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Crary Bank – a Deep Foraging Habitat for Emperor Penguins in the western Ross Sea

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Abstract

Although most dives of emperor penguins (*Aptenodytes forsteri*) are less than 100 m, penguins from the Cape Washington colony regularly perform deep dives > 400 m. To evaluate the significance and location of these deep dives of birds on foraging trips from Cape Washington, we report the satellite tracks of three birds. We also review the frequency of deep dives in the 35 of 42 birds that performed deep dives during seven research seasons over 22 years. Records included 83,314 dives, of which 1,418 were > 400 m deep (deepest 552 m). Durations of these deep dives ranged from 7 to 13 min, up to more than twice the aerobic dive limit. Inter-deep-dive-intervals (IDDIs) between most deep dives were 10-20 min. The travel routes of satellite-tagged birds showed that all three spent time over Crary Bank, about 100 km from Cape Washington. Dives > 400m only occurred over Crary Bank in the two satellite-tracked birds that were also equipped with dive recorders. The depths of the dives were consistent with the distribution of the most common, and energy-dense prey item found in their diet, *Pleuragramma antarctica*. We conclude that significant food resources are located over Crary Bank, accounting for the deep dives and success of birds from Cape Washington, the second largest, stable colony of emperor penguins known.

Keywords: penguin, Crary Bank, Antarctic silverfish, Ross Sea, inter-deep-dive-interval, Ross Sea Region MPA

Introduction

Emperor penguins (*Aptenodytes forsteri*) dive to different depths to forage on underwater prey. While they are known to dive as deep as 564 m, the vast majority of dives are <100 m deep (Kirkwood and Robertson 1995; Kooyman and Kooyman 1995; Wienecke et al. 2007). However, dives >400 m deep have been documented among birds breeding at several colonies: Cape Washington (Sato et al. 2011), Coulman Island (Kooyman and Kooyman 1995), Taylor, Auster and Amanda Bay colonies (Kirkwood and Robertson 1997a, b; Wienecke et al. 2007), and at the Pointe Géologie colony (Zimmer et al. 2010).

The specific purpose of deep diving has not been established. One possibility is that penguins are feeding on or near the bottom at sea mounts or banks proximate to their colonies. For example, dives made by emperor penguin females and males in winter and spring from the Pointe Géologie colony showed preferences for bottom dives of 200-300 m (Zimmer et al. 2008; Rodary et al. 2000). And emperor penguins from Coulman Island and Cape Washington routinely perform deep dives during spring foraging trips (Kooyman and Kooyman 1995; Sato et al. 2011).

The topography of the Ross Sea shelf is characterized by glacier-gouged troughs, some > 1000 m deep, between which are banks, some rising to within 250 m of the surface and thus within reach of foraging emperor penguins (Anderson 1999; Davey 2004). One such bank is Crary Bank, located within 100 km of the Cape Washington colony, one of the largest of known colonies (Kooyman and Ponganis 2012). This bank contains a rich benthic invertebrate assemblage (Barry et al. 2003) as well as dense shoals of mid-water Antarctic silverfish (*Pleurogramma antarctica*) (O'Driscoll et al. 2011), a known favored prey of emperor penguins and Weddell seals (*Leptonychotes weddellii*) (Cherel and Kooyman 1998; Fuiman et al. 2002). Crary Bank is also within the recently established Ross Sea Region Marine Protected Area (MPA). This adds a collective importance to the bank for the ecology of the large emperor penguin colonies nearby and to the rationale of the MPA location.

Based on the satellite track and dive record of one bird from Cape Washington (Ancel et al. 1992), we suspected that deep dives conducted by emperor penguins from the Cape Washington colony represented foraging over Crary Bank. To explore this idea and help understand the prevalence, purpose and location of these deep dives, we examined dive records and satellite tracks from seven years of field projects over a span of 22 years at Cape Washington, from 1989 to 2011. Our objectives were to use satellite tracking data to determine: (1) penguin movement from the Cape Washington colony during the chick nurturing time, (2) the location of dives > 400 m; (3) features of deep dive profiles, and (4) the Inter-Deep-Dive-Interval (IDDI: the time between serial deep dives) to evaluate the physiology and swim effort of 400+ m deep dives (as in Tyack et al. (2006)).

Materials and Methods

Study site

All seven studies were conducted between October and November from a remote field camp approximately 2 km from the Cape Washington (74° 39' S; 165° 22'E) emperor penguin breeding colony while penguins were rearing their chicks. Researchers accessed the colony by foot, ski or snow mobile. Depending on the year and ice conditions, the distance from the colony to the edge of seasonal sea ice where emperors enter and return from the ocean, varied from 3 to 10 km.

Capture and Instrumentation

Penguins were captured about 0.5 km seaward of the colony perimeter. All deployments occurred in the last week of October and the first week of November. Birds were randomly selected from a departure path that we estimated to be used by 90% of breeding adults. Body masses were obtained using a Pesola 50-kg hanging spring scale to within 0.5 kg (Pesola Schindellegi CH), or a model FW-150K platform load scale to within 0.02 kg (A&D Weighing San Jose CA USA) Sex of birds was determined by the difference in the trumpet call of birds during or after capture (Jouventin et al., 1979)**.** Data loggers, including a time depth recorder (TDR), radio transmitter, and occasionally a satellite transmitter, were attached to the central back using super glue and stainless steel cable ties as previously described (Kooyman and Kooyman 1995; Goetz et al. 2018), or using waterproof Tesa tape (Beiersdorf AG Hamburg DE) and stainless steel cable ties in 2005 penguins (Sato et al. 2011).

We used various models of TDRs and satellite transmitters (see Table 1 for details). Sampling rate and maximum depth of the TDRs ranged from 1 to 15 s, and from 500 to 1,000 m, respectively. In addition to the previously published track and dive profiles of one bird (Ancel et al. 1992), tracking data were obtained from three more birds. Two birds had Toyocom satellite transmitters from the 1990's experiments (Ancel et al. 1992; Kooyman et al., 2004) (one of which also had a TDR). The third bird had a Wildlife Computers Splash 10 in the 2011 experiment.

Penguins were recaptured as they returned to the colony or when they were already in the colony. Body masses were usually obtained on recovery to assess mass gain after the foraging trip. However, penguins captured in the colony may have already fed their chicks which would have reduced post-foraging mass. After instruments were removed, the data were downloaded in camp.

Satellite data analysis

ARGOS tracking data for birds CW1-11 (Fig. 1), CW7-92 (Fig. 4), and CW12-92 (Fig. 5), were processed through a horizontal speed filter of > 30 km h^{-1} to remove erroneous points (McConnell et al. 1992). ARGOS locations were then interpolated every 90 mins using a forward-looking particle filtering model (Tremblay et al. 2009), which accounts for the errors associated with each ARGOS location class. Note that only 3, 2 and 1 location classes were available for CW7-92 and CW12-92 as poor quality location classes (A, B and Z) had been previously removed from the data and were no longer available. Dive locations were determined by linking dive time with time along the track line, and linearly interpolating to the nearest minute. ArcGIS 10.3.1 (ESRI, 2015) was used to produce all geographic maps and the ggplot2 package (Wickham 2009) in R (R Core Team 2019) were used to produce dive plots.

