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Influences of natural and anthropogenic habitat variables on Indo-Pacific humpback dolphins *Sousa chinensis* in Hong Kong

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ABSTRACT: Indo-Pacific humpback dolphins *Sousa chinensis* in Hong Kong (HK) waters are part of a large (ca. 2000–2500), but declining, population that occurs in the Pearl River Estuary of southern China. To understand the factors that may influence dolphin densities in 4 different parts of HK, a 25 yr (1996–2020) database containing 66 439 km of line-transect survey effort and 4052 dolphin sightings was used. Seventeen variables representing natural and anthropogenic habitat factors were evaluated using generalized additive models (GAMs) to identify the preferred habitat of humpback dolphins in HK waters. In the environmental GAMs, rainfall, salinity, and river discharge were significant factors related to dolphin density, consistent with their observed strong preference for estuarine habitat. Sea surface temperature was also important for one of the 4 subareas. In the anthropogenic GAMs, the only significant variable was the amount of habitat area lost to land reclamation in North Lantau. This finding is consistent with previous hypotheses that heavy coastal engineering in North Lantau has contributed to observed declines in dolphin abundance during the study period. This study provides some of the first quantitative indications of factors that are potentially influencing the density of the animals in various parts of HK. As such, it will be a valuable tool for evaluating and mitigating potential impacts of both natural and anthropogenic factors on the population in the future.

KEY WORDS: Chinese white dolphin · Density · Abundance · Habitat modeling · Southeast Asia · China

1. INTRODUCTION

Over the past 27 yr, we have developed an improved understanding of the population biology and habitat preferences of Indo-Pacific humpback dolphins *Sousa chinensis*, locally known as Chinese white dolphins, in Hong Kong (HK) waters. These dolphins are part of a large population that occurs within the Pearl River Estuary and inhabits Chinese waters off HK, Macau, and the Guangdong Province. The population abundance estimates range between 2000 and ca. 2500 individuals (Chen et al. 2010), and the population is thought to be declining at a rate of about 2.5% or more annually (Huang et al. 2012). Present knowledge of habitat preferences and requirements of the dolphins in HK and Pearl River Estuary waters is still qualitative and subject to data gaps. There are many different environmental factors suspected to impact the animals, both natural and anthropogenic, and the specific degree to which certain elements of the habitat affect the movements and density of the dolphins is not adequately understood (see Hung 2008, Chan & Karczmarski 2017, Jefferson 2018).

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Knowledge of the influences of environmental factors is important for comprehensive and unbiased environmental impact assessment as well as for sound management and conservation of the population. While the dolphins are part of the much larger Pearl River Estuary population that transcends the jurisdictions of different administrative sectors, the HK government has intensively attempted to manage human impacts on the dolphins within its waters since the early 1990s, largely through the environmental impact assessment process (see Jefferson et al. 2009 for a description). Despite the large amount of effort and funds that have been spent managing these animals, the abundance of humpback dolphins in HK waters has been declining since the early 2000s (Jefferson 2018). Current protection measures are widely established but their efficacy remains questionable. There is great concern that the dolphins using HK waters may dwindle to insignificant numbers unless the population can be stabilized and, hopefully, can recover to some extent (Karczmarski et al. 2016, Chan & Karczmarski 2017, Jefferson 2018).

In recent years, the availability of large and long-term databases of consistently collected data on cetacean density and abundance, along with the availability of habitat data (such as remotely sensed and *in situ* environmental variables, prey densities, and metrics of habitat modification) have allowed habitat models to be built for many species of whales and dolphins globally (see below). Models have been developed using well-established methods, such as generalized linear models or generalized additive models (GAMs), and results have been used to investigate various biological aspects that are highly relevant to the conservation and management of the species of interest. Models built with high-quality data have been used to understand how habitat variables and prey abundance affect the density and abundance of the focal species (Zerbini et al. 2016), reduce uncertainty in abundance trends (Forney 2000), produce spatially explicit density estimates for evaluating habitat disturbance (Forney et al. 2012, 2015), estimate rate of change in population size (Ward et al. 2011), and assess seasonal variability and predict future changes in density and abundance (Becker et al. 2012, 2014, 2016, 2017, 2018). The predictive and forecasting capabilities of these studies make them especially attractive to wildlife managers, who can use the models to predict and compare different scenarios of environmental change, both natural and anthropogenic.

The general approach of the current project was to build a habitat-based density model for humpback dolphins in HK waters, using the line-transect data collected by the Agriculture, Fisheries, and Conservation Department (AFCD) and Airport Authority Hong Kong (AAHK) since 1996. Bao et al. (2019) demonstrated the importance of using systematic survey data to construct habitat models. In the present study, a series of environmental variables of interest (e.g. sea surface temperature [SST], freshwater river input, rainfall, water depth, salinity) and metrics of anthropogenic changes in habitat (e.g. fisheries activity, vessel traffic, amount of reclamation and dredging, environmental contamination) were integrated into the long-term data set of line-transect data collected since late 1995 (Jefferson 2000, 2018). GAMs were then developed to provide an improved understanding of how the abundance of humpback dolphins in HK waters is influenced by environmental and anthropogenic variables. Ultimately, we hope the models will be used in a predictive capacity to assess alternative future scenarios important to developing sound management strategies.

2. MATERIALS AND METHODS

2.1. Study area

The study area encompasses the western waters of HK[1] (Fig. 1), known to be used as important humpback dolphin habitat over the past 27 yr. HK is subtropical, with 2 primary seasons: the wet season (defined here as May–October), when the weather is hot and there is frequent rain, and the dry season (November–April), when it is cooler and there is much less rainfall. The study area was divided into 4 geographic strata (termed survey areas in this paper) for analysis: North Lantau, Deep Bay, West Lantau, and Southwest Lantau (see Fig. 1). The study area is described in further detail in Jefferson (2000). Development in the western part of HK has been increasing since the new airport (Hong Kong International Airport, HKIA) was built in the area in the mid-late 1990s, just at the start of the current study period. The airport was built mostly on reclaimed land, and it began operations in mid-1998 (Plant & Okervee 1998, Wu et al. 2020). A number of construction pro-

[1]Since 1997, Hong Kong has been a Special Administrative Region (SAR) within the People's Republic of China (PRC), and as such, has its own government and a certain degree of autonomy. The boundary between the HK SAR and mainland China was redrawn in 1997, which affected access by our survey vessel.

