MANAGEMENT OF NEPALESE RIVERS TO CONSERVE GANGES RIVER DOLPHIN

by

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To my parents, who gave me lessons in spiritual things and encouraged me to go on every adventure;
To the hundreds of men and women living in the community in pursuit of healthy living;
and most especially to our endangered Ganges River dolphins.
This research is dedicated to you.

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ABSTRACT

The aim of this dissertation is to use evidence-based research to better understand the ecology of the endangered Ganges River dolphins (GRD, *Platanista gangetica gangetica*) in Nepalese waterways to account for the potential roles that river dolphins play in riverine ecosystems and to guide effective restoration and protection. Previous studies failed to systematically and rigorously capture globally heightened hydro-ecological issues that threaten GRDs, a shortcoming that this thesis addresses. As a large and mobile apex predator in riverine ecosystems whose conservation supports the protection of a wide diversity of species, I first reviewed how evolutionary trap mechanisms—which threaten the ecological structure of the river basin—affect the dynamics and viability of GRD populations in South Asian waterways. Further, to improve the persistence of GRD, I examined ecological preferences and responses of GRD to environmental and anthropogenic stressors by using systematically replicated field-based datasets at finer spatial and wider temporal scales in large river systems (e.g., Sapta Koshi and Karnali) of Nepal. Globally, I detected six potential mechanisms that likely affect the GRD populations discretely or in combination: (1) habitat modification; (2) occurrence of finite and geographically restricted local populations; (3) ratio of effective to estimated population size; (4) increased risk of inbreeding depression in genetically isolated groups; (5) at-risk behavioral attributes; and (6) direct fisheries–dolphin interactions. The effects of water regulation on native freshwater biodiversity, especially for megafauna like GRD, are extreme and place populations under a greater risk of extinction by isolation and habitat loss. My study reveals that GRD exhibit ecological responses to flow variations that determine habitat quality and availability; variation in flow resulted in substantial response differences across time and space. This suggests that GRD occupy a variety of habitats to support their life histories and maintain viable populations. A decline in suitable habitats coupled with uninformed water regulations likely places GRDs under severe physiological stress during the low-water season (i.e., January–April), suggesting that reduced flow regimes contribute to the process of endangerment and extirpation of highly endemic aquatic mega species as an immediate response. I found that *ad hoc* or proportional-based flow management is no longer tenable to maintain the integrity and functionality of aquatic ecosystems. My research highlights that quantifying the relationships of GRDs ecological responses to flow variation is crucial for monitoring the effects of water alteration and determining the minimum flow regime needed for balancing human needs and

promoting economic advancement while conserving GRD and riverine biodiversity. Furthermore, high fisheries exploitation rates of GRD-preferred prey sizes (>60% of the total catch per effort), especially during the low water season combined with the risks of 48% (CI: 43–52%) increased behavioral change probability among dolphins exposed to fisheries, increasing the risks of social and biological impairment for exposed dolphins. My study reports drivers and consequences of GRD-fisheries interactions, and can be used to mitigate impacts on small cetaceans. I also found considerable overlap in GRD diel activity coefficients across space, season, and time of day, indicating environmental factors marginally regulate diel activity patterns. Instead, GRD consistently exhibited nocturnal activity peaks despite substantial variation in diurnal activity. This indicates a compromising shift in GRD diurnal behavioral activity as a response to human disturbance, especially fishing events. Interestingly, GRD exhibit behavioural variability in response to spatial heterogeneity, adjusting in highly regulated and modified river systems. My research advances our empirical understanding of ecological needs and life history of GRD in relation to space and time, and supports the development of freshwater cetaceans recovery strategies as well as conservation and management of priority habitats in combination with assisting the processes of societal needs. As a top predator of the riverine ecosystem, effective riverine cetacean conservation strategies can directly or indirectly support the restoration of the degraded riverine ecosystem by maintaining their functions and integrity.

INTRODUCTION

The Ganges–Brahmaputra–Meghna and Karnaphuli River Basin in Nepal, India, and Bangladesh is home to the world's most endangered freshwater river dolphin—the Ganges River dolphin (GRD). Unfortunately, several anthropogenic and natural factors jeopardize the future of this species by changing habitat quality and disrupting their dispersal corridors. The dams and barrages at or near the international borders (e.g., Nepal–India and India-Bangladesh) threaten the Ganges River dolphin ecology by reducing or modifying habitats (Rahman et al., 2010). These processes present sizeable irreversible extinction risks for Ganges River dolphins, similar to those that contributed to the recent human-induced extinction of the Yangtze River dolphin (Turvey et al., 2007). Although, as a mega species and highly mobile organism in an aquatic ecosystem, this species offers opportunity to measure the quality of river systems health (Turvey et al., 2012), the extinction risk for the Ganges River dolphin is poorly understood, and how small isolated groups of the Ganges River dolphin will respond to novel environmental changes while maintaining genetic diversity is unknown. Whereas habitat loss and fragmentation are the most critical documented factors (Sinha & Kannan, 2014; Paudel et al., 2015), a combination of several factors likely put the Ganges River dolphin at risk of extinction. Different factors may act, and interact, to drive the Ganges River dolphin populations to extinction by reducing population size and stability and creating downward cycles to demographic extinction. Our ability to understand the extent and potential magnitude of such threats is limited, yet essential to develop an integrative conservation strategy in a changing environmental setting to restore the degraded river systems.

As the significant loss of the Ganges River dolphin is largely attributed to dams/water-related development structures, hydrological alteration resulting from natural water availability or human-interventions is threatening freshwater ecosystems and their native biotic inhabitants faster than these habitats can be restored (Baron et al., 2004). Such modifications affect ecosystems and their aquatic biota in many ways, including effects on physical habitat, life history, and lateral and longitudinal connectivity (Bunn & Arthington, 2004). Preserving a freshwater ecosystem’s natural flow regime, in terms of quantity, quality, and seasonality, is essential to protect native biota and environmental processes. Previous studies have typically developed flow-ecology relationships using lower trophic species, such as small fishes and riparian plants, limiting their scope of application. Such relationships might not represent the full integrity of ecosystems, because megafauna require diverse habitats and connectivity and are often sensitive to natural flow regimes across a considerable geographic scale. Past studies have often have not studied the essential ecological roles and function of freshwater megafauna (i.e., body mass ≥30 kg; He et al., 2017), which help to develop relationships that are transferrable to regional landscapes. As the ecological traits of focal taxa might explain much of the variation in response to altered flows (Poff, 2018), freshwater apex predators may be ideal candidates to develop flow-ecology relationships that could benefit a broad range of species that share the same riverine and adjacent riparian habitats (Leo et al. 2018).

The human-induced extinction of a Yangtze River dolphin (*Lipotes vexillifer*) from China has led to growing concern that similar extinctions of other river dolphins are likely unless human uses and river ecology are better understood and conflicts mitigated (Turvey et al., 2007). Particularly at risk are other river dolphins with distributions that are mostly restricted to human-dominated river systems under the immense pressure of multiple factors, including habitat loss and river-dependent human communities. Conflicts between small cetaceans and artisanal fishing have increased globally in recent years (Kreb et al., 2007; Loch et al., 2009; Turvey et al., 2010; Paudel et al., 2015; Kelker et al., 2018). Despite available studies on interactions between small cetaceans and fisheries, competition between small cetaceans and subsistence fisheries poses a severe and growing problem, and meaningful management thus requires an effective and appropriate assessment of the factors that drive the interaction.

The risk of small cetaceans’ endangerment and extinction was highlighted globally after the functional extinction of the Yangtze River dolphin. Small cetaceans, such as the Ganges River dolphins, particularly those with a small population size limited to a certain geographic range, are more vulnerable to the risk of extinction in the Anthropocene. Although the social and behavioral needs of cetaceans have been identified as potential factors that determine their vulnerability to human disturbance, how GRD adjust their underwater behaviors and diel activity patterns in response to spatial and temporal variation remains poorly understood. Previous studies on GRD underwater behaviors were mostly performed in laboratory settings (Herald et al., 1969; Andersen & Pilleri 1970; Mizue et al., 1971). Recent studies have focused on capturing the sound source of the free-ranging GRD to characterize annual behavioral patterns (i.e., habitat use) (Sugimatsu et al., 2008; Sasaki-Yamamoto et al., 2012) and click characteristics; but these studies did not explicitly report the underwater behaviors and diel activity patterns in response to ecological factors (for example, ecological factors that controlled the number of clicks) across space and time; thus, they failed to report how GRD underwater behaviors and diel activity respond across environmental variability throughout the length of a day.

Herein, I collected and analyzed demographic, behavioral, environmental, and genetic-based information in an integrative way to predict the evolutionary potential of the Ganges River dolphin in South Asian waterways. I highlight possible mechanisms that could affect the dynamics and viability of the Ganges River dolphin populations across the region. To balance the conservation of endangered species like GRD and development in the regulated river system, I quantified the relationships between flow-ecology considering habitat selection traits of GRD, which is crucial for monitoring the effects of water alterations and determining the minimum flows needed to maintain healthy and functional freshwater ecosystems in the Anthropocene. Furthermore, I also assessed aspects of the interaction between artisanal fisheries and cetaceans in Nepalese waterways not previously studied by examining 1) niche overlap between GRD and fisheries in the prey size collected by each; 2) overlap in diel activity by fisheries and GDR; and 3) effects of fisheries on GDR behavior. By understanding underwater behaviors and diel activities of GRD, I reported the significance of spatial heterogeneity to GRD, which offers the opportunity to estimate spatial and time overlap, and understand how cetaceans compromise their ecological needs in response to human activity. My findings fulfill the current gaps in endangered freshwater cetaceans population management and protection of their priority habitats that eventually contribute to maintain the functions of fragile riverine ecosystems where aquatic species survival is at risk during the Anthropocene. This study will support development of conservation and protection strategies for riverine ecosystems in Nepal, extending to other regions that share similar aquatic species and hydro-physical characteristics.

PRESENT STUDY

This dissertation comprises four manuscripts. The first manuscript published in *Ecology and Evolution* (Appendix A), “Factors affecting the persistence of endangered Ganges River dolphins (*Platanista gangetica gangetica*)”, which aims to review how evolutionary trap mechanisms may affect the dynamics and viability of the GRD populations after rapid declines in their population size and distribution. We detected six potential trap mechanisms that might affect the Ganges dolphin populations discretely or in combination: (a) habitat modification; (b) occurrence of finite and geographically restricted local populations; (c) ratio of effective to estimate population size; (d) increasing risk of inbreeding depression in genetically isolated groups; (e) at-risk behavioral attributes; and (f) direct fisheries–dolphin interactions. The second manuscript, submitted for consideration in *Nature Scientific Reports* (Appendix B), “Ecological responses to flow variation inform river dolphin conservation” quantified flow-ecology responses in the Karnali River of Nepal during the low-flow season when habitat was heavily reduced and water demand was highest. We define ecological responses as suitable habitat templates with enough usable surface area to support GRD fitness by improving reproduction and survival. The third manuscript, published in *Nature Scientific Reports* (Appendix C), “Seasonal flow dynamics exacerbate overlap between artisanal fisheries and imperiled Ganges River dolphins” quantify the effects of artisanal fisheries on the ecology of a small cetacean, the Ganges River dolphin (*Platanista gangetica gangetica*, GRD), in a large river system of Nepal. We examine the size-classes of fisheries’ catches, behavioral changes in GRD in response to fishing activities, and diel overlap between GRD and fishing activity. The fourth manuscript, intended for submission to *Animal Conservation* (Appendix D), “Behavioral responses to spatial heterogeneity in endangered Ganges River dolphins” examined the underwater behavioral activities of GRD differently than previous studies: we collected echolocation pulses (a series of clicks) from three hydro-physically stratified habitats most preferred by the GRD over a wide temporal scale. Using click patterns and time of acoustic detection of GRD, we addressed to the ways in which diel activity patterns and their behaviors developed across environmental variability.

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APPENDIX A: FACTORS AFFECTING THE PERSISTENCE OF ENDANGERED GANGES RIVER DOLPHINS (*Platanista gangetica gangetica*)

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Factors affecting the persistence of endangered Ganges River dolphins (*Platanista gangetica gangetica*)

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Running title: Evolutionary potential of endangered Ganges River dolphins

Abstract

The Ganges-Brahmaputra-Meghna and Karnaphuli River Basin (GBMK) in Nepal, India, and Bangladesh is among the world's most biodiverse river basins. However, human-induced habitat modification processes threaten the ecological structure of this river basin. Among the GBMK's diverse flora and fauna of this freshwater ecosystem, the endemic Ganges River dolphin (*Platanista g. gangetica*) is one of the most charismatic species in this freshwater ecosystem. Though a >50% population size reduction has occurred since 1957, researchers and decision-makers often overlook the persistence (or evolutionary potential) of this species in the highly fragmented GBMK. We define the evolutionary potential as the ability of species/populations to adapt in a changing environment by maintaining their genetic diversity. Here we review how evolutionary trap mechanisms affect the dynamics and viability of the Ganges River dolphin (GRD) populations after rapid declines in their population size and distribution. We detected six potential trap mechanisms that might affect GRD populations discretely or in combination: 1) habitat modification; 2) occurrence of finite and geographically restricted local populations; 3) ratio of effective to estimate population size; 4) increasing risk of inbreeding depression in genetically isolated groups; 5) at-risk behavioral attributes; and 6) direct fisheries-dolphin interactions. Because evolutionary traps appear most significant during low water season, they adversely affect demographic parameters, which reduce evolutionary potential. These traps have already caused local extirpation events; therefore, we recommend translocation among populations, including restoring and preserving essential habitats as immediate conservation strategies. Integrative evolutionary potential information based on demographic, genetic, and environmental data is still lacking. Thus, we identify gaps in the knowledge and suggest integrative approaches to understand the future of Ganges dolphins in South Asian waterways.

Keywords: Ganges River dolphin, evolutionary potential, freshwater species, evolutionary traps, management implications, South Asian waterways

Introduction

While many landscapes, including freshwater ecosystems, around the world are being transformed by humans at unprecedented rates, understanding the evolutionary potential of endangered species is often ignored (Moritz & Potter, 2013). South Asian rivers are under threats as almost all the surrounding countries (e.g., Nepal, India, Bangladesh, and China) scramble to harness hydropower and water extraction for expanding agrarian economies (Pereira et al., 2009). The Ganges-Brahmaputra-Meghna and Karnaphuli River Basin (GBMK; Figure 1) in Nepal, India, and Bangladesh is home to the world's most endangered freshwater river dolphin—the Ganges River dolphin (GRD). Unfortunately, several anthropogenic and natural factors jeopardize the future of this species. The dams and barrages made by the Indian government at or near the international borders (e.g., Nepal–India and India–Bangladesh) threaten GRD ecology by reducing or modifying habitats (Rahman et al., 2010). These processes present sizeable irreversible extinction risks for Ganges dolphins, similar to those that contributed to the recent human-induced extinction of the Yangtze River dolphin (Turvey et al., 2007). However, the extinction risk for GRD is poorly understood, and how small isolated groups of the Ganges dolphin will respond to novel environmental changes while maintaining genetic diversity is unknown. While habitat loss and fragmentation are the most critical documented factors (Sinha et al., 2014; Paudel et al., 2015a), a combination of several factors likely put the Ganges dolphin at risk of extinction. Different factors may act, and interact, to drive GRD populations to extinction by reducing population sizes and stability and creating downward cycles to extinction demographically. Our ability to understand the extent and potential magnitude of such threats is limited, yet essential to develop an integrative conservation strategy in a changing environmental setting.

A large number of dams and water-related projects are planned or under construction in the main reaches and tributaries of the GBMK (Verma et al., 2009). Such flow-regulating barriers (e.g., 19 hydro-power dams and 23 barrages; Figure 1) were created from the 1950s through the 1980s in the GBMK (Smith et al., 2000). Barriers not only contract the range of GRD distribution but also create small, local subpopulations, which reduces the evolutionary potential of the Ganges dolphin. Such small fragmented subpopulations with restricted gene flow are exposed to increased inbreeding and loss of genetic diversity, likely leading to higher extinction risks. Genetically isolated small sub populations of GRD have already been extirpated from some river segments in the GBMK Basin (e.g., upstream of Gandak and Sapta Koshi Rivers in Nepal). In such an intensively human-modified landscape, several evolutionary traps (i.e., an adaptive trait suddenly becomes maladaptive, leading to extinction) are more prominent and hinder the further process of GRD evolution (Schlaepfer et al., 2002; Robertson et al., 2013).

Though the Ganges dolphin is one of the most endangered cetaceans and constantly under pressure throughout the GBMK Basin, the evolutionary potential of the GRD has not yet been assessed. As the species faces severe threats of extinction, understanding evolutionary potential helps us to predict the rate of adaptation to ongoing environmental change. Our review will evaluate the genetic stability of the Ganges dolphin and its adaptation to the changing environment. Because of several threatening ecological and physiological traits [e.g., highly seasonal migration in relation to flow (Anderson, 1879); patchy distributions with finite habitat preference (BasHir et al., 2010; Paudel et al., 2015b); small litter sizes (Anderson, 1879); and solitary behavior; see details in Sinha & Kannan, 2014 for biology, ecology and conservation status of GRD], the comprehensive evaluation of GRD evolutionary potential could improve our understanding of their potential viable populations.

The few previous conservation studies of the GRD examined habitat components (Smith & Reeves, 2012; Khanal et al., 2016), feeding and foraging behaviors (Kelkar et al., 2018), and flow regimes (Choudhary et al., 2012; Khanal et al., 2016). Critically, these previous efforts did not integrate ecological, demographic, and environmental factors that might accelerate extinction risk before genetic deterioration (Lande, 1988). In response to this issue, ecological and evolutionary information is critical while predicting species extinction risks. A fifty percent reduction in global population size since the 1990s along with increasingly isolated populations exacerbates extinction risks for the endangered GRD (Braulik & Smith, 2017). Thus, an accurate account of how the Ganges dolphin responds to a changing environment is fundamental to the establishment of meaningful conservation actions, including managing reintroductions, and long-term monitoring.

In this review, we collected and analyzed demographic, behavioral, environmental, and genetic-based information in an integrative way to predict the evolutionary potential of the Ganges dolphin in South Asian waterways. We highlight possible mechanisms that could affect the dynamics and viability of GRD populations throughout their range in Nepal, India, and Bangladesh. To our knowledge, this is the first study that demonstrates the effects of genetic, demographic, and environmental factors on the evolutionary potential of small isolated subpopulations of GRD. This information could be applied to forecast the fate of endangered small cetaceans (i.e., river dolphins in south/east Asia and South America) along with developing integrative conservation management strategies for waterways they inhabit. We also identify research gaps that hinder our understanding of the Ganges dolphin evolution and ecology.

Materials and Methods

We reviewed published peer-reviewed journal articles and books related to GRD from January 1900 through December 2018 through the ‘Google Scholar’ and Thomson Reuters ‘Web of Science' databases. We refined our review by using the following keywords in different combinations: Ganges River dolphin, evolution potential, demographic, environmental process, behavior, dams/barrage, catastrophic, and genetic viability. We found 85 publications comprising journal articles (*n*=61), review articles (*n*=4), notes (*n*=2), proceedings articles (*n*=16), and book chapters (*n*=2) related to GRD population (*n*=20), biology (*n*=12), ecology (*n*=7), anthropogenic threats (*n*=12), echolocation and communication (*n*=14), phylogenetics (*n*=6), evolution (*n*=2), biochemistry (*n*=8), anatomy (*n*=3) and disease (*n*=1). We did not find publications devoted to interactive evolutionary potential of GRD; however, two partially dealt with the integrative evolutionary potential of the Ganges dolphin (Smith & Reeves, 2012; Kelkar et al., 2018).

We grouped all the potential persistence-threatening processes under six potential evolutionary trap mechanisms that might drive the evolutionary potential of the Ganges dolphin in the GBMK Basin: 1) habitat modification (change in GRD preferred hydro-physical habitat in terms of feature (e.g., pool, riffle, and run) and quality (e.g., depth and velocity)); 2) occurrence of finite and geographically restricted local populations; 3) ratio of effective to estimate population size (N_e<500); 4) increasing risk of inbreeding depression in genetically isolated groups; 5) at-risk behavioral traits; and 6) direct fisheries-dolphin interactions (Table 1). We describe and discuss each mechanism individually; however, we merged genetic mechanisms (i.e., traps #3 and #4) to present potential relationships between genetic isolation and risk of inbreeding in GRD. Because of a lack of knowledge on potential evolutionary trap mechanisms of the Ganges dolphin, we focused on identifying evolutionary trap mechanisms that represent demographic, genetic, and environmental factors and suggest future study to priorities these mechanisms and their interactive effects. We used the ratio of effective (N_e) to estimate population size (N_c) to quantify the relative rate at which genetic diversity eroded, a fundamental process of evolutionary change (Frankham, 2003). Knowledge of the relative magnitudes of these two parameters is essential to understand population persistence, mainly because N_e is generally much lower than N_c in natural populations (Frankham, 1995). Here, we estimated long-term historical N_e as an informative tool to determine the risk of population extinction assuming average ratio value (N_e/N_c) = 0.11 (Frankham, 1995). To reduce the potential risk of redundancy and to make findings more interactive, we discuss our results under four headings that cover identified evolutionary traps mechanisms: physical habitat modification, genetics, GRD behavioral ecology, and dolphin-fisheries interactions. Maps related to distribution, isolated, and extirpation segments were prepared using ArcGIS Pro 2.3.2 (ESRI Inc., 2018). We also used the Ganges dolphin natural picture from the field to support a hypothesis that we deduced from literature reviews.

Results

We found only two papers that partially incorporate the evolutionary potential of GRD in response to a changing environment. Kelkar et al. (2018) focused on adaptive capacity by combining anatomy, physiology, and morphology. Further, Smith & Reeves (2012) assessed whether the Ganges dolphin is a specialist or generalist using systematic animal taxonomy and behavioral facts to understand their adaption in a human-modified landscape. Our review of potential mechanisms that might hinder the evolutionary potential of the Ganges dolphin is defined in detail below.

Habitat modification

When habitat was modified, we noticed local extirpation and spatial disequilibrium of isolated subpopulations of GRD increased (Sinha & Kannan, 2014; Paudel et al., 2015b). Aquatic animals have adapted to existing cycles of silt, nutrients, and discharge. Land use strongly influences the habitat quality of streams and rivers (Allan, 2004). Therefore, a dramatic transformation of landforms into human uses, together with tripling human population size, in South Asia might alter the hydro-physical habitats in South Asian waterways (Richards & Flint, 1994). With such massive land transformation and increased social pressure, presumably characteristics of mesohabitats available in the GBMK Basin change through alterations of the magnitude of discharge, pollution, sedimentation, and riparian attributes. As a result, foraging grounds and migratory pathways might block, fragment, or destroy the Ganges dolphin populations (Dudgeon, 2000). This further exacerbates ongoing GRD isolation and habitat fragmentation in the GBMK Basin. We identified six extirpated populations in various rivers segments (Table 3)—an 18% reduction in the global distribution range of the GRD—and nine geographically isolated small groups (with the possibility of connectivity) that might have resulted from this trapping mechanism (Table 4).

Water pollution due to land transformation might also adversely affect the health of the Ganges dolphin populations. GRD's cannot adequately metabolize contaminants (Senthilkumar et al., 1999), and might suffer from skin, reproductive, and immunological diseases from water pollution (Helle, 1976; Kannan et al., 1993; Colborn, 1996; Acevedo-Whitehouse & Duffus, 2009; Van Bressem et al., 2009). We observed several instances of skin lesions (e.g., a circular scar on the back, long scars on the abdomen, cross-hatch like scars on the dorsal ridge and dorsal fins) in most animals sighted below the Sapta Koshi Barrage in Nepal (Figure 3; personal observation). Furthermore, Senthilkumar et al. (1999) linked a reduction in abundance of the GRD in the Ganges River to a higher level of contamination (e.g., DDTs and PCBs). Similarly, Behera et al. (2013) also found pollution as a cause of local extirpation in the middle Ganges River (between Kachlaghat and Kanpur) of India.

Development of finite and geographically restricted local populations

We identified various water development projects in the GBMK Basin (Nepal=8; India=42; Bangladesh=16; Figures 1 & 2) that affect rivers historically or currently supporting the Ganges dolphins. These large structures across rivers have contributed to local extinction and genetically isolated small local populations of GRDs with small geographic ranges in the GBMK Basin. We found four genetically restricted subgroups in Nepal and India with small effective geographic ranges, and possibly unidirectional movements (Figure 2; Table 2). Higher effects of fragmentation occur in the major tributaries (e.g., Nepal and India) of the Ganges River compared to rivers in Bangladesh (Smith et al., 2000; Sinha & Kannan, 2014). For example, the Girijapuri Dam located 20 km below the Nepal/India border in the Karnali River of Nepal offers less than 30 km of effective upstream habitat, with a sub-population size smaller than 50 individuals. Out of 5,317 total km of available stream habitat in the GBMK, the GRD was completely extirpated from 18%. Further, we found nine naturally isolated subpopulations (possibility of inter-connectivity depends on water level), with group sizes smaller than 20 individuals (Table 4, Figure 1; Sinha et al., 2014). These subgroups localized in a limited area of the river segment because of the non-linear hydro-physical habitat.

The ratio of effective to estimate population size and increasing risk of inbreeding depression

Roxburgh (1801) made the first documentation about the Ganges dolphin. Then Anderson (1878) reported on the distributional range, morphology, and anatomy of this species. Approximately 100 years later, only a few papers offered further details on the population status of the GRD (Jones, 1978; Lal Mohan, 1989). Its global population size was estimated to be 4,000–5,000 in the GBMK Basin (Jones, 1978). The species had declined to 3,526 in 2014 (Sinha & Kannan, 2014), indicating a 30% loss in four generations (assuming a nine-year generation rate). We estimated N_e of 550 with an estimate size of 5,000 for the year of 1982 (Jones, 1978) and 388 for 2014 (Sinha & Kannan, 2014). This value reveals that the GRD is suffering from insufficient effective population sizes (N_e<500) required to maintain viable genetic diversity (Franklin, 1980). Because of such a small current N_e ($\leq$ 500) and fragmented into isolated small subpopulations, inbreeding depression could be the most immediate and significant hindrance to the evolutionary potential of the Ganges dolphin (Vilas et al., 2006).

At-risk behavioral traits

The GBMK Basin undergoes seasonal flow patterns that define and inhibit access of GRDs to particular foraging or surfacing grounds. The GBMK's natural flow regime provides GRDs cues to migrate, reproduce, forage, etc.; thus, the rhythm of the river is tied intimately to the functional ecology of this animal. In the context of rapidly changing environmental settings, such GRD dependence on water level could be maladaptive. An inability to adapt to these changes not only subjects GRD to an evolutionary trap but also reduces their evolutionary potential by affecting their important life-history stages (e.g., resting period, preparation for reproduction period). At risk behavioral activities (e.g., habitat specialization) in combination with different biological traits, such as small litter size, late sexual maturity, and long gestation period, might also reduce persistence of the Ganges dolphin (Purvis et al., 2000). The surfacing and foraging behavior of Ganges dolphins are mostly confined to deep pools and eddies, which provide critical shelter and large prey species (Paudel et al., 2015 a & b). Because of such habitat sensitivity (e.g., selection of vertical water column and water velocity; Dudgeon, 2000), the Ganges dolphins may hinder their evolutionary potential by reduction of genetic diversity.

Fisheries-dolphin interactions

Increasing pressure from artisanal fisheries heightens the potential for river dolphin and fisheries interactions, mainly through direct competition for certain fish size-classes as well as habitat and diel activity overlap. Conflicts between Ganges dolphins and artisanal fishing increased dramatically in recent years across the GBMK Basin (Kelkar et al., 2010; Paudel et al., 2016; Kelkar et al., 2018). Although bycatch data was not available for the Ganges dolphin, this is considered one of the prime consequences of the direct fisheries-dolphin interaction (Read, 2008), which further threatens their survivorship of GRDs, especially young calves. For example, two young calves (< 20 kg) entangled in a gillnet in the Sapta Koshi River of Nepal between 2013 and 2015 (Paudel, 2017).