Dive analysis

We examined only deep diving bouts (> 400 m) of birds although they also could and did dive on small isolated patches of the bank that were < 400 m from the surface. For dives collected by Wildlife Computer TDRs, we used purpose derived programs by Wildlife Computers to determine dive profiles, dive duration and maximum dive depth. The 2005 dive data, collected by the Little Leonardo recorders, were processed with Igor Pro (WaveMetrics Lake Oswego OR USA) as previously described (Sato et al. 2011).

To focus on the potential recovery periods from a series of deep, 400-m+ dives, we calculated the IDDI as the time from the end of a deep dive to the beginning of the next deep dive As a result, often a few shallow dives, usually <100 m as well as some time spent on the surface of the ice were included as part of the IDDI. We selected two of the deepest serial dive bouts from two birds, for which we had strip chart records. The IDDI interval on the chart paper was measured with dial calipers accurate to 0.1 min. In addition, we examined the IDDI for all dives > 400 m (even if not performed in long serial dive bouts) in the 2005 birds (Sato et al. 2011). ArcScene 10.7 was used to produce the 3D dive track presented in Fig. 2. The ggplot2 package in R was used to plot the dive profile of CW1-11 (Fig. 3).

Results

Deep dive characteristics

Deep dives (> 400 m) were recorded in 35 of 42 birds equipped with dive recorders over the seven field seasons (Table1). Trip durations ranged from 4 to 23.3 days, and maximum dive depth for all birds was 552 m during a "search" dive of 11.7 min. All search and feeding dives were determined subjectively based on the strip chart profile, occurrence within a series of dives, and the consistency of the depth of the dives. The sample rate of 5 to 15 s of the Wildlife Computer TDRs was too coarse to consider depth deflections during the bottom time as feeding events.

Emperor penguin CW9-90 had a remarkable record in which a depth of 482 m was measured numerous times. However, the flatness of the record indicated that the dives went beyond the maximum capacity of the recorder, and probably > 500 m.

Trip tracks

Fig. 1 shows the track of emperor penguin CW1-11 relative to the water depth and association with Crary Bank. All dives while crossing the Drygalski Basin were < 300 m (Figs. 2, 3). The detailed dive record of penguin CW1-11 shows that the bird dove deepest (> 400 m) during its foraging trip only when it was over the Crary Bank (Fig. 3).

We examined the foraging trips of two other emperor penguins in detail (CW7-92, Fig. 4; CW12-92, Fig. 5). Both of these birds showed some degree of association with the Crary Bank similar to that of CW1-11 (Fig. 1). The compressed diving depth record of CW12-92 showed that this bird conducted deep dives near and over Crary Bank (Fig. 6).

Of the three tracked birds in this study, CW7-92 did not have a TDR and, therefore, is not listed in Table 1. This 25-kg bird had a net gain of 2.5 kg on return from a 16-day trip. It was equipped with the Toyocom transmitter described in Table 1 for CW12-92 and for CW13-92. CW13-92's track was previously published (Ancel et al. 1992) and is not illustrated in this paper.

Although CW 4-95 was not equipped with a satellite transmitter, the exceptional deep-diving record of emperor penguin CW4-95 (Fig. 7a) suggested that the bird opted for feeding on Crary Bank, similar to CW1-11 (Fig. 1). Dives to depths > 400 m were found in 8 of 11 dive bouts (88 dives) during the 14.1-day trip of CW4-95.

Inter-deep-dive-interval (IDDI)

The IDDI was calculated in CW9-90 during a 10.4-h dive bout with average depth of 474 m, and in CW4-95 during a 9-h bout with average dive depth of 471 m. Both of these birds exhibited the longest dive bouts with consistent, serial dives to > 400 m depth. The mean IDDI was 35.1 min for CW9-90 for 12 dives over 7.9 h of the 10.4-h period. Dive profiles during a deep-diving bout by CW4-95 illustrated long IDDIs which were at least 20 min but ranged up to 28 min (Fig. 7b). The average IDDI for one bout was 27.8 min for 14 dives over an 8.5 h of the 9-h period. Analysis of the 2005 data for all dives > 400m (Fig. 8) revealed that most IDDIs were > 10 min, but that shorter IDDIs between 400-m+ dives could occur, some as short as 4.2-4.4 min.

Persistence of deep diving behavior

Over a decade later, the 2005 birds persisted in deep dive tendencies with such dives appearing in 9 of the 10 instrumented birds (Sato et al. 2011) (Table 1). The single 2011 record of this study (Figs. 1-3, Table 1) included periods of intense deep-diving activity.

Discussion

Consistency and extremes

83% of all TDR-tagged birds from 1989 to 2011 performed deep dives > 400 m (Table 1). CW9-90, CW10-92, CW4-95 and CW1-11 were exceptional in the number of deep dives. For CW9-90, 11 of 18 dive bouts were > 400 m, for a total of 137 deep dives. CW1-11 dived to >400 m in almost every dive bout and made 136 deep dives in 11 days. CW4-95 made numerous deep dives and set a depth record for emperor penguins in the Ross Sea of 552 m (Table 1, Fig. 7a). The only deeper dive (564 m) ever recorded from an emperor penguin was from Auster colony in 1994. The bird performed 11 dives >500 m and 61 dives >400 m over 6 days (Wienecke et al. 2007). Clearly this bird from Auster colony was a high intensity deep diver, and the 500+ m dives may set the boundary of how deep emperor penguins will dive.

Location

Because of advances in biologging capability, the detailed tracking data obtained from bird CW1-11 introduced a new perspective to us (Figs.1-3). The track shows that the deep dives did not begin until after passing the Drygalski Basin. Most of the track days and all of the deep dives were over Crary Bank. Review of CW12-92's track and dives also confirmed deep dives over Cary Bank. The consistency of the deep diving depths suggested that the bird was over a depth boundary, the top of Crary Bank, and was pursuing demersal prey rather than a concentration of mesopelagic prey that would likely change depth in avoidance behavior of a penguin that was taking 20-min breaks between dives.

The other track obtained in 1992 showed the bird spending much of its time over Crary Bank (Fig. 4). In addition, in the first report of foraging trip tracks from Cape Washington (CW13-90), most of the locations were over the bank (Ancel et al., 1992). The similarity of the satellite tracks and the documentation of deep dives over the Crary Bank (CW7-92, CW12-92, CW1-11) emphasizes the importance of the bank as a foraging area, and the need for further research.

Physiological consequences of deep dives

The physiological constraints of these deep dives can be evaluated with results from published reports of stroke rates, and heart rates during dives of emperor penguins at sea as well as prior documentation of both muscle oxygen depletion and the aerobic dive limit (ADL, dive duration associated with post-dive blood lactate accumulation) of birds diving at an isolated dive hole (Kooyman 1985; Ponganis et al. 1997; Williams et al. 2011, 2012; Wright et al. 2014).

