POP2020-05

Utilisation of the marine habitat of hoiho/yellow-eyed penguins from Rakiura/Stewart Island

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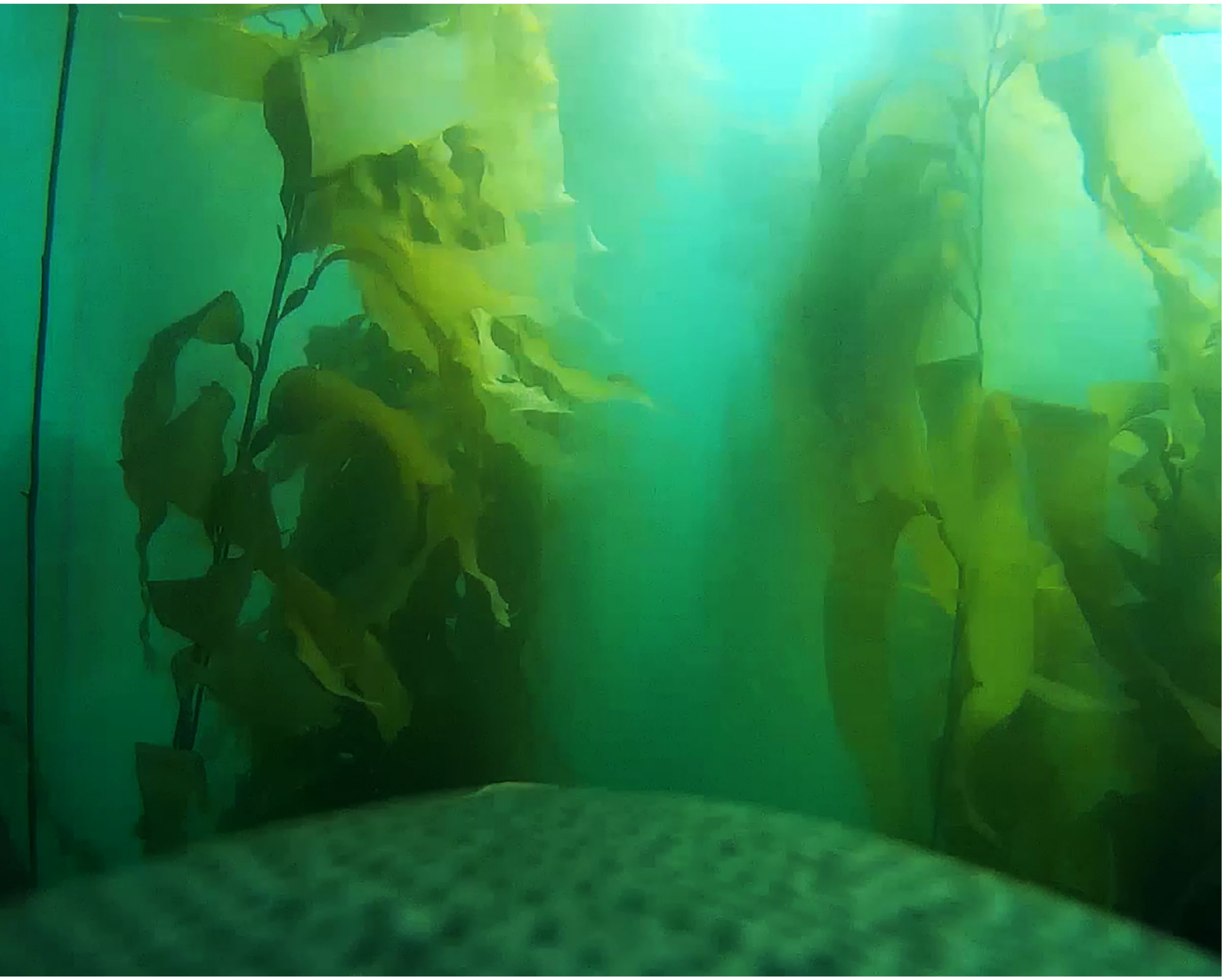

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Executive summary

Between November 2020 and July 2021, foraging of hoiho/yellow-eyed penguins from three different breeding locations on and around Rakiura/Stewart Island was studied using GPS dive loggers, satellite trackers, and animal-borne cameras to establish the penguins' utilisation of their local marine habitats. The sites ranged from southern Rakiura (Port Pegasus/Pikihatiti), the Bravo Island Group in Paterson Inlet/Whaka a Te Wera, to Whenua Hou/Codfish Island where penguins have access to the Foveaux Strait. At the former two sites, penguins were tracked during the early chick rearing phase (chick-guard, November & December 2020), whereas two visits to Whenua Hou ensured that tracking data was recorded during late chick rearing (post-guard, January 2021) as well as the non-breeding period in winter (July 2021).

We tracked seven breeding hoiho from the four nests remaining active at Pigeon House East/Port Pegasus. All penguins consistently foraged in a well-defined area <5 km from their breeding sites, foraging primarily over sandy seafloor at depths of around 80 m.

Work on the Bravo Is. Group/Paterson Inlet focussed on Groper Island, where all six breeding adult penguins were tracked. Except for one bird, all penguins foraged exclusively within the inlet focussing their prey searching efforts on near shore habitat, some of them foraging in extremely shallow water (<2 m). One of the tracked penguins foraged in a group of up to three other hoiho in Big Glory Bay, whereas its mate left the inlet to forage in bays along Rakiura's northeast coast. Comparison with the preliminary tracking data from our 2019 pilot study revealed remarkably consistent individual foraging preferences within and across years.

On Whenua Hou, six breeding hoiho were GPS tracked during the post-guard stage; an additional five penguins were fitted with satellite transmitters during the non-breeding period. Regardless of time of year, the penguins foraged primarily to the north of Whenua Hou in areas previously determined to be important hoiho foraging habitat in 2005. Two individuals foraged south of the island. Again, individual foraging preferences remained remarkably consistent and, hence, easy to predict.

With most of the terrestrial threats the species faces on the New Zealand mainland virtually absent on Rakiura, the impact of fisheries is likely the most important factor besides climate change contributing to population declines. Set net fisheries, which unlike on the mainland are allowed to operate directly inshore are the greatest threat for Rakiura hoiho.

This study provides decision makers with the information required to adequately address this issue and, thus, follow the strategies outlined in Te Kaweka Takohaka mō te Hoiho.

Introduction

Background/context

The mainland population of hoiho/Yellow-eyed penguin (*Megadyptes antipodes*) has been undergoing a significant decline since the late 1990s with future projections indicating functional extinction of the species outside of the subantarctic region within the next 20 years (Mattern et al., 2017). The study established increasing sea surface temperatures as an important driver for hoiho population trends, but also stresses that this only explained about a third of the observed variation in penguin numbers. The importance of factors not related to climate change is highlighted, particularly fisheries interactions, pollution, disease outbreaks, predators, as well as human disturbance impacts. However, neither of these factors are easy to include in models due to a lack or inaccessibility of relevant and detailed data, making it difficult to assess their exact contribution to the hoiho's demise.

Fisheries impacts have been repeatedly highlighted as having a significant effect on penguin survival and population trajectories, especially in species that live and breed in the vicinity of humans (Trathan et al., 2015; Crawford et al., 2017). For hoiho, several studies have pointed out the potentially crucial impact fisheries interactions have on the species' survival on the New Zealand mainland and Rakiura/Stewart Island. Incidental bycatch in set net operations directly affects the survival of juvenile and adult birds (Darby & Dawson, 2000; Crawford et al., 2017). In addition, modification of the species' foraging habitats at the seafloor by bottom trawling or dredging contributes indirectly via alteration of hoiho prey diversity and abundance (Mattern et al., 2005, 2013; Mattern, Ellenberg & Davis, 2007; Browne et al., 2011; Ellenberg & Mattern, 2012; Mattern & Ellenberg, 2018).

Development of mitigation measures that reduce the impact of fisheries on hoiho are reliant on solid knowledge of their utilisation of the marine habitat. Most hoiho tracking studies in the past decades were conducted opportunistically and were spatially as well as temporally limited (e.g. Moore et al., 1995; Mattern et al., 2007, 2013, 2018). Moreover, these studies indicated substantial regional differences in hoiho foraging behaviour so that extrapolation of results to the entire mainland population provided an inadequate representation of the species' actual habitat use (Mattern, 2020a).

Consequently, a comprehensive tracking study of hoiho across their mainland range was conducted between 2018 and 2020 (Mattern & Ellenberg, 2021). However, while this study indeed managed to fill many data gaps in our knowledge of the habitat use of hoiho, logistic constraints meant that the Foveaux Strait region and Rakiura, which still represents one of the mainland strongholds for the species (Webster, 2018), was not properly covered. A pilot study on a few penguins breeding on the Bravo Island group located in Paterson Inlet (Mattern & Young, 2019) highlighted that Rakiura may indeed represent a safe haven for the species, as many of the mainland threats (pollution, introduced predators, human disturbance) were of little to no relevance for the penguins breeding on and around the island.

Along most of the mainland's hoiho distributional range, set netting restrictions to reduce Hector's dolphin bycatch also reduce potentially harmful interactions of the fisheries and penguins within four-nautical miles from the coast. While the current set netting restriction have only limited benefits for mainland hoiho (Mattern & Ellenberg, 2021), even these limited benefits do not apply around Rakiura as all the islands in the Foveaux Strait are exempt from the set net restrictions, i.e. nets can be set immediately inshore at important penguin landing sites. Compared to the mainland, fisheries impacts are likely to have the greatest impact on Rakiura hoiho numbers. Hence, gaining a better understanding of the at-sea distribution of hoiho around Rakiura is essential to be able to limit fishing impacts and maintain the region as a potential sanctuary for mainland hoiho.

Objectives

Gain an overview of the marine habitat use by hoiho around Rakiura by studying penguin foraging with various tracking methodologies. Working with birds from different areas provides an indication about the variability of their at-sea behaviour in relation to local conditions (e.g., topography, bathymetry) and help the identification of areas with high hoiho occurrence where set net impacts are likely to be greatest. Obtain tracking information during different life-stages of the species to assess variability of foraging ranges and behaviour and at-sea distribution throughout the annual cycle. Focus on chick-rearing and post-moult (i.e., winter) as previous studies indicated greatest variability in penguin behaviour between these two stages (Moore, 1999; Mattern & Ellenberg, 2021).

Methods

GPS dive loggers

For the chick-rearing tracking studies (i.e., chick-guard and post guard stage), Axy-Trek Marine (TechnoSmart, Italy) GPS dive loggers (40 x 15 x 60 mm, 35 g: Figure 1) equipped with 2000 mAh batteries were used to determine foraging movements and diving behaviour in hoiho.

Figure 1. *TechnoSmart Axy-Trek Marine GPS dive loggers used in this study; SD card shown for scale.*

All devices were programmed to record GPS fixes every 1.5 minutes and sample water depth at 1 second intervals (1 Hz). Devices would fall back to a 15-minute GPS routine when birds were inactive, e.g., on the nest, triggered by an accelerometer incorporated in the devices.

Using these settings, battery life for each deployment ranged between 5-10 days. Hence, recovery attempts of devices commenced 5-7 days after deployment. Because of the archival, non-transmitting nature of GPS loggers, the units had to be recovered to access data; device loss also resulted in data loss.

Satellite transmitters

SPOT-275 satellite transmitters (Wildlife Computers, USA; W x H x L: 17 mm x 20 mm x 86 mm, weight: 40 g; Figure 2) were used in combination with an Axy4 TDR (TechnoSmart, Italy; dimensions 15 mm x 9 mm x 34 mm, weight: 7 g; see also Figure 1) to track hoiho from

Whenua Hou/Codfish Island during the winter period. The transmitters operate through the ARGOS satellite network and were programmed to broadcast their location 30 times per hour.

Satellite transmitters were chosen over GPS dive loggers to overcome the unpredictable landing times and locations of tracked birds in the non-breeding season and guarantee availability of data even if the device could not be recovered.

