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RESEARCH ARTICLE

The early life of king penguins: ontogeny of dive capacity and foraging behaviour in an expert diver

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ABSTRACT

The period of emancipation in seabirds, when juveniles change from a terrestrial existence to a life at sea, is associated with many challenges. Apart from finding favourable foraging sites, they have to develop effective prey search patterns and physiological capacities that enable them to capture sufficient prey to meet their energetic needs. Animals that dive to forage, such as king penguins (*Aptenodytes patagonicus*), need to acquire an adequate breath-hold capacity, allowing them to locate and capture prey at depth. To investigate the ontogeny of their dive capacity and foraging performance, we implanted juvenile king penguins before their first departure to sea and also adult breeders with a data-logger recording pressure and temperature. We found that juvenile king penguins possess a remarkable dive capacity when leaving their natal colony, enabling them to conduct dives in excess of 100 m within their first week at sea. Despite this, juvenile dive/foraging performance, investigated in relation to dive depth, remained below the adult level throughout their first year at sea, probably reflecting physiological limitations as a result of incomplete maturation. A significantly shallower foraging depth of juveniles, particularly during their first 5 months at sea, could also indicate differences in foraging strategy and targeted prey. The initially greater wiggle rate suggests that juveniles fed opportunistically and also targeted different prey from adults and/or that many of the wiggles of juveniles reflect unsuccessful prey-capture attempts, indicating a lower foraging proficiency. After 5 months, this difference disappeared, suggesting sufficient physical maturation and improvement of juvenile foraging skills.

KEY WORDS: Ontogeny, Foraging proficiency, Wiggles, Seabirds, Bio-logging, Diving

INTRODUCTION

Juvenile birds, like other vertebrates, face a challenging situation during their period of emancipation (Burger, 1980; Wunderle, 1991). At this point they should have acquired the basic set of tools required for survival. This includes, most importantly, the ability to avoid predation and the successful localization and capture of sufficient food of the right kind. The latter requires a number of behavioural skills (e.g. finding productive foraging areas, effective search patterns, prey recognition/selection), as well as proficiencies associated with their anatomy/morphology and biochemistry/physiology (locomotion, neuromuscular coordination, thermoregulation) (Marchetti and Price, 1989; Wunderle, 1991). It is probably not surprising that in long-lived animals mortality is generally higher during the juvenile phase than during adult life, affecting the recruitment into the breeding stock of a population and, consequently, population dynamics (Charlesworth, 1980; Stearns, 1992; Weimerskirch, 2002; Levitis, 2011). One aspect that has received particular attention in explaining this greater mortality of juvenile animals is their generally lower foraging proficiency, which typically lags behind that of adults for a considerable period of time (Wunderle, 1991). This might be related to differences at particular stages of a foraging sequence (the choice of foraging site, prey search patterns, prey capture and handling) and improvements in foraging skills occur over time through physical maturation and learning (Wunderle, 1991; Wheelwright and Templeton, 2003; Castillo-Guerrero and Mellink, 2006; Gomes et al., 2009).

In the marine realm, numerous studies have reported lower success rates for juvenile and immature seabirds during prey-capture attempts (Orians, 1969; Brandt, 1984; Morrison et al., 1978) and a generally lower foraging efficiency/proficiency (Daunt et al., 2007a,b; Gomes et al., 2009; Grecian et al., 2018). Juvenile birds might compensate for their lower foraging proficiency in a number of ways. For example, they may increase their foraging effort by allocating more time to foraging (Dunn, 1972; Morrison et al., 1978). However, this might ultimately be constrained by seasonal changes in environmental conditions (reduced day length and deterioration of light conditions in winter, limiting visual foraging) and/or prey availability, challenging their energy balance and, consequently, survival (Daunt et al., 2007a). Apart from the lack of experience, a lower foraging proficiency might be the result of an insufficient biochemical/physiological development affecting locomotion (lower muscle efficiencies and/or mismatches between muscle biochemistry and fibre-type composition; Shero et al., 2012, 2019) and the required motor skills for prey capture and handling (Marchetti and Price, 1989; Wunderle, 1991).

In addition, for animals that dive to forage, breath-hold capacity will be of great importance, enabling them to locate and capture prey at depth. Such capacity relies on sufficiently developed oxygen stores, a meticulous use of the limited oxygen underwater (‘dive response’) and the ability to rapidly refuel oxygen and remove CO_2 at the surface between dives (Kooyman, 1989; Butler and Jones, 1997; Butler, 2004). In contrast to marine mammals, where numerous studies investigated in detail the development of dive capacity (e.g. Burns, 1999; Folkow et al., 2010; Noren and Suydam, 2016), little is known about the ontogeny of dive capacity in seabirds. A few studies have investigated oxygen stores [blood haemoglobin (Hb) and pectoral muscle myoglobin (Mb) content] and muscle enzyme activity in chicks/fledglings and adults of a number of penguin and alcid species (Weber et al., 1974; Haggblom et al., 1988;

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Williams, 1992; Ponganis et al., 1999, 2010). These studies found considerably lower Mb levels in chicks/fledglings, while Hb levels and muscle enzyme activity approached those of adults and suggested that Mb might be a critical determinant of juvenile dive capacity. Only one of the above groups also looked into the actual dive behaviour of birds upon fledging. Ponganis and colleagues (1999, 2010) found that juvenile emperor penguins (*Aptenodytes forsteri*), which possess ∼30% of the Mb concentration and ∼60% of the body mass of adults at the time of fledging, conduct shallower and shorter dives during their first 2.5 months at sea than adults during foraging trips. Similar dive patterns were observed during post-natal dispersal of juvenile emperor penguins from a different colony (Thiebot et al., 2013; Labrousse et al., 2019). Hence, a fully developed and sufficiently large muscle O_2 store appears to be of great importance for these birds to facilitate their extreme dive performance (Ponganis et al., 1999, 2010).

King penguins (*Aptenodytes patagonicus* Miller) are the second largest penguin species and, in the avian world, their dive performance is surpassed only by the larger emperor penguins (Pütz et al., 1998; Pütz and Cherel, 2005; Wienecke et al., 2007). Recently, studies have investigated behavioural and physiological aspects of king penguins during their early life at sea (Orgeret et al., 2016, 2019; Enstipp et al., 2017, 2019). These birds spend the first year of their life at their natal colony and, upon completion of their first moult into waterproof plumage, enter the sea during the austral spring. During the following 1–3 years, they roam over a large oceanic area (Orgeret et al., 2016, 2019), only returning to land for their annual moult (Enstipp et al., 2019). Unfortunately, no information concerning their physiological status at the time of fledging is available (e.g. oxygen stores in blood and muscle). Given their considerably longer developmental period on land (Bost et al., 2013; Kooyman et al., 1996), one might expect that the physical/physiological maturation (especially dive capacity) of juvenile king penguins is further advanced than is the case for juvenile emperor penguins. Besides dive capacity, detailed behavioural patterns of juvenile king penguins during their initial phase at sea are unknown (depth utilization, temporal organization of foraging). Previous studies investigated the dive behaviour and movement patterns of juvenile king penguins by deploying satellite relayed loggers that provided summary data for dive behaviour and location (Orgeret et al., 2016, 2019). This led to the suggestion that the development of dive capacity is crucial for the survival of juvenile king penguins (Orgeret et al., 2016). However, a more detailed analysis of dive capacity development, notably investigating the important effect of depth on various parameters, was not possible with the acquired summary data. Investigating the foraging patterns and, especially, direct predator–prey interactions in deep-diving animals that forage far away from land remains a technical challenge, despite the fast developments in biologging technology (Wilmers et al., 2015; Andrews and Enstipp, 2016; Forin-Wiart et al., 2019; Fahlman et al., 2021). While general foraging patterns can be assessed from pressure recordings (dive profiles), there are no practical methods to reliably document the outcome of predator–prey interactions. Consequently, proxy variables, such as rapid changes in dive profile (i.e. wiggles) have been used as indicators of prey encounters in diving animals, including king penguins (Bost et al., 2007; Hanuise et al., 2010).

The purpose of this study was to investigate the ontogeny of physiological capacity and dive/foraging behaviour in juvenile king penguins during their first year at sea and to contrast these parameters with those of adult breeders. In particular: (1) we studied how indices of dive capacity differ between juvenile and adult penguins and how they develop in juveniles; (2) we explored how foraging behaviour and effort of both juveniles and adults change with season; (3) we investigated presumed differences in foraging proficiency between juvenile and adult birds; and (4) we studied the ontogeny of the spatial (depth utilization) and temporal organization of foraging behaviour in juvenile king penguins.

MATERIALS AND METHODS

Bird capture, logger implantation and recapture

Our study was conducted at the king penguin colony of 'Baie du Marin' on Possession Island, Crozet Archipelago, in the Southern Indian Ocean (46°25′34″S, 51°51′36″E). All procedures concerning bird capture, logger implantation, recovery from surgery, bird release and recapture were detailed in previous papers (Enstipp et al., 2017, 2019). In brief, we implanted 30 juvenile king penguins of both sexes (∼1 year old; November/December 2013) and 8 adult males (>3 years old; December 2014) with a data logger (LUL, MIBE, IPHC, Strasbourg, France) that recorded pressure and temperature. The logger was positioned on the right flank of a bird and placed within the subcutaneous fat layer (see fig. 1 in Enstipp et al., 2017). At the time of implantation, juveniles were at the end of their first moult and nearly ready to leave the colony for the first time and disperse at sea, while adults were incubating eggs. All birds also received a passive transponder tag that allowed detection upon return to the colony. Following extended periods at sea, 19 immature birds and 6 adult birds were successfully recaptured and underwent surgery for logger removal.

All experimental procedures were approved by the French ethics committee (APAFIS, permit no. 02015041411414001) and the French Polar Environmental Committee (permit nos 2013-76, 2014-121, 2015-145; TAAF) and conducted in accordance with its guidelines.