Discussion

Physical habitat modification

Altering natural streamflow imperils native biodiversity and increases freshwater functional complexity (Dudgeon, 2000). Given that GRDs show a strong preference for particular habitats, the presence of small finite GRD groups with limited geographic range indicates that they are under severe risk of habitat loss and fragmentation (Fahrig, 1997). Although there is a lack of research quantifying and characterizing the Ganges dolphin breeding habitats, studies of closely related species suggest that loss of suitable hydro-physical habitats (e.g., required depth) might affect GRDs indirectly by reducing or eliminating their reproductive success (Robinson et al., 1992). For example, the presence of suitable habitats (e.g., water depth) significantly predicts female reproductive success in bottlenose dolphins (Mann et al., 2000). To improve survival prospects of the Ganges dolphin, we must, therefore, identify suitable hydro-physical habitats that contribute to its demographic processes, and increase efforts to reduce habitat loss. Since the 1990s, researchers have recommended conservation efforts that focus on recovering declining populations in their natural habitats (e.g., Smith, 1993), yet efforts to date have failed to make an impact. Instead, local extinction rates and isolated small population groups have increased (Table 2 & 4), mostly in the upstream range of the Ganges River. Among all the groups, the Nepalese subpopulations size is too small to support long-term viability (Paudel et al., 2015a). Because of the heightened risks in such small isolated groups, these subgroups need an immediate effective conservation plan. The need of effective conservation plans for such small isolated populations is clearly illustrated by the recent conservation status of small cetaceans like the Hector’s dolphin (*Cephalorhynchus hectori*) in New Zealand, the Indo-Pacific humpback dolphin (*Sousa chinensis*) in Taiwan and Hong Kong, and the Irrawaddy dolphin (*Orcaella brevirostris*) in Asia (Cagnazzi et al., 2013). Even though the Indian government declared the Ganges dolphin as the national aquatic animal (Sinha et al., 2014) and formulated the Conservation Action Plan for the Ganges dolphin (2010-2020), structures made by the Indian government at international borders have highly modified the environmental structure of the GBMK, thus threatening the same species they declared important. Despite several initiated river dolphin-based conservation projects (e.g., Vikramshila Gangetic Dolphin Sanctuary, Bhagalpur District of Bihar, India; WCS dolphin conservation project in Bangladesh), our findings suggest more science-driven regional level conservation initiatives are needed.

Although the loss of the Ganges dolphin is largely attributed to dams/water based development structures, we clearly noticed evidence of population increase in some segments, such as between Bijnor (middle Ganges Dam) and Narora (lower Ganges Dam) (Sinha & Kannan, 2014). This implies that effects of fragmentation by dam/barrage are trivial in comparison to the effects of habitat loss (Fahrig, 1997). However, wildlife managers and policymakers often overlook the issue of the quality and quantity of the foraging habitats that influence the GRD's reproductive success between barriers. While the reproduction only occurs in suitable foraging grounds, it is also imperative to determine the minimum amount of habitat that needs to be preserved to allow for the persistence of the GRD. The combination of needs for both reproduction and persistence means that maintenance of habitat quality is critical for the long term survival of the Ganges dolphin. Based on the increased Ganges dolphin population size between dams, further study is warranted because the effects of large water-based structures, like dams, could be minimal if we sustain the required water levels that allow animal movement and reproduction between barriers. This review stressed that barriers (e.g., dams/barrage) are not a single cause but rather an interaction of multiple issues (e.g., flow release plan, fisheries-dolphin interactions) causing the Ganges dolphin declines. Additional systematic studies that integrate habitat quality assessment, population census, and a genetic approach could support our findings.

Genetic

The most notable barrage is the Farakka Barrage, which divides the global population of GRDs at approximately the center of their geographical range, making several regional subpopulations. The Girija, Gandak, upper Sharda, and Koshi Barrage further isolate dolphin populations in their furthest upstream range in Nepal, in which some groups already became extirpated. Because of weak selective pressure in small and isolated populations, animals might tolerate inbreeding despite the cost (Rioux-Paquette et al., 2010). Since the aquatic mammals are sensitive to the effects of dams (Wu et al., 2004), the questionably viable subpopulations in a limited geographic range (Tables 2 & 3; Figures 1 & 2) are more prone to immediate extinction. This occurs in different ways that ruin genetic diversity (e.g., inbreeding depression, and reduction of genetic variability) and reduce the fitness of the population overall. The addition of each new dam further fuels the fragmentation of habitat and development of small local subpopulations. In such scenarios, where genetic heterozygosity declines and inbreeding increases, the risk of GRD local extinctions seems inevitable. Since species extinctions proceed more rapidly in freshwater than terrestrial environments (Ricciardi & Rasmussen, 1999), we expect to find many small local subpopulations and continued extirpation in the future. However, the rates of decreasing genetic diversity and increasing inbreeding are still unknown and should be further studied.

As demographic and environmental stochasticity drive small populations to extinction before genetic erosion (Lande, 1988), recent local extinction of subpopulations from certain regions, and an increase in questionably viable subpopulations might be attributed to demographics (e.g., fluctuation in population size) and environmental factors. Presently, GRDs might not face immediate extinction but are under imminent risks. They might suffer from the gradual depletion of genetic diversity, inbreeding within local groups, and reduced fitness. The declining pattern of N_e eventually reduces the ability of the Ganges dolphin to adapt to novel environmental threats. This pattern can be used to predict the rate of adaptation of the GRD in the South Asian rivers, but we acknowledge this as uncharted territory in the prospects of evolutionary potential. It is true that relying exclusively on estimate data for estimating effective population size might underestimate N_e value. However, estimate data as a proxy to determine cues of genetic loss or extinction risk could be a reasonable option to interpret population health in data crises in regions like the GBMK Basin. Curtailing the decline of N_e is critical for the conservation of this endangered species and thus it could be useful to urge concerned authorities in South Asia. In particular, the most striking finding of this analysis is the declining and inadequate N_e of GRD populations. Effective population size can be depressed due to fluctuation in population size, including a variety of biological traits, such as high endemism, long gestation period, small litter size, unequal sex ratio, and variance in group size (Jones, 1978; Frankham, 2003). Further, N_e is likely to reduce decrease in such small local subpopulations with short geographic range by limited access to suitable foraging sites that may influence the reproductive success of the GRD. As a consequence, the number of individuals contributing to reproduction may be less than predicted.

A vital population management implication of low and declining N_e populations is that substantial population sizes are required for long-term maintenance of genetic variation (Frankham, 1995). Conservation actions may take the form of more benign environments or managing dolphins to increase reproduction and survival. If heterozygosity loss is capped at 5% or less in the next 50 years, hope to sustain GRD populations still exists. The relatively small and isolated GRD subpopulations may require individual translocation among subpopulations to maintain genetic variation. Also, human interventions (e.g., habitat management or preservation activities) to ensure their survival and reproduction with sufficient water level at the proper time (e.g., December-April, peak breeding period) are urgently required. Jones (1975) suggested a similar management approach, the translocation of animals to the Chambal and Rihand tributaries of the Ganges River in India. Smith (1993) also stressed habitat intervention along the stretch of Karnali River (below the Chisapani Bridge) to manage the remaining questionably viable population to prevent its extinction.

GRD behavioral ecology

Long term persistence of specialist species has been adversely affected by current global and local environmental changes (Clavel et al., 2010). During the past decades, several studies revealed declines in specialist mammals (e.g., Fisher et al., 2003). Given that the GRD is more specialized in its circadian rhythms concerning habitat selection (e.g., depth profile selection for reproduction and foraging), human impacts to its habitat may are likely to affect these use patterns that might in turn affect their functional ecology and important life-history stages. Hydrological cues highly guide GRD functional activities, like locating prey species and reproductive success, which particularly affect functional ecology of the Ganges dolphin (Smith & Reeves, 2012). Further, the Ganges dolphin adopts seasonal movement patterns between the mainstream and tributaries using a cyclic range of water levels. For instance, presence of high-water flow in the mainstream reach stimulates GRDs to migrate to other tributaries (Paudel et al., 2015b). In certain instances, water regulation by anthropogenic structures (e.g., hydropower dams or development structures) could falsely present as an environmental cue, rendering these evolutionary responses maladaptive. Such evolutionary traps could be more effectively studied in certain locations (e.g., seasonal migration patterns to the Mohana tributary of the Karnali River of Nepal, and habitat occupancy below the Sapta Koshi Barrage). Further, Braulik et al. (2015) found low mtDNA variability in GRDs, indicating habitat-specific behavior or more localized occupancy behaviors might further contribute to the loss of genetic diversity. However, they argued that this could be the result of interactive effects of low population sizes and localized sensitive behaviors. Using different behavioral strategies adopted by the Ganges dolphin, in combination with extinction-promoting traits, presumably, render Ganges dolphins species extremely vulnerable to extinction.

Human-dolphin conflicts

Interactions between artisanal fisheries and the Ganges dolphin is one of the most significant conservation concerns in the GBMK Basin, leading to endangerment and extinction (Read, 2008). The recent extinction of the baiji (*Lipotes vexillifer*), a freshwater dolphin endemic to the Yangtze River, China, showcases how such interactions can cause dramatic declines (Turvey et al., 2007). Unsustainable by-catch in local fisheries attributed to the loss of baiji. Similarly, the vaquita (*Phocoena sinus*) with less than 30 individuals, and 95 Indus River dolphins (*Platanista gangetica minor*) in Pakistan killed in a fishing gear between 1993 and 2012 were all associated with human-dolphin interactions (Jefferson, 2019). Dietary and diel activity, and spatial and temporal overlap with fisheries could be the reasons for Ganges dolphin endangerment associated with fisheries (Read, 2008). Thus, interactions between the Ganges dolphin and subsistence fisheries is a serious and growing problem, and effective management requires an assessment of the factors driving these interactions. Quantitative and qualitative documentation of drivers (e.g., dietary competition, spatial overlap, behavioral distractions, etc.) that lead to negative fisheries-river dolphin interactions could help better manage and promote co-existence between fisheries and river dolphins.

Future management implications

Because of conservative policies and limitation of resources, there currently exists a void in the application of genetic tools to explore the population viability of the Ganges dolphin in the GBMK Basin. Initiating a regional inter-governmental project promoting genetic-based research to examine genetic viability and factors associated with the risk of extinction is essential. As the Ganges dolphin is facing serious population loss issues, use of non-invasive tools, like environmental DNA (eDNA), for genetic monitoring might be effective (Foote et al., 2012). But understanding the viability of such a tool is imperative before its application. Conservation projects that build transboundary cooperative mechanisms (e.g., joint venture conservation initiatives among countries) on upstream tributaries of the Ganges and Brahmaputra rivers could promote restoration of the GRD hydro-physical habitat. Nepalese and Indian (Uttar Pradesh) authorities should not wait for critical situations, learning from the extinction lessons of the Indus River dolphin (*Platanista gangetica minor*) and Yangtze River dolphin (*Lipotes vexillifer*). Since we noticed a large fluctuation in population size, we emphasize the importance of understanding this fluctuation effects on demographic structure, which might produce a minimal value of the ratio of effective to census population size. Because of weak selective pressure in a small and isolated population, GRD subpopulations might be severely affected by the risk of inbreeding and thus could exhibit a unique genetic structure. Using modern gene sequencing methods would improve our ability to test articulated assumptions we made in this article (for example, Parsons et al., 2002). We suggest the integration of genetic data with census data to predict more accurate population trends of the Ganges dolphin. If we have a better population genetic knowledge, we could develop appropriate “genetic rescue” to recover this declining species into its natural habitat. At this point, one potential “genetic rescue” tool to improve genetic stability could be translocation of individuals among subpopulations by developing proper capture and handling techniques (Krutzen et al. 2018).

From a conservation perspective, our findings imply that making extinction predictions from a single ecological factor may be risky because of synergistic effects of several factors. Thus, we highlight the integration of genetics, demographics and environmental factors in future studies, which can aid future research and provide a better understanding of conservation and management purposes. In general, isolated, small subpopulations warrant immediate conservation attention, regionally and internationally. Maintenance of minimum stream flow and restoration and preservation of essential foraging and surfacing habitats appear to be the best methods to limit or prevent any further declines of the GRD.

Conclusions

The evolutionary potential of the Ganges dolphin in the GBMK Basin may be hindered by several mechanisms like spatial and genetic isolation, small N_e group size, risky behavioral activities, direct dolphin-fisheries interaction, and habitat modification. As an interactive function of these different mechanisms, we note the reduced evolutionary potential of the GRD in the fragmented South Asian waterways as GRDs are vulnerable to changing environments. Despite this, recent research mostly focuses on discrete conservation issues, and science-based integrative knowledge of GRD evolutionary potential remains limited. Populations with such spatial disequilibrium can have significant ecological and evolutionary outcomes. Therefore, integration of robust genetic and novel population data, merged with historical information, could significantly aid the trajectory of future GRD evolutionary potential. We recommend an integrative approach of demographic, genetic, and environmental aspects, an essential combination to improve our understanding of the future of this charismatic species in the GBMK Basin.

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Data Accessibility Statement

The authors declare that all data supporting the findings of this study are available within the article (Tables 2, 3 and 4).

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Table 1. 1 The different mechanisms and their associated processes, and types of mechanism that might affect the dynamics and viability of the Ganges River dolphin (GRD). Based on the animal sensitivity to the mechanism, scaled persistence was assigned to each mechanism involved. (Type of mechanism: E-environmental; A-anthropogenic; D-demographic; G-genetic; B-behavioral; I-intrinsic)

Mechanisms thought to drive evolutionary potential	**Type**	**Processes that might affect the dynamics and viability of GRD**	**Persistence scale of species**
Habitat (or quality) modification	E/A	Because of high tropic level, dolphins migrate to their preferred environmental optima or adapt *in situ* to avoid extinction. Resulting extirpation or local small groups of population	low
Occurrence of finite and geographically restricted local populations	A	Increase homozygosity and the expression of deleterious recessive alleles; loss of allelic diversity at functional genes and thus, increase risk of inbreeding	low
Ratio of effective to estimate population size (<500)	D/G	Increase risks of inbreeding and genetic drift affecting the adaptive potential of species	low
Risk of inbreeding in small local populations	G	50% reduction of population size over 3 generations; loss of genetic diversity in small populations reduce the ability of population to evolve with environmental change, as genetic diversity acts as raw materials for adaptive evolutionary	low
At-risk behavioral attributes (including biological attributes)	B/I	Adaptive behaviors can become maladaptive in the new setting and eventually caught in an evolutionary trap. Rates at which behaviors realign themselves after being caught in a trap depend on the strength of selection imposed by the trap and the degree to which the behaviors are phenotypically plastic. Looking at localized habitat preference, taking water level as cues, non-gregarious trait, fish removal from gillnet	variable

		could reduce potential persistence scale.	
Increased fisheries-dolphin interaction	A	Increase mortality rate reduce the potential of evolution by increasing the cost of survivorship	variable

Table 1.2 Locations of genetically isolated groups of GRDs in the GBMK River Basin with their group size. The dams/barrages isolate these groups.

Country	Location of isolated group	Estimated Group size
India	Between middle and lower Ganga Barrage	56
	Between Bicchi in Madhya Pradesh to Banjari in Bihar	10
Nepal	Above Gandak Barrage	2
	Above Girijapuri Barrage in India to upstream Nepal	50-60

Table 1.3 Details of complete populations' extirpated segments in the GBMK River Basin with their length size.

Country	Location of population's extirpated segment	Length (km)
India	Between Haridwar and middle Ganga Barrage	100
	Lower Ganga Barrage to Kanpur	358
	Sone River to its confluence with Ganga	300
	Sharda River	100
Nepal	Upstream Mahakali River from Sharda Barrage	40
	Upstream from Sapta Koshi Barrage	49

Table 1.4 Questionably viable groups in the GBMK River Basin that require immediate conservation action with their populations size. These groups were isolated either by the effect of dams (water extraction effect in the downstream) or naturally reduced habitat (low water level, mainly in the upstream tributaries of the Ganges River) and are reported historically from the region as localized population.

Country	Location/river segment	Length (km)	Estimated population size in a river segment
India	Rapti River	20	8
	Surya River	22	16
	Between Bicchi in Madhya Pradesh to Banjari	130	10
	Ken River (to Yamuna and Sindhan confluence)	30	8
	Betwa (confluence with Yamuna to Orai)	84	6
	Sind (confluence with Yamuna to 110 Km upstream)	110	5
	Rupnarayan (Gadiara to Mankar)	424	18
	Kulsi (from Gharamara to its confluence with the Brahmaputra at Nagarbera)	76	17
Nepal	Narayani (above Gandak Barrage)	85	2

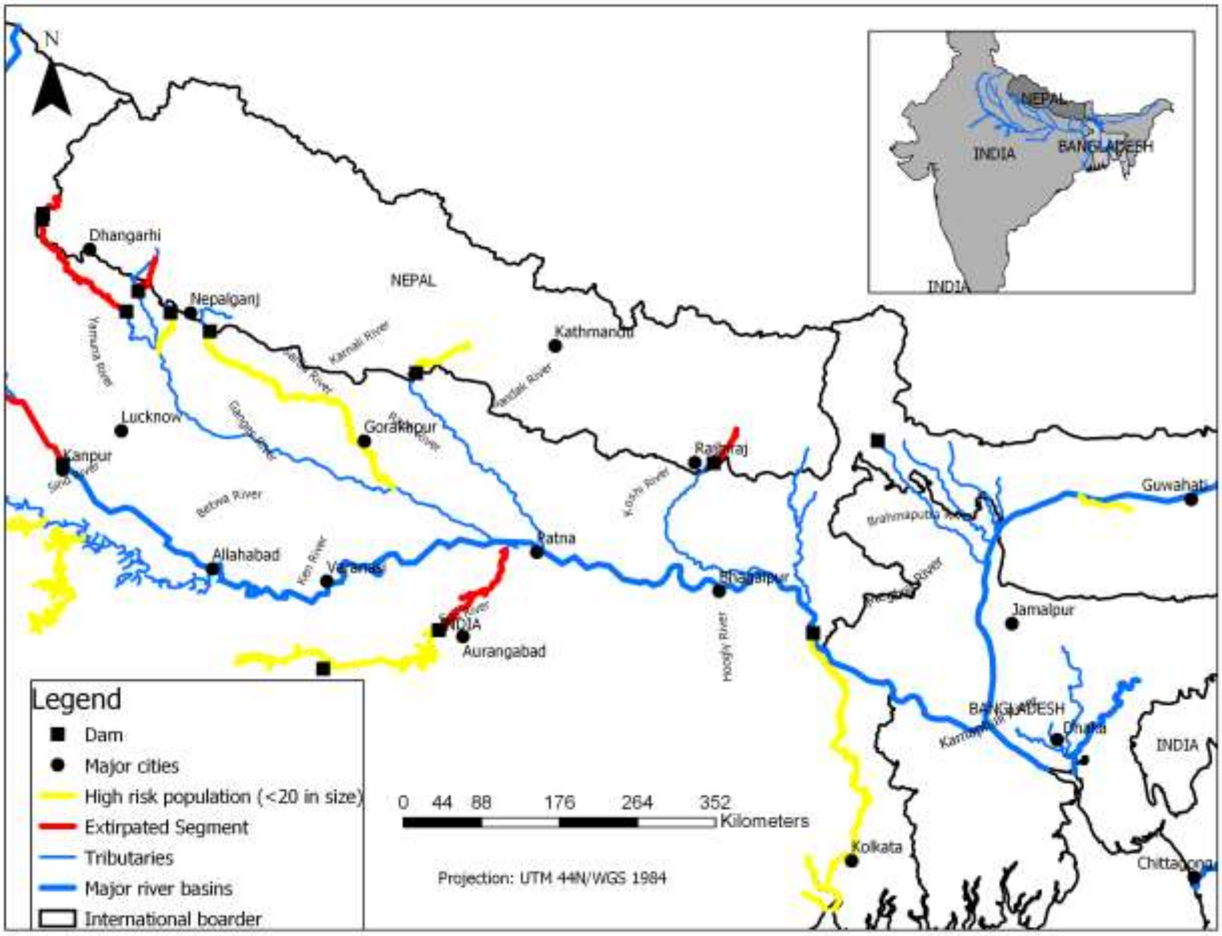

Figure 1.1 The Ganges-Brahmaputra-Meghna and Karnaphuli (GBMK) Basin in South Asia showing the river dolphin distribution river networks and location of major dams that isolated the dolphin groups. Most of the dams are located at the border between countries resulting in high-risk small groups. For the last couple of years, around 20% of the habitat was reduced because of these dams. Yellow color indicates the river segment with high risk subpopulations (<20 population size) and red depicts segments with the extirpated population.

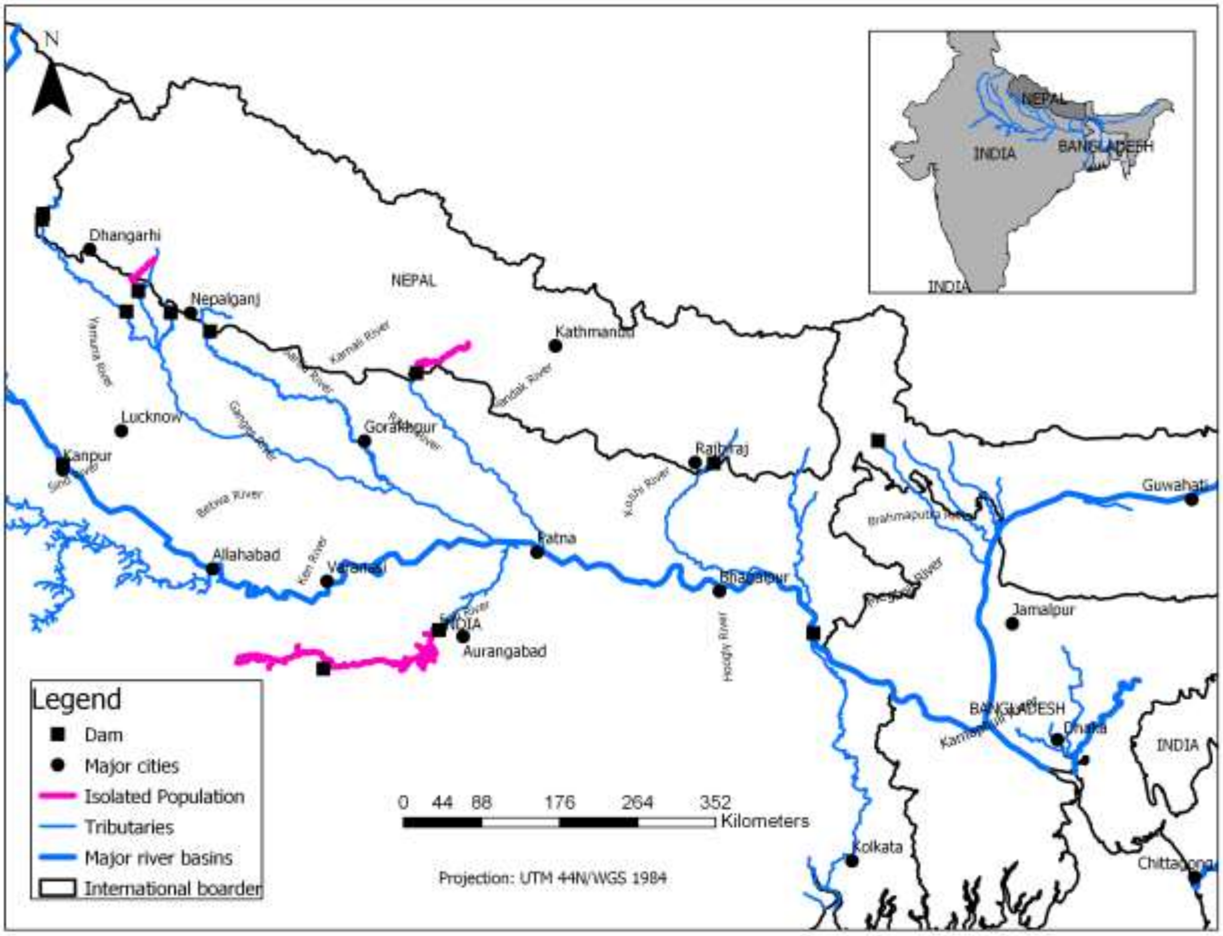

Figure 1.2 Genetically isolated groups (which might overlap with high risk groups) of Ganges dolphins by dams/barrages in Nepal and India rivers' segments. Because of dams, there is an assumption of unidirectional movement (downstream only) of dolphins in the GBMK Basin. As a result, dolphins in the upstream tributaries are more sensitive, and as result most extirpated segments were reported only from the upstream of the Ganges.

Figure 1.3 Skin lesions recorded on the GRD below Sapta Koshi Barrage in Nepal. Highly fluctuating hydro-physical properties and acute interaction with fishing nets might be the reasons that increase dolphins’ susceptibility to skin-related disease.

APPENDIX B: ECOLOGICAL RESPONSES TO FLOW VARIATION INFORM RIVER DOLPHINS CONSERVATION

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(Submitted to *Nature Scientific Reports*)

Ecological responses to flow variation inform river dolphin conservation

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Running title: *ecological responses to flow alternations*

Abstract

Many environmental flow (e-flow) studies and applications have predominantly used state- (i.e., at a single time point) and rate- (i.e., temporal change) based demographic characteristics of species representing lower trophic levels (e.g., fish communities) to build flow-ecology relationships, rather than using a process that incorporates population dynamics. Recent studies have revealed the importance of incorporating data on species traits when building flow-ecology relationships. The effects of flow on keystone megafauna species (i.e., body mass ≥30 kg) reverberate through entire food webs; however, the relationships between flow and these species are not well understood, limiting the scope of the relationships used in flow management. Here, we fill this gap by incorporating the habitat selection traits at different flows of a freshwater apex predator, Ganges River dolphin (GRD, *Platanista gangetica gangetica*), which plays a significant role in maintaining the structure, functions and integrity of the aquatic ecosystem. Using temporally and spatially measured GRD habitat selection traits, we quantified flow-ecology responses in the Karnali River of Nepal during the low-flow season when habitat was heavily reduced and water demand was highest. We define ecological responses as suitable habitat templates with enough usable surface area to support GRD fitness by improving reproduction and survival. We measured the available and occupied habitats to develop flow-ecology responses. Variation in flow resulted in substantial differences in the ecological response across time and space, suggesting that aquatic species adjusted in a variety of habitats to support their life histories and maintain viable populations. The limited availability of suitable habitats combined with uninformed water regulations by humans likely places GRDs under severe physiological stress during low-water seasons (i.e., January–April), suggesting that critical flows contribute to the process of endangering and extirpating highly sensitive endemic aquatic biodiversity. Our study reveals that ad hoc or experience-based flow management is no longer tenable to maintain the integrity and functionality of aquatic ecosystems. We stress that quantifying the flow-ecology relationships of foundational species, particularly megafauna, in response to flow variation is crucial for monitoring the effects of water alterations and determining the minimum flows needed for maintaining healthy and functional freshwater ecosystems in the Anthropocene.

Keywords: Ganges River dolphin, flow alteration, ecological responses, hydro-physical habitats, freshwater ecosystem, South Asian waterways, environmental flow

Introduction

Functionally intact and biologically complex freshwater ecosystems play a critical role in nature and have long-term benefits to society, especially in the Anthropocene [1]. However, hydrological alteration is threatening freshwater ecosystems and their native biotic inhabitants faster than they can be restored [2]. Such modifications affect ecosystems and their aquatic biota in many ways, including having effects on physical habitat, life history, and lateral and longitudinal connectivity [3]. Preserving a freshwater ecosystem's natural flow regime, in terms of quantity, quality, and seasonality, is essential to protect native biota and environmental processes. Hence, understanding how variation in natural flow drives ecological processes can provide a scientific basis for protecting and maintaining aquatic ecosystems when establishing the appropriate balance between societal and ecosystem needs. For this reason, flow-ecology relationships are globally recognized as a means by which freshwater ecosystems' integrity and dynamic potential can be protected and maintained [3,4,5,6].

