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Hector's dolphin distribution at Kaikōura before and after a major earthquake

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ABSTRACT: Catastrophic natural events can have major impacts on marine ecosystems, but effects on mobile predators, such as cetaceans, remain poorly understood. This study investigated whether the coastal distribution patterns of Hector's dolphins *Cephalorhynchus hectori hectori* off Kaikōura, New Zealand, changed after the powerful Kaikōura earthquake in November 2016. Dolphin sightings from boat-based surveys conducted before (2013–2016) and after (2016–2020) the earthquake were binned into 18 sectors of 4 km length each. The dolphins' occurrence across sectors was then compared during pre- and post-earthquake periods using generalised linear models. Areas of high and low occurrence probability were temporally stable for Hector's dolphins from before to 1.5 yr post-quake. Historic sighting data (from the 1990s) matched with the observed high-occurrence areas, indicating decadal stability in distribution patterns. An increase in dolphin occurrence was noted in the final 2–4 yr post-quake period across most nearshore sectors. This was particularly noticeable in the historically low-use areas along the narrow shelf at the head of the deep Kaikōura Canyon. This observation could indicate increased population connectivity between dolphins using the northern and southern sections of the Kaikōura Peninsula. The dolphins' occurrence patterns pre-quake at the sector level were broadly explained by water depth, distance to rivers, sea surface temperature and chlorophyll when explored with generalised additive models. We discuss scenarios that may explain the species' persistent distribution patterns during natural perturbation events as well as synergies with other conservation measures.

KEY WORDS: Catastrophic events · *Cephalorhynchus hectori* · Distribution persistence · Kaikōura earthquake

1. INTRODUCTION

Catastrophic events can fundamentally alter the structure and function of ecosystems due to the mortality of key species, dramatic changes in nutrient and energy flux and physical alterations of important habitats (Ramachandran et al. 2005, James et al. 2008). In the marine realm, natural catastrophes can result from climatic events such as hurricanes and heatwaves (Johnson & Winker 2010, Wild et al. 2019) or geological events such as volcanic eruptions, tsunamis and earthquakes (EQs) (Fraile-Nuez et al. 2012, Schiel et al. 2019). Catastrophic events can also be of anthropogenic origin, the most prominent being large-scale marine pollution events such as oil spills (Peterson et al. 2003, Frasier et al. 2020, Murawski et al. 2021).

Catastrophic events are, by definition, infrequent, abrupt and unpredictable. A relatively short and intense impact phase followed by potentially cascading long-term consequences can affect an ecosystem over months if not years via direct and indirect pathways (Schiel et al. 2019, Murawski et al. 2021). Detecting and determining population-level effects of catastrophic events requires substantial *a priori* knowledge of the system (pre-event studies) and

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appropriate post-event monitoring. Understanding the impacts of catastrophic events on populations of mobile and long-lived marine predators such as cetaceans is particularly challenging, as such studies are resource-intensive to undertake and require long time scales to investigate population-level effects (Bassos-Hull et al. 2013, Wild et al. 2019, Frasier et al. 2020, Coxon et al. 2022, Schwacke et al. 2022). There appear to be only 3 studies that have investigated the effects of rare geological events such as EQs on wild cetaceans (Gallo-Reynoso et al. 2011, Guerra et al. 2020, Barlow et al. 2022).

Documented short-term responses of cetaceans to EQs include behavioural changes in captive bottlenose dolphins *Tursiops truncatus* (Turner et al. 2015) and a fin whale *Balaenoptera physalus* abandoning an affected area likely due to the intense underwater noise associated with the seismic activity (Gallo-Reynoso et al. 2011). Longer-term changes in the distribution of pelagic, deep-diving sperm whales *Physeter macrocephalus* in the aftermath of the 2016 Kaikōura EQ in New Zealand are thought to be linked to altered trophic pathways and habitat modifications (Guerra et al. 2020). Here, we investigate the effects of the same Kaikōura EQ on the distribution of a coastal, shallow-water delphinid, the Hector's dolphin *Cephalorhynchus hectori hectori* using data from systematic sighting surveys.

Hector's dolphins are endemic to the neritic waters of New Zealand. They are predominantly found inshore of the 100 m depth contour and display high site fidelity to shallow nearshore and often turbid areas (Bräger et al. 2002, 2003, Weir & Sagnol 2015, Roberts et al. 2019) and have also been found to associate with sandy bottom substrate (Brough et al. 2023). These habitat characteristics are thought to correlate with areas of higher prey abundance, particularly during the summer months (Miller 2015, Brough et al. 2020). Hector's dolphins are considered to be generalist predators of small benthic and epipelagic fish and squid (Miller et al. 2013). The turbid nearshore habitat might also convey shelter from predators, particularly during the dolphins' calving season in austral spring and summer (Bräger et al. 2003, Brough et al. 2019).

The Kaikōura coastline is estimated to be home to 300–400 Hector's dolphins during the summer (304, 95% CI: 211–542, Weir & Sagnol 2015; 421, 95% CI: 132–1346 over a much larger study area, MacKenzie & Clement 2016). Previous evidence of demographic and genetic population structuring suggests limited dispersal between Hector's dolphins north and south of the Kaikōura Canyon (Weir & Sagnol 2015, Hamner et al. 2016). The deep Kaikōura Canyon and associated oceanographic features are thought to represent unfavourable dolphin habitat that might discourage dolphin dispersal (Bräger & Bräger 2018).

The Kaikōura EQ was a very powerful, multi-fault EQ of magnitude 7.8 that struck the north-east South Island of New Zealand near the coastal township of Kaikōura on 14 November 2016 (in the austral spring). It caused widespread damage and resulted in thousands of inland landslides, complex coastal subsidence and uplift processes (Dellow et al. 2017, Hamling et al. 2017) as well as substantial sediment flushing within the deep offshore Kaikōura Canyon (Mountjoy et al. 2018). The underwater sediment slides into the canyon removed large quantities of benthic biomass (Mountjoy et al. 2018), which in turn is thought to have affected the habitat of sperm whales that depend on the deep canyon's prey resources (Guerra et al. 2020). Nearshore habitats where Hector's dolphins reside were also affected. Coastal and inland landslides caused large and recurrent increases in terrigenous sediment loading in the rivers that discharge into the sea along the Kaikōura coast with additional sedimentation caused by coastal uplift processes (Schiel et al. 2019, McEwan et al. 2023). Coastal uplift also altered the intertidal and nearshore zones, leading to mass mortality of brown macroalgae (i.e. kelp forests) and other habitat-forming species, which in turn affected the dependent invertebrate communities and nursery grounds for various fish species (Schiel et al. 2019, Alestra et al. 2021, Orchard et al. 2021). Thus, both geomorphological and biological processes caused by the EQ could have affected the quality and availability of Hector's dolphin habitat.

This study used dolphin sighting data collected over an 8 yr period (2013–2020) to investigate whether Hector's dolphin distribution significantly changed after the Kaikōura EQ and in relation to a historic sighting data set from the mid-1990s (Bräger 1998). We also explored dolphin occurrence in relation to environmental characteristics to better understand whether broad abiotic conditions are underpinning the observed stable distribution pattern.

