A Jack of All Trades - Fiordland penguins/Tawaki are able to utilise diverse marine habitats during winter migration

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Abstract

Migration and non-breeding dispersal is a common in many animal groups and often driven by seasonal changes in a species' habitat. It is a prevalent behaviour in crested penguins (Eudyptes sp.) that have evolved in and still principally inhabit the subantarctic regions of the southern hemisphere. Tawaki/Fiordland penguins are an exception as they live and breed in the temperate zone breed of southern New Zealand. Nevertheless, they do leave their colonies outside the breeding period and undertake significant pre-moult and winter migrations. Using satellite telemetry, we examined the winter dispersal of tawaki across the species' entire breeding range, to see if dispersal patterns varied depending on where birds originated from, and to gain an understanding of the environmental drivers behind these dispersal patterns via maximum entropy modelling of habitat suitability. All penguins showed the same dispersal patterns irrespective of their origin. The birds travelled southwest with destinations located in the subantarctic region approximately 1,000 km due south of Tasmania. Penguins achieved maximum distances of a median 1,585 km away from their point of origin, covering total distances of a median 6,086 km over the course of a median 135 days. Most birds reached the subantarctic ocean front during the first half of their journeys with several penguins returning to the mainland via a northern route along the subtropical front. Mixed layer depth of around 80 m was a strong predictor of penguin presence matching the usual foraging dive depth recorded for this species. Maxent modelling showed that the species utilises a variety of ocean habitats ranging from polar to subtropical waters, which stands in contrast to general lateral dispersal patterns apparent in other crested penguins. This suggests a high degree of behavioural flexibility in tawaki, which is likely a significant advantage in a changing oceanic environment.

Commented [KS1]: Revise some sentences as some seem incomplete.

Commented [KS2]: But also in temperate zones, birds do commonly migrate.

Commented [KS3]: This may be a bit of a strange start, what about taking a more question-centered introduction.

Commented [KS4]: I believe what you call dispersal, is actually migration, or just movements from summer to winter area and back.

Commented [KS5]: Vague wording.

Commented [KS6]: i.e. before arriving back in the colony?

Commented [KS7]: What is this?

Commented [KS8]: Flexibility over what? Maybe the conditions that they live in are relatively similar throughout the season due to seasonality? Are they then flexible?

Commented [KS9]: Not necessarily: it may also mean they are looking for alternative feeding waters if their original habitat has degraded.
BTW. Migratory birds can be still threatened by e.g. climate change.

Introduction

Migration and non-breeding dispersal is common in many animal groups, but is particularly prevalent in birds (Newton, 2007). With the ability to fly, birds can cover vast distances resulting in collective travel routes spanning the globe (Shaffer et al., 2006; Quillfeldt, Voigt & Masello, 2010; Weimerskirch et al., 2015). Migratory movements are often apparent in species that live and breed in regions affected by seasonal resource variability, effectively forcing the animals to travel to more productive environments at certain times of the year (Bowler & Benton, 2005; Newton, 2007; Ainley & Wilson, 2023). Because long distances might need to be travelled, the dispersal phase of a species' annual life-cycle is often energy demanding (Arizmendi-Mejía et al., 2013), requiring animals to optimise their dispersal movements accordingly (Hennin et al., 2016). This should be especially relevant for non-flying bird species such as penguins.

Of the 18 species of penguins listed on the IUCN Redlist (iucnredlist.org), six species are considered sedentary, remaining at their breeding sites all year without migratory movements being inherent part of their annual cycle, whereas the remainder disperse when not breeding (Garcia Borboroglu & Boersma, 2013). Although latitudinal effects have been reported in species breeding closer to or on the Antarctic Continent, either because breeding sites are ice-bound in winter (Trathan & Ballard, 2013; Wienecke, Kooyman & LeMaho, 2013) or due to seasonality of available prey resources (Pütz et al., 2006; Raya Rey, Trathan & Schiavini, 2007), there are at the very least exceptions to this rule. Gentoo penguins (*Pygoscelis papua*), for example, that co-exist with crested penguins (*Eudyptes spp.*) in various locations in the subantarctic region or with other *Pygoscelis* species in Antarctica, do not disperse over long distances away from their colonies outside of the breeding season, whereas all Eudyptes undertake obligate migration (Croxall & Davis, 1999). Conversely, on the New Zealand mainland, adult hoiho/Yellow-eyed penguins (*Megadyptes antipodes*) and kororā/Little penguins, remain at or near their breeding colonies throughout the non-breeding period (Wilson & Mattern, 2019; Hickcox et al., 2022), whereas tawaki/Fiordland penguins (*Eudyptes pachyrhynchus*) outside the breeding season disperse far into the subantarctic region (Mattern et al., 2018; Thiebot et al., 2020; Green et al., 2022). As such, latitudinal and seasonal changes in the species' environments alone do not fully explain why some species are migratory and others are not.

