Risks, resources, and refugia: Spatial overlap between yellow-eyed penguin foraging distribution and prey, commercial fisheries, and marine protected areas

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ABSTRACT

Conservation of the endangered yellow-eyed penguin (*Megadyptes antipodes*) in New Zealand has principally sought to manage terrestrial threats, while relatively little has been done to understand or address marine threats, such as reduced prey availability, commercial fisheries interactions, and habitat destruction. We assessed spatial similarities between mainland yellow-eyed penguin marine distribution and resources (prey), risks (fisheries interactions), and areas of refugia (marine protected areas, MPAs). We determined if suitable penguin foraging habitat, based on environmental predictors using a Maxent species distribution model (SDM), also supports a high diversity of key prey species identified using a stacked SDM. We also created a novel index to predict areas of potential commercial fisheries interactions and mapped the overlap of penguin distribution and MPAs. Areas along the middle of the continental shelf had the highest prey diversity and probability of penguin presence, which overlapped with gillnet fisheries in these regions. Suitable penguin habitat also overlaps with trawl fisheries inshore along much of the South Island coast. <1 % of the penguin range overlaps with current MPAs, and the proposed South-East Marine Protected Areas network would protect only 3.6 % of the current penguin foraging distribution. This study takes an ecosystem approach to assess complex interactions between commercial fisheries, marine ecosystems, and MPAs, which is urgently required for marine spatial planning and adaptive ecosystem management of not only this endangered seabird but for southeast New Zealand coastal habitat and biota also.

1. Introduction

Penguins are one of the most threatened groups of seabirds due to the combined impacts of direct, indirect, terrestrial, marine, anthropogenic, and natural threats (Boersma et al., 2019; Hickcox et al., 2019; Ropert-Coudert et al., 2019). Actions are necessary to improve penguin population resilience to these threats, such as climate change, fisheries interactions, poor diet quality/starvation, disease, and predation (Mattern and Wilson, 2019). The creation and implementation of adaptive and evidence-based management plans through marine spatial planning (MSP) is one of the highest conservation priorities for penguins (Boersma et al., 2019). As an ecosystem-based management approach to conservation, MSP considers the spatiotemporal interactions between species, threats, services, stakeholders, and other factors to achieve conservation management objectives in areas of biological significance (Frazão Santos et al., 2019). Likewise, studies of these interactions can be used to inform MSP decisions.

The endangered yellow-eyed penguin (*Megadyptes antipodes;* hoiho or takaraha in te reo Māori), is endemic to New Zealand/Aotearoa (BirdLife International, 2020; Seddon et al., 2013). The mainland/northern population of yellow-eyed penguins breeds along the southeastern coast of the South Island/Te Waipounamu of New Zealand, from Banks Peninsula (northernmost extent) to North Otago, Otago Peninsula, Catlins, and Stewart Island/Rakiura and adjacent Codfish

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Island/Whenua Hou (southernmost extent). The subantarctic/southern population breeds on the Auckland Islands/Motu Maha and Campbell Island/Motu Ihupuku. Adults are year-round central-place foragers (Mattern, 2006; Mattern et al., 2007) that primarily target benthic communities of abundant and diverse prey including finfish, cephalopods, and occasionally crustacea in coastal waters over the continental shelf (Mattern and Ellenberg, 2018; Mattern et al., 2018; Young et al., 2020). Individuals exhibit a more flexible foraging strategy when environmental conditions necessitate (Elley et al., 2022; Muller et al., 2020, 2021). Predator-prey interactions shape the distributional patterns of a species (Wisz et al., 2013), and the most important predictors of yellow-eyed penguin distribution in New Zealand also affect prey (Hickcox et al., 2022). There has been a dietary shift in yellow-eyed penguins over the past 35 years (Young et al., 2020), likely a response to changing prey availability, distribution, and/or abundance. Prior to this study, an investigation of the spatial overlap between yellow-eyed penguin foraging ranges and prey distributions had not been conducted.

Yellow-eyed penguins are vulnerable in areas subjected to commercial and recreational fishing activities, due to accidental bycatch risk, overfishing, seafloor habitat degradation caused by trawling and dredging, and other indirect threats like pollution (Mattern and Wilson, 2019; Webster, 2018). Fisheries influence the spatial distribution and density of prey, leading to altered trophic cascades affecting the entire marine ecosystem (Planque et al., 2010). Bottom-contact fishing (e.g., trawling, dredging) causes benthic habitat degradation, increased sedimentation, destruction of biogenic reefs and bryozoan thickets, and altered fish populations and community assemblages (Carbines et al., 2004; Thrush and Dayton, 2002), which in turn may negatively impact penguin foraging and reproductive success (Browne et al., 2011; Ellenberg and Mattern, 2012; Mattern et al., 2013). Commercial gillnet (setnet) fisheries pose a medium-to-extreme risk to the mainland population of benthivorous yellow-eyed penguins (Richard et al., 2020; Rowe, 2013), with bottom gillnets responsible for >100 confirmed or reported penguin deaths over the past forty years (see Darby and Dawson, 2000; Rowe, 2013; Webster, 2018). Young et al. (2022) found that juvenile penguin foraging hotspots, which cover a larger area than that of adult penguins, overlap with the extent of commercial gillnet fishing by 52.0 %. Despite some bans, voluntary closures, and restrictions on the east coast, it is unknown the extent to which penguins forage within gillnet and trawl commercial fishing areas.

Marine protected areas (MPAs) mitigate some marine and fisheries-related threats, particularly in areas of high fishing intensity and co-occurrence with endangered animals (Davies et al., 2018). In New Zealand, three spatial management tools are used to protect marine biodiversity: (i) type 1 marine reserves (no-take or extraction of any resource), (ii) type 2 MPAs (some restrictions to fishing), and (iii) "other marine protection tools" including customary areas and marine mammal sanctuaries (Davies et al., 2018; Department of Conservation and Fisheries New Zealand, 2020). More specifically, mātaitai reserves only allow customary fishing through local management, and marine mammal sanctuaries limit activities such as seismic surveys and some fishing methods. There are 44 type 1 and 19 type 2 MPAs, which are managed and monitored by the Department of Conservation (DOC). They cover 12.3 % of New Zealand territorial sea that extends 12 nautical miles from the coast; however, they protect only 0.4 % of mainland coastal waters and <1 % of the New Zealand exclusive economic zone (EEZ; DOC et al., 2019). The New Zealand government is currently considering the 1267 km^2 South-East Marine Protected Area (SEMPA) network, comprising six type 1 and five type 2 MPAs off the southeast coast of the South Island (DOC and FNZ, 2020; South-East Marine Protection Forum, 2018). However, there is little spatial information on the overlap between the proposed/established MPAs and penguin distribution, nor on the likely effectiveness of MPAs in protecting the species and their prey resources.

