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Movement ecology and foraging behaviours of oceanic manta rays *Mobula birostris* in the coastal waters of Aotearoa, New Zealand

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Cite this article: Cooper TM, Green L, Setyawan E, Erdmann M, Duffy CAJ, Constantine R, Della Penna A. 2025 Movement ecology and foraging behaviours of oceanic manta rays *Mobula birostris* in the coastal waters of Aotearoa, New Zealand. *R. Soc. Open Sci.* **12**: 250838.
https://doi.org/10.1098/rsos.250838

Received: 30 April 2025
Accepted: 29 October 2025

Subject Category:
Ecology, conservation, and global change biology

Subject Areas:
ecology, environmental science, oceanography

Keywords:
mobulid, manta ray, foraging, bio-logging, satellite tracking, generalized additive models, New Zealand

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Understanding the movements and associated behaviours of animals is critical for informed management decisions. This is particularly important for species such as the Endangered oceanic manta ray (*Mobula birostris*), which has a conservative life history and is therefore vulnerable to population disturbances. Twelve oceanic manta rays were tracked for 9–84 days using high-resolution SPLASH10F-321A/E Fastloc GPS tags during their seasonal presence in northeastern Aotearoa, New Zealand, which indicated broad variation in fine-scale (100 m to 10 km) movements in Tīkapa Moana—Te Moananui-ā-Toi—the Hauraki Gulf and the nearby shelf. While in this region, the tagged oceanic manta rays spent most of their time in surface waters <5 m, with occasional dives up to 365 m. Generalized additive mixed-effect models indicate that movement patterns associated with daytime foraging in the region are linked to northerly winds but inhibited by high wind speeds (10+ ms^{-1}). Dives deeper than 5 m were more frequent at night, and during gibbous moon phases. A key challenge of this study is the lack of knowledge about oceanic manta ray prey composition and distribution: gathering and

Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8142774.

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incorporating this information into modelling is necessary to better understand the movement ecology and behaviours of manta rays at the southernmost part of their range.

1. Introduction

Animal interactions with the environment are shaped by internal factors such as physiological constraints, and external cues such as social interactions and the heterogeneity of environmental conditions and resources [1]. Understanding these drivers is a fundamental aspect of behavioural ecology and is useful to predict how populations respond to ecosystem variability and inform conservation management (reviewed in [2]). For marine species, movement takes place in the three-dimensional ocean environment. While much of our understanding of behaviour comes from field observations [3], movements below the surface are typically difficult to observe. These challenges are particularly pronounced for highly migratory oceanic species. Satellite telemetry and remote sensing technology are invaluable for investigating the movements of such wide-ranging and cryptic animals [2]. These technologies enable the tracking of individuals over large distances, facilitating behavioural studies related to horizontal movement, diving behaviour and habitat use, as well as research focused on the relationships with environmental conditions and resources (reviewed in [4]).

The oceanic manta ray (*Mobula birostris*) is a large planktivorous mobulid ray, distributed throughout tropical to subtropical regions and occasionally occurring in warm temperate habitats [5,6]. Although global trends in oceanic manta ray populations are not well understood, there has been a sharp decline in sightings and landings in some parts of their range [6]. The species' conservative life history makes it particularly vulnerable to population disturbances and baseline information on its biology and ecology is lacking. The concern for oceanic manta ray populations has contributed to their current classification as Endangered on the International Union for Nature's (IUCN) Red List of Threatened Species [6]. Similar to other planktivorous species, including the closely related reef manta ray (*M. alfredi*), oceanic manta ray movements are assumed to be closely linked to prey abundance and distribution and influenced by factors such as temperature, lunar cycle and tidal range [7]. Little is known about oceanic manta ray foraging, though vertical movement records reveal high occupation of zooplankton-rich surface waters (~5–10 m), punctuated by occasional deep dives [8], while several studies have documented oceanic manta rays feeding on mesopelagic prey (e.g. [9–11]). While some populations exhibit year-round residency patterns, documented seasonal patterns of oceanic manta rays indicate that they may also take long-distance migratory movements, likely linked to seasonal temperature variability and prey availability [12–14].

Oceanic manta rays are protected in Aotearoa, New Zealand (NZ), the southernmost limit of their distribution. Yet the national classification of this species is data deficient due to a lack of knowledge on their ecology in this region [15]. Over the past 6 years, research dedicated to collecting citizen science and non-systematic sightings data and deploying satellite tags on oceanic manta rays has focused on northeastern NZ waters. Sightings, which include photo-identification (photo-ID) records and telemetry, revealed that oceanic manta rays occur in NZ throughout the late austral spring (~November) to late austral autumn (~April) [16] and migrate to lower latitudes (e.g. to Fiji [14]) during winter. Oceanic manta rays' fine-scale movements and behaviours in NZ waters, as well as the triggers of their northern migrations into warmer Pacific waters in late summer to early autumn, remain unknown.

Here, we investigate the fine-scale spatial distribution and foraging ecology of manta rays in the Tīkapa Moana—Te Moananui-ā-Toi—the Hauraki Gulf (hereafter the Gulf) and its surrounding waters as part of a larger satellite telemetry study on the overall movement patterns and behaviour in coastal NZ waters and beyond. We interpret these movement patterns with the aid of high-resolution remotely sensed and *in situ*-measured environmental variables. Our study provides the first assessment of oceanic manta ray behavioural ecology in NZ and contributes to the global understanding of this endangered species at the southernmost part of their distribution.

2. Material and methods

2.1. Study area

The Gulf is a shallow (<100 m) semi-enclosed embayment located on the northeast coast of the Te Ika-ā-Māui North Island of NZ, near Tāmaki Makaurau Auckland (figure 1). The Gulf and its adjacent waters are highly productive, supporting diverse year-round communities of large marine species such as sharks, cetaceans and seabirds [17,18]. Over winter mixing and upwelling contribute to some of the highest primary productivity levels in coastal NZ waters [19,20]. It is suggested that this productivity persists through late spring and summer as stratification increases [20]. Zooplankton community structure shows marked seasonal variation, which influences prey availability and trophic interactions [21]. Localized summer increases in ocean temperature, increased stratification and intrusions of subtropical warmer waters from the East Auckland Current may influence seasonally occurring tropical species, including the oceanic manta ray, which are frequently observed in the outer Gulf and adjacent shelf [22,23]. Oceanic manta ray fine-scale movements were tracked within the Gulf (figure 1) and adjacent coastal shelf. We focused our analyses on locations in the coastal waters of the Gulf, excluding those north of 34.9° S where we expect mantas are initiating their migrations towards lower latitudes at the end of the season. The ocean in this area is mostly shallower than 100 m depth, and the nearby shelf north of 38° S is where manta rays typically occupy areas where the seafloor is shallower than 200 m, but occasionally venture to deeper shelf and slope waters [24].

