

Diving ontogeny and lunar responses in a highly migratory mammal, the northern fur seal *Callorhinus ursinus*

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ABSTRACT: Diving ontogeny studies enable the examination of both the evolution of diving strategies and the physiological constraints and environmental factors determining foraging behaviour. Northern fur seal (NFS) *Callorhinus ursinus* pups that undertake far-ranging migrations in their first year are an ideal species for examining such factors. The diving behaviour of 64 NFS pups from 4 North American breeding sites was studied using satellite-dive recorders deployed on pups prior to weaning. Summarised diving activity (6 h histograms of dive depth and duration) was recorded during the pups' first 8 mo at sea and transmitted via satellite. During the first month at sea, pups adopted the nocturnal diving patterns characteristic of adults, with average maximum nightly and crepuscular dive depths and durations exceeding daytime values by a factor of from 4 to 4.5. Diving capacity in terms of maximum depths (112 m) and durations (285 s) attained also increased linearly with age until ~8 to 10 mo of age. Overlaid on diving capability development was the significant influence of environmental cues, such as lunar phase, on migratory diving behaviour. During full moons, pups dived deeper and for longer periods than during other lunar phases, as pups likely mimicked the behaviour of their vertically migrating prey. These findings indicate that prey accessibility, particularly for younger pups with reduced diving capacity, may prove more challenging during higher lunar illumination periods.

KEY WORDS: Foraging · Lunar · North Pacific · Polar ecosystems · Postnatal development

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INTRODUCTION

Diving behaviour of marine vertebrates is influenced by both intrinsic (physiological) and extrinsic factors—such as diel cycles linked to the vertical behaviour of pelagic prey (Hays 2003, Shepard et al. 2006), predation (Hays et al. 2001), lunar cycles (Horning & Trillmich 1999, Ream et al. 2005) and other climatic, oceanographic and environmental signals correlated with prey availability (Lea et al. 2006)—as well as and reproductive (Weng et al. 2007) and life-history cycles (Teo et al. 2007). Individual responses to these factors are likely a function of age (and experience), diving capacity, evolutionary and physiological adaptations and skill (Kooyman 1989, Hindell & Lea 1998, Rich-

mond et al. 2006, Fowler et al. 2007b). Until recently, dive data time series for many marine vertebrates were largely restricted to adults, providing an understanding of physical capability in diving and the correlations between dive activity and external factors, but only in mature age classes. For most species only scant knowledge exists regarding the development of foraging strategies (including diving behaviour) in naïve animals and their consequences for survival (Salmon et al. 2004, Fowler et al. 2006).

Studies of diving ontogeny in pinnipeds, particularly otariids prior to weaning, indicate that pups steadily develop their capacity to dive with increasing age (Baylis et al. 2005, Spence-Bailey et al. 2007). In species exhibiting a short lactation period (~4 mo), such as

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northern *Callorhinus ursinus* and Antarctic fur seals *Arctocephalus gazella*, pups have little time to develop their diving skills prior to weaning and, hence, generally dive shallowly (McCafferty et al. 1998, Baker & Donohue 2000, Baker 2007). However, species with longer suckling periods (8 to 36 mo) have ample opportunity to develop diving abilities while exploring their surroundings, travelling with their mothers (Horning & Trillmich 1997, Raum-Suryan et al. 2004, Rehberg & Burns 2008), and/or while attempting prey capture prior to weaning and nutritional independence (McCafferty et al. 1998, Baylis et al. 2005, Fowler et al. 2007a).

The diving behaviour of northern fur seal (NFS) pups and juveniles (Baker & Donohue 2000, Sterling & Ream 2004, Baker 2007) has recently been documented, but only at a single breeding site, St Paul Island (SP) in the Pribilof Islands, Alaska (57°11'N, 170°16'W). NFS breeding sites are distributed across the North Pacific Ocean from California to Russia, with animals undertaking large annual migrations to seasonally productive feeding areas (Kenyon & Wilke 1953, Kajimura 1982, Bigg 1990, Ream et al. 2005). Historically, this species has primarily been studied during the summer months when adult female foraging effort is concentrated in the Bering Sea (Goebel et al. 1991, Robson et al. 2004, Call et al. 2008). However, recent studies have documented the far-ranging winter migratory movements and diving behaviour of a small sample of adult females (Ream et al. 2005, Sterling 2009) and pups (Baker 2007, Lea et al. 2009). Adults and pups both forage primarily nocturnally while undertaking round trips of >9000 km across shelf and pelagic habitats during the non-breeding period (Ream et al. 2005, Sterling 2009).

Currently, the largest populations of NFS, at the Pribilof Islands (southeast Bering Sea), are undergoing significant declines (Towell et al. 2006), while other populations are stable or increasing. Given the likely

role juvenile survivorship plays in influencing population trajectories (Baker & Fowler 1992, York 1995, Fowler et al. 2006), an understanding of the evolution of diving behaviour, capabilities and foraging strategies of newly weaned animals from different colonies during their first annual migration is of particular importance.