In this study, we used a spatial approach to (i) quantify the overlap between suitable yellow-eyed penguin foraging habitat and prey, (ii)

determine areas of risk due to commercial fisheries interactions, (iii) assess existing and proposed MPA overlap with penguins. We aimed to illustrate potential applications of spatial distribution modelling (SDM) in future marine spatial planning and conservation management of the species. We predicted that (i) species richness of key prey species will be high in areas of high habitat suitability for yellow-eyed penguins, (ii) penguin suitable habitat overlaps significantly with all types of commercial fisheries but especially gillnet fisheries, and (iii) penguin suitable habitat minimally overlaps with established/proposed MPAs. This research is the first comprehensive spatial analysis of potential interactions between yellow-eyed penguins and biotic factors within their marine environment.

2. Materials and methods

2.1. Yellow-eyed penguin distribution

Hickcox et al. (2022) found that variations of marine habitat impacted the foraging distribution of mainland yellow-eyed penguins. They used Maxent, a machine-learning, presence-only method (Phillips et al., 2006), to predict a marine probability of presence (POP) for yellow-eyed penguins using dive locations from 135 individuals (2003–2021) and nine environmental predictors. Two mainland POP distributions were predicted: (1) a breeding season distribution limited by the distance to colony predictor and (2) an annual/non-breeding distribution not limited by distance to colony which better represents the foraging range of breeding/non-breeding adults and juveniles. Since prey and fisheries data were not specific to the breeding season, we used the mainland annual distribution map for the analyses in this study, with grid cells ranging from 0 (low POP) to 1 (high POP). We reclassified this penguin POP using the threshold that maximised the sum of sensitivity and specificity (Freeman and Moisen, 2008; Hunter-Ayad et al., 2021). This binary environmental suitability map assumes that areas where penguins are more likely to be present are more suitable habitat, so grid cells where POP >0.35 were considered suitable habitat (see Hickcox et al., 2022).

2.2. Prey distribution

We compiled a dataset of location coordinates for eight finfish species frequently detected in current yellow-eyed penguin diet using DNA metabarcoding of faecal samples (Young et al., 2020): blue cod/rāwaru (*Parapercis colias*), opalfish/kohikohi (*Hemerocoetes monopterygius*), silverside (*Argentina elongata*), common or blue warehou/warehou kahurangi (*Seriolella brama*), redbait (*Emmelichthys nitidus*), red cod/hoka (*Pseudophycis bachus*), and sprat/kupae (*Sprattus antipodum* and *S. muelleri*). The two species of sprat were considered together due to few occurrence points for each species separately. These species were chosen based on their frequency of occurrence in faecal samples, data availability, and previous detection in diet studies (e.g., van Heezik, 1990; Moore and Wakelin, 1997). Blue cod, red cod, blue warehou, silverside, and opalfish are demersal species, while redbait is benthopelagic, and sprat and juvenile red cod are pelagic species (McMillan et al., 2011).

We obtained presence records from the open-source Ocean Biogeographic Information System repository (OBIS; http://www.obis.org) using the *robis* package (v2.6.1; Provost and Bosch, 2021). Presences are representative of an annual sample to correspond with the annual marine distribution of yellow-eyed penguins, so the data prevented a temporal component, both seasonal and yearly, from being considered in this study. Based on quality and collection methods, we retained points from multiple datasets from 1964 to 2018 to improve sample size and reduce sampling bias. For blue cod, we used occurrences from the New Zealand research tagging database (dataset 1) released by the Ministry for Primary Industries (MPI, 2014a). For all species except sprat and opalfish, we obtained occurrences from bottom/midwater trawls contained in the MPI and National Institute of Water and Atmospheric

Research (NIWA) *Trawl* database, which includes: New Zealand fish and squid distributions from research bottom trawls 1964–2008 (dataset 2; NIWA, 2014), catch data from New Zealand research trawls since 2008 (dataset 3; Anderson et al., 1998; SWPRON, 2017), and Soviet trawl fishery data in New Zealand waters 1964-1987 (dataset 4; MPI, 2014b). Dataset 2 is available in its entirety from the New Zealand Ocean Data Network (http://nzodn.nz), which we used to supplement incomplete or missing OBIS records for sprat and opalfish. Any data from MPI or NIWA is licensed for re-use under the Creative Commons Attribution 4.0 New Zealand licence.

We removed points collected pre-1964 and those on land or outside a 75 km buffer off the coast based on the Topo50 NZ Coastlines and Islands Polygons layer obtained from the Land Information NZ (LINZ) geospatial database (Fig. 1; LINZ, 2020). This buffer was based on maximum distances travelled by penguins and matches the study extent used in the

penguin SDM. We spatially thinned each prey dataset to a minimum distance of 500 m between points. Data manipulation and analyses were conducted in R version 4.0.3 (R Core Team, 2021) using packages associated with the *tidyverse* (Wickham et al., 2019) and *sp* (v1.4–5; Bivand et al., 2013; Pebesma and Bivand, 2005), *raster* (v3.3–13; Hijmans, 2020), *rgeos* (v0.5–5; Bivand and Rundel, 2020), and *spThin* (v0.2.0) (Aiello-Lammens et al., 2015). See Appendix Table A.1 for sample sizes.

