

SEASONAL CHANGES IN DIVING AND FLYING ACTIVITIES OF RHINOCEROS AUKLETS *CERORHINCA MONOCERATA* THROUGHOUT THE NON-BREEDING PERIOD

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ABSTRACT

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To understand how migratory seabirds meet the energetic challenges associated with wing molt and wintering, a full annual cycle behavioral study is needed. We studied the diving and flying activities of three Rhinoceros Auklets *Cerorhinca monocerata* migrating in the northwestern Pacific. The auklets decreased daily flight time and dive depth for seven weeks from the end of summer, presumably associated with primary feather molt. In winter, they increased dive depth (~81 m) and daily dive time. We suggest that Rhinoceros Auklets adjust their diving and flying behaviors in response to wing molt and energy demands in winter.

Key words: Seabird, foraging, behavioral time budgets, migration, Sea of Okhotsk, molt

INTRODUCTION

Full annual cycle research is essential to understanding the effects of natural and anthropogenic changes on migratory bird species (Marra *et al.* 2015). Accordingly, several studies on the movement patterns of migratory seabirds during the non-breeding period have been conducted using geolocator tracking; at the same time, relatively little information has been obtained about seabird behavior that is concurrent with the movement data (e.g., Gutowsky *et al.* 2014, Orben *et al.* 2015, Dunn *et al.* 2020). During the non-breeding period, seabirds often face challenges not faced during breeding, such as low food abundance, extreme weather conditions, and foraging opportunities reduced by shortened day length (Harris & Wanless 1996, Daunt *et al.* 2006, Fort *et al.* 2013, Dunn *et al.* 2020). Such factors might affect their populations through elevated mortality (Harris & Wanless 1996, Jones *et al.* 2019). The period of wing molt can also be energetically challenging, as some seabird species reduce flying activities or become completely flightless (Thompson & Kitaysky 2004, Elliott & Gaston 2014, Gutowsky *et al.* 2014, Harris *et al.* 2014, Chérel *et al.* 2016, Elliott *et al.* 2017), which constrains their ability to track changes in prey distribution (Davoren *et al.* 2002). A concurrent study of behavior and movements would be valuable to understand how birds adjust their behaviors to meet these challenges.

Rhinoceros Auklets *Cerorhinca monocerata* are medium-sized alcids (500–600 g) that forage on pelagic schooling fish by wing-propelled diving (Watanuki & Ito 2012). A recent study reported on the post-breeding migration of this species from Teuri Island, Japan, where the largest known breeding colony is located (Takahashi *et al.* 2015). However, behaviors such as diving and flying have not been examined during the non-breeding period. We hypothesized that the auklets experience a flightless period in the fall for wing molt and that they increase their diving effort in winter to meet the

limited foraging opportunities presented by shortened day length and high energetic demands, as recently demonstrated in murre *Uria* spp. (e.g., Elliott & Gaston 2014, Burke & Montevecchi 2018, Dunn *et al.* 2020, Takahashi *et al.* 2020). To test these hypotheses, we attached geolocation/depth loggers on Rhinoceros Auklets to examine seasonal changes in their diving and flying activities.

METHODS

The study was conducted at Teuri Island (44°25'N, 141°18'E), Japan, where approximately 300,000 pairs breed (Watanuki & Ito 2012). Rhinoceros Auklets first return to this colony in late March or April and lay a single egg in April or May. The chicks hatch in May–June and fledge in July. In June 2015, we captured five chick-rearing birds from their nest burrows. We attached a geolocation/depth logger (LAT2500: 8×35 mm, 3.6 g, Lotek Wireless, Canada) to the tarsus of each bird using a plastic ring (total mass of the logger including the ring: 4.5 g, which is 0.8% of mean body mass at deployment). The birds were weighed and sexed based on morphometrics (Niizuma *et al.* 1999).

The geolocators recorded the times of sunrise and sunset via onboard processing of light data (Ekstrom 2007). They were set to record saltwater immersion and depth every 120 seconds and temperature every hour. First, we analyzed the bird locations from the recorded times of sunrise and sunset using an iterative forward step-selection process, which was performed 200 times to calculate a median geographic track (R package “ProbGLS”, Merkel *et al.* 2016). Second, we analyzed diving activities from the time-depth records by calculating daily dive time (i.e., the sum of durations with depths > 1 m) and daily mean and maximum dive depths. Although the depth sampling interval of 120 seconds does not resolve individual dives, these daily metrics would reliably reflect the daily diving effort and seasonal patterns of depth use.

