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Modelling marine habitat utilisation by yellow-eyed penguins along their mainland distribution: baseline information

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Using Global Positioning System tracking data obtained from yellow-eyed penguins (*Megadyptes antipodes*) over the course of the past 20 years, habitat models were developed to assess the species' utilisation of the continental shelf when at sea. A total of 29 494 locations of dive events were recorded for birds from Codfish Island/Whenua Hou and Stewart Island/Rakiura (Foveaux Strait region), the Catlins, Otago Peninsula, Aramoana, and Oamaru. Regions suffering from data deficiency, and thus unreliable model outputs, are the southern ranges of Stewart Island (Port Pegasus to Paterson Inlet), the Catlins, and Banks Peninsula. The maximum entropy method was used to develop habitat utilisation models, based on foraging data and environmental variables for bathymetry, seafloor sediment, and colony distance.

Model outputs for the data deficient Banks Peninsula, Catlins, and the southern regions of Stewart Island cannot be considered representative. Further investigation is required.

During the breeding season, the core yellow-eyed penguin foraging habitat from Aramoana to Oamaru spans from the Blueskin Bay to Waitaki River within 5–35 km from the coast. South of the Otago Peninsula, foraging occurs primarily to the south and west between 5 and 30 km from the coast; the penguins generally utilise waters no deeper than 80 m. Models predict that the entire Foveaux Strait from Te Waewae Bay to the 80-m depth contour to the east should represent suitable habitat. However, seafloor ecosystems for large parts of the eastern and central Foveaux Strait have been altered by the Bluff oyster fishery, and the actual habitat utilised by the penguins is probably concentrated to the west largely outside the oyster fishery's Quota Management Area. This is reflected in the regional model outputs for Stewart Island/Rakiura.

To assess non-breeding distribution, the constraining variable 'colony distance' was removed from the models, and the model outputs indicated that the penguins may utilise most of the continental shelf from Stewart Island to North Canterbury. Core foraging habitat ranges from the shore to about 70 km offshore in the Canterbury Bight and 40–50 km from the coast in the southern regions.

The diving activity of breeding penguins is concentrated in the hours between 6 a.m. and 9 p.m. (90.9% of 79 982 recorded dives); the diving intensity reaches its peak at 7 a.m. and remains constant until 7 p.m. During the breeding season, 94% of the penguins' dives were along the seafloor; outside the breeding period, the penguins covered greater distances diving closer to the surface and 70% of all dives were benthic.

The dispersal of fledgling penguins has only recently been studied via satellite telemetry. Although this research is ongoing, preliminary results indicate that the region north of the Otago Peninsula and the region around the Rangitata River mouth in the Canterbury Bight are important congregation points for young penguins after fledging (February-July).

No data on set netting operations were available for analysis so only very general conclusions can be drawn. Yellow-eyed penguins are particularly vulnerable to set net operations that target benthic species, operate in the penguins' core foraging grounds (as specified by the models), and are active during daylight hours. Setting nets between 7 p.m. and 7 a.m. may significantly reduce the risk of incidental bycatch of yellow-eyed penguins.

1. INTRODUCTION

1.1 Overview

With an estimated 1700 breeding pairs, the yellow-eyed penguin is the second rarest penguin world-wide (Seddon et al. 2013). The species lives and breeds on the subantarctic Campbell Island and Auckland Island, as well as the south-eastern shores of New Zealand's South Island. On the mainland (described here as the eastern and southern coasts of the South Island and Stewart Island), yellow-eyed penguins breed between Port Pegasus in southern Stewart Island and Oamaru in North Otago where their presence contributes to the local tourism economy. A few breeding pairs are found on Banks Peninsula, although their reproductive output is close to zero (Ellenberg & Mattern 2012).

On the mainland, the species has undergone a significant decline in the past two decades and current population projections predict functional extinction of the mainland population in the next 20–40 years (Mattern et al. 2017a, Houseman 2018). Rising sea surface temperature as a result of climate change has been identified as a key problem for the species reducing its resilience towards other non-climatic factors such as pollution and fisheries bycatch (Mattern et al. 2017a). Incidental set net bycatch of yellow-eyed penguins has been identified as an issue that can be managed to enhance the species' chance of survival in the face of climate change (Darby & Dawson 2000, Ellenberg & Mattern 2012, Crawford et al. 2017).

As the population declines, the impact of even small numbers of fishing related mortalities increases, and Fisheries New Zealand required information about the utilisation of the marine habitat by the species from their mainland habitat.

Based on tracking data recorded during various studies carried out by the University of Otago using GPS dive loggers on yellow-eyed penguins, habitat models were developed to inform investigations to examine the likelihood of captures and the resulting risk to yellow-eyed penguins from set net fishing.

1.2 Literature Review

Several extensive literature reviews covering fisheries interactions of yellow-eyed penguin have been published in recent years (Ellenberg & Mattern 2012, Crawford et al. 2017, Mattern & Wilson 2019, Webster 2018). A condensed summary of these reviews is presented below.

Bycatch of yellow-eyed penguins in set nets poses a significant threat. The risk of yellow-eyed penguin entanglement in set nets has been categorised as "extreme" in the "Level 1 Risk Assessment for Incidental Seabird Mortality" (Rowe 2010). Between 1979 and 1997, 72 confirmed deaths of yellow-eyed penguins due to set net entanglement were recorded, the majority of which occurred near the Otago Peninsula (Darby & Dawson 2000). The peak of the set netting effort coincides with the penguins' breeding season (November–March) (Ellenberg & Mattern 2012). During this period, foraging ranges of yellow-eyed penguins are restricted because penguins have to return to their nest daily to feed their offspring (Darby et al. 1990). This reduces the penguins' ability to disperse widely so that penguin numbers at sea are concentrated generally within a 10–40 km radius of their breeding colonies (Moore 1999, Mattern et al. 2007).

Yellow-eyed penguins are predominantly benthic foragers that search for and catch their prey (e.g., blue cod *Parapercis colias*, opalfish *Hemerocoetes monopterygius*, and arrow squid *Nototodarus sloanii*) at or close to the seafloor (Mattern et al. 2007, 2013, 2018; Mattern & Ellenberg 2018) (Figure 1). This makes them vulnerable to bottom fishing operations. Set netting in New Zealand primarily targets demersal fish species such as tarakihi *Nemadactylus macropterus*, jock stewart *Helicolenus percoides*, rig *Mustelus lenticulatus*, and school shark *Galeorhinus galeus*. These fisheries overlap spatially with the benthic foraging areas used by yellow-eyed penguin (Crawford et al. 2017).

In 2008, a set net ban within a 4-nautical mile zone from the coast was established along most of the yellow-eyed penguins' mainland breeding range, the exception being Stewart Island and its outliers (Ellenberg & Mattern 2012). However, although this ban certainly eliminated the risk of set net and penguin interactions within this zone, tracking studies showed that the penguins principally forage between 5 and 25 km from the coast (Moore 1999, Mattern et al. 2007, 2013). Moreover, the set net ban meant that fishing operations moved away from the coast and, thus, further into the penguins' foraging habitat where benthic diving is more prevalent (Ellenberg & Mattern 2012). Thus, incidental bycatch of yellow-eyed penguins in set nets not only remains a significant threat, but the inshore set net ban may in fact have increased the risk for the penguins.

The only measure of the frequency of incidental bycatch mortality in yellow-eyed penguins derives from observer reports (Rowe 2008). Reported figures are believed to underestimate the true mortality of yellow-eyed penguins in set netting operations. For example, for the five year period 2005–10, only nine incidents of yellow-eyed penguin bycatch were reported; no self-reporting by fishers was evident so that the true number of bycatch incidents was likely masked by low observer coverage (Crawford et al. 2017). Model-based estimates of penguin fatalities in set netting operations range between 16 and 60 birds annually (mean 35 birds y^{-1}) (Richard & Abraham 2015). In the 2018–19 breeding season nest searches on the mainland found 216 breeding pairs (DOC, unpublished data). Hence, between 3 and 14% of the mainland yellow-eyed penguin population may be lost due to set net mortality every year.

Figure 1: Yellow-eyed penguin swimming past a spiny dog fish at the seafloor off the Otago Peninsula. Screen capture of video footage recorded with an animal-borne video logger (Mattern et al. 2018).

2. METHODS

2.1 Dive data structure

Yellow-eyed penguins have been tracked infrequently using GPS dive loggers since late 2003 (Mattern et al. 2007, 2013, 2018, Ellenberg & Mattern 2012, Mattern & Ellenberg 2018). These devices deliver accurate locations of dive events allowing it to put behavioural patterns – derived from dive profile analysis (Wilson 1995) – into a spatial context (Mattern et al. 2007). In the ideal case, Global Positioning System (GPS) positions are recorded immediately before or after a dive event. If GPS fixes are not recorded close to a dive event, dive locations can still be estimated by linear extrapolation using the nearest fixes recorded before or after a dive event.

Between December 2003 and March 2019, GPS dive data from a total of 79 yellow-eyed penguins were recorded at six locations spanning the species' distributional range on the mainland (Table 1).

Yellow-eyed penguins are generally benthic foragers that use pelagic dives to commute between their breeding colonies and foraging sites (Mattern et al. 2007). However, environmental conditions can prevent the penguins from benthic foraging; for example, when strong algal blooms reduce light levels at the seafloor. Under such circumstances yellow-eyed penguins may switch to pelagic foraging, although the birds revert back to benthic foraging as soon as visibility permits (Mattern & Ellenberg 2018).

The determination of whether a dive event recorded as benthic or pelagic is derived from various factors. Firstly, dive profiles of benthic dives have a characteristic U-shape with a bottom phase that is characterised by little to no vertical undulations (Figure 2). Secondly, in combination with the GPS location of the dive, the maximum depth of the dive event can be compared with bathymetry data (e.g., Mitchell et al. 2012). If a dive depth is within 2 m of the charted water depth, the dive is considered a benthic dive.

Considering that inshore set net fisheries target principally demersal species (Crawford et al. 2017) only benthic dives were used for the development of species distribution models (SDM). A total of 58 050 benthic dives were recorded during the 79 deployments of GPS dive loggers on yellow-eyed penguins.

For the analysis, dive data were filtered for spatial quality. Extrapolated dive locations (i.e., dives where no GPS fix was recorded immediately before or after the event) were increasingly unreliable the longer the time period between dive event and nearest GPS fix. A maximum Time-To-Fix of 10 minutes was used as a cut-off point for accepted dive locations; i.e., any dive location that occurred >10 minutes from a GPS fix was omitted. This reduced the number of dive locations used for the analysis to 29 494.

The volume of data recorded for each individual penguin varied greatly, with some birds being tracked for a single day, whereas other deployments recorded data for up to three weeks. To avoid an undue individual bias, for each bird a random subsample of 100 accepted benthic dive locations was drawn, so that a total of 7900 dive locations were used to develop the models.

Table 1: Summary of yellow-eyed penguin GPS dive data recorded since 2003.

Date range	Site	Life history stage	Number of birds	Number of dive events	Number of benthic dives
12/2003–12/2004	Oamaru (North Otago)	Breeding	8	3 096	2 347
12/2004–02/2015	Boulder Beach (Otago Peninsula)	Breeding	33	33 980	27 022
01/2005–11/2006	Anglem Coast, Stewart Island	Breeding	13	5 723	4 022
12/2005–12/2006	Codfish Island/Whenua Hou	Breeding	17	13 240	5 906
12/2017–12/2018	Nugget Point & Penguin Bay, Te Rere (Catlins)	Breeding	4	2 224	1 655
02/2019–03/2019	Aramoana	Pre-moult	4	24 184	17 098

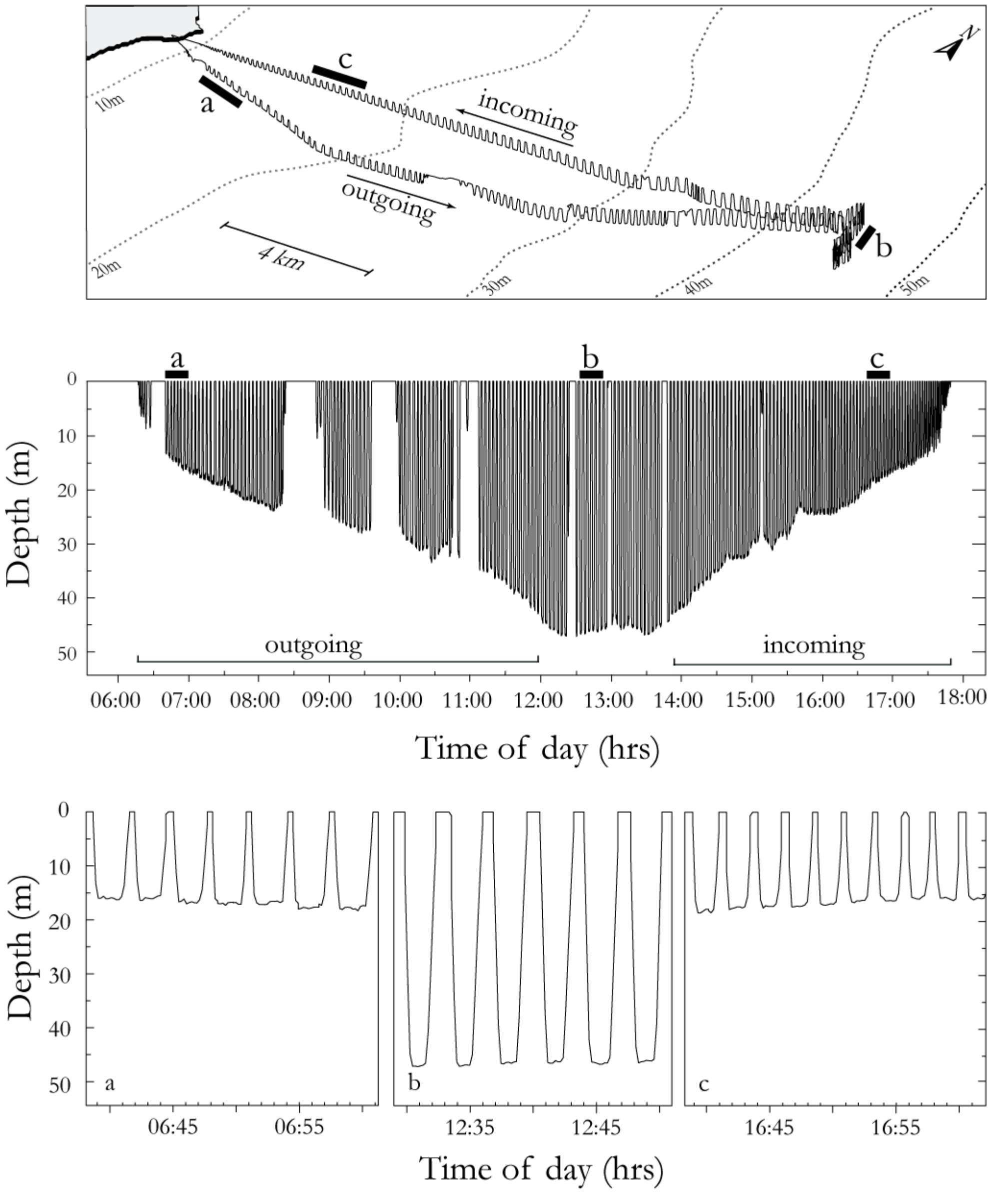

Figure 2: Example of benthic dive profiles recorded in a yellow-eyed penguin from Oamaru, North Otago. Figure reproduced from Mattern et al. (2007).