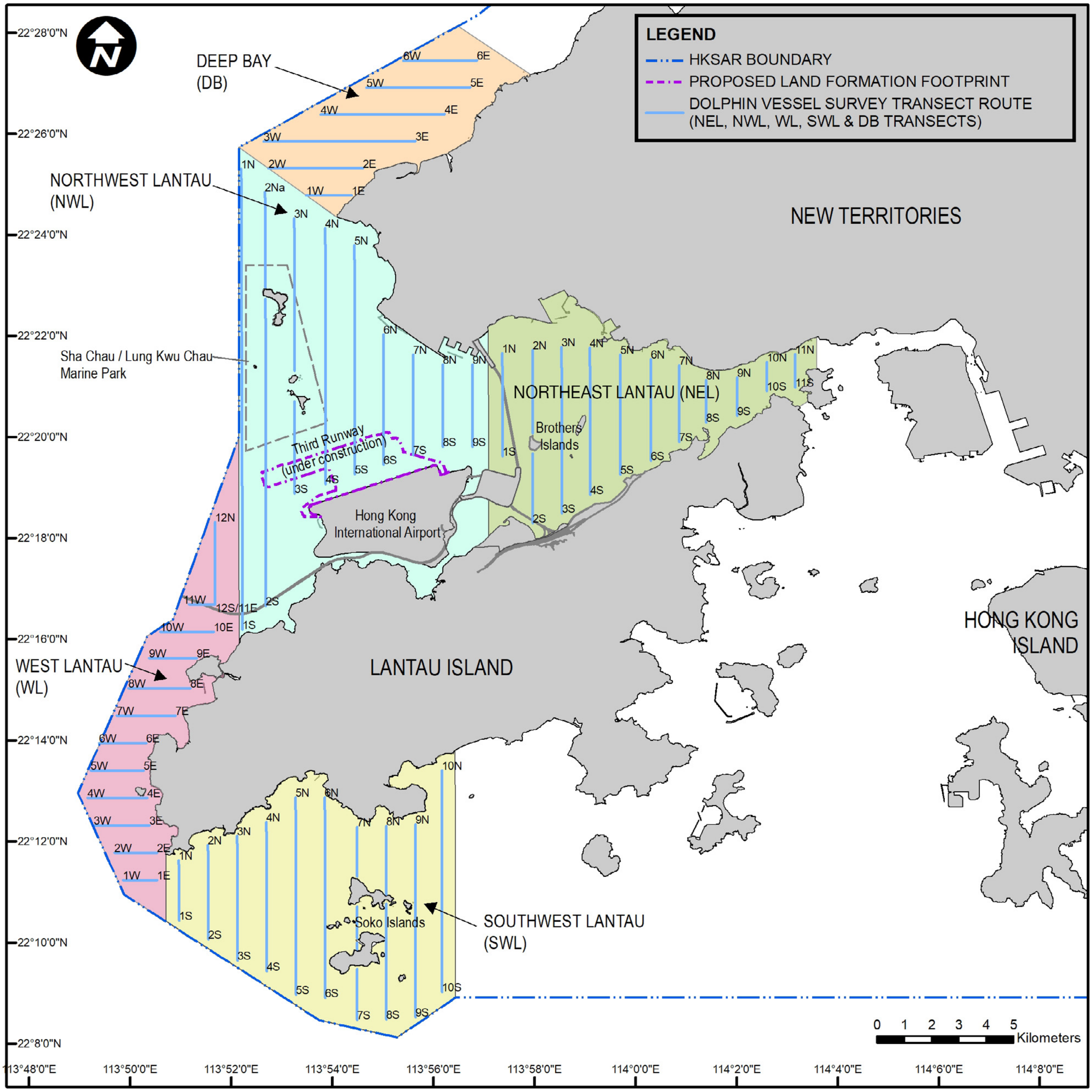


Fig. 1. Hong Kong study area, showing the 4 survey areas (note that Northwest and Northeast Lantau are analyzed together as a single survey area). Figure produced by Mott MacDonald Hong Kong Ltd.

jects that might have affected the dolphins took place in western HK during the study period (Table 1).

2.2. Dolphin density data

Cetacean monitoring surveys have been conducted in western HK waters since September 1995. Surveys are run throughout the year, with relatively even effort in each month. We conducted visual surveys using several inboard research vessels; all had similar structures and ranged from 12–15 m in length. These were mostly junk-style vessels with elevated open upper decks (flying bridges) and all had a full 180° unobstructed view ahead of the vessel. Searches were conducted by 2 on-duty observers from sitting positions at the front of the flying bridge, which afforded an eye height of 4–5 m above the water's surface.

Two different teams conducted surveys to examine dolphin density and abundance by line-transect meth-

Table 1. Construction projects in Hong Kong (HK) during the study period that may have affected dolphins. HKIA: Hong Kong International Airport

Project	Survey areas affected	Dates of marine works	Reclamation area (km^2)	Major impacts
HKIA Aviation Fuel Receiving Facility	North Lantau	Feb 1995–Jun 1997	Negligible	Percussive piling, small-scale dredging
River Trade Terminal	North Lantau	Oct 1996–Dec 1998	0.65	Dredging, small-scale reclamation
Deep Bay coastal reclamation	Deep Bay	Jan 2000–Dec 2006	7.21	Land reclamation
HKIA Permanent Aviation Fuel Facility	North Lantau	Nov 2005–Jul 2006; Jul 2007–Dec 2009	0.068	Hydraulic/bored piling, small-scale reclamation
HK Boundary Crossing Facilities	North Lantau	Jan 2011–Aug 2014	1.5	Large-scale land reclamation
HK-Zhuhai-Macao Bridge	West Lantau, North Lantau	Jun 2013–Jan 2018	Negligible	Bridge viaduct, tunnel construction, vibratory piling
HKIA Third Runway	North Lantau	Jul 2017–Jul 2021	6.5	Large-scale land reclamation

ods in HK: the AFCD survey team (from late 1995 to present; covered all survey areas in HK), and the Mott Macdonald team (from late 2015 to present; covered all 4 survey areas evaluated in this study). Both teams used the same methods, developed by the senior author in the mid-1990s for small cetacean line-transect surveys in HK, and used very similar vessels and equipment (these are detailed in Jefferson & Leatherwood 1997, Jefferson 2000, Jefferson & Moore 2020). Briefly, search effort data collected included time and position for the start and end of each leg, Beaufort sea state, and visibility; sighting data included species, time and position of initial detection, sighting angle, radial distance, group size and composition, behavior, and response to vessel. Trackline detection probability was assumed to be 1.0, based on the experiment reported by Jefferson (2000). Though the study period covered 1996–2020, in some of the early years of the study survey effort was not conducted in certain subareas due to funding limitations.

2.3. Habitat variables

To obtain data on variables that represent factors known or suspected to affect humpback dolphin abundance in HK waters and could be used as covariates in the habitat models, we conducted searches of a variety of sources, including online websites, published literature, nautical charts, HK government statistical records, environmental impact assessment reports, and graduate theses. We were able to extract numerical data on most variables described above, with different levels of temporal resolution (monthly, quarterly, annual). Most variables were either averages specific to the individual survey areas or averages for the entire study area (Table 2 & Table S1 in the Supplement at www.int-res.com/articles/suppl/n051p143_supp.pdf).

Natural factors include:

(1) Prey availability — although it is common knowledge within the marine mammal research community that prey availability (which is related to productivity) is the primary determining factor in the distribution and density of most marine mammals, this has been difficult to statistically demonstrate for humpback dolphins in HK waters. This is due to the absence of long-term data on fish and fisheries resources in HK. Nonetheless, there is ample circumstantial evidence that prey availability is a critical factor for this population (Jefferson 2000, Hung 2008).

(2) Season — dolphin distribution and density in all of HK's waters has been shown to be strongly related to season, though seasonal fluctuations in freshwater and nutrient inputs may be the important factors (Jefferson 2000, Hung 2008).

(3) Freshwater input — as stated above, freshwater input (which is related to rainfall), primarily from the adjacent Pearl River, has been demonstrated to be a critical element influencing the distribution of HK's dolphins. This may occur mainly through differential

Table 2. Natural and anthropogenic covariates used in the study. GAMs: generalize additive models; EPD: Environmental Protection Department; HK: Hong Kong; AAHK: Airport Authority; AFCD: Agriculture, Fisheries and Conservation Department; n/a: not available

Variable name	Natural/ Anthropogenic	Dynamic/ Static/Cumulative	Resolution	Source	Used in GAMs?
Sea surface temperature	N	D	Monthly	EPD website[a]	✓
Rainfall	N	D	Monthly	HK Observatory website[b]	✓
Salinity	N	D	Monthly	EPD website[a]	✓
Pearl River discharge	N	D	Monthly	Wei etal. (2020), Xue et al. (2004)	✓
Water depth	N	S	n/a	Nautical charts	✓
Chl *a*	N	D	Monthly	EPD website[a]	✓
Finless porpoise abundance	N	D	Quarterly	Jefferson & Moore (2020)	✓
Reclamation (proportion of area lost)	A	C	Annual	AAHK records, S. L. Huang unpubl. data	✓
Fisheries — total production	A	D	Annual	FAO website[c]	
Fisheries — trawlers, gillnetters	A	D	Annual	AFCD statistics[d], Lin et al. (2019)	
Vessels — ocean cargo arrivals	A	D	Monthly	Marine Dept. website[e]	✓
Vessels — Macau ferry arrivals	A	D	Quarterly	Marine Department website[e]	✓
Vessels — other ferry arrivals	A	D	Quarterly	Marine Department website[e]	✓
Vessels — construction	A	D	Monthly	AA records, HZMB EIA	✓
Fecal coliforms	A	D	Monthly	EPD website[a]	✓
Proportion of artificial coastline	A	C	n/a	Hung (2008)	
Proportion of protected area	A	C	Monthly	AFCD website[d]	✓

[a]https://cd.epic.epd.gov.hk/EPICRIVER/marine/?lang=en
[b]https://www.hko.gov.hk/en/cis/climat.htm
[c]https://www.fao.org/fishery/en/statistics
[d]https://www.afcd.gov.hk/english/fisheries/fish_cap/fish_cap_latest/fish_cap_latest.html
[e]https://www.mardep.gov.hk/en/fact/portstat.html

levels of salinity and productivity (Parsons 1998a, Jefferson 2000, Hung 2008).

