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Editorial

Welcome to this the twentieth volume of the *Journal of Cetacean Research and Management*. This volume contains seven papers covering a wide range of conservation and management issues.

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G.P. DONOVAN
Editor

Spatial analysis on the occurrence of inshore and offshore bottlenose dolphins (*Tursiops truncatus*) in Osa Peninsula waters and Golfo Dulce, Costa Rica

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ABSTRACT

The aim of this assessment is to advance our understanding in the spatial ecology of the resident inshore and offshore population of bottlenose dolphins in Golfo Dulce (GD) and Osa Peninsula Waters (OPW). Our approach used niche-based models (Phillips *et al.*, 2006, Thorne *et al.*, 2012, Friedlaender *et al.*, 2011), which provided details of how dolphins use coastal and oceanic habitats, describing the factors that influence their distribution in the study area and identifying the critical habitats to be considered for management and conservation. Our analyses indicate several important aspects of the distribution of these two ecotypes of bottlenose dolphins. As expected in the study area, these two ecological races occur in close proximity, but differ in the structural factors of the habitat they occupy. The inshore population uses areas close to the mouths of the rivers as critical foraging habitats, being influenced by tidal cycles and seasonal changes in water temperature and salinity. The offshore population in oceanic habitats must rely on prey species found in rare but profitable patches, therefore pelagic dolphins in the open ocean would often need to travel long distances searching for these patches. Distribution models illustrating the difference in habitat use presented in this assessment are key to effective management of the marine mammals' diversity in Costa Rica.

KEYWORDS: COMMON BOTTLENOSE DOLPHIN; PACIFIC OCEAN; HABITAT; MODELLING; DISTRIBUTION; FEEDING GROUNDS

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) inhabit most temperate and tropical waters around the world (Hale *et al.*, 2000; Wells and Scott, 2008; Fernandez *et al.*, 2011), including coastal inshore waters of all continents, around most oceanic islands and atolls, as well as in pelagic offshore waters, displaying strong behavioural and ecological plasticity that allows them to inhabit marine and estuarine ecosystems, even ranging into rivers. It appears that *T. truncatus* may have once or repeatedly, adapted to different environmental conditions resulting in several different forms or ecotypes (Tezanos-Pinto *et al.*, 2009). These populations exhibit notable morphological (Hersh and Duffield, 1990; Well and Scott, 2008), osteological (Perrin *et al.*, 2011), hematological (Duffield *et al.*, 1983; Hersh and Duffield, 1990) and molecular differences (Hoezel *et al.*, 1998; LeDuc *et al.*, 1999; Segura *et al.,* 2006; Perrin *et al.* 2011; Lowther-Thieleking *et al.*, 2015). Such differences are associated with their ecology (Rossbach and Herzing, 1999; Segura *et al.*, 2006; Klatsky *et al.*, 2007; Bearzi *et al.*, 2009). Therefore, they are recognised as distinct ecological races. According to Perrin *et al.* (2011), *Tursiops nuuanu* was described in the offshore eastern tropical Pacific by Andrews in 1911, and later synonymised with *Tursiops truncatus* by Hershkovitz (1966). However, the occurrence of the inshore and offshore ecotypes was first described by Norris and Prescott, (1961) in the eastern North Pacific.

According to Segura *et al.* (2006), ecological and environmental pressures can affect the evolution of phenotypic traits involved in reproductive isolation and the subsequent splitting of lineages into separate species. These phenotypic variations between the populations of *T. truncatus* throughout their geographic range have been used to characterise their distribution. Factors such as depth (pelagic forms have been reported to range primarily between the 200m and 2,000m isobaths), salinity, primary productivity, surface temperature, distance to the coast (coastal form occurs at least up to 7.5km from shore), habitat use, residence patterns and social strategies, could be the cause of these phenotypic and genetic variations (Natoli *et al.*, 2004; Natoli *et al.,* 2005; Torres *et al.*, 2005; Segura *et al.*, 2006; Querouil *et al.*, 2007; Bearzi *et al.*, 2008; Fernández *et al.*, 2011; Diaz *et al.*, 2017). According to several theoretical and empirical analyses, organisms' ecology is considered to be a driving force in speciation (Schluter, 2009). Novel ecological niches are colonised by ancestral populations that have been subjected to divergence and radiation processes. Gavrilets and Losos (2009) suggest that such processes of adaptive radiation into novel and divergent ecological niches is differentiated by a burst of phenotypic diversification, which progressively slows as available ecological niches become filled.

The territorial Pacific waters of Costa Rica are an important portion of the Eastern Tropical Pacific (ETP). They are characterised by a remarkable seascape diversity, including: coral reefs; mangrove forests; mudflats; rocky shores; sandy beaches; cliffs; seagrasses; a seasonal upwelling area; an oceanic thermal dome; an oceanic trench (more than 4,000m deep); a submarine mountain range (Coco Ridge); many coastal islands; one oceanic island

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(Coco Island); a cold seeps and even a tropical fjord (Cortés and Werhtmann, 2009; Alvarado *et al*., 2011; Alvarado *et al*., 2012). Such diversity of marine habitat is reflected in the cetacean's diversity patterns (May-Collado *et al*., 2005; Oviedo *et al*., 2015), even at different scales.

Pacheco-Polanco *et al*. (2011) documented the occurrence of the inshore and offshore ecotypes of *T. truncatus* off Osa Peninsula and Golfo Dulce respectively, Oviedo *et al*. (2015) detailed the relevance of each ecotype within the diversity pattern of the habitats they occur. In many regions of the world, however, there is insufficient evidence to distinguish between differential habitat use by individuals and true ecotype specialisation of particular *T. truncatus* genetic lineages. That is why the study of species-environment relationships can provide important information about the species' habitat use and distribution. Species' distribution models can provide quantitative predictions of geographic distribution and are useful tools for conservation purposes, as they can be used to predict locations where ecotypes are likely to occur, in areas that have not been thoroughly surveyed.

The aim of this assessment is to advance our understanding in the spatial ecology of bottlenose dolphins in Golfo Dulce and Osa Peninsula Waters (henceforth GD and OPW), test if there are dissimilar environmental variables influencing habitat suitability between the inshore and offshore ecotypes, use niche-based models (Phillips *et al*., 2006; Thorne *et al*., 2012; Friedlaender *et al*., 2011) to describe the factors that influence their distribution in the study area and identify the critical habitats to be considered for management and conservation.

METHODS

Study area

Osa Peninsula Waters: This study area was framed within a polygon limited to the East by the shorelines of Terraba-Sierpe River System, Drake Bay and Corcovado National Park to Punta Salsipuedes. The area within the polygon is the target location of whale watching boats (the platform of observation) and is characterised by a great portion of shelf waters, which progressively shrinks southward along the western coast of the Peninsula; just outside of GD's entrance, water depths reach 1,000m at less than 4nm from Cabo Matapalo. Within shelf waters, the most remarkable topographic unit is Isla del Caño (Fig. 1).

Golfo Dulce: This embayment is characterised by a deep inner basin (> 215m of maximum depth) and a shallow sill (70m), that connects the inner basin with the open ETP (Wolff *et al.* 1996; Quesada-Alpizar and Cortez, 2006; Svendsen *et al*., 2006).The total surface area is close to 750km^2. Water circulation is restricted, a characterisation of true fjords, and there is a slow, deep water renewal by occasional intrusion of dense subsurface waters. Productivity in GD is most likely subsidised by riparian discharge to the inner basin, particularly by contributions from the Esquinas, Rincón, Tigre and Coto Colorado Rivers (Fig. 1)

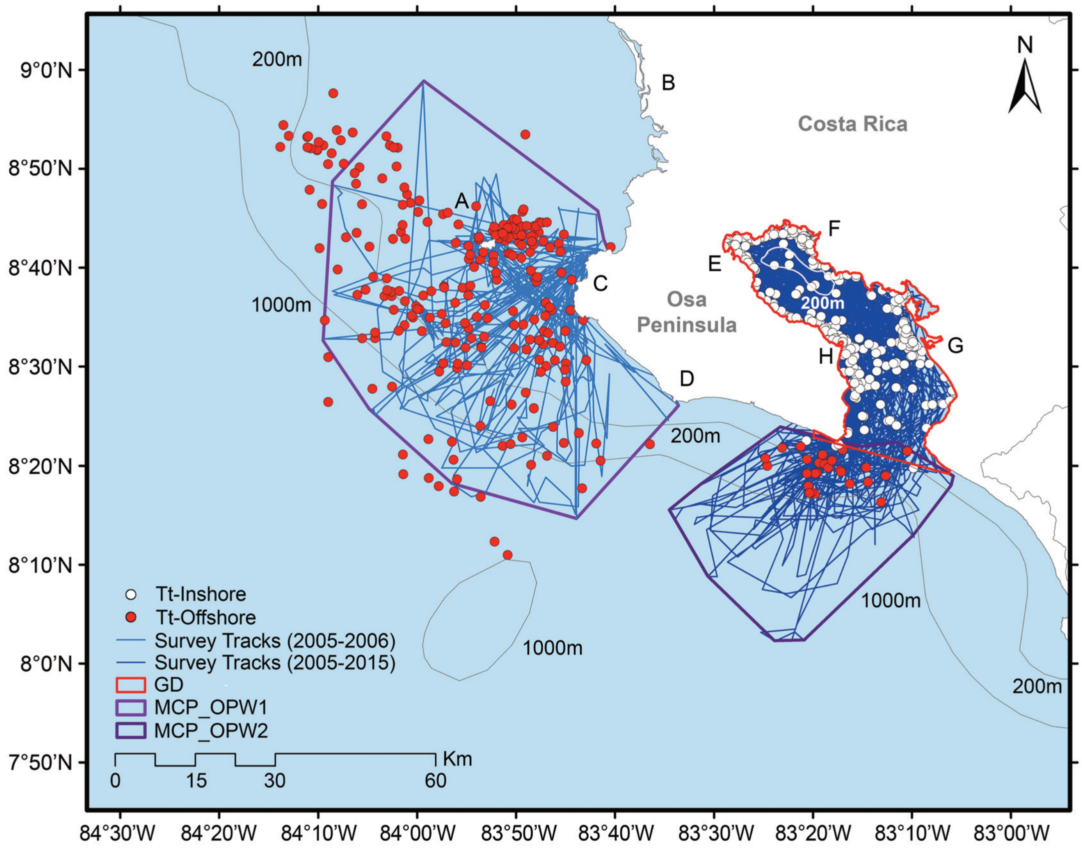

Fig. 1. Research efforts: search effort in OPW is distributed in two polygons (MCP_OPW1 and MCP_OPW2). Search effort in GD is illustrated by the tracks corresponding to 611 surveys inside GD and 165 surveys in MCP_OPW2. Encounters of inshore bottlenose dolphins (white circles) inside GD and offshore bottlenose dolphins (red circles) off OPW. Reference locations: A = Isla del Caño, B = Terraba-Sierpe River, C = Drake Bay, D = Punta Salsipuedes, E = Rincon River, F = Esquinas River, G = Coto Colorado River, H = Tigre–Platanares Rivers.

Dolphin locations

During field observations of bottlenose dolphins in the study area (GD and OPW), the putative classes of inshore and offshore ecotypes were assigned a priority by trained surveyors, following the visual and bathymetric cues described in Oviedo *et al*. (2015), which are based in those reported in Segura *et al*. (2006), Wells and Scott (2008), Perrin *et al*. (2011) and Diaz-Gamboa *et al*. (2017).

Data detailing the occurrence of bottlenose dolphin groups in the study area were derived from two databases: (1) sightings records gathered in Drake Bay-Isla del Caño and Corcovado National Park from 2001 to 2006 (Vida Marina Foundation, n = inshore: 0 sightings, offshore: 238 sightings); (2) presence-only records collected in GD from 2005 to 2015 (Centro de Investigación de Cetáceos Costa Rica CEIC, n = inshore: 450 sightings, offshore: 35 sightings). Each sighting recorded yielded information on date and location (GPS coordinates), best estimates on group size, group composition and behaviour at first encounter. Behaviour data collected in GD was more consistent and homogeneous due to the systematic utilisation of an ethogram by trained observers (LO, DHM, JDPP) and constraints related with environmental conditions and detectability (behaviour data was deemed valid when collected at a Beaufort sea condition < 3), whereas behaviour records taken in OPW during 2001–2006 were *ad libitum*.

The detection probability of the target species and subgroups are not specifically reported, however we acknowledge that detection probability would differ between locations. Dolphin encounters in GD (2005–2015) were collected using a more controlled protocol aided by the physiography of the research area; a semi-closed inner sea which facilitates a relatively high encounter rate, therefore there is a thorough documentation of the search effort. Whereas, sightings in OPW were entirely opportunistic in nature and effort tracks were only available for 2005–2006 (111 surveys), despite the search effort done since 2001 in the same sub-area (Fig. 1).

Eco-Geographic Variables (EGVs)

The variables taken into account to build the ecological niche models, were chosen according to their ecological relevance for the target species (*T. truncatus*) and availability of the data. The dataset contains three physiographic-related variables describing '*shelf tendency'* (McLeod *et al*., 2007; Bouchet *et al.,* 2015): depth, slope and curvature, which were obtained using the extracted data from the global 30 arc-second grid of the GEBCO_08 Grid dataset. Slope and curvature, a measure of the bottom topography, were processed using the *DEM tools* in the ArcGis 9.3.1 software.

Three more variables were selected for both areas (GD, OPW): the distance to the coastline, the distance to the 200m bathymetric lines and the distance to the major rivers' mouth. These variables were constructed using the *Euclidean Distance Tool* of the Spatial Analyst Toolbox in ArcGis 9.3.1. Non-physiographic variables were included in the modelling process: the mean Sea Surface Temperature (SST), Sea Surface Salinity (SSS) and the Surface Chlorophyll α (Chlor-α). Seasonal means for SST and SSS were obtained from MARSPEC dataset (Sbrocco, 2013). A 0.01-degree grid (approx. 1.6km × 1.6km) was used as resolution for the environmental layers to mimic the MARSPEC dataset original resolution. Due to the small size of GD no Chlor-α data with proper resolution was available. Chlor-α means were produced using the MODIS Aqua L2 images downloaded from Ocean Color Web (Feldman and McClain, 2012) and processed using SEADAS 7.0 (Baith *et al*., 2001). Maps were created (one for each variable) using the mean value of all the images available from 2001 to 2006 for the seascape off OPW and 2005–2015 for GD. A correlation analysis of all the variables was performed using a Pearson's correlation analysis integrated in the ENMTools (Warren *et al*., 2010). All correlated variables (significant Pearson's correlation greater than 0.5) were excluded. Selection between autocorrelated variables was done according to the field knowledge and literature existent for the species.

Modelling approach

We developed ecological niche models for bottlenose dolphins using a maximum entropy modelling approach to look at the potential distribution of these flagship species in the study area during the dry and rainy seasons, to describe differences in habitat suitability predictions and variables contribution between seasons. Maxent program (v. 3.3.3) was used in order to obtain habitat suitability (*HS*) predictions for our target ecotypes, as detailed in Phillips *et al*. (2006; 2009). Maxent estimates a target species' probability of presence by finding the probability distribution of the maximum entropy (i.e. the closest to uniform distribution), subject to a set of constraints that represent the availability of suitable habitat for the target species. In the present study, the model outputs were used as an approximation to the abiotic fundamental niche, or the species physiological range of tolerance to environmental factors in the absence of biotic interactions (Hutchinson, 1957). Due to the potential heterogeneity in detection probability in presence-only data depicting the location of bottlenose dolphins in GD and OPW, we applied a sample selection bias approach (Elith *et al*., 2010), following the recommendations in Merow *et al*. (2013) and Yackulic *et al*. (2013) to mediate an effort correction for both seasons. Two different files were constructed for each season using a Minimum Convex Polygon analysis with all the species sightings along with the effort tracks to obtain two sampled area polygons. The sample area polygons delimited the abiotic EGVs evaluated, in a way that biased variable sampling is reduced. Maxent models were run using the auto features with 100 replicates and using cross-validation to assess the model fit. To evaluate the model accuracy, we used the Area Under the Curve (AUC) metric of the Receiving Operator Characteristic (ROC) curve (Phillips *et al*., 2006). The AUC value provides a threshold-independent metric of overall accuracy; it ranges between 0.5 and 1.0. Values of 0.5 indicate that scores of specificity and sensitivity do not differ, while scores of 1.0 indicate that the distributions of the scores do not overlap. We assessed AUC values of the ROC curve of the models following the scale suggested in Hosmer and Lemeshow (1989): 0.5 indicated no discrimination; 0.5 to 0.7 represented poor discrimination; 0.7 to 0.8 indicated an acceptable discrimination; 0.8 to 0.9 indicated an excellent discrimination; and over 0.9 represented outstanding discrimination.

The permutation importance index was used to identify the most important EGVs for both ecotypes of bottlenose dolphins. This index measures the level of contribution of each EGV to the fit of the final model, in contrast to other heuristically defined metrics that depend on the path taken to obtain the models. The values of a particular variable are randomly permuted among the training points (presence and background) to measure the decrease in training AUC, a relevant decrease shows that the model is greatly dependent of such variable. The values were normalised to provide percentages (Kalle *et al.,* 2013; Svendsen *et al.*, 2015). In order to be consistent with the aim of understanding the effect of abiotic predictors in delimiting the distribution (Merow *et al.*, 2013), for both inshore and offshore bottlenose dolphins, the response curves to those variables that contributed the most to the average model (≥ 50%) were used to assess habitat suitability.

Behaviour and group size analysis

Data collected on group size and behaviours was analysed to test for differences between ecotypes. All statistical tests were performed with Statgraphics v. 2-1. We present the

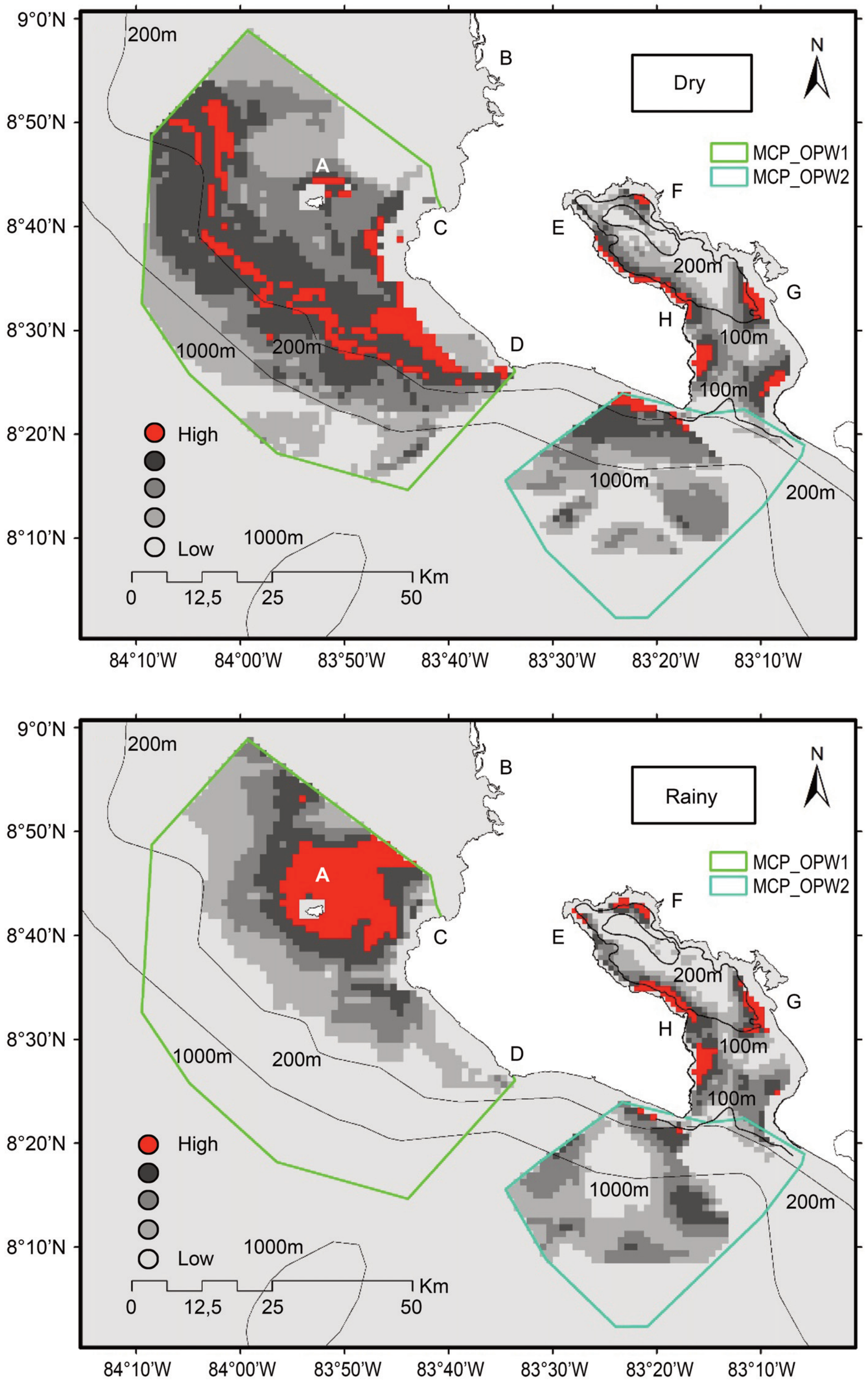

Fig. 2. Average habitat suitability model for *T. truncatus* with details in bathymetric contours in OPW (inserted polygons: OPW1 and OPW2) and GD. Reference location: A = Isla del Caño, B = Terraba-Sierpe River, C = Drake Bay, D = Punta Salsipuedes, E = Rincon River, F = Esquinas River, G = Coto Colorado River, H = Tigre–Platanares Rivers.

activity budget of both inshore and offshore bottlenose dolphins using behaviour observation at first encounter from 2010 to 2015 (*n* = 383 records) based on the ethogram used in Sceneider (1999) and modified by Garcia and Dawson (2003), which is made of five basic behavioural states: Forage, Travel, Social, Rest and Mill.

RESULTS

Survey effort was not evenly distributed between the two portions of the study area, with higher survey effort recorded in GD: a total of 775 cetaceans surveys were conducted between 2005 and 2015, including the inner basin (426 surveys ≈ 2,130hrs), the sill area (184 surveys ≈ 920hrs) and the transition to oceanic waters (165 surveys ≈ 825hrs). In contrast, earlier survey effort (2001–2006) off OPW accounted for 564 surveys equivalent to approximately 2,200hrs.

Ecological niche modelling for inshore bottlenose dolphins in GD

The average models for inshore bottlenose dolphins in GD derived from 100 replication runs are presented in Fig. 2. The major proportion of suitable habitat for *T. truncatus* in GD during the dry and rainy seasons corresponded with the coastline related to adjacent areas to the rivers' mouth, such as Esquinas and Coto Colorado, with particular reference to the sub-system conformed by the Tigre and Platanares Rivers.

The mean AUC value for the cross-validated model for inshore bottlenose dolphins in GD during the dry and rainy seasons were 0.759 (+/–0.120) and 0.775 (+/–0.076) respectively (Fig.3), which were deemed to offer an acceptable discrimination during the dry season and the rainy season. EGVs contributions to the final models of runs in GD are shown in Fig. 4. From all the set, distance to the rivers and distance to the 200m isobaths were found to be the strongest predictors during the dry season, while distance to the rivers, slope and distance to the 200m isobaths were the most influential environmental variables during the rainy season.

The seasonal model gain for GD during the dry season is notably decreased by major distance to the rivers and increased at far distance to the 200m isobaths (Fig. 5). Rainy season model gains are primarily described by distance to rivers and distance to 200m isobaths. Slope is also considered in Fig. 5 since it gains in combination with the latter and contributes by more than 50%. There is a negative

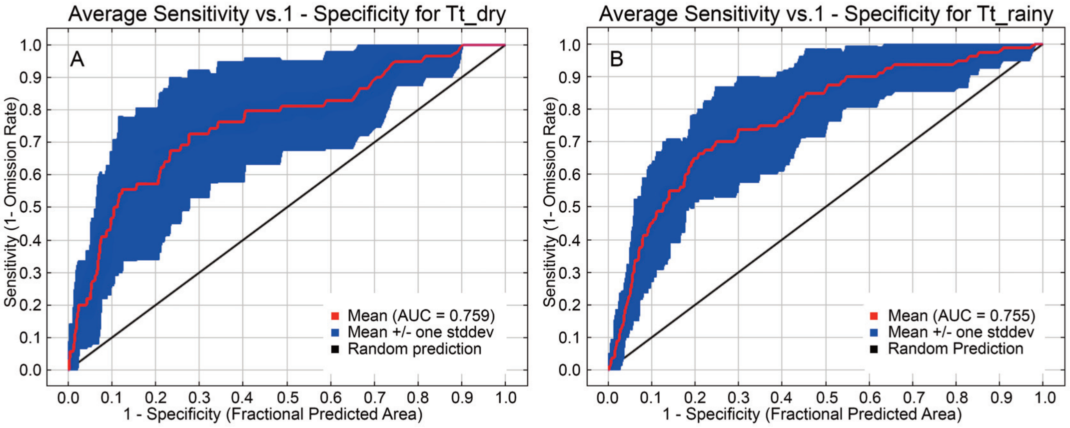

Fig. 3. Diagnostic plots for Maxent modelling of bottlenose dolphins in GD 2005–2015. Plot A indicates the receiver operator characteristic (ROC) curve for the model of the dry season (mean AUC for all the model runs equals 0.759); plot B shows the receiver operator characteristic (ROC) curve for the model of the rainy season (mean AUC for all the model runs equals to 0.775). The blue area indicates the standard deviation for the 100 model runs. The black diagonal line represents a random prediction (AUC = 0.5).

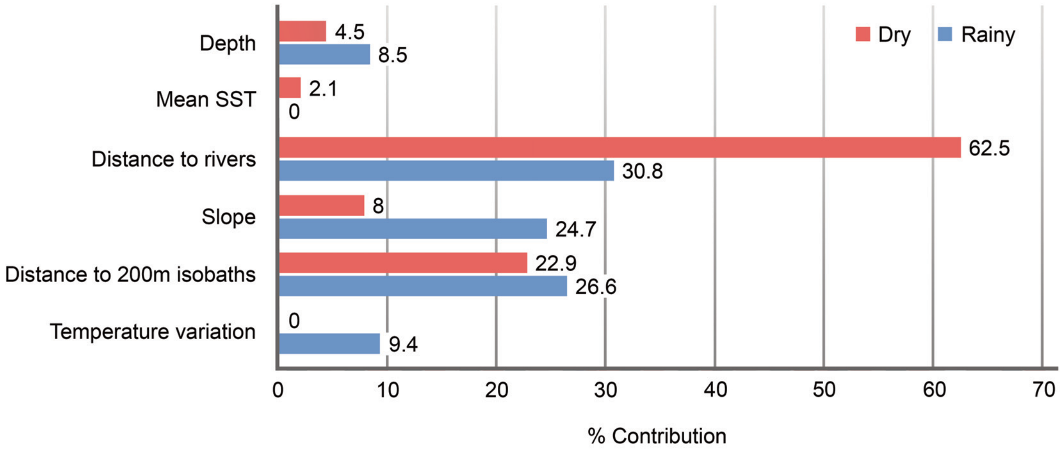

Fig. 4. Depiction for the estimates of relative contributions of the environmental variables to the Maxent model describing the abiotic fundamental ecological niche of inshore bottlenose dolphins in GD. The bars indicate the percent contribution for each variable to the overall models in the dry (blue bars) and rainy (red bars) seasons respectively, exact percentage in number at the top of each bar.

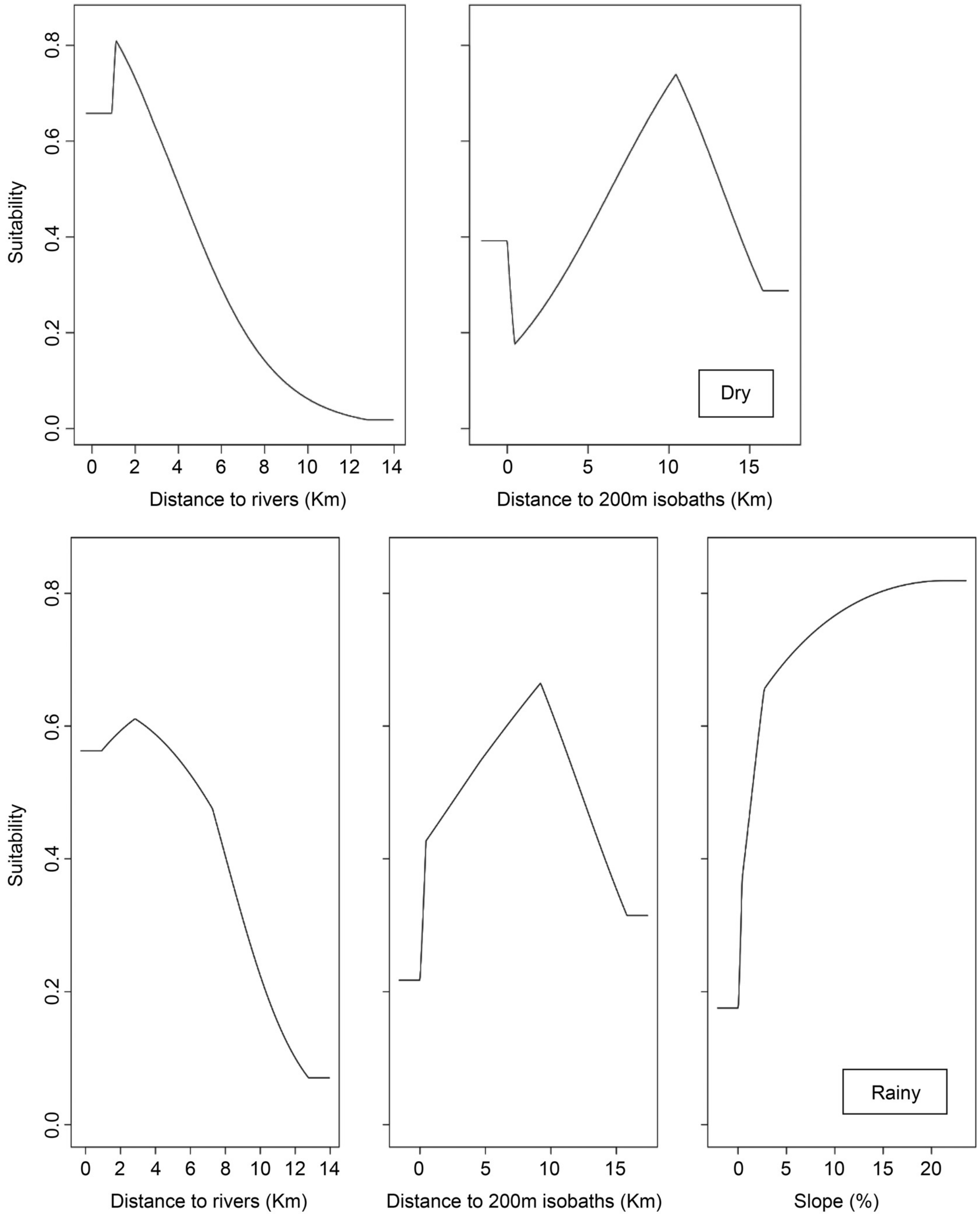

Fig. 5. Response curves for each of the main environmental variables influencing the ecological niche of bottlenose dolphins in GD during dry (distance to rivers and to 200m isobaths) and rainy (slope, distance to rivers and to 200m isobaths) seasons.

response to distance to the rivers beyond 2km, while the response associated with distance to the 200m isobaths is maximised at around 10km.

Ecological niche modelling for offshore bottlenose dolphins in OPW

The average models for OPW was obtained from 100 replication runs (Fig. 2) following the same procedure with inshore bottlenose dolphins in GD. The suitable habitat for the offshore ecotype of *T. truncatus* in OPW during the dry season is located within or close to the 200m isobaths, while in the rainy season it shifted around Caño Island and in front of the Térraba-Sierpe wetland.

Offshore bottlenose dolphins' models validation, showed a mean AUC value for the cross-validated model of the dry and rainy seasons of 0.759 (+/–0.089) and 0.888 (+/–0.098) respectively, which were deemed to offer an *acceptable discrimination* during the dry season and *excellent discrimination* for the rainy season. Plots in Fig. 6, illustrate the predictive performance of the model, highlighting low spatial autocorrelation.

The contributions of EGVs to the final models of offshore bottlenose dolphins in OPW are shown in Fig. 7. From all the set, depth and distance to the 200m isobaths were found to be the strongest predictors, both during rainy and dry seasons contributing to more than 50% to the gain in discrimination.

The seasonal models of OPW are primarily dominated by depths; during the dry season the ecological niche of bottlenose dolphins are better predicted by depths close to

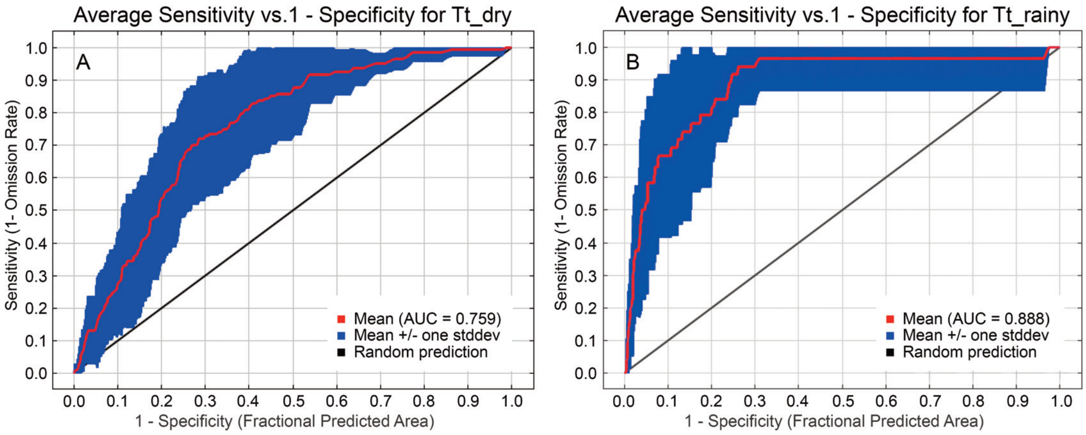

Fig. 6. Diagnostic plots for Maxent modelling of bottlenose dolphins in OPW 2001–2006. Plot A indicates the receiver operator characteristic (ROC) curve for the model of the dry season (mean AUC for all the model runs equals to 0.759); plot B shows the receiver operator characteristic (ROC) curve for the model of the rainy season (mean AUC for all the model runs equals to 0.888). The blue area indicates the standard deviation for the 100 model runs. The black diagonal line represents a random prediction (AUC = 0.5).

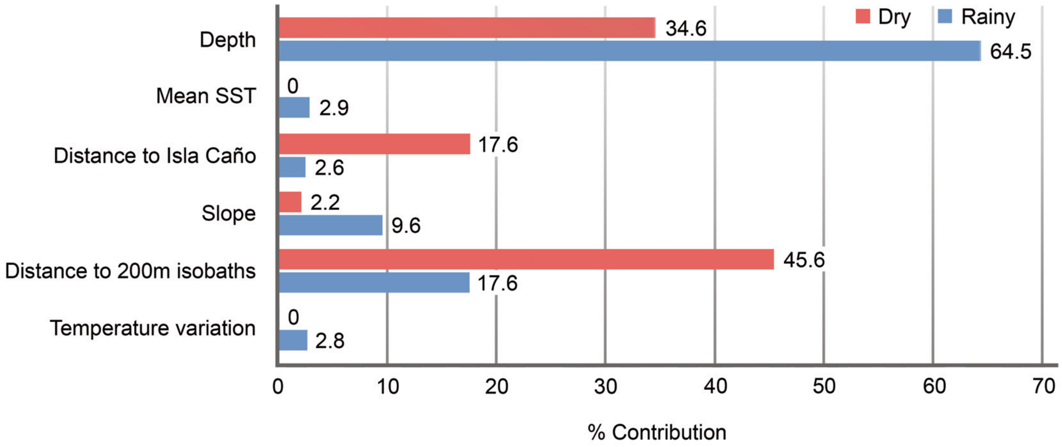

Fig. 7. Depiction for the estimates of relative contributions of the environmental variables to the Maxent model describing the abiotic fundamental ecological niche of inshore bottlenose dolphins in OPW. The bars indicate the percent contribution for each variable to the overall models in the dry (blue bars) and rainy (red bars) seasons respectively, exact percentage in number at the top of each bar.

the 200m bathymetric contour. This characteristic shifted during the rainy season to platform water depths of less than 200m. Distance to the 200m isobaths is the second best predictor of the ecological niche of *T. truncatus* in OPW. During the dry season the maximum gain is more consistent with short distances as opposed to the trend during the rainy season, where the niche is best described by distances close to 20km from this bathymetric contour (Fig. 8).

Behaviour and group size

The activity budget of inshore bottlenose dolphins showed the relevance of foraging in GD in relation to all other behaviours, while travelling is second in importance but closely associated with foraging. Dolphins will travel from one foraging spot to the other along the rivers draining in the inner basin of GD. Contrastingly, the activity budget of offshore bottlenose dolphins in the same dataset evidence the opposite trend; travelling is the most important activity for groups of the offshore ecotype of *T. truncatus*, followed by foraging as the second most important behaviour. The differences in the structure of the activity budget between putative forms is supported statistically (Kruskal Wallis test: $H(1) = 18.98$, $p < 0.05$), whereas the dissimilarities in foraging and travelling between the inshore and offshore bottlenose dolphins are not.

There was a statistically significant difference in group size between inshore and offshore bottlenose dolphins in the GD dataset (Kruskal Wallis test: $H(1) = 45.95$, $p < 0.05$), with dolphins observed in the inner basin and sill area of GD aggregated in smaller groups ($\bar{X} = 6.64$, SD = 5.93, N = 348 Range:1–30), in comparison to those documented in the transitional oceanic area off the mouth of the gulf ($\bar{X} = 43.74$, SD = 52.86, N = 35 Range 2–200), with a trend of increase in group size with oceanic depths ($r^2 = 0.346$, $p < 0.05$).

DISCUSSION

The results detailed above support the differences in distribution of inshore and offshore bottlenose dolphins in GD and OPW. Based on the environmental requirements that affect their habitat suitability and considering the dissimilarities in external morphology and behaviour, we have distinguished the abiotic environmental factors influencing the spatial ecology between these two ecotypes: in GD, the EGVs that best describe the ecological niche of

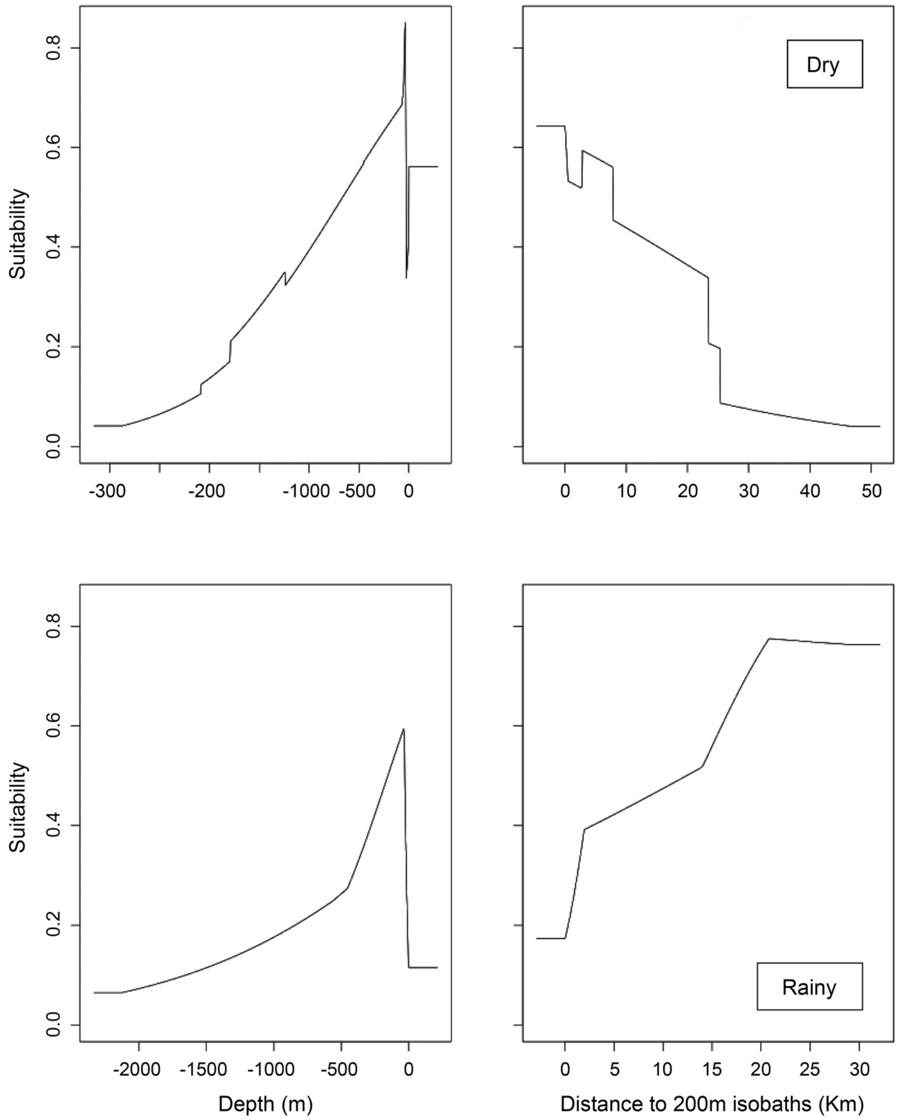

Fig. 8. Response curves for each of the main environmental variables influencing the ecological niche of bottlenose dolphins in OPW during dry and rainy seasons (depth and distance to 200m isobaths).

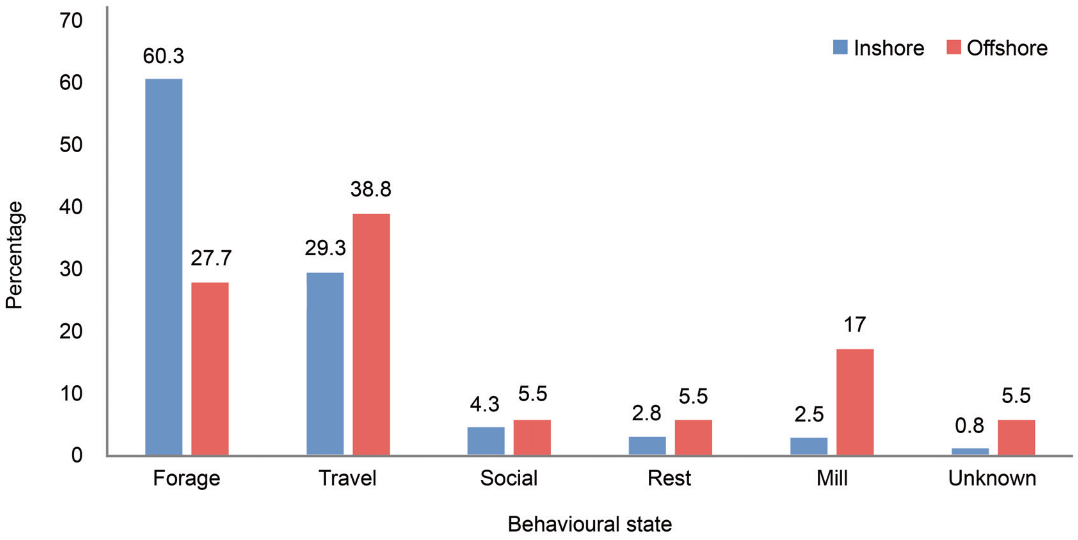

Fig. 9. Activity budget of inshore and offshore bottlenose dolphins in the study area. Exact percentage of every behaviour state on top of each bar.

the inshore form of bottlenose dolphins were distance to the rivers, distance to the 200m isobaths and slope, whereas depth and distance to the 200m isobaths were found to be the strongest predictors that describe the ecological niche of the offshore *T. truncatus* in OPW, during both seasons. Water depth, distance to the coast and distance to the 200m depth contour have been used for different authors to identify boundaries between species and ecological races in bottlenose dolphins elsewhere (Hale *et al*., 2000; Segura *et al*., 2006).

As expected in the study area, we have found the two ecological races of bottlenose dolphins to occur in close proximity, but to remarkably differ in the environmental requirements of the habitats they occupied. We do not rule out the potential for mixed encounter of both ecotypes: on 1 January 2016, we found a couple of inshore bottlenose dolphins at 10 miles from Caño Island travelling among an offshore group. We recognised the inshore ecotype individuals by the pigmentation pattern (as explained elsewhere in this study) and by the incidence of Lacaziosis Like Disease (LLD), which have been documented for the bottlenose dolphins in GD (Bessessen *et al*., 2014) and for another population off the port of Caldera at 300km north of GD (Herra-Miranda and Pacheco-Polanco, unpublished obs.). Additionally, the behaviour differentiated those inshore dolphins; even though they were travelling with a group of offshore conspecifics, they were at the periphery of the group and constantly avoided by other members within the group. We argued a confounding factor that despite the possibility for mixing, which occurs in an area where overlap between ecotypes exists, the general pattern of distribution evidencing a differential habitat use between ecotypes remains.

Based on the analysis of behavioural observations in the field, the inshore population that inhabits GD uses the areas close to the mouths of the rivers as critical foraging habitats (Herra Miranda *et al*., 2016). Estuarine habitats represent secured resources where potential prey species may be found individually, rather than in large schools. The prey species (and thus the dolphins) are being influenced by tidal cycles and seasonal changes in water temperature and salinity (Allen *et al*., 2001; Bearzi *et al*., 2008; Gowans *et al*., 2007; Perrin *et al*., 2011); hence aggregations are based in few individuals; competition at intra-specific levels for food and other factors may limit the option of forming large groups in inshore habitats (Bearzi, 2005; Pacheco-Polanco and Oviedo, 2007; Gowans *et al*., 2007; Bearzi *et al*., 2008; Oviedo *et al*., 2012; 2018). Additionally, individuals' encounter history derived from mark-capture-recapture sampling, has shown that the majority of resident dolphins are females with calves, usually gathering in the same protected locations year-round (Oviedo, 2018). In complex sheltered estuarine habitats, the dolphins can hide and notably reduce their predation risk (Gowans *et al*., 2007). According to our field observations, offshore bottlenose dolphins are usually encountered when travelling and showed an increase in group size with water depth. Likely, the offshore population in oceanic habitats would rely on prey species found in rare but profitable patches, with large areas of habitat with little to no available food sources at all, therefore, pelagic dolphins in the open ocean often would need to travel long distances searching for these patches (Gowans *et al*., 2007). Likewise, larger group sizes may benefit from cooperative feeding on patchy, rich food resources found in deeper habitats and may have a better chance of detecting predators and protecting against them. There are encounters in this spatial analysis, of fewer than five individuals, that have been assigned to the oceanic ecotype. Those smaller groups were considered as scout groups. In those instances, smaller groups, after being followed for an extended period of time, ended up being part of a major aggregation of offshore bottlenose dolphins.

Our assessment is based on presence only data, which yield several limitations regarding the inferences to be derived (Phillips *et al*., 2009). The use of a presence background algorithm (such as Maxent) limits the potential inferences to be done, as they produce different niche estimates than presence-absence models. As exemplified by Soberon and Nakamura (2009), the use of presence-absence will deliver an estimative of the occupied niche, while presence-background methods will calculate something more similar to the realised niche. A model constructed with true absences data has the potential to deliver better estimates of the actual distribution of the species studied. Nevertheless, due to the dynamic nature of the oceanic environment and the motility of the studied species, obtaining true absences might be an impossible objective when working with cetaceans. The use of methodological absences (false absences due to insufficient sampling) during the modelling process will produce incorrect distributional estimates (Lobo *et al*., 2010). Consequently, for cetaceans, it would be risky to use presence-absence algorithms, those procedures should be applied only in cases with a small area and extremely well sampled, with data in all the variety of environmental conditions available.

Opportunistic datasets, such as the ones used in this assessment, are important sources of information on distribution patterns, having the inherent potential of overcoming the caveats of presence-only data and Maxent, due to the high periodicity of the field observations in a relatively small area, which is improved by the addition of related behavioural data (Fernandez *et al*., 2018). While the inferences made from the present study might be limited due to the data available, there are several elements worth considering: (a) sightings are obtained from direct field observation using opportunistic boat-searches, therefore, instead of inferring the sampling process (as in museum collection data), the search effort during the collection of dolphin sightings, allowed for the correction of sampling bias by delimiting an effective subarea of observed records; and (b) the main drawback in modelling species distributions would not be the spatial bias in itself but the bias in the available environmental variables (Guillera-Arroita *et al*., 2015). In this assessment we established the variables that were good predictors to discern the difference in distribution of two ecotypes of bottlenose dolphins, from those variables, the fixed ones (e.g. 'shelf tendencies') which were unlikely to be misrepresented in the sample polygon, since spatio-temporally stable physical structures are easier to record or map, and require less resources to be characterised (Bouchet *et al*., 2015). Whereas those more dynamic in nature (e.g.

SST, SSS) were obtained from remote sensors, covering a much wider geographic resolution than that portrayed in the delimiting polygons.

Factors such as habitat structure, habitat boundaries, resource specialisation, and site fidelity in sheltered environments may promote phenotypic differentiation between dolphin groups like those found in OPW and GD (Natoli *et al.,* 2005; Torres *et al*., 2005; Segura *et al*., 2006; Querouil *et al*., 2007; Bearzi *et* al., 2008; Gowans *et al*., 2007; Fernandez *et al*., 2011; Pacheco-Polanco *et al*., 2011; Guevara-Aguirre and Gallo-Reynoso, 2016; Diaz *et al*., 2017). These aspects might equally have a crucial role in defining eco-morphological differences within a species. We hypothesise that the coastal habitat of GD might have stronger implications beyond the level of ecotypes, with potential localised genetic differentiation, such as that reported by Möller *et al.* (2007). Research efforts on discerning population structure are underway. We expect to couple photo-ID surveying with genetic sampling in forthcoming sampling seasons to confirm our hypothesis.

It is fundamental to understand the factors that influence the morphological differences within species, to increase our knowledge of evolutionary and ecological responses that affect a population in its natural environment, and to help us in the formulation of effective conservation measurements. The Pacific shoreline of Costa Rica is facing an increase in coastal urban-tourist development, most of which is being carried out without considering potential ecosystem effects. On the other hand, in 2010, GD was declared by the Institute for Fisheries and Aquaculture of Costa Rica (INCOPESCA) as a Marine Area for Responsible Fishery. This differs from Marine Protected Areas in goals and objectives, where the only restriction is the use of destructive fishing gear inside the Gulf. This leaves the critical foraging and calving habitats of these populations of dolphins inhabiting this embayment unprotected, defenseless and vulnerable to coastal development and degradation of their marine coastal habitats.

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Observations of cetaceans off southern Sri Lanka, April 2007–2013

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ABSTRACT

Cetaceans were observed off the South coast of Sri Lanka in the month of April, every year over a seven-year period, 2007–13. During 48 days at sea a total of 290 cetacean sightings were recorded. Blue whales were abundant, accounting for 61% (*n* = 177) of all sightings. This concentration of blue whales was predicted and discovered based on a migration hypothesis and there was evidence of the expected net westward movement in April. Nevertheless, most blue whales seen were not obviously on passage and many appeared to be feeding. Mothers with calves and likely reproductive behaviour (breaching and rushing) were also observed. There were five sightings of Bryde's-type whales (*B. brydei/edeni*); four were identified as *B. brydei*, one was identified as *B. edeni*. Sperm whales were sighted 16 times within a narrow band centred just outside the 1,000m isobath. Modal group size was 10–12; based on size most individuals appeared to be mature females or immatures. Spinner dolphin (*n* = 35 sightings) was the most abundant species, accounting for 67% of all cetaceans seen by number of individuals. They were frequently associated with tuna and seabirds. Risso's dolphin was only seen once, despite being reported as common around Sri Lanka in the early 1980s. They were taken in large numbers by local fisheries, which may have reduced local abundance. Other species recorded were: dwarf sperm whale (*n* = 3 sightings); short-finned pilot whale (*n* = 3); common bottlenose dolphin (*n* = 9); Indo-Pacific bottlenose dolphin (*n* = 3); pantropical spotted dolphin (*n* = 4); and striped dolphin (*n* = 4). Since the discovery of blue whales off southern Sri Lanka, commercial whale watching centred on the fishing port of Mirissa has developed rapidly, bringing new revenue to the region but also the potential for disturbance to the whales.