The biodiversity of native aquatic species is better maintained in streams in which flow regimes are the most natural [2]. As earth's larger rivers are obstructed with approximately >40000 large dams [7], the effects of infrastructure on freshwater native biodiversity have been extreme [8]. Previous broad-scale freshwater research focused on the environmental and social consequences of flow variation [9], but recent studies have emphasized empirical ecology-flow relationships to ensure the sustainability of aquatic ecosystems [10,11]. Previously, e-flow studies and applications relied heavily on regime-averaged metrics (mean seasonal flow characteristics) to explain changes in ecosystem state variables (abundance of species). However, scientists have suggested greater adoption of ecological responses related to process-based (processes contributing to population size) and species traits (e.g., habitat selection traits to improve species fitness) that are rooted in a strong ecological foundation [11,12,13,14]. A recent study described these approaches broadly and stressed the importance of performing repeated measurements of ecological responses over time, focusing on reactions that can be linked directly or indirectly to demographic processes [12].

Flow-ecology relationships can be developed for local or regional scales. Previous studies have typically developed flow-ecology relationships using lower trophic species, such as small fishes and riparian plants, limiting their scope of application. Such relationships might not indicate the full integrity of ecosystems, because megafauna require diverse habitats and are often sensitive to natural flow regimes across a considerable geographic scale. Past studies have often overlooked the essential ecological roles and functions of freshwater megafauna (i.e., body mass ≥30 kg; [15]), which help to develop relationships that are transferrable to regional landscapes. The presence of native freshwater megafauna is associated with high native organism biodiversity, and megafauna share common threats with small freshwater species [15]. For these reasons, megafauna-based strategies could potentially maintain key processes and relationships that are robust and able to persist under the anticipated changes in social and environmental conditions [15,16].

Further, selecting appropriate ecological response variables is key to understanding flow-ecology relationships. Identification of demographic process(es) that strongly influence population dynamics is integral to defining the nature and applicability of relationships [13]. To this point, flow-ecology relationships have generally been developed using multi-species fish models, with the rate of change in species richness as an ecological response [12]. These models overlooked potential trait-based approaches that support ecosystem integrity by maintaining natural flow variability across temporal scales. Further, freshwater megafauna also declined by 88% between 1970 and 2012, which was attributed to habitat loss—the primary response to flow alteration changes in habitats [15]. In this paper, we build flow-ecology relationships, assuming associations between reproduction and habitat use, in which habitats with enough usable area act as a template for the reproductive success of species [17].

Our flow-ecology relationships assume that the GRD, as a freshwater apex predator, is a foundational umbrella species of South Asian aquatic ecosystems (detail ecology, biology and distribution of GRD is available in [18]). If this key species is reduced or extirpated, trophic pathways will change drastically (i.e., there will be higher order effects), and the total ecosystem productivity will decrease [19]. Here, we examine flow-ecology relationships in the Karnali River system of Nepal, a large tributary of the Ganges River in India, by linking GRD ecological responses to flow variation during the low-water season, when hydro-physical habitat is a limiting factor. As a native to South Asian river systems, GRD is distributed from the mouth of Ganges (main river) in India to the foothills of the Himalaya in Nepal. Because of its long-life span and trophic position, the GRD exhibits heterogeneous traits across multiple habitat scales and in critical life-history stages. As a result, the GRD's status as a keystone predator indicates that it could be a potential bio-indicator for assessing the health of the aquatic system [20,21,22,23]. The GRD uses a variety of aquatic habitats across diverse velocities and depths, comprised of stable hydro-physical habitats and eddy counter-currents that trap nutrients and woody debris, thereby enhancing nutrient deposition and aquatic diversity [24]. In line with this hypothesis, GRD habitat-use traits could influence the demographic processes of other aquatic species, and conserving critical habitats of the GRD could improve species diversity and maintain important resources for the rest of the community [25].

To develop flow-ecology relationships using GRD habitat selection traits, we first examined GRD habitat selectivity (disproportionately selected habitats) across space and time to develop a habitat suitability curve (HSC) based on data of occupied and available areas. Typically, suitable habitat is estimated based on how often species use a particular habitat across time and space, and it is assumed that such habitats are used by species to maximize their fitness. Developing flow-ecology responses based on apex predator habitat selection traits could be useful for water-resource managers, who are commonly tasked with balancing multiple competing socioeconomic and conservation priorities. Further, by considering the requirements of an apex predator, this research offers generalizable flow-ecology relationships that aid the formulation of flow management guidelines applicable across regional scales that share common species diversity and geomorphic characteristics. This enables the protection of diverse habitats and taxonomic groups by avoiding the risk of crossing ecological thresholds that threaten endemic aquatic biodiversity.

Results

GRD detection based on depth and the velocity of the flow

The mean depth of the habitat used was higher in December (mean=2.119 m, SD=0.858; preferred range=3.5-4.2 m, *w*=1.71, SE (*w*) =0.13) than in March (mean=1.953 m, SD=0.569;

preferred range=6.3-7 m, *w*= 1.9, SE (*w*)=0.6) or May (mean=1.620 m, SD=0.324; preferred range=4.9-5.6 m, *w*=9.22, SE (*w*)=1.62) [Figure 2]. However, we noticed higher water velocity in the habitat used for May (mean=0.934 m/s, SD=0.330; preferred range=0-0.3 m/s, *w*=1.67, SE(*w*)=0.13) than for December (mean= 0.840, SD=0.228; preferred range=0.6-0.9 m/s, *w*=1.9, SE(*w*)=0.6) or March (mean=0.788, SD=0.292; preferred range=1.8-2.1 m/s, *w*= 3.62, SE(*w*)=0.47) [Figure 2]. The model that best predicted the presence of GRD contained the additive effect of depth and velocity [Model 1: depth (AIC=4665.5, R^2=0.02), Model 2: velocity (AIC=4637.2, R^2=0.03), Model 3: depth*velocity (AIC=4560.8, R^2=0.062), and Model 4: depth+velocity (AIC=4559.1, R^2=0.061)]. We noticed a significant impact of both depth (GLM, β=1.370, SE=0.036, Z= 8.671, P< 0.001) and velocity (GLM, β= -0.454, SE=0.077, Z = -10.114, P< 0.001) on the presence of the GRDs. Depths >2 m had a substantial positive effect on the presence of GRD (Figure 3). Even though velocity and GRD presence had an inverse relationship, velocities < 1 m/s had a positive effect; velocities greater than 1 m/s had substantial negative effects (Figure 3).

The effect of flow fluctuations on hydraulic habitat availability

The mean AWS (suitable physical habitat templates as a function of depth and velocity at particular geomorphologies that offer enough usable surface area to support GRD fitness) recorded in December was higher (24.531 m^2/m, SD= 29.193, Figure 4) than that in March (17.220 m^2/m, SD= 18.759) or May (13.253 m^2/m, SD= 29.379). The upstream mean AWS (31.330 m^2/m, SD=39.401) was higher than that of the midstream (12.884 m^2/m, SD=18.755) or downstream segments (20.095 m^2/m, SD=18.801, Figure 4). No significant difference in the average AWS among seasons was observed (ANOVA, F (2,174) =2.832, P=0.0616). However, we noticed substantial variation in the average AWS by segment (ANOVA, F (2, 174) = 7.899, P<0.0001, df=2).

Fluctuations of 10%, 20%, 40%, and 60% in the current base flow (536.11 m^3/s) resulted in AWS losses of 2.076 m^2/m (9% loss of the base flow's AWS), 3.538 m^2/m (15% loss of the base flow's AWS), 6.191 m^2/m (26% loss of the base flow's AWS), and 11.998 m^2/m (50% loss of the base flow's AWS), respectively (Table 1). For the retention of 80% and 65% of the GRD habitats (or AWS), minimum flows of 383.967 m^3/s and 348.51 m^3/s, respectively, are required (Figure 5, Table 2).

Quantifying flow-ecology relationships to determine flow regimes

The GAM models based on AWS velocity and AWS depth explained deviances of 45.7% (R^2= 0.502) and 38.1% (R^2=0.458), respectively, with significance of the smooth term (velocity: edf=6, F= 12.69, $P<0.001$; depth: edf= 16.33, F=7.079, $P<0.001$). Our AWS-flow GAM model explained only 35.6% (R^2=0.431) of the deviance but had a significant predictor smoothing term (flow: edf=10.04, F=2.954, P= 0.0361). All of the predictors were found to have smoothing terms significantly different from zero ($P<0.005$) and thus contributed to the model fit of the AWS. All the models exhibit a non-linear relationship, showing positive and negative biological responses to flows, depth, and velocities. Flow <200 m^3/s had a negative influence on the AWS. Although flows ranging from 210–230 m^3/s, 280–350 m^3/s, and 400–417 m^3/s contributed positively to the AWS, they might not be proportionally supportive, as they are close to the zero-effect line (Figure 6). Flows between 351 and 389 m^3/s had the greatest positive impact on the estimated AWS. Therefore, we recommended flow ranges <200 m^3/s, from 210–230 m^3/s, from 280–350 m^3/s, and >400 m^3/s under a critical flow level of 351–389 m^3/s as optimum flow levels. Flow ranging from 417–500 m^3/s also had a negative effect on the estimated AWS. Values higher than 500 m^3/s likely reflect errors associated with the interpolation of environmental data. Using the 39-year average monthly 90% exceedance flows shows that the winter season (November–May) suffers from low flows (below the optimum flow range, Figure 7). Therefore, the winter months (January through April), excepting May and November, could be taken as critical low-flow months. Two distinct depth ranges, 1.7–3.7 m and 4.2–5.2 m, had positive effects on the estimated AWS; three depth peaks (2.4 m, 3.2 m, and 4.6 m) contribute the greatest amount to the AWS (Figure 8). Velocity showed an inverse relation with the estimated AWS. However, velocities up to 0.6 m/s had a positive effect on the estimated AWS and then fell sharply.

Discussion

Quantifying the adequate amount and timing of water flows to sustain aquatic biota and environmental processes is a global management priority in freshwater ecosystems [12,16]. To cope with the emerging threats to and persistent conservation challenges of freshwater biodiversity, a highly context-dependent, cautious, applied research approach is emphasized [16]. Thus, the process of maintaining ecological integrity is increasingly expensive due to escalating out-of-stream water demand and as a consequence of climate change [26]. To our knowledge, this is the first study to develop flow-ecology responses using top predator or mega-species (body mass >30 kg) traits to show physiographical and ecologically distinct flow-ecology relationships that support emerging flow-ecology science (e-flow). We present here flow-ecology relationships that are generalizable, quantitative, and able to generate temporally specific predictions of ecological responses to flow alterations. Our approach offers a platform for evaluating the environmental outcomes of water withdrawals or water resource management decisions in larger river systems that share major megafauna, such as river dolphins, particularly rivers in South/East Asia, and South America, which harbour most populations of endangered river dolphins.

We noticed significant changes in the ecological response, as the most fundamental responses to flow variations, across a wide range of temporal and spatial scales, which suggests that our approach is responsive to and can be used to quantify flow-ecology relationships [11]. As habitat acts as a template for species life-history traits or demographic processes [17], this underpins the importance of the early adoption of flow regulation guidelines for sustaining endangered aquatic life in highly regulated rivers. Thus, our approach, which considers temporally distinctive habitats of the GRD for establishing flow-ecology relationships, could have several advantages for the protection and restoration of the ecological integrity of streams and rivers that share similar hydrological and taxonomic groups (river cetaceans) [27]. These relationships can be applied in two different contexts: to evaluate the probable environmental consequences of flow modification or to establish guidelines for flow restoration in impaired streams. For instance, we used this approach to examine flow release plans [e.g., the proposed minimum flow (10–20% of the monthly minimum flow)] adopted by the massive Upper Karnali hydropower project in our study area. The results indicate that this reference plan is ecologically inadequate and no longer tenable to ensure the long-term functionality of the aquatic ecosystem.

Our findings reveal GRD are more sensitive to depth and velocity of natural flows that cumulatively define the suitable habitat template at specific geomorphologies, suggesting a substantial risk to population persistence if the species selects these attributes of flow preferentially under a critical flow. As a result, we observed both positive and negative biological responses to flow alterations, suggesting non-linear flow-ecology relationships, and negative consequences of both high and low flows to the ecology of the GRD (e.g., [28, 29]). This non-linearity likely indicates the salience of time-varying habitat availability for species life-history traits in the environments in which aquatic species occur. We noticed a negative contribution to the AWS from flows beyond certain points, supporting the hypothesis that the natural flow regime does not necessarily optimize all ecological functions of the target species [30]. This offers an opportunity to harvest flow, using caution if the flow exceeds the maximum level. Thus, an approach that specifies when flows are limited and predicts well-defined ecological outcomes using species traits is needed to build trust with managers and gain social support for environmental flows [12]. Using traits from freshwater megafauna species, which offer a preferred multi-species template for fostering demographic processes [17, 27], our approach may allow the construction of reliable flow-ecology relationships that integrate social and ecological demands. However, we stress that the incorporation of non-flow environmental factors, including climatic variability, might further improve the predictive power of our approach [12].

Significant adverse impacts of water withdrawals during the critical water level season are widely recognized in aquatic species conservation and are the most concerning with larger regulated rivers [31]. This is a significant challenge for aquatic biodiversity or species conservation, since it might cause substantial disproportionate changes in the biological response or result in diminishing ecological returns [11]. We identified ecological thresholds that offer opportunities to address this significant concern in rivers that share similar taxonomic and hydro-physical habitats. Thus, we stress that there is a crucial research and management need globally in the field of aquatic ecology to use species' life history-specific traits, particularly reproduction and migration traits, to determine the magnitude and timing of appropriate ecological flows [32].

Strong non-linear ecology-flow relationships across broader temporal scales are often associated with particular requirements of species at various stages of their life histories [11]. Thus, the timing of important life history stages (e.g., the preparatory period for reproduction or the timing of growth or reproduction) should coincide with the optimum water level to sustain aquatic life [16]. The peak reproduction time of the GRD and the timing of the critical water level overlapped to a large extent [33], which suggests that there is a high risk of mismatch between demographic phenology (i.e., birthing period) and suitable area availability (or usable area), which determines reproductive success. The effects further increase through the synergistic interactions of altered hydrology and anthropogenic impacts, such as overfishing and habitat degradation. Given the importance of water level in determining the breeding and survival success of lotic animals (e.g., [34]), timely and reasonable water allocation strategies will be needed to sustain aquatic biodiversity while optimizing water availability for human use [35]. To avoid species loss and habitat degradation, conservation approaches that address ecological attributes (e.g., obligatory breeding migrations, use of different habitats at different stages of the life cycle, and the extent of habitat occupancy) are essential [36]. In general, our approach could serve as a fundamental basis in riverine ecosystems, where river dolphin conservation falls short of ecological expectations, while addressing anthropogenic needs. Assuming the temporal patterns of flow variation that determine the habitat templates on which some species adaptations have been established [37, 38], maintaining a pattern of natural variability using proposed ecological thresholds might serve as an effective conservation measure. This approach benefits diverse aquatic taxa by offering temporally dynamic habitats that are useful for the completion of aquatic species life-history events.

We noticed a change in the amount of hydro-physical habitats as the first ecological response to flow variation, which supports the previous study findings [35]. Consequently, we found that GRD is forced to use low-quality habitats over a superior when the flow is reduced, as demonstrated by the considerable low value of use habitat characteristics (depth and velocity) over a habitat with high selection strength (preferred habitats). For example, as the flow declined, GRD were forced to use the habitats with a higher flow velocity as the season progressed towards peak dry season, which had a negative contribution to AWS. The magnitude and direction of such changes are poorly known. In response to this issue, we quantify the variation in ecological responses or usable areas (AWS) as a function of flow fluctuations. Our simulation models predict a loss of 26% of the currently available maximum AWS with a 40% fluctuation in the base flow (536.112 m^3/s, see detailed flow fluctuation levels in Table 1). To maintain ecological integrity and functionality and retain 80% of the AWS, we recommended maintaining a minimum flow of 383.967 m^3/s (Table 2) in the Karnali River. To minimize the adverse effects of flow fluctuations, traditionally adopted flow maintenance rules must be revisited in terms of hydro-ecological prospects. Further, while undertaking environmental impact assessments for mega hydropower or water-related projects, investigators must respond to the distribution and abundance of key species, which are affected by the interactions between the species and the changing environment [39]. In our case, the natural variability in flows from January through April seems more critical (below the threshold) for aquatic biodiversity, and perhaps, the severity of environmental impacts can be expected to increase with the duration of low flows during these months. Therefore, hydrological changes need to be considered when assessing the risk to endangered aquatic species in the face of persistent and increasing human activity during the Anthropocene [40].

As an immediate ecological response by aquatic biota to natural flow alteration (particularly during the dry season when flow naturally reduced and water extraction further accelerated) is the rapid loss of native and sensitive species mediated by the fragmentation of linear habitat corridors that limit their dispersal ability or gene flow between habitats [41-42]. Because of the long-life, low reproductive rate and habitat specialists (highly selective depth and velocity that define their habitats at particular geomorphic), habitat fragmentation certainly exposes river dolphins to the risk of ecological traps, a severe threat to their reproduction and survival. A sharp decline in population size (~50%), local extirpation (~18% reduction in distribution range), the formation of small isolated groups with a risk of inbreeding, and acute interactions with fisheries were commonly reported consequences of flow reduction in GRD populations in South Asian waterways [33]. Smith [43] described such ecological traps as “rare hydro-physical” in the same study area of this research, making the GRD more rare. Further, competitive interactions in feeding niches mediated by the reduced flow exacerbate overlap between river dolphins and fisheries, which likely escalates the endangerment and extinction of river dolphins through bycatch or adverse impacts on their health [44]. Although little is known about the flexibility of river dolphins habitat preferences or ability to adjust to changed environmental conditions, the current population size likely determines the fate of these trapped populations in highly regulated river systems [41]. Considering the current rate of decline of South Asian River dolphins (*Platanista gangetica*), the demographic effects of an ecological trap should be substantial and pose an immediate risk of extinction unless social and economic benefits of flow alteration are evaluated against ecological outcomes. Recent extinction of Chinese River dolphins, in addition to the sharp decline of *Platanista gangetica,* suggests immediate attention of conservation or water management authorities in South America, an important home to river dolphins, which is relatively less impacted by water development projects at present. As hundreds of hydroelectric dams have been planned throughout the Amazon, including many in the Orinoco and Tocantins-Araguaia basins [45], we suggest immediate actions to incorporate flow-ecology relationships in their water use management plans to avoid the risks of native and sensitive aquatic species extinctions.

Considerable interest in flow-ecology analysis exists globally, and our physiographic and ecologically distinctive flow-ecology relationships could reasonably support the global environmental flow guideline development process. Given the complicated non-linear relationships in aquatic ecosystems, relying on the habitat use of megafauna species could offer an opportunity to develop flow-ecology relationships that are scientifically robust, regionally flexible, and ecologically predictable. Foundation species (e.g., top predators), which are structurally and functionally significant taxa, offer critical resources for communities [25]; therefore, ecological thresholds based on the distinctive ecology of river dolphins might serve as a scientific basis for maintaining the environmental integrity of riverine ecosystems. The broader need for concerted, targeted, and timely conservation of freshwater biodiversity has been highlighted globally [46], and our findings could assist in developing an appropriate and broad biotic integrity plan to improve the resilience of riverine ecosystems. However, ecological responses to flows might differ in different landscapes, so understanding the spatial pattern of flow responses is essential. Our approach can be replicated carefully in other riverine systems that share similar hydrological and geomorphological characteristics, including the presence of mammalian carnivores (e.g., the Indus River dolphin, *Platanista gangetica minor*; Irrawaddy dolphin, *Orcaella brevirostris*; Amazon River dolphin, *Inia geoffrensis*; Tucuxi, *Sotalia fluviatilis*; Araguaian river dolphin, *Inia araguaiaensis* and Bolivian River dolphin, *Inia boliviensis*). As such relationships are unlikely to remain static in a changing environment [47-

48], managers need to anticipate how this dynamism may affect future environmental flow needs and develop appropriate management regimes that are robust to environmental change [49-50].

Methods

Study area

This project was conducted in the downstream segment of the Karnali River basin of Nepal (Figure 1), which is the largest of Nepal's three major river systems and is characterized by the steep terrain of the Himalayan Mountains. The highest runoff occurs during the monsoon season (e.g., June–October), and the lowest occurs during the winter season (e.g., December–May). Below the Siwalik Mountain range (a physiographic zone, Figure 1), a vast network of small tributaries combines to form a single narrow channel of the Karnali River with well-defined banks. Originating from the Tibetan Plateau, the Karnali River is the largest tributary to the Ganges River in India, which harbours the most significant density of GRDs in the world. The lower Karnali River basin provides the furthest upstream range for GRDs, critically endangered gharials (*Gavialis gangeticus*), smooth Indian otters (*Lutrogale perspicillata*), and 36 native fish species [51]. The GRD population size in the Karnali River has declined from 26 to six individuals [52]. Such a sharp decline in the GRD population is due to the effects of habitat degradation, mainly from water-based development projects (i.e., water diversion, [53]). Concurrently, several upstream development projects are proposed, under construction, or completed [e.g., planned: the Karnali Chisapani multipurpose dam, 10800 megawatt (MW); under construction: the upper Karnali hydropower project, 900 MW, and Bhari Babai diversion project; completed: Rani Jamara Kulariya irrigation intakes] and further threaten downstream aquatic life. All projects adopt traditional preconstruction environmental impact assessments procedure to define flow proportions (generally 10–20% of natural regimes) anecdotally and unscientifically. Thus, traditional flow proportions might be inadequate to sustain native aquatic biodiversity. Our study focused on the lower catchment area of the Karnali River basin, which is downstream from all megaprojects. All measurement protocols, including dolphin observation methods, were carried out in accordance with the Department of National Parks and Wildlife Conservation, Government of Nepal, guidelines and regulations. Habitat measurement protocols, including dolphin observation methods, were approved by the Department of National Parks and Wildlife Conservation, Government of Nepal (No 1129; 12 December 2016).

Available habitat assessment

Reduced water levels during the low-water season (e.g., December–May) escalate threats to aquatic biota by limiting physical habitat availability. Here, habitat refers to the hydro-physical habitat, which is defined by the flow and depth interactions at a particular geomorphic condition over space and time. Therefore, habitat availability (i.e. the area accessible to species) is assumed to be the greatest bottleneck, critically limiting species reproduction and survival [48, 49]. We measured the available habitats in the low-water season when suitable habitat is critically limited (i.e., December–May in 2018/2019), excluding the monsoon season (June–November). Further, to capture dynamic flow variation within the dry (i.e., low) water season, we selected three temporal periods—March (mid dry season), May (late dry season), and December (early dry season)—based on 39 years of flow records available from the Department of Hydrology, Government of Nepal. Assessing available habitat includes habitat mapping and bank and instream surveys. We divided the study area into three segments [upper segment (S1): length = 11 km, average width = 218 m; middle segment (S2): length = 29 km, average width = 121 m; and lower segment (S3): length = 10 km, average width = 198 m; Figure 1] based on uniform flow and channel geomorphology mapped along the selected stretch of the river. The three segments vary hydrologically and structurally. S1 consists of river channels with natural flows without any infrastructural diversion. Because of water diversion operations (e.g., Rani Jamuna irrigation intake and several traditional agricultural irrigation channels) and distributaries, the natural flow volume in S2 was low compared to that in S1. S3 benefited slightly from distributaries and received more water than S2.

Within each segment, the study reach (the linear segment where cross-sections are established) was established in such a way that the length of each reach was at least higher than the mean width (so the number varies among segments) of the respective segment. We also tried to maintain relatively similar flow at the top and bottom of the reach. Within each reach, random cross-sections were established to capture the hydraulic properties based on flow variation. As the flow variability of the stream increased, the number of cross-sections increased, and each section was kept at least 300 m apart from the other sections. Therefore, the number of cross-sections was based on the flow variation within a reach instead of the length of the reach. Bank and instream surveys started in an upstream direction, wherein directional readings of the cross-sections were noted. For the bank and instream measurements, pin heights were established at either side of the cross-section using GPS and a permanent reference marker for repeated flow measurements. Water surface elevations were estimated using a total station (an optical instrument for land surveying; Leica 772737 Builder 503) across the pin heights for each cross-section required for hydrological simulation. A new benchmark was established for each effort to measure the water surface elevation at each cross-section. The total number of cross-sections examined for the available habitats was 177 (March=60, May=47, and December=60). The hydraulic parameters (see habitat characterization section below) at each cross-section were measured using a RiverSurveyor S5 acoustic water current profile reader [Sontek, Acoustic Doppler Profiler (ADP S5)].

Occupied habitat assessment

We conducted a GRD population survey to capture occupied (selectivity) habitat characteristics (n=97) at three temporal scales (previously mentioned) using the approach developed by Paudel et al. 2015a. Within each temporal scale, we conducted three replications to capture the temporal and spatial variability in the characteristics of the occupied habitat. When we first detected dolphins, we observed surfacing behaviours for at least five minutes before establishing a cross-section. The habitats that were used for at least five minutes were considered occupied habitats, and then cross-sections were established to measure habitat characteristics using the ADP. If the dolphins disappeared after the location of the first sighting in less than five minutes, we excluded those habitats from our analysis. The Dolphin observation (only observation done) protocols were approved and permitted by the Department of National Parks and Wildlife Conservation, Government of Nepal.

Data Analysis

Data preparation and software

The ADP S5 hydraulic data were imported into *Excel* databases (Microsoft v. 2010) to format for *System for Environmental Flow Analysis* (SEFA, version 1.5; Aquatic Habitat Analysts Inc.) software. All the hydraulic properties [depth (m), velocity (m/s), wetted perimeter-WP (m), width (m), cross-sectional area-CSA (m^2), Froude number, and discharge (m^3/s)], suitability, and flow regime determination were calculated using SEFA software and analysed at the cross-section and segment levels. The average flow of each segment was used as a base flow while running the habitat simulation model for the respective segment. We found critical flows (<210 m^3/s, an insufficient flow that has a negative contribution to habitat suitability) in December and March and excess flows (>417 m^3/s, excess flow with a negative contribution to habitat suitability) in May. Therefore, the habitat retention hydraulic simulation model was performed only with excess flow (for May) using 39 years of 90% exceedance flow (the flow that is equaled or exceeded 90% of the time).

Habitat characterization

The cross-sectional hydro-physical parameters—width, flow, depth, velocity, wetted perimeter, cross-sectional area, and habitat (types)—were reported spatially and temporally. The habitat type (e.g., pool, run, and riffle) was classified based on the Froude number (F_r), where Froude is an index of hydraulic turbulence (the ratio of velocity by the acceleration of gravity). Points with Froude numbers exceeding 0.41 were considered riffles, points with Froude numbers less than 0.18 were considered pools, and intermediate values were classified as run habitats. The proportion of run, riffle, and pool habitats within each study reach was calculated from the Froude numbers. The GRD's seasonal hydro-physical habitats were characterized using basic descriptive statistics (mean and 95% CI). The variation in these hydraulic parameters among seasons, habitat types, and segments was examined by an analysis of variance (ANOVA), and post hoc pairwise comparisons were performed using Tukey's honestly significant difference (HSD) test. A two-way ANOVA test was used to investigate any interactive effects of season and habitat on hydraulic variations. The level of significance was set at $p < 0.05$ for all the statistical tests. All the analyses were conducted using R Studio.

Hydro-physical habitat modelling

The GRD's suitable habitat (i.e., habitat selectivity) is defined as the range of hydro-physical conditions in which GRDs are most likely to be found (excluding water quality). The habitat simulation approach comprised two steps: developing the habitat suitability curve (HSC) and estimating the area-weighted suitability (AWS) using the HSC and flow relationships. The HSC was developed using the GRD *occupied* and *available* habitat datasets. To develop the HSCs, understanding the strength of selection for a particular habitat is essential. Therefore, we measured habitat selectivity (w) at equal intervals of both depth and velocity to measure the preference strength (preferred category) for a specific category of habitat. Habitat selectivity was calculated as the proportion of a habitat class that was occupied divided by the proportion of that category available in the whole sample [50]. A value of w = one indicates neutral preference, $w <$ one indicates that the habitat was used less commonly than expected by chance, and habitats with $w >$ one are used more frequently than expected by chance. Using the selectivity values (w), we transformed the depth and velocity categories into a binary scale of zero and one. We assigned a value of one to those categories for which $w >$ one and zero to those categories for which $w \leq$ one. By assigning one and zero to each group, we developed an HSC to calculate the area weighted suitability (AWS) at each measured point. Hydraulic habitat suitability is expressed as AWS in terms of usable area in metres of width or square metres per metre of reach (m^2/m).