For example, in one penguin's dive to 465 m (Williams et al. 2012), there was an increase in stroke rate during the bottom phase from 0.7 Hz in late descent to 1.1 to 3 Hz. This indicates extra effort at this time despite reduced buoyancy at such depth. During early ascent, the stroke rate returned to 0.7 Hz. The extra effort at the bottom could mean increased burst speed in pursuit of prey. In contrast to the increased stroke rate at the bottom of deep dives, heart rate decreased (Wright et al. 2014). In one case of a deep dive to 423 m, heart rate changed from about 30 beats min^{-1} (bpm) during late descent and early ascent to a mean of 17 bpm during the bottom phase. The minimum heart rate was 8 bpm. At such low heart rates, in the presence of increased swim effort, we think there is a redistribution of blood flow away from muscle and peripheral organs (i.e., the classical Irving-Scholander dive response). Under such conditions, there is potential depletion of myoglobin-bound oxygen and a rise in anaerobic glycolysis in propulsive muscles.

Based on muscle oxygen depletion patterns and the measured ADL in emperor penguins at an isolated dive hole (Ponganis et al. 1997; Williams et al. 2011), the estimated muscle metabolic rate during a 10-min dive would result in a muscle lactate concentration of 7 mmol lactate kg^{-1} muscle (Williams et al. 2012). Given that the increased stroke rate at the bottom of a deep dive is higher than that at the isolated dive hole (Williams et al. 2011, 2012), the end-of dive muscle lactate concentration is probably closer to 10 mmol kg^{-1} muscle for a 10-min, 400-m dive. This concentration is equivalent to that in humans exercising at 75% maximal oxygen consumption for 6 min, or to that in horses running at 6-8 m s^{-1} for 2 min (Karlsson et al. 1970; Harris et al. 1991). Notably, in that horse study and in humans after sub-maximal exercise (Freund et al. 1990), the time required for venous blood lactate concentrations to return to resting levels was 15-30 min, remarkably similar to many of the IDDIs for 400-m+ dives of emperor penguins.

Such muscle lactate accumulation during deep dives of emperor penguins does not prevent penguins from making short dives after 400-m dives (Sato et al. 2011). In addition, the actual end-of-dive lactate concentration probably varies dependent on the locomotory effort of a given deep dive. However, metabolic recovery probably does explain why the IDDI between deep dives often becomes extended to 10-20 min or more (Figs. 7, 8). We assume rapid blood oxygen loading (Meir and Ponganis 2009; Williams et al. 2011), but a longer metabolic recovery before performance of another deep dive. Alternatively, the prolonged IDDI may allow for excess nitrogen elimination as has been debated in beaked whales (Hooker et al 2009), or it may simply be secondary to digestion and emptying of a stomach packed with prey. We think metabolic recovery is the most probable.

With a measured aerobic diving limit (ADL) of 5.6 min in emperor penguins (Ponganis et al. 1997), these deep dives of 7 to 12 min frequently exceed the ADL. In comparison to marine mammals, the small size of diving birds, lower mass specific oxygen stores, and higher mass specific oxygen consumption result in shorter ADLs (Noren and Williams 2000). In order to expand their foraging realm to deeper depths, emperor penguins exceed this limit at the cost of a longer recovery time.

Efficiency, energetics and prey of deep dives

An overall appreciation of the effort in a deep dive bout can be determined by calculating the dive efficiency (DE) as DE= BT/(DT+IDDI) after Cherel et al. (1999) and Ydenberg and Clark (1989), where BT = bottom time (from Kooyman and Kooyman (1995), a typical BT in 400+ m dives = 2 min). Considering only dives >400 m as in Fig. 7b (IDDI = 20 and DT (dive time) = 10 min), DE = 2/(10 + 20) equals 0.07. In contrast, in the northern rockhopper, *Eudyptes moseleyi*, feeding epipelagically at 15 to 35 m, DE is 0.39 (Cherel et al. 1999). In other words, the diving efficiency of emperor penguins' exceptionally deep dives is one fifth that of northern rockhopper penguins. Therefore, one would expect that the deep dives should be exploiting an exceptionally rich food source.

A small shallow diving penguin, such as the northern rockhopper that is a near surface forager, relies primarily on aerobic metabolism. Emperor penguins commit to prey some distance from the surface. We hypothesize that they must rely on a calorically rich prey that results in a big benefit for the cost of such a long recovery after a deep dive. For emperor penguins over the Crary Bank, the adult Antarctic silverfish, which are in dense, slow moving benthic or demersal distribution (Fuiman et al. 2002), represent high caloric prey items (Lenky et al. 2012).

How much emperor penguins feed epi- to meso-pelagically while crossing the Drygalski basin is unknown. Figs. 1 and 2 show less time over deep water than over the Crary Bank. However, some birds did not perform many deep dives (*i.e*., CW1-92, 18-92, 3-96, 3-05, 11-05), and seven of 42 deployments had no dives > 400m. This suggests that favorable fish distribution for mesopelagic feeding may be present at times. A large, dense school of fish over the Drygalski Basin would have been a good alternative to deep diving. However, as a food source, one of the best features of the Crary Bank is its availability. In early spring, when fast ice is most extensive, access to the Crary Bank from Cape Washington is still possible because fast ice does not extend so far offshore. This is not always the case at Auster, Amanda Bay, and Pointe Géologie where fast ice is more widespread and may extend over the shelf shallows, and the birds are forced to search further from the colony, off the shelf where the benthos cannot be reached (Wienecke and Robertson 1997; Zimmer et al. 2008).

We hypothesize that emperor penguins from Cape Washington often put much of their effort into demersal or benthic prey based on the tracks in Figs. 1 and 2, and on the dive profile series of Fig. 7b. The penguins spend time over the Crary Bank, the depth of which is about 250 to 500 m below the surface. We suggest the prey near the bottom at 400 m is dense, reliable, not dispersed by many penguins searching the area, and easy to catch. Regarding the prey of emperor penguins in the Ross Sea, there is no better known possibility than Antarctic silverfish. It has widespread distribution in the Ross Sea (Dewitt et al. 1990; O'Driscoll et al. 2011). It is the dominant species found in stomachs samples of birds at Cape Washington (Cherel and Kooyman 1998). As mentioned earlier, O'Driscoll et al (2011) found that adult silverfish were the most abundant fish caught in demersal trawls over Crary and Mawson Bank. Adults, which can be up to 25 cm in length, occur at depths of ~ 400 m. The energy density of the Antarctic silverfish, although of about half those of Antarctic tooth fish (*Dissostichus mawsoni*) and some Antarctic lanternfish, is equivalent to or greater than the energy densities of many other Antarctic nototheniid fish (Lenky et al. 2012).

Conservation

Over a 22 year span of observations from Cape Washington, we conclude that the purpose of dives >400 m is for demersal or benthic feeding. Given the consistency of the travel and deep dives of these penguins, it is logical that the favored location is Crary Bank. The supreme effort and low dive efficiency of the birds to reach these depths is evidence for the importance of the bank as a productive foraging area. It is fortunate that long-line fishing is prohibited over the banks of the Ross Sea, especially since commercial fishing is permitted in deeper waters, outside the boundaries of the recently enacted Ross Sea Region MPA. The close proximity of Mawson Bank (also within the MPA) to the Coulman Island and Cape Roget emperor penguin colonies, and the known deep-diving effort from Coulman Island (Kooyman and Kooyman, 1995) and Cape Roget (Kooyman *unpub data)* add further support for continued protection of the banks in the Ross Sea. The reliability of the banks as a food source, and of the sea ice as a stable platform are significant attributes for the location and success of the largest Ross Sea colonies.