The primary objectives of the present study were consequently: (1) to quantify the progression in diving capability of NFS pups from across their North American range as they conduct their first annual migration and (2) to examine the influence of various external factors (time of day, sex, natal site and seasonal and lunar phase) on pup dive behaviour during migration; to better understand the factors that affect dive behaviour, prey availability and, consequently, foraging success, for this vulnerable age class.

MATERIALS AND METHODS

Field sites and device deployment. In autumn (October/November) 2005 and 2006, 64 SPLASH satellite-linked dive tags (Wildlife Computers) were deployed on *Callorhinus ursinus* pups from all 4 North American breeding sites (Fig. 1, Table 1; SP, St George Island [SG], Bogoslof Island [BG], San Miguel Island [SM]). The SPLASH tags (60 × 50 × 25 mm, <1.5 % body mass) were glued to fur on the dorsal midline posterior to the scapulae with a fine layer of epoxy (Devcon). Tags that incorporated rear-facing antennae to reduce hydrodynamic drag effects were only deployed on pups weighing >11 kg to maximise the likelihood of survival. The deployment sex ratio was relatively even (1.2:1 males/females), and recorders were deployed an average 13.0 ± 15.8 d (0 to 62 d) prior to departure from natal sites (Table 1).

SPLASH tags were programmed to record water temperature and dive depth every second. This information was summarized over 6 h periods (all times are Greenwich mean time, GMT): 05:00 to 10:59, 11:00 to 16:59, 17:00 to 22:59, 23:00 to 04:59 h, and transmitted via satellite. Maximum dive depth and dive duration were attributed to 1 of 14 bins (see Table S1 for details, in the Supplement at www.int-res.com/articles/suppl/m419p233_supp.pdf). At deployment in Alaska, 6 h bins corresponded to 09:00 h (n = 57) and at SM in 2006 to 08:00 h (n = 7). During migration, local time of day (dawn, day, dusk and night) for the 6 h periods varied considerably from the GMT times due to seasonal changes in day length and the E/W scale of movements. Dive depth (± 0.5 m) and duration were recorded in 14 bins (Table 2). Dive depths <1 m were not considered dives, and instruments were pressure-tested to ~1000 m.

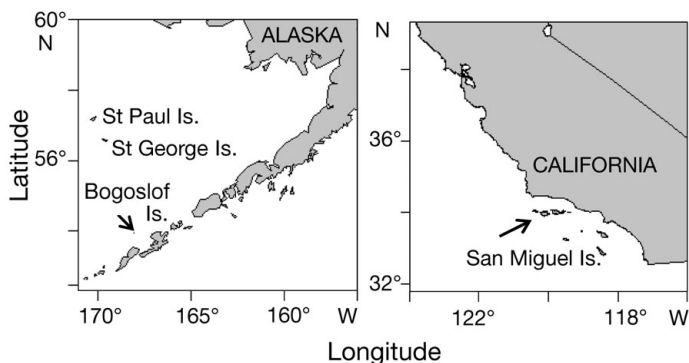


Fig. 1. North American northern fur seal *Callorhinus ursinus* breeding sites

Table 1. *Callorhinus ursinus*. Deployment characteristics and morphometrics of northern fur seal pups equipped with dive recorders in 2005 and 2006. Mean values (\pm SD), parentheses: number of pups departing natal sites. SP: St Paul Is.; SG: St George Is.; BG: Bogoslof Is.; SM: San Miguel Is.; M/F: males/females

Site	Mean deployment date	n	M/F	Mass (kg)	Length (cm)	Mean age at departure (d)	Deployment length at sea (d)
2005							
SP	6 Nov \pm 3.8 d	20 (20)	10/10	15.4 \pm 2.8	84.1 \pm 3.5	124.4 \pm 4.3	1.5–228.6
SG	7 Nov \pm 1.2 d	10 (10)	5/5	16.6 \pm 1.4	86.3 \pm 3.5	126.8 \pm 1.8	23.8–236.7
BG	16 Oct \pm 2.4 d	10 (8)	7/3	15.8 \pm 2 ^a	86.7 \pm 4.9	129.6 \pm 10.2	84.2–208.3
Total		40 (38)	22/18	15.8 \pm 2.3	85.3 \pm 4.0	126.3 \pm 6.0	128.8 \pm 79.6
2006							
SP	9 Nov \pm 1.2 d	10 (10)	5/5	18.2 \pm 1.9	84.8 \pm 3.4	133.7 \pm 6.6	0.6–238.3
BG	2 Oct \pm 1.6 d	7 (7)	4/3	13.9 \pm 1.4 ^a	84.0 \pm 1.8	134.6 \pm 13.0	1.0–186.8
SM	14 Nov \pm 0 d	7 (7)	4/3	12.7 \pm 1.3	84.8 \pm 4.2	146.3 \pm 9.8	3.2–63.8
Total		24 (24)	13/11	15.3 \pm 2.9	83.4 \pm 3.6	137.6 \pm 10.9	101.2 \pm 83.7
Overall		64 (62)	35/29	15.6 \pm 2.6	84.6 \pm 3.9	130.6 \pm 9.9	118.1 \pm 81.7

