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Fine-scale habitat partitioning of Chilean and Peale's dolphins and their overlap with aquaculture

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Running head: ***Habitat partitioning in coastal dolphins***

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Abstract:

1. Predictive species distribution models (SDMs) have become powerful tools to determine habitat use patterns of mobile marine predators and their spatial overlap with potentially impacting anthropogenic activities.
2. This study used SDMs to investigate fine-scale habitat use patterns of two poorly known and broadly sympatric coastal delphinids, Chilean dolphins (*Cephalorhynchus eutropia*) and Peale's dolphins (*Lagenorhynchus australis*), and their spatial interactions with intense aquaculture farming activities in the Chiloé archipelago, southern Chile.
3. A long-term dataset (2002-2012) of boat-based dolphin sightings and concurrently *in situ* collected environmental and anthropogenic variables was analysed using binomial GAMs to investigate ecological drivers of each species' fine-scale distribution and to predict dolphin occurrence spatially.
4. Chilean dolphins preferred shallow (<30 m deep), turbid waters, close to shore (<500 m) and river mouths which often placed them in sheltered bays and channels used intensively by shellfish farms. Peale's dolphins were also found in shallow waters but occurred over a wider range of conditions along more open or exposed coastlines. Both species had to navigate extensive salmon and shellfish farming sites to transit between areas of important habitat.
5. Sightings and predicted occurrence maps showed a clear pattern of spatial habitat partitioning between species, which remained stable across the 11-year study period. The identification of important habitat for Chilean dolphins warrants the consideration of spatially explicit conservation measures to limit the potential effects of overlapping salmon and shellfish farming.
6. The observed differences in ecological plasticity of the two sympatric species should be considered when evaluating and mitigating the effects of environmental change and ongoing anthropogenic pressures on their nearshore habitat. The estimated species-environment relationships could also be used to predict where dolphin habitat and anthropogenic activities are most likely to overlap in other parts of the species' ranges.

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Keywords: predictive species distribution models, habitat use pattern, niche partitioning, *Cephalorhynchus eutropia*, *Lagenorhynchus australis*, aquaculture

INTRODUCTION

Where animals occur, what drives their distribution and how they use their habitat are some of the fundamental questions in ecology. Understanding how these patterns relate to the spatial distribution and extent of human activities, and how they might be affected by environmental change, is essential to conservation. Sympatric species may respond differently to environmental change and anthropogenic pressures, making the identification of species-specific habitat use patterns a key requirement for effective conservation (Schaefer, Jetz, & Böhning-Gaese, 2008; Silber et al., 2017).

Predictive species distribution models (Guisan & Zimmermann, 2000), SDMs, have emerged as powerful tools to identify important habitats for species and for use in biodiversity conservation (Gregr, Baumgartner, Laidre, & Palacios, 2013; Guisan et al., 2013; Lecours, 2017). SDMs can provide important ecological insights into species-environment relationships (Bräger, Harraway, & Manly, 2003; Redfern et al., 2006) enable comparisons among species (Ingram, Walshe, Johnston, & Rogan, 2007; Mannocci et al., 2014; Redfern et al., 2013), identify key areas and habitats (Esteban et al., 2014; Pérez-Jorge et al., 2015), and help predict where species might be most at risk from anthropogenic activities (Ashe, Noren, & Williams, 2010; Redfern et al., 2013). They can also inform conservation and management by guiding spatially explicit mitigation actions such as the designation and management of marine protected areas (Bailey & Thompson, 2009; Cañadas, Sagarminaga, De Stephanis, Urquiola, & Hammond, 2005; IUCN-MMPATF, 2016).

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This study uses SDMs to investigate the habitat use patterns of two poorly known coastal delphinids, which occur in sympatry in southern Chile, one of the most intensively used marine aquaculture farming regions in the world (Bostock et al., 2010). The study species, Chilean dolphin (*Cephalorhynchus eutropia,* Gray 1846) and Peale's dolphin (*Lagenorhynchus australis,* Peale 1848), inhabit the nearshore waters of southern Chile, with Peale's dolphins also occurring over the continental shelf waters of the southern South Atlantic where they are sympatric with another *Cephalorhynchus* species (*C. commersonnii,* Lacépède 1804) (Heinrich, Elwen, & Bräger, 2010).

Cephalorhynchus dolphins and Peale's dolphins are unusual amongst the delphinids in that their acoustic repertoire seems to consist only of narrow-band high frequency clicks which may be an adaptation to life in acoustically cluttered inshore waters (Götz, Antunes, & Heinrich, 2010; Kyhn et al., 2010) and/or facilitates acoustic crypsis from their main potential predator, killer whales (*Orcinus orca,* Linnaeus 1758) (Morisaka & Connor, 2007). Peale's dolphins are bigger than Chilean dolphins, and seem to show more ecological plasticity inhabiting a wider geographic and habitat range (Cipriano, 2018). Detailed information on diet is lacking for both species, but they are thought to forage on a variety of schooling and demersal fish and cephalopod species (Goodall, Norris, Galeazzi, Oporto, & Cameron, 1988; Schiavini, Goodall, Lescrauwaet, & Alonso, 1997). Both Chilean and Peale's dolphins seem to prefer nearshore shallow waters (Heinrich, 2006; Viddi, Hucke-Gaete, Torres-Florez, & Ribeiro, 2010), but differ substantially in their encounter rates in southern Chile. Peale's dolphins are usually the most frequently sighted delphinid, whereas Chilean dolphins are rarely seen and appear to have a more patchy distribution concentrated in sheltered bays and channels (Aguayo-Lobo, Torres Navarro, & Acevedo Ramírez, 1998; Viddi et al., 2010; Zamorano-Abramson, Gibbons, & Capella, 2010). Both species are regularly sighted in the Chiloé

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archipelago where Peale's dolphins appear to outnumber small localized populations of Chilean dolphins (Heinrich, 2006).

Since the early 1990s the Chiloé region has become the centre of Chile's lucrative salmonid and shellfish farming enterprises, leading to substantial increases in human population and infrastructure, and affecting the health of the coastal marine ecosystem (Buschmann et al., 2009; Buschmann, López, & Medina, 1996; Sepúlveda, Arismendi, Soto, Jara, & Farias, 2013). Potential direct effects of aquaculture farming on cetaceans include increased mortality due to entanglement in cage netting and ropes (Díaz López & Bernal Shirai, 2007; Kemper & Gibbs, 2001). However, most effects likely operate via multiple indirect and possibly synergistic pathways such as exclusion from important habitat, habitat degradation, food web alterations, noise pollution, contamination and spread of disease (Buschmann et al., 2009, 2012; Kemper et al., 2003; Markowitz, Harlin, Würsig, & McFadden, 2004; Pearson, Vaughn-Hirshorn, Srinivasan, & Würsig, 2012; Ribeiro, Viddi, Cordeiro, & Freitas, 2007; Watson-Capps & Mann, 2005). Fish farms can also affect dolphin habitat use patterns (Bonizzoni et al., 2014), because farmed fish or cage-associated wild fish can act as attractive food sources (Piroddi, Bearzi, & Christensen, 2011).

This study uses a long-term dataset to model fine-scale habitat use of sympatric Chilean and Peale's dolphins in relation to environmental and anthropogenic variables in the Chiloé archipelago. It explores differences in habitat use patterns between the two species, identifies their key habitats using spatial predictions, and provides evidence of decadal stability in habitat use, supporting spatially explicit management measures as a suitable tool to protect dolphin key habitats.