KEYWORDS: BLUE WHALE; BRYDE'S WHALE; COMMON BOTTLENOSE DOLPHIN; DWARF SPERM WHALE; INCIDENTAL CATCHES; INDIAN OCEAN; INDO-PACIFIC BOTTLENOSE DOLPHIN; MIGRATION; PAN-TROPICAL SPOTTED DOLPHIN; RISSO'S DOLPHIN; SANCTUARIES; SCHOOL SIZE; SHORT-FINNED PILOT WHALE; STRIPED DOLPHIN; WHALE WATCHING

INTRODUCTION

Blue whales in the northern Indian Ocean are believed to belong to a distinct subspecies, *Balaenoptera musculus indica* Blyth, 1859 (Perrin *et al*., 2010; Anderson *et al*., 2012). These whales have been known to occur around Sri Lanka for well over a century (Blyth, 1859; Fernando, 1912). Deraniyagala (1948) even characterised blue whales as 'common off Ceylon' (Sri Lanka). However, during the mid-1960s Soviet whalers took 1,294 blue whales from the Arabian Sea, including waters that are now part of the Exclusive Economic Zone (EEZ) of Sri Lanka (Berzin, 2008; Brownell, 1995; Clapham and Ivashchenko, 2009; Mikhalev, 1996; Mikhalev, 2000; Yablokov, 1994). Those Soviet catches were illegal and unreported at the time, and greatly reduced the northern Indian Ocean blue whale population, perhaps to just 10% of its original size (Zemsky and Sazhinov, 1994).

In 1979 the International Whaling Commission (IWC) established the Indian Ocean Sanctuary (IOS). One outcome was the sponsoring, by the World Wildlife Fund (WWF, Netherlands), of an expedition to the IOS to conduct non-lethal cetacean research. That research was carried out from the yacht *Tulip*, and resulted in a wealth of new information (e.g. Alling, 1986; Alling *et al*., 1991; Gordon, 1987; 1991). One finding was blue whales off the northeast coast of Sri Lanka near Trincomalee during January–April 1983 and 1984. This came as a surprise at the time (Whitehead, 1983; 1989), perhaps in part because the reduction in whale numbers by Soviet whaling may have contributed to a complete dearth of contemporary reports of blue whales from the region.

Later, a review of cetacean strandings in the neighbouring Maldives (roughly 400 n.miles, 750km, West of Sri Lanka) confirmed that blue whales strand year-round on the coasts of South Asia (India, Sri Lanka and the Maldives) (Anderson *et al*., 1999). That review also demonstrated that most strandings occurred during the northeast monsoon season (December to March: see Methods for an outline of the monsoon seasons). Where blue whales went during the southwest monsoon (May to October) was unknown, but it was suggested that many might be feeding in the highly productive seasonal upwellings of the western Arabian Sea (Anderson *et al*., 1999). Anderson (2005) subsequently demonstrated that sightings of blue whales in the Maldives were also seasonal (occurring during November to April), and again suggested that at least some of the blue whales which were known (from the *Tulip* research) to spend the early part of each year off northeast Sri Lanka might also feed off Somalia and Arabia in May–October. If this were the case, then it was predicted that those whales should pass eastwards from the Maldives to southern Sri Lanka in about December, returning westwards in April.

On the South coast of Sri Lanka, April tends to bring better weather than December, so a visit was planned for April 2005 to test this prediction. Inspection of Admiralty charts of Sri Lanka showed that Dondra Head was a likely site from which to look for blue whales, not only because it is the island's southernmost point but also because a minor canyon just offshore brings deep water to within about 5km of the coast. The visit was postponed for two years following the devastating tsunami of December 2004.

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[2] *Jetwing Lighthouse Hotel, Dadalla, Galle, Sri Lanka.*

Dondra Head was finally visited on 18 April 2007. Looking out to sea with a telescope, the first blue whale blow was spotted after just 12mins of searching. Further observations of blows and whales showing their flukes followed, with at least three blue whales in view. A second visit the next day produced a first blue whale blow within just 10mins, and recorded a minimum of four animals in less than two hours of watching. Following the success of these land-based observations, observations were continued using boat-based surveys. Some findings on blue whales have been reported by Anderson *et al*. (2012). This paper reports additional cetacean observations from visits during April in seven years, 2007–2013.

METHODS

Survey area

The survey area was initially selected as the waters off Dondra Head, the southernmost point of Sri Lanka (Fig. 1). The nearest port to Dondra Head at which a charter boat was available in April 2007 was Mirissa (approximately 15km West). Subsequently all boat-based surveys were conducted from there. The edge of the continental shelf lies approximately 7–8km South of Mirissa and runs roughly East–West. The continental slope curves northwards South of Dondra Head forming a submarine canyon, the head of which lies about 5km offshore (Fig. 1). Much shipping passes around the South coast of Sri Lanka, indeed this is one of the busiest shipping routes in the world, and a traffic separation scheme is in force (Hydrographic Office, 2007). Nearest to the coast is an inshore traffic zone, then a westbound shipping lane (centred around 5°48.5’N), and furthest offshore an eastbound shipping lane (centred around 5°42.5’N) (Fig. 2).

The meteorology of Sri Lanka (and this study site) is dominated by the monsoons (Fein and Stephens, 1989; Pant and Kumar, 1997). During the southwest (SW or boreal summer) monsoon, winds are predominantly southwesterly or westerly, blowing from over the Arabian Sea. During the northeast (NE or boreal winter) monsoon, winds are predominantly northeasterly, blowing off the Bay of Bengal. Winds in the northeast monsoon are generally lighter than those of the southwest monsoon. Furthermore, Mirissa is sheltered from northeast winds, but fully exposed to those from the southwest. The southwest monsoon blows from about May to October (although the later months are less windy, and sometimes referred to as the post-monsoon). The northeast monsoon lasts from about December to March. April is an inter-monsoon month, when winds are generally

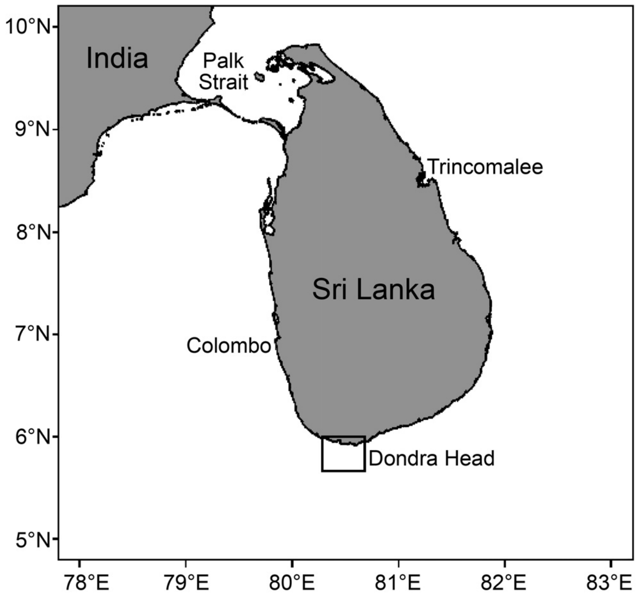

Fig. 1. Location map (the South coast study area is outlined by the rectangular box).

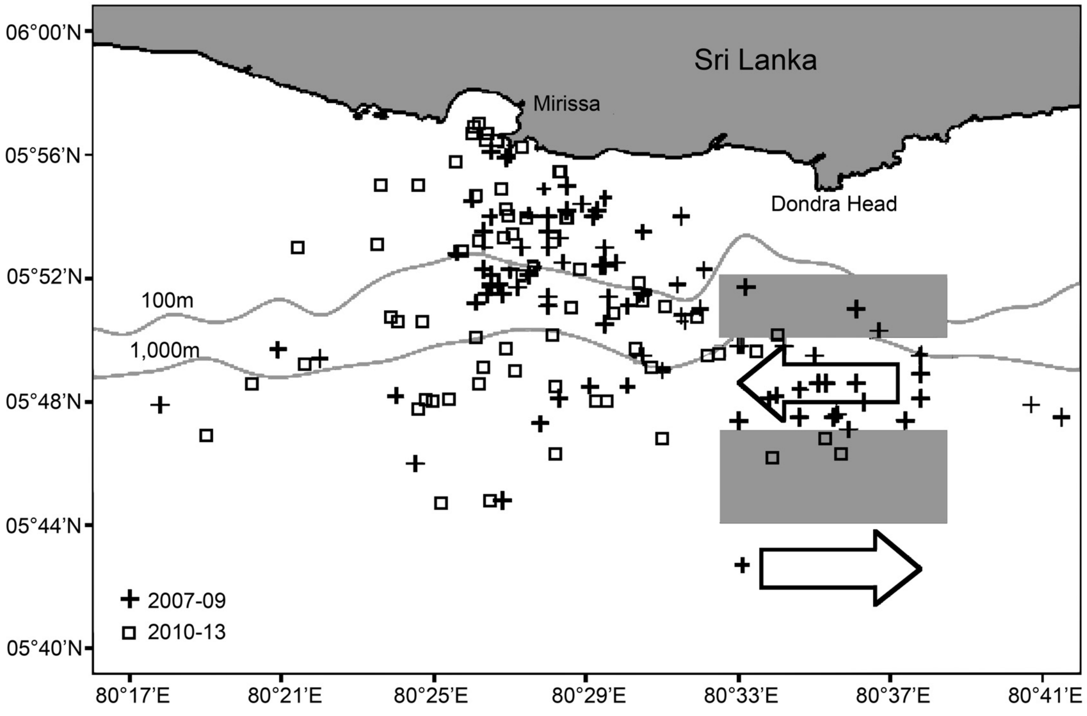

Fig. 2. Distribution of sightings effort off the South coast of Sri Lanka (the markers show 2-hourly boat positions, the grey blocks denote shipping separation zones, while arrows denote shipping lanes). Scale: 4’ latitude = 4 n.miles = 7.4km.

light and variable, although the southwest monsoon has usually set in by the end of the month. In addition to the prevailing monsoon winds, strong sea breezes develop on many days. As a result, April sea conditions are usually relatively calm in the mornings, but often become rough by midday or early afternoon.

The oceanography of this site is strongly affected by the seasonally reversing monsoon winds (Wyrtki, 1973; Molinari *et al*., 1990; Schott and McCreary, 2001; Shankar *et al*., 2002; Hydrographic Office, 2007; de Vos *et al*., 2014a). During the southwest monsoon, the Southwest (or Summer or Indian) Monsoon Current flows eastwards past the South of Sri Lanka from the Arabian Sea into the Bay of Bengal. It is joined by the southward flowing West Indian Coastal Current which passes down the West coast and around the South coast of Sri Lanka. During the northeast monsoon, most currents in the region reverse. The eastward flowing Southwest Monsoon Current is replaced by the westward flowing North Equatorial (or Winter Monsoon) Current. During early April currents can be variable, but are generally eastward by the end of the month, although there may be differences between years (*cf* de Vos *et al*., 2014b).

The longshore flow of these currents produces coastal upwellings, which, together with other physical oceanographic processes, promote primary productivity along the West and South coasts during the southwest monsoon and along the East and South coasts during the northeast monsoon (Krey, 1973; Longhurst, 1998; Vinayachandran and Mathew, 2003; Vinayachandran *et al*., 2004; 2005; de Vos *et al*., 2014a). In addition, rivers flowing into the sea along the South coast (including the Nilwala Ganga which enters the sea at Matara, between Dondra Head and Mirissa) bring nutrients into the inshore waters, again promoting primary productivity in this area.

Survey methodology

Surveys were carried out from the fishing port of Mirissa on the 16m motorised vessel *Spirit of Dondra*, for 2–14 days each April (and the last two days of March in 2009) over seven years, 2007–13 (Table 1). In 2007 and 2008, *Spirit of Dondra* was operating as a general charter boat; by 2009 it was operating as a whale watching vessel. All trips reported here were operated as whale watching trips, under the direction of the authors. The vessel had an average cruising speed of 7–8kts (13–15km h^{-1}) and a maximum speed of 11kts (20km h^{-1}). Two to four observers maintained a watch, from both the main deck (eye height about 2m above the waterline) and the roof of the wheelhouse (about 3.5m) at all times between leaving and returning to port. A total of 48 days of observation were completed, amounting to some 308hrs at sea (Table 1). The boat's position was recorded every two hours (at 08:00, 10:00, 12:00, 14:00 and 16:00h); these positions are charted in Fig. 2. During 2007–09, most effort was spent East of Mirissa, towards Dondra Canyon. However, as it became apparent that blue whales were to be found all along the outer shelf and slope, including immediately South of Mirissa, more time was spent in that area during 2010–2013 (Fig. 2). During 2007 and 2008, *Spirit of Dondra* was the only vessel whale watching in the area; in subsequent years the number of other vessels watching whales each day was recorded.

Table 1

Summary of at-sea cetacean survey effort.

Year	Start date	Finish date	No. days	No. hours	No. sightings	Blue whale sightings
2007	21 Apr.	23 Apr.	2	9:30	13	7
2008	9 Apr.	22 Apr.	14	99:15	95	64
2009	30 Mar.	11 Apr.	12	72:45	69	44
2010	10 Apr.	16 Apr.	6	42:25	30	6
2011	18 Apr.	24 Apr.	5	29:30	37	27
2012	16 Apr.	21 Apr.	5	32:20	33	21
2013	6 Apr.	11 Apr.	4	22:30	13	8
Total	**30 Mar.**	**24 Apr.**	**48**	**308:15**	**290**	**177**

For each cetacean encounter, boat position was recorded (with estimated distance and bearing to the cetacean(s) if not close by), group size estimated, presence of calves noted, and behavioural observations noted (including direction of travel if obvious, and interactions between species). Most cetaceans were approached closely enough to allow identification; in the few instances when this was not possible (e.g. while engaged with other cetaceans or when returning to port) identification was made to the lowest taxonomic level possible. For blue whales, defecations were noted and dive times were recorded. Blue whale dive cycles typically consisted of several short shallow dives and surfacings ending with a strongly arched back (and in most cases raised flukes) prior to a long (and presumably deep) dive. Long dive times were recorded (to the nearest minute) whenever there was little likelihood of confusing animals (due to the presence of multiple whales in the area).

RESULTS AND DISCUSSION

Species accounts

A total of 12 species were recorded from sightings at sea during 2007–13 (Table 2). Selected accounts of species follow.

Blue whale

Blue whales (*Balaenoptera musculus*) were abundant, with 177 sightings (61% of all sightings) and an estimated 270 individuals recorded. Note that this number included several resightings (on different days) of well-marked individuals, so will overestimate the actual number of animals seen. Nevertheless, the South coast of Sri Lanka is clearly home to a significant population of blue whales, for part of the year at least (Anderson *et al*., 2012; Ilangakoon, 2012a). The apparent abundance of blue whales was not constant throughout the month. Twice as many were seen in the second half of April as were seen during the first half (Table 3). In addition, direction of travel in April was recorded for 33 animals; in the early part of the month equal numbers were heading West and East (1–14 April, 8 v. 8), whereas in the latter part more were heading West than East (15–24 April, 11 v. 6). The numbers are small, but these data are consistent with the hypothesis of blue whales returning westward from the East coast during April (Anderson *et al*., 2012). Nevertheless, most blue whales were not obviously travelling. Many were diving repeatedly in the same general area, apparently feeding. Many instances of defecation were observed, with bright orange faeces suggesting predation on krill or other crustaceans.

Table 2

Summary of cetacean sightings by species.

		No. of sightings	No. of individuals	Group size	
				Mean	Range
Blue whale	*Balaenoptera musculus*	177	270	1.6	1–14
Probable blue whale		9	9	1.0	1
Bryde's whale	*Balaenoptera edeni*	5	5	1.0	1
Sperm whale	*Physeter macrocephalus*	16	179	11.2	1–35
Dwarf sperm whale	*Kogia sima*	3	9	3.0	1–6
Beaked whale	Ziphiidae	1	2	2	–
Short-finned pilot whale	*Globicephala macrorhynchus*	3	120	40	30–50
Risso's dolphin	*Grampus griseus*	1	30	30	–
Common bottlenose	*Tursiops truncatus*	9	727*	90.6	25–200
Indo-pacific bottlenose	*Tursiops aduncus*	3	24	8.0	4–12
Unidentified bottlenose dolphin	*Tursiops* sp.	2	11	5.5	1–10
Spinner dolphin	*Stenella longirostris*	35	4,986	142	6–600
Spotted dolphin	*Stenella attenuata*	4	410	102	40–200
Striped dolphin	*Stenella coeruleoalba*	4	198	49.5	8–150
Unidentified dolphin		14	421	–	–
Unidentified whale		1	1	–	–
Unidentified cetacean		3	4	–	–
Total		**290**	**7,406**		

*Note: Includes one distant sighting of at least two individuals, not included in group size estimates

Table 3

Numbers of blue whales seen per day off Mirissa in early and late April.

Period	Mean	95% CI	Range	Days
1–14 April	3.8	± 1.2	0–10	24
15–24 April	7.7	± 2.3	2–20	22

Dive times (for presumed deep dives, not shorter breathing sequences) were recorded on 132 occasions from 36 whales. Mean dive time was 11.1mins, and modal time was 10–12mins. These dive times are similar to the mean deep dive time of 10.7mins recorded by de Vos *et al.* (2013b) in the same area, and may be indicative of foraging depth (*cf* Doniol-Valcroze *et al*., 2011). In contrast, among a (smaller) sample of dive times recorded from blue whales (presumed to be on passage) in the Maldives, dives of 10–11mins were particularly uncommon (Anderson, 2005).

In addition to being a feeding area, Sri Lanka also appears to be a breeding area for blue whales. Eleven mother and calf pairs were noted and there were five instances of activity that appeared indicative of courtship or male competition. Breaching by individual animals was observed during four of these five occasions of presumed courtship, while two animals rushing at the surface side-by-side was observed three times. On one of these occasions spinner dolphins (*Stenella longirostris*) sped in to ride alongside the blue whales, with some dolphins bowriding in front of them. All of these observations occurred during the period 18–22 April (in three different years). All occurred when relatively large numbers of blue whales were in the area (minimum daily counts 8–20).

The observations of calves and apparent breeding behaviour, and of relatively large numbers of blue whales, suggest that this population might have largely recovered from the effects of whaling in the 1960s. Following Soviet whaling, it was suggested that the northern Indian Ocean blue whale population was reduced to perhaps just 10% of its original size (Zemsky and Sazhinov, 1994). The Antarctic blue whale population may be increasing at about 7% per year (Branch *et al*., 2004). Hypothetically, for northern Indian Ocean blue whales, assuming a population reduced to 10% of its original size, and a conservative 5% rate of population increase since 1967 (when Soviet whaling in the region ceased), then the population may have returned to 100% (i.e. its original size) by 2015. These numbers can be debated, but there appear to be many blue whales (certainly many 10s, perhaps low 100s) off Sri Lanka, and it is possible that the population may have recovered from the effects of commercial whaling. Nevertheless, there are now real concerns in this region regarding fisheries interactions and other anthropogenic threats. In particular, blue whales off Mirissa are at risk of ship strikes, especially if disturbance by whale watching vessels displaces some offshore into the shipping lanes (Ilangakoon, 2012c, 2013; Randage *et al*., 2014; de Vos *et al*., 2013a, 2016; Priyadarshana, 2016). Mean latitude of blue whale sightings was 5°50'N (range 5°43' to 5°56'N) i.e. roughly centred along the 1,000m isobath, and in the westbound shipping lane (Fig. 3). There was no difference in mean latitude (i.e. distance offshore) in 2007–09 versus 2010–13 (i.e. before and after the expansion of commercial whale watching at Mirissa) (Table 4). However, blue whales were more latitudinally dispersed in 2010–2013 (5°43' to 5°56'N) than in 2007–2009 (5°46' to 5°53'N). The issue of disturbance by whale-watching vessels is discussed further below.

Bryde's whale

During this study there were five sightings of 'Bryde's whales' (*B. edeni/brydei*). The taxonomy of these whales is not yet resolved, but it is likely that there are two species within the northern Indian Ocean, including Sri Lanka: the larger offshore Bryde's whale (*B. brydei*), and the smaller inshore Eden's whale (*B. edeni*). These taxa are currently recognised as forms, ecotypes or subspecies, although they probably warrant full specific status (e.g. Sasaki *et al*., 2006; Yamada *et al*., 2006; Kershaw *et al*., 2013; Luksenburg *et al*., 2015). However, an outstanding issue is that the holotype of *B. edeni* (in Kolkata, India) has yet to be genetically typed.

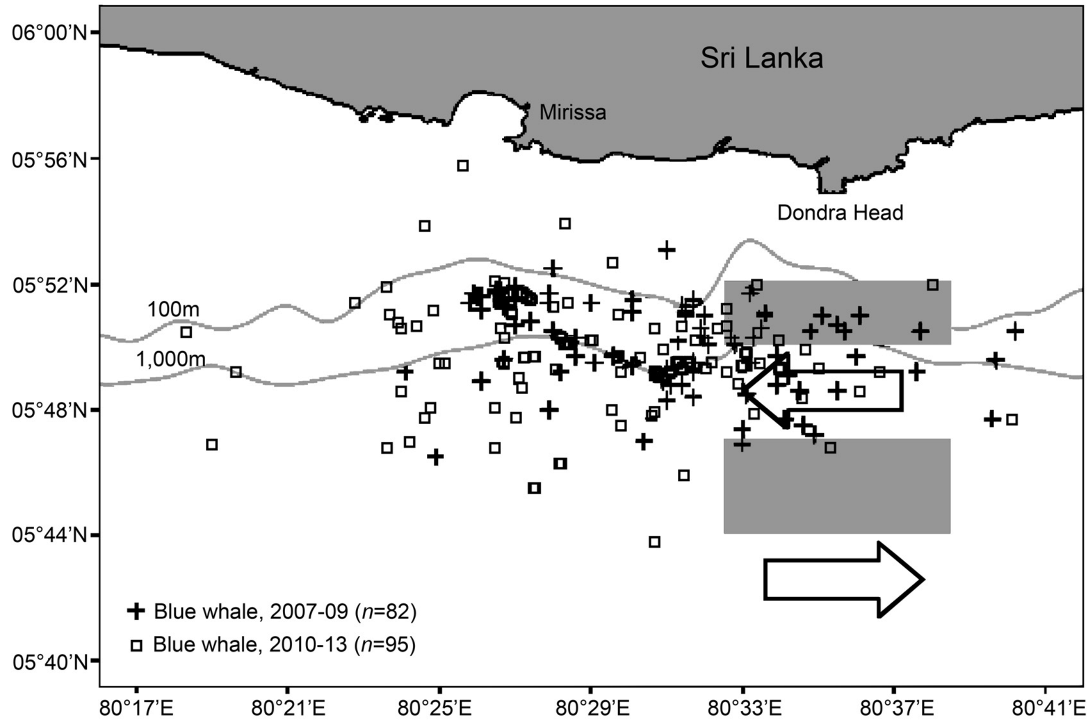

Fig. 3. Blue whales: distribution of sightings off the South coast of Sri Lanka during two time periods (2007–09 and 2010–13).

Table 4

Blue whale numbers, sightings rates and mean latitudes off Mirissa during two time periods (April only, excludes two days in March 2009).

	2007–09	2010–13	2007–13
Sighting effort			
No. days	26	20	46
Mean latitude of boat positions	5°50.9'N	5°51.2'N	5°51.0'N
Mean longitude of boat positions	80°30.2'E	80°27.4E	80°29.0'E
Blue whales			
No. encounters	108	62	170
Encounters per day (mean ± 95% CI)	4.2 ± 0.8	3.1 ± 0.8	3.7 ± 0.6
No. blue whales	150	110	260
Blue whales per day (mean ± 95% CI)	5.8 ± 1.0	5.5 ± 1.1	5.7 ± 0.7
Mean latitude (± 95% CI)	5°50.1'N ± 0.3'	5°49.4'N ± 0.5'	5°49.9'N ± 0.2'
Latitude range	5°46.9'–5°53.1' N	5°43.8'–5°55.8' N	5°43.8'–5°55.8' N

Of the five animals sighted during this study, four were moderately large (about 11–15m) and appeared very much like whales seen in the Maldives which have been identified genetically as *brydei*-type (Kershaw *et al*., 2013). One animal (seen on 17 April 2012 at 5°50.6'N, 80°26.6'E) was much smaller (about 6m). Some of its features were consistent with a *brydei*-type animal: it was dark coloured dorsally (apparently uniformly so); had a relatively large, upright, sickle-shaped dorsal fin; had a tall, thin, vertical blow; and did not fluke when diving. Other features were different: it appeared to have five ridges on its rostrum, which seemed somewhat narrow and pointed; it was of a size at which a *brydei*-type animal would likely still be a calf closely associated with its mother; and it moved particularly fast, faster than the larger *brydei*-type animals, just beneath the water surface. It was tentatively identified as *edeni*-type.

The identification of small baleen whales in Sri Lanka is problematic. There have been previous reports of strandings and sightings, mostly from the northwest coast, which have been identified as minke whales, *B. acutorostrata* (e.g. Deraniyagala, 1948; 1960; 1963; Ilangakoon, 2002; Bröker and Ilangakoon, 2008). This identification seems to have started with Deraniyagala (1948), who identified a baleen whale of 6.4m length stranded in May 1937 at Mannar (northwest coast) as *B. acutorostrata*, based on a newspaper photograph (which could not be found in the National Archives in March 2014) and measurements sent by an informant. Deraniyagala (1960) subsequently identified that stranded animal (together with a second one of 7.9m from near Jaffna in January 1954) as a 'southern little piked whale' (i.e. Antarctic minke whale) *B. a. bonaerenis*. Rice (1998) dismissed Deraniyagala's 'use of the name *B. a. bonaerensis* for a whale (which he did not examine) [as] arbitrary and unwarranted.' There may be some validity in that assessment, but the reason for Deraniyagala's choice of name possibly followed from his belief that many whales and other marine animals were entering Sri Lankan waters from the southern hemisphere (Deraniyagala, 1960; 1965). Furthermore the only other two subspecific names then available applied to minke whales from the North Atlantic and North Pacific, both of which seem even less likely to occur in Sri Lanka. Then in July 1962, another five small baleen whales (8.5–10.7m) stranded on the northwest coast. Deraniyagala (1963) again does not seem to have inspected the strandings in person, but he did secure some specimens for the National Museum (including some multi-coloured yellow/white and grey/black baleen plates). These additional strandings convinced him that there was in fact a local ‘tropical race’ of minke whale, which he named as a new subspecies, *B. a. thalmaha*. Rice (1998) drily noted that this ‘alleged subspecies… remains enigmatic; the unique color pattern of its baleen plates… if not aberrant, leaves doubt whether it is really a minke whale.’ Intriguingly, Deraniyagala (1963) considered *B. edeni* (Anderson, 1879) to be a junior synonym of *B. a. bonaerensis* (Burmeister, 1867). Deraniyagala (1963) gave no justification for this decision, but he may have been following Gibson-Hill (1950). The identity of these small Sri Lankan whales remains in question, but one possibility is that they are indeed *B. edeni*. In support of this suggestion, a small baleen whale (estimated length about 12m) which stranded just across the Gulf of Mannar on the South Indian coast in August 2006 has been genetically identified as *edeni*-type (Jayasankar *et al*., 2006). Subsequently four further whales (two measured as 3.9m and 9.6m) were genetically identified as *edeni*-type from strandings on the Kerala coast of southwest India (George *et al*., 2011; Bijukumar *et al*., 2012). To the best of our knowledge there have been no minke whales genetically identified from India or Sri Lanka so far. Furthermore, Kershaw *et al*. (2013) found that among 56 genetic samples from ‘Bryde’s’ whales collected in the northern Indian Ocean (Oman, the Maldives and Bangladesh) there were 11 *brydei*-type and 45 *edeni*-type animals but no *B. acutorostrata*. Nor were there any Omura’s whales, *Balaenoptera omurai*, in those samples, although this species has now been recorded from Sri Lanka with one sighting off Mirissa (de Vos, 2017) and another off Trincomalee (RCA and Nilantha Kodithuwakku, pers. obs. 7 April 2016).

Sperm whale

Sperm whale (*Physeter macrocephalus*) sightings were concentrated along 5°49’N (range 5°47’ to 5°51’N), i.e. just deeper than the 1,000m isobaths (Fig. 4). This is only slightly South of the mean latitude of blue whale sightings (but with much less variability), and again is within the westbound shipping lane. There was no obvious net movement along the coast: four groups were noted to be travelling East, and four groups West. However, sperm whales have been seen heading eastwards in large aggregations in March (AA, pers. obs.).

Mean group size was 11.2 ± 1.8, rather similar to the 12.8 reported by de Vos *et al.* (2012). Modal group size was 10–12. Most individuals appeared to be mature females or immatures, being estimated at ≤10m (although precise length estimations were not made). Only one individual was thought to be a mature male, because of its particularly large size (length uncertain but estimated to be > 12m). That was seen on 24 April 2011, the latest date on which observations were made. Remarkably, the only mature male sighted by Gordon (1989) was on 24 April 1984, again the last day of his observations.

Short-finned pilot whale

Three sightings of short-finned pilot whales (*Globicephala macrorhynchus*) were made on consecutive days (9–11 April 2009), all in the same general area (about 10–13km off Dondra Head). These sightings may possibly have all been of the same group. Certainly, distinctive individuals, including a pale brown animal (presumed to be an adult female because it was accompanied by a calf, of normal colour) and another animal with no dorsal fin, were seen on both 10 and 11 April, although not on 9 April. On all three days the pilot whales were accompanied by common bottlenose dolphins (*Tursiops truncatus*), with about 200 bottlenose on 9 April and about 40–50 on 10 and 11 April.

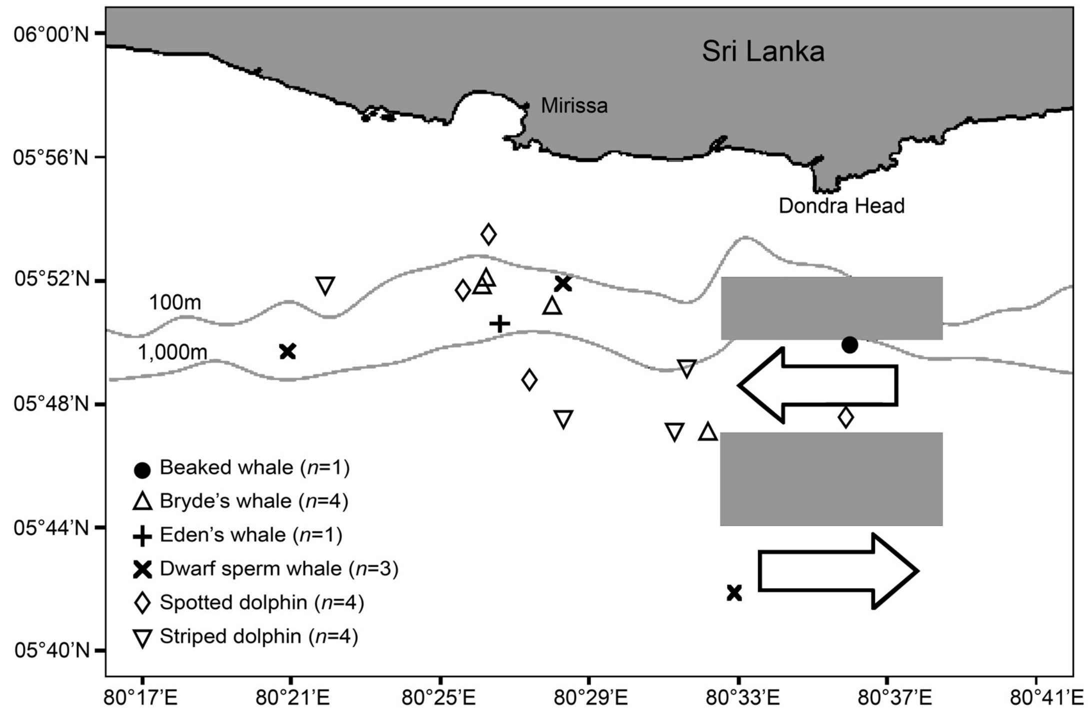

Fig. 4. Miscellaneous cetacean sightings off the South coast of Sri Lanka during 2007–2013.

On 11 April Risso's dolphins (*Grampus griseus*) were also present. The Risso's were particularly active at the surface, breaching and tail-slapping. On that occasion, after some time the pilot whales moved towards the East at about 9–10km h^{-1}, followed by the bottlenose dolphins. It seemed likely that this was an aggressive encounter, resulting in the displacement of the pilot whales, as has been documented elsewhere (Shane, 1995; Anderson, 2005).

Bottlenose dolphin

Two species of bottlenose dolphin were identified: common (*Tursiops truncatus*) and Indo-Pacific (*Tursiops aduncus*). Animals identified as *T. truncatus* appeared somewhat larger, with stubbier beaks; were often a darker and less uniform grey in dorsal colouration; were seen in close association with pilot whales on three occasions; occurred in larger schools (mean size 90.6); occurred more offshore (Fig. 5); and readily bowrode. Animals identified as *T. aduncus* appeared slightly smaller, with slightly longer beaks; had relatively large dorsal fins; were more uniformly and slightly paler grey in dorsal colouration; in one instance revealed ventral spotting; were never seen in association with other cetaceans; occurred in smaller schools (mean size 8.0); occurred more inshore (Fig. 5); and avoided our boat.

T. aduncus appears to have been formally recorded from Sri Lanka only recently (Kurihara and Oda, 2007; Martenstyn, 2013), although its presence is not unexpected. Whitehead (1989, p.61) observed bottlenose dolphins close to the coast of Sri Lanka which were 'smaller, less vocal and less demonstrative' than *T. truncatus* and which he considered might be *T. aduncus*. Ilangakoon (2002) recorded only *T. truncatus* among bottlenose dolphin bycatch, but did note the presence of 'both the coastal and offshore forms' and that 'mature animals may sometimes have dark spots on the pale ventral surface'; this is a characteristic of *T. aduncus*. Sri Lanka is within the expected range of *T. aduncus* and is included in the general distribution maps of this species by Jefferson *et al*. (2008) and Reeves *et al*. (2002). On the other hand, the reports of *T. aduncus* from Sri Lankan waters by Afsal *et al*. (2011) require confirmation: they only recorded this species, not *T. truncatus*, despite most of their bottlenose dolphin records being from offshore.

Spinner dolphin

Spinner dolphins were the most abundant species recorded (Table 2), accounting for some 67% of all cetaceans sighted, by number of individuals. This agrees with previous studies, which have recorded high numbers of spinner dolphins in Sri Lankan waters (e.g. Leatherwood and Reeves, 1989; Dayaratne and Joseph, 1993; Ilangakoon, 2002), and indeed in the wider tropical Indian Ocean (e.g. Ballance and Pitman, 1998; Anderson, 2005).

Spinner dolphins were mostly sighted over the outer shelf, in roughly 100–200m depth (Fig. 6). Mean latitude of sightings was 5°51.5'N, which is 5km North (inshore) of the mean latitude of sperm whale sightings. It is assumed that these spinner dolphins feed mainly at night off the edge of the continental slope, and come into relatively shallower shelf waters during the day, as is comparable to the situation in other areas (e.g. Anderson, 2005; Norris *et al*., 1994; Silva and Da Silva, 2009). Although these spinner dolphins are assumed to feed mainly at night, they clearly associate with tuna during the daytime. Eleven groups of spinner dolphins were accompanied by seabirds, in every case including bridled terns (*Sterna anaethetus*). Other birds recorded were flesh-footed shearwater (*Puffinus carneipes*), wedge-tailed shearwater (*Puffinus pacificus*), Persian shearwater (*Puffinus persicus*), lesser crested tern (*Thalasseus bengalensis*), common tern (*Sterna hirundo*), little tern (*Sternula albifrons*), whiskered tern (*Chlidonias hybridus*) and white-

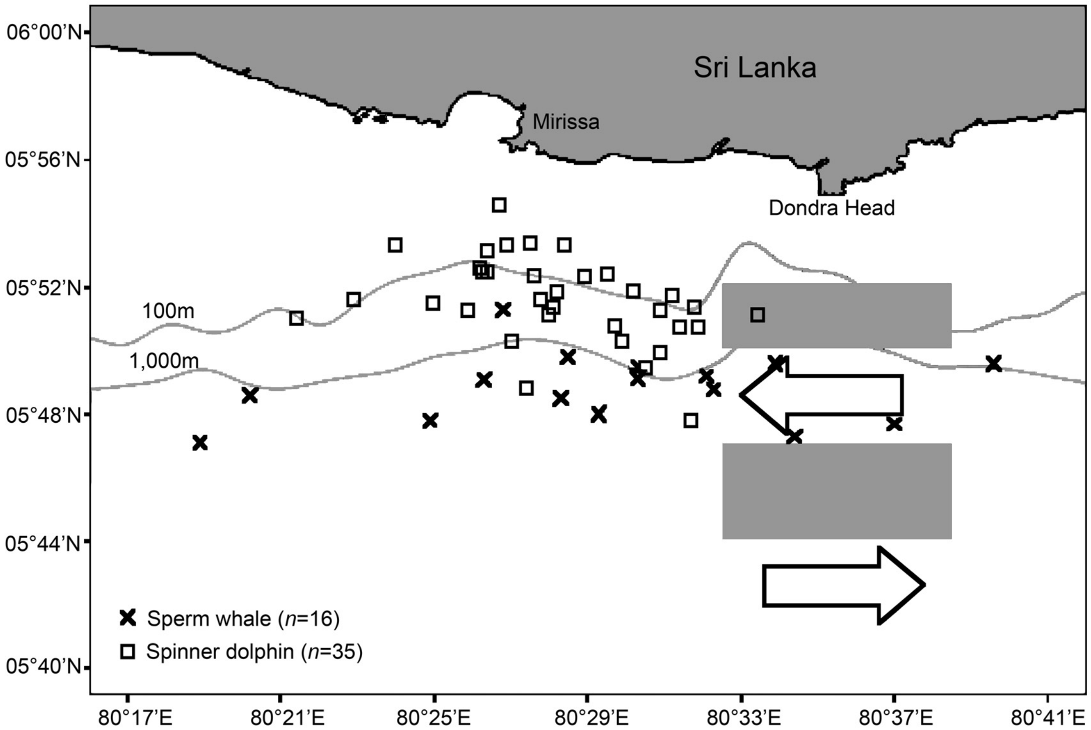

Fig. 5. Sperm whale and spinner dolphin sightings off the South coast of Sri Lanka during 2007–2013.

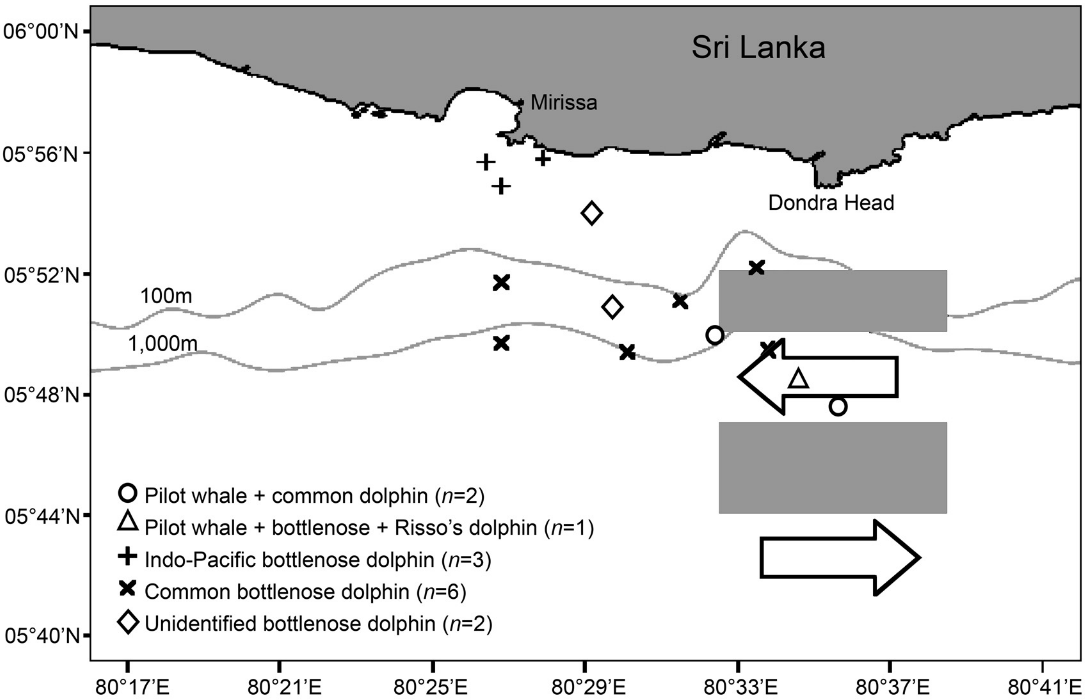

Fig. 6. Short-finned pilot whale, common bottlenose dolphin, Indo-Pacific bottlenose dolphin and Risso's dolphin sightings off the South coast of Sri Lanka during 2007–2013.

winged tern (*Chlidonias leucopterus*). In five of these 11 cases, tuna were seen, or fishing boats were present. The association of dolphins, particularly spinner dolphins, with tuna in Sri Lankan waters has been previously documented (e.g. Sivasubramaniam, 1970; De Silva and Boniface, 1991; Ilangakoon, 2002). More generally, the association of dolphins with yellowfin tuna (*Thunnus albacares*) is widespread in the tropical Indian Ocean (Anderson, 2014).

Of 19 groups of spinner dolphins for which direction of movement was recorded, 12 (63%) were heading to the East and 7 to the West. Although the numbers are small, this might suggest a possible net movement of spinner dolphins eastwards around the South coast of Sri Lanka in April. If spinner dolphins are indeed moving eastwards in April (and perhaps westwards during the other inter-monsoon in October–November) then they might be more abundant on the East coast during the southwest monsoon, and on the West coast during the northeast monsoon. This is certainly consistent with published information, including the following:

(1) From a tuna fisheries aerial survey, Sivasubramaniam (1970) reported many dolphins with tuna (probably mostly spinner dolphins) off the East coast in July but not the West coast.

(2) From a 3-year (1984–86) survey of dolphin landings at Trincomalee fish market, Leatherwood and Reeves (1989, Table 12) presented data showing that spinner dolphins were on average landed twice as often during the southwest monsoon as during the northeast monsoon (13.0 spinners/mo. in April to October versus 6.8 spinners/mo. in November to March).

(3) Following a one-year national survey of dolphin landings, Dayaratne and Joseph (1993) reported that there were two clear peaks in dolphin (mostly spinner dolphin) landings on the South coast (mostly at Mirissa), in October–November and in April, which is consistent with two periods of movement around the South coast. While Dayaratne and Joseph (1993) attributed these peaks to an increase in deliberate taking of dolphins (by harpoon) during periods of low tuna catches, Ilangakoon *et al.* (2000a) suggested that harpooning of dolphins (by West coast fishermen) was not strongly affected by tuna catch, and therefore that landings reflected abundance.

(4) During a year-round survey off the northwest coast, Bröker and Ilangakoon (2008) observed spinner dolphins during the northeast monsoon, but not during the southwest monsoon.

(5) Spinner dolphins are much more abundant off Trincomalee on the northeast coast during the southwest monsoon than the northeast monsoon (Nilantha Kodithuwakku, naturalist at Trinco Blu hotel, pers. comm).

Risso's dolphin

There was just a single sighting of Risso's dolphin (Table 2; Fig. 5). This was surprising since this species has in the past been reported to be common in Sri Lankan waters (Alling, 1984; Leatherwood and Reeves, 1989; Ilangakoon, 2002). Although this single observation from a restricted area and time period is of limited interest by itself, combined with other sightings data from other areas and seasons (Table 5) it suggests a decline in the abundance of Risso's dolphins around the Sri Lankan coast over the past three decades. The comparatively high sightings rate noted by de Vos *et al.* (2012) in 2003 came from a remote area off the uninhabited southeast coast. Risso's dolphin bycatch landings show the same downward trend (Anderson, 2014). Sri Lanka has significant pelagic gillnet and harpoon fisheries. Kruse *et al.*

(1991) identified Sri Lankan Risso's dolphins as being particularly vulnerable to overexploitation. They reviewed available catch and biological data and concluded that 'the current take of Risso's dolphins in the Sri Lankan drift gillnet fishery is not sustainable.' It appears that they may have been right.

Fisheries interactions

Sri Lanka is a major fishing nation. Studies in the 1980s and early 1990s demonstrated that large numbers of small cetaceans were being caught, both as bycatch in pelagic gillnets and as direct catch by harpoon (Alling, 1985; Ilangakoon, 1997; Ilangakoon *et al*., 2000a; 2000b; Leatherwood and Reeves, 1989; Prematunga *et al*., 1985). There was some controversy over the exact numbers being landed annually, although landings were clearly in the thousands. Leatherwood (1994) reworked earlier studies and conservatively estimated a catch of 8,042–11,821 dolphins per year during 1984–86. Dayaratne and Joseph (1993) estimated total annual landings of 5,181 dolphins during 1991–92. Reported tuna catches from the pelagic fisheries have increased roughly fourfold from about 20,000t per year in the 1980s and early 1990s to over 80,000t per year recently, with gillnets remaining the main fishing gear (e.g. Perera *et al*., 2013; tuna catch data available from *www.iotc.org*). Although there has been no monitoring of cetacean landings since the mid-1990s, it is believed that some dolphin catching continues, despite cetaceans being legally protected (Ilangakoon, 2012a; Reeves *et al*., 2013).

The scarcity of Risso's dolphin sightings during this study highlights the possible impact these fisheries may be having on at least some cetacean populations. A recent global review (Jefferson *et al*., 2013) confirmed that Risso's dolphins range widely across inshore to oceanic habitats but have a strong preference for continental slope and outer shelf waters. The continental shelf and slope of Sri Lanka is contiguous with that of India. It seems likely that Risso's dolphin abundance has also been reduced in Indian waters, where there are also major gillnet fisheries which catch Risso's dolphins (e.g. Yousuf *et al*., 2009). Only four sightings of Risso's dolphins were reported from an extensive survey of Indian and adjacent seas (including Sri Lankan waters) conducted during 2003–2007 (Afsal *et al*., 2008). In contrast, the Maldives (which though adjacent to Sri Lanka and South India are not connected to their continental shelf, and do not have gillnet fisheries) have a much higher relative abundance of Risso's dolphins, of the order of 11–14% of sightings (Anderson, 2005; Clark *et al*., 2012; RCA, unpublished data, 2003–2016), which is comparable to what was seen off Sri Lanka in the 1980s (Table 5).

Unlike Risso's dolphins, spinner dolphins remain relatively abundant in Sri Lankan waters, despite large numbers having been taken by local fisheries (e.g. Dayaratne and Joseph, 1993). This suggests that large numbers may be continually entering Sri Lankan waters from elsewhere in the Indian Ocean; they are certainly abundant in the Maldives (Ballance *et al*., 2001; Anderson, 2005; Clark *et al*., 2012) and elsewhere in the Indian Ocean including the waters between the Maldives and Sri Lanka (Ballance and Pitman, 1998; RCA, pers. obs.). However, it seems unlikely that this situation can continue indefinitely, given the high and increasing extent of gillnet fishing and spinner dolphin bycatch in the wider Indian Ocean (Reeves *et al*., 2013; Anderson, 2014).

Movements of whales and shipping

The waters off southern Sri Lanka appear to be a migratory corridor for some cetacean species. The whole northern Indian Ocean is affected by the monsoons, experiencing twice-yearly reversals of ocean currents. This affects the distribution of phytoplankton, and thus also the distribution of zooplankton and micronekton (e.g. Longhurst, 1998). Any cetacean wanting to move between the Arabian Sea and the Bay of Bengal to take advantage of such seasonal productivity would have its passage blocked by the landmass of peninsular India and Sri Lanka. This may act like a giant inverted funnel, forcing animals to pass around the southern tip of Sri Lanka (the Palk Strait between Sri Lanka and India being too shallow for most species). The same land barrier ensures that one of the busiest shipping lanes in the world passes just off the southern coast of Sri Lanka. Ships travelling between the West (Europe, via the Suez Canal, as well as the Gulf) and East Asia, pass back and forth, just off Dondra Head. With the continental slope lying just 5–8km offshore, both whales and ships are visible from land.

Table 5

Sightings of Risso's dolphins recorded during surveys around Sri Lanka, 1983–2013.

		No. of sightings				
Date	Location	Risso's	Cetaceans	Small cetaceans	% Risso's	Source
1983	NE coast	2	26	–	7.7%	Leatherwood *et al.* (1984)
1994	West coast	0	25	–	0%	Ilangakoon *et al.* (2000a)
2003	Sri Lanka	6	76	–	7.9%	De Vos *et al.* (2012)
2004–05	NW coast	0	33	–	0%	Bröker and Ilangakoon (2008)
2003–07	Sri Lanka	1	86	–	1.2%	Afsal *et al.* (2008)
2008–09	South coast	0	69	–	0%	Ilangakoon (2012a)
2007–13	South coast	1	290	–	0.3%	This study
2010–12	NE coast	0	215	–	0%	Nanayakkara *et al.* (2014)
1982–84	Sri Lanka	29	–	170*	17.1%	Alling (1986)
2003	Sri Lanka	6	–	46	13.0%	De Vos *et al.* (2012)
2008–09	South coast	0	–	48	0%	Ilangakoon (2012a)
2007–13	South coast	1	–	82	1.2%	This study

*Note: Alling (1986) reported on cetaceans excluding large whales seen during the *Tulip* expedition. Small cetacean data from other studies (where n > 40) are presented for comparison.

April, and also October–November, are the inter-monsoon periods, when ocean currents change. So too does the distribution of phytoplankton, and subsequently zooplankton. It is therefore to be expected that some cetaceans will change coasts at these times. As noted above, blue whales and spinner dolphins may both be moving around the South coast in April, but in opposite directions. Blue whales appear to be more abundant on the East coast of Sri Lanka during the northeast monsoon season (particularly February–April) and on the West coast during the southwest monsoon season (April–October) (Anderson *et al*., 2012). In contrast, the reverse seems to be true for spinner dolphins, which appear to prefer the downstream sides of the island (see above). There is an intriguing comparison to be made with the adjacent Maldives, where several species of cetacean also appear to 'swap sides' with the changing monsoons but in the opposite direction (RCA, unpublished data, 2000–16). In the case of Sri Lanka, the solid mass of the island deflects the monsoon currents, promoting upwelling on the upstream coast (and also along the South coast because currents from both East and West wrap around this shoreline). This, together with nutrient input from rivers flooded by rains coming in off the sea, promotes seasonally high primary productivity on the seasonally alternating upstream side as well as along the southern coast (e.g. Vinayachandran and Mathew, 2003; Vinayachandran *et al*., 2004; Yapa, 2009; de Vos *et al*., 2014a). The greatest numbers of blue whales might be expected on the more productive upstream side. In contrast, spinner dolphins, perhaps because of their small size, which may increase predation risk or competitive exclusion, appear to be most abundant on the apparently less productive downstream side (although the distribution and abundance of their mesopelagic prey is unknown). The situation is different in the Maldives. The Maldivian chain of coral atolls is a porous barrier, allowing the monsoon currents to pass through, and promoting upwelling in the process, which leads to a plankton bloom on the downstream side (Anderson *et al*., 2011). Therefore blue whales and other plankton feeders are more abundant on the downstream side (Anderson *et al*., 2011; 2012), while spinner dolphins seem to be most abundant on the apparently less productive upstream side (RCA, pers. obs.).