(4) Water depth/benthic slope — Jefferson (2000) noticed that water depth appeared to affect the distribution of humpback dolphins in HK waters, especially in terms of feeding habitat. Hung (2008) demonstrated the importance of both depth and benthic slope to dolphin distribution. In other habitats, such as the northern Beibu Gulf (Wu et al. 2017a) and Donsak in the Gulf of Thailand (Jutapruet et al. 2017), water depth is one of the major variables affecting humpback dolphin distributions.

(5) Coastline type — the type of coastline was shown by Hung (2008) to be an important determinant of dolphin occurrence and behavior, with dolphins preferring rocky over sandy or artificial coastlines. In the Xiamen area, Wang et al. (2017) found that humpback dolphins prefer natural over artificial coastlines.

(6) Water temperature — although water temperature correlates with dolphin presence and use, this may be secondary to its effects on prey (Parsons 1998a, Hung 2008). In the northern Beibu Gulf, SST is as important as marine primary production in determining humpback dolphin distribution in winter (Huang et al. 2019).

(7) Finless porpoise presence — in most areas of HK, Indo-Pacific finless porpoises *Neophocaena phocaenoides* and humpback dolphins show little or no overlap in distribution, but where they are sympatric, there tends to be a negative temporal correlation (Parsons 1998a, Jefferson 2000). Although this may mainly be related to dolphin exclusion of porpoises, there is indeed a relationship between the occurrence of the 2 species.

There are also several anthropogenic factors, as described below:

(1) Vessel traffic — vessel traffic is known to be an important threat to dolphins, both in terms of behavioral disturbance and the risk of vessel collision. In HK, humpback dolphins appear to be affected by vessels (especially high-speed ferries and construction vessels), both in terms of long- and short-term impacts (Jefferson 2000, Hung 2008, Klein 2016).

(2) Anthropogenic noise — noise created by human activities has come to be recognized as one of the greatest threats to a variety of marine mammal spe-

cies. Previous work has demonstrated the importance of noise levels in determining dolphin movements and occurrence patterns (Würsig et al. 2000, Würsig & Greene 2002, Klein 2016, Piwetz et al. 2021).

(3) Marine construction — HK has been rapidly developing for many decades, and marine construction projects are ubiquitous, especially in western waters in recent decades. These projects have clear impacts on the local dolphins, especially when they involve reclamation and/or piling operations (Jefferson 2000, Würsig et al. 2000, Würsig & Greene 2002, Jefferson & Hung 2004). A recent review article summarizes both the physical and ecological consequences of marine construction on humpback dolphins and their habitats (Huang et al. 2022).

(4) Dredging/dumping of spoils — used in the maintenance of shipping channels and harbors as well as in marine construction, dredging and the associated dumping of dredge spoils/sediments can affect dolphins in HK (Hung 2008).

(5) Fishing activity — there is little doubt that besides the risk of bycatch, fishing activities can also influence dolphin distribution. In HK, trawling and, to a lesser extent, gillnetting, are known to affect dolphins (Jefferson 2000, Parsons & Jefferson 2000, Hung 2008). A trawl ban has been in effect in HK since 2013, but some level of illegal trawling still occurs in the territory, especially at night (T. A. Jefferson pers. obs.). Before the trawl ban, dolphins were frequently observed feeding actively behind trawlers, and often traveling from some distance to approach them (see Jefferson 2000).

(6) Contaminant levels — environmental pollution is rampant in HK and is a serious concern for its effects on dolphins. This is particularly the case for organochlorines and heavy/trace metals (Parsons 1998b, Parsons & Chan 1998, Jefferson et al. 2006). Human and domestic animal sewage flows into HK from several point sources, and it is likely that this threat also affects dolphin health and mortality.

2.4. Modeling database structure

Dolphin sighting data used to build the habitat-based density models were collected within the waters of the study area using line-transect methods (Buckland et al. 2001). Only on-effort data collected in Beaufort sea state conditions ≤3 were used to build the models (see Jefferson & Leatherwood 1997 for justification), and for consistency among years, included the 2 days per month with the most complete survey effort. Samples for modeling consisted of a single day of survey effort, with the number of sightings and total number of dolphins sighted assigned to each daily sample, as well as total daily effort (km) and effective strip half-width. Seasons were defined as winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and autumn (Sep–Nov). Two sets of covariates were used as potential predictor variables: (1) environmental covariates, and (2) anthropogenic covariates. The environmental covariates included monthly averages of salinity (psu), SST (°C), and the natural logarithm of chlorophyll *a* (chl *a*; μg l^{-1}), all specific to each individual survey area; as well as Pearl River freshwater discharge (10^8 m^3) and rainfall totals for HK (mm). Water depth (m) was also available as a single mean value for each of the 4 survey areas.

Anthropogenic covariates were also available as monthly averages and included fecal coliform counts (cfu per 100 ml) specific to each survey area, number of passenger ferries arriving from Macau (relevant to Southwest Lantau), number of passenger ferries arriving from other ports (relevant to North Lantau), number of ocean cargo vessel arrivals in HK (relevant to North Lantau), number of working construction vessels (relevant to North Lantau), and cumulative proportion of area lost as habitat due to reclamation (%; relevant to North Lantau). In addition, based on empirical data that suggest there is an inverse relationship between the abundance of humpback dolphins and finless porpoises (T. A. Jefferson unpubl. data), the latter was also considered as a potential covariate (relevant to Southwest Lantau only).

Given the documented effect of fisheries on the dolphins (Parsons & Jefferson 2000, Jefferson et al. 2006), statistics such as the number of fishing vessels and catch totals were evaluated as potential covariates for this analysis. Unfortunately, fisheries data were available only for the entirety of HK and not for the individual survey areas, thus limiting their use as effective predictors. Fisheries data should ideally be collected at spatial and temporal resolutions suitable for evaluating their potential effects on the dolphin population.

2.5. Modeling framework

Given the inherent differences in the 2 types of covariates and the area-specificity of the anthropogenic covariates, a multi-stage modeling process was used in this study (Jacobson et al. 2022). First, the probability of detection was estimated using methods described by Jefferson (2018), with detection functions estimated separately for each year. Next, an environmental density model was developed to identify correlative covariates. Finally, the estimated density from the environmental model was included in a separate anthropogenic model to identify potential effects of anthropogenic factors on dolphin occurrence in the survey areas. All models were built using a GAM framework (Wood 2017) in R v.4.0.2 (R Core Team 2020) with the 'mgcv' package (v.1.8-31; Wood 2011).

2.5.1. Environmental GAMs

In the first GAM, potential predictor variables were limited to the environmental covariates to evaluate which of these habitat factors might be affecting the abundance of dolphins in the study area. The 'environmental GAMs' were fitted using the number of dolphins per survey day (n_j, where the survey day is indexed by j) as the response variable. Models assuming a Tweedie and negative binomial distribution were initially considered for the response variable, given that they are essentially over-dispersed 'count' data. Based on inspection of model residuals and diagnostic plots, the Tweedie distribution with a log link was ultimately selected for the final models (Miller et al. 2013). Environmental covariates for each day (x_{kj}, where k indexes the covariates) were included as smooth functions (f_k). Effort was accounted for by including an offset of the area effectively searched (A_j), which was computed as the product of the length of the daily effort, the effective strip half-width (calculated separately for each year from standard design-based analyses), the number of sides surveyed (i.e. 2), and the probability of detection per survey day ($\hat{p}_j$). The probability of detection was derived using methods described by Jefferson (2018) and summarized above. Trackline detection probability ($g(0)$), was assumed to equal 1. Although effort and sighting data were limited to Beaufort sea state conditions ≤3, resulting abundance estimates are likely biased low (Barlow 2015). The environmental models thus take the following form:

$$E(n_j) = \hat{A}_j \exp\left\{\beta_0 + \sum_{k=1}^{K} f_k(x_{kj})\right\} \quad \text{where } n_j \sim \text{Tweedie}(\phi, q) \tag{1}$$

In this equation β_0 is a model intercept and Tweedie parameters ϕ (scale) and q (power) are calculated during model fitting and refer to the mean-variance relationship of the distribution, such that $Var(n_j) = \phi E(Xn_j)^q$. The index for day is denoted by j.