We considered an initial set of 11 high-resolution environmental predictors that directly or indirectly impact availability and occurrence of fish (Appendix Table A.2). We followed the Hickcox et al. (2022) methodology for predictor selection and multicollinearity reduction. A final dataset of seven predictors was used for modelling (Appendix Fig. A.1): bathymetry (bathy), tidal current speed (current), annual mean concentrations of dissolved oxygen (sf_do) and salinity (sf_salinity)
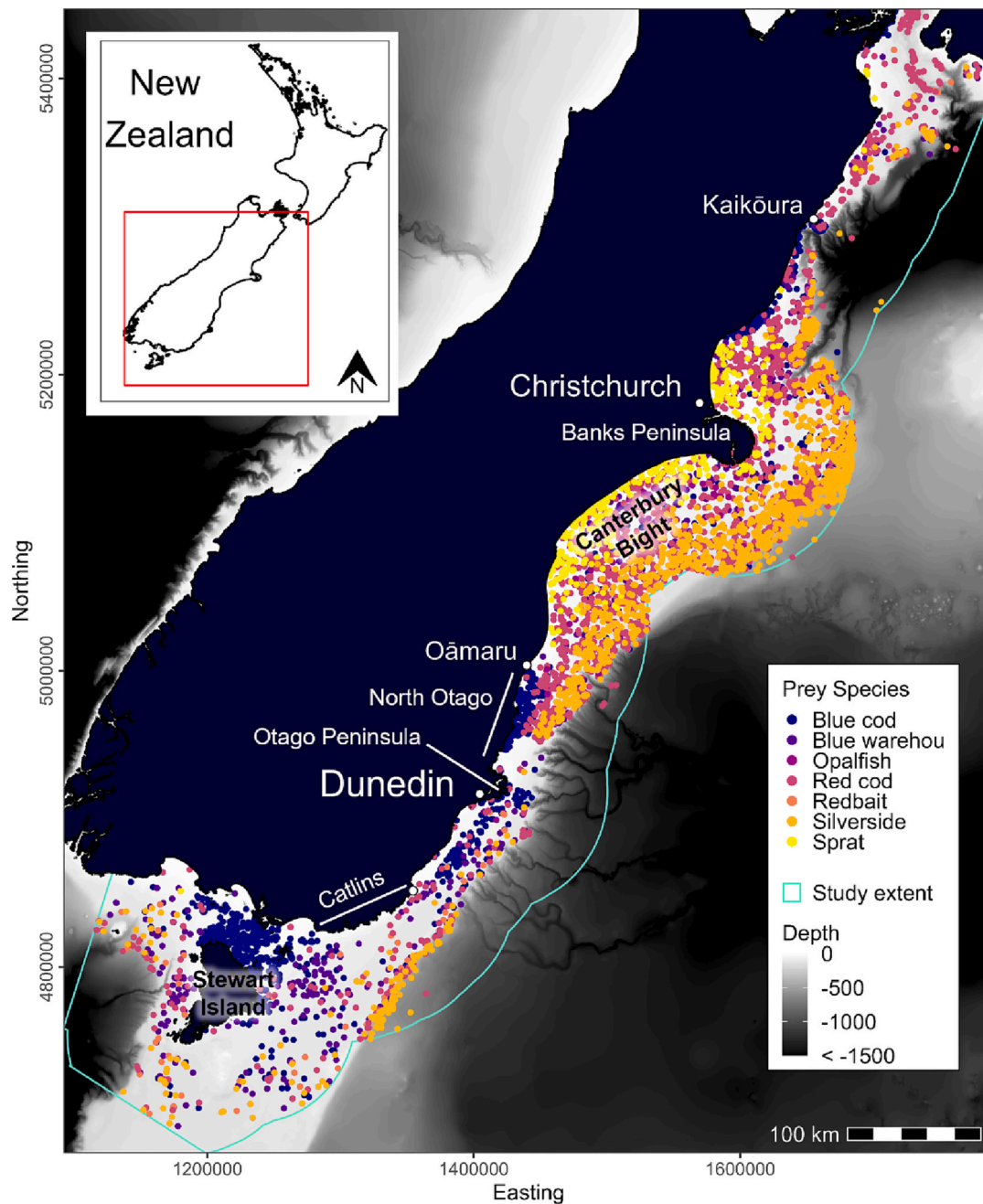
Fig. 1. Occurrences of seven key prey species of yellow-eyed penguins off the east coast of New Zealand used for modelling. The greyscale base map shows seafloor depth in metres (Mitchell et al., 2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at the seafloor, and mean annual (2002–2018) sea surface temperature (sst_mean), chlorophyll-*a* (chla_mean), and water turbidity (turb_mean).

We fitted Maxent SDM for each prey species using default regularisation values, all possible feature classes (LQHPT, where L = linear, Q = quadratic, H = hinge, P = product, T = threshold function; Elith et al., 2011), and 20,000 random background points with the *SSDM* package (v0.2.8.9002; Schmitt et al., 2017). We cross-validated with 70 % training and 30 % testing points, which was repeated five times for each model. Model performance was assessed using the Area under the Receiver Operating Characteristic curve (AUC; Phillips et al., 2006; Radosavljevic and Anderson, 2014). There are spatial, environmental, and detectability sampling biases inherent in these data, particularly in areas like the Canterbury Bight (a shallow region <100 m deep south of Banks Peninsula with a sand and mud seafloor) where survey effort was highest. To account for this bias, we repeated the modelling procedure ten times using a random sample of background points (Fourcade et al., 2014) and averaged the models, following recommendations from Barbet-Massin et al. (2012) and the *SSDM* package methodology.

We combined species-level finfish distribution models into a community-level representation of species richness based on an index of species diversity by summing or "stacking" all prey species continuous probability of occurrence maps (Schmitt et al., 2017; Zurell et al., 2020) using *SSDM* (Guisan and Rahbek, 2011; Schmitt et al., 2017). This method produces a probability-stacked species distribution model (pSSDM; D'Amen et al., 2015; Schmitt et al., 2017):

$$E(S_j) = \sum_{k=1}^{n} p_{j,k} \qquad (1)$$

where $E(S_j)$ is the expected species richness (S) at site j, n is the number of species, and $p_{j,k}$ is the occurrence probability prediction for species k (Calabrese et al., 2014). We applied the probability ranking rule (PRR) to the final pSSDM (D'Amen et al., 2015); for each grid cell, POP was summed in decreasing order for the number of species equal to the predicted species richness. This method improves assemblage predictions and minimises over-prediction inherent in *SSDM* (D'Amen et al., 2015; Zurell et al., 2020). The prediction was evaluated using (i) species richness error, or the difference between predicted and observed species richness, (ii) prediction success, or the proportion of correct predictions, (iii) specificity, or the proportion of true negatives where a species is both predicted and observed as being absent, and (iv) sensitivity, or the proportion of true positives where a species is both predicted and observed as being present.

We calculated an index of resource co-occurrence by multiplying POP and prey diversity and reclassifying into three categories: (i) no/ little likelihood of co-occurrence for values <1, (ii) moderate co-occurrence for values 1–2, and (iii) high co-occurrence for values >2 (top 5 % of all grid cells). This index is commutative, so there is little co-occurrence between predator and prey if a grid cell has a high species richness (SR)/low POP or a low SR/high POP (Fig. 2).