Conclusions

1. Dives >400 m were an important component of most emperor penguin foraging trips from the Cape Washington colony during seven studies over a span of 22 years.
2. The exceptional number of deep dives for CW9-90, CW4-1995 and CW1-11 show great reliance on deep-dive foraging by perhaps all penguins from Cape Washington.
3. The extreme depth of these dives results in an oxygen debt/metabolic recovery that often requires inter-deep-dive-intervals of 10 - 20 min.

4. The main prey of birds from Cape Washington is Antarctic silverfish (*P. antarctica*) during both shallow and deep diving. It is hypothesized that adult Antarctic silverfish are easy prey during deep dives, and that deep dives may at times provide a major part of the total catch per trip.
5. The Crary Bank location is vital to the success of the Cape Washington colony.
6. It is likely that Crary Bank and other banks are the main feeding location for emperor penguins from other large Ross Sea colonies at Coulman Island, Cape Roget and Franklin Island.
7. The recent designation of the Ross Sea Region Marine Protected Area provides important protection for most western Ross Sea emperor penguins because it includes Crary and Mawson Banks.

Compliance with Ethical Standards

The authors have no conflicts of interest. All procedures and research were conducted under multiple UCSD IACUC protocols and Antarctic Conservation Act permits.

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Table 1. Body masses, trip durations, dive characteristics, and recorders of emperor penguins that had dives to >400 m (1989-2011). From 42 depth records deployed in this time period, these 35 had maximum dives >400 m, and eight of these had depths >500 m. Of all dives recorded, 1.70% were > 400 m in depth. For individual birds, deep dives ranged from 0.02% to 10.05% of dives recorded. Three of the birds also had satellite tracks; the track of CW13-90 was published previously (Ancel et al. 1992). Only one of the nine 2005 results was a complete trip record. The length of data collection for each bird in 2005 is shown in parenthesis.

Year	Bird ID	Body Mass (kg) (before/after trip)	Trip Duration (days)	Max Dive Depth (m)	Total Deep Dives	Total Dives	% Deep Dives	Type of Recorder or Transmitter
1989	CW11-89M	28.0/31.6	11	531	55	3315	1.66	A
	CW12-89F	25.0/27.8	12	464	68	3322	2.05	B
1990	CW2-90M	27.0	8	471	44	2255	1.95	C
	CW3-90	22.7/26.2	15	471	59	4313	1.37	C
	CW9-90	27.7	18	482+	143	2255	6.34	C
	CW10-90F	21.5	9.5	438	16	2103	0.76	C
	CW11-90	22.0	11	531	54	2625	2.06	C
	CW13-90M*	27.1/29.7	17.4	483	11	2728	0.40	C,H
	CW14-90M	24.9/29.7	8.7	528	34	2470	1.38	C
	CW23-90M	30.3/31.6	8.3	436	51	1179	4.33	C
	CW31-90F	29.2/28.0	7.9	464	57	1464	3.89	C
1992	CW1-92	24.5/24.5	15.9	477	7	3854	0.18	C
	CW2-92	22.5	7	486	99	2631	3.76	C
	CW3-92	24.7	4	492	34	1141	2.98	C
	CW10-92	24.2	23.3	492	136	4286	3.17	C
	CW11-92	22.0	16.3	441	30	3141	0.96	C
	CW13-92*	25.4/26.3	17.4	468	19	1964	0.97	C, H
	CW15-92	26.0	9.3	450	21	3043	0.69	C
	CW16-92	23.8	9.3	444	7	1706	0.41	C
	CW18-92	24.3/25.2	10	405	21	1706	1.23	C
	CW21-92	27.9	8.2	462	4	2134	0.19	C
	CW22-92	22.9	14.3	484	25	2151	1.16	C
1995	CW4-95	24.2	14.1	552	93	2771	3.36	C
1996	CW3-96M	26.5	13	460	17	2683	0.63	C
	CW8-96M	28.4	7	480	24	1125	2.13	C
2005	CW2-05	23.0/25.5	10.0 (4.1)	418	8	1479	0.54	E
	CW3-05	21.5/25.5	18.0(4.1)	423	1	1153	0.09	E
	CW4-05	23.5/25.5	13.5(3.9)	514	16	1264	1.27	E
	CW7-05	24.0/26.5	16.1(4.0)	476	41	1376	2.98	E
	CW8-05	27.5/30.5	13.7(3.9)	502	23	1167	1.97	E

	CW9-05	24.0/26.5	15.0(4.0)	500	31	953	3.25	E
	CW10-05	25.5/30.5	19.7(14.3)	459	13	3447	0.38	F
	CW11-05	22.0/22.5	16.5(14.5)	400	1	5859	0.02	F
	CW13-05	26.0/30.0	11.5(11.5)	509	19	2959	0.64	G
2011	CW1-11 *	25.5	11	470	136	1292	10.05	D
		Mean of total trip (± s.d.)	12.6 (± 4.30)	473 (± 36.0)			1.98 (± 2.07)	
		Totals			1418	83314		

Abbreviations: * = satellite track; M–male, F-female, identified by vocalizations. Types of TDRs included: A - Wildlife Computers (Redmond WA USA) mark 3 or C - mark5, with sampling rates of 10 to 15 s, depth range of 500 to 750 m. Other details as reported in Kooyman and Kooyman (1995). The custom Konoff and Croll (B) recorder sampled every 4 s, and weighed 35 g as reported in Croll et al. (1992). The Wildlife Splash 10 TDR/transmitter mass (D) was 99 g; other details as reported in Goetz et al. (2018). The Little Leonardo (Tokyo, JP) W1000-PD2GT (E), W1000L-PD2GT (F), and W1000L-3MPD3GT (G) details for 2005 were as described in Sato et al. (2011). It should be noted that in 2005, that each value in parentheses is the trip length and the non-parenthetic number is the recorded length. All recorders in 2005 had delay starts of 4 to 96 h. The 2005 recorders ranged in weight from 73 to 101 g. The Toyocom (Long Beach CA USA) satellite transmitter (H) weighed 475 g. Other details are as in Ancel et al. (1992); Kooyman et al. (2004).