2.2 Model development

Data for three variables were available to put dive locations into a spatial, environmental context. Water depth was derived from the 250-m gridded bathymetry data set generated by the National Institute of Water and Atmospheric Research (NIWA) in 2016 (Mitchell et al. 2012) (Figure 3.1). Sediment and substrate were extracted as geospatial layers (modelled by NIWA on request from DOC, NIWA Project: DOC15302, and associated metadata are available at https://seasketch.doc.govt.nz/seas_otago/rest/services/Folk_Substrate_Class/MapServer) from the South-East Marine Protection Forum’s Seasketch project (http://southeastmarine.seasketch.org). Seafloor habitat was broadly categorised into three main sediment types: gravel, sand, and mud (Figure 3.2). Using known locations of yellow-eyed penguin colonies on the New Zealand mainland and in the Foveaux Strait region, distance of each GPS fix to the nearest colony (‘colony distance’) were calculated for a 1-km grid covering the entire east coast South Island continental shelf (Figure 3.3). Bathymetry and sediment data were resampled to match this 1-km grid. Accepted yellow-eyed penguin dive positions were projected onto the environmental grids for subsequent analysis (Figure 3.4).

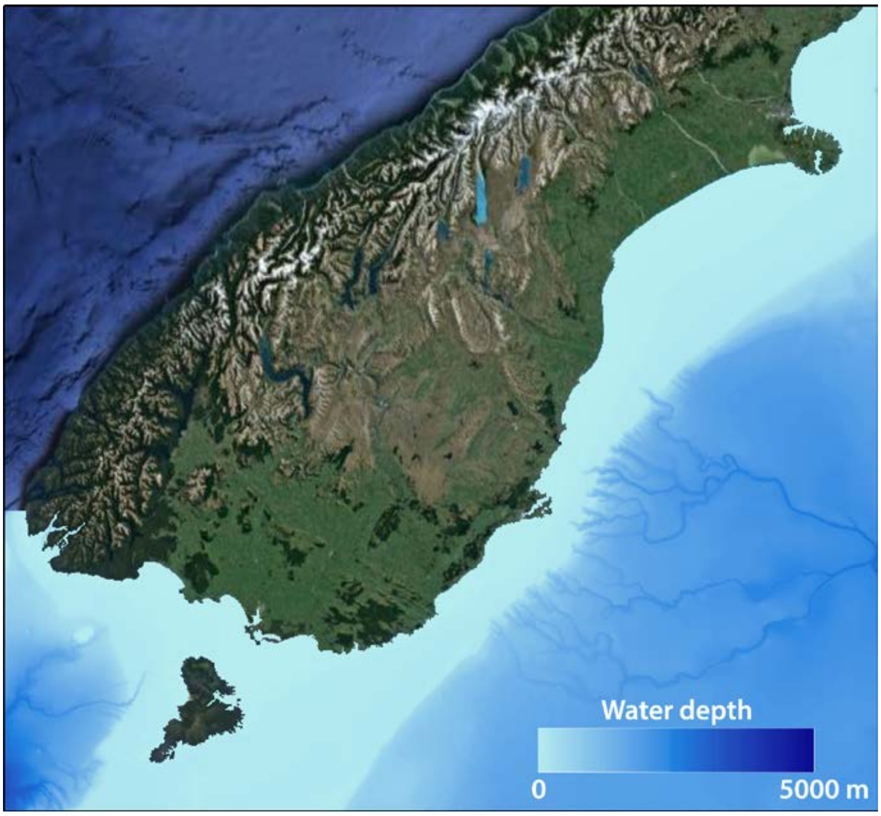

Figure 3.1: 1-km gridded bathymetry within the mainland yellow-eyed penguin distributional range. Source: [https://www.niwa.co.nz/our-science/oceans/bathymetry/download-the-data.](https://www.niwa.co.nz/our-science/oceans/bathymetry/download-the-data)

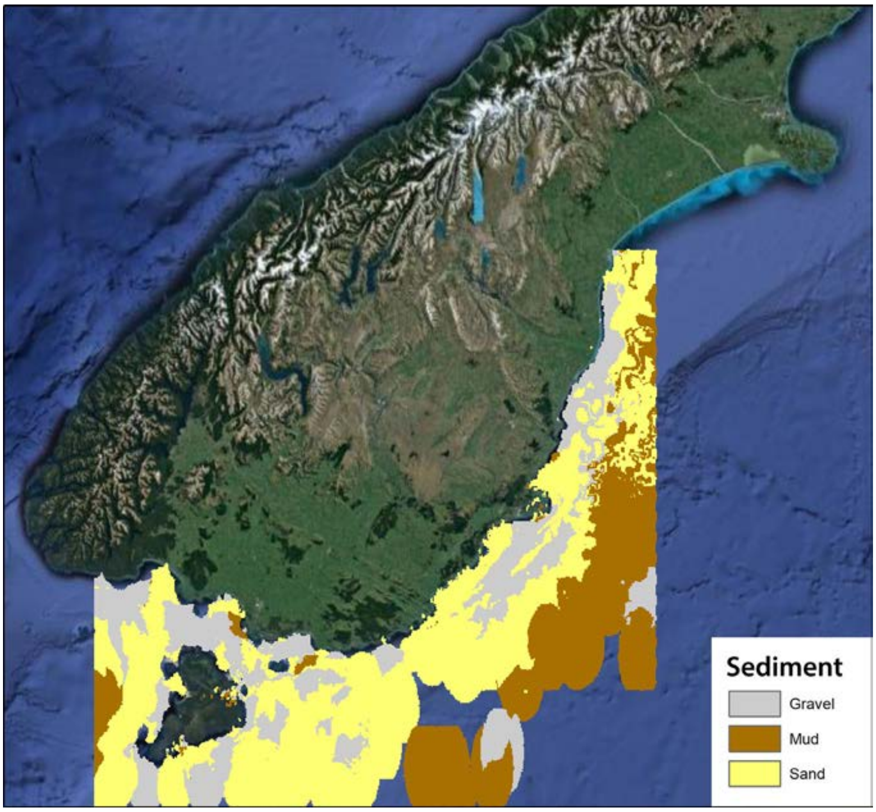

Figure 3.2: 1-km gridded sediment structure within most of the mainland yellow-eyed penguin distributional range. Source: http://southeastmarine.seasketch.org/

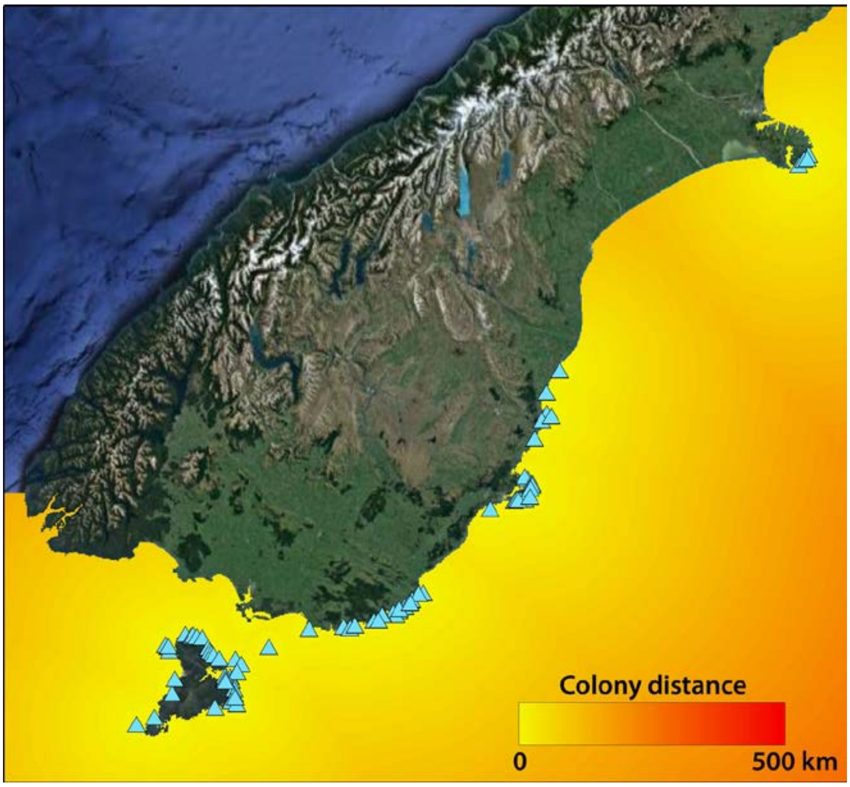

Figure 3.3: 1-km gridded colony distance data calculated from recorded breeding locations featured in the yellow-eyed penguin (YEP) database. Blue triangles indicate active as well as historic yellow-eyed penguin breeding colony locations (n=86) extracted from the YEP database used for distance calculations.

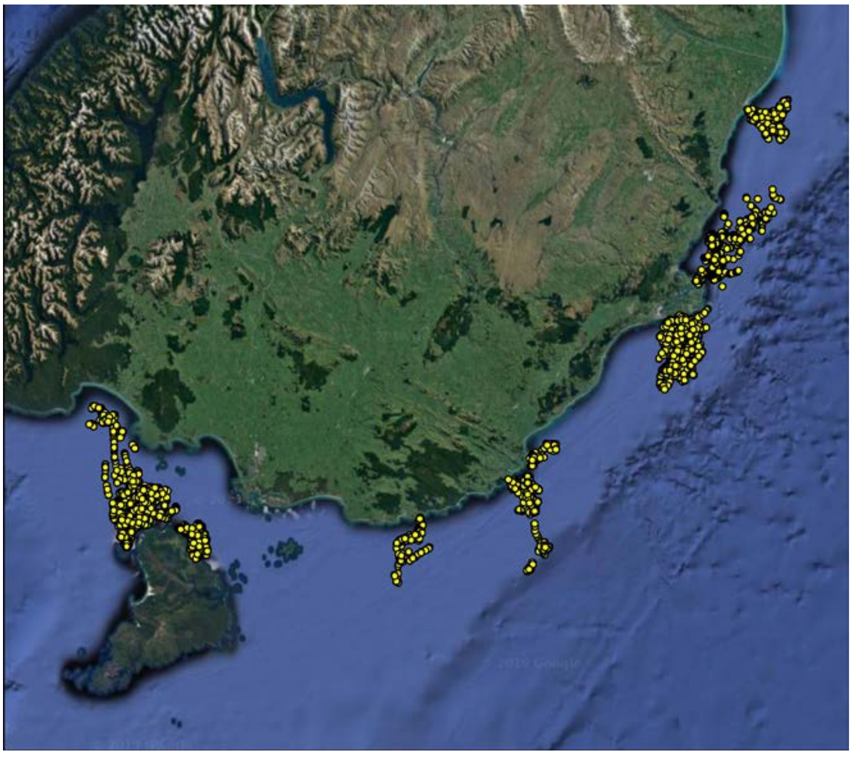

Figure 3.4: Filtered dive locations (n=7900) of yellow-eyed penguins recorded between December 2003 and March 2019 used for developing species distribution models.

Initially simple probabilistic models were developed by counting the number of dives in each grid cell. However, the reliability of the model outputs was unsatisfactory, and a more comprehensive modelling approach was required.

Maximum entropy (Maxent) models proved to be more reliable even though this approach also could not overcome the data deficiency for important yellow-eyed penguin regions, namely Banks Peninsula, the Catlins, and southern Stewart Island. Additional data for the region north of the Otago Peninsula (i.e., Aramoana) became available in March 2019 and these data substantially enhanced the model output.

Maxent is a general-purpose, machine- learning method for making predictions or inference from incomplete spatial information (Phillips et al. 2006). Its core idea is to estimate a species distribution (using presence-absence data derived from the penguins' GPS fix locations at sea) by finding the probability distribution of maximum entropy, subject to a set of environmental parameters (e.g., water depth, sediment type, and colony distance) that represent incomplete information about the species distribution.

There are considerable differences in the characteristics of marine habitat utilised by yellow-eyed penguins from the different regions. For example, penguins from Otago Peninsula forage predominantly over gravelly habitat at depths down to 80 m (Mattern et al. 2018), whereas penguins from Stewart Island may either forage over sandy seafloor habitat or oyster beds (on gravel) at depths generally shallower than 30 m. Although data for detailed analysis are lacking for the Catlins and southern Stewart Island, deployments of dive recorders have shown that in these regions yellow-eyed penguins often forage at depths over 100 m (Moore et al. 1995, Chilvers et al. 2014); whereas dive data available from other regions never exceeded 80 m. Therefore, individual SDMs were developed for each of the regions outlined in Table 1. Data were then pooled to derive a SDM for the species New Zealand mainland range of occurrence (i.e., southern Stewart Island to eastern Cook Strait) to provide a general overview of all suitable habitat regardless of regional foraging strategies.

