid-channel depth requirements were estimated at 5.2 m for dolphin adults and between 2.2 and 2.4 m for mother–calf pairs.

4. Adult dolphins showed highly similar habitat preferences across regulated or unregulated rivers, for depths >5 m, and meandering channels. Dry-season habitat availability was reduced as the degree of flow regulation increased across rivers, mainly owing to loss of lateral and longitudinal channel connectivity.

5. Overall encounter rates were reduced from >3 km^{-1} in less regulated stretches, to <0.3 km^{-1} in regulated rivers. Clustering of dolphins in deep pools increased along the gradient of river flow reduction, with dolphins almost absent from intervening segments because of low flow rates. These results indicate the importance of maintaining adequate dry-season flows to ensure river habitat availability and connectivity for dolphins.

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KEY WORDS: flow regulation; Ganges river dolphins; river depth; channel morphology; Bayesian zero-inflated spatial models; Gandak River; Gangetic basin

*Correspondence to: Nachiket Kelkar, Nature Conservation Foundation, 3076/5, IV Cross, Gokulam Park, Mysore 570002, India. Email: rainmaker.nsk@gmail.com.

INTRODUCTION

Regulation of river flows for human use seriously threatens freshwater biodiversity across the globe (Bunn and Arthington, 2002; Nilsson *et al*., 2005). Large dams, flood-control structures, and embankments for irrigation projects and hydroelectric power (Dudgeon, 2000, Dudgeon *et al*., 2006; Collen *et al*., 2008) have had substantial impacts on river ecosystem services and biodiversity at both local and landscape scales (Dudgeon, 2000; Nilsson *et al*., 2005). River flow regulation primarily leads to the loss of longitudinal and lateral connectivity of habitats along the river continuum (Vannote *et al*., 1980; Ward, 1998; Ward *et al*., 1999; Bunn and Arthington, 2002). Flow regulation also causes local habitat fragmentation, reduction of variability in river discharge, and simplification of channel morphology, e.g. straightening of rivers and loss in hydraulic complexity (Ward and Stanford, 1995; Ward *et al*., 1999; Tockner and Stanford, 2002; Doll *et al*., 2009; Arthington *et al*., 2010). Habitat loss through flow regulation can have drastic effects on distribution, gene flow, movement, migration patterns, and behaviour of riverine species (Bunn and Arthington, 2002; Lytle and Poff, 2004). Several freshwater species adapted to natural river flow dynamics have been seriously affected, and many have become endangered (McAllister *et al*., 2001; Robinson *et al*., 2002). Also, freshwater diversions have led to declines in water quality, biological productivity and geomorphological processes, especially in developing countries (Bannerjee, 1999; Adams, 2000; Dudgeon, 2005). Management and maintenance of adequate and ecologically relevant flows is thus one of the most important challenges for freshwater conservation today (Richter *et al*., 2003; Smakhtin *et al*., 2007).

In the Indian subcontinent, large-scale flow regulation and impending water development projects seriously threaten the unique biodiversity of large rivers (Dudgeon, 2000). A prolonged dry season (6–8 months) in major floodplain rivers in India is a critical period for riverine species as river flows gradually decline until the arrival of the monsoon floods (Heiler *et al*., 1995; Richter *et al*., 1997; Jain and Sinha, 2003). Freshwater diversions for irrigation and power projects further aggravate the scarcity of river water in this 'pinch period', causing major declines in habitat connectivity and resource availability (Payne and Temple, 1996; Adams, 2000; Adel, 2001; Dudgeon, 2005). Survival of endangered and charismatic river fauna such as the Ganges river dolphin *Platanista gangetica gangetica* and Gharial *Gavialis gangeticus* is also increasingly threatened by dry-season flow reduction by large dams and barrages (Smith and Braulik, 2008; Hussain, 2009). The resulting loss of river channel connectivity may have caused fragmentation of populations, and possibly even local extinctions in some areas (Reeves and Leatherwood, 1994; Smith *et al*., 1994; Smith and Smith, 1998; Sinha *et al*., 2000).

Documenting distributional responses of river dolphins to alterations in fluvial characteristics caused by dry-season flow regulation might yield a vital understanding of their adaptive resilience to environmental stress (Smith and Reeves, 2009). This can contribute towards the case for better estimation and maintenance of adequate flows to ensure river habitat availability and connectivity in the dry season, for conservation of river dolphins and other freshwater species (Reeves *et al*., 2000; Das *et al*., 2005; Smakhtin *et al*., 2007). Surveys of river dolphin populations have been conducted across most parts of their distribution range (Sinha *et al*., 2000; Behera, 2006; Choudhary *et al*., 2006), and long-term observations have helped identify general habitat requirements of the species (Smith *et al*., 2009, 2010). Dolphins are known to prefer deeper pools, counter-currents, muddy-rocky substrates, meandering channels, and confluence joins that offer hydraulic refuge (Reeves and Leatherwood, 1994; Smith *et al*., 1998, 2009, 2010; Kelkar *et al*., 2010). The impacts of flow alteration on river depth and channel morphology, within-river and across-floodplain exchanges and connectivity, flow volume, sediment accretion and scouring patterns are also reasonably well understood (Ward, 1998; Ward *et al*., 1999; Thoms, 2003; Benda, 2004; Bragg *et al*., 2005; Vietz *et al*., 2007; Arthington *et al*., 2010). A multitude of observations and surveys indicates how dolphin distributions might change (a) across the dry season and monsoonal floods, with respect to downstream distance of dolphins from barrages, (b) at local scales because of the presence of important habitats such as confluences and hydraulic refuges from counter-current pools and meandering channels, and (c) by extirpation of populations from areas upstream of barrages (Smith *et al*., 1994, 1998; Reeves *et al*., 2000; Sinha *et al*., 2000; Chaudhary, 2003; Sinha and Sharma, 2003). Nevertheless, more empirical studies that include rigorous quantitative approaches are needed for a detailed understanding of dolphin-habitat relationships altered by flow regulation across multiple spatio-temporal scales.

The distribution of dolphins is generally patchy and not uniform across the river stretch, with hotspots in specific areas (Smith *et al*., 1998; Choudhary *et al*., 2006). The known 'natural' or common distribution may confound inference about effects of altered river flows on dolphin distribution, since it can be difficult to assess whether dolphins can move between these 'patches' if flows in the intervening shallow areas are reduced. The magnitude of spatial clustering across segments (autocorrelation in dolphin encounter rates vis-a-vis depth and channel morphology) and dolphin use of 'marginal' habitats between hotspot areas could be used as simple indicators of habitat connectivity. In an ideal situation, assessments of dolphin distribution at pre- and post-water release events can help calculate the effect sizes or magnitudes of impact. However, it may be logistically difficult to conduct such surveys at large scales. A space-for-time comparison across similar rivers could help assess dolphin distributional responses across a gradient of flow regulation.