In the case of ships, one of the world's busiest shipping lanes passes just off Dondra Head. There is a traffic separation scheme in place with the inshore, westbound lane passing just outside the 1,000m contour (Fig. 2). Much shipping therefore passes through waters where both blue whales and sperm whales are most abundant. Ship strikes are therefore inevitable (Ilangakoon, 2012c; de Vos *et al*., 2013a; Randage *et al*., 2014). There is a need to address this issue (perhaps by introducing speed restrictions within the existing shipping channels, or moving them further offshore) if such mortality is to be reduced (Priyadarshana *et al*., 2016). However, moving the shipping lanes offshore could open the way for gillnetting over the continental slope, with consequent greater cetacean mortality (Randage *et al*., 2014). In the meantime, concern has been expressed that the rate of ship strikes has increased as a result of whale watching from Mirissa disturbing blue whales and pushing them offshore into the shipping lanes (Ilangakoon, 2012c; 2013).

Whale watching

Since the discovery of large numbers of blue whales off the South coast of Sri Lanka, Mirissa has become a major centre for whale watching. Previously, the whales' presence, although well-known to local fishermen, was not more widely realised. In both 2007 and 2008, the vessel chartered for the excursions reported here was operating not as a whale watching boat but as part of a game-fishing and water-sports venture (set up in the wake of the 2004 tsunami by a philanthropic Belgian businessman resident in Sri Lanka). No other vessels were whale watching at that time. However, following widespread publicity starting in late 2008 (e.g. Wijeyeratne, 2008) whale watching activities have expanded rapidly (Fig. 7), as too has boat-based cetacean research (e.g. Ilangakoon, 2012a; 2012b; 2013; de Vos *et al*., 2013a; 2013b; 2014b; Randage *et al*., 2014; Priyadarshana *et al*., 2016).

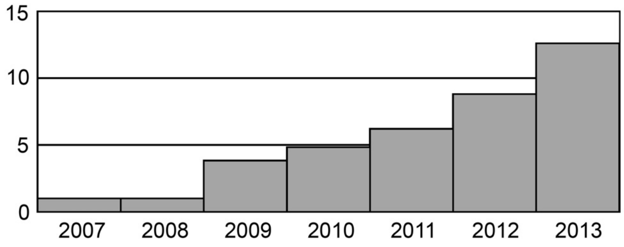

Fig. 7. Mean number of whale-watching boats per day, seen operating out of Mirissa, southern Sri Lanka, in April, 2007–2013.

While some boat operators do behave responsibly around the whales, others do not. Ilangakoon (2012c; 2013) has highlighted unregulated whale watching as a threat to blue whales off southern Sri Lanka. She further suggested that increased whale watching out of Mirissa was driving the blue whales further offshore, into the shipping lanes, with consequent increase in ship-strike mortality. The study reported here provides no evidence of blue whales being displaced offshore: the mean latitude of blue whale sightings was the same in the early years (2007–2009) as in the later years when many whale-watching boats were operating (2010–13) (Table 4). Randage *et al*. (2014) also present data which show no net movement offshore during three 'high' seasons (December–April), 2009–2010, 2010–2011 and 2011–2012. And while de Vos *et al*. (2014) did find an interannual shift in blue whale distribution offshore, that was related to interannual differences in oceanographic conditions. Furthermore, de Vos *et al*. (2013b) found no change in the frequency of fluking up before deep dives in the presence or absence of whale-watching vessels. Nevertheless, the data presented here do suggest that blue whales were more latitudinally dispersed during 2010–13 than in 2007–2009; one possible explanation could be disturbance by whale-watching vessels.

Blue whales were present over the continental slope, and in the shipping lanes, even in 2007–08, before the explosive growth of whale watching from Mirissa (Fig. 3). If blue whales are being disturbed by whale watching, then there is no obvious reason why they should not move along the continental slope, rather than offshore. One reason for the recent increase in numbers of blue whale carcasses being reported is probably the great increase in the number of observers, following the expansion of whale watching. In addition, over recent decades, the general increase in the volume and speed of international shipping passing southern Sri Lanka (Priyadarshana *et al*., 2016), together with the likely increase in blue whale numbers (assuming that the northern Indian Ocean population has largely recovered from whaling in the 1960s) may have contributed to an increase in the actual number of ship strikes.

Whatever the case, it is clear that both unregulated whale watching and ship strikes are causes of concern for blue whales and other cetacean species off the southern coast of Sri Lanka. At the same time, bycatch of cetaceans in gillnet and other fisheries is impacting several species. All of these issues need to be addressed if cetacean watching is to continue to be a profitable enterprise for the people of southern Sri Lanka and if the cetacean populations of the region are to be sustained.

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Best practice guidelines for cetacean tagging

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ABSTRACT

Animal-borne electronic instruments (tags) are valuable tools for collecting information on cetacean physiology, behaviour and ecology, and for enhancing conservation and management policies for cetacean populations. Tags allow researchers to track the movement patterns, habitat use and other aspects of the behaviour of animals that are otherwise difficult to observe. They can even be used to monitor the physiology of a tagged animal within its changing environment. Such tags are ideal for identifying and predicting responses to anthropogenic threats, thus facilitating the development of robust mitigation measures. With the increasing need for data best provided by tagging and the increasing availability of tags, such research is becoming more common. Tagging can, however, pose risks to the health and welfare of cetaceans and to personnel involved in tagging operations. Here we provide 'best practice' recommendations for cetacean tag design, deployment and follow-up assessment of tagged individuals, compiled by biologists and veterinarians with significant experience in cetacean tagging. This paper is intended to serve as a resource to assist tag users, veterinarians, ethics committees and regulatory agency staff in the implementation of high standards of practice, and to promote the training of specialists in this area. Standardised terminology for describing tag design and illustrations of tag types and attachment sites are provided, along with protocols for tag testing and deployment (both remote and through capture-release), including training of operators. The recommendations emphasise the importance of ensuring that tagging is ethically and scientifically justified for a particular project and that tagging only be used to address *bona fide* research or conservation questions that are best addressed with tagging, as supported by an exploration of alternative methods. Recommendations are provided for minimising effects on individual animals (e.g. through careful selection of the individual, tag design and implant sterilisation) and for improving knowledge of tagging effects on cetaceans through increased post-tagging monitoring.

KEYWORDS: BIO-LOGGING; RADIO-TAGGING; SATELLITE TAGGING; TELEMETRY

1. INTRODUCTION*

The understanding of the biology of cetaceans and their habitat requirements, and our ability to mitigate threats to them, are challenged by the difficulty of observing animals that spend most of their time beneath the water surface, often in remote areas. This challenge can be at least partly overcome by using animal-borne monitoring instruments (bio-logging tags; hereafter referred to as 'tags'). Depending on the design, these tags can provide a variety of data, such as environmental (e.g. water temperature, salinity), physiological (e.g. heart rate, body temperature) and behavioural (e.g. dive depth and duration, acceleration, geographic position). Although the first time a tag of this type was applied to a cetacean was as early as the 1930s (Scholander, 1940), it took several decades and the advent of VHF transmitters, digital time-depth-recorders and eventually satellite-linked transmitters, for these tags to be regularly used in the study of wild cetaceans. Modern tags can archive data for eventual recovery and downloading, or they can transmit data via electromagnetic and/or sound waves. Tags are now a critical component in advancing cetacean science. Compared with other types of observations, tags can provide nearly continuous data as opposed to snapshots in time and are observer-independent. They have yielded data important for answering basic science and life history questions and for the management and conservation of cetaceans, including data on population

*Note: In-text references have been used sparingly here as we aim to offer recommendations broad enough to be relevant to all those interested in cetacean tagging, to be as concise as possible, and also to aid readability. An exhaustive list of references (over 500) related to cetacean tagging is provided in the Supplementary Bibliography (see Appendix B).

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[18] *Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA, 98115, USA.*

structure and stock discreteness. Tag data have also been valuable in the development of mitigation measures to protect cetacean species. For example, they have been used to document previously unknown migratory routes and important habitats, to determine the fate of stranded and rescued animals post-release and responses to human disturbance, as well as to provide basic knowledge about cetacean physiology, behaviour and ecology (see Appendix B for a comprehensive list of references that document such studies).

The use of tagging in cetacean research has increased considerably in the past 20yrs (Fig. 1). With tags designed specifically for cetaceans becoming commercially available only recently, their use is likely to further increase and continue to expand our knowledge of cetacean biology. Tagging does, however, present potential risks to tagged individuals, so users need to be aware of possible health and welfare concerns. Tags have the potential to alter the physiology and behaviour of the tagged animal, and thus the validity of the interpretation of the data collected. As tag designs and tagging methods develop, information about the most successful refinements and innovations should be shared to facilitate the use of techniques that are most appropriate for a project and that minimise any potential adverse effects on tagged animals. The objectives of this paper are to provide a summary of key topics to consider before tagging cetaceans and best practice recommendations based on the experience of the authors and reviews of the literature. Whilst the intention is that these recommendations are applicable globally, we recognise that not all of them may be feasible in all situations. Variations in local laws, customs and cultures, and the challenges of fieldwork in remote and difficult environments, can all require adjustments to the recommendations we propose. Therefore, the recommendations presented here should not be interpreted as mandatory but rather as standards to strive for. The text preceding the key recommendations for each section of this document is intended to provide additional context and detail to assist with the adjustment of protocols as possible.

No previous single document has provided guidelines for cetacean tagging, but there are a few highly relevant resources that the guidelines presented here are intended to build upon. The Society for Marine Mammalogy has published 'Guidelines for the Treatment of Marine Mammals in Field Research' (Gales *et al.*, 2009) that scientists contemplating tagging of cetaceans should follow. Morton *et al.* (2003) provided useful recommendations for refining telemetry procedures, and although their focus was on laboratory animals, many of the recommendations are relevant to cetacean tagging. Casper (2009) provided a valuable framework for minimising the negative effects of instrumenting wild birds and mammals, and Mulcahy (2011; 2013) reviewed asepsis and antibiotic usage associated with implanted electronic tags. Two recent documents have provided best practice recommendations for the use of tags with pinnipeds; one for implanted tags (Horning *et al.*, 2017), and one for external tags (Horning *et al.*, 2019). Specific recommendations for cetacean tagging can be found in some recent book chapters (e.g. Lander *et al.*, 2018; McConnell *et al.*, 2010) and workshop reports (ONR, 2009; Weller, 2008;

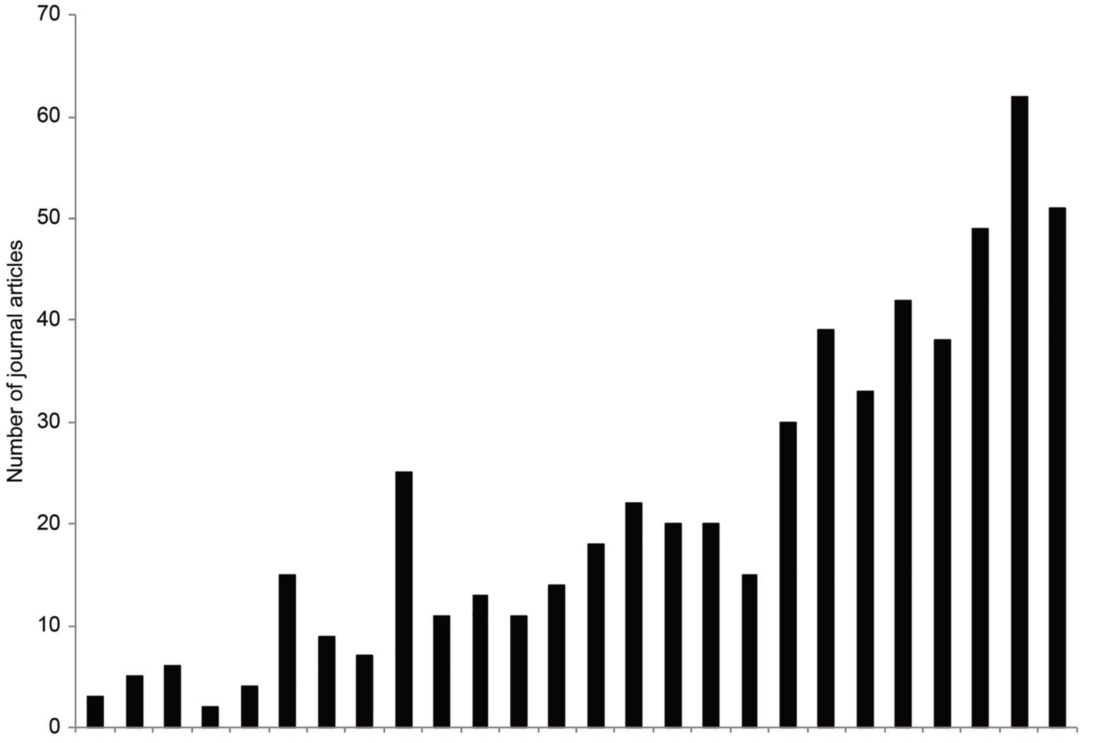


Fig. 1. Number of journal articles published between 1993 and 2018 that included some aspect of cetacean tagging. Web of Science, Scopus and Google Scholar were searched using a broad list of key words to identify scientific papers that included any aspect of the topic of cetacean tagging, including development of tags, deployment of tags and studies of effects of tags. The full reference list is provided in the Supplementary Bibliography (see Appendix B).

Wells, 2005). This document will focus on updating and clarifying key topics important for cetacean tagging to provide a resource for researchers, veterinarians, ethics boards and regulatory agency staff to interpret and implement high standards of practice, and to identify necessary training. We hope that this paper will further efforts to improve tags, attachments and techniques.

1.1 Approach

These guidelines originated with the Cetacean Tag Design Workshop sponsored by the Office of Naval Research in 2009 (ONR, 2009) and were further developed at the Workshop on Living Whales in the Southern Ocean in 2012 (Baker *et al.*, 2012), at the 20th Biennial Conference on the Biology of Marine Mammals in 2013, and at the Workshop on Cetacean Tag Development, Tag Follow-up and Tagging Best Practices sponsored by ONR, the International Whaling Commission (IWC) and the National Marine Fisheries Service/National Oceanic and Atmospheric Administration (NMFS/NOAA) in September 2017 (IWC, in press). Each author has expertise in one or more of the following disciplines as it relates to cetaceans: general biology, capture and release, tagging, veterinary medicine and tag technology. Each author volunteered to participate and has contributed significantly to the development of the guidelines by identifying, evaluating and summarising the most current information on cetacean tagging. The guidelines are not meant to be a detailed description (or instruction manual) of methods, but rather provide key recommendations to inform practitioners and regulators (e.g. animal welfare/ethics and permitting authorities) about appropriate methods and circumstances for tagging cetaceans.

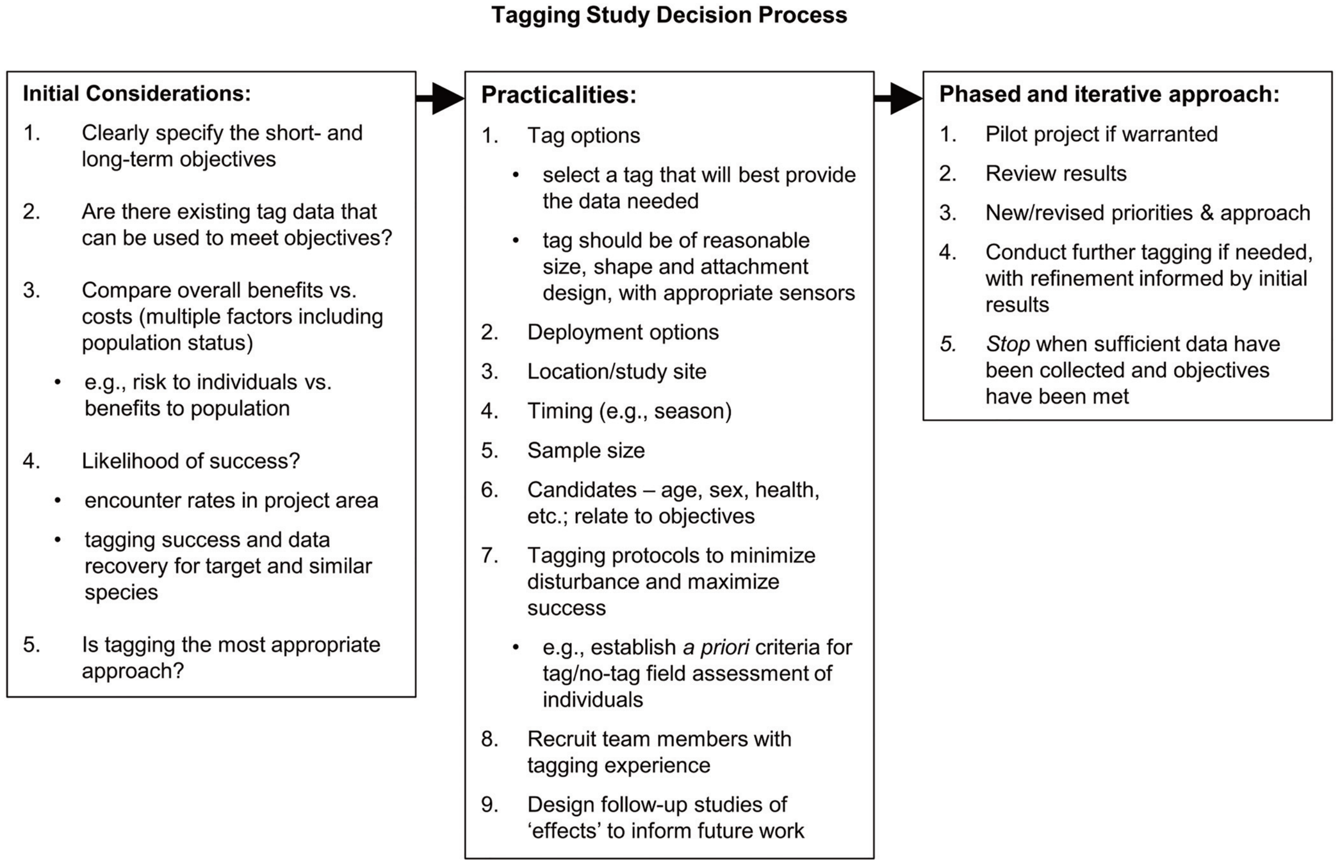
To be most effective, such guidelines need to be readily available and up-to-date. Therefore, in addition to this publication, the guidelines will be available on the *cetaceantagging.info* website, where a forum will be hosted for the discussion of modifications and additions to ensure the document and recommendations reflect current best practices.

2. KEY TOPICS AND RECOMMENDATIONS

2.1 Ethical and legal considerations of tagging

While there are scientific and conservation benefits of tagging cetaceans (see Supplementary Bibliography in Appendix B), there can also be negative effects on individuals (Section 2.7). Therefore, prior to any decision to use tags, researchers should weigh the positive and negative factors to determine if tagging is scientifically and ethically justified. The Bateson cube, comparing animal suffering with research merit and population benefit, is one good approach to this decision-making process (McMahon *et al.*, 2012). All methods available to address identified research questions (including thorough examination of existing data), should be evaluated prior to the decision to use tags to ensure that the data required can best be provided by these instruments. To help guide those that are considering a cetacean tagging study, a flow chart of an example decision process is presented in Fig. 2.

If tagging is justified, effects on the target animals should be minimised by following the best principles of research design (Gales *et al.*, 2009). Refinements in tagging



Tagging Study Decision Process

Initial Considerations:

1. Clearly specify the short- and long-term objectives
2. Are there existing tag data that can be used to meet objectives?
3. Compare overall benefits vs. costs (multiple factors including population status)
    - e.g., risk to individuals vs. benefits to population
4. Likelihood of success?
    - encounter rates in project area
    - tagging success and data recovery for target and similar species
5. Is tagging the most appropriate approach?

Practicalities:

1. Tag options
    - select a tag that will best provide the data needed
    - tag should be of reasonable size, shape and attachment design, with appropriate sensors
2. Deployment options
3. Location/study site
4. Timing (e.g., season)
5. Sample size
6. Candidates – age, sex, health, etc.; relate to objectives
7. Tagging protocols to minimize disturbance and maximize success
    - e.g., establish *a priori* criteria for tag/no-tag field assessment of individuals
8. Recruit team members with tagging experience
9. Design follow-up studies of ‘effects’ to inform future work

Phased and iterative approach:

1. Pilot project if warranted
2. Review results
3. New/revised priorities & approach
4. Conduct further tagging if needed, with refinement informed by initial results
5. *Stop* when sufficient data have been collected and objectives have been met

Fig. 2. A recommended approach to guide the decision process for those considering a cetacean tagging study. Additional details are presented in Section 2.2, including an explanation of what constitutes a ‘reasonable’ tag design for a species.

procedures, such as using methods that cause no more than momentary pain or discomfort, reflect elements of good experimental design encapsulated in the principle of the Three Rs (Russell and Burch, 1959): Replacement (with procedures not using animals), Reduction (in the number of animals used) and Refinement (using methods which decrease any adverse effect). Tagging studies should only be conducted when the research or management questions require new data from live animals, so it is the latter two Rs that are relevant. For example, researchers must identify a sample size that minimises animal use while answering the study objective. In many types of cetacean studies, ideal sample size is not easily determined or attainable. This is especially true in tagging studies because of difficult logistics (e.g. animals that can be hard to find and approach). Further, estimating the appropriate sample size in advance is complicated by our limited knowledge of the natural variability of most of the parameters that tags are being used to measure. As for any technique, whether the likely achievable sample size will be sufficient to answer the research question must be considered before deciding to use tags. Given how little is known about some species however, even a sample size of one may provide valuable information that will inform future research designs or management questions. Further, due to the wide variation in tag attachment duration, a larger number of deployments may be required to obtain the target number of tags with sufficient attachment duration to answer the research questions. Nevertheless, when possible, scientists should address sample size questions with statistical power analyses. Tagging data collected from similar species will likely be useful for estimating parameter variability.

This paper assumes that researchers will comply with all laws and regulations that govern animal care and welfare at the local, national and international levels. Tagging procedures may have effects on animals during all phases (i.e. approach, deployment, on-animal operation, detachment and post-detachment). Effects should be identified, and if significant, mitigated where possible and justified to administration/regulatory/ethical oversight authorities. Scientists planning to tag cetaceans must also consider possible unintended effects of tagging activities on the environment, including capture-release operations and inadvertent animal disturbance, especially when conducting research in protected or sensitive areas. Furthermore, tags include electronics that may be regulated at the local or federal level, and even though a tag is available commercially, it may not be legal to use it in some locations without permits. Other laws and regulations that apply to cetacean tagging include those that protect the health and safety of the human participants. Tagging large, wild animals from small boats is challenging and poses risks to humans and animals, therefore it is critical that researchers maintain high safety standards to protect themselves, their study subjects, other animals and bystanders. Adequate preparation includes a thorough risk assessment, possession of, and competency in the use of appropriate safety equipment, and a contingency plan for emergencies involving either humans or the study animals. Detailed recommendations regarding training and qualifications are found in Section 2.5.

Researchers should consider the importance of cetaceans to various groups of people for subsistence, cultural, scientific and economic reasons. Stakeholders interested in cetacean tagging projects may include subsistence and commercial whalers, fishers, cultural leaders and participants in wildlife tourism. There is, therefore, a need to identify and work with members of interested communities at all stages of a project, to convey the research objectives and possibly to solicit and include research questions raised by local stakeholders. This may encompass coordination during the planning stages and, just as importantly, communication of results both as the project proceeds and at its end. Consideration of the rights, concerns and interests of indigenous peoples can be regionally critical, as is recognition of the value of local and traditional knowledge. One example of the international acceptance of these principles is the 'Agreement on Enhancing International Arctic Scientific Cooperation', signed at the 10th Arctic Council Ministerial meeting in Fairbanks, Alaska, 11 May 2017. Although local and traditional knowledge and use of cetaceans are important issues far beyond the Arctic, a good example of guidance for outreach to local stakeholders can be found in the US National Science Foundation's 'Principles for the Conduct of Research in the Arctic' (*https://www.nsf.gov/od/opp/arctic/conduct.jsp*).

At the end of this section, as in all subsequent sections of these guidelines, the main recommendations are summarised for the section topic in bullet points.

2.1.1 Recommendations for ethical and legal considerations of tagging

- Determine if tagging is appropriate.
    - Consider alternative methods for addressing research questions.
    - Review relevant existing data for the species and area of consideration.
    - Ensure that there is a scientific or conservation justification for obtaining new data and that those data are best provided by tags.

- Follow best practices of research design.
    - Develop the research plan with animal welfare as a high priority.
    - Evaluate equipment options and choose the instrument and attachment that provide the data needed.
    - As much as possible, ascertain required samples sizes and statistical approaches in advance, obtaining expert advice if needed.
    - Tag the fewest number of individuals necessary in the least invasive and impactful manner possible to achieve the project goals.

- Prepare adequately for field work.
    - Conduct a thorough risk assessment in advance.
    - Prepare for unexpected risks to the safety of animals and humans.
    - Ensure the capture/tagging team is trained in the safe and proper procedures for boat approaches (and capture-release techniques if required) and use of tagging equipment.

- Comply with all applicable local, national and international legal requirements.
- Obtain review and approval by an animal ethics committee, even if not locally required.
- Reach out to stakeholders, including those with subsistence, cultural and economic interests in the study subjects, by:
  - sharing research goals and soliciting input;
  - coordinating during planning; and
  - communicating results throughout and at the completion of the study.

2.2 Tag design and deployment

The first known bio-logging tags deployed on cetaceans were capillary manometers, which provided a single data point for the depth of the deepest dive while attached. In the 1930s, Scholander (1940) and colleagues secured such a tag to a harness on a harbor porpoise (*Phocoena phocoena*) and placed one on a harpoon line to measure the dive depth of a harpooned fin whale (*Balaenoptera physalus*). Since then, both the tags and the methods for attaching them have improved significantly. However, refinements are still needed, especially in the way instruments are attached to cetaceans, so that attachment durations are more consistent, and therefore more predictable, and provide the required duration of observations while minimising effects on the tagged individuals. There is a wide variety of tag designs, including custom-made tags such as those with external leads for monitoring physiological parameters, and those that transmit data from one part of the body to another device secured elsewhere. Here, the focus is on tags considered a single unit for deployment which, based on the method of attachment, can be either invasive or non-invasive. Invasive is defined here as a tag attachment that intentionally breaks the skin, regardless of the degree of the break.

2.2.1 Invasive tags

There are currently three common configurations of invasive tags (Fig. 3). Each of these include percutaneous implants (i.e. implants that create and maintain a hole through the skin until the tag is lost).

Type A = Anchored. Anchored tags are tags with the electronics package external to the skin, attached by one or more anchors that puncture and terminate below the skin. The anchors, often solid shafts with retention barbs or petals, are designed to terminate in the internal tissue of the dorsal fin or in dermal or hypodermal tissue along the dorsum. Anchored tags are usually deployed using remote-attachment methods that do not require restraint of the animal, such as projection from a crossbow or air-gun, or placement with a pole.

Type B = Bolt-on. Bolt-on tags have external electronics and one or more piercing anchors. An element of the tag is attached to the external end(s) of one or more 'bolts' that pierce tissue, creating a tunnel around the bolt with an entry and exit site (like a human ear-ring or a pinniped flipper tag). For example, single-point dolphin tags that trail behind a v-shaped piece that is 'bolted' to the dorsal fin, or the three-pin design with the tag

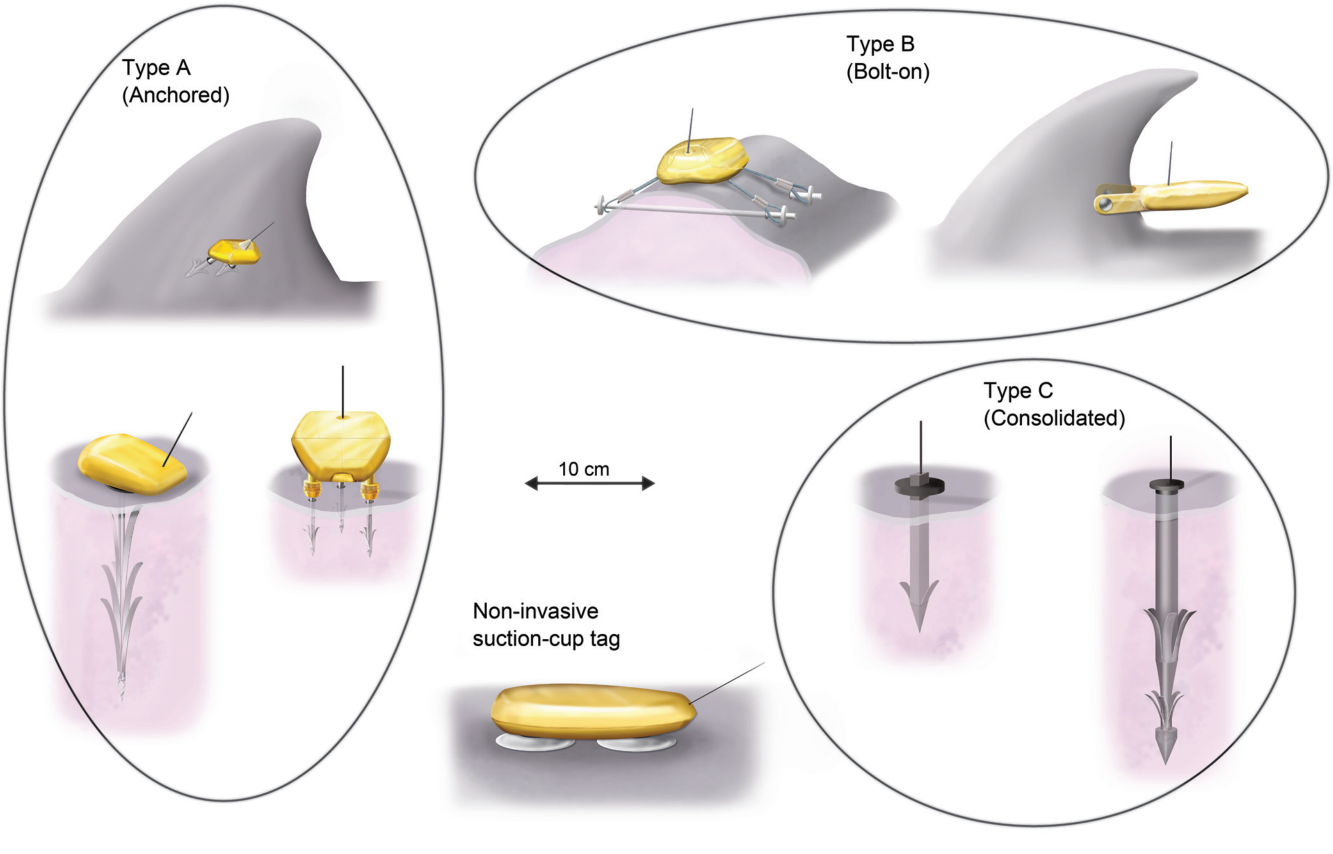


Fig. 3. Illustrations of a non-invasive (= no break in the skin) suction cup tag (bottom center) and the three most common configurations of invasive tags, Type A: Anchored; Type B: Bolt-on; Type C: Consolidated. [Illustrations by Michael Ortiz]

bolted on one side and a flat plate held on the opposite side. Another example of a bolt-on design is sometimes called a 'spider-legs' tag, where the tag sits as a saddle over or near the dorsal ridge, connected via cables to piercing pins, rods or bolts. Creating the hole for the bolt currently requires capture and restraint of the animal, and manual contact with the skin.

Type C = Consolidated. The electronics and retention elements are consolidated into a single implanted anchor. The electronics are typically inside a metal case, usually a cylinder, designed to be partially implanted in the body, with only a small part of the top of the tag and antenna and/or sensors projecting above the skin. Retention barbs, or petals, are connected directly to the implanted package. Puncture of the skin typically occurs on the body or the base of the dorsal fin (not the central part of the dorsal fin), and the distal end of the tag sometimes terminates internally to the muscle/blubber interface. Application of these tags does not require restraint and they are deployed with remote methods.

2.2.2 Non-invasive tags

Non-invasive tag attachments include harnesses, peduncle belts and suction cups. Suction cups (Fig. 3) are the most common non-invasive attachment and have been used with success in many species. Suction cups pose little to no negative impact on the study animal, but their duration of attachment typically ranges from a few hours to at most a few days.

2.2.3 Choice of tag type

When selecting tags and attachment systems, scientists should explore all design and deployment options, using scientific journal articles, reports from vendors and by contacting researchers with extensive tagging experience. Direct communication is the most valuable way to obtain the information needed and to access results from unpublished work.

Key criteria for determining whether a tag is appropriate for a particular research project include:

(1) ability to provide the type, quantity and resolution of data required;

(2) being of a reasonable size, shape and configuration for the species and sex/age class to be studied; and

(3) having the least impact possible on the animals.

2.2.4 Tag design

A reasonable tag design is one that does not pose unacceptable risks to the health, welfare and reproductive success of the tagged individual, and that does not significantly alter behaviour or otherwise affect the tagged animal in a way that could bias the results. A reasonable tag should also not interfere with body movements or appreciably increase energy expenditure. The latter can partly be addressed by minimising the external dimensions and the forces imposed by the tag, primarily drag and lift. This applies to all parts of non-invasive tags and the external parts of invasive ones. Design features that improve hydrodynamics will reduce metabolic cost and may also reduce predation risk and the possibility of entanglement or premature tag detachment or failure. The shape and characteristics that result in minimal drag are not necessarily obvious, so focussed testing of different designs is recommended, which can be done empirically and/or by simulation using computational fluid dynamics. In environments where bio-fouling is likely to occur and long attachment durations are needed, making the external portion of tags smooth (e.g. with a slick coating) can reduce attachment ability of marine organisms (bio-fouling) and therefore prevent an increase in drag while protecting external sensors on the tag. An external part of the tag should be labeled with an ID# and researcher contact information to facilitate identification by beach combers in case a tag washes up on shore, or by stranding responders if a tag is still attached to a cetacean that strands while carrying a tag.

Tags that generate sound, e.g. to transmit data underwater or to facilitate acoustic tracking, may have unanticipated effects on cetaceans. Despite having a low duty cycle, these transmitters may be audible to the tagged animal (and possibly also to its predators) and could cause startle or other behavioural responses. The sounds generated by these tags should be assessed in the context of the hearing range, sensitivity and integration time of the target species and their predators, as well as the likely ambient noise level, to the extent that these are known. Pilot trials with cetaceans in captivity and with devices containing additional behavioural sensors may help to evaluate the acceptability of the acoustic output.

Non-invasive tag attachments are those that are not designed to penetrate the skin. These include suction cups, harnesses and peduncle belts. Non-invasive tags, especially those attached with suction cups, may often be the best choice when short-term tag attachment is all that is required. However, even though these tags are classified as non-invasive, some of these methods can nevertheless cause negative effects on animals, so a reasonable non-invasive tag design should aim to minimise adverse effects, such as excessive drag. Harnesses that encircle the body can impose significant drag loads, an increased risk of entanglement and lead to skin chafing (Scott *et al.*, 1990). Therefore, the use of harnesses is not recommended with free-ranging cetaceans. Peduncle belts are still experimental but placing an object on part of the body that moves as much as the caudal peduncle presents obvious challenges that have yet to be resolved, including the potential for altering the biomechanics of swimming and/or skin chafing. In many cetaceans, the peduncle is laterally compressed with a hydrodynamically efficient shape, the drag of which could be strongly affected by a belt. Non-invasive tags are most commonly attached with suction cups, and the number and arrangement of the cups should be part of the design and testing. The shore hardness or durometer of the material used to make the suction cups is important as attaining the best suction is a balance between stiffness to maintain shape and softness to achieve a good seal with the skin. The volume of the cup should be considered as this relates to the suction, or vacuum, pressure that can be achieved inside the suction cup. Although a greater vacuum pressure is likely to allow the tag to resist greater external forces that might dislodge a suction cup, it is important to consider whether excessive vacuum pressure can cause complications such as blistering or hematomas below the cup (Shorter *et al.*, 2014). A suction cup that does not cause significant discomfort is also likely to reduce the possibility that the tagged animal will intentionally remove the tag.

Many non-invasive tags are archival and must be retrieved to recover the data; the tag must therefore float upon release and some system(s) to track the tag must be incorporated (e.g. VHF beacon and/or Argos transmitter). The tracking antenna needs to be oriented correctly, i.e. free of the water surface, after the tag releases, requiring that floatation is integrated strategically into the tag package. Finally, while non-invasive tags are sometimes dislodged by other animals, they can remain attached for relatively long periods of time (e.g. 24+ hrs), so many of these tags incorporate an automatic release system to facilitate retrieval.

For invasive tags, whilst it is generally preferable to use the smallest sizes possible for both external and internal parts, smaller is not always better. For example, the ability of an implanted anchor or bolt to resist withdrawal by external forces is likely to be positively related to its length. Further, the retention elements for anchored or consolidated tags are typically designed to anchor in or under a particular tissue and therefore need to be long enough to reach the target tissue, whether it be blubber, muscle or in the central tissue of the dorsal fin or ridge. However, the maximum depth of penetration and placement on the body require careful consideration to ensure the sharp, rigid elements of the anchor do not damage bones or internal organs. Most tags are implanted on the dorsal surface of cetaceans where the closest bones are the vertebral processes (neural spines and transverse processes) and the ribs (Fig. 4). In small cetaceans, these structures may only be a few centimeters below the skin. In larger cetaceans the distances are greater, but age, season and body condition can alter these distances within a species. Therefore, attention to a tag's intended maximum depth of penetration and the anatomy, size and body condition of the target animal is critical. Figs 4 and 5 illustrate the basic anatomical features to be aware of when placing tags in the typical places on a representative mysticete (humpback whale) and an odontocete (killer whale).

Tags should be constructed of materials that are biocompatible and safe for skin contact (for external parts) or long-term implantation in mammalian tissue (for implanted parts), regardless of the anticipated retention time. Although most tags with implanted parts are likely to be fully shed within a few months, there are reports of implanted tags or parts of tags that have been retained within the tissue of cetaceans for many years. Therefore, for the implanted parts of tags it would be prudent to choose materials that are not likely to cause significant complications that could harm the tagged cetacean if retained permanently. Material choices should also consider the corrosive nature of the tag

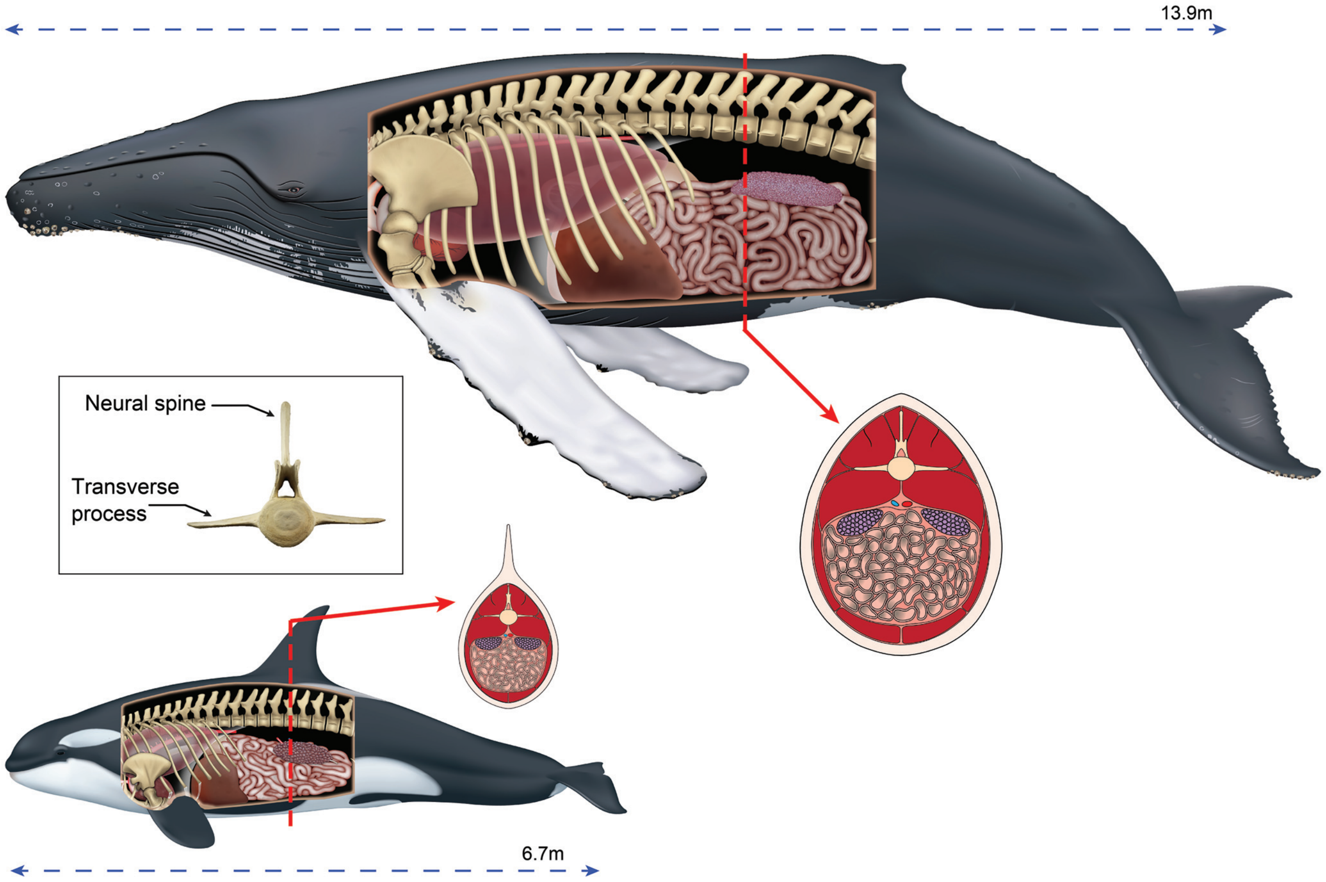


Fig. 4. Schematic illustrations of a humpback whale (top) and killer whale (bottom); both based on non-pregnant adult females. Anatomical features are shown in a cut-away sagittal section and a transverse section at the level of the body where invasive tags are most often attached. In the sagittal sections, many tissues, including muscles and connective tissue, have been omitted for clarity. [Illustrations by Uko Gorter]

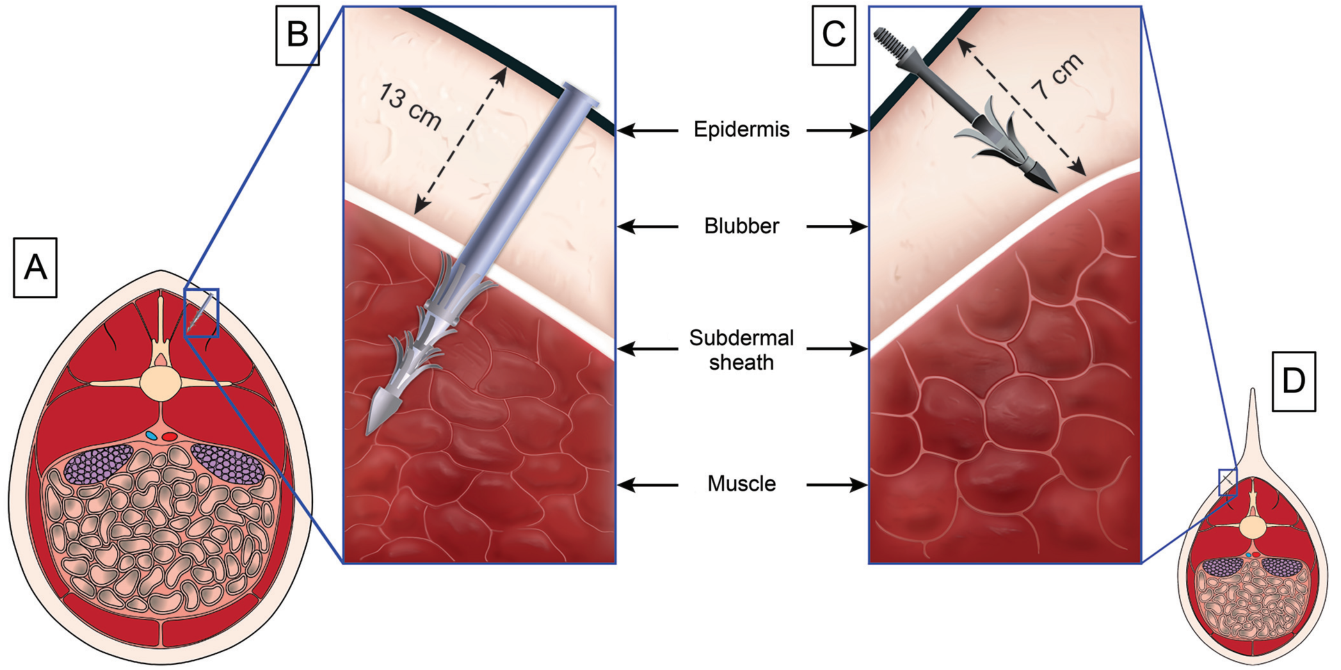


Fig. 5. Schematic illustrations of representative tag implants *in situ*, based on the transverse sections of a humpback whale (A) and a killer whale (D), drawn to the same scale, as illustrated in Fig. 4. Left (A and B): The humpback whale transverse section with an implanted Type C (Consolidated) tag. Right (C and D): The killer whale transverse section with an implanted dart from a Type A (Anchored) tag. Note that the expanded boxes (B and C) are not drawn to the same scale; they have been scaled so that the blubber layer thicknesses, which are different for the two species, appear at the same size in B and C. The implants are drawn here as if they entered the tissue at a 90° angle to the plane of the penetrated skin, which results in the maximum possible depth of penetration, even though most Type C tags and Type A anchors enter at a smaller angle. The term blubber includes the dermal and hypodermal layers of the integument. The subdermal sheath is the fascia layer of interwoven collagen fibers surrounding the axial musculature (Pabst *et al.*, 1990). [Illustrations by Uko Gorter]

environment, inside and outside of the body. Comprehensive guidance on the topic of biomaterials can be found in Ratner *et al.* (2013), and recommendations for conducting biocompatibility evaluations for implant devices are presented in the International Standard ISO 10993-1:2018, 'Biological evaluation of medical devices – Part 1: Evaluation and testing within a risk management process'.

2.2.5 Sterilisation

All implanted parts of a tag must be thoroughly cleaned of particles and chemical contaminants (e.g., machining oils that are often not removed by manufacturers) by washing and rinsing, and then must be sterilised before implantation. In the past, disinfection (reduction, but not complete elimination, of pathogen contamination) of implanted tags was common practice, yet likelihood of infection at tag sites was unknown due to minimal opportunity for post-tagging assessment of animals. Sterilisation means the killing or removal of all microorganisms, including viruses, fungi, protozoa and bacterial spores. Low level disinfection can only kill most vegetative bacteria, some (enveloped) viruses and some fungi; intermediate level disinfection can eliminate most bacteria (vegetative and mycobacteria), most fungi and most viruses; and high level disinfection (HLD) can destroy all microbes, with the exception of some bacterial spores (see Govindaraj and Muthuraman, 2015). With enhanced understanding of the response of tissues to tag insertion (see Fig. 6), coupled with improved animal welfare standards globally, full sterilisation, as required for surgical implants used in humans and domestic and laboratory animals, is now recommended. Although infection at tag sites can result from organisms entering the tag site at any time after insertion, sterility at the time of implantation is important, as this is the time when blood vessels can be cut during tag insertion, allowing direct entry of pathogens into the blood stream should they be present. As improvements are made to attachment methods, attention should be paid to developing anchors that are not likely to carry skin and its associated microbes deep into the implant site.

Sterilisation of all implantable tag parts is recommended, while any other part of the tag that contacts the implantable pieces of the tag or the whale should be treated with HLD. A variety of sterilisation methods exist, based on heat, radiation or chemical exposure, but dry heat and steam sterilisation are not safe for most electronics. Chemical gas sterilisation is thus a good choice for tag sterilisation. Gas sterilisation with ethylene oxide (EtO) can be used and is widely available in human and veterinary clinics. After EtO sterilisation, approximately 24hrs of off-gassing is required before tag deployment because EtO is toxic. Additional chemical sterilants include hydrogen peroxide, peracetic acid, glutaraldehyde and hydrogen peroxide/peracetic acid mixtures (FDA, 2015; Rutala *et al.*, 2008), but care must be taken when using these on tags to ensure that all exposed parts of the tags are compatible with the chosen chemical. For example, HLD concentrations of hydrogen peroxide and peracetic acid can degrade Buna N (nitrile rubber), but Viton rubber and EPDM are resistant to these chemicals. Each chemical must be used at a specific temperature, concentration and contact time period for effective disinfection or sterilisation. For example, when soaking devices by immersion in a 2.4% glutaraldehyde solution, HLD conditions will be reached in 45mins at 25°C, but 10hrs of soaking is required to achieve sterilisation (FDA, 2015).

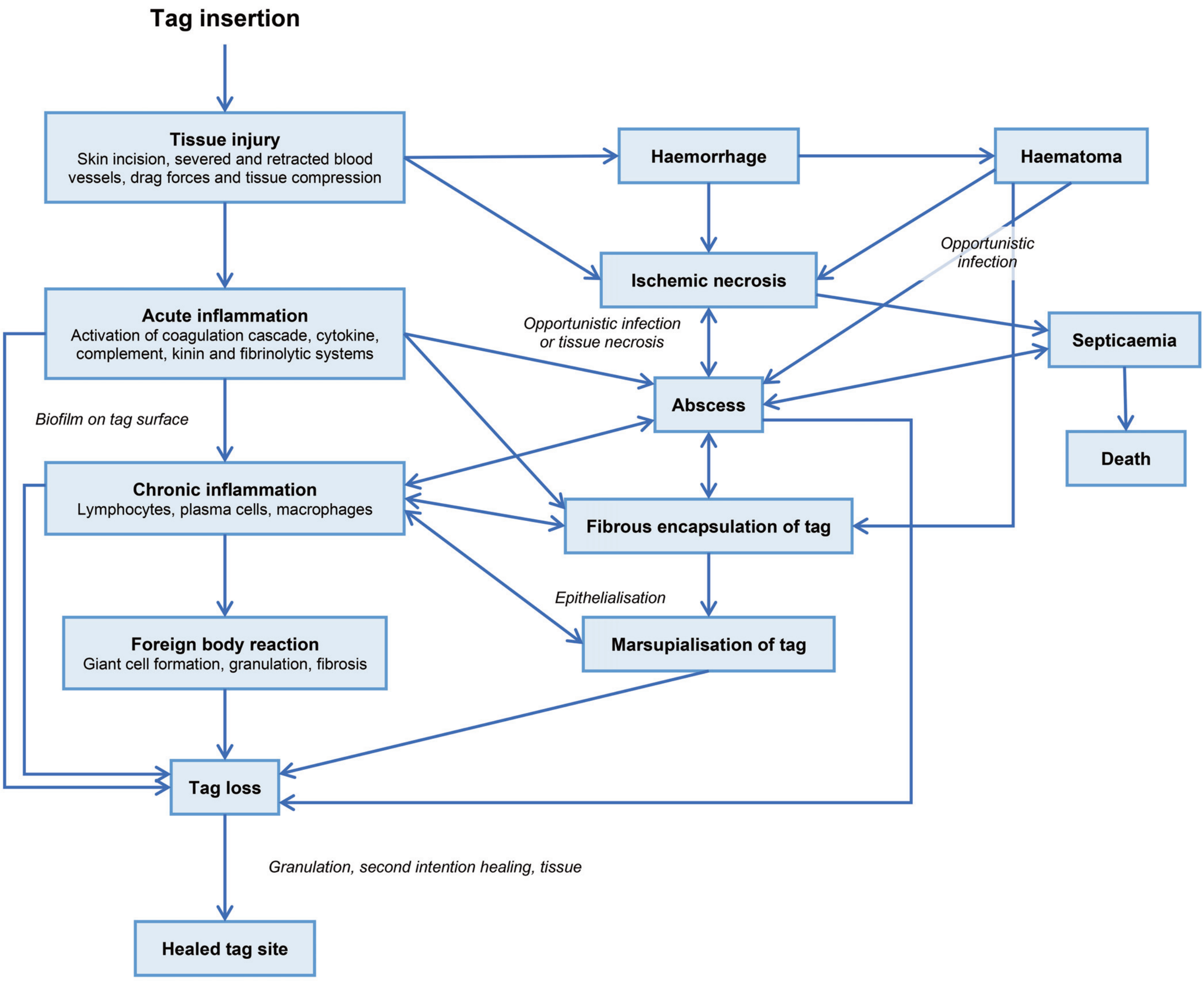


Fig. 6. Schematic diagram of the succession of potential physiological responses to application of an invasive tag. Text in the demarcated boxes describes stages of responses, italic text describes the processes occurring during progression between these stages.