Except for data recorded in Aramoana in February and March 2019, all available data represent yellow-eyed penguin at-sea distribution during the breeding period. To estimate the species utilisation of the marine habitat outside the breeding season, the constraining variable 'colony distance' was removed from the models. This approach assumed that the general benthic foraging strategy is retained by yellow-eyed penguins over the winter months as well. Dive analysis of the Aramoana data support this assumption.

3. RESULTS AND DISCUSSION

In the following sections model outputs for the different regions are presented, including generalised models using a pooled data set. In each section, a figure indicates habitat utilisation as determined by the best fitting regional models (Figures 4.1–4.7 for the breeding season in section 3.1 and Figures 5.1–5.7 for the non-breeding season in section 3.2). Different coloured raster cells indicate the utilisation likelihood for each cell. In dark red areas the chance to encounter foraging yellow-eyed penguins is 90–100%, and dark green raster cells indicate where yellow-eyed penguins are less likely to forage (under 20% chance). Empty raster cells show areas that the models identified as of no relevance for penguin foraging. However, that is not to say that these areas are not visited by commuting birds (Figures 4.1–4.8).

A table in each section gives estimates of relative contributions of the environmental variables to the Maxent model (Tables 2.1–2.7 in section 3.1 and Tables 3.1–3.7 in section 3.2). To determine the first estimate, in each iteration of the training algorithm, the increase in regularised gain is added to the contribution of the corresponding variable or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training the presence data and background data are randomly permuted. The model is re-evaluated on the permuted data, and the resulting drop in the training AUC is shown in the table, normalised to percentages.

3.1 Species distribution models – breeding season

3.1.1 Oamaru (North Otago)

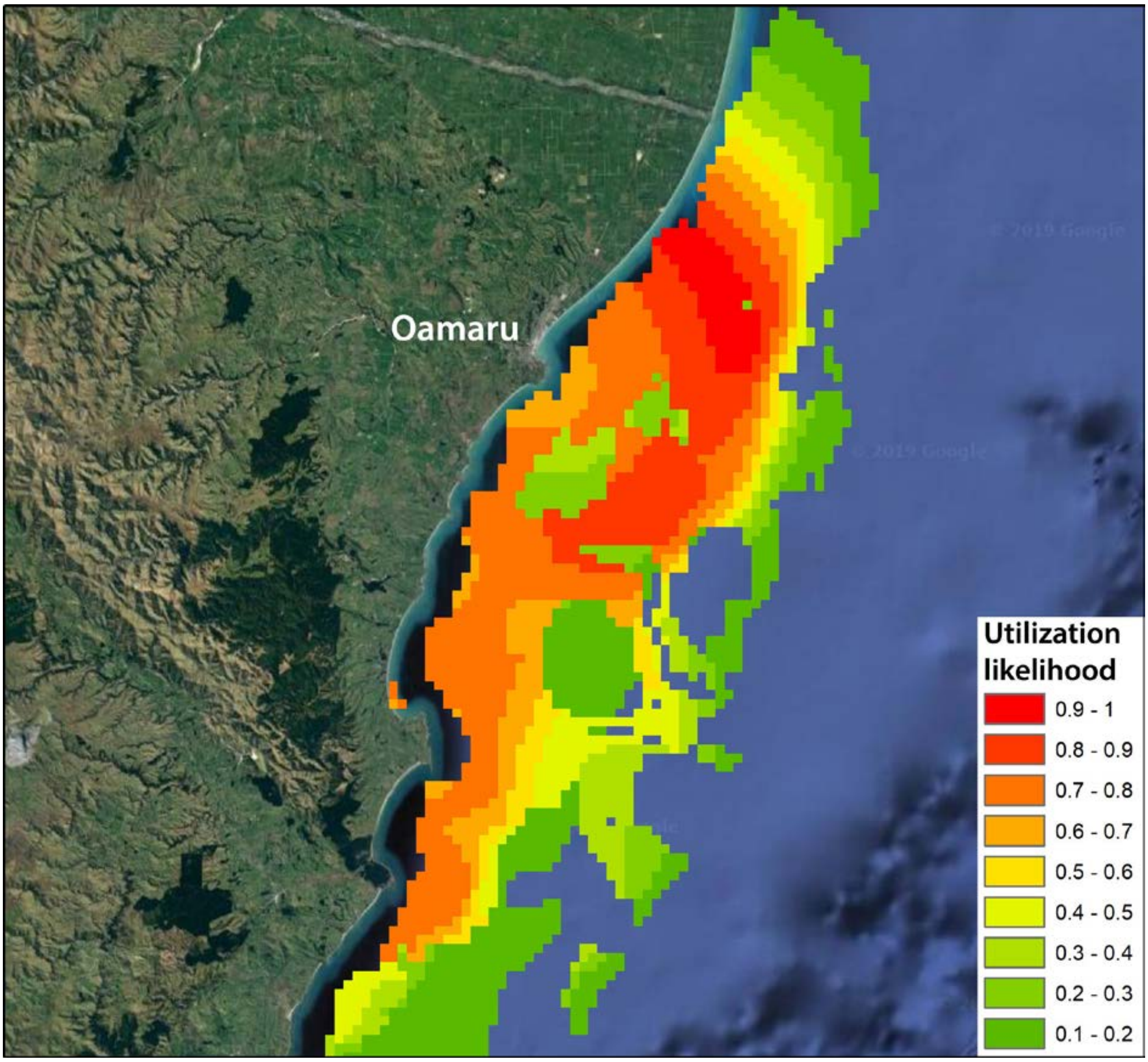

Figure 4.1: Marine habitat available to yellow-eyed penguins off northern North Otago based on foraging data recorded at Oamaru (n=10 birds, 2003–2004). The penguins prefer to stay within 20-30 km of their respective colonies and forage primarily over gravelly habitat in depths of 20–50 m.

Table 2.1: Relative contribution of environmental variables to model – North Otago.

	Percent contribution	Permutation importance
Colony distance	40.4	67.5
Bathymetry	30.4	6.8
Sediment type	29.2	25.8

3.1.2 Aramoana

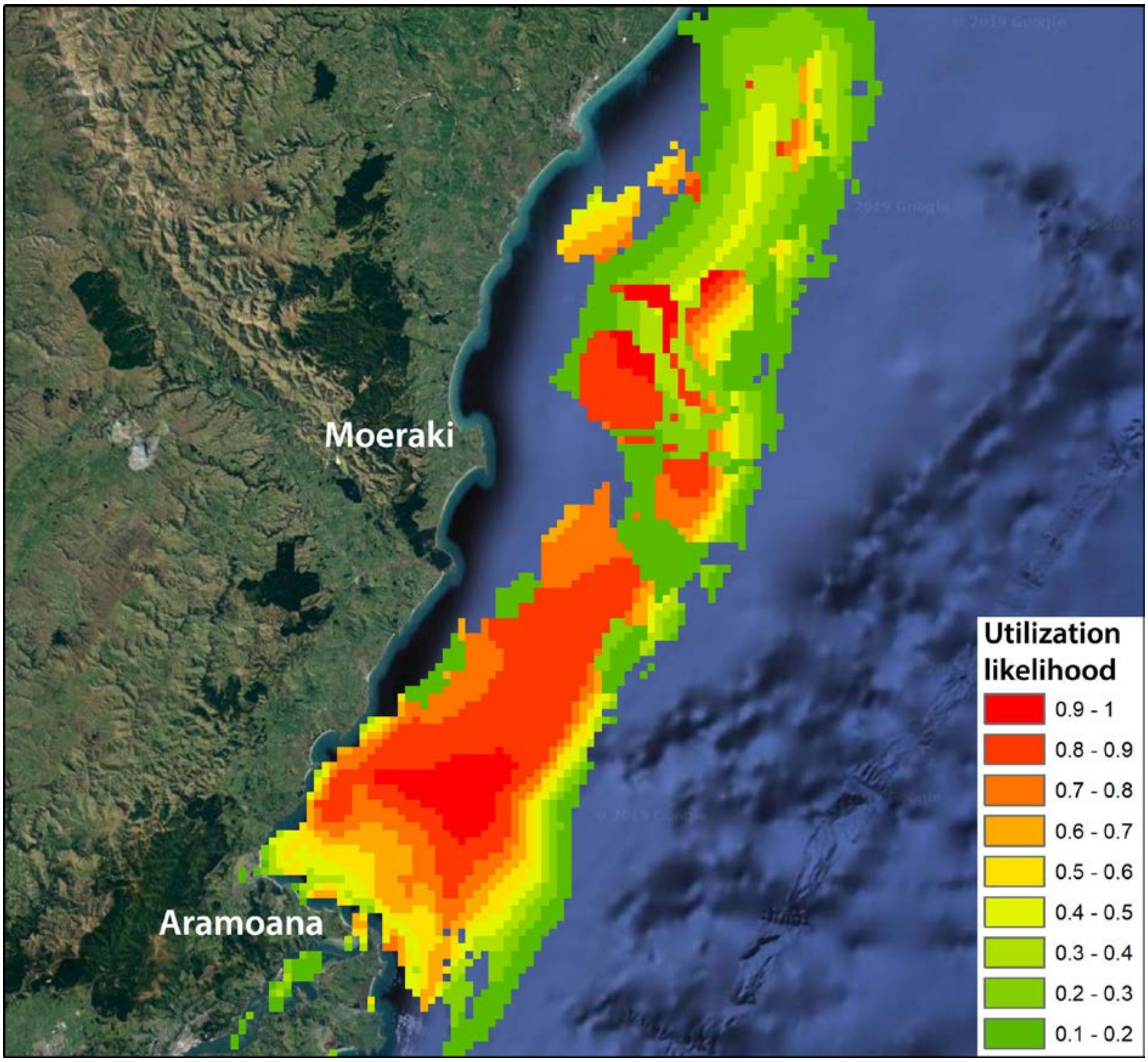

Figure 4.2: Marine habitat available to yellow-eyed penguins off southern North Otago based on foraging data recorded at Aramoana (n=4 birds, February 2018). The birds utilise large swaths of the continental shelf (1-40 km from coast) and stay in waters shallower than 70 m). Unlike most other sites, sediment does not play a significant role in predicting penguin distribution; birds forage over any available sediment.

Table 2.2: Relative contribution of environmental variables to model – Aramoana.

	Per cent contribution	Permutation importance
Colony distance	58.0	68.6
Bathymetry	27.7	25.0
Sediment type	14.3	6.3

3.1.3 Otago Peninsula

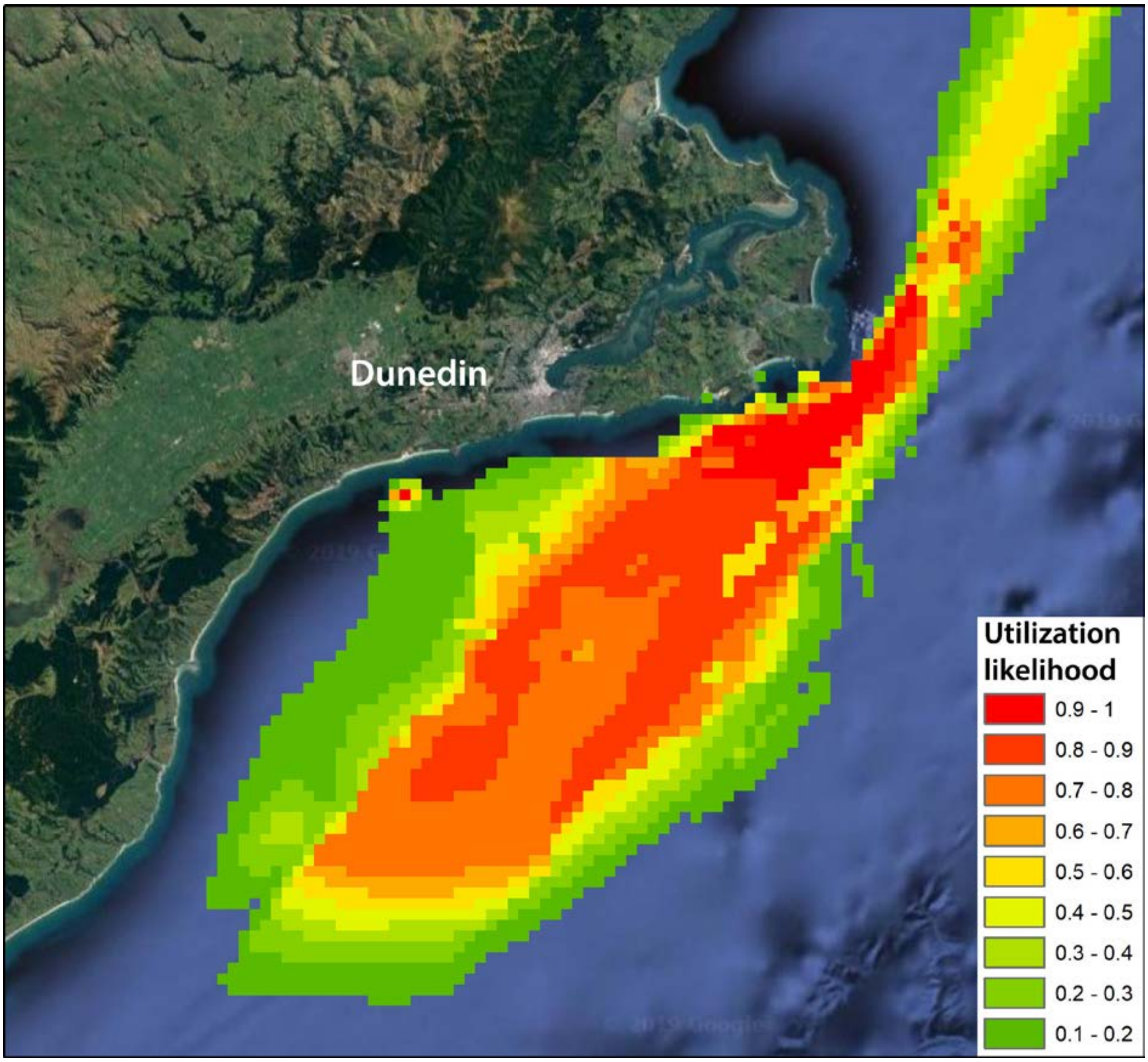

Figure 4.3: Marine habitat available to Yellow-eyed penguins off the Otago Peninsula based on foraging data recorded at Boulder Beach (n=26 birds, 2004-2016). Most important predictors for penguin presence are colony distance and water depth. The birds prefer to forage between 10 and 35 km from their colonies utilizing water depths of 40-80 m. Although sediment type hardly contributes to the final model (see Table 2.3) the birds forage predominantly over gravelly substrate.