2.2. Satellite tagging

The data used in our study were collected from 26 Wildlife Computers SPLASH10F-321A/E satellite tags deployed on adult and subadult oceanic manta rays between 2021 and 2024 (table 1). Manta ray sex was determined through the presence or absence of male reproductive organs (claspers). Mature males were categorized by the elongation and calcification of claspers, past the pelvic fin margin. Female maturity was determined by the presence of mating scars on the pectoral fins and/or evidence of pregnancy. Maturity was further inferred from visual estimations of body size, subadults having a disc width of 360 cm or less. Tags were attached to an 85 cm stainless steel tether with a titanium dart tip and deployed using a pole spear, anchoring the titanium dart tip into the dorsum of the animal in the muscle band between either the right or left pectoral and the central body cavity as described in [25]. Drones were used to guide the tagger in the water towards the feeding or cruising animal and continued to follow it post-tagging in order to document any behavioural responses. Tags recorded Fastloc GPS and Argos locations whenever the antennae breached the surface of the water. Tags were programmed for a 3–6 months deployment, with the aim of revealing oceanic manta movements in coastal NZ waters throughout the Austral summer (December–February) and autumn (March–May). Attempts were made to recover tags after they detached from the oceanic manta rays, though this was rarely feasible due to the majority of tags popping off in remote Pacific waters beyond our study area due to seasonal northward migration of the rays [14].

2.3. Horizontal movement data processing

Data processing and statistical analyses were carried out using the R programming language (version 4.2.2) [26]. Only Fastloc GPS location data were used in this study. GPS locations were pre-processed to remove unrealistic points by applying a speed filter of 5 ms^{-1} and excluding low-quality locations (from the LocSolve algorithm used to estimate the animal's location; Wildlife Computers). We also excluded locations where instrument clock errors were suspected based on snapshot time and downloaded RINEX files. After this filtering, only one location was mapped on land and was manually removed. Only tracks with 15 or more locations within the study region were retained for further analyses.

To be able to detect movement patterns typically associated with foraging, we fitted a time-varying move persistence state space model to the data using the 'fit_ssm' function from the 'aniMotum' R package [27]. This process regularized each track to regular 6 h time-steps between locations. This time step was chosen as a compromise between gaining insight into the fine-scale drivers of movements, while considering the limited number of locations for some tracks and avoiding overfitting. Portions of the regularized tracks located more than 10 km away from measured locations were excluded from

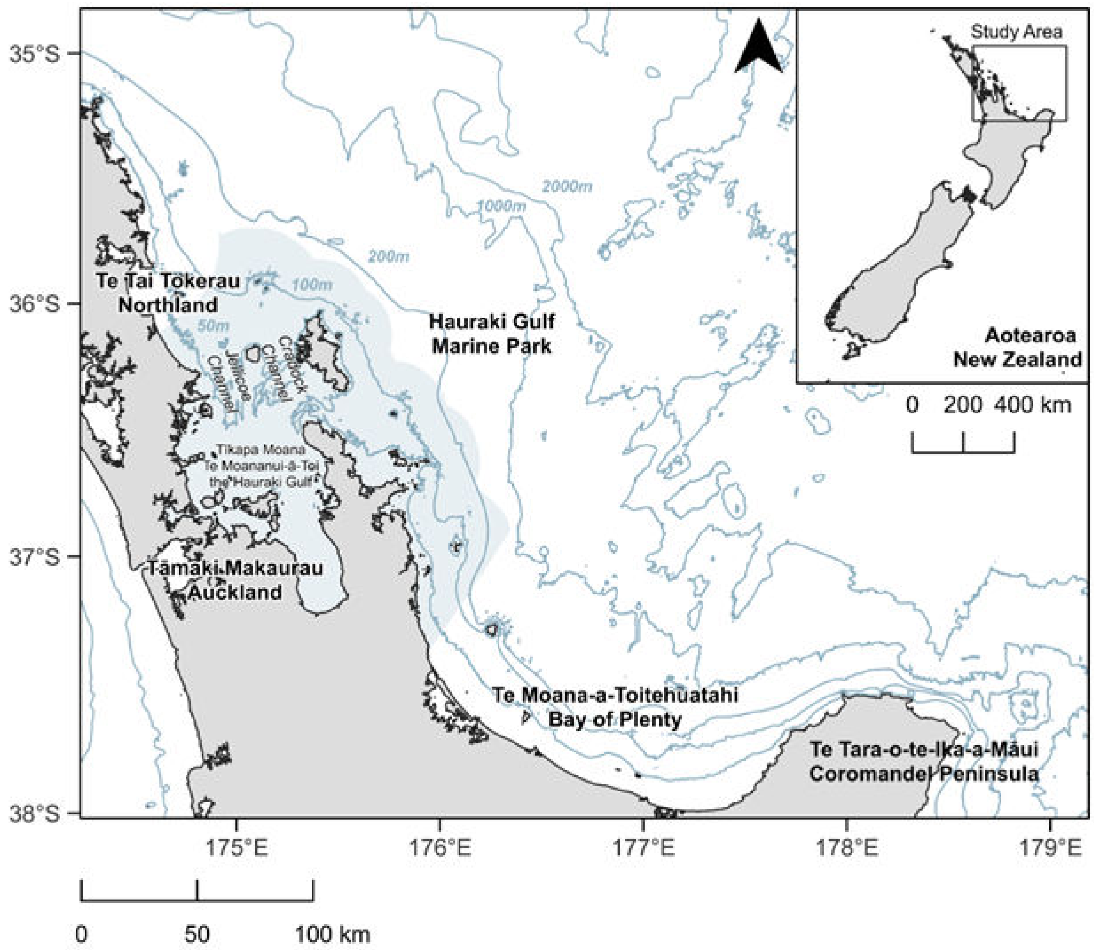

Figure 1. Map of the study region outlining key island groups/regions. Inset shows position in relation to Te Ika-ā-Maui North Island of Aotearoa, New Zealand. Isobaths are shown in blue. Blue shading indicates the Hauraki Gulf Marine Park.

further analyses. Paths were re-routed off land using a 1 km buffer using the 'pathroutr' package [28] integrated in the aniMotum package. Oceanic manta ray movement behaviour was characterized using move-persistence (γ_t) on a 6 h basis, a metric which provides a continuous scale from 0 to 1 where lower values represent area restricted search (ARS) behaviours, associated to with slower speeds and increased turning frequency (and expected to occur when animals are foraging intensively [29]), and higher values represent transiting behaviours involving faster, more directional movements. This was estimated from the rerouted tracks using the 'fit_mpm' function in 'aniMotum' with the joint move persistence model ('jmpm'). Tracks that could not be regularized (e.g. because of the sparsity of locations) or for which the estimate of the move persistence did not converge were excluded from the analysis.