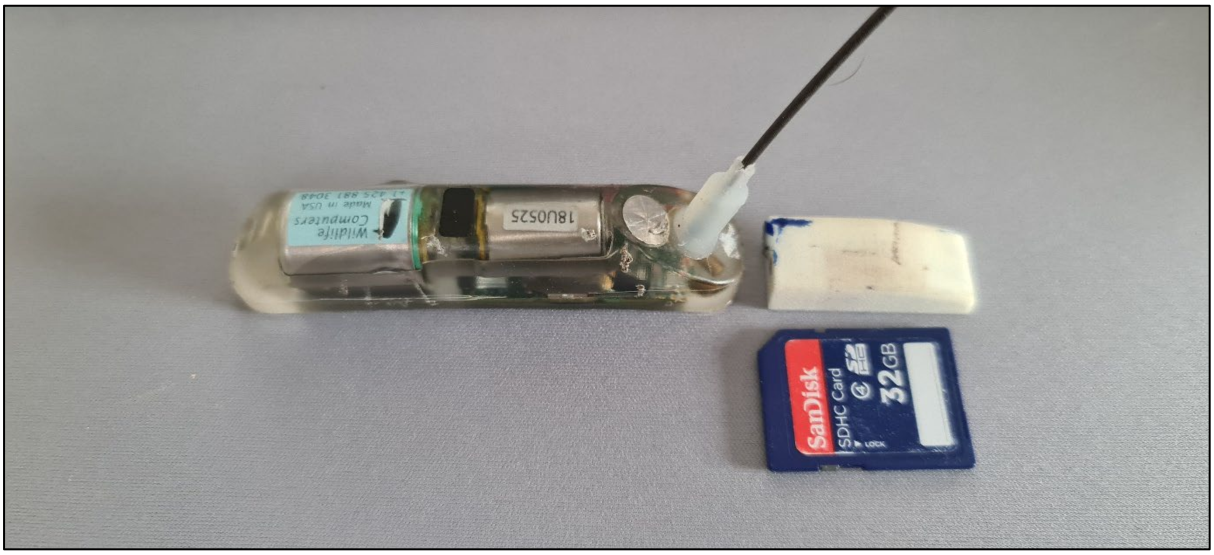


Figure 2. *Wildlife Computers SPOT-275 satellite transmitter (left) and TechnoSmart Axy4 dive logger (right) that were deployed in combination to study hoiho foraging and dive behaviour in winter 2021; SD card shown for scale.*

Camera loggers

To get insights into the penguins' feeding habits, i.e., prey composition, pursuit behaviour and prey capture rates, novel animal-borne camera loggers (PenguCam, Eudyptes Ltd, New Zealand; dimensions W x H x L: 35mm x 20 mm x 85 mm, weight: 85 g; Figure 3) were deployed at all sites. These devices record continuous full HD video footage and have an operating time of 2-3 hours. Camera deployments were only conducted when short foraging trips were predictable (i.e., during chick-rearing stages) so that the units could be recovered after a single foraging trip. The devices are equipped with a salt-water switch that triggers a pre-programmable delayed start of the video recording, allowing it to focus on the penguins' active foraging period. Devices were set-up to start recording four hours after the penguin had entered the water when penguins were expected to have reached their main foraging destinations.

Cameras were deployed in conjunction with GPS dive loggers, so that foraging tracks and dive data were recorded as well.

While cameras were recovered after one foraging trip, GPS dive loggers remained on the penguins for 5-7 days. Detailed analysis of the camera data has been undertaken as part of a Master's thesis at the Department of Zoology, University of Otago (Elley, 2022). In this report, only preliminary results of this part of the study are presented.

Figure 3. *Eudyptes PenguCam animal-borne camera logger deployed on some hoiho during this project. SD card shown for scale.*

Device attachment

All devices were attached using the well-established "Tesa-tape" method (Wilson et al., 1997) which uses adhesive tape threaded under rows of feathers and then wrapped around the device. Additionally, a thin layer of rubber-based glue was applied to the top side of the device to prevent the ends of the tape to loosen over time. This method is fully reversible and does not cause damage to the plumage when devices are recovered (Figure 4).

As hoiho in the past have shown a habit of preening off devices, the loggers were additionally secured using cable ties. To that end, a cable tie was threaded under the base of the device after attaching it to the bird's plumage with tape, looped around the unit, and then tightened using a cable tie gun, which also ensured that the protruding end of the cable tie was cut off cleanly at the tie fastener. Apart from the camera logger, all devices were attached to the birds' lower backs so that the units would sit behind the penguin's arched back which significantly reduces drag (Bannasch, Wilson & Culik, 1994) (Figure 4).

Figure 4. *AxyTrek GPS dive logger attached with tape and a cable tie to a hoiho (left) and state of plumage after recovery of the device five days of deployment. Pigeon House East, Port Pegasus, Rakiura, 30 November and 5 December 2020.*

The same tape/cable tie method was used to deploy a combination of camera and GPS loggers. The two units were attached individually so that the camera sat directly in front of the GPS logger (Figure 5).

Figure 5. *Combination of PenguCam video camera and AxyTrek GPS dive logger attached with tape to the lower back of a penguin (left) and after recovery of the camera the day after initial deployment. Groper Island, Bravo Group, Rakiura, 14 & 15 December 2020.*

Satellite transmitters and TDRs were also attached using tape. However, unlike the camera-GPS logger combination, satellite transmitter and TDR were attached as a single unit (Figure 6).

Figure 6. *Combination of Satellite transmitter and Axy4 TDR attached with tape to the lower back of a penguin (left) and after recovery (right). Whenua Hou/Codfish Island, 2 & 7 July 2021.*

Animal Ethics statement

All manipulations described above were approved by the Department of Conservation's Animal Ethics Committee, AEC reference numbers (AEC 336, AEC389).

Study sites, timing & number of deployments

At Port Pegasus (southern Rakiura, Figure 7), water depths off the coast swiftly drop to >100 m while the port region itself features water depths <50 m. Both areas were accessible to the penguins, which raised the question whether the birds as benthic foragers prefer the shallower Port habitat over the deeper offshore waters. Only four active nests were available for us to work with. Deployments were carried out on seven of the eight breeding adults between 25 November and 7 December 2020.

Paterson Inlet is rather shallow with water depths not exceeding 25m. On the Bravo Group of Islands, only Groper Island featured more than a single breeding pair of hoiho. The work was carried out with the six breeding adults (three nests) from this island. Device deployments were conducted between 10 and 20 December 2020.

Whenua Hou, the site with direct access to Foveaux Strait (water depth: 20-50 m) was selected as third study site after the number of breeding hoiho along the north-eastern coast of Rakiura proved to be too limiting for this project. Moreover, historic tracking data exists for this site allowing a comparison of current with past penguin behaviour (Ellenberg & Mattern, 2012). Two trips were conducted to Whenua Hou, one in January 2021 (7.-19.) to deploy cameras and GPS loggers during the post-guard stage of breeding, and another trip in July 2021 (1.-15.) to study winter foraging movements using satellite transmitters.

Table 1. *Study sites of the Rakiura hoiho tracking study conducted between November 2020 and July 2021.*

Region	Site	Stage*	Deployments
Port Pegasus *Pikihatiti*	Pigeon House East *-47.226197, 167.654534*	CG	4x CAM/GPS 3x GPS
Paterson Inlet *Whaka a Te Wera*	Groper Island, Bravo Group *-46.953303, 168.145895*	CG	4x CAM/GPS 2x GPS
Codfish Island *Whenua Hou*	Sealers Bay *-46.766901, 167.649222*	PG, WI	3x CAM/GPS 3x GPS 5x SAT/TDR

** CG – Chick-guard, PG – Post-guard, WI – winter*

Figure 7. *Rakiura/Stewart Island and the Foveaux Strait region. Overview of the study sites, timing, and number of device deployments on hoiho.*

Data handling & analysis

Processed GPS and satellite data have been uploaded to the Movebank tracking data repository (Movebank ID: 1594883659 , URL: https://bit.ly/hoiho-rakiura-2020-21).

Dive data was analysed using custom scripts programmed in Matlab (Mathworks, Inc., USA). Dive events were identified and dive phases determined following methods outlined in Mattern et al. (2007). Main dive parameters determined were

- **surface time**, time spent at the sea surface prior to each dive
- **dive time**, time spent underwater before resurfacing
- **descent duration**, time spent descending to depth from the surface
- **bottom time**, time spent after the descent and before ascending again
- **bottom start depth**, depth at which the bottom phase started
- **bottom end depth**, depth at which bottom phase ended
- **max dive depth**, dive depth reached during each dive
- **ascent duration**, time spent ascending back to the surface after conclusion of bottom phase
- **diving efficiency**, ratio of dive time to duration of a full dive cycle, i.e. dive time / (surface time + dive time)
- **foraging effort**, ratio of bottom time to duration of full dive cycle, i.e. bottom time/ (surface time + dive time)
- **benthic dive**, binary parameter indicating if the dive was pelagic (0) or benthic (1)

The benthic dive parameter is an important metric in hoiho due to their predominantly benthic foraging strategy (Mattern et al., 2007). Benthic dives were identified by their characteristic dive profile, which resembles a square wave with a linear descent, followed by a bottom phase with little to no vertical undulations, and concluded by a linear ascent. Benthic dives often occur in sequences during which the penguin reaches similar depths of previous dives; sequences of pelagic dives generally vary in the maximum depth reached.

See also monthly report for April 2020 for further details about the dive analysis process (DOI: https://doi.org/10.6084/m9.figshare.12203168).

Results & Discussion

Compared to the previous project (POP2018-02), which was hampered by extremely poor breeding seasons in 2018/19 and 2019/20 with plenty of nest failures resulting in device loss (Mattern & Ellenberg, 2021), the Rakiura study presented here has been highly successful. Of the 24 deployments, all but one bird fitted with satellite transmitter could be recaptured, resulting in 24 spatial and 23 dive data sets.

GPS dive loggers remained on the birds for 5.9±1.6 days (mean±standard deviation; range: 4-10 days), yielding GPS and dive data representing between 27 and 33 foraging trips at the different study sites (Table 2). Foraging trip lengths seldom exceeded 10 hours in guard-stage hoiho from Pigeon House and Groper Island, with many pairs alternating nest attendance around midday so that both parents were able to forage on the same day. This never occurred on Whenua Hou where trip durations averaged nearly 16 hours.

A total of 8,706 at-sea locations were recorded by the GPS loggers at all three sites (Figure 8). On average the devices recorded 45.0±15.7 GPS fixes per hour which allowed to determine accurate geographic locations for nearly half of the recorded dive events (fix rate per dive event: 0.46±0.1, range: 0.07-0.88, n=24 birds).

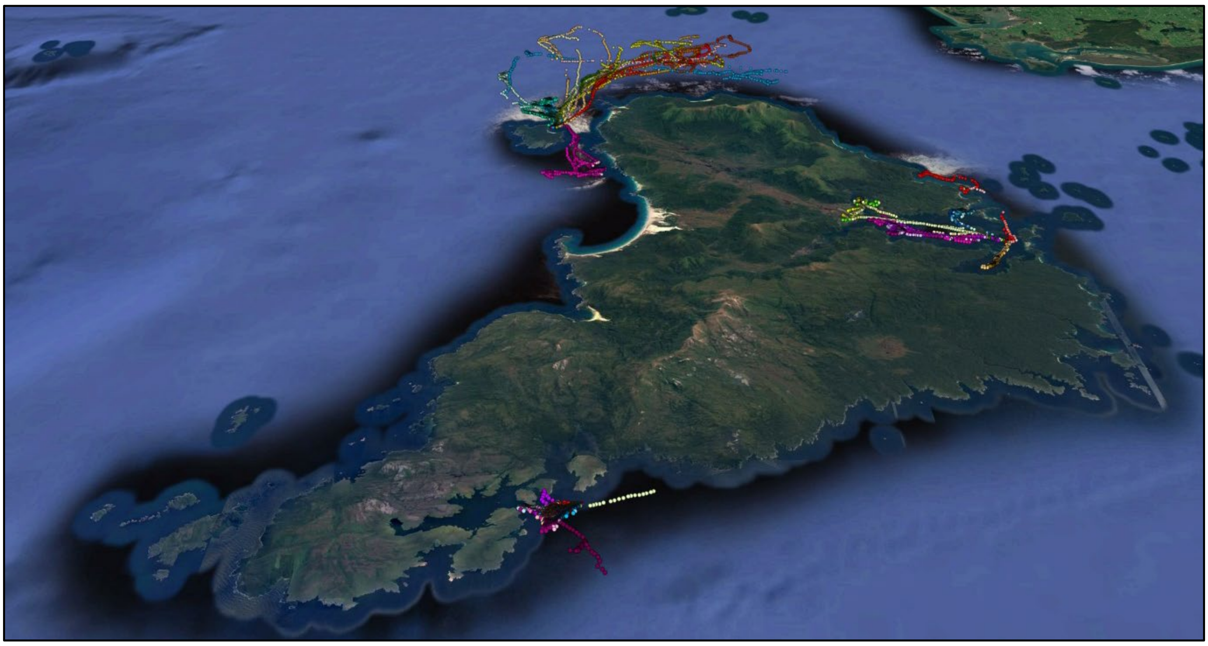


Figure 8. *Overview of distribution of GPS data recorded on breeding hoiho during the chick rearing period 2020/21 at the three main study sites on Rakiura and Whenua Hou/Codfish Island.*