^aBogoslof Island deployments occurred 2 to 6 wk prior to deployments at other sites

Table 2. *Callorhinus ursinus*. Linear mixed-effects models fit to migratory behavioural dive parameters during night periods for northern fur seal pups at St Paul, St George, Bogoslof and San Miguel Islands. The simplest high-ranking model with Δ AIC < 2 and only those fixed-factor models with AIC > 0 are presented. (AIC: Akaike's information criterion). ω AIC: weighted AIC; LL: log likelihood; D: days post-departure; S: site, L: lunar illumination fraction; Sex: sex of pup; Y: year; PV: percentage random effect (pup) variance

Response	Rank	Model	df	AIC	Δ AIC	ω AIC	LL
Mean depth (m)							
PV = 13.8 %	1	L + D + Sex + S + D:L + L:Sex + S:L + D:Sex	16	5177.9	0	0.99	–2573.0
	10	L	5	5362.6	184.6	0	–2676.3
	14	D	5	5616.8	438.9	0	–2803.4
	16	S	7	5735.7	557.8	0	–2860.9
	19	Null	4	5737.6	559.7	0	–2864.8
Mean duration (s)							
PV = 12.1 %	1	L + D + Sex + S + D:L + L:Sex + S:L	15	3109.8	0	0.65	–1539.9
	2	L + D + Sex + S + D:L + L:Sex + S:L + D:Sex	16	3111.0	1.2	0.35	–1539.5
	10	L	5	3237.0	127.2	0	–1613.5
	15	D	5	4023.8	914.0	0	–2006.9
	17	Sex	5	4069.0	959.1	0	–2029.5
	18	S	7	4070.4	960.6	0	–2028.2
	21	Null	4	4072.8	963.0	0	–2032.4
Max. depth (m)							
PV = 11.5 %	1	L + D + Sex + S + D:L + L:Sex + S:L + D:Sex	1	7793.4	0	1.0	–3880.7
	8	L	10	8092.0	298.5	0	–4041.0
	12	D	14	8119.2	325.8	0	–4054.6
	16	Null	16	8347.3	553.9	0	–4169.7
Max. duration (s)							
PV = 15.8 %	1	L + D + Sex + S + D:L + L:Sex + S:L + D:Sex	16	5382.5	0	0.93	–2675.3
	10	L	5	5717.4	334.9	0	–2853.7
	14	D	5	5889.7	507.2	0	–2939.9
	17	S	7	6114.0	731.5	0	–3050.0
	19	Sex	5	6121.1	738.6	0	–3055.6
	20	Null	4	6121.9	739.4	0	–3056.9
Dive freq. (per 6 h)^a							
PV = 5.2 %	1	L + D + Sex + S + D:L + L:Sex + S:L + D:Sex	16	10753.4	0	1.0	–5360.7
	10	L	5	10890.9	137.5	0	–5440.5
	14	D	5	11013.1	259.7	0	–5501.6
	16	S	7	11046.8	293.4	0	–5516.4
	19	Null	4	11062.2	308.7	0	–5527.1

^aDive frequency calculated from dive depth bins

Dive data analyses. Data were extracted using the WC-DAP programme (V.1.0.56, Wildlife Computers) and the following filtering methods were applied:

1. Duplicate records within 6 h periods were removed by selecting the data with the highest number of repeated transmissions from the satellite;
2. Maximum dive depth and duration per 6 h period were calculated as the midpoint of the deepest or largest bin for which frequency data were available, as no measure of dive depth within the bin is given. Although maximum dive depth was treated as a discrete variable with a limited number of possible bins, it was a representation of a true continuous variable and was treated as such in subsequent analyses;
3. Only dives > 2 m and > 15 s were included in analyses. The shallowest dive depth bin (1 to 2 m) recorded the maximum values of 255 dives per 6 h period in 98.1 % of cases. This bin was removed from analyses as it likely represented surface travel or resting behaviour (as for Baker 2007);
4. Mean dive depth (m) and duration (s) per 6 h period were then calculated as:

$$\frac{[\text{Freq}(b_2) \times \text{midpoint}(b_2)] + \dots + [\text{Freq}(b_{14}) \times \text{midpoint}(b_{14})]}{\sum [\text{Freq}(b_2; b_{14})]}$$

where b_2 to b_{14} represent the dive depth or duration bin values.