Restricted maximum likelihood (REML) was used to obtain parameter estimates (Wood 2011). Marra & Wood's (2011) shrinkage approach was used to remove potential terms from each model by modifying the smoothing penalty, allowing the smooth effect to be shrunk to zero. This effectively performed model selection automatically during fitting. We used REML and a shrinkage approach to remove variables, as this combination yields superior results compared to selecting variables and smoothing levels using Akaike's Information Criterion (Marra & Wood 2011), and this approach has been used successfully in similar GAM studies (e.g. Roberts et al. 2016, Becker et al. 2020). Correlations among the predictor variables in our study ranged from 0.001 to 0.67 (absolute values), but 'mgcv' is robust to such effects (termed 'concurvity'; Wood 2008).

The resulting 'environmental density models' were then used to predict on the environmental conditions during the survey periods (all the environmental covariates were available as monthly averages) to derive yearly abundance estimates for each of the 4 survey areas. We concentrated on yearly abundance (vs. seasonal) for consistency with Jefferson (2018), who used yearly design-based estimates (i.e. derived from systematic line-transect data collected on surveys designed to provide representative coverage of a study area; Buckland et al. 2001) to demonstrate a decline in dolphin abundance in HK waters over the period of this study.

To estimate density, predictions from the environmental models were incorporated into the standard line-transect equation (Buckland et al. 2001) to derive density ($\hat{D}_j$); number of animals per km^2 on day j) for each of the 4 survey areas:

$$\hat{D}_{js} = \frac{n_{js}}{\hat{A}_{js}} \tag{2}$$

where j is the survey day, (n_j) is the model-predicted number of dolphins on day j in survey area s, and $\hat{A}_{js}$ is the effective area searched on day j in survey area s as defined in Eq. (1). An effort-weighted average of the daily density predictions was multiplied by the size of the study area to derive a yearly abundance estimate for each of the 4 study areas.

Given the multiple sources of uncertainty inherent in model-predicted abundance estimates (e.g. variance associated with model parameters, model selection, sampling error, detection parameters, error in the estimation of habitat covariates, etc.), it is often not possible to account for all sources when estimating variance, but it is important to account for the dominant source (Barlow et al. 2009). The greatest source of uncertainty in the model-predicted abundance estimates in this study is the seasonal variability in population density due to movement of dolphins outside of the survey areas (Jefferson 2018). Coefficients of variation and confidence intervals for the model predictions were thus based on the monthly variability in density, calculated based on the variation in predicted density estimates within each year using standard statistical formulae. For the models here, uncertainty will be underestimated to some degree, but the most important source of uncertainty has been accounted for.

We used established metrics (e.g. % explained deviance, area under the receiver operating characteristic curve [AUC; Fawcett 2006], and true skill statistic [TSS; Allouche et al. 2006]) to assess the fit of the environmental GAMs. The AUC (range: 0 to 1) indicates how well predictions can discriminate between observed presences and absences; a value >0.5 reflects a better-than-random skill of the model. The TSS (range: −1 to +1) accounts for both false negative and false positive errors; a value of +1 indicates perfect agreement, while values ≤0 denote that the model did not perform better than random. We followed the sensitivity–specificity sum maximization approach described in Liu et al. (2005) to obtain thresholds for dolphin presence (for calculating the TSS). We also evaluated the potential bias in the environmental-based model predictions by comparing the model-based abundance estimates based on the sum of individual modeling segment (i.e. daily) predictions to standard design-based estimates derived from the same data set used for modeling. We derived the design-based estimates from survey data for the years 1996–2020 using Eq. (2) above but excluded the environmental predictors (i.e. observed rather than predicted number of dolphins during the survey period). Although there is no statistical threshold for significance, values closer to 1 indicate better agreement between model-based and design-based estimates of density.

2.5.2. Anthropogenic GAMs

The next stage of modeling was designed to assess if any of the anthropogenic variables potentially affected dolphin abundance during our study period. In these 'anthropogenic GAMs', yearly design-based abundance estimates (i.e. standard design-based estimates derived from the same survey data but without the inclusion of habitat predictors) were used as the response variable, the model-predicted abundance estimates as the predictor variable, and each of the impacts added separately as relevant to the area and available for modeling (Table 2). The anthropogenic GAMs were built using the natural log of the yearly design-based abundance estimates as the response variable (a_i, where i indexes the year), and a Gaussian response distribution, because abundance is generally log-normally distributed. The natural log of the yearly model-predicted abundance estimates derived from the environmental GAM (see above) was the main predictor variable (m_i, and the natural log of each of the yearly averaged anthropogenic variables was offered separately as a second predictor (y_i). The variables were log transformed, because the effects are expected to be multiplicative (i.e. a proportional change), not additive. The anthropogenic models were therefore of the following form:

$$E(\log_e a_i) = \beta_0 + f(\log_e m_i) + f(\log_e y_i)$$
$$\text{where } a_i \sim \text{Normal}(\mu, \sigma^2) \tag{3}$$

Yearly design-based estimates were specifically used in the model to tease out the potential effect of the anthropogenic variables on dolphin abundance. Other studies have compared habitat-based density model predictions to design-based predictions as a way to assess model performance (e.g. Barlow et al. 2009, Forney et al. 2015, Becker et al. 2020). The environmental GAMs developed in stage one were used to capture changes in dolphin abundance that could be due to changes in environmental conditions, while the anthropogenic GAMs were designed to account for additional abundance changes due to human effects. An initial GAM was built with model-predicted yearly abundance estimates derived from the environmental GAM as the only predictor variable to provide a baseline for assessing the importance of the subsequently added anthropogenic predictor variables. Each yearly averaged anthropogenic variable was then tested in a forward-stepwise selection process to assess the significance of each variable. As described for the environmental GAMs, REML and a shrinkage approach were used to select covariates; an anthropogenic variable was deemed significant if it remained in the model after fitting (i.e. the smooth was not shrunk to zero) and its p-value was greater than 0.05. Separate anthropogenic GAMs were developed for each region since the potential impacts are specific to each survey area. Theoretically, if the anthropogenic variable was affecting dolphin abundance, the variable would be significant and the resulting yearly abundance estimates derived from the anthropogenic GAM would be closer to the design-based estimates. The abundance estimates from the environmental GAM were thus treated as point estimates to examine the potential for anthropogenic effects. For any anthropogenic GAM that included a significant anthropogenic variable, yearly abundance estimates from the model were compared to both the yearly design-based and environmental GAM estimates.

3. RESULTS

3.1. Data used for analysis

A total of 66 439 km of on-effort survey data collected between 1996 and 2020 within the study area of HK waters was used to develop the environmental-based GAMs. This included 4230 km in the Deep Bay survey area, 37 914 km in the North Lantau survey area, 9334 km in the West Lantau survey area, and 14 961 km in the Southwest Lantau survey area. A total of 4052 dolphin sightings were collected during this systematic survey effort and were usable in the line-transect analyses: 72 from Deep Bay, 1754 from North Lantau, 1723 from West Lantau, and 503 from Southwest Lantau.

3.2. Habitat modeling results

Initially, a single environmental GAM was developed using data from the entire study area; however, subsequent analyses revealed that there were substantial differences in the functional forms of significant variables among the 4 survey areas. Survey-area-specific environmental GAMs were therefore more appropriate. Environmental GAMs were thus developed separately for each of the 4 survey areas. The deviance explained by the environmental GAMs was low and varied from 3.6 to 10.6% (Table 3). The models exhibited better than random skill at predicting true positives and negatives, as indicated by AUC values for all models being greater than 0.6. Performance better than random (i.e. all values were >0) was also indicated by the TSS values, which account for both omission and commission errors, which ranged from 0.18 to 0.37. The observed-to-predicted density ratios provide an indication of how well the sum of the daily-based abundance predictions from the model compared to survey area abundance as derived from design-based line-transect methods, and these values were close to 1.00 for all 4 survey areas (Table 3).