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MATERIAL AND METHODS

Study Area

This study took place in the Chiloé archipelago in southern Chile (41.8°–43.4°S, 73.2°–73.9°W) and comprised two survey areas (northern and southern, Figure 1) separated by about 70 km and covering a range of coastal habitats including islands, channels, bays and estuaries. This region is characterized by considerable freshwater input and variations in sea surface temperature (SST) and salinity (Dávila, Figueria, & Müller, 2002; Iriarte, González, Liu, Rivas, & Valenzuela, 2007; this study). The northern study area (near Castro) spanned roughly 260 km^2, with water depths up to 130 m and average depth of about 50 m. The southern area (near Quellón) spanned roughly 275 km^2, with water depths rarely exceeding 50 m and average depth of about 25 m.

Sampling Design and Data Collection

Systematic boat-based habitat and sighting surveys for small cetaceans were carried out annually from January to April of 2002–2012, using 4.2 m inflatable boats with outboard engines. Surveys were conducted at 20 km/h in favourable conditions, defined as Beaufort ≤3, good visibility and little or no precipitation. Surveys were designed to ensure full coverage of the available habitat in the chosen study areas. Transects had variable start and end points and were placed in regularly spaced randomized zigzag patterns crossing bays and channels from shore to shore and extending up to 3,000 m offshore.

Two to four observers scanned the sea surface ahead and out to 90° of the transect line for visual cues of dolphins. When dolphins were sighted, the observers recorded the position of the vessel on the transect line using Global Positioning System (GPS), the distance (estimated by eye in m) and angle (estimated in degrees using a small angle board) to the

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sighting before approaching the dolphins to record more detailed information. This included species identification, group size, presence of offspring, dolphin behaviour and a suite of *in situ* environmental measurements (Table 1) made as close as possible to the original location where dolphins were first seen prior to approach (position also marked by GPS). This position constituted a presence point. Any further dolphin groups seen while working with the initial sighting were not included in the analyses presented here.

Environmental measurements (Table 1) included biologically relevant physiographic and oceanographic variables that served to characterize dolphin habitat (depth, distance to shore, distance to rivers, SST, water clarity, salinity) and anthropogenic variables (distances to nearest salmon and nearest shellfish farms). Distance variables were measured *in situ* using a Bushnell laser range finder for distances of <1000 m (i.e. maximum range of equipment). Distances to coastline and rivers of ≥1000 m were derived in a GIS (Geographic Information System; Manifold System vers 8.0, using coordinate system WGS 1984 UTM Zone 18S and GSHHS high resolution coastline data). It was not possible to use GIS to calculate *post-hoc* distances to salmon and shellfish farms because the farms regularly changed location, extent and activity status. Mapping these frequent changes *in situ* was not feasible given the number of farms involved. However, the maximum distance between any given point in the study area and the nearest aquaculture farm was 7000 m. Therefore, distances of ≥1000 m which could not be measured *in situ* (or when no farms were in visual range), were assigned random values from 1000 to 7000 m to facilitate the inclusion of distance to farms as continuous variables in the models. Thus, direct effects of aquaculture sites on dolphin distributions were only interpreted for distances within the measured range of <1000 m, and greater distances were considered uninformative for the modelled relationships.

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After all measurements had been taken during a sighting, survey effort resumed at the initial point of departure from the transect line and continued along the original trajectory. If no dolphins were sighted while moving along the transects, the vessel was stopped at regular 15-min intervals to collect the same *in situ* environmental data as recorded during dolphin presence (Table 1). These 15-min stops for sampling without dolphins constituted the absence points of the analysis, and were considered true absences because sighting conditions and survey protocol would have allowed any dolphins present at that location to be detected. The randomized transect design and regular 15-min sampling at absence points along the transects ensured that the habitat types available to the dolphins in each study area were sampled representatively.

Modelling

All absence and presence points with their associated *in situ* measurements constituted the sample data for analyses. Dolphin probability of occurrence was modelled using binomial Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1990) with a logit link function. Analyses were carried out in software R 3.4.2 (R Core Team, 2017), using the *mgcv* library (Wood, 2006). Pairplots and variance inflation factors (Brauner & Shacham, 1998) were used to inspect potential collinearity among covariates, but none was detected. The choice of variables (Table 1) was guided by their potential biological relevance as well as availability of reliable data measured at appropriate spatial and temporal resolutions, which ruled out using remotely sensed data (e.g. SST, chlorophyll concentration) or tidal predictions for the study areas.

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Each predictor variable entered the model as a smooth term (except Year, which was included as factor, see below), where the degree of smoothness was determined as part of the model fitting process (Wood, 2006). Thin plate regression splines were used, because they allow smoothing with respect to any number of covariates and do not require 'knot' locations to be specified (Wood, 2006). GAMs have a tendency to over-fit (Wood, 2006), so the degrees of freedom of each smooth was limited to 4.

Two types of models were fitted: the 'environmental (or explanatory) model' and the 'spatial model'. In the environmental model, all variables except latitude and longitude were included. Beaufort scale was included to take account of variation in detection probability as a function of sea conditions (Evans & Hammond, 2004). Year was added as a factor, to explore differences among survey years. In the spatial model, additional spatial information (latitude and longitude) was included as an isotropic smooth (Wood, 2006), as a proxy for potentially spatially structured habitat characteristics that were not accounted for with the available environmental data. The best models were used to visualize the predictions of dolphin occurrence on the maps.

Two model selection methods were used. Shrinkage smoothers (Wood, 2006) were used on the full model (all candidate covariates) as an automated model selection. Shrinkage smoothers introduce an additional penalty that enables smooth terms to be penalized ('shrunk' away) when the term makes no contribution to the model (Wood, 2006). Forward stepwise selection was used as a complementary method to assess the contribution of each covariate to the explained deviance, and to choose among models with or without factor variables. Here, each covariate was added to the null model (intercept only), one at a time. The covariate that made the greatest model improvement was retained. All remaining covariates were then individually tested again for potential inclusion in this new model. This

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continued until the inclusion of new covariates no longer improved the model, as judged by the UBRE score and the approximate Akaike's Information Criterion (AIC) for GAMs (Wood, 2006). Covariates were retained if they reduced the AIC by at least 2 (Burnham & Anderson, 2002).

The best models were used to visualize the predictions of dolphin occurrence in the study areas. The 95% confidence intervals (CI) for predictions were calculated through non-parametric bootstrap of the sample data, with replacement, using 500 replications and the percentile method (Borchers, Buckland, & Zucchini, 2002). The mean probability of occurrence and the lower and upper CI bounds were then plotted on maps to visualize the probability of occurrence as a measure of importance of different areas. All point-based predictions were exported into Manifold GIS and kriging was used to generate smooth colour-coded surfaces for the habitat use maps. Information on the location and extent of registered aquaculture concessions for the year 2015, obtained from the Chilean Fisheries Service (wwww.subpesca.cl), was then overlaid on the combined predicted habitat use surfaces for both species to illustrate their recent spatial overlap in both study areas.