Figure Legends

Fig. 1. Complete foraging trip track for emperor penguin CW1-11 relative to bathymetric depth. The 500-m isobath denotes the boundary of Crary Bank. Note the insert with the 300 m shallows in red. Depth difference indicates the difference between maximum depth of dive and bottom depth

Fig. 2. Complete foraging trip track and depth profile for emperor penguin CW1-11 showing dive data relative to bathymetric depth. The 500-m isobath denotes the boundary of Crary Bank. During this 11-day, the bird made 1292 dives, including 136 dives to depths > 400 m

Fig. 3. Complete dive record for emperor penguin CW1-11. Deep dives occurred in the shaded area that indicates when the bird was over Crary Bank

Fig. 4. Complete 16-day foraging trip track for emperor penguin CW7-92, which was equipped with only a satellite transmitter. The 500-m isobath denotes the boundary of Crary Bank

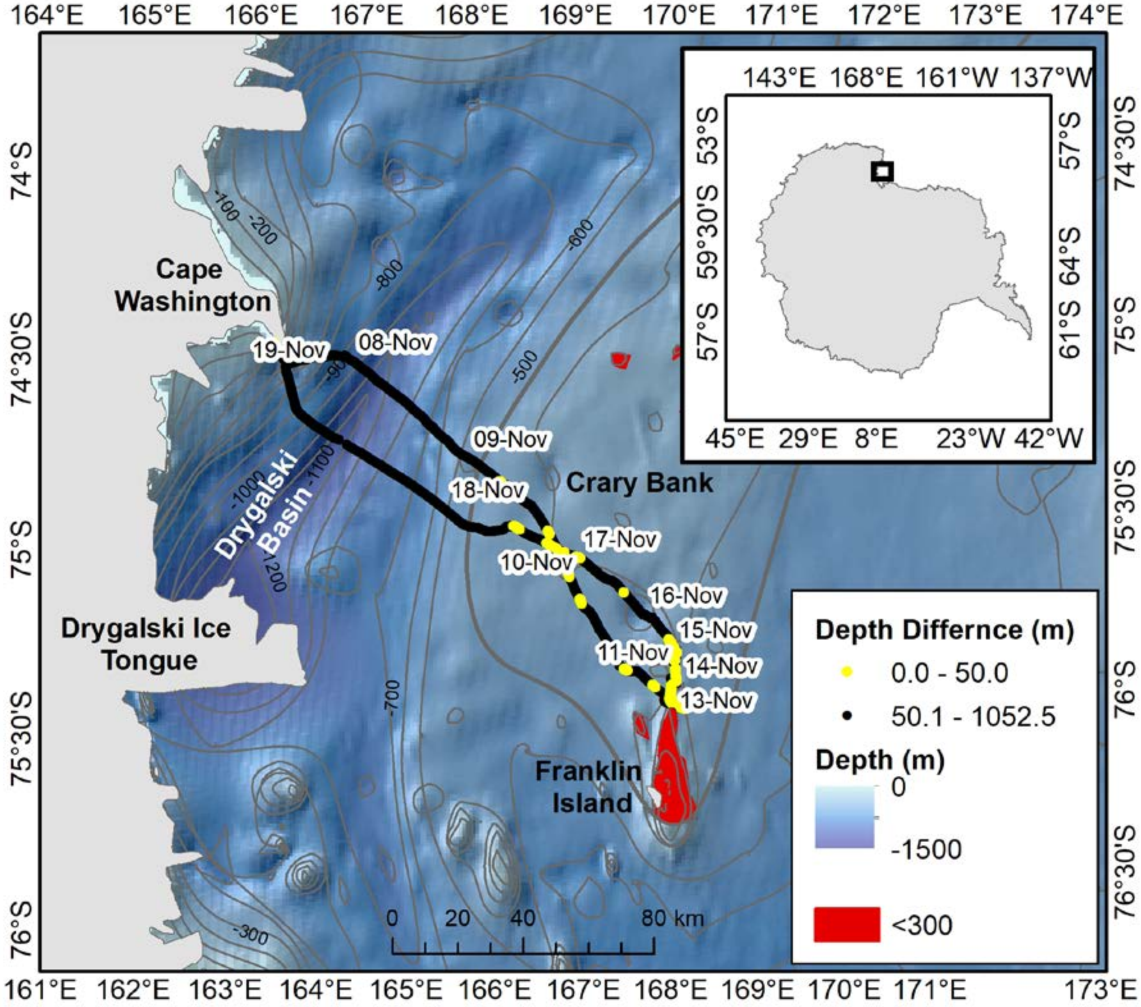
Fig. 5. Complete 20-day foraging trip track for emperor penguin CW12-92. The 500-m isobath denotes the boundary of Crary Bank. Depth difference indicates the difference between maximum depth of dive and bottom depth

Fig. 6. Complete dive record for emperor penguin CW12-92. The shaded area shows where the bird was over Crary Bank. This record shows about 25 dive bouts of which 11 included dives to >300 m and four to >400 m

Fig. 7. Complete 14.1-day foraging trip track for emperor penguin CW4-95 (**a**) and partial dive bout of serial deep dives to about 470 m during that trip (**b**). Eighty-eight dives > 400 m occurred during eight dive bouts in **a**. The second deepest dive reported for an emperor penguin (552 m) occurred on the sixth day of the trip. Inter-deep-dive intervals (time between the deep dives) in **b** were 20-27 min during this series of dives by CW4-95

Fig. 8. Scatterplot of inter-deep-dive -intervals (IDDI, the time between deep dives) in the 2005 emperor penguins for dives > 400 m in depth that had an IDDI < 30 min. 59% of dives > 400 m had an IDDI < 30 min; for these 90 dives, mean IDDI (± S.D.) was 15.8 (± 6.01) min

Fig 1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74°S
74°30'S
75°S
75°30'S
76°S
74°30'S
75°S
75°30'S
76°S
76°30'S
143°E 168°E 161°W 137°W
45°E 29°E 8°E 23°W 42°W
53°S
59°30'S
57°S
57°S
64°S
61°S
Cape Washington
Drygalski Basin
Drygalski Ice Tongue
Crary Bank
Franklin Island
19-Nov
08-Nov
09-Nov
18-Nov
17-Nov
10-Nov
16-Nov
15-Nov
11-Nov
14-Nov
13-Nov
-100
-200
-800
-600
-500
-900
-1000
-1100
-1200
-700
-300
0 20 40 80 km
Depth Differnce (m)
● 0.0 - 50.0
● 50.1 - 1052.5
Depth (m)
0
-1500
🟥 <300