Table 2.3: Relative contribution of environmental variables to model – Otago Peninsula.

	Per cent contribution	Permutation importance
Bathymetry	44.1	33.2
Colony distance	39.2	65.0
Sediment type	16.7	1.9

3.1.4 Catlins (data deficient)

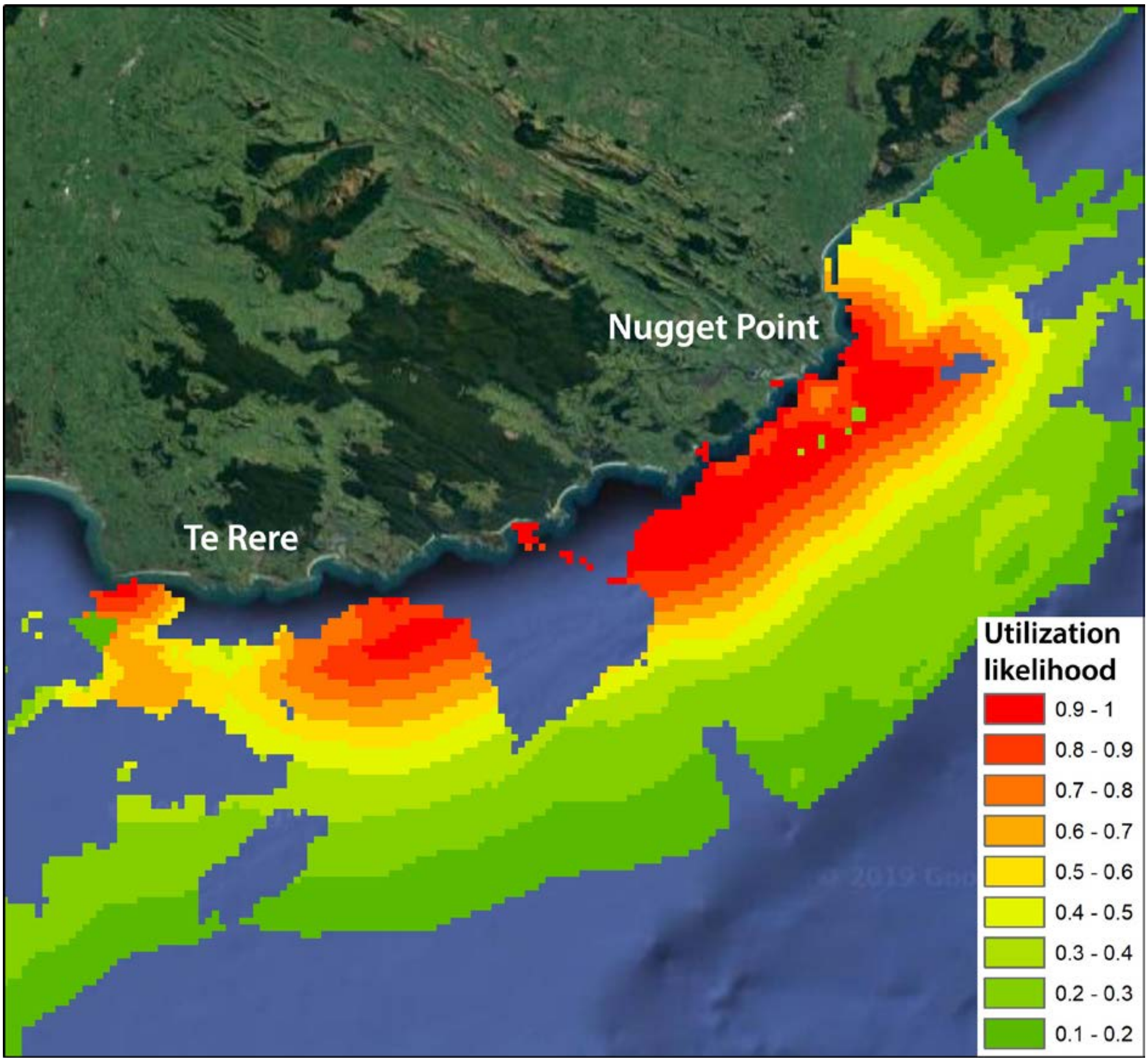

Figure 4.4: Low confidence model outputs of yellow-eyed penguin habitat utilisation off the Catlins coast. Data for only four birds from Nugget Point (n=3 birds, 2016) and Te Rere (n=1 bird, 2016) were available at the time of this project.

The marine habitat around the Catlins is highly variable, ranging from shallow, inshore habitat in Molyneux Bay to deep shelf-edge environment off Hinahina Cove and biogenic reef habitat off the western Catlins (Herzer 1981). With data from only four penguins, the range of the yellow-eyed penguin utilisation of available habitat is grossly under-represented. Therefore, model outputs must be considered unrepresentative. Further data are required.

Table 2.4: Relative contribution of environmental variables to model – Catlins.

	Percent contribution	Permutation importance
Colony distance	59.1	65.5
Sediment type	32.7	21.5
Bathymetry	8.2	13

3.1.5 Anglem Coast (Stewart Island)

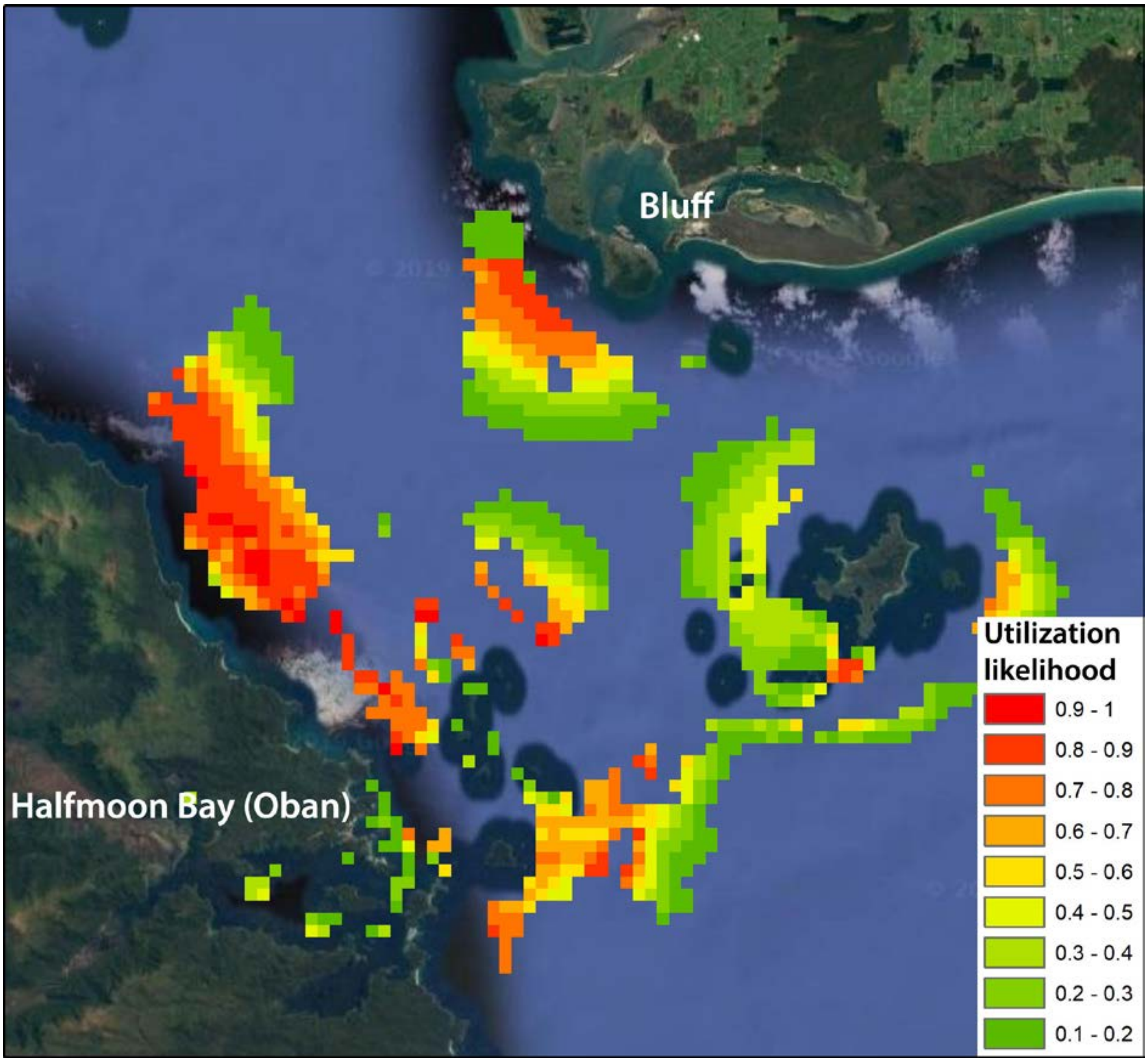

Figure 4.5: Highly fragmented habitat available to yellow-eyed penguins in the eastern Foveaux Strait based on data recorded along the Anglem coast (n=25 birds, 2004–2006). Birds predominantly foraged within 4 km of the Stewart Island coast, in shallow (under 30 m waters) over gravelly habitat. Colony distance is the most important determinant for the distribution of foraging behaviour. It is noticeable that the birds do not range into the central Foveaux Strait, presumably because of alteration of the seafloor habitat by the Bluff Oyster fishery (Ellenberg & Mattern 2012).

Table 2.5: Relative contribution of environmental variables to model – Anglem Coast.

	Per cent contribution	Permutation importance
Colony distance	66.6	81.1
Sediment type	17.9	10
Bathymetry	15.6	8.9

3.1.6 Codfish Island / Whenua Hou

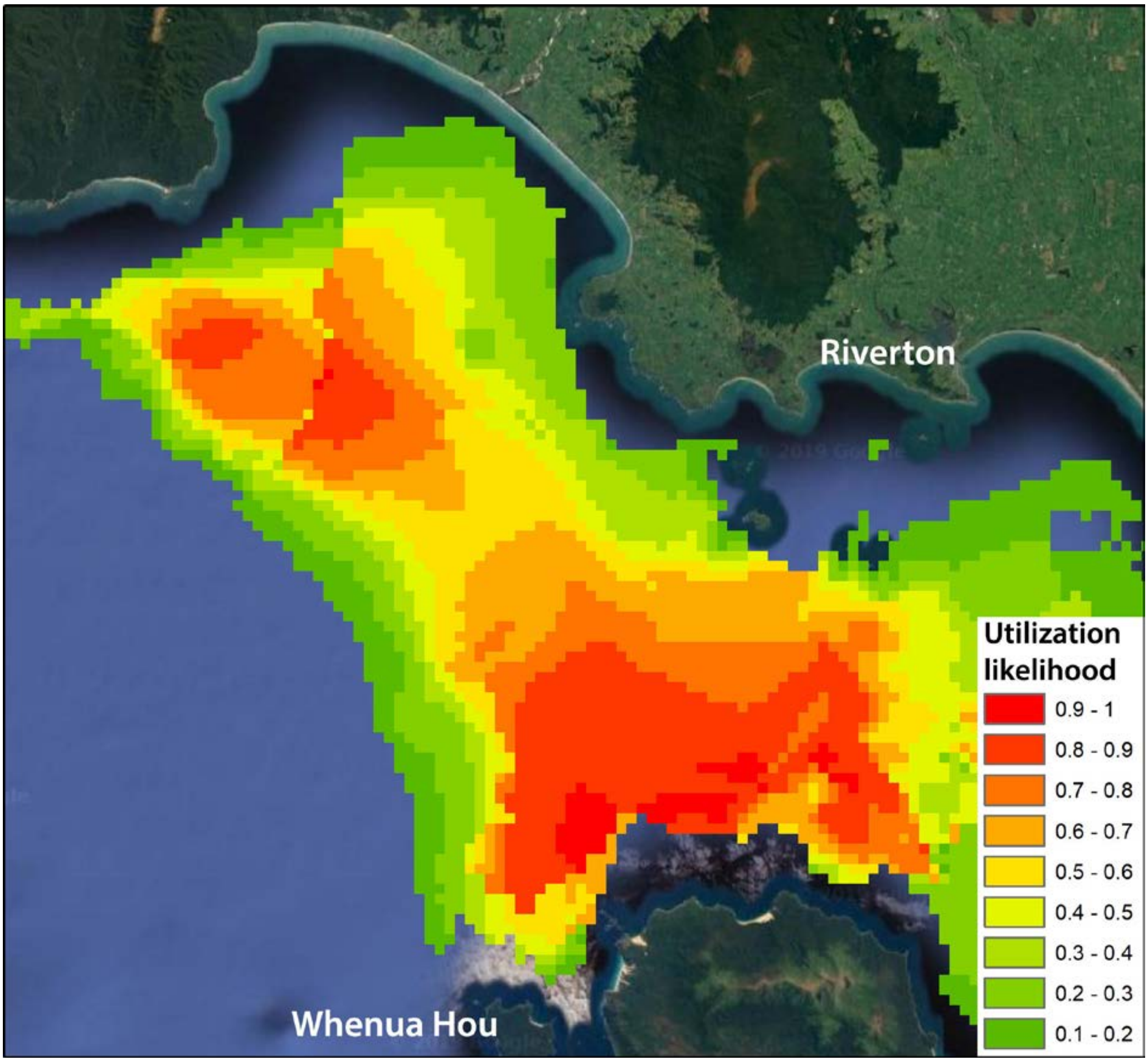

Figure 4.6: Marine habitat available to yellow-eyed penguins in the western Foveaux Strait based on foraging data recorded at Codfish Island/Whenua Hou (n=18 birds, 2005–2006). Most suitable habitat is over gravel, 30–60 m deep, north of Stewart Island/Rakiura, or sand outside Te Waewae Bay. Birds travelled considerable distances, and in some instances made overnight trips.