Tawaki are a particularly interesting species in this regard. After completion of the breeding season in December, at the height of the austral summer, the birds leave their breeding colonies for ca. 10 weeks in preparation for their annual moult, which the birds generally complete when back in their colonies (Mattern, 2013; Mattern & Wilson, 2019a). Considering the energetic demands of the breeding season and the moulting period (Brown, 1989), it is surprising that tawaki migrate considerable distances during the pre-moult period (Mattern et al., 2018) even though the productivity around the NZ mainland reaches its peak at this time (Murphy et al., 2001; Goebel, Wing & Boyd, 2005). But instead of accessing local marine resources, tawaki disperse southwest into the subantarctic region and forage in water masses that originate in the Antarctic Circumpolar Current. As such, seasonal patterns

Commented [KS10]: I think you use the words erroneously. I think you mean migration.

Commented [KS11]: But swimming is also a very energy-efficient way of movement right? And it is also about the gain of energy.

Commented [KS12]: In my understaning this refers to sitting. I think you should use 'resident'. I know that sedentary is often used, but I think this is erroneous use of the word.

Commented [KS13]: Dispersal has a specific meaning in biology. This is not it, and you might want to be careful to avoid confusion for the reader.
Please revise in the whole text.

Commented [KS14]: On what?
Split long sentence

Commented [KS15]: Are they also from mainland?

Commented [KS16]: You make the reader expect that you will study which factors determine whether a species shows seasonal migration of not, but this is not the goal of your study.

Commented [KS17]: Why? Swimming can go together with feeding. Does their food migrate?

Commented [KS18]: Explain this abbreviation the first time.

Commented [KS19]: Do you have a reference?

Commented [KS20]: In = from?

Commented [KS21]: For me as a landbird ecologist, it seems odd that they go south, as those areas must be only colder than their summer areas. Can you mention this contrast somewhere (in discussion e.g.)?

in local productivity do not seem to be a defining factor for the tawaki migration, at least not during the pre-moult period.

The key to understanding the drivers behind penguin migration ultimately requires knowledge about the resources that the birds consume at the destination of their journey (Croxall & Davis, 1999). Obtaining this information, however, is extremely difficult given the logistical constraints of making observations and obtaining samples at the non-breeding destination. An alternative approach, therefore, is to examine the seasonally occupied regions in the context of a species' known foraging behaviour. The marine ecology of tawaki has been studied extensively in the past decade, allowing some inferences to be made about their diving behaviour. When breeding, tawaki exhibit a high degree of behavioural plasticity that allows them to utilize variable marine habitats, ranging from coastal shelf and shallow inshore habitats (Mattern & Wilson, 2019a), to fjord systems and pelagic environments (Otis, 2021; Hornblow, 2022). As such it is plausible that penguins utilising different regional habitats when breeding may also show different approaches to their non-breeding migration. Previous studies of tawaki dispersal focussed on birds from single locations (Mattern et al., 2018; Thiebot et al., 2020) which may provide a site-biased representation their migration.

Commented [KS22]: Remove "the key to"

Commented [KS23]: But also on their way. Not only the furthest point or place where they stay longest is relevant.

Commented [KS24]: Various?

Commented [KS25]: Vague wording

Commented [KS26]: Of their

We examined the distribution of tawaki over the winter of 2019 using satellite transmitters. Our aims were to (a) track individual tawaki from across the species' distributional range to account for potential breeding location effects on migration behaviour, (b) evaluate environmental conditions at the birds' non-breeding destinations to model the physical factors associated with these locations and, (c) consider potential advantages of tawaki movement patterns outside of the breeding season in the context of other crested penguin species.

Commented [KS27]: And you test whether it differs per sex.

Commented [KS28]: Conditions and physical factors are vague, can you say it more explicitly?

Commented [KS29]: ...which do not migrate?
But why would those other species not migrate if migration is advantageous for this species?

Materials & Methods

Study species

Tawaki/Fiordland penguins are one of seven crested penguin species (*Eudyptes sp.*) currently recognized by the IUCN Redlist (https://www.iucnredlist.org/) and is the only crested penguin that breeds in a temperate and continental setting along the southwestern coastlines of Aotearoa/New Zealand (Mattern & Wilson, 2019a). Long thought to be one of the rarest penguin species, recent population surveys revealed their numbers to much considerably larger than previously assumed with estimates ranging up to 50,000 mature individuals (IUCN, 2020). Exact population estimates are difficult due to the species' cryptic breeding behaviour in remote and difficult to access regions of New Zealand's South Island (Mattern & Wilson, 2019a).

Commented [KS30]: What do you mean with that?

Commented [KS31]: Much = be

Tawaki have been described as "winter breeders" (Poupart et al., 2019) although this overly generalises the species' annual cycle with eggs hatching in the early austral spring (September) and chicks fledging in early summer (December). At the conclusion of the breeding season, the penguins undertake an extensive pre-moult migration that lasts until late January and early February before undergoing their annual moult (Mattern et al., 2018). By the end of February and beginning of March, tawaki leave their colonies on their winter

Commented [KS32]: Autumn and winter

migration. Although this migration starts in the austral Autumn (March-May), the majority of tawaki remain at sea for the first 6-8 weeks of winter (Green et al., 2022).