Fig 2

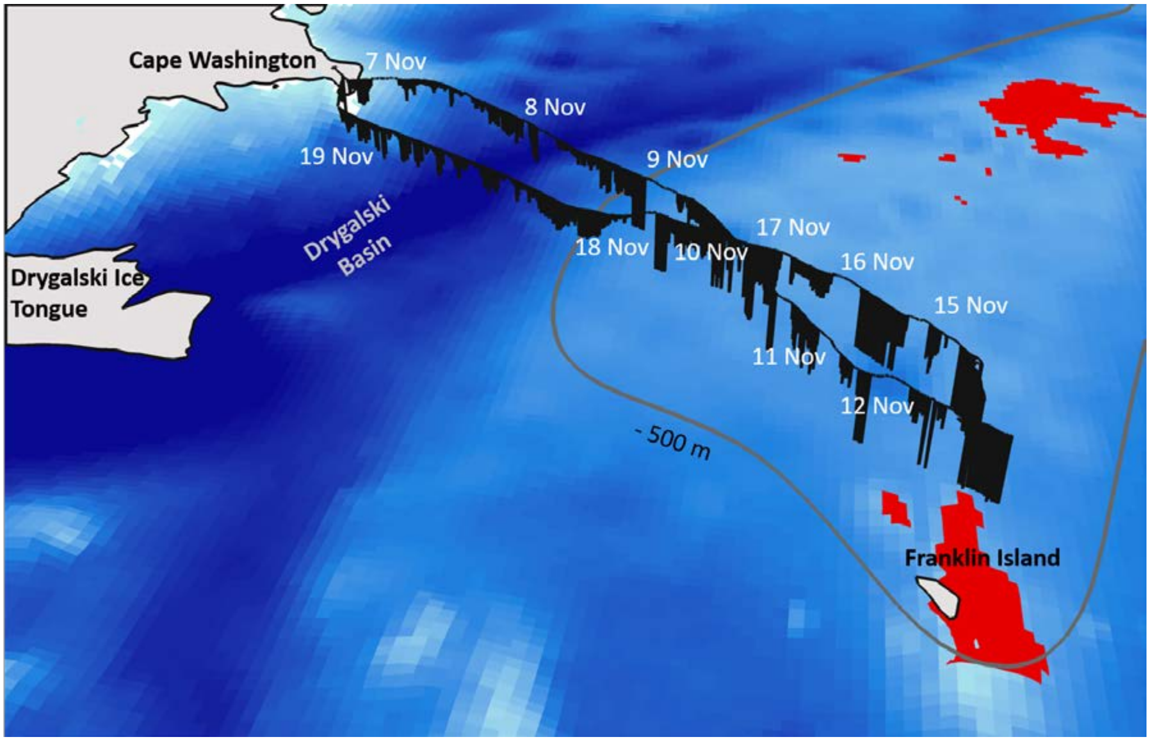

Cape Washington
7 Nov
8 Nov
9 Nov
19 Nov
Drygalski Basin
Drygalski Ice Tongue
18 Nov
10 Nov
17 Nov
16 Nov
15 Nov
11 Nov
12 Nov
- 500 m
Franklin Island

Fig 3

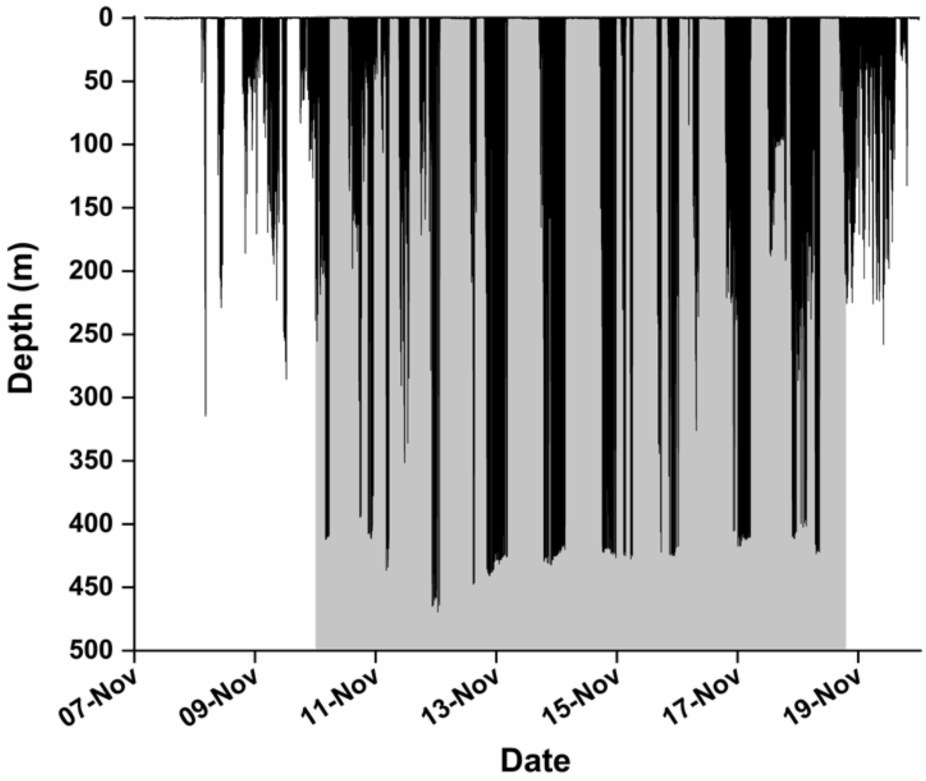

0
50
100
150
200
250
300
350
400
450
500
Depth (m)
07-Nov
09-Nov
11-Nov
13-Nov
15-Nov
17-Nov
19-Nov
Date