To infer maximum dive depths from the 120-second sampling interval, we detected the inflection point of depth (where the recorded depth switched from descending to ascending), then we calculated daily mean and maximum depths of inflection points as mean and maximum dive depths (see Takahashi *et al.* 2018 for details). We validated this approach using the high-resolution depth data (sampling interval: 1 s) obtained from 10 Rhinoceros Auklets (N. Sato unpubl. data) during the chick-rearing period. Daily mean dive depth (interval: 1 s) correlated significantly with the daily mean depth of inflection points (120-second interval, resampled from one-second intervals; $y = 1.01x - 1.07$, $R^2 = 0.75$, $P < 0.001$, $n = 19$ d). Daily maximum dive depth (interval: 1 s) correlated significantly with daily maximum depth of inflection points (120-second interval $y = 0.965x + 8.75$, $R^2 = 0.75$, $P < 0.001$, $n = 19$ d) but were underestimated (by 8.75 m, on average) with the 120-second sampling interval. As daily dive time appeared to be related to mean daily dive depth (see Results), we performed linear regression analysis of daily dive time against daily mean dive depth for each bird. Third, we analyzed colony attendance and flying activities from saltwater immersion records. We defined colony attendance when the geolocator was 'dry' for a prolonged period (> 5 h) through midnight (Takahashi *et al.* 2015). Daily flight time was calculated as the sum of the 'dry' readings of the immersion records between sunset and sunrise (derived from estimated bird locations). This is because Rhinoceros Auklets fly mostly during daytime (Kato *et al.* 2003), and they may show leg-tucking behavior frequently during the night, as observed in Thick-billed Murres *U. lomvia* (Elliott & Gaston 2014). Fourth, we calculated the daily mean water temperature experienced by the birds using data recorded when their loggers showed a continuous 'wet' period (> 30 min) prior to the temperature measurement.

As the birds showed a clear period of reduced daily flight time (see Results), we considered the period when daily flight time remained under one hour as the period of wing molt (Cherel *et al.* 2016). We compared diving activities between 'molt' (the period of wing molt, Table 1), 'breeding' (the period from three days after the logger attachment to migratory departure), 'post-molt' (the period starting two weeks after the wing molt), and 'winter' (the period starting four weeks before heading north toward the colony; Table 1). A generalized linear mixed model was used to compare daily dive time, mean diving depth, maximum diving depth, and mean temperature between molt and other three periods; Bird ID was included as a random factor (R package "lme4"; <https://cran.r-project.org/web/packages/lme4/index.html>).

RESULTS

We recaptured three of the five tagged birds during the 2016–2018 breeding seasons (three males). Two devices recorded the data until

March 2016, and another stopped recording on 12 October 2015. The birds left their colony on 13 July 2015 (± 11.0 days, standard deviation (SD)), based on immersion data (Table 1). They first moved northward and reached areas off northern Sakhalin Island or north of Hokkaido Island, and they stayed until late September or early October (Fig. 1). Then, all three birds migrated southward to the eastern Sea of Japan. The two birds that were tracked over the winter stayed in this region until mid-February or mid-March. They then returned northward to the area around Teuri Island in March. Bird C arrived at the colony on 18 March 2016.

Throughout the non-breeding period, the birds limited their daily diving activity to daylight hours (sunrise to sunset, Fig. 2). The daily dive time changed seasonally and increased during winter (Fig. 3, Table 2). Overall, the daily maximum dive depth during the non-breeding period was 25.8 ± 8.5 m on average (SD, $n = 3$ birds, 82–251 days of records for each bird) and tended to be deeper during winter, with the maximum depth of 81 m (recorded on 01 March 2016, Fig. 3). Daily dive time increased linearly with daily mean dive depth for each bird (Fig. 4).