Table 2.6: Relative contribution of environmental variables to model – Codfish Island / Whenua Hou.

	Per cent contribution	Permutation importance
Bathymetry	74.6	72.9
Sediment type	14.8	2.2
Colony distance	10.6	24.9

3.1.7 New Zealand mainland (pooled regional data)

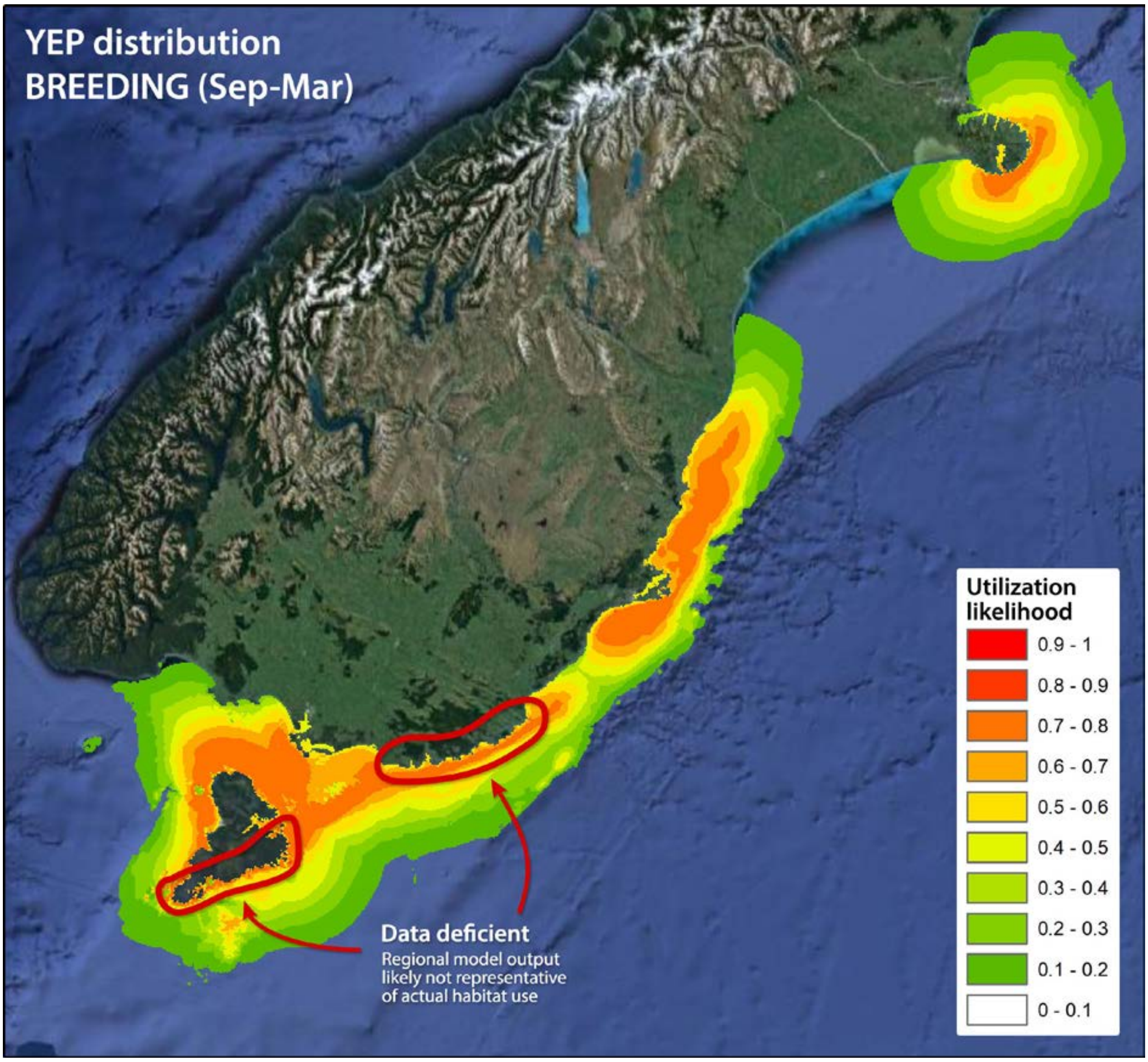

Figure 4.7: Marine habitat available to yellow-eyed penguins along the south-east coast of the South Island, based on pooled foraging data from sites summarised above (n=87 birds, 2003–2019).

Table 2.7: Relative contribution of environmental variables to model – southern mainland region.

	Per cent contribution	Permutation importance
Colony distance	50.4	35.2
Bathymetry	46.6	64.1
Sediment type	3.0	0.7

3.2 Species distribution models – non-breeding season

3.2.1 Oamaru (North Otago)

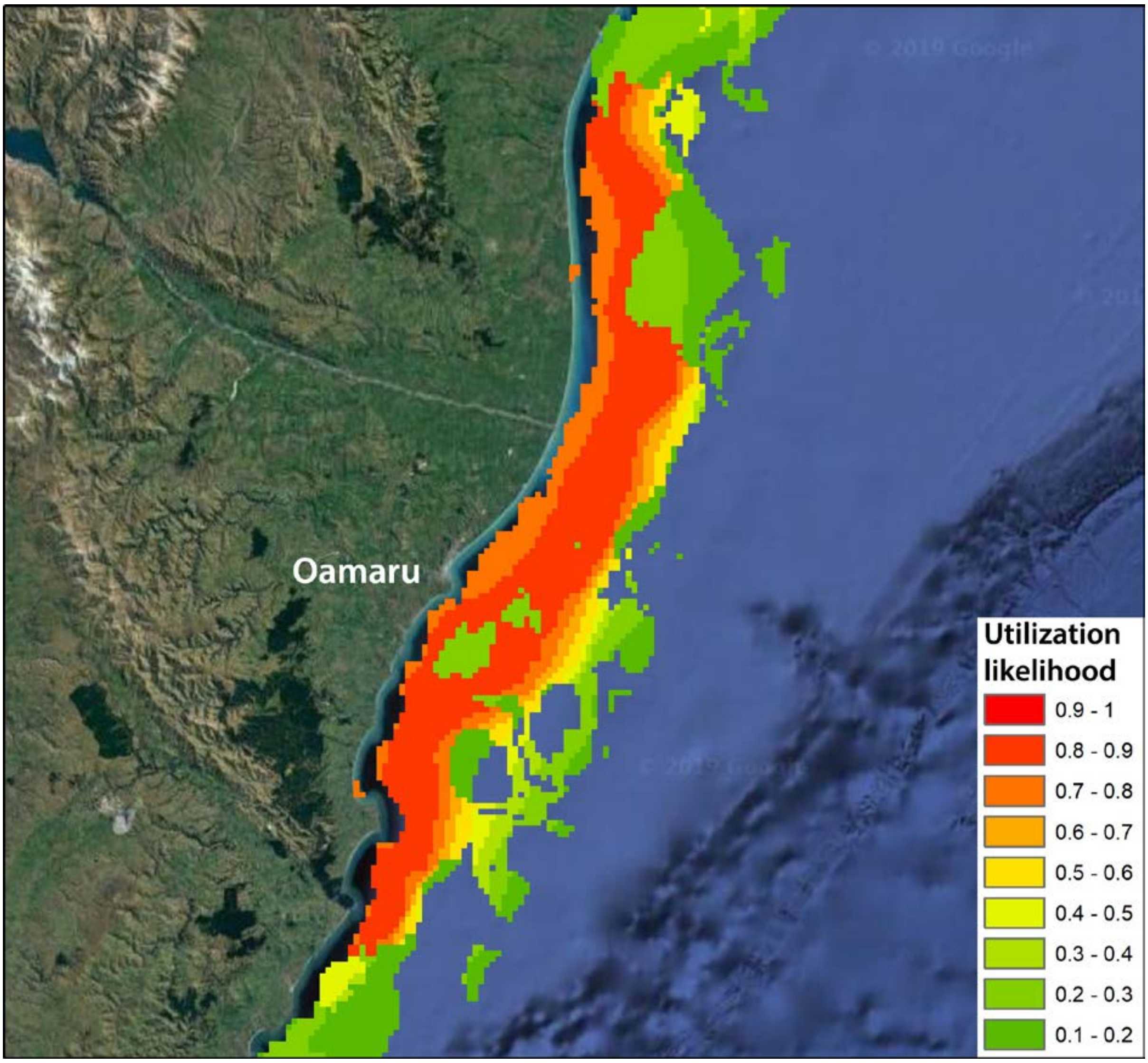

Figure 5.1: Model outputs for northern North Otago omitting colony distance as predictor variable to simulate habitat utilisation during the non-breeding period. It predicts that the entire continental shelf with depths to 70 m are suitable for foraging yellow-eyed penguins between March and September.

Table 3.1: Relative contribution of environmental variables to model – North Otago.

	Per cent contribution	Permutation importance
Bathymetry	63.2	89.9
Sediment type	36.8	10.1

3.2.2 Aramoana

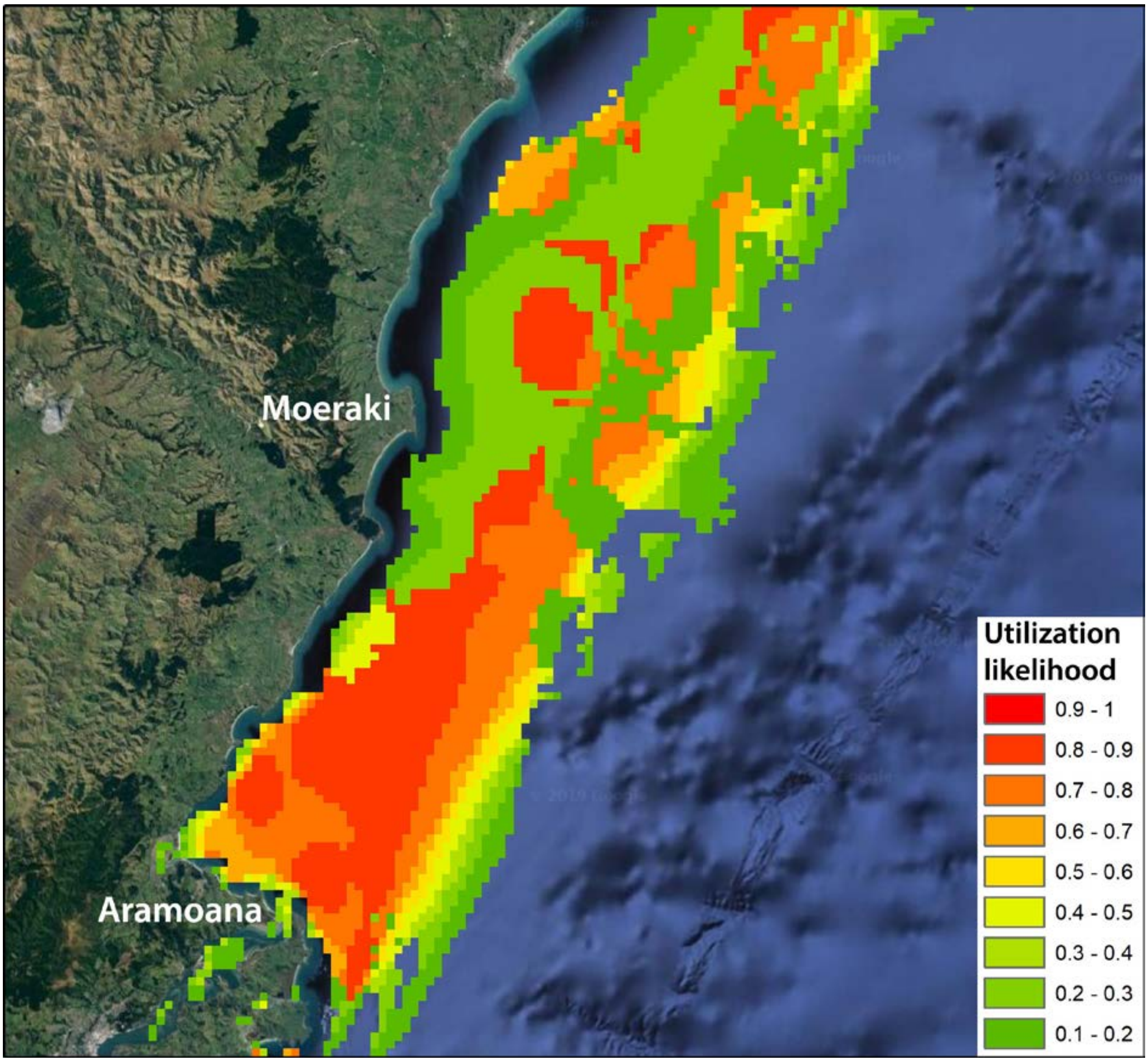

Figure 5.2: Model outputs for habitat utilisation of yellow-eyed penguins in southern North Otago during the non-breeding period. Predicted regions of suitable habitat are located between the northern Otago Peninsula and Moeraki. Model predictions have since been confirmed as representative by subsequent non-breeding tracking (Mattern 2018).

Table 3.2: Relative contribution of environmental variables to model – Aramoana.