Data analysis

Logger data and analysis

Of the 19 loggers retrieved from immature birds, 14 loggers recorded data for periods ranging between 2 weeks and 2.5 years before battery failure. Loggers from 6 adult birds were retrieved and recorded data over periods that ranged from 3 weeks to 10 months (Table 1). All juvenile birds conducted extended trips at sea before returning to their natal colony (Table 1). In the current analysis, we focused on the first year spent at sea ('juvenile stage'), which starts with the departure from the colony and ends with the beginning of their second moult, which started on average 380.8±7.7 days after departure (mean±s.e.m. from 6 juveniles). Adult birds conducted multiple foraging trips that started during the incubation period, continued throughout the winter (June–September) and extended into the following spring (September–December; Table 1). All but one adult bird, from which loggers were retrieved, failed their breeding attempt during the autumn, when chicks disappeared from the créche.

All data were analysed using custom-written programs in Matlab (version R2015b; MathWorks, Natick, MA, USA; for details, see Enstipp et al., 2017, 2019). After a zero offset correction of depth data, various dive parameters were extracted for all dives >1 m, using a custom-written Matlab program that classified dive behaviour as described in detail in Halsey et al. (2007). In the current analysis, we included data from 8 juvenile and 6 adult birds (Table 1) that had been fitted with the same logger coating ('oil and wax'; see Enstipp et al., 2019). Sampling intervals for pressure and temperature recordings were originally set to 5 s for juveniles and 4 s for adults. To avoid any potential bias resulting from sampling

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Table 1. Summary of logger deployments (oil and wax-coated loggers only)

Bird	M_b (kg)	Start trip 1 (dd/mm/yyyy)	End trip 1 (dd/mm/yyyy)	Duration trip 1 (days)	Time at sea recorded (year 1) (days)	No. of trips recorded (year 1)
Juveniles						
LuL04	9.8	08/12/2013	06/11/2014	330.9	380.9	2
LuL05	12.3	08/12/2013			194.5	
LuL11	8.6	08/12/2013	06/12/2014	363.5	391.8	2
LuL18	11.5	18/12/2013			10.5	
LuL22	10.2	05/01/2014			89.2	
LuL23	10.8	06/01/2014			255.5	
LuL25	11.1	04/01/2014			35.8	
LuL29	11.3	07/01/2014	03/11/2014	300.1	340.5	2
Mean	10.7±0.4	23/12/2013 (±5.1 days)	15/11/2014 (±10.7 days)	331.5±18.3	212.3±54.5	2.0±0.0
Adults						
LuL31	9.7	29/12/2014	14/01/2015	16.7	173.5	13
LuL32	9.7	31/12/2014	18/01/2015	18.8	72.4	5
LuL33	10.1	01/01/2015	13/01/2015	12.3	23.7	2
LuL34	10.2	09/01/2015	21/01/2015	12.4	12.4	1
LuL36		03/01/2015	16/01/2015	13.2	139.6	7
LuL37	11.7	05/01/2015	12/01/2015	7.5	257.9	17
Mean	10.3±0.4	02/01/2015 (±1.8 days)	16/01/2015 (±1.5 days)	13.5±1.8	113.3±42.5	7.5±2.6

'Mean' indicates grand means±s.e.m. 'Duration trip 1' for juvenile birds refers to their first trip upon moult completion, when they leave their natal colony for the first time in their life and stay at sea until the following moult cycle (their second trip being their pre-moult trip, undertaken in preparation for the moult fast ashore); only complete trips are indicated. For adults, the first trip recorded occurred during the incubation period.

interval differences between both groups, all adult data were resampled at 5 s intervals during initial data processing using a linear interpolation function in Matlab ('interp1'; Wilson et al., 1995).

Ontogeny of dive/foraging performance and effort

We investigated a number of parameters concerning both dive/foraging performance and effort throughout the first year of juveniles at sea and during the corresponding period in adult breeders. Performance parameters (e.g. dive and post-dive surface interval duration; Fig. 1), especially when investigated in relation to dive depth, may be indicative of physiological capacity. By contrast, effort parameters (e.g. daily foraging time, dive effort) indicate 'how hard a bird worked', such as how much daily time it allocated to foraging.

We investigated dive/foraging parameters in three ways. (1) To investigate the effect of dive depth on performance parameters, we sorted all deep dives (≥50 m) into 10 m depth bins, according to the maximum depth reached during a dive. Throughout our study, dive depth refers to the maximum depth reached during a dive, unless specified differently. The 50 m depth threshold has been used in previous investigations (Ropert-Coudert et al., 2000; Charrassin et al., 2002; Halsey et al., 2007), as most foraging of adult king penguins seems to occur during dives exceeding this depth (Pütz et al., 1998). Hence, in our study we distinguished between shallow dives (<50 m), most likely associated with travelling, and deep ('foraging') dives (≥50 m). We only considered depth bins for which sufficient data for both juveniles and adults were available, effectively truncating the depth range at 250 m because only adult birds conducted a sufficient number of deeper dives. We then investigated how performance parameters changed with dive depth and contrasted juvenile and adult birds (Fig. 1). (2) The same analysis was conducted to investigate longitudinal changes in performance parameters of juveniles, in relation to dive depth, during their initial period at sea. Here, we contrasted juvenile performance parameters during their first and fourth month at sea (Fig. 2). As body mass at departure varied between juveniles (Table 1), potentially indicating differences in physical maturation, we also tested whether initial body mass affected any of the investigated performance parameters during the first month at sea. (3) To study the ontogeny of dive/foraging performance and effort, and potential seasonal changes, we computed the weekly grand means±s.e.m. (based on the daily means of individual birds) of various parameters (e.g. dive depth and duration; Fig. 3), contrasting juvenile penguins with adult breeders. For one parameter (dive efficiency), this was done according to dive depth (50 m bins), to take into account the strong effect of depth on dive efficiency (Fig. 4). We also computed the 95th percentile for all performance parameters of juveniles as a proxy for physiological limitation (Bennett et al., 2001, 2010). All data from juveniles and adults were sorted according to the cumulative time spent at sea (from week 1 to week 48). The mean departure date of juveniles was 25 December 2013 (±5.1 days) with a maximum difference of ∼4 weeks between birds (Table 1). The mean departure date for adults was 2 January 2015 (±1.8 days), with a maximum range of ∼1.5 weeks (Table 1). The time spent at sea was assigned to particular seasons of the annual cycle, starting with 'week 1' during the austral summer in mid-December. Hence, the maximum individual deviation from this temporal alignment was ∼3 weeks.

In the definition of dive/foraging performance and effort parameters, we followed the classification system for seabird diving behaviour given in Halsey et al. (2007). The following parameters were computed as an index of dive/foraging performance of birds in relation to dive depth: dive duration, post-dive surface interval (PDSI), bottom duration, dive efficiency and number of wiggles per dive. Dive duration is the period spent submerged during a dive. PDSI is the total time spent at the surface between two foraging dives (≥50 m) and excludes periods spent submerged during shallow dives (<50 m), which occasionally occurred between foraging dives. In our analysis, we only included dives conducted within a foraging bout, excluding isolated deep dives (with a PDSI duration exceeding 15 min; Halsey et al., 2007).

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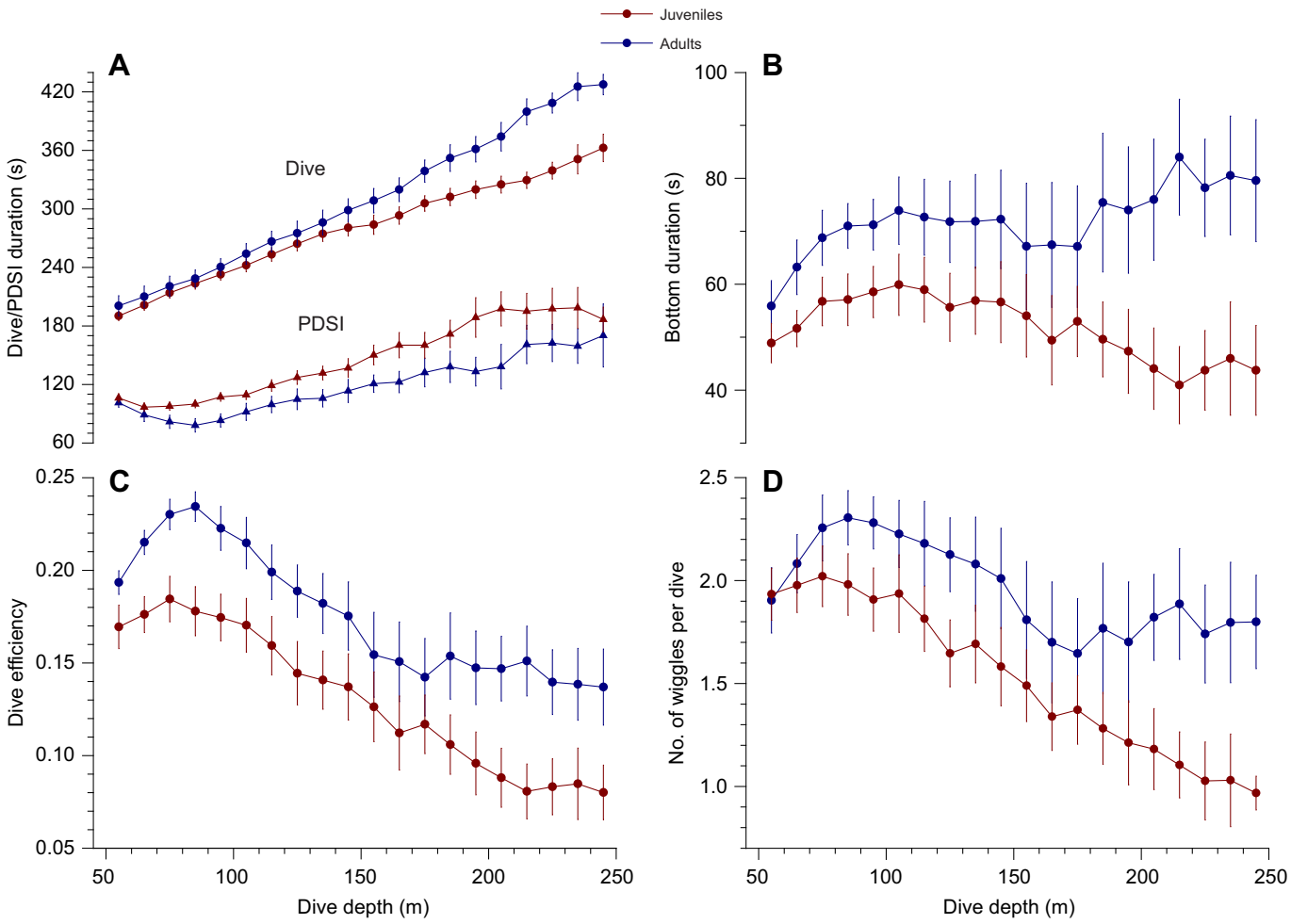

Fig. 1. Effect of depth on the dive performance of juvenile and adult king penguins. (A) Dive (circles, top) and post-dive surface interval (PDSI; triangles, bottom) duration, (B) bottom duration, (C) dive efficiency (bottom duration/dive cycle duration) and (D) number of wiggles per foraging dive of adult (blue) and juvenile (red) king penguins versus dive depth. Values are grand means±s.e.m. (10 m depth bins; all dives ≥50 m). For adults N=4–6 birds, n=43,556 dives and for juveniles N=4–8 birds, n=106,586 dives.