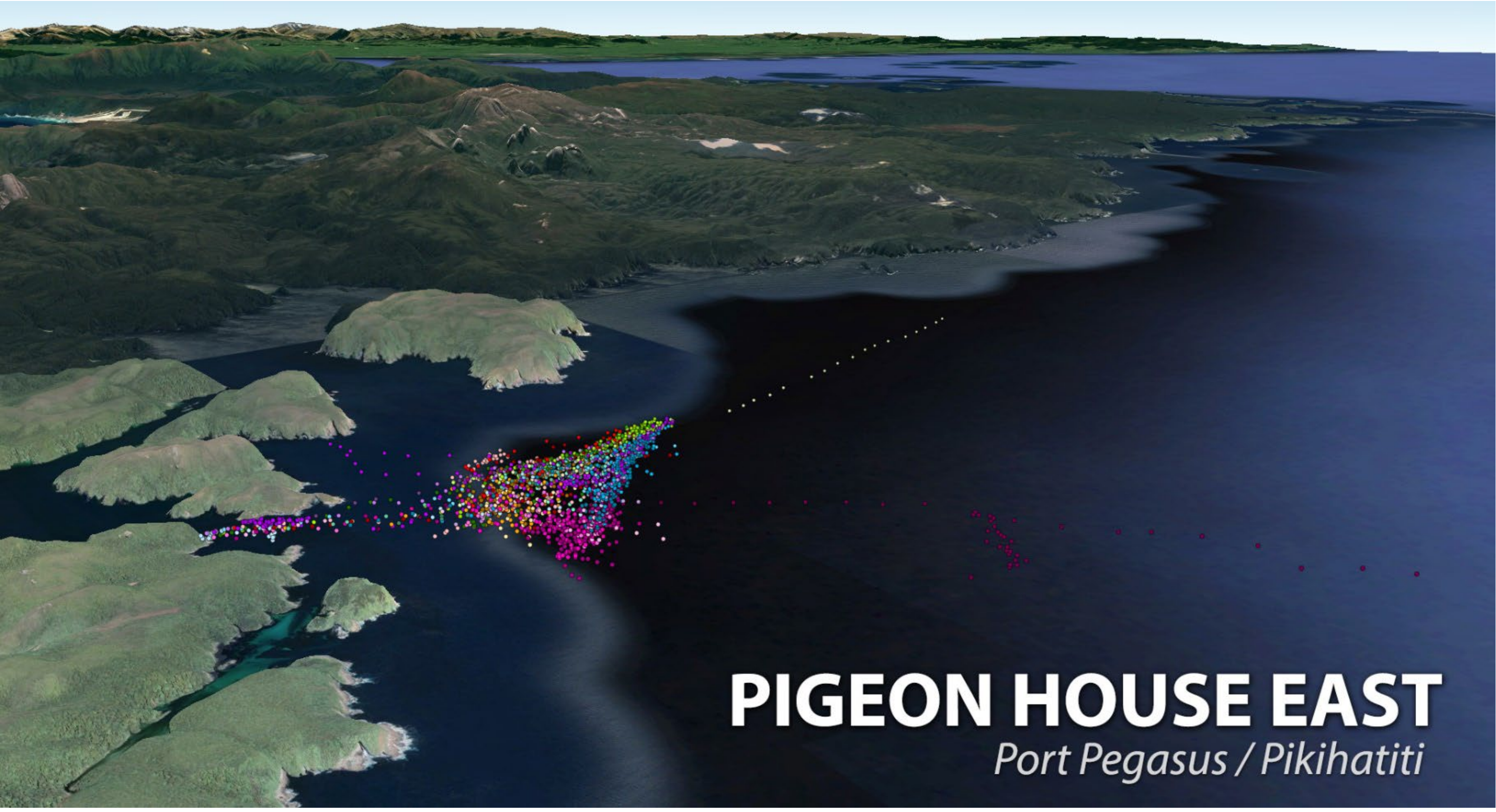
Winter tracking using a combination of satellite transmitters and dive loggers was limited by the number of satellite tags available (n=5). Four of the five birds deployed with devices could be recaptured after a mean 7.2±0.4 days (range: 6.9±8.0 days), the fifth bird eluded recapture so that the devices could not be recovered but naturally fell off and, consequently, no dive data is available for this bird.

Birds fitted with satellite transmitters in the winter period that could be recaptured (n=4) performed between two and seven foraging trips (mean: 4.3±1.8 trips) while carrying the devices. Average trip durations varied between 7.4 and 21.4 hours but were overall comparable to what was observed during the post-guard stage (January 2021) at the same site (Table 2) especially when the shorter daylength in winter is taken into consideration. The temporal resolution and spatial accuracy of satellite transmitters is substantially inferior to GPS loggers, so that after filtering of invalid position fixes from the raw satellite data, a total of 73 at-sea locations were accepted across the four birds. This only corresponds to 1.8±0.6 fixes recorded per hour allowing it to determine locations of merely 2% of all recorded dives.

Satellite data for the bird that eluded recapture suggests that it carried the device until 2 November 2022 (i.e., for 122 days) inflating the trip data recorded for this individual compared to the other birds. Over the course of the bird's prolonged deployment period a total of 1,089 valid position fixes remained after filtering of the received satellite data. Without valid dive data, the determination of accurate trip start and end times is impossible so that data from this bird was omitted from analysis presented in various tables in this report.

Table 2. *Overview of foraging trip durations of hoiho at the three study sites on Rakiura and Whenua Hou.*

Site	Stage	Number of trips [n]	Foraging trip duration [hrs]		
			Min	Max	Mean ± SD
Pigeon House East	Chick-guard	30	6.4	10.0	8.1±1.2
Groper Island	Chick-guard	33	5.6	8.8	7.2±1.3
Whenua Hou	Post guard	27	13.5	19.6	15.8±2.1
	Winter	17	7.4	21.4	12.1±5.5



GPS tracking

A total of four active nests were present when the tracking study took place a Pigeon House East. Of these, three nests were located in the forested area around the rock formation that gives the area its name, see (Mattern, 2020b) for further details. A fourth nest (PH2003); was found on steep coastal slope to south of the inlet cutting inland from the Pigeon House Bay; access to this nest was difficult due to the unstable ground, which was exacerbated by wet conditions during the second week of the study. Because of this, only one of the breeding birds from this nest was fitted with a device, bringing the total number of deployments to seven birds.

Of these seven birds, four birds were fitted with a combination of camera and GPS logger. Three of the birds carried the camera during the first foraging trip while deployed with GPS logger; one bird was fitted with a camera for the last foraging trip after it had already performed four foraging trips with GPS logger only.

Foraging ranges were remarkably short with birds seldom travelling more than 3.5±0.4 km from their breeding colony (mean range: 3.2-4.4 km, n=7) covering distances of a mean 34.7±7.0 km (mean range: 20.0-43.3 km) (Table 3).

Trip duration averaged 7.2±1.3 hrs which, considering a daylength of around 15.5 hours at the time of the study, such short ranges and duration facilitated that both birds in a pair were able to forage daily. On 2 December 2020, the male hoiho from nest PH2004 even performed two foraging trips, one in the morning (05:36 am – 10:45 am, 5.2 hrs) and a second trip in the evening (07:47 pm – 09:37 pm, 1.8 hrs) after his partner had returned from a six-hour foraging trip in the afternoon.

Similarly remarkable was that all seven birds foraged in an extremely well-defined triangular area ca. 2.5 km due east of Pigeon House mainly confined to water depths of 50-80 m (Figure 10). Distribution of the GPS fixes shows a clear linear demarcated eastern boundary of the penguins foraging area. The trajectory of this boundary does not align with the local bathymetry and instead seems to be governed by substrate changes at the seafloor. Preliminary video data suggests that the penguins concentrated their foraging effort on a seafloor habitat dominated by sand (Figure 9).

Two birds ventured further (10- 12 km) away on single trips, one drifting due east-north-east during a period of inactivity (PH2002 female, trip 1, 26.11.2020), and the other one travelling south-east (PH2003 male, trip 7, 05.12.2020). However, all other foraging trips performed by these two birds took them to the main foraging area shared with all other birds (Figure 10).

Figure 9. *Screenshot of camera footage recorded in the core hoiho foraging area off Pigeon House, Port Pegasus. Change of seafloor substrate (sand in front, gravel background) probably explains the clear demarcation of the foraging area's eastern boundary.*

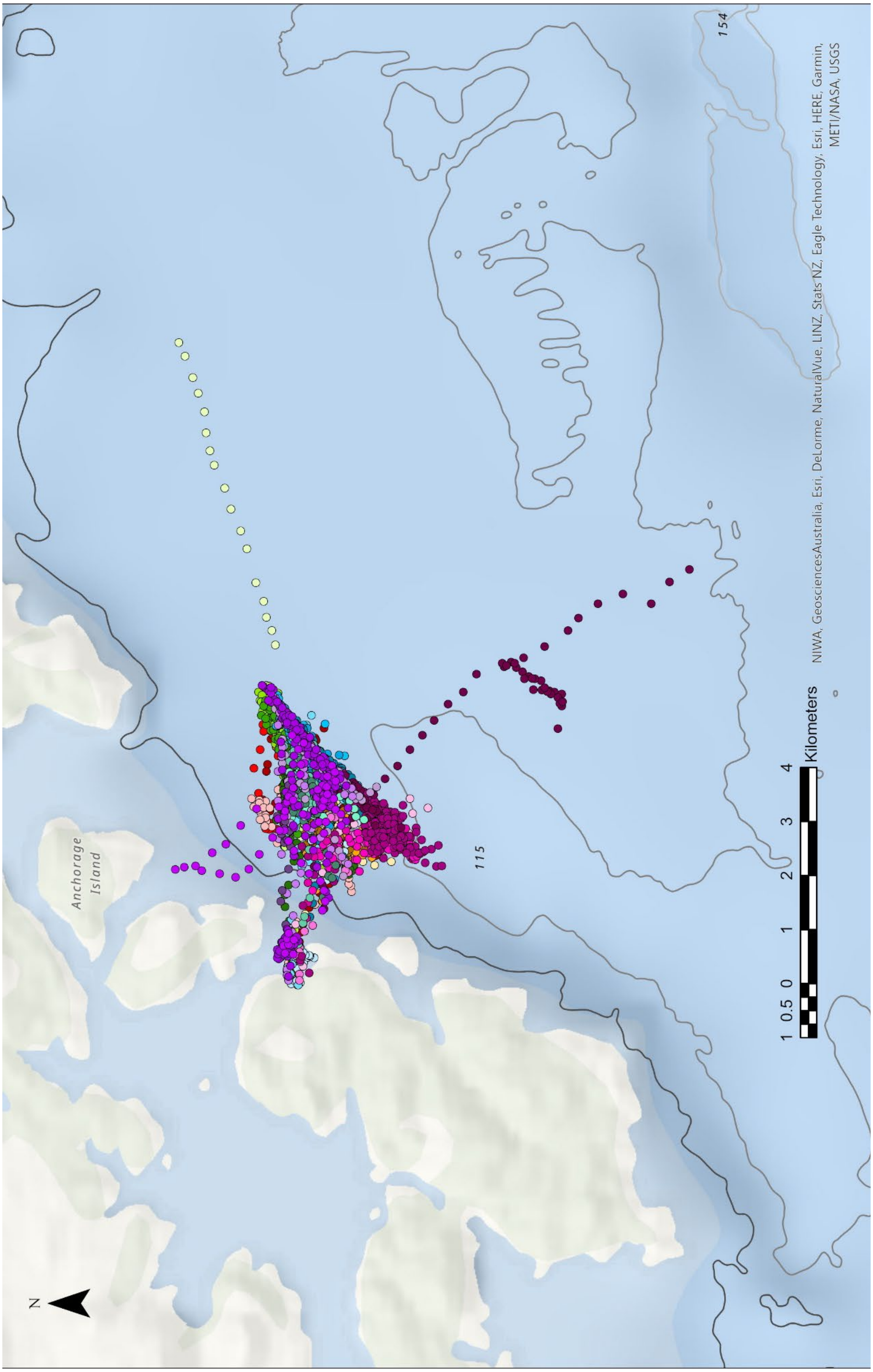


Figure 10. *Overview of distribution of foraging locations in hoiho from Pigeon House East, Port Pegasus/Pikihatiti*

Table 3. *Foraging trip statistics recorded on seven adult hoiho breeding at Pigeon House East during the 2020/21 breeding season.*