To obtain the AWS value for the reach, we multiplied the combined suitability index (CSI, which is the product of the suitability of depth and velocity at a point) and the proportion of the reach area represented by that point. Using a 39-year average base flow of 536.11 m^3/s (90% exceedance flow) in May, we predicted the fluctuation (decrease by 10%) in the currently available maximum AWS (i.e., 22.718 m^2/m, AWS of May) in the range of flows from 200–900 m^3/s. We simulated the AWS in this particular range because this range represents the 39-year low and maximum values of the 90% exceedance flow for the low-water season (November–May). Covering this variation over a broader scale increases the applicability of our ecological thresholds across time. Using the same base flow and range, we also estimated the minimum flows that retain various standards (%) of habitat protection. Further, we also determined the minimum flow that provides the maximum AWS for the low-water season.

Ecological thresholds using flow-ecology relationships

As water depth and velocity are the result of instream habitat features, such as pools, riffles, and runs, we only incorporated depth and velocity when estimating the hydraulic habitat suitability. Additionally, GRD habitat selection is strongly guided by the depth and velocity of a river section [24, 48]. Generalized linear models (GLMs) using logit functions were used to examine the relationship between GRD presence and hydraulic properties (depth and velocity). Four different GLMs (depth, velocity, depth*velocity, and depth+velocity) were developed, and the Akaike information criterion (AIC) was used to select the best models. The additive effect of depth and velocity on the GRD presence was found in the model with the best performance; therefore, we further used a generalized additive model (GAM) to capture the possible non-linear influence of depth and velocity on GRD presence. Because of the possibility of both linear and non-linear relationships [11], we again used a GAM to capture the functional relationships between ecology (AWS) and flow. The degree of smoothness for all the GAMs identified by the iterative approach (up to 25 smoothing factors were checked) and the selected smoothing parameter (i.e., 20 for all the GAM models) that yielded a significant covariate (at the 0.005 level of significance) explained the maximum deviance and adjusted R^2. Both the GLM and GAM models were fitted using the *lm* and *mgcv* packages in R Studio.

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Competing Interests Statement

The authors declare no conflict of interest, financial or otherwise.

Author Contributions

S.P. and J.L.K. conceived the study. S.P. and J.L.K. designed the work and S.P., U.T., R.S. and R.C.G. involved in the data acquisition processes. S.P. conducted data analyses. S.P., J.L.K., and U.T. wrote the manuscript and all the authors reviewed the manuscript and approved the final version.

Data availability

All data supporting the conclusions of this article are within the paper.

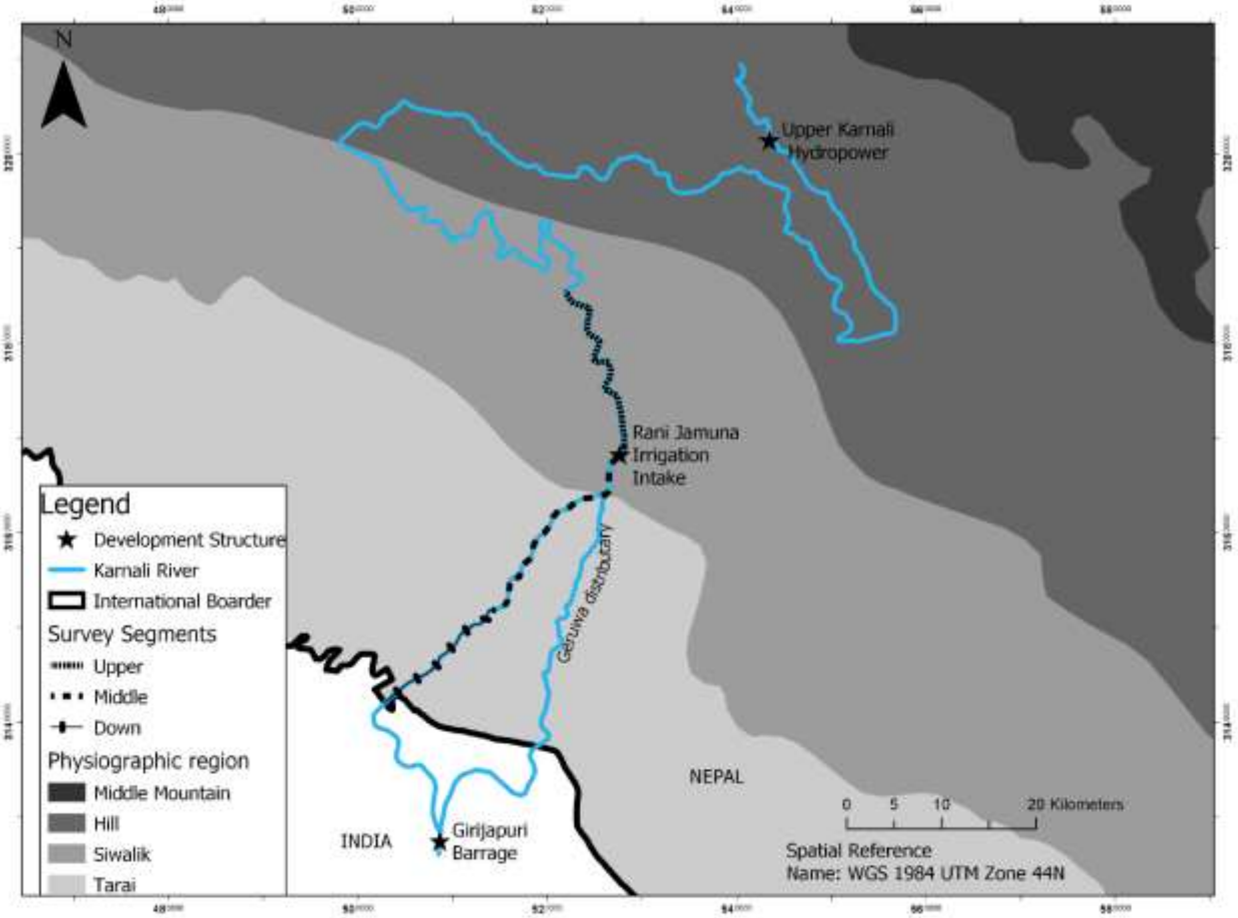

Figure 2.1 Map of the Karnali River system of Nepal showing locations of Upper Karnali Hydropower, Rani Jamuna Irrigation Intake and Girirajpuri Dam (in India) that extract the water from the mainstream Karnali River. Survey segments (S1, S2 and S3) represent the historically and presently occupied potential habitat of the Ganges River dolphins. The map was prepared using ArcGIS Pro 2.6 (Esri Inc.; www.pro.arcgis.com), and data (physiographic and river) developed by the Government of Nepal were used to prepare this map.

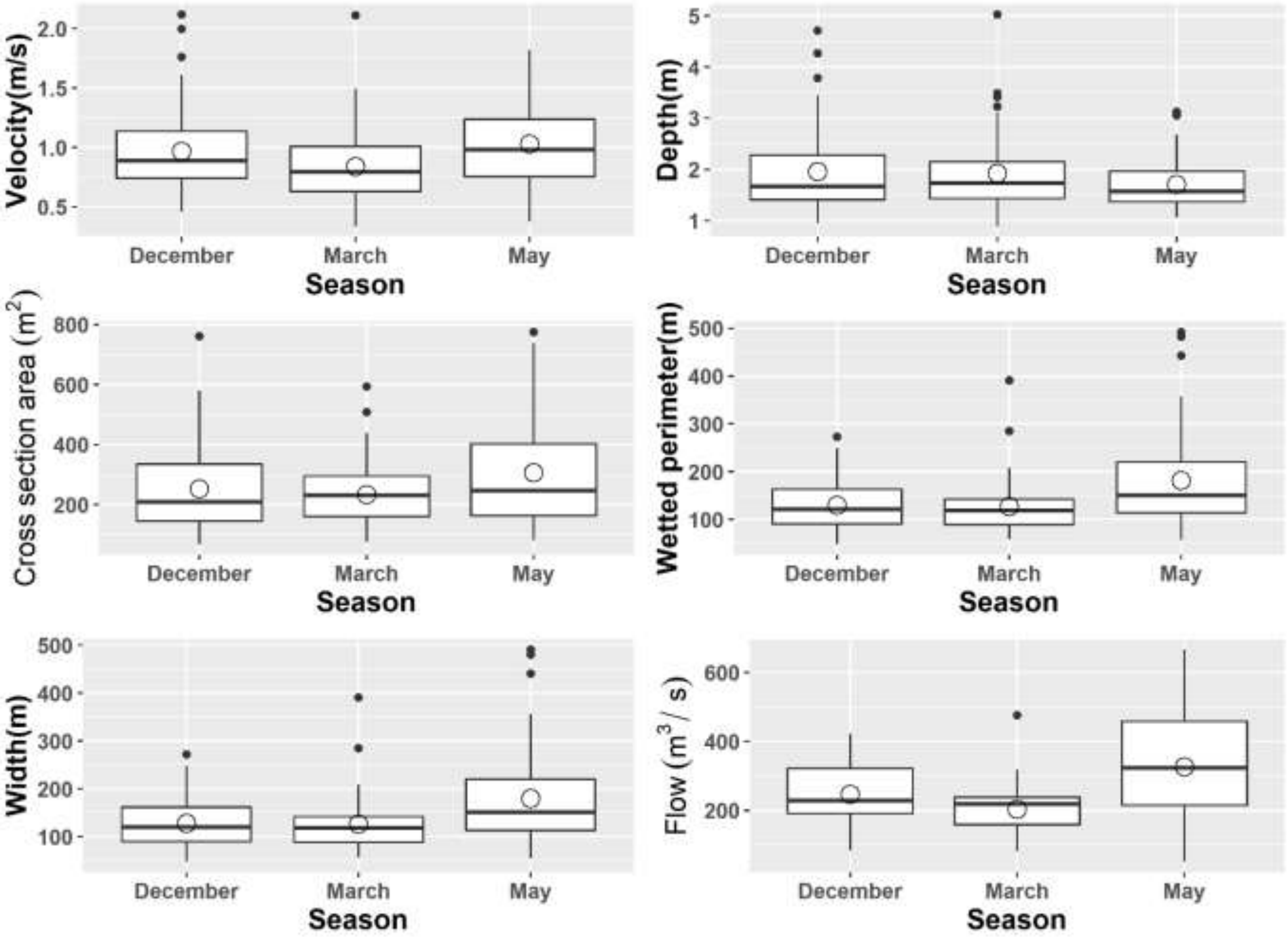

Figure 2.2 Ganges River dolphins ecological attributes across the dry water season (Dec-early dry, Mar-middle dry and May-late dry; Dry season = December-May; Transition season for both dry and wet respectively= November, June; Wet = July-October) show that individuals are often found in specific hydro-physical habitats, suggesting strong habitat selection. The line's median value divides the box and means value represented by a hollow circle.

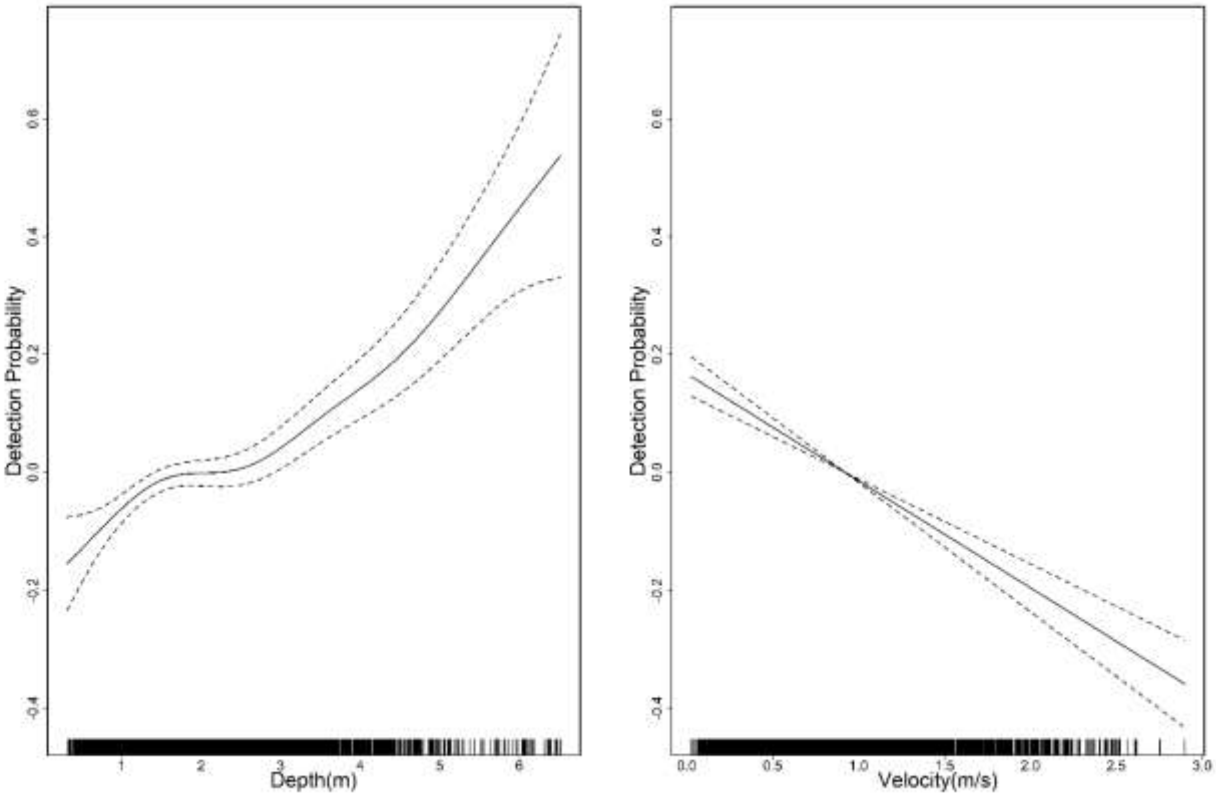

Figure 2.3 Smoothed curve of the additive effect of depth and velocity to the detection probability of Ganges River dolphins in the General Additive Models, where dotted lines represent 95% CI, and the lower axis represents single observations of depth and velocity, respectively, in the Karnali River of Nepal.

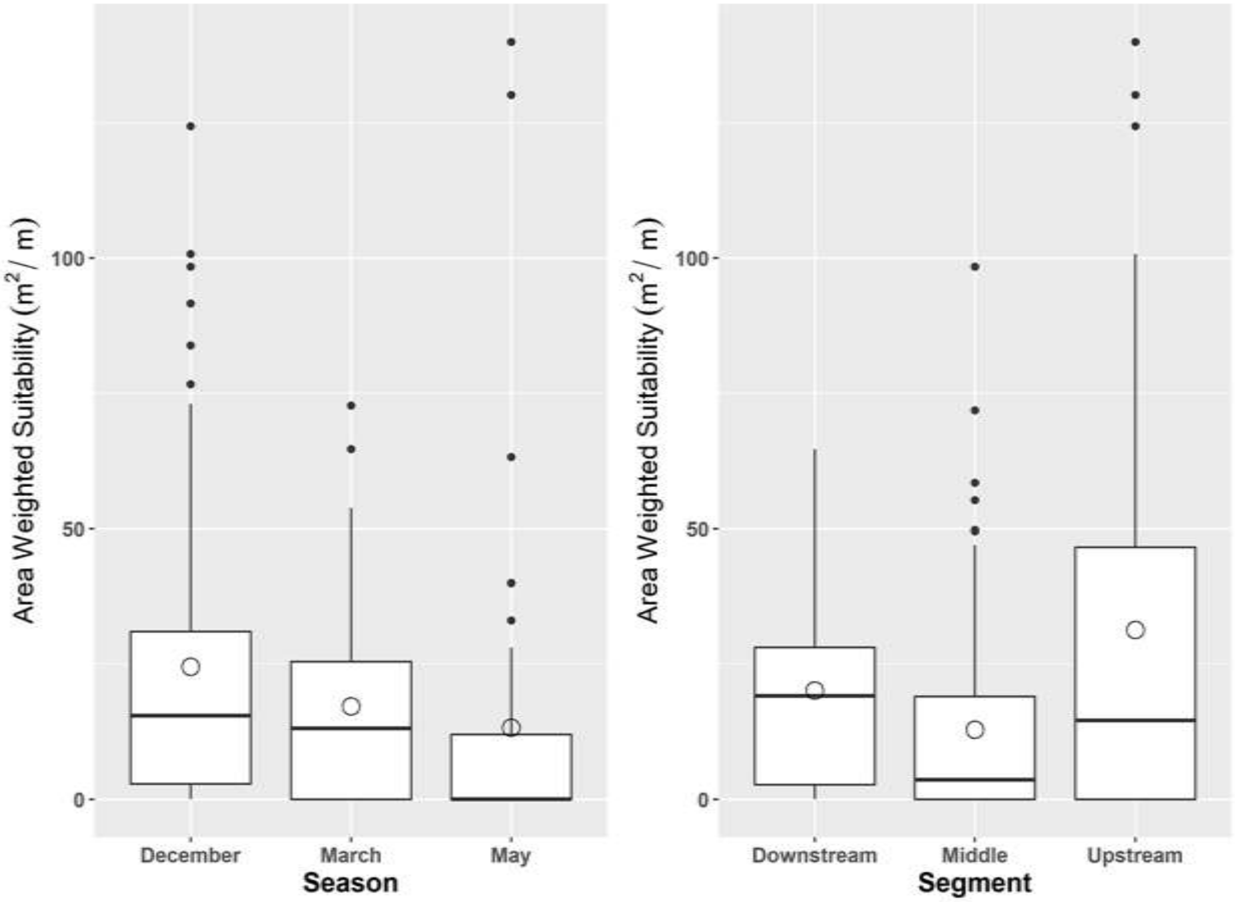

Figure 2.4 Area Weighted Suitability (AWS) distribution across dry season (Dec-early dry, Mar-middle dry and May-late dry; Dry season = December-May; Transition season for both dry and wet respectively= November, June; Wet = July-October) and segments (upper, middle and downstream), which shows higher availability of AWS in the confined and unregulated upper segment compared to affected segments from distributaries and human extraction, and seasonally more AWS noticed during the early dry season compared to the middle and late dry season. The line's median value divides the box and means value represented by a hollow circle.

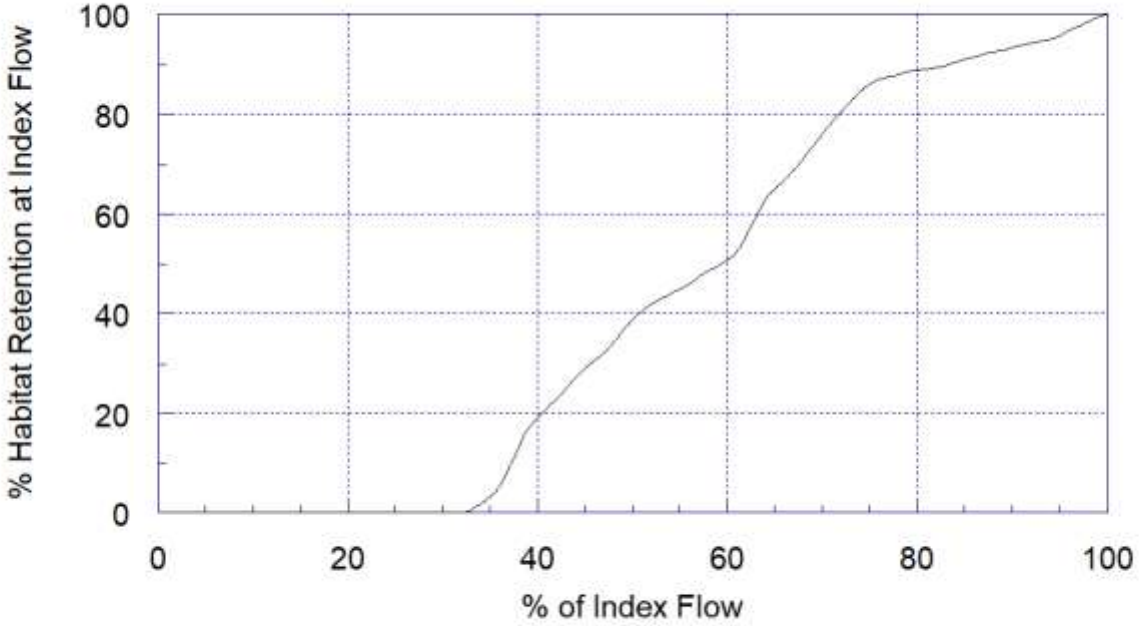

Figure 2.5 Habitat retention (%) at the different proportion of the base flow. For example, if we maintain 40% of the base flow, at least 20% of the GRDs' hydro-physical habitats will have remained in the stream.

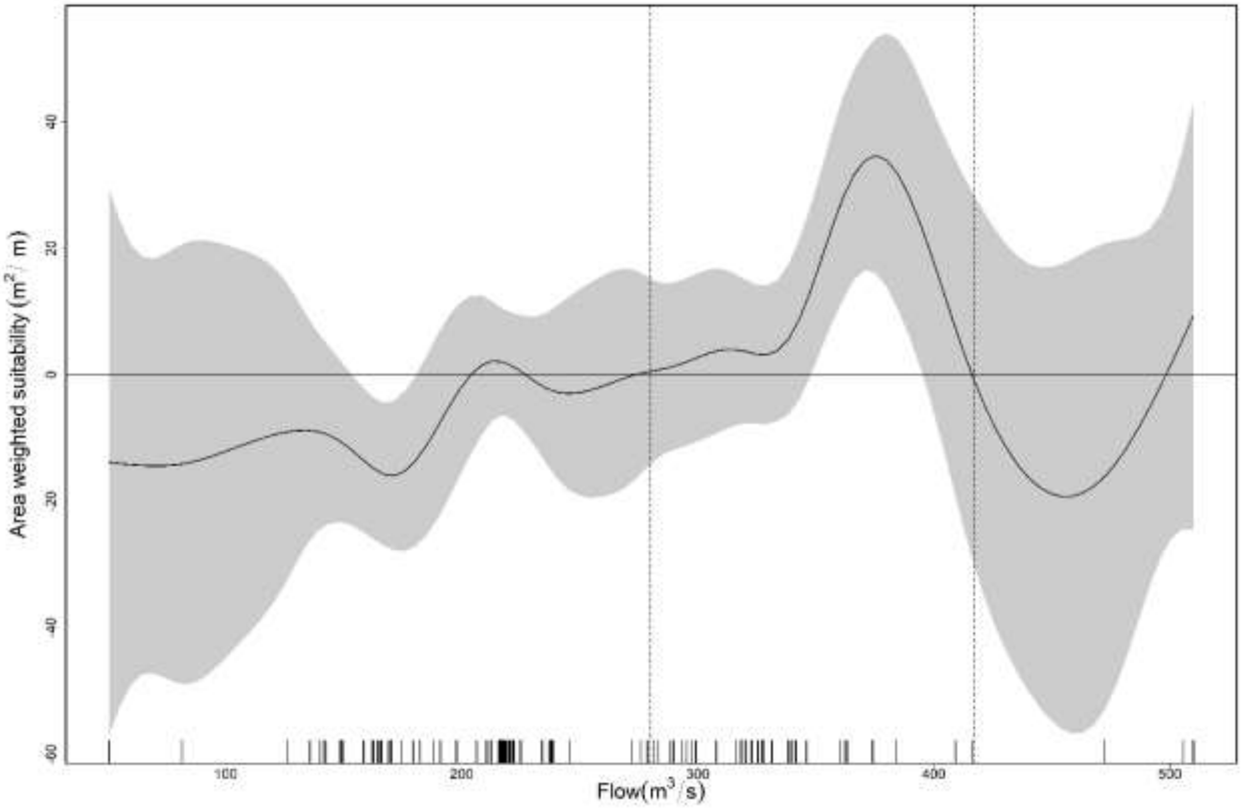

Figure 2.6 Ecological response (Area Weighted Suitability) of Ganges River dolphins as a function of flow in a continuous scale, where the smoothed curve line shows the estimated AWS as a function of flow variation, gray color represents the 95% CI level, and marks along the lower axis represent a single observation of the flow level. The two dotted vertical lines identify the limits for the optimum range, whereas the black horizontal line represents the zero effects zone.

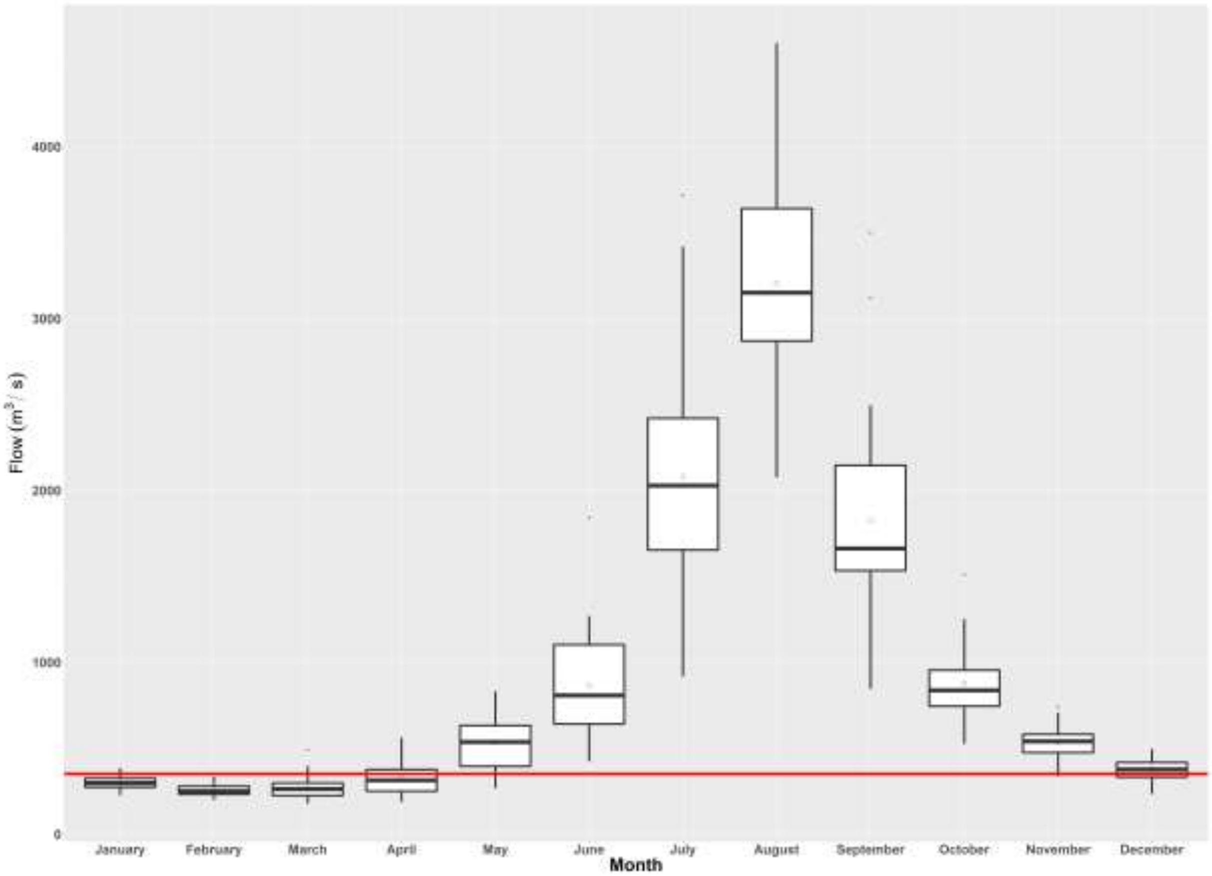

Figure 2.7 Monthly average 90% time equaled or exceeded flows for the 39 years shows that from January through March, aquatic species suffer from low flows, putting them at risk of evolutionary traps by hugely reducing suitable hydro-physical habitats. The horizontal red line indicates the lower limit of the optimum range.