Typically, during a dive, steps and wiggles are detectable as specific changes in the dive profile and are used to define further parameters (Halsey et al., 2007). Accordingly, bottom duration was defined as the time between the first and last wiggle or step of a dive occurring at a depth deeper than 75% of maximum dive depth. Dive efficiency represents the fraction of a dive cycle spent in the bottom phase (bottom duration/dive cycle duration; Ydenberg and Clark, 1989; Charrassin et al., 2002). We also considered the number of wiggles per dive as a relative index of prey encounter/pursuit events (Wilson and Wilson, 1995; Simeone and Wilson, 2003; Bost et al., 2007; Hanuise et al., 2010). Three performance parameters (dive depth, dive duration, dive efficiency) were computed throughout the year to investigate the ontogeny of dive/foraging parameters (Figs 3A,B and 4). The ontogeny of dive/foraging effort of birds was studied using two parameters: daily foraging time and dive effort. Daily foraging time represents the sum of the cumulative time per day that a bird spent underwater in dives ≥50 m and the recovery time spent at the surface between these dives. The last dive of a foraging bout and the occasional isolated deep dives were excluded. Dive effort was calculated as the product of the total time spent submerged per day (dive depth >1 m) and mean depth during submergence (here: mean of all depth values during submergence) and integrates both temporal and spatial (depth) aspects of diving/foraging.

Indices of foraging proficiency and foraging strategies of juvenile and adult king penguins

We used the number of wiggles detected during dives as an index of foraging proficiency. There are a number of caveats associated with this index and they will be discussed in detail below. Nevertheless, most researchers seem to agree that wiggles in the dive profile represent prey-encounter events (Bost et al., 2007; Hanuise et al., 2010), while the outcome of these events remains unknown. Despite this, investigating the number of wiggles detected during the dives of juveniles and adults and potential differences over time might provide us with insights concerning the efficacy of their search patterns and/or prey pursuits. A similar number of wiggles per time spent underwater (wiggle rate) in juveniles and adults presumably indicates a similar capacity to detect prey, while the capacity to capture and ingest prey might still differ between these groups. Hence, we investigated foraging proficiency in juveniles and adults (1) by plotting the daily number of wiggles against the associated time spent submerged in foraging dives, to explore the general relationship, and (2) by computing the weekly grand means of various parameters related to the number of wiggles during foraging dives (longitudinal investigation): ‘dive rate’ (number of foraging dives per hour submerged), ‘bottom fraction’ (bottom duration per hour submerged), ‘wiggle rate’ (number of wiggles per hour bottom

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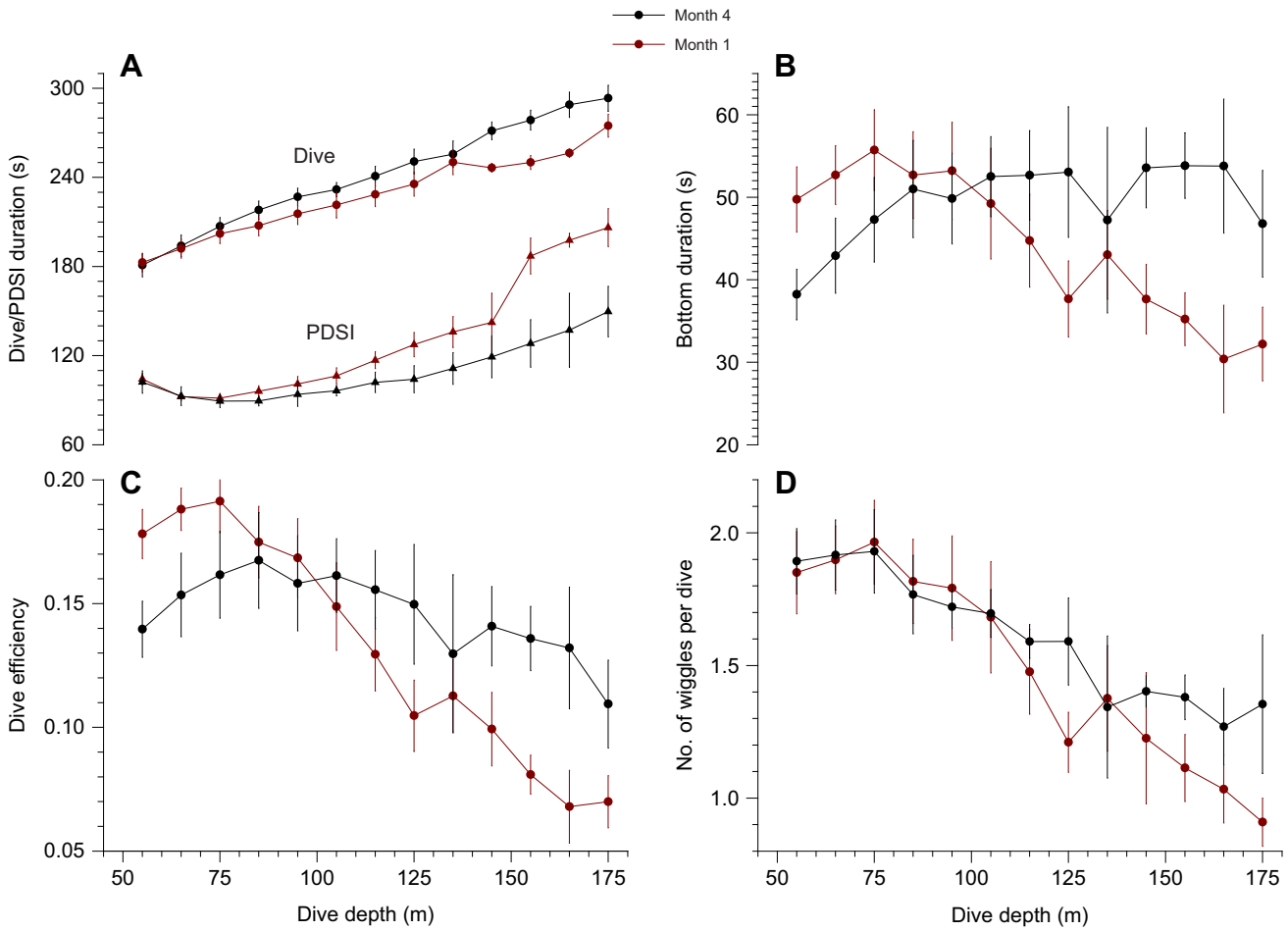

Fig. 2. Longitudinal changes in performance parameters of juveniles in relation to depth. (A) Dive (circles, top) and PDSI (triangles, bottom) duration, (B) bottom duration, (C) dive efficiency and (D) number of wiggles per foraging dive of juvenile king penguins during their first month at sea (red) and 3 months later (black) versus dive depth. Values are grand means±s.e.m. (10 m depth bins; all dives ≥50 m). For month 1 (austral summer) *N*=2–8 birds, *n*=15,047 dives and for month 4 (austral autumn) *N*=4–5 birds, *n*=9960 dives.

duration), and the relative distribution of wiggles across 50 m depth bins. Furthermore, we investigated the spatial (depth utilization) and temporal (diurnal/nocturnal) foraging patterns of juvenile and adult king penguins.

Depth utilization in juvenile king penguins

To investigate how juvenile king penguins utilized the water column when leaving their natal colony and to assess potential changes over time, we computed daily plots of dive depth against time of day for all individuals for their first month at sea. The same analysis was conducted with the dive records from adult breeders.

Temporal foraging patterns: evidence for nocturnal foraging?

Investigation of whether juvenile birds engage in nocturnal foraging activity requires the identification of night periods. As we did not record the geographical position of birds and because juvenile king penguins roam over large oceanic areas during their first year at sea (Orgeret et al., 2016, 2019), moving between time zones, the exact start and end of night periods, as experienced by the birds, were unknown. Accordingly, we used changes in bird diving behaviour to estimate the approximate night periods. Birds typically discontinue deep-diving activity when light levels become insufficient in the evening until the following morning. Furthermore, they also show a systematic increase in dive depth near dawn and a systematic decrease near dusk (Pütz et al., 1998). Hence, we calculated the duration of daily 'rest' periods between the end of deep-diving activity in the evening and the start of deep-diving activity the following morning and plotted these over the entire period investigated. These plots typically showed a regular pattern that changed according to season (i.e. the rest/night period increased from summer to winter and decreased from winter to summer). The dive records of outliers (i.e. days that showed a shorter 'rest' period than typical for the period in question) were visually inspected for evidence of nocturnal foraging (dives ≥50 m). The same analysis was conducted with the dive records from adult breeders.