In this study the spatial distribution and habitat use of Ganges river dolphins was investigated (a) within the regulated Gandak River in India downstream of the Indo-Nepal barrage, from primary data, and (b) across the moderately regulated Gandak, Kosi and highly regulated Chambal and Sone rivers, and a stretch in the upper Ganges; from available literature (largely similar to the Gandak in biophysical characteristics). A relatively less regulated stretch from the lower Ganges was considered a control site, to estimate relative impacts of flow reduction on dolphin distribution. Channel morphology and river depth were investigated as the key variables influencing dolphin distribution. Bayesian spatial models were used to incorporate multiple sources of information about dolphin habitat use. The main contribution of this study is a preliminary impact assessment of dry-season flow alterations on an endangered riverine species across five rivers. From the results, potential impacts of flow reduction on the ecology of river dolphins, implications for future research, and linkages of observed trends to conservation are discussed.

METHODS

Study area

The study took place on the Gandak River, but available information from literature and opportunistic observations on dolphins from other similar and dissimilar stretches within the Gangetic basin was also used. Two sections of the main stem of the Ganges, and two each of antecedent snowmelt-fed tributaries (Gandak, Kosi) and semi-arid-origin, plain-fed tributaries (Chambal, Sone) were included (Jain and Sinha, 2003; Singh *et al*., 2007). A map of the sites is shown in Figure 1.

Gandak River

The Gandak River (known as Narayani in Nepal) originates in the Nepal Himalaya. It is one of the major north–south flowing antecedent tributaries of the Ganga, with a drainage area of 7620 km^2 in India (Jain and Sinha, 2004). It flows through the states of Bihar and Uttar Pradesh for a distance of 335 km until it joins the Ganga at Patna. At the India–Nepal border, a barrage with a large irrigation and power project was constructed at Valmikinagar, Bihar. The depth profile of the flow-regulated river stretch within India is shallow overall (<1 m) with some deep pools with depths between 7 and 12 m. The Gandak River also has many flood-control embankments. This river has a high frequency of channel avulsion and is one of the most flood-prone rivers in the alluvial megafans of northern Bihar (Jain and Sinha, 2004). Industrial activity in this region is low, and floodplain agriculture, despite the high human population densities, is not widespread in the upper reaches. Large tracts of alluvial grassland and scrub forest still persist along the banks, and fishing activity is common and widespread. The length of the dry season (low-flow period) is from November to May. Interviews revealed that hunting of dolphins is absent from many parts due to religious beliefs (Authors, unpublished data).

Kosi River

The Kosi is one of the most dynamic antecedent tributaries of the Ganges, and has moved about 112 km eastward over the last century. The Gandak–Kosi interfan forms one of the largest floodplains on the Indian subcontinent (Sinha and Jain, 1998). Unfortunately, a series of embankments has been constructed along the Kosi for flood control, which has only aggravated the problem of floods in the area (Sinha and Jain, 1998). The Kosi barrage in Nepal is a major diversion that has led to severe declines in flow, especially in the dry season (Chaudhary, 2003). Deep pools occur only beyond 50 km from the barrage (Sinha and Sharma, 2003). After flowing 270 km in India, it meets the Ganges near Kursela in Bihar. Agriculture and grassland scrub

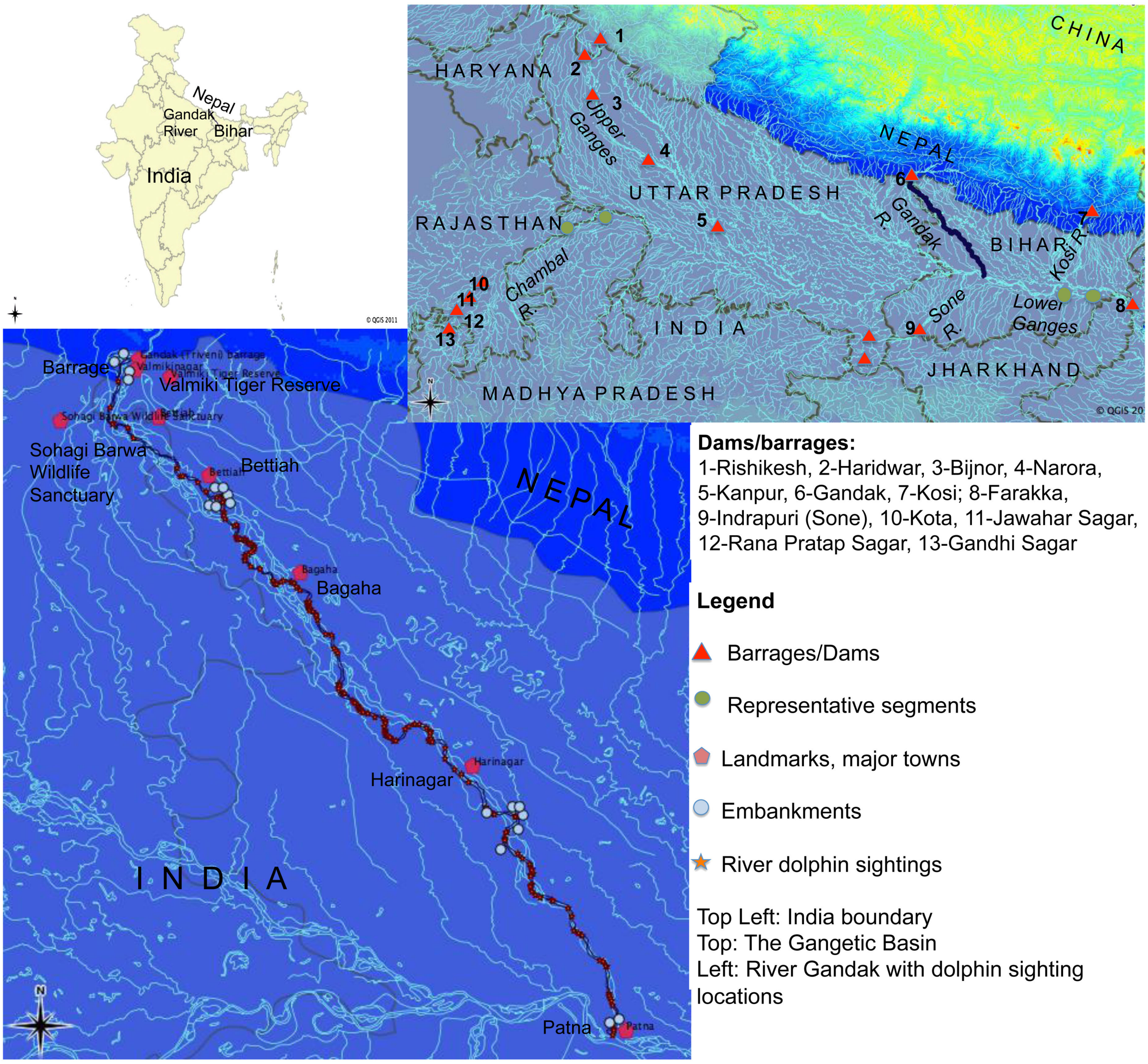

Figure 1. The Gangetic basin with the Gandak and other rivers, major dam/barrage sites on these rivers and other important landmarks indicated. Dolphin sighting points in the Gandak River are also shown.

form the major land-use types. Hunting of dolphins for oil has been recorded (Sinha and Sharma, 2003).