2. MATERIALS AND METHODS

2.1. Survey area and field methods

This study used boat-based sighting data of Hector's dolphins collected by KORI (the Kaikōura Ocean Research Institute) from November to March of 2013 through to 2020, which corresponds seasonally to late austral spring, summer and early autumn. The study area comprised around 55 km of coastline extending from Haumuri Bluffs (42.6° S, 173.5° E) to the Hapuku River mouth (42.3° S, 173.8° E) with the Kaikōura Peninsula in the centre (Fig. 1). A variety of shore types dominate this coast, including wave-cut rocky platforms around the Kaikōura Peninsula, mixed sand and gravel beaches to the north and alternating beaches and rocky reefs to the south. Local river discharge contributes sediment directly into the coastal waters (Lewis & Barnes 1999), often leading to turbid conditions near river mouths. The Kaikōura Canyon, a U-shaped submarine canyon with a maximum depth of 1.2 km, is situated only 1 km offshore at its most proximal point (Lewis & Barnes 1999) (Fig. 1).

Surveys started and ended at the South Bay Marina on the Kaikōura Peninsula and followed 2 routes either heading north or south of the Peninsula, hereafter termed 'north' and 'south' respectively (Fig. 1). Occasionally, both north and south sections of the study area were visited on the same day, but more often only one or the other route could be completed. All surveys were conducted only in favourable weather conditions with Beaufort sea states of 3 or less. Surveys were primarily aimed at dolphin photo-identification (Weir & Sagnol 2015) and followed pre-planned routes within 2 km of and roughly parallel to the coastline and more offshore transects at about 5 km from the coast (Fig. 1). For surveys conducted from 2013 to 2018, the planned route was programmed into a Garmin 76 GPS and was usually followed closely; however, the realised tracks were not recorded, precluding track-based spatial analyses (see Section 2.2). Notes were kept of the time and location if a survey had to be terminated prematurely (e.g. because of deteriorating sighting conditions). During late 2018 to 2020, realised survey tracks (GPS fix frequency of $\leqslant$1 min) were recorded using a customised CyberTracker v.3.510 (Liebenberg & Steventon 2013) application running on a Samsung Galaxy tablet computer (Fig. 1).

All surveys were conducted from rigid-hull inflatable vessels powered by an outboard engine (length: 5.5–5.8 m; power: 80–100 hp) at speeds of 10–15 knots. At least 2 dedicated observers searched by naked eye in discrete sections from ahead to abeam of the survey vessel. When a sighting was made, vessel speed was reduced to no-wake speed, and the sighted animals were approached for photo-identification purposes and to ascertain group size. Surveys were primarily focussed on Hector's dolphins, but other marine mammals and birds were also recorded. For each sighting, the GPS location, time, species, group size and number of calves or newborns were noted on paper datasheets (2013–2018) or entered directly into the CyberTracker application (2019–2020). Correctly identifying Hector's dolphins from other commonly encountered delphinid species was straightforward, given their smaller body size, distinctly rounded dorsal fins and lighter body colour than other dolphins (Carwardine 2019). After all data had been collected, the survey was continued in the direction of the planned route. Hector's dolphins are well known for their tendency to approach boats (Dawson et al. 2004) and for forming temporary aggregations with fluid group membership (Bräger 1999, Constantine 2019). Every effort was made to avoid repeat sightings of the same dolphins by increasing vessel speed briefly upon departure. Sightings that were deemed a confirmed re-sighting of the same individuals in a similar-sized group in close proximity to the previous encounter on the same day were excluded from further analysis.

2.2. Delineation of spatial and temporal units for analysis

To investigate potential effects of the EQ, this study's primary aim was a temporal comparison of dolphin distributions before and after the EQ, using a measure of occurrence. Full coverage of the entire study area was intended; however, differences in the recording of spatial survey effort precluded a high-resolution transect-based analysis. Instead, we created a 1.2 km buffer around all of the planned daily survey routes followed from 2014 to 2018 and split these into 4 km segments along the planned route that gave 18 polygons of roughly equal area, hereafter termed sectors (Fig. 1). Sectors were assigned unique ID numbers and formed the spatial unit for all further analysis. The buffer was chosen based on the distribution of all Hector's dolphin and non-Hector's dolphin locations, e.g. other marine mammal species and environmental stations (as plotted in Fig. 1), to account for slight deviation from the planned track. Specifically, straight-line distances from all recorded GPS locations to the planned track lines were measured in QGIS. Truncation at the 97th percentile of distances was set to determine the buffer size (1.2 km), which indicated the area around the planned track through which the vessel had travelled over the study. The buffered area also encompassed the survey tracks from November 2018–2020 (Fig. 1). The way each