Importantly, the birds showed a period of reduced daily flight time starting in mid-August and lasting for 53, 44, and 46 days (Table 1). Birds flew an average of 0.2 ± 0.02 hours per day (SD) during this period. Daily dive time and residual daily dive time (from the regression of daily dive time against mean daily dive depth; Fig. 4) were shorter, and daily mean and maximum dive depths were shallower during the period of wing molt than during the breeding, post-molt, and winter periods (Table 2; $P < 0.05$ for all comparisons). During the winter, the birds more than doubled their daily dive time and dived nearly three times deeper on average compared to the molt period (Table 2). The daily mean water temperatures during the post-molt and the winter periods were lower than during the breeding and molt periods, with temperatures during the post-molt period being the coldest throughout the entire period (Fig. 3, Table 2; $P < 0.001$ for all comparisons).

DISCUSSION

Diving and flying activities of Rhinoceros Auklets changed seasonally. In autumn, they showed a period of reduced flying, which likely corresponded with their wing molt (Thompson & Kitaysky 2004, Elliott & Gaston 2014, Gutowsky *et al.* 2014, Cherel *et al.* 2016, St. John Glew *et al.* 2018, Dunn *et al.* 2020). This result agrees with a previous study of wing molt timing in alcids, which included Rhinoceros Auklet specimens (Pyle 2009). During this molt period, the auklets dived for less time per day to shallower depths, compared to other times of the year (Table 2). These changes in diving activities during wing molt could be related to their reduced wing area. A previous study on captive Common

TABLE 1
Migratory and molt timings of three Rhinoceros Auklets

Bird ID	Left from colony	Moving northward, crossing 45°N	Beginning of wing molt	End of wing molt	Beginning of moving southward	Beginning of moving toward colony	Arrived at colony
A	23 Jul 2015	27 Jul 2015	13 Aug 2015	04 Oct 2015	29 Sep 2015	-	-
B	28 Jun 2015	18 Jul 2015	17 Aug 2015	29 Sep 2015	14 Oct 2015	16 Feb 2016	-
C	19 Jul 2015	20 Jul 2015	16 Aug 2015	30 Sep 2015	18 Oct 2015	15 Mar 2016	18 Mar 2016