Ideally, the sterility of the implanted parts of a tag should be maintained until deployment. This is often difficult in field situations, but with care and forethought, sterility can be maximised (Mulcahy, 2013). Shrouds, hoods, bags, sheaths or other sterile covers, and sterile gloves can be used to minimise environmental contamination of the tag. Additionally, packaging or containers with peripheral handles could be designed to facilitate easy, aseptic handling of implantable components without sterile gloves. Training, practice and experience with aseptic technique will help ensure compliance. As soon as sterile wrappings are removed, surfaces begin to accumulate contaminants in a time-dependent fashion, at a rate influenced by the environment in which they are being used (Dalstrom *et al.*, 2008). At some point, the surfaces may become contaminated enough to require HLD or re-sterilisation. The length of time that adequate sterility is maintained can be extended by protecting the implantable surfaces with water-impermeable sterile drapes, wrappings or containers until immediately prior to use. We suggest that a conservative approach is to disinfect or re-sterilise after a few hours of exposure to air. In field situations, availability of sterile gloves, bags, tape and handling instruments, as well as baths for HLD solution immersion, can be useful in maintaining sterility of tags. If the penetrating elements of a tag become contaminated (e.g. implant parts come into direct contact with nonsterile surfaces, including missing the target animal and landing in seawater), they should be re-sterilised prior to use.

To address the potential for infection associated with percutaneous tag deployment, antibiotic coatings have been added to some tags with implanted parts (Mate *et al.*, 2007). The efficacy of antibiotic use in reducing tag site infection is unclear (due to the spectrum of potential organisms involved, including fungi). It may potentially have deleterious effects on beneficial flora and can enhance development of specific antibiotic resistance, and thus use should be conducted with caution and be subsequently evaluated. Any use should only occur after thorough research and in conjunction with improvements in implant preparation and implant technique, use of microbial resistant materials and implant sterilisation. The choice of antibiotic agents and dosage should be determined in consultation with a veterinarian and be effective in killing the range of organisms of concern. A comprehensive review of antibiotic use with electronic tag implants in fish provides recommendations that are applicable to tag implants in cetaceans (Mulcahy, 2011). The use of antimicrobials does not preclude the need to sterilise the implantable portions of a tag.

2.2.6 Tag operation

Researchers should check that tags are operating properly after receiving them from the manufacturer, and again in the field, prior to deployment. For multi-sensor tags, researchers should develop a protocol for testing each sensor in the tag for correct operation prior to deployment. For all types of transmitting tags, researchers are encouraged to carry receivers to check for transmissions from the tag immediately after deployment, which is important for troubleshooting problems later. Well-documented field procedures greatly aid in diagnosing problems. All relevant deployment data should be recorded in real-time (Section 2.8), either on 'traditional' data sheets or by electronic means. Photographs and videos should be taken of the tag deployment to document the tag attachment site on the body of the animal in sufficient resolution for subsequent evaluation of the condition and placement of the tag (see Section 2.7).

Dedicated follow-up studies should be conducted whenever possible, to assess tag effects and the fate of tags. This is especially important when using new or significantly modified tags and attachment designs (see below). However, even designs with a long history of successful performance have some probability of failure. Tags that transmit data or use a radio beacon to aid recovery may cease transmissions for a variety of reasons, including failure of the tag electronics or battery, tag damage or loss, or animal mortality (Hammerschlag *et al.*, 2014; Hays *et al.*, 2007). Sometimes it is possible to infer the likely cause from data that were transmitted prior to cessation or it is obvious from visual evidence (either from direct observations or photographs). However, in most cases, tags cease transmitting and the cause is never known. Table 1 lists some of the possible causes for lack of transmissions and observable signs or clues that are sometimes found in data or diagnostic messages transmitted by the tag, or from analysis of photographs (also see Section 2.7).

Tag failure can be defined as those events other than the cessation of transmissions at the expected end of the battery life or tag loss by the expected foreign body response with eventual tag detachment or outward migration of retention elements (or the whole tag in the case of Type C tags). The possibility of tag failure (i.e. cases where there is evidence that the tag electronics or mechanicals, including the retention elements, have failed; Table 1), should be discussed during the planning stage. An acceptable tag failure rate should be decided in advance, and if that failure rate is exceeded, a comprehensive review of technology and procedures should be conducted (Morton *et al.*, 2003). The conditions under which most cetacean tags will operate are extreme, and therefore what constitutes an acceptable failure rate for each cetacean tagging study should be evaluated in advance and published with the other study results (Section 2.8). A summary of any tag failures experienced during the study along with the suspected causes should also be published.

2.2.7 Tag deployment

Protocols for the successful deployment of tags are as important as the appropriate design, selection and preparation of equipment. Those considering tagging cetaceans should carefully research attachment methods, fully plan their research design including the selection of which individuals should be tagged (Section 2.6) and obtain adequate training (Section 2.5). Whether tagging free-swimming cetaceans (Section 2.3) or captured and restrained animals (Section 2.4), a plan for the tagging operations should be developed in advance and shared with all participating personnel.

Tags should be deployed using methods and equipment that are appropriate to the study species and the sex and age class of targeted individuals. For tags that are deployed on unrestrained animals where there is incomplete control over attachment location, suitability of the penetration depth of anchors over the entire potential attachment surface of the body should be considered. Planning, patience and practice are necessary to ensure that tags are applied where intended.

Projectile devices, such as pneumatic or chemical propellant rifles and crossbows are commonly used to deploy tags onto free-swimming (unrestrained) animals. Projectile devices can be quite powerful; therefore, it is important to adjust the force according to the weight and aerodynamics of the tag and distance to the animal. Poles, whether held or thrown, can also result in tags being delivered with a substantial amount of force. With many pneumatic and chemical propellant devices, adjustments can be made during an approach. Projection force should be no more than required for accurate flight and sufficient implantation. Implant force, whether on a tag at the end of a pole or the end of a projected tag carrier, should not exceed that required for the implanted parts of the tag to reach their designed penetration depth when launched from the expected distance. Projected tag packages are typically not very aerodynamic in the deployment configuration, meaning that their velocity will slow significantly over the range of likely distances between the tagger and the target animal. Therefore, if no adjustments are made to the initial projection velocity, then the impact force at close tagging distances will be much greater than at longer distances. Too much force can cause excessive tissue trauma, limiting retention, exacerbating wounds and potentially damaging the electronics. Consolidated tags should have an adequate section of increased dimension (like the head of a nail) to limit penetration depth, so that excessive deployment force does not cause the tag to implant deeper than designed. Excessively deep implantation can cause unacceptable injury to the animal and prevent tag transmission if the wet/dry sensors or the base of the antenna are also implanted. However, using too little force will result in incomplete penetration, causing shorter retention duration. More detail is presented in Section 2.3 on boat approach for tagging free-swimming cetaceans.

Tag deployments on captured and temporarily-restrained animals are performed under controlled conditions, allowing accurate and consistent tag placement. Restraint and manual placement of tags allows researchers to choose an exact attachment site, but even for well-studied species, there is currently no consensus on what part of the dorsal fin or body

Table 1

Ultimate causes of lack of transmissions from telemetry tags. Possible proximate causes of each category of unexpected failure are also provided, along with signs or sequelae that may be observed in previously transmitted messages or in photographs or follow up field observations (some may be obvious, like broken dart shafts, others inferred from visual signs, such as purulent discharge suggesting infection, or even less obvious signs, such as swelling). The causes of loss of transmissions listed are not mutually exclusive and there may be multiple issues that occur either simultaneously or in succession after tag deployment.

Ultimate cause	Proximate cause		Notes re: Signs or consequences
Undetermined	Any of the below		Typically, transmissions are suddenly lost with no warning messages and no resightings of the tagged animal. Evidence from follow-up studies demonstrates that this is rarely because of mortality. Therefore, dedicated follow-up studies can be critical for diagnosing problems and improving tag design and deployment methods.
Tag electronics failure	Battery failure		Unexpectedly low battery voltage or high rate of decreasing voltage
	Antenna breakage		Poor signal strength or visual confirmation of frayed or broken antenna
	Wet-dry sensor fouling or breakage		Unexpectedly high rate of transmissions due to transmission underwater (corrosion or biofouling will increase the resistance between the electrodes, mimicking surfacing). Alternatively, water absorption in the tag material may decrease the resistance leading to apparent continuous immersion.
	Firmware bug		Unlimited variety of disappointing revelations.
Tag attachment failure (tag loss)	Improper attachment		Retention elements fail to implant at all or to an adequate depth, or tag fails to attach to the desired target anatomic location (due to animal behavior, environmental conditions, operator issues, or other challenges of deploying onto moving animals from unstable platforms).
	Failed attachment	Migration of bolt, pin or rod	In Type B (bolt-on) tags, if attachment rod(s) migrate caudally through dorsal fin tissue, drag may increase dramatically, resulting in progressive changes in swimming and dive behavior.
	Mechanical breakage	Tag package breakage	Lacking visual confirmation, fractures can result in water intrusion which may manifest in unexpected sensor readings, accelerated battery voltage decline, or just sudden electronics failure.
		Implanted element breakage	Retention of observable parts after tag loss. Migration to the surface may take weeks to years. Type A (anchored): visual evidence of retained dart shafts snapped or separated from electronics package; Type B (bolt-on): pierced elements (e.g., bolts/pins/rods) snapped or connections to tag severed. Type C (consolidated): anchors separated from main tag package.
	Typical foreign body response		Wound margins well delineated and even with adjoining skin, healthy granulation tissue visible at surface; typically results in complete wound healing, although in some species, repigmentation of the tagged area may not occur.
	Secondary infection		Swelling and retraction of the penetrating site margins, dependent swelling, blood or discharge either overlying or draining from the tag site and secondary effects, such as loss of condition and potential behavioral changes.
	Large external force		Wound and surrounding epidermis may appear similar to normal foreign body response; in some cases, retention elements can leave tell-tale scratch marks, or cause unusual wound margins. Recovered tags can also show evidence of being scraped against another animal or some object, including the seafloor.
Mortality	Natural		Possibly unusual movement or other behaviors leading up to time of death; body temperature sensors may reveal abnormally high temperature due to inflammation, infection or an unexplained cause of hyperthermia.
	Tag-related	Puncture of bone or internal organ	Never reported in tagged cetaceans (but only a few dead tagged animals have had full post mortem examination). Depending on the extent of injury, organ involved and possible secondary microbial invasion, clinical signs may be inapparent on external exam or there may be swelling or depression and discharge from tag site, subcutaneous swelling within the vicinity of the penetrating wound, loss of nutritional condition, difficulty with swimming and other factors.
		Introduction of secondary infection	Not likely confirmed without fresh carcass recovery and thorough necropsy. Taggers should coordinate with stranding networks so tag sites can be assessed during stranding responses. Based on external lesions alone, it is difficult to infer either a localized abscess or granuloma at the tag site, vs widespread or systemic infection. Overall nutritional condition, activity and behavior prior to death may provide clues to the health status of the animal.
		Entanglement	We are unaware of any occurrence in cetaceans, but anecdotes from fish tagging studies have been reported.
		Tag-induced predation	Never reported in cetaceans, but uncommonly observed in fish studies. This should be considered if contemplating the attachment of ultrasonic tags to cetaceans that are prey of other cetaceans.

is optimal for attachment, so additional research on morphology, physiological function and hydrodynamics of potential attachment sites is required. Trocars, drill bits or other instruments used to pierce tissue should be cleaned and sterilised before each use consistent with the sterilisation of implantable tag components described in Section 2.2.5. Other opportunities for sampling (blood, morphometrics, tissues) are available with a temporarily-restrained animal, and the pros and cons of longer holding times should be considered in deciding whether to collect health assessment data when tagging is the primary purpose. Likewise, when the primary purpose of capture and temporary restraint is to collect health assessment or physiological data, the purpose, type and pros and cons of tagging should be thoroughly considered before deciding to include tagging in the project. More detail is presented below in Section 2.4 on capture-release methods.

2.2.8 Identification of tagged individuals

Whenever possible, researchers should obtain data so that the tagged individual can be identified in the future, especially after the tag has detached. For many individuals, this can be done with photographs or video of the anatomical features that allow individual recognition in that species, such as the dorsal fin, saddle patch, fluke, callosity, barnacle, or colouration patterns. For poorly marked animals, photographs are more likely to produce recognisable images than video, but a genetic sample may be the only way to identify an individual later. Genetic sampling has the advantage that it can permit sex determination, and it can allow identification even when post-mortem decomposition makes visual recognition impossible, or if markings change such that the individual may not be recognisable from subsequent photos. Biopsy dart sampling and tagging can sometimes be performed at nearly the same time (by two different operators) and some tag deployment devices (e.g. a tag holder on the end of an arrow or pole mounted next to a biopsy dart) perform simultaneous tagging and skin collection. In other cases, multiple approaches can be made to collect skin samples by biopsy dart sampling during a separate approach from tagging, but the additional stress to the animal of another close approach should be considered. This consideration may be especially relevant for non-invasive short-term (e.g. suction cup attached) tags for which the period of disturbance could represent an important fraction of the deployment time.

2.2.9 Development of new equipment and methods

Refinements of all aspects of cetacean tagging are important, and innovation in tag attachment technology and procedures is encouraged. However, new equipment must be tested, and its effective and consistent operation should be demonstrated before use on live animals. For attachment elements, especially invasive ones, testing should include tissue surrogates (such as fiber-reinforced rubber or foam blocks) and carcass tissue. For equipment that will be deployed by projectile devices, testing using whole carcasses, or at least large tissue blocks representative of the characteristics of *in situ* tissue, should be conducted. Such tests will allow for the determination of the appropriate projection velocity at a given distance to the animal, which is necessary to ensure proper implantation while minimising tissue damage and tag breakage.

Innovation is also required for non-invasive attachments. Many multi-sensor tags, especially those recording audio and video, can record for a longer duration than most suction cups will remain attached. Therefore, increasing the duration of suction-cup attachments would be valuable. To address this need, suction cups with microtextures and adhesives are being considered, but these may still have effects that should first be explored with tissue surrogates. For all non-invasive tags, initial deployments on cetaceans under human care are encouraged because detailed observations of tag performance and effects on the animals can be more easily conducted.

Efforts to improve tag electronics, sensors, batteries and antennas, while much needed, can introduce unanticipated failures. New tag designs should be tested in a manner that replicates, as closely as reasonably possible, the conditions under which they will be used in the field (e.g. temperature, pressure, salt water and UV light exposure). The effects of rapid acceleration and deceleration on the tag during tag deployment should also be evaluated.

Researchers should be extremely cautious when deploying a new tag attachment design on individuals sensitive to disturbance, especially endangered populations. Most refinements and improvements in tagging equipment and methodology build on previous knowledge and are therefore often modifications of proven technology, limiting the potential for unanticipated effects. However, more substantial innovations may be necessary to provide longer attachment durations to address research questions without increasing the effects on tagged individuals. After thorough testing in the laboratory and under simulated field conditions with tissue surrogates and/or carcass tissue, radically new attachment designs must be shown to be safe and effective on a similar species/population before being applied to one at risk. In such pilot studies, the opportunity for resight observations is critical (see Section 2.7 for more details on the need for pilot and follow-up studies and how they should be designed).

2.2.10 Recommendations for tag design and deployment

- Researchers must choose appropriate tags, tools and methods by reviewing previous work and obtaining advice from others with hands-on experience in cetacean tagging, preferably with similar species.

- All elements of the tags must be a reasonable (detailed above) size, shape and configuration for the species, sex and age class that will be targeted.

- Tag configurations should produce the desired data with the least impact possible to the tagged individual for the necessary duration of attachment.
  - Tags should minimise: trauma; energetic costs; interference with body movements; predation risk; risk of entanglement; and interference with social interactions.

- Implanted elements should be:
  - constructed only of materials known to be biocompatible and safe for long-term implantation (regardless of the intended duration of implantation);

    - thoroughly cleaned and sterilised (not simply disinfected) and maintained sterile until deployment; and
    - be of a small enough size and placed appropriately so there is no risk of contact with bones or internal organs upon deployment.

- Researchers should ensure that tags are operating before heading to the field, and if possible, shortly before and after deployment.

- Tagged individuals should be identified.
    - Obtain photographs of the tag attachment site and of identifying features of the animal, provided this does not greatly extend the disturbance to the animal.
    - Whenever possible, obtain a tissue sample for genetics to aid future identification.

- Refinement and innovation of tags and tagging methods are strongly encouraged but should proceed with caution.
    - Testing of new equipment and methods should be thorough and should include tissue surrogates and/or carcass testing before application to live animals. When feasible, such as for non-invasive tags, consider deployments with cetaceans under human care.
    - New tags and attachment designs that are so substantially different from previously deployed designs that effects cannot be predicted must be shown to be safe and effective on a similar species before applying to endangered species or populations.
    - Dedicated follow-up observations should be conducted whenever feasible, but especially when using new or significantly modified attachment designs.
    - An acceptable tag failure rate should be determined before tagging, and if exceeded, protocols should be reviewed.

2.3 Boat approach for tagging free-swimming cetaceans

The protocols for boat approaches will vary depending on multiple factors, including species, weather conditions, the type of tagging and the type of boat. However, vessel approaches for tagging are typically closer to the animals than vessel approaches for other cetacean research activities (e.g. photo-identification and biopsy sampling), and thus there is an increased risk of disturbance (and potential injury) to the cetaceans being approached, as well as risks to human safety. Serious accidents have occurred during tagging operations and appropriate caution must be taken. There are several basic principles that should be applied to all boat approaches for tagging free-swimming animals. All crew should be prepared for accidents, including being familiar with safety gear, as well as emergency communication and rescue protocols. The appropriate safety equipment will vary, but key items such as personal floatation devices, helmets for those operating in small boats and rough seas, and emergency locator beacons should be considered. For boats tagging larger whales in remote areas, operation of a second, safety/support boat should be considered. When the use of a second vessel is not feasible, a float plan should be filed and check-in times with someone on shore should be scheduled. When operating in challenging environments, such as in cold waters or rough seas, even more stringent safety protocols should be considered, such as limits on the distance from an assistance vessel.

Boat approaches should be undertaken in a way to minimise risk to both the cetacean and the personnel on board. Vessel/cetacean collisions could occur either by the vessel striking the animal or by the animal striking the vessel, including potentially breaching onto a vessel. Both possibilities can be minimised with the use of a boat driver with extensive experience in driving in close proximity to cetaceans as well as familiarity with the behaviour of the species being approached. Cetacean responses to vessel approaches vary dramatically by species, by population, by age or sex, and even by individual. Thus, the experience of the boat driver with the behaviour of the target and similar species is key to minimising harassment and ensuring safety. Such experience can improve deployments and reduce risk by providing more steady approaches involving the slowest possible speed, minimal throttle adjustments and fewest course changes while near the animal. Furthermore, the ability of the crew to recognise behaviours or escalating patterns that may indicate the potential for the animal striking the vessel can be as important as familiarity with the vessel controls to minimise the chances of the vessel striking the animal.

Good communication between the boat driver and tagger (e.g. direct concise dialogue, hands-free headsets) and other crew members is paramount for the boat driver to be aware of other animals in a group or behaviour of individuals not visible to the driver beyond the target individual. Such communication also increases general safety aboard the vessel. The tagger will usually have both hands on the deployment device, thus may not be holding onto the boat. Unexpected rapid acceleration or deceleration could have significant consequences for the tagger, crew and animals near the boat.

Minimising disturbance to that required to deploy a tag should be a goal of vessel approaches. Disturbing non-target animals in a group during the approach may be necessary to deploy tags on some species, but patience and caution can minimise approach-related disturbance. Care is especially important if approaching groups with calves. Criteria for when to terminate tagging attempts on an individual or group should be agreed upon before starting fieldwork, and all personnel on board should be familiar with the criteria. Example criteria include repeated display of behavioural cues that would be interpreted as strong avoidance. The total disturbance to recognisable individuals over a field season should be kept within pre-agreed limits. In field sites in which multiple research groups are approaching the same animals, whether for tagging or other research requiring close boat approaches, there should be communication between the groups to assess and minimise the total disturbance on individuals.

2.3.1 Recommendations for boat approach for tagging free-swimming cetaceans

- Vessel approaches should be undertaken in a way that minimises risk to the personnel on board and minimises harassment and risk of injury of cetaceans being approached/tagged.

- Be prepared for accidents: safety and first aid equipment should be on board always, and the tagging crew should have first aid, 'man overboard' and general emergency response training.
- Clear communication and rescue protocols should be agreed before tagging efforts commence, and all personnel on the boat should be familiar with the protocols.
- Boat drivers should have as much prior experience as possible with the behaviour of the species being tagged, especially any species-specific risks of dangerous response, and need to be aware of all individual animals in a group, not just the target individual.
- Approaches should be made at the slowest feasible speed and at angles of approach that will minimise possible collisions with either target or non-target individuals.

2.4 Capture-release and tagging of restrained animals

2.4.1 Rationale for capture-release

Although capture-release techniques in general involve greater risk to animals and to people than remote tagging techniques that do not involve restraint and handling, for some cetacean species of smaller body size or whose behaviour does not allow for remote tagging, capture-release may be the more effective option. Responses to capture vary by species, and risks must be weighed carefully against the benefits of tagging. Temporarily restrained animals provide opportunities for careful and optimal placement of tags for long-term attachment and collection of information and samples not available using remote tag deployments. Sex can be determined, age can be estimated, ultrasound can be used to measure blubber stores as a proxy for body condition or for assessing reproductive status, blood, blow, swabs and other samples can be collected for health assessment and life history analyses (Townsend *et al.*, 2018). Disinfection of the tag attachment site should occur just before surgical tag attachment. Local anesthesia should be used for small odontocetes when time permits, especially for multiple piercings, and in other cases at the discretion of the consulting veterinarian.

Because of logistical and safety considerations, capture-release efforts typically are limited to smaller odontocetes, and a variety of species have been tagged during capture-release operations, conducted either specifically for tagging, or as part of a broader research programme, such as population health assessments. Larger odontocetes and most mysticetes are not good candidates for this approach. Response to capture and handling differs by cetacean species but can also differ by individual within a species.

2.4.2 Methods for capture-release

As summarised by Loughlin *et al.* (2010) and Asper (1975), specific capture techniques have been developed for different species, habitats and situations. In shallow water, large-mesh seine nets have been deployed to corral or create barriers to enclose small groups of animals. Individual belugas have been caught in shallow water by driving animals into nets and by leaping from a boat and placing a hoop net around them. In intermediate water depths, fishing structures such as weirs have been used to contain porpoises. In deep water, break-away hoop nets have been used to catch individual bow-riding cetaceans of a range of sizes (Asper, 1975). Purse seines and surface gillnets have been used to capture individuals or groups of small cetaceans in deep, open waters (Loughlin *et al.*, 2010). The duration of active pursuit should be minimised, and a limit should be determined in advance, along with a limit on the number of capture attempts made on an individual. Tagging of restrained cetaceans may occur on the deck of a boat, on a floating mat alongside a vessel, or in shallow water. One variant of tagging restrained animals occurs when stranded or rescued animals are tagged prior to release.

2.4.3 Recommendations for capture-release

- Capture teams must be very experienced with the capture and restraint techniques and familiar with how the gear might behave under different environmental conditions.
- An experienced marine mammal veterinarian should be included as part of the capture-release team.
- Safe capture-release sites should be scouted and selected in advance whenever possible. For shallow water encircling seine net situations, a capture site should be free of underwater obstacles, with minimal currents and mud.
- Duration of pursuit should be as short as possible.
- Disturbance to non-target animals should be minimised. When possible, the numbers of animals involved in capture attempts should be limited to those targeted for tagging.
- Weather conditions, tides and daylight should be suitable for the entire length of a capture-release event, for animal and human safety.
- Presumed mother/calf pairs should be avoided unless part of the research goals; they should not be separated during capture or handling, and they should be released together.
- The animal should be able to breathe at will, with unimpeded access to the surface; respiration rate and behaviour should be monitored carefully and capture attempts abandoned if necessary.
- Identify and assess potential stressors before proceeding with capture or handling (e.g. vulnerability from life history or physiological state such as extreme young/old age, compromised health).
- If feasible, establish contingency plans to recapture tagged animals and remove tags if health or behavioural problems associated with the tags become evident and the risks related to re-capture are outweighed by the need to remove the tag.

2.4.4 Recommendations for restraint and handling

- Include more personnel than the number needed to handle the expected number of captured individuals at any given time and include a dedicated veterinarian to monitor each individual cetacean throughout the procedures.

- Restraint and handling should be at the minimum level and for the briefest time required to conduct the procedures safely and humanely, which requires an efficient handling plan with organised tool kit and data forms, and a practiced team.
- Restraint system should provide for the animal's comfort (padded, shaded, quiet) and allow rapid, safe, controlled release of the animal in the event of problems.
- Airways should not be obstructed during restraint for tagging.
- Careful monitoring should occur throughout the restraint period, including respiration interval/effectiveness (with pre-defined species-specific thresholds triggering veterinary response), heart rate (including assessing sinus arrhythmia), eye appearance, colour/response of the mucous membranes of the mouth, vocalisations and general behaviour.
- Thermal stress to the animal should be avoided by keeping it shaded, wet and cool.
- General anesthesia should not be used, but emergency medications should be readily available. The attending veterinarian should be highly familiar with indicators, drug administration and recovery protocols for the species being handled.
- A basic health assessment should be conducted when feasible without greatly increasing restraint time, including blood collection, physical exam, ultrasonic pregnancy and lung health check, morphometrics and sampling for genetics. To assess response to handling, blood can be analysed in near-real-time for parameters such as lactic acid. Determination of late term pregnancy provides guidance on duration and method of handling and procedures to be used but should not necessarily preclude tagging with currently available small tags.

2.5 Training/qualifications of personnel

Having qualified personnel participating in tag deployment projects (as taggers, boat drivers, photographers, data recorders) or capture-release, is paramount for the safe and successful use of these methods. Inexperience or lack of familiarity with any of the many steps involved can present real risks to the health and safety of the study animals and humans alike, as well as compromise data quality. As it may often be difficult to obtain the necessary training and supervision, people wishing to begin tagging or capture-release operations should approach those with extensive tagging experience, and those with experience should offer opportunities to gain experience and training.

2.5.1 Importance of training for remote tagging

Considerable attention is often given to the qualifications of the tagger, who may bear the most obvious risks and responsibility for a successful remote deployment, particularly when powerful projectors (e.g. crossbows, pneumatic or black-powder guns) are employed. However, the success of the tagger is directly related to the skill and experience of the boat driver. A boat driver not familiar with the behaviour of the species of interest, the boat (that must have suitable characteristics for safely approaching whales) or the specific requirements of the tag deployment will greatly reduce the chances of a successful attachment and increase the chances of injury to animals and personnel (e.g. through poor tag placement or vessel/cetacean contact). Thus, adequate training is essential for all methods prior to their use.

Minimum training and competency qualifications for tagging will vary depending on the type of tag being deployed and the species being tagged. However, certain basic principles apply to all tagging scenarios, and researchers considering tagging should ensure that their protocols address these principles so that the entire team is adequately trained to safely and effectively deploy tags. The specific recommendations below apply most to taggers and boat drivers, but it is important that all personnel aboard the boat are prepared to assist and that their actions do not jeopardise the safety of the study animals, the other researchers, or themselves. The entire tagging team should consider conducting training deployments aboard the tagging vessel, targeting a simulated cetacean (e.g. a floating target).

2.5.2 Importance of training for capture, handling, tagging and release

Well-trained and experienced personnel can greatly expedite the process, and they can detect adverse situations and other problems early, contributing to safe release of the animals. Training should include literature review, mentoring, familiarity with the species from field observations, direct experience with the target and related species, and practicing techniques without animals present.

2.5.3 Recommendations for training of taggers

- Spend time observing, photographing, or engaging in other data collection techniques on the study population to become familiar with the general behavioural patterns of the species of interest.
- Become familiar with use of all equipment used in tag deployment through repetition (including use of the tag, tag attachment elements and deployment device):
  - practice deployments on land with a dummy tag projected at a target placed at different distances and angles; and
  - practice boat approaches and deployments aboard the tagging vessel, or one that is similar, with a dummy tag and floating target, preferably in conditions (e.g. comparable sea state and vessel speeds) that will likely be encountered during your research.
- For taggers deploying tags onto free-swimming animals using a projection device (e.g. crossbow, pneumatic rifle):
  - be competent with biopsy sampling of the target species or similar species; and
  - complete a firearms or archery safety course or receive instruction from an individual experienced in the safe handling of firearms or crossbows and practice until proficient.
- New taggers should conduct initial deployments under the supervision of an experienced individual who can provide feedback and assess when qualified to proceed unsupervised.

2.5.4 Recommendations for training of boat drivers

- Become proficient in the safe operation and handling of the vessel used for tagging before approaching cetaceans.
- Spend time observing, photographing, or engaging in other data collection on the study population to become familiar with the general behaviour of the species of interest.
- Have prior experience driving near cetaceans during biopsy sampling or other data collection methods that require specific positioning of the boat.
- For tags that require approaches closer than 5m to large cetaceans, the boat driver's first approaches for deployment should be supervised by an experienced individual (which could include the tagger), who can provide feedback and assess when qualified to operate unsupervised.

2.5.5 Recommendations for training in capture, handling and release methods

- Spend time observing, photographing, or engaging in other data collection techniques on the study population to become familiar with the general behavioural patterns of the species of interest:
  - under free-ranging conditions; and
  - during handling.
- Become directly familiar with the physical characteristics and field conditions of the capture site, and/or engage local experts.
- Become familiar with all aspects of the equipment used in tag deployment through repetition (including use of the tag, tag attachment elements) to expedite process and minimise time animal is restrained.

2.6 Selection of candidates for tagging

2.6.1 Conservation status

Some basic research questions, especially physiological ones, might effectively be addressed by studying any one of many different species. In such cases, the selection of a candidate species/population should take into consideration their conservation status, population size, trends in abundance and geographic range. The use of the most invasive techniques in endangered or declining populations should be considered only if less invasive tags are not able to provide the necessary data for the project (that must have identified conservation benefits). These may include pilot or feasibility studies, which are described in more detail in Section 2.7. One option to providing safeguards and minimising risks of negative effects in a threatened species/population might be to tag only males, if they are representative of the population from the perspective of the research questions. This may not always be feasible, however, especially in species that are not sexually dimorphic, or where the sex of only a few animals is known through individual identification. Furthermore, there may be cases where males are more sensitive than females to adverse effects of tagging. Therefore, this should be evaluated on a case-by-case basis.

2.6.2 Timing

There are times when cetaceans may be more vulnerable to potential adverse effects of tagging and tagging operations. These include periods when animals are fasting (e.g. the breeding season) or when seasonal or cyclical temporal environmental stressors (e.g. El Niño or harmful algal blooms) can affect food availability, body condition or health status. The objectives of some studies may require tagging during these times, therefore it is important to consider the timing and location of tagging to fully appreciate the risks during periods when animals may be more sensitive to potentially negative effects of tagging.

2.6.3 Age class

Tagging of calves/young-of-the-year (often identified by their small size and behaviour), especially with invasive techniques, should be well justified and only conducted under special circumstances. Disturbance and the energetic effects of tagging will likely have greater impacts on calves. Tagging of females with calves, however, can be a valuable way to address certain questions. Disturbance associated with tagging approaches, tag deployment and from tag effects, however, could restrict suckling opportunities and disrupt social bonds between mother-calf pairs. If tagging of mothers is required, special care must be taken to avoid separating mothers and calves. Conservative protocols should be developed (e.g. avoid tagging of mothers with neonates [e.g. animals with fetal folds], restrict tagging attempts to a short period of time compared with animals of other sex/age classes, abort tagging attempts if behavioural indicators of disturbance are detected).

2.6.4 Physiological status and health

The health of the population should be considered so that potential stressors from tagging (disturbance, tag effects) do not further compromise the health of individuals in the population. Tagging studies should use available data from longitudinal studies on age, sex, reproductive condition and/or prior reproductive and health history, to select target animals (when such animals can be easily identified in the field). In such cases, taggers should collaborate with research groups conducting longitudinal studies to ensure that as much knowledge of individuals as possible is considered in the study design to minimise risks to the population. In some types of studies, a more random sample may be appropriate.

Potential effects of tagging may vary with animal age, sex, reproductive status, health and social status and level of exposure to environmental and anthropogenic stressors. When selecting individuals to tag, care should be taken to select animals in apparent good health, unless there is strong justification for using tags to monitor sick or injured animals. For typical tagging projects, individuals to avoid include those with evidence of emaciation (e.g. post-nuchal depressions, visible ribs or scapula), higher than normal external parasite load, unusual skin conditions, presence of significant pre-existing wounds (e.g. from an entanglement, predator bite, or ship strike) that have not healed or are of an unknown extent, or that are displaying unusual behavioural or respiratory patterns. For those populations for which there is significant longitudinal (long-term) information and individuals are easily identified in the field, candidates for tagging could be evaluated before going into the field, and/or in the field before deploying a tag. The *a priori* development of criteria for assessing each individual and making a tag/no-tag field decision is recommended.

There are occasional circumstances when the decision to tag a compromised animal may be intentionally made to monitor its movements and survival. For example, cases of individual cetaceans that have been refloated after stranding, or that have been herded or harassed to move them from out-of-habitat situations or ice entrapments, may require monitoring post intervention to evaluate the success of the methods used. Entangled animals might require tagging to facilitate location and disentanglement efforts on subsequent days. In these rare but often highly publicised events, the decision to tag, choice of tag type to use, evaluation of alternative methods to achieve goals and monitoring efforts should be evaluated on a case-by-case basis, preferably by a group of experts with pertinent expertise in the species' biology, tagging technology and veterinary medicine. Tagging a compromised animal may be justified for identifying the cause of poor health within a population, or a population decline, or the monitoring of a specific individual for its health assessment or the need to improve its welfare.

2.6.5 Multiple tags

Attaching more than one tag at a time, or tagging the same individual repeatedly, may be useful to address some questions. In certain cases, deploying two tags at the same time can be used to assess tag failure rate. It is important, however, to note that this inevitably increases the disturbance to the individual due to increased tagging effort, a larger number of attachment points and added drag. When considering tag deployment on an animal that was tagged in a previous field effort, if possible, first assess the health of the individual between tagging events, and for invasive tags, assess wound healing of the implant sites. In instances where individuals have been tagged multiple times, assessing the state of wound healing in these individuals should be a priority to better understand potential effects of multiple tag deployments.

2.6.6 Recommendations for selection of candidates for tagging

- Selection of species/populations for tagging.
  - Basic (as opposed to applied or species-specific) research questions should be addressed in healthy species/populations.
  - Tagging of endangered/threatened or declining species/populations should be conducted with the least invasive technique possible that will provide the necessary data over a sufficient observation period.
  - To avoid impacts on females in endangered/threatened populations, consider whether tagging males only is a feasible option that can address the questions.
  - Tagging of endangered/threatened populations should generate data that are useful in guiding actions that lead to an improvement in their conservation status.
  - Avoid tagging populations with known health problems and in locations and/or time periods when animals are expected to be more vulnerable, unless the project objectives require this.
- Selection of individuals for tagging.
  - Consider sex, age, health and reproductive history in the selection of individuals to tag, ensuring the selection criteria do not compromise the goals of the study.
  - Tag deployment should be focused on animals in apparent good body/health condition. Develop pre-tagging evaluations criteria for a tag/no-tag decision in the field.
  - Tagging of individuals in poor health should only be considered if tagging has the potential to significantly improve welfare or if necessary for conservation goals that require such data.
  - Tagging calves/young-of-the-year should be carefully justified, especially if invasive techniques are required.
  - Develop conservative tagging protocols for calves and females with calves.
  - If deployment of multiple tags on one individual is necessary, ensure the animal is in good health condition and use the least invasive tags possible.
  - Prioritise collection of follow-up health data from individuals that are tagged multiple times.

2.7 Assessing effects with follow-up studies

During the planning stages of any cetacean tagging project, researchers should consider the likely effects on the tagged animals and their population. If tags or tagging cause adverse effects on physiology and health, the results of the study may be invalid due to alteration of the animal's behaviour by the procedure itself. The potential effects of tagging include behavioural and physiological changes, infection, pain and mortality; they may be short-term (minutes to days), medium-term (days to months), or long-term (months to years).

Behavioural effects include short-term responses to the boat approach and tag deployment, but might also include longer-lasting effects, such as avoidance of the area where tagging occurred, anomalously slow or fast movements, or unusual diving behaviour, such as extended surface time. The presence of the tag may increase drag or the risk of entanglement or biofouling. For invasive tags, physiological effects (Fig. 6) may include the foreign body response, local healing processes and other more serious consequences such as abscesses, granulomas, haematomas, bone fractures, systemic infections or reduced reproductive success. Non-invasive tags with attachments not intended to break the skin, can also have physiological effects due to skin chafing, haematomas resulting from strong suction cups, or excessive drag. Tagged animals may experience discomfort or pain at some point over the course of the research. In the worst-case scenario, invasive tagging could lead to the death of the tagged individual, from acute trauma at the time of attachment (due to tag hitting vital organs), inward migration of the tag through time, or systemic infection. Capture and temporary restraint of animals can also lead in exceptional circumstances to extreme behavioural/physiological responses and mortality. Unanticipated issues can arise, such as an increase in the vulnerability of the tagged animals (e.g. because of a previously unrecognised prey shortage), or a defect during manufacture of the equipment discovered after tag application, and therefore some of the impacts may not be recognised until after tags have been deployed (or never discovered).

Due to the range of potential impacts, whenever tagging effects are likely to be unpredictable or significant, deployments should start with a pilot study using a precautionary approach, with limits on the initial numbers of deployments and the rate at which tags are deployed to allow time for assessment of initial results and effects. To adequately assess the effects of tagging, follow-up studies using photography, health assessments and post-mortem examinations are required. A few such studies have generated valuable information on behavioural effects, the wound healing process and the fate of individuals (Andrews *et al.*, 2015; Balmer *et al.*, 2011; Best *et al.*, 2015; Gendron *et al.*, 2015; Heide-Jørgensen *et al.*, 2017; Norman *et al.*, 2018; Robbins *et al.*, 2013; Wells, 2013). However, existing data with which to assess effects remain limited, even for some frequently tagged species and tag types that have a long history of use. While follow-up monitoring may not be feasible or warranted in all cases, it is especially recommended when projects use a substantially new tag design, target an individual/species/population of particular concern, or in circumstances when existing knowledge on effects may not apply.

2.7.1 Designing an effective follow-up study

Follow-up studies aim to assess animal behaviour, tag site tissue responses, health and condition of the tagged animal and the appearance/condition of the tag when it is still present on the animal. They can be enhanced by collaborations among population biologists, veterinarians, naturalists and whale watching operators and the group that deployed the tags. When planning a follow-up study for a new or significantly modified tag design, the best option is to choose a species/population that has been the subject of a long-term demographic study with a comprehensive catalogue of known individuals and a high individual re-sighting rate. This will greatly improve the ability to assess both short- and long-term tagging effects, although the need to tag such individuals must be justified. Although challenging, a tagged individual can potentially be found and observed at systematic intervals using telemetry data while the tag is still transmitting. This may only be practical in projects in which the study population is resident in an area or expected to pass by accessible sites. Opportunistic re-sightings can also be valuable, particularly regarding long-term effects after tags are no longer present or transmitting. Such data may be available from individual identification catalogues and/or facilitated by enlisting a collaborating network of knowledgeable observers in the areas used by tagged individuals. However, opportunistic data are likely to be of lower quality and to span a narrower range of data types than available from planned re-sightings. Occasionally, tagged animals may strand, so coordination amongst the tagging community and the stranding network is essential to ensure examination of stranded animals includes thorough documentation of the tag site and health status of the animal (see Section 2.8).

Researchers should attempt to obtain relevant baseline data from a 'control' sample of individuals that can be compared to the tagged animals. In species with strong social bonds, the control sample should typically be members of the same social group, because re-sighting probabilities and exposure to environmental factors that may influence wound healing and other responses can vary among social groups. These measures will help to differentiate tagging effects from other intrinsic or extrinsic causes of variation among individuals.

Behavioural assessments should be based on an ethogram that is relevant to the species and, where applicable, type of habitat. Assessments should occur in real-time whenever possible, but simultaneous collection of high definition video can allow for retrospective viewing and assessments. Ideally, observations should include the immediate response to deployment, as well as extended pre- and post-tagging observations to facilitate the detection of significant tag-related effects. However, monitoring the behaviour of an individual prior to tagging can be challenging because it may not be possible to predict in advance which individual will ultimately be tagged. Focal follows that are limited to the period after tagging can still be valuable for assessing the nature and duration of some tag responses and for diagnosing tag failures related to deployment. However, researchers should consider the possible effect of the vessel on animal behaviour and either maintain adequate distance or use an alternative method (e.g. unmanned aerial vehicles) to make visual observations or video recordings to prevent unnecessary disturbance. Some tags collect frequent data on dive depth, foraging duration, speed and direction of travel, or overall activity level such that short-term responses can be studied based on changes in those parameters over time. However, many tags do not have these capabilities and tag-related responses may manifest in ways that tags cannot detect.

The best way to directly quantify physiological effects is by conducting a thorough health assessment of a well-known individual before tag attachment, monitoring the individual via observations through the duration of tag attachment and conducting a follow-up assessment after tag loss. Such health assessments can include blood analysis, ultrasound examination, hormonal status, microbial culture and in some cases histological examination of tissue. However, access to most tagged cetaceans will be limited and so reliable methods for assessing effects through remote observation need to be developed and applied when feasible. Assessment of microbiome and hormonal status can be achieved through collection of blow, faecal, or tissue samples. Hormone levels in these samples can be used to evaluate stress (corticosteroids) and reproductive status (progesterone). For a review of potential methods that could be applied, see Hunt *et al.* (2013).

High-resolution photographs of the tag site should be taken at the time of deployment and during each re-sighting. Images should be zoomed-in as close as possible and at several angles to the tag site. Images should also be taken of the entire animal and with a wide field of view around the tag site to evaluate skin and body condition. Tagging projects should also consider ways to enhance and quantify information later obtained by photographs and observation. For example, features such as etched rings on the body of consolidated tags can improve the precision of visual estimates of penetration depth and tag rejection.

A systematic scoring system can be used to standardise assessments of the tag site and animal health from photographs or video stills, with numerical scores applied to features of varying severity. An example is presented in Table 2 (see also Norman *et al.*, 2018). Tag site features that can be scored include the presence, size and shape of raised skin areas and/or depressions at and around the tag site, extent of skin loss around the tag, tissue extrusion, changes in skin pigmentation or texture, wound margin integrity and the presence, characteristics and extent of cyamid distribution. By contrast, some tag site features, such as haemorrhage, serious discharge or inflammatory exudate, may be difficult to consistently detect in photographs as these are readily washed from the tag site during animal movement. Overall health scoring from photographs should also consider body condition, skin condition and cyamid distribution, and any known species-specific health indicators (e.g. Pettis *et al.*, 2004). If a consistent time series of photographs is available, evaluation of whether the tag site changes are increasing or decreasing may assist in detection of tag site responses through numerical scoring of photographs. Prior to scoring, image quality should be explicitly evaluated and accounted for to minimise errors in interpretation. Similar assessment of healing of other types of injuries (e.g. shark bites) may also be useful for comparison of wound healing processes.

Once data are scored, appropriate qualitative and quantitative approaches should be used to assess the progression of changes in features over time and to predict their severity. Mark-recapture statistical models can also be used to quantify survival and reproduction relative to control groups and tag-associated covariate data. However, the effectiveness of the latter depends on sample sizes and detection probabilities that can be challenging to achieve in tagging studies.

2.7.2 Recommendations for follow-up studies

- Follow-up studies are desirable to assess tag effects. They are recommended in these situations:
  - when using completely new or substantially modified tag attachment designs;
  - when tagging species whose characteristics might limit the transferability of results from effects studies conducted on other species;
  - when tags are deployed on individuals/species/populations of particular concern; and
  - when evidence emerges to suggest that tags are not performing as expected (see Section 2.2).
- Follow-up studies should be designed in advance and incorporate the elements below.
  - Be based on robust statistical methods, especially given likely limitations on sample size and statistical power for determining effects. Sample design should include a cohort of control (un-tagged) animals for comparison.
  - Include dedicated re-sighting attempts to evaluate the individual, preferably at pre-determined intervals.

Table 2

Example of a scoring system to characterise tag site features from photographs (from Gulland *et al.* unpublished).

Feature	Description	Score
Swelling	No visible swelling	0
	Localised, focal, under 30cm diameter	1
	Regional, focal, over 30cm diameter	2
	Irregular size and shape, over 30cm diameter	3
Skin loss	No visible skin loss	0
	Up to 1 cm greater than tag diameter	1
	Up to 3 times tag diameter	2
	Larger than 3 times tag diameter	3
Exudate	No visible exudate	0
	Clear	1
	Blood	2
	Purulent	3
Tissue extrusion	No visible tissue extrusion	0
	Fresh tissue	1
	Necrotic tissue	2
Pigmentation change	Normal pigmentation	0
	Change in color of skin around tag site	1
Depression/divot	No visible divot	0
	Diameter of tag or less	1
	Up to approx. 3 times tag diameter, shallow	2
	Significantly larger than tag diameter, deep	3
Cyamids in tag site	Absence of cyamids in tag site	0
	Within tag site margins	1
	Patch extending beyond tag site margins	2

  - Promote opportunistic re-sighting by fostering collaborations with population biologists, veterinarians, naturalists, whale watching operators and stranding responders working with the same animals or in the same area.
  - Include behavioural observations (preferably in real-time and video) based on an ethogram that is relevant to the species and local habitat.
  - Include high-resolution photographs of the tag, tag site and as much of the entire animal as possible, from multiple angles, as well as of other body areas critical for body condition and health assessments.
  - If feasible, include systemic health assessments (e.g. metabolomics, stress and reproductive hormone assessment, in blow samples, feces, biopsy tissue).
- A systematic scoring system using pre-established criteria should be used to assess tag attachment site and overall animal health.

2.8 Reporting and data sharing

Despite the accelerating use of tags in cetacean studies, tagging is still an evolving and experimental field, with developments in some cases occurring without broad and timely sharing of information on successful innovations, or their instructive failures. Therefore, the scientific and regulatory communities would benefit from learning the details of what did and did not work. Specifically, reports and publications that include tagging results should provide details on the tags used (maximum dimensions, volume, frontal surface area, mass), especially for implanted parts (including maximum implant depth), manufacturer, specifics of materials and configuration, the deployment method and equipment, the basic metrics of tag performance (attachment duration, data telemetry throughput or other relevant tag operation results) and information on tag effects. Those involved with tagging, including tag designers and manufacturers, should also be encouraged to share more detailed information on failures, whether electronic, mechanical, attachment or deployment related. Details and rationales for excluding data collected in the first hours or days after tagging (e.g. to reduce data bias from disturbance and/or a tagging locale effect), should be fully explained for consideration by others.

Research groups working on the same population should share information on the individuals that are tagged to facilitate follow-up, prevent unintended repeat tagging and to reduce cumulative impact on individuals and their population. Researchers should also share the identity of tagged animals, or photographs of tagged but unidentified individuals, with stranding coordinators and response groups to increase the likelihood that previously tagged animals can be recognised in advance of necropsy. In some cases, for example bottlenose dolphins and humpback whales, region-wide collaborative individual identification catalogues exist that could expedite notification to researchers about a sighted or stranded, previously tagged individual. This would facilitate the collection of additional data relevant to tagging effects, including examination of the tag attachment site. See Appendix A for recommendations regarding the necropsy and dissection of the tag implant site for a previously tagged cetacean.

A 'tagging database' that includes information on individual animals, health assessments, tag data and photo-identification would greatly improve the ability to quantify potential tagging effects; such a database would also help in determining whether new tagging studies should be contemplated or if sufficient data already exist to answer a particular question. With the broader acceptance of the need to make government-funded data publicly available, more data repositories are becoming available. However, many of these repositories do not have the capability to host the essential data and photographs that should be included in a comprehensive cetacean tagging database, so until the cetacean tagging community or an academic society establishes an appropriate repository site, individual researchers could host the information on their own websites and make its existence known to interested parties. Wherever possible, this information should be provided in a machine-searchable form using standard data formats. An example of the data fields that could be included in such a form is provided in Table 3. If real-time posting of movement data is contemplated, researchers should consider the potential for unintended use of telemetry data (Hammerschlag *et al.*, 2014), but in most cases the ability to follow animals in real-time will engage the public and outweigh disadvantages. As with most decisions regarding tagging of cetaceans, the pros and cons must be weighed, but with use of best practices, researchers should be able to ensure that benefits dominate.

Table 3

Examples of some of the data fields that should be collected by tag users. Most fields could also be included in a standard data form for sharing with other researchers.

FIELD	FIELD DESCRIPTION
Device information	
Tag (device) type	Type of device used (e.g., archival tags, satellite tags, satellite archival tags, acoustic tags).
Tag (device) manufacturer	Name of the manufacturer or, in the case of instruments from multiple manufacturers, list all manufacturers.
Tag model name/number	The name or number of the tag model.
Tag serial number	The unique serial number of the device.
PTT ID number	The Argos ID number of the Platform Transmitting Terminal (PTT) (if applicable, i.e., for tags equipped with Argos transmitters).
Transmitter frequency	The frequency in Hz of any transmitter not on the standard Argos frequency (e.g., a VHF beacon or ultrasonic transmitter).
Anchor type	A description of the anchoring system used to attach the tag to the animal (if applicable).
Anchor manufacturer	If the anchor manufacturer is different from the tag manufacturer, provide the name here.
Tag firmware	Version number of the firmware encoded in the tag.