Generalized additive mixed-effects models (GAMM; 'mgcv' package; function: 'bam'; family = betar [30]) were used to analyse oceanic manta ray behavioural response to environmental variables. GAMMs are non-parametric regression models that do not rely on a linear relationship between explanatory and explained variables, support non-normally distributed explained variables and allow the inclusion of random effects such as individual differences or tagging effects. This flexibility makes them a commonly used tool to investigate ecological relationships where nonlinearity is expected [31,32]. We modelled move-persistence (1-γ_t , 0-1, following a beta-regression distribution [33]) as the response variable. Temporal autocorrelation was assessed with an autocorrelation function ('afc'), and autocorrelation coefficients were estimated to be <0.05, so it was not included in the models. Manta identity was included as a random effect. As fixed effects, we considered environmental descriptors including sea surface temperature (SST), chlorophyll-*a*, diffuse attenuation coefficient at 490 nm (kd490; commonly used as an indicator for water clarity), bathymetry, hourly mean wind speed, direction and maximum gust, tidal phase, fraction of moon illuminated (at night), and solar

Table 1. Details of 16 satellite tag deployments on oceanic manta rays in Aotearoa, New Zealand. (A) 12 tags analysed for horizontal and vertical movements. (B) 4 tags analysed for vertical movements only. Bold indicates the three recovered tags that provided high-resolution data.

ID	tag type SPLASH 10 F-321	tag no.	sex	dw (m)	deployment date	tracking duration in study area (days)	total GPS locations in study region
(A) horizontal and vertical movements							
9	A	204511	M	3.6	10 Jan 2022	32	89
14	E	238014[a]	F	4.4	22 Jan 2023	22	34
16	**E**	238016	**M**	**4.3**	**22 Jan 2023**	**20**	**113**
17	E	238018[a]	F	4.4	22 Jan 2023	9	38
18	E	238019	M	4.2	22 Jan 2023	19	37
19	E	252520	F	4	27 Dec 2023	37	255
20	E	252522	F	4	27 Dec 2023	76	314
21	E	252524	F	3.5	27 Dec 2023	77	43
22	E	252525	M	4	27 Dec 2023	64	266
23	E	252526	F	4.5	19 Dec 2023	84	36
24	E	252528*	F	4	27 Dec 2023	76	462
25	E	252778	F	3.4	04 Jan 2024	45	293
(B) vertical data movements only							
5	**A**	**197235[a]**	**F**	**5.2**	**03 Feb 2021**	**31**	**14**
11	E	215016[a]	F	4.8	17 Feb 2022	12	2
15	E	238015	M	4.2	22 Jan 2023	11	31
26	**E**	**252779[a]**	**F**	**5**	**04 Jan 2024**	**40**	**14**

[a] Indicates pregnant manta rays. dw = estimate disc width (wingtip to wingtip). Number of GPS locations refers to those after cleaning of the data and only includes data from within the study area (figure 1). Despite having sufficient GPS locations ($n = 31$), the aniMotum package was unable to calculate move persistence for manta no. 15, suspected as a consequence of the animals' sporadic movements, including large data gaps relative to the prediction interval. Therefore, the data for this tag (238015) were only used for the vertical movement analyses.

angle (during the day; table 2). Correlations between environmental variables were assessed (Pearson correlation coefficient) and for each pair of variables correlating with each other, only one was retained. Correlations above 0.80 were found for mean wind speed and maximum hourly gust and between chlorophyll-*a* and kd490. While chlorophyll-*a* is a commonly used parameter to quantify phytoplankton stocks, because our study region encompasses coastal areas, where coloured dissolved organic matter may introduce bias, we chose kd490. Mean wind speed was chosen over maximum hourly gust speed as we expect it to have a stronger impact on the mixing properties of the near-surface ocean. Smooth functions parameterized using the fast restricted maximum likelihood (fREML) method. Regularized and rerouted location data were separated into two models—one for daytime observations ($n = 1047$), and one for nighttime observations ($n = 417$). In the day model, the altitude of the sun was included as a proxy for daylight. In the night model, the illuminated fraction of the moon was included as a proxy for moonlight intensity.

2.4. Vertical movement data processing

Diving data were analysed from the 12 tags used for the horizontal analysis, plus an additional 4 tags with an insufficient number of GPS locations (<15) for the horizontal analysis or for which the move persistence algorithm did not converge. Diving data were analysed differently based on whether a tag was recovered or not. Diving data from the 13 unrecovered tags only provided a summarized account of diving behaviours (data transmitted from the tag to the Argos satellite network) at a lower

Table 2. Environmental variables investigated for influence on oceanic manta ray foraging behaviour.

variable	temporal resolution	spatial resolution	description	source
bathymetry (outside the Hauraki Gulf, m)	—	15 arc-second interval	continuous global terrain model produced using gridded bathymetric data augmented to the SRTM15+ base grid; bathymetric data sets are developed by the four Seabed 2030 regional centres and largely based on multibeam data	GEBCO Compilation Group Grid [34]
bathymetry (within the Hauraki Gulf, m)	—	20 m	combination of multibeam, single beam acoustic surveys (offshore) and light detection and ranging (LiDAR; nearshore) measurements compiled by MetOcean for Waikato Regional Council and Auckland Council	MetOcean Auckland Council Waikato Regional Council [35]
Kd490 (m^{-1})	daily	4 km	diffuse attenuation coefficient of light at 490 nm	Copernicus Marine Service [36]
period (night/day)	—	—	time of day is identified based on times of Sunrise (top edge of the sun appears on the horizon) and Sunset (sun disappears below the horizon, evening civil twilight starts); extracted using the getSunlightTimes function.	*Suncalc* R package
solar altitude (°)	based on the precision of the location	based on the precision of the location	sun altitude above the horizon in radians, e.g. 0 at the horizon and 90° at the zenith (overhead)	*Suncalc* R package
fraction of moon illumination	daily	—	fraction of lunar illumination from 0 (new moon) to 1 (full moon)	*Suncalc* R package
sea surface temperature (°C)	hourly, aggregated to six hours	2 km		Himiwari-08 (2021/2022) and Himiwari-9 (from 2023) [37,38]
tide (rising/falling/slack)	minute	50 km	high tide times extracted from the NIWA Tide Forecaster Model; slack tide is identified as the period within 30 min on either side of high tide	NIWA Tide Forecaster Model
wind direction (°T)	hourly	measured from the nearest wind station	direction the wind is blowing from, measured over the 10 min preceding	Meteorological Service of New Zealand Ltd (Metservice)