Bird ID	No	Date	Duration	Range	Distance covered
			hrs	*km*	*km*
PH2001 female 982 0002102 13035	1	02.12.2020	9.9	3.6	18.0
	2	03.12.2020	2.9	3.5	28.9
	3	05.12.2020	13.3	2.9	46.8
PH2001 male 982 0004055 31761	1	26.11.2020	8.5	2.9	13.8
	2	27.11.2020	8.7	3.4	34.9
	3	28.11.2020	9.1	3.2	54.3
PH2002 female 982 0002102 13827	1	26.11.2020	10.4	8.3	17.4*
	2	27.11.2020	4.7	3.9	25.9
	3	28.11.2020	4.3	3.8	37.6
	4	29.11.2020	4.2	3.8	49.7
	5	30.11.2020	4.1	3.7	60.0
	6	01.12.2020	7.0	3.1	78.4
PH2002 male 982 0002102 12196	1	01.12.2020	6.3	3.1	10.7
	2	02.12.2020	5.8	3.5	21.6
	3	03.12.2020	6.1	3.7	31.5
	4	04.12.2020	11.5	3.6	51.1
	5	05.12.2020	8.8	3.4	67.0
PH2003 male 982 0002102 13596	1	28.11.2020	6.5	2.9	5.8
	2	30.11.2020	3.8	2.6	15.8
	3	01.12.2020	8.9	2.6	27.8
	4	02.12.2020	3.5	2.7	33.8
	5	03.12.2020	12.2	2.7	50.3
	6	04.12.2020	9.0	2.9	59.9
	7	05.12.2020	10.6	7.4	84.7
PH2004 female 982 0002102 12967	1	04.12.2020	4.5	3.3	10.8
	2	05.12.2020	5.4	3.3	19.3
	3	06.12.2020	7.0	2.9	29.9
PH2004 male 982 0002102 12155	1	01.12.2020	6.3	3.6	8.9
	2	02.12.2020	5.2	3.7	22.3
	3	02.12.2020	1.8	2.6	26.4
	4	03.12.2020	7.0	3.9	42.5
	5	04.12.2020	8.3	3.8	53.6
	6	05.12.2020	7.7	3.2	71.8

** Incomplete GPS coverage, true distance covered likely greater*

Diving behaviour

Considering the highly consistent at-sea movements apparent in hoiho tracked at Pigeon House East, it is not surprising, that their diving behaviour was also comparable amongst the tracked individuals (Table 4).

While number of dives performed per trip are obviously closely linked to the duration of the respective trips and vary accordingly between as well as within individuals, mean maximum dive depths across all birds are comparable with individual means averaging 54.6±4.5 m (range: 47.6-59.8 m, n=7 birds) with maximum depths reached by each penguin ranging between 84.1 m and 104.0 m (mean: 91.9±6.1 m, n=7). The penguins spent an average 131±6 seconds underwater when preforming a dive (range: 121-139 s, n=7). Between 56 and 80% of all recorded dives were classified as benthic, i.e., dives on which the penguins foraged along the seafloor; on average two thirds (67%) of all dives were benthic dives.

The average dive depths recorded in hoiho from Pigeon House East were deeper than what has been observed in hoiho from other mainland sites in the past few years, with the exception being penguins breeding in the Catlins, that have been found to regularly forage at depths exceeding 100 m (Mattern & Ellenberg, 2021). While at a first glance this may give the appearance of hoiho from southern Rakiura showing a greater foraging effort when compared to other regions, short foraging ranges and trip durations (Table 3) suggest otherwise. Analysis of video footage showed that the penguins foraged for opalfish (*Hemerocoetes spp.*) an easy to ingest fish species, as well as arrow squid (*Nototodarus sloani*), both of which appear to be quite abundant in the vicinity of the breeding colony (Elley, 2022).

The diving behaviour of hoiho from Pigeon House has been studied in November 2011 (Chilvers, Dobbins & Edmonds, 2014). While their study did not record any spatial data, the dive statistics reported are comparable to what we have observed. As such, it seems plausible that foraging ranges in hoiho from Port Pegasus remained consistent over the past decade.

On several occasions, large feeding flocks of red-billed gulls (*Larus novaehollandiae*, 50+ individuals), white fronted terns (*Sterna striata*, 50+ individuals) and tawaki (*Eudyptes pachyrhynchus*, 30+individuals) were seen foraging close to the surface in the passage between Pigeon House Bay and Noble Island. Generally, one or two hoiho were part of these feeding flocks, underlining that hoiho do engage in pelagic foraging if the opportunity arises.

Table 4. *Summary of core dive parameters recorded for the seven breeding hoiho fitted with GPS dive loggers at Pigeon House East, southern Rakiura, between 26 November and 7 December 2020.*

Bird ID	Trip	Dives	Benthic dives		Dive time	Max depth	Mean depth
		n	*N*	*%*	*s*	*m*	*m*
PH2001 female 982 0002102 13035	1	159	95	59.7	120±69	91.9	47.9±35.3
	2	75	35	46.7	109±74	94	43.6±36.8
	3	190	136	71.6	150±66	92.4	57.0±30.6
PH2001 male 982 0004055 31761	1	144	105	72.9	143±63	98.1	61.2±33.3
	2	147	102	69.4	135±63	92.7	55.1±33.4
	3	160	112	70	138±62	90.1	56.1±32.8
PH2002 female 982 0002102 13827	1	191	132	69.1	141±53	93.3	59.8±28.8
	2	108	66	61.1	115±58	88.8	52.7±35.2
	3	87	56	64.4	120±57	88.8	54.7±33.6
	4	92	63	68.5	127±53	89.3	59.5±32.5
	5	91	64	70.3	129±57	88.7	57.6±32.1
	6	135	95	70.4	134±55	87.1	58.3±31.0
PH2002 male 982 0002102 12196	1	196	45	23	65±60	92.5	19.5±28.4
	2	118	57	48.3	105±72	90.6	40.5±35.9
	3	113	71	62.8	132±70	90.9	52.9±35.2
	4	187	141	75.4	155±66	97.1	64.2±33.0
	5	124	86	69.4	150±68	98.2	60.9±35.0
PH2003 male 982 0002102 13596	1	105	69	65.7	136±67	101.1	61.4±39.1
	2	70	42	60	126±71	103.8	54.2±39.3
	3	150	84	56	124±68	110	58.2±44.0
	4	72	40	55.6	118±66	100.5	57.1±41.4
	5	204	117	57.4	123±71	114	56.8±42.8
	6	146	100	68.5	141±71	99.7	65.7±40.1
	7	172	112	65.1	153±58	99.1	65.2±34.0
PH2004 female 982 0002102 12967	1	88	70	79.5	136±55	88.6	61.3±29.8
	2	101	82	81.2	140±50	83.3	59.5±27.0
	3	126	99	78.6	138±58	80.4	55.3±27.6
PH2004 male 982 0002102 12155	1	104	85	81.7	145±61	89.1	58.5±31.5
	2	94	70	74.5	140±58	86.8	54.8±31.8
	3	50	31	62	106±53	73.4	37.1±25.8
	4	133	102	76.7	131±56	89.6	48.6±30.7
	5	155	111	71.6	137±69	88.5	56.0±34.1
	6	136	113	83.1	151±47	85.5	57.4±27.3

GPS tracking

Nest numbers on the Bravo Group have been declining in the past years. In the 2020/21 season, Groper Island had the greatest number of nests still active in December 2020 (n=3), so that we focused our tracking effort to this site. Over the course of 10 days (10-20 December), all six breeding adults were fitted with GPS dive loggers; four birds also carried cameras for a single trip at the beginning of their respective deployment period. GPS dive loggers were recovered after a mean 6.8±2.0 days (range: 5.0-10.1 days). In one pair (GP2001), device deployments overlapped by six days, i.e., both birds carried devices simultaneously (13-18 December).

As already observed in the 2019/20 season (Mattern & Young, 2019), penguins from the Bravo Group foraged exclusively within Paterson Inlet / Whaka a Te Wera, with one exception, the female from nest GP2001 (transponder number: 982 0000334 54002).

The female from GP 2001 regularly left Paterson Inlet to forage very close inshore along the Rakiura coast reaching as far north as Port Williams (Figure 11). Due to the penguin's tendency to spend only a short time at the surface, GPS coverage of the bird's foraging trips is spotty. However, camera footage revealed that it spent substantial time in Halfmoon Bay (Figure 12a) where it foraged along the seafloor catching predominantly spotty/paketi (*Notolabrus celidotus*). Particularly noteworthy is the bird's prevalence for foraging inside of kelp forests along the coast, a habitat teeming with butterfish/rarī (*Odax pullus*) (Figure 12b), a fish species that is targeted around Rakiura using inshore set nets.

The bird also carried a GPS device in the 2019/20 season and showed a similar preference for foraging close inshore along the Rakiura coast north of the inlet (Mattern & Young, 2019). Similarly, its partner, the male from GP2001 (982 0002102 13011) showed individual foraging preferences consistent between years. On all eight foraging trips recorded, the penguin travelled directly into Big Glory Bay where it foraged in the vicinity of salmon farm operations (Figure 11). However, camera footage recorded by this bird did not show any direct interaction with the salmon farms, instead it foraged predominantly at the seafloor despite poor visibility (Figure 12c). The footage also showed that the penguin was foraging in a group of at least three other hoiho. Considering the consistency of all tracked birds at-sea movements, it is safe to assume that the birds accompanying the GP2001 male were from other breeding locations, such as Goat Island or Little Glory Bay. Group foraging behaviour may point towards cooperative foraging (Figure 12c), although camera footage did not show any such behaviour. Big Glory Bay appears to represent an important foraging location for local hoiho populations. Whether this is because or despite of the substantial aquaculture operations in the bay remains unclear.

The hoiho from the other two nests all exhibited near shore foraging strategies; the central Paterson Inlet was only visited while transiting between breeding island and foraging destination (Figure 11). The birds concentrated their foraging effort on water depths <15 m. The pair from nest GP2003 stands out foraging in extremely shallow water of <2m depth in the Freshwater River delta in the western end of Paterson Inlet. The birds foraged over shell covered, sandy habitat as well as seagrass meadows catching spotty. Camera footage shows that the area is also frequented by other hoiho (Figures 12d-f).

Overall, it appears as if most hoiho breeding within Paterson Inlet / Whaka a Te Wera are the least likely penguins to be affected by commercial fishing activities. However, whether the observed preference for foraging within the inlet may be representative for the non-breeding season requires further investigation.

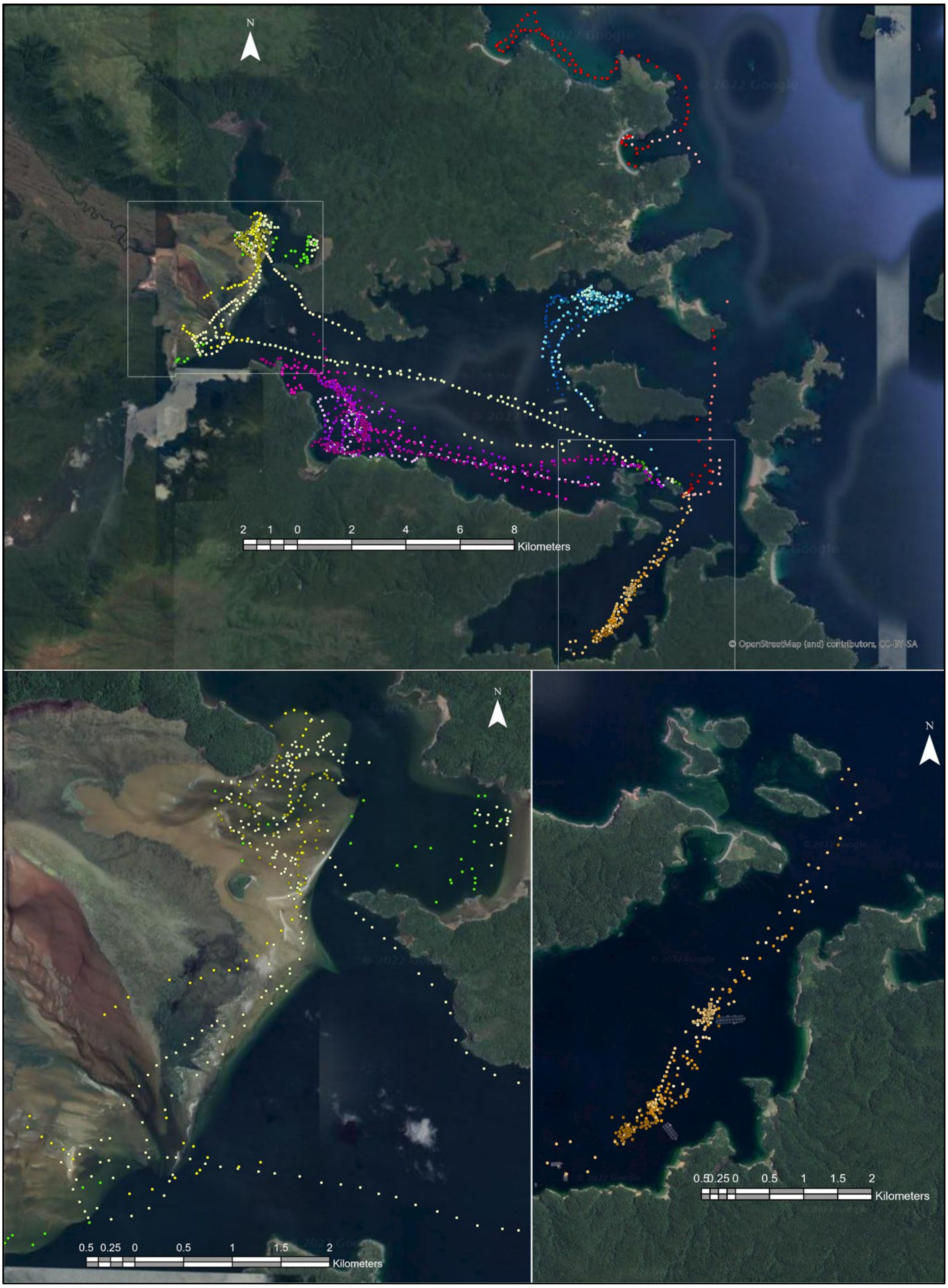


Figure 11. *Overview of foraging locations recorded on hoiho breeding on Groper Island, Bravo Group in December 2020 (top). Details of the main foraging locations of the pair of birds from nest GP2003 (bottom left) that foraged in extremely shallow waters (<2 m) of the Freshwater River delta, and the male from GP2001 (bottom right) that consistently swam into Big Glory Bay to forage in the vicinity of salmon farms, a behaviour this bird had already exhibited in the previous season.*