RESULTS

Field surveys covered a distance of 30,736 km during 489 days spread over 11 years. A total of 531 Chilean dolphin sightings (32–80 annually) and 353 Peale's dolphin sightings (22–70 annually) were used for modelling, together with 2,461 absence points (178–408 annually, Figure 1). Both species were encountered in all years and in both study areas, yet with different encounter rates. Chilean dolphins were uncommon in the northern compared to the southern study area (0.3 dolphin compared to 2 dolphins per 10 km surveyed), whereas

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Peale's dolphins were sighted more frequently in the northern than the southern study areas (1 dolphin compared to 0.5 dolphin per 10 km surveyed).

Detection probabilities were not calculated because distance and angle estimates lacked precision, were not available for all sightings and were affected by the low position of the observers (<2m). However, average radial distances of detection were almost identical for both species (Chilean dolphins: 249 m, SD = 188 m, Peale's dolphins: 256 m, SD = 204 m), thus differences in detection probability are unlikely to affect comparison of model results between species. For both species, the different model selection methods resulted in the same covariates retained in the final environmental and spatial models. Table 2 shows the results of the forward stepwise selection for the environmental models, including the relative contribution of covariates to the explained deviance.

Chilean dolphins

The final environmental model for Chilean dolphins retained all candidate covariates except Year, and explained 33.2% of the deviance (Table 2). The model fitted the data well (adjusted R^2 for binary data = 0.43). Fitted smooth functions are shown in Figure 2. Distance to shore was the most important predictor, explaining 17.8% of the deviance (Table 2). Probability of occurrence decreased with increasing distance to shore, and 95% of all sightings of Chilean dolphins occurred within 500 m from shore. Depth was also an important predictor, with probability of occurrence decreasing with increasing depth, and 95% of all sightings were made in waters with depths shallower than 30 m. Probability of occurrence decreased with increasing distance to shellfish farms, but increased with increasing distance to salmon farms. It was higher closer to rivers, in more turbid, somewhat less saline and relatively warmer waters. As expected, it decreased with increasing Beaufort scale. Year was not retained in the model, suggesting no significant inter-annual differences.

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The final spatial model included distance to shore, depth, SST, water clarity, distance to nearest river, distance to nearest shellfish farm, distance to nearest salmon farm and Beaufort scale, plus the interaction of latitude and longitude, explained 42.1% of the deviance (adjusted $R^2 = 0.52$), and was used to generate prediction maps. Visual comparison of prediction maps with the observed sightings indicated that the model correctly predicted areas of high occurrence probability where sightings were concentrated (Figures 1, 3 and 4).

Key areas for Chilean dolphins, based on high predicted probability of occurrence, were situated mostly in the southern study area: in Yaldad Bay, along the western shore of Isla Coldita, and in the channels around Isla San Pedro (Figure 3). These areas were predicted as important even when uncertainty (lower 95% CI bound) was taken into account (Figure 3c). Areas with few or no sightings were also correctly predicted as areas with low probability of occurrence, regardless of uncertainty. Mean model predictions appeared to under-predict occurrence at Isla Cailín; however, the upper 95% CI did predict this area to be important, while still predicting low probability of occurrence in adjacent waters (Figure 3b). The model predicted low overall probability of occurrence in the northern study area (Figure 4), with the exception of a few sheltered bays where the upper 95% CI indicated potentially higher probability of occurrence (Figure 4b).

Peale's dolphin

The final environmental model for Peale's dolphins retained depth, distance to nearest shellfish farm, distance to shore, distance to nearest river, salinity, SST and Beaufort scale, explaining 16.1% of the deviance (Table 2) with an adjusted $R^2 = 0.21$. Fitted smooth functions are shown in Figure 5. Depth was the most important predictor, explaining 8.5% of the deviance. Probability of occurrence decreased with increasing water depth, and dolphins appeared to prefer waters shallower than 20 m. The second most important predictor was

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distance to nearest shellfish farm, with probability of occurrence increasing with increasing distance from shellfish farms. Predictions suggested Peale's dolphins were more likely to be found within 400 m from shore, in SST 12.5–15°C, further from river mouths, and in somewhat more saline waters.

The final spatial model retained fewer environmental variables than identified in the environmental model, and included depth, distance to shore, SST and distance to nearest river, plus the interaction of latitude and longitude. The model explained 32.3% of the deviance (adjusted R^2 = 0.40), double the deviance explained by the environmental model, and was used to generate prediction maps. The mean predictions highlighted areas of highest occurrence in Canal Dalcahue and the channel of Castro in the northern study area (Figure 4), and off the southern shores of Islas Laitec and Cailín in the southern study area, but seemed to under-predict occurrence on the eastern side of Isla Coldita (Figure 3). As with Chilean dolphins, Year was not retained in any of the models for Peale's dolphins, indicating no significant inter-annual differences.

Habitat predictions and aquaculture overlap

Predictions of occurrence for both species were overlaid with officially registered concessions for salmon and shellfish farms in 2015 (Figure 6). Aquaculture concessions, in particular for shellfish farms, were widespread along the coasts and in sheltered bays of both study areas, and overlapped with or occurred close to predicted habitat, particularly for Chilean dolphins. Salmon farms were generally located a bit further away from predicted Chilean dolphin habitat, except for the channels around Isla San Pedro in the southern study area where farms occurred near or within core habitat of Chilean dolphins. Peale's dolphins showed less overlap with aquaculture sites than Chilean dolphins in the southern study area,

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but some of their predicted core habitat in the northern study area (particularly near Dalcahue) abutted or overlapped with both salmon and shellfish concessions.

DISCUSSION

This study provides the first quantitative assessment of how sympatric Chilean and Peale's dolphins rely on different environmental characteristics of nearshore habitat, which appears to lead to fine-scale habitat partitioning in the Chiloé archipelago. Habitat use patterns for both species showed decadal stability with persistent key areas of occurrence. Aquaculture farming and associated activities were intense in both study areas and abutted or overlapped with areas identified as key dolphin habitats. Investigating habitat use patterns across fine spatial but large temporal scales using *in situ* data on environmental variables is a unique feature of this study, resulting in spatially explicit conservation and management implications for the species and region of study.

Species-habitat relationships

Habitat use patterns of Chilean dolphins in the Chiloé archipelago appeared to be strongly influenced by certain environmental conditions. Chilean dolphins occurred almost exclusively in waters shallower than 30 m, and within 500 m from shore. Probability of occurrence was higher closer to river mouths and in bays with estuarine characteristics (e.g. lower water visibility, lower salinity). The presence of deep waters within channels and bays in the northern area might explain why Chilean dolphin occurrence was lower there compared to the southern area.

Shallow, nearshore waters influenced by rivers seem to be defining habitat characteristics for Chilean dolphins. These findings echo the few other habitat studies off the open coast north (Pérez-Álvarez, Alvarez, Aguayo-Lobo, & Olavarría, 2007) and in channels

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south of Chiloé (Viddi, Harcourt, & Hucke-Gaete, 2015), as well as most of the incidental sighting locations reported for this species (Aguayo-Lobo et al., 1998; Capella, Gibbons, & Vilina, 1999; Goodall et al., 1988; Morgenthaler, Fernández, Moraga, & Olavarría, 2014; Zamorano-Abramson et al., 2010). The four dolphins of the genus *Cephalorhynchus*, to which the Chilean dolphin belongs, are all characterized as coastal shallow-water species (Dawson, 2018), with Commerson's dolphins (*C. commersonnii*) and Hector's dolphins (*C. hectori,* Van Beneden 1881) also commonly sighted in turbid waters or near river mouths (Bräger et al., 2003; Goodall, 1994).