Fig 4

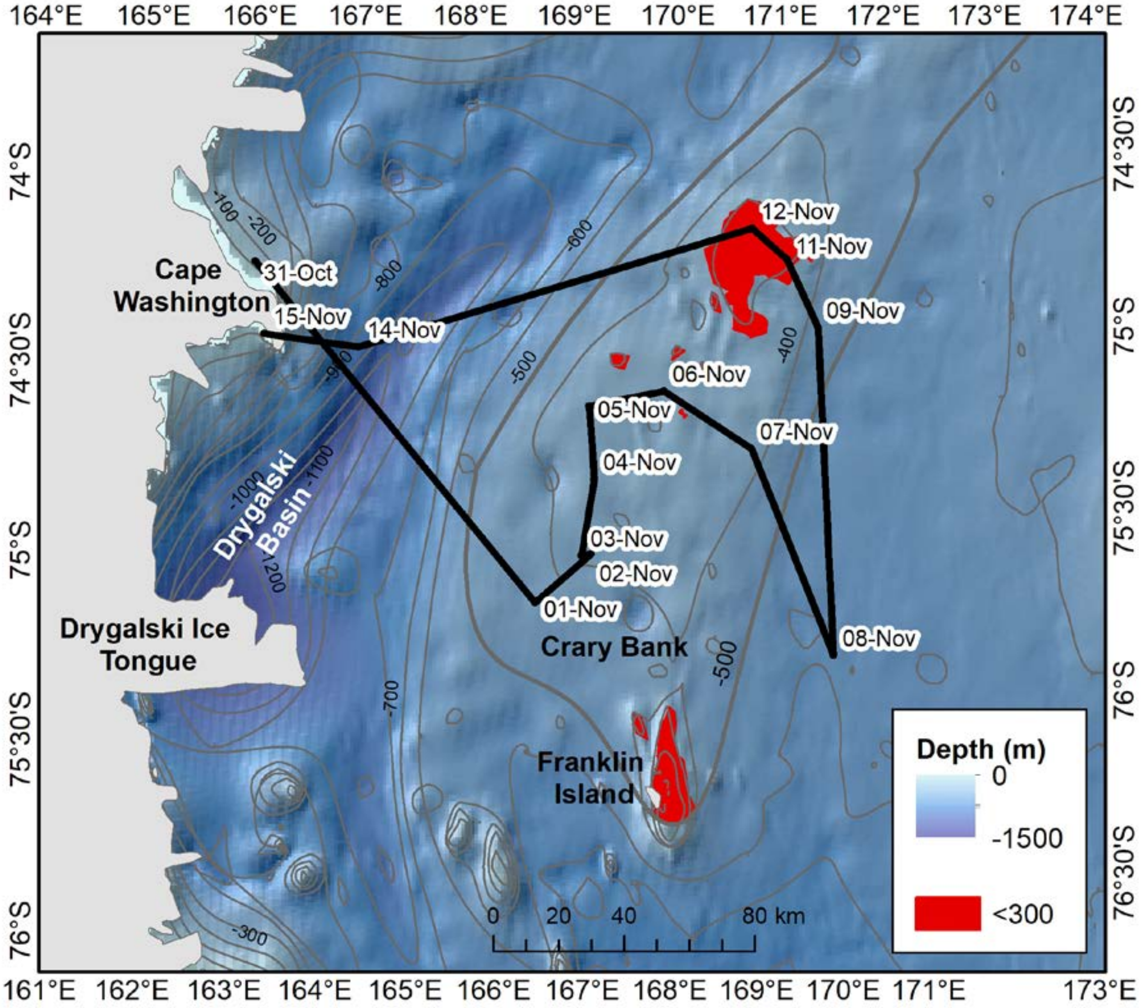

164°E
165°E
166°E
167°E
168°E
169°E
170°E
171°E
172°E
173°E
174°E
74°S
74°30'S
75°S
75°30'S
76°S
74°30'S
75°S
75°30'S
76°S
76°30'S
161°E
162°E
163°E
164°E
165°E
166°E
167°E
168°E
169°E
170°E
171°E
173°E
Cape Washington
Drygalski Basin
Drygalski Ice Tongue
Crary Bank
Franklin Island
31-Oct
01-Nov
02-Nov
03-Nov
04-Nov
05-Nov
06-Nov
07-Nov
08-Nov
09-Nov
11-Nov
12-Nov
14-Nov
15-Nov
-100
-200
-300
-400
-500
-600
-700
-800
-900
-1000
-1100
-1200
0 20 40 80 km
Depth (m)
0
-1500
🟥 <300

Fig 5

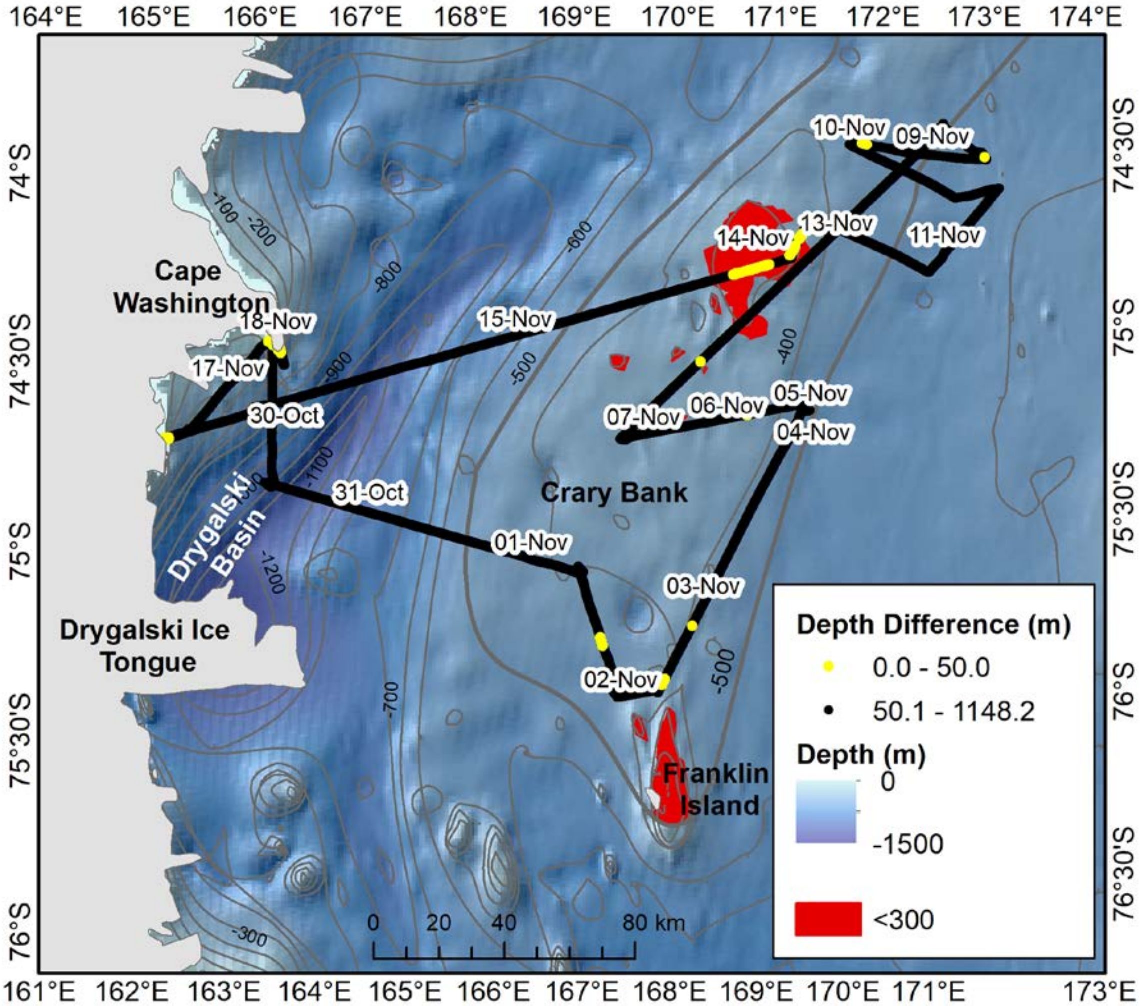
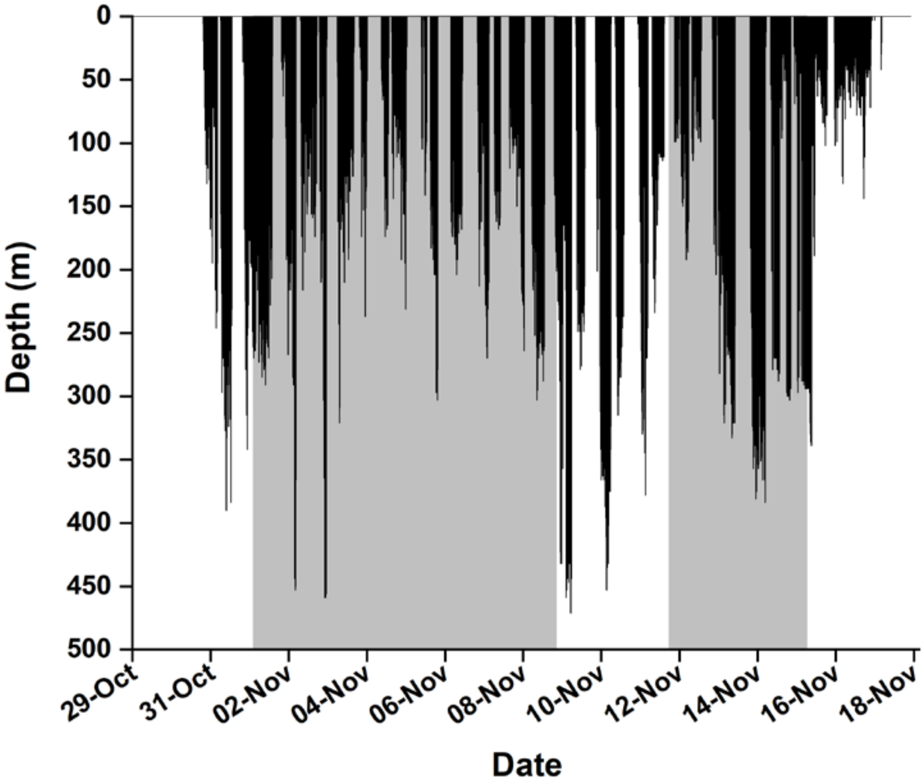