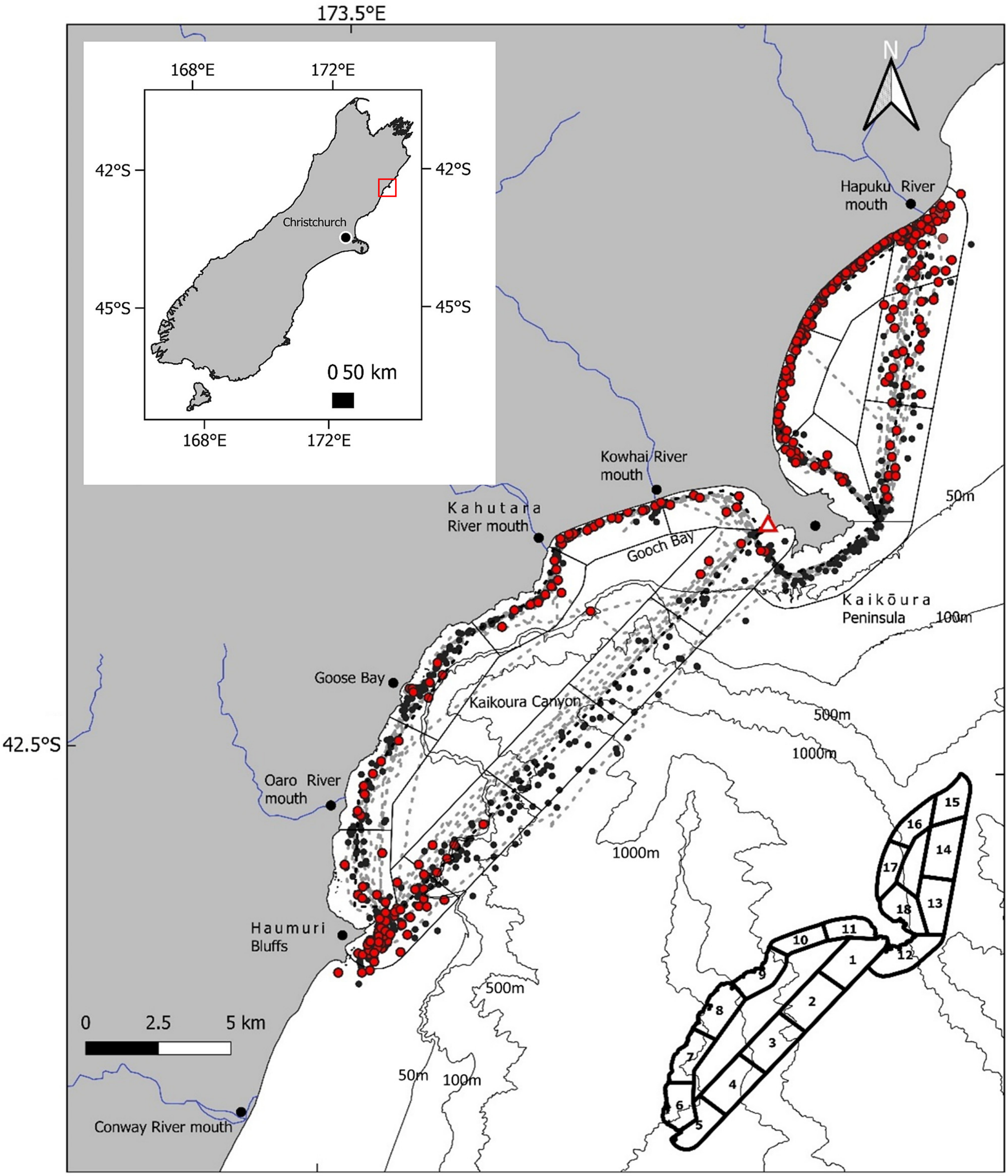

Fig. 1. Study site (red square in inset), extending from the Haumuri Bluffs to the Hapuku River mouth along the east coast of South Island New Zealand. Spatial units of analysis (black outlined sectors, see bottom right inset for sector ID numbers), created around a planned survey track line (dashed black line) commencing from South Bay (open red triangle to the south (Sectors 1–11) and to the north (Sectors 12–18) of the Kaikōura Peninsula. GPS locations of Hector's dolphin sightings from complete boat-based surveys conducted November 2013 to March 2020 (red dots). Non-Hector's dolphin sightings and environmental station readings from 2014 to 2018 used to inform the sector size are shown as small black dots. GPS Track lines from 2018–2020 (dashed grey lines). The 50, 100, 500 and 1000 m depth contours are labelled, and key river centrelines are shown (blue lines)

sector was traversed (broadly following the same preplanned route parallel to shore with some variations in distances from shore) meant that observers should have been equally likely to detect dolphins in any sector before and after the EQ (see Section 4). Our research question and analytical approach did not require that all dolphins in each sector be detected during a survey.

For each survey day, the field notes and GPS data were checked to ensure that all sectors had been surveyed as planned. Sectors not surveyed at full length were removed from further analysis for that survey day. The basic unit of analysis was each completed passage through a sector on a given survey day, termed 'sector visit' hereafter. In each sector, Hector's dolphin occurrence was recorded as either seen (present) or not seen (i.e. not detected). Occurrence per sector visit provides a robust measure of sector use, which was used to compare across space and time periods.

For the temporal comparisons, survey effort was grouped into 6 annual survey periods and 3 episodes in relation to the EQ. Each survey period spanned November to March, which included austral spring to autumn when Hector's dolphins tend to be concentrated within a few kilometres from shore (Rayment et al. 2010). There were not enough systematic surveys conducted from January to March 2014 or from November 2015 to March 2016, and these months were excluded from further analysis. Thus, 6 annual periods with roughly equal survey effort in austral summer were used: 2013 (Jan–Mar and Nov–Dec 2013), 2014–2015 (Nov 2014–Mar 2015), 2016–2017 (Nov 2016–Mar 2017), 2017–2018 (Nov 2017–Mar 2018), 2018–2019 (Nov 2018–Mar 2019) and 2019–2020 (Nov 2019–Mar 2020) (see Table 1). The 3 EQ periods were pre-EQ (2013 to Nov 2016), 1.5 yr post-EQ (Dec 2016 to March 2018, i.e. 1.5–18 mo post-EQ) and 2–4 yr post-EQ (Nov 2018 to March 2020) (see Table 1 for periods and effort). EQ time periods were selected to give approximately equal survey effort and to explore medium to longer-term effects of the EQ. Annual periods were selected to investigate whether annual variations provided a better explanation for any differences over time.

2.3. Statistical analysis: temporal effects on distribution

The temporal and spatial patterns in Hector's dolphin distribution were explored considering occurrence as a function of time (annual or EQ periods) and space (sector ID) using generalised linear models (GLMs). Independent variables were factors (sector ID with 18 levels, annual period with 6 levels and EQ period with 3 levels). All model variations (i.e. intercept only (null), sole terms only, both the spatial and a temporal term, and an interaction between spatial and a temporal term) were considered. Note temporal terms 'year' and 'EQ period' were not considered in the same model, as we were only interested in determining whether EQ periods better explained the data than annual variation. Candidate models were compared using Akaike's information criterion (AIC), with the final model selected based on the lowest-scoring AIC and when differing by more than 2 points from the next best model. Dolphin occurrence was modelled using binomial GLMs with a logit link function. The best-fitting (final) model was examined by plotting the distribution of deviance residuals and by plotting the variance of deviance residuals against fitted values. Cook's distance was examined to check for overly influential values. The base level for categorical variables in the final model was set to pre-EQ for the EQ period, and Sector 7 for Sector ID. Sector 7 was selected because it had the median number of overall sightings and was therefore a suitable comparison to higher and lower sighting rates in other sectors. Subsets of the dolphin occurrence data set were also overlaid with Sector ID to produce distribution maps for each of the 3 EQ periods and facilitate visual comparisons of spatial patterns over time.

Statistical analyses were conducted in R software v.4.1.2 (R Core Team 2019). Mapping and spatial analyses were undertaken in QGIS v.3.4.9 (QGIS Development Team 2020) using the projected coordinate reference system UTM 59S, and the spatial analysis libraries QGIS, GRASS (GRASS Development Team 2020) and SAGA (Conrad et al. 2015).

2.4. Long-term distribution patterns

We explored the temporal persistence of the observed nearshore distribution patterns by comparing them with historic sighting data of Hector's dolphins collected in the same study area from 1994 to 1997. The field methods are described in detail in Bräger (1998), with the raw sighting data available in the thesis appendix. The methods were comparable to those used in this study. At least 2 observers conducted boat-based photo-identification surveys for Hector's dolphins from a 4.5 m long rigid hull vessel with a 40 hp outboard engine covering more of the Kaikōura coastline than this study. Locations where dolphins were present were recorded in addition to sites where dolphins were not detected. For comparison purposes, only data collected during the same months and matching the current study's extent are shown here. Surveys also started and ended at the Kaikōura Peninsula (see Fig. 2D), with the north and south sections surveyed on different days. Survey effort was concentrated within 1 km from the shore, thus allowing for a comparison of sightings to more recent surveys in this area. Locations of Hector's dolphin sightings were recorded using GPS and group size was estimated in a similar manner to this study. The historic sighting locations were compared visually to the current distribution patterns (see Fig. 2).

2.5. Environmental conditions and dolphin occurrence across sectors

Given the patterns in Hector's dolphin distribution described by the temporal–spatial models (Section 2.3), we then explored whether static and dynamic environmental variables could help explain the observed patterns in sector use. Environmental variables were selected based on their known influence on Hector's dolphin habitat use and their availability in appropriate temporal and spatial resolutions.

We would have liked to model dolphin habitat use in relation to environmental conditions as likely changed by the EQ. Unfortunately, data were not available at the required temporal or spatial resolutions. Key environmental variables such as depth were not available at scales comparable to pre-EQ. The use of sectors to bin sightings and effort data precluded modelling the dolphins' fine-scale habitat use given the wide environmental space in some sectors i.e. depth in sectors overlapping the canyon rim. We therefore used available variables to explore differences in the sectors' overall characteristics pre-EQ (e.g. shallow versus deep, sandy versus muddy bottom substrate).

Static variables considered were distance to river mouth, distance to land, bottom substrate type, bathymetry and slope. Dynamic variables differed both spatially and temporally and were available for the entire study area; these were sea surface temperature (SST) and surface chlorophyll *a* (chl *a*) concentration.