River mouths and estuaries are known areas of enhanced productivity, often aggregating fish and serving as fish nurseries, in turn attracting piscivorous predators such as dolphins (Arso Civil et al., 2019; Parra, Schick & Corkeron, 2006). Intense seasonal phytoplankton blooms occur in the inshore waters off Chiloé (Iriarte et al., 2007) and in estuaries such as Yaldad Bay (Navarro & Jaramillo, 1994) identified as key Chilean dolphin habitat in this study. Systematic information on Chilean dolphin diet is lacking, but field observations (this study, Viddi et al., 2015) suggest that they might feed on schooling sardines (*Strangomera* spp.), Patagonian blenny (*Eleginops maclovinus,* Cuvier 1830) and silversides (*Odontesthes* spp.), which are known to spawn in and inhabit estuaries as juveniles (Dyer, 2000). Chilean dolphins at Chiloé spent a large proportion of their time foraging (Heinrich, 2006; Ribeiro et al., 2007), which is typical for small bodied cetaceans with high energetic demands requiring high rates of energy intake (Wisniewska et al., 2016). Thus, Chilean dolphin habitat use appeared to be driven by environmental features that may serve to aggregate and maintain sufficiently abundant and reliable prey resources. Mark-recapture studies of identifiable individuals at southern Chiloé indicate that the local population of Chilean dolphins is small (~ 60 adults) with individuals showing high site fidelity and limited along-

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shore movements (Heinrich, 2006). The availability of suitable habitat and resulting effects on dolphin carrying capacity could be important factors in determining overall distribution, abundance and population structure.

Genetic studies have shown clear population differences between Chilean dolphins along the open coast north of Chiloé and to the south in the deep fjords (Pérez-Alvarez et al., 2015). Similar, and even more fine-scale, genetic differences and strong population structuring have also been found in congeneric Commerson's dolphins (Cipriano, Hevia, & Iñíguez, 2011) and Hector's dolphins (Hamner, Pichler, Heimeier, Constantine, & Baker, 2012; Pichler, Dawson, Slooten, & Baker, 1998), and might be a feature of *Cephalorhynchus* dolphins, generally. Unfortunately, Chilean dolphins in the intermediate Chiloé region have not been sampled (Pérez-Álvarez et al., 2015), so finer-scale population structure remains unknown, but obtaining such information should be a priority given the distinct and stable habitat use patterns described here.

Sheltered, shallow nearshore waters might also confer a lower risk of predation. Killer whales are rarely seen in the Chiloé archipelago and have not been observed in Chilean dolphin habitat, but they are known to predate marine mammals in the Chilean fjords (Häussermann, Acevedo, Försterra, Bailey, & Aguayo-Lobo, 2013). Fear and predator avoidance are powerful sub-lethal forces that shape behaviour and habitat use patterns of prey even when predation events appear rare (Wirsing, Heithjaus, Frid, & Dill, 2008).

Depth, distance to shore and distance to rivers were also important predictor variables for the occurrence of Peale's dolphins. They also used shallow waters (<20 m) close to shore (<400 m) but also occurred further offshore (>1,000 m) over shallow sandbanks and shoals. In contrast to Chilean dolphins, Peale's dolphins were found further from rivers, and along more open or exposed shorelines and along the shores of wider and deeper channels in the northern

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study area. The diet of Peale's dolphins in the Chiloé archipelago is not known, but they were never observed feeding on small schooling fish as Chilean dolphins were (S. Heinrich, pers. obs.). In other parts of their range, Peale's dolphins seem to have a generalist diet based on demersal and shallow water prey (e.g. fish, octopus, shrimp; Iñíguez & de Haro, 1994; Schiavini et al., 1997). Therefore, Peale's dolphin habitat use might reflect different foraging strategies involving transit between more patchily distributed or less productive prey patches, and is likely also influenced by other ecological needs. The only other distribution modelling studies of Peale's dolphins, both on spatial scales an order of magnitude greater than this study, seemed to support broader habitat use patterns. Peale's dolphins in the Chilean fjords and southern Argentina were seen 10s of km from shore but always in the neritic zone (usually in <100 m water depth) (Dellabianca et al., 2016; Viddi et al., 2010). Compared to Chilean dolphins, greater ecological plasticity in Peale's dolphins is to be expected given their much wider distributional range spanning both southern South Pacific and South Atlantic continental shelf waters (Cipriano, 2018).

Identifying key habitat and habitat partitioning

For both species, including spatial components improved the predictive ability of the models, but particularly so for Peale's dolphins. While spatial covariates do not elucidate ecological relationships, they helped to improve predictions by capturing spatially linked differences in habitat characteristics that were or could not be measured. The predictive habitat use maps closely matched the distribution of the actual sighting locations. Core areas for Chilean dolphins remained consistent even when model uncertainty was mapped as lower and upper 95% confidence intervals (CIs). Spatial occurrence patterns of Peale's dolphins were

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more ambiguous across lower and upper CIs, reflecting greater variability in the sighting data and less strong relationships with the available environmental covariates.

There was very little fine-scale spatial overlap between the two species, particularly in southern Chiloé, where Peale's dolphins were never seen in core Chilean dolphin habitat. Short-term associations or direct interactions between the two species were rarely observed, even where their selected habitats seemed to overlap (Heinrich et al., 2010). This differs markedly from the regular co-occurrence and frequent, at least short-term mixed group associations reported for Peale's dolphins and Commerson's dolphins in Argentina (de Haro & Iñíguez, 1997; Goodall et al., 1997).

Sympatric co-existence of similar species is shaped by resource availability (e.g. abundance of prey), predation pressure and habitat complexity. Within their physiological and ecological constraints, different strategies enable sympatric species to co-exist, including spatial or temporal differences in habitat use, dietary divergence and specialization, as well as differences in activity patterns and socially mediated behaviours (Bearzi, 2005; Parra, 2006). In some sympatric cetaceans, aggressive interactions act to maintain patterns of fine-scale habitat partitioning, with usually the smaller species avoiding the larger, more dominant one (Parra, 2006; Thompson, White, & Dickson, 2004). Aggressive interactions between Chilean and Peale's dolphins have not been documented, and the observed fine-scale habitat partitioning at Chiloé likely reflects the more specialist habitat preferences of Chilean dolphins, and the greater ecological plasticity of Peale's dolphins enabling them to exploit a wider range of habitats and resources.

Dolphins and aquaculture

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Aquaculture activities were intense and wide-spread throughout the study areas. For both species, distances to farm sites were retained as predictor variables in the environmental habitat models. There was a strong positive relationship between Chilean dolphin occurrence and proximity to shellfish farms, but the opposite pattern for salmon farms. In contrast, Peale's dolphin occurrence increased with increasing distance to shellfish farms, with no apparent relationship with distance to salmon farms. These relationships should not be interpreted as Chilean dolphins being attracted to shellfish farms, or Peale's and Chilean dolphins actively avoiding shellfish and salmon farms, respectively. A more plausible explanation is that the location of the two types of aquaculture overlapped more or less with the dolphins' preferred habitat, and thus acted as a proxy for a set of habitat characteristics.