Salinity, freshwater discharge from the Pearl River, and SST were the most common environmental predictor variables (Table 3), and their functional forms (Fig. 2) were consistent with what would be expected given the different survey area locations.

The environmental model for the Deep Bay survey area indicated that higher numbers of dolphins are found in relatively cooler waters with low chl *a* content (Fig. 2). In the North Lantau survey area, dolphins prefer habitat with lower rainfall, high salinity, and high freshwater discharge from the Pearl River (Fig. 2), consistent with previous observations that the dolphins tend to be associated with estuarine habitat. Conversely, in Southwest Lantau, the model function indicates that greater numbers of dolphins are found in lower salinity waters (Fig. 2). In West Lantau, dolphins prefer waters with high SSTs and high freshwater discharge from the Pearl River (Fig. 2). The differences in habitat preferences among the 4 survey areas are likely related to their relative geography and proximity to the Pearl River, with some areas more heavily affected by freshwater outflow from the river.

In preparation for the second stage of modeling, each environmental model was used to predict the monthly environmental conditions of the survey periods and derive yearly average abundance estimates for each of the 4 survey areas (Fig. 3). The anthropogenic GAMs were then developed using the design-based abundance estimates as the response variable, the model-predicted abundance estimates as the predictor variable, and each of the impacts added separately as relevant to the area and available for

Table 3. Final environmental models built with the 1996–2020 survey data for each of the 4 survey areas. Variables are listed in the order of their significance (SST: sea surface temperature; PR: Pearl River; Ln: natural logarithm). All models were corrected for effort with an offset for the area searched (see Section 2.5.1 for details). Performance metrics included the percentage of explained deviance (Expl. dev.), the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and the ratio of observed to predicted density for the survey area (Obs:Pred)

Survey area	Predictor variables	Expl. dev.	AUC	TSS	Obs:Pred
Deep Bay	Ln chl *a* + SST	6.9	0.70	0.35	1.00
North Lantau	PR discharge + salinity + rainfall	10.6	0.62	0.27	0.96
West Lantau	PR discharge + SST	3.6	0.69	0.37	0.96
Southwest Lantau	Salinity	4.6	0.61	0.18	0.96

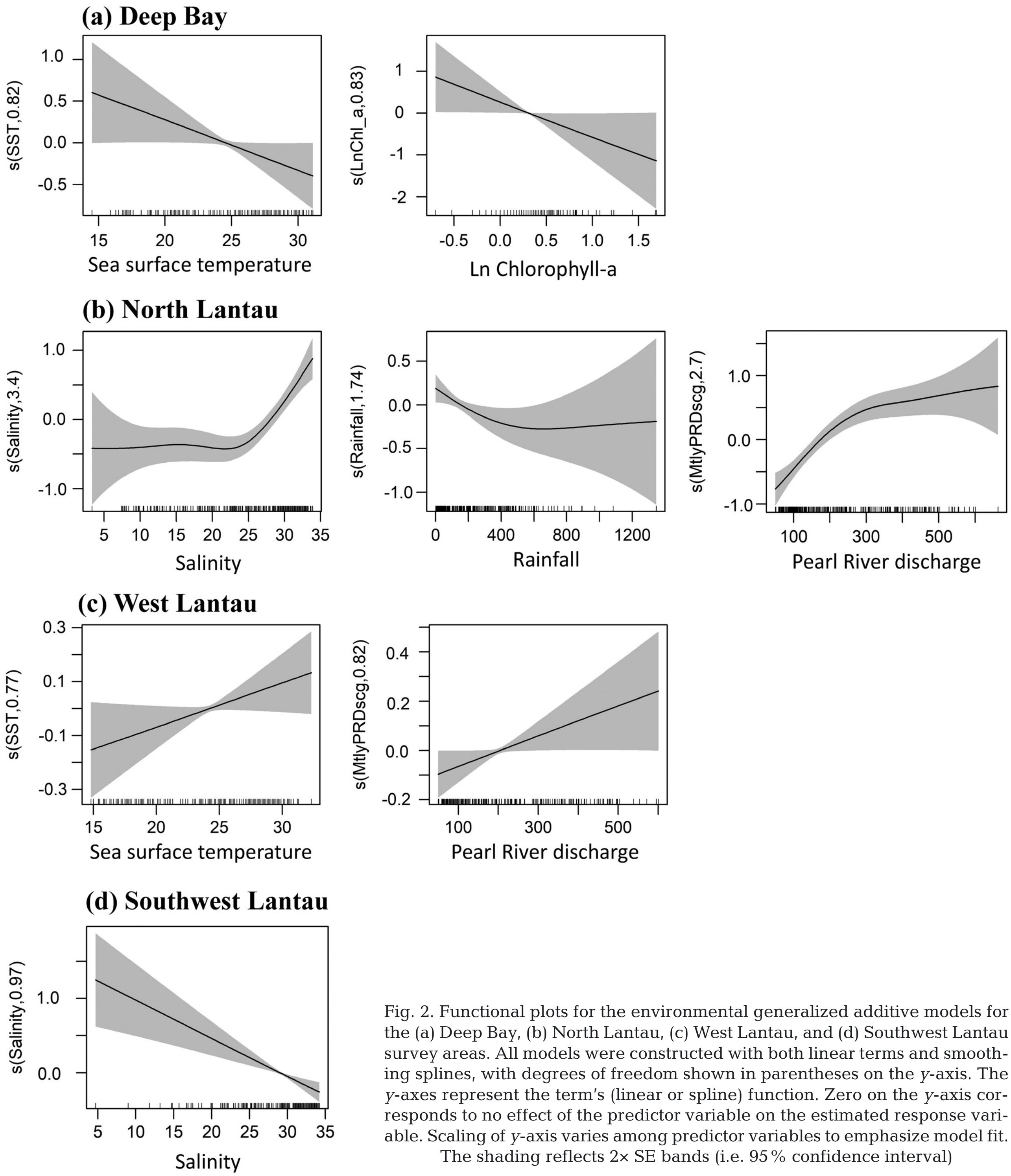
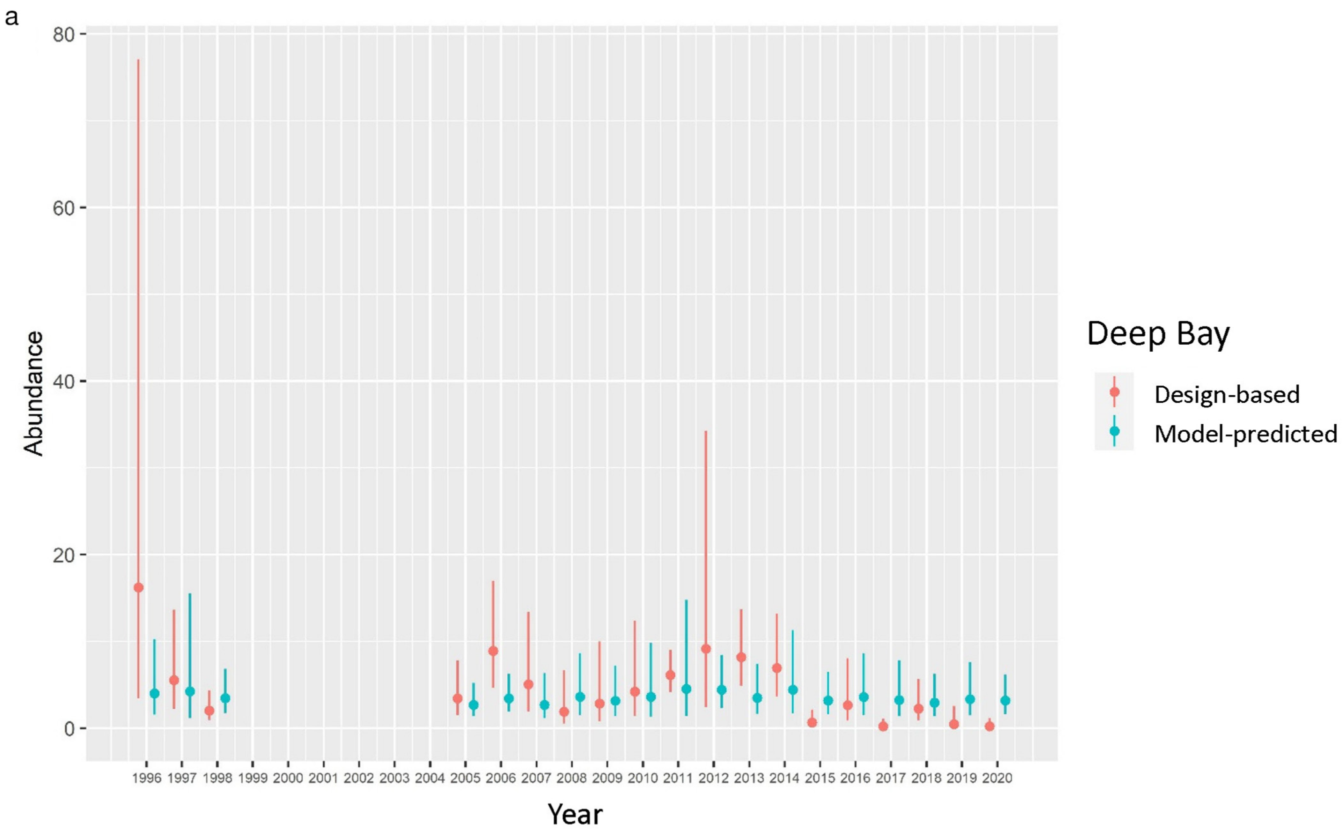