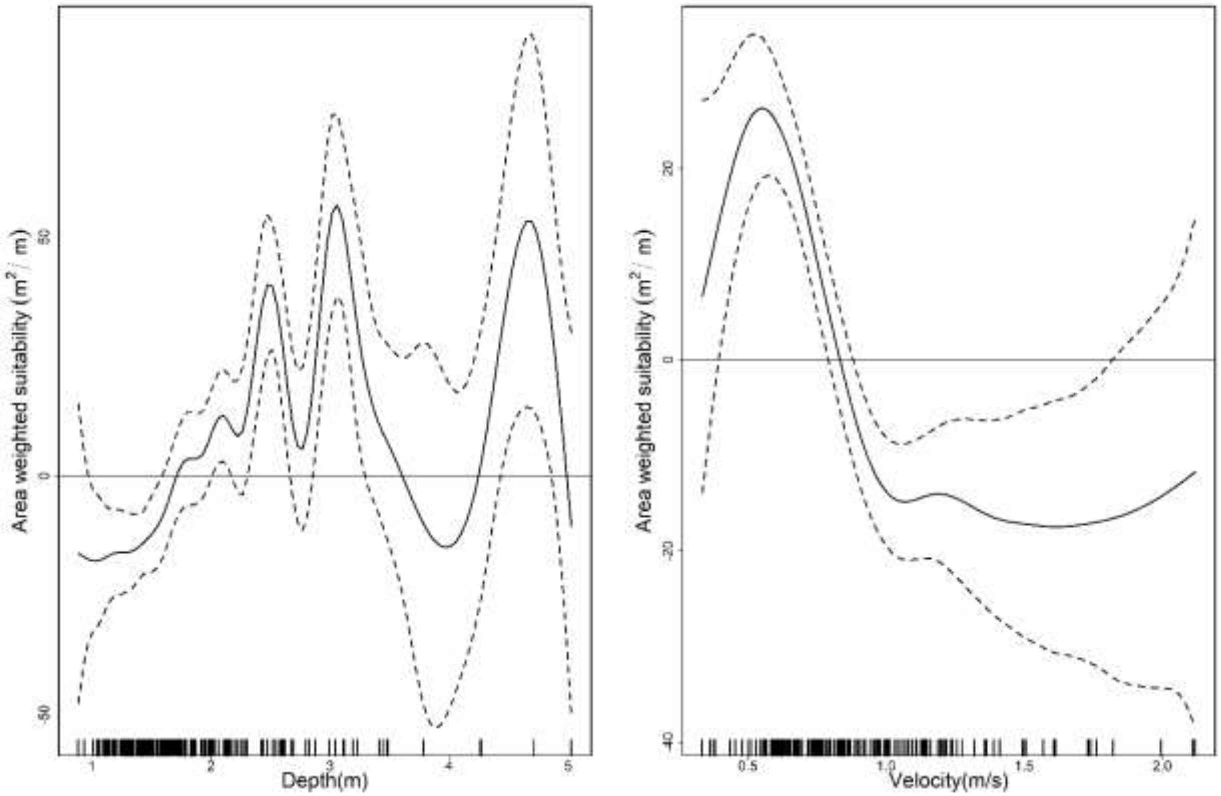

Figure 2.8 Effects of the depth and velocity on the Area Weighted Suitability (AWS), where several peaks indicate positive and negative (or non-linear relationships) GRD responses.

Table 2.1 Area Weighted Suitability (AWS) loss with flow fluctuations around a base flow of 536.112 cubic meter per second for May

The proportion of maximum fluctuation	Loss (AWS m^2/m)	% Loss of AWS at base flow
0	0	0
0.1	2.07	8.67
0.2	3.53	14.78
0.3	4.97	20.77
0.4	6.19	25.87
0.5	8.54	35.71
0.6	11.99	50.14
0.7	15.05	62.92
0.8	18.19	76.01
0.9	22.13	92.49
1	23.69	99.02

Table 2.2 Minimum Flows (in cubic meter per second) that retain a % of Area Weighted Suitability at a base flow of 536.112 cubic meter per second

Retention %	**Minimum Flows (m^3/s)**
95	503.08
90	446.96
85	398.23
80	383.96
75	372.58
70	361.44
65	348.51
60	337.84
55	330.11
50	317.92
45	294.58
40	270.79
35	258.19
30	244.12
25	229.62
20	216.15
15	205.51
10	198.47

APPENDIX C: SEASONAL FLOW DYNAMICS EXACERBATE OVERLAP BETWEEN ARTISANAL FISHERIES AND IMPERILED GANGES RIVER DOLPHINS

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Seasonal flow dynamics exacerbate overlap between artisanal fisheries and imperiled Ganges River Dolphins

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Running title: Fisheries interactions with small cetaceans

Abstract

Here we quantify the effects of artisanal fisheries on the ecology of a small cetacean, the Ganges River dolphin (*Platanista gangetica gangetica,* GRD), in a large river system of Nepal. We examine the size-classes of fisheries' catches, behavioural changes in GRD in response to fishing activities, and diel overlap between GRD and fishing activity. We observed high human exploitation rates (> 60% of the total catch per effort) of GRD-preferred prey sizes, indicating risks of high resource competition and dietary overlap, especially during the low water season when resource availability is reduced. Competitive interactions in the feeding niches during the low water season, plus temporal overlap between the peak exploitation and critical life-history events (e.g., reproduction), likely have ecological consequences. Furthermore, we detected 48% (95% CI: 43–52%) increase in the chance of behavioural changes among dolphins exposed to anthropopressure (fishing activity), risking social behaviour impairment in exposed dolphins. The higher diel overlap and increased diel coefficient as the surveys progressed towards the monsoon season suggest temporal shifts in GRD socio-behavioural states and seasonal effects on resource partitioning, respectively. This work identifies drivers of small cetaceans-fisheries interactions and their consequences, and can be used to help reduce biologically significant fishing impacts on small cetaceans. Mitigation strategies, together with river sanctuary and distanced-based approaches, should be urgently included in a framework of ecosystem-based management.

Introduction

Freshwater ecosystems provide vital resources for humans and are a habitat for a plethora of endemic and sensitive fauna and flora [1]. However, human pressures on freshwater ecosystems have risen sharply over the past century, leading to substantial and growing threats to global biodiversity [1]. Freshwater fisheries around the world are increasingly overexploited by humans [1,2]. Humans have caused rapid and significant declines in abundance and distribution of freshwater fauna that could reduce future viability of various taxa [2]. Freshwater river systems –

exhibiting some of the richest fish biodiversity resources in the world– are no exception to these global trends [3].

Fisheries in the cold-water systems of the Hindu Kush region of the Himalayas are considered vital sources of nutrition and food security, where large human populations living downstream rely on these natural resources for their daily survival [4]. Large artisanal fishing communities predominantly depend on subsistence and semi-intensive fisheries for their livelihoods. For many Nepalese, fishing is a way of life [5]. Nearly three million fishermen from India and Bangladesh rely on fishing in Himalayan Rivers for income, food security, and nutrition [6]. For example, the Koshi River in Nepal, a major tributary of the Ganges River, harbours 103 fish species and contributes about half of Nepal's total fish production of 33,000 metric tons per year; with more than 30,000 people depending on fishing in the Koshi and other rivers in Nepal for their livelihoods [6]. Consequently, local dependence on river systems, documenting losses of biodiversity, diagnosing their causes, and finding mitigation have become significant issues.

The first human-caused extinction of a Yangtze River dolphin (*Lipotes vexillifer*) from China has led to growing concern that similar extinctions of other river dolphins are likely unless human needs and river ecology are better understood, and conflicts mitigated [7]. Particularly at risk are other river dolphins with distributions that are mostly restricted to human-dominated river systems under the immense pressure of river-dependent communities. Conflicts between small cetaceans and artisanal fishing have increased globally in recent years [8–12]. Despite available studies on interactions between small cetaceans and fisheries, competition between small cetaceans and subsistence fisheries poses a severe and growing problem, and meaningful management thus requires an effective and appropriate assessment of the factors driving the interaction.

The conflict between small cetaceans and artisanal fisheries is mainly through ecological niche overlap, for example, food and habitats [12-17]. Such interactions have resulted in small GRD population sizes of questionable viability in two major river systems of Nepal, the Karnali and Sapta Koshi [17]. At least 95 Indus River dolphins (*Platanista gangetica minor*) were killed between 1993 and 2012 in fishing gear in the main sections of the rivers of Pakistan [18].

Similarly, the majority of Irrawaddy dolphin (*Orcaella brevirostiris*) deaths were attributed to entanglement in gillnets in the Mekong River of Cambodia and Laos [8]. Furthermore, the survival of South American river dolphins is threatened by fisheries [15], and the vaquita (*Phocoena sinus*) in Mexico is in severe danger of extinction due to non-target capture in nets [19]. Globally, human activities leading to intense small cetaceans-fisheries interactions must be examined to manage and promote the co-existence between fisheries and small cetaceans.

Previous research has quantified the strength of the interaction between cetaceans and fisheries. However, no studies have examined potential ecological niche overlap, for example, overlap in the dimension of prey size (focusing preferred prey size), diel activity (the distribution of activity throughout the daily cycle), and behavioural distraction (change from one behavioural state to other). Most studies have used fisheries datasets (biological catch) to measure such interactions. For example, by-catch (number of entangled dolphins), harvest details (catch per unit effort), and social dimensions [20-24] while ignoring the potential relationship between niche overlap and competition [25].

Globally, a sharp decline in population status (~50%) and distribution of GRD is attributed to anthropogenic activities [26]. In Nepal, out of four rivers of distribution, currently only two river systems are occupied by GRD with questionably viable population size (<50) [17]. Here, we assessed aspects of the interaction between artisanal fisheries and cetaceans in Nepalese waterways not previously studied by examining 1) niche overlap between GRD and fisheries in the dimension of prey size; 2) overlap in diel activity by fisheries and GDR; and 3) effects of fisheries on GDR behaviour. To characterize the interactions, we collected fishery data at wider temporal scale, visually observed GRD response to fishing events, and estimated overlap coefficients to compare activity patterns of fishers and GRD. We analysed the fishery data using generalized linear models within a Bayesian hierarchical framework to obtain exploitation rates of GRD preferred prey sizes and their contributing factors.

Results

Preferred prey size exploitation over space and time

The top deviance information criterion (DIC) supported model included gear and season as predictive covariates (Model 1, Table 1). On average, gear and season contribute with β coefficients of 2.438 (95% Credible interval: 2.122–2.743) and 0.193 (95% Credible interval: -0.121–0.502), respectively. The proportion of exploitation (β coefficient) was higher in the Sapta Koshi river [Gill = 0.623 (95% CI 0.45–0.807), Cast = 0.877 (95% CI 0.719–0.955)] than in the Karnali [(Karnali: Gill = 0.521 (95% CI 0.338–0.73), Cast = 0.677 (95% CI 0.518–0.797). Contrary to our *a priori* predictions, cast nets were associated with higher average exploitation of the proportion of preferred fish size caught during the dry season (October–March), whereas, most of the time (April–November), gill nets were associated with stronger effects.

In both river systems, the dry season (October–March) had a higher mean proportion of preferred fish sizes caught compared to other seasons (except February through March in the Karnali River), which were the most common months for the highest percentage of preferred fish size captured (Fig. 1). We detected minimal variation of mean proportional rates during dry seasons, which had the largest mean proportion values compared to other seasons (Fig. 1). The mean annual exploitation proportion rates were 0.6 (95% CI 0.297-0.952) and 0.78 (95% CI 0.732-0.952) in the Karnali and Sapta Koshi rivers (Fig. 1), respectively.

Fisheries over space and time

Average total catch per effort exhibits distinct seasonal patterns in both river systems, lowest in summer (April–November: mean=1.454 kg, SD=1.719), and higher during the dry season (October–March: mean=3.063 kg, SD= 3.236). Across the seasons, June-July (mean=5.062 kg, SD=4.620) in the Sapta Koshi and December–January (mean= 2.145 kg, SD=0.906) in the Karnali attained the highest peaks of fish biomass captured, which then declined to the onset of the summer season. Average total catches varied more widely within a season in the Sapta Koshi

River, whereas in the Karnali catches tended to remain constant (Fig. 2). The lowest average catch records were observed through August to November in both river systems, which were less than or equal to 2 kg (Fig. 3). Average catch per effort across gear type [(Cast: Karnali- mean=0.932 kg, SD=0.845; Sapta Koshi- mean=4.470 kg, SD=4.404), (Gill: Karnali- mean=1.420 kg, SD=1.104; Sapta Koshi- mean=3.141 kg, SD=2.428)] varied, which considerably contributed to the average seasonal biomass catches observed (Fig. 3).

Behavioural changes to the artisanal fishing boat

Time of the day (GLM, estimate= 0.685, 95 % CI 0.526-0.887, Z=-2.843, P=0.004) associated with a higher probability of dolphins being subjected to anthropopressure. Compared to the afternoon (estimate= 1.1875, 95% CI 0.7427-1.910), risk of behavioural change in the morning and evening increased by 1.753 (95 % CI 1.070- 2.879) and 2.470 (95% CI 1.438- 4.276) respectively. The propensity scores varied from 0.328 to 0.746 (mean= 0.48), with high overlap of scores between two treatment groups. Behavioural change rates (with 95% confidence intervals) by treatment groups in each propensity quintile group revealed that behavioural change rates were higher in dolphins exposed to anthropopressure than those in the control group (Fig. 4). Overall, we noticed an average 48% (95% CI: 43–52%) increase in chance of behavioural change rates (or risks) in dolphins exposed to anthropopressure compared to control group dolphins (Fig. 4). Under a human presence, we noticed substantial change in behaviour state from surface feeding to long (44%, n=180) and travel dive (33%, n=135) respectively.

Temporal activity/diel overlap

We detected GRDs and artisanal fishing boats in all months surveyed, with substantial variation in GRD detections, ranging from 45 and 51 detections in the winter surveys (November–February) to 127 detections during March–April as the monsoon season approached. Artisanal fishing boat detections were fairly constant, ranging from 187 to 195 detections across the same survey periods. Dolphin activity in the dry season (November–February) exhibited trimodal activity curves with a peak in early morning activity around 0700 h, followed by a peak in mid-day (1200 h), and a less pronounced peak towards the end of daylight 1800 h (Fig. 5). Dolphin activity in March–April exhibited similar activity peaks in the early morning (0700 h), but with a distribution of activity that plateaued throughout the rest of the day. Artisanal fishing boat activity across all seasons approached uniformity throughout the day, with minor declines in activity around mid-day. These observations led to moderate diel overlap between the artisanal fishing boats and GRDs in November–December with the coefficient of overlap estimates Δ = 0.604 (95% CI = 0.478–0.726, Table 2). Overlap coefficients increased across the next two survey seasons: Δ = 0.725 (95% CI = 0.615–0.850) and Δ = 0.832 (95% CI = 0.756–0.912) in January–February and March–April, respectively (Table 2).

Discussion

Globally, interactions between artisanal fisheries and small cetaceans are one of the most significant conservation issues leading to endangerment and extinction [42]. The recent extinction of the Yangtze River dolphin and the critically small size of the vaquita population showcase how such interactions can contribute to dramatic declines of small cetaceans [18]. Our study reveals that interactive and cumulative effects of artisanal fishing with seasonal resource variations – the high dietary overlap of preferred prey exploitation, substantial risk of impairment of ecological and social behaviour, and significant diel activity overlaps – is putting the small cetaceans under acute pressure that could affect dolphin persistence. These factors might have contributed to the decline in dolphin populations in Nepal over the past two decades [12] and will continue to affect river dolphin population growth in the future.

We observed high human exploitation rates of GRD-preferred prey sizes in the major river systems of Nepal, where an already small number of the dolphins (28–52 individuals) persist [12]. Greater than 60% of the total catch per effort in each river was within the preferred prey size range. Fishing gear and seasons were identified as significantly contributing to the higher proportion of GRD-preferred fish size-classes captured in fisheries. Among these contributing factors, the contribution of gear was two-fold stronger than that of season. Specifically, we saw a higher proportion of GRD-preferred fish caught by cast nets relative to gill nets, particularly during the dry season. Because of non-selective behaviours of the cast net, impacts of cast nets could be significant relative to gill net during dry seasons when resource availability is reduced. Medirose et al. [43] reported similar effects of cast nets in aquatic systems of Brazil and urged fishing gear specific fisheries management schema. As the variation on fish stock and size distribution is likely regulated by fishing and temperature (regulated by season), seasonal variation in resource overlap highlights seasonal gear-specific regulations as the appropriate and effective mitigation effort to sustain resources and minimize potential conflict between small cetaceans and artisanal fisheries in highly exploited river system.

Also, these high exploitation rates peaked during the dry season when habitat was reduced, which suggests that there is typically more significant overlap in the feeding “niches” of river dolphins and fishermen during this time of year. Narrow habitat breadth coupled with limited availability of habitat and overlap in prey resources likely increases competition between GRD and fisheries in that both GRD and artisanal fisheries overlap in high productivity foraging sites, such as deep pools and confluence habitats [44]. The direct effects of these interactions have likely increased by-catch of small cetaceans. For example, we recorded by-catch leading to the death of three young calves in the Sapta Koshi River and one adult in the Karnali River during 2015–2018, especially between December-February. Such mortality could be attributed to either small cetaceans increasing their foraging time in the area with high overlapped, which forces small cetaceans to forage further in areas with higher depredation risks [45]. Although fish availability or stock data is not available for the study site, the high exploitation of small cetacean’s preferred prey by fisheries during the resource-limitation period suggests there is high overlap between the diets of small cetaceans and the catch of artisanal fisheries, which might play an indirect role in compromising the health of these cetaceans [46]. We did not find any species that are devalued by the fisheries, but we noticed fisheries opting for a few species in terms of taste. Fishers directly sell these captured fishes in a local market, where fishes are consumed in multiple ways.

Furthermore, we noticed GRD reproduction predominantly occurs during the low water season when fishery exploitation is highest. Limited habitat availability, along with the risk of phenological mismatch between predator and prey in the changing Anthropocene, further exacerbate the risk of population decline or extirpation in small cetacean (such as GRD) by adversely affecting reproduction [47]. For instance, the loss of four small cetaceans in the Mediterranean and Black Seas has been attributed to overfishing or prey depletion [48].

It would be difficult to establish a clear link between fisheries and the decline of dolphins. Nevertheless, under the lack of the most preferred food or prey size could play a significant role to reduce potential reproduction, and is considered as the most important population size regulator [48]. Thus, small cetaceans are highly vulnerable to such competition effects, which likely affects their survival, fecundity, and overall fitness [49].

We observed a difference in the behavioural change rate of GRDs between anthropopressure and control zones. A chance of higher dolphin behavioural change rates (40–60%) were observed in artisanal fishing boat areas compared to control areas. Although there is no direct evidence of the adverse impact of such behavioural changes on small cetaceans' ecology, we suspect that artisanal fishing activities might threaten individual social or behavioural roles that are essential to maintain a cohesive functioning society [18]. Chilvers et al. [50] also noticed the change in the behaviours of the bottlenose dolphin communities (*Tursiaps truncaría*) as a function of fishing activity. Disruption of the behaviours and social life of Indo-Pacific humpback dolphins (*Sousa chinensis*) by fishers is argued to be a form of short-term stress that leads to a permanent impairment of behavioural functioning and social life [51]. Thus, among small cetaceans, changes in behaviours, direction and speed of travel, and diving styles (short, long) were all common consequences of such interactions [52], possibly reducing survival and reproductive success of individuals and declining populations size over time [53].

Furthermore, distraction in surfacing ecology might reduce energy reserve, which also accelerates physiological stress [54]. While the influences of human-made noise and other human actions on cetacean behaviour have been widely highlighted, cases of increased sensitivity following harassment are emerging in the field of small cetacean conservation [55]. Additional work is needed to determine if the observed behavioural changes we noted in GDR due to fishing activities result in reduced survival. Increasing human-related activities like fishing pressure and changing environment could potentially reduce the space by eliminating access to suitable foraging sites and further fuel physiological harassment. Therefore, possible regulations, including buffer zones or a river sanctuary covering small cetacean hot spots, could reduce both chronic and acute interactions between artisanal fisheries and small cetaceans.

Globally, a lack of information exists on the “area of influence” within which human activities might displace small cetaceans. In line with the findings of Richman et al. [30], we suggest that 400–500 m can be considered as the maximum GRD observable distance. Furthermore, our maximum response distance (200 m) could be a guide to determine whether small cetaceans experience stress from human activities, and inform co-existence management plans and buffer zones for critical hotspots or observed individual dolphins. The National Oceanic and Atmospheric Administrations of the United States (NOAA-Fisheries) prohibit approaching or remaining 460 m of an endangered Atlantic right whale (*Eubalaena glacialis*), and the distance is considered as a safe distance to enhance their self-sustaining population. Thus, our proposed distances support a strategy to identify specific areas that are important to the survival of small cetacean populations and restricting human access [56]. A recent study [24] suggests a spatial approach as a cost-effective tool for reducing all fishery-cetacean interactions. In light of this evidence, our response distance might be cost-effective and allow managers to prioritize locations and apply different management strategies, offering potential beneficial outcomes for small cetaceans and fisheries.

Given that many biological activities are under photoperiodic control, allowing very narrow periods for critical life-history events within the annual cycle [57], shifts in the timing of the essential ecological and social states caused by the diel overlap or human disturbances might have significant fitness consequences in small cetaceans [58]. We noticed a high diel overlap between fisheries and GRD behavioural events, and as a consequence, GRD are displaced from their active surfacing time window. As a result, the optimal timing of critical life history activities that are based on environmental cues, for example, the timing of reproduction, the timing of hibernation or resting, and accumulation of body reserve could be severely affected and thus, reduce the fitness by failing to respond optimally to time-sensitive behaviours [59]. Specific biological effects of timing shifts in small cetaceans have not yet been explored, but broadly deleterious effects have been noted that might influence reproduction success, health, ranging patterns, and availability of preferred habitats, and potentially trigger a decline in abundance [60]. Given the recent human-caused extinction of Yangtze River dolphin [7] and Mediterranean striped dolphins in 1990–1992 [46], it is likely that small and isolated subpopulations of cetaceans will be severely affected by temporal activity displacement, leading to adverse impacts on the processes that retain demographic dynamics. These might include river dolphins in South and East Asia (e.g., Indus River dolphin, GRD, Irrawaddy dolphin) and some species [e.g., Bolivian River dolphin (*Inia geoffrensis boliviensis*), Chilean dolphin (*Cephalorhynchus eutropia*) in South America.

Knowledge of temporal activity patterns should improve understanding of surfacing or foraging strategies of small cetaceans and further help to minimize potential conflicts between cetaceans and fisheries [61]. Our temporal activity overlap analysis between GRD and artisanal fisheries revealed relatively high diurnal overlap during the dry seasons (particularly between November to April). The overlap coefficients show an increasing rate as the season gets closer to the onset of the monsoon, suggesting more competition (including spatial overlap) during the post dry season (or pre-monsoon period: February–May). There appear to be inverse peaks in activity between GRDs and artisanal fishing, suggesting that small cetaceans might be temporally avoiding peaks in artisanal fishing activity. We visually observed three distinct temporal fishing patterns adopted by the fishermen: early morning (0530 h), early afternoon (1300 h), and late evening (1600 h). Thus, dolphins exhibit clear peaks in the early morning (0600–0900 h), around noon (1100–1300 h), and late evening (1700–1800 h), suggesting that management plans implementing active time windows might help to minimize long-term effects on small cetaceans. In the past, most small cetacean management efforts have focused on the number of individuals (or by-catch) and have not considered behavioural ecology in management schemes. Our study shows that regulating fishing activity using small cetaceans surfacing ecology as a basis further helps to reduce the adverse effects of human activities. For example, in our case, restricting fishing activity in the early morning (0300–0900 h) and later afternoon (1500–1900 h) could reduce dolphin and artisanal fisheries temporal conflict by ~40% and promote co-existence of GRD and fisheries in highly fragmented waterways. However, further understanding of underwater behaviours or feeding strategies of small cetaceans in relation to fishing [62], body nutritional condition [63], and examining temporal dynamics of catches [64] will help to more precisely understand the extent and level of interaction.

Globally, a major threat to small cetaceans (and their subspecies) is their interactions with fisheries, either directly or indirectly, which put them in danger of extinction [69]. Careful monitoring and regulation of the artisanal fisheries, including the development of river sanctuaries, are generally essential for providing sustainable benefits to both small population cetaceans and communities [29]. Given the global demise of small cetaceans, existing conservation policies and structure of protected areas still do not afford sufficient protection for small cetaceans from disturbances. For example, in Nepal, conservation policies and establishment of protected areas are entirely based on terrestrial species, and there have been no river sanctuaries established to date to address the issue of aquatic species and safeguard their migratory pattern. The Vikramshila Gangetic dolphin sanctuary in India is one promising conservation effort to recover the GRD population along the continuum of the Ganges River. If the establishment of protected areas is not feasible, using the GRD's maximum observable or response distance supports to establish the distance-based regulations between the boats and the dolphins for no interactions. Thus, recovering viable populations of small cetaceans into their natural habitat is potentially costly due to overlap with human economies in the changing environments. Improving and managing fisheries activities is a feasible and cost-effective approach to minimize conflict; however, incorporating river ecology and cetacean behaviour when formulating a management plan is critical. Thus, further understanding of GDR and other small cetacean diel activity patterns (e.g., via noninvasive surveys throughout the 24-h clock) is required to understand life-history strategies and their requirements, thus supporting efforts to maintain co-existence of fishers and small cetaceans. Managing fisheries should not be limited to satisfying consumers, and should incorporate a wide array of ecological and social benefits [65]. Unregulated fisheries practices threaten not only small cetaceans but also the ecology of the rivers and the biotic communities that rely on them. Thus, setting up the appropriate institutional structure and practical legal framework that allows stakeholders to participate in resource management activities is essential for the successful implementation of artisanal fisheries management. Such approaches have demonstrated some success in fisheries management in Brazil [66] and China [67]. Similarly, Dewhurst-Richman et al. [68] highlighted the importance of institutional regulations to minimize by-catch of GRD in Bangladesh. Given the burden that freshwater systems are experiencing, peer-based off-farm group activities (e.g., aquaculture in ponds), combined with economic incentives using locally available resources and creating cetacean-based market (eco-tourism), should be included within a framework of integrated river basin management.

Methods

Study sites

We conducted this study in two river systems (Sapta Koshi and Karnali) of Nepal (see [5, 12] for geographic distribution, and socio-economic and ecological description of study sites), where the last GRD populations remain [12]. Both river systems represent the upstream range for the GRD distribution in the Ganges River basin [26]. The high dependency of local fishers (78.5%) [5] on these river systems corresponds with heightened fishing intensity and as a result, deep pools which are most preferred by dolphins occupied by fisheries that reduce habitat availability to dolphins, particularly during the dry seasons (October–March) when flow reduced. Though systematic data on the total number of local fishers depending on river systems is not available, a high proportion of the people living close to river systems derive income primarily from the fishing. Greater than 70% of fishers fish more than 4 days per week in these two river systems using a wooden boat comprised of two boat passengers [5]. The Karnali and Sapta Koshi Rivers provide 55 km and 35 km of potential dolphin habitat, respectively. However, this habitat shrinks considerably during the dry season when available space is reduced, and pressure from fishers escalates [5].

Data collection

Dolphin preferred prey size exploitation

Since niche overlap (either diet or space) is considered as a prerequisite of competition, interactions should be understood in connection with the niche concept [25]. Diet overlap (in terms of fish size class) could serve as an effective indicator of current interaction levels [27]. We examined the abundance of dolphins' preferred prey size in the total catch per effort to predict the current direct competitive interactions between GDR and fisheries and the pressure of fisheries on the feeding habits of river dolphins. A catching effort to each net type was defined as an average duration of effective fishing activity of a single trip, excluding travel time (Cast: n= 203, average fishing duration= 3.95 hrs, SD= 2.04; Gill: n=198, average fishing duration= 6.68 hrs, SD= 3.90). Mean catch per effort for each gear type, and average total catch per trip (combined data) by season and river were estimated.