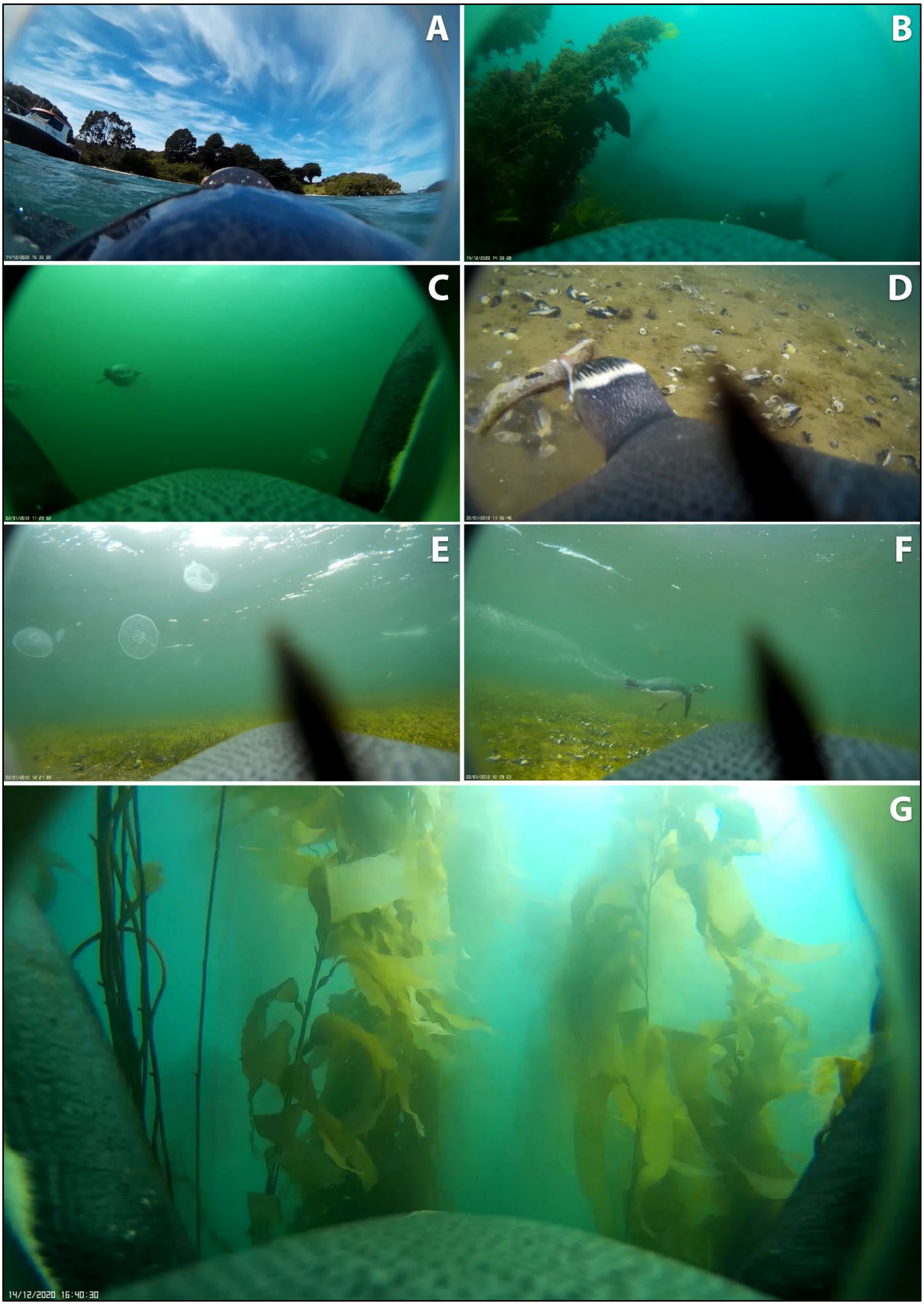


Figure 12. *A-F: Frame grabs from camera footage recorded on hoiho from Groper Island, Bravo Group, Peterson Inlet / Paterson Inlet / Whaka a Te Wera, December 2020. Lower frame (G), female hoiho from nest GP2001 swimming through kelp forest, 14.12.2020.*

Table 5. *Foraging trip statistics recorded on seven adult hoiho breeding on Groper Island, Paterson Inlet, Rakiura in the 2020/21 breeding season.*

Bird ID	Trip	Date	Duration	Range	Distance covered
			hrs	*Km*	*Km*
GP2001 female 982 0000334 54002	1	14.12.2020	10.2	9	13.2
	2	15.12.2020	12	4.9	32.8
	3	16.12.2020	8.9	12.5	58.3
	4	17.12.2020	9.9	8.5	75.7
	5	18.12.2020	8.9	0.6	85.0
GP2001 male 982 0002102 13011	1	11.12.2020	6.9	3.8	*8.0**
	2	12.12.2020	6.7	3.9	9.2*
	3	13.12.2020	7.2	4.0	12.7
	4	14.12.2020	6.2	4.0	19.1
	5	15.12.2020	6.6	3.9	27.7
	6	16.12.2020	8	4.4	44.1
	7	17.12.2020	6.6	4.9	58.1
	8	18.12.2020	7.3	4.3	68.1
GP2003 female 982 0000334 54063	1	11.12.2020	9.3	13	18.9
	2	12.12.2020	8.1	12.7	35.4
	3	13.12.2020	8.1	12.7	75.8
	4	14.12.2020	7.2	12.7	105.1
GP2003 male 982 0002102 13011	1	15.12.2020	15.8	12.9	21.9
	2**	16.12.2020	0.3	0.1	34.2
	3**	17.12.2020	1.7	1.1	38.0
	4	19.12.2020	14.3	12.7	81.5
GP2004 female 982 0000334 60002	1	15.12.2020	7.2	5.5	11
	2	16.12.2020	10.1	5.5	32.7
	3	17.12.2020	8.2	5.7	55.7
	4	18.12.2020	7.6	5.7	77.2
GP2004 male 982 0002102 12574	1	11.12.2020	8.3	9.2	30
	2	12.12.2020	8.2	10.3	56.1
	3	13.12.2020	11.3	9.5	98.7
	4	14.12.2020	7.8	10.9	132.1

** Poor GPS coverage, therefore, distance covered likely greater*
*** Brief evening trips serving primarily for washing and preening*

Diving behaviour

The diving behaviour of hoiho from Groper Island proved to be highly unusual, especially for a penguin species of this size. Large body size in diving animals are generally linked to their ability to stay under water for longer and reach greater depths (Kooyman & Ponganis, 1998). As the fourth largest of all extant penguin species (Garcia Borboroglu & Boersma, 2013), hoiho therefore are well-equipped to forage at depths exceeding 100 m; the maximum theoretical dive depth following Wilson (1995) for a hoiho ranges between 140 and 170 m.

In this light, the dive depths recorded in hoiho from Groper Island were surprising (average individual mean dive depth: 11.6±6 m, range: 4.6-21.9 m; max depths reached: 27.1±5.9, range: 16.3-36.4 m, n=6 birds). Three of the six tracked birds showed average maximum dive depths <10 m across their foraging trips (Table 6). Particularly, the birds from nest GP2003 that consistently foraged in the Freshwater River delta (see above), showed very low mean maximum dive depths, which only exceed 5 m depths because the birds travelled at greater depths while commuting between the island and their foraging destination. While in the delta, foraging depths ranged between 0.3 and 1.5 m (see also Figure 12e & f). Dive times for these two birds were also substantially shorter (45±7 s, n=2) when compared to the other penguins (85±12 s, n=4), presumably at least in part owing to the higher energy requirements for such extremely shallow dives[1].

The third shallow diving hoiho was the female from GP2001, which consistently foraged out of Paterson Inlet. Although this bird exhibited benthic foraging, she did so mostly in the shallow bays <10 m deep north of Paterson Inlet. Moreover, her tendency to forage in kelp forests was associated with shallower near surface dives.

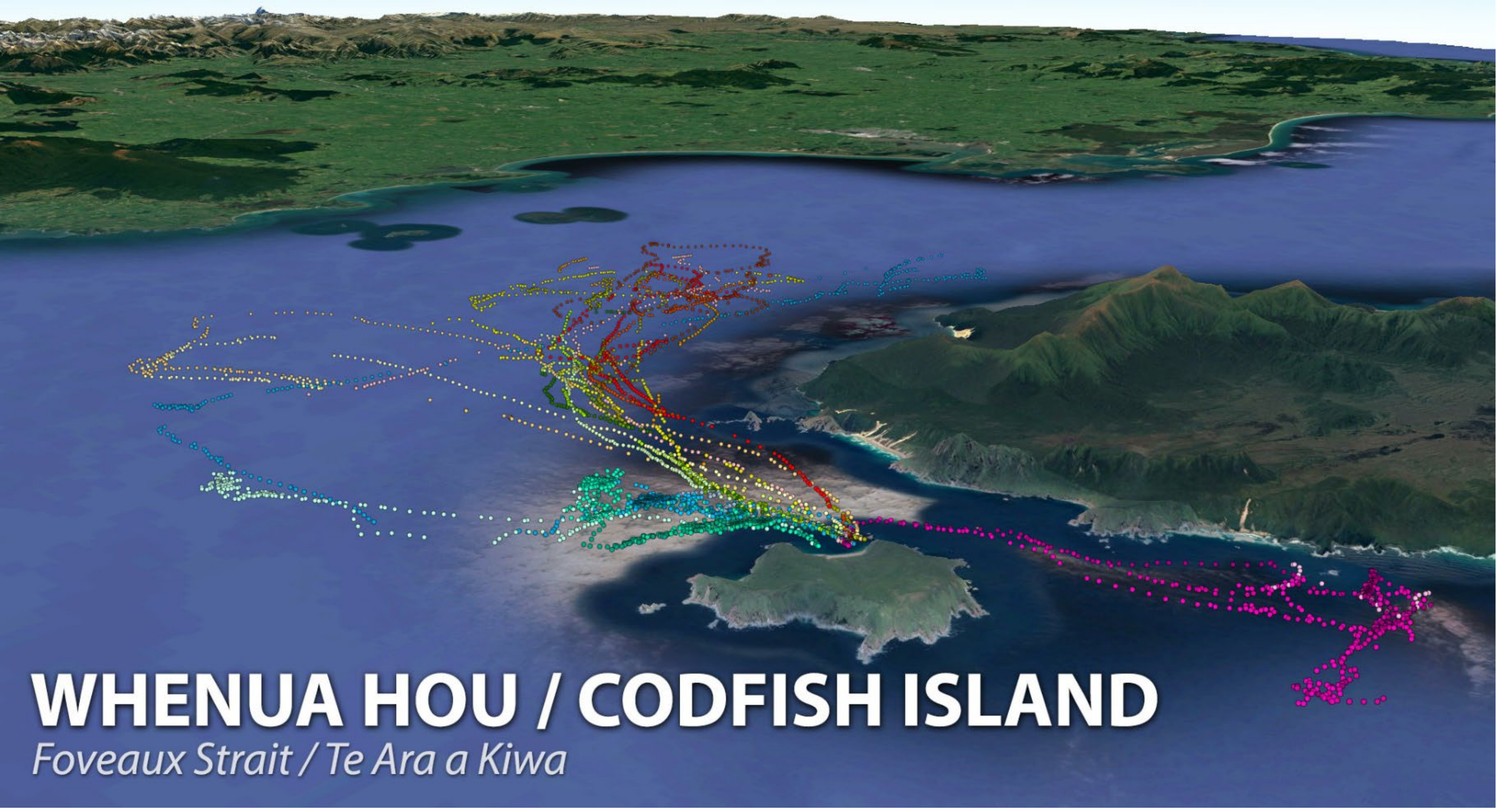
Only the penguin foraging in Big Glory Bay regularly frequently reached depths >20 m pursuing a benthic foraging strategy. However, in comparison to hoiho studied along the New Zealand mainland as well as at the other sites during this study, the penguins from Paterson Inlet exhibit the lowest diving effort which could be beneficial, provided adequate prey quality and quantities.