	Per cent contribution	Permutation importance
Bathymetry	83.8	89.9
Sediment type	16.2	10.1

3.2.3 Otago Peninsula

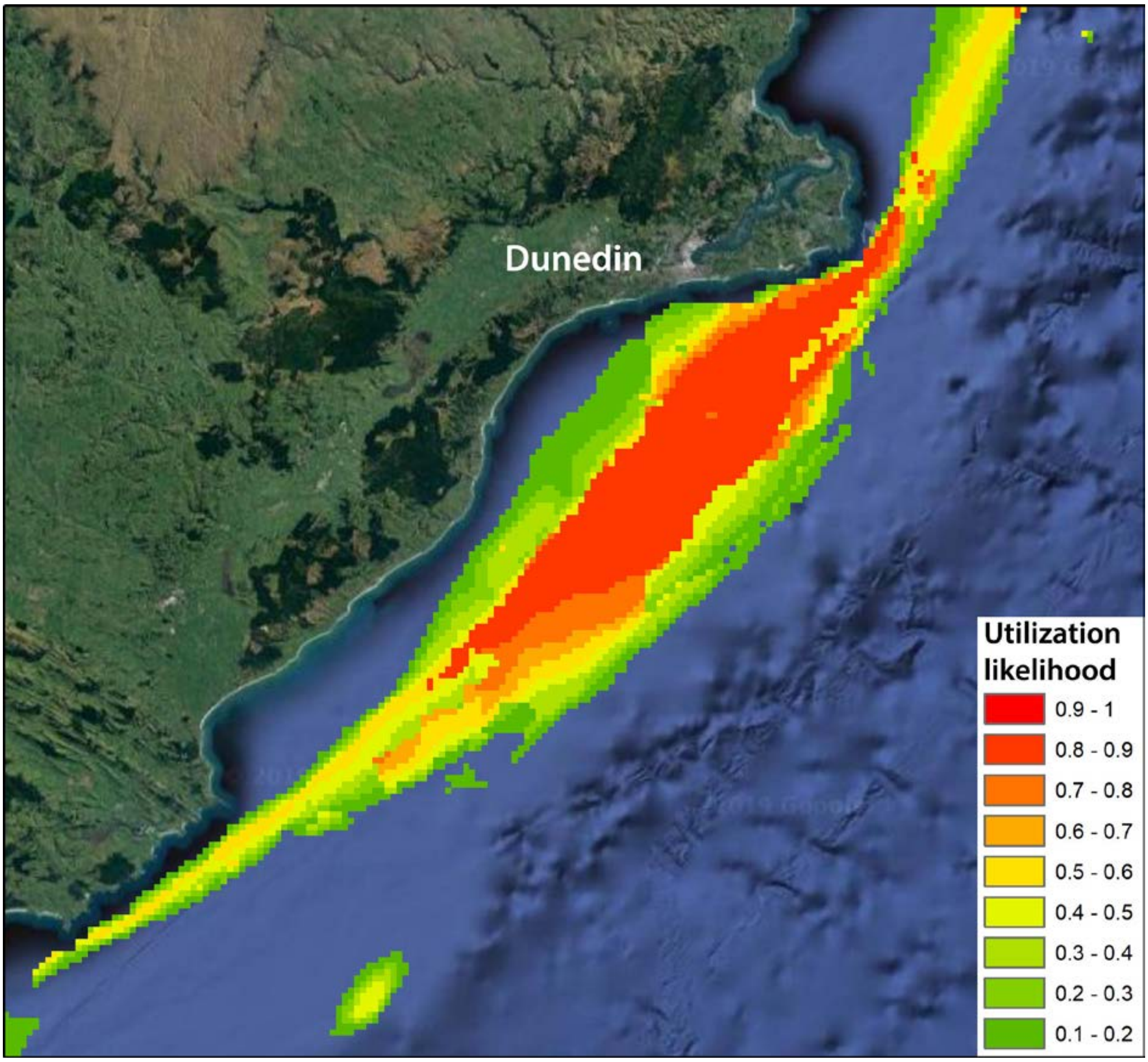

Figure 5.3: Model outputs for habitat utilisation of Otago Peninsula yellow-eyed penguins during the non-breeding period. Predicted regions are comparable to those for the breeding period, although penguins are likely to travel further away from their colonies. Model predictions have since been confirmed as representative by subsequent non-breeding tracking (Mattern 2020).

Table 3.3: Relative contribution of environmental variables to model – Otago Peninsula.

	Per cent contribution	Permutation importance
Bathymetry	76.1	97.2
Sediment type	23.9	2.8

3.2.4 Catlins (data deficient)

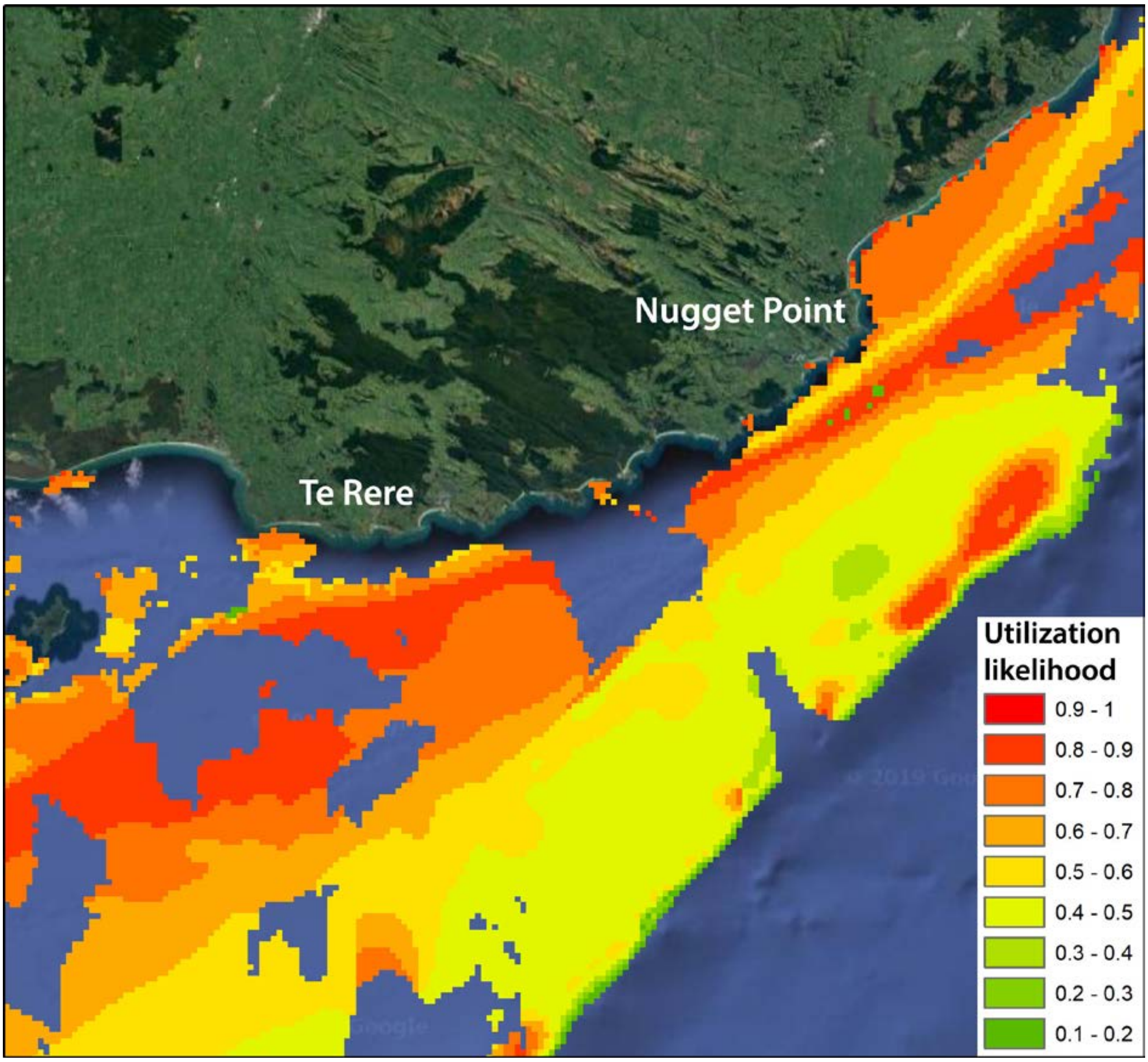

Figure 5.4: Model outputs for predicted non-breeding habitat utilisation of yellow-eyed penguins in the Catlins. Model outputs suffer from data deficiency and are considered unrepresentative.

Table 3.4: Relative contribution of environmental variables to model – Catlins.

	Per cent contribution	Permutation importance
Sediment type	53.5	32.9
Bathymetry	46.5	67.1

3.2.5 Anglem Coast (Stewart Island)

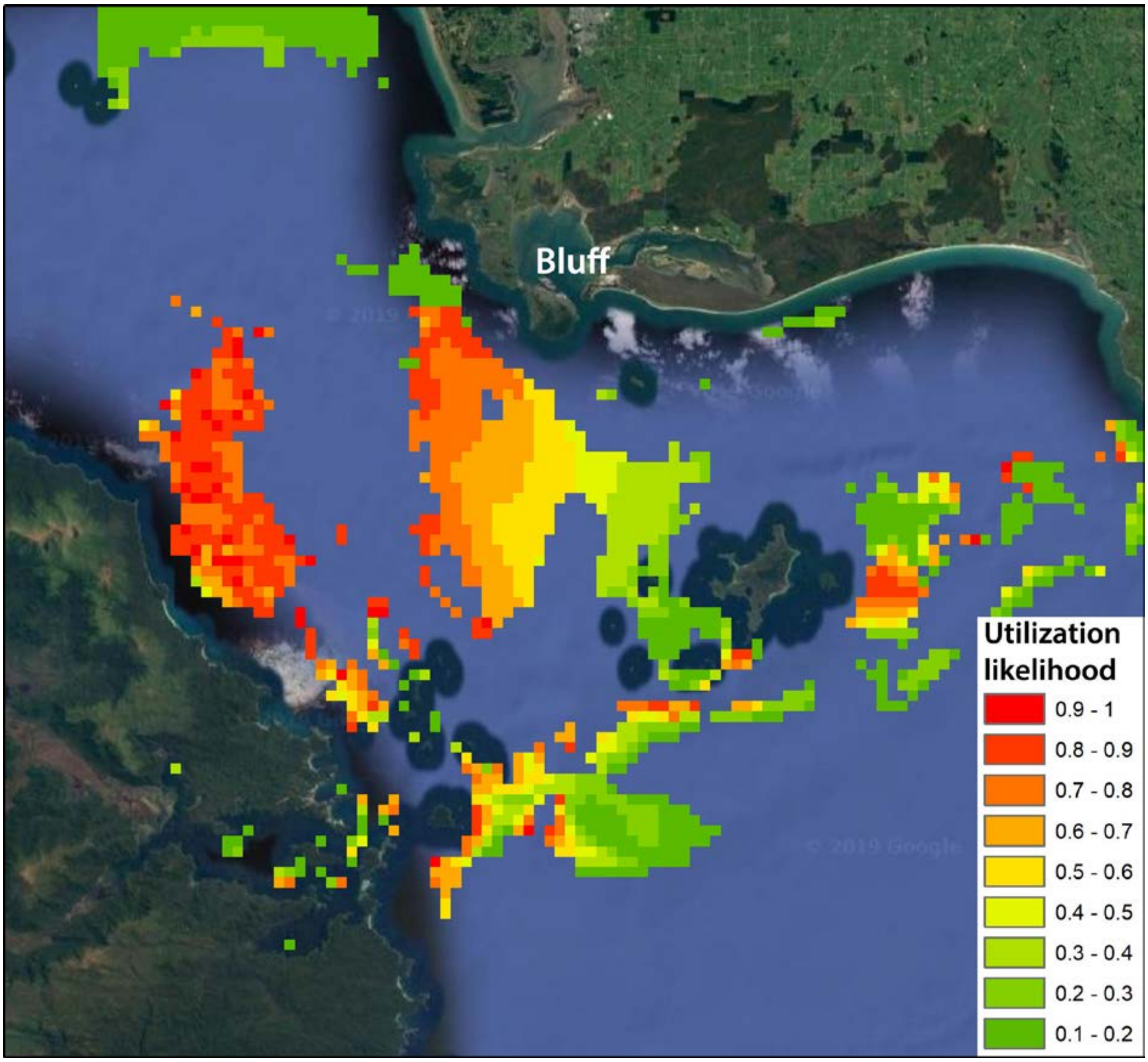

Figure 5.5: Model outputs for habitat utilisation of Stewart Island/Rakiura yellow-eyed penguins during the non-breeding period. Outputs are largely comparable to those for the breeding season.

Table 3.5: Relative contribution of environmental variables to model – Anglem Coast.