2.3. Fisheries overlap

We obtained annual commercial fishing intensity (kg/ha) rasters from MPI (Official Information Act OIA21-0221; MPI Open Geospatial Data Portal OGDP; https://data-mpi.opendata.arcgis.com). Fishing intensity (FI) was estimated as an 11-year annual mean of total commercial catch per unit area for (i) midwater/bottom trawling, (ii) netting (including gill, ring, and drift netting), and (iii) all fishing methods (including line, jig, and pot fishing) from 1 October 2007–30 September 2018. These data were reported to MPI by permitted commercial fishers in statutory catch and effort returns. The locations of fishing events were reported by statistical area or as start coordinates (and end coordinates, where available), which are precise to one (trawling) or two (netting) nautical miles (nm). Grid cell values equalled NA where fishing did not occur or where there were fewer than three commercial fishing
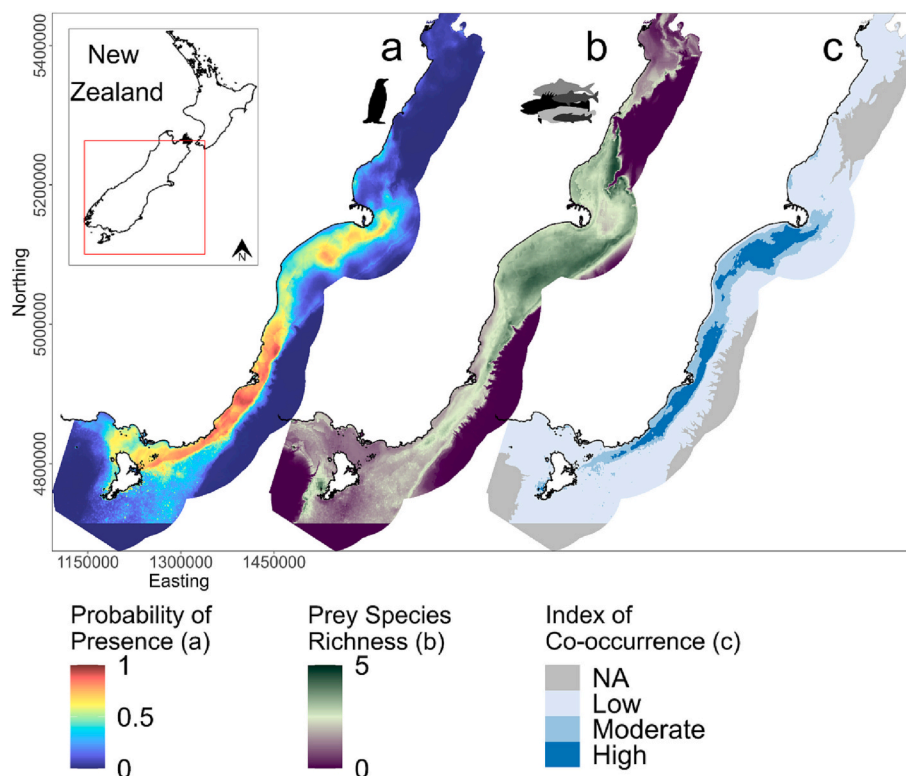
Fig. 2. Co-occurrence between yellow-eyed penguins and their prey, including (a) penguin predicted Maxent probability of presence, (b) prey species richness or diversity, predicted by a probability-stacked species distribution model with a probability ranking rule applied (PRR-pSSDM), and (c) the index of penguin/prey co-occurrence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

operators (MPI, 2021a). Fishing intensity ranged from no/0 to high/10. We clipped and resampled these data to match the extent and 500 m resolution of the penguin SDM.

For trawling, netting, and all methods, we calculated two measures of overlap between commercial fishing activities and penguin distribution. First, we estimated potential interaction risk (e.g., Cuthbert et al., 2005; Dodino et al., 2021; Fossette et al., 2014; Fox et al., 2021) by multiplying penguin probability of presence (POP 0-1) with fishing intensity (ten FI classes) and standardising the output from 0 (no/minimal interaction) to 1 (high interaction).

$$\text{Interaction Score} = \text{FI}^* \text{POP} \tag{2}$$

Next we determined a categorical index of overlap. We reclassified each FI layer into three categories as follows: 0 = 'low' (FI ≤ 1), 1 = 'average' (FI > 1 and ≤ to 5), and 2 = 'high' (FI > 5). High FI represents the top 5 % or the 95 % quantile of cells. Then we reclassified the binary environmental suitability map for penguins (PES) as follows: 4 = low/ 0 suitability, 5 = high/1 suitability. We multiplied the reclassified FI and PES rasters, which resulted in six categories of overlap. For ease of visualisation and analysis, we combined grid cell values of the overlap map into four final categories: (i) no/low FI, low PES; (ii) average/high FI, low PES; (iii) no/low FI, high PES; (iv) average/high FI, high PES.

There is a four nautical mile gillnet ban off the east coast of the mainland, which increased to 12 nm in some areas in 2020 (MPI, 2021b; Fig. 3a). We obtained gillnet prohibition shapefiles from the MPI OGDP and calculated the area of overlap between the current gillnet closure area and PES within the study extent.

2.4. Marine protected areas overlap

We obtained two types of spatial data for established MPAs from LINZ: (1) type 1 marine reserves and type 2 MPAs, and (2) other marine protection tools not included in the marine reserves layer. We combined ('union') and cropped ('clip') both layers to the study area in ArcGIS Pro (v2.7.0; ESRI Inc., 2019), which retained four type 1 MPAs, two type 2

MPAs, three marine mammal sanctuaries established under the *Mammals Protection Act 1978,* and four areas established under the *Kaikōura (Te Tai o Marokura) Marine Management Act 2014.*

Next, we converted spatial data for the proposed and consulted SEMPA network, obtained from SeaSketch (https://seasketch.doc.govt. nz; South-East Marine Protection Forum, 2018), into a shapefile in ArcGIS Pro. In R, we grouped established and proposed MPA polygons by type and calculated their area of intersection with the penguin binary suitability raster. Penguin overlap was calculated as.

$$R_{p,m} = R_p \cap {}_m / R_p \tag{3}$$

$R_{p,m}$ is the proportion of penguin range (R_p) that overlaps with MPAs (R_m). MPA overlap, or $R_{m,p}$, was also calculated using R_m as the denominator (Fox et al., 2021).

All maps, shown in the New Zealand Transverse Mercator 2000 projection with axes in easting and northing (metres), were created using *ggplot2* (v3.3.3) (Wickham, 2016) and *ggpubr* (v0.4.0) (Kassambara, 2020).