Chambal River

The Chambal River is 960 km long, flows northward across the states of Madhya Pradesh, Rajasthan and Uttar Pradesh to join the Yamuna. It is one of the relatively pristine and clean large rivers in India, with tracts of scrub forests along its rocky ravines. Four barrages for irrigated agriculture, hydel power and atomic energy have been constructed along the Chambal, which have led to severe flow reduction in the river (Nair, 2010). A large length of the Chambal River lies within a protected area as it still holds the largest breeding population of the critically endangered gharial *Gavialis gangeticus*, as well as some rare bird species.

Sone River

The Sone is 784 km long, and flows north-eastward until it meets the Ganges before Patna. Apart from two smaller barrages, the Indrapuri barrage constructed on the Sone is the main reason for drastic declines in dry-season freshwater flows. The length of the Sone within Bihar is *c.* 300 km (downstream of the barrage), from which, in the dry season, dolphins have been reported entirely absent (Sinha and Sharma, 2003). The Sone holds an important population of wild gharial, and a fairly large riverine tract has been declared a wildlife sanctuary.

Upper Ganges (Haridwar to Narora)

This highly regulated *c.* 300 km stretch of the Ganges has two important barrages at Bijnor and Narora in Uttar Pradesh. Characterized by significantly reduced flows throughout the year, this stretch has a low population of dolphins (*c*. 35–39 dolphins) but has been monitored and protected with local support for a long period of time (Behera and Mohan, 2005). Historically, this stretch has recorded major declines in the upstream range of river dolphins, even upstream of Bijnor, to Haridwar. Reports suggest that dolphins have not been seen in a stretch of 140 km over the last few decades. However, a recent increase in dolphin populations between the barrages has been reported (Behera, 2006).

Lower Ganges (Sultanganj to Kahalgaon, the Vikramshila Gangetic Dolphin Sanctuary)

The Vikramshila Gangetic Dolphin Sanctuary is located in the Bhagalpur district of Bihar, India. It is a river stretch *c*. 65 km long between the towns of Sultanganj and Kahalgaon (Choudhary *et al*., 2006). The river channel is characterized by meanders, wide straight channels, alluvial islands, point and spit bars, and rocky mid-channel islands, with eddy counter-current pools also being common habitat features (Singh *et al*., 2007). Despite being a sanctuary, fishing and agriculture are highly intensive and widespread in this area. This section lies more than 450 km downstream of Kanpur barrage and over 150 km upstream of Farakka barrage, and due to several large river confluences between Kanpur and Farakka has relatively higher flows. As such, it stands as a control site for the present comparison between rivers. Dolphins in this stretch have been relatively better protected from hunting through civil society initiatives over the last decade (Choudhary *et al*., 2006).

Data collection

Within the Gandak River

In January 2010, a 15-day boat-based survey of river dolphins was conducted across 332 km of the Gandak River in India, starting from the Gandak barrage and ending at the confluence with the Ganga, near Patna. An average of 22.6 km of the river was covered each day. The river stretch was divided into equal-length sampling units of 1 km each (n = 332 km) and dolphins surveyed along shoreline contours. Three trained observers recorded dolphin counts in each stretch (based on Smith and Reeves, 2000). Sampling was undertaken only in excellent sighting conditions. Observers recorded the number of dolphins and estimated distance and angle of each dolphin encounter from the boat's GPS location at the time of survey, with a range finder and compass. Dolphin age-classes (neonate/calf, sub-adult, adult) were intuitively estimated based on observation. Care was taken to avoid double counting of dolphins, by recording simultaneous resurfacings of more than one dolphin, and correcting the time interval between resurfacing of individuals relative to the approach time of the boat. Channels that could not be crossed by boat (water less than 0.5 m deep) were surveyed on foot, and boat surveys continued from the nearest navigable channels. For each segment sampled, ecological and anthropogenic covariates were recorded mainly in relation to physical attributes (e.g. depth, channel morphology), human use (e.g. fishing, ferry crossing), and land-use type (e.g. forest, agriculture, town) at the start and end of each segment (Table 1). Since river flow data were not available (being confidential in accordance with rules of the Government of India), proxy variables were recorded, such as river depth, width and channel morphology, relevant to the dry season low-flow period. Detectability bias was assumed constant across segments surveyed. Dolphin encounter rates (counts per km) indicated habitat use.

Across rivers

Information on dolphin encounter rates, reported distance of the first dolphin sighting from the barrage, dolphin occurrence in habitats between deep pools, flood-season occurrence nearer to and further from the barrage, and known historical distribution in the dry season was compiled from this study and other similar surveys in rivers within the Gangetic basin (Sinha and Sharma, 2003; Behera and Mohan, 2005). These were compared across rivers that were biophysically more or less similar to the Gandak, and along a gradient of flow regulation (based on number of barrages upstream, within a distance of 300 km in the Kosi, Sone, and a stretch of the upper Ganges). It was also assumed that declines in dolphin numbers caused by other threats (e.g. pollution, by-catch, hunting) were similar across all rivers. To assess whether the presence of barrages upstream can have distant effects (>250 km) downstream as well, dolphin encounter rates (encounter rates in primary and marginal intervening habitats) were compared along similar lengths of the Gandak and Chambal rivers, and with a 60 km stretch of the relatively less regulated lower Ganges (distance from the last barrage downstream was over 450 km).