5. Dive parameter records (mean, maximum and dive frequency) greater than a pup's monthly average value (+2 SD) were removed (1.6 to 5 % records) ensuring the removal of spurious satellite data transmissions.

Time of day, lunar- and age-related covariates. As pups were handled towards the end of lactation, their age at the time of capture was estimated using published mean or median pupping dates: SP—9 July; SG and BG—6 July; SM—2 July (Gentry 1998, Melin et al. 2008) as the date of birth.

Day and night duration varied considerably throughout the study in response to both change in season and the extent of the migratory movements of the pups (see Baker 2007). For example, day length at the Pribilof Islands (~58° N) in November is 8.1 h and in the central North Pacific Ocean in April (40° N) is 13.1 h. Consequently, the attribution of time of day (dawn, day, dusk and night) to the 6 h dive periods was highly variable throughout the migration. Argos satellite location data collected in addition to dive data were incorporated in a correlated random-walk model to predict locations for the start and end of each 6 h dive period using the crawl package (Johnson et al. 2008, Johnson 2009) in R software (R Development Core Team 2005). We then assigned the actual time of day (dawn, day, dusk and night) to each 6 h diving period based on solar elevation values at each modelled pup location. Solar eleva-

tion was calculated using the elevation function in the tripEstimation package in R (Sumner & Wotherspoon 2008). Positive solar elevation values equate to day and negative values to night. The start and end of day, dusk, night and dawn periods were determined using solar elevations.

Lunar phase (full, waning, new and waxing) and lunar illumination fraction (0 to 1, where full moon is 1) were then attributed to each 6 h record (see Bestley et al. 2008). Lunar phase and fraction data were sourced from www.ga.gov.au/geodesy/astro/moon-phases/moonphases.jsp and <http://www.usno.navy.mil/USNO/astronomical-applications/data-services/frac-moon-ill>, respectively.

Pup body size effects on diving capability. A simple diving capability index (DCAP) was derived from standardised residuals of the mean duration/mean depth linear regression relationship. Positive DCAP values represent dive periods in which pups spent a longer time diving at a given average depth than predicted by the model and vice versa for negative values. A body condition index (BCI) was then derived from the residuals of the multiple linear regression equation: pup mass ~ log(length) + log(girth), where pup mass is in kg, and length and girth are in cm. The influence of pup body size (length, mass, girth, BCI) on pre-migratory dive parameters (mean depth, duration, diving frequency and DCAP) was assessed using general linear models. Dive parameters within 1 wk of device deployment were selected to minimise the effect of growth on possible relationships. Data from all sites were pooled due to sample size (1 to 21 data points per individual).

Behavioural analysis and model testing. Linear mixed-effect models incorporating time of day, days since departure, lunar illumination fraction, sex and natal site were used to assess their influence on migratory behavioural response variables (mean and maximum dive depth [m], duration [s] and dive frequency per 6 h period) using the R-software V2.8.2 package nlme V3.1-89 (Pinheiro et al. 2009). All response variables were log-transformed.

Migratory dive data from pups at all sites were incorporated in mixed models with 'pup' selected as the appropriate random effects structure. Inter-annual effects were examined only for pups from the 2 sites studied in both years, SP and BG. A least-squares fit model was applied with log-transformed dive parameters as the response variable and days since departure (D, migration) as the fixed (continuous) factor. An autocorrelation function (ACF) was then applied to the normalised residuals of the least-squares output, and the ACF plot of lags (days since departure) was then inspected visually for periodicity in high correlation values (Fig. 2; ACF plots combined for mean, maxi-

num and dive frequency). A lag periodicity consistent with lunar cycle was detected for all migratory behavioural response variables. Consequently, the lunar illumination fraction and an autoregressive correlation function were included in the models to account for a lack of temporal independence for each pup (Zuur et al. 2009). Model simplification of nested models was used prior to the application of an information-theoretic model selection procedure (Bolker et al. 2009). Potential models were ranked according to the