Statistical analysis

All statistical analyses were conducted in JMP (version Pro 11.2.0, SAS Institute Inc., Cary, NC, USA). Linear mixed-effects model analysis (LME) with restricted maximum likelihood (REML) estimation was used to test for differences of performance parameters (dive duration, PDSI, bottom duration, dive efficiency, number of wiggles per dive) in relation to dive depth between juveniles and adults and between month 1 and month 4 for juveniles. Depth and status (juveniles versus adults or month 1 versus month 4) were included as fixed effects, while bird ID was included as a random effect to account for repeated measures. Where appropriate, interaction terms were included in the respective

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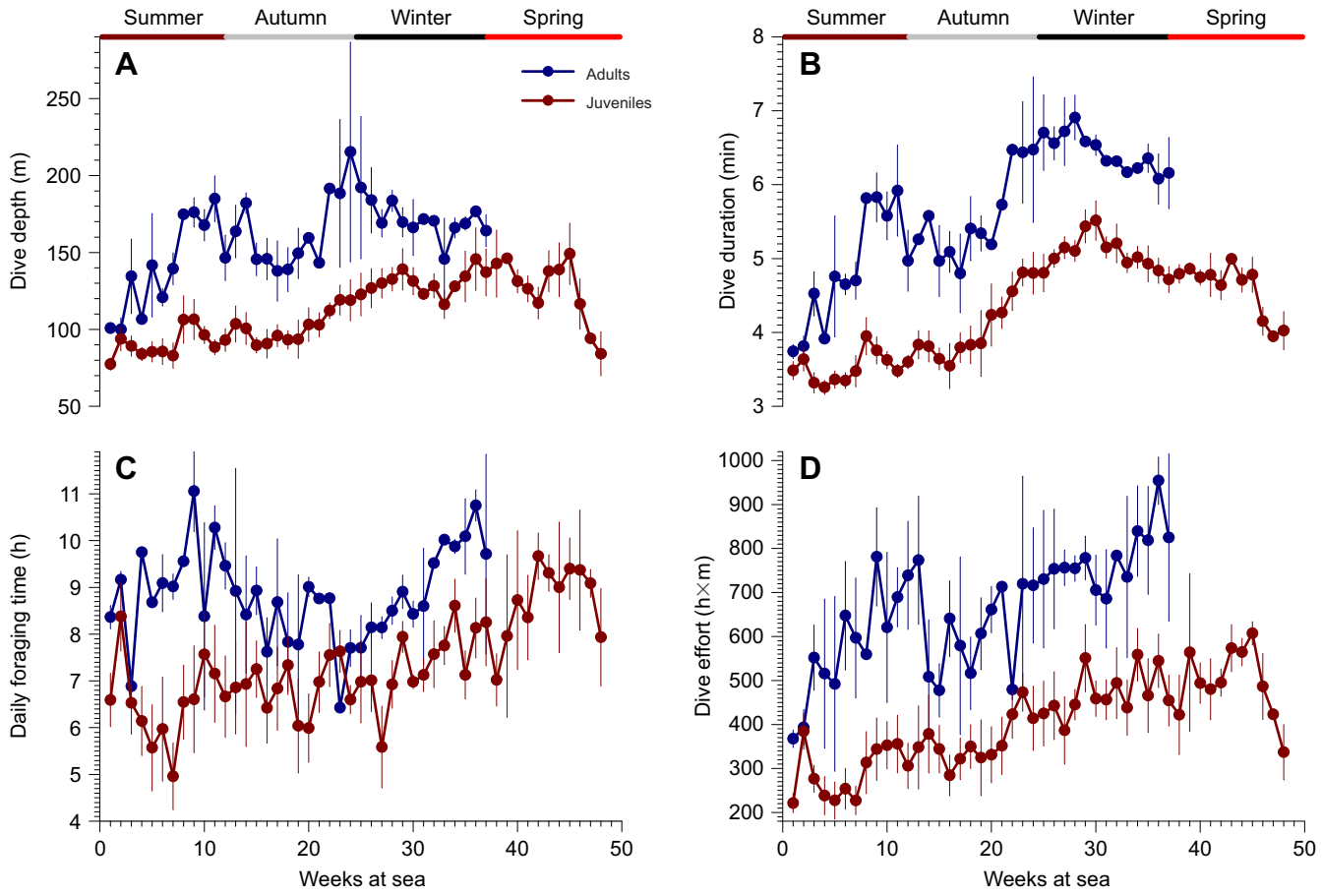

Fig. 3. Longitudinal/seasonal changes in dive/foraging behaviour and effort. (A) Development of dive depth, (B) dive duration, (C) daily foraging time and (D) dive effort [time (h) submerged per day×mean depth (m) during submergence] in dives of adult (blue) and juvenile (red) king penguins (weekly grand means±s.e.m.). In A–C, only foraging dives (≥50 m) are included (for adults *N*=1–6 birds, *n*=46,211 dives; for juveniles *N*=2–8 birds, *n*=108,751 dives), while D includes all dives >1 m (*n*=134,611 and 306,997 dives for adults and juveniles, respectively).

model and removed if not significant. Similarly, differences in the ontogeny of performance (dive depth, dive duration, dive efficiency, dive rate, bottom fraction, wiggle rate) and effort parameters (foraging time, dive effort) between juveniles and adults were tested with LME analysis. We first tested for overall differences between groups by including status as a fixed effect and bird ID as a random effect in the model. Then we tested whether the parameters changed over time and whether this differed between groups by adding 'weeks at sea' and the interaction term 'weeks at sea×status' as fixed effects to the model. If a parameter included different depth bins (dive efficiency), analysis was also run separately for each bin. Lastly, we used LME analysis to test for differences in the relationship between the number of wiggles per day and time spent submerged in foraging dives between juveniles and adults. Significance for all statistical tests was accepted at $P<0.05$. *F*-values are presented with degrees of freedom and denominator degrees of freedom. All values presented are grand means±s.e.m., established from individual bird means, unless specified differently.

RESULTS

Ontogeny of dive performance, dive/foraging behaviour and effort

Effect of depth on dive performance as an indicator of physiological capacity

There was a strong effect of dive depth on all investigated performance parameters in both juvenile and adult king penguins ($P<0.0001$ for all parameters but bottom duration, for which $P=0.02$; Fig. 1). While dive and PDSI duration increased with depth, dive efficiency and the number of wiggles per dive decreased. Bottom duration increased with depth in adults but declined in juveniles ($F_{1,231}=35.66$, $P<0.0001$; Fig. 1). Most importantly, when considering the different depth bins, all parameters differed significantly between juveniles and adults ($P<0.0001$ for all parameters but dive efficiency, for which $P=0.04$). Whereas for dives to a given depth, dive duration, bottom duration, dive efficiency and the number of wiggles per dive were significantly greater in adults, PDSI duration was significantly greater in juveniles (Fig. 1). On average, for a given dive depth, dive duration was 8% shorter and PDSI duration 28% longer in juvenile birds, when compared with adults. The time spent near the bottom of a dive, during which most foraging takes place, was, on average, 25% shorter in juveniles, so that overall dive efficiency was similarly reduced, when compared with adult birds. Accordingly, the number of wiggles per dive to a given depth was, on average, 19% lower in juveniles than in adults.

Longitudinal changes in performance parameters of juveniles in relation to depth

LME analysis investigating the development of performance parameters of juvenile king penguins in relation to dive depth between their first and fourth month at sea showed that with the exception of the number of wiggles per dive, all parameters were

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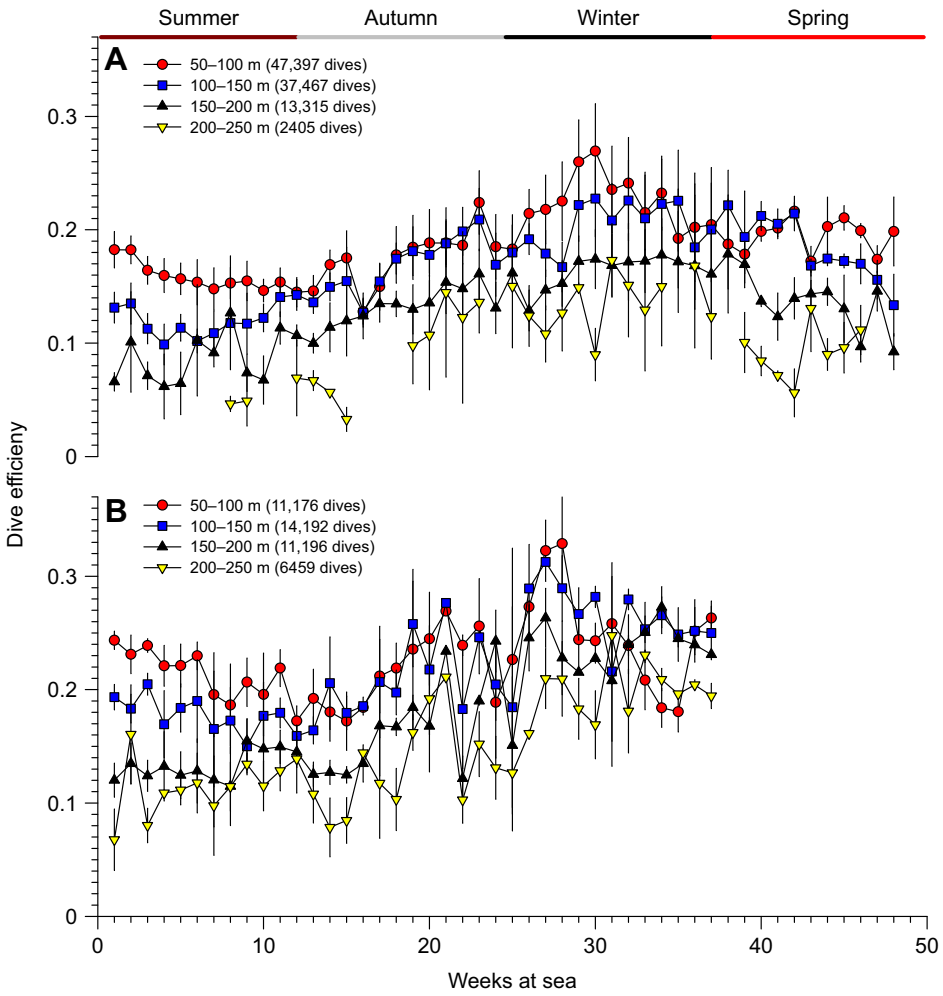

Fig. 4. Longitudinal/seasonal changes in dive efficiency of juvenile and adult king penguins. Changes in dive efficiency over time in juvenile (A; *N*=2–8 birds, *n*=100,584 dives) and adult king penguins (B; *N*=1–6 birds, *n*=43,023 dives) for various depth bins (weekly grand means±s.e.m.).

significantly improved after birds had spent 3 months at sea (P<0.0001 for all parameters but the number of wiggles per dive, for which P=0.14, $F_{1,137}$=2.24; Fig. 2). Especially noticeable was the reduction in PDSI duration after 3 months, particularly after deeper dives. Similarly, bottom time during dives to a given depth remained nearly constant for much of the depth range after 3 months at sea and the decline in overall dive efficiency with depth was also considerably reduced (Fig. 2). Despite the considerable body mass variation between juveniles at departure (8.6–12.3 kg; Table 1), no effect of body mass on any of the performance parameters during their first month at sea (investigated in relation to dive depth) was detectable (P-values between 0.57 and 0.98 for all performance parameters indicated in Fig. 2).