Table 3 (continued)

FIELD	FIELD DESCRIPTION
Deployment device	
Deployment device	Description of the device used for deployment (e.g., pole, crossbow, pneumatic rifle) and manufacturer.
Type of applicator	Description of the applicator or tag carrier used with the deployment device (e.g., 30 cm "rocket" or carrier, 45 cm crossbow bolt, 81 cm arrow for air rifle, etc.) and manufacturer/vendor, if applicable.
Deployment force parameters	For pneumatic deployment devices, the pressure used to deploy the tag (in psi, bars, or Pascals) and the diameter of the barrel. For crossbows, the draw strength and the power stroke length.
Deployment information	
Field number	Number assigned in the field for the tag deployment (e.g., a unique deployment or animal identification code).
Deployment date/time	Date and time the instrument was deployed.
Deployment location	Locality, State/Province, Country or water mass (such as the Large Marine Ecosystem) where the deployment occurred.
Deployment coordinates	Latitude and longitude of the deployment.
Height of the tagging platform	For tags that are remotely deployed, specify the height of the platform where the tagger was located relative to the surface of the water for each deployment.
Horizontal distance to the whale	Estimated horizontal distance between the tagger and the animal upon tag deployment. Include a description of the method used to estimate horizontal distance (e.g. visual approximation, laser range finder).
Tag Placement, Animal Reaction and Follow-up	
Tag placement	The location on the body where the tag was placed (e.g., left or right side, dorsum or flank, on the dorsal fin). Whenever possible provide horizontal and vertical references, for example, 1 m ahead (cranial) of the dorsal fin and 50 cm circumferentially from the dorsal midline of the body. Specify whether full tag penetration was achieved and, if possible, provide information on the penetration angle relative to the plane of the local skin surface.
Reaction to tagging	Description or numerical classification (e.g., Weinrich *et al.*, 1991) of the behavioral reaction (if any) to the tagging process (e.g., boat approach, tag deployment) that was observed. If possible, separately record responses to the approach (e.g., evasive behavior, changes in displacement speed or direction) and to the deployment of the tag (e.g., tails flicks, startle).
Behavior post tagging	The behavior of the tagged individual shortly after tag deployment (if observed).
Reapproach	Specify whether the animal was reapproached after tagging on the same day.
Time lapse for reapproach	The time lapse between tagging and reapproach.
Closest distance on reapproach	The closest distance to the tagged animal on reapproach.
Reaction to reapproach	Description of the behavioral reaction to the reapproach.
Animal information	
Species	Species of the cetacean that was tagged.
Sex	The sex of the tagged individual, and how it was determined (e.g., morphological features, molecular methods from a biopsy sample).
Size	Approximate size of the tagged individual.
Age or age class	The age (in years) or maturity/age class (juvenile, sub-adult) of the tagged animal and how this was determined.
Animal ID	If a catalogued individual is recognized in the field, or later from photographs, note the catalog ID number.
Group composition	The group composition (e.g., mother-calf pair, competitive group), if the animal was tagged while in a group.
Role in the group	The role of the animal in the group (e.g., a mother in a mother-calf pair, an escort in a competitive group).
Other documentation	
Biopsy sample	If a biopsy sample was collected from the tagged animal, specify the biopsy sample identification number and how preserved.
Photographs	Indicate whether photographs were obtained for photo-identification and of the deployment and the tag placement at the time of tagging, immediately after deployment and during follow-up. Specify photo frames and file names.
Video	Indicate whether video images were made of the deployment, the tag placement and during follow-up. Specify video file names.
Tagging Platform Information	
Vessel name	Name of the vessel used for deployment of the tag, if applicable.
Vessel crew	Names of the boat crew, including their roles (e.g., driver, tagger, photographer).
Position of tagger within vessel	Specify where the tag was deployed from (e.g. bow of the boat, a tagging platform such as a bow pulpit, other).
Environmental Conditions	
Weather	Weather conditions (e.g., rain, fog) at the time of deployment.
Visibility	The distance at which an object ($\geq$ human size) can be visibly identified against the background (e.g., Very poor (< 1 km), Poor (1 – 4 km), Moderate (4 – 9 km), Good (> 9 km)
Sea state (Beaufort)	Sea state condition based on the modern Beaufort wind force scale.
Other Observations	
Notes	Additional information deemed relevant regarding tag deployment.

2.8.1 Recommendations for reporting and data sharing

- All tagging reports/publications should include:
  - details on tag manufacturer, size, shape, materials and configuration, especially of implanted sections (including the maximum implant depth);
  - photographs of the tags from multiple angles;
  - information on deployment method, including devices used (note power of projectile devices, or velocity);
  - information on tag performance, including at least mean/median and range of attachment duration; include numbers of tags that failed and when and how they failed;
  - information on whether a follow-up study was conducted and, if so, provision of numbers of re-sights and details of any unexpected issues that occurred, including photographs; and
  - information on data exclusion and inclusion criteria.
- Researchers should deposit metadata describing tag data holdings and any information from which to assess effects (e.g. including key photographs for individual ID and of tag and tag site) into publicly accessible data portals.

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APPENDIX A

RECOMMENDATIONS FOR NECROPSY AND DISSECTION OF THE TAG IMPLANT SITE FOR A PREVIOUSLY TAGGED CETACEAN

This protocol will help taggers, stranding responders and necropsy teams investigate the effects of tagging and integrate *ante mortem* history of the stranded individual with postmortem findings. Information obtained from using this protocol will also be valuable to all others involved with cetacean tagging, including researchers, veterinarians and marine mammal managers, especially as we strive to understand implant-tissue interactions and healing processes, and to improve tag design and deployment methodology. The authors of these guidelines may be contacted for additional advice, collaborative proposals and recommendations of other resources. For those unfamiliar with some of the methods recommended below, we strongly recommend working with stranding coordinators, other marine mammal research scientists with tagging expertise and regional veterinary diagnostic pathologists, prior to dissection of a tag implant site. If local resources are not available to accomplish the post-necropsy examinations of the implant site tissue block as detailed in steps 11–15 below, shipment of an entire tissue block to a marine mammal pathologist is recommended; please contact the authors of these guidelines to discuss collaborative opportunities.

When a previously-tagged cetacean is confirmed dead or a tag is observed on initial examination of a stranded animal and a postmortem examination is scheduled, the principal investigator (PI) or other representative of the study that deployed the tag should provide stranding and necropsy responders with annotated photographs of the animal, highlighting the anatomic site of attachment. They should also provide images and specifications of the model of tag deployed, especially the shape and dimensions of the implanted parts. The tagging project PI should collaborate closely with responders and provide shipping supplies (containers and labels) and courier account numbers to facilitate shipping of tissues to diagnostic laboratories or marine mammal pathologists. Responders should review the photographs to confirm the tag implant site, if possible, prior to commencing the necropsy (although this may not be logistically feasible in some situations). In addition to following conventional necropsy protocols, include a scale marker with the Field ID# and date in each photograph, and avoid obscuring the areas of interest in the field of view. Document gross findings in a necropsy report and include photos and sketches. If the tag implant site is partly or completely healed, then steps 5–15 may not all be necessary or possible. However, whenever the tag implant site can be identified, we recommend that all steps be followed, even for carcasses that are not fresh.

(1) Photo-document the animal and the tag site. Photograph the tag site from three different perspectives: (a) wide angle images of the carcass to place the tag location in anatomic context; (b) intermediate scale images to illustrate adjoining tissues and potential changes; and (c) external macroscopic images of the implant site to detail host response. Rulers or other objects that may lend scale to each image are imperative.

- These photographs will be used to help assess overall impact of the tag and to make more precise measurements of the exact tag placement than could be made from photographs of the live animal and will be invaluable to the taggers and others.

(2) Compile as complete a set of morphometric data as possible from the animal.

- See, for example, Chapter 10 in Geraci and Lounsbury (2005) and Appendix F in Pugliares *et al.* (2007).

(3) Collect a 1.0 × 0.5cm × full depth skin sample including the dermis, away from the implant site and freeze it in a sterile container for genetic analysis.

(4) If possible, measure the straight-line and curvilinear distance between the tag implant site and the tip of the rostrum.

(5) Swab the implant wound aperture. If no parts of the tag are visible, and if the implant site is open (patent), or in the early stages of resolution, five sterile (*Teflon* or cotton tip) swabs should be obtained prior to excision of the implant site tissue block. Collect two of these swabs from the external aperture and three swabs from deeper in along the penetration tract. The swabs should be collected as gently as possible to avoid tissue damage. Place one of the external swabs and two of the deeper swabs in transport media for routine microbiology (bacteriology and fungal culture). If the microbiology samples will be submitted to a diagnostic lab within 24–48 hours, they may be chilled and shipped on ice; otherwise they may be frozen, although this will reduce the viability of the bacteria. One external and one deeper swab for microbiome studies should be placed in sterile containers and either chilled for immediate transport or frozen (preferably in liquid nitrogen) for later submission to a laboratory. If RNAlater or other tissue stabilisation or culture media are available, these may be suitable alternatives and the swabs should be maintained chilled. If swabs are not available in the field, tissue and swabs may be collected later at the lab from the excised implant site tissue block (step 6).

(6) Excise the implant site and surrounding tissue, to include unaltered tissue at the edges of the block, for diagnostic imaging and subsequent lab analyses (steps 11–15). If no parts of the tag are externally evident, outline a 20 × 20cm square around the original implant site and excise the skin and blubber around the site down to and including underlying muscle. If the tag (or parts of the tag) are present, they should be retained *in situ* within the surrounding soft tissues excised as a block; include at least 10 cm of tissue beyond all margins of the implant. Depending upon the body curvature or potential swelling at the tag site, additional tissue may need to be incorporated into the excised sample to ensure all altered tissue is within the block. Photograph the cut surfaces and examine them for any discoloration or other abnormality.

(7) After excising the implant site tissue block, if abnormal tissues are observed beneath or in the vicinity of the implant site, collect specimen swabs or tissue samples (using a sterile blade) from those areas for subsequent laboratory analyses. Samples of regional or local lymph nodes and any associated gross lesions in the underlying or adjoining soft tissues may be collected and chilled or frozen for microbiology, with subsamples preserved in formalin for microscopic evaluation. Document gross lesions with photographs and include a scale marker with field number.

(8) If feasible, retain the excised block on ice, and arrange for subsequent examinations within 48 hours (steps 11–15).

(9) If conditions during necropsy do not permit the full execution of steps 5–8, collection of a single sample, measuring at least 2 × 2cm on the surface, cut down to the full thickness of skin and blubber, including a margin of the implant site, would be valuable. If the tissue sample can be submitted to a diagnostic lab within 24-48 hours after collection, the sample may be secured in a sterile plastic bag, chilled on wet ice or gel ice packs and submitted for evaluation; on receipt, the tissues may be subsampled for molecular studies and microbiology as well as representative subsamples preserved in formalin. If the carcass is condition code 2 or 3 and only a single portion of tissue is available, this sample may be subdivided (dissected in half) on site, with a portion chilled (if laboratory analysis is likely with 48h, otherwise frozen) and retained for microbiology and molecular studies and a formalin fixed sample for histopathology. If late code 3 or 4, the tissue may be preserved in formalin for diagnostic evaluation.

(10) The necropsy of the whole animal should be completed by conventional protocols and systemic pathology recorded with appropriate tissue samples archived for additional studies.

(11) Back at the lab, and before further sectioning of the excised tag implant site tissue block, obtain precise measurements, photographs, radiographs (x-rays), CT and, if possible, MR scans, to document the degree of tissue penetration by the tag, possible implant structural failures (if any parts were retained), and any associated inflammatory exudate or tissue necrosis.

(12) Serial slices (every 5–10mm; bread-loafing) through the tissue block should be made parallel to the long axis of the tag implant tract, examining each cut surface for any abnormalities or retained tag elements. These slices should be placed on a cutting board in sequence for photography (with scale) and further analyses. Preservation of multiple representative samples in 10% formalin and separately at –80°C (no formalin) is required for additional histopathologic and microbiologic analysis. If a significant portion or an entire Type C tag or anchor from a Type A tag (e.g., a LIMPET dart), or rod, pin or bolt from a Type B tag remained implanted, instead of starting serial slices from one margin of the tissue block, start by cutting

along opposing margins of the percutaneous tag body or dart from the surface of the skin down to the bottom of the tissue block, separating the tissue block in two. The approach should expose the tag tract from the skin through the blubber (and possibly muscle) and facilitate removal of half of the excised tissue block, gently separating tissue from implant protrusions, such as retention petals. The two halves can then be sectioned serially as above.

(13) Swab the penetration site and any parts of the tag or implanted pieces that are encountered during serial sectioning of the tissue block with bacteriology and dry swabs, and place swabs and tag parts in separate sterile containers for microbiology, microbiome studies and potential mechanical or metallurgic analyses.

(14) Label each tissue slice with a laundry tag or other identifier, then fix abnormal tissue and surrounding normal tissue. Ensure that the laundry tag clip is placed as far away from the site of interest, so that it does not damage visibly abnormal tissues.

(15) Have an experienced veterinary pathologist examine the sections and if the tissues are sufficiently well preserved, follow-up transmission electron microscopy may be considered.

(16) Ensure a full report is collated with gross, histological and ancillary (imaging, microbiology) diagnostic findings.

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APPENDIX B

SUPPLEMENTARY BIBLIOGRAPHY

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Seasonal and interannual variations in the distributions of tuna-associated dolphins in the eastern tropical Pacific Ocean

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ABSTRACT

Seasonal and interannual (El Niño–La Niña) variations in dolphin distributions in the eastern tropical Pacific Ocean have not been quantified, in spite of an extensive research vessel database. Fisheries observer data from the yellowfin tuna purse-seine fishery, collected year-round from 1986 through 2015, were used to construct a binned spatiotemporal dataset of the presence/absence of spotted, spinner and common dolphin schools by month and 1° area. Distribution patterns were predicted from generalised additive logistic regression models applied to the binned data, with dynamic predictors of surface temperature and salinity, thermocline depth and a stratification index. The dolphin taxa, especially common dolphins, show some niche separation in relation to these variables. Predicted distributions for each taxon showed seasonal and interannual differences. Spotted and spinner dolphins responded to changes in the position and size of the eastern Pacific warm pool and avoided the equatorial cold tongue in September–October and during La Niña. Common dolphins responded to seasonal and interannual changes in the Costa Rica Dome, the cold tongue, and the coastal upwelling habitat along Baja California, Peru and Ecuador. These predicted temporal variations are consistent with changes in preferred habitat driven by environmental variability.

KEYWORDS: DISTRIBUTION; EL NIÑO; MODELLING; OCEANOGRAPHY; PACIFIC OCEAN

INTRODUCTION

Species distribution patterns and changes in these patterns over time are integral to studies of habitat use, population dynamics, and ecological and evolutionary relationships. Species distribution models relate spatial patterns of species to environmental variables that vary in space and perhaps time. Such models are fundamental to understanding habitat utilisation in both geographical and ecological (niche) space. More practically, they are also useful to objectively fill gaps in survey data, although extrapolation beyond the spatial or temporal extent of the observations is challenging (Redfern *et al.*, 2017).

The eastern tropical Pacific Ocean (ETP) is a significant part of the global tropical ocean and includes several water masses and habitat types (Fig. 1) that can influence the distribution of species (Ballance *et al.*, 2006; Fiedler and Talley, 2006). Among the 10 or more species of dolphins that reside in the ETP, three species have been the focus of much research and management concern because of their involvement with the yellowfin tuna (*Thunnus albacares*) purse-seine fishery (Hall, 1998; National Research Council, 1992): the spotted dolphin; the spinner dolphin; and the common dolphin. The association between tuna and dolphins in the region is thought to be related to unusual habitat conditions (Scott *et al.*, 2012).

The eastern Pacific warm pool, characterised by warm surface temperature and high stratification, is part of the warm, low-salinity tropical surface water (TSW) mass. Surface salinity is lowest in the Gulf of Panama. This water mass is highly stratified, with a shallow mixed layer depth, which results in a shallow oxygen minimum layer (Fiedler and Talley, 2006). The warm pool is the centre of the ETP tuna purse-seine fishery (IATTC, 2018) that targets yellowfin tuna associated with dolphins. South of the warm pool, the equatorial cold tongue is cool, moderate-salinity water overlying an equatorial thermocline ridge resulting from equatorial upwelling. The equatorial front is the northern boundary of the equatorial cold tongue. The countercurrent thermocline ridge lies along 10°N, associated with the eastward North Equatorial Countercurrent on the south side and the westward North Equatorial Current on the north side. The Costa Rica Dome is the eastern end of this thermocline ridge and is a site of oceanic upwelling and enhanced productivity (Fiedler, 2002).

Cold, low-salinity eastern boundary currents, the California and Peru Currents, flow into the ETP along the coasts of North and South America. These currents are the eastern, equatorward segments of the North and South Pacific subtropical gyres. The subtropical gyres encompass warm, high-salinity subtropical surface water masses. Productivity is enhanced seasonally in the regions of coastal and oceanic upwelling: the eastern boundary currents, the equatorial cold tongue and the Costa Rica Dome.

The spatial patterns illustrated as climatologies in Fig. 1 are dynamic both within and between years. Seasonal and ENSO (El Niño-Southern Oscillation)-related variability in ETP oceanography are reviewed in Fiedler and Talley (2006) and Wang and Fiedler (2006). Interannual variability due to ENSO and seasonal variability are known to be of comparable magnitude in the ETP (Fiedler *et al.*, 2013). The intertropical convergence zone (ITCZ) reaches its northern extreme in September (Hastenrath, 2002) and southeast trade winds blow across the equator. Equatorial upwelling is high and the cold tongue is pronounced. To the north of the cold tongue, seasonal temperature changes are slight, but warming and cooling do occur to the north and south of a

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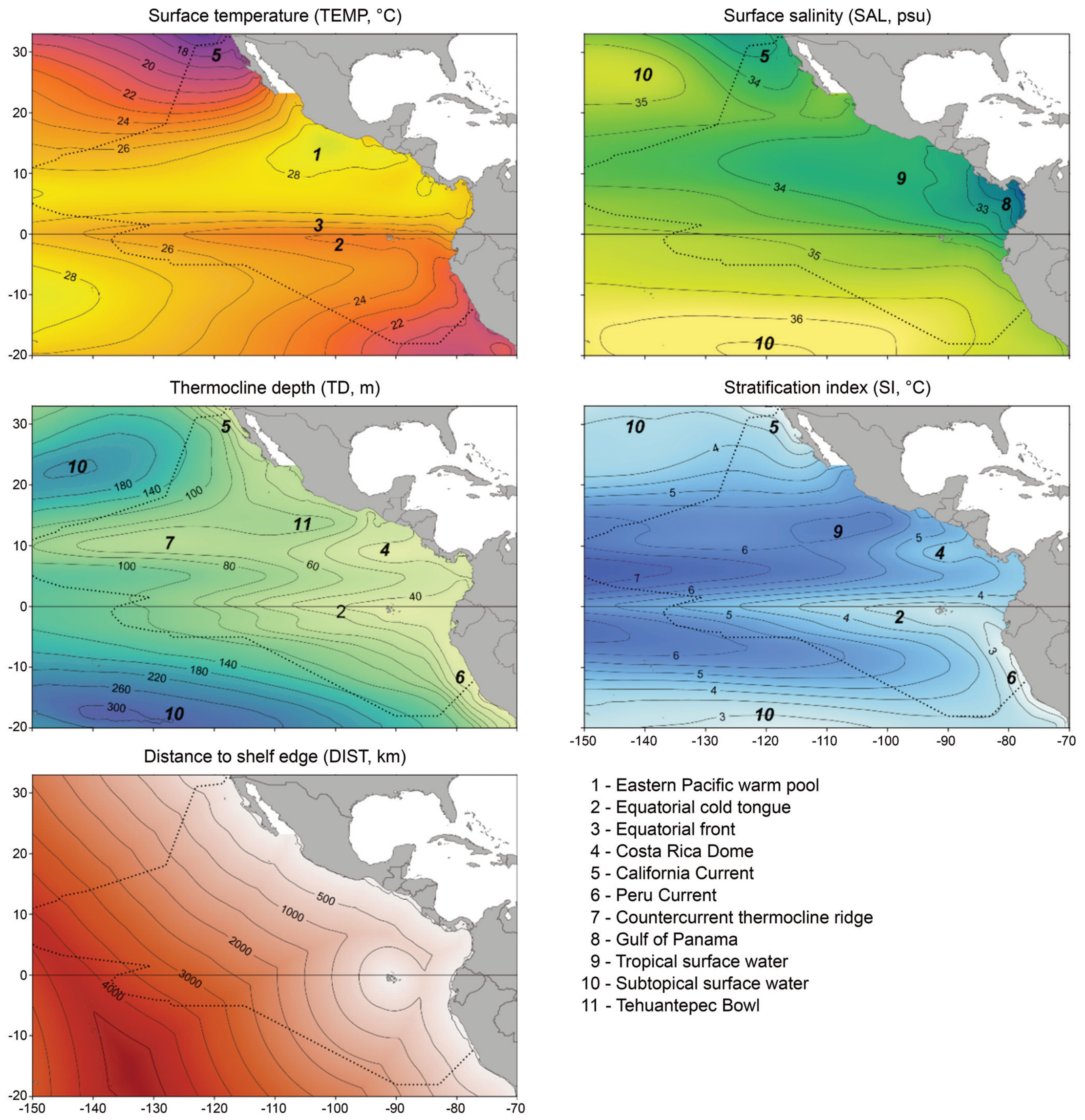


Fig. 1. Climatologies of oceanographic predictor variables (1980–2015) and important environmental features in the eastern tropical Pacific. Dotted line marks the extent of Southwest Fisheries Science Center (SWFSC) research vessel surveys.

thermal equator at ~10°N. Salinity of tropical waters north of the equator is lower in October–November due to seasonal rains associated with the ITCZ. Seasonal winds force local changes in surface temperature, circulation and upwelling along the equator, the Central American coast and at the Costa Rica Dome.

ENSO changes are only partially analogous to seasonal changes. ENSO changes in winds and in surface and subsurface temperature are most pronounced along the equator, but similar changes occur in tropical waters north of the equator (Wang and Fiedler, 2006). During warm El Niño events, surface waters are warmer and the thermocline is deeper throughout the region, more so along the equator than to the north. Trade winds are weak, so that wind-driven upwelling and nutrient input for phytoplankton production are decreased. During La Niña, the cold phase of ENSO, the changes in the ETP go the opposite way, but with a somewhat lesser magnitude (An and Jin, 2004).

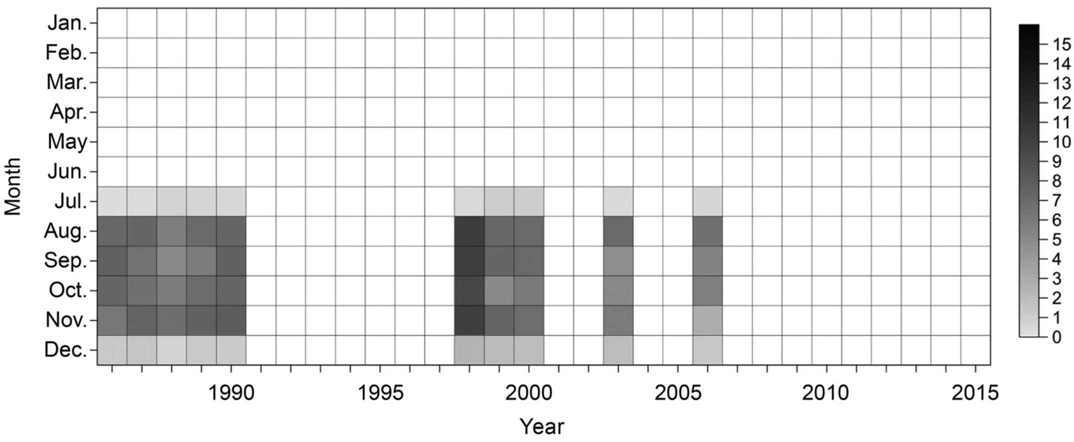
Comparison of the species distributions estimated from research vessel surveys (Gerrodette *et al.*, 2008) for the dominant dolphin species in the ETP in warm and cold years suggests that species/stock ranges may expand or contract in response to environmental changes (Fiedler and Reilly, 1994; Ballance *et al.*, 2006). Pantropical spotted dolphins are globally distributed in tropical and some subtropical waters, from 30-40°N to 20-40°S. Offshore pantropical spotted dolphins (*Stenella attenuata attenuata*, Gray 1846) are the most abundant species in the ETP (Gerrodette and Forcada, 2005). Spinner dolphins (*S. longirostris*, Gray 1828), in common with spotted dolphins, are circumtropical but show a different pattern of sub-specific differentiation in the eastern Pacific than spotted dolphins do (Leslie and Morin, 2018). There are several distinct sub-species of spinner dolphin, with the most abundant being the eastern spinner dolphin (*S. l. orientalis*, Perrin 1990). A third ETP spinner stock, referred to as 'whitebelly' spinners, is thought to be a hybrid of the eastern spinner and Gray's spinner (*S. l. longirostris*, Perrin 2010; Perrin, 2018b). Whitebelly spinners are found in the region to the west and south of eastern spinner dolphins in the ETP. Two forms of common dolphins occur within the ETP: short-beaked common dolphins (*Delphinus delphis delphis* Linnaeus 1758) are the offshore warm-temperate form found throughout the ETP and globally, while the long-beaked form (*D. d. capensis*, formerly *D. capensis*; Committee on Taxonomy, 2017) are found in cooler nearshore waters to the north and south of the yellowfin tuna fishery (Hamilton *et al.*, 2009).

Although the ETP has some of the most extensive cetacean line-transect survey coverage in the world (Kaschner *et al.*, 2012), there are gaps in temporal coverage (Fig. 2), which results in an incomplete picture of inter-annual and inter-seasonal changes in dolphin species distributions. For example, the only recent ENSO warm/cold event adequately covered by research vessel surveys was 1986-88; the first year of the major 1997-99 event was missed. In addition, all research vessel surveys that completely cover the ETP have been in August–November (Gerrodette *et al.*, 2008), and therefore these data cannot resolve seasonality of distributions.

An alternative source of data for dolphins in the ETP are the marine mammal sightings data collected by fisheries' observers onboard tuna vessels searching for and setting on tuna associated with dolphins (Bayliff, 2001; Wahlen, 1986). For decades, purse-seiners fishing for yellowfin tuna set nets on dolphins, primarily pantropical spotted dolphin, eastern spinner dolphin and common dolphin, to catch the associated tuna (National Research Council, 1992). Observers have been placed aboard large purse-seiners to monitor dolphin bycatch (Bayliff, 2001; National Research Council, 1992) and, more recently, to collect catch and bycatch data for many more species involved in the purse-seine fishery (Joseph, 1994). The tuna vessel observer data (TVOD) spatial coverage within the ETP is similar to that of the research vessel data, while the temporal coverage is much more extensive (Fig. 2). However, as fishery-dependent data, the TVOD have a variety of known biases (Buckland and Anganuzzi, 1988; Lennert-Cody *et al.*, 2001; 2016; Ward, 2005) that must be taken into consideration.

The objectives of this paper were to extend understanding of dolphin distributions in the ETP by describing seasonal and interannual variation in dolphin habitat use and to demonstrate that useful inferences about dolphin populations

(A) SWFSC effort, 10^3 km



(B) TVOD effort, 10^3 km

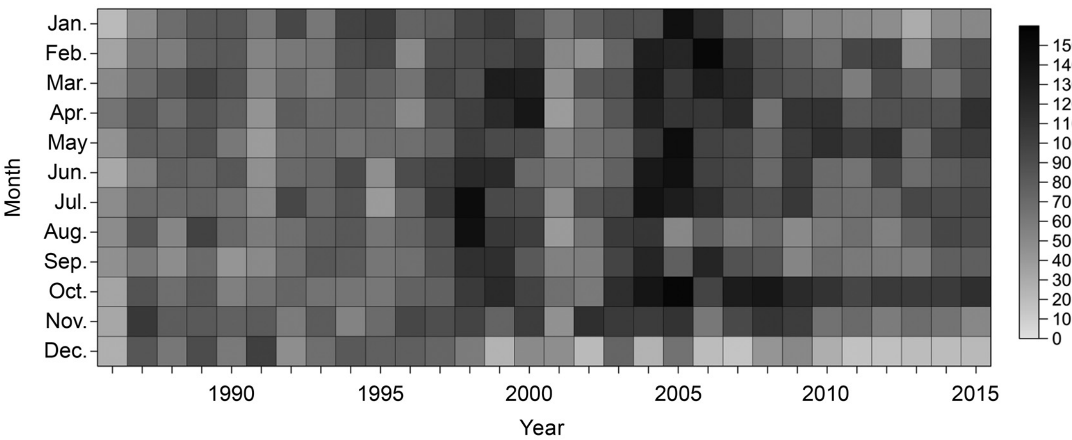


Fig. 2. Total search effort for ETP dolphins by month and year: (A) SWFSC research vessel surveys; and (B) tuna vessel observers. Search effort is km of search, or tuna vessel trackline, while observers were on duty.

can be derived from fishery observer data. TVOD, post-processed to minimise the effects of known biases on the analyses, were used to explore questions that cannot be addressed using research vessel data, yielding original insights into seasonal and interannual movement patterns of tuna-associated dolphins. Species distribution models of presence-absence (the probability of one or more dolphin schools) were built for three taxa: spotted dolphin, spinner dolphin and common dolphin. Model projections are presented for the climatological spatial distributions and for differences between the seasonal extremes of March–April and September–October and between El Niño and La Niña years. These differences are interpreted as responses to seasonal and interannual changes in dolphin habitat, extending our knowledge of variability in the distributions of these rare top predators. Finally, the ecological significance of the modelled distributions and implied responses to seasonal and interannual variations in the environment are discussed.

MATERIALS AND METHODS

Tuna vessel observer data

TVOD were collected by Inter-American Tropical Tuna Commission (IATTC) observers aboard vessels of the international fleet and by National Marine Fisheries Service (NMFS) observers aboard US-flagged vessels. These data were processed and binned into 1° monthly 'cells' for each of the years from 1986 through 2015. Prior to 1986, the sampling did not adequately represent all vessels participating in the fishery (Joseph, 1994). Spatial coverage of the 1986–2015 TVOD search effort is shown in Fig. 3. As has been observed previously (cf. Hall *et al.*, 1999), fishing effort tends to increase south of the equator in the austral summer and extend much farther to the west, north of the equator in the boreal summer. Temporal variability of total search effort is illustrated in Fig. 2. TVOD dolphin sightings are collected when purse-seiners fishing on dolphin-associated tuna are actively searching. Thus, changes in coverage may be influenced by tuna availability and weather.

The unbinned data included information on vessel activity (e.g. searching, running, setting), positions, dates and times of various vessel activities, observer status (on/off duty) and dolphin school sighting information (species, school size) for each day during a vessel's trip. Data processing was designed to minimise known biases in the TVOD, which include non-random distribution of search effort and a tendency for dolphin sightings to be of schools associated with tuna (Buckland and Anganuzzi, 1988; Lennert-Cody *et al.*, 2001; 2016), and a positive correlation between dolphin school size and tuna catch (Hall *et al.*, 1999).

Search effort per 1° monthly cell was computed and used to exclude cells where effort was too low to have been likely to represent adequate search for dolphin schools. Very low effort per cell could have occurred because vessels were simply transiting the area, and search during transit appears to have different characteristics to non-transit search (Lennert-Cody *et al.*, 2016). Search effort by cell was computed as follows. Trip-days that did not have at least two valid positions and any days that had no period of on-duty searching (i.e. observer on-duty and vessel in search mode) were dropped. Then, during a trip-day, a 'search segment' was defined as any pair of records that corresponded to a period of on-duty searching. For every search segment that did not have known start and/or end positions, the positions were estimated from known position information as close in time as possible to the segments without position information. The distance spent searching (in km) was then computed from each segment and summed over segments (or fractions thereof) within each cell. Only those cells with at least 50km of search effort were retained for further analysis, assuming that this level of effort would have been adequate to detect dolphin schools if present; this excludes 38.7% of cells (mean search effort = 164.7km, median = 99.4km).

Dolphin sightings were summarised by cell for those cells with more than 50km of search effort. Spotted and spinner dolphins associated with tuna in the ETP can form pure- or mixed-species schools (Hall *et al.*, 1999). In this analysis, sightings assigned to each species included both pure- and mixed-species schools. The majority of sightings recorded by observers were initially detected by the vessel crew although observers were instructed to make their own estimates of species composition and school size whenever possible. Because observers did not have access to high-powered searching equipment (and were not allowed to interfere with the searching process of the vessel crew), any sightings made only by the observer, without being referred by the crew, were deemed to be of questionable quality and therefore were also excluded from the analysis.

For sightings referred by the crew, observers made initial estimates of dolphin school size and species composition if they were able to adequately view the school. The observer made a final ('best') estimate of school size and species composition if the dolphins were later involved in a purse-seine set. When available, observers' best estimates of school composition were used, otherwise their initial estimates were used (Table 1). For spotted dolphins, the estimates of species composition by the vessel crew were used if no observer estimates were available. Vessel crew sightings of spinner dolphins were not used because they were not recorded to stock. In addition, no vessel crew sighting data were used for common dolphins because the vessel crew did not distinguish between common dolphins and whitebelly spinner dolphins (the crew record both species as 'whitebelly' dolphin). To minimise potential bias in the reporting of dolphin schools that were associated with tuna (Lennert-Cody *et al.*, 2016) and the positive correlation of school size with tuna catch (Hall *et al.*, 1999), neither the number of dolphin schools nor estimates of school size were used. The number of sightings per cell was converted into presence (one or more schools sighted) or absence (no schools sighted), independent of school size.

Predictor variables

Oceanographic predictor variables were extracted from composites of six ocean reanalysis datasets (Fiedler *et al.*, 2017): ECDA v3.1[3]; ESTOC v02c[4]; GECCO2 v34_55[5];

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[3] *www.gfdl.noaa.gov/ocean-data-assimilation/*

[4] *www.godac.jamstec.go.jp/estoc/*

[5] *icdc.zmaw.de/1/daten/reanalysis-ocean/gecco2*

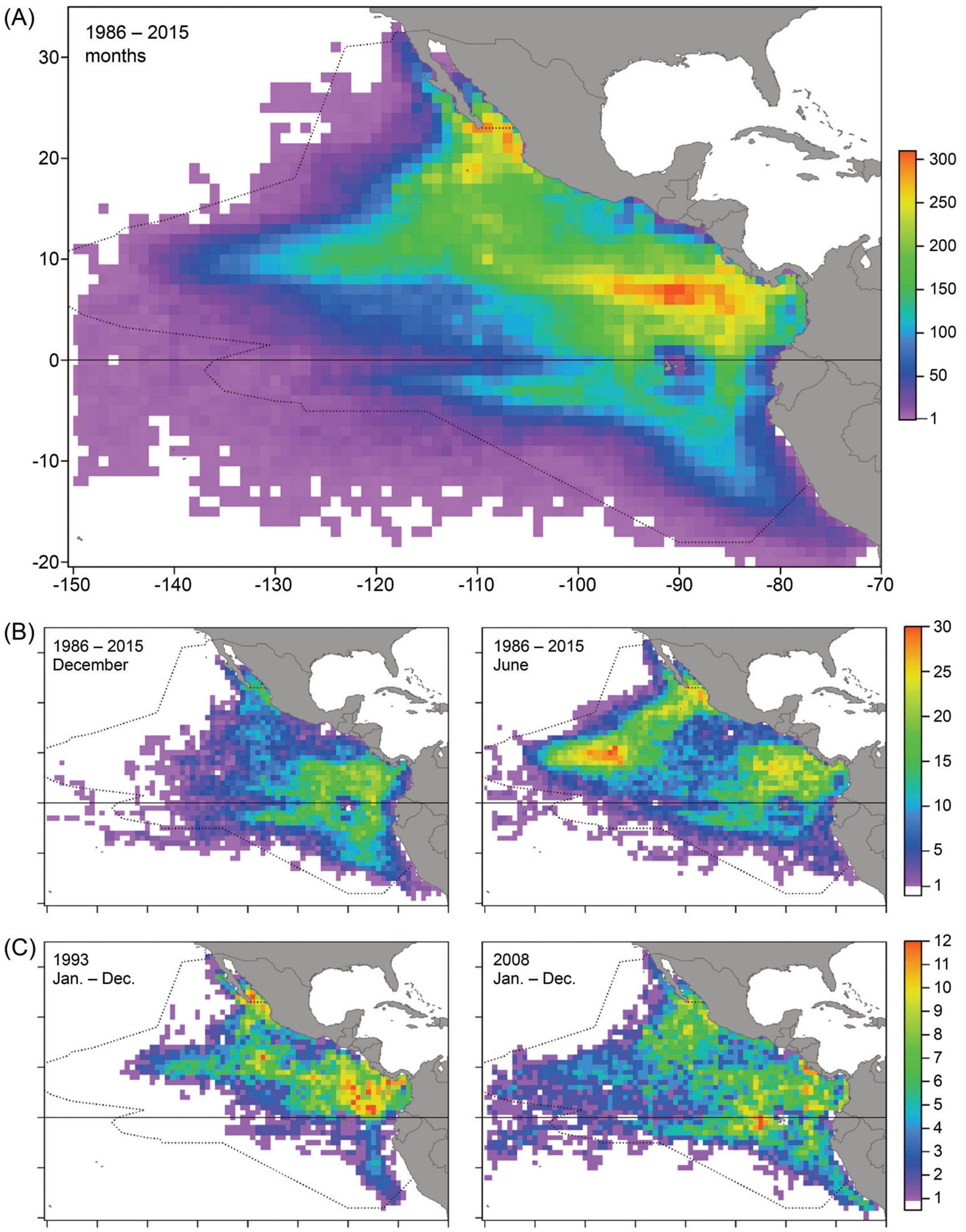

Fig. 3. (A) Coverage of tuna vessel observer data (TVOD) dolphin sightings, total number of months during 1986–2015 (scale is months, 360 total). (B) Yearly coverage of TVOD dolphin sightings data for the months of December and June, number of years during 1986–2015 for each month (scale is years, 30 total). (C) Monthly coverage of TVOD dolphin sightings data for two years, 1993 and 2008, illustrating extremes of yearly coverage. Dotted lines indicate the study area for SWFSC research vessel surveys (August–November in 1986–1990, 1998–2000, 2003, and 2006).

Table 1

TVOD dolphin sighting identifications, 1986–2015, proportions in pure and mixed schools and by quality of the identification: best (final, post-set) or initial estimate by the observer, or estimate by crew only. *N* is the total number of sightings in the monthly 1° cells.

		Spotted	Eastern spinner	Common
Observer best estimate	Pure	0.36	0.10	0.44
	Mixed	0.32	0.64	0.01
Observer initial estimate	Pure	0.15	0.07	0.54
	Mixed	0.08	0.18	0.01
Crew-only estimate	Pure	0.06		
	Mixed	0.02		
N =		173,556	53,266	18,357

GODAS[6]; ORAS4[7]; and SODA 3.3.1[8]. Each of the monthly reanalysis data fields (temperature and salinity) were linearly interpolated onto 0.25-deg longitude-latitude grids and at depths of 0, 5, 10, 20, 30,…500m (MATLAB interp3). The six interpolations were then averaged to produce a composite to minimise biases and uncertainties in each of the six reanalyses, which use different inputs and methodologies (Balmaseda *et al.*, 2015). Variables derived from the reanalysis data (thermocline depth and stratification index) were derived from the composited temperature and salinity fields. The monthly composites were then averaged on 1° longitude-latitude grids for four oceanographic predictor variables: surface temperature (TEMP, °C); salinity (SAL, psu); thermocline depth (TD, m); and stratification index (SI, °C). The thermocline was defined as the depth interval that included the upper decile (10%) of 1m temperature gradients in a 0–300m depth profile of temperature; thermocline depth is the weighted mean of the depths of this set, with each depth weighted by the value of the 1m temperature gradient. Stratification index is the standard deviation of temperature in the near-surface layer, 0–300m (Fiedler, 2010). A static fifth predictor variable, distance to the edge of the continental shelf (DIST, km), was derived from the geomorphic features map (GSFM) of the global ocean (Harris *et al.*, 2014), excluding smaller islands.

Generalised additive models

A logistic regression model was used to model the probability of one or more dolphin schools (p) as a function of covariates using the R (v.3.4.0; R Development Core Team, 2017) generalised additive model (GAM) package 'mgcv' (v.1.8-4; Wood, 2011):

$$\begin{aligned}\mathrm{logit}(p) \sim \mathrm{te}(\mathrm{SAL},\mathrm{TEMP}) + \mathrm{s}(\mathrm{TD}) + \mathrm{s}(\mathrm{SI}) \\ + \mathrm{s}(\mathrm{DIST}) + \mathrm{s}(\mathrm{effort})\end{aligned} \tag{1}$$

where TEMP and SAL were modelled as a tensor product smooth surface (te) to differentiate surface water masses, and the other predictors were modelled as univariate smooth terms based on thin plate regression splines. Correlations among the environmental predictor variables in our study ranged from 0.03 to 0.73 in absolute value (Table 2), but mgcv is robust to strong functional relationships among predictor variables (termed 'concurvity'; Wood, 2008). The gamma parameter was set to 1.4 (Wood, 2006) and a maximum of two degrees of freedom was allowed for each spline to capture non-linear relationships but limit over-fitting. Search effort per cell (effort) was included as a covariate in the model to account for its possible effect on the probability of detecting presence.

A model was built for each species using all observed 1° year-month presence/absence cells for the 1986–2015 period, with corresponding environmental data. Predictions for seasonal and ENSO periods used estimated parameters from these models but applied to climatological variable fields for the respective period. Seasonal extremes are represented by the periods of March–April and September–October. An empirical orthogonal function analysis of the monthly climatologies of the four predictor variables showed a primary mode that explained 89% of the total variance and peaked in these months (not shown). These periods resolve important seasonal variations in the oceanography of the region (Fiedler and Talley, 2006). Two contrasting ENSO categories were based on mean NINO3.4 SSTa[9] from July through June of the following year:

El Niño (NINO3.4 > 0.5 °C): 1986, 1987, 1991, 1994, 1997, 2002, 2004, 2009, 2014, 2015

La Niña (NINO3.4 < –0.5 °C): 1988, 1995, 1998, 1999, 2000, 2007, 2010, 2011

Table 2

Correlations between environmental predictor variables for monthly, 1° binned TVOD presence/absence data (n = 126,460). Variables are surface temperature (TEMP), surface salinity (SAL), thermocline depth (TD), stratification index (SI) and distance to shelf edge (DIST).

	SAL	TD	SI	DIST
TEMP	–0.54	+0.03	+0.73	+0.10
SAL		+0.34	–0.18	+0.29
TD			+0.58	+0.56
SI				+0.46

Both these groups of years extend over the entire period of the 1986–2015 TVOD sightings data used to construct the model, which should help to reduce the influence of any temporal changes in data biases on the ENSO predictions. The effects of each of the predictor variables were assumed to be the same for each season or ENSO period, i.e. separate models were not built for each period, nor were interactions between season or ENSO periods (as factors) and the environmental variables included in the model. This means that the predicted model responses to season or ENSO period are directly determined by seasonal or ENSO-related changes in the predictor variables rather than by changes over time in the species-environment relationships.

The relative importance or contribution of predictor variables to a model prediction was estimated as in Thuiller *et al.* (2009). For a given model, each of the five variables were randomly permuted before being used in prediction. The correlation of the original prediction with the prediction using a permuted variable is related to the importance of the variable: permuting an unimportant variable will change the prediction only slightly and result in a high correlation, while permuting an important variable will result in more change in the prediction and a lower correlation. The scores of variable importance are equal to 1 minus the mean correlation for 20 random permutations of each variable, rescaled to sum to 1 across all predictor variables.

RESULTS

Distributions in space: effects of season and El Niño/La Niña

Spotted dolphin predicted probability of presence (Fig. 4) is highest in the eastern Pacific warm pool, although to the west of the warmest surface water off southern Mexico, Guatemala and Honduras (Fig. 1). Moderate levels of presence are predicted south of the equator, except in the cool Peru Current region off Peru and Ecuador. During

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[6] *www.cpc.ncep.noaa.gov/products/GODAS*

[7] *ecmwf.int/en/research/climate-reanalysis/ocean-reanalysis*

[8] *apdrc.soest.hawaii.edu/data/*

[9] *www.cpc.ncep.noaa.gov/data/indices/sstoi.indices*

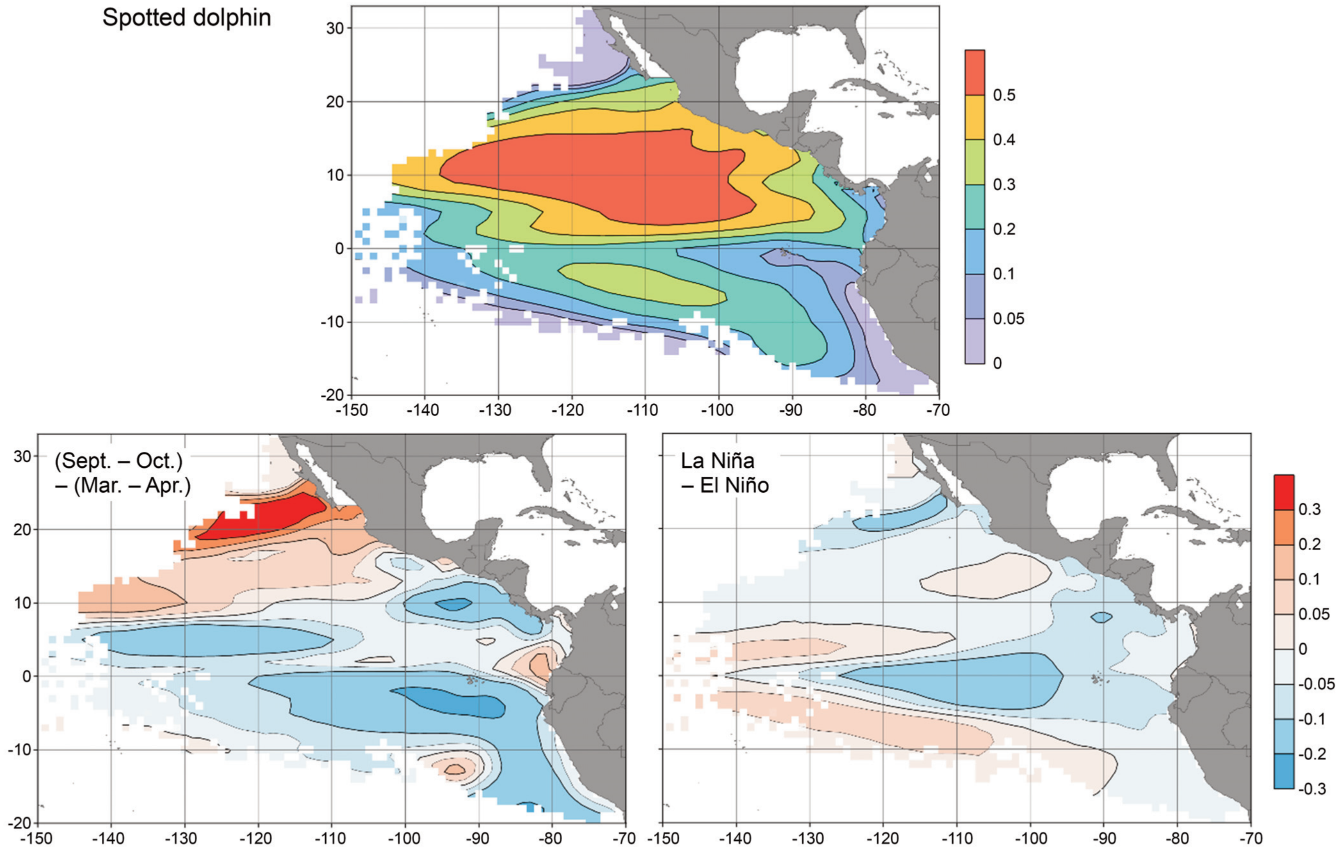

Fig. 4. Spotted dolphin probability of presence climatology (top), and differences between seasonal extremes and El Niño and La Niña years (bottom), predicted by GAM from TVOD, 1986–2015. Cells with <300km total TVOD effort are masked.

September–October and La Niña years, the normally low presence in the equatorial cold tongue declines (blue in the difference maps). From March–April to September–October, shifts are predicted from south to north across ~10°N, the thermal equator in the ETP (Fiedler and Talley, 2006) and away from Central American coastal waters, particularly the Costa Rica Dome. From El Niño to La Niña years, predicted presence shifts away from the equatorial cold tongue both to the north and south and also declines slightly in the region of the Costa Rica Dome and Gulf of Panama.

Spinner dolphin predicted probability of presence (Fig. 5) is restricted to the eastern Pacific warm pool between the equatorial front and the California Current off Baja California (Fig. 1). From March–April to September–October, presence shifts toward the northwest extreme of the warm pool, similar to the prediction for spotted dolphins. From El Niño to La Niña years, changes are relatively minor. However, the increased probability of presence off southern Mexico during La Niña suggests that suitable habitat contracts to the warmest waters of the warm pool during cool years.

Common dolphin predicted probability of presence (Fig. 6) is high along the coast of southern Baja California, in the region of the Costa Rica Dome, and in the Peru Current and equatorial cold tongue. From March–April to September–October, predicted presence increases in the region of the Costa Rica Dome and in the equatorial cold tongue, but decreases in the Gulf of Panama region; the predicted presence maximum along Baja California moves to the north. Predicted presence along the countercurrent thermocline ridge (~10°N) increases slightly during September–October, when research vessel surveys had sightings here (see Fig. 8). From El Niño to La Niña years, predicted presence increases in the equatorial cold tongue and decreases in the Gulf of Panama, but there is no clear response to changes in the region of the Costa Rica Dome. The ENSO phase changes along southern Baja California are also not consistent with the seasonal changes.

Table 3 summarises the performance of the GAMs. AUC (area under the receiver operating characteristic curve) is an integral measure of the ability of the model to distinguish observed presences and absences, and COR (point biserial correlation) measures model goodness-of-fit to observations (Elith *et al.*, 2006). The models explained a fair proportion of variance in the data and successfully predicted presence of dolphins. Correspondence between model-predicted presence and observed dolphin sightings in a research vessel database are examined below.

Distributions in niche space

Plots of available and utilised habitat (Fig. 7) illustrate the distributions of dolphins in ecological or niche space

Table 3

Performance of the GAM models in predicting the observed presence of three dolphin taxa: deviance explained, AUC and COR.

	Deviance explained	AUC	COR
Spotted	21.4%	0.85	0.64
Spinner	23.6%	0.95	0.78
Common	23.2%	0.82	0.43

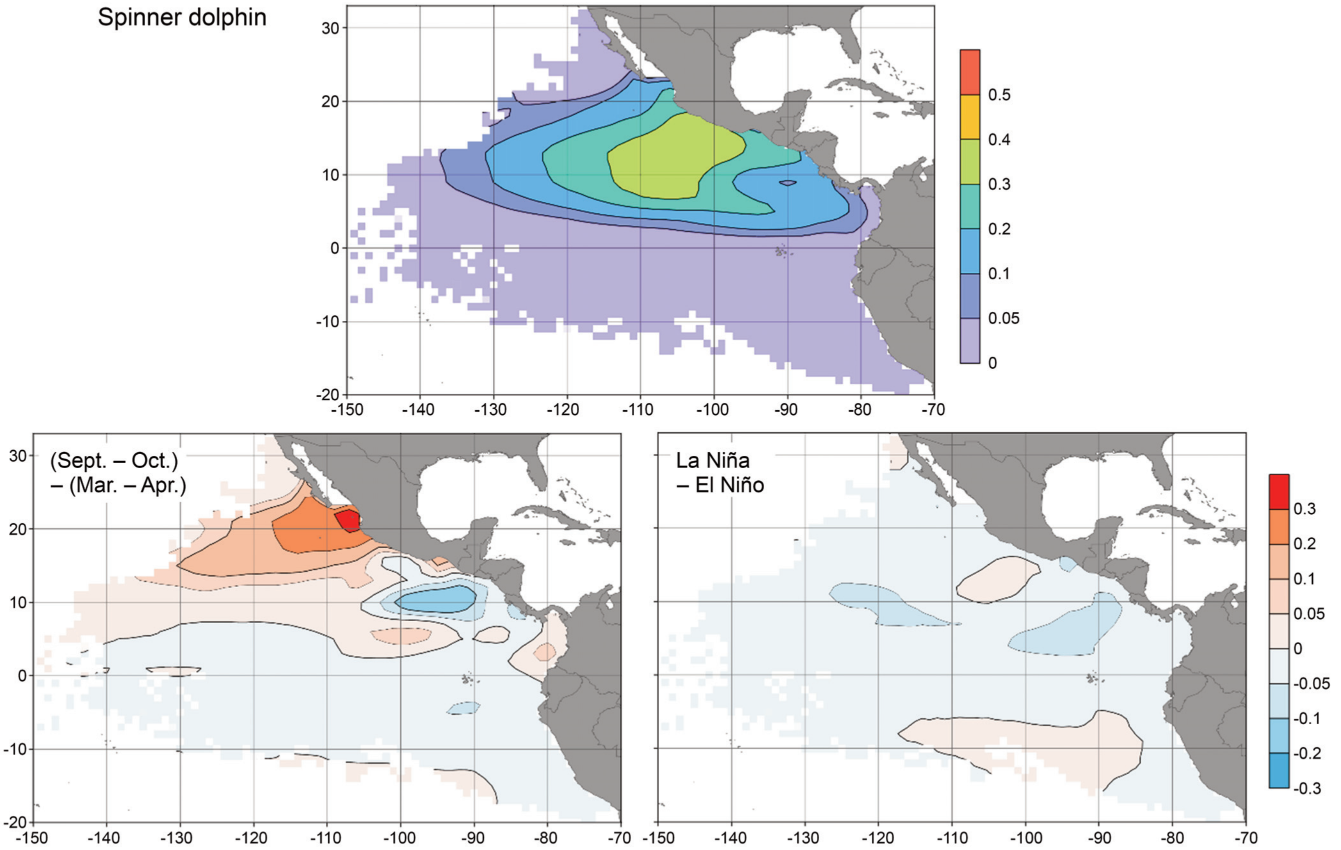

Fig. 5. Spinner dolphin probability of presence climatology (top), and differences between seasonal extremes and El Niño and La Niña years (bottom), predicted by GAM from TVOD, 1986–2015. Cells with <300km total TVOD effort are masked.