Satellite transmitter deployments

Between 22 February and 7 March 2019, a total of 16 adult tawaki post-moult were fitted with Argos satellite transmitters (SPOT-275 Platform Transmitter Terminals, dimensions: W x L x H – 15mm x 85mm x 17 mm; weight: 40 g; Wildlife Computers, Redmond, WA, USA). All birds were captured at the moulting sites, weighed with 5 Kg Pesola spring balance (division: 50 g), individual marked with passive integrated transponders, and had morphometric measurements taken to determine sex (White et al., 2021). Deployments occurred at three sites in New Zealand's Southwest (Figure 1).

Commented [KS33]: Put in more logical place in the sentence, say "in the post-moult period"

Commented [KS34]: How is this attached? And is it just battery-powered?

Commented [KS35]: How?

Commented [KS36]: But how can you call these already post-moult then? Do they still stay there for some time after moulting?

Commented [KS37]: individually

Commented [KS38]: Use this as 1st sentence of next paragraph

It was intended to deploy five devices at three sites spanning the species' breeding range, namely Jackson Head, West coast (S43.9633,E 168.6107); Harrison Cove in Milford Sound/Piopiotahi, Fiordland (S 44.6202,E 167.9097); and Whenua Hou, Foveaux Strait (S46.7582,E 167.6407). However, Jackson Head was practically devoid of moulting birds when visited so that only a single female could be fitted with a transmitter. Instead, two of the remaining devices were deployed on additional birds on Whenua Hou, while another two transmitters were fitted to two tawaki that moulted outside of the tawaki breeding range in the care of the Oamaru Blue Penguin Colony on the east coast of the South Island (S45.1103,E 170.9801). The two Oamaru deployments yielded very little data as both devices ceased 3-19 days after the birds were released from care and were, therefore, omitted from further analysis. Overall, three female and two male penguins in Harrison Cove (22.02.2019), three females and five males from Whenua Hou (25.02.2019), and a single female from Jackson Head (27.02.2019) were fitted with SPOT-tags (Table 1).

The devices were attached using the Tesa-tape method (Wilson et al., 1997) with a thin layer of Pattex rubber glue (Henkel AG & Co. KGaA, Düsseldorf, Germany) applied to the feathers below the transmitter base, with an additional layer of Araldite 5-minute epoxy glue (Selleys, Auckland, New Zealand) covering the tape wrapped around the devices. The entire deployment procedure from catching to release took between 10-15 minutes, during which the birds were kept in a cloth bag that covered their heads. Birds were eventually released back into the burrow in which they had moulted.

Commented [KS39]: Move up 1 paragraph

Basic satellite data analysis

The satellite transmitters were programmed to start operating once the device's saltwater switch detected immersion, i.e., when a penguin had finished moult and entered the sea to launch the winter journey. The devices were programmed to broadcast a signal to Argos satellites 15 times per hour, which ensured that the battery of the units would last around six months and therefore the entire winter dispersal period could be covered. With these settings an average 10 locations per day could be obtained for each bird. Not all these locations were classified as reliable by the Argos system (e.g. Thomson et al., 2017). Therefore, for spatial analysis any locations for which the locational error could either not be determined (Argos classes A,B,Z) or was >1500 m (Argos class 0) were omitted from analysis. Accepted satellite data was furthermore filtered using the function 'sdafilter' from the package 'argosfilter' library (Freitas, 2012) in R 4.2.2 (R Core Team & R Development Core Team,

Commented [KS40]: This seems low if it transmits 15 times per hour

Commented [KS41]: So what was your final sample size per day on average? Did the subsetting not result in large gaps for a several days?

2022). This function removes locations identified as being outliers based on swimming speed, distance between successive locations, and turning angles (Freitas et al., 2008).

Accepted data were then used to determine individual foraging tracks and to calculate basic trip statistics, providing basic metrics to compare movement of penguins from the different study sites. These were trip duration, maximum distance from start point, distance travelled per day, and mean daily swimming speed. Swimming speed was calculated as the distance between two consecutive locations on the same day divided by the time difference when these two locations were recorded. These speeds must be considered minimum as they do not integrate the diving phase of the birds with additional vertical and lateral movements. We used general linear mixed models, employed in R 4.2.2. (R Core Team & R Development Core Team, 2022) to examine differences in trip statistics between birds from the different sites.

Maxent modelling of suitable dispersal destinations

We used the maximum entropy approach ("Maxent"; Phillips, Anderson & Schapire, 2006; Phillips & Dudík, 2008; Phillips et al., 2017) to model the distribution of tawaki at their dispersal destination in the subantarctic region. Maxent employs a machine-learning method that uses presence-only data to estimate a target probability distribution by finding the probability distribution of maximum entropy. Maxent examines an a priori set of environmental variables at locations where animal presence is recorded and compares these with the same variables at generated pseudo-absence locations, to identify which variable best explain animal selection of used sites and to project these conditions to wider areas that should also be suitable for the animals even though no actual presence data was recorded. Maxent's similarity to inhomogeneous Poisson point processes means that outputs can be scaled to probability of presence using a complementary log-log link (*cloglog*) function so that habitat suitability can be visualised in a 0-1 raster set, where cell values closer to 0 are indicative of unsuitable, and values closer to 1 of suitable habitat conditions.