	Per cent contribution	Permutation importance
Bathymetry	74.1	89.3
Sediment type	25.9	10.7

3.2.6 Codfish Island / Whenua Hou

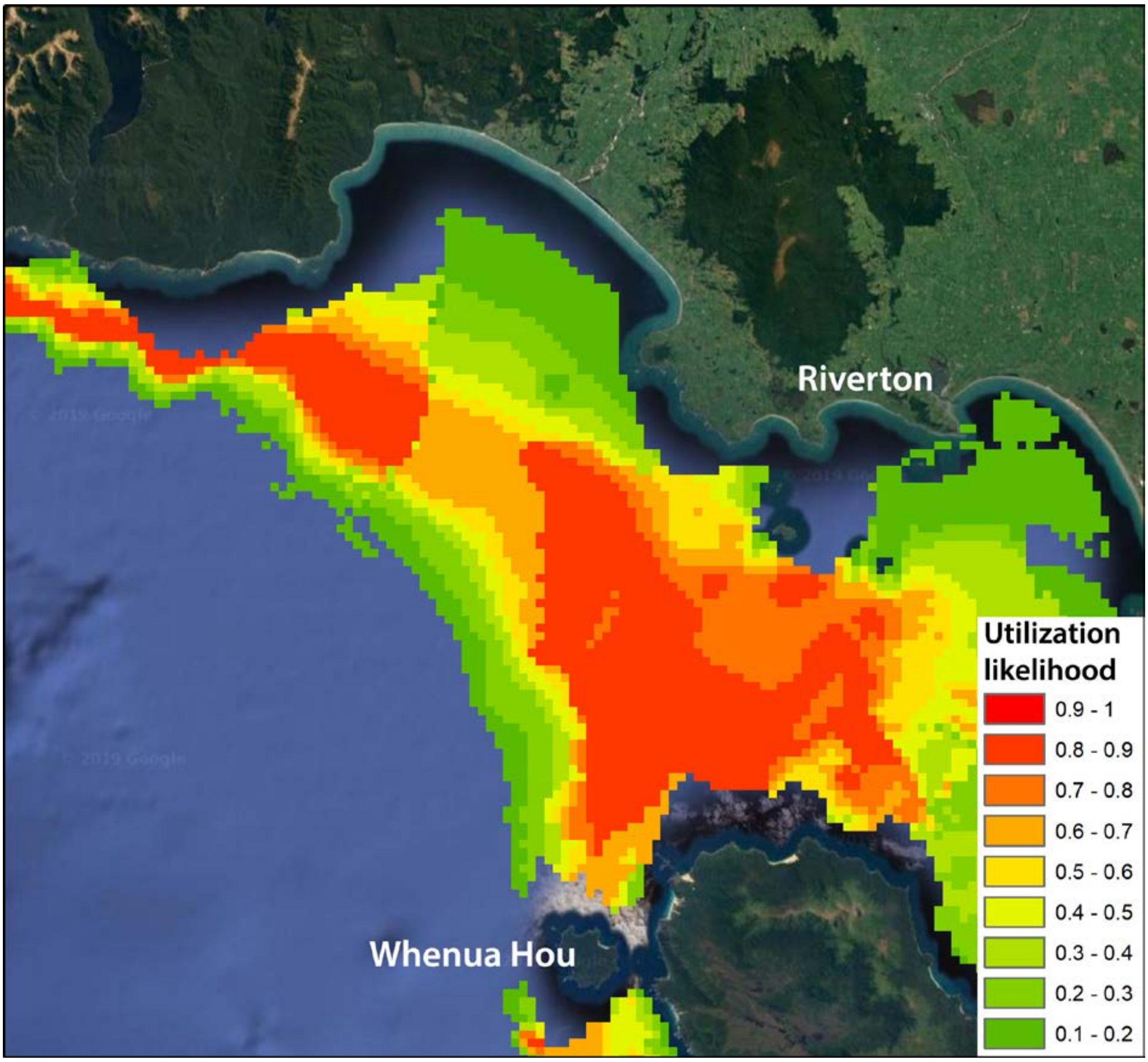

Figure 5.6: Model outputs for habitat utilisation of Codfish Island/Whenua Hou yellow-eyed penguins during the non-breeding period. With breeding penguins already showing extremely long foraging ranges, the elimination of colony distance to simulate non-breeding habitat utilisation gives a similar output to that for the breeding period.

Table 3.6: Relative contribution of environmental variables to model – Whenua Hou.

	Per cent contribution	Permutation importance
Bathymetry	82.4	95.3
Sediment type	17.6	4.7

3.2.7 New Zealand mainland (pooled regional data)

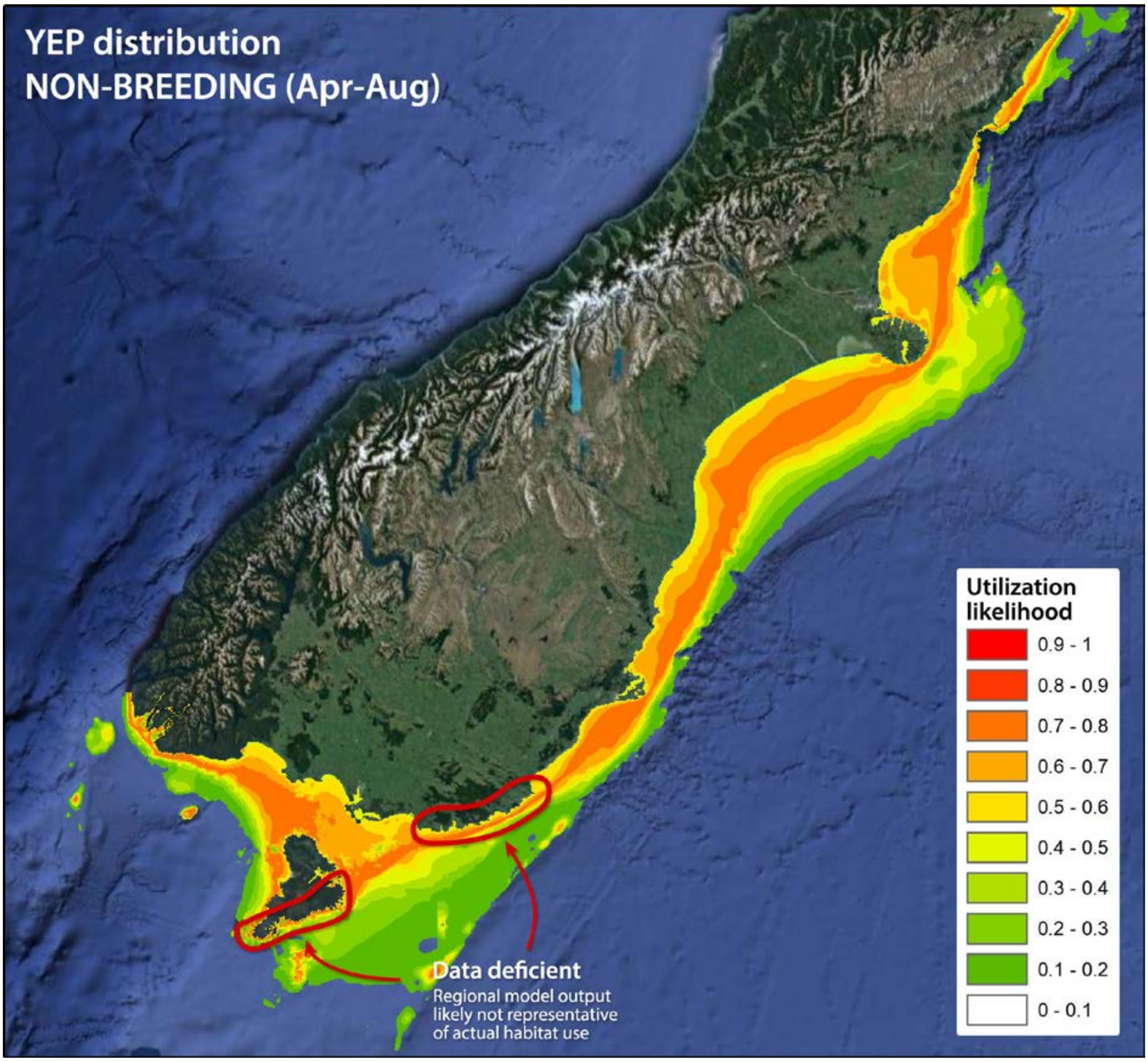

Figure 5.7: Marine habitat available to yellow-eyed penguins along New Zealand's South Island coastline based on pooled foraging data from sites with the colony distance variable eliminated to simulate non-breeding utilisation. Essentially any habitat with water depths between 20 and 90 m is predicted to be suitable habitat for the species between March and September.

Table 3.7: Relative contribution of environmental variables to model – southern and eastern South Island mainland.

	Per cent contribution	Permutation importance
Bathymetry	97.5	97.1
Sediment type	2.5	2.9

3.3 Diurnal activity of yellow-eyed penguins

Yellow-eyed penguins are visual hunters that rely on sufficient underwater light levels to find prey (Davis & Renner 2003). As a result the species exhibits strong diurnal foraging behaviour; even when penguins remain at sea over night, they do not dive. Using onset times for all available dive events recorded in yellow-eyed penguins thus far (n=75 892 dives) from all sites shows that foraging activity intensifies from 5 a.m. onwards, reaches its peak between 7 a.m. and 7 p.m., and concludes by 9 p.m. (Figure 6).

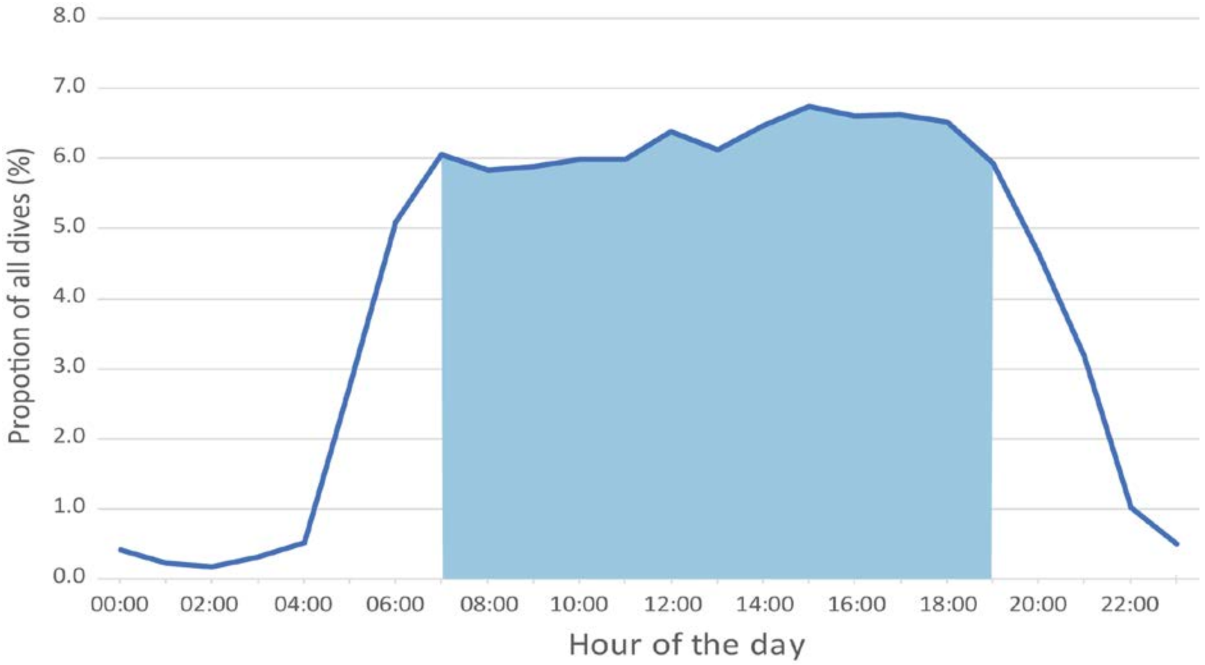

Figure 6: Diurnal diving activity of yellow-eyed penguins during the breeding season (September-February). The blue shaded area under the curve highlights the time of day when foraging activity is at its most intensive.

There is considerable individual, as well as regional variability, with some birds only performing foraging trips in the late afternoon and evening and others returning to their nest in the early afternoon. Thus, it is impossible to derive more detailed activity patterns than the one presented above.

Except for dive data for four birds that were tracked from Aramoana in the weeks following completion of the breeding season (February and March), all dive data available at this stage derive from breeding penguins. Preliminary analysis of tracking work conducted in winter 2019 (May-September) indicates that penguins tend to leave the land around sunrise (i.e., 7.30–8.30 a.m.) and, if returning to land at all, do so between 4 p.m. and 6 p.m. However, at this stage of their annual cycle, birds tend to stay at sea for up to two weeks at a time (Mattern & Young 2019), eliminating the need for commuting at the beginning and the end of the day; hence, intensive foraging activity occurs within the same hours of the day in winter as in summer.

3.4 Benthic vs pelagic dives

Studies of yellow-eyed penguin foraging behaviour conducted since 2003 found that the species predominantly foraged at the seafloor (Mattern et al. 2007, 2013, 2018). The data set used in this project consisted of 82 447 dive events, and 58 050 of these were benthic dives (70.4%). It should be noted that this ratio is somewhat biased by data recorded from penguins from Codfish Island/Whenua Hou (see Table 1), which travelled (in pelagic depths) over 50 km to their foraging grounds in Te Waewae Bay (Ellenberg & Mattern 2012). Excluding Codfish Island/Whenua Hou data, the ratio between benthic and pelagic dives is 3:1 (75.3% of all dives are benthic).

Pelagic dives by yellow-eyed penguins are generally associated with travelling behaviour (Mattern et al. 2007, see Figure 2). Accordingly, pelagic diving is more prevalent in the morning and late afternoon when birds are travelling to and returning from their foraging grounds (Figure 7).

Recent deployments of camera loggers revealed that dives classified as 'pelagic' due to their vertical profile can be directly associated with benthic foraging behaviour. Penguins catching relatively large demersal prey items (e.g., blue cod) were found to take the fish to the surface, where the prey (often killed during the ascent phase) was then dropped. The penguin would then return to the prey on a series of pelagic dives until it managed to ingest it (Mattern & Ellenberg 2018).

In November 2016, unusually high phytoplankton concentration in the water column off the Otago Peninsula severely impacted the visibility at the seafloor. Four penguins fitted with camera loggers during this time foraged predominantly in pelagic depths, although some attempts of benthic feeding were made. During pelagic dives, penguins would target fish larvae associated with jellyfish in the upper 20–30 m of the water column. All penguins resumed benthic foraging in December 2016, when the phytoplankton bloom had dissipated (Mattern et al. 2017b).

Density analysis of the spatial distribution of pelagic and benthic dive types indicates that most pelagic dives are performed during the commute from colony to foraging grounds further offshore (Figure 8). Hence, pelagic dives occur primarily within the 4 nautical mile set net exclusion zone; the only exception are data recorded on penguins from Codfish Island/Whenua Hou; these penguins crossed Foveaux Strait using pelagic travelling dives (mean dive depth: 12.5 m; n=7976).