Specific fish sizes have been previously reported as GRD-preferred prey regardless of species [10,28,29]. We considered fish in the range of 3–15 cm total length as preferred fish size regardless of species. We sampled across six 2-month temporal sampling periods between April and March in 2017–2018. We collected 30 landing observations (equal sample size across seasons and between rivers) representing catches per trip for each sampling period. These temporal periods were differentiated to account for potential seasonal variations in fishing stocks. We approached fishers randomly at landing sites immediately before they sold their daily catch of fish. Fish were caught using cast and gill nets during the morning and late afternoon, which are the dominant fishing strategies in both the Karnali and Sapta Koshi rivers. To improve the precision of the estimate, we further stratified landings based on gear types (cast or gill net) and time of the day [morning (0500-1100) or evening (1500-1900) shift] they fished. From the total fish caught, we placed fish greater than 2 cm in total length in a temporary holding tank and then randomly selected ~20–100% of the fish to be measured. We recorded fisheries biological information with fishers at landing sites per event [fish total length or size (cm), total fish caught (kg), distance travelled while fishing (km), gear type, and time of the day they fished their gear]. All fishers survey procedures were carried out in accordance with the ethical standards of the Human Subjects Protection Program at the University of Arizona. Informed consent was obtained from all fishers for being included in the study. All the experiment protocols involving humans were approved by the University of Arizona, Institutional Review Board committee charged with the protection of human research subjects. All methods involving fish and dolphin observations were carried out in accordance with the Department of National Parks and Wildlife Conservation, Government of Nepal, guidelines and regulations. Fish measurement protocols, including dolphin observation methods, were approved by the Department of National Parks and Wildlife Conservation, Government of Nepal (No 1129; 12 December 2016).

Behavioural responses to fishing events

We examined behavioural responses of river dolphins to artisanal fishing boats as an index of disturbance. Here we defined “behavioural response” as any alteration of behavioural state (from one to another state) as a putative consequence of interacting with a fishing boat. Because of immense threats from fisheries to GRD survival (i.e. entanglement) in the Sapta Koshi [12], we observed behavioural states from November through May during 2017–2018 only in the Sapta Koshi River of Nepal. This temporal window represents the dry season, in which conflicts between dolphins and fisheries is heightened as a function of reduced deep pool habitats [17]. As artisanal fisheries in Nepal primarily use only unpowered wooden boats (absence of engine boat or any other heavy commercial traffic vessels) and adopt spatial partitioning of fishing activities (isolated from other fishers) among fishers to avoid potential fishing competition, this assisted us to record behavioural response to each fishing activity. If multiple fishing boats were present or travelling through the area, we excluded such observations from the study. Assuming < 500 m as the maximum observation distance of GRD [30], we divided the river into shore-based transects of 400 m, with one elevated fixed observation station (3 m from the river bank to avoid possible disturbances) in the centre of each transect (at 200 m). This allowed us to classify the dolphin-fisheries interaction points into pressure (treatment) or control zones. We classified the dolphin presence area into control (without boats, control group) or pressure (presence of fishing boat, treatment group) zones using the maximum dolphin response distance to a fishing boat. To classify the zones, we defined maximum dolphin response distance as 200 m (SD 25 m, n = 156); this decision was based on the findings of a pilot study. We conducted a shore-based pilot survey to estimate the approximate response distance, with a distance < 200 m from the fishing boat considered as anthropopressure treatment, and > 200 m classified as the control zone. We classified dolphin behaviour into five states that we could distinguish at a distance from these observation stations: [Dive (D), steep dives with long dive interval showing tails out at the surface before the dive; Travel (T), persistent and directional movement with constant speed and relatively short dive intervals (< 60 s); Surface-Feeding (SF), chase fish with rapid circular dives, rapid directional changes, and circle swimming; Socializing (S), engage in diverse interactions with some physical contact with other dolphins; and Resting (R), low swimming speed with short dive intervals and no group activity].

We applied focal animal scan-sampling surveys as the strategy to record sequential behaviours, but if dolphins were observed together, we considered these groups as a single analysis unit. When a dolphin was first sighted, we classified the initial behavioural state and the behaviour exhibited at the end of a 3-min time interval following the initial sighting. Any individual that disappeared before the 3 min period expired was excluded from analyses. When dolphin was sighted in a group, we recorded the predominant behaviours observed in the group (usually each member engaged in similar behaviour patterns). We recorded a total 406 behavioural observations (n) throughout the season, representing evenly distributed (n=67~68) observations across the months. Out of the total observations, 208 observations were in the control zone, and 198 were in the pressure zone.

Data analysis

Preferred prey size exploitation by fisheries

We used generalized linear mixed models within a Bayesian hierarchical framework to quantify the proportion of catch by fishers that fell within the preferred prey size of dolphins (i.e., the proportion of all fish caught that were within 3–15 cm). The model structure followed:

$$Y_{i,t,j} \sim \text{Binomial}\left(n_{i,t,j}, p_{i,t}\right) \text{ eq (1)}$$

$$logit\left(p_{i,t}\right), \sim \text{Normal}\left(X'_{i,t}\beta, \sigma^2\right)$$

$$\beta_{,} \sim \text{Normal}\left(0, \sigma_\beta^2\right)$$

$$\sigma^2 \sim \text{IG}\ (a, b),$$

$$\sigma_\beta^2 \sim \text{IG}\ (c, d),$$

where $y_{i,t,j}$ is the number of fish caught that were between 3 and 15 cm at site i = 1,…n, during time period t = 1,…T, for boat j = 1,…J. We represent the total number of fish caught at site i by boat j during time t with $n_{i,t,j}$. We were interested in estimating the expected proportion of total fish caught that were between 3 and 15 cm, $p_{i,t}$, given the characteristics of the site described by covariates in the vector $x_{i,t}$. The β coefficients characterize the direction and strength of the relationship between the covariates $x_{i,t,}$ and the logit of the proportion of fish between 3–15 cm.

We developed a suite of *a priori* predictive models to describe differences in proportions $p_{i,t}$ among sites and times (e.g., different combinations of covariates in the vector $x_{i,t}$, Table 1). We assessed the relative strength of these hypotheses by fitting equation 1 to our data for each $x_{i,t}$ in Table 1, and calculating the Deviance Information Criterion (DIC) for each model [31]. We used vague priors for all parameter distributions. Specifically, we used inverse gamma (IG) priors for σ^2 and σ^2_β and set a = b = c = d = 0.0001. We fit each model to our data using a custom Markov chain Monte Carlo algorithm written in R statistical software [32]. For each model fit, we obtained two chains of 50,000 iterations after a suitable burn-in period. We assessed chains visually and also used the Gelman-Rubin convergence diagnostic. All chains appeared to converge and had Gelman-Rubin diagnostic values < 1.01. We further assessed model fit using Bayesian P-values [33,34]. We used a random effect for each location and time (i.e., line 2 in equation 1) because preliminary analyses suggested that a generalized linear model without a random effect had extreme lack of model fit (i.e., Bayesian P-value = 1). After incorporating the random effect, we found no evidence for lack of model fit for any model we considered (Table 1). Furthermore, we estimated the posterior distributions for each of these covariates using a Beta posterior distribution function, with the binomial distribution as a sampling distribution type. We simulated 10,000 random samples from this posterior distribution taking a uniform Beta before summarizing results for each gear type and season.

Behavioural changes to artisanal fishing boats

We applied propensity matching score analysis (PMS, conditional probability) to estimate the causal effects of treatment (presence of fishing boat) on GRD behaviour change [35]. As our observations were non-random, we used PMS to mimic the conditions of a randomized controlled trial using all the information (covariates) sufficient to predict the probability of receiving the treatment effect. Thus, in PMS, the likelihood that each observation gets a particular treatment effect is the same for all observations (either control or treated), such that they depend only on the known explanatory variables of an observation. Targeting fishing activity as the primary factor, other than natural processes, for behavioural distraction, we included seasons (month) and time of the day [morning (400-11:59), afternoon (1200- 14:59), evening (1500- 1900)] as additional explanatory variables. As we are concerned only with the fishing activity, we assumed that these covariates are sufficient to predict the effect of the treatment. To estimate the propensity score, we used a Generalized Linear Model (GLM) using logit link function in which treatment status (treatment vs control environment) regressed on the baseline characteristics of seasons (month) and time of the day. We compared four *a priori* models with the explanatory variables [model1: time of the day, model2: seasons, model3: time of day + seasons, model4: time of day*seasons] and used the model with the lowest AIC value (Akaike information criterion) to predict the effect of the treatment. The model with the covariate time of the day (model1-AIC 549.640; model2- AIC 555.585; model3 AIC-550.024, model4- AIC 549.996) was best fitted to estimate the effects of explanatory variable on the probability of receiving treatment (e.g., anthropopressure-fishing boat). We forwarded this model to estimate the propensity scores. To ensure that our observations were randomly assigned, we visually checked propensity scores overlap between two treatments and found a good degree of overlap (between 0.32 and 0.78). Furthermore, to ensure that our covariate (time of day) provides sufficient information to tell the dolphin's probability of receiving the treatment, we visually checked the balance of covariate across treatment groups by stratifying propensity matching scores into equal-sized quintile strata (Q1, Q2, Q3, Q4, and Q5) [36]. We examined the distribution of covariate within the quintiles of the propensity scores and observed that the distribution of propensity scores closely aligned (no major differences) between treatment groups for explanatory variable. The balanced covariate within quintiles of the propensity score gives an opportunity to estimate unbiased treatment effect (fishing boat presence) within each propensity score stratum [37]. Thus, we estimated the average treatment and control effects in each propensity score quintile and also derive the overall probability of receiving the treatment. All statistical analysis was done in R and PMS estimated using package 'matching'.

Activity overlap analyses

We used the behavioural response (time of dolphin first detection) and fishing (time of fishing activity lasting ≥ 10 min) event observational datasets to analyze the diel activity overlap between fisheries and river dolphins. We treated the times of dolphin behavioural observations and the times of actively engaged fishing with cast or gillnet observations as random samples from the continuous distribution of the 24-h clock. However, our inferences were limited to the diurnal portion of the day (0600–1900 h), because we did not make observations at night and fishing activity was mostly absent during night hours. We used the kernel density overlap approach to fit a von Mises kernel density to each activity distribution for dolphins and humans [38]. We calculated the coefficient of overlap (Δ) as the proportion of diel overlap between activity patterns of dolphins and humans, which bounded between 0 (no overlap) and 1 (complete overlap) [38]. We estimated the overlap coefficients for bimonthly periods to account for seasonal variation in these activity patterns and to ensure robust sample sizes for inferences [39]. We performed 10,000 iterative bootstraps to determine the 95% confidence intervals within the 'overlap' package in R to account for uncertainty in our estimates [40,41].

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Author Contributions

S.P. and J.L.K. conceived the study. S.P. and J.L.K. designed the work and S.P. involved in the data acquisition processes. S.P. and M.V. C. conducted data analyses. S.P., J.L.K., and M.V. C. wrote the manuscript and all the authors reviewed the manuscript and approved the final version.

Data availability

All data supporting the conclusions of this article are within the paper.

Competing Interests Statement

The authors (S.P., J.L.K., and M.V.C.) declare no competing interests.

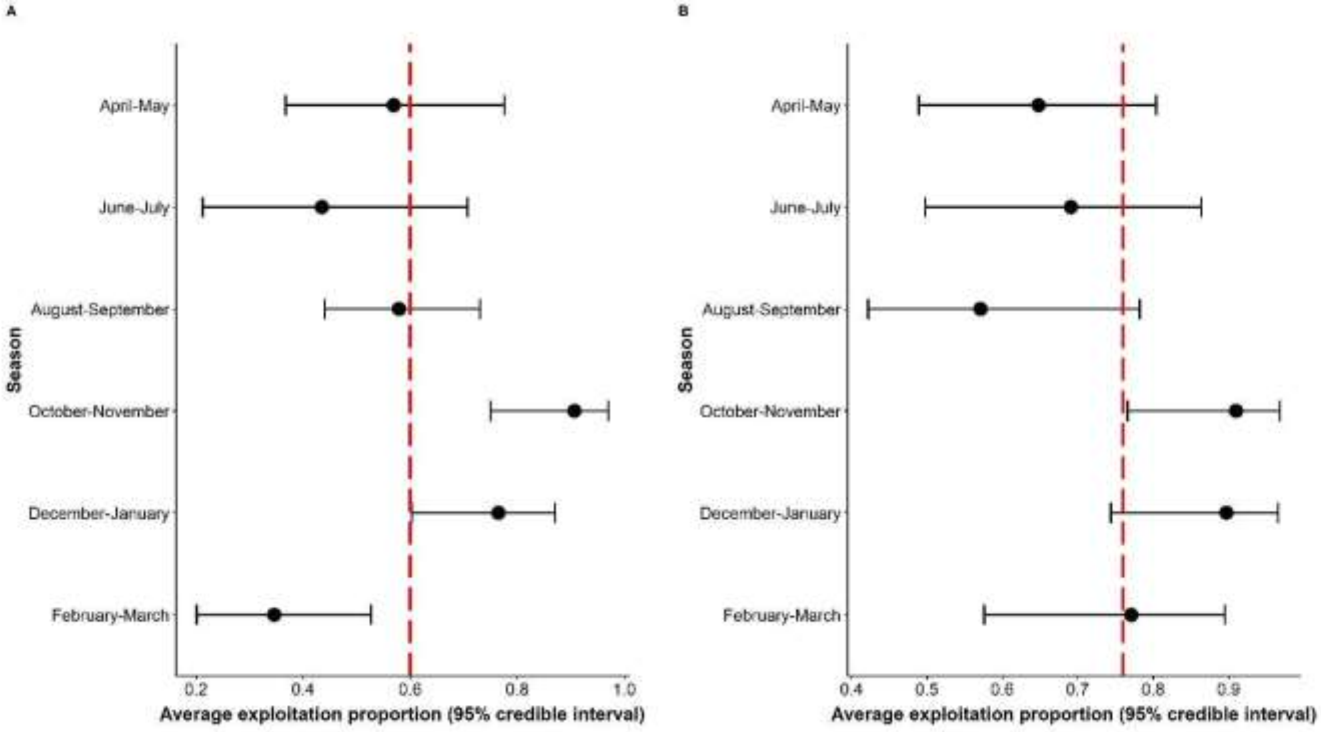

Figure 3.1 Mean exploited proportion over season, where the red vertical line represents the annual average (A- Karnali; B-Sapta Koshi). For both river systems, October–January received a higher amount of exploited proportion, which is greater than the yearly average. The black dot in each error bar represents the mean exploited value for the respective season.

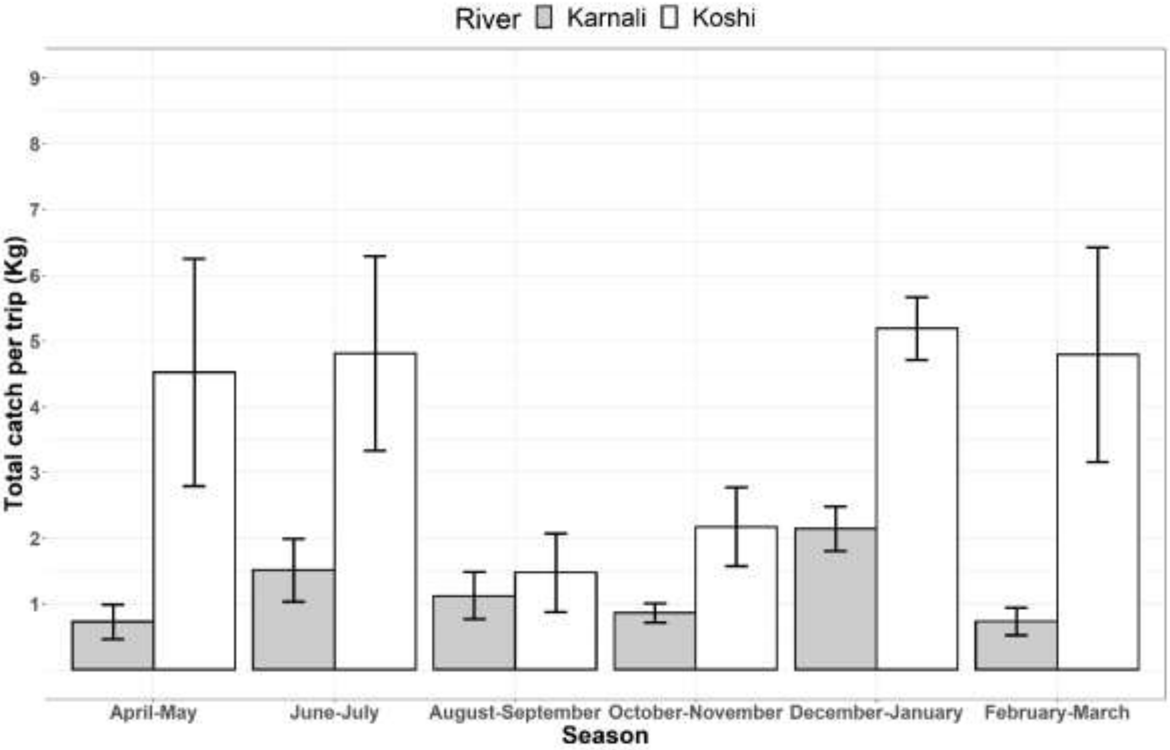

Figure 3.2 Seasonal average total catches per effort (with 95% CI level) in the Karnali and Sapta Koshi River systems. The Sapta Koshi River shows a two-fold higher level of harvest compared to the Karnali River, suggesting a high rate of resource exploitation in the Sapta Koshi river of Nepal. The rate of exploitation is higher from December through July, which is the temporal range with most top fisheries-dolphin conflicts recorded.

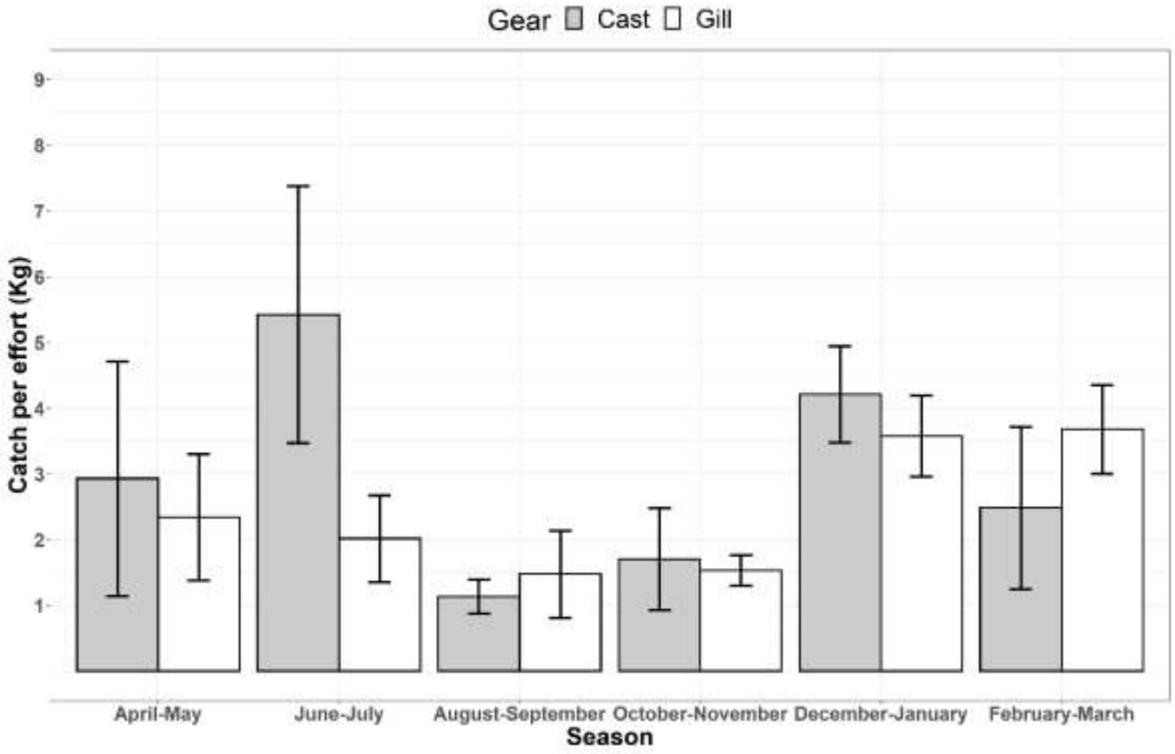

Figure 3.3 Average catch per effort in terms of gear types (Gill and Cast nets). During the low water season (December–July), the effect of the Cast net is higher compared to the Gillnet, suggesting the significance of the regulation of the cast nets to minimize the resource competition and potential risk of animal depredation.

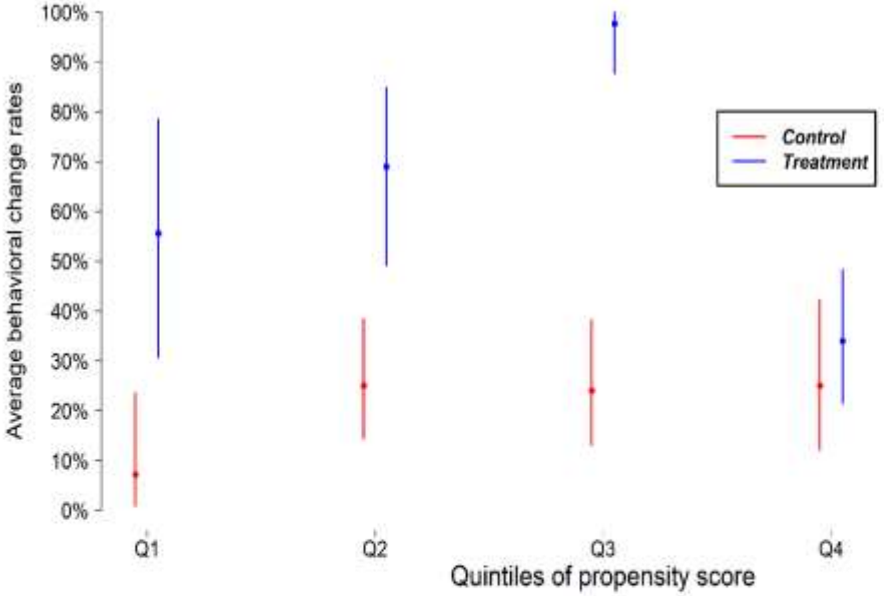

Figure 3.4 The average behavioural change (overall) percentage by group (treatment and control) within an equal size propensity matching score strata with 95% confidence intervals. Blue and red bars represent treatment (boat presence) and control effects (without fishing boat), respectively. In each pair, the average treatment effect is higher than in the control effect.

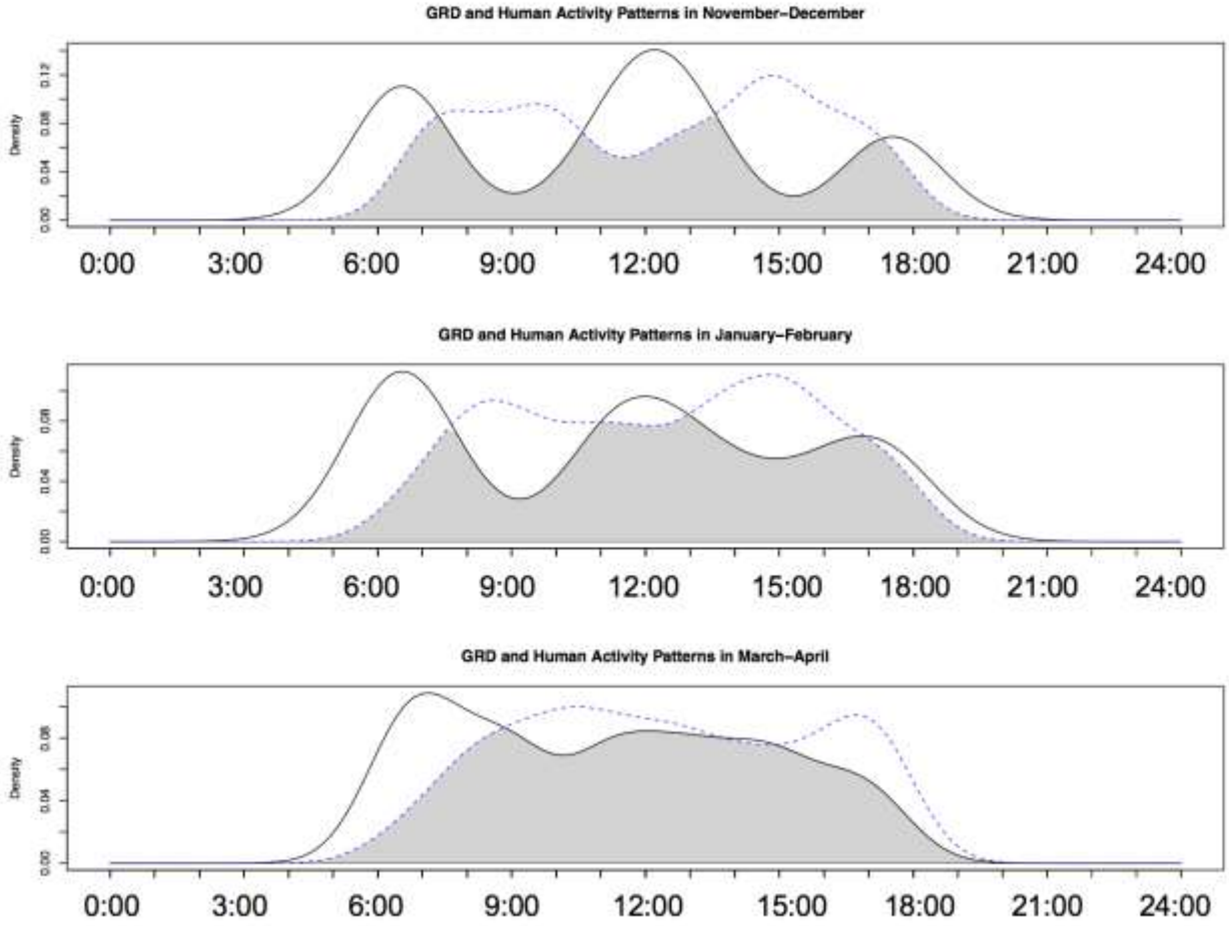

Figure 3.5 Black lines indicate activities of dolphins, and the humans are blue dotted lines. The overlap increases during each period and from one period to the next (shaded grey), showing a clear trend that there are inverse peaks of activity between dolphins and humans.

Table 3.1 Proposed covariates for the model described in equation 1, model comparison via Deviance Information Criterion (DIC), effective number of parameters (pD), and Bayesian P-values used to assess model fit for the fishing data. Models that contained interactions also contained the additive covariate. Among the tested models, model 1 performed best.

ID	**Model ($x_{i,t}$)**	**DIC**	**pD**	**Bayesian P-value**
1	**Gear+Season**	**1203.789**	**217.033**	**0.479**
2	Gear+Season+Gear*Season	1203.939	215.142	0.488
3	Gear*Season+River	1210.288	215.074	0.515
4	Gear+Season+River	1211.893	216.385	0.484
5	Season+Time+Effort	1214.754	222.301	0.491
6	Season*Time	1217.129	222.483	0.5
7	Season+Time	1219.104	223.016	0.504
8	Season	1219.676	222.91	0.504
9	Time+Effort+Distance	1220.401	225.234	0.503
10	Season+Time+Effort+River	1221.328	221.329	0.51
11	Weight+Season	1221.518	222.514	0.5
12	Effort	1222.943	226.32	0.502
13	NULL	1223.651	225.923	0.509
14	Weight+Season+ Weight*Season	1224.025	222.837	0.516
15	Season*Time+River	1225.449	222.444	0.515
16	Weight+Season+River	1226.818	222.617	0.508
17	Season+River+Time	1227.149	222.9	0.512
18	Time+Effort+Time*Effort	1227.832	226.035	0.516
19	Season+River	1228.121	223.183	0.51

20	Season+River+Season*River	1228.513	222.499	0.511
21	Time+Effort+River	1228.983	226.851	0.517
22	Season*River	1229.077	223.013	0.513

Table 3.2 Coefficient of overlap (Δ) estimates and 95% confidence intervals of the diel activity patterns of Ganges River dolphins (GRD) and humans during three sampling periods: November–December, January–February, and March–April in the Sapta Koshi River, Nepal.