Depth data were available for the entire study area from before the EQ at a 250 m resolution gridded raster from the New Zealand 250 m Bathymetry Grid (NIWA 2016). Slope values were calculated from the pre-EQ depth raster at the same 250 m resolution using the slope tool in QGIS. Bottom substrate type was available as separate raster layers of the proportion of sand, mud and gravel at 1 km^2 resolution from before the EQ (Bostock et al. 2019).

Locations of river mouths were determined at the cross-section between the Kaikōura coastline (derived from NZ Coastlines and Islands Polygon Topo 1:50k; LINZ 2020) and river centre lines (NZ River Centreline Topo 1:500k; LINZ 2011) and were verified on satellite images from Google Earth (accessed online 2020). Seasonal minor streams and creeks were not included. A GIS shapefile of the wider east coast was then converted into a raster of 50 m resolution, with each cell assigned a value depending on whether it contained land with no river mouth, sea or land with a river mouth. The shortest distances between cells that included sea and the nearest river mouths were calculated (avoiding crossing land-only cells) in R software using the 'gridDistance' tool in the package 'raster' (Hijmans 2020). The shortest distance between any cell at sea and the nearest cell on land was also calculated using the same package.

The zonal statistics tool (in QGIS) was used to calculate the median value per sector for each static variable to be used as a predictor variable in the environmental models of dolphin sector use. Median values were chosen to limit the influence of large values for coastal sectors; for instance, where the proximity of the canyon to the shore meant that depths greater than 100 m were present at the edge of a predominantly shallow sector. In the 2 sectors over the canyon (Sectors 2 and 3), median depth values are in the region of 700 m and do not represent likely habitat for the species. The consistent lack of sightings in our results supported this assumption, so we decided to exclude these 2 sectors from the environmental analyses.

Satellite-derived multi-scale ultra-high resolution (MUR) level 4 SST (°C) data were available from the Group for High Resolution Sea Surface Temperature (GHRSST) as daily composites at 1 km^2 spatial resolution (JPL NASA 2020). Surface chl *a* data were obtained as raster layers at a resolution of 2.7 km^2 produced by the National Oceanic and Atmosphere Administration (NOAA) Coast Watch program using data derived from the MODIS sensor on the Aqua satellite by the Goddard Space Flight Center (NOAA 2020). Eight-day composites were used as the best compromise between data loss due to cloud cover and the need for high temporal resolution to match the sector visits. SST and chl *a* data were matched as closely as possible to the corresponding survey date. In nearshore waters, satellite-derived chl *a* measurements not only capture plankton activity (as in the open ocean) but also likely include contributions of terrigenous sediments and re-suspended materials (Matsushita et al. 2012), thus may capture turbidity derived from river-run off and coastal currents.

We used generalised additive models (GAMs) to investigate whether the observed spatial patterns of dolphin occurrence could be explained by the environmental characteristics of the different sectors. Dolphin occurrence was modelled using GAMs with binomial error structure, logit-link function and thin-plate regression splines to select the appropriate level of smoothing (Wood 2003). Degrees of freedom for each smooth were set to a maximum of 5 to prevent model overfitting. Pairs of environmental predictor variables were investigated for collinearity using Pearson's correlation, and only variables with a coefficient of less than 0.6 were included in the same model. Manual forward stepwise selection was used to identify the most parsimonious model with the best fit to the data. Each variable or interaction was first entered as the sole term. The term that had the lowest AIC or improved the AIC the most and explained most of the deviance was retained, and the process was repeated for the remaining variables until the model AIC no longer improved. Smooth plots from the final model for pre-EQ periods were created to visualise relationships between the probability of occurrence and environmental variables.

Table 1. Survey effort and total number of Hector's dolphins recorded during surveys from 2013 to 2020. Data are shown in 2 temporal categories i.e. by year and by earthquake (EQ) period

Temporal category	Survey period	Surveys North	Surveys South	Surveys Total	Groups Total	Individuals Total
Year	2013	9	8	17	55	270
	2014–2015	10	7	17	59	296
	2016–2017	8	9	17	52	237
	2017–2018	14	14	28	66	405
	2018–2019	11	11	22	79	462
	2019–2020	2	4	6	23	123
	TOTAL	54	53	107	334	1793
EQ Period	Pre-EQ	22	18	40	121	584
	<1.5 yr post-EQ	19	20	39	111	624
	2–4 yr post-EQ	13	15	28	102	585
	TOTAL	54	53	107	334	1793

3. RESULTS

3.1. Survey effort and sightings

A total of 903 sector visits from 107 surveys (54 north and 53 south) conducted from January 2013 to March 2020 (Table 1) formed the units of analysis. Of those surveys, 40 (324 sector visits) occurred during the pre-EQ period, 39 (360 sector visits) occurred in the 1.5 yr post-EQ period and 28 (219 sector visits) occurred in the 2–4 yr post-EQ period (Table 1). The 2017–2018 survey period saw the most surveys conducted, and the 2019–2020 survey period, the fewest (Table 1). A total of 334 groups of Hector's dolphins were sighted during the 8 yr study period (Table 1), with 121 groups encountered during the pre-EQ period, 111 groups during the 1.5 yr post-EQ period and 102 groups in the 2–4 yr post-EQ period. Mean (±SD) dolphin group size was 5.5 ± 4.3 and was similar across EQ periods (pre-EQ: 5.2 ± 3.8; 1.5 yr post-EQ: 5.6 ± 4.9; 2–4 yr post-EQ: 5.9 ± 4.3). The first north and south surveys post-EQ took place 39 and 41 d, respectively, after the end of the main seismic events on 14 November 2016. A total of 10 group sightings of Hector's dolphins were made with 15 animals in the north (Sectors 15 and 16) and 25 animals to the south (Sectors 4, 5, 6, 7 and 9). No unusual behaviours were observed relative to those seen on any other surveys, although this was not tested empirically.

Over the 8 yr study period, Hector's dolphins were seen throughout the study area but were notably absent from the offshore sectors over the Kaikōura Canyon (Sectors 2–4) and off the eastern side of the Kaikōura Peninsula (Sector 12) (Figs. 1 & 2). Sightings were generally more frequent north of the Kaikōura Peninsula (Sectors 14–18) than to the south (Sectors 5–11) (Figs. 1 & 2). Sightings at either end of the study area, near Haumuri Bluffs (Sector 5, south) and the Hapuku River (Sector 15, north), were consistently more frequent during all periods (Fig. 2). Interannual sighting frequency varied in the nearshore waters to the south of the Peninsula, with Hector's dolphins frequently sighted at the head of the Kaikōura Canyon (Sectors 7 and 8) only during the 2018–2019 and 2019–2020 survey periods (i.e. 2–4 yr post-EQ) (Fig. 2).