(*Continued.*)

Table 2. (*Continued.*)

variable	temporal resolution	spatial resolution	description	source
			the observation time and in degrees clockwise from geographic north	
wind speed (ms^{-1})	hourly	measured from the nearest wind station	average wind speed recorded during the 10 min preceding the observation time	Meteorological Service of New Zealand Ltd (Metservice)

resolution due to bandwidth constraints. These were regularized to the coarsest temporal resolution of transmission (5 min) and classified into one of 4 depth groups (0–5 m, 5–50 m, 50–100 m, 100+ m). Dives were defined as beginning from 10 m depth to exclude surface behaviours and analysed as time-series using the 'diveMove' package [39]. Diving behaviour was first assessed by comparing the distribution of each depth group during the day and night using a Mann–Whitney *U* test.

By contrast, diving data from the three recovered satellite tags provided a full dataset of high-resolution (1–10 s) temperature and pressure measurements. For each dive metric, i.e. mean bottom depth (mean depth during the bottom phase of the dive; m), maximum depth (m), total dive time (s) and post-dive duration (the time spent at the surface following the dive; s), we fitted a GAMM model using the mgcv 'bam' function. Because diving metrics were expected to be highly skewed to short, shallow dives, GAMMs were fitted using functions of the tweedie family ('tw') [30]. Temporal autocorrelation was estimated using an autocorrelation function ('afc') and autocorrelation coefficients (ranging between 0.20 and 0.35) were included in the GAMMs with an autoregressive order 1 (AR(1)) structure. The explanatory variables included temperature (minimum recorded during dive) and solar altitude for day observations, or moon illumination for night observations. Manta identity was included as a random effect.

3. Results

3.1. Tagging results

Between February 2021 and January 2024, 26 SPLASH10F-321A/E satellite tags were deployed on oceanic manta rays in the study region. Tagged rays consisted of 17 females (range = 3.5–5.6 m in disc width (DW)), and 9 males (range = 3.4–5.5 m DW). Tag deployment durations ranged from 9 to 84 days within the study area—noting that, while in many cases the tag deployments continued after the manta ray left the study area and migrated north, our analyses are restricted to only those movements within the Gulf and nearby shelf.

Of the tags deployed, 12 transmitted sufficient (i.e. more than 15 valid locations) GPS locations for analysis of their horizontal movements. Despite having sufficient GPS locations ($n = 31$), the aniMotum package was unable to calculate move persistence for manta ray 15 (table 1). This was suspected to be a consequence of the large data gaps relative to the prediction interval in this animal's track. Sixteen tags transmitted concurrent GPS data and diving histograms, allowing us to assess their vertical movements (table 1).

3.2. Horizontal movements

Tracking data for the 12 tagged individuals with sufficient horizontal data were recorded between late December and March (2022–2024), after which the tags either released or the individuals travelled outside of the study area. The data were analysed for horizontal movements, providing 1980 GPS locations collected from transmission periods from 9 to 84 days (table 1). Individuals ranged in size from an estimated 3.4 to 4.4 m DW and comprised 8 adult females (3 of which were visually assessed as being pregnant at the time of tagging), and 4 males (2 adults, 2 subadults).

Tracks revealed broad variations in individual movements, mostly within the Hauraki Gulf Marine Park area and within the 200 m isobath (99% of locations; figure 2). More specifically, approximately 50% of locations were in the Jellicoe and Cradock Channels (figure 2). While manta rays 9, 17, 18 and 25 remained west of Te Tara-o-te-Ika a Māui, the Coromandel Peninsula, mainly within the Gulf region, the majority of manta rays travelled further south-east, along the Coromandel Peninsula. Manta ray 19 and 23 travelled further, into Te Moana-a-Toitehuatahi the Bay of Plenty, with #19 reaching the southernmost extent of tracked movement at 37.72° S, 177.4° E and manta ray 23 reaching the easternmost extent of tracked movement at 36.95° S, 179.02° E. Manta ray 24 travelled north, before returning south, and then travelling east. ARS behaviour was frequent in Jellicoe Channel and the northern sides of Te Hauturu-o-Toi Little Barrier Island and Aotea Great Barrier Island (electronic supplementary material, figure S1).

Environmental variables for the day and night GAMMs accounted for 26.8% and 42.6% of the deviance observed in move persistence, respectively (figures 3 and 4).

Both day and night models suggest that bathymetry ($p < 0.001$) was the most significant predictor of ARS behaviour, with estimated foraging activity increasing at shallower depths. For day observations: solar altitude ($p < 0.01$), wind direction ($p < 0.05$), wind speed ($p < 0.05$) and SST ($p < 0.05$) were also significant predictors. ARS activity increased during northerly winds and decreased when wind speeds exceeded 10 ms^{-1}. Foraging activity decreased at temperatures greater than 23°C. During the day, ARS behaviour was highest when the sun was at peak elevation and around 20° elevation. While solar altitude was significant in predicting ARS behaviour, as a consequence of the 6-hour-timestep selected for ssm analysis, there is a lack of observations distributed uniformly throughout the day. Therefore, this finding should be interpreted with caution.

For night observations, bathymetry ($p < 0.001$), wind speed ($p < 0.05$) and direction ($p < 0.05$) were significant, displaying patterns mostly similar to those detected during the day (figures 3 and 4), as well as moon illumination ($p < 0.001$) and kd490 ($p < 0.01$), indicating a decrease during periods of the new moon and increased ARS behaviour in clear waters (lower k490). Both models showed significant variation between individuals.