Fig. 2. Functional plots for the environmental generalized additive models for the (a) Deep Bay, (b) North Lantau, (c) West Lantau, and (d) Southwest Lantau survey areas. All models were constructed with both linear terms and smoothing splines, with degrees of freedom shown in parentheses on the *y*-axis. The *y*-axes represent the term's (linear or spline) function. Zero on the *y*-axis corresponds to no effect of the predictor variable on the estimated response variable. Scaling of *y*-axis varies among predictor variables to emphasize model fit. The shading reflects 2× SE bands (i.e. 95% confidence interval)

modeling (Table 2). The proportion of area lost to reclamation was identified as a significant variable ($p < 0.0001$; Table 4) in the North Lantau anthropogenic GAM; none of the other variables, including finless porpoise abundance in South Lantau (a natural variable) were identified as significant in their respective GAMs (Table S2).

The baseline North Lantau anthropogenic GAM (i.e. using model-predicted abundance as the only predictor variable) explained 73.8% of the deviance



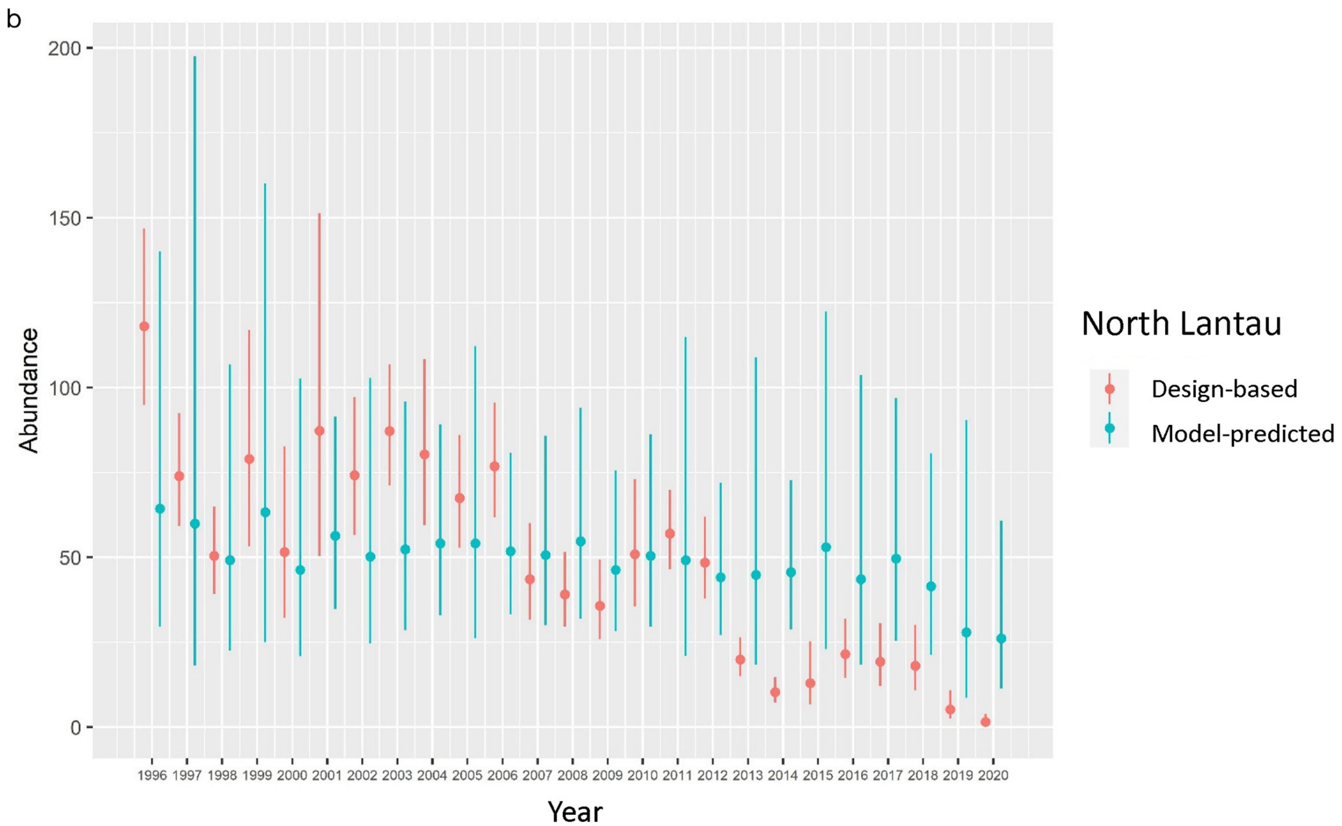


Fig. 3. Yearly line-transect and model-predicted abundance estimates and 95% confidence intervals for the (a) Deep Bay, (b) North Lantau, (c) West Lantau, and (d) Southwest Lantau survey areas. Years without an abundance estimate indicate that either the area was not surveyed that year or that environmental covariates were not available for that year

(*Fig. 3 continued on next page*)