Seasonal changes in dive/foraging behaviour and effort

Table 2 presents mean values for various investigated dive parameters for juveniles and adults during their first month at sea (foraging dives; ≥50 m) and illustrates the degree of observed variation between individuals. The longitudinal investigation of dive/foraging behaviour (dive depth and duration; Fig. 3A,B) showed that: (a) adult birds dived to greater depth ($F_{1,11}$=9.23, P=0.01) and for a longer duration ($F_{1,12}$=7.07, P=0.02) than juveniles over the entire period investigated; (b) during their first 5 months at sea, mean dive depth of juveniles rarely exceeded 100 m, with a corresponding mean dive duration below 4 min; (c) after that period, during the autumn, dive depth ($F_{1,817}$=168.47, P<0.0001) and duration ($F_{1,1477}$=509.45, P<0.0001) increased steadily in juveniles, and remained high throughout winter, before both declined in spring; (d) in adult birds, both parameters also increased over time, with a pronounced step in mid-autumn and the scope of the overall increase did not differ between groups ($F_{1,13}$=0.01, P=0.91 and $F_{1,13}$=3.49, P=0.09 for depth and duration, respectively). Dive efficiency was generally greater for shallower depth bins and increased significantly throughout the period investigated in both juveniles and adults ($F_{1,1150}$=148.41, P<0.0001; Fig. 4). For a given depth bin, dive efficiency was greater in adults than in juveniles ($F_{3,1144}$=185.63, P<0.0001) and its increase over time was also significantly greater in adults ($F_{1,13}$=13.56, P=0.003; Fig. 4).

Effort parameters (daily foraging time and dive effort; Fig. 3C,D) showed a similar picture: (a) adult birds had consistently greater values than juveniles throughout the studied period ($F_{1,13}$=6.42, P=0.03 and $F_{1,13}$=18.71, P<0.001 for daily foraging time and dive effort, respectively); (b) following an initial peak and subsequent decline, the daily foraging time ($F_{1,232}$=65.08, P<0.0001) and dive effort ($F_{1,330}$=64.89, P<0.0001) of juveniles increased gradually until spring; (c) in adult birds, both parameters peaked during summer and late winter; (d) the scope of the increase in both parameters over time did not differ between groups ($F_{1,232}$=0.18, P=0.67 and $F_{1,330}$=0.96, P=0.33 for daily foraging time and dive effort, respectively). During spring, all performance and effort parameters declined in juvenile penguins, while data for adult birds are, unfortunately, lacking.

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Table 2. Mean values for dive parameters of juveniles and adults during their first month at sea

Bird	Dive depth (m)	Dive duration (s)	PDSI duration (s)	Bottom duration (s)	Dive efficiency	No. of wiggles per dive
Juveniles						
LuL04	86.3	203.9	94.5	51.2	0.18	1.7
LuL05	95.2	218.4	120.6	51.6	0.16	2.0
LuL11	87.4	214.6	104.7	61.4	0.20	2.0
LuL18	86.1	245.9	107.8	71.3	0.21	2.4
LuL22	114.9	221.1	143.1	36.4	0.11	1.3
LuL23	73.0	166.6	88.5	29.7	0.12	1.1
LuL25	84.6	200.2	102.2	43.5	0.15	1.6
LuL29	88.7	214.6	82.1	57.5	0.20	1.9
Mean	89.5±4.2	210.7±8.0	105.4±6.8	50.3±4.8	0.16±0.0	1.7±0.2
Adults						
LuL31	98.8	234.4	71.6	67.0	0.22	2.0
LuL32	85.9	215.0	90.5	62.9	0.21	2.0
LuL33	98.1	218.6	65.4	57.4	0.21	1.9
LuL34	99.8	222.3	66.7	62.1	0.22	2.0
LuL36	102.3	234.2	73.3	69.5	0.23	2.2
LuL37	127.5	255.2	75.9	63.4	0.20	2.0
Mean	102.0±5.6	229.9±6.0	73.9±3.7	63.7±1.7	0.22±0.0	2.0±0.0

Data are for foraging dives ≥50 m. PDSI, post-dive surface interval. Dive efficiency is the fraction of a dive cycle spent in the bottom phase, i.e. bottom duration/dive cycle duration. 'Mean' indicates grand means±s.e.m.

Extreme performance reflects development of physiological capacity?

In addition to the above investigation, which provides an average picture and allows a direct comparison between juveniles and adults, it is also rewarding to look at extreme performance values, which may provide a glimpse into the development of physiological capacity in juveniles. All juveniles, which had never been at sea, apart from short/shallow 'bathing' activity inside the bay, exceeded a dive depth of 100 m during their first week at sea, with one bird diving to 170 m. Computation of the 95th percentile for performance parameters showed that all parameters improved gradually during the first 4 months at sea, after which performance increased sharply during mid-autumn. For example, dive depth (95th percentile) increased from an average of 118 m during the first week to 163 m after 2 months and 204 m after 7 months. Correspondingly, dive duration (95th percentile) increased from an average of 4.3 min during the first week at sea to 4.9 min after 2 months and 6.5 min after 7 months. The greatest depth (293 m) and the longest dive duration (8.8 min) were achieved by one juvenile during winter. However, despite the occurrence of such exceptional performance, most foraging dives of juveniles during their first 5 months at sea targeted a depth shallower than 100 m, with a corresponding dive duration below 4 min.

Indices of foraging proficiency and potential differences in foraging strategy

The general relationship between the daily number of wiggles and the associated foraging time spent submerged did not differ between juvenile and adult king penguins ($F_{1,12}$=0.15, P=0.71). However, there was an appreciable inter-individual variation, so that for the same time spent submerged, some birds conducted a consistently greater number of wiggles than others. There was also considerable intra-individual variation between days, so that for the same time spent submerged, the number of wiggles differed, often by a factor of 2–3.

Investigating the distribution of wiggles across 50 m depth bins showed that most wiggles conducted by juveniles occurred during dives to 50–100 m up to late autumn, after which this shifted to the 100–150 m depth bin (Fig. 5). By contrast, in adults, wiggles occurred throughout the water column in similar proportions during the summer. In the autumn, most wiggles of adults occurred at a depth layer of 100–150 m and this shifted during winter to even greater depth (150–200 m; Fig. 5).

As juveniles conducted shorter/shallower dives than adults, their dive rate was consistently higher ($F_{1,12}$=6.84, P=0.02; Fig. 6A). Over time, dive rate declined in both groups ($F_{1,1490}$=583.49, P<0.0001), especially during the autumn, so that it reached the lowest level during winter, when dive depth and duration were greatest. The greater dive rate of juveniles and the longer/deeper dives of adults resulted in a similar relative bottom duration. Hence, the fraction of each hour underwater spent at foraging depth did not differ between groups ($F_{1,12}$=2.09, P=0.17). The latter increased during the autumn in both groups ($F_{1,313}$=40.25, P<0.0001), with a more pronounced increase in adults, when compared with juveniles ($F_{1,11}$=5.42, P=0.04). Wiggle rate was significantly greater in juveniles, when compared with adults, especially during their first 5 months at sea ($F_{1,13}$=12.96, P=0.003; Fig. 6B). The number of wiggles conducted per hour of bottom duration declined significantly in juveniles during mid-autumn ($F_{1,225}$=9.4, P=0.002) and reached similar levels to that of adults after ∼5 months at sea, during winter (Fig. 6B).

Depth utilization

Visual analysis of dive depth distribution showed that during the first days at sea, juveniles conducted dives throughout daylight that rarely exceeded 50 m (Fig. 7). The number of detected wiggles during these dives, probably indicating prey encounters, was low. After a few days at sea, depth utilization changed and shallower dives occurred predominately during the early morning and late evening, when light levels limit visual foraging. During these periods, dive depth progressively increased and decreased, respectively, while during the remaining daylight hours juveniles targeted a greater depth (Fig. 7). On average, juveniles required 4.9±0.7 days (range: 3–8 days) before they consistently targeted a depth layer near or beyond 100 m (Fig. 7). Concurrently, the number of detected wiggles reached a higher and more stable level. This pattern of depth utilization persisted for the rest of their first year at sea. By contrast, all adult breeders targeted a depth layer exceeding 100 m from their first day at sea during all recorded foraging trips.