Table 1. Details of ecological and anthropogenic covariates measured in river dolphin surveys, and possible effects of flow regulation on these factors

Independent variable	Description	Potential effects of flow regulation*
Biophysical		
River depth	Measured at centroid of each segment, in metres (m) with a depth sounder	Reduction of depths, deeper pools in clumped patches
Channel area	Channel width (m) calculated with laser rangefinder, area estimated for units with segment length 1 km	Floodplain spread reduction, channel width reduction
Water temperature	Measured at centroids of segments, in degrees Celsius	Increase in temperature
Channel morphology	Meanders, mid-channel islands, braided stretches and confluences	Transitions from meanders to braided channels, confluences isolated from main stem
Land-use type	Land-use types noted for both banks – village/town, forest, floodplain, plantation, agriculture, flood-control structures	Seasonal agricultural expansion; construction of embankments
Anthropogenic		
Fishing	Presence or absence of different fishing practices noted per segment - gillnets, basket-nets, seine-nets, hook-lines, large drag-nets, and barrier fishing using mosquito-nets, and cast-nets	Decline in fisheries production, fragmentation of fish populations
Boat traffic	Number of boats per segment	-
Other	Sand-mining, river channel dredging, embankments	-
Miscellaneous		
Latitude and Longitude	In degrees decimal, later converted to WGS 84/UTM-45 North projection	-
Weather and Visibility	Sighting conditions from best to worst on an ordinal scale from 1 to 6, based on presence and intensity of fog, haze, winds, and rains.	-

*From studies on flow regulation impacts: Ward and Stanford, 1995; Poff *et al*., 1997; Ward, 1998; Adel, 2001; Bunn and Arthington, 2002; Nilsson *et al*., 2005.

Data analysis

Within the Gandak River

River dolphin counts were mapped in relation to segment number (indicating distance from the barrage). Biophysical and anthropogenic covariates were also mapped across the entire stretch, at 1 km resolution with the open source software Quantum GIS Mimas 1.3.0 (Quantum GIS Development Team, 2010). Encounter rates and proportion of segments out of the total that had dolphin presence were calculated. Ecological and anthropogenic covariates correlated with dolphin counts (total counts, and counts of adults, sub-adults and calves per segment) were identified using exploratory analyses. Mantel tests were used for correlation of covariates with dolphin counts to incorporate spatial autocorrelation. A Mantel correlogram was plotted to represent change in correlation in dolphin counts with dissimilarity in river depth. Euclidean and Jaccard indices of dissimilarity were used for the correlograms.

To assess the importance of river depth and channel morphology on relative abundance of different age-classes of river dolphins, Classification and Regression Trees (CART) were used (De'ath and Fabricius, 2000). In CART, the variation in adult, sub-adult and calf encounter rates is partitioned into homogeneous sub-clusters based on combinations of covariates included in the model. This binary, recursive partitioning continues until residual deviance for tree models is minimized. Based on the tree model output, it is possible to compare important contrasts between dolphin encounter rates as explained by a certain combination or a 'minimum depth'. For instance, the tree might produce a last split in the depth data at x m, above which dolphin encounter rates (output nodes) are, say, 2 km^{-1} and below which, they fall to 0.2 km^{-1}. CART can thus be used to identify the channel depth or type below which dolphins might avoid them. CART model outputs for 'minimum depth requirements' were compared with observations from other studies across rivers (Smith *et al*., 1998, 2009; Sinha and Sharma, 2003; Behera and Mohan, 2005; Kelkar *et al*., 2010).

Based on the CART output (i.e. variables selected), statistical models were used to test the individual effect of depth, channel type, etc. on dolphin counts. To make use of prior information on channel preferences of dolphins, Bayesian regression models were used. Bayesian analysis treats different model parameters as stochastic values drawn from an appropriate underlying natural 'distribution process'. This is called the prior distribution, and has mean and variance (or shape and scale) parameters that can be constructed from known previous information (literature, expert opinion, historical data, local knowledge, etc.) (Ellison, 1996). The prior distribution can also have virtually no information, represented usually as a 'flat' or 'diffuse' prior distribution (Spiegelhalter *et al*., 2007).

The likelihood (actual data) is updated with a suitable prior distribution, and a posterior distribution is estimated for parameters, using Bayes Theorem:

$$p(\theta|x) \propto p(x|\theta).p(\theta)$$

where θ represents the candidate model and x represents the data. Using priors helps in explicit validation of response (in this case, habitat preference) from known data and this can help in comparisons across studies (useful for single-species models).

Bayesian analysis can thus have many advantages for complex analyses with robust inference on parameter estimates, over other non-parametric methods (GAMs) or even conventional regression (GLMs). A Bayesian hierarchical approach helped construct intuitive models by explicitly incorporating covariate effects, spatial effects and segment-level random effects influencing the process of interest (distribution of river dolphins) across levels. Excess zero-counts are a special case of over-dispersion (of clustered zeros), and present an additional modelling challenge, as they add extra-Poisson variation in the data distribution (Martin *et al*., 2005; Ntzoufras, 2009). Excess zeros may have also arisen from segment lengths of 1 km. The frequency distribution of dolphin counts per segment was zero-inflated, with zero-counts forming 60% of the total dataset (Figure 2). For better inference and accuracy of estimates, it was necessary to model the source of zero observations.

Zero-inflated Poisson and negative binomial GLMs (Martin *et al*., 2005; Minami *et al*., 2007) provide ease in modeling such data. GLMs were used in a full Bayesian hierarchical modelling framework, with the explanatory variables depth, meander presence, and gillnet fishing; and a conditional autoregressive (CAR Normal) term for spatial random effects for a first-order neighbourhood structure (Jin *et al*., 2005; Gschlol and Czado, 2006; Lee and Durban, 2009). In this model, dolphin occurrence for any segment

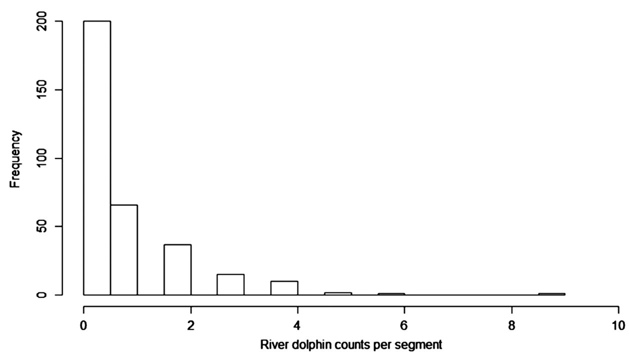

Figure 2. Zero-inflated nature of dolphin abundance across river segments.

was assumed to be dependent on the previous and next adjacent segments only. All models included a Gaussian error term for site-level unstructured random effects (Lee and Durban, 2009). The models were based broadly on Martin *et al*. (2005) and Ntzoufras (2009).

Process model distributions for dolphin count per segment were specified as $dolphincount[i] : Poisson(mean[i])$ OR $dolphincount[i] : NegativeBinomial(p[i], r[i])$ and $mean[i] < -\mu[i]gz[i]$ or $(p[i] < -\mu[i]gz[i])$ where $\mu[i]$ refers to the observed dolphin count per segment, with $z[i]$ representing the probability of a zero count $z[i] : Bernoulli(p)$; p: $Uniform(0, 1)$.