Six environmental data features previously identified to best describe habitat preferences of tawaki in the high seas (Mattern et al., 2018) were selected to develop a Maxent distribution model in the subantarctic region. Two features were derived from NASA's satellite-based AUQA-Modis ocean colour program (https://oceancolor.gsfc.nasa.gov), namely night-time sea surface temperature (*nsst*) and chlorophyll-a concentration (*chlo_a*). We also used sea level anomaly (*sla*; Copernicus Climate Data, https://doi.org/10.24381/cds.4c328c78), surface current velocity (*velo*; OSCAR 3rd degree surface currents, https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg), Mixed Layer Depth (*mld*; SEANOE, https://doi.org/10.17882/91774), and bathymetry (*bathy*; GEBCO 2022; https://www.gebco.net/data_and_products/gridded_bathymetry_data/).

Tawaki disperse south over the austral fall and winter period, which greatly limits completeness of satellite-based environmental data. Short day lengths and frequent cloud cover means that raster layers that are derived from optical measurements from space often contain cells without valid data and, thus, are not suitable for Maxent modelling. To overcome this limitation, we had to use seasonal averages that combine measurements taken from March to June 2019. SST and Chlo_a data were directly available for download as

Commented [KS42]: Which cut-off values did you use?

Commented [KS43]: How was it possible to see if a bird was foraging?

Commented [KS44]: Why these and not others? E.g. total distance.

Commented [KS45]: So this is a second reason

Commented [KS46]: variables

Commented [KS47]: But during which period, and in which area? What does your study add to that study?

Commented [KS48]: But is that comparable to the area that you study?

Commented [KS49]: AQUA

Commented [KS50]: Maybe you can shortly mention what each measure represents, e.g. productivity, depth, etc.

Commented [KS51]: But please discuss in discussion which insights may you miss because variables were taken only on the year-level.

Commented [KS52]: This is a shame, but I think there is no alternative?

Commented [KS53]: Please be consistent with the notation above.

seasonal averages for focal period. However, current velocity and sea level anomaly data were only downloadable as 5-day grids. For these variables, all data sets for March to June were downloaded and combined into a single mean raster by using the 'Raster Calculator' in ArcGIS Pro 3.1.0 (ESRI Inc., Redlands, CA, USA). Sea surface current data consisted of vertical (v) and horizontal component (u) rasters. Using the 'Raster Calculator' the vectorial current velocity raster was calculated as velocity=$\mathrm{sqrt}(u^2+v^2)$. The Mixed Layer Depth raster was only available as a composite of direct measurements taken between 1970 and 2021 so that seasonal discrimination of the data was not possible. Obviously, bathymetry also is a temporally static variable.

All environmental rasters clipped to the same extent of 30°S to 65°S and 80°E to 45°W (i.e. across the date line) in ArcGIS Pro 3.1.0 (function 'Clip raster'). As the data sets were available in different spatial resolutions, the respective rasters were first projected to UTM datum using the ArcGIS function 'Project raster', then resampled ('Resample') to have the same resolution with cell sizes of 25x25 km. The resulting clipped and resampled rasters were then exported as ASCII raster files that could be processed by the Java software Maxent 3.4.4 (Phillips, Dudík & Schapire, 2023).

Tawaki dispersal movements can be differentiated into three phases, the outgoing travel phase, the foraging phase at the destination, and the incoming return phase (Mattern et al., 2018). For each bird, locations that were >75% of the maximum distance from the point of origin were classified as "at destination". To model the environmental suitability of the subantarctic region for tawaki during their winter migration, only locations classified as "at destination" were used. The Maxent analysis was set up to use a randomly chosen 25% of the location data as test samples with the remaining data used for model training over 500 iterations. The model produces response curves for each environmental variable that are then used for jack-knife analysis of variable importance expressed as percent contribution (PC) to the model (Phillips, 2017).

Commented [KS54]: I am sceptical of this, because from the tracks on the map it seems that the journey is just one continuous gradual trip outward and backward, without clearly one destination and a travel to and from it. Foraging likely occurs during all stages.

Permits and Animal Ethics

This study complies with the relevant national, international, and institutional guidelines regarding animal care. It was conducted under a research permit (38882-RES) issued by the Department of Conservation under the New Zealand Wildlife Act 1953. All manipulations were approved by the Ethics Committee of the University of Otago (D69/17).

Commented [KS55]: Which?

Results

Satellite tracking

Between 23 February and 11 September 2019, a total of 15,010 locations was received for the 14 tawaki fitted with satellite tags. After filtering, 5,024 locations were accepted for the reconstruction of the birds' travel paths (Figure 1) and subsequent analysis.

Birds from the three main groups departed on their winter migration at around the same time with average departure dates of 27 February (Milford Sound/Fiordland, n=5), 28 February (Jackson Head/West Coast, n=1), and 1 March (Whenua Hou/Foveaux Strait, n=8) (Table 1).

Commented [KS56]: This is not really a group

A median of 280 locations (range: 5-870) were received per bird and penguins transmitted for a median of 127 days (range: 52-192 days) which allowed the reconstruction of complete winter trips for five birds, with an additional six birds transmitting well into the third, return stage of their journey. Three birds stopped transmitting before they had embarked on their return to the mainland.