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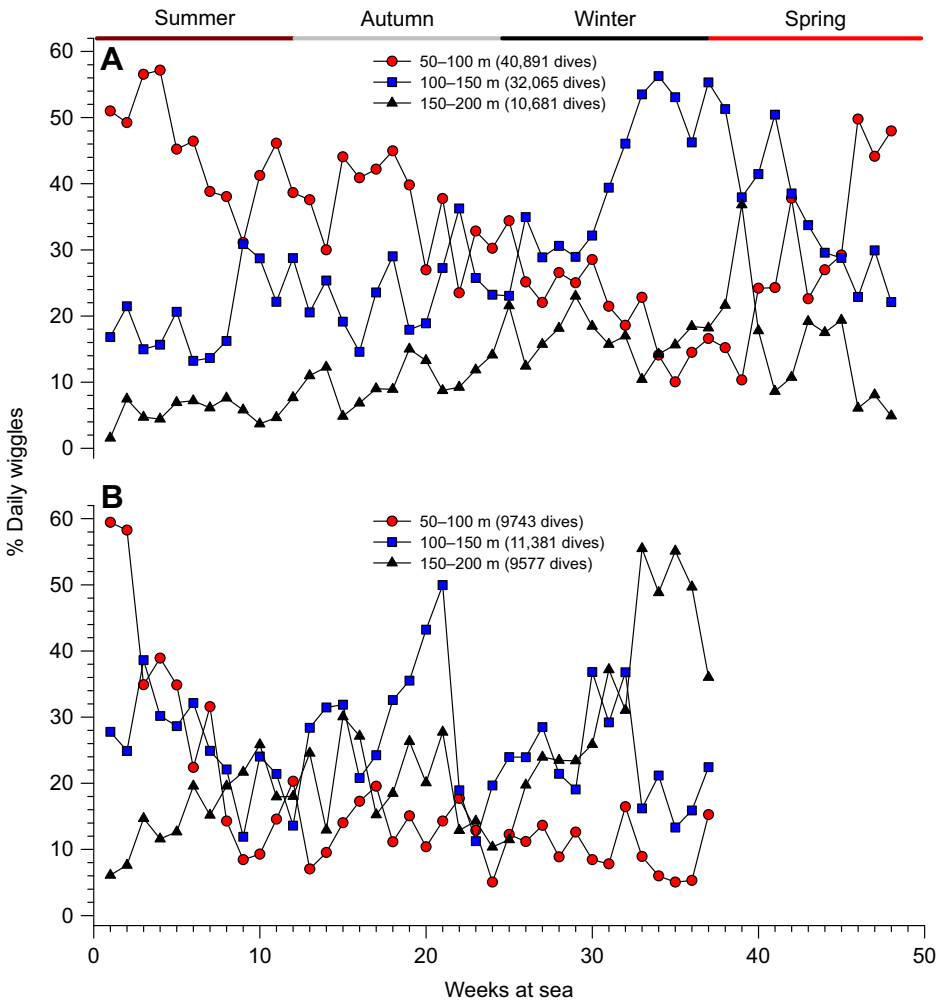

Fig. 5. Depth distribution of wiggles during foraging dives of juveniles and adults. Relative distribution of wiggles across various depth bins over time for juvenile (A; *N*=2–8 birds, *n*=83,637 dives) and adult king penguins (B; *N*=1–6 birds, *n*=30,701 dives; weekly grand means±s.e.m.).

Temporal foraging patterns: evidence for nocturnal foraging?

In our analysis, the 'rest' periods at night (no deep-diving activity) were suspiciously short in a small number of cases for two juvenile penguins only. Visual inspection of the dive records showed that one bird (Lul05) conducted 4 dives ≥50 m within a bout of shallow travelling dives (to ∼5 m) during a single night. The other bird (Lul11) conducted nocturnal dive bouts during 4 nights that mostly targeted a depth of ∼30–40 m, with some dives extending beyond 50 m. For both birds, such nocturnal behaviour occurred during late summer, after birds had been at sea for at least 2.5 months. In all other juveniles and the adult breeders, there was no evidence of nocturnal foraging.

DISCUSSION

Juvenile king penguins possessed a remarkable dive capacity when leaving the colony at the end of their ∼11 month developmental period on land, allowing them to reach a depth in access of 100 m within days. Nevertheless, their dive/foraging performance remained below the adult level during their first year at sea, probably reflecting physiological limitation resulting from incomplete maturation. Most juvenile foraging dives during their first 5 months at sea did not exceed a depth of 100 m, while adults during that period foraged predominately at between 150 and 200 m. Apart from a difference in maturation status, this might also indicate differences in foraging strategy and targeted prey. The wiggle rate of juveniles during their first months at sea was significantly greater than that of adults, potentially indicating opportunistic foraging of inexperienced and hungry juveniles on smaller/less energy dense prey. However, a greater wiggle rate might also reflect a greater number of unsuccessful capture attempts by inexperienced juveniles, indicating a lower foraging proficiency. During late autumn and winter, when juveniles had spent ∼5 months at sea and when changes in food availability forced birds to increase dive depth and duration, this difference in wiggle rate between groups disappeared, probably indicating sufficient physical maturation and improvement of foraging skills in juveniles.

Ontogeny of dive capacity and seasonal changes in dive/foraging behaviour and effort

The shorter dive and bottom durations of juveniles compared with adults for dives to a given depth and their longer PDSI durations are indicative of their inferior physiological capacity that persisted throughout their first year at sea (Fig. 1). However, juvenile capacity developed rapidly at sea (Fig. 2) and the performance also varied between individuals (Table 2), so that some juveniles reached a depth of nearly 300 m during exceptional dives (maximum depth and dive duration: 272 m and 7.0 min, respectively) after only 2 months. Surprisingly, there was no relationship between departure body mass and dive performance during their first month at sea, suggesting that body mass differences did not reflect differences in physical maturation. However, the relatively small number of individuals in our study might have prevented detection of such a relationship.

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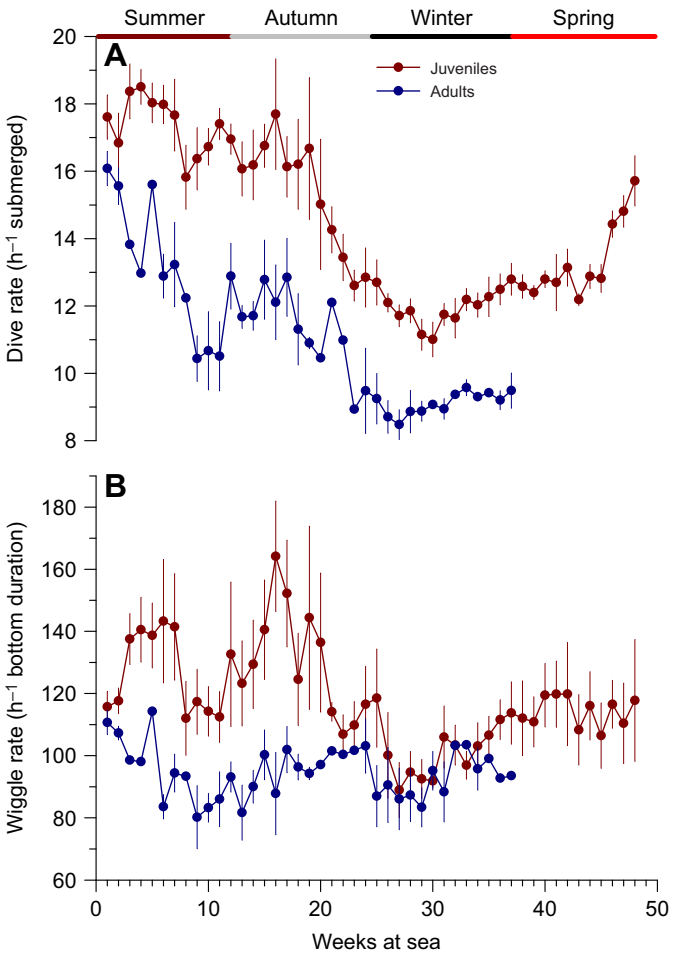

Fig. 6. Development of wiggle rate: an index of foraging proficiency? Development of dive (A) and wiggle rates (B) during foraging dives of juvenile (*N*=2–8 birds, *n*=108,751 dives) and adult king penguins (*N*=1–6 birds, *n*=46,211 dives; weekly grand means±s.e.m.). Juveniles conducted shallower/shorter dives than adults, so their dive rate was significantly greater (A). However, the fraction of time underwater spent at foraging depth (h bottom duration/h submerged) did not differ between groups, allowing direct comparison of wiggles conducted during the bottom phase of dives (B).

Owing to their long developmental period on land, it is likely that by the time juvenile king penguins left the colony, their oxygen stores (particularly in muscle) were further developed than is the case in juveniles of many other marine endotherms. Orgeret and colleagues (2016) suggested that the development of dive capacity is crucial for the survival of juvenile king penguins. Five out of the 17 juveniles they equipped with Splash tags (satellite-transmitting summary data) were unable to improve their dive capacity sufficiently and vanished when oceanographic conditions changed in the autumn. Unfortunately, given the summary character of their data, a more detailed analysis of dive capacity development was not possible. By contrast, the current study necessarily focused on the development in surviving birds, as we have no data from birds that failed to return.

The ontogeny of dive capacity has been studied best in marine mammals, particularly in pinnipeds. The picture emerging from a variety of species shows that body oxygen stores are not fully developed in juvenile marine mammals during their first year of life (e.g. Burns and Castellini, 1996; Weise and Costa, 2007; Noren and Suydam, 2016). Hence, it is not surprising that juvenile dive capacity lacks behind that of adult animals for a considerable period, constraining dive behaviour and foraging proficiency. For example, Burns (1999) found that the time juvenile Weddell seals (*Leptonychotes weddellii*) spent at foraging depth during deep dives was lower than in adults, reducing the time available for prey searching/capture.

Similarly, for avian divers, a number of studies indicate that juvenile muscle oxygen stores are not fully developed (Weber et al., 1974; Haggblom et al., 1988; Williams, 1992; Ponganis et al., 1999, 2010). The consequences of lower muscle oxygen stores for dive performance were illustrated by the relatively shallow and short dives of juvenile emperor penguins during their first 2.5 months at sea (Ponganis et al., 1999). In that study, one-third of all dives recorded in juveniles were below 10 m and lasted for less than 0.5 min. Similarly, two studies that tracked the dispersal of juvenile emperor penguins from a different colony found that most dives were relatively shallow, when birds dived within the pack ice or close to the sea ice edge, but increased when birds moved away from the ice edge over time (Thiebot et al., 2013; Labrousse et al., 2019). For comparison, when foraging, breeding emperor penguins frequently exceed a depth of 400 m and a duration of 10 min (Kooyman and Kooyman, 1995). Upon leaving their natal colony, juvenile king penguins dived consistently deeper and for a longer duration than juvenile emperor penguins, suggesting a relatively better developed aerobic dive capacity in the former at this initial period at sea. However, the relatively shallow foraging depth of juvenile emperor penguins during their first months at sea is probably explained by the availability of food at shallower depth, not requiring deeper dives.