3.2. Hector's dolphin distribution pre- and post-EQ

Neither candidate occurrence model with the sole temporal term 'year' or 'EQ period' improved upon the null model by more than 2 AIC points (Table 2)

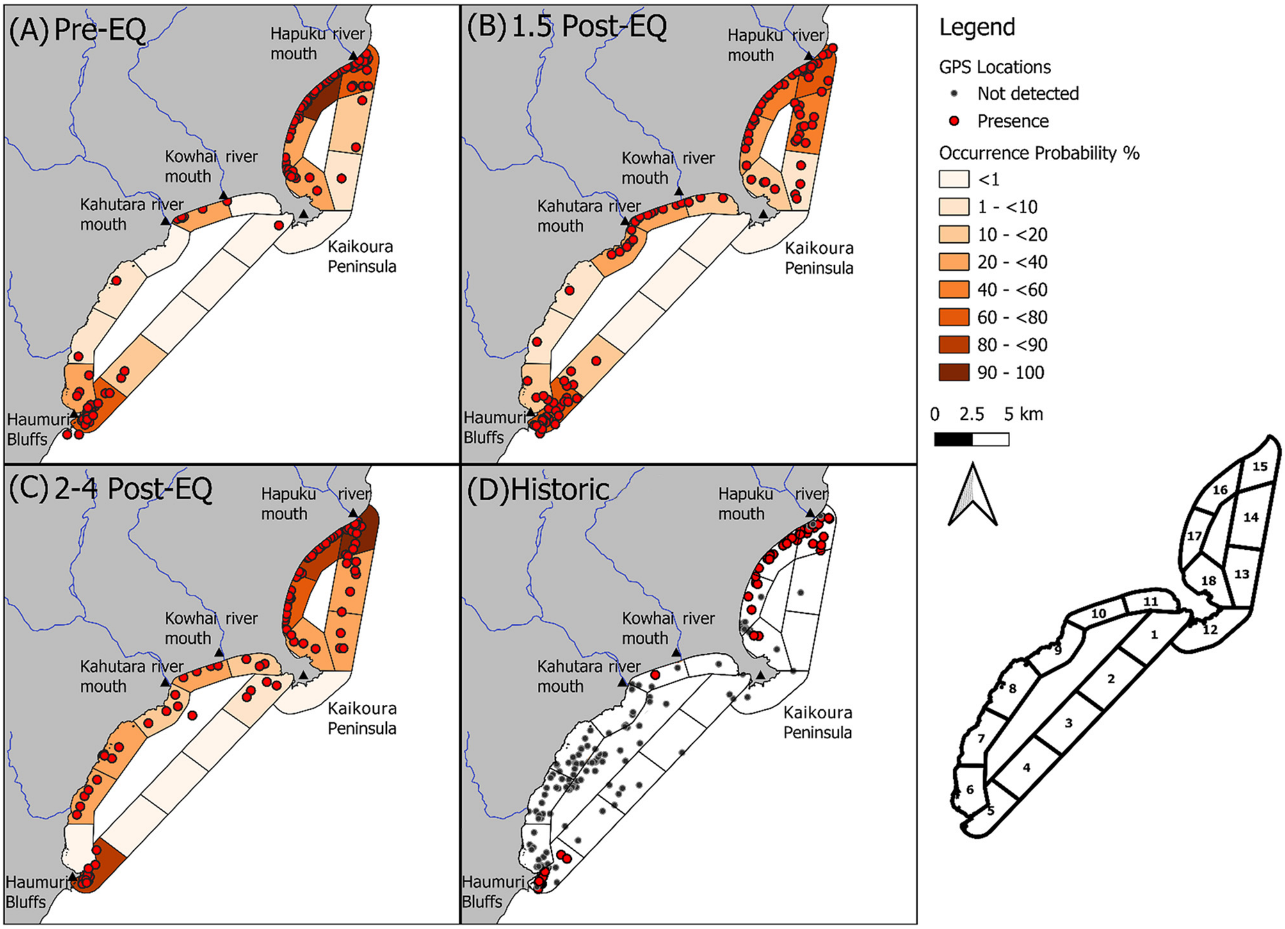

Fig. 2. Fitted values of probability of occurrence of Hector's dolphins off Kaikōura per spatial unit of analysis (sector) generated using 3 binomial generalised linear models with sighting data (red dots) recorded during boat-based surveys conducted (A) pre-earthquake (EQ), (B) 0–1.5 yr post-quake and (C) 2–4 yr post-quake. (D) Locations of sightings (red dot) and non-sightings of Hector's dolphins from historic boat-based surveys conducted November–March 1994–1997

Table 2. Candidate models of Hector's dolphin occurrence in order of lowest to highest Akaike information criterion (AIC) value. The best model, identified by the lowest AIC value, is highlighted in **bold**. ΔAIC from the best model and log likelihood is shown for each model. EQ: earthquake

Model type	AIC	ΔAIC	Log likelihood
Sector_ID + EQ period	**724.7**		**342.3**
Sector_ID	728.2	3.5	346.1
Sector_ID + year	729.5	4.8	341.8
Sector_ID × EQ period	731.5	6.8	311.8
Sector_ID × year	783.2	58.5	283.6
EQ period	1011.1	286.4	502.1
Null (intercept only)	1011.5	286.8	504.7
Year	1014.2	289.5	501.1

suggesting that these terms did not explain much variability in the data. However, the best occurrence model included the spatial term (Sector ID) and the temporal term (EQ period) without an interaction term, demonstrating support for an EQ period effect over annual effects (Table 2). The best model indicated that the probability of Hector's dolphin occurrence varied between sectors across the study area and also differed between some of the 3 EQ periods (Table 3). Model diagnostic plots showed no cause for concern (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m748p175_supp.pdf).

Spatial variation in occurrence probability across the study area was notable. For example, in all EQ periods, Sectors 5 (Haumuri Bluffs, South), 15 and 16 (Hapuku River, North) consistently had the highest predicted probability of dolphin occurrence with over 65% (Figs. 2 & 3). Sectors 10 (Kahutara River, south), 14, 17 and 18 (north) also had a high probability of dolphin occurrence ranging from 22 to 52%. By contrast, Hector's dolphins were not predicted to occur (0–1% probability) in Sectors 12 (eastern face of

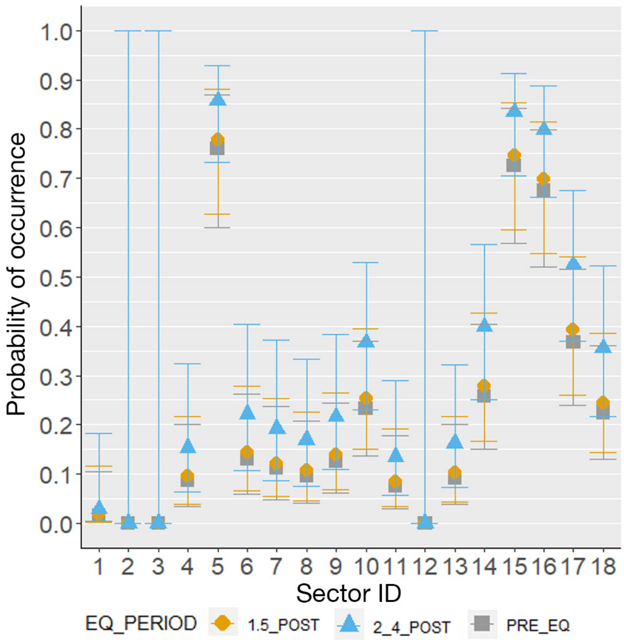

Fig. 3. Fitted values of occurrence probability ±95% confidence interval for Hector's dolphins per spatial unit of analysis (sector) for each earthquake (EQ) (Pre-EQ: 2013–Nov 2016; 1.5 yr post-EQ: Dec 2016–March 2018; 2–4 yr post-EQ: Nov 2018–Mar 2020) period at Kaikōura, New Zealand, generated using a binomial generalised linear model

Kaikōura Peninsula) and Sectors 2–3 (directly over the Kaikōura Canyon) (Figs. 2 & 3).