[1] At shallower depths, air captured in the birds' plumage is not compressed increasing their positive buoyancy which has to be compensated by higher muscular effort (Sato et al., 2002).

Table 6 *Summary of core dive parameters recorded for the seven breeding hoiho fitted with GPS dive loggers on Groper Island, between 10 and 20 December 2020.*

Bird ID	Trip	Dives	Benthic dives		Dive time	Max depth	Mean depth
		n	*n*	*%*	*S*	*m*	*m*
GP2001 female 982 0000334 54002	1	365	259	71	81±33	28	9.3±5.4
	2	305	197	64.6	78±42	44.6	9.7±7.4
	3	402	269	66.9	67±29	26.7	7.6±5.0
	4	490	297	60.6	64±36	42.5	6.7±5.2
	5	402	258	64.2	66±38	40.4	7.7±6.1
GP2001 male 982 0002102 13011	1	173	131	75.7	96±36	31.3	21.0±9.0
	2	178	141	79.2	99±34	27.7	20.8±8.4
	3	177	140	79.1	104±33	30	22.2±7.7
	4	150	120	80	105±39	31.3	21.2±7.9
	5	168	143	85.1	110±28	31.4	22.0±7.0
	6	191	155	81.2	106±34	29.6	22.0±7.7
	7	163	144	88.3	108±30	27.1	22.8±5.8
	8	154	135	87.7	108±24	27.7	23.1±4.9
GP2003 female 982 0000334 54063	1	379	189	49.9	55±38	27.5	7.0±8.0
	2	315	143	45.4	58±42	27.5	8.3±8.6
	3	321	153	47.7	50±37	27.6	7.1±8.7
	4	346	279	80.6	46±28	27.2	4.1±7.2
GP2003 male 982 0002102 13011	1	796	522	65.6	46±34	26.1	4.7±6.3
	2*	7	0	0	13±9	4.6	1.2±1.5
	3*	45	39	86.7	84±33	22.4	12.4±5.2
	4	502	229	45.6	44±44	27.8	4.5±6.7
GP2004 female 982 0000334 60002	1	232	180	77.6	85±32	25	16.7±6.7
	2	345	251	72.8	82±36	27.7	15.9±7.9
	3	266	181	68	79±29	24.2	15.4±7.1
	4	268	202	75.4	77±34	25.9	16.7±8.0
GP2004 male 982 0002102 12574	1	239	175	73.2	80±33	24.9	10.9±5.3
	2	239	219	91.6	87±37	27.9	13.0±6.4
	3	317	256	80.8	87±42	28	13.0±6.8
	4	260	198	76.2	80±39	27.4	11.2±6.3

* *Brief evening trips serving primarily for washing and preening*



GPS tracking – Post-guard (January 2021)

A total of 13 breeding pairs were active on Whenua Hou in the 2020/21 season. Of the initial nine breeding pairs in Waikoropupu/Sealers Bay, only four nests were still active and thus available for the GPS tracking study during the post-guard stage of breeding (9-21 January 2021). During post-guard, nest attendance patterns of the breeders are less predictable and can vary. Considering the temporal constraints of the work on the island for logistical reasons, deployments had to be conducted opportunistically so that on two nests, both adult hoiho could be fitted with GPS dive loggers. The remaining four deployments were on female penguins from the other nests. Cameras were fitted for the first day of the deployment on three birds, the pair from nest WH2003 as well as the female from WH2002.

While fitted with GPS dive loggers, five of the penguins foraged to the North of Whenua Hou as well as Rakiura (Figure 13). Foraging ranges were generally substantially greater when compared to hoiho from Pigeon House and Groper Island. The exception were the females from WH2003 and WH2022.

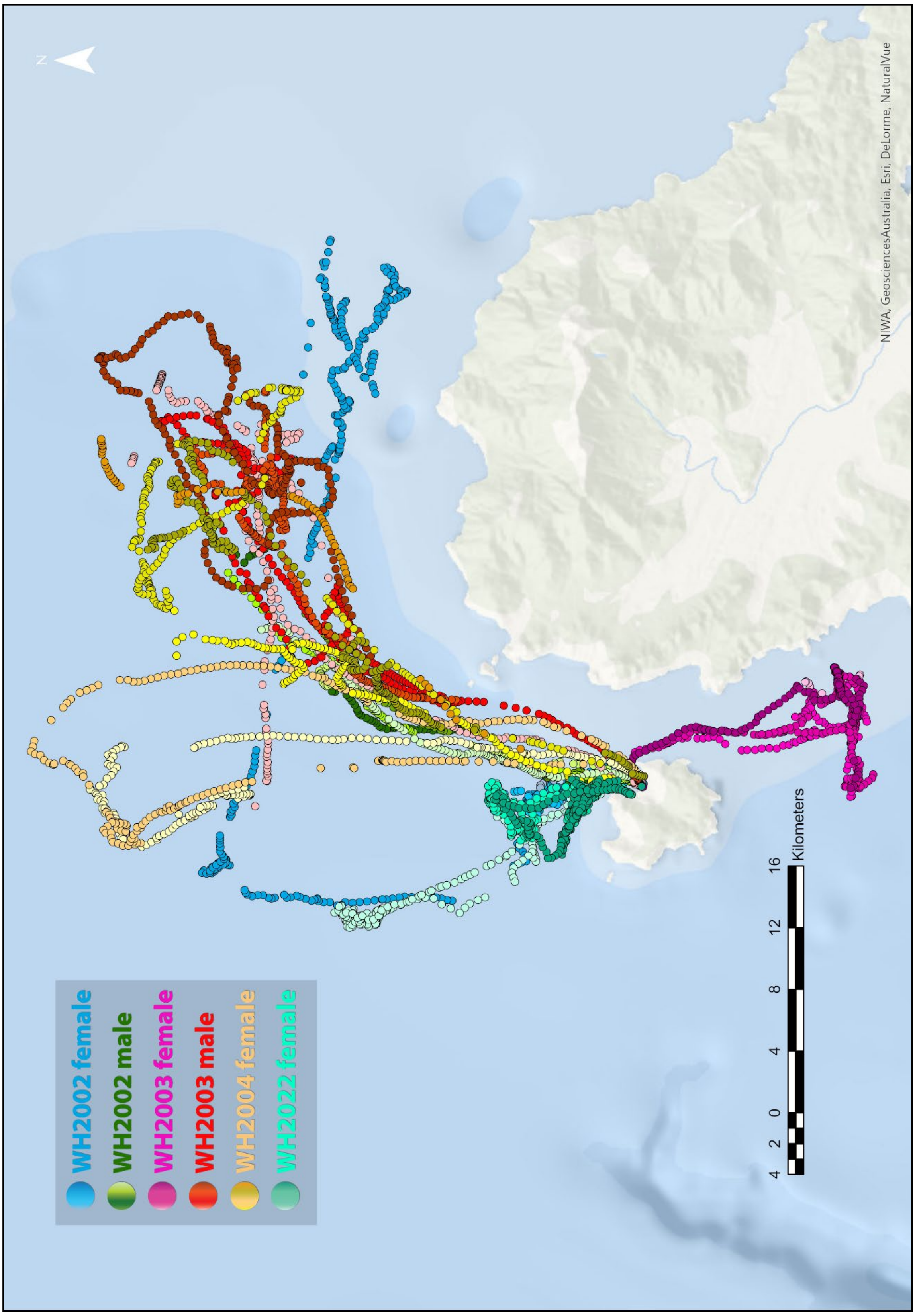


Figure 13. *Overview of distribution of foraging locations in hoiho from Whenua Hou during the post-guard stage of the 2020/21 season (January 2021). Colours of similar hue represent different tracks performed by the same bird (e.g. dark red, red, light red = WH2003 male).*

WH2003 female foraged 5 km to the South of Whenua Hou, which is a first record of a bird from the island not foraging to the north of it (Ellenberg & Mattern, 2012). The penguin focused her foraging effort on an area extending westward one kilometre southwest of Richards Point on Rakiura (markers with pink hue in Figure 13). The other short-ranged bird was WH2004 female which stayed within six kilometres of Northwest Bay on Whenua Hou (turquoise hue, Figure 13).

The remaining birds all foraged between 15 and 30 km north from their breeding sites. No penguin crossed Foveaux Strait to forage in Te Wae Wae Bay as had been observed during previous studies in 2005 and 2006 (Mattern, 2006; Ellenberg & Mattern, 2012). However, overall, the birds stayed within the foraging ranges determined in 2005 and 2006 for breeding penguins tracked during the late chick-guard and early post guard-stage (Figure 14), underlining habitat preferences and the long-term consistency in hoiho foraging patterns.

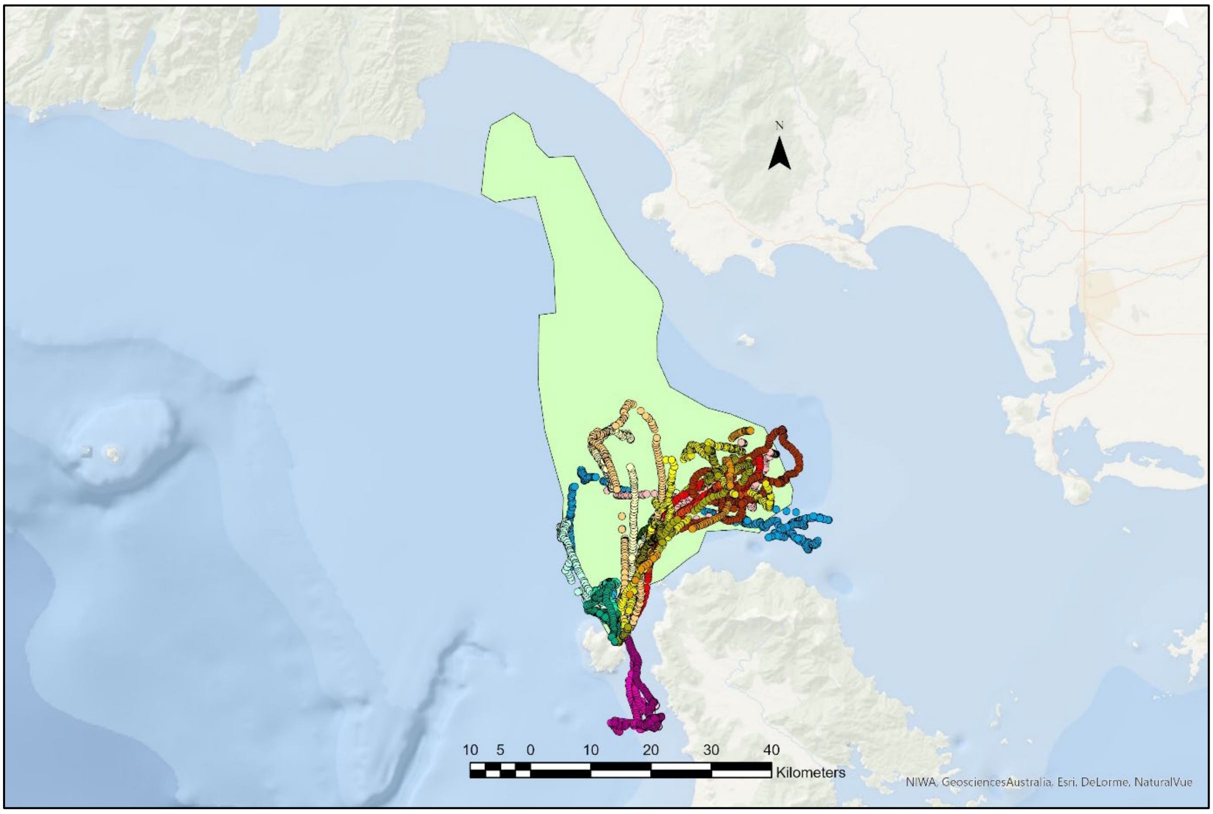


Figure 14. *The 2021 hoiho tracking data from Whenua Hou/Codfish Island in relation to foraging ranges determined in 2005 and 2006. The green polygon indicates the convex hull of GPS locations recorded during late chick-guard and early post guard in those years.*

Overnight trips, apparent in the earlier 2005 and 2006 studies, were uncommon. Only two birds stayed at sea overnight on a single trip. All other birds returned to their nest daily (average individual means of trip duration: 15.7±2.1 hrs, range: 13.5-19.6 hrs: n=6 birds).