3.3. Vertical movements

Dive data from 16 tagged individuals revealed high occupancy of the top 5 m of the water column, punctuated by occasional excursions to deeper waters (maximum dive = 365 m; mean = 7.79 ± 14.86 s.d.). Manta rays displayed patterns of reverse diel vertical movements, spending a greater proportion of time in surface waters in the day (0–5 m; 70% compared to 52.0% at night) and undertaking more deep-dives during the night (figure 5), although this difference was not statistically significant.

The three recovered tags (numbers 5, 16 and 26) provided a full dataset of high temporal resolution data (10 s for number 5 and 1 s for numbers 16 and 26) of depth and ambient temperature. The average temperature recorded by oceanic manta ray 5 was 21.13°C ± 0.43 s.d. (range = 15.9–23.65°C), for manta ray 16 this was 20.89°C ± 1.09 s.d. (range = 13.7–26.7°C) and for manta ray 25 it was 21.6°C ± 0.88 s.d. (range = 14.2–24.85°C). Water temperatures decreased with depth (figure 6).

During the day, maximum depth (71.6% deviation explained), mean bottom depth (68.5% deviation explained) and longer dive duration (35.2% deviation explained) correlated with colder minimum temperatures and lower sun altitude (figure 6). For night observations, maximum depth (74.6% deviation explained), mean bottom depth (72.6% deviation explained) and dive duration (34.8% deviation explained) correlated with colder minimum temperatures, and peaked during the gibbous moon phase (figure 7). The models examining post-dive duration were only able to account for less than 10% of the deviance, suggesting that this metric is driven by variables that have not been considered in this analysis.

4. Discussion

Our study focuses on the movements of oceanic manta rays in the coastal waters of NZ, highlighting the value of telemetry in providing insights into movement patterns and foraging behaviour in relation to environmental variables at the southernmost extent of this species' range. Satellite tag data revealed fine-scale movements of oceanic manta rays in the Gulf and broader northeastern shelf, greatly advancing our understanding of this Endangered species [6], currently listed as data deficient

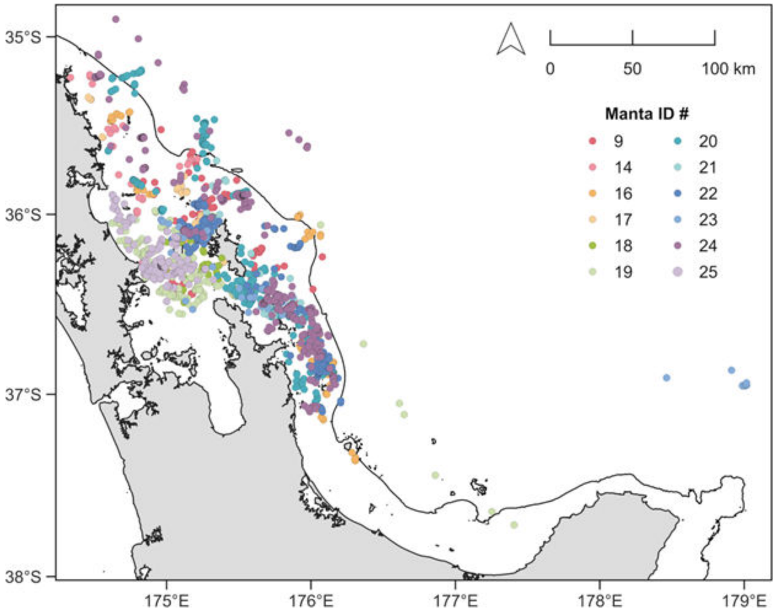

Figure 2. Quality-controlled filtered horizontal tracks of 12 oceanic manta rays tagged with SPLASH10F-321A/E tags in north-east Aotearoa, New Zealand. Points indicate Fastloc GPS positions. The solid dark line indicates the 200 m isobath.

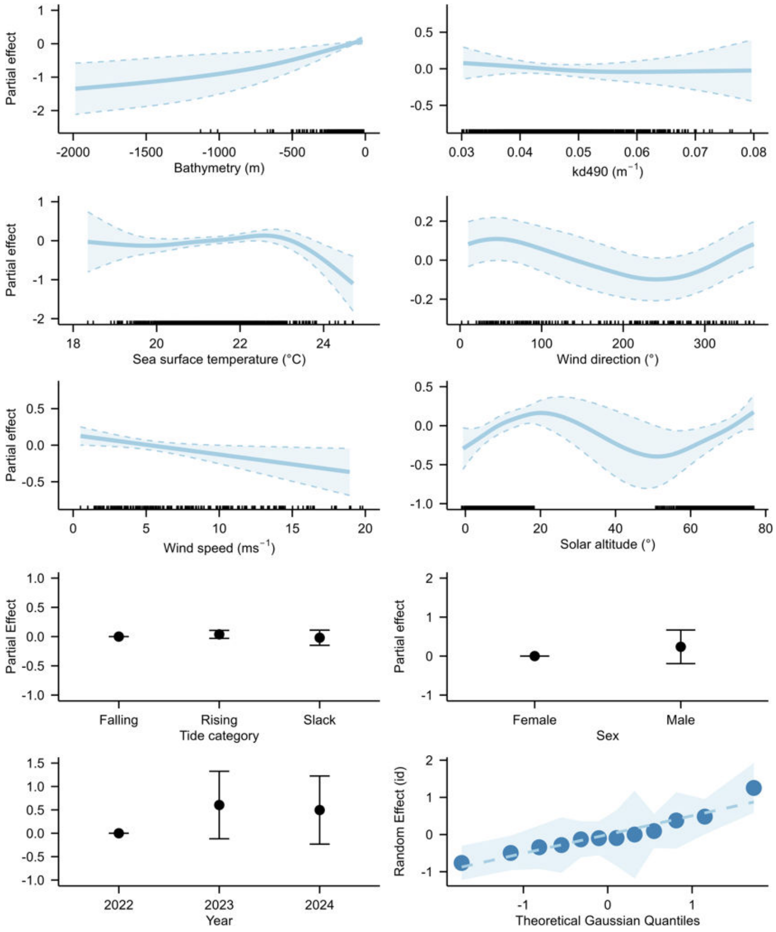

Figure 3. GAMM smooth, parametric and random effects predictors of oceanic manta ray area restricted search behaviour during the day. Solid lines and circles represent estimates, while shaded areas represent estimated standard errors. To aid visualization the *y*-axis scales differ between terms.