The GLMs were represented as: dolphin count $< -$ Intercept + Parameter B (Covariates) + CAR spatial term + Gaussian errors term. The spatial conditional autoregressive (CAR Normal, Spiegelhalter *et al*., 2007) term for spatial random effects and smoothing is given as $\rho[1:N] : CAR \cdot Normal(adj[], num[], weights[], tau)$; $tau : Gamma(0.001, 0.001)$where tau is the term for precision (1/variance) of spatial random effects. The terms num, adj and $weights$ refer to the number of neighbours, adjacency matrix (first-order neighborhood structure) and spatial weights. The Gaussian random effects term was denoted by $mu[i] : Normal(0, tau.h)$; $tau.h : Normal(0, 0.001)$ where $tau.h$ is a precision term for site-level random effects was also added.

Spatial random effects were tested at 1 km resolution for dependence in dolphin counts. High values for the precision term indicated lower spatial effects, whereas low values indicated high spatial effects (similar counts in segments due to spatial adjacency). Prior distributions were constructed as follows: (a) for a positive slope lognormal prior distributions were used with appropriate mean and relatively high variance; (b) for uninformative or negative effects normal distributions with zero or negative mean, and an appropriate high variance term were used. For parameter estimation 30 000 Markov Chain Monte Carlo (MCMC) iterations were used after discarding the burn-in period for the first 4000 iterations. All statistical analyses were conducted with the software R 2.10.1 (R Development Core Team, 2010) and WinBUGS 1.4.3 (Spiegelhalter *et al*. 2007).

Across rivers

Qualitative comparisons were conducted to assess general trends in dolphin distributional response across a gradient of flow regulation in rivers of the Gangetic basin (similar lengths of the Gandak, Kosi, Sone and upper Ganges at river basin level, and at sub-sampled stretches of similar lengths distant from barrages, in the Chambal, Gandak and lower Ganges). Overall dolphin encounter rates per km were used as an index of habitat use. Dolphin use of intervening marginal habitats between deep pools was assessed as a measure of habitat availability from upstream–downstream connectivity. Dry-season connectivity of the main-stem with confluences (as an index of lateral connectivity) was ranked for three rivers. Proportion of zero counts out of the total number of segments surveyed was used as an index of unavailable habitat for dolphins. The scale of spatial clustering in the Gandak was compared with the lower Ganges with Mantel correlograms.

RESULTS

Within the Gandak River

Dolphin presence was recorded in 39.7% of the total number of segments (n = 332). A total best count of 257 (range 250–267) and individual overall encounter rate was 0.75 (SD 0.89) dolphins km^{-1}. Dolphin counts per segment were positively influenced by river channel depth and presence of meanders (Table 2). Gillnet fishing activity and dolphin distribution showed high spatial overlap. Dolphins showed clustering close to deep pools and meanders (Figure 3). High spatial clustering of dolphin groups was observed within 1 km segments, indicated by the small value of the spatial variance parameter, estimated at 0.004 (SD 0.007) (Table 2, Figure 3). Encounter rates were highest in the middle reaches of the Gandak (1.13 km^{-1}), compared with 100 km adjacent to the barrage (0.52 km^{-1}), and the lower reaches closer to the Ganges main stem (0.7 km^{-1}). The first adult dolphin sighting was beyond 10 km from the barrage whereas mother–calf pairs were first observed beyond 57 km. Classification and regression trees estimated a minimum depth of 3.8 m for sub-adult habitat preference, and adult dolphins showed higher preference for segments >5.2 m deep (Figure 4). Adult–calf pairs were found mainly in shallow areas with depth range 2.2–2.4 m, but encounter rates were low in channels with mid-channel islands and presence of gillnet fishing (Figure 4). Dolphin counts were highly correlated with depth profile across segments (pair-wise dissimilarity; Mantel's

Table 2. Parameter estimates for effect sizes (with Bayesian credible intervals) of zero-inflated Poisson (ZIP and Pois) and (zero-inflated) negative binomial (ZINB and NB) regression models for dolphin relative abundance. Conditional autoregressive (CAR normal) spatial and unstructured random effects per segment (URE) are also modelled. Deviance Information Criterion (DIC) values are provided as the model selection criteria for the 7 best models. Lowest DIC value indicates best model.

Model	Parameter estimates			DIC
	Regression coefficients[a]	Random effects[b]	Overdispersion and zero-inflation terms[c]	
ZIP ~ depth, meander, gillnet, CAR, URE	*b0*: -0.008 (−0.57-0.51) *b1*: 0.18 (0.11-0.25) *b2*: 0.03 (−0.34 – 0.40) *b3*: -0.32 (−0.61- -0.03)	*tau*: 265.8 (106.7-587.2) *tau.h*: 24.14 (2.26-76.63)	*p*: 1.28 (1.19-1.51) z: 0.28 (0.19-0.50)	757.8
ZIP ~ depth, gillnet, URE	*b0*: 0.04 (−0.59-0.68) *b1*: 0.165 (0.09-0.24) *b3*: -0.2847 (−0.58- -0.03)	*tau.h*: 6.23 (1.97-15.76)	*p*: 1.3 (1.12-1.45) z: 0.3 (0.11-0.46)	765.2
ZIP ~ depth, gillnet, CAR, URE	*b0*: 0.16 (−0.69-0.82) *b1*: 0.175 (0.10-0.25) *b3*: -0.335 (−0.64- -0.009)	*tau*: 1121 (407.4-2442) *tau.h*: 20.45 (2.07-49.08)	*p*: 1.32 (1.12-1.46) z: 0.32 (0.12-0.46)	769.6
NB ~ depth, meander, CAR	*b0*: -1.003 (−1.34- -0.68) *b1*: 0.218 (0.13-0.31) *b2*: 0.214 (−0.11- 0.55)	*tau*: 131.4 (14.6-405.3)	*p*: 1.29 (1.04-1.62)	770.4
NB ~ depth, meander, gillnet, CAR, URE	*b0*: -0.5 (−1.2-0.08) *b1*: 0.21 (0.11-0.29) *b2*: 0.29 (−0.06-0.65) b3: -0.29 (−0.57- -0.06)	*tau*: 569.9 (160.2-1752) *tau.h*: 25.56 (2.8-70.93)	*p*: 1.49 (1.08-2.27)	776.4
ZINB ~ depth, meander, gillnet CAR URE	*b0*: -0.06 (−0.62-0.53) *b1*: 0.183 (0.104-0.26) *b2*: 0.12 (−0.32-0.56) b3: -0.31 (−0.67- -0.01)	*tau*: 420.4 (37.87-3174) *tau.h*: 24.73 (3.343-66.82)	*p*: 27.46 (2.20-154.4) z: 0.20 (0.012-0.40)	789.4
ZINB depth, gillnet URE	*b0*: -0.12 (−0.74-0.48) *b1*: 0.18 (0.10-0.28) *b3*: -0.232 (−0.55- -0.06)	*tau.h*: 14.78 (1.72-51.54)	*p*: 27.85 (2.23-156.1) z: 0.25 (0.013-0.42)	791.2

[a]Parameters of the basic regression model with covariates: *b0* = intercept, *b1* = slope for depth, *b2* = slope for presence of meander, *b3* = slope for absence of gillnet (meander and gillnet are binary variables); [b] *tau* = precision (1/variance) of spatial random effects, *tau.h* = precision of URE (unstructured random effects); [c] *p* = parameter for overdispersion, z = zero-inflation parameter (for ZIP, z = *p*−1); CAR term for conditional autoregressive spatial random effects.