Table 7. *Foraging trip statistics recorded on seven adult hoiho breeding on Whenua Hou/Codfish Island during the post-guard stage of the 2020/21 breeding season.*

Bird ID	Trip	Date	Duration	Range	Distance covered
			hrs	*km*	*km*
WH2002 female 982 0000636 20146	1	09.01.2021	11.3	4.9	13.2
	2	10.01.2021	12.0	6.2	33.8
	3	12.01.2021	36.6	27.9	155.4
	4	13.01.2021	9.8	5.1	179.6
WH2002 male 982 0000560 90833	1	15.01.2021	14.1	18.2	22.5
	2	16.01.2021	15.3	15.2	75.9
	3	17.01.2021	15.5	22.9	101.1
	4	18.01.2021	11.8	20.7	146.8
	5	19.01.2021	15.0	20.7	213.5
WH2003 female 982 0000636 29336	1	14.01.2021	14.4	10.9	26.7
	2	15.01.2021	15.9	10.7	66.5
	3	16.01.2021	13.3	10.5	110.5
WH2003 male 982 0000053 30974	1	08.01.2021	26.7	28.1	89.3
	2	12.01.2021	18.1	26.8	167.9
	3	13.01.2021	18.2	25.5	231.0
	4	14.01.2021	15.3	30.7	310.5
WH2004 female 982 0000053 31750	1	11.01.2021	15.6	24.5	45.1
	2	12.01.2021	15.6	27.1	125.2
	3	13.01.2021	11.9	22.1	158.8
	4	14.01.2021	14.5	25.9	220.4
	5	15.01.2021	15.8	25.4	272.2
	6	16.01.2021	15.5	28.5	309.7
WH2022 female 982 0000334 55741	1	11.01.2021	15.5	14.7	51.6
	2	12.01.2021	14.8	6.8	97.2
	3	13.01.2021	10.6	4.4	125.2
	4	14.01.2021	13.1	6.5	168.3

Diving behaviour

Consistent with foraging behaviour observed previously (Browne et al., 2011; Ellenberg & Mattern, 2012), hoiho from Whenua Hou showed primarily benthic foraging behaviour with a mean 67±16% of dives being classified as benthic dives (Table 8). The long foraging ranges recorded make it likely that the pelagic dives were principally associated with travelling/commuting behaviour.

Mean maximum dive depths of the different birds ranged between 55.7 and 68.1 m (mean: 64.4±4.1 m, n=6 birds) which reflects the water depths in central Foveaux Strait. Dive times (mean: 118±15 s, range: 105-150 s) were on average 20 s shorter than what was observed at Pigeon House East likely resulting from the shorter transit times from surface to seafloor required in shallower Foveaux Strait.

Camera deployments showed that the benthic habitat utilized by hoiho north of Whenua Hou is very similar to what is found off the Otago Peninsula (Mattern et al., 2018). That is, swaths of coarse sand (Figure 15a) or gravel/shell fragment ripples (Figure 15b) which appear to be the preferred habitat for opalfish (*Hemerocoetes monopterygius*) a species targeted by Whenua Hou hoiho (Browne et al., 2011; this study). The seafloor habitat south of the island is dominated by fine sand with floating seaweed and small rock boulders and rocky reefs which provide shelter to juvenile fish, like tarakihi (*Nemadactylus macropterus*) and blue cod (*Parapercis colias*) that are being successfully targeted here (Seed et al., 2018) (Figure 15c).

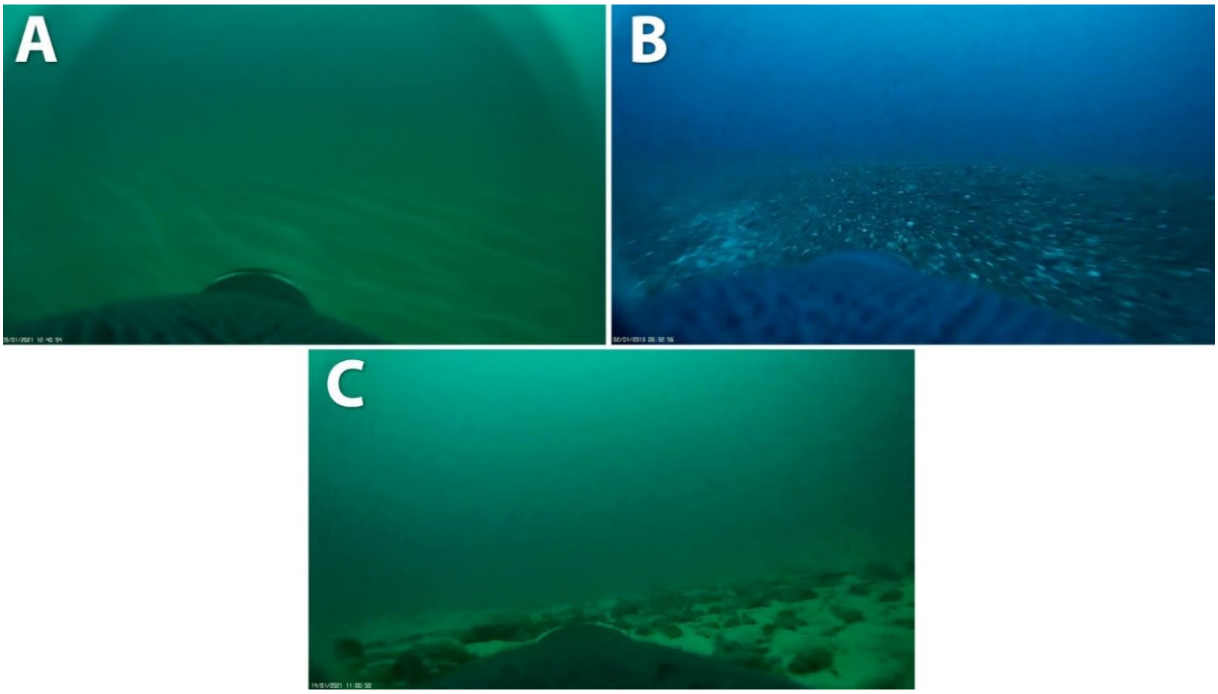


Figure 15. *Frame grabs of video footage recorded in Jan 2021 north (a & b) and south (c) of Whenua Hou.*

***Table 8** Summary of core dive parameters recorded for the seven breeding hoiho fitted with GPS dive loggers on Whenua Hou/Codfish Island, between 9 and 19 January 2021.*

Bird ID	Trip	Dives	Benthic dives		Dive time	Max depth	Mean depth
		n	*n*	*%*	*s*	*m*	*m*
WH2002 female 982 0000636 20146	1	257	223	86.8	115±41	62.1	45.7±18.7
	2	249	203	81.5	125±46	66.5	47.9±21.3
	3	728	441	60.6	117±49	76.2	37.6±23.0
	4	191	176	92.1	125±39	63	49.2±20.2
WH2002 male 982 0000560 90833	1	335	221	66	116±47	65.8	42.5±22.9
	2	400	256	64	106±52	66.6	39.6±23.8
	3	409	194	47.4	98±51	61.6	32.4±22.7
	4	293	172	58.7	102±47	61.7	37.7±22.7
	5	346	185	53.5	102±45	65.1	36.0±22.1
WH2003 female 982 0000636 29336	1	343	241	70.3	107±46	56.2	32.3±17.5
	2	363	293	80.7	116±40	55	35.7±15.4
	3	280	217	77.5	115±48	55.2	32.9±17.0
	4	472	279	59.1	101±46	56.2	27.9±17.7
WH2003 male 982 0000053 30974	1	589	191	32.4	96±53	67.2	23.5±22.5
	2	357	184	51.5	128±60	67.1	33.8±22.7
	3	311	161	51.8	123±66	68.9	33.0±24.3
	4	343	207	60.3	123±60	63	36.6±20.2
WH2004 female 982 0000053 31750	1	396	217	54.8	103±64	66.5	36.4±27.4
	2	401	202	50.4	107±65	66.1	34.7±26.6
	3	187	125	66.8	118±63	62.9	36.1±25.2
	4	384	176	45.8	104±51	65.1	31.4±19.9
	5	345	185	53.6	113±56	63.5	34.3±23.7
	6	513	128	25	85±44	65	25.6±18.1
WH2022 female 982 0000334 55741	1	255	227	89	167±52	77.8	60.0±23.9
	2	252	223	88.5	161±54	67.1	54.5±20.9
	3	231	225	97.4	130±29	59.4	39.2±13.1
	4	260	250	96.2	141±34	68.2	44.9±15.1

Satellite tracking – Winter (July 2021)

Tracking hoiho in winter is inherently difficult as birds do not necessarily return to their nests so that individuals can make landfall at varying locations. Hence, their quasi-random occurrence on land complicates capturing birds for device deployments. Nevertheless, it was possible to deploy the full number of satellite trackers (n=5) available for this study on hoiho in the first two days of the 14-day period our team had on the island in July 2021. The devices remained on the birds for seven to nine days after which four of the five penguins could be recaptured. The final bird was a male that had its first sighting after being marked as a chick on Whenua Hou in 2010. This penguin was a roaming bachelor not associated with any particular breeding area, which made recapture impossible despite all our efforts over several nights with two different catch teams at a range of likely landing locations. Surveillance camera footage revealed that the male was stalking a number of paired females apparently without success.

While data recorded with the TDRs deployed in combination with satellite trackers provided the same quality of diving data as recorded during chick-rearing (see below), the spatial and temporal resolution of the satellite data was far inferior to GPS data. Only between three and 11 position fixes (mean: 5±2 fixes, n=14 trips) were recorded per foraging trip in penguins that returned dive data. As a result, location-based foraging trip statistics are unreliable and likely unrepresentative (Table 9).

Nevertheless, the distribution of the obtained spatial data suggests that the Whenua Hou hoiho still foraged in the same general areas to the north of the island that was utilised during chick-rearing in January 2021, as well as during the tracking studies conducted in 2005 and 2006 (Figure 15).

Durations of one-day trips were shorter (mean: 14.0±4.7 hours, range: 9-21 hours, n=4 birds) than what was observed in January. The same seems to be true for the foraging ranges that seldomly exceeded 20 km (Table 9) and averaged 13±1.5 km in the four birds that could be recaptured. Whether this difference in foraging ranges is in fact a result of the poor spatial quality of the satellite data cannot be ruled out. However, given the shorter trip durations it seems logical that foraging ranges are also shorter. On one hand, the shorter daylength in July (ca. 8.5 hours) when compared to the chick-rearing study in January (ca. 15.5 hours) likely affects both trip duration and foraging range. On the other hand, when not breeding, hoiho only must focus on self-sustenance so that energy requirements and foraging effort to meet these is likely reduced also.

Thus, the most important outcome of the winter study is the insight that hoiho from Whenua Hou forage in a well-defined region to the North and Northeast and likely have done so for at least the past 15 years (Figure 16). One of the males tracked during winter occasionally foraged to the South of the island using the same area as has been observed in one of the breeding females.