Shellfish, in particular mussels (Mytilidae), are cultivated on vertical lines suspended from horizontal surface longlines buoyed by floats. These farms require a minimum water depth of around 8-10 m and high primary productivity and nutrient flow, conditions often encountered in or near estuaries (e.g. Yaldad Bay). These characteristics match those selected by Chilean dolphins, but not so much those of Peale's dolphins. Where shellfish farms and Chilean dolphins co-occurred, the dolphins were observed to move in the corridors between the shore and the outer shoreward longlines of the farms (Heinrich & Fuentes, pers. obs.). Although they occasionally were observed inside the perimeter of shellfish farms, Chilean dolphins appeared to avoid areas with more than 30% coverage of surface longlines in Yaldad Bay (Ribeiro et al., 2007). Thus, large shellfish farms might reduce the availability of habitat important to Chilean dolphins. Similar exclusion effects and potentially lost foraging opportunities have been reported for shellfish farms and dusky dolphins (*L. obscurus*, Gray 1828) in New Zealand (Markowitz et al., 2004; Pearson et al., 2012) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, Ehrenberg 1833) in Australia (Watson-Capps & Mann,

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2005). In contrast, shellfish farms in Spain that used floating rafts instead of longlines were found to attract common bottlenose dolphins (*T. truncatus*, Montagu 1821); these structures might provide predictable and enhanced foraging opportunities for the dolphins by attracting and harbouring wild fish (Díaz López & Methion, 2017). A recent review found that the responses of mobile organisms associated with farming structures differed substantially in nature (from attraction to repulsion) and across spatial and temporal scales (Callier et al., 2017). Thus, scale and species-specific responses should be carefully considered in studies and management of aquaculture effects on wild fauna.

Predicted occurrence of Chilean dolphins increased with distance to salmon farms (within 1000 m), but neither Chilean nor Peale's dolphin habitat selection seemed to be directly influenced by the distribution of salmon farms. These farms were more abundant in the northern study area and tended to be located in deeper waters (>20 m) which limited their spatial proximity to preferred Chilean dolphin habitat. Acoustic harassment devices aimed at deterring predatory attacks of pinnipeds on caged farm fish can induce area avoidance in small cetaceans (Olesiuk, Nichol, Sowden, & Ford, 2002), but such devices were not used by fish farms in the Chiloé archipelago during the study period (Sepúlveda & Oliva, 2005; Heinrich, pers. obs.).

Even though the modelling results show limited direct spatial overlap between dolphins and salmon farms, the expansion and intensification of fish farming in the coastal marine environment might still affect both species through cascading ecosystem effects. The Chilean salmon farming industry has faced substantial criticism for their inadequate handling of disease outbreaks, misuse of antibiotics, and regular accidental (and intentional) releases of millions of farmed salmon into the coastal waters off Chiloé, all of which threaten the health and function of the coastal marine ecosystem (Asche, Hansen, Tveteras, & Tveterås, 2009;

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Buschmann et al., 2012; Gomez-Uchida et al., 2018; Niklitschek, Soto, Lafon, Molinet, & Toledo, 2013; Sepúlveda et al., 2013). Managing and adapting aquaculture practices to reduce negative effects might be a more promising mitigation strategy than excluding anthropogenic activities outright. If this approach was adopted, monitoring and enforcement of appropriate aquaculture practices in general, and close to key dolphin habitat in particular, should be a priority. Supporting measures that should be put in place include a requirement for proper maintenance of existing aquaculture farms and removal of structures no longer in use (e.g. shellfish long-lines and floats) to reduce potential habitat exclusion effects, particularly for Chilean dolphins. Under the precautionary principle restrictions on new farming concessions should be introduced until better information about the risks and magnitude of impacts of the farming activities on the coastal marine ecosystem and its dependent species is obtained (Niklitschek et al., 2013).

The identified differences in the responses of the two dolphin species to aquaculture farms also highlights important methodological considerations. Species distribution models should include anthropogenic variables in areas of intense human activities, as the latter might be interacting with or even altering the natural habitat use patterns of the species of interest. Species interactions with aquaculture should be investigated on a species- and context-specific basis.

Conservation implications

A distinguishing feature of this study was the use of long-term (11 years), systematically *in situ* collected data to investigate fine-scale habitat use patterns of two sympatric cetacean species in a coastal environment under pressure from human activities. The observed species-environment relationships and resulting habitat use patterns for both

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species remained stable over a decade. Such long-term stability in habitat use is important when considering spatially explicit conservation measures, such as marine protected areas (Hartel, Constantine & Torres, 2015; Wilson, Reid, Grellier, Thompson, & Hammond, 2004). The channels around Isla San Pedro, Coldita and Yaldad Bay in southern Chiloé constitute key habitat for a small, resident population of Chilean dolphins (this study; Heinrich, 2006), and should be considered as the first priority conservation area for Chile's only endemic cetacean in regional marine spatial planning and coastal zoning.

Our study was limited to austral summers and autumns. Winter field activities in southern Chile are hampered by challenging logistics, poor light and inclement weather conditions (Darwin, 1860). Observations from short sighting surveys during winter (2004, 2010) and year-round static passive acoustic monitoring (PAM) (2013-14) indicated that Chilean dolphins continued to use the same key areas in Yaldad Bay and around Isla San Pedro throughout the year (Heinrich, unpublished data). Static PAM appears to be a particularly useful tool to monitor patterns of seasonal habitat use in the identified core habitat or dolphin occurrence around aquaculture farms given the method's independence of weather and light conditions (Mellinger, Stafford, Moore, Dziak, & Matsumoto, 2007).

Although our study identified several high-occurrence areas for Peale's dolphins (e.g. Canal Dalcahue, shoals south of Islas Laitec and Cailín), fine-scale spatial conservation measures might be less suitable due to this species' wider ranging habits. While their more generalist nature might make Peale's dolphins less susceptible to localized habitat impacts, it might also expose them to a wider range of anthropogenic pressures regionally. Therefore, Peale's dolphins and other highly mobile marine predators would likely benefit most from an integrated, region-wide ecosystem approach to managing ongoing and intensifying

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anthropogenic activities, such as the continued expansion of aquaculture into more remote and less impacted southern fjords (Fernández & Castilla, 2005).

The identified important habitats for Chilean and Peale's dolphins are highly relevant for coastal and marine spatial planning in the Chiloé archipelago. The results also have implications beyond the boundaries of our study areas. The established species-environment relationships could be used to predict potentially important habitats for each species in the southern fjords. This region is the focus for major planned expansions of the Chilean salmon farming industry (Niklitschek et al., 2013), yet conducting systematic marine surveys in this vast fjordic region is logistically challenging and prohibitively expensive. Range-wide abundance estimates are lacking for both species, but have been deemed a conservation priority for Chilean dolphins given concerns about the species' past exploitation, suspected low abundance, and potentially declining populations (Heinrich & Reeves, 2017). While extrapolated habitat predictions should be treated with caution, they could serve to identify potentially important areas where dedicated studies of dolphin abundance should be conducted or where dolphin habitat use and anthropogenic activities are most likely to overlap (Elith & Leathwick, 2009; Mannocci, Roberts, Miller, & Halpin, 2017). Spatial predictions of important dolphin habitat could also be included in region-wide marine spatial planning and conservation zoning initiatives (Guisan et al., 2013; Vila et al., 2016).