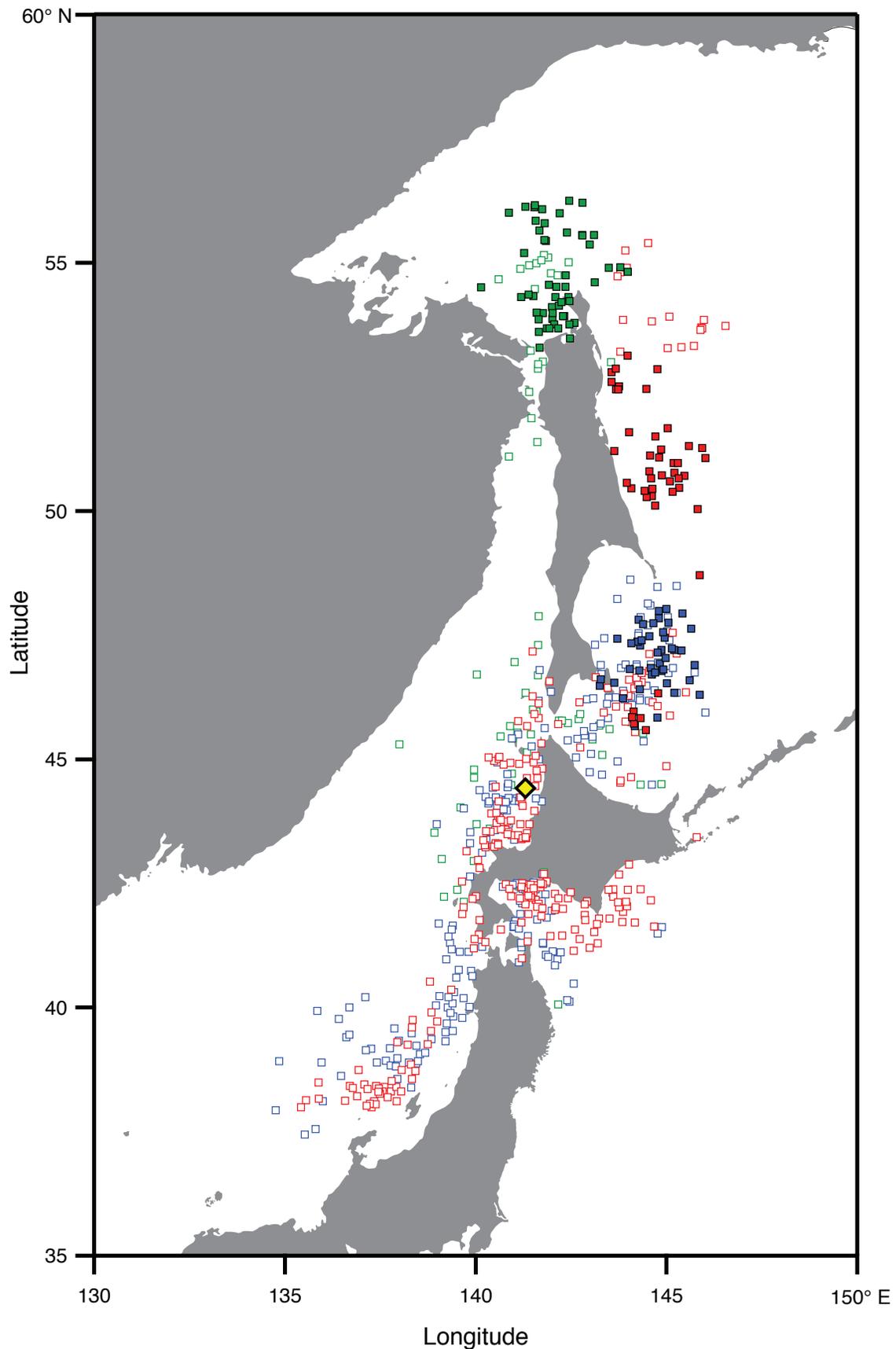


Fig. 1. Seasonal changes in daily locations of three Rhinoceros Auklets during the post-breeding migration, estimated from geolocation data. Each color shows different individuals (green, blue, and red for Birds A, B, and C, respectively). The location of the Teuri Island breeding colony is shown as a yellow diamond. Bird locations during the period of short daily flight time (< 1 h) are shown as filled squares.

Murres *U. aalge* and Tufted Puffins *Fratercula cirrhata* showed that diving birds needed to flap more frequently during wing molt to overcome the reduced work per flap, a result of wing area reduction (Bridge 2004). Rhinoceros Auklets probably have slightly lower diving ability during wing molt compared with the breeding, post-molt, and winter periods. Davoren *et al.* (2002) suggested that molting Common Murres have less capacity to adjust their horizontal distribution to prey availability due to the lack of flying ability. Our results indicate that wing molt may also constrain the birds' adjustment of vertical movements to the depth distribution of their prey, reinforcing the idea that molting alcid are more vulnerable to variability in prey distribution. Rhinoceros Auklets may also face anthropogenic threats during wing molt. Oil and gas platforms are located off northeastern Sakhalin Island in the Sea of Okhotsk (Blanchard *et al.* 2019), where one of our auklets stayed

during wing molt. Molting auklets with limited flying ability could be severely affected by oil spills in this region.

In winter, Rhinoceros Auklets progressively dived deeper and showed higher diving effort (Fig. 3, Table 2). The diving depths appeared to be deeper than those reported during the breeding period (maximum breeding-period dive depth: 57 m in Kuroki *et al.* 2003, 52 m in Cunningham *et al.* 2018). Deeper diving might reflect the larger depth distribution of forage fish in winter (e.g., Burke & Montevecchi 2018) or a change in birds' responses to reduced foraging opportunities due to shorter day lengths (Burke & Montevecchi 2018). The latter explanation, however, does not seem to apply in our case, as the dive depths were relatively shallow around the winter solstice compared to the subsequent winter periods (Fig. 3). Deeper diving partly explained the increased daily dive time