3. Results

3.1. Prey distribution

Prey species richness derived from the Maxent PRR-pSSDM (AUC = 0.83) was greatest in the south and southeast of the Canterbury Bight along the outer continental shelf, while co-occurrence with penguins was highest north of the Canterbury Bight (Fig. 2a). Prey richness and co-occurrence was lowest around Stewart Island (Fig. 2b). For more central areas of yellow-eyed penguin foraging distribution, from North Otago to the Catlins, species richness was higher over the mid and outer continental shelf in waters 50–100 m deep (Fig. 2c) near the largest subpopulations of yellow-eyed penguins on the Otago Peninsula and North Otago (Mattern and Wilson, 2019). Likewise, co-occurrence was high in these areas and moderate in waters <50 m deep. For individual Maxent prey SDM from which PRR-pSSDM was derived (Appendix
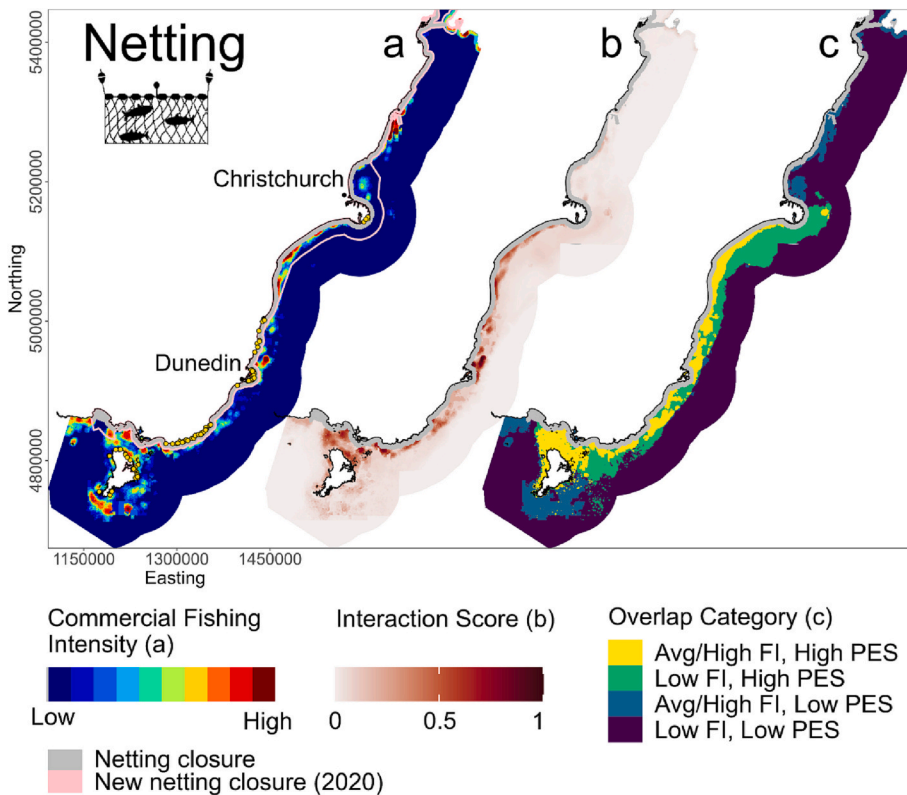
Fig. 3. Commercial gillnet fishing intensity (a; FI) from 2007 to 2019 ranging from low to high (Ministry for Primary Industries, 2021; licensed for re-use under the Creative Commons Attribution 4.0 International licence). Yellow circles are breeding sites with at least one nest since 2003. The netting prohibition area (grey) is 4 nm off the coast, which increased to 12 nm in some areas in 2020 (pink outline). The spatial overlap between commercial gillnet fisheries and yellow-eyed penguin probability of presence (PES) was visualised as an interaction score (b) ranging from 0 to 1 (no/low to high interaction) and four categories of overlap (c). Yellow indicates areas of high risk, with a high probability of penguin presence and an average/high fishing intensity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

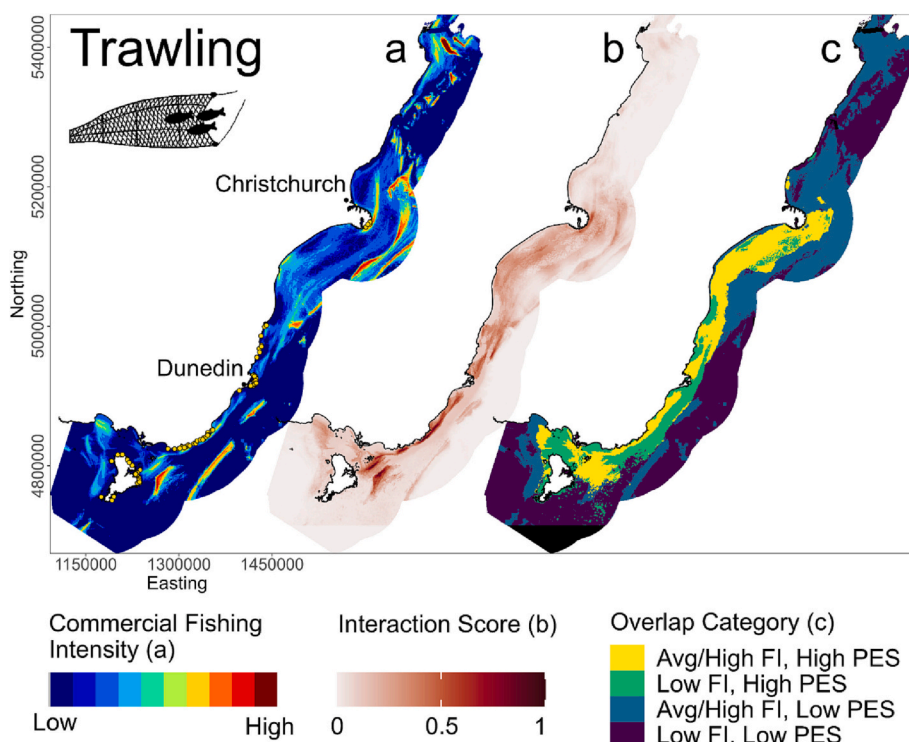Fig. A.2), AUC values ranged from 0.76 to 0.94 (Table A.3).