Table 9. *Foraging trip statistics recorded on seven adult hoiho breeding on Groper Island in the 2020/21 breeding season. Due to the low temporal and spatial accuracy of satellite data, foraging ranges and travel distances (values in italic font) presented here are only indicative values and do not provide an accurate representation of the penguins' foraging movements. Where fixes were clustered too close together, values were omitted.*

Bird ID	Trip	Date	Duration	Position Fixes	Range	Distance covered
			hrs	*n*	*km*	*km*
WH-D02 male 982 0002102 14392	1	07.07.2021	9.6	7	*5.4*	*17.7*
	2	10.07.2021	33.2	11	*25.0*	*54.6*
WH-D03 female 982 0000636 29336	1	05.07.2021	33.4	5	*31.8*	*83.3*
	2	06.07.2021	8.5	3	*7.8*	*18.6*
	3	07.07.2021	8.5	4	*5.4*	*14.3*
	4	08.07.2021	9.0	3	*6.3*	-
	5	09.07.2021	9.4	3	-	-
WH-D04 male 982 0000053 30974	2	04.07.2021	14.6	8	*20.4*	*42.5*
	3	07.07.2021	9.2	4	*10.7*	*22.3*
	4	09.07.2021	9.6	5	*6.4*	*13*
WH-D06 female 982 0000021 17937	1	04.07.2021	8.4	7	*11.8*	*27.6*
	2	07.07.2021	9.4	3	*7.6*	*15.3*
	3	08.07.2021	9.4	3	*11.5*	*23.6*
	4	10.07.2021	8.9	3	*12.7*	*26*

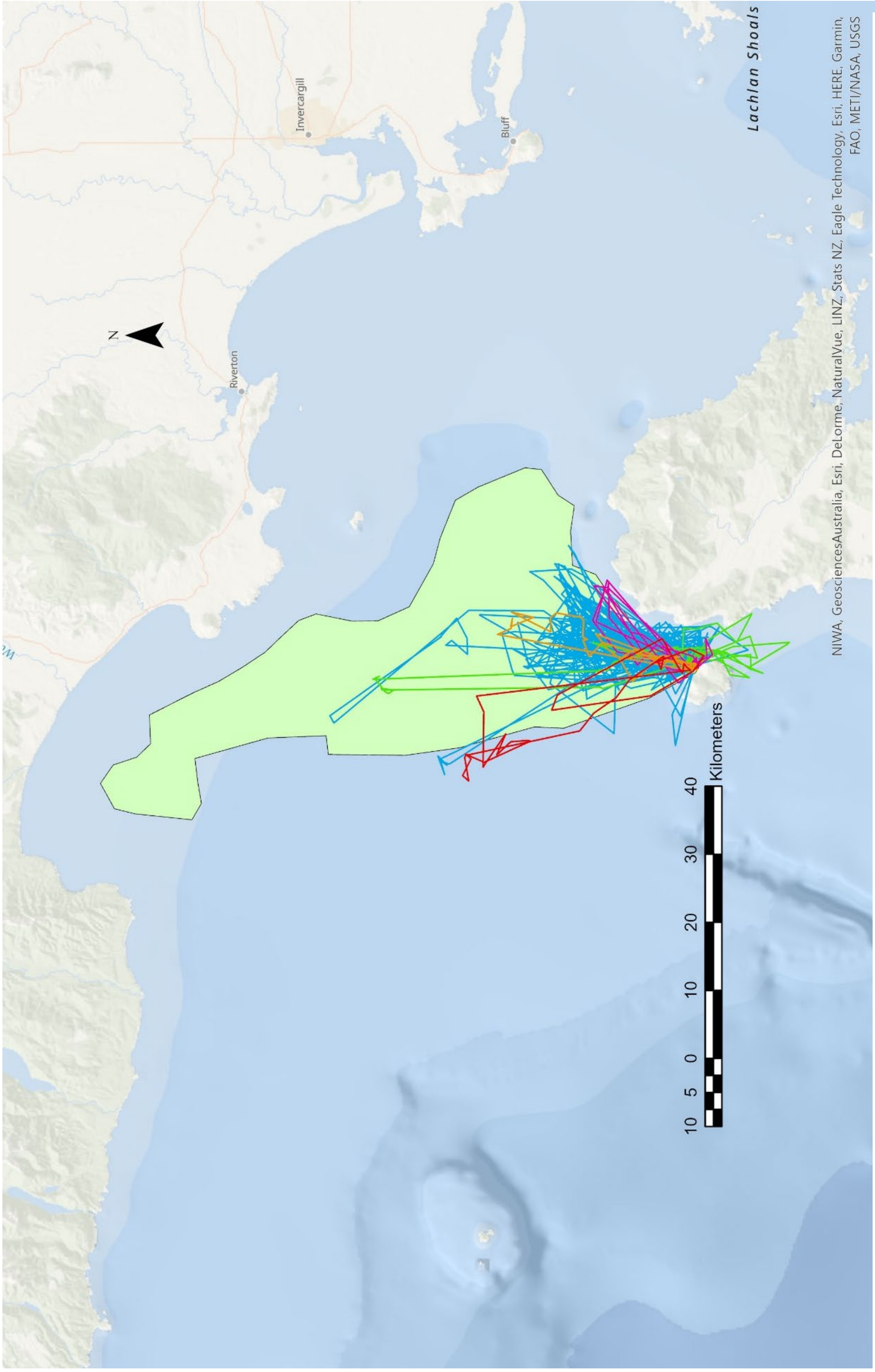


Figure 16. *Overview of distribution of foraging locations in hoiho from Whenua Hou during the non-breeding season/winter, July 2021.*

Diving behaviour

Diving behaviour recorded in the four hoiho that could be recaptured indicates that in winter hoiho from Whenua Hou expend less energy when foraging (Table 10). Dive times (average individual means: 100±9s, range: 82-122 s, n=4 birds) were around 20 seconds shorter when compared to data recorded during post-guard (see Table 8). The ratio of benthic to pelagic dives was also moved towards shallow and pelagic dives with only a mean 46±9% of all dives being classified as going down to the seafloor. The higher prevalence of pelagic dives also likely explains the lower mean dive depths of 29±3 m (range: 25-30 m) even through absolute max depths (65±8 m, range 54-76 m, n=4 birds) reached by the birds is comparable to those max depths observed six months earlier (see Table 8).

In terms of the habitat utilization this changes little in terms of which parts of the water column are used by the penguins. It is unclear whether the penguins displayed more pelagic dives due to lower light levels and poorer weather prevalent during winter, and consequently lower visibility, or whether birds may target different prey during the non-breeding season.

***Table 10** Summary of core dive parameters recorded for the seven breeding hoiho fitted with GPS dive loggers on Groper Island, between 10 and 20 December 2020.*

Bird ID	Trip	Dives	Benthic dives		Dive time	Max depth	Mean depth
		n	*n*	*%*	*s*	*m*	*m*
WH-D02 male 982 0002102 14392	1	274	116	42.3	89±61	73.8	33.2±30.3
	2	725	218	30.1	82±50	78.6	26.9±26.8
WH-D03 female 982 0000636 29336	1	880	265	30.1	94±43	65.2	20.9±20.8
	2	227	133	58.6	90±40	47.8	24.7±17.7
	3	208	156	75.0	108±42	54.7	32.6±17.4
	4	186	152	81.7	114±47	48.6	32.7±15.8
	5	216	140	64.8	95±51	54.2	28.0±17.4
WH-D04 male 982 0000053 30974	1	174	89	51.1	122±69	61.5	37.3±25.2
	2	176	80	45.5	110±64	64.1	31.5±24.9
	3	240	95	39.6	102±62	62.7	29.4±24.5
WH-D06 female 982 0000021 17937	1	146	61	41.8	111±50	63.1	26.2±21.7
	2	186	96	51.6	109±50	65.7	30.5±20.6
	3	223	71	31.8	91±45	69.5	22.2±18.3
	4	194	63	32.5	95±44	66.1	21.1±18.1

Conclusions

Comparing the foraging movements and diving behaviour of hoiho from the Rakiura/Foveaux Strait sites reveals remarkable regional variation in the penguins' behaviour. Each of the hoiho subpopulations have adapted their behaviour to suit the marine environment that is most accessible to them. While this suggests behavioural flexibility, the fact that individual penguins show highly consistent foraging routines negates this notion to some degree and further underpins the hypothesis that once individuals have found their preferred foraging strategy, they tend not to deviate from it (Mattern et al., 2007, 2013). This renders hoiho a highly predictable species and means that the results presented in this report likely provide an accurate representation of the utilisation of the respective marine habitats by hoiho from the different sites. This conclusion is supported by the fact that home ranges of birds from Whenua Hou do not seem to have changed significantly since the early 2000s. However, it has to be kept in mind that there is no foraging data for either Pigeon House or the Bravo Is. Group outside of chick-rearing, so that reported results can only be considered representative for this period.

Rakiura hoiho likely face the most significant threats in their marine environment. The presented data provide a solid base for informing the development of effective management guidelines to safeguard hoiho at sea. Given the species' ongoing population decline on the mainland, which is also evident on Rakiura (Yellow-eyed Penguin Trust, 2021), there is a real opportunity to mitigate threats to hoiho and their foraging habitat and consequently provide hoiho populations the opportunity to recover.

Terrestrial threats have negligible impacts for Rakiura hoiho

Whereas predation by feral cats cannot be ruled out entirely on Rakiura, there is little (Mattern, 2020b) to no (King et al., 2012) evidence that this affects hoiho in a significant way. Dogs which continue to negatively impact hoiho on the mainland, are prohibited in Rakiura National Park. Similarly, human disturbance plays no role for the penguins as none of the breeding areas are easily accessible and thus are hardly frequented by humans[2].

[2] The exception may be Long Harry Bay in the north of Rakiura, that is accessible from the North-West Circuit walking track.

Disease outbreaks frequently observed on the mainland (Webster, 2018), appear to be less prevalent on Rakiura. Although disease has been found to be associated with reduced breeding success in hoiho from north-eastern Rakiura, this appears to be related to malnutrition caused by a degraded marine environment rather than an emergence of new disease vectors (King et al., 2012); the same study found disease to be a negligible factor on the Bravo Group and Whenua Hou.

Hence, sea-based factors likely impact hoiho from Rakiura and the Foveaux Strait region the most. Based on studies conducted on the South Island (Darby & Dawson, 2000; Crawford et al., 2017) commercial inshore set netting fisheries likely represent the main threat for the species.

Set netting as main threat for Rakiura hoiho

The hoiho from Port Pegasus foraged exclusively within two nautical miles from the coast. With the foraging movements of all breeding birds concentrated on a small area, the entire local population could experience a catastrophic mortality event, if a set net would be brought out in the area, especially given that there is a maximum permitted set net length of 3000 m for gear set at depths deeper than 2 m (New Zealand Legislation, 2022).

In November 2021, a set net operator accidentally caught six tawaki in the Pigeon House region (Ministry of Primary Industries, 2022), highlighting the threat level of set net fisheries. The only plausible explanation for the dramatic disappearance of an entire hoiho breeding colony (Yellow-eyed Penguin Trust, 2021) at Golden Beach on Rakiura's northeast coast, at this stage, is a catastrophic bycatch event involving inshore set nets. A similar event is believed to have resulted in the sharp drop in penguin numbers on Whenua Hou in 2016 (Crawford et al., 2017). Around Whenua Hou there is now a voluntary set net restriction observed by most of the local operators (Graham Parker, pers. comm.) which appears to coincide with a stabilization of penguin numbers.

This study provides decision makers with the information required to adequately address this issue and, thus, follow the strategies outlined in Te Kaweka Takohaka mō te Hoiho.

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Appendix - Quarterly report summaries

1. **Q1 - 21 Oct – 20 Dec 2020** *DOI: 10.6084/m9.figshare.14256503*

   Field work for the project commenced on Pigeon House peninsula, Port Pegasus/Pikihatiti on 25 November 2020. Initially the locations of three active nests in the eastern hoiho breeding area were known, so that further nest searches were conducted between 26-29 November. Searches covered the eastern ranges of the Pigeon House area as well as Fright Cove on the west side of the peninsula. GPS positions of only two of the three nests were initially available to our team; the third nest was located during the search on 26 November. A fourth active nest was found on 29 November; a failed, fifth nest was discovered by chance on 4 December. GPS dive and camera logger deployments were conducted between 25 November and 7 December 2020. Seven of the breeding birds (four males, three females) were fitted with GPS dive loggers; devices remained on the birds for 4-8 days (mean: 5.4 days). Foraging data showed highly consistent foraging behaviour in all birds.

   Full report: https://figshare.com/ndownloader/files/26919887

2. **Q2 - 21 Dec 2020 - 20 Mar 2021** *DOI: 10.6084/m9.figshare.14374385*

   Between 21 December 2018 and 4 January 2019, a total of six breeding hoiho carried GPS dive loggers. Of these, only three devices could be recovered. One penguin managed to preen off the device while at sea shortly after deployment. Two devices were lost because recapture of the penguins proved very difficult. As a result, deployment periods were extended by more than a week facilitating device loss. Of the three recovered devices, the GPS unit of one device was destroyed as the penguin pierced the casing causing leakage; this did not affect dive data, though. The other units yielded full GPS and data sets. Tracking data from Penguin Bay, highlight increased foraging effort with the penguin performing several overnight trips during which it visited the edge of the continental shelf. At Te Rere, the situation was markedly different with birds performing one-day and short-term trips. GPS data indicates interaction with inshore fisheries, as the penguin performed several trips during which it exhibited linear foraging which is generally associated with bottom trawl fisheries.

   Full report: https://figshare.com/ndownloader/files/27458564