Commented [KS57]: This is very low, 5 locations. How did you deal with that?

All tawaki travelled southwest with destinations located in the subantarctic region approximately 1,000 km due south of Tasmania in international waters outside of the New Zealand Exclusive Economic Zone (Figure 1). Penguins for which complete winter trips could be recorded achieved maximum distances of between 1,002 and 2,193 (median: 1,585 km, n=5) kilometres away from their point of origin, covering total distances of a median 6,086 km (range: 3,917-7,200 km) over the course of 131-156 days (median: 135 days) (Table 1). Penguins that entered the return phase before transmissions stopped reached a median maximum distance of 1,689 km (range: 1,002-2,688 km, n=11) from their place of moult.

Comparing the birds' mean distances from their place of moult on a weekly basis shows little difference in the distances reached each week when comparing birds from Milford Sound and Whenua Hou (Figure 2). Penguins from Milford Sound and Whenua Hou had reached their non-breeding destinations by the first week of April. The return journeys in both groups started as early as the first week of May, with all birds moving back towards the mainland by the first week of June. The female from Jackson Head did not distance herself as much or as fast from the mainland, but her home distances still fall well within the range of the other groups.

Commented [KS58]: Please indicate sample size per group in figure captions

Commented [KS59]: What do you mean?

Linear mixed effect models of the birds' spatial distribution using the means of recorded longitude and latitude show no major differences in the distribution of penguins from the three main groups during any of the trip stages (Table 2). The only significant difference is that males tend to forage around 3 degrees further south while at the winter destination. Thus, data from all groups were pooled to model habitat suitability of the subantarctic ocean region as a non-breeding destination for tawaki.

Commented [KS60]: Would it also be intersting to look at a relation with body mass?

Maxent modelling of habitat suitability

Calculating daily average locations for each bird and limiting the resulting data set to locations ≥75% of the maximum distance from each bird's point of origin, reduced the data set to 605 locations that were the used to estimate penguin distribution at their winter destination using six environmental variable rasters (Figure 3).

The resulting Maxent model (Figure 4) indicates that suitable habitat for tawaki is located south of the subantarctic front (SAF), principally south of latitude 50°S and west of longitude 160°E. Overall bands of suitable conditions can be found at variable rates along the southern fringes of subantarctic front throughout the western Pacific and into the eastern Indian Ocean. The exception being the area of the Campbell Plateau directly south of New Zealand. Except for a small band of suitable conditions along the south-eastern limits of the Plateau, the subantarctic waters within the NZ EEZ seem largely unsuitable for tawaki.

The model indicated that mixed layer depth (MLD) was the most important predictor suitability of the subantarctic ocean (percent contribution to the model – MLD: 57%) followed by ocean temperature (NSST: 28.3%) and bathymetry (BATHY: 12.5%). Chlorophyll-a (CHL_A: 0.9%), sea level anomaly (SLA: 0.7%), and surface current velocity (SLA: 0.6%) played next to no role in determining environmental conditions preferred by tawaki at their winter dispersal destination. The response curves resulting from the model provide deeper insights into the range over which the environmental variables are of importance. The response curve for mixed layer depth peaks around at depths of 81-83 metres; most suitable conditions for tawaki presence (probability >0.75) range at MLDs between 71 and 91 m (Figure 5). Sea surface temperature (NSST) peaks around 6°C with probability of presence being higher than 0.75 in water temperatures between 4°C and 8°C. For the last relevant variable, bathymetry (BATHY), has no distinct peak but water depths between 1,800 m and 4,500 m best predict tawaki presence.

Discussion

Tawaki migrating over winter showed similar movement patterns and ranges as has previously been determined for their pre-moult journeys (Mattern et al., 2018). However, whereas before the moult the penguins have only 8-10 weeks to complete their journeys, they can take twice as much time over winter. This underlines the remarkability of the tawaki long-distance pre-moult movements (Mattern et al., 2018) as well as the importance of the subantarctic region south of Australia for the species' non-breeding distribution and survival (Thiebot et al., 2020; Green et al., 2022).

Effects of devices on penguin performance and survival

While externally attached devices inevitably influence the performance of diving animals (e.g., Chiaradia et al., 2005; Wilson & McMahon, 2006; Ludynia et al., 2012), previous studies on crested penguins found little evidence that the effects are significant enough to alter their migratory behaviour or affect their survival (e.g., Pütz et al., 2006; Mattern et al., 2018; Houstin et al., 2022). Although cessation of transmission can indicate the death of a study animal, malfunctions and especially loss of the device are also possible causes (Sergio et al., 2019). Devices on five of the eight tawaki from Whenua Hou stopped transmitting before the birds had completed their journeys (Table 1), yet all birds fitted with transmitters in February 2019 were re-sighted in their home colony in August 2019. The single female from Jackson Head was encountered incubating a fresh clutch of eggs in mid-August 2019,

Commented [KS61]: How did you deal with non-independence (because you track individuals) and also auto-correlation (because the next location is probably close to the previous location, again not independent).

Commented [KS62]: Where can i see the captions?