3.2. Fisheries overlap

Approximately 33.4 % and 61.2 % of suitable penguin habitat overlapped with areas of high netting (Fig. 3) and trawling fishing intensity, respectively (Fig. 4). High commercial fishing intensity using any method occurred across 80.8 % of suitable penguin foraging habitat (Appendix Fig. A.3), and interaction scores for gillnetting were highest north of the Otago Peninsula and around the northern coast of Stewart Island. High trawl interaction scores occurred more inshore especially offshore of the Catlins and east Foveaux Strait (Fig. 4).

The four nautical mile gillnet ban off the South Island's east coast reduced the inshore overlap, although key interaction areas tended to occur along the border of this prohibition zone (Fig. 3a). In 2020, this zone was increased to 12 nm in the Canterbury Bight and north of Banks Peninsula (Fig. 3a). Although fishing intensity data was obtained from 2007 to 2018, current intensity in these areas is negligible; hence, interaction scores are reduced to 0. About 34 % or 8179.5 km of penguin foraging range overlaps with netting prohibition zones (Table 1). While commercial trawl fishing for vessels over 46 m in length is prohibited within the same gillnet prohibition zone, an outright ban of trawling has not been implemented.

3.3. Marine protected area overlap

Only 0.04 % of the predicted range of mainland yellow-eyed penguins (23,978 km^2) is currently protected by a type 1 or type 2 MPA (Table 1). The overlap between marine mammal sanctuaries (Fig. 5) and penguin distribution is 35.8 %, although there is little protection from fisheries interactions in these areas. The proposed SEMPA network of 11 type 1 and type 2 MPAs (Table A.4) would cover an area of 1266 km^2, or 3.6 % of the yellow-eyed penguin mainland distribution; however, 67.6 % of the total SEMPA range would overlap with suitable penguin foraging habitat (Table 1). Although the Moko-tere-a-torehu type 2 MPA, central to the study extent north of Ōamaru (Fig. 5C), has the greatest overlap with penguin distribution, there are no adjacent

Table 1

Area (km^2) of established and proposed MPAs and their overlap area with the distribution of yellow-eyed penguin. Area was summed across each MPA type and for all MPAs combined, with n equal to the number of MPAs per type. See Table A.4 for MPA names and sizes. Also included is the area of overlap between penguins and gillnet closure areas (including established type 1 marine reserves).

MPA Type	n	Area (km^2)	Overlap (km^2)	Penguin Overlap (%) [c]	MPA Overlap (%) [d]
Established MPAs					
Type 1 MPA	4	121.9	2.5	0.01	2.01
Type 2 MPA	2	88.9	6.0	0.03	6.8
Marine Mammal Sanctuaries	3	15,280.9	8586.2	35.8	56.2
Other	4	6221.9	2.6	0.01	0.04
Total [a]	13	21,713.6	8597.2	35.9	39.6
Total (Type 1 + 2) [b]	6	210.8	8.5	0.04	4.02
Proposed MPAs (SEMPA)					
Type 1 MPA	6	404.7	300.7	1.3	74.3
Type 2 MPA	5	861.7	555.8	2.3	64.5
Total [a]	11	1266.3	856.4	3.6	67.6
Gillnetting prohibited	–	15,505.1	8179.5	34.1	52.8

[a] Sum for all MPAs.
[b] Sum for Type 1 and Type 2 MPAs only.
[c] Penguin overlap = overlap area/area of penguin distribution*100.
[d] MPA overlap = overlap area/total area*100.

colonies, so any adult penguins foraging here likely to originate from North Otago or will be juveniles dispersing from further south. As shown in Fig. 5, the Kaimata type 2 MPA (E), Papanui marine reserve (H), and Te Uma Koau marine reserve (D) are the largest MPAs closest to penguin breeding sites and will have the most overlap with penguins. There is only one proposed MPA in the Catlins, and it does not overlap with
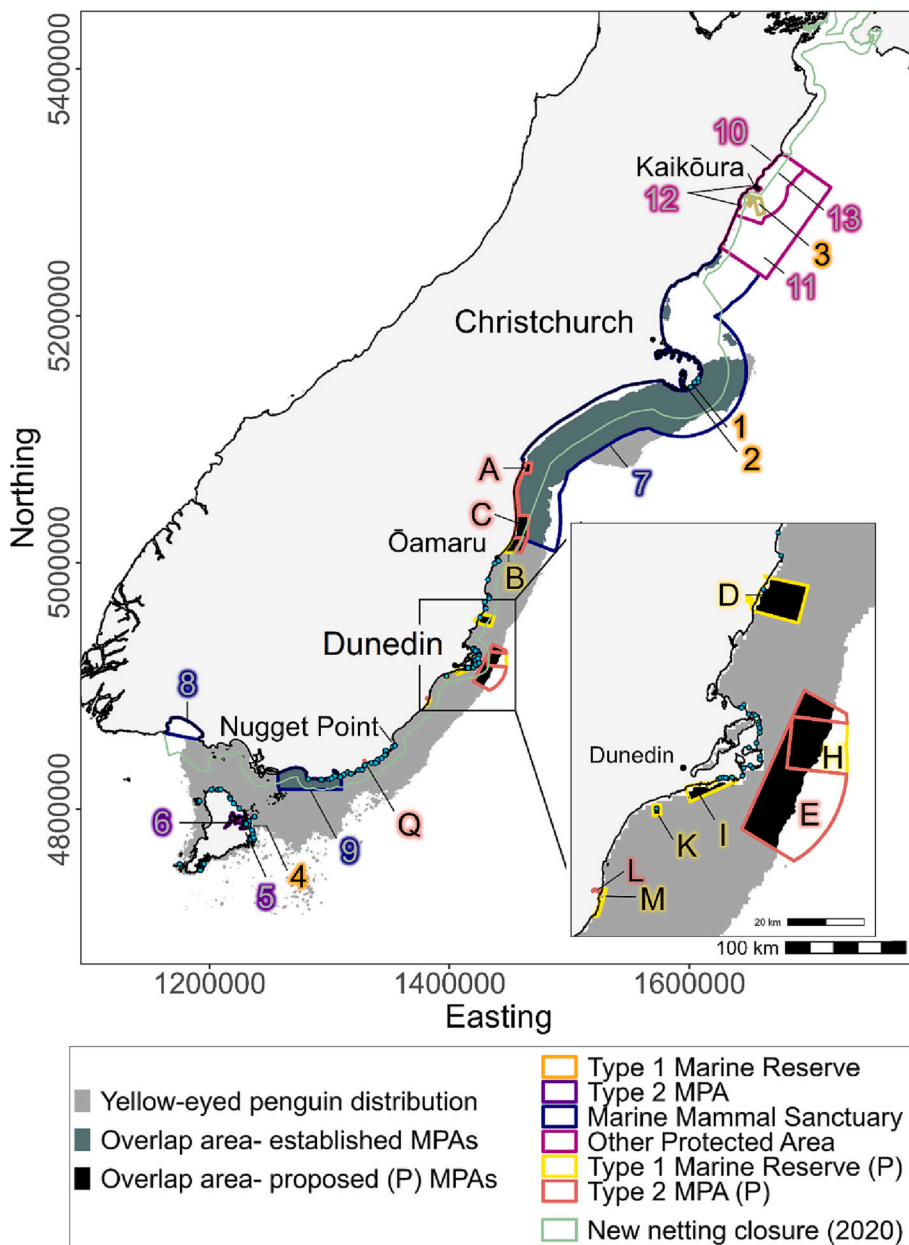