Period	Number of Detections		Coefficient of overlap (Δ)	Lower CI	Upper CI
	GRD	Humans			
November-December	51	189	0.604	0.478	0.726
January-February	45	187	0.725	0.615	0.850
March-April	127	195	0.832	0.756	0.912

APPENDIX D: BEHAVIORAL RESPONSES TO SPATIAL HETEROGENEITY IN ENDANGERED GANGES RIVER DOLPHINS

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(In the format of *Animal Conservation*)

Behavioral responses to spatial heterogeneity in endangered Ganges River dolphins (*Platanista gangetica gangetica*)

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Abstract

Risks to small riverine cetaceans were highlighted after the recent extinction of the Chinese River dolphin (*Lipotes vexillifer)*. Cetaceans, such as the Ganges River dolphins (GRD; *Platanista gangetica gangetica*), with small population sizes and limited geographic distributions, are more vulnerable to the risk of extinction in the Anthropocene. Although the social and behavioral needs of cetaceans have been identified as potential factors influencing their vulnerability to human disturbances, how small riverine cetaceans adjust their behavior and activity patterns in response to space (habitat)-time (time of day) variations remains poorly known. We examined the behavioral activities of endangered riverine cetaceans, GRD, by collecting echolocation clicks using underwater stereo acoustic data loggers from three spatially stratified habitats over a six months temporal scale in the Sapta Koshi River system of Nepal. Our research revealed that GRD exhibit behavioral variability in response to spatial heterogeneity, indicating diverse environmental requirements to GRD persistence. Such unevenly distributed behavioral activity and their movement duration across the habitats but not across the time of the day suggested variability in GRD behavior is likely regulated by the habitat structure irrespective of the time of the day. A higher value of the diel coefficients (the proportion of animals active throughout the day) across space, season, and time of the day indicate that environmental factors marginally regulate activity patterns. Instead, GRD consistently displayed nocturnal activity peaks despite considerable variation in diurnal activity, indicating that river dolphins may adopt nocturnal refuges as a temporal response to human disturbance in highly regulated river systems. Significance of heterogeneity in habitats and the management of human disturbances improving the persistence of riverine cetaceans is emphasized and discussed. We reported behavioral ecological information in relation to space-time variations, which is essential for formulating river dolphin recovery plans that aims to connect ecological perspective to planning and management.

Introduction

Increasing interactions between freshwater endangered cetaceans and fisheries has been reported around the globe (Dewhurst-Richman et al. 2020; Basran & Rasmussen 2020; Paudel & Koprowski 2020). Current research suggests that over 300,000 whales and dolphins die annually due to entanglement in fishing gear (IWC 2020), suggesting a need for an extensive research effort to understand cetaceans life histories and their likely exposure levels to human activities. Social and behavioral needs of cetaceans are potential factors that define vulnerability to human exploitation and disturbance. Survival and reproductive success of cetaceans, may be influenced by social and behavioral factors, making them more vulnerable to exploitation (Wade et al. 2012). Recently, the direct killing of cetaceans has been reduced, but the indirect deaths of small cetaceans have increased (Jefferson 2019), putting some small riverine cetaceans in danger of extinction. The majority of the ten most endangered cetaceans belong exist in freshwater ecosystems (Jefferson 2019). Several small freshwater cetaceans are in danger of extinction due to human activities, and may follow the Chinese River dolphin (*Lipotes vexillifer*), which became functionally extinct in 2006 (Turvey et al. 2007). Therefore, it is imperative that we understand how susceptible small cetaceans are to human impacts.

Habitat degradation, prey depletion, noise pollution, bycatch, and depredation risks upon freshwater cetaceans from anthropogenic activities are recognized as primary drivers of their decline (Jefferson 2019). One human activity that influences the lives of river cetaceans is the disturbance by damage or destruction of preferred locations where they perform essential life history activities such as birthing, calf rearing, or feeding. Thus, species confined to particularly small geographic region, such as the vaquita (*Phocoena sinus*), Chilean dolphin (*Cephalorhynchus eutropia*), and South Asian river dolphins (*Platanista gangetica*), are at higher risk to human disturbance, and could go extinct unless responsible management is implemented. Thus, behavioral and ecological requirements need to be understood to minimize the habitat pressure. One way to reduce pressure on habitat is to understand cetacean behaviors and diel activity patterns that influence a wide range of ecological and physiological processes (Vazquez et al. 2019). These behaviors can help us understand the overlap between species' ecological needs (e.g., foraging, resting, social or surfacing activities) and human activity (e.g., fishing activity). In this way, anthropogenic pressure can be minimized. Unfortunately, our knowledge of underwater behaviors and diel activity of river dolphins, especially endangered Ganges river dolphins (GRD), which appears to have narrow habitat requirements and geographic range, is limited and hindering conservation efforts intended to reduce human pressures.

Previous studies on GRD underwater behaviors primarily occurred in laboratory settings (Herald et al. 1969; Mizue et al. 1971). Although recent studies have focused on capturing the sound source of free-ranging GRD to characterize annual behavioral patterns (Sasaki-Yamamoto et al. 2012) and click characteristics (Jensen et al. 2013), these studies did not explicitly report the underwater behaviors and diel activity patterns in response to space and time variations. Further, the number of clicks exhibited by GRD also offers the opportunity to understand their underwater surfacing behaviors. The number of clicks changes significantly when behavior transitions from traveling to foraging/diving activity in odontocetes (Au 1993; Akamatsu et al. 2007; Sugimatsu et al. 2009), offering an opportunity to classify and compare underwater behaviours in relation to space and disturbances. A study showed that the number of clicks by GRD drastically declines while changing movement from stationary to travel in Ganges River, India (Sugimatsu et al. 2009). Similarly, the number of clicks increased during foraging/or deep diving than traveling in white-beaked dolphins (Rasmussen et al. 2013). In addition to the number of clicks, the acoustic trajectory (a series of click trains which is separated by >5 minutes from previous or subsequent click trains) duration also offers information regarding the duration of the dolphin’s habitat use near the hydrophone area offering an opportunity to understand species-space relationships.

To advance knowledge in the understanding of the ecology of GRD behaviours and diel activity, we ascertained underwater movement behaviors and diel activity patterns of the GRD using dolphin-emitted echolocation clicks collected by stereo acoustic data loggers from three spatially and temporally stratified habitats in the Sapta Koshi River system of Nepal. The findings of this study provide insight on the timing of activity peaks (proportion of day animals are active) and significance of spatial heterogeneity to GRD life history activities, thus helping broaden our knowledge regarding how GRD compromises their social and behavioral activities while responding to human activities, particularly fishing and noise, in the Anthropocene.

Methods

Study area

This study was conducted in the Sapta Koshi River system of Nepal (Fig. 1). We collected GRD echolocation clicks representing three hydro-physically stratified sites [deep pool (DP), confluence (CF), and straight channel (SC), see Table 1 for definition] frequently occupied by the GRD (Paudel et al. 2015) assuming dolphin echolocation clicks differ significantly across sites and behaviors (Jones & Sayigh 2002). This study area is heavily used by the artisanal fishing communities using wooden boats throughout the daylight hours (Paudel et al. 2016). As a result, a high day-hour temporal activity overlap between GRD and fisheries was recorded in the study area that intensifies interactions (Paudel et al. 2020).The clicks were recorded from November 2017 through May 2018, and for each habitat a two-month continuous recording were made [November–January (DP), December–February (CF), and March–May (SC)]. This survey period represents diverse seasons so we consider this temporal scale as a season. This research was conducted under a research permit issued to the principal author of this paper by the Department of National Parks and Wildlife Conservation (DNPWC), Government of Nepal. All the observation procedures comply with regulations developed by the DNPWC.

Data collection

Underwater stereo acoustic data loggers (A-tags; Marine Micro Technology, Saitama, Japan) were used to capture the click trains emitted by the GRD. A long-life A-tag with extended life battery cases was deployed, which possessed the capacity to capture data continuously for one month. GRD clicks were monitored and captured using fixed type A-tag; this permitted us to attach A-tags (T-shape hydrophone) firmly on a fixed bamboo stick positioned at half of the depth of the selected habitat (DP, CF and SC) and 4 m away from the riverbank (see detail in Table 1). The A-tag, which consists of two hydrophones, a passive band-pass filter (55–235 kHz), CPU, flash memory (128 MB), and batteries (two UM-1 batteries), was fixed parallel to the direction of the river flow. Details about the A-tag hardware specification, signal processing (sensitivity range), and auto-removal of noise contamination by A-tag has been documented previously in detail (Akamatsu et al. 2005). The A-tag records intensity of each click, the absolute time of the sound arrival, and the sound source direction of clicks encoded in the time arrival difference between the two hydrophones. When a sound is triggered, either in the primary or secondary hydrophone, an independent high-speed counter begins to measure the sound arrival time difference until the other hydrophone is triggered. That means only a series of clicks recorded at both hydrophones is considered a valid click train, and also offers the opportunity to exclude extraneous noise. The A-tags sample click trains at 2 kHz, the time resolution of the click detection equal to 0.5 milliseconds (ms). The hydrophone sensitivity was calibrated in advance and a detection threshold level set at 132 $dB_{p\text{-}p}$ re. 1µPa. Acoustic sensing distance was estimated using a standard formula (Akamatsu et al. 2007). This estimated sensing distance was further bootstrapped ($N = 10000$) to obtain the uncertainty on the estimated acoustically sensing distance.

Acoustic moving type and its relevance to GRD behavioral activity

Previous studies on underwater behaviors of GRD relied heavily on captive environment settings (Herald et al. 1969; Andersen & Pilleri 1970; Mizue et al. 1971) and visual observations(Sinha et al. 2010). We followed the procedure developed by (Sasaki-Yamamoto et al. 2012) for classifying underwater movement into three categories based on the relative sound source angle of GRD clicks: Staying (S), Movement A (A), and Movement B (B). Movement A is defined as an acoustic trajectory in which the relative sound source angle constantly changes to the positive or negative direction over time, representing animal traveling in either direction (upstream or downstream), whereas movement B is defined as tortuous trajectory with at least one flexion point, indicating animal engaging in diving behavior related to foraging or long surfacing activity in a particular area (See details in Sasaki-Yamamoto et al. 2012 regarding the trajectory differentiation). Staying is a trajectory with a very narrow range (i.e., 10–20°) change in a relevant source of sound direction.

We further differentiated these movement categories using the pattern of the number of clicks and trajectory duration. We defined two different movement types (A and B) if the trajectory duration and click number were significantly different across the moving types. But in the case of remaining stationary, we only considered the relative angle of the sound source direction as its number of clicks and trajectory duration can vary. Before making ecological inferences about underwater behaviors of GRD, we examined the differences in the number of clicks and trajectory duration among all the pairs of three moving types to avoid the risk of misleading conclusions related to GRD behaviors. Collectively, we refer to all underwater moving types (A, B and S) as behaviors of GRD (hereafter behaviors).

Acoustics click processing and analysis

Recorded clicks were pre-processed in Igor Pro 7 software (WaveMetrics, version 2020.) using custom software written by Tomonari Akamatsu for A-tags (Marine Micro Technology, Saitama, Japan). This custom written file is primarily used for noise reduction and to create a time-sequential statistical data of each click train captured. Dolphins emit series of echolocation clicks that exhibit a click train, which is a series of pulses (or clicks) with click intervals $\leq$ 100 ms (Au 1993). To exclude extraneous noises from our datasets, we kept a click train with intervals ranging from 20 –70 ms with $\geq$ 5 pulses in a pulse train, which with high probability represents signals coming from the GRD (Sasaki-Yamamoto et al. 2012). Before defining animal movement type, we first identified the acoustics trajectory of the dolphin, separated by > 5 minutes from previous or subsequent click trains. The time of the first click train in the trajectory is considered as the start time, and the time of the last click train is considered as the end time of a trajectory, which enables us to calculate trajectory duration. Then, within a trajectory, pulse trains were visually analyzed to assign movement type to the trajectory based on the changes in relative angle of the sound source direction. We discarded a trajectory if more than one animal was present to avoid underestimating click and/or inter-pulse intervals. Trajectories in the ranges of 0-50° and 130-180° were also eliminated to avoid the risk of false classification of the movement type. Only valid trajectories were forwarded for subsequent analysis. All analyses are based on the relative angle of the animal's sound production; thus, it only indirectly considers animal body movement.

Statistical analysis

Because of the unequal sample size and unequal variance in observations across sites, we used Dunnett-Tukey-Kramer pairwise multiple comparison tests (DTK) to compare the pairwise mean of the number of clicks and the trajectory duration among the pairs of habitats and moving types using the DTK package in R-Studio (Dunnett 1980). We bootstrapped (N = 10,000) parameters – number of clicks, trajectory duration, click interval – to report uncertainty on the estimates using *boot* package in R-Studio.

Chi-square test (χ^2) was used to examine the association between: movement and habitat, movement and time of day [**Twilight** (activity around sunrise and sunset time: 0500–0659, 1700 –1859; **Day** (activity during day-time): 0700 –1659; **Night** (activity during night-time): 1900 – 0459). The relation between trajectory duration and habitat type was examined by simple linear regression (LR) using the *lm* package in R Studio. Before fitting the model, trajectory duration was normalized using the log transfer.

Because of overdispersion on the number of clicks, we used a negative binomial Generalized Linear Model (GLM) to examine the relationship between the number of clicks and click-interval using the *glm.nb* function available in the MASS package in R-Studio. Ecological variables [explanatory variables: season (November–February, March–May), habitat type, time of the day, moving type)] that controlled the number of clicks were examined using Poisson GLM by adding trajectory identification number as a random effect in the model to account for the issue of overdispersion on dependent variable using *glmer* function available in the lme4 package in R. We built six possible models (Table. 2) and used Akaike Information Criteria (AIC) to select the best model that explains the variation of click numbers.

We estimated the overlap coefficient to examine the similarity of click-interval across space, season, and time of the day. Diel activity (the proportion of animals active throughout the day) of GRD was calculated using the time of acoustic detection. We fitted von Mises kernel density to the time of acoustic detection and estimated the overlap coefficient (with bootstrapped N = 10,000) to identify the similarity or difference in the diel activity pattern across space, season, and time of the day. The overlap coefficient was estimated using the *overlap* package in R-Studio (Ridout & Linkie 2009). Differences among parameters were considered significant when the probability (p) was equal to or less than 0.05 in all the data analyses.

Results

Trajectory characteristics and moving type

Acoustic recordings were made over 4110 hrs (deep Pool 1405 hrs; confluence 1266 hrs; straight channel 1439 hrs), in which the total number of valid trajectories recorded was 1413 (conflunce-99, deep pool-1042, straight channel-234) comprising a total of 861 hr. The average trajectory duration of confluence (mean = 57.50 min, bias = 0.14, SE = 6.86) and deep pool (mean = 39.66 min, bias = 0.002, SE = 3.40) was substantially higher than for the straight channel (mean = 15.05 min, bias = 0.002, SE = 1.54, Fig. 2). We detected pairwise significant differences in the trajectory duration among all habitat pairs, except deep pool and confluence (DTK test, p = 0.05). We found habitat type to be a significant contributor to the trajectory duration (LR, R^2_{Adj} 0.04, F = 33.55, $p < 0.001$).

Disproportionate distribution of the movement type across habitats reveals that movement type is dependent on habitat ($\chi2 = 123.17$, $p < 0.001$; Fig. 3). Average trajectory duration of diving was longer than remaining stationary and travelling, respectively (Fig. 2, Table 3). Trajectory duration differed among all the movement type pairs (DTK test, $p = 0.05$). The proportion of each movement type was equally distributed across the time of the day ($\chi^2 = 0.89$, df = 4, $p = 0.92$, Fig. 3).

The average number of clicks in each trajectory was considerably higher in the deep pool than in the confluence and straight channel (Fig. 4, Table 3). Number of clicks was higher in diving than in stationary and travelling behaviors (Table 3). The average number of clicks differed among all pairs of habitat and movement types (DTK, $p = 0.05$). The number of clicks was higher during the night time ($N = 607$, mean = 100.31, 95% CI 22.89) compare to day time ($N = 540$, mean = 171.33, 95% CI 70.56) and twilight hours ($N = 228$, mean = 136.40, 95% 36.29).The number of clicks did not differ among any pairs of behaviors across time of day (DTK, $p > 0.05$).

Our results show no relationship between number of clicks and click interval [GLM, $\beta = –1.002$, SE = 0.03, $Z = –0.07$, $p = 0.94$]. The variation in the number of GRD clicks is controlled by the additive effect of habitat and movement type (Table 2); however, the parameter, habitat type, was weakest over movement type. While GRD shift from travelling to diving behaviour, the number of clicks increases in diving ($\beta = 3.78$, SE= 0.73, $Z = 1.82$, $p = 0.05$) and decreases when stationary ($\beta = -0.70$, SE= 1.02, Z= –0.33, $p = 0.73$). The second-best model included only movement type with a slight decrease in AIC without habitat type.

A shorter average click-interval length was recorded in straight channel ($N = 234$, mean = 31.80 ms, 95% CI 1.41) than in deep pool ($N = 1042$, mean = 33.38 ms, 95% CI 0.85) or confluence ($N = 99$, mean = 51.54 ms, 95% CI 3.69) respectively. Average click-interval duration differed among all pairs of habitats, except the pair of the straight channel and deep pool (DTK, $p = 0.05$). Average click-interval duration is longer in diving ($N = 1040$, mean = 35.08 ms, 95% CI 0.95) than in remaining stationary ($N = 85$, mean=32.74 ms, 95% CI 2.14) or travelling ($N = 250$, mean = 32.24 ms, 95% CI 1.45). The average click intervals differed only between traveling and diving, except for the pairs of traveling and stationary and diving and stationary (DTK, $p = 0.05$). The average click interval of all movement types was higher in the deep pool (except diving) compared to straight channel and confluence, respectively. The estimated average acoustic sensing range of GRD was 25.817 m (range= 0.648-74.55, 95 % CI 25.248-26.40). The higher average sensing distance was recorded in CF (N=99, mean=38.66 m, SE= 1.39) than in DP (N=1042, mean= 25.03 m, SE= 0.32) and SC (N=234, mean= 23.85 m, SE=0.53) habitats respectively. The marginal difference was recorded on sensing distance across movement types (A: N= 250, mean= 24.19 m, SE=0.55; B: N=1041, mean= 26.30 m, SE= 0.36; S: N= 84, mean= 24.57 m, SE= 0.81).

The average click interval was 34.43 ms (95% CI range 26.61835.96) in a pooled dataset, with a good degree of overlap of click intervals across movement and habitat type (Fig. 5). Considerable overlap was observed among all pairs of movement types [travelling–diving: estimate = 0.77, bias = –0.01, SE = 0.03; travelling–stationary: estimate= 0.64, bias = –0.03, SE = 0.06; diving–stationary: estimate = 0.69, bias = –0.03, SE = 0.05). Across the habitats, only the pair of deep pool–straight channel (estimate = 0.81, bias = –0.03, SE = 0.03) holds substantial overlap of click intervals compared to confluence–deep pool (estimate = 0.28, bias = –0.001, SE = 0.02) and confluence–straight channel (estimate = 0.26, bias = –0008, SE = 0.03). Season did not influence the duration of click intervals (LR, F = 0.18, $R^2_{Adj} = -0.0005$, $p = 0.66$).

Diel activity pattern

Diel activity of GRD substantially overlapped across space [straight channel-deep pool: estimated overlap = 0.841, bias = –0.015, SE = 0.029; straight channel-confluence: estimated overlap = 0.783, bias = –0.016, SE = 0.042; deep pool-confluence: estimated overlap = 0.869, bias = –0.024, SE = 0.031) [Fig. 6] and season [seasonal overlap: estimated overlap = 0.838, bias = –0.0162, SE = 0.028] [Fig. 7]. Over all habitats, GRD consistently demonstrated bimodal nocturnal activity with peaks before sunrise and after sunset, avoiding human activity (mostly fishing activity) during the day for most of the time (Fig. 6 & 7). But in the case of Confluence, GRD showed trimodal peaks, short duration highest peak immediately during afternoon and two peaks before sunrise and after sunset.

Seasonal diel activity patterns of GRD displayed similar nocturnal activity with bimodal peaks before sunrise and after sunset. However, the density of the day hours activity was substantially reduced in the post dry season (March–May) compared to peak dry season (November–February) [Fig. 7]. High proportion of activity was recorded during the night hours (N = 1238, mean = 0.450, 95% CI 0.431-0.469) compared to twilight (N = 437, mean = 0.158, 95% CI 0.1458-0.173) and day hours (N = 1075, mean = 0.390, 95% CI 0.3728-0.409).

Discussion

Trajectory duration and the number of clicks differed among movement types (Fig. 2 & 4), which supported our assumptions of the movement classifications based on echolocation recordings. As this acoustic approach of underwater behavior classification was validated by Sasaki-Yamamoto et al. 2012 using an independent visual survey, acoustically we confirm that movement A refers to traveling, and movement B indicates diving or surfacing activity in a particular area for a long duration. Substantial differences in the trajectory duration across habitats suggest that GRD disproportionally use deep pools and confluences most. Further, unevenly distributed frequency of the movement type across the habitats but not across the time of the day suggested variability in GRD behaviors may be regulated by the habitat structure irrespective of the sunrise and sunset time or the time of the day. This result is consistent with an interpretation that variations in light intensity did not influence the riverine cetaceans sonar behaviors (Herald et al. 1969). Our results also predict that trajectory duration significantly correlates with habitat type.

Heterogeneity in habitats likely improves survival and recruitment by mediating life history strategies in riverine ecosystems (Stoner 2009). Studies on riverine cetaceans frequently report use of deep pools and confluences by riverine dolphins (Pavanato et al. 2019). Such habitats are valuable to river cetaceans due to rich biological productivity, which in turn increases prey availability and modulates easier prey capture (Smith et al. 1998). However, the primarily mechanism for selecting such hydro-physical habitats is likely associated with improved diving physiology, facilitated by suitable hydro-physical attributes of such habitats (Skrovan et al. 1999). As the diving and swimming movements of river cetaceans is energetically costly, the biological significance of using such habitats may offer opportunity to conserve energy and limit blood oxygen, which may improve their foraging efficiency by extending the duration of dives (Skrovan et al. 1999). Further, hydro-physical attributes of such habitats are characterized by larger cross-sectional area combined with suitable depth and velocity, which likely support dolphin's energetic efficiency by offering maximum usable area.

Habitat-driven behaviors and disproportionate distribution of trajectory duration across space likely indicate productive and diverse environmental requirements to riverine cetacean persistence. Previously, patchy occupancy of GRD was reported across the species distribution (Smith et al. 1998; Paudel et al. 2015). Similar heterogeneity in habitat was reported in common bottlenose dolphins (*Tursiops truncatus*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Ingram & Rogan 2002). The majority of the small cetaceans in the western Ligurian Sea and southwestern Mediterranean short-beaked common dolphin (*Delphinus delphis*) also exhibited specific preference of physical habitats (Azzellino et al. 2008). Such specific habitat preferences were often linked to the heterogeneity in their habitat (Samuel et al. 1985). However, incorporating prey availability information with acoustics data can provide a better understanding of the behavior.

As human pressure increases and riverine habitats are colonized, adopting diverse habitats and modifying behaviors indicate the degree of plasticity of a species in adjusting to human-induced disturbance and habitat alteration. However, such behavioral responses may be maladaptive or insufficient to offset the animal's fitness loss (Wong & Candolin 2015). A recent study indicates that increases in ambient noise level in the riverine ecosystem altered the GRD acoustic activity, which may induce metabolic stress (Dey et al. 2019). Even though habitat-driven variation in behavioral patterns likely improves their persistence under human pressure, this will likely affect processes that regulate their population's size. The declining population size and recent increased bycatch of riverine cetaceans indirectly indicate the effects of anthropogenic effects in the long term (Dewhurst-Richman et al. 2020). This finding highlights the importance of heterogeneity in the spatial environment for riverine dolphins' persistence along with mitigating deleterious impacts on the dolphins' population size. Maintenance of a natural flow regime along with habitat management and protection may offer diverse physical habitats, allowing cetaceans to persist and contribute to the ecosystem diversity.

Variation on number of clicks associated to the behavioral type in which biosonar clicks dramatically changed when movement shifts from one mode of locomotion to another, such as traveling to foraging (Au 1993) . In line with this finding, our model also predicted that behavior controls the number of clicks. This result further supports our movement classification assumption as well as that of previous studies. We also noticed appreciable overlap of the click-interval across space, season, and time of the day. We suggest considering the number of clicks and trajectory duration to differentiate movement type is a more reliable indicator than click-interval to classify behaviors of riverine cetaceans. Further, understanding the click number and click-interval pattern across search, approach, and catch phases of cetacean clicks may add further insight on click patterns (see details in Rasmussen et al. 2013 for more information about phases of clicks).

The substantially reduced density in diel activity patterns during the day hours indicating that GRD uses hours when anthropogenic activities are less active (night hours). The three distinct temporal patterns of fishing activity (early morning, early afternoon, and late evening) adopted by fisheries in the same study site were reported by previous study (Paudel et al. 2020). This temporal pattern of fishing in the artisanal fishery is evidently reflected in diel activity patterns of GRD (day hours avoidance, Fig. 6), and avoidance of humans by GRD further accelerated during the post dry season (March-April, Fig. 7) when artisanal fishing pressure is intensified and habitat reduced (Paudel & Koprowski 2020). Although high dolphin activity during night is commonly attributed to the foraging of the vertical migrating prey species (Sasaki-Yamamoto et al. 2012; Cascão et al. 2020), our study shows that intense night activity (diel density) of GRD is likely associated with consequences of anthropogenic effects (fishing activities), shifting river dolphin activity towards nocturnality due to more risky day foraging. Furthermore, the highest number of clicks occurred during the night, compared to daylight hours supported this assertion, in which GRD diel density reduced in response to human disturbances during day hours.

A shift in dial activity as a temporal response to anthropogenic pressures may alter species diets toward prey that is more accessible when species is active (Gaynor et al. 2018). Such secular shift exhibited by GRD likely increases dolphins' activity during the night to fulfil their foraging requirements. Although coexistence between fisheries and riverine cetaceans may be enhanced by increased nocturnal activity, the risk effects induced are expected to be significant, which can compromise reproduction and survival (Gaynor et al. 2018). Incorporating knowledge of freshwater cetaceans' temporal dynamics into conservation planning through developing temporal zonation seems imperative (Paudel & Koprowski 2020). Thus, regulating human behavior and resource exploitation with respect to the diel activity or time/habitat specific behavioral responses help cetacean species to survive and recover even within areas of heavy human disturbances.

Foraging in the proximity of fishing gear or human disturbances exposes cetaceans to a greater risk of becoming entangled or killed. Consequently, bycatch has become the leading threat to many riverine dolphin populations (Bearzi et al. 2019). Identification of appropriate conservation measures to mitigate the most common and documented small cetacean's conservation issue—fisheries and cetaceans interactions—is highlighted globally (Bearzi et al. 2019). Our previous study also revealed that close approaches to GRD by humans, particularly by fishers, likely impede social, feeding, and resting behaviors of GRD (Paudel & Koprowski 2020). Similar risks were reported by (Cribb et al. 2013) in Indo-Pacific bottlenose dolphins, and a recently increasing trend in the bycatch of GRD in small-scale fisheries was discovered (Dewhurst-Richman et al. 2020). Our identified acoustic sensing distance could facilitate development of regulation by defining minimum approach distance to riverine cetaceans, reducing or avoiding potential adverse biological effects.