There was no significant difference between pre-EQ and 1.5 yr post-EQ (Table 3), but the probability of occurrence was significantly higher in the 2–4 yr post-EQ period than both pre-EQ ($p < 0.01$) and 1.5 yr post-EQ ($p < 0.05$) (Figs. 2A–C & 3). Predicted probability of occurrence was consistently higher across all sectors, excluding 2, 3 and 12 (no sightings) during the 2–4 yr post-EQ period but did not differ significantly between periods when considering individual sectors (Fig. 3; overlapping 95% confidence intervals). Overall, the pattern of the predicted occurrence values from the best model matched well the underpinning sighting data (Fig. 2A–C).

3.3. Long-term distribution patterns

The historic sighting data matched the current distribution patterns of observed and predicted Hector's dolphin high occurrence sectors very closely (Fig. 2D). There were 51 dolphin sighting locations and 133 locations without dolphins present available from 51 surveys conducted between November to March from 1994 to 1997 (Fig. 2D). The majority of historic sightings (82%) were in sectors with high predicted probability of occurrence (65% and above; Fig. 2). In the south, almost all historic sightings occurred off Haumuri Bluffs (Sector 5), while in the north, historic sightings were concentrated off Hapuku River (Sector 15) and south along that stretch of coastline (Sectors 16 and 17). Effort offshore was limited; however, there were no historic sightings in the offshore sectors (Sectors 2–4), which matched the near-zero predicted probability of occurrence in those sectors (Fig. 2 & 3). There were 65 historic locations without dolphins but only one historic sighting (in Sector 10) along the entire south coast between the Kaikōura Peninsula and Haumuri Bluffs (Sectors 6–11) (Fig. 2D). This historical lack of occurrence contrasts with the gradual increase in Hector's dolphin occurrence along the south coast (Sectors 7–11), with predicted probabilities of occurrence ranging from 10 to 25% (Figs. 2 & 3) since the EQ.

Table 3. Model output from a final fitted binomial generalised linear model of Hector's dolphin occurrence. Parameter estimates show the difference to each level of the 2 independent factors (Sector_ID or EQ_period) from the base level intercept (Sector 7 or pre-EQ) with standard error (SE), test-statistic (Z) and significance (Pr) levels (**$p < 0.01$; ***$p < 0.001$)

	Estimate	SE	Z	Pr(>|Z|)
(Intercept)	−2.08	0.467	−4.453	<0.001***
SECTOR_ID1	−2.06	1.103	−1.867	0.061
SECTOR_ID2	−16.68	926.402	−0.018	0.986
SECTOR_ID3	−16.69	956.001	−0.017	0.986
SECTOR_ID4	−0.27	0.648	−0.418	0.676
SECTOR_ID5	3.23	0.569	5.677	<0.001***
SECTOR_ID6	0.18	0.605	0.302	0.763
SECTOR_ID8	−0.15	0.621	−0.249	0.804
SECTOR_ID9	0.15	0.587	0.254	0.799
SECTOR_ID10	0.89	0.537	1.657	0.097
SECTOR_ID11	−0.42	0.646	−0.653	0.514
SECTOR_ID12	−16.71	890.128	−0.019	0.985
SECTOR_ID13	−0.20	0.620	−0.329	0.742
SECTOR_ID14	1.02	0.540	1.894	0.058
SECTOR_ID15	3.05	0.554	5.510	<0.001***
SECTOR_ID16	2.81	0.539	5.203	<0.001***
SECTOR_ID17	1.53	0.524	2.929	<0.01**
SECTOR_ID18	0.84	0.542	1.554	0.120
EQ_PERIOD1.5_POST	0.10	0.226	0.471	0.638
EQ_PERIOD2_4_POST	0.64	0.247	2.595	<0.001**

3.4. Environmental conditions and dolphin occurrence across sectors

A total of 230 sector visits from 2013 to 2016 had complete static and dynamic covariate data and were available for the environmental models. The following variables had Pearson's correlation coefficients that exceeded 0.6 and were therefore not included in the same models: depth and distance to land; depth and slope; slope and percent sand; slope and percent mud; percent sand and percent mud; and percent mud and percent gravel.

Depth was the most important predictor of Hector's dolphin occurrence in a sector out of all environmental variables in the single-term models (Table 4) and in the final model (Table 4). The single-term model with depth was improved by adding distance to river, SST and chl *a* (log), with the final model explaining 53.3% of the deviance (Table 4).

The relationship between Hector's dolphin occurrence probability and depth showed no clear trend in the GAM (Fig. 4A). However, sectors 5, 15 and 16 with the highest predicted probability of occurrence (Section 3.2) had median depth values of 20 m or less (Table S1 in the Supplement).

The predicted probability for Hector's dolphin occurrence from the nearest river mouth was greater between 4 to 7 km (peak at 5–5.5 km) and was lower at nearer and greater distances (Fig. 4, Table S1). Sectors 5, 15 and 16 had median values of distance to river of 5.1, 1.5 and 3.9 km respectively (Table S1). The probability of Hector's dolphin occurrence increased with SST in an almost linear relationship up

Table 4. Explanatory terms in the single-term models and the final (best) model of Hector's dolphin occurrence pre-earthquake. edf: estimated degrees of freedom; % Dev: percentage of deviance explained by a term. For the final model, changes in % Dev and AIC value resulting from the addition of each term to the Depth only model are shown

Smooth term	edf	% Dev	AIC
Single-term models			
Depth (m)	3.92	26.9	194.8
Sand (%)	3.81	26.0	196.9
Gravel (%)	3.91	20.5	211.1
Mud (%)	3.58	17.2	218.7
Slope (%)	1.26	6.98	239.9
SST (°C)	1.00	3.3	248.6
Distance to land (m)	3.11	4.68	249.4
Chl *a* (log) (mg m^{-3})	1.00	0.375	256.1
Distance to river (m)	1.00	0.02	257.0
Final model			
Depth (m)	3.10	26.9	
Distance to river (m)	3.94	+18.5	−40.9
SST (°C)	3.18	+3.9	−5.7
Chl *a* (log) (mg m^{-3})	1.00	+4.0	−5.5
TOTAL		**53.3**	