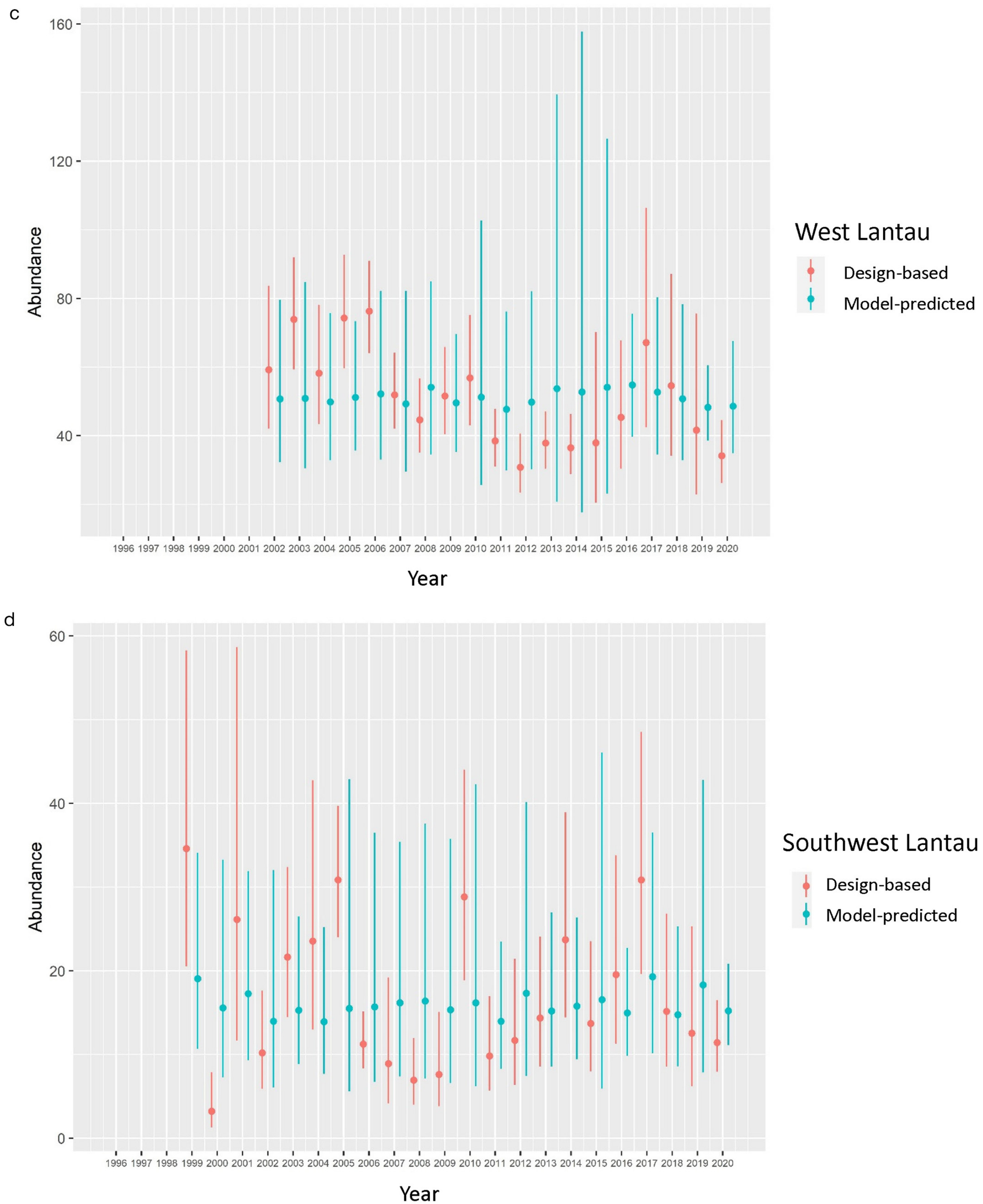


Fig. 3. (continued)

Table 4. Baseline and final anthropogenic models built for North Lantau. Variables are listed in the order of their significance (Ln Pred.Abund: natural logarithm of predicted abundance from the environmental generalized additive model; reclamation: proportion of area lost to reclamation in North Lantau), with their approximate p-values in parentheses. Performance metrics included the percentage of explained deviance (Expl. dev.) and root mean squared error (REML)

Model	Predictor variables (p-value)	Expl. dev.	REML
Baseline	Ln Predicted Abund. (<0.0001)	73.8	0.51
Anthropogenic	Reclamation (<0.0001) + Ln Predicted Abund. (0.0431)	91.5	0.29

and, as expected, had an almost linear functional plot (Fig. 4). When the proportion of area lost to reclamation was added to this baseline model, explained deviance increased to 91.5%, and the functional plot showed a threshold effect, with line-transect abundance estimates decreasing once the cumulative proportion of reclamation reached approximately 0.0067 (Fig. 5). The root mean squared error also improved when the anthropogenic variable was added, from 0.51 for the baseline GAM to 0.29 when the anthropogenic variable was added to the model (Table 4). Most yearly abundance estimates from this model were much closer to those estimated using design-based methods, particularly from 2013 on, when the difference between the design-based and environmental-model predicted abundance estimates were largest (Fig. 6). Interestingly, in 2013, there was a large increase in the proportion of habitat lost to reclamation, increasing from 0.0068 in 2012 to 0.0103 in 2013, and much of this was in preferential dolphin habitat.

4. DISCUSSION

To our knowledge, this is the first study to develop habitat-based density models for Indo-Pacific humpback dolphins using systematic line-transect data in concert with comprehensive environmental and anthropogenic variables. The results provide valuable information for our understanding of humpback dolphin use of HK waters, and especially for management authorities that are charged with protecting these animals. Based on the environmental GAMs, several natural variables (salinity, rainfall, river discharge, chl *a*, SST) affect dolphin abundance in the study area. The significance of salinity and freshwater discharge is not surprising, as previous research has suggested that freshwater input (river discharge and salinity are both strongly related variables) is a major factor in dolphin use of particular areas (Jefferson 2000, 2018, Hung 2008). The significance of SST was not fully expected, as there have been few indications from previous work that this is an important factor in dolphin movements in our study area (though Huang et al. 2019 found it to be important in the Beibu Gulf).

The anthropogenic GAM indicated that at least one factor (land reclamation) correlated with dolphin abundance in HK. Though we cannot necessarily infer causation from this result, these findings do provide important information that should be considered in future management actions. The multi-stage modeling approach used in this study provides a technique for potentially distinguishing between environmental and anthropogenic effects and can easily be applied to other species and study areas.

4.1. Caveats and potential biases

Effective habitat models require covariates at temporal and spatial resolutions consistent with the scale of the ecological or management question (Mannocci et al. 2017). The objectives of this study were to develop a better understanding of habitat variables that correlate with the abundance of humpback dolphins in HK waters as well as to investigate which anthropogenic impacts may be related to the documented declining numbers of dolphins (Jefferson 2018). Consistent with Jefferson (2018), we focused our analysis on yearly abundance for each of the 4

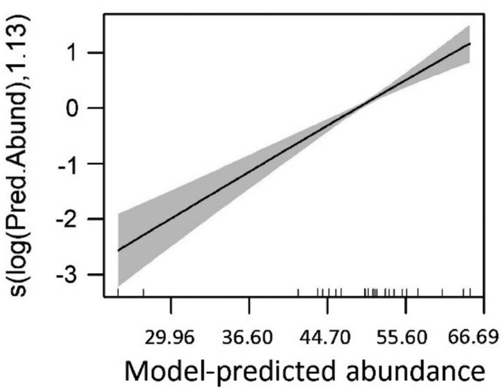


Fig. 4. Functional plot for the North Lantau baseline anthropogenic generalized additive model. Shading reflects 2× SE bands (i.e. 95% confidence interval)

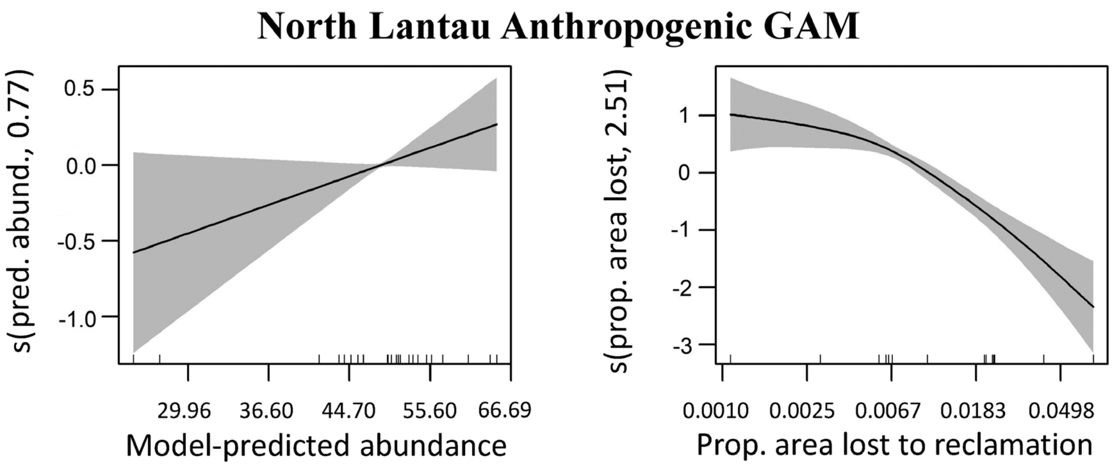


Fig. 5. Functional plots for the North Lantau anthropogenic generalized additive model (GAM). The *y*-axes represent the term's (linear or spline) function. The model was constructed with both linear terms and smoothing splines, with degrees of freedom shown in parentheses on the *y*-axis. Zero on the *y*-axis corresponds to no effect of the predictor variable on the estimated response variable. Scaling of *y*-axis varies among predictor variables to emphasize model fit. Shading reflects 2× SE bands (i.e. 95% confidence interval)

survey areas, which was supported by the resolution of the available habitat covariates (i.e. the finest resolution was monthly for each individual survey area as a whole). The current habitat models thus reflect yearly mean abundance in each of the 4 survey areas, without explicitly accounting for seasonal or within-survey-area variation.