Commented [KS63]: Could there be a dichotomy? Either they go on the STF, or south of the SAF?

Commented [KS64]: What do you mean? Say in easier way? E.g. different places of different size?

Commented [KS65]: Predictor for

Commented [KS66]: Be consistent in abbreviations

Commented [KS67]: Velo.
Also, be consistent in using small or capital letters.

Commented [KS68]: I don't see how this is underlined by the fact that winter migration is longer than pre-moult migration

Commented [KS69]: You can mention in the methods that potential tagging effects are discussed in the discussion.

Commented [KS70]: But did those studies tag birds in the same annual moment as you did?

with the device still attached and recoverable. Four of the five birds fitted with transmitters in Milford Sound have subsequently been observed by an automatic wildlife monitoring system, so that only one of the birds fitted with transmitters remains unaccounted for. Hence, device loss was the main explanation for the cessation of signal transmission in this study.

Movements of penguins from different breeding sites

Tawaki from the species' entire breeding range exhibited similar movement patterns. With all birds heading towards the same subantarctic area south of Tasmania (Figure 1), it could be expected that on average penguins from Milford Sound would distance themselves slightly more from their home colony than their Whenua Hou counterparts – Milford Sound is located approximately 200 km further north. But this is not the case (Figure 2). Instead, the distance between Whenua Hou and Milford Sound may reflect in the fact that some of the Whenua Hou penguins reached further west than their Milford Sound conspecifics. However, on the scale that the tawaki winter migration occurs, the origin of the birds had no significant effect on how penguins from the three main groups distributed themselves during the various stages of their winter journeys (Table 2). Individual variation likely masks any potential effect of the spatial distance between the birds' origins.

Commented [KS71]: But in that figure, you use per group an average per week, so you cannot say whether they go further, because differences may be cancelled out by averaging (birds may reach their maximum distance at different moments).

The tawaki winter migration has previously been studied via geolocators (Thiebot et al., 2020; Green et al., 2022). Although not as spatially accurate as satellite transmitters, the penguins' reconstructed movement patterns match our observations. While both studies were conducted with birds from colonies in close proximity to or at the same sites of this study, it confirms consistency in the penguins' winter movements across the years. This relative uniformity in the movement patterns of tawaki that moulted along the western shores of southern New Zealand underlines the importance of the birds' non-breeding destination, the ocean south of the subantarctic front (SAF).

Commented [KS72]: And/or precise

Commented [KS73]: How many years in total?

Characterisation of environment in the destination region

Physical ocean boundaries, such as fronts, are of significant biological relevance as physical processes can result in an accumulation of nutrients and, therefore, increased prey abundance for oceanic predators (Bost et al., 2009a). Tracking data showed that the penguins' dispersal destination was located south of the Subantarctic Front (Figure 1), which matches observations previously reported using geolocation data (Thiebot et al., 2020; Green et al., 2022). This ocean region is characterised by colder surface temperatures (3-8°C) and low chlorophyll-a concentrations (Figure 3).

Commented [KS74]: results

Commented [KS75]: Colder than what?
And low compared to what?

During their winter migration, tawaki leave the areas of subtropical waters north of the subtropical front (STF) characterized by temperatures >12°C, with which the species is exclusively associated during the breeding season (Mattern & Wilson, 2019a; Poupart et al., 2019; Otis, 2021; Hornblow, 2022). Within 3-4 weeks most of the penguins passed through the subantarctic region (8-11°C) and crossed the Subantarctic Front into the waters of the Polar Frontal Zone (PFZ), that is, the oceanic region located between the Subantarctic Front (SAF) and the Antarctic Polar Front (APF). This is consistent with temperature profiles reported in Thiebot et al. (2020).The PFZ is characterized by an entrainment of nutrients that originate from upwelling forces in the Southern Ocean which can sustain intense diatom

Commented [KS76]: Within 3-4 weeks time window, or 3-4 weeks after departure?

blooms (Sarmiento et al., 2004). As such, this nutrient richness probably explains why the PFZ is targeted by tawaki.

The closely-related Snares penguins (*E. robustus*), similarly to tawaki, move westwards to the oceans south of Australia in winter, but stay predominantly along the subtropical front (Green et al., 2022). However, Snares penguins leave on their winter journeys 4-6 weeks later than do tawaki and reach their non-breeding destinations only when tawaki are well into the return phase of their winter movements. Thus, seasonal differences in the ocean productivity during both species' winter migration appear to play a vital role in the spatial segregation of both species' marine habitat in the eastern Indian Ocean south of Australia. Seasonality likely also explains why chlorophyll-a concentration plays only a minor role in determining the habitat suitability of tawaki during the winter migration.

Commented [KS77]: Similarly, this could explain the dichotomy seen in this species tawaki. Either to the STF, or south of the SAF? Did that correlate with departure date?

Although chlorophyll-a concentrations are considered a good proxy for ocean productivity and increased prey availability for seabirds (Suryan, Santora & Sydeman, 2012), this may not always be the case (Grémillet et al., 2008). Moreover, chlorophyll-a concentration data are generally derived from optical satellite measurements and therefore limited to the surface layer of the oceans (Morales & Acker, 2011). As such, chlorophyll-a concentration represents the environmental conditions at the surface and might not reflect what is happening at greater depth. This is likely to be particularly relevant in deep diving species, such as tawaki (Grémillet et al., 2008). Although the satellite transmitters did not record any information about diving behaviour, the Maxent model nevertheless allows to make inferences about tawaki diving behaviour while in the subantarctic region.