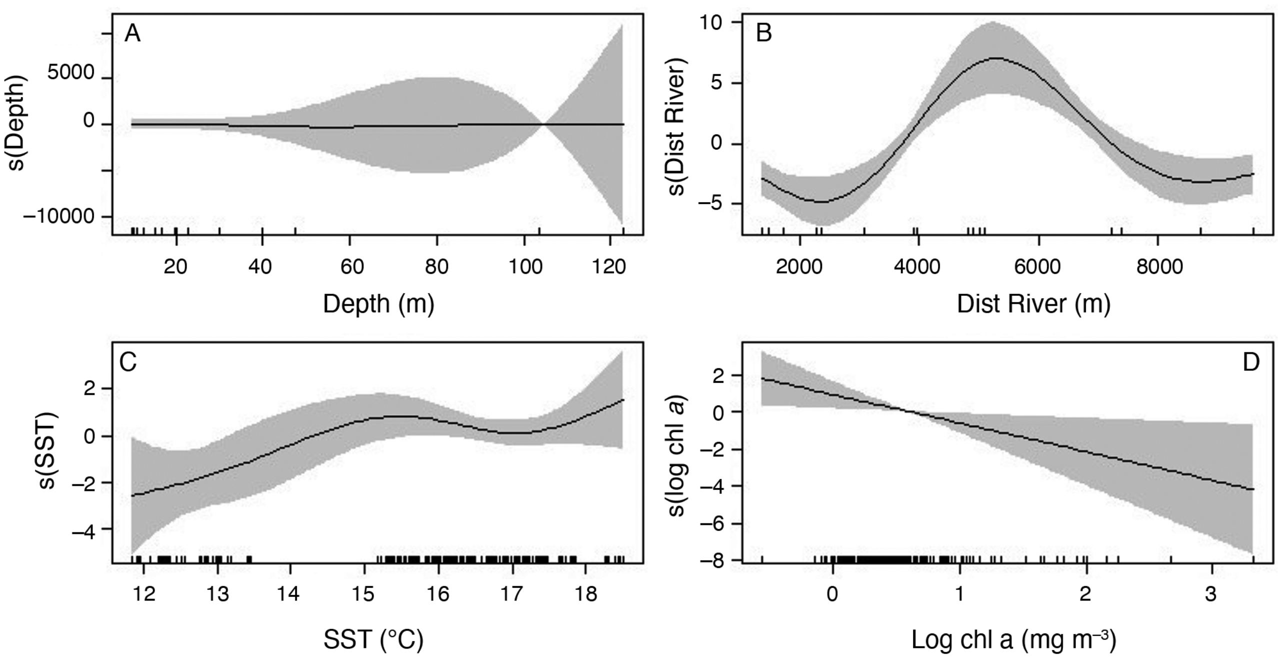

Fig. 4. Probability of Hector's dolphin occurrence along the Kaikōura coast pre-earthquake as a function of (A) depth (m), (B) distance to river (km), (C) sea surface temperature (SST; °C) and (D) chlorophyll *a* (chl *a*; log, mg m^{-3}). Plots were generated using the outputs from the best generalised additive model. Rug plots: observations of covariate values; grey shading: 95% confidence bands

to 15°C, with a second peak above 18°C (Fig. 4C). The variable chl *a* showed a negative linear correlation with dolphin occurrence (Fig. 4D).

4. DISCUSSION

This study detected no major changes in the distribution of Hector's dolphins along the Kaikōura coastline before and after the 2016 Kaikōura EQ. Instead, comparing historic sighting data with contemporary distribution patterns showed consistent use of several coastal sectors by the dolphins for more than 2 decades with more variability in less frequently used sectors through time. Hector's dolphins mainly occurred in sectors that had median water depths of less than 20 m, increasing summer SST and were in the broader vicinity of river mouths and low chl *a* concentration.

Few studies have investigated the effects on cetacean distribution from naturally occurring yet infrequent or unpredictable catastrophic events (e.g. Bassos-Hull et al. 2013, Fandel et al. 2020, Guerra et al. 2020). Such studies require the fortuitous circumstances of suitable longer-term data collection already in place pre-catastrophe to allow for before and after comparisons. Data used in our study were originally collected for photo-identification purposes, and most surveys did not record fine-scale spatial survey effort. We standardised survey effort to reduce potential bias from unequal spatial sampling by binning sighting data into coarser spatio-temporal units (sector visits) for which consistent effort information could be compiled from field notes and which ensured that each sector was covered in its full length. This approach also facilitated an informative comparison with historical data for which GPS effort tracks were not available but which were collected using the same alongshore survey approach. We acknowledge that the chosen sector width exceeded the typical sighting distance of Hector's dolphins from small boats (Dawson et al. 2004), but this spatial unit was necessary to encompass variation between survey track locations through time. Thus, occurrence here represents the probability of sighting a dolphin group on any given transect traversing through a sector at full length. As we assumed that dolphins were equally likely to have been missed by the observers in any sector before and after the EQ, relative comparisons are reasonable using the same survey methods. Only sector visits with good sighting conditions were analysed to minimise detection bias across sector visits.

Our sector-based approach precluded examining the drivers of fine-scale habitat selection or changes in habitat use in relation to the EQ. We explored only the broad environmental characteristics of the sectors to better help understand the temporal persistence in dolphin distribution (or spatial) trends. Even at our coarse spatial scale, differences in occurrence across sectors were well explained by environmental conditions known to influence Hector's dolphin habitat use (Bräger et al. 2003, Rayment et al. 2010, Weir & Sagnol 2015, Brough et al. 2023). It would have been interesting to investigate the potential EQ effects on dolphin habitat use directly given the evidence of substantial environmental changes in the nearshore zones and the Kaikōura Canyon post-quake (Mountjoy et al. 2018, Orchard et al. 2021, Thomsen et al. 2021). Unfortunately, the required environmental data for such a fine-scale comparison were not available at the relevant spatial resolutions or for the post-quake period.

4.1. Kaikōura EQ and Hector's dolphins

The first post-EQ survey was conducted 39 d after the main quake event. Therefore, we have no information on acute or short-term effects on the dolphins in the 6 wk immediately after the EQ. Once surveys resumed, however, we did not detect any large spatial changes in the overall distribution of Hector's dolphins between the Hapuku River and Haumuri Bluffs. The probability of occurrence remained stable across almost all sectors from before to 1.5 yr after the EQ. This finding matched results from photo-identification and mark–recapture analyses that also showed no detectable changes in Hector's dolphin total abundance in the study area over the same period (Weir & MacKenzie 2021).

Similarly, the presence and overall abundance of sperm whales using the nearby Kaikōura Canyon did not change in the weeks to months after the EQ (Guerra et al. 2020). Thus, overall, the coastal Kaikōura EQ did not appear to have had any major short-term impacts on resident cetaceans inhabiting the shallow neritic (Hector's dolphins) or deep-water pelagic (sperm whales) realms. However, some sperm whales shifted foraging areas away from the usual canyon habitat to the surrounding deep-water areas (Guerra et al. 2020). They also spent longer at the surface recovering from dives, which the authors interpreted as the whales having to dive and search for longer for their deep-water prey (Guerra et al. 2020). The EQ triggered sediment slides and turbidity currents at the canyon head, which destroyed benthic communities, altered trophic pathways and likely reduced prey availability for sperm whales (Guerra et al. 2020, Bigham et al. 2023).

In the nearshore sectors of our study area, the Kaikōura EQ caused coastal uplifts of one to 2 m in the intertidal zone (Orchard et al. 2021), which severely damaged ecological communities, coastal reefs and associated kelp forests (Schiel et al. 2019, Alestra et al. 2021, Orchard et al. 2021, Thomsen et al. 2021). In this study, depth was the most important covariate of Hector's dolphin occurrence, with sectors less than 20 m median depth being areas of highest use. Changes in depth across the scale of our sectors post-EQ are unknown; however, any physical alterations could have affected habitat quality including the availability, composition and catchability of prey for Hector's dolphins. There is no information available on Hector's dolphin diet at Kaikōura. In general, Hector's dolphins are described as generalist predators that take a variety of small prey — often juveniles of various benthic or pelagic fish species that associate with shallow and estuarine waters (Miller et al. 2013). Along the east coast of New Zealand, Hector's dolphins do not appear to feed on reef-associated prey species (Miller et al. 2013), and rocky reefs were not typical habitat used by Hector's dolphins elsewhere in their range (Brough et al. 2023). This matches our finding that Hector's dolphins were not commonly encountered near the rocky reefs surrounding the Kaikōura Peninsula (Sectors 1, 11, 12 and 18). Thus, the EQ damage to reef communities might not have affected Hector's dolphins in a way that would manifest itself in large-scale changes to their distribution. As generalist predators (Miller et al. 2013), Hector's dolphins might also have been able to switch from preferred to alternative prey species without having to move in space. A dietary study of the Māui dolphin subspecies *Cephalorhynchus hectori maui* using stable isotope analysis supports this idea. Ogilvy et al. (2022) demonstrated temporal shifts in Māui dolphin dietary niche in response to potential changes in prey availability.