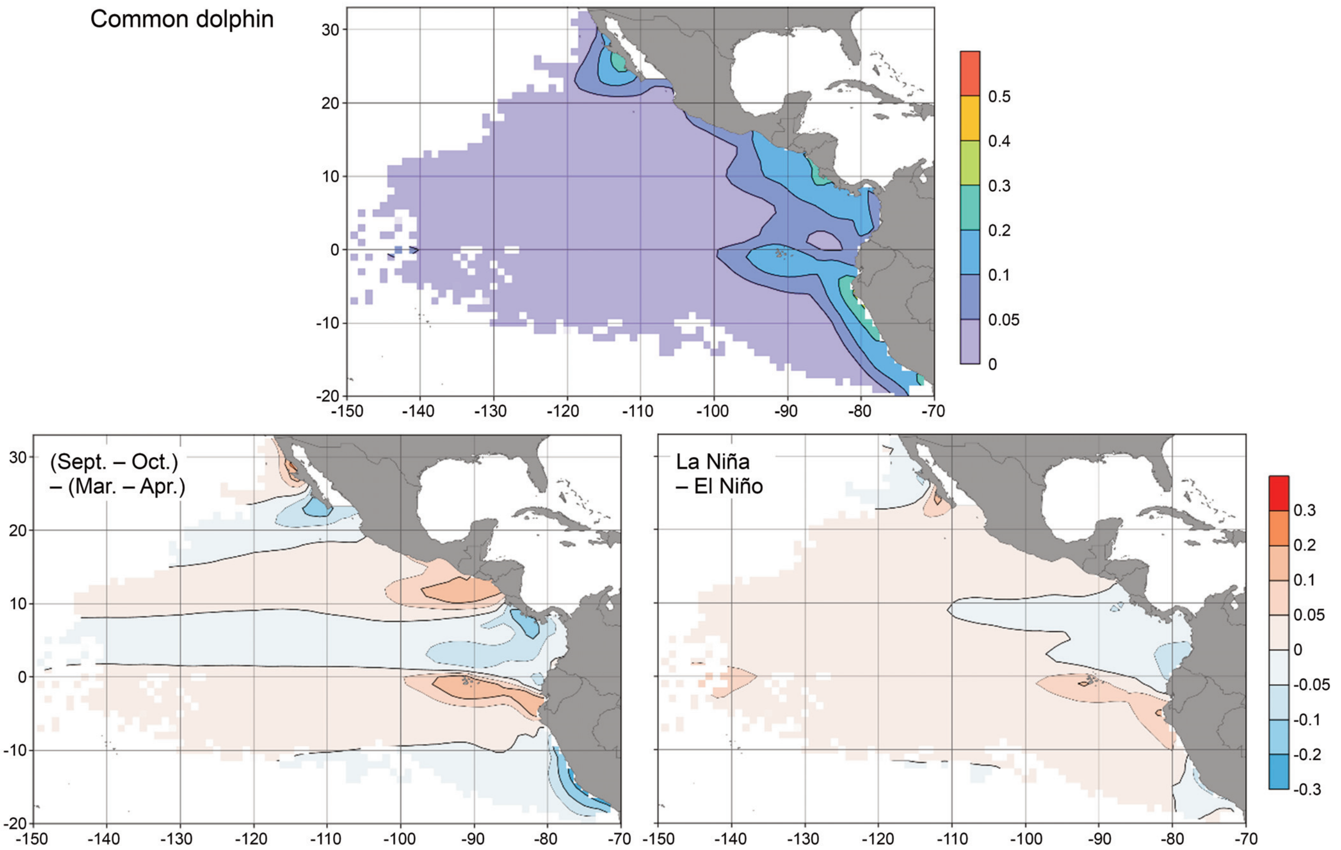

Fig. 6. Common dolphin probability of presence climatology (top), and differences between seasonal extremes and El Niño and La Niña years (bottom), predicted by GAM from TVOD, 1986–2015. Cells with <300km total TVOD effort are masked.

sampled by the fishery as it searches for tuna associated with dolphins (for GAM partial response curves see the Appendix). These are essentially estimates of realised niches (Colwell and Rangel, 2009). The plot for the surface temperature-salinity interaction (TEMP-SAL) shows a predominance of the two major surface water masses in the region (Fiedler and Talley, 2006). The first is warm, moderate-salinity TSW centred at 28–29°C and 33–34psu. The second is cooler, higher-salinity equatorial surface water (ESW) centred at 25–26°C and 34–35psu. Spinner dolphins are more strongly associated with TSW, while spotted dolphins show a broader distribution extending into ESW. Common dolphins too show a preference for ESW, but also for cooler waters representing coastal upwelling.

The other oceanographic variables, thermocline depth (TD) and stratification index (SI), are of similar relative importance as TEMP-SAL for all three dolphin taxa (Table 4). Spotted and spinner dolphins show a preference for a relatively strong but less shallow thermocline. Common dolphins show a distinctly different response to SI than spotted and spinner dolphins do; they prefer relatively unstratified near-surface waters, typical of coastal and oceanic upwelling regions. Distance to shelf edge (DIST) is a relatively important predictor variable only for the more narrowly distributed spinner and common dolphins. For all of these predictor variables, the preferences of spotted and spinner dolphins, often found in mixed schools, are relatively similar, while they tend to be more distinct from the common dolphin preferences.

Table 4

Relative importance or contribution of predictor variables to GAM predictions of distributions of three dolphin taxa.

	TEMP-SAL	TD	SI	DIST	Effort
Spotted	0.36	0.27	0.26	0.03	0.08
Spinner	0.18	0.25	0.35	0.20	0.02
Common	0.19	0.20	0.23	0.34	0.04

DISCUSSION

The GAMs of species–environment relationships using TVOD sightings were used to predict distributions for seasonal and ENSO periods from the climatological environmental conditions specific for those periods. These predictions could be made without extrapolating outside the limits of the TVOD observations, as would be necessary with

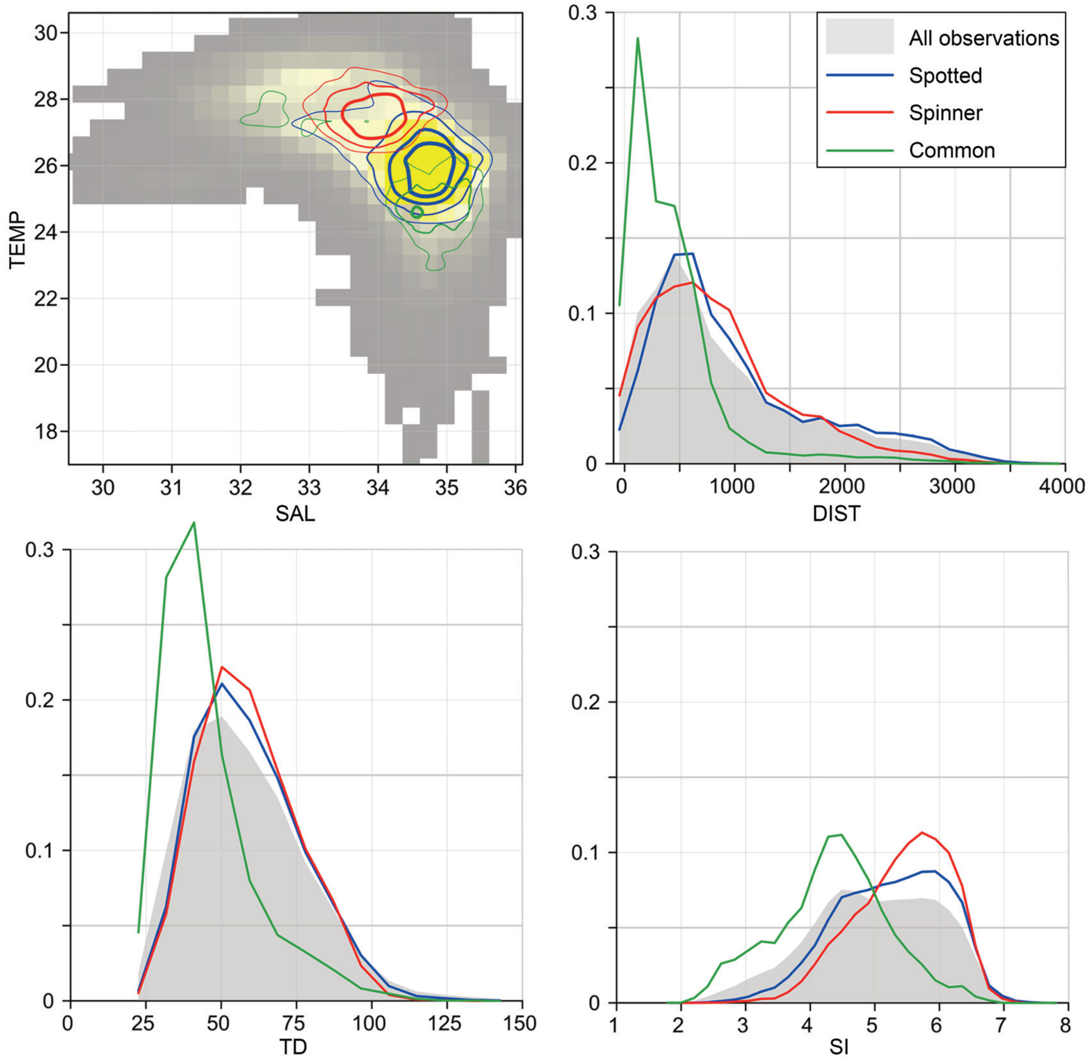

Fig. 7. Observed distributions of presence of three dolphin taxa (used habitat) and all month-deg observations (available habitat) relative to predictor variables: TEMP (surface temperature, °C); SAL (surface salinity, psu); TD (thermocline depth, m); SI (stratification index, °C); and DIST (distance to shelf edge, km). For the TEMP–SAL plot, contours are at 0.05, 0.1, 0.2 and 0.3, colour-coded by taxon; availability ranges from 0 (darker grey) to 0.015 (yellow).

models built from research vessel observations. The GAMs of species–environment relationships using TVOD sightings had explained deviance values of 21.4, 23.6 and 23.2% for spotted, spinner and common dolphins, respectively (Table 3). In comparison, GAMs of species encounter rates using SWFSC research vessel sightings and effort data had explained deviances of 11.6, 25.2 and 18.3% for offshore spotted, eastern spinner and short-beaked common dolphins (Forney *et al.*, 2012). The results presented here give new insight into how these resident dolphins respond to seasonal and interannual changes within their habitat. Before discussing the ecological significance of the results, consideration is given to whether it is reasonable to make inferences about ETP dolphins based on observations of tuna-associated dolphins.

Do TVOD results represent ETP dolphin populations? The overall correspondence between TVOD predicted distributions and the general distribution of Southwest Fisheries Science Center (SWFSC) research vessel sightings is good (Fig. 8), with correlations from 0.38 to 0.62, although there are some discrepancies. For spotted dolphins, the

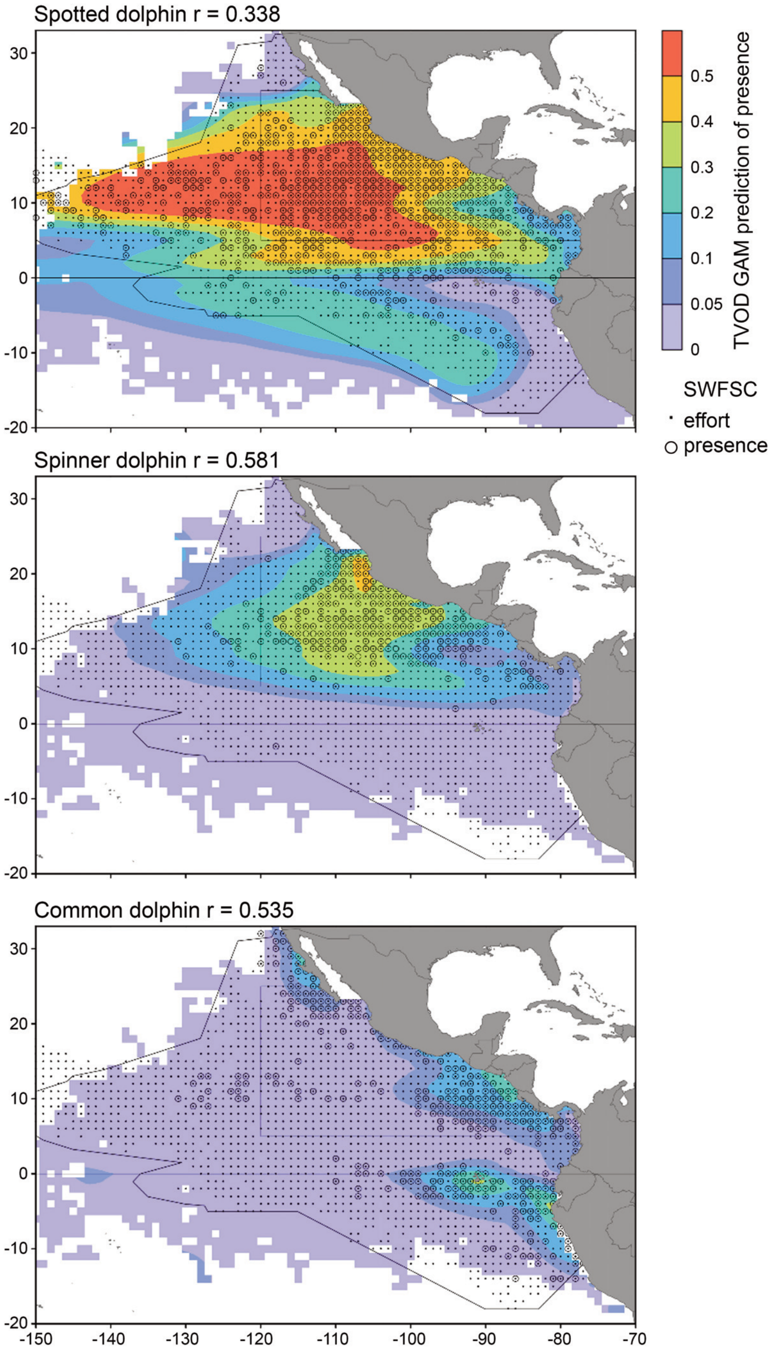

Fig. 8. Presence of three dolphin taxa predicted by GAMs from TVOD for August–November (colour contours) and observed on 10 SWFSC research vessel surveys (symbols, no or at least one sighting 1986–2006) The outer line is the SWFSC study area and the inner line shows the core area for SWFSC surveys (Gerrodette *et al.*, 2008). Predictions for cells with no TVOD effort are not shown. Correlations (r) between TVOD model prediction and SWFSC observed presence/absence in 1° squares covered by both datasets.

TVOD prediction tends to be higher to the west in the warm pool region, while SWFSC sightings are more prevalent to the east, likely because research vessel survey effort was nominally 2–3 times higher in the core area east of 120°W. For spinner dolphins, research vessel sightings are most frequent in the warm pool area where TVOD predictions are highest. For common dolphins, research vessel sightings are frequent in three areas of coastal or equatorial upwelling as predicted: southern Baja California, the Costa Rica Dome and the coast of Peru-Ecuador extending west into the equatorial cold tongue. However, the TVOD predictions do not capture the research vessel sightings to the west of the Costa Rica Dome along the countercurrent thermocline ridge at 10°N. Given the similarities, the spatial distributions and patterns of change presented here represent the responses of these dolphins to their environment in the ETP, whether or not they are associated with tuna.

Species distribution models for these species have been built from SWFSC research vessel survey data from the ETP, and also from the Central North Pacific and California Current. These models all estimate climatological distributions and may estimate distributions for individual survey years. For the ETP, Forney *et al.* (2012) show an eastern spinner dolphin distribution similar to that presented here (Fig. 5), with moderate expansion and contraction between surveys. Their predicted distributions for pantropical spotted dolphins show a preference for warm tropical water north of the equator, as in Fig. 4, but predicted levels are lower at the centre of the TVOD-predicted maximum (120–110°W) and higher to the west. Predicted density levels vary among surveys, but changes in distribution were not predicted. A related study that combined SWFSC data from the ETP and other regional surveys to model distributions in the central North Pacific found spatial patterns for pantropical spotted dolphins and spinner dolphins that are consistent with our results (Forney *et al.*, 2015), even though spinner dolphins included whitebelly and Hawaiian spinners.

The distributions predicted for common dolphins by Forney *et al.* (2012) show the same three regional maxima in upwelling centres as in Fig. 6, but they emphasise the eastern equatorial maximum relative to the Costa Rica Dome and southern Baja California maxima. Pardo *et al.* (2015) used a single variable – absolute dynamic topography of the sea surface – to predict the distribution of short-beaked common dolphin population density using SWFSC survey data from the ETP and California Current. The pattern of preferred habitat was very similar to that presented here, but also had a moderate high corresponding to sightings to the west of the Costa Rica Dome.

Ecological relevance

The model-predicted presence of spotted dolphins is highest in a band along the countercurrent thermocline ridge at 10°N, declining towards the coast of Central America, but extending towards the coast of southern Mexico (Fig. 4). Warm tropical surface water occupies this region, in a shallow layer overlying a strongly stratified thermocline (Fig. 1). Values of predicted presence tend to be greater to the west of 120°W, although the prevalence of research vessel sightings of offshore spotted dolphins is greater to the east, in the core stratum of higher survey effort (Fig. 8).

Moderate levels of predicted presence of spotted dolphins extend to the south of the equator, but with a minimum along the equator corresponding to the equatorial cold tongue. Predicted presence is lower during September–October and during La Niña (Fig. 4), when the equatorial thermocline ridge is shallower and stronger trade winds increase equatorial upwelling and cool the surface waters. This exclusion is more pronounced for September–October than for La Niña. The primary seasonal change resolved by the difference map in the lower left of Fig. 4 is a summer–autumn increase in the northern offshore part of the range and a decrease south of ~10°N. A decrease in predicted presence in the region of the Costa Rica Dome occurs during September–October, when the Dome is most fully developed (Fiedler, 2002). A similar, but smaller, change occurs during La Niña, when the Dome is slightly shallower than during El Niño (Fiedler and Talley, 2006).

The centre of predicted presence of spinner dolphins is confined to the warm, stratified eastern Pacific warm pool (Fig. 5), corresponding to the known distribution of the eastern spinner dolphin subspecies. The range limits of spinner dolphins correspond to the equatorial front to the south, and the presence of California Current and subtropical surface waters to the northwest. Seasonal changes in predicted presence of spinner dolphins are less than for spotted dolphins but are similar in showing a boreal summer–autumn increase towards the northwest. Changes in the region of the Costa Rica Dome are not marked. There are slight September–October and La Niña decreases at the Tehuantepec bowl off southern Mexico, which is also evident for spotted dolphins in Fig. 4. The Tehuantepec bowl, like the Dome, is associated with seasonal gap winds and the regional dynamics of surface circulation (Kessler, 2006).

Common dolphins have a distribution complementary to spotted and spinner dolphins in the ETP. Au and Perryman (1985) used early SWFSC abundance survey data to contrast the ‘tropical water’ habitat of spotted and spinner dolphins with the ‘upwelling-modified’ habitat of common dolphins. The model predictions indicate a strong response to the seasonal cycle of the Costa Rica Dome, with higher predicted presence of common dolphins in September–October (Fig. 6). There is no strong response to the Dome predicted for La Niña years, but the increase in presence for the cold tongue region suggests a similar response to enhanced upwelling conditions during those periods. The concurrent decrease in predicted presence in the Gulf of Panama suggests that common dolphins might move to upwelling areas when habitat conditions are more favourable in those areas.

In both geographic and niche space, spotted dolphins and eastern spinner dolphins are partially sympatric, in that the range of the latter lies entirely within the range of the former, while common dolphins are more parapatric relative to the other two. All three dolphin species feed on a variety of small fishes, cephalopods and crustaceans, but diet differences may contribute to niche separation. Spotted dolphins in the ETP are known to feed on mesopelagic fishes and squids of the deep scattering layer, as it moves toward the ocean surface at night, and also on epipelagic fishes such as flyingfish (Robertson and Chivers, 1997). In contrast, spinner dolphins are known to dive deeper to feed more exclusively on mesopelagic prey (Perrin *et al.*, 2008), potentially reducing niche overlap even though they are commonly found in mixed schools with spotted dolphins for at least part of the day (Scott and Chivers, 2009). Common dolphins feed on a variety of prey, including small mesopelagic fishes and squids found in the deep scattering layer and epipelagic schooling species such as small scombroids, clupeoids and market squids (Perrin, 2018a). The niche differentiation among these three species in the ETP is consistent with studies of other sympatric dolphins (Bearzi, 2005).

Useful information about the temporal and spatial distribution of dolphin prey species in the large oceanic region of the ETP does not exist. The predictor variables likely influence prey availability, notably thermocline depth and stratification (Scott *et al.*, 2012). Spotted and spinner dolphins, which feed on vertically migrating mesopelagic prey, are associated with shallow thermoclines and high stratification, while common dolphins that feed on pelagic fish in upwelling areas show somewhat different associations with these proxy variables.

Our species distribution models for spotted, spinner and common dolphins based on TVOD have yielded new information about how the dolphins respond to seasonal and ENSO-related changes in their environment. These animals are highly mobile, opportunistic predators. The variations in habitat quality that determine model-predicted presence probably reflect prey availability influenced by the environmental proxies that were used as predictor variables. Tagging data for spotted dolphins have shown that they typically move 100–200km per day, apparently in foraging activity (Scott and Chivers, 2009). Earlier tag-recapture studies found that some spotted dolphins moved several hundred km along the thermocline ridge at 10°N (Perrin *et al.*, 1979). These observed movements are not true migration, as observed for some whales between distinct feeding and breeding/calving grounds (Stern and Friedlaender, 2018), but they are consistent with our results suggesting seasonal movements related to habitat seasonality. Both seasonal and interannual distributional responses to changes in habitat may indicate future effects of climate change in the region. Observing or predicting population responses will require more extensive collection and analysis of species density and life history data.

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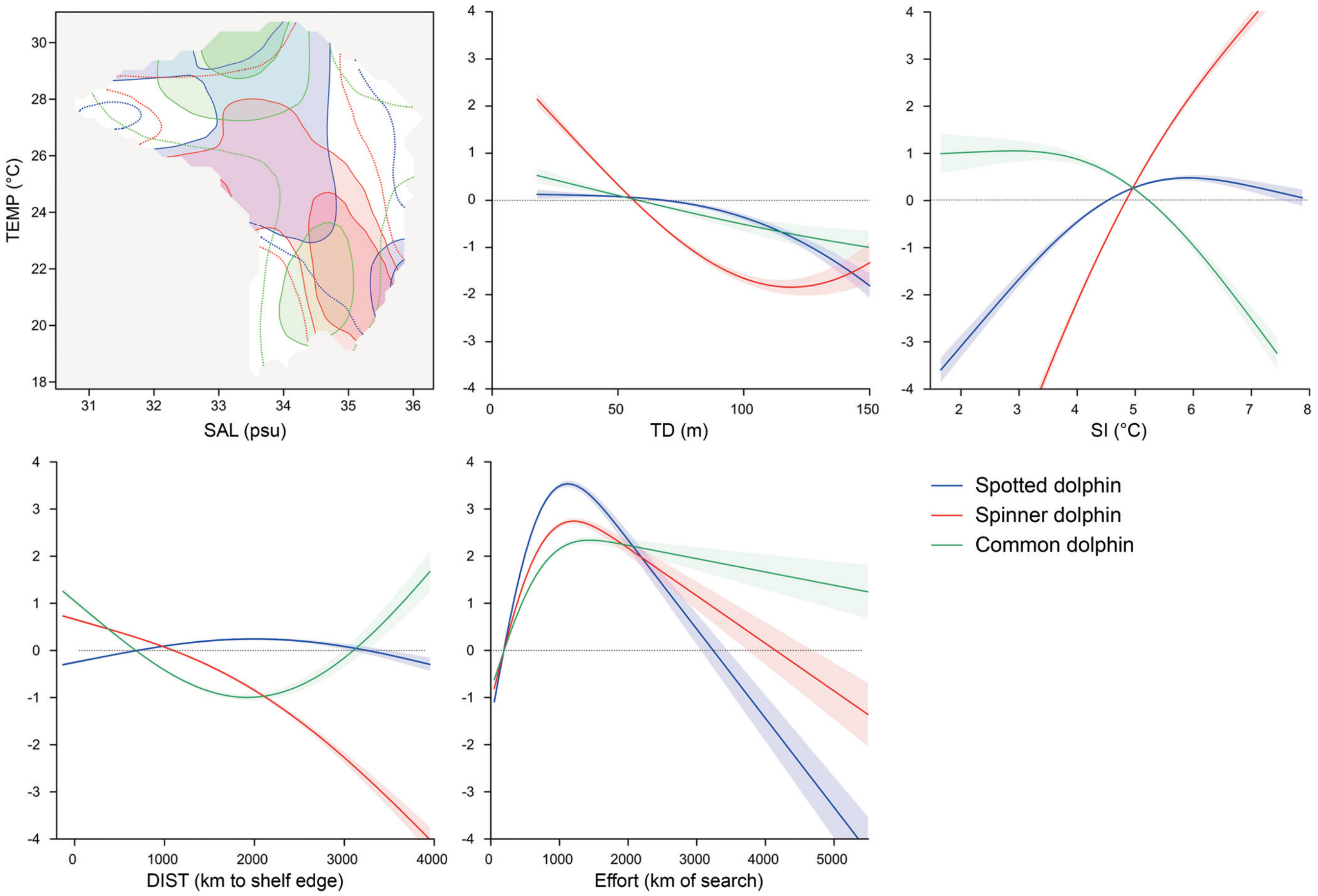
APPENDIX: MODELLED RESPONSES TO PREDICTOR VARIABLES



Appendix Fig. 1. Modelled responses to predictor variables for three dolphin taxa: TEMP (surface temperature); SAL (surface salinity); TD (thermocline depth); SI (stratification index); and DIST (distance to shelf edge). For the TEMP-SAL interaction plot, contours are at –1 (dashed), and at 0 and 1 (solid and filled); the grey area is outside the sample range.

A note regarding conditioning simulation trials for data-poor management strategy evaluations

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ABSTRACT

Management Strategy Evaluation is a key tool used by the Scientific Committee of the International Whaling Commission to identify appropriate management strategies for commercial and aboriginal subsistence whaling. In several cases, Bayesian approaches have been used to condition the operating models and the assumed priors may substantially impact the conclusions regarding appropriate management strategies in data-poor situations. Three approaches for defining a prior on the 'scaling' parameter (on 'initial depletion', 'current depletion', and 'carrying capacity') are compared in terms of the proportion of draws from the prior that are rejected during the construction of the post-model-pre-data distribution and hence the resulting implied distribution for initial and current depletion. Overall, placing a prior on initial depletion leads to the fewest rejected draws but the implied distribution for current depletion depends on the catch history. In contrast, placing a prior on carrying capacity leads to less optimistic distributions for initial and current depletion and perhaps to unreasonably optimistic distributions for MSY. The issue of the appropriate distribution for the 'scaling' parameter in population models should be an explicit component of Management Strategy Evaluation and Bayesian assessments in data-poor situations in general.

KEYWORDS: BAYESIAN METHODS; MANAGEMENT STRATEGY EVALUATION; WHALING

INTRODUCTION

The Scientific Committee of the International Whaling Commission (IWC) uses Management Strategy Evaluation (MSE)[3] to compare the abilities of alternative candidate management strategies to achieve pre-specified management goals for commercial and aboriginal subsistence whaling recognising the inherent scientific uncertainty (Punt and Donovan, 2007; Punt *et al*., 2016). The IWC was the first organisation to make extensive use of MSE, but MSE is now considered state of the art by most marine renewable resource management bodies. The MSE approach has been used to evaluate management strategies for fish and invertebrate resources (e.g. Plagányi *et al*., 2007; Hillary *et al*., 2016) as well as in a broader ecosystem context (e.g. Dichmont *et al*., 2013; Fulton *et al*., 2919), and has been proposed for use in the terrestrial realm (Bunnefeld *et al*., 2011).

A key component of MSE is the operating model, which is a mathematical model of the system being managed, its current status and how future data will be generated. The values for the parameters of the operating model are specified (or the operating model is 'conditioned') by fitting it to the available data. In general, the operating models used to compare alternative variants of the Revised Management Procedure (RMP; IWC, 2012) are conditioned using a bootstrap-like procedure (e.g. western North Pacific Bryde's whales: IWC, 2019a; North Pacific minke whales: IWC, 2014a; North Atlantic minke whales: IWC, 2017). In contrast, the operating models used to compare alternative candidate *Strike Limit Algorithms* for aboriginal subsistence whaling have often been fitted using Bayesian methods (e.g. Bering-Chukchi-Beaufort Seas [B-C-B] bowhead whales: IWC, 2003; West Greenland bowhead, humpback and fin whales: IWC, 2014b, IWC, 2019b)[4].

Bayesian methods allow (and in fact require) prior distributions to be imposed on the parameters of the population dynamics model, with these updated into posterior distributions based on the available data. The (estimated) parameters of the operating model relate to biological parameters (survival, age-at-maturity, the oldest age at which the juvenile survival rate applies), productivity (usually quantified by the Maximum Sustainable Yield rate; MSYR), current abundance (N_{cur}), and a parameter that determines the current status of the population relative to carrying capacity (the 'scaling' parameter). The last three parameters have the greatest influence on the performance of candidate management strategies, which has led most IWC MSEs to develop trials in which MSYR is set to default values agreed by the Scientific Committee after considerable review (IWC, 2014c) rather than being treated as estimable (often $\text{MSYR}_{1+} = 1\%$ and $\text{MSYR}_{mat} = 4\%$). The prior for current abundance is usually treated as 'informative' and set to the sampling distribution for a recent estimate of abundance (equivalent to placing a uniform prior on current (year y_{cur}) abundance and including the recent estimate of abundance in the likelihood function). The 'scaling' parameter has usually been taken to be carrying capacity (K), with the prior for K taken to be uniform over a suitably broad range.

This paper explores options for choosing the prior for the scaling parameter. It would be desirable for this choice to be irrelevant, as would be the case for a stock such as the

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[3] Usually termed the Management Procedure approach in IWC literature.

[4] Exceptions are the most recent trials for the Eastern North Pacific gray whales (maximum likelihood approach; IWC, 2019c) and West Greenland minke whales (based on the operating model used to evaluate RMP variants).

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B-C-B bowheads for which the available data are fairly informative (but cannot place an upper limit on [present] carrying capacity). Desirable properties of this parameter are that (a) a wide range of scenarios are represented in the trials that would be conducted if there were no data, and (b) the posterior for the parameter closely matches the prior if there were no data (i.e. the specified prior is actually used as expected by those developing trials; A.E. Punt, pers. obs.) and hence relatively few of the draws from the priors are rejected because the population model is inconsistent with the generated values for the parameters. For example, an inconsistency would arise if the catch series was a constant 100 whales annually, the value for carrying capacity was set to 1,000 and the value for current population size to 999 unless the population growth rate parameter was set to a very (unrealistically) high value. Ideally, the set of parameters from the posterior should be such that the true population trajectory is included within the set of implied population trajectories.

The focus for this paper is the case in which the population projections do not start at carrying capacity but at some lower value in some year y_I, as is the case for all the recent operating models on which evaluations of *Strike Limits Algorithms* are based (IWC, 2014b; 2019). The paper considers the following three (almost exhaustive) options for defining the scaling parameter:

(A) The scaling parameter is taken to be the ratio of abundance in year y_I (year 25 for this paper) relative to carrying capacity ('initial depletion') D_I, with the prior for initial depletion assumed to be uniform over 0.01 to 0.99, i.e. $D_I \sim U[0.01,0.99]$, with carrying capacity for each draw from the prior set such that current abundance equals a value drawn from the sampling distribution for N_{cur} (denoted 'Year 25 depletion prior');

(B) The scaling parameter is taken to be current (y_{Cur}; year 75 for this paper) depletion, with the prior for current depletion assumed to be uniform over 0.01 to 0.99, i.e. the implied prior for current abundance N_{cur} is uniform between 1 and 99% of carrying capacity. This assumption leads to the following prior for carrying capacity $K \sim U[\tilde{N}_{cur}/0.99, \tilde{N}_{cur}/0.01]$ where is $\tilde{N}_{cur}$ is the mean of sampling distribution for current abundance (denoted 'Carrying capacity prior (A)'); and

(C) The scaling parameter is taken to be carrying capacity, *K*, with a uniform prior over a 'wide range' placed on the logarithm of *K*, illustrated by $K \sim U[\ell n\tilde{N}_{cur}, \ell n(100\tilde{N}_{cur})]$ (denoted 'Carrying capacity prior (B)').

The last two options are based on the same support range for carrying capacity.

METHODS

Overview of the testing procedure

Two analyses (one that ignores observation error and one that accounts for observation error) are conducted to compare the three approaches for specifying the scale parameter (A–C above). All of these assume that catches started in year 0 and continued to year 75, and that the catches from years 25 to 75 are known. This reflects a case where the earlier catches are either not known well or there is concern that the abundance changed over years 0 to 25 for reasons not captured by the known catch history (e.g. if the stock is found in a region where catches are taken, but they are not included in the catch history for the stock; e.g. fin whales off West Greenland, or carrying capacity changed). The stock is assumed to be 1,000 animals at the start of year 75 (i.e. $N_{75} = 1{,}000$), although the methods are such that the results are independent of the choice of the value for N_{75}.

The two analyses are:

(1) Conduct projections from year 25 to year 75 where the abundance in year 75 is known to be 1,000, for 99 values of the 'scaling' parameter (initial depletion or carrying capacity) across its assumed plausible range (this is referred to as a 'hitting' analysis within the IWC Scientific Committee).

(2) As for (1), except that 1,000 values for N_{75} are drawn from a prior (lognormal with mean 1,000 and standard error of the log 0.3[5]) rather than N_{75} being known to be 1,000 (the 'post-model-pre-data distribution' analysis[6]).

Results are shown for three values for N_{75}/K (0.25, 0.5 and 0.75) for each of five effort series (Fig. 1, left column; resulting catches in Fig. 1, columns 2–4). The results of the first analysis are evaluated in terms of the extent to which the resulting trajectories cover an adequate range of scenarios, while the results of the second analysis are evaluated in terms of a range of outcomes, including the extent to which the priors for D_I ('Year 25 depletion prior'), *K* (the two carrying capacity priors), and N_{cur} are updated simply by projecting the model forward and rejecting parameter combinations that are not consistent with the assumed population dynamics.

Population dynamics

The model of the population dynamics is a deterministic Schaefer production model, i.e.:

$$N_{t+1} = N_t + rN_t(1 - N_t/\mathrm{K}) - \phi E_t N_t; \qquad N_0 = K \qquad (1)$$

where N_t is the population size at the start of year t, *r* is the intrinsic rate of growth (set to 0.05, equivalent to an MSYR of 0.025[7]), *K* is carrying capacity (set to the current abundance, $N_{75} = 1{,}000$, divided by current depletion D_{75}, i.e. $K = 1{,}000/D_{75}$), E_t is the relative effort in year *t* (Fig. 1, column 1), and ϕ is a catchability parameter, selected so that the pre-specified depletion D_{75} is achieved. The value of ϕ is set separately for each of the five effort scenarios. The term $\phi E_t N_t$ is replaced by the catch for year *t* from the operating model when applying the Bayesian estimation methods.

RESULTS AND DISCUSSION

Results of 'hitting' analyses

Fig. 2 shows the time-trajectories of true population size (thick red line) for each of the five effort scenarios (rows) in

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[5] 0.3 is within the range of the CVs of the estimates of abundance used when conditioning operating models, but the results would be insensitive to this value.

[6] The post-model-pre-data distribution for a parameter is the distribution for that parameter that arises once parameter combinations that are inconsistent with the population dynamics model are excluded; post-model-pre-data distributions can be computed for model outputs (derived variables) as well as parameters.

[7] Results (not shown here) confirm that the qualitative results are insensitive to decreasing (to 0.02) or increasing (to 0.1) the value assumed for *r*.

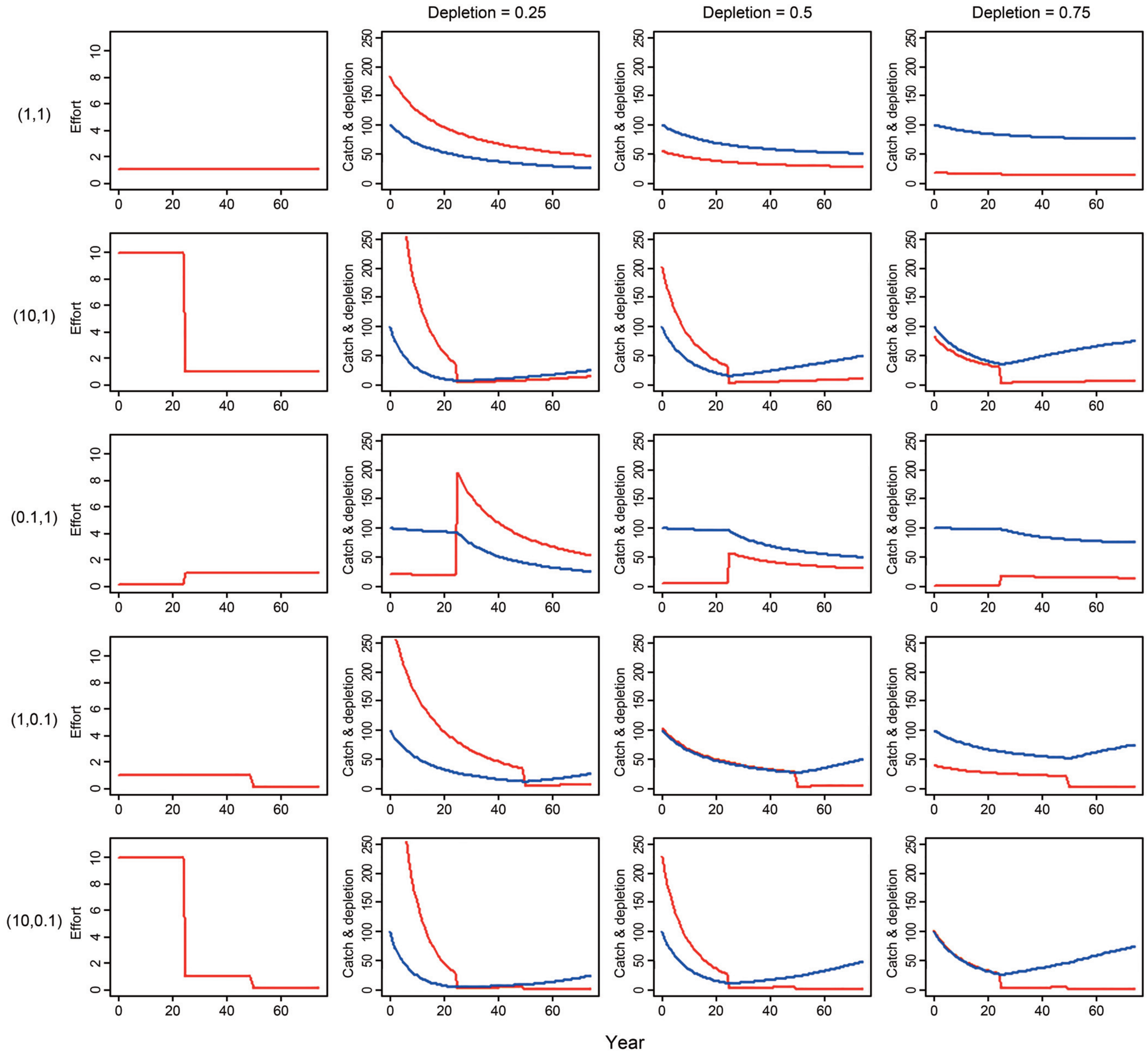

Fig. 1. Time-trajectories of effort (left column), and of catch [red lines] and depletion [blue lines] (columns 2–4). Results are shown for five scenarios regarding the time-trajectories of relative effort (rows).

absolute terms and relative to carrying capacity, along with the range of time-trajectories of inferred population size in absolute and relative terms for each of the three priors (columns). The results in Fig. 2 pertain to *N/K* = 0.5 in year 75 (results for *N/K* = 0.25 and *N/K* = 0.75 are shown in supplementary Figs S.1 and S.2). As expected, all of the time-trajectories of inferred population size (the blue lines) pass through the 1,000 in year 75. The distributions of time-trajectories of inferred population sizes, in absolute terms, are quite tight irrespective of the method used to account for uncertainty. However, there is less variability in the time-trajectories of population size when the priors on carrying capacity are used, which is most noticeable for relative population size.

Post-model-pre-data distribution

Allowing for uncertainty in current abundance (log-normal with a log-scale standard deviation of 0.3; *N/K* in year 75 of 0.5 in Fig. 3 and of 0.25 and 0.75 in Supplementary Figs S.3 and S.4) led to results that are generally qualitatively similar to those when current abundance is known. However, carrying capacity prior (B) leads to samples from the prior that do not include the true trajectory for the 1–1 effort scenario and particularly the 0.1–1 effort scenario for much of the time-series (first and third rows in Fig. 3). This discrepancy is related to the value of *N/K* in year 75, with the effect being smaller for D_{75} = 0.25 and larger for D_{75} = 0.75 (Supplementary Figs S.3 and S.4). None of the three methods do well at including the true trajectory in the sampled trajectories for the 0.1–1 effort scenario, particularly for D_{75} = 0.75 (Supplementary Fig. S.4).

The number of draws from the priors that are not consistent with the model (and are rejected in the process of constructing the post-model-pre-data distribution) differs among the various prior assumptions (Table 1). It is possible to find acceptable values for carrying capacity for almost all

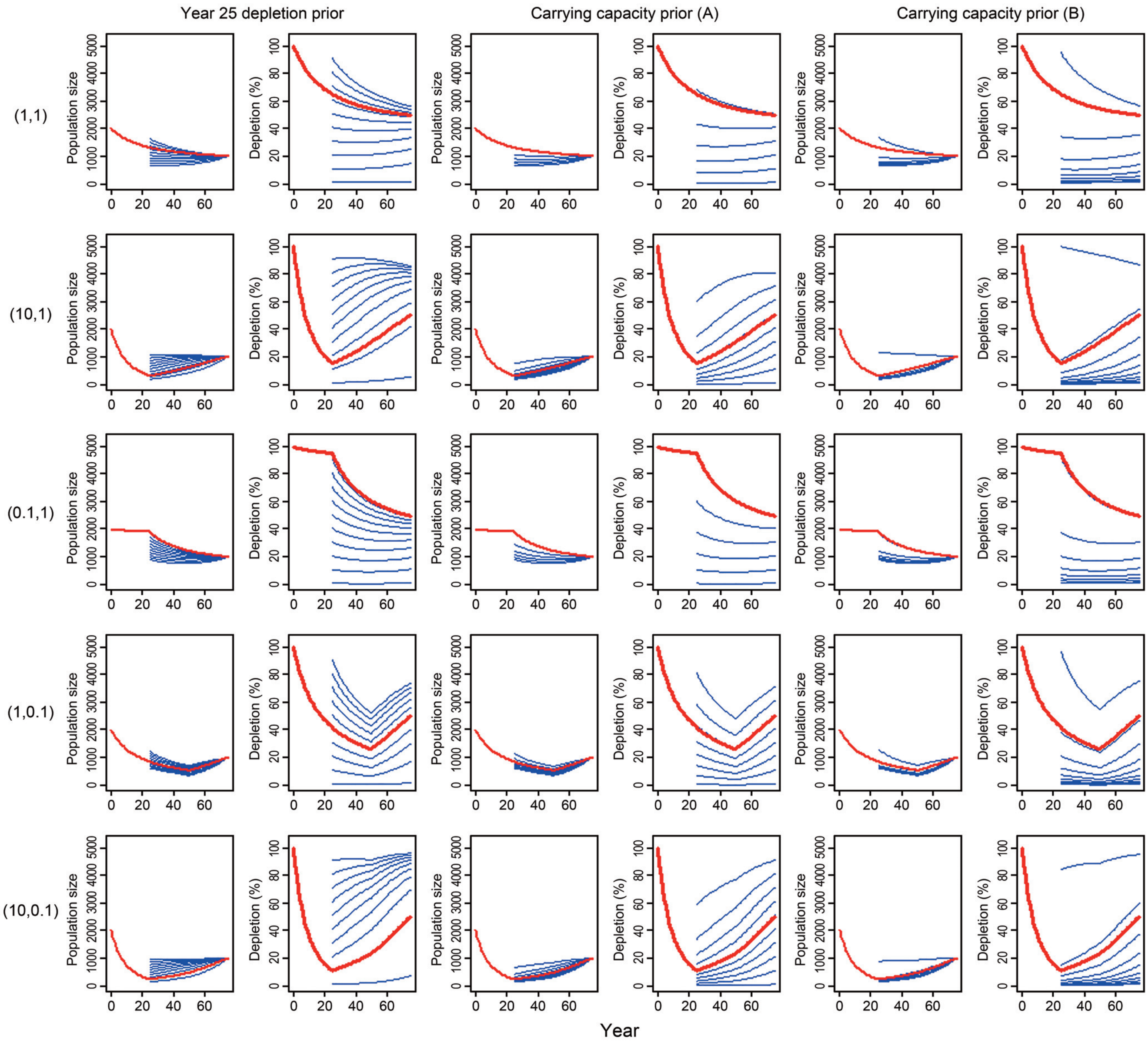

Fig. 2. Time-trajectories of true population size (thick red line) for each of the five effort scenarios (rows) in absolute terms and relative to carrying capacity (depletion), along with the range of time-trajectories of inferred population size (thin blue lines) in absolute and relative terms when sampling from each of the three priors (columns). The results in this figure pertain to *N/K* = 0.5 in year 75.

Table 1

Proportion of 100,000 draws from the prior that were not rejected as infeasible as a function of the relative population size (depletion) in year 75 and the effort scenario.

Relative population/ effort scenarios	Year 25 depletion prior	Carrying Capacity prior (A)	Carrying Capacity prior (B)
N_{75}/K=0.25			
1, 1	0.996	0.375	0.788
10, 1	1.000	0.848	0.961
0.1, 1	0.986	0.257	0.710
1, 0.1	1.000	0.644	0.902
10, 0.1	1.000	0.908	0.976
N_{75}/K=0.5			
1, 1	1.000	0.589	0.883
10, 1	1.000	0.865	0.965
0.1, 1	1.000	0.513	0.856
1, 0.1	1.000	0.784	0.943
10, 0.1	1.000	0.910	0.976
N_{75}/K=0.75			
1, 1	1.000	0.803	0.948
10, 1	1.000	0.885	0.970
0.1, 1	1.000	0.782	0.942
1, 0.1	1.000	0.857	0.963
10, 0.1	1.000	0.911	0.977

values for year 25 depletion (the few exceptions being – somewhat surprisingly – the constant effort scenario). In contrast, up to 29% of the 'Carrying capacity prior (B)' draws can be rejected, but it is generally possible to find values for initial population size to match the generated current abundance and carrying capacity values. The poorest performance in terms of rejecting draws during the post-model-pre-data stage is 'Carrying capacity prior (A)' for which it is seldom possible to find an initial depletion that matches the generated current abundance and carrying capacity values, and the proportion of rejected draws can be as high as 74%, with most of the rejections occurring for higher levels for current depletion (i.e. population sizes close to carrying capacity). Although a large proportion of draws may be rejected, this does not (visually at least) impact the post-model-pre-data distribution for current abundance (Fig. 4).

Fig. 5 shows the post-model-pre-data distribution for initial (year 25) and current (year 75) depletion. The distributions (except for initial depletion for the 'Year 25 depletion prior') are far from uniform, suggesting that any of the choices of prior lead to *a priori* implications regarding stock status at various points in time. The sensitivity of the post-model-pre-data distributions for current depletion to the effort scenario is greatest for the 'Year 25 depletion prior, with three of the distributions centered somewhere close to the true depletion and two centered on much more optimistic values (Fig. 5, column 2). In contrast, 'Carrying capacity prior (A)' implies that the stock was fairly depleted in year 25 irrespective of the effort scenario. The distribution for current depletion is shifted towards lower values for this prior, even though this method was developed based on a uniform distribution for current depletion. 'Carrying capacity prior (B)' leads to the most

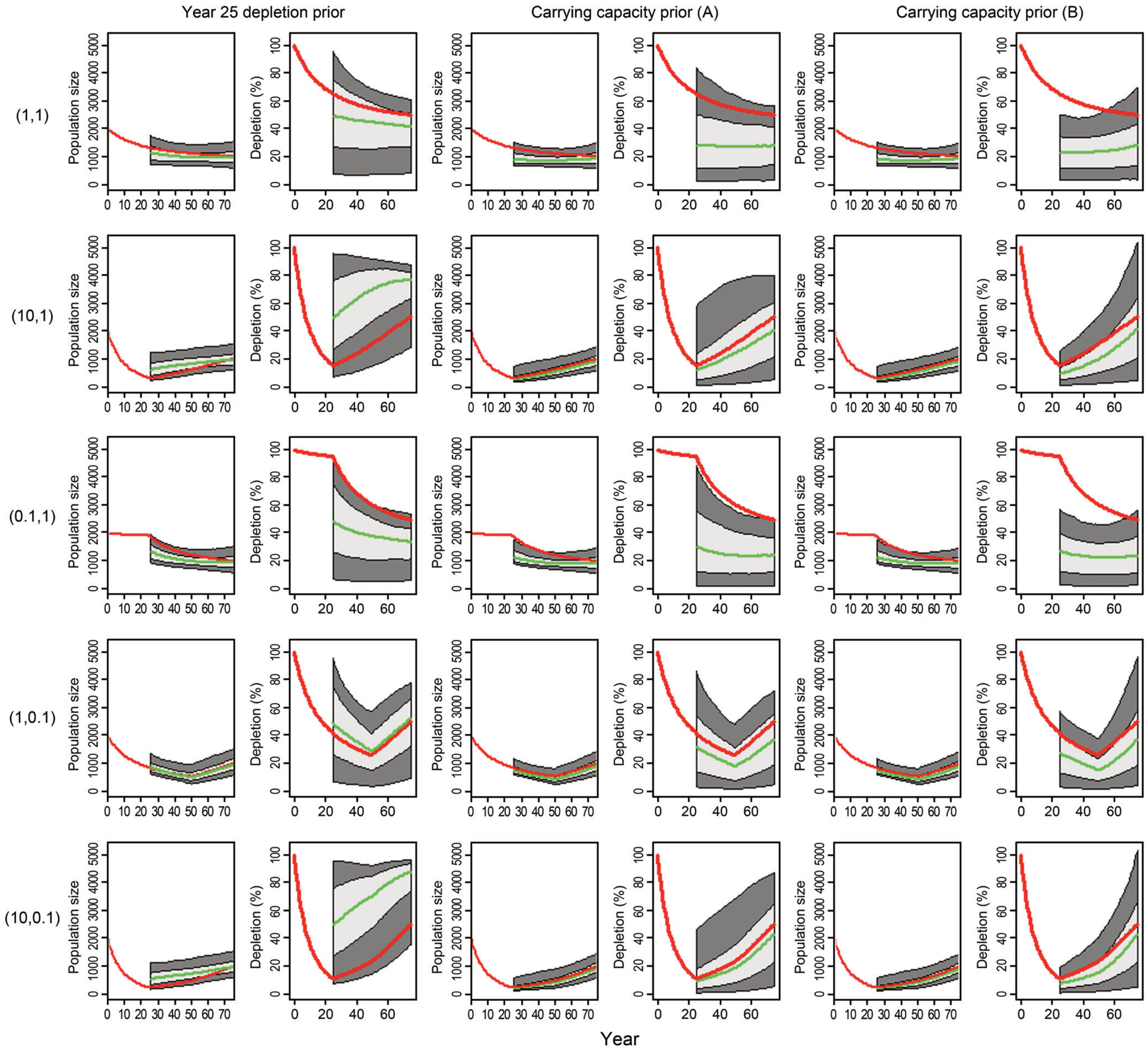

Fig. 3. Time-trajectories of true population size (thick red line) for each of the five effort scenarios (rows) in absolute terms and relative to carrying capacity (depletion), along with the range of time-trajectories of inferred population size in absolute and relative terms for each of the three priors when account is taken of uncertainty in current population size (columns). The green lines denote the distribution medians, the light gray shading the 50%iles of the distributions and the dark gray shading the 90%iles of the distributions. The results in this figure pertain to $N/K = 0.5$ in year 75.