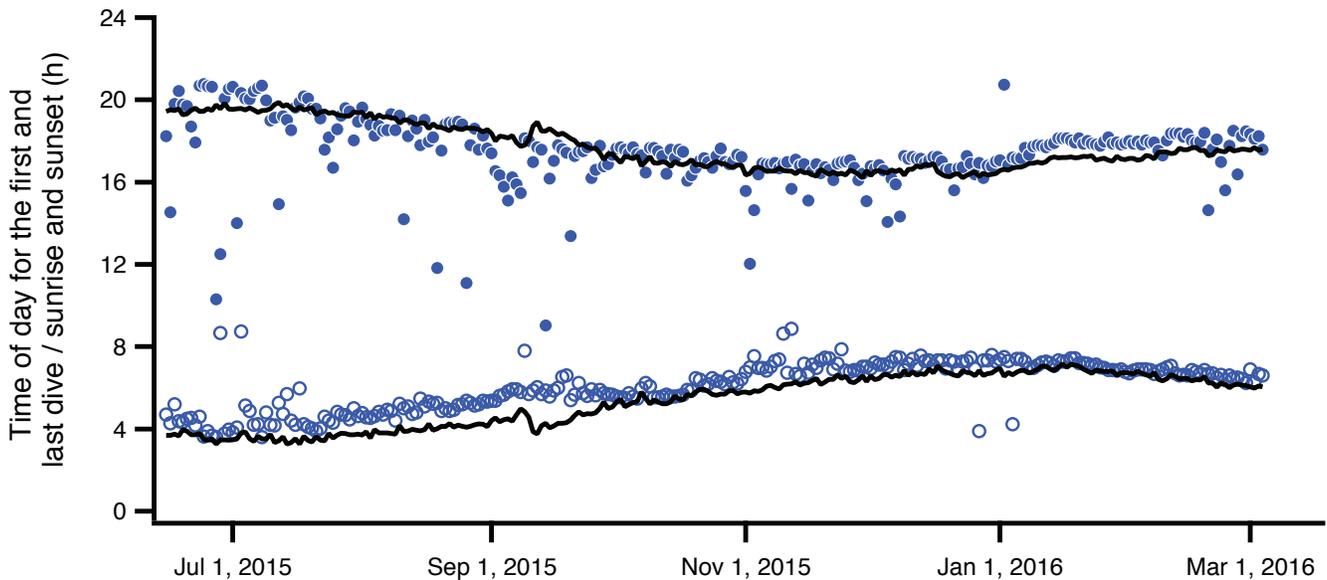


Fig. 2. Seasonal changes in the daily timing of Rhinoceros Auklet diving activities. Start (open circles) and finish (filled circles) time of diving activity for Bird B for each day during the non-breeding period. Time of day is shown as the local time at the colony (GMT+9). Black lines show times of sunrise and sunset, calculated from the geolocator data.

TABLE 2

Seasonal changes in daily diving activity and water temperature experienced by three Rhinoceros Auklets. Values are given as a mean \pm standard deviation with the number of days (*n*).

Bird ID	Daily dive time (h) ^a				Daily dive depth (m) ^b				Daily water temperature (°C)			
	Breeding	Molt	Post-molt	Winter	Breeding	Molt	Post-molt	Winter	Breeding	Molt	Post-molt	Winter
A	3.5 \pm 1.6	0.9 \pm 0.4	-	-	13.1 \pm 3.7	6.4 \pm 1.6	-	-	14.8 \pm 3.6	14.9 \pm 2.2	-	-
	0.43 \pm 1.5 (<i>n</i> = 36)	-0.49 \pm 0.6 (<i>n</i> = 53)			29.1 \pm 9.1 (<i>n</i> = 36)	12.1 \pm 3.2 (<i>n</i> = 53)			(<i>n</i> = 37)	(<i>n</i> = 53)		
B	4.1 \pm 2.4	1.3 \pm 0.6	3.3 \pm 1.5	5.6 \pm 1.3	11.0 \pm 1.7	12.2 \pm 3.4	15.2 \pm 5.9	26.6 \pm 4.7	13.6 \pm 2.8	14.4 \pm 1.1	10.5 \pm 4.0	11.2 \pm 1.0
	1.94 \pm 2.5 (<i>n</i> = 11)	-1.03 \pm 0.8 (<i>n</i> = 44)	0.31 \pm 1.1 (<i>n</i> = 14)	0.48 \pm 1.1 (<i>n</i> = 28)	24.3 \pm 6.7 (<i>n</i> = 11)	20.8 \pm 6.6 (<i>n</i> = 44)	31.4 \pm 11.0 (<i>n</i> = 14)	50.5 \pm 6.6 (<i>n</i> = 28)	(<i>n</i> = 11)	(<i>n</i> = 44)	(<i>n</i> = 14)	(<i>n</i> = 28)
C	2.6 \pm 1.8	1.4 \pm 0.6	2.6 \pm 0.9	4.2 \pm 1.6	11.7 \pm 5.9	10.4 \pm 3.9	19.1 \pm 4.3	31.5 \pm 5.3	13.5 \pm 1.9	11.4 \pm 2.5	8.1 \pm 1.4	11.3 \pm 0.6
	0.92 \pm 1.6 (<i>n</i> = 31)	-0.10 \pm 0.6 (<i>n</i> = 46)	0.12 \pm 0.7 (<i>n</i> = 14)	0.32 \pm 1.7 (<i>n</i> = 28)	25.6 \pm 11.9 (<i>n</i> = 31)	22.6 \pm 6.8 (<i>n</i> = 46)	39.5 \pm 8.7 (<i>n</i> = 14)	59.2 \pm 10.0 (<i>n</i> = 28)	(<i>n</i> = 32)	(<i>n</i> = 46)	(<i>n</i> = 14)	(<i>n</i> = 28)