Preceding the departure of juvenile king penguins to sea is their first moult, when birds change into their first waterproof plumage. During their annual moult fast, king penguins lose substantial parts of their subcutaneous fat and their pectoral muscle, with consequences for their dive/foraging performance and thermal energetics (Cherel et al., 1994; Enstipp et al., 2019). Juveniles leave their natal colony in a lean state and are under considerable pressure to improve their body condition. In particular, the rapid deposition of an insulating subcutaneous fat layer is of critical importance to withstand the thermal challenges of polar waters. Hence, the first weeks at sea are critical for juvenile birds and the initial improvement of dive capacity parameters might be the outcome of two different processes: physiological maturation as a result of ontogenesis and/or physiological recovery from the preceding moult fast (Enstipp et al., 2019). Accordingly, during the first 3 weeks at sea, juvenile birds spent many hours searching for and presumably catching prey (Fig. 3C). Daily foraging time peaked during week 2 and was similar to that of adults during weeks 2–3 (Fig. 3C). Similarly, overall dive effort, which includes both shallow (travelling) and deep foraging dives, peaked during week 2 and was as high as adult dive effort (Fig. 3D). Following these first three weeks, daily foraging time and dive effort of juveniles declined for some weeks, before both parameters increased gradually thereafter until the following spring (Fig. 3C,D). Similarly, after the first weeks, mean dive depth declined for ~4 weeks (Fig. 3A) and juveniles conducted many shallow dives, suggesting that they travelled towards different foraging areas after a first quick improvement of body condition. This interpretation is supported by similar observations in juvenile king penguins from the same colony, equipped with Splash tags, that provided Argos locations and a summary of dive parameters (Orgeret et al., 2019). This showed that juveniles conducted many travelling dives during their first week at sea, which was followed by an intense 3 week

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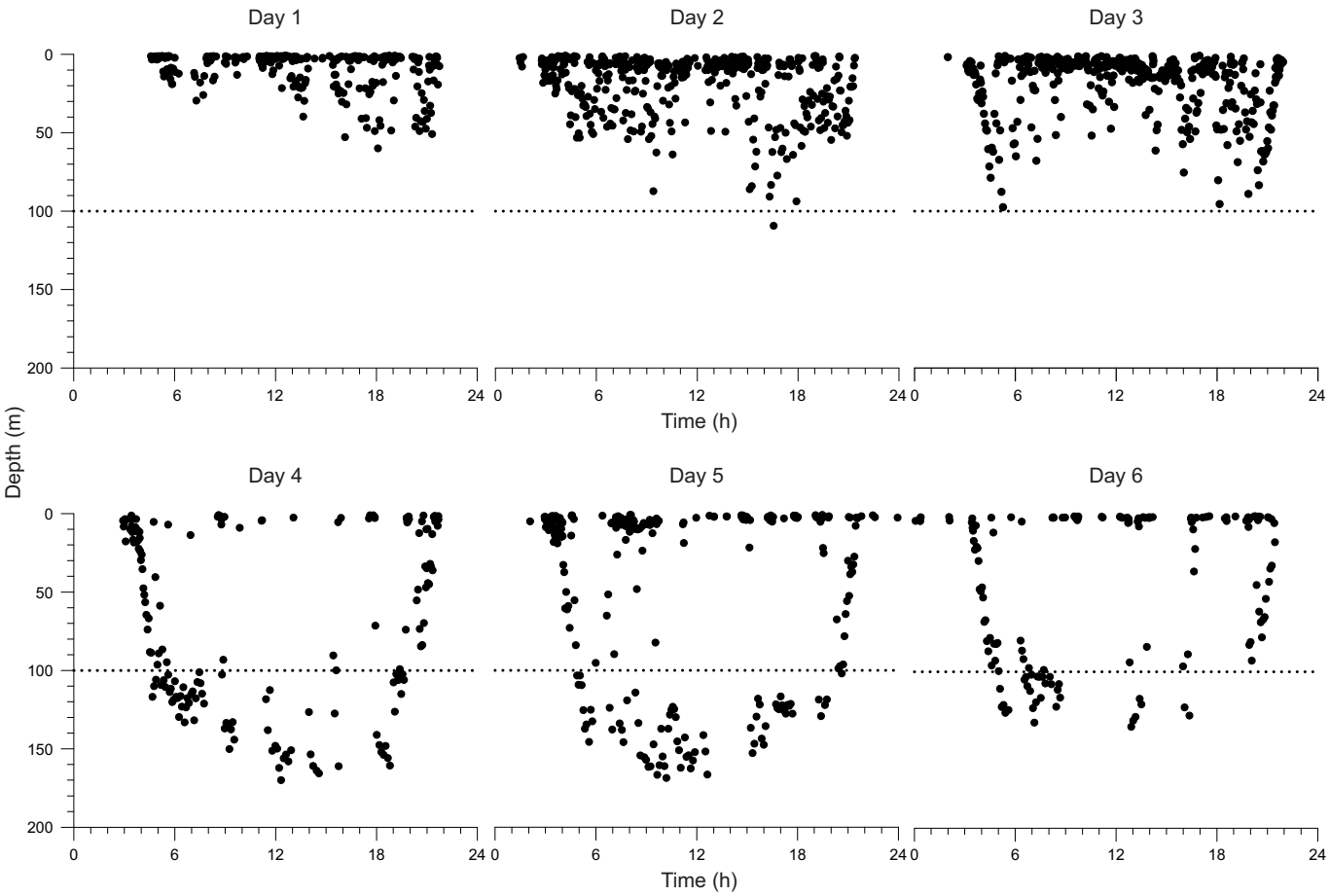

Fig. 7. Depth utilization of juveniles during their first week at sea. Continuous record of diving activity shown by a juvenile king penguin (Lul22) during its first 6 days at sea. Each dot indicates the maximum depth reached during a dive (n=1815 dives), shown against time of day. The dotted line indicates the typical position of the thermocline within the water column near the Polar Front during summer, where adults and juveniles forage. During the first 3 days, diving activity was restricted to shallower depths and probably occurred within the surface mixed layer. Thereafter, the bird transited this layer and directly targeted a deeper depth layer, apart from shallow 'travelling' dives and dives conducted during dawn/dusk, when light levels limit dive depth.

period of foraging with little travelling, before travelling increased again more gradually.

During autumn, in April, a sudden and continuous increase in all performance and effort parameters occurred in both juvenile and adult king penguins and values remained high until the following spring (Figs 3 and 4). The best indicator of dive performance might be dive efficiency, which represents the fraction of the dive cycle the animal spends at feeding depth (bottom phase). According to optimal foraging models, this parameter should be maximized by divers (Ydenberg and Clark, 1989) and there is evidence for this occurring in king penguins (Hanuise et al., 2013). In our study, dive efficiency was generally lower in juveniles than in adults for all depth bins but increased significantly during the autumn in both groups (Fig. 4). Additionally, the depth distribution of wiggles reflected these seasonal changes, whereby the majority of wiggles occurred at greater depth during the autumn and winter in both groups (Fig. 5). Such increases in performance and effort parameters are probably the consequence of seasonal oceanographic changes affecting prey availability (Kozlov et al., 1991; Charrassin and Bost, 2001; Charrassin et al., 2002). In particular, a thicker surface mixed layer (SML) would require birds to dive to greater depth to access their prey, while a lower prey density at depth would require increased bottom/dive durations to facilitate prey search and capture. Adult king penguins have been shown to react to seasonal changes in local prey availability by exploiting different foraging areas (Polar Front during spring/summer and Antarctic pack ice region during autumn/winter; Charrassin and Bost, 2001). Furthermore, dive depth and especially bottom and overall dive duration of adult birds (for dives to the same depth) are greatly increased during winter, when compared with the other seasons (Charrassin et al., 2002). Such an increase in apnoea capacity is probably a consequence of physiological acclimatization during the long periods spent at sea in winter and might be facilitated by means of hypothermia and hypometabolism (Handrich et al., 1997; Schmidt et al., 2006). While we could not track our birds, juvenile king penguins from the Crozet Archipelago have been shown to remain within the vicinity of the Polar Front during summer before they move to the south-west during autumn, so that some birds reach the edge of the pack ice (Orgeret et al., 2019). Hence, the observed increase in performance and effort parameters of juveniles during autumn in our study are probably also associated with seasonal changes in prey availability, facilitated by their continuing physiological maturation and acclimatization. For dispersing juvenile emperor penguins, similar seasonal changes in dive depth have been reported and are also believed to reflect seasonal changes in prey distribution (Thiebot et al., 2013; Labrousse et al., 2019).

Foraging and overall dive effort were consistently greater in adult king penguins, when compared with the juveniles (Fig. 3C,D). A

number of studies have shown that juvenile seabirds might try to compensate for their lower foraging proficiency by allocating more time to foraging (Dunn, 1972; Morrison et al., 1978; Daunt et al., 2007a). However, given the unique breeding cycle of king penguins, which requires on average 14–15 months to rear one chick (Bost et al., 2013), a comparison of foraging effort between juveniles and adult breeders is biased by the different energy requirements associated with these different life history stages (de Grissac et al., 2017). Adult breeders foraged for themselves and their chick and were also constrained by the requirement to commute between remote foraging areas and their breeding colony. By contrast, juvenile birds had to provision only for themselves and could roam freely (Orgeret et al., 2019).