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TABLES

Table 1. Environmental, spatial and temporal variables measured during boat surveys and considered as candidate predictors in the modelling.

Variable	Working name	Description	Measurement method	Unit
Depth	Depth	Water depth	Hand-held depth sounder	m
Distance to shore	ShoreDist	Linear distance to nearest shore	Laser range finder (< 1,000 m) & GIS (≥1,000 m)	m
Distance to river	RiverDist	Distance (linear or alongshore) to nearest permanent river mouth	GIS	m
Water clarity	WaterClar	Water clarity	Secchi disk depth	m
Sea surface temperature	SST	Sea surface temperature at 1 m depth	Digital conductivity-temperature meter	° C
Salinity	Salinity	Salinity at 1 m depth	Digital conductivity-temperature meter	‰
Distance to shellfish farm	ShellfishFarm	Linear distance to nearest shellfish farm	Laser range finder (< 1,000 m) & GIS (>1,000 m)	m
Distance to salmon farm	SalmonFarm	Linear distance to nearest salmon farm	Laser range finder (<1,000m), random value from 1000 m to 7000 m	m
Beaufort scale	SeaCond	Sea conditions	Field observation	-
Latitude / Longitude	LatLon	Geographic position expressed in decimal degrees (-N, -E)	Hand-held Garmin GPS receiver	°
Year	Year	Year in which research was carried out		-

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Table 2. Environmental models based on forward stepwise selection. Covariates are shown in order of importance and sequential entry into the model. Effective degrees of freedom for each smooth are given in the 'edf' column. The % Dev shows the contribution of each term to the explained deviance. Δ AIC is the reduction of AIC when the covariate was added to the model.

Chilean dolphin			
Smooth	**edf**	**% Dev**	**Δ AIC**
s(ShoreDist)	1.9	17.8	
s(ShellfishFarm)	2.0	+4.8	–89.7
s(Depth)	2.4	+2.6	–49.5
s(WaterClar)	3.5	+2.5	–42.5
s(RiverDist)	3.8	+1.9	–32.1
s(SST)	3.9	+1.3	–18.0
s(SeaCond)	1.7	+1.0	–17.4
s(SalmonFarm)	3.2	+0.9	–10.3
s(Salinity)	1.0	+0.4	–7.7
Total		**33.2**	

Peale's dolphin			
Smooth	**edf**	**% Dev**	**Δ AIC**
s(Depth)	3.6	8.5	
s(ShellfishFarm)	3.0	+2.2	–29.2
s(ShoreDist)	2.8	+1.4	–16.9
s(RiverDist)	3.7	+1.6	–16.8
s(Salinity)	2.1	+1.1	–14.1
s(SST)	2.1	+0.7	–6.8
s(SeaCond)	2.1	+0.6	–5.4
Total		**16.1**	

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FIGURES (legends)

Figure 1. Distribution of sightings and absence sampling points in the northern and southern study areas in the Chiloé archipelago, southern Chile. Red points: Chilean dolphins; Yellow points: Peale's dolphins. Small blue points: sampling locations without dolphins (absences). Light blue area: extent of the coastal survey areas. Inset: Location of Chiloé archipelago in South America.

Figure 2. Occurrence of Chilean dolphins as a smooth function of covariates: distance to shore, distance to nearest river, depth, water clarity, salinity, SST, distance to nearest shellfish farm and distance to nearest salmon farm. Shaded areas represent 95% CI. Data points are represented as rug plots on the horizontal axes.

Figure 3. Predicted mean occurrence of Chilean dolphins (a) and Peale's Dolphins (d) in the the southern study area, together with upper (b, e) and lower (c, f) 95% CI.

Figure 4. Predicted mean occurrence of Chilean dolphins (a) and Peale's Dolphins (d) in the northern study area, together with upper (b, e) and lower (c, f) 95% CI.

Figure 5. Occurrence of Peale's dolphins as a smooth function of different covariates: depth, distance to shore, salinity, SST, distance to nearest river and distance to nearest shellfish farm. Shaded areas represent 95% CI. Data points are represented as rug plots on the horizontal axes.

Figure 6. Predicted mean dolphin occurrence of Chilean and Peale's dolphins overlaid with concessions for salmon and shellfish farms in 2015 in the southern (a) and northern (b) study areas. For details on the colour scheme for predicted occurrence see Figures 3 and 4.

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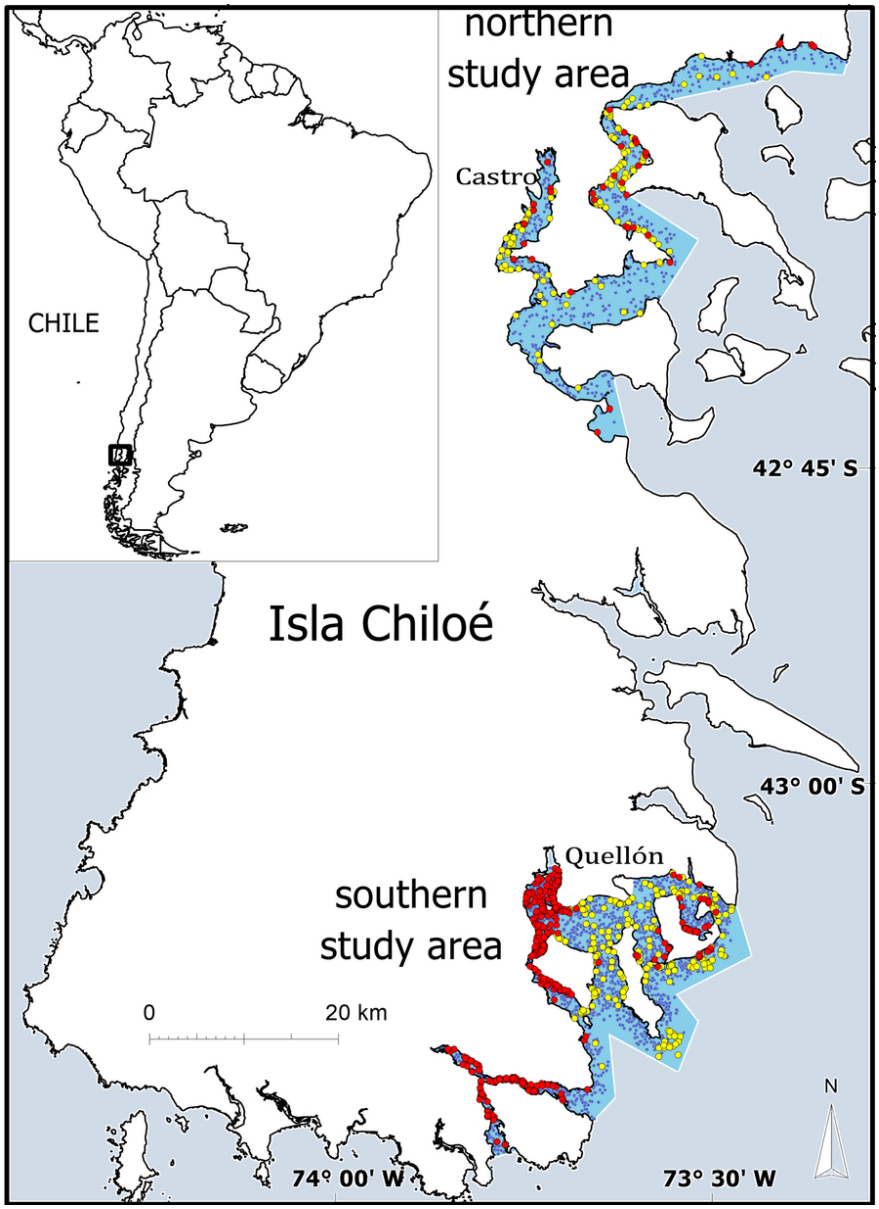