Commented [KS78]: How deep do they go?

Commented [KS79]: Which inferences exactly?

The models of habitat suitability indicate a substantial effect of the mixed layer depth (MLD) on the likelihood of tawaki presence. With a contribution of 57% to the model, MLD must be described as a stand-out parameter during this second stage of the winter migration. MLD provides an indication of at which depth the thermocline, an abrupt change in water temperature and/or salinity, is located (Kara, Rochford & Hurlburt, 2000). Just like oceanic fronts, the thermocline represents a physical boundary at which nutrients and biomass can accumulate (Bost et al., 2009a). The model suggests that the highest likelihood of tawaki being present was in regions with the shallowest MLD over most of the Pacific and Indian Ocean's subantarctic regions (Sarmiento et al., 2004). In this region, MLD ranges around 80 m (Figure 5), which corresponds to dive depths recorded in tawaki during the breeding season when foraging outside of fjord environments (Otis, 2021; Hornblow, 2022). Thus, the thermocline is certainly accessible by tawaki at their non-breeding destination. Foraging at the thermocline has already been described as a strategy used by penguins to pursue predictably-distributed prey (Bost et al., 2009a; Labrousse et al., 2019). During winter, juvenile emperor penguins are believed to be foraging at the thermocline for myctophid fish and squid (Labrousse et al., 2019). Given that the abundance of krill – known to be an important food source for Snares penguin (Mattern et al., 2009) – is decreased over the winter period of the year (Young et al., 1993) it seems likely that tawaki are also primarily targeting fish and squid when venturing south. This dietary preference also matches what is known about the species' prey composition during the breeding season (van Heezik, 1989, 1990; Poupart et al., 2019; Hornblow, 2022).

Commented [KS80]: Preferably mention this also earlier, in methods.

Commented [KS81]: OK, but diet in different seasons may differ.

Variable ocean habitats, variable diet

Crested penguins all move far from their breeding areas over winter (e.g., Pütz et al., 2002; Rey et al., 2007; Bost et al., 2009b; Thiebot et al., 2011; Green et al., 2022). Populations that live and breed in pelagic environments principally show a lateral movement where the birds travel eastwards or westwards, focussing their activities on water masses located at or near frontal zones, be it the Subtropical Front (e.g. Snares penguins, Northern Rockhopper penguins *E. moseleyi*), the Subantarctic Front (Eastern Rockhopper *E. filholi*), and/or the Polar Frontal Zone (Macaroni/Royal penguins *E. chrysolophus/schlegeli*) (Green et al., 2023). What sets tawaki apart from the other crested penguin species, is that their migration spans three major fronts and the associated water masses ranging from subtropical to polar. Foraging in oceanic regions characterised by significantly different environmental conditions should also reflect in the prey consumed by tawaki during their winter migration.

Commented [KS82]: Not possible?

Commented [KS83]: But were other penguins sampled in the same way?

This raises the question, whether prey abundance or quality can explain tawaki travelling thousands of kilometres to the regions south of the Subantarctic Front. Clearly, a substantial amount of prey must be consumed on the penguins' return journey, which, compared to the outgoing phase of the winter migration, is prolonged (Figure 2). Even though they breed south of tawaki, Snares penguins move further north and remain in the vicinity of the Subtropical Front over winter (Thompson, 2016; Green et al., 2022). The tawaki satellite tracks show that several of the birds return to the mainland via routes along the STF also (Figure 1), indicating this area is as suitable for tawaki as it is for Snares penguins. Tawaki start on their winter journeys two months earlier than Snares penguins (Green et al., 2022) which might make visiting the southern regions in autumn (March-May) more viable for tawaki, as the reduction in ocean productivity during winter has yet to take effect (Moore & Abbott, 2000; Murphy et al., 2001). However, considering that many other crested penguins forage exclusively at these latitudes through the winter (Green et al., 2023), seasonality seems unlikely to be an inhibiting factor and, conversely, not a compelling explanation as to why tawaki favour subantarctic over subtropical waters.

Commented [KS84]: Not easy to say from the figure, as that is averaged per week. See also comment on L. 326.

Commented [KS85]: In line 362 you say 4-6 weeks.

Without knowledge about prey consumed over the non-breeding period, it is difficult to unravel why tawaki cross two major fronts during the winter migration. However, the fact they do may provide some insight into why the tawaki population is doing better than other NZ crested penguins.

Commented [KS86]: Avoid 'why' as it is vague. Please be concrete.

Commented [KS87]: Please be aware in your interpretation of results that measuring an outcome alone (i.e. migration route), does not prove what strategy the bird had, or what it favours. For that you need to know what would have been the outcome of alternative routes as well.

Accessing different water masses a key for population stability?