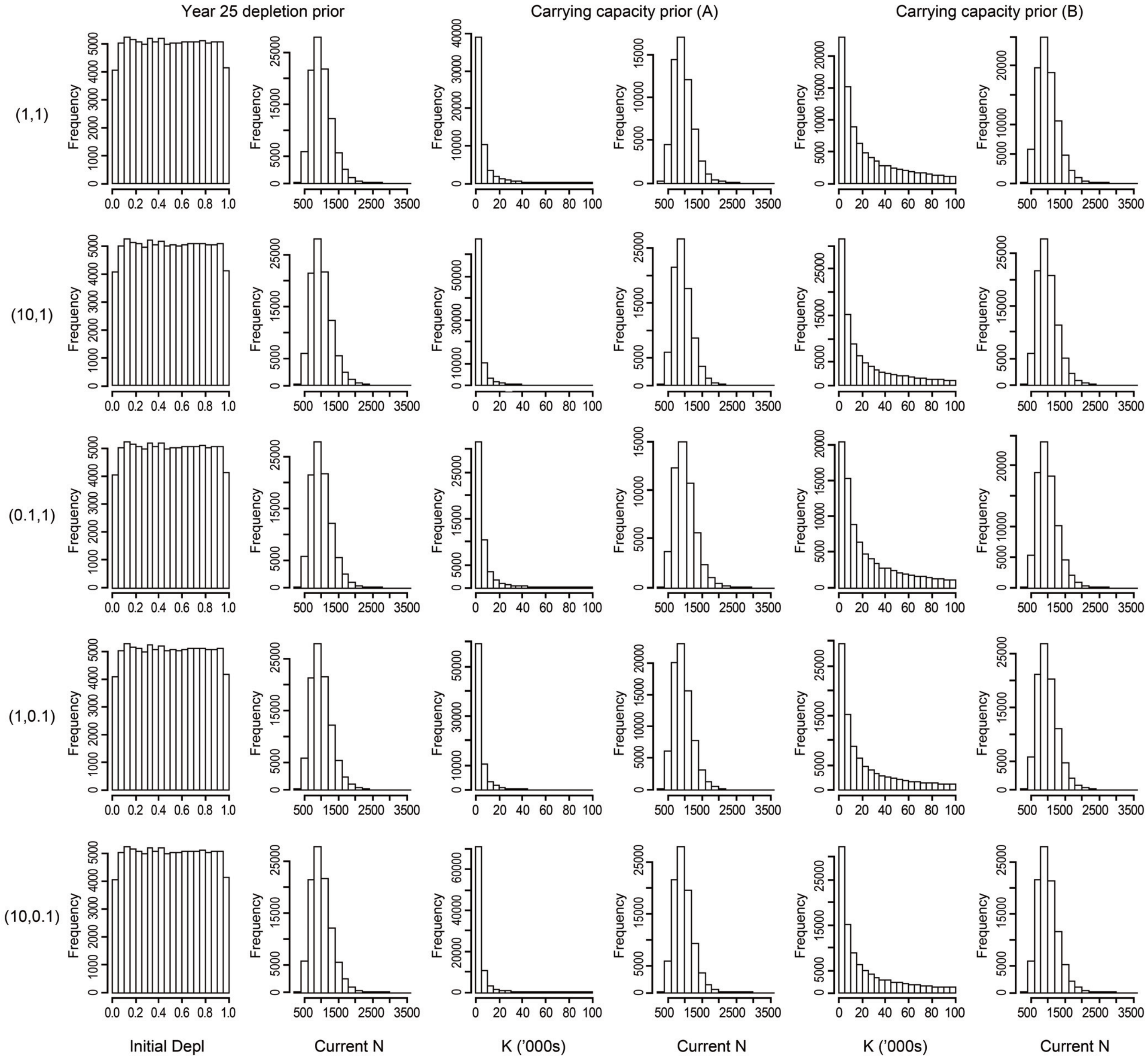

Fig. 4. Histograms of the post-model-pre-data distribution for the variable that is generated to create the scaling parameter (first column for each prior) and the post-model-pre-data distribution for population size in year 75. The results in this figure pertain to $N/K = 0.5$ in year 75. The results for other values of N/K in year 75 are very similar and are not shown.

extreme depletion distributions, with the implication *a priori* that the stock was highly depleted and still is, irrespective of how effort (and hence fishing mortality) has changed over time.

CONCLUSIONS, CAVEATS AND FINAL REMARKS

The process of constructing the post-model-pre-data distribution has long been known to lead to rejected parameter combinations (e.g. Brandon *et al*., 2007). However, those analyses tended to focus on biological parameters such as survival and the age-at-maturity. The analysis of this paper suggests that the choice of the prior for the 'scaling' parameter (carrying capacity or initial depletion) has a large impact on the proportion of rejected draws and that the resulting post-model-pre-data distributions are sensitive to the choice of the scaling parameter and the prior assigned to it (and for 'year 25 depletion prior' to the series of historical catches). In the case of 'Carrying capacity prior (A)' the post-model-pre-data distribution for the parameter on which the prior is based is updated, sometimes quite substantially, which is undesirable because priors should be only be updated due to data.

The effects found here will, of course, be 'mitigated' by the availability of data, as the data will update the priors, and the 'scaling' parameter should be updated substantially if there is a time series of estimates of abundance. Nevertheless, some IWC MSEs (e.g. for West Greenland bowhead whales) are based on limited data, and the extent of updating may be low. This can have an effect on the final outcomes. For example, 'carrying capacity prior (B)' implies higher levels of carrying capacity than the other two priors. As MSY is the product of r and K, this implies higher MSY for this choice of prior (which is close to the default for recent IWC MSEs for aboriginal subsistence whaling operations) and hence that more 'aggressive' *Strike Limit*

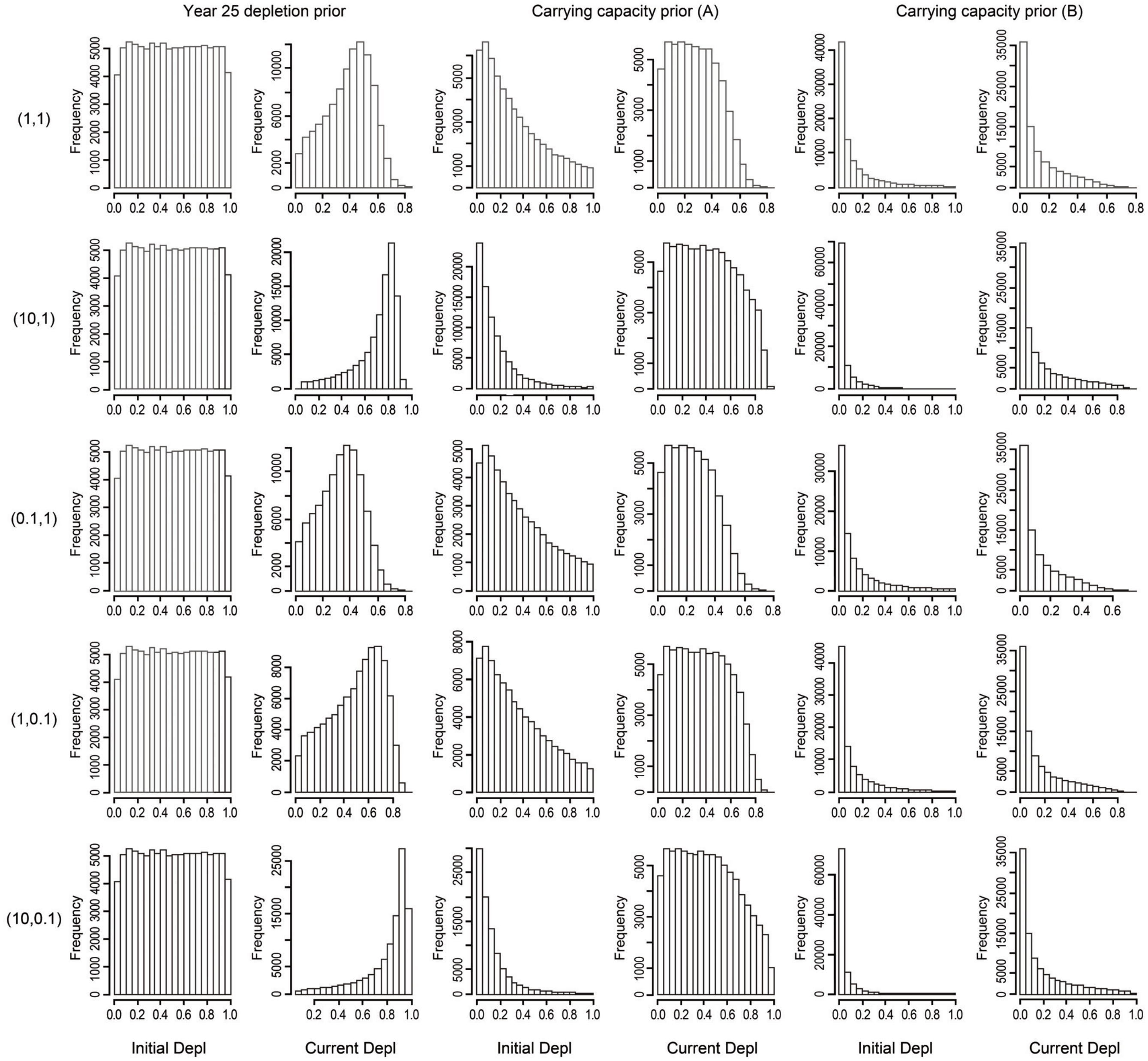

Fig. 5. Histograms of the post-model-pre-data distribution for initial (year 25) and current (year 75) relative population size (depletion). The results in this figure pertain to *N/K* = 0.5 in year 75. The results for other values of *N/K* in year 75 are very similar and are not shown.

Algorithms could be concluded to be 'safe' from a conservation viewpoint.

The analyses of this paper are based on a simple population dynamics model and actual simulation trials are usually based on more complex (e.g. sex- and age-structured, and often spatial) models. These models contain additional reasons for rejecting draws from prior distributions (e.g. parameter combinations that lead to adult survival being lower than that for juveniles). However, the general concerns raised here would be robust to more complex model structures because the fundamental population dynamic process that leads to the results (the *r-K* trade-off) is a basic property of all population models.

Overall, the results of this paper lead to some recommendations regarding future best practices for Bayesian MSEs (particularly those for which data are sparse and/or uninformative) as well as Bayesian and Bayesian-like data-poor methods for assessment stocks (e.g. Martell and Froese, 2013).

(1) The issue of the appropriate distribution for the 'scaling' parameter should be an explicit component of the IWC *Implementation* and *Implementation Review* process, and in general in best practice guidelines for MSE (e.g. Punt *et al.*, 2016).

(2) The post-model-pre-data distribution (and posterior) for key parameters (such as initial and final depletion and MSY) should be reported and evaluated, particularly if the prior distribution for the scaling parameter is not updated substantially. It is necessary to assess the extent to which the posterior for key model outputs reflects the data or the prior/the post-model-pre-data distribution.

(3) There may be value in 'redrawing' parameters when the implied post-model-pre-data distribution does not match that intended (c.f. Brandon *et al.*, 2007).

(4) There would be value in considering more than one assumption (e.g. the three approaches considered in this

paper) regarding the 'scaling' parameter in MSEs if the post-model-pre-data distributions (and posteriors) are sensitive to the choice of 'scaling parameter'.

ACKNOWLEDGEMENTS

Gisli Vikingsson (Marine and Freshwater Research Institute, Iceland) is acknowledged for noting during an AWMP meeting in Copenhagen surprise that all simulation trials led to very low initial depletions when using a 'Carrying capacity prior (B)'-like prior. I apologise for taking so long before being to address the issue. Natalie Dowling (CSIRO), Malcolm Haddon (CSIRO, Retired), and two anonymous reviewers are thanked for their comments on an earlier version of this paper.

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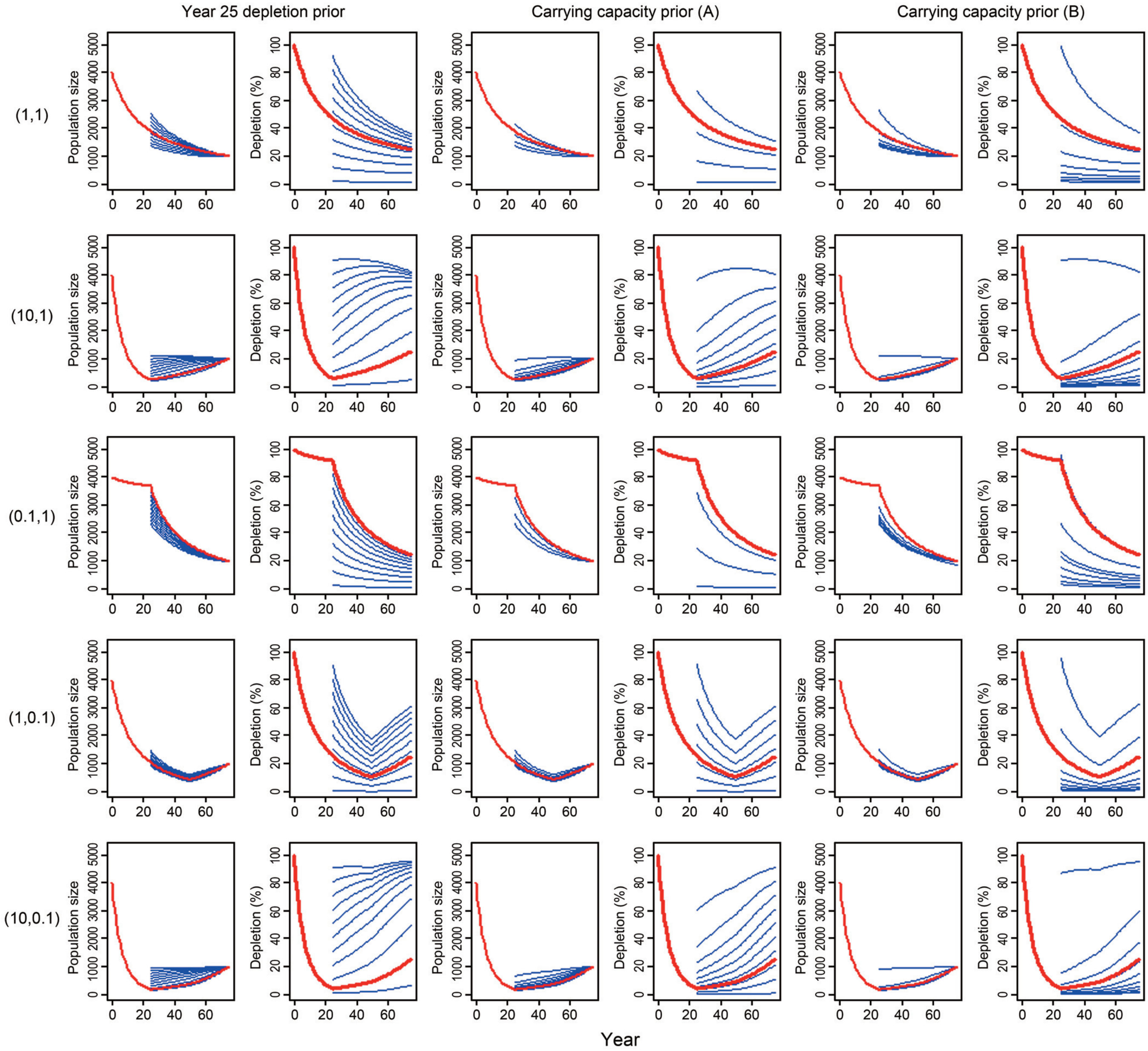
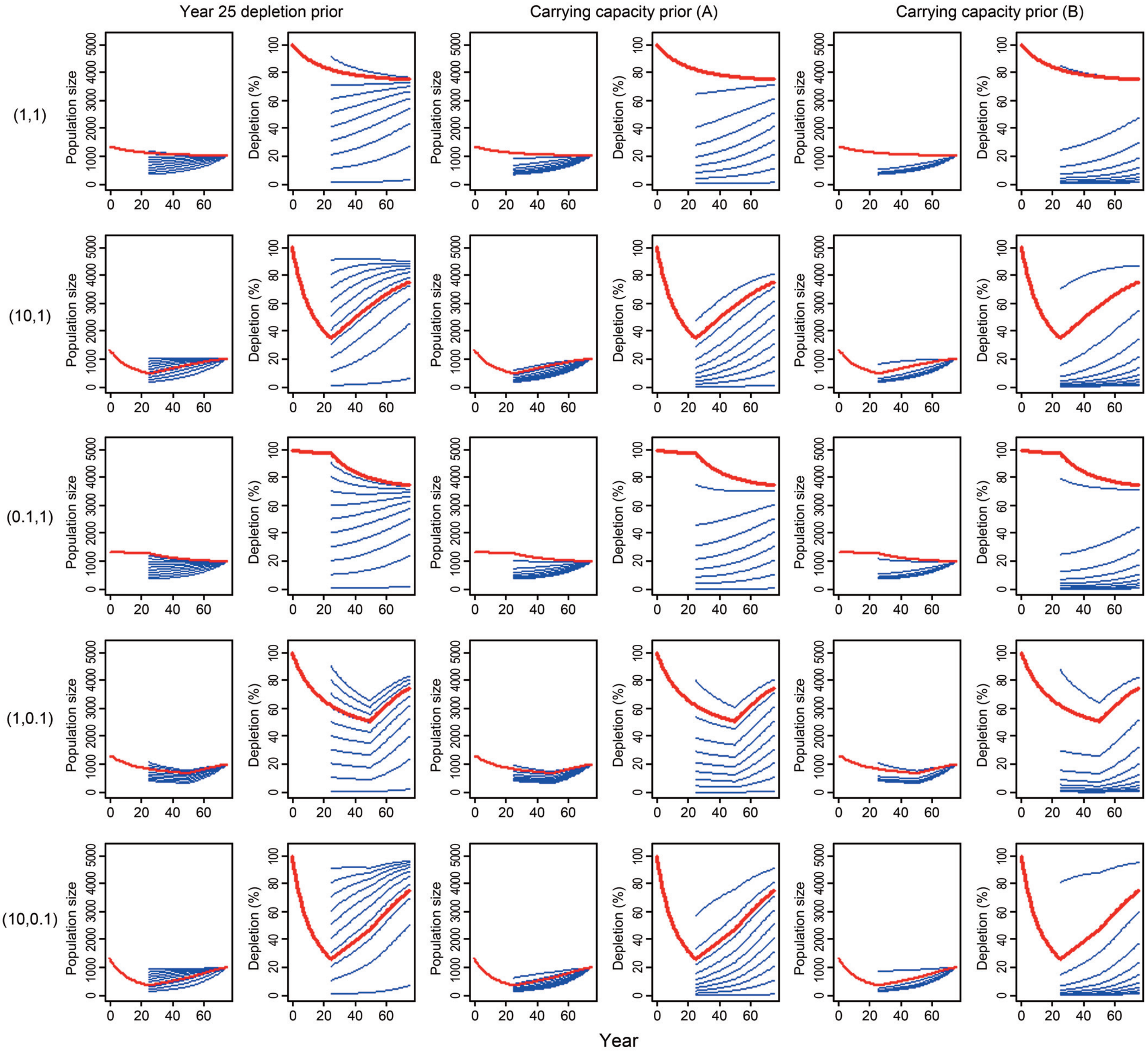
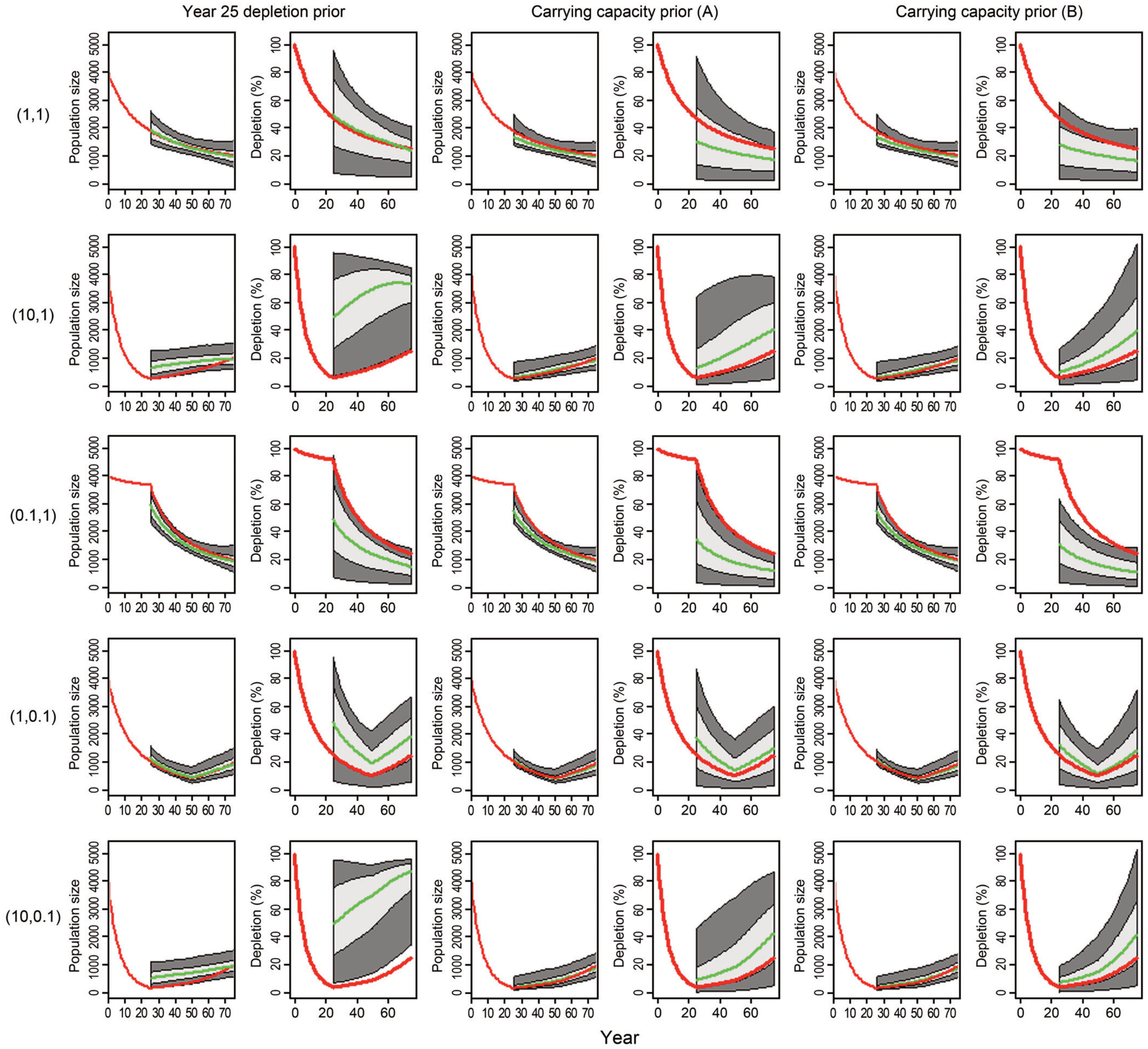
[Supplementary Figures are on following pages]



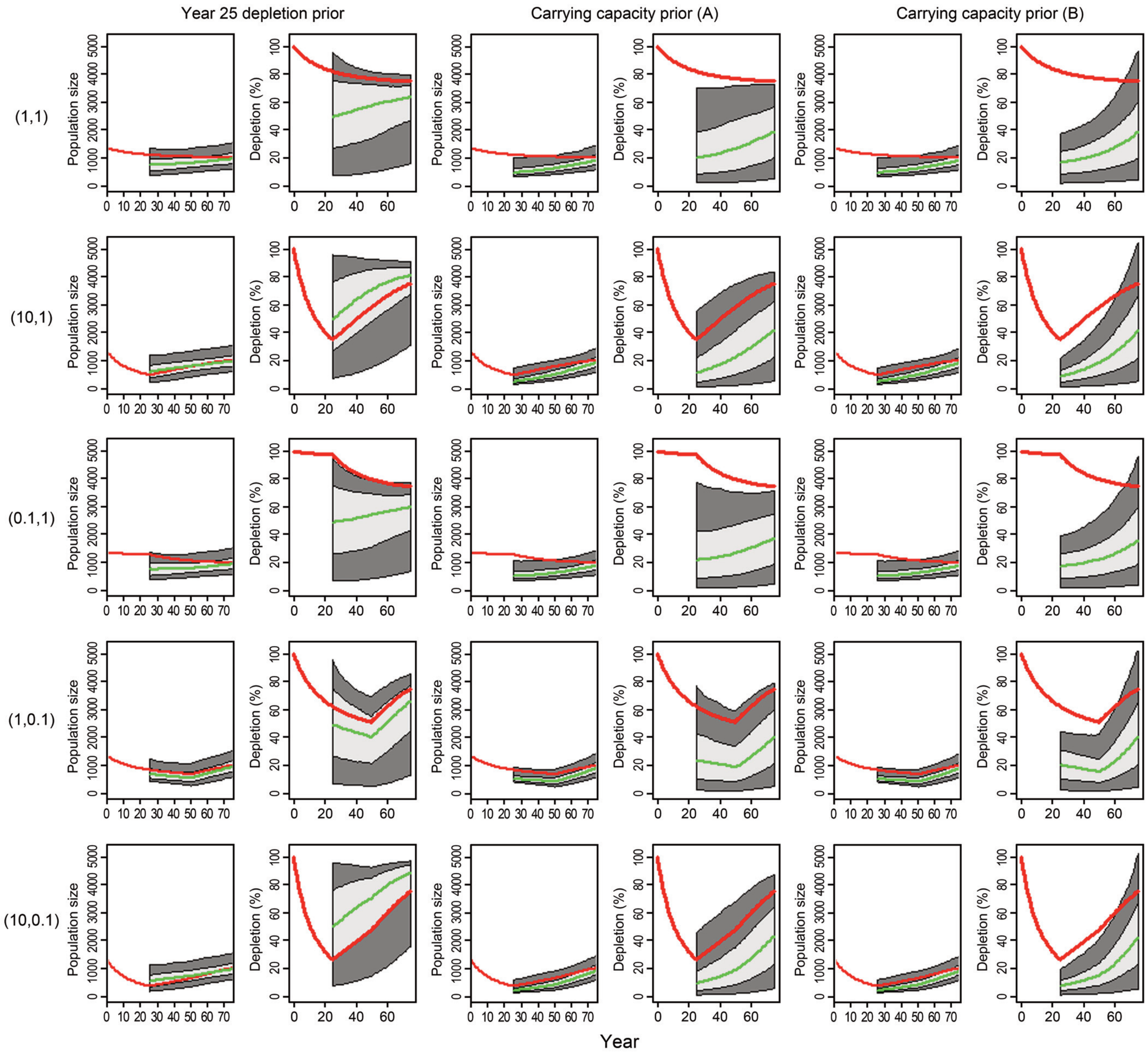
Supplementary Fig. S.1. Time-trajectories of true population size (thick red line) for each of the five effort scenarios (rows) in absolute terms and relative to carrying capacity, along with the range of time-trajectories of inferred population size in absolute and relative terms (thin blue lines) for each of the three priors (columns). The results in this figure pertain to $N/K = 0.25$ in year 75.



Supplementary Fig. S.2. Time-trajectories of true population size (thick red line) for each of the five effort scenarios (rows) in absolute terms and relative to carrying capacity, along with the range of time-trajectories of inferred population size in absolute and relative terms (thin blue lines) for each of the three priors (columns). The results in this figure pertain to *N/K* = 0.75 in year 75.



Supplementary Fig. S.3. Time-trajectories of true population size (thick red line) for each of the five effort scenarios (rows) in absolute terms and relative to carrying capacity, along with the range of time-trajectories of inferred population size in absolute and relative terms for each of the three priors when account is taken of uncertainty in current population size (columns). The green lines denote the distribution medians, the light grey shading the 50%iles of the distributions and the dark grey shading the 90%iles of the distributions. The results in this figure pertain to N/K = 0.25 in year 75.



Supplementary Fig. S.4. Time-trajectories of true population size (thick red line) for each of the five effort scenarios (rows) in absolute terms and relative to carrying capacity, along with the range of time-trajectories of inferred population size in absolute and relative terms for each of the three priors when account is taken of uncertainty in current population size (columns). The green lines denote the distribution medians, the light grey shading the 50%iles of the distributions and the dark grey shading the 90%iles of the distributions. The results in this figure pertain to N/K = 0.75 in year 75.

Density, abundance and group size of river dolphins (*Inia geoffrensis* and *Sotalia fluviatilis*) in Central Amazonia, Brazil

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ABSTRACT

A boat-based survey was conducted in the Tefé river and lake (Brazil) in December 2013, during the transitional water period. A combination of strip-width transects parallel to the river, lake-margins and confluences, and cross-channel line transects in the lake, were used to cover a total distance of 670 linear kilometres of the dolphins' habitat. A total of 383 groups of Amazon river dolphin and 124 groups of tucuxi were observed. Group size, density and abundance estimates were obtained per species and habitat (tributary, lake-margin and confluence). Group sizes ranged from one to six individuals for the Amazon river dolphin and from one to eight individuals for the tucuxi. The abundance of river dolphins was higher for the Amazon river dolphin (911, CV = 0.15) than the tucuxi (511, CV = 0.26). Higher densities were found in the lake-margin and tributary for the Amazon river dolphin and in the confluences for the tucuxi. Lake-margins, confluences and tributaries are therefore proposed as critical habitats for the conservation of river dolphins in central Amazonia. The Tefé lake is identified as an area of concern due to a high number of human stressors such as boat traffic, fishing and habitat degradation.

KEYWORDS: ABUNDANCE ESTIMATES; HABITAT; SURVEY-VESSEL; MONITORING; SOUTHERN HEMISPHERE; SOUTH AMERICA

INTRODUCTION

The Amazon river dolphin (*Inia geoffrensis*, Blainville 1817) and the tucuxi (*Sotalia fluviatilis* Gervais and Deville, 1853), are widely distributed in the Amazon, Orinoco and Tocantins river basins of South America (Best and da Silva, 1993; Hrbek *et al.*, 2014; Santos *et al.*, 2012). The Amazon river dolphin is listed as 'Endangered' by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (da Silva *et al.*, 2018) and the National List of Brazilian Fauna Threatened with Extinction (Brazilian Ministry of the Environment, 2014); the tucuxi is listed as 'Data Deficient' in both of the lists primarily due to the lack of data and associated assessments to evaluate the risk of population decline (Secchi, 2012). Lack of data is of concern, particularly because river dolphins are facing increasing human threats such as negative interaction with fisheries, population isolation by dams, bio-contamination by heavy metals (mining) and their illegal harvest for use as bait in fisheries for the *piracatinga* catfish, *Calophysus macropterus* (Gómez *et al.*, 2008; Hoyt, 2005; Iriarte and Marmontel, 2013; Trujillo *et al.*, 2010). Furthermore, the Action Plan for South American River Dolphins 2010–20 (Trujillo *et al.*, 2010) recommended that density and abundance estimates be generated to evaluate and monitor the status of dolphin populations and to prioritise conservation and management actions, particularly in areas with absence of information.

This study provides estimates of density and abundance of river dolphins in a sub-basin of the Amazon river in central Amazonia as part of an initiative to strengthen an existing network of researchers and managers known as the South American River Dolphin Protected Area Network (SARDPAN). The overarching goal of this study is to contribute to the evaluation and monitoring of the conservation status of river dolphins in South America. The research reported here constitutes the first estimate of density and abundance of river dolphins for the Tefé river and lake.

METHODS

Study area

Boat-based surveys were conducted in the Tefé lake and river (a tributary of the Solimões river), a narrow river and lake system of central Amazonia (3°21'0.35''S, 64°42'54.04''W), see Fig. 1. The Tefé river is a narrow tributary whose headwaters rise in lowlands dominated by sandy soils (Goulding *et al.*, 2003; Sioli, 1984). The tributary and lake are formed by black waters that are poor in nutrients, with high concentrations of organic compounds leading to an acidic pH (Goulding *et al.*, 2003; Sioli, 1984). The lake has low water quality near the town of Tefé because of household sewage and solid waste disposal (Borges *et al.*, 2013). Fisheries activity is widely spread in the Tefé river and lake (Barthem, 1990), contributing to almost 30% of the fish landed in the town of Tefé (Ilha, pers. comm.).

Sampling protocol

A regional boat-decker, navigating at an average speed of 12kmh^{-1}, was used to conduct a survey from 3–11 December 2013, during the transitional water period at the beginning

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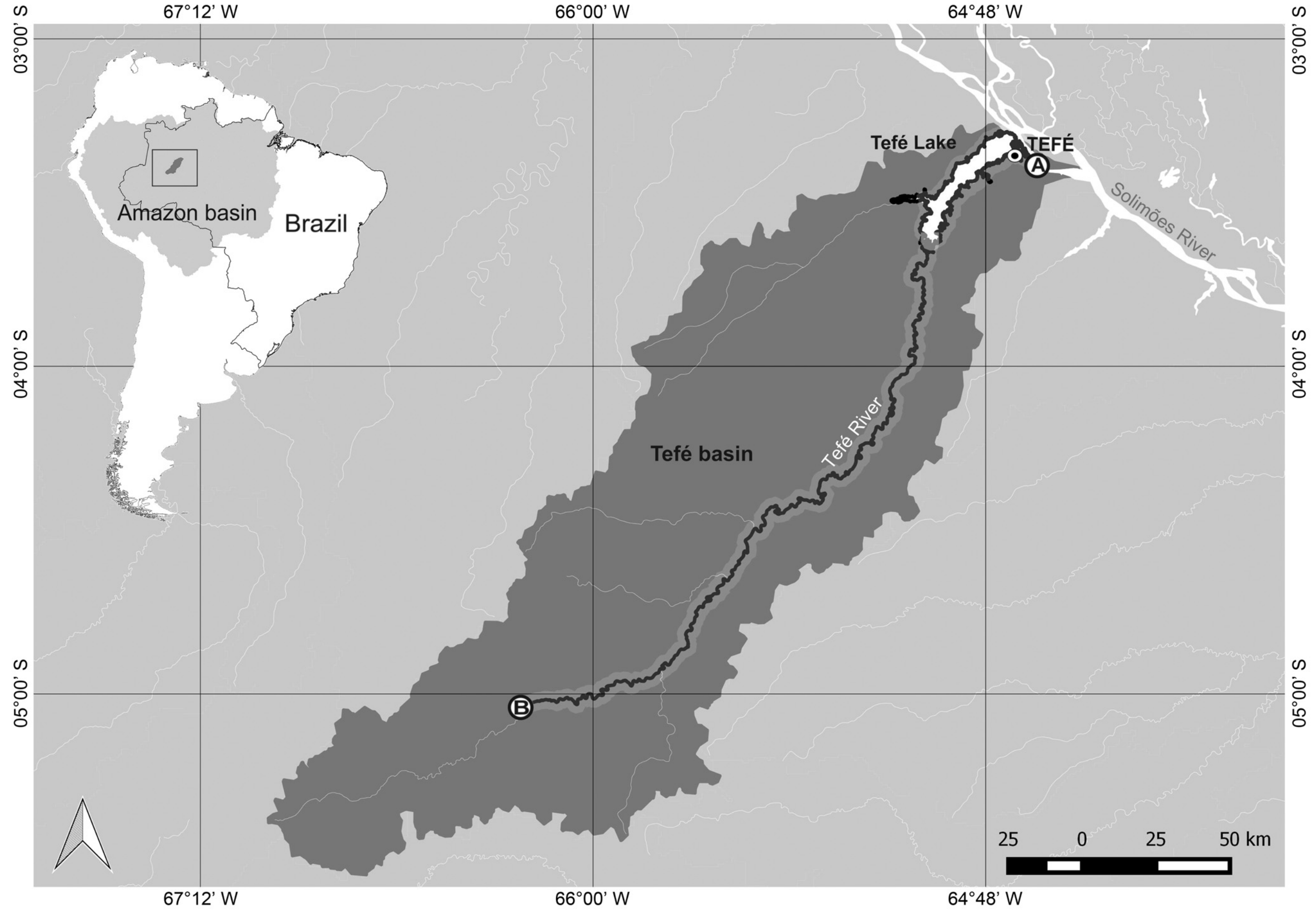

Fig. 1. Map of Central Amazonia (light grey) specifying the sub-basin of Tefé river (dark grey) and Tefé town. Point A indicates the survey starting location at the confluence between the Tefé lake and the Solimões river and point B the survey end location at the Tefé river.

Table 1
Definition of habitat types surveyed during December 2013 in central Amazonia

Habitat type or stratum	Location in this study	Definition
Tributary	Tefé river	Small and medium size rivers with maximum width of 400m (Gomez-Salazar *et al*., 2012a). Most of the small blackwaters rivers are concentrated in the central Amazon, just as Tefé river (Goulding *et al*., 2003).
Confluence	Tefé lake and Solimões river	Connection areas between small or large rivers and lakes with others, including channels. May or may not present a mix of waters (Martin *et al*., 2004, Gomez-Salazar *et al*., 2012a). The confluence between Tefé lake and Solimões river is an example of black and white waters mixing.
Lake	Tefé lake: General	Can present oval, elongated or dendritic shapes and shallow waters with maximum depth ranging from 6-12m in the high-water level. Large lakes, such as Tefé, are connected to rivers most of the time through small channels (Junk *et al*., 2012).
	Tefé lake: Margin area	Area of the lake with a width of 200m from the margin to the channel (Martin *et al*., 2004, Gomez-Salazar *et al*., 2012a).
	Tefé lake: Channel area	Area of the lake excluding the area of lake-margin, *i.e*., channel further away than 200m of the margin in any perimeter of the lake (Martin *et al*., 2004, Gomez-Salazar *et al*., 2012a).

of the flooding season (between 'low' and 'high' water levels).

River dolphins' habitat comprises rivers, channels, lakes and confluences, all of which have diverse characteristics (Table 1). They are distributed differentially amongst these various habitats, with densities generally higher at the river margins, confluences and lakes (Gomez-Salazar *et al.*, 2012a; Martin and da Silva, 2004; Martin *et al.*, 2004). Recognising the need to take this into account in the sampling design, data collection as well as data analysis were carried out by means of stratification (Buckland *et al.*, 2001; 2004). A combination of strip and cross-channel line transect field protocols were implemented (Gomez-Salazar *et al.*, 2012a; Martin and da Silva, 2004; Vidal *et al.*, 1997). Cross-channel line transects were conducted by crossing the lake from one margin to another in a zigzag pattern. Strip-width transects of 200m or less (depending on the river width) were conducted parallel to the margin of the lake and the tributary, where the distance to the shore was controlled using a laser range finder. Only strip transects were conducted in the Tefé river due to the limited width of this tributary (mean width of 152m).

Two independent platforms were present, each 7.3m above water level (Gomez-Salazar *et al.*, 2012a; Laake and Borchers, 2004). The first platform was located at the front of the boat (forward platform), and the second platform at the back, facing the opposite direction (rear platform). There were three observers and one data recorder on each platform, an additional effort data recorder in the forward platform and a 'referee' transiting between both platforms. The observers actively searched for the river dolphins from 0° (trackline) to 90° on each side of the platform. For each sighting, the following information was collected: geographic position, species, group size, presence of calves, distance from the dolphins to the margin (collected only for strip transects), angle of the observer to the dolphins and distance from the observer to the dolphin group. Distances to the dolphins and from the dolphins to the margins were estimated by naked eye by observers with previous experience with the survey method described above (CG-S and FT).

Sighting data from both platforms were integrated into a single data sheet at the end of the survey and the correspondence between the dolphins detected by the forward and rear platform was determined (i.e. whether a sighting from the rear platform was a confirmation of one from the front platform or a new detection). This was based on the judgment of the referee regarding time of the sightings, side, angle, species and group size (i.e. whenever the referee had not been able to track the group in real time from the forward to the rear platform).

Following Gomez-Salazar *et al.* (2012a), environmental conditions were recorded every 30 minutes and included river state (0 to 3, increasing turbulence scale), glare (0 to 3, increasing intensity scale) and visibility (1 to 4, 1 being poor and 4 excellent).

Density estimates: strip transects

Density of river dolphins for each habitat *i* (tributary, lake-margin, confluence) were obtained based on a Horvitz-Thompson-like estimator:

$$\hat{D}_i = E(s)\frac{\hat{D}g_i}{w\hat{g}(0)'}$$

where *E(s)* is the mean group size, *w* is the transect width (truncated at 200m or mean width when the distance across the tributary was < 200m) and $\hat{g}(0)$ is the detection probability on the transect line.

River dolphins have been found to be distributed according to a gradient with higher densities closer to the margin in the first 50m lessening towards the river channel up to 200m out (Gomez-Salazar *et al.*, 2012a; Martin *et al.*, 2004). Considering that detection probability decreases with distance, a conflict between density and detection variation may occur. For this reason, corrections for undetected clusters in the 200m strip-width transects were incorporated (*P1* and *P2*) by using a detection function fitted for the cross-channel line transects (Gomez-Salazar *et al.*, 2012a). Therefore, density of clusters ($\hat{D}g_i$) is defined as:

$$\hat{D}g_i = \frac{ER_{i(0\text{–}50)}}{P_2} + \frac{ER_{i(50\text{–}100)}}{P_1} + \frac{ER_{i(100\text{–}150)}}{P_1} + \frac{ER_{i(150\text{–}200)}}{P_2}$$

Where *ER* is the mean encounter rate by transect, $P1_{\text{Amazon river dolphin}} = 0.955$ and $P1_{\text{Tucuxi}} = 0.994$ are the detection probabilities between 0–50m from the transect line (i.e. 50–100m or 100–150m from the margin), and $P2_{\text{Amazon river dolphin}} = 0.523$ and $P2_{\text{Tucuxi}} = 0.675$ are the detection probability between 50–100m from the transect line (i.e. 0–50m or 150–200m from the margin).

The $\hat{g}(0)$ was estimated with the Petersen estimator:

$$\hat{g}(0) = 1 - \frac{n_{\text{rear new}^2}}{n_{\text{rear}}}$$

Where n_{rear} is the number of river dolphins detected by the rear platform and $n_{\text{rear new}}$ is the number of dolphins detected by the rear platform which were not detected by the forward platform.

Finally, abundance was derived from density as:

$$\hat{N}_i = \hat{D}_i A_i$$

Where A_i is the size of the area surveyed, calculated using Geographic Information Systems (GIS). For tributary and lake-margin habitats, the areas were calculated as the perimeter of the Tefé river and lake multiplied by the average strip width of 152 and 200m respectively. For lake-channel habitat, the area resulted from the difference between the total area of the lake and the area of the lake-margin. For confluence, the width of each confluence was multiplied by the transect length, and then summed to obtain the total area.

The variances of encounter rates were derived empirically, the variances of the detection probability (*P1* and *P2*) were estimated following Gomez-Salazar *et al.* (2012a) and the variances of $\hat{g}(0)$ calculated through the delta method (Seber, 1982). These were used to compute the final variance and correspondent standard deviation (SD) and coefficient of variation (CV).

Density estimates: line transects

It was expected that density estimates of river dolphins in the lake-channel area would be obtained by fitting detection probability models to perpendicular distance data using conventional line transect sampling methods (Buckland *et al.*, 2001). However, only 7 and 2 sightings were recorded for the Amazon river dolphin and the tucuxi respectively, an insufficient sample to properly estimate detection probability (Buckland *et al.*, 2001). For populations that occur in clusters, such as in the present study, the sample size should be larger (~60–80) to accurately estimate abundance of individuals (Buckland *et al.*, 2001). For this reason, the results in the lake-channel were omitted and only the encounter rates were presented in order to compare with relative densities estimated for other habitats. The majority of river dolphins are found in areas closer to the river bank (Gomez-Salazar *et al.*, 2012a; Martin *et al.*, 2004), and thus, it is not expected that omitting estimates from cross-channel line transects will have a large impact in the overall abundance estimate of dolphins for this region.

RESULTS

A total of 590 and 80 linear kilometres of sampling effort were conducted using strip and cross-channel line transects respectively, with a total of 383 sightings of Amazon river dolphins and 124 sightings of tucuxis recorded. Overall, the transects were surveyed during good sighting conditions:

Table 2

Area of stratum (A) (km^2), mean group size $E(s)$ with correspondent standard deviation ($SD(s)$), number of sightings (n), mean encounter rate by transect (ER), abundance ($\widehat{N}$) and density ($\widehat{D}$) (ind km^{-2}) with correspondent standard deviation (SD) and coefficient of variation (CV) for Amazon river dolphin (*I. geoffrensis*) and tucuxi (*S. fluviatilis*) by stratum.

	Amazon pink dolphin									Tucuxi							
Habitat	A	$E(s)$	$SD(s)$	n	ER	$\widehat{N}$	$\widehat{D}$	SD	CV	$E(s)$	$SD(s)$	n	ER	$\widehat{N}$	$\widehat{D}$	SD	CV
Tributary	104	1.44	0.70	395	0.72	582	5.59	0.99	0.18	2.32	1.49	140	0.38	210	2.01	2.58	1.28
Lake-margin	76	1.40	0.73	139	0.65	327	4.28	1.13	0.26	2.35	1.44	122	0.73	290	3.79	1.71	0.45
Lake-channel	328	1.43	0.79	10	0.28	–	–	–	–	1	0.00	2	0.08	–	–	–	–
Confluence	1.2	1.67	1.03	10	0.91	2	1.54	1.03	0.67	3.2	1.90	16	1.60	9	9.08	1.10	0.12
Overall**	509.20	1.48	–	554	0.64	911	3.80	–	0.15	2.22	–	280	0.70	511	4.96	–	0.26

* The values are rounded for two decimal places to fit in the table. Therefore, the multiplication of density and area does not result exactly in the abundance.

** The overall estimates of $E(s)$, ER and $\widehat{D}$ correspond to the mean among habitats.

100% during low turbulence (levels 0 and 1), 84% during minimum glare (levels 0 and 1) and 68% during good and excellent visibility.

Group size ranged from one to six individuals for Amazon river dolphin and from one to eight for tucuxi. Differences in group size across habitats were not observed for both species (Kruskal Wallis test, $\alpha = 0.05$). Almost all animals present were detected: $\hat{g}(0)$ was estimated at 0.99 (CV = 0.002) for the Amazon river dolphin and 0.99 (CV = 0.003) for tucuxi. The highest density of Amazon river dolphins was found in the tributary (5.85 ind km^{-1}, SD = 0.99), while the lowest density was found in the confluences (1.54 ind km^{-1}, SD = 1.03; Table 2). Conversely, the tucuxi's highest density was in the confluences (9.03 ind km^{-1}, SD = 1.29), followed by the lake-margin habitat (3.77 ind km^{-1}, SD = 1.71) (Table 2). Overall, the abundance of river dolphins in the Tefé river-lake system was higher for Amazon river dolphin (911, CV = 0.15) than tucuxi (511, CV = 0.26) (Table 2).

DISCUSSION

This study provides a benchmark for river dolphin abundance estimates in the Tefé river and lake. Group size, density and abundance were explored in different habitats to enable a comparison among them and with other studies.

Group sizes of both species of river dolphins (ranging from 1 to 8) were consistent with previous studies in other regions of Amazonia (Gomez-Salazar *et al.*, 2012b; Martin *et al.*, 2004). Differences in group size across habitats were not identified. As stated by other studies (Gomez-Salazar *et al.*, 2012b; Martin *et al.*, 2004), these differences might arise from repeated surveys conducted in different seasons. Repeated surveys could for example identify the behavioural responses of river dolphins to freshwater floods.

The preference of river dolphins for lakes and confluences instead of narrow rivers has been reported in other regions of Amazonia, as these areas have higher productivity compared with other habitats (Aliaga-Rossel, 2002; Gomez-Salazar *et al.*, 2012b; Martin *et al.*, 2004; McGuire and Wienemiller, 1998). For instance, the mixing of black and white waters in the confluence between the Japurá and Solimões rivers (an area adjacent to our study area) has also been reported as a preferred habitat for tucuxi (Martin *et al.*, 2004). Similarity of features is likely to explain the high density of tucuxi in the confluence between the Tefé lake and Solimões river.

Although confluences represent less than 1% of the proportion of the total study area, this habitat is particularly important in Amazonia for the movement of aquatic life between rivers, tributaries and lakes during and after freshwater floods (Barthem and Goulding, 1997; Fernandes, 1997; Henderson, 1990). Every year during the highwater period, an area of approximately 170,000km^2 in the Amazon is inundated, forming the floodplains (Hamilton and Lewis, 1990). Seasonal freshwater floods enhance the total aquatic productivity in the Amazon and trigger the migration of fish and dolphins between habitats (Barthem and Goulding, 1997; Lewis *et al.*, 2000; Martin and da Silva, 2004).

Contrary to the tucuxi, densities of Amazon river dolphins were the highest in the Tefé river (tributary). Amazon river dolphins have morphological adaptations (e.g. flexible bodies, small dorsal fins and large pectoral fins) that allow them to exploit narrow areas with limited water depth without getting stranded (Martin and da Silva, 2004). This may explain the higher density of Amazon river dolphins in the tributary, and the higher density of tucuxi in habitats that are easier to navigate (i.e. confluences and lakes) during the present study due to the season when the study took place.

Comparing monitoring efforts in Amazonia

Density and population size of river dolphins in South America have been estimated from surveys conducted in small areas using varied methodologies. Earlier surveys were mainly focused on obtaining encounter rates instead of densities and abundance estimates (da Silva, 1994; Herman *et al.*, 1996; Kasuya and Kajihara, 1974; Layne, 1958; Meade and Koehnken, 1991; Pilleri and Gihr, 1977; Trujillo, 2000). More recent surveys have been conducted using standardised sampling methods (Aliaga-Rossel, 2002; Leatherwood, 1996; Martin and da Silva, 2004; Martin *et al.*, 2004; McGuire, 2002; Utreras, 1996; Vidal *et al.*, 1997). However, these latter studies have differences in sighting protocols (e.g. number of observers), analysis (e.g. assumptions about $g(0)$, corrections by the detection probability as a function of perpendicular distances), and the season surveyed. Consequently, caution should be applied when comparing results across areas and studies. Here, the sampling and analytical methods proposed by Gomez-Salazar *et al.* (2012a) were followed, which allowed for a preliminary and relatively simple comparison with density estimates reported in other areas of Amazonia (Figs 2 and 3).