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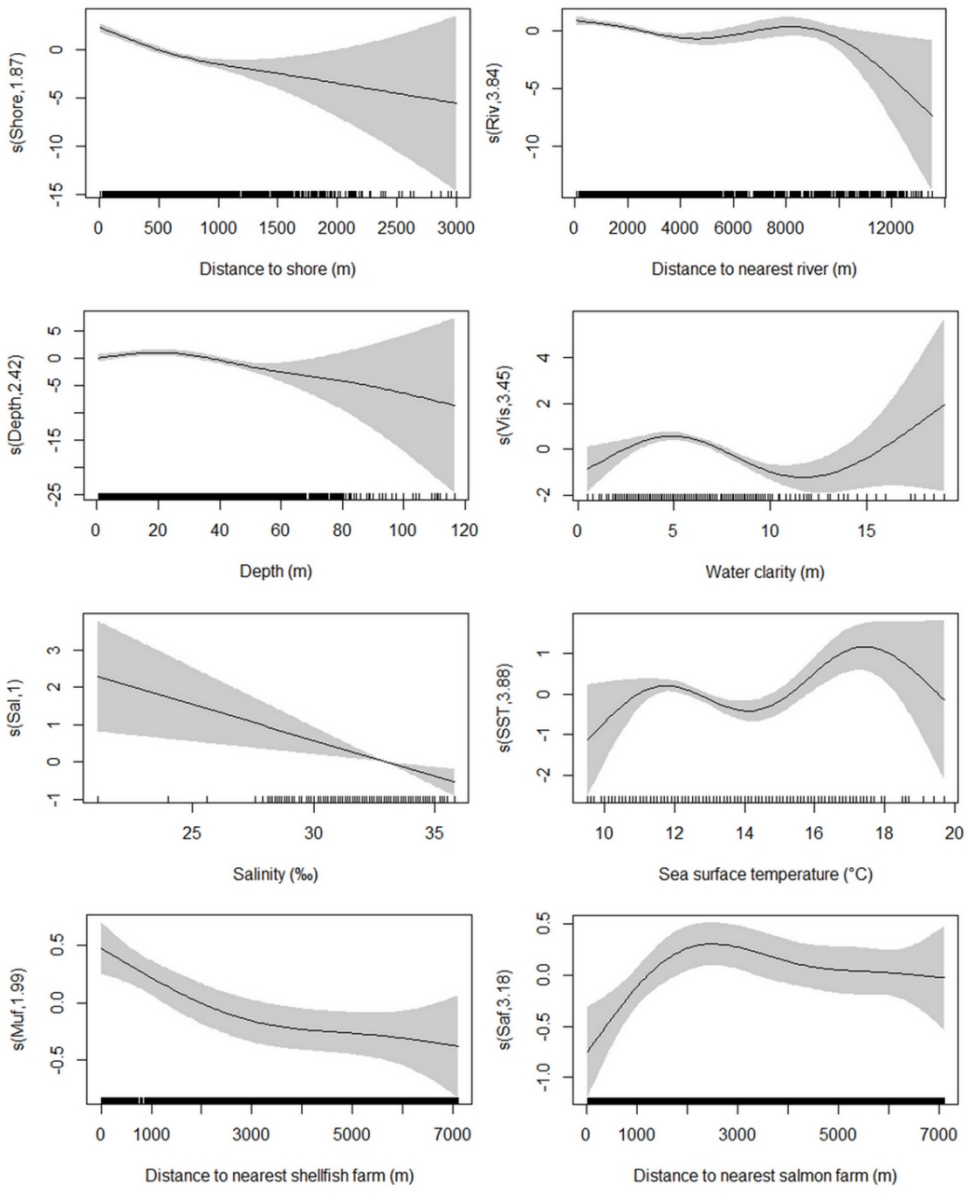

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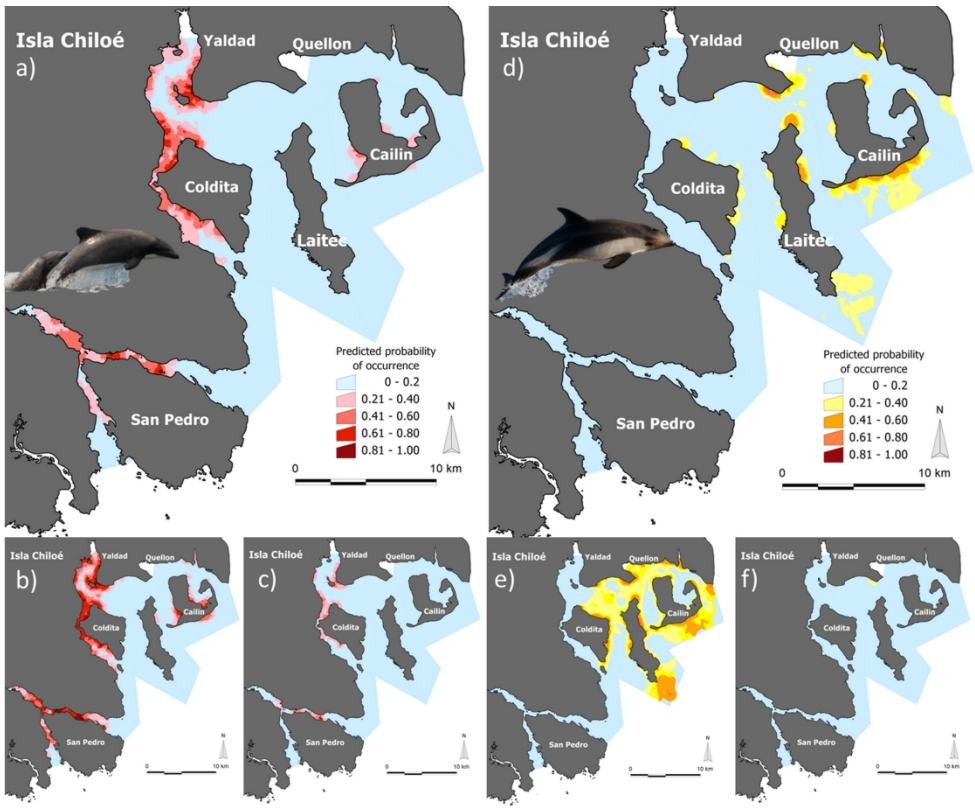