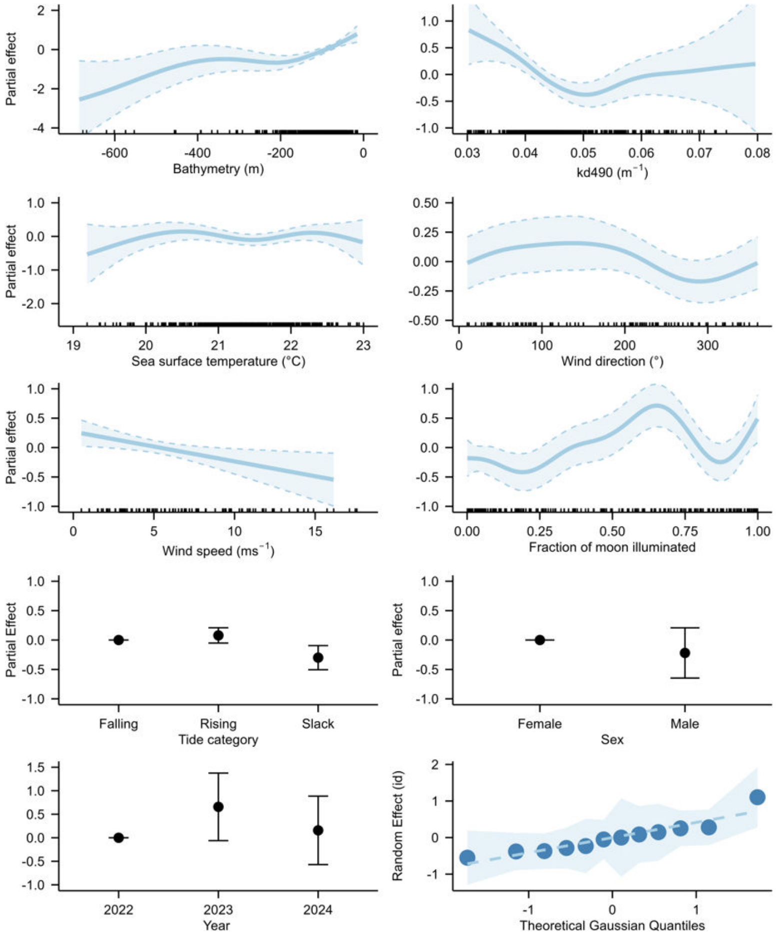

Figure 4. GAMM smooth, parametric and random effect predictors of oceanic manta ray area restricted search behaviour at night. Solid lines and circles represent estimates, while shaded areas represent estimated standard errors. To aid visualization the *y*-axis scales differ between terms.

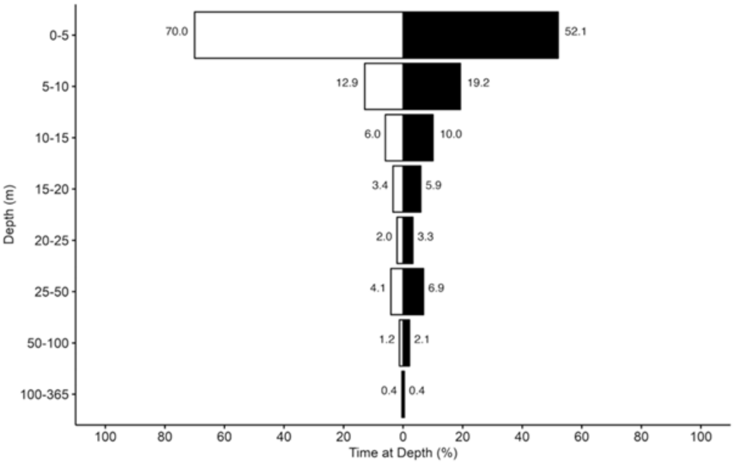

Figure 5. Proportion of time at depth for 16 oceanic manta rays tagged with SPLASH10F-321A/E tags. White bars indicate vertical habitat use during the day; black bars indicate vertical habitat use during the night. Analysis for figures calculates percentage based on the total recorded movements, excluding periods where data were not transmitted.

in NZ [15]. The fine-scale movement patterns support the current understanding that the distribution of manta rays in NZ is centred around the Gulf, information based largely on non-systematic photo-ID and encounter records [16]. We found that oceanic manta rays were predominantly confined within the 200 m isobath along the northeast shelf of NZ and that the majority of tagged individuals occurred

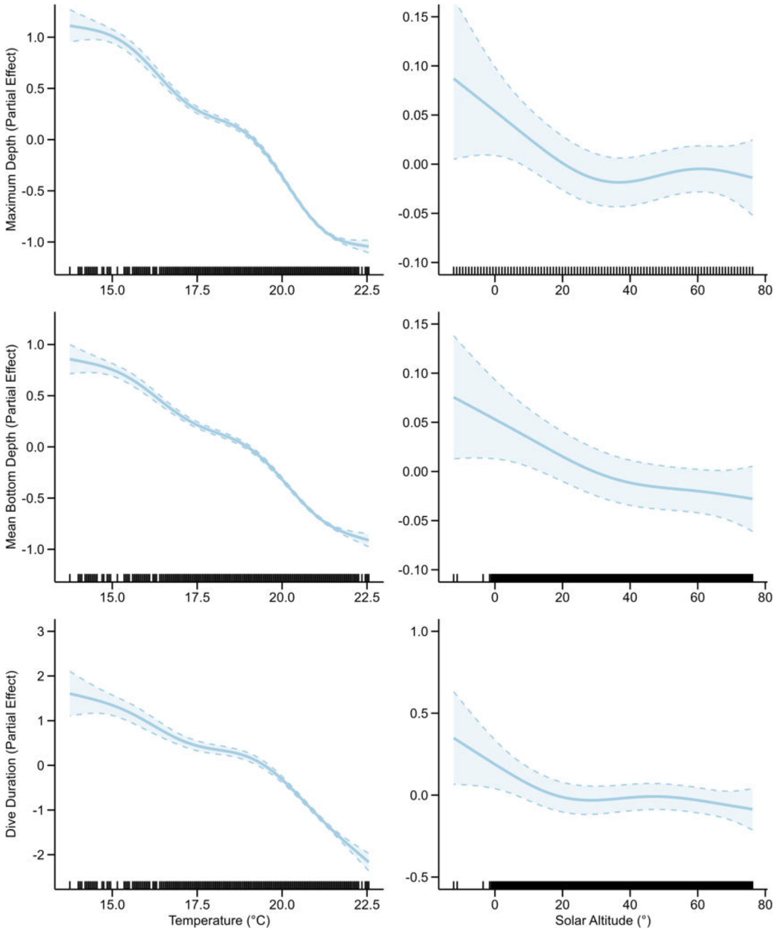

Figure 6. GAMM smooth terms of environmental predictors of three tagged oceanic manta ray diving behaviours during the day. Solid lines and circles represent estimates, while shaded areas represent estimated standard errors and bars. To aid visualization the *y*-axis scales differ between terms and all dive descriptors are log-transformed.

and displayed ARS behaviour at some point in Jellicoe and/or Cradock Channels, areas of known high zooplankton productivity [40]. Our findings align with those of Ozaki *et al.* [16], who also observed the significance of the 200 m isobath separating the spatial distributions of oceanic manta rays inshore and spinetail devil rays (*Mobula mobular*) offshore. Further research is needed to determine whether this is niche separation driven by inter-species competition or different prey preferences for the two species of mobulid ray.