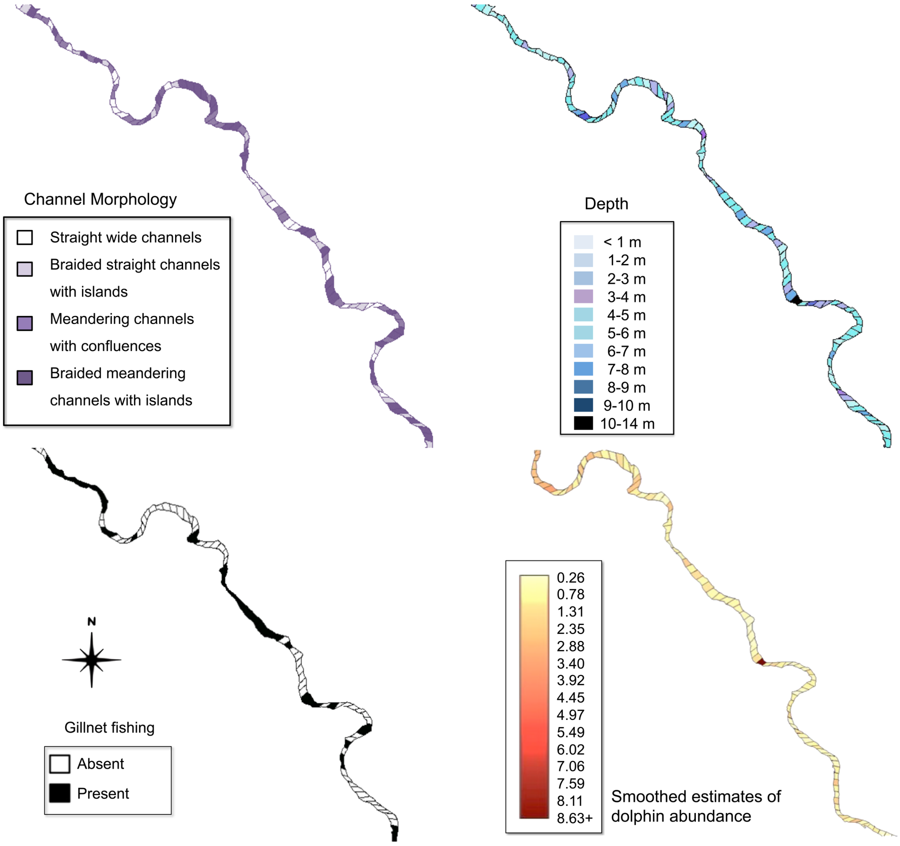

Figure 3. Section of the Gandak River showing (top panel): variation in channel types, depth profile; and (lower panel) occurrence of gillnet fishing, with smoothed estimates of dolphin counts: the output from selected spatial zero-inflated Poisson regression model.

$r = 0.285$, $P = 0.001$). Dolphin encounter rate in intervening channels between deep pools/meanders was 0.284 km^{-1} (Table 3, Figure 5).

Across rivers

Dolphin habitat use across rivers was influenced by similar covariates, i.e. channel depths of around 5 m (mostly deep pools) and presence of meandering stretches. This habitat preference held true along the gradient of flow regulation in these rivers, but overall habitat availability was reduced as flow alteration increased (Table 3). Dolphin encounter rates were lower and the sighting distances downstream of barrages increased with the number of barrages. The Sone and Chambal Rivers (which do not receive snowmelt water) had drastic flow reduction caused by barrages and recorded very low dolphin encounter rates compared with other stretches. The scale of spatial clustering of dolphins in the Gandak was smaller (<1 km), compared with the lower Ganges (<2 km) (Figure 5). Also, most of the intervening branches between 'hotspots' had regular dolphin presence in the Ganges. In contrast, river dolphins in the Chambal were found restricted to deep pools, as intervening stretches had almost no water and confluences mostly cut off in the dry season (Nair, T., pers. obs.). Across river stretches more than 250 km downstream of any barrage, the same trend in encounter rates and unavailable habitat was noted (Table 4). Confluence–main-stem connectivity was lower in the Chambal and Gandak compared with the lower Ganges. Habitat use of deep pools as well as intervening habitats by dolphins declined as flow alteration increased and availability was reduced (Tables 3 and 4).

DISCUSSION

River dolphin distribution within the flow-regulated Gandak River showed extreme clustering at small spatial scales, and positive association with river depth and meandering habitats. Along a gradient of flow regulation across rivers in the Gangetic basin, results from this study, offer suggestive evidence for reduction in availability of primary habitat for river dolphins, and disruption in longitudinal and lateral connectivity with increased flow regulation. These comparisons were possible not only due to biophysical similarities of the rivers considered,