Although tawaki have long been considered one of the rarest penguin species (McLean et al., 1997) and one that may be undergoing a steady decline in population numbers (Otley et al., 2018), recent population surveys indicate the species is considerably more numerous than previously thought (Long, 2017; Mattern & Long, 2017; Long & Litchwark, 2021), and might even be expanding its range (Young, Pullar & McKinlay, 2015; Mattern & Wilson, 2019a). As a result, the IUCN Red list downlisted tawaki from "Vulnerable" to "Near Threatened" in 2020 (IUCN, 2020). This stands in stark contrast to two other crested penguins breeding in the New Zealand subantarctic region, the Erect-crested penguin (*E. sclateri*) and the Eastern Rockhopper penguin. Both species have experienced significant declines in the past 50 years (Taylor, 2000; Hiscock & Chilvers, 2014; Davis et al., 2022), a trend that largely continues, albeit at a reduced rate in recent years (Morrison et al., 2015). They breed on remote subantarctic Bounty, Antipodes, and Campbell Islands southeast of New Zealand, about halfway between the Subtropical and Subantarctic Fronts. The winter migration of Eastern Rockhopper has been recently examined and birds tended to move eastwards along the Subantarctic Front into the southern Pacific ocean, which conforms with the lateral movement patterns common in crested penguins (Thompson, 2016; Green et al., 2023). Data from GLS tracking of Erect-crested penguins seem to suggest similar trajectories in Erect-crested penguins (Green, 2023). Hence, the penguins primarily remain within the same water mass throughout the non-breeding period, which also means that changes to the productivity within these water masses may affect their foraging success and survival, ultimately driving population changes (Hilton et al., 2006). Environmental phenomena, such as El Niño or La Niña which significantly influence intensity and distribution of ocean productivity, have a more uniform effect within certain water masses (Racault et al., 2012), which then in turn could negatively affect penguin species that are concentrating their winter migration within a limited band of latitudes. Compared to other crested penguins found in New Zealand, tawaki inhabit a diverse array of water masses. It is likely that plastic behaviour observed during the breeding season (Otis, 2021; Hornblow, 2022) also enables them to adapt their behaviour during the winter migration to the varying foraging conditions in different water masses.

Commented [KS88]: Be consistent in whether you abbreviate this or not.

Commented [KS89]: This is unknown and too speculative. Please be aware that you don't know what they eat and thus you don't know whether the foraging conditions differ and whether they have adapted to that. In the worst case, they are making 'the best of a bad job'.

Conclusion

During the non-breeding period, tawaki exhibit the same behavioural plasticity that allows them to utilize different marine habitats that is also apparent during the breeding period (Mattern & Wilson, 2019a). This could be a significant advantage in the face of ongoing and rapid change in our oceans, especially when compared to the strategies of other crested penguin species in the New Zealand region. According to recent population estimates, tawaki and Snares penguins, two species that breed in the warm waters north of the Subtropical Front, both show stable if not increasing population trends (Mattern & Wilson, 2019a,b). Snares penguins even move along the Subtropical Front when not breeding (Green et al., 2022). In contrast, Erect-crested and Eastern Rockhopper penguins that both breed exclusively in subantarctic waters are declining (Hiscock & Chilvers, 2014). As such, the secret of success seems to lie in access to warmer waters. In this light, tawaki's affinity to move into the subantarctic region appears to be counter intuitive. However, travelling to the Polar Front at least does not seem to negatively affect the penguins' survival. This is likely due to a combination of physical characteristics at the penguins' non-breeding destination that make this region adequate foraging habitat, and the fact that tawaki can utilize resources in warmer waters on their slow return to their breeding sites. In the end, their non-breeding movements to the south are what roots tawaki in in the Subantarctic region, from where crested penguins originated (Cole et al., 2019).

Commented [KS90]: See previous comment.

Commented [KS91]: This is not a conclusion. And I doubt the validity of this statement. It could also be that tawaki try out different habitats because their original preferred habitat is in decline or degrading. So it doesn't mean directly that they are coping well.

Commented [KS92]: It is not possible to say this.

Commented [KS93]: This is pure speculation.

Acknowledgements

We thank the members of our field teams for the assistance with satellite transmitter deployments and recoveries, especially Richard Seed, Andrea Faris, and Mel Young. The Antarctic Research Trust is grateful to all those who contributed financially to this study, in particular Erika Bodmer, Sylviane Brunner-Bodmer, Ernst Frei, K-Tec AG, Verena & Ulrich Knoblauch, Alexandra Logan, Jrma Pittard, Eva & Erwin Mayer Anouch & Karin Reckinger, Royal Zoological Society of Antwerp, Klaus Peter Schmidt, Pia & Peter Schudel, Katharina Steiner, Anita & Georg Weibel, Ursula Wölfli and Barbara & Wilfried Wulfers. We are ever so grateful for the logistical support we keep receiving from Southern Discoveries in Milford Sound, and the Department of Conservation crew in Invercargill (Rhuaridh Hannan, Sharon Trainor) that have helped us to get to Whenua Hou for this study. Very special thanks to David Ainley for extensive review of an earlier draft of this manuscript.

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Commented [KS94]: Please indicate what kind of publication Hornblow 2022 is. MSc dissertation?

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