Indices of juvenile and adult foraging proficiency

Our analysis of rapid changes in the dive profile of birds (wiggles) showed that the overall relationship between the time birds spent submerged in foraging dives per day and the associated number of wiggles conducted did not differ between juveniles and adults. However, given the considerable inter- and intra-individual variation, presumably reflecting differences in individual foraging proficiency and in prey availability, respectively, such a relationship might be too coarse to detect potential differences in foraging proficiency between groups. Our longitudinal investigation found that the wiggle rate of juveniles was significantly greater than that of adults during their first 5 months at sea (Fig. 6B). Thereafter, in mid-autumn, it started to decline and reached levels similar to those of adults during winter. This longitudinal investigation should not be confused with the reported number of wiggles per dive in relation to depth, which, for a given depth, was greater in adults (Fig. 1D). As dive rate was greater in juveniles (Fig. 6A), they conducted an overall greater number of wiggles per hour submerged (Fig. 6B). However, the fraction of each hour spent underwater that birds remained at foraging depth did not differ between groups, allowing a direct comparison of wiggle rates. Two scenarios might explain this initially higher wiggle rate of juveniles. (1) Juveniles targeted different prey items from adults, in particular smaller and/or less energy dense prey items (e.g. macro-zooplankton, squid). Inexperienced and hungry juveniles will probably attempt to capture any prey item that fits into their prey spectrum and will learn with time to target the most beneficial prey in terms of energy balance. (2) Juveniles targeted the same prey items as adults (myctophids) and a great number of detected wiggles reflect unsuccessful prey-capture attempts, suggesting a lower foraging proficiency of inexperienced juveniles. Improvements in foraging skills will occur over time with experience and a completion of physical maturation (Wunderle, 1991). Given that the majority of foraging dives of juveniles during their first months at sea targeted a depth where myctophid density during daylight is relatively low (Figs 3A and 5; Kozlov et al., 1991), juveniles probably foraged opportunistically on a variety of prey species, contributing to the greater wiggle rate. The decline in wiggle rates of juveniles during the autumn presumably reflects physical maturation and an improvement in foraging skills, enabling birds to persistently target a greater depth layer with a higher myctophid density, resulting in greater capture success.

However, a few caveats with our wiggle analysis have to be considered. (1) Our sampling frequency (0.2 Hz) was relatively low and most likely led to an underestimation of the total number of wiggles conducted during foraging dives (Simeone and Wilson, 2003). If the prey-capture sequence characteristics differed between juveniles and adults (e.g. experienced adults might pursue and capture prey in a shorter time), wiggle detectability might have differed between groups, potentially leading to a greater underestimation in adults. (2) Environmental conditions and, therefore, foraging conditions (prey availability) might have differed between juveniles and adults. (3) Lastly, it is also possible that juvenile birds, at least initially, use wiggles as a search technique, whereby birds frequently revert their orientation during descent to scan for prey items against the brighter surface, enhancing detectability.

In recent years, a number of studies have investigated the ontogeny of seabird foraging behaviour (from fledglings to adults) in a variety of species through the deployment of small bio-logging devices. However, most of these studies have focused on the development of spatial and temporal foraging patterns as an indicator of foraging proficiency (Riotte-Lambert and Weimerskirch, 2013; de Grissac et al., 2016, 2017; Mendez et al., 2017; Votier et al., 2017; Grecian et al., 2018). By contrast, studies on the detailed foraging performance of juvenile/immature seabirds that forage far from land are rare (but see Fayet et al., 2015).

Age-related differences in foraging performance of pursuit-diving seabirds, such as penguins, have been investigated during foraging trips but concern animals of at least 3 years of age. In the absence of visual observations, wiggles have been used to indicate various aspects of predator–prey interactions. For example, Le Vaillant et al. (2013) found that older king penguins (9 years) conducted more wiggles at greater depth than younger birds (5 years) and also gained mass more rapidly. By contrast, Zimmer et al. (2011) found that the hunting efficiency and prey pursuit frequency (wiggles) did not differ between young (3 years) little penguins (*Eudyptula minor*) and older birds (up to 14 years), but middle-aged birds used a different, presumably less costly, hunting tactic. This was suggested to reflect limitations caused by physical immaturity/inexperience and physical deterioration with age in young and old individuals, respectively, while middle-aged birds were presumably experienced and in a good physical condition (Zimmer et al., 2011). However, evidence from juvenile pursuit-diving birds during their first year after fledging is lacking. To investigate predator–prey interactions in greater detail than was possible in the current study and to reliably detect the outcome of prey-encounter events, accelerometry emerges as a promising technique, especially when a prey-capture signature is first determined from concomitant video footage during captive trials (Kokubun et al., 2011; Carroll et al., 2014).

Foraging strategies of juvenile and adult king penguins

The most striking difference between juvenile and adult foraging patterns was the preference for shallower dive/foraging depth in juveniles, particularly during their first 5 months at sea (Fig. 3A). On the one hand, such a pattern might reflect physiological limitations concerning their aerobic dive capacity. While juveniles were able to dive to considerable depth within days of leaving their colony, deep dives were relatively rare and were associated with a reduced bottom duration and, most importantly, a greatly increased PDSI duration (Fig. 1A,B), often ending foraging bouts. Hence, during these prolonged dives, juveniles probably approached their physiological limits and dives might have been exploratory in nature, also helping to gradually improve aerobic capacity (Noren et al., 2001; Ponganis et al., 1999, 2010).

On the other hand, the shallower dive depth of juveniles during their initial period at sea might also represent a foraging strategy that differed from that of adult king penguins. If compatible with sufficient prey capture, then a shallower foraging depth should be

preferable from both a behavioural and physiological perspective. At a shallower foraging depth (i.e. <100 m), the time available near the bottom, where most prey captures occur, remained relatively high in juveniles, while PDSI duration was relatively short, resulting in an overall higher dive efficiency, when compared with deeper dives (Figs 1 and 2). Because of the faster recovery at the surface, shallower foraging also allows a greater dive rate, so that once a bird has detected a prey patch, it can maximize the time spent within the prey patch before it disintegrates (Hanuise et al., 2013; Tessier and Bost, 2020).

Lastly, heat loss will also be lower at shallower depth. Enstipp et al. (2017) found that the peripheral temperature of juvenile king penguins during foraging bouts fell to progressively lower levels during their first 6 months at sea, presumably reflecting increases in thermal insulation. Perhaps it is not a coincidence that juveniles prefer a shallower foraging depth until peripheral insulation has increased sufficiently and they are eventually forced to increase foraging depth during the autumn/winter?

Still, if juveniles managed to capture sufficient food at a mean foraging depth <100 m during summer, why did adults forage at considerably greater depth? Presumably, foraging on myctophid fish at greater depth was more profitable for adults, providing sufficient energy for their reproductive attempt. Juveniles, in contrast, probably fed opportunistically during this time, including smaller/less energy dense prey in their diet, captured at shallower depth.

Depth utilization and potential links with oceanographic features

Adult king penguins from the Crozet Archipelago typically target regions with a strong vertical stratification (Polar Front). Here, they descend towards the thermocline, where they target a prey source, lanternfish (myctophids), that is predictably concentrated below the SML by oceanographic processes (Charrassin and Bost, 2001; Bost et al., 2009). However, it is conceivable that inexperienced juvenile birds might first explore the SML, before learning to associate oceanographic features (e.g. thermocline) with a more concentrated and predictable prey source. As we do not know the exact foraging location of our birds, we also cannot know the vertical position of the thermocline at that site. However, during summer, when adult king penguins forage at the Polar Front, the thermocline there is typically located at a depth of between 60 and 110 m (Charrassin and Bost, 2001). Juvenile king penguins, leaving the Crozet Islands in early summer, also move southward and remain within the vicinity of the Polar Front during summer (Orgeret et al., 2019). Hence, the oceanographic conditions encountered by juveniles were probably similar to those of adults. Within their first week at sea, all juveniles targeted a depth layer near or beyond 100 m, which was probably close to or beyond the thermocline (Fig. 7). The observed rapid changes in their pattern of depth utilization are intriguing and could suggest that birds learn to avoid the SML that is void of prey. Hence, juveniles might learn rapidly to recognize the association between an oceanographic feature (e.g. thermocline) and predictable prey abundance. Such capacity for recognizing oceanographic features has been shown in juvenile emperor penguins during their first odyssey and in juvenile wandering albatrosses (*Diomedea exulans*), that were able to exploit oceanographic features in a way that was similar to adults (Labrousse et al., 2019; de Grissac et al., 2017).

Temporal foraging patterns: evidence for nocturnal foraging?

As visual predators, adult king penguins forage predominately during daylight and twilight hours (Wilson et al., 1993; Pütz and Bost, 1994; Bost et al., 2002). Depending on the season, their main targeted prey undertakes vertical migrations and can be found at shallower depth during the night, albeit more scattered (Kozlov et al., 1991). However, there seems to be little nocturnal foraging activity in adult king penguins, which is presumably explained by the 4 times greater foraging success of birds during the day, when compared with the adjacent night (Pütz et al., 1998). Whether juvenile birds follow a similar temporal organization of foraging or whether they might engage in more nocturnal foraging activity, especially at the start of their extended period at sea, when birds need to rapidly replenish their fat stores after moult (Enstipp et al., 2017, 2019), is unclear.

We found little evidence for nocturnal foraging activity of juvenile king penguins. All but two juveniles conducted foraging dives (i.e. ≥50 m) exclusively during daylight/twilight hours from the beginning of their trip. The four deep dives conducted during 1 night by Lul05 were probably of an exploratory nature, conducted during shallow travelling dives. However, the repeated targeting of a depth >30 m (with some dives exceeding 50 m) during 4 nights by Lul1 probably represent nocturnal foraging dives, conducted occasionally, when foraging conditions were favourable (sufficient moonlight and prey at shallow depth). However, the number of wiggles detected during these dives was low, suggesting little foraging success.

In conclusion, similar to other studies investigating the ontogeny of dive/foraging behaviour in marine mammals and seabirds, juvenile king penguins require an extended period at sea to reach physical maturity. While the lack of full physical maturity might have constrained juvenile birds to a shallower depth range, they foraged successfully and survived this critical period. Clearly, overall energy requirements of juveniles must have been lower than in adult breeders, so that opportunistic foraging at a depth, where myctophid availability was probably low, was sufficient for juveniles. The development of wiggle rates provides support for opportunistic foraging of juveniles during their first months at sea, while foraging proficiency might also have lacked behind that of adults. Hence, similar to other avian divers, juvenile king penguins require experience and physical maturation to improve dive capacity and foraging skills. With ongoing technological development, future studies will be able to use additional techniques (e.g. accelerometry) throughout the extensive roaming periods of juveniles, to shed more light on the early ontogeny of their foraging behaviour.

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Competing interests

The authors declare no competing or financial interests.

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Visualization: M.R.E.; Supervision: C.-A.B., H.W., Y.H.; Project administration: C.-A.B., H.W., Y.H.; Funding acquisition: C.-A.B., H.W., Y.H.

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