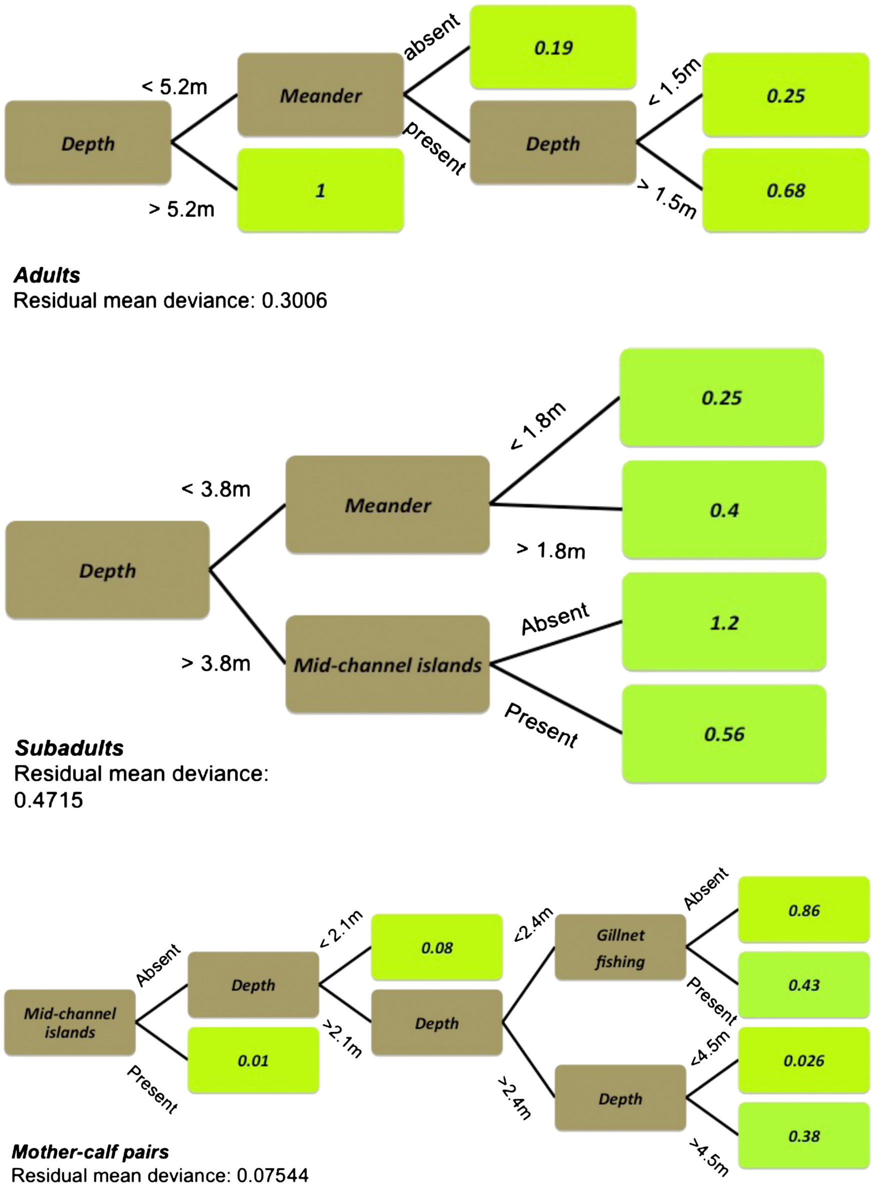

Figure 4. Selected best tree models showing habitat preferences of different age-classes of dolphins in the Gandak River: (Top) adults prefer channels with depths >5.2 m and meanders; (Middle) minimum depth required by sub-adults is less than that of adults (3.8 m); and (Bottom) mother–calf pairs prefer shallower channels between 2.2 and 2.4 m, preferring areas without alluvial islands and presence of gillnet fishing. Green boxes indicate mean encounter rates for the respective covariates (brown boxes).

but also because dolphin habitat preferences across different rivers were found to be very similar. However, long-term direct studies are needed to compare pre- and post-water release effects on dolphin distribution, directed dispersal, emigration, and other movements. Such comparisons could help with a clear understanding of how human modifications to flow regimes might influence the extent of ‘crowding’ in the commonly observed ‘clustered’ distribution of dolphins. Although general patterns conform to known patterns of dolphin distribution (Smith *et al.*, 1998) at the reach scale, habitat use at finer scales can also be responsive to flow regulation and associated stress.

We believe that the broad qualitative comparison presented is a useful preliminary attempt to reveal dolphin habitat-use patterns as flow alterations increase in magnitude, and with the nature of different rivers. In addition, the study forms an important baseline for future monitoring in the Gandak, with updated estimates of abundance (previously <150 reported) (Behera, 2006). Another contribution of the study is the application of Bayesian spatial models for quantifying dolphin–habitat relationships. Bayesian analysis allows the intuitive use of natural distributions representing animal abundance (Gelfand *et al.*, 2006), such as Poisson or negative binomial with zero-inflation and spatial effects (Gschlol and Czado,

Table 3. Comparison across rivers of the Gangetic basin with reference to dolphin habitat use in biophysically similar rivers along a gradient of flow regulation, (demonstrating negative trend in habitat use with flow regulation). (SD=Standard Deviation)

River	Gandak[a]	Kosi[b]	Sone[b]	Upper Ganges (Haridwar to Narora)[c]
Flow regulation attributes				
Length surveyed	332 km	c. 270 km	c. 300 km	c. 300 km
Number of dams/barrages upstream	1	1	3	4
Snowmelt or plains-fed?	Snowmelt	Snowmelt	Plains	Snowmelt
Dry-season channel depth	Mostly 0.5–2 m, with some deep pool sections 7–12 m	Depth > 5 m after 60 km from barrage, river channels fragmented into pools of water because of excessive embankment constructions	0.5 to 1 m in most areas	Some deep pools with very shallow stretches in between (<1–1.5 m)
Degree of channel avulsion	High	High	Low	High
Meanders and braided channels	Common	Common	Common	Common
Dolphin distribution patterns				
Reported first occurrence downstream of last barrage	10 km (Gandak barrage)	42 km (Koshi barrage)	-	82 km (Bijnor barrage)
Dolphin encounter rates per km	0.75 (SD 0.89)	0.31	0	0.23
Dolphin encounter rates per km in intervening marginal habitats between deep pools	0.284	Difficult to estimate given nature of dry-season flows	Absent (no dolphins seen or reported in dry-season, throughout the stretch)	Almost absent from intervening areas
Flood-season occurrence of dolphins close to barrage and feeder canals	Yes	Yes (movements reported across 200 km)	Yes (sporadic sightings only in the monsoons)	Yes
Historical dolphin distributional change	Upstream extirpation likely, downstream occurrence changes not drastic	Upstream extirpation likely, reported reduction in downstream occurrence	Drastic, dolphins possibly abundant before construction of Indrapuri barrage	Drastic, at least 130–140 km reduction in upstream occurrence limit

[a]This study.
[b]Based on Sinha and Sharma, 2003.
[c]Based on Behera and Mohan, 2005.

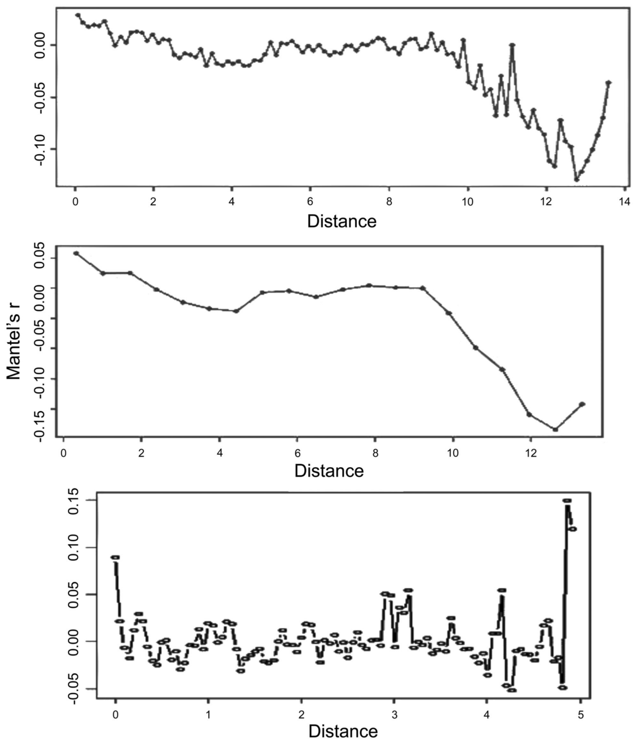

Figure 5. Mantel correlograms showing change in spatial correlation of dolphin counts with distance in km (lag) in the Gandak River (top and middle), and the Ganges (bottom). The magnitude of spatial autocorrelation on dolphin counts is higher in the Ganges, indicating higher clustering of dolphin groups in the Gandak.