The characteristics of echolocation clicks of GRD have been extensively studied, however, underwater behaviors and diel activity patterns in response to spatial and temporal changes remain poorly understood. To our knowledge, this study is the first that explains behaviors and diel activity patterns of GRD explicitly by accounting for spatial and temporal variations in the click trains emitted by GRD. Our results support and inform conservation efforts for endangered freshwater cetaceans, with reference to GRD; for example, the need to identify, delineate, and protect cetaceans priority habitats (spatial heterogeneity), minimize river dolphins' interactions with fisheries by regulating the activity overlap, and limit human or fisheries approach river dolphins using sensing distance. This study supports the significance of environmental heterogeneity in the natural history of riverine cetaceans that likely improve survival and foraging efficiency. As a result, adjusting to human-modified habitats by widening behavioral plasticity is likely common in riverine cetaceans. This adaptation might improve their persistence in the short term while, in the long term, as the cumulative effect of human disturbances on the temporal dynamics of riverine cetaceans ecology increases, they might suffer from different physiological and morphological stresses as observed in a number of other cetaceans (Ng & Leung 2003). Identifying priority habitats and defining temporal zonation along with protecting travel corridors that connect geographically proximate protected areas by developing appropriate regulations might help to balance the viable populations of small riverine cetaceans in the highly regulated rivers.

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Table 4.1 Spatial and temporal characteristics of the study sites, including hydro-physical details of each habitat type

Habitat type	Location	Survey period	Hydro-physical characteristics
Confluence	26º N, 86º E	December 6, 2017–February 13, 2018	Meeting point of two small distributaries with 3 m depth; moderate flow; substrate type: silt/clay
Deep pool	26º N, 86º E	November 6, 2017–January 19, 2018	Straight river channel with 4 m depth; low flow current; substrate type: small cobbles
Straight channel	26º N, 86º E	March 22, 2018–May 25, 2018	Straight channel with shallow depth (1.7 m); fast running flow; substrate type: small boulder

Table 4.2 Poisson generalized linear models (GLM) showing the relationships between the number of clicks and explanatory variables. The top model (lowest AIC) shows that the number of clicks significantly regulated by the interactions of movement type and habitat structure.

Model	**Df**	**AIC**
Number of clicks ~ Moving type*Habitat	10	14462.3
Number of clicks ~ Moving type	4	14463.59
Number of clicks ~ Moving type + Habitat	6	14466.47
Number of clicks ~ Moving type+ Habitat Type+ Time of day	7	14467.92
Number of clicks ~ Habitat Type	4	14721.26
Number of clicks ~ Time of day	3	14730.47

Table 4.3 Characterization of trajectory duration (minutes) and number of clicks by habitat and movement type.

	Habitat type			
	CF **(N=99)**	**DP** **(N=1042)**	**SC** **(N=234)**	**Overall** **(N=1375)**
Trajectory duration (min)				
Mean (SD)	57.5 (67.3)	39.7 (111)	15.1 (23.1)	36.8 (98.9)
Median [Min, Max]	30.4 [0.4, 352]	11.4 [0.1, 1960]	7.73 [0.4, 220]	11.4 [0.1, 1960]
Number of clicks				
Mean (SD)	95.7 (151)	155 (648)	55.9 (113)	134 (569)
Median [Min, Max]	41.0 [6, 909]	32.0 [1, 15900]	26.5 [6, 1280]	31.0 [1, 15900]

	Acoustic movement type			
	Moving A **(N=250)**	**Moving B** **(N=1041)**	**Staying** **(N=84)**	**Overall** **(N=1375)**
Trajectory duration (min)				
Mean (SD)	4.74 (4.3)	46.5 (112)	11.0 (14)	36.8 (98.9)
Median [Min, Max]	3.52 [0.1, 39.3]	16.4 [0.2, 1960]	6.89 [0.4, 69.1]	11.4 [0.1, 1960]
Number of clicks				
Mean (SD)	16.8 (17.5)	171 (649)	28.1 (40.3)	134 (569)
Median [Min, Max]	11.0 [6, 187]	45.0 [1, 15900]	12.5 [6, 228]	31.0 [1, 15900]

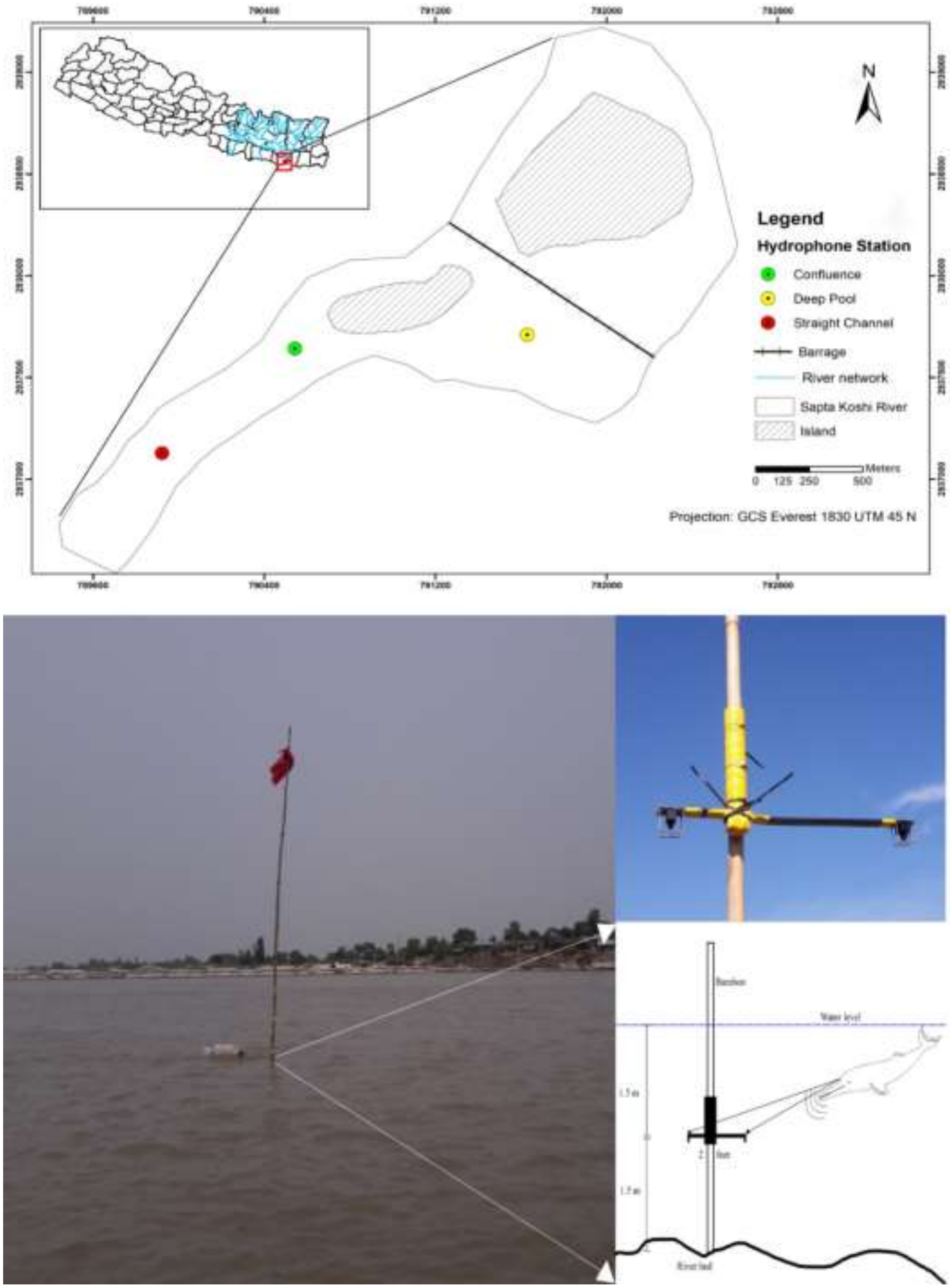

Figure 4.1 The study area showing hydrophone locations at three spatially stratified habitats, confluence (CF), deep pool (DP), and straight channel (SC) in the Sapta Koshi River system of Nepal.

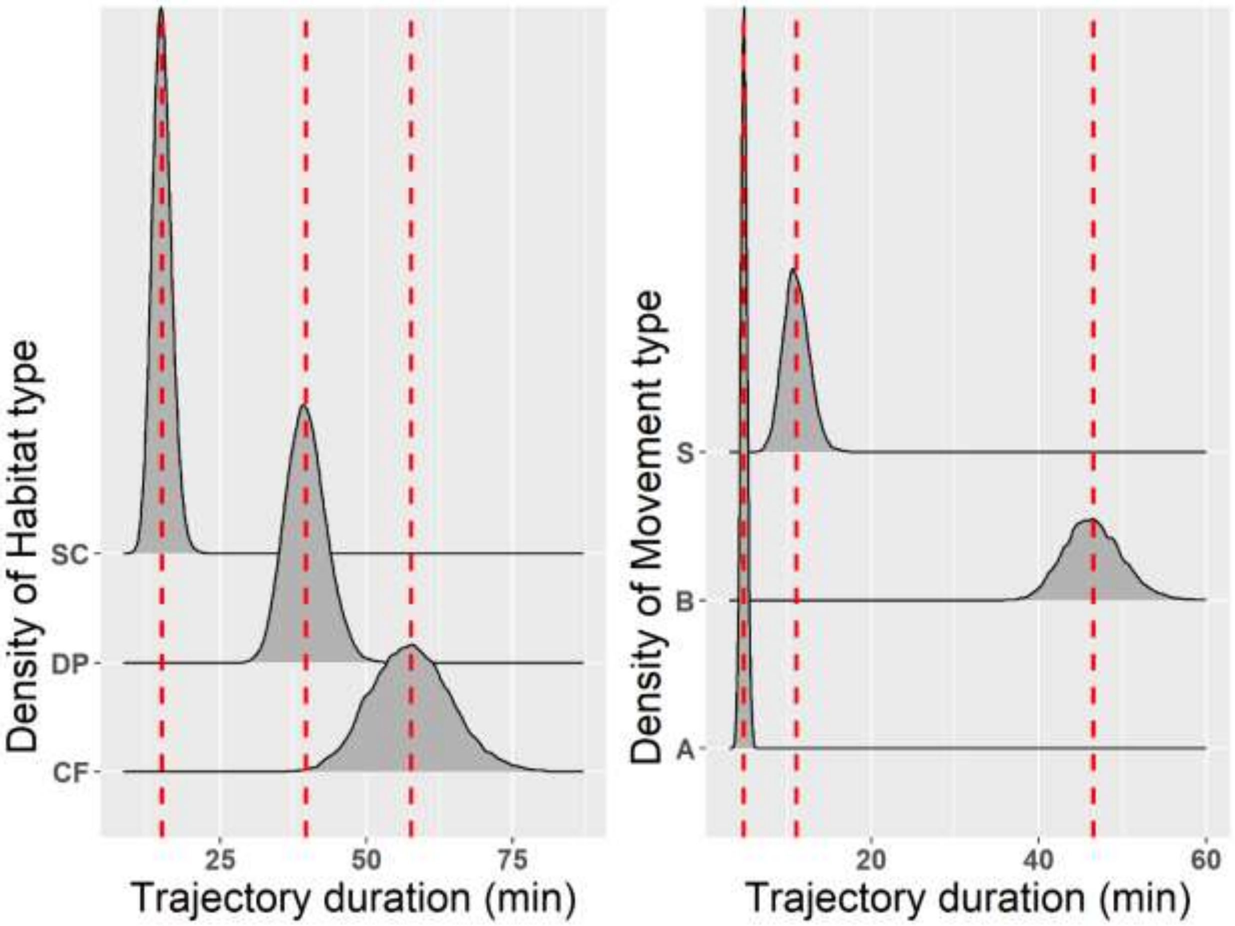

Figure 4.2 The density graph showing trajectory duration distribution across habitats [confluence (CF), deep pool (DP) and straight channel (SC)] and moving types [movement A-travelling; movement B- diving)] depicts significant differences in the trajectory duration (a red vertical line indicates the average value) across space and moving type, indicating different preferences and behaviours adopted by GRD across habitats.

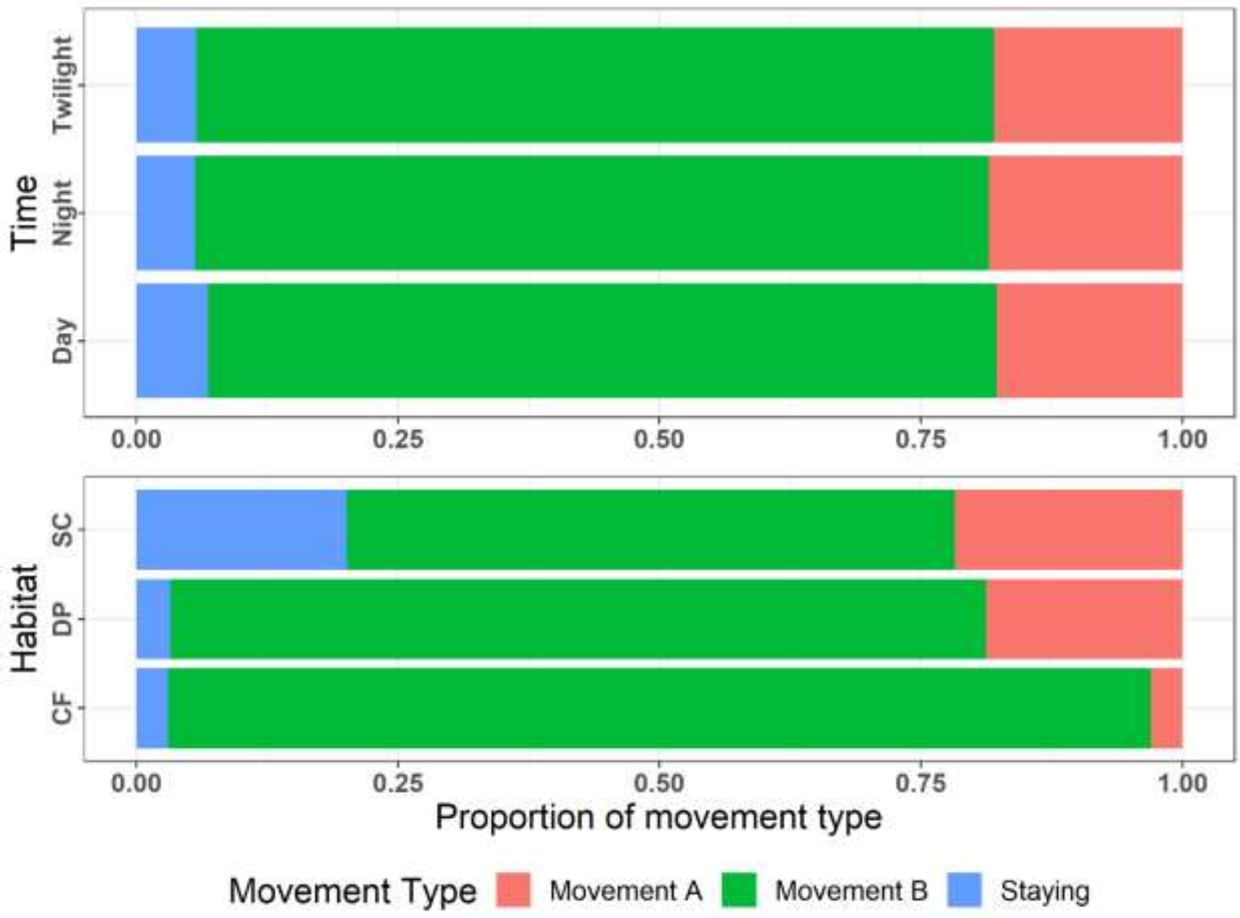

Figure 4.3 Moving type (movement A-travelling; movement B- diving) distribution across habitat and time of the day (twilight, day, and night) depicts significant differences in the moving type of GRD across the habitat but not during the day length indicating variability in GRD behaviours is habitat-driven.

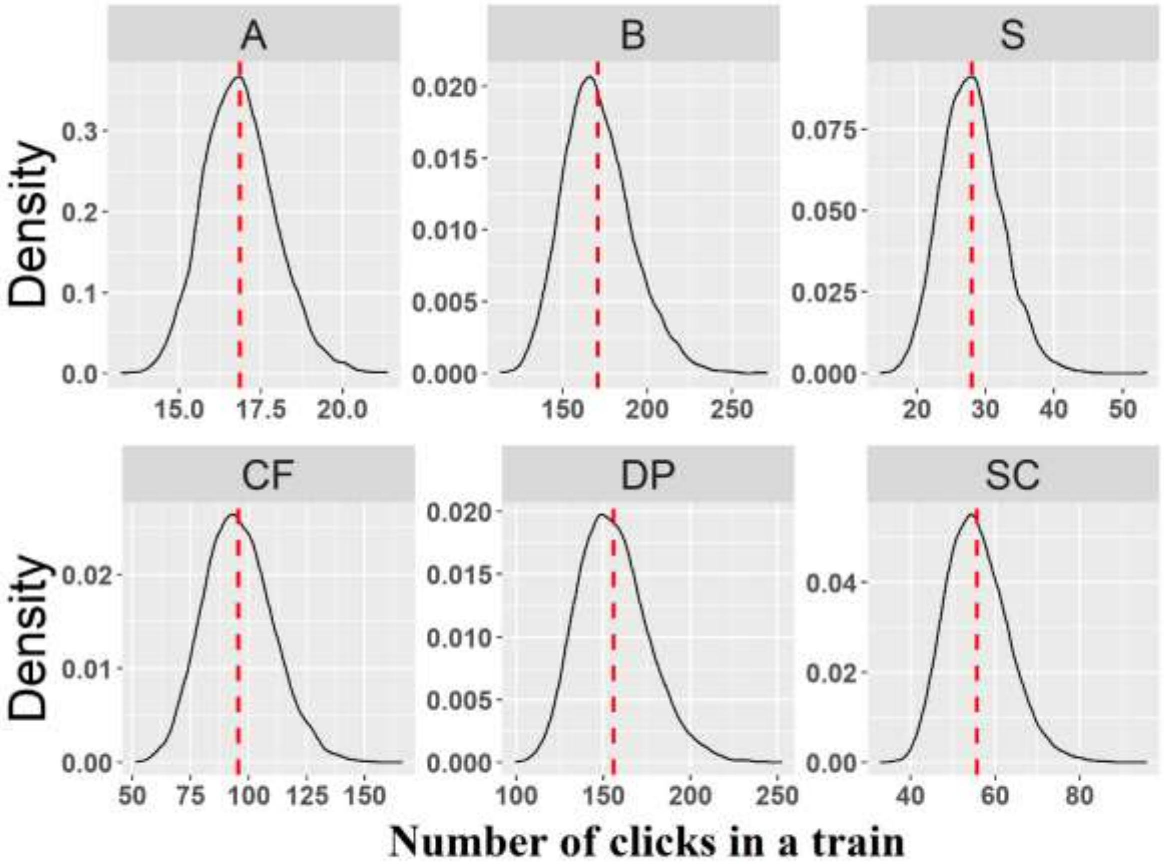

Figure 4.4 The click distribution density plot (the red vertical dashed line indicates an average click number) reveals the significant differences in the number of clicks over habitat [confluence (CF), deep pool (DP) and straight channel (SC)] and moving type (movement A-travelling; movement B- diving), indicating that GRD behavioural activity varies in response to spatial heterogeneity and suggesting that the different behavioural activity adopted by GRD to improve their persistence.

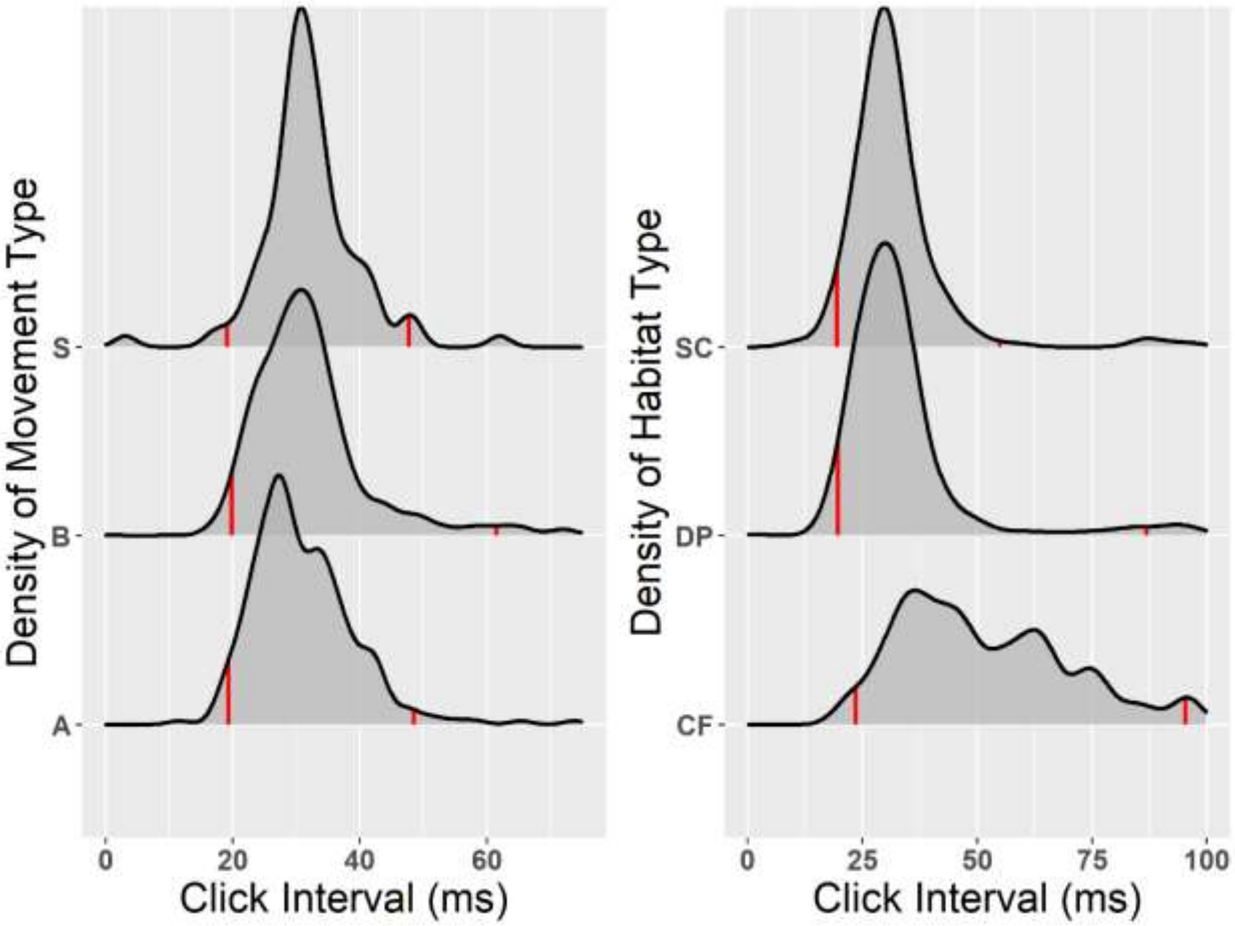

Figure 4.5 High overlap of density distribution of the click-interval (the vertical red lines indicate lower and upper 95% confidence interval of click interval) across space and moving type indicates the similar click-interval distribution of GRD bio-sonar clicks across space and moving type.

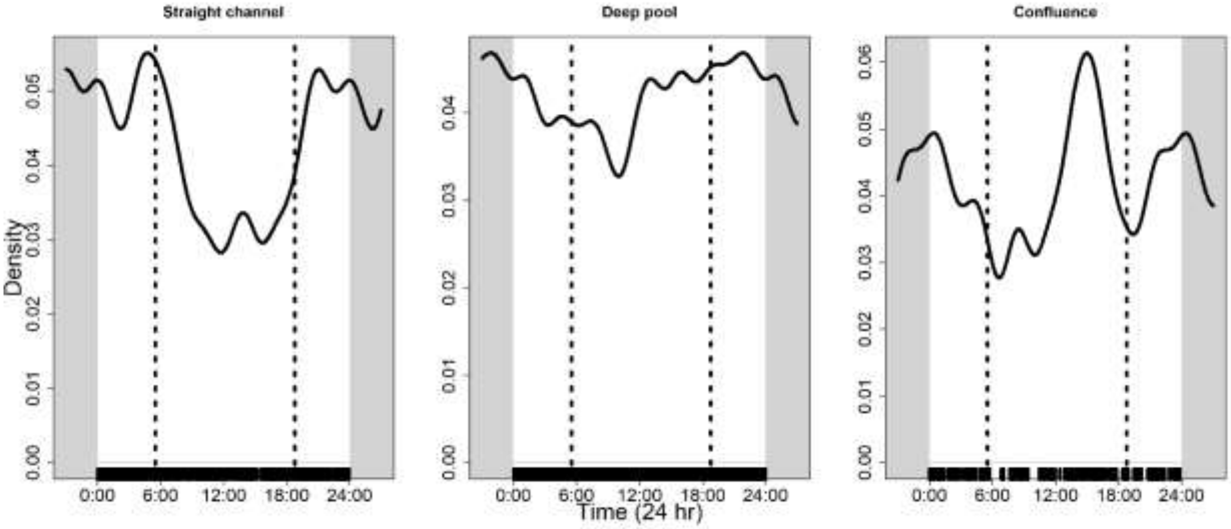

Figure 4.6 Diel density (proportion of GRD active) patterns [the black dash lines indicate sunrise (0530) and sunset (1830) time respectively, on a 24-hour time scale] of GRD across habitats indicate GRD highly active during the night hours, avoiding the day hours when human disturbances are highest.

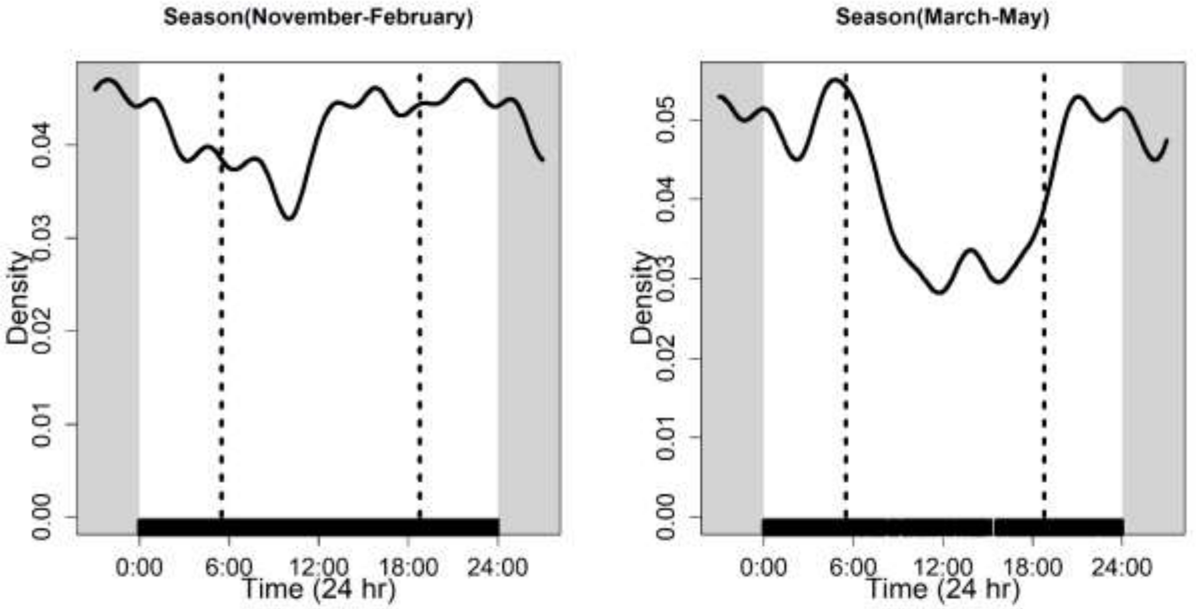

Figure 4.7 Seasonal diel (proportion of GRD active) patterns of GRD showing day hours avoidance rate intensified during the late dry season (March–April) compared to peak dry season (November–February). The black dashed lines indicate sunrise (0530) and sunset (1830) time respectively, on a 24-hour time scale.