One major shortcoming of the current study was the unavailability of relevant data to describe fisheries in HK waters. Fisheries, especially trawl fisheries, are well known to be important elements that impact the dolphins. These impacts can be negative (e.g. entanglement in nets and lines, resulting in injury and death; habitat damage and reduction of prey resources for the dolphins; Parsons & Jefferson 2000, Jefferson et al. 2006), or positive (e.g. dolphins feeding on prey stirred up by the nets, allowing easy access to food for the dolphins; Jefferson 2000). The data available on fisheries in HK are largely qualitative and non-systematic. There are no long-term records of the spatial or temporal distribution of fishing effort, capture or discard rates, or dolphin by-catch rates. The limited data that are available come primarily from vessel registration records, occasional port surveys (largely dependent on fishers' self-reporting), and for dolphin by-catch as gleaned from stranding records. On-board fisheries observer programs, or even programs that collect catch data from remote platforms, are not available and may not be suitable for fishing vessels presently used in HK. There has been a dramatic change in fishing activity in HK over the study period, with a trawl ban going into effect in 2013. Wilson et al. (2008) pointed out that changes in trawling effort in HK may be important in influencing humpback dolphin use of the area.

As this is a novel attempt to use habitat-based modeling methods for this population of humpback dolphins, some lessons were learned in the process that can be applied to future work along these lines.

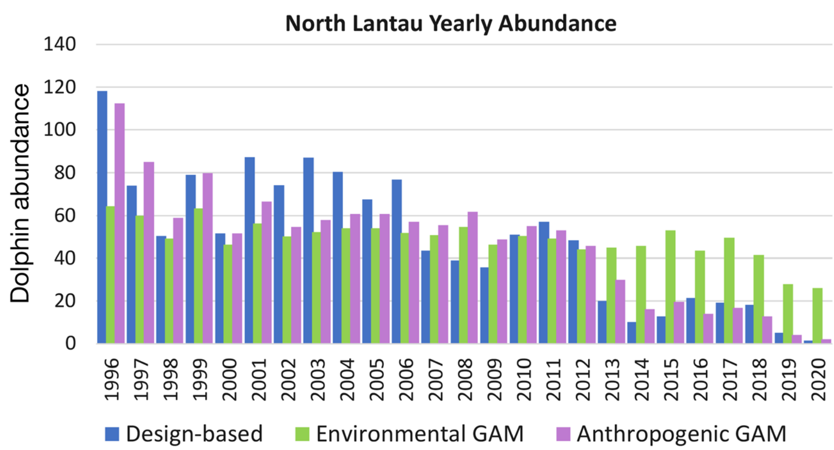


Fig. 6. Yearly abundance for the North Lantau survey area as derived from design-based analyses (blue bars), the environmental generalized additive model (GAM) (green bars), and the anthropogenic GAM (purple bars). Note the much closer relationship of the anthropogenic GAM estimates (vs. the habitat GAM estimates) to the design-based estimates, and the dramatic drop in the design-based estimates starting in about 2013

The most important lesson is that better predictor variables would be valuable, especially at finer temporal and spatial scales. Since this study used covariate data collected through other projects, in some cases there was not a good match with our dolphin survey data, and this certainly affected the results to some extent. Clearly, much better data on fishing effort, catches, and, ideally, dolphin and porpoise bycatch, would be extremely helpful.

Finally, while we found a strong correlation between dolphin abundance and the proportion of habitat lost to reclamation, we cannot effectively distinguish causation from simple correlation. While the impacts of reclamation on humpback dolphins were recently summarized (Huang et al. 2022), is difficult to determine the mechanistic link between habitat loss and dolphin abundance. In addition, even if we assume that reclamation is causative of dolphin declines, it is challenging to distinguish the impacts of the construction phase (i.e. the noisy and disruptive activities involved in creating the 'reclaimed' land) vs. the operational phase (i.e. the effects of the long-term loss of that part of the dolphins' habitat). As our long-term database of consistently collected dolphin density data accumulates, we will be better able to examine this in the future. However, further work on this important issue is needed, including ongoing studies to determine if dolphin numbers stabilize (or increase) as reclamation work for the airport's Third Runway expansion in North Lantau comes to a halt, and with the subsequent creation of a large marine park that would largely prohibit such operations after 2024 (see Jefferson 2018).

4.2. Management implications

The results of this study provide information that is directly relevant to the management of humpback dolphins in HK waters and the Pearl River Estuary. Recognizing that salinity, freshwater discharge from the Pearl River, and SST are important habitat features that affect dolphin abundance can be useful in sorting out potential reasons that may explain changes in dolphin density in different areas of HK. For example, the environmental models developed in this study can be used to evaluate if future changes in dolphin abundance are consistent with changes in habitat conditions or if other factors are driving the differences. In 2 of the survey areas (i.e. North Lantau and West Lantau), increases in freshwater discharge from the Pearl River are associated with increases in dolphin density. Future changes that result in a decrease of freshwater discharge from the Pearl River would likely result in a decrease in dolphin density in these areas. Similarly, if water temperatures rise in response to climate change or changes in regional currents due to maritime engineering, there could be an increase in the number of dolphins using West Lantau and a decrease in the number of dolphins in Deep Bay. Ultimately, given the availability of additional sighting and environmental data, a logical next step in model development is to tease out seasonal variability in dolphin abundance and distribution among survey areas. For government authorities, the environmental GAMs indicate that monitoring of salinity, freshwater discharge from the Pearl River, and SST should be included in conservation actions for the humpback dolphin population.

Even more important is the finding that area lost to reclamation stands out as the most significant anthropogenic factor in fluctuations of dolphin numbers in the heavily developing North Lantau area (there has been less development in the other survey areas). This has long been suspected, but this study provides the first quantitative evidence of such a link (Fig. 6). It is possible that there was some fundamental shift in the environment around 2013 that changed the nature of the (correlative) relationship between the dolphins and the river-based environmental variables. If so, then the model-based estimate would not be accurate because it assumed stable species–habitat relationships that may no longer exist in the same way. We are not aware of any significant shift or change in the environmental variables related to the river at around this time. However, around this time there was a major construction project (i.e. the Hong Kong-Zhuhai-Macao Bridge), which involved large-scale piling and reclamation work in a central part of the dolphins' habitat in the PR China-adjacent waters of the Pearl River (Wang et al. 2014) as well as smaller-scale bridge work in HK. In addition, the trawl ban went into effect in 2013, and as dolphin movements are known to have been affected by trawling activity (Jefferson 2000, Wilson et al. 2008), this may have been a factor.

Coastal engineering, especially involving land reclamation, is frequently used in Chinese waters and has been linked to conservation issues for the humpback dolphin in other habitats, such as those in the eastern Taiwan Strait, Xiaman, and the northern Beibu Gulf (e.g. Chen et al. 2016, Karczmarski et al. 2017, Wang et al. 2017, Wu et al. 2017b, 2021, Huang et al. 2022). Teasing out the relative importance of behavioral disturbance during the noisy construction phases involving reclamation vs. the effects of actual physical loss of habitat caused by the 'reclaiming' of shallow seas will require further study (Huang et al. 2022). Clearly, improvements are needed in both our scientific understanding of determining factors for changes in dolphin abundance, and in management approaches to effectively conserve these animals. The approaches outlined by Bao et al. (2019) and Huang et al. (2022) have great potential to aid in future modifications to management efforts for humpback dolphins in coastal habitats. Despite the challenges, our finding of the importance of reclamation may provide further support for the creation of marine parks (in which such construction processes are forbidden) and for general calls to restrict reclamation projects in important dolphin habitat.

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