164°E
165°E
166°E
167°E
168°E
169°E
170°E
171°E
172°E
173°E
174°E
74°S
74°30'S
75°S
75°30'S
76°S
161°E
162°E
163°E
164°E
165°E
166°E
167°E
168°E
169°E
170°E
171°E
173°E
Cape Washington
Drygalski Basin
Drygalski Ice Tongue
Crary Bank
Franklin Island
10-Nov
09-Nov
11-Nov
13-Nov
14-Nov
15-Nov
18-Nov
17-Nov
30-Oct
31-Oct
01-Nov
02-Nov
03-Nov
04-Nov
05-Nov
06-Nov
07-Nov
-100
-200
-300
-400
-500
-600
-700
-800
-900
-1100
-1200
0
20
40
80 km
Depth Difference (m)
0.0 - 50.0
50.1 - 1148.2
Depth (m)
0
-1500
<300

Fig 6


Depth (m)
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100
150
200
250
300
350
400
450
500
29-Oct
31-Oct
02-Nov
04-Nov
06-Nov
08-Nov
10-Nov
12-Nov
14-Nov
16-Nov
18-Nov
Date

Fig 7

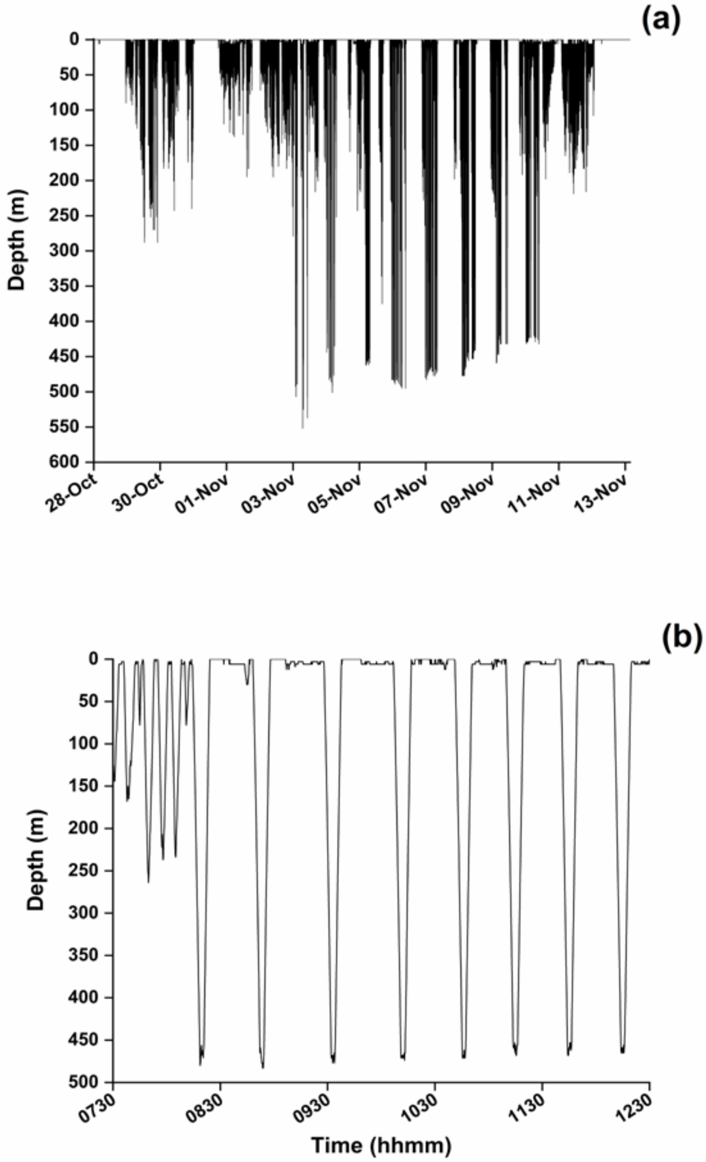
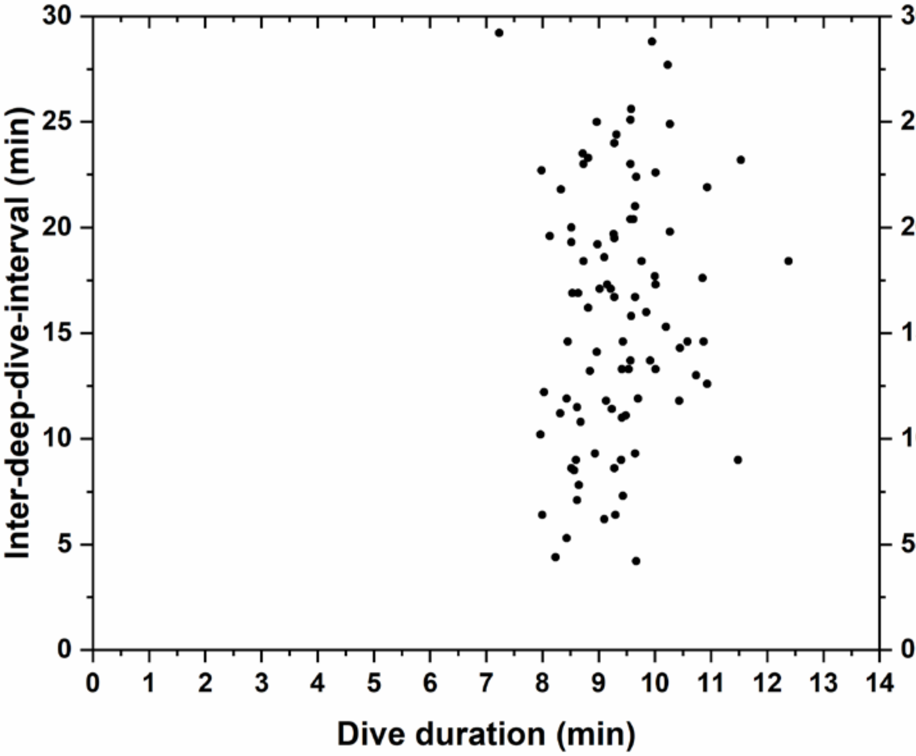

(a)
Depth (m)
0
50
100
150
200
250
300
350
400
450
500
550
600
28-Oct
30-Oct
01-Nov
03-Nov
05-Nov
07-Nov
09-Nov
11-Nov
13-Nov
(b)
Depth (m)
0
50
100
150
200
250
300
350
400
450
500
0730
0830
0930
1030
1130
1230
Time (hhmm)

Fig 8


Inter-deep-dive-interval (min)
Dive duration (min)
0
5
10
15
20
25
30
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14