4.1. Horizontal movements

During the day, movement patterns associated with foraging behaviours were more common during northerly winds. During summer, prevailing northerly and northeasterly winds drive intrusions of oceanic water south through Jellicoe Channel and contribute to sediment transport through Cradock Channel [24,40]. These intrusions of warmer, oligotrophic East Auckland Current waters may allow oceanic manta rays to inhabit warmer waters while capitalizing on the higher productivity within the Gulf. Assumed foraging behaviours decreased significantly at wind speeds of greater than 10 ms^{-1} possibly due to disruption of prey patches.

Oceanic manta rays were only present in the Gulf from late spring to early autumn, in association with the increased influence of the warm East Auckland Current and localized heating. Consequently, environmental conditions remained relatively stable during this time—95% of SST observations were between 19.5°C and 23.4°C. Assumed foraging activity decreased at SST temperatures greater than 23°C, when observations coincided with movement away from NZ waters.

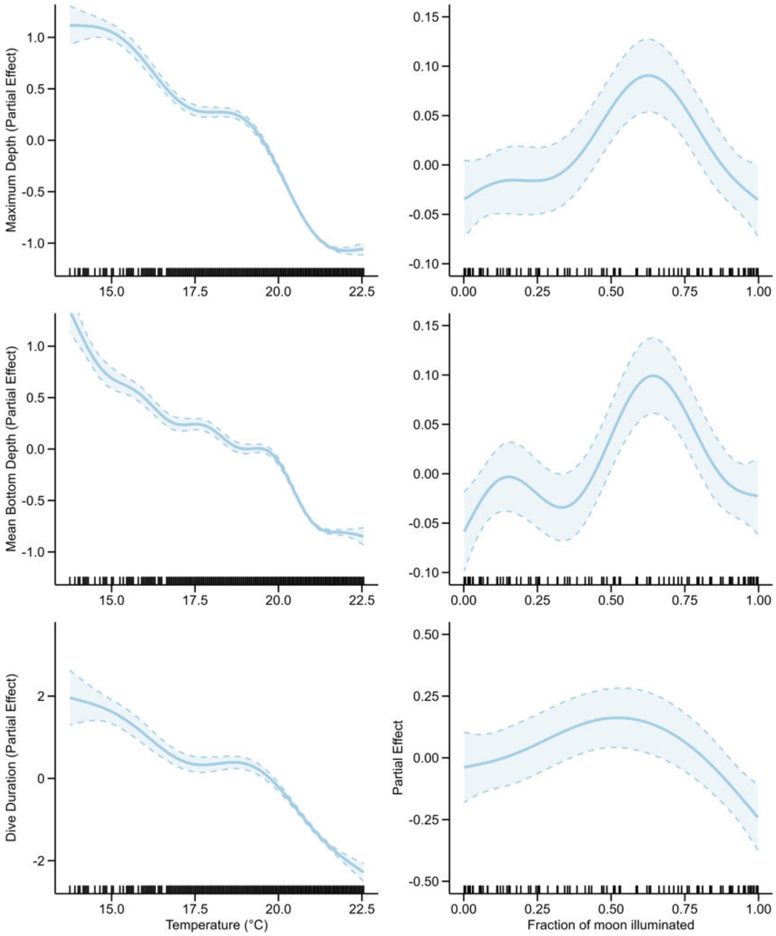

Figure 7. GAMM smooth terms of environmental predictors of three tagged oceanic manta ray diving behaviours during the night. Solid lines and circles represent estimates, while shaded areas represent estimated standard errors and bars. To aid visualization the *y*-axis scales differ between terms and all dive descriptors are log-transformed.

4.2. Vertical movements

Oceanic manta ray diving behaviour in the Gulf was consistent with findings from other regions [8], where manta rays displayed a preference for surface waters (<5 m) with occasional deeper dives. As expected, deeper dives were correlated with colder temperatures, and vertical movements of manta rays exposed them to greater variability in temperature, from a minimum of 13.7°C to maximum of 26.5°C. However, temperature did not limit dive depth or duration and was a poor predictor of post-dive duration. This suggests that oceanic manta rays may not need to spend time basking at the surface to rewarm, as has been described for other planktivorous elasmobranchs which undergo deep dives (e.g. [41]). Oceanic manta rays can dive much deeper than was recorded in this study, experiencing far colder temperatures. During their migrations from NZ to the Pacific Islands, tagged individuals have recorded dives of up to 1376 m, encountering temperatures as low as 3.9°C [14]. During the day, oceanic manta rays tended to undertake longer, deeper dives when the solar altitude was lower, corresponding to dusk and dawn periods. Shifts in diving patterns around dusk and dawn have been observed in plankton-feeding Bryde's whales (*Balaenoptera edeni brydei*) in the Gulf [42] and might be in response to zooplankton movements and aggregation patterns [43,44]. At night, dives were shorter and shallower during the new moon phase, peaking during the gibbous moon. The new moon is linked to increased abundances of zooplankton in surface waters [45] and to the decreased emergence of demersal zooplankton in Puerto Rico, Australia and the Gulf of California [46,47]. If oceanic manta rays in the Gulf are targeting demersal species, it may not be energetically profitable for them to dive during the new moon; instead, they may opt to forage on surface zooplankton during this part of the lunar cycle.