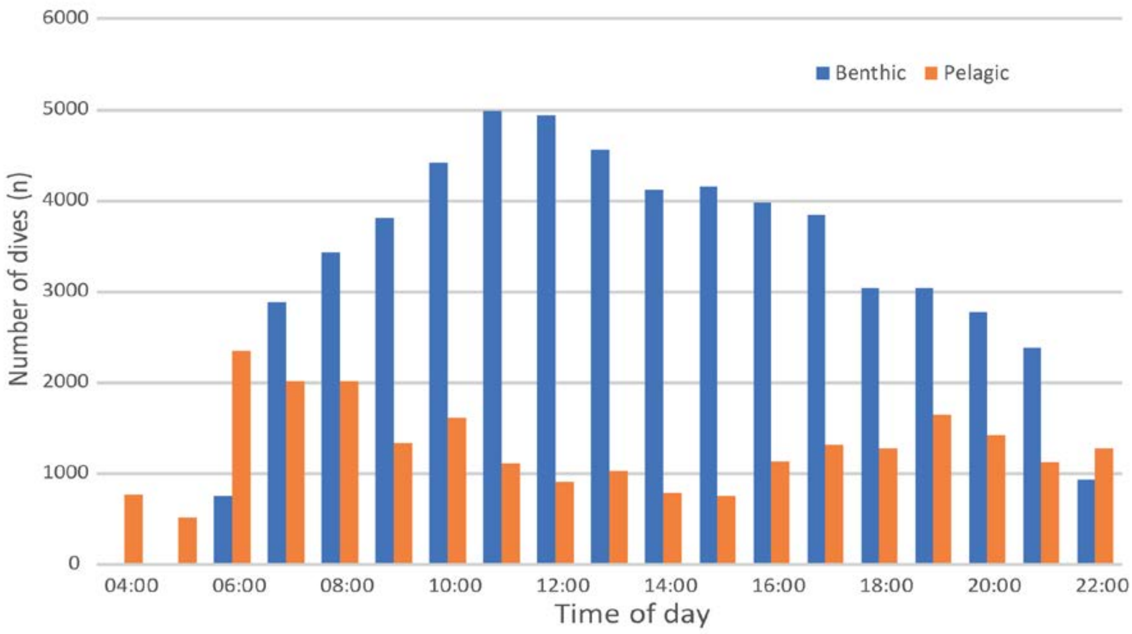

Figure 7: Frequency of benthic and pelagic dives in yellow-eyed penguins over the course of the day during the breeding season.

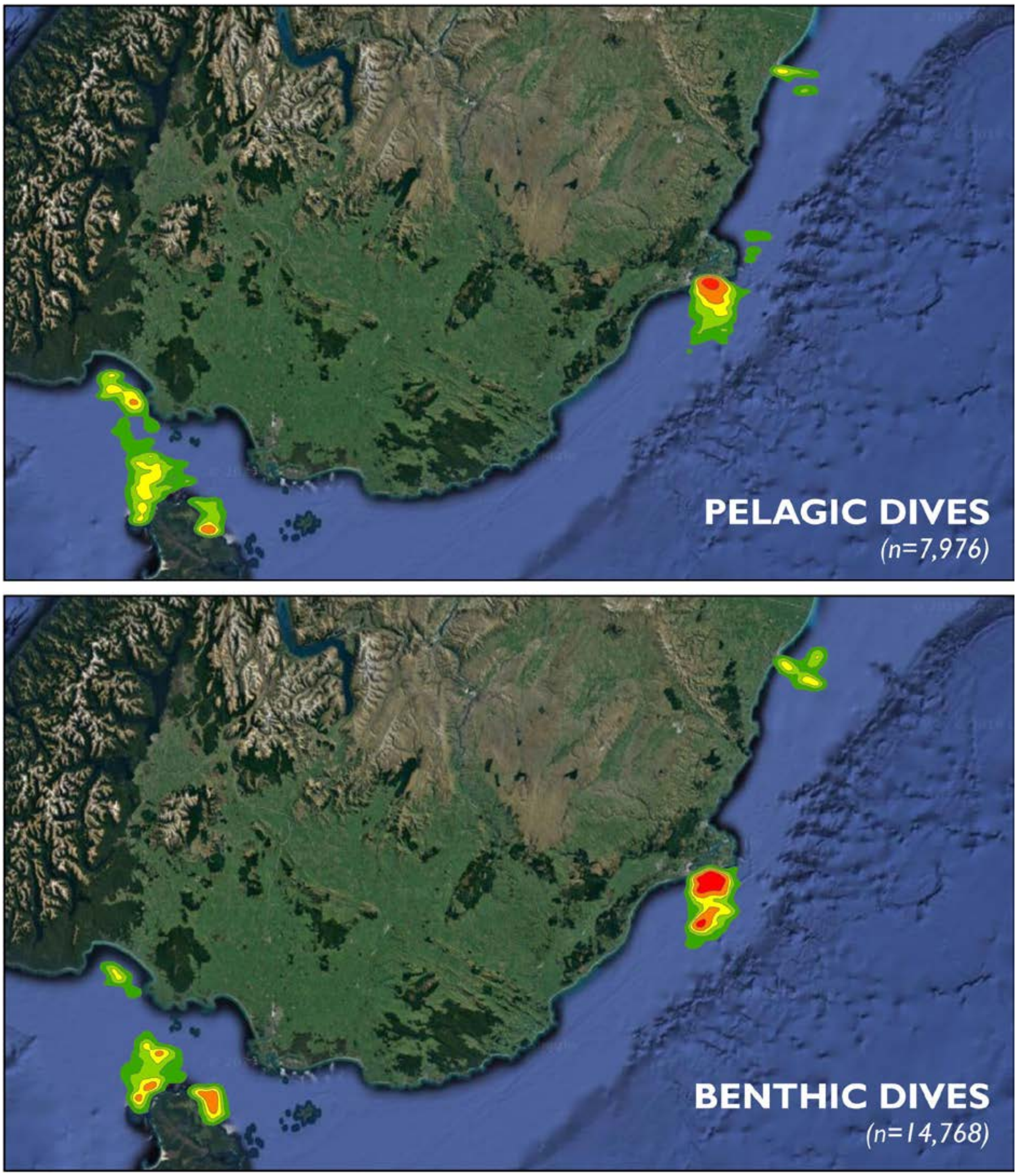

Figure 8: Kernel density distribution of yellow-eyed penguin dive types. Note that only dives with actual or accepted interpolated dive location were used. Coloured polygons indicate the 20% (dark green) to 95% (red) density kernels, red being the regions where dive types were most common.

3.5 Fledgling dispersal

Fledgling yellow-eyed penguins are notoriously difficult to track. This is partly due to the low numbers of chicks that survive until fledging (Browne et al. 2011, King et al. 2012) and because the majority of those that fledge never return (Mattern et al. 2017a). This means that archival data tags like GPS dive loggers cannot be used to track these birds because the devices need to be recovered to access the data. In the past two years, some fledgling penguins have been tracked with satellite transmitters that provide a few rough locations (positional error 250–1500 m, Freitas et al. 2008) and no information about diving behaviour.

It is therefore unknown if young yellow-eyed penguins exhibit principally benthic foraging behaviour from their first days at sea onwards or whether this strategy is only adopted by birds that eventually survive their first year. In the context of the utilisation of the inshore environment by yellow-eyed penguins, the satellite data have very limited power for advanced modelling. A simple kernel density analysis is most appropriate for this data set.

The kernel density analysis (Figure 9) indicates that the region north of the Otago Peninsula, as well as the southern to central Canterbury Bight, are of particular importance for fledgling yellow-eyed penguins. Interestingly, there is a substantial overlap with the non-breeding SDM output for adult yellow-eyed penguins from Aramoana (cf. Figure 5.2). Off Moeraki and Oamaru, fledglings appear to prefer deeper waters, about 15–20 km from the coast; whereas adult penguins forage closer to the coast (cf. Figure 5.1).

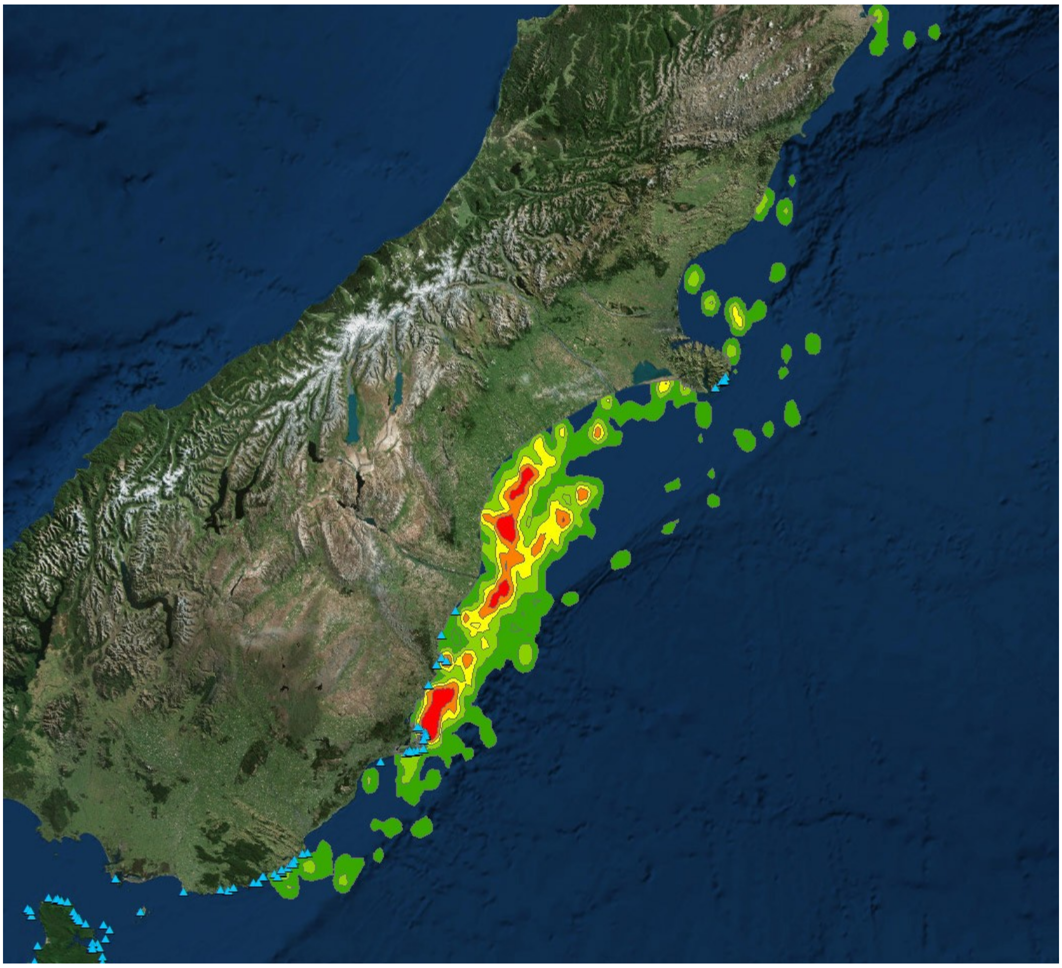

Figure 9: Kernel density distribution of yellow-eyed penguin fledgling dispersal in February-June. Isolines indicate the 20% (dark green) to 95% (red) density kernels, red being the regions most utilised by fledglings during their first forays at sea. Blue triangles indicate historic and current locations of yellow-eyed penguin breeding colonies as listed in the YEP database.

Individual fledglings frequently travel up to Cook Strait. However, the kernel density analysis suggests that these are most likely to be outliers. Therefore, to assess the potential impact of the set net fishery on fledgling yellow-eyed penguins, emphasis should be placed on the region north of the Otago Peninsula and the Canterbury Bight.

4. MANAGEMENT IMPLICATIONS

The species distribution models developed in this study provide a spatial and temporal framework for the development of measures to mitigate impact of set netting operations on the endangered yellow-eyed penguin. Observed bycatch of yellow-eyed penguins suggests that Foveaux Strait and North Otago (Aramoana to Waitaki River) may be regions where measures to reduce bycatch are needed the most. Probably the most feasible mitigation measure would be to have set net fisheries operate outside the hours of increased penguin presence at their foraging grounds.

During the yellow-eyed penguin breeding season, limiting set net operations to the early hours of morning (before 7 a.m.) or from early evening (from 6 p.m. onwards) would likely lead to a substantial reduction of bycatch risk. Similarly, setting nets at depths greater than the penguins' preferred foraging depths (shallower than 80 m for North Otago, Otago Peninsula, and Foveaux Strait) would further reduce the risk of penguin interactions with fishing gear.

For Stewart Island and its outlying islands, banning set netting immediately inshore would substantially reduce the risk of penguin bycatch as they leave or return to their colonies. It appears that the local fishing community has established a voluntary set net ban around Codfish Island/ Whenua Hou (Richard Wells, pers. comm.). Similar restrictions elsewhere in Foveaux Strait, particularly around Stewart Island's northeast coast, the Tītī Islands, and Port Pegasus, would also be effective for reducing bycatch risk.

Outside the breeding season, penguins appear to disperse over greater distances. This will reduce the bycatch risk in the vicinity of major breeding colonies; however, in areas usually not frequented by breeding penguins (e.g., Canterbury Bight) the bycatch risk will inevitably increase.

For fledgling penguins, Canterbury Bight seems to play an important role. The young birds generally travel there from February/March onwards and may stay in the area until the following spring. Although there is not any information about the diving behaviour of young yellow-eyed penguins, it is assumed that they may be foraging demersally so that near-bottom set net operations, particularly around the Rangitata River mouth, may negatively influence their survival rate and, thus, contribute to the extremely low recruitment, as observed in recent years.

Although the distribution models for some of the core problem areas — namely North Otago and Foveaux Strait — can be considered representative, the lack of foraging data from the Catlins and southern Stewart Island prevents reliable predictions of the yellow-eyed penguins' utilisation of the regional marine habitat. Therefore, it is vital to gather foraging data to remodel the habitat utilisation by the penguins in these under-represented regions. Currently a research programme conducted by the Department of Conservation's Conservation Services Programme is attempting to fill some of these data gaps. However, the limited 2-year runtime of this programme may not yield enough data to substantially improve model outputs.

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