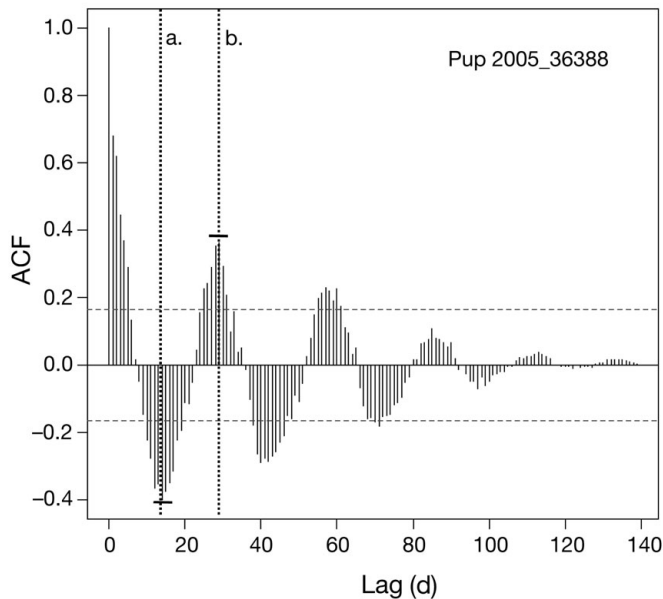


Fig. 2. *Callorhinus ursinus*. An autocorrelation function (ACF) plot by time lag highlighting lunar periodicity within nightly mean depth. Vertical dotted lines depict a negative correlation at half lunar cycle (a) and a positive correlation after a full lunar cycle (b). Horizontal dashed lines denote limits of significance

Akaike information criterion (AIC), with the lowest AIC value ranking highest.

Finally, given the predisposition of many otariids, particularly fur seals, to nocturnal foraging (Georges et al. 2000, Lea et al. 2002, Page et al. 2005) and the apparent influence of lunar phase on diving behaviour, we also tested the log-transformed behavioural response variables for time of day effects using mixed models including pup as a random factor. A comparison of model outputs with null models showed time of day to be an influential factor in predicting behavioural dive responses (see Fig. 3, and Baker 2007). Models for behavioural response variables during day, night, dawn and dusk were consequently run separately.

Analyses of migratory behavioural response variables (average mean and maximum dive depths and duration in relation to time of day) were performed for pups for which a minimum of three 6 h dive records per month per time of day period (dawn, day, dusk and night) were recorded to minimise the influence of small sample sizes on average monthly values for any single pup. Variance attributed to the random effect (PV, between pup variability) was calculated as a proportion of the combined random effect and residual variances. Statistics are presented as means \pm 1 SD unless stated otherwise.

RESULTS

Dive and location data were transmitted via satellite for 5 h d⁻¹ to maximise tag operational life (180 to 220 d). Two tags failed prior to pup departure at BG in 2005 (Table 1). Migration dive data for $n = 56$ *Callorhinus ursinus* pups are presented, excluding failed tags ($n = 2$),

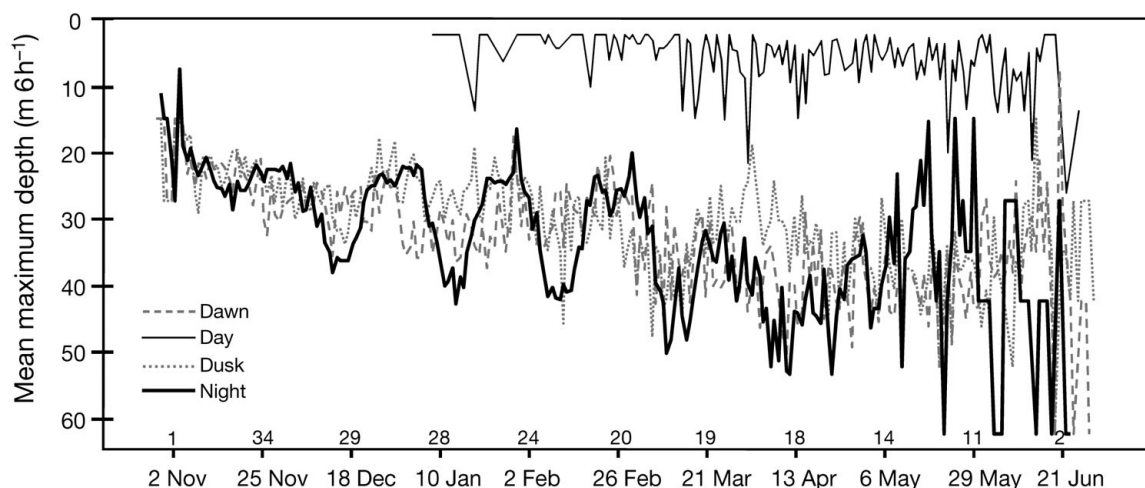


Fig. 3. *Callorhinus ursinus*. Average daily maximum dive depth (over 6 h periods) in relation to time of day for pups from St. Paul, St. George and Bogoslof Island in 2005/2006. Pup sample sizes listed above dates