^a Daily dive time (above) and residual daily dive time (below, in bold) are shown in the same column. Residual daily dive times are calculated from the linear regression of daily dive time against mean daily dive depth (as in Fig. 4).

^b Daily mean dive depth (above) and maximum dive depth (below, in bold) are shown in the same column.

in winter (Fig. 4). However, the birds showed higher diving effort in winter than was predicted by mean daily dive depths, as indicated by positive values of residual daily dive times (Table 2).

The high diving effort during winter might also reflect the increased energy demand for thermoregulation (Fort *et al.* 2013, Burke & Montevecchi 2018, Dunn *et al.* 2020). However, our Rhinoceros Auklets experienced relatively low water temperatures during the post-molt period in the fall compared to the winter period, indicating that the increase in the thermoregulatory costs might be mitigated by moving to warmer southern regions in winter. We suggest that the high diving effort in winter might reflect pre-breeding accumulation of body reserve (e.g., Daunt *et al.* 2006, Takahashi *et al.* 2020), which could have positive effects on subsequent breeding performance (Daunt *et al.* 2006, Sorensen *et al.* 2009). Our results confirmed that Rhinoceros Auklets breeding on Teuri Island use the Sea of Japan as a wintering area, corroborating a previous two-

year study (Takahashi *et al.* 2015), even though the longitudinal distributions in our study were further east. We suggest that the foraging conditions in this wintering area, where fish community changes have been associated with past shifts in climate (Tian *et al.* 2006), are crucial for the Teuri Island population of Rhinoceros Auklets.