Effects of the Kaikōura EQ on soft-sediment coastal areas and associated biotic communities have not been studied; thus, ecological changes in many of the coastal sectors relevant to Hector's dolphins remain unknown. Immediately after the EQ, landslides increased terrigenous sediment loading in the rivers that discharged into the study area (Dellow et al. 2017, Hamling et al. 2017), likely increasing sedimentation and turbidity in the nearshore waters. Most high-use sectors were in the broader vicinity of river mouths, with a peak at 5 km distance (Fig. 4B) but did not always contain a river within that sector. At the sector level, there was a negative correlation between dolphin occurrence and chl *a* concentration (Fig. 4D) (considered by some to be a proxy for turbidity in coastal waters; Matsushita et al. 2012, Derville et al. 2016). Hector's dolphins have evolved to occupy highly dynamic and turbid nearshore environments. They use narrow-band, high-frequency echolocation clicks to navigate and forage and are well adapted to detecting prey in cluttered environments (Kyhn et al. 2009). Thus, increased sediment loading was unlikely to have hampered the dolphins' acoustic ability to detect prey or navigate in more turbid habitat, allowing persistent use of the same high-use areas post-EQ.

An increase in Hector's dolphin occurrence probability at Kaikōura with warmer temperatures (Fig. 4C) may reflect seasonality in inshore movements likely associated with prey movements in warmer months (Rayment et al. 2010). The Kaikōura EQ is unlikely to have had any major impact on SST in the region. However, it is also important to recognise other catastrophic events which occurred over the same period. Globally, marine heatwaves are becoming more frequent (Oliver et al. 2018) with extreme events in 2017–2018 and 2018–2019 leading to record temperature anomalies in the New Zealand region (Salinger et al. 2019). Overall, our findings suggest that habitat variables important to these dolphins do not appear to have been largely affected by the EQ or other catastrophic events.

4.2. Temporal persistence in Hector's dolphin distribution patterns

The observed distribution pattern of Hector's dolphins at Kaikōura, particularly in the north, seems to have persisted for at least several decades, as evidenced by our comparison with historic sighting data. Long-term stability in fine-scale habitat selection has been shown for Hector's dolphins at Banks Peninsula (Brough et al. 2019) and other coastal delphinids such as congeneric Chilean dolphins *Cephalorhynchus eutropia* (Heinrich et al. 2019). Persistent high-use areas are usually interpreted as core habitat where dolphins meet their needs for survival (e.g. foraging, reproduction, safety from predators) (Brough et al. 2019, Heinrich et al. 2019). Given our results, it seems unlikely that the Kaikōura EQ substantially degraded the dolphins' core habitats. However, evidence in other regions demonstrates that a resident population can also persist in degraded habitat (e.g. *Sousa chi-*

nensis; Karczmarski et al. 2017) if alternative habitat is not available or there are substantial fitness costs to movements, such as resource uncertainty in unfamiliar habitat or increased predation risk. Detailed habitat studies are needed to identify the composition and extent of suitable habitat for Hector's dolphins at Kaikōura. Current New Zealand-wide predictive maps for Hector's dolphin distribution (Roberts et al. 2019, Stephenson et al. 2020) indicate suitable habitat further north and south of our Kaikōura study area, but these modelling approaches are too large-scale to allow for meaningful comparisons with the findings described here.

An alternative explanation for dolphins persisting in an area after a catastrophic event could be that some individuals moved out of their impacted habitat but were replaced by an influx of immigrants from further afield. Such emigration—immigration replacements could mimic stable distribution patterns and even appear as an increase in abundance. Following 2 powerful hurricanes in the Bahamas, 30% of resident bottlenose dolphins abandoned the area only to be replaced by the same number of immigrants (Elliser & Herzing 2011). Individual recognition (photo-identification) data exist for Hector's dolphins at Kaikōura for pre- and post-EQ periods (Weir & MacKenzie 2021) and could be used to investigate changes in individual site fidelity and social dynamics. In general, Hector's dolphins are known to have small home ranges and high site fidelity (Bräger et al. 2002, Rayment et al. 2009), which promotes stable distribution patterns. However, these characteristics also make resident populations vulnerable to spatially explicit impacts such as habitat degradation and direct mortality events (Burkhart & Slooten 2003, Karczmarski et al. 2017).

Hector's dolphins north and south of the Kaikōura Canyon are thought to belong to different communities with low rates of exchange between them (Weir & Sagnol 2015, Hamner et al. 2016, Bräger & Bräger 2018). These authors suggested that the deep canyon (Sectors 2 and 3) and very narrow shelf at the canyon head (Sectors 7—9) represented unfavourable habitat and a potential oceanographic barrier to population connectivity. Our results from sighting data up to 2018 supported that notion, with consistently low probabilities of occurrence (<15%) and few dolphins being seen in those narrow shelf sections (Sectors 7—9). However, in the 2—4 yr post-EQ period (2018—2020), dolphin sightings across the study area appear to have increased, including in those narrow low-use shelf sectors between Haumuri Bluffs and the Kaikōura Peninsula. Further research is needed to determine whether an increase in area use is indeed reflected in an overall increase in population abundance or what the underpinning mechanisms might be. Mark—recapture surveys should extend to investigate trends in abundance and changes in population dynamics such as survival rates and rates of emigration—immigration (e.g. Fearnbach et al. 2012, Bassos-Hull et al. 2013, Lin et al. 2022).

4.3. Wider implications

The effects of catastrophic events also need to be considered in the context of how they might affect other natural and anthropogenic pressures on a species as these can also modify population-level effects. In the 2 yr after Hurricane Katrina, foraging encounters of bottlenose dolphins in Mississippi Sound increased by up to 15% (Smith et al. 2013) and calf encounter rates and the proportion of calves increased over the same time (Miller et al. 2010). The authors suggested that an increase in dolphin prey due to substantially reduced commercial fishing effort following the hurricane could have had positive effects on the dolphins' foraging success and calf survival. Hector's dolphins in the Banks Peninsula Marine Mammal Sanctuary have shown increased survival rates after commercial set nets were banned, leading to a reduction in bycatch-related mortality (Gormley et al. 2012). Off Kaikōura, a commercial set net ban to between 1 and 4 nautical miles has been in place since 2008. Whether this has had positive effects on the wider dolphin populations in our study area through reduced capture remains to be investigated. Up-to-date abundance estimates and more detailed habitat studies are needed to understand whether changes to the dolphins' habitat from the Kaikōura EQ may have affected survival rates, increased local abundance and affected use and potential population connectivity along the narrow shelf sections at the head of the Kaikōura Canyon (i.e. Sectors 8 and 9).

4.4. Concluding remarks

This is the first study to investigate the effects of an EQ on the distribution patterns of a coastal delphinid. Distribution patterns of Hector's dolphins at Kaikōura seem to have remained relatively stable over decades before and in the first few years after the EQ. Broad-scale habitat characteristics were useful in interpreting the environmental conditions that set apart high- and low-use areas, but more detailed studies are needed to identify the extent of any changes to the dolphins' core habitat. Potential increases in occurrence in the 2–4 yr post-EQ require further investigation; in particular, any possible synergies with ongoing conservation and fisheries management measures.

Data availability. The research data underpinning the analysis in this publication can be found in Ellis et al. (2024). https://doi.org/10.17630/72dd0c2f-f4ad-4276-8aee-3d3d18a598ae

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