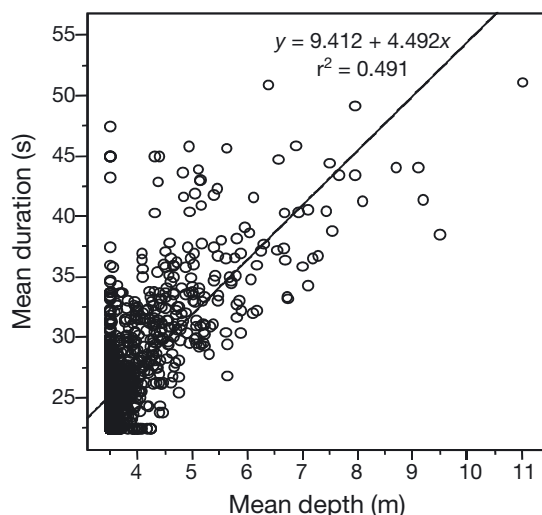


Fig. 4. *Callorhinus ursinus*. The linear relationship between mean dive duration and mean dive depth (over 6 h periods) for pre-migratory northern fur seal pups

animals whose transmissions ceased within 2 d of departure ($n = 4$) and animals with insufficient records up to 7 d post-departure ($n = 2$). Tag transmissions were recorded for 4 to 242 d (mean = 127.5 ± 83.3 d). The body mass of pups at the time of deployment was not correlated with transmission duration at any site.

Relationship between diving capability and pup size

Prior to migration, average dive duration per 6 h period was positively related to mean dive depth by a linear function when data were pooled across all sites ($F_{2,1318} = 1271.3$, $p < 0.001$, $r^2 = 0.491$; Fig. 4). A dive capability index (DCAP) was then derived based on standardised residuals for this relationship. Positive DCAP values represent dive periods when pups spent more time at a given depth than predicted by the model and vice versa for negative values.

To assess the influence of body size on diving capability prior to weaning, a BCI was derived from the residuals of the multiple linear regression of body mass (11.2 to 21.4 kg) against length (73 to 95 cm) and girth (55 to 81 cm). The body size of pups varied between sites and years in relation to time of capture and age (Table 1). General linear models for 59 pups indicate that body size and/or condition are correlated with a variety of pre-migratory diving parameters. The fixed-factor model for pup body mass ranked highest in influencing maximum dive depth (AIC = 302.512; Fig. 5a) and mean dive duration (AIC = -97.299; Fig. 5b). While maximum dive duration prior to weaning was correlated with both body mass (AIC = 5.056; Fig. 5c) and girth (AIC = 5.804; Fig. 5d) models.

Migratory dive behaviour

The post-departure diving behaviour of 56 NFS pups was recorded during 7212 seal days (2005: 4823; 2006: 2389) for 17 857 dive depth periods of 6 h (17 706 dive duration periods), encompassing 3 387 526 dives > 2 m. Pups departed natal sites at approximately 115 to 161 d of estimated age, and were likely younger at departure in 2005 than in 2006 ($F_{1,53} = 40.84$, $p < 0.001$) and older at SM than at other sites ($F_{3,53} = 5.65$, $p < 0.01$; see Table 1) based on published median birth dates. No appreciable difference in age at departure between the sexes was evident when tested by 1-way ANOVA.

The length of deployments post-departure averaged 118.4 ± 81.5 d, but ranged up to 8 mo in duration (0.6 to 238.3 d; Table 1). Of 4 possible 6 h dive records that could be transmitted daily, we received $69.3 \pm 13.4\%$ ($n = 36$) and $62.0 \pm 15.8\%$ ($n = 21$) due to incomplete records in 2005 and 2006, respectively. The overall proportional representation of dive depth and dive duration in relation to pup sex and season is presented in Fig. 6. The majority of dives recorded for the 55 individual pups were from 2 to 20 m depth and 15 to 90 s duration ($98.4 \pm 1.7\%$ and $97.0 \pm 3.1\%$, respectively). A maximum dive depth of 112.5 m and 285 s duration was attained by pups during this period (Fig. 6).

Migratory diving development

Mean dive depth and duration increased until ~ 4 mo post-departure (~ 8 mo age; Table S2, in the Supplement at www.int-res.com/articles/suppl/m419p233_supp.pdf), while mean maximum dive depth and duration increased steadily from 4 to 6 mo post-departure (~ 8 to 10 mo of age; Table S3, in the Supplement). This trend is slightly different between sites and years. Nightly maximum dive depth and duration, however, continued to slowly increase with age (Table S3).

Corresponding dive depths and durations were matched for 14 425 dive periods of 6 h. Mean and maximum dive depth and dive duration were positively correlated at all sites in each month, except BG 2006 at 7+ mo post-departure (Fig. 7a, b). The slope of these relationships generally decreased the longer pups were at sea (Fig. 8a, b). An ANOVA of log-transformed mean dive duration in relation to dive depth, site, year, months since departure and pup sex highlighted the increasing trend in dive capacity with time. The significance of the month \times site \times year \times mean depth term ($F_{4,14410} = 23.605$, $p < 0.0001$; Table S4, in the Supplement) also indicated that after 7+ mo at sea (10 to 11 mo of age) pups from SP in 2005, SG in 2005 and SM in 2006 (for which only 2 mo data are available) were capable of attaining equivalent depths in significantly