Table 4. Comparison across rivers of the Gangetic basin with reference to dolphin habitat use in similar lengths of the Gandak, Chambal and lower Ganges, > 250 km downstream of barrages (similar trend as Table 3).

River	Chambal[a, c]	Gandak[b, d]	Lower Ganges[e]
Distance downstream of last barrage	c. 300 km	270 km	Above 450 km
Length surveyed	75 km	63 km	65 km
Dolphin encounter rates per km	0.09 (SD 0.34)	0.67 (SD 0.99)	3.35 (SD 2.87)
Proportion of segments with zero counts	0.933	0.603	0.071
Dolphin encounter rates per km in intervening marginal habitats between deep pools	Absent from intervening habitats, restricted to deep pools	0.49 (SD 0.96)	2.92 (SD 2.09)

[a]This study, contribution of Tarun Nair.
[b]This study.
[c]Chambal has four barrages and heavy flow-regulation.
[d]Gandak has one important barrage.
[e]From dataset used in Kelkar *et al.* (2010).

2006). The models include parameter estimation on the effects of spatial adjacency on counts, an aspect often ignored in many habitat studies. Zero-inflated models aid in better inference from models of survey data for rare species such as river dolphins that often yield many zero counts (Minami *et al.*, 2007). The estimation procedure is highly rigorous yet flexible and allows for explicit incorporation of known (prior) information in models (Ellison, 1996). These techniques can be very useful in developing refined habitat suitability models for river dolphins.

Surveys of river dolphins from the biophysically similar, flow-regulated Kosi, Sone and upper Ganges (Sinha and Sharma, 2003; Behera and Mohan, 2005) suggest that river dolphins have declined from a large proportion of river habitat following the construction of barrages. Other regulated rivers have seen drastic declines in dolphin distribution, e.g. in the highly regulated and polluted Yamuna River (Sinha *et al.*, 2000; Chaudhary, 2003; Das *et al.*, 2005; Smith and Reeves, 2009). These results quantitatively validate findings of Das *et al.* (2005), who noted a reduction in the distribution of dolphins downstream of barrages with reduction in river flow. Across a series of barrages on the Indus River (Braulik, 2006) an increase in dolphin abundance was reported from middle and lower reaches distant from barrages, possibly owing to emigration (involuntary attrition) to downstream areas. However, most upstream populations seem to have been extirpated (Sinha *et al.*, 2000). Barrages on rivers flowing from Nepal to India (Kosi and Gandak), and from India to Bangladesh (Farakka) have had potentially adverse impacts on upstream and downstream dolphin populations (Smith *et al.*, 1994; Sinha *et al.*, 2000, Smith and Braulik, 2008).

Reduction in connections between adjoining river segments can affect longitudinal connectivity and dolphin movement along the river, especially between 'hotspots' in deep pools. In addition, confluence habitats are highly preferred by dolphins, as they are areas of stable flows facilitating fish movement and aggregation (Benda, 2004). Lateral connectivity, i.e. tributaries joining the main stem augment reduced flows downstream of barrages (Ward, 1998; Tockner and Stanford, 2002), which is evident in the Gandak River as well. High levels of water abstraction for dry-season irrigated agriculture could affect tributary flows and cause a reduction in main-stem–floodplain connectivity (Adel, 2001; Doll *et al.*, 2009; Kelkar *et al.*, 2010). Straightening of regulated river channels can directly affect meanders preferred by dolphins for hydraulic refuge (Smith *et al.*, 1998; Sinha *et al.*, 2000). Dolphin habitat selection is linked to foraging on small-sized schooling fishes (Kelkar *et al.*, 2010). In deeper pools with counter-currents, dolphins often aggregate for feeding in side-channels near deep pools, to maximize foraging efficiency (Smith *et al.*, 1998). Overlap and competition for resources between fishers and river dolphins may be escalated by habitat loss (Kelkar *et al.*, 2010), as fishing activity is also concentrated in these areas. Extreme flow reduction may also affect female–calf pairs as they mostly reside in shallow channels during the peak dry season, possibly the calving period (Authors, personal observations over the last 5 years).

Minimum depth requirements (depth thresholds) estimated for dolphins might indicate that dolphins, in any river, may not adapt to reduced flows beyond a certain point. Flow requirements for the critically endangered gharial *Gavialis gangeticus* (Hussain, 2009; Nair, 2010) are highly similar, and both species are vulnerable to flow alteration. It is also necessary to identify impacts of flow alteration on, and minimum depth requirements of, river fisheries, as fish resources become scarce and patchy in the peak dry season. Minimum depth requirements could thus be used as 'signals' of flow reduction effects and habitat availability for protecting both the needs of river fisheries and biodiversity (Adams, 2000; Acreman and Dunbar, 2004). Ensuring the provision of adequate environmental flows at the policy and implementation level must be made mandatory and high priority in the Gangetic basin (Richter *et al*., 1997; Dudgeon, 2000, 2005, Smakhtin *et al*., 2007).

Dry-season river flow reduction is among the most important threats to freshwater biodiversity as well as local livelihoods in the Indian subcontinent. At present, any institutional or civil monitoring of flow regimes from the viewpoint of wildlife conservation or livelihood safety is largely lacking. At the local level, dry-season abstraction of tributary water, construction of weirs and channel diversions must also ensure that near-natural flows are maintained throughout the year. Generating public support for mandatory provision of adequate and ecologically relevant river flows will be a key step. Quantitative estimation of spatio-temporal, multi-scale monitoring of water needs of the agriculture, industry and fisheries sectors is necessary for balancing them with the ecological flow requirements of endangered riverine biota (Richter *et al*., 2003; Acreman and Dunbar, 2004; Smakhtin *et al*., 2007). At the subcontinental scale, international trans-boundary negotiations for ensuring environmental/natural adequate flows (Smith *et al*., 1998; Chatterjee and Dey, 2006) will also go a long way in safeguarding habitat availability and connectivity for river dolphins and other species. In conclusion, these results suggest that local and landscape-level alteration of river flows in the Gangetic basin can have serious impacts on river dolphins, and support the need for maintenance of ecological flow regimes for their conservation.

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