Fig. 4. Commercial trawling fishing intensity (a; FI) from 2007 to 2019 ranging from low to high (Ministry for Primary Industries, 2021; licensed for re-use under the Creative Commons Attribution 4.0 International licence). Yellow circles are breeding sites with at least one nest since 2003. The spatial overlap between commercial gillnet fisheries and yellow-eyed penguin probability of presence (PES) was visualised as an interaction score (b) ranging from 0 to 1 (no/low to high interaction) and four categories of overlap (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 5. Overlap between yellow-eyed penguin distribution and established MPAs (numbered with areas of overlap shown in dark grey) and proposed MPAs (P; lettered with areas of overlap shown in black). See Appendix Table A.4 for the full names of the referenced MPA names. The inset shows the Otago Peninsula, and the green boundary shows the current gillnet closure area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

current yellow-eyed penguin distribution.

4. Discussion

This study is a practical application of predictive SDM that examined the overlap of yellow-eyed penguins with resources, risks, and areas of refugia at sea. Analyses relied on publicly available and accessible data to show how SDM can be applied to marine spatial planning and conservation management. We aimed to understand penguin-prey and penguin-fisheries spatial interactions while assessing the location of established and proposed MPAs and fishing prohibition zones.

4.1. Prey distribution

High prey diversity increases the chance of prey capture success and resilience to environmental change. Compared to areas along the mid-continental shelf where there is considerable spatial overlap between penguins and their prey, low to moderate co-occurrence occurred inshore and adjacent to breeding colonies. In these areas, prey species richness is relatively low, and penguins are either travelling through these areas to and from foraging grounds or using them for surface activities like resting. Birds forage further offshore over the mid-shelf in average depths of 50-100 m where species richness is higher.

Most of the time penguins are restricted in their foraging movements based on distance to their breeding site (Hickcox et al., 2022) and show high fidelity to certain areas (Mattern et al., 2007; Moore, 1999). For instance, adult penguins rarely travel to the Canterbury Bight, approximately 170-270 km north of the Otago Peninsula. For most of the population that breed from the Catlins to North Otago, it is too far to travel during the breeding season. A penguin travels up to 55 km in a typical single-day foraging trip (Elley et al., 2022; Mattern et al., 2007; Mattern et al., 2013), despite the area's high prey species richness. Noted, however, is the potential bias in sampling effort in areas like the Canterbury Bight, which could impact species richness estimations.

We would expect to see a change in penguin distribution, dive behaviour, breeding success, or diet in response to recent prey distribution shifts observed in New Zealand (e.g., Chiaradia et al., 2003; Sherley et al., 2013). However, several foraging studies separated by

decades indicated mostly consistent foraging behaviours, such as distance travelled, trip frequency and duration, in the South Island population (Mattern, data unpub.; Young, data unpub.; Moore et al., 1995; Moore, 1999; Mattern et al., 2007; Elley et al., 2022). Recent shifting prey distributions were not captured in the species richness metric due to the long time series, but key prey identified in the 1990s (Moore and Wakelin, 1997; van Heezik, 1990) are still present in the current yellow-eyed penguin diet, albeit in lower frequencies and abundance (Young et al., 2020). These species are still found within penguin foraging range. Rather, their abundance or availability at correct sizes may have changed as the effects of commercial fishing and climate change have intensified over time (Morrison et al., 2014; OPMCSA, 2021), thus contributing to the yellow-eyed penguin population decline. If prey greatly expand or shift their distributional range outside the maximum penguin foraging range, it is more likely that penguins would change their diving behaviour, diet, or foraging effort, such as pelagically diving (Mattern et al., 2007; Muller et al., 2020, 2021) or switching key prey species (Chiaradia et al., 2003; Sherley et al., 2013), rather than significantly changing their horizontal range.

Key prey were identified in a single season (Young et al., 2020), while species richness and penguin distribution were modelled using long-term and large-scale data. Our findings may not reflect prey compositions during periods of relative population stability. Another limitation to this study is the prey data represents all size classes of fish, despite yellow-eyed penguins often foraging on juveniles rather than adults (e.g., red cod, silverside). Future work is required to ascertain if temporal and spatial distributional shifts of adults, juveniles, or spawning grounds have occurred at different scales and size classes.

4.2. Fisheries overlap

Yellow-eyed penguins forage in areas used by all types of fisheries along the South Island's eastern continental shelf. While prey composition determines the attractiveness of an area to both fisheries and penguins, the type of commercial or recreational fishery affects the magnitude of direct and indirect risks to fish and penguins (Crawford et al., 2017; Dodino et al., 2021; Richard et al., 2020). For instance, the unsustainable removal of adult fish from a population greatly affects spawning stock, population structure, and recruitment over time (Planque et al., 2010). Minimum allowable sizes of commercially fished species are typically larger than the small or juvenile prey yellow-eyed penguins prefer (Browne et al., 2011; Moore and Wakelin, 1997; van Heezik, 1990), so penguins and fisheries do not always compete directly for the same resources (Pichegru et al., 2009). Rather, declining juvenile fish biomass likely affects penguins more.