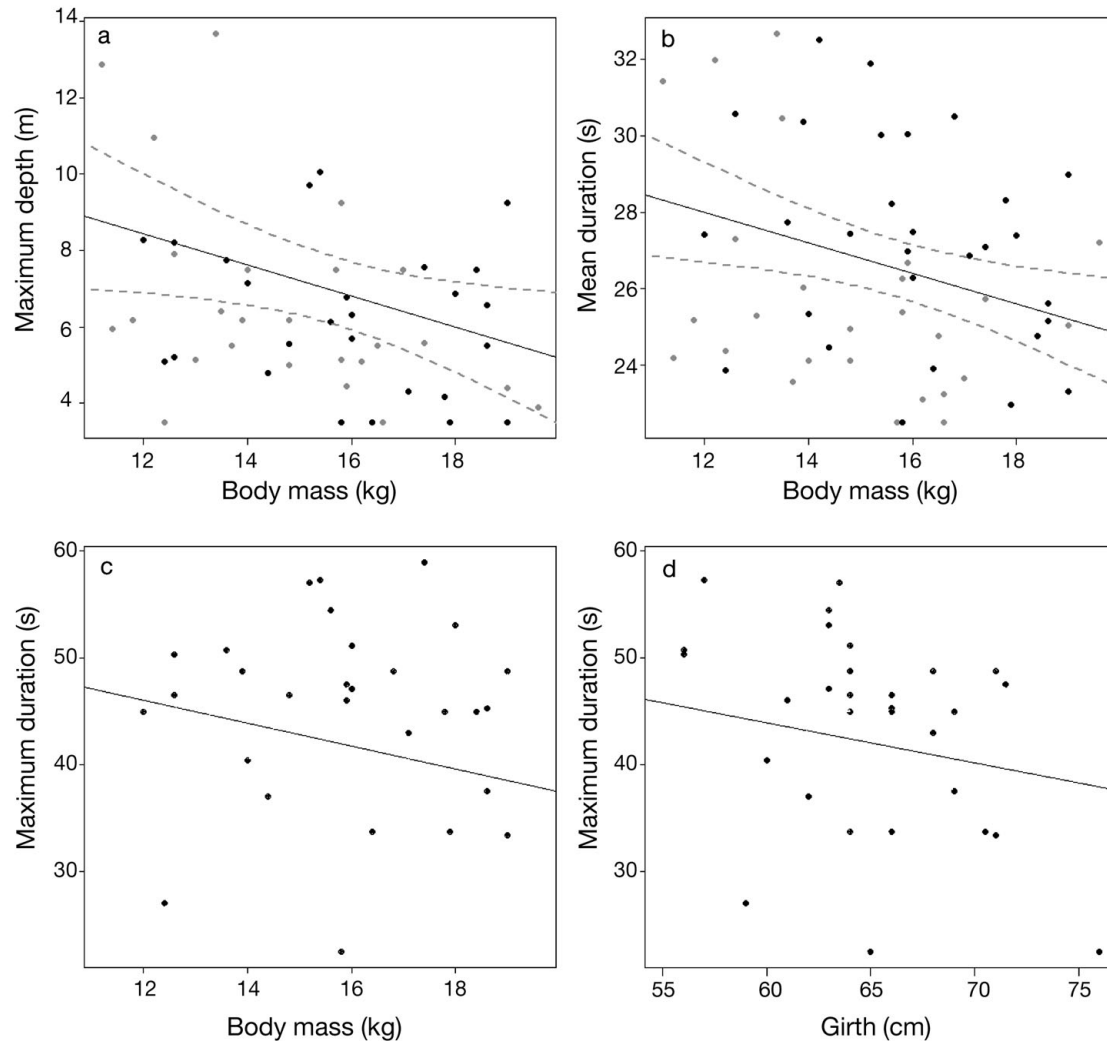


Fig. 5. *Callorhinus ursinus*. Pre-migration relationships between the diving parameters (a) maximum dive depth, (b) mean dive duration and (c & d) maximum dive duration, and pup body condition (body mass or body girth), for 59 northern fur seal pups. Black: male pups; grey: female pups; continuous line: generalised linear model fit; broken lines: 95% confidence limits

less time. Fig. 8b describes a similar trend for maximum depth/duration relationships, although the slope coefficients are generally lower for maximum depth/duration monthly regressions (see Fig. 7a). A marked decrease in slope coefficients is not apparent until after 4 mo post-departure (~8 mo of age), potentially indicating that when diving deeply, pups are operating at their diving limit until this age (Fig. 8b). Analysis of variance again showed the month \times site \times year \times maximum depth term to be highly significant in relation to maximum dive duration ($F_{4,14410} = 20.498$, $p < 0.0001$; Table S4).