4.3. Relationships between prey and the environment

A key factor hindering our understanding of oceanic manta ray foraging behaviour is the limited knowledge about the distribution and dynamics of their prey. While oceanic manta rays have been observed in the Gulf feeding on zooplankton (*Nyctiphanes* spp.) during the day, their additional preferred prey species remain unknown (L.G. 2025, unpublished data). Prey plasticity in oceanic manta rays and other mobulids is well-known in other regions (e.g. [9,10]) and could be determined using methods such as isotope analysis or camera tags. Zooplankton assemblages in the Gulf are diverse and vary spatially and seasonally, with a number of large planktivores having preferred prey (e.g. Bryde's whales [21]). We have observed oceanic manta rays foraging on zooplankton in proximity to Bryde's whales and being displaced by the whales, suggesting there may be interspecies competition in the nearshore Gulf waters (L.G. 2025, unpublished data). Prey availability is a strong year-round predictor for the distribution of several shark and cetacean species in the Gulf, especially in the later summer months [18], so this may also hold true for oceanic manta rays. Without knowing the oceanic manta ray prey preferences in NZ waters, we cannot predict the effect of shifts in prey distribution in response to environmental change—a common 'missing link' in marine ecological studies which can be highly valuable when included. Future work should focus on coupled measurements of prey and environmental variables in areas where manta rays are feeding. This will clarify the mechanisms underpinning the links between manta ray distribution, habitat use, behaviour and their environment.

5. Conclusion

This research is the first tracking study of oceanic manta rays in NZ, highlighting the importance of the Gulf habitat during the Austral summer to autumn months. There was strong variability in oceanic manta ray movement patterns, with almost all satellite-derived locations occurring within the 200 m isobath. Daytime assumed foraging occurred more frequently with northerly winds and was hindered by strong wind velocities. Diving patterns reveal that, when in the Gulf, oceanic manta rays mostly occupy the near surface during the day and dive deeper at night, suggesting the potential for foraging on different species at different times of the day or a movement of their prey following the reverse diel migration. Future studies are needed to clarify what oceanic manta rays feed on in the study region, how their prey is distributed, and how prey and predators respond to environmental change.

Ethics. All tagging and drone procedures were conducted under Wildlife Act 1953 permit 96119-FAU issued by the New Zealand Department of Conservation, the University of Auckland Animal Ethics Committee approval AEC23490 and NZ Department of Conservation Animal Ethics Committee approvals AEC-377 and AEC-426, Department of Conservation after consultation with mana whenua (Māori, the Indigenous people of the region). The authors of this work recognize the rights of Indigenous peoples to make decisions about the future use of information, biological collections, data and digital sequence information that derives from associated lands, waters and territories. To support the practice of proper and appropriate acknowledgement into the future of these rights, we request that those seeking to reuse these data contact L.G. (lydia.green@mantatrust.org) ahead of use and publication.

Data accessibility. The tracking data used in this study can be accessed through https://doi.org/10.17608/k6.auckland.28774631.v1 (horizontal data), https://doi.org/10.17608/k6.auckland.28836848.v1 (vertical recovered data) and https://doi.org/10.17608/k6.auckland.28774634.v1 (vertical unrecovered data). The authors of this work recognize the rights of Indigenous peoples to make decisions about the future use of information, biological collections, data and digital sequence information that derives from associated lands, waters and territories. To support the practice of proper and appropriate acknowledgement into the future of these rights, we request that those seeking to reuse the tracking data from this study contact L.G. (lydia.green@mantatrust.org) ahead of use and publication.

Himawari-8 and Himawari-9 satellite data can be accessed through the GHRSST NOAA/STAR online portal [48,49]. Large-scale bathymetric data can be downloaded from GEBCO (https://www.gebco.net) [50]. Diffuse light attenuation coefficients can be obtained from the Copernicus Marine Service (CMEMS) (https://doi.org/10.48670/moi-00281). Tide data can be extracted from the NIWA Tide Forecaster model: https://niwa.co.nz/coasts/tide-forecaster. High-resolution bathymetric data for the Hauraki Gulf Marine Park and local wind data extracted at the locations of interest can be found on https://doi.org/10.17608/k6.auckland.28786052.v1. The R code developed to analyse these datasets can be found on GitHub at https://github.com/AliceDellaPenna/MantasNZ.

Supplementary material is available online [51].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. T.M.C.: conceptualization, data curation, formal analysis, investigation, visualization, writing— original draft, writing—review and editing; L.G.: conceptualization, investigation, supervision, writing—review and editing; E.S.: conceptualization, investigation, supervision, writing—review and editing;

M.E.: conceptualization, funding acquisition, investigation, supervision, writing—review and editing; C.A.J.D.: conceptualization, funding acquisition, writing—review and editing; R.C.: conceptualization, funding acquisition, supervision, visualization, writing—original draft, writing—review and editing; A.D.P.: conceptualization, data curation, formal analysis, funding acquisition, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This research was generously funded by MAC3 Impact Philanthropies, Daniel Roozen, Audrey and Shannon Wong and Save the Blue Foundation, Live Ocean Foundation, Wolcott Henry Foundation, Katrine Bosley, Barry and Fiona Gray, Marie-Elizabeth Mali and the Wolcott Henry Foundation. T.M.S. was supported by a University of Auckland Research Master's Scholarship, and L.G. was supported by Live Ocean Foundation, Pub Charity and Lion's Foundation.

Acknowledgements. We thank mana whenua (local Māori) who supported our work: Ngāti Manuhiri, Ngāti Rehua Ngātiwai ki Aotea, Ngātiwai and the Tuhua Trust Board. Thanks to Alexandre Lhériau-Nice (University of Auckland), Neal Osborne (Meteorological Service), Sarah Gardiner (MetOcean), Kevin Lay (Wildlife Computers) and Karen Middlemiss (Department of Conservation) for technical assistance. Many thanks to the following for fieldwork assistance: Rikako Ozaki, Scott and Sue Tindale and the Tindale Marine Research Charitable Trust, Schannel van Dijken, Kina Scollay, Irene van der Ven, Richard Robinson, Leo Panganiban, Melissa White and SeaKeepers, David and Janet Wyeth, James and Johanna Klein, Shane and Julia Riddle and Northland Dive. The authors are grateful to all data providers including the Copernicus Marine Service, the National Centers for Environmental Information from the National Oceanic and Atmospheric Administration (NOAA, U.S.A.), the National Institute of Water and Atmospheric Research (NIWA, New Zealand), MetService and MetOcean Solutions (New Zealand), Waikato Regional Council and Auckland Council (New Zealand) and the GEBCO programme. We thank the two anonymous reviewers whose feedback improved the quality of our manuscript.

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