Penguins can drown while entangled in gillnets (Crawford et al., 2017), and areas along the mid-shelf have both high gillnet fishing intensity and high penguin probability of presence. Although bycatch in trawls has only been documented twice (Webster, 2018; DOC, data unpub.), the effects of trawling on yellow-eyed penguins are more indirect and long-term. Bottom disturbance reduces habitat complexity, increases homogenisation by damaging seafloor structures such as reefs or sand waves, removes organisms from the environment, and stirs up sediment (Mattern et al., 2013; Thrush and Dayton, 2002). For a finite time after the trawl event, tolerant fish species, often scavengers like blue cod, consume dead, exposed, or damaged macrofauna in the regenerating benthic habitat (Baird et al., 2015; Mattern et al., 2013; Thrush and Dayton, 2002). Increases of blue cod in yellow-eyed penguin diet (Young et al., 2020) might be indicative of increased habitat disturbance or trawling intensity where these penguins are foraging (Mattern et al., 2013, 2007; Moore, 1999).

In November 2022, a voluntary gillnetting closure was implemented in two additional areas around Stewart Island in addition to the current 4 nm voluntary closure around Codfish Island (Fisheries Inshore New Zealand, 2023). Gillnet prohibition areas have been extended to 12 nm around Banks Peninsula, the Canterbury Bight, and Ta Waewae Bay in Southland since October 2020. Although adults rarely forage around Banks Peninsula, the extensions benefit juvenile yellow-eyed penguins during their natal dispersal period (Young et al., 2022). Although positively impacting other wildlife in the area, these bans may inadvertently increase the interaction risk between penguins and gillnet fisheries (Boersma and Parrish, 1999). While penguins are protected from gillnets while they travel, often pelagically, through the 4 nm gillnet ban area, they typically forage and feed beyond its boundaries (mean distance from breeding colony 8.7–12.0 km) over the mid-continental shelf in waters 50-150 m deep (Hickcox et al., 2022), exactly where fisheries have relocated outside of the ban area. 'Fishing the line' with increased intensity is due to increased prey abundance adjacent to but outside of the ban area, which attracts both fisheries and penguins (Greenstreet et al., 2009).

This analysis relied on temporally analogous fisheries and penguin data (2007–2018 and 2006–2021, respectively) to establish a long-term interaction potential but did not quantify rates of bycatch or impacts of habitat degradation. Future evaluation of the effects of commercial fishing on yellow-eyed penguins need to account for discrepancies in reported fisheries-related penguin mortalities across agencies and databases (Webster, 2018), unreliable reporting of bycatch, and a lack of available, precise location data for fishing activities and penguin captures. Moreover, a data deficit has prevented assessments of the effects of recreational fishing on protected species, arguably of more consequence in some areas in New Zealand. Current protection strategies often discount recreational fisheries, but further studies and advocacy for restrictions in methods, catches, and reporting, if necessary, should be prioritised (Crawford et al., 2017). Current fisheries management practices are not sufficiently reducing protected species captures and protecting the marine environment, despite quota management and vessel monitoring systems, electronic catch reporting, and increased observer and camera coverage on inshore vessels (Office of the Prime Minister's Chief Science Advisor, 2021; available from www.pmcsa.ac.nz).

4.3. Marine protected areas overlap

Marine threats are the main cause of yellow-eyed penguin population decline (Mattern and Wilson, 2019; Young et al., 2020). MPAs are a key tool used to mitigate these negative anthropogenic impacts, particularly related to fisheries (Davies et al., 2018), but <1 % of the penguins' mainland total predicted distributional range overlaps with a type 1 marine reserve or type 2 MPA. While there is widespread use of mainland coastal waters by commercial fisheries, the largest MPAs occur offshore within the EEZ (DOC et al., 2019). The proposed SEMPA network would protect only 3.6 % of the penguins' range. Approximately 34 % of the foraging range of yellow-eyed penguins overlaps with a gillnet prohibition area, although these areas are not considered formal MPAs. Marine protection is required in fisheries-penguin interaction hotspots including the Catlins coast and North Otago.

Since MPAs are spatially explicit management tools, they require substantial geographic data, such as seabird tracking data and SDM (Domisch et al., 2019), to identify areas of high biodiversity, important habitat, or exploitation areas (Thaxter et al., 2012). There are some fundamental problems with MPAs, however, like lack of enforcement/compliance, cross-national connectivity, and governance (Frazão Santos et al., 2019). The costs to fisheries are often considered over the cost to the environment, which can result in poorly structured, patchy, and small MPAs. From an ecological perspective, MPAs may inadvertently alter the size, abundance, and diversity of formerly fished predators which affects larvae communities and recruitment (Boersma and Parrish, 1999), particularly in smaller reserves. When MPAs are considered within the wider framework of marine spatial planning, although an imperfect system, some of these problems can be addressed (Frazão Santos et al., 2019).

Other tools besides MPAs need to be implemented. For instance, a

holistic adaptive management approach considering the interactions between a variety of prey, protected species, and humans could support temporary, but stricter, closures that allow fishing in certain areas at certain times (e.g., outside the penguin breeding season or only at night) as an alternative to permanent no-take MPAs. Moreover, continual assessments of the effects of fishing in localised areas could dictate the level of use and potential discontinuity of activities if certain thresholds are reached (Scott, 2016). Moreover, integrating threatened species, prey, fisheries, and MPA data, like the results of this study, could focus observer coverage in high-risk commercial fisheries (i.e., past bycaught penguins or targeting penguin prey species) in areas of high penguins-fisheries overlap. This could not only improve protection for penguins and reporting of bycatch but also reduce overall observer effort. Other alternatives include promoting traditional fishing methods and customary use allowances, developing sustainable fisheries, incentivising compliance, improving legislature and permitting, increasing education and public awareness, and encouraging behaviour changes to mitigate anthropogenic overexploitation and environmental change (Jarvis and Young, 2019; Scott, 2016).

Naturally, penguins, seabirds, marine mammals, and other predators are not the only animals to target assemblages of abundant and diverse fish species. Commercial fishing operations also target these areas, elevating the risk of bycatch, habitat destruction, disturbance, pollution, and other threats. This study was the first to consider how all three factors, prey, commercial fisheries, and MPAs, affect yellow-eyed penguins, an approach that could be applied to other marine species. Moreover, there is an opportunity to integrate this information, including SDMs and spatial analyses, into future marine spatial planning opportunities and to reform the national approach of marine spatial planning in New Zealand so that international standards and cultural values are met (Scott, 2016).

Ethics statement

Funding

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability

Most data analysed for this study are stored on Movebank (www. movebank.org) and can be made available by the authors upon reasonable request (Movebank study IDs: 1129010560, 7690187, 1348934678, 1594883659, 1507150714). Prey data were obtained from the open-source Ocean Biogeographic Information System repository. Data for fishing intensity was obtained from MPI/Manatū Ahu Matua through an Official Information Act request OIA21-0221.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110197.

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