Linear mixed-effects models (Table 2) indicated that of all behavioural response variables, maximum nightly dive duration showed the strongest positive ontogenetic relationship with days since departure (~age). Even so this is a relatively weak response and

is largely due to the strong interaction effects between days since departure and sex of the pup and the interaction between days since departure and lunar illumination (see top model mean dive duration). Inter-pup variability was relatively low at 5.2 to 15.3% variance, being highest for maximum dive duration during night periods (Table 2).

Diel, lunar and year effects

NFS pups exhibit a strong diel pattern in maximum and mean dive depth and duration and dive frequency, consistent with adult nocturnal dive behaviour (see 'Materials and methods'). From departure onwards, the daytime dives of pups were always shallower, shorter and less numerous than night-time dives

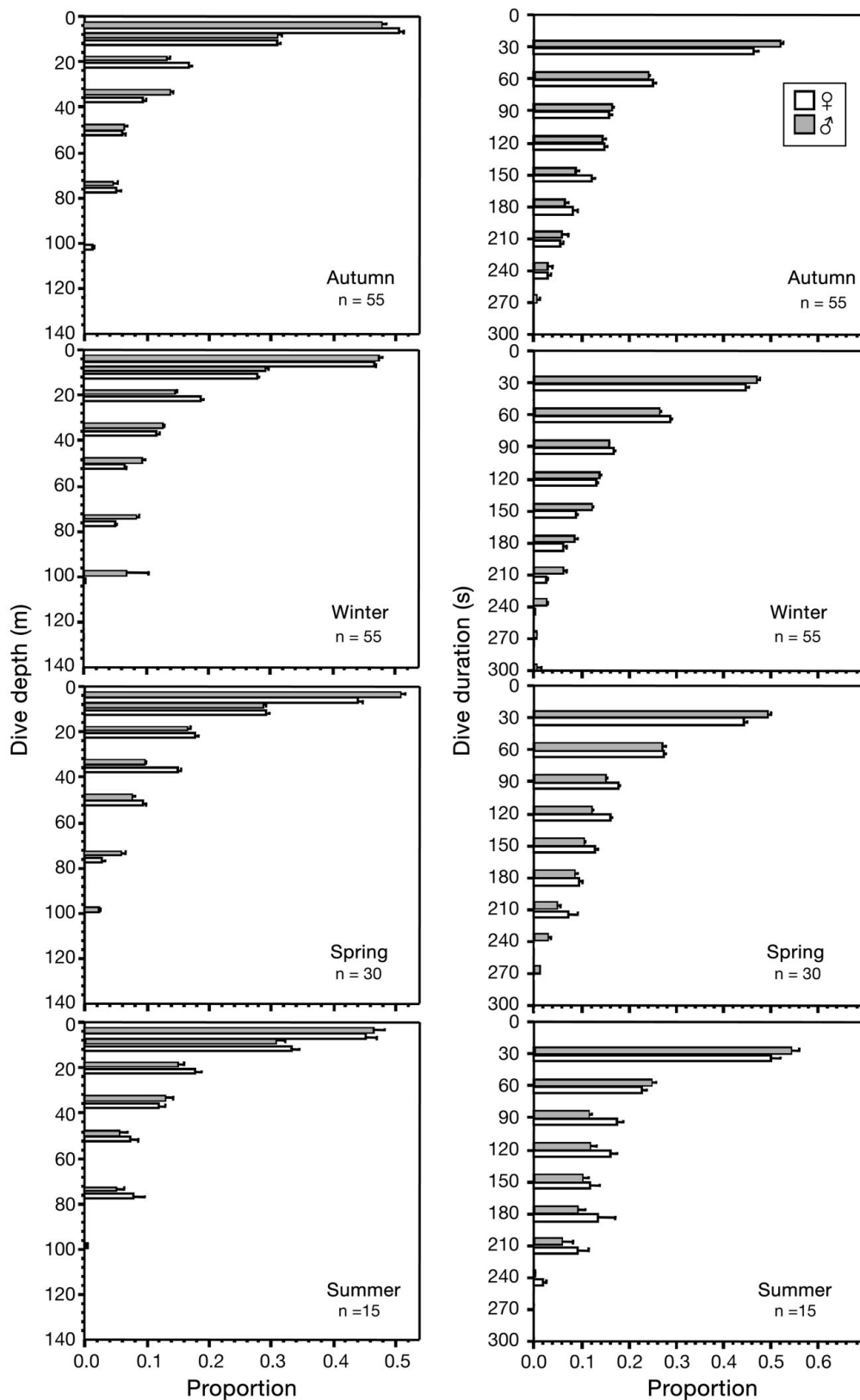


Fig. 6. *Callorhinus ursinus*. Proportional histograms of dive depth and duration for migratory northern fur seal pups by pup sex and season (Autumn: September to November; Winter: December to February; Spring: March to May; Summer: June to August). Number of pups per season expressed as sample size