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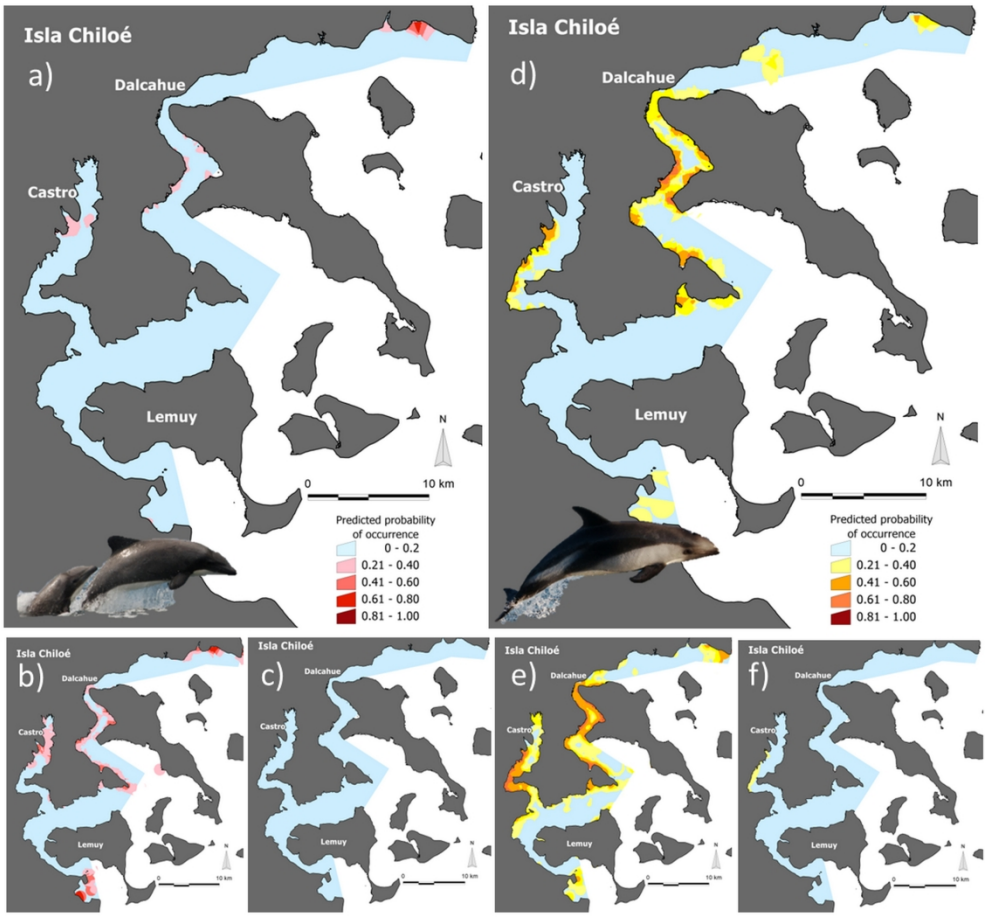

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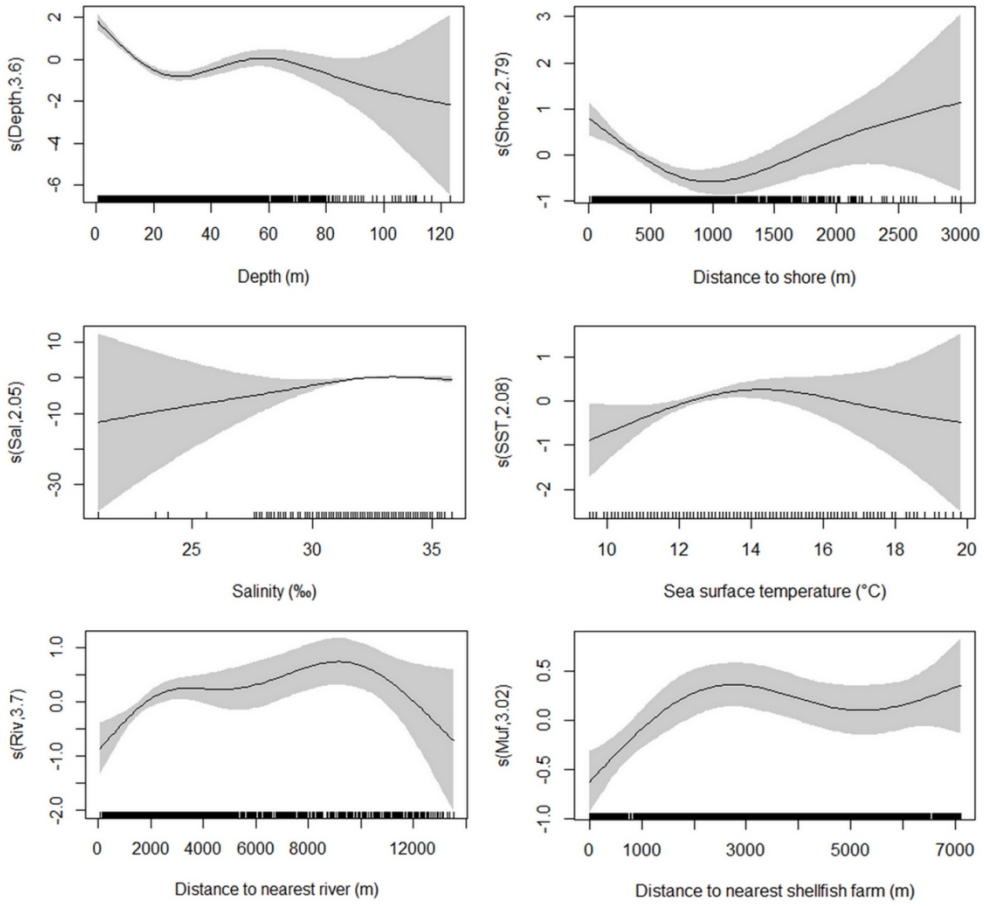

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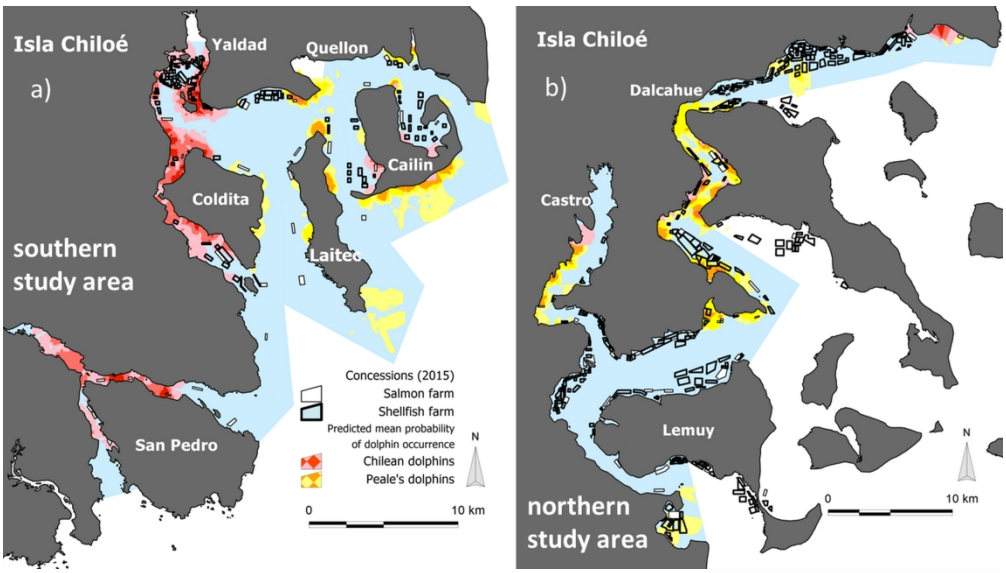

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