The density of the Amazon river dolphin in the Tefé river was higher than the densities reported in tributaries located in Bolivia, Venezuela, Colombia and Ecuador, and similar to one of the highest densities ever reported – in a Peruvian

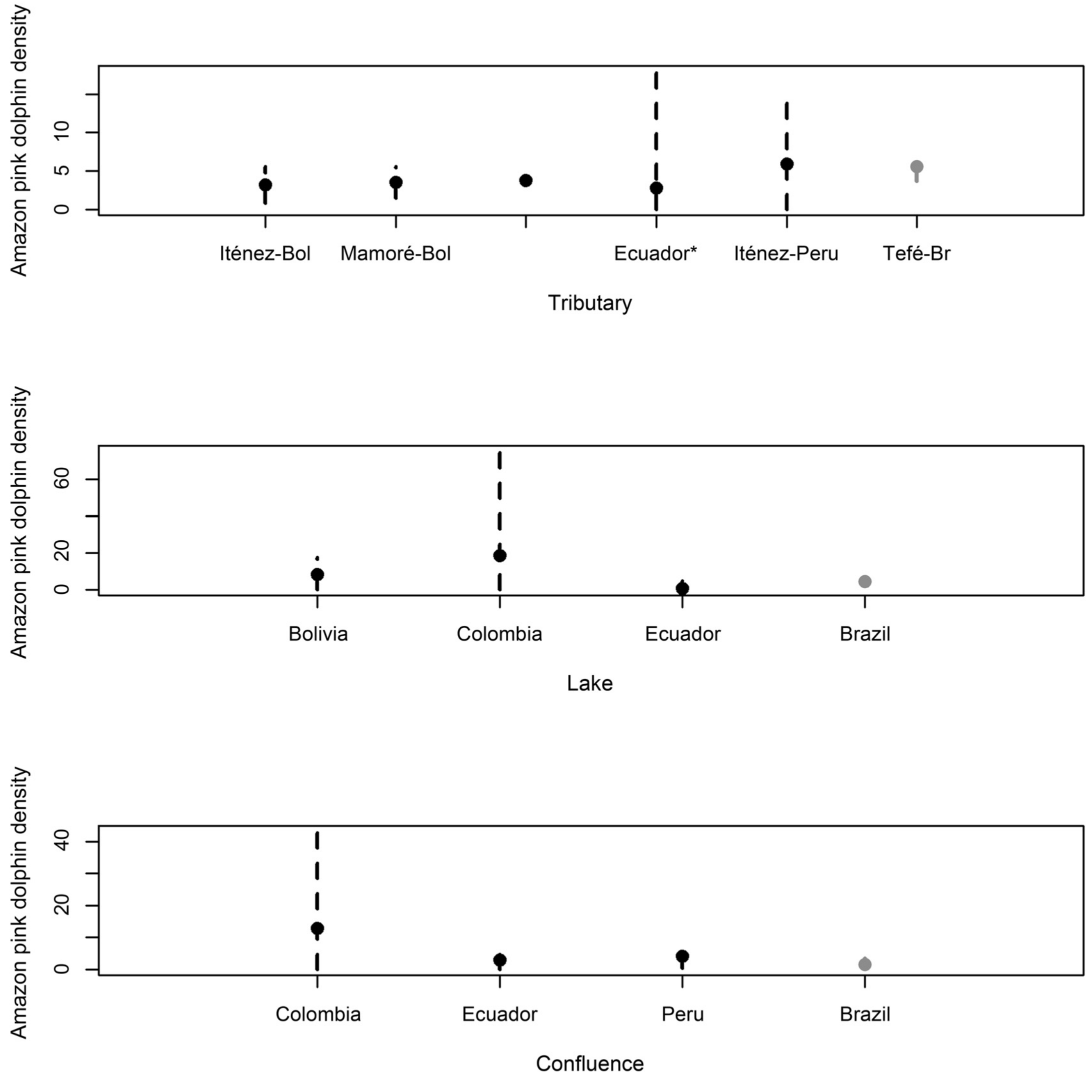

Fig. 2. Density of *I. geoffrensis* estimated in tributaries, lakes and confluences of Colombia, Ecuador, Peru and Bolivia (from Gomez-Salazar *et al.* (2012a) (black) and Brazil (grey). Dots represent the mean estimates and dashed lines the standard errors. *Refers to Cuyabeno, Yasuni, Lagartococha and Aguarico rivers.

tributary (Gomez-Salazar *et al.*, 2012a). This suggests that the Tefé river, together with the Pacaya Samiria Reserve in Peru, the Mamirauá Sustainable Development Reserve in Brazil, and the Iténez and Mamoré rivers in Bolivia, are hotspots for the Amazon river dolphin at a regional scale (hotspots of river dolphins were previously defined and identified as locations with the highest density estimates of dolphins in South America; Gomez-Salazar *et al.*, 2012a).

Conversely, the density estimates of the Amazon river dolphin reported in the Tefé lake and in the confluence were smaller than those obtained in other countries, being only comparable to the low densities of Ecuador (Gomez-Salazar *et al.*, 2012a). Further surveys which take into account seasonality might clarify the importance of the Tefé lake for Amazon river dolphins.

For tucuxi, the density was smaller than estimates reported in rivers of Colombia and higher than in rivers of Ecuador (Gomez-Salazar *et al.*, 2012a). Conversely, density at confluences was similar to that estimated in Peru (Gomez-Salazar *et al.*, 2012a). Nevertheless, caution is warranted when interpreting these results due to the large CVs associated with the density estimates.

It is also important to highlight that because the abundance of river dolphins in the lake-channel was not estimated due to the small number of detections in this habitat, the overall abundance in the Tefé lake will be negatively biased to an unknown extent. The low abundance of river dolphins in the lake-channel corroborates other studies in which the encounter rates in lake or river channels are usually low (Gomez-Salazar *et al.*, 2012a; Martin *et al.*, 2004).

Human activities impacting river dolphin populations in the Tefé lake

Although density estimates for river dolphins in lake-margin habitats are usually the highest in other areas of Amazonia, this is not the case in the Tefé lake. Due to its proximity with the city of Tefé (human population of 62,662 in 2014), a variety of potentially harmful (to dolphins) human activities take place within the lake region, including fisheries, logging and riverine vessel traffic. A systematic survey reported 11 Amazon river dolphin and 4 tucuxi carcasses in the Tefé lake in 2013 (unpublished data). Taking into account the abundance point estimate provided in this study, these mortalities represent approximately 1.15% of the Amazon river dolphin and 0.8% of the tucuxi population being removed from the Tefé lake in a single year. Evidence of

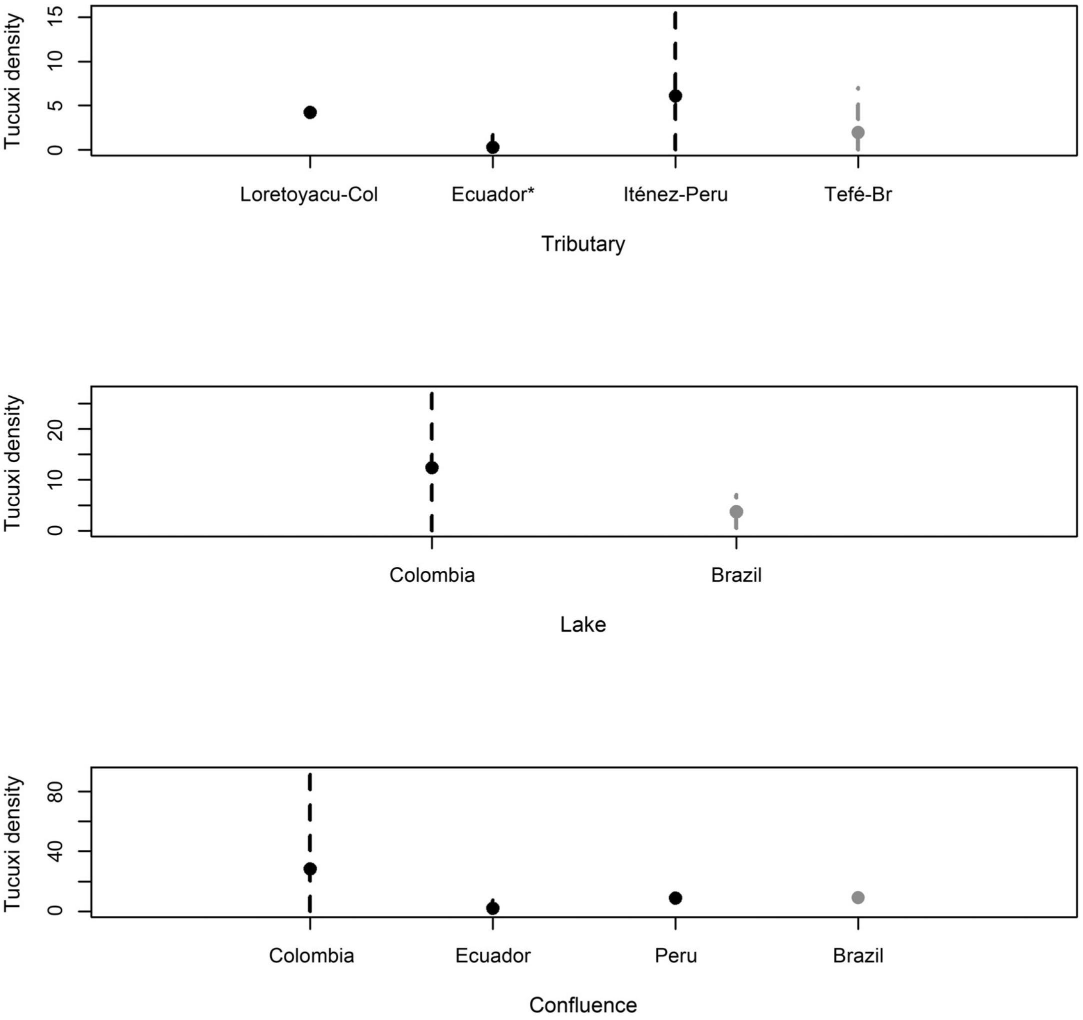

Fig. 3. Density of *S. fluviatilis* estimated in tributaries, lakes and confluences of Colombia, Ecuador and Peru (from Gomez-Salazar *et al.* (2012a) (black) and Brazil (grey). Dots represent the mean estimate and dashed lines the standard errors. *Refers to Cuyabeno, Yasuni, Lagartococha and Aguarico rivers.

interaction with fisheries based on possible marks of gillnets (entanglement) and of intentional killing (spear and axe marks) were observed in 55% of the carcasses (Santos *et al.*, 2014). Another threat to these populations includes habitat degradation, in particular chemical pollution. The city of Tefé does not have basic sanitation services and as a consequence, household sewage, wastewater and solid waste have been released into Tefé lake (Borges *et al.*, 2013). The poor water quality of the lake may explain findings of abscesses in the river dolphins necropsied which may be due to infectious diseases such as tuberculosis, pneumonia, golf ball disease and others (Bueno, pers. comm.). It is important to highlight that the number of carcasses reported probably represent a minimum mortality value as they do not account for unobserved records.

Of most serious concern is the decline in apparent survival of Amazon river dolphins for the past ten years in an area adjacent to the Tefé lake (Mintzer *et al.*, 2013). This decline has been attributed to the illegal harvesting of dolphins to be used as bait for the *piracatinga* catfish fishery. Moreover, the harvest rates reported seemed to exceed conservation limits and may be unsustainable (Mintzer *et al.*, 2013). In response, the Brazilian government has banned the commercial capture of the *piracatinga* catfish for five years starting on January 2015. There is no sign that this illegal harvesting is currently occurring in the Tefé river-lake system, although purchase, storage and disposal of *piracatinga* catfish still occur in the town of Tefé (Botero-Arias *et al.*, 2014).

In addition, disturbance due to elevated levels of noise generated from human activities can cause sub-lethal impacts (New *et al.*, 2013; NRC, 2005; Pirotta *et al.*, 2014). The potential impacts of noise on river dolphin populations in general have not as yet been studied (e.g. possible displacement from important habitats and foraging disruption), and noise exposure is potentially an additional human stressor to river dolphins in the Tefé lake.

Overall, human activities in South America riverine areas are increasing and some of these activities are causing lethal and/or sub-lethal impacts on river dolphin populations. The local and regional magnitude of these potentially cumulative impacts is not as yet fully understood.

FINAL REMARKS AND RECOMMENDATIONS

This study represents the first attempt at a standardised monitoring programme with the goal of assessing population trends of Amazon river dolphins and tucuxi in the Tefé river-lake system. Confluences, which are important areas for river connectivity, as well as lake-margin areas, had the highest density estimates of tucuxis. Conversely, the Tefé river had some of the highest density estimates ever reported for the Amazon river dolphin. Therefore, we propose these confluences and Tefé lake as areas of high priority for tucuxi conservation at a local scale, and the Tefé river as an important area for the conservation of the Amazon river dolphin at both local and regional scales.

The relatively low density estimates of river dolphins in the Tefé lake, as well as the high number of increasing human activities observed in this study and in the Amazon as a whole, should be further investigated. Estimating and monitoring the potential lethal and sub-lethal impacts of human activities on river dolphin populations is recommended as a process to be undertaken in parallel to efforts to monitor river dolphin distribution and abundance. This information is fundamental to informing conservation priorities in the region.

As previously reported, repetitive surveys conducted in riverine areas using comparable methodology are required to investigate how seasonality, habitat, and other potential environmental and human variables drive variation in the density of river dolphins. However, due to funding constraints, repetitive surveys cannot be always implemented in these remote areas. In those cases, it has been proposed to survey areas during the transitional water periods, where most of the habitat types are available (e.g. channels are not completely dry and lakes are still connected to the main rivers) to make studies more comparable (Gomez-Salazar *et al.*, 2012a).

This study reports on current efforts, which are being replicated in several rivers of South America, to improve knowledge on river dolphin population parameters. Equally important, these studies are being designed with the goal of strengthening SARDPAN and enhancing capacity building in South America.

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Participatory science and directed survey methods: A case study with odontocetes in the Maui Nui region of the Hawaiian Islands

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ABSTRACT

Given the difficulties and costs often associated with surveying cetaceans, enlisting members of the public to collect data offers a promising alternative approach. Comparison of cetacean ‘participatory science’ (also known as ‘citizen science’) data with data collected during traditional scientific studies helps reveal the strengths and weaknesses of a participatory science approach. With a large number of vessel operators on the water throughout the year, including dolphin-oriented tour boats, the Hawaiian Islands offer an ideal study site to employ such a dual-method comparison. The study aimed to enhance understanding of nearshore dolphin distributions relative to bathymetry. Operators of tour and fishing vessels within the shallow Maui Nui basin of the Hawaiian Islands were recruited to report delphinid sightings. Researchers conducted standard dolphin surveys within the same region. The participatory science approach was successful in generating a large sample size of sightings from five different species. Findings here demonstrate the potential value of participatory science and of using a multimethod approach to infer odontocete distribution trends relative to bathymetry in areas where both methods are feasible. Important refinements for future projects are highlighted.

KEYWORDS: CONSERVATION; DISTRIBUTION; INCIDENTAL SIGHTINGS; SURVEY-VESSEL; WHALE WATCHING

INTRODUCTION

‘Participatory science’, also known as citizen science, is a burgeoning field that uses volunteers to collect scientific information and help answer questions that otherwise would be logistically or financially infeasible (Bhattacharjee, 2005; Dickinson *et al.*, 2010). In return, the public becomes more aware of conservation issues and gains a sense of ‘earth stewardship’ (Dickinson *et al.*, 2012). As charismatic megafauna, cetaceans are the focus of many participatory science projects. These include shore-based monitoring studies to determine habitat use and temporal variation (Evans and Hammond, 2004; Pierpoint *et al.*, 2009), using photos taken by tour operators or members of the public to help understand site fidelity via individual identification ((Baird *et al.*, 2009; Baird *et al.*, 2008), as well as stranding surveys to document mortality events and collect information on the basic biology of species (Ford *et al.*, 1998; Gannon *et al.*, 1997; MacLeod *et al.*, 2005; Mignucci-Giannoni *et al.*, 2000; Mignucci-Giannoni *et al.*, 1999). Due to the ongoing popularity of marine mammal research programmes, some such as SeaWatch in the UK and the Great Whale Count in Hawaiʻi, have been occurring for decades. Given the costs and inherent difficulties of studying marine animals, tapping into a large-scale workforce of volunteers has resulted in greater spatiotemporal coverage of cetacean data, which, with appropriate analyses, can help inform policy and management decisions through a greater understanding of marine mammal biology and threats (Baird *et al.*, 2002; Cheney *et al.*, 2013; Ford *et al.*, 1998; Gannon *et al.*, 1997; Hauser *et al.*, 2006; Weinrich *et al.*, 2000).

However, participatory science cetacean studies are prone to numerous biases, and thus results must be critically evaluated when drawing inferences. Accurate taxonomic identification is an inherent requirement for wildlife studies, but this is often difficult to achieve with participatory science research as similar species can often be confused (Bell, 2006), and this is certainly the case with cetaceans in Hawaiʻi (Baird, 2016). Non-random distributions of volunteer effort and under-detection of species may also skew data (Bird *et al.*, 2014; Crall *et al.*, 2011; Robinson *et al.*, 2018). However, when these biases are controlled in the initial design of participatory science studies and when volunteers are supervised by researchers, accurate data can be collected (Delaney *et al.*, 2008).

In the absence of direct supervision of volunteers, the accuracy of participatory science data usually requires validation that it meets a certain standard (Bird *et al.*, 2014), yet only about half of published participatory science studies include some sort of verification process to ensure data quality (Thiel *et al.*, 2014). Furthermore, only one cetacean study has compared frequency of dolphin sightings made by volunteers to those made during directed surveys (Bristow *et al.*, 2001). To address the issue of data quality, some cetacean studies have compared and combined several independent approaches, allowing for estimation of biases by method and strengthening scientific conclusions (Baird *et al.*, 2002; Cheney *et al.*, 2013).

Numerous opportunities exist to enhance the capabilities of cetacean participatory science projects to produce more comprehensive and robust scientific data. Captains and crew of commercial vessels offer a valuable resource to marine mammal studies, as they are generally familiar with their local waters and marine fauna and thus may more accurately identify species. In addition, data such as sighting

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coordinates collected by volunteers on vessels may be analysed post-hoc relative to other biological data such as water depth to better understand cetacean habitat preference. Mobile technology also holds great potential in participatory science projects as an easy, cost-efficient, real-time communication tool to help facilitate data collection and reporting (Baker and Oeschger, 2009). The widespread use of Short Message Service (SMS) text messages has helped streamline marine field efforts, with texts now used to relay information from tagged animals as well as to report catch and effort information from fishermen (Baker and Oeschger, 2009; Cronin and McConnell, 2008; McConnell *et al.*, 2004).

Around the Hawaiian Islands, historically much of the cetacean science by both citizens and experts has centered on the humpback whale (*Megaptera novaeangliae*). Until recently, most odontocete species have received comparatively little attention (Baird, 2016; Baird *et al.*, 2013). While many single species studies have been conducted around the islands, including research on common bottlenose dolphins (*Tursiops truncatus*; hereafter bottlenose dolphins) (Baird *et al.*, 2009), pantropical spotted dolphins (*Stenella attenuata*) (Baird et al., 2001; Courbis *et al.*, 2014), spinner dolphins (*Stenella longirostris*) (Benoit-Bird and Au, 2003; Lammers, 2004; Norris *et al.*, 1994; Thorne *et al.*, 2012), false killer whales (*Pseudorca crassidens*) (Baird *et al.*, 2008; Baird *et al.*, 2010), and short-finned pilot whales (*Globicephala macrorhynchus*) (Abecassis *et al.*, 2015; Mahaffy *et al.*, 2015; Van Cise *et al.*, 2017), relatively few comprehensive, systematic multispecies assessments have been made of the eighteen odontocete species known to inhabit Hawaiian waters (Baird, 2016; Barlow, 2006).

Since 2000, there has been an ongoing multispecies assessment of odontocetes around the main Hawaiian Islands (Baird, 2016; Baird *et al.*, 2013). Among other findings, these results showed that the sighting rates of most species varied with depth, with some species such as spinner dolphins most often found in depths less than 1,000m and other species such as rough-toothed dolphins (*Steno bredanensis*) commonly using depths greater than 3,000m (Baird *et al.*, 2013). However, relatively little effort was made in the shallow basin of the Maui Nui region (Maui, Lānaʻi, Molokaʻi, Kahoʻolawe; see Fig. 1), an area of high commercial tour vessel traffic. Thus, this area remains understudied with much still to be described and learned about how odontocetes use this distinct local environment. Bathymetry is an important criterion of habitat selection for many delphinids, related to, for example, enhanced foraging success or refuge from predators (Davis *et al.*, 2002; Davis *et al.*, 1998; Hastie *et al.*, 2004; Thorne *et al.*, 2012). Thus understanding the interspecific distribution of delphinids in this shallow water region of substantial human activity can help guide odontocete management.

This study implemented a participatory science delphinid-sighting project in the Maui Nui region, capitalising on the numerous vessel crew and captains operating in the region to report odontocete sightings around the four islands. In addition, existing odontocete observations collected via dedicated surveys by Baird *et al.* (2013) and the Cascadia Research Collective around Maui and Lānaʻi allowed for a comparative analysis of the two methods, increasing confidence in our understanding of delphinid distributions in insular Hawaiian waters.

METHODS

At the beginning of June 2015, the captains and/or crew members of sport fishing and commercial tour vessel

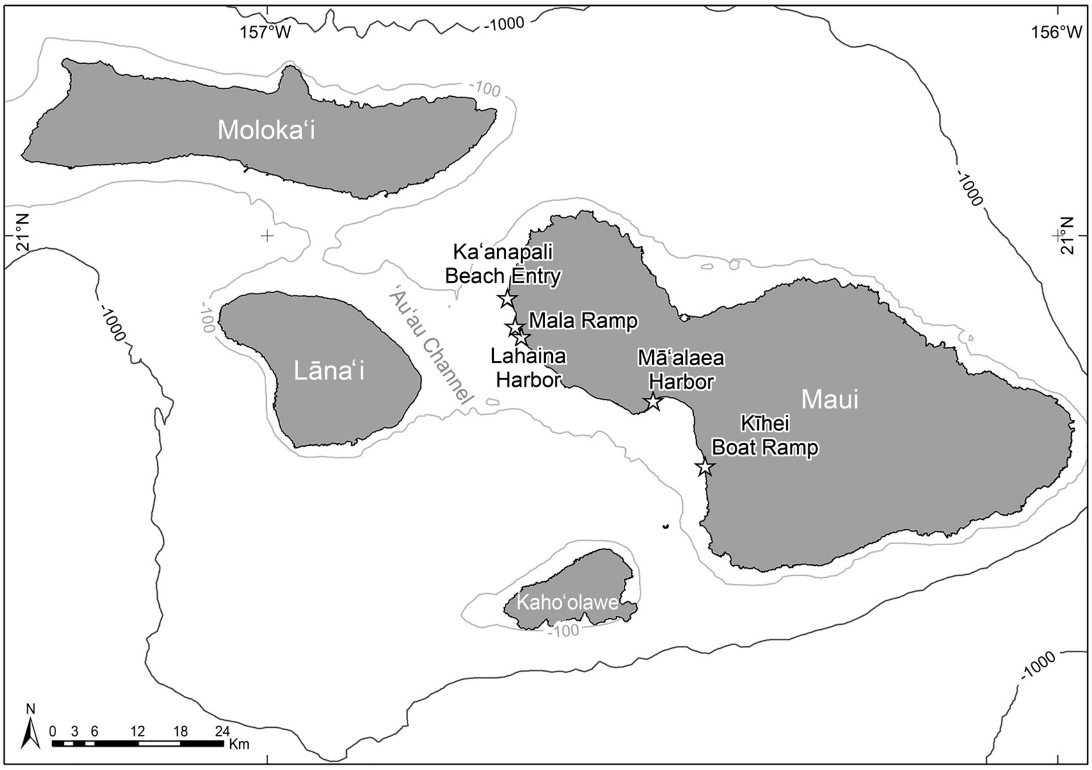

Fig. 1. Reference map of the Maui Nui region. Harbours are displayed on the map where volunteer participation in the community science project was solicited. The 100m isobath is shown in light gray, and the 1,000m isobath is shown in dark gray.

operators were approached at launch ramps and harbours along the leeward coast of Maui, including the Kihei Boat Ramp, Māʻalaea Harbor, Lahaina Harbor, Mala Boat Ramp and Kāʻanapali Beach Entry. Each harbour was visited once between the hours of 14:00 and 16:00 from 1 June 2015 and 15 June 2015, and during that time period, researchers attempted to approach and talk to personnel associated with every tour or fishing vessel present at the docks/ramps. The purpose of the community sighting project and the ecological importance of odontocetes were explained and discussed with the crew. If a captain or crew member expressed interest in participating in the project, he/she was given a laminated protocol sheet that gave the project goals and procedures. The protocol asked for several key pieces of information whenever a delphinid group was sighted in the Maui Nui region, including: (1) the date, the time of day and the GPS coordinates of the vessel; and (2) an identification of the species using a dorsal fin photo key of the most common species in the area, which included spinner dolphins, bottlenose dolphins, pantropical spotted dolphins, false killer whales and short-finned pilot whales. It was requested that all sighting information be communicated via SMS text messages. If an observer was uncertain about the identity of the species, they were encouraged to send photos of the sighting along with the data. No permits were required for the citizen science effort, as all vessel operators observed passively and were assumed to abide by the approach regulations set forth by the Marine Mammal Protection Act (MMPA). Although we cannot verify the behaviour of the vessels involved in this study, the authors have not witnessed any blatant violations of the MMPA by vessel operators in the Maui Nui region. The project lasted for six months through November 2015. Updates and reminders were periodically communicated to all observers involved in the project.

In addition, sighting data were used from Baird *et al.* (2013) from odontocete surveys conducted by the Cascadia Research Collective in the leeward Maui Nui region in 2000, 2001, 2002, 2003 and 2012. Survey areas had been chosen to maximise geographic scope and depth range within Maui Nui, while remaining in areas with relatively calm conditions with minimal swell (Beaufort Sea State < 3). While on survey effort, two to six observers scanned 360 degrees around the vessel primarily with the naked eye and occasionally with binoculars. When an odontocete group was spotted, the group was approached for identification and GPS coordinates and time of day were recorded. In addition, photographs were taken for most encounters for photo-identification catalogues (Baird *et al.*, 2009; Baird *et al.*, 2008; Mahaffy *et al.*, 2015).

All sightings from both survey approaches were compiled and filtered. Species that were observed only once using either method were omitted from the analysis. In addition, sightings were excluded if they were made outside the 1,000m isobath, the designated edge of the Maui Nui region in this study. Sightings reported with approximate locations, such as 'Manele Bay,' were still included in the analyses, and GPS coordinates were estimated for the location. To ensure the independence of each community project sighting, all sightings reported for the same species occurring within a 5km radius during the same hour on the same day as another sighting were discarded. Sightings were plotted using the R package 'ggmap' (Kahle and Wickham, 2013). With the restricted sighting information, water depths were generated for each encounter using the GPS coordinates input in the 'get.depth' function from the R package 'marmap'. Depths of sightings from the participatory science approach were compared with those from the standard surveys across all observed odontocete species using an unpaired two-sample test. The specific test, either a parametric Student's t-test or a non-parametric Wilcoxon rank sum test, was determined on the basis of the normality of the data visually assessed via QQ plots. Data were then pooled across methods and median depths of sightings were examined relative to species.

RESULTS

Thirty vessels were approached during the two-week solicitation period in early June 2015, and by the end of the project in November 2015, 37 observers representing 24 different vessels (80% response rate) had provided sightings of delphinids. The vessels included 19 commercial tour operators and five sport-fishing operations. Observers reported 320 total sightings of six species including bottlenose dolphins, spinner dolphins, pantropical spotted dolphins, false killer whales, short-finned pilot whales and melon-headed whales (*Peponocephala electra*). Half of the sightings came from three observers, while the mean number of sightings for the other 34 observers was considerably lower ($\bar{x} = 4.3$, SD = 3.7). When observations were corrected for duplicate sightings, the total number of sightings decreased to 276 independent reports (Fig. 2). Sightings were made between 06:00 and 18:00. Only one sighting was made of melon-headed whales so the species was removed from the depth analysis. The most frequently sighted species were spinner dolphins ($n = 151$) followed by bottlenose dolphins ($n = 83$) and pantropical spotted dolphins ($n = 30$), while short-finned pilot whales ($n = 5$) and false killer whales ($n = 7$) were the least often sighted (Fig. 3). July had the greatest number of observations ($n = 97$), with reporting effort diminishing each subsequent month until the end of the project.

There were 111 sightings of eight odontocete species from the Maui Nui region in the Baird *et al.* (2013) surveys. In addition to the six species observed by the community observers, these included rough-toothed dolphin (*Steno bredanensis*) and dwarf sperm whale (*Kogia sima*). As with the community project, sightings were made during the hours of 06:00 and 18:00. Only one sighting was made each of melon-headed whales, rough-toothed dolphins and dwarf sperm whales, so these three species were excluded from further analysis relative to depth. Across all surveys, the most commonly observed species was the bottlenose dolphin ($n = 60$), while false killer whales ($n = 4$) and spinner dolphins ($n = 9$) were the least sighted (Fig. 4), in contrast with the large number of spinner dolphin reports from the participatory science efforts.

Distributions of depths of sightings were skewed for most species, and thus a two-tailed non-parametric Wilcoxon rank sum test was chosen to compare sighting depths between the directed survey approach and the community sighting project for each species. Test results showed that the two approaches produced significantly different sighting depths of spinner dolphins ($W = 1068$, $p = 0.001$) and short-finned pilot

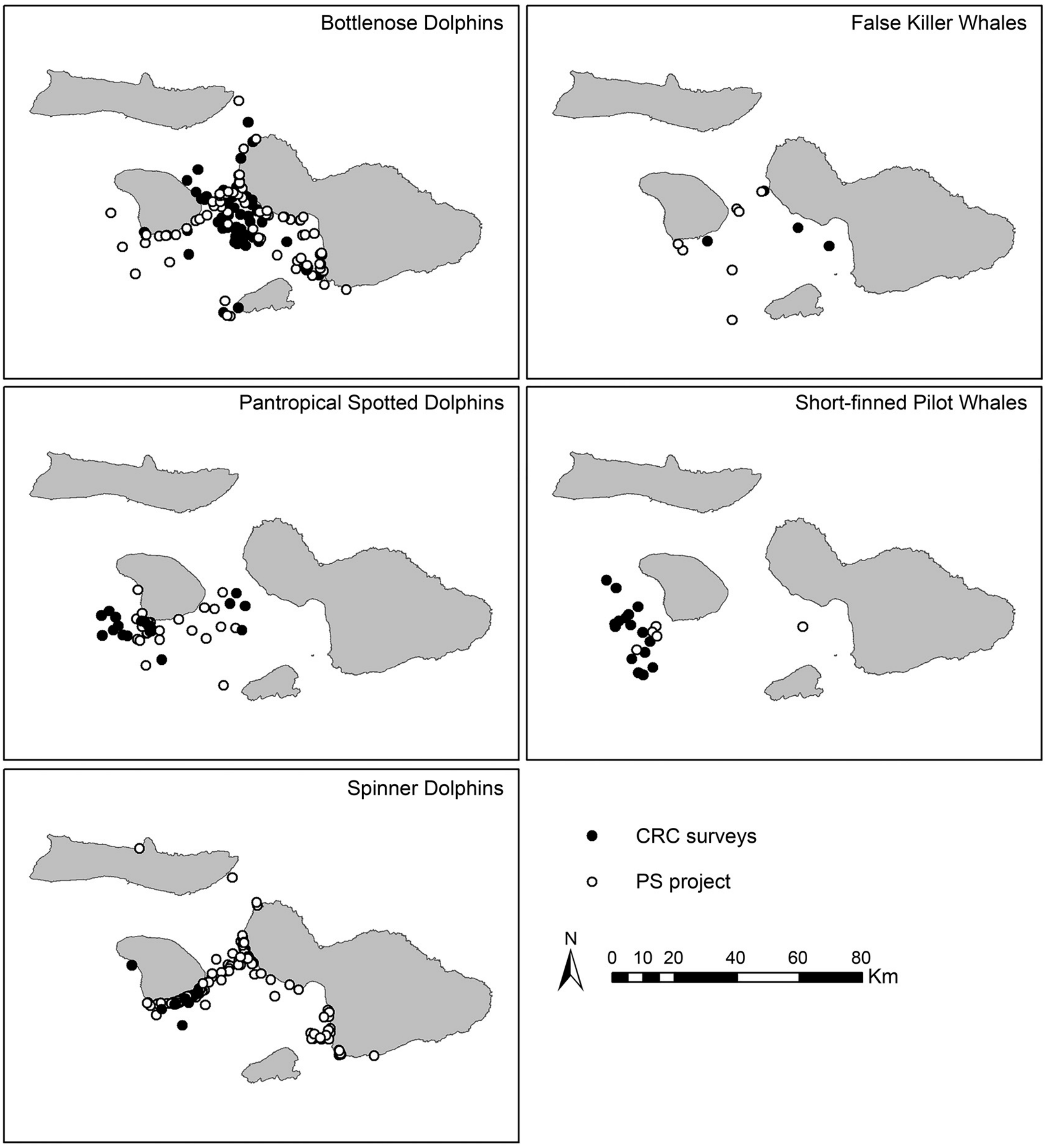

Fig. 2. Map of odontocete sightings from the Cascadia Research Collective (CRC) surveys (n = 108) and Participatory Science (PS) project (n = 276) in the Maui Nui region. Observations were corrected for replicate sightings and exclude species sighted only once.

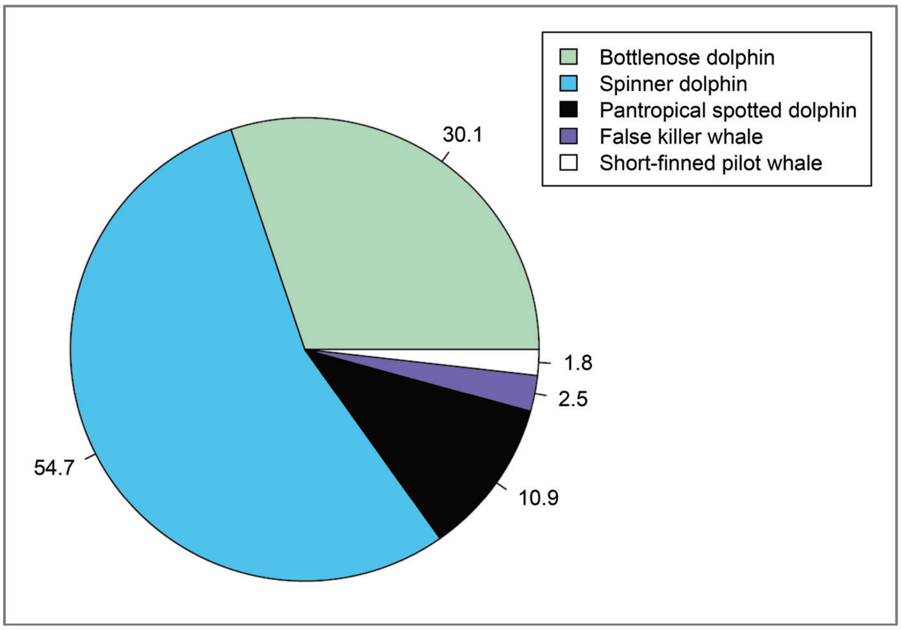

Fig. 3. Sighting proportions of odontocete species in the Maui Nui region based on the Participatory Science project. Slices are labeled with percentages representing the proportion of observations of each species.

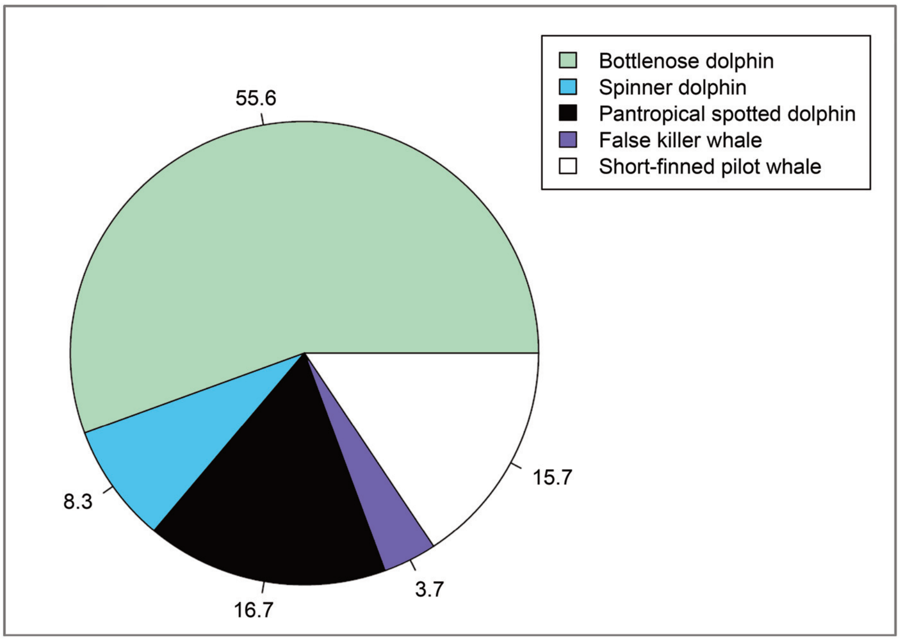

Fig. 4. Sighting proportions of odontocete species in the Maui Nui region based on the Cascadia Research Collective surveys. Slices are labeled with percentages representing the proportion of observations of each species.

Table 1

Hodges-Lehmann estimators of depth of sightings (m) by method. 95% confidence intervals are shown in parentheses. *88 % confidence intervals shown. CRC = Cascadia Research Collective; PS = Participatory Science.

	CRC surveys		PS project	
Species	Sample size	Depth of sighting (m)	Sample size	Depth of sighting (m)
Bottlenose dolphin	60	102.5 (81.5–125.5)	83	86.5 (67.5–107.5)
Spinner dolphin	9	167.0 (88.0–257.0)	151	71.5 (62.5–80.0)
False killer whale	4	89.8 (48.0–225.0)*	7	173.8 (61.5–302.0)
Pantropical spotted dolphin	18	387.5 (276.0–506.5)	30	272.0 (214.5–327.5)
Short-finned pilot whale	17	676.0 (637.0–702.0)	5	452.8 (411.0–668.0)*

whales ($W = 60$, $p = 0.007$), with directed surveys sighting pilot whales and spinner dolphins in deeper waters than community observers (Fig. 4). However, for the other three species, there were no significant depth differences between the two survey types ($W_{\text{bottlenose}} = 2{,}766$ $p = 0.1614$, $W_{\text{spotted}} = 351$ $p = 0.0862$, $W_{\text{falsekiller}} = 10.5$ $p = 0.5699$; Table 1). For both methods, pilot whales were seen in the deepest waters (Table 1; Fig. 4), while pantropical spotted dolphins were found in intermediate depths. The other three species (bottlenose dolphins, spinner dolphins, and false killer whales) were all observed in relatively similar, shallower waters of approximately 80m.

DISCUSSION

The Maui Nui delphinid community sighting project was successful in generating a large data set of odontocete sightings from five different species and laying a groundwork for future studies in the region. The request for minimal sighting information combined with the ease of text message reporting likely contributed to participation by many different vessel operators and the large number of observations that were received. Reporting was initially high during the beginning of the project and peaked a month after its start date; reported sightings steadily decreased over the course of the project. Given that several of the populations are known to be resident to the area (Baird, 2016), this decrease is probably a reflection of diminished reporting over time, with crew occupied by other responsibilities and/or forgetting to report. Sharing unusual sightings with all volunteers or creating reporting incentives, such as prizes for the most sightings (Hochachka *et al.*, 2012), may help maintain reporting levels for future projects.

Species identification is of critical importance to this study and identification ability may not be consistent across all volunteers (Falk *et al.*, 2019); mistakes may be more prevalent for species of similar appearance (e.g. spinner and spotted dolphins). However, the few observers that submitted the majority of the reports may have initially been more interested in marine science and/or delphinids (Thiel *et al.*, 2014) and it is possible that they were more knowledgeable of the dolphin species in the region and thus to more likely to provide accurate reports.

When the depth data for the participatory science project were compared with those from directed surveys, there was little difference for three of the five species (bottlenose and pantropical spotted dolphins, false killer whales) although sample sizes for the last species were small in both cases ($n = 4$ and 7, respectively). This similarity provides support for the participatory science approach as well as the results from the directed approach relative to bathymetry, at least in the areas where observers regularly spend time. However, spinner dolphins and short-finned pilot whales were sighted

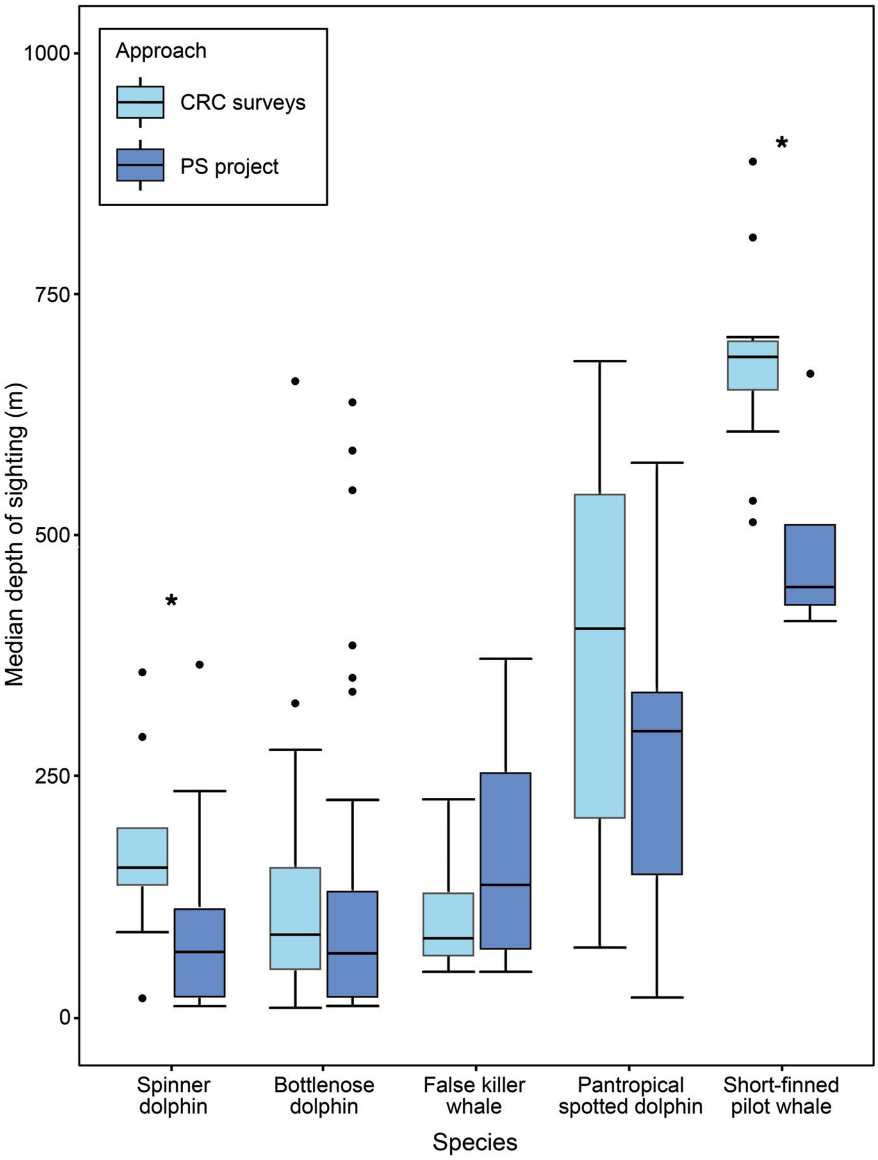

Fig. 5. Comparisons of depth of sighting (m) by survey type. The middle line in each box represents the median, the box designates Q1 and Q3, and the ends of the whiskers mark the minimum and maximum values within the '1.5 rule'. Points represent outliers that are either less than Q1–1.5*IQR or greater than Q3+1.5*IQR. * = Indicates significant difference between Hodges-Lehmann estimators at p = 0.05 based on Wilcoxon rank sum tests. CRC = Cascadia Research Collective; PS = Participatory Science.

in depths that were significantly different between the directed surveys and the community sighting effort, with the former observing both species in deeper waters. The two species also comprised different proportions of the total delphinid sightings for the two surveys approaches, likely due to different distributions of effort. For example, to find spinner dolphins for their passengers, tour operators often transit across relatively shallow depths and search in shallow near-shore areas, since spinner dolphins are known to occupy shallow coastal areas during the daytime (Lammers, 2004; Norris *et al.*, 1994; Thorne *et al.*, 2012).

In contrast, the Baird *et al.* (2013) surveys in the Maui Nui region targeted less common odontocete species and thus took place farther away from the coastline. This accounts for the relatively small sample size of spinner dolphin observations from these surveys. For pilot whales, different distributions of effort probably led to the considerable difference in total sightings, with participatory science vessels typically not transiting near the majority of the Baird *et al.* (2013) pilot whale sightings along the slope of Maui Nui. Indeed, all participatory science pilot whale observations were opportunistically made by fishing vessels, which engage in more offshore transits than tour operators. A larger sample size of participatory science pilot whale sightings, including more observations from fishing vessels, may have produced results more similar to the directed surveys. Non-random distributions of effort can be an issue with participatory science projects (Crall *et al.*, 2011), and this bias was apparent in the community sighting approach. On the other hand, the Baird *et al.* (2013) directed surveys were conducted farther away from the coastline in deeper waters, and thus this sampling approach likely captured the preferred depths of some, but not all the common dolphin species. The results suggest that comprehensive participatory science projects would need to direct effort over both deep and shallow waters of the archipelago.

In the past, a variety of methods have been used to assess habitat use of odontocetes around the main Hawaiian Islands, including sighting surveys, satellite tagging and acoustic monitoring. Depending on the species being studied there are advantages and disadvantages to each method. For rarely seen species, such as beaked whales, satellite tagging and acoustic monitoring may be the most useful approaches (e.g. Abecassis *et al.*, 2015; Baird, 2016; Schorr *et al.*, 2009). Both of these approaches are also particularly valuable in areas with consistently strong winds and poor sighting conditions, as tagged animals may be tracked as they move into areas difficult to access by vessel, and dolphin movement patterns may be acoustically monitored using hydrophones within these areas. Participatory science approaches similar to the one presented here are likely to be most valuable in areas of high vessel activity, relatively good viewing conditions and in areas used extensively by the species of interest, provided the species are relatively easy to identify (Bell, 2006).

While the preferred depth ranges of the species presented here have been relatively well established throughout the Hawaiian Islands (Baird *et al.*, 2015; Baird *et al.*, 2010; Baird *et al.*, 2013; Thorne *et al.*, 2012), the results of this study contribute useful scientific information regarding the daytime depth ranges most used within the Maui Nui region. With some knowledge of these preferred daytime depths, spatial distributions of odontocete populations, both resident and non-resident, around the basin may also begin to be inferred. Based on the observed means, these results also complement and further elucidate passive acoustic monitoring in the Maui Nui region, which revealed diel distribution differences relative to bathymetry between larger-bodied odontocetes and smaller species. Based on this study, as well as results from satellite tagging efforts and surveys from throughout the main Hawaiian Islands (Baird, 2016), pilot whales appear to primarily occupy deeper insular waters, likely in order to forage more efficiently on their epipelagic squid prey (Abecassis *et al.*, 2015; Pauly *et al.*, 1998). In contrast, within the Maui Nui basin, false killer whales do use the shallower depths, reflecting that their prey, which consists of larger fish such as mahi mahi (*Coryphaena hippurus*) and tuna (*Thunnus sp.*) (Baird *et al.*, 2008; Connor and Norris, 1982; Shallenberger, 1981), also use these shallow waters. Individual false killer whales from the insular population may also use shallow waters to capture prey more efficiently, i.e. they may be able to leverage the bottom to limit their prey's ability to escape to greater depths beyond their reach. Interestingly, based on both nearshore and offshore surveys as well as satellite tagging data, false killer whales from this population also use habitat beyond the island shelf of depths up to nearly 5,000m (Baird *et al.*, 2012; Baird *et al.*, 2010), revealing the importance of the spatial scale considered when assessing results.

The three other species sighted during this study, the smaller pantropical spotted dolphins, bottlenose dolphins and spinner dolphins, were found in mid- to shallow-depth ranges during the daytime. Based on acoustic monitoring results in the Maui Nui basin, these smaller species typically prefer coastal habitats that are in close proximity to the 1,000m contour, particularly during the nighttime. This likely enables efficient foraging on the productive mesopelagic boundary layer of micronekton that migrates towards shore during nighttime hours (Benoit-Bird and Au, 2003; Reid *et al.*, 1991). It may also be inferred that areas farther out from the island shelf may offer limited protection and prey resources for small delphinids and therefore represent less desirable resting and foraging habitats. The results of this study show that spotted dolphins, sighted at mid-depth ranges, do not rely as heavily on shallow resting areas during the day and instead occupy deeper water coastal areas for resting. Off other islands in the archipelago spotted dolphins can also be found in deeper offshore areas (Baird, 2016; Baird *et al.*, 2013). In contrast, spinner dolphins appear to depend on shallow water habitats during the daytime, which is consistent with prior research on spinner dolphins (Norris and Dohl, 1980; Norris *et al.*, 1994; Thorne *et al.*, 2012). Many of the sightings of spinner dolphins between Maui and Lāna‘i in the ‘Au‘au Channel (Fig. 2) were likely either groups transiting between shallow-water resting areas adjacent to one or the other islands or resting within the relatively shallow waters of the channel.

In summary, certain biases are inevitable in any participatory science project but they can be better estimated and assessed when the results are examined in light of those from directed scientific studies (Baird *et al.*, 2002) and integrated into larger efforts to characterise species distributions. In addition, using a multi-method approach, even with the presence of confounding factors, may provide greater confidence in the overall results than if only one method was used. For cetacean studies, further comparison of results with those generated using approaches with better temporal or spatial coverage (e.g. passive acoustic monitoring or satellite tagging) should further contribute to a better understanding of the overall system. Future cetacean participatory science projects should leverage volunteers such as fishermen and other vessel operators who possess valuable knowledge of their marine environments and understand local delphinid distribution patterns. Vessel captains and crew may also occasionally sight rare and unusual cetaceans, which is valuable information that often remains undocumented.

Improvements could also be made to future participatory science projects based on the results of this work. Along with using an incidental sighting methodology, such as the one used in this project, participatory science cetacean studies could also make an effort to measure the level of effort expended by volunteers and the geographical extent of their observations in order to generate rates of observations and further expand the utility of the data. In addition, with greater personnel support to help develop and implement participatory science projects, training sessions could be provided to all volunteer recruits in order to uniformly prepare volunteers for their tasks, thereby raising levels of participation. Finally, the specific tools used for data collection and communication have been shown to be a critical factor determining the success or failure of self-reporting programmes (McCluskey and Lewison, 2008). Therefore, participatory science projects should aim to utilise user-friendly technologies such as smartphone apps or SMS text messages that facilitate the transmission of data from volunteers to coordinators.

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