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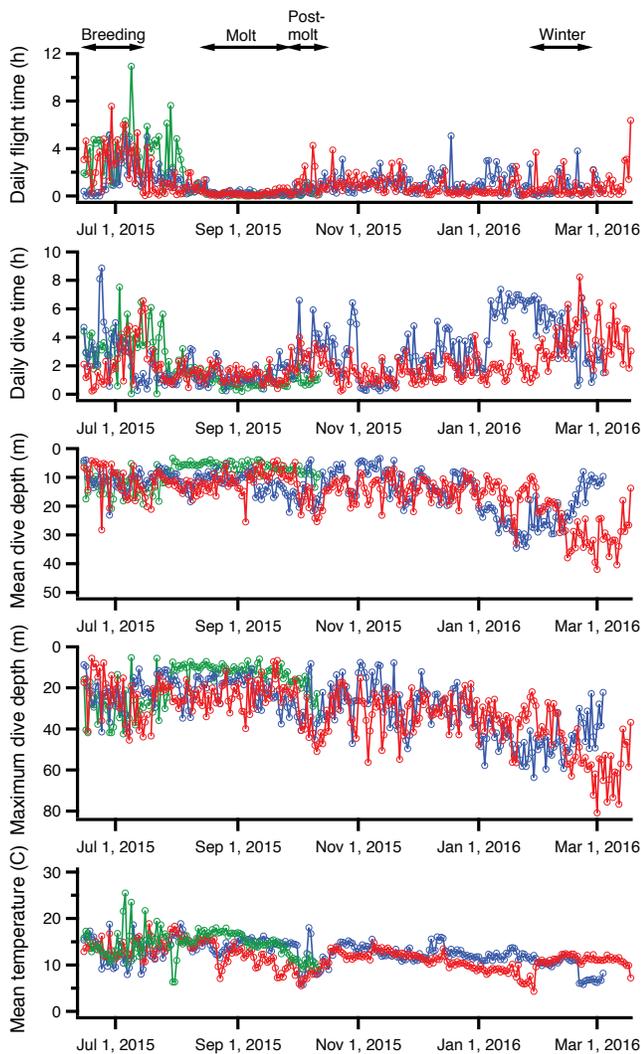
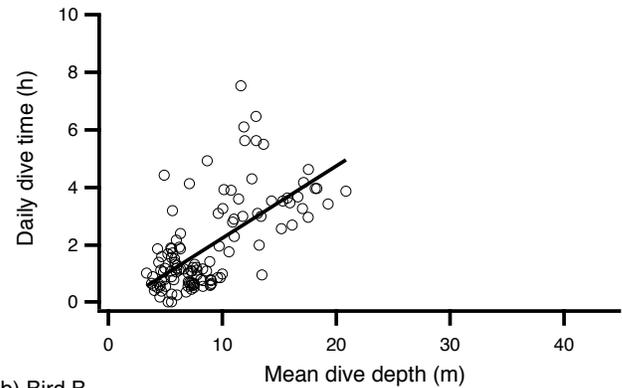
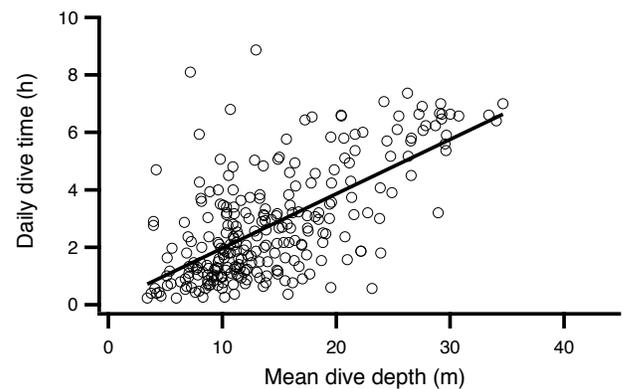


Fig. 3. Seasonal changes in daily flight and dive times, mean and maximum dive depths, and mean water temperature experienced (from top to bottom) of three Rhinoceros Auklets. Each color shows different individuals (green, blue, and red for Birds A, B, and C, respectively). Double-headed arrows show the approximate timing of the four periods (breeding, molt, post-molt, and winter) used in Table 2.

(a) Bird A



(b) Bird B



(c) Bird C

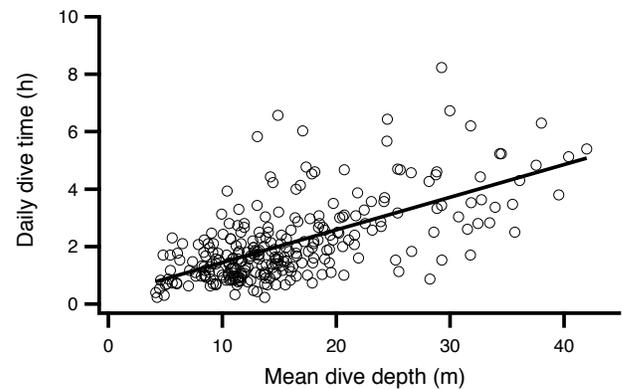


Fig. 4. The relationship between daily dive time and daily mean dive depth. The linear regression line is shown as a solid line for each bird (Bird A: $y = 0.250x - 0.264$, $n = 119$, $R^2 = 0.420$, $P < 0.001$; Bird B: $y = 0.190x + 0.066$, $n = 264$, $R^2 = 0.429$, $P < 0.001$; Bird C: $y = 0.114x + 0.309$, $n = 277$, $R^2 = 0.406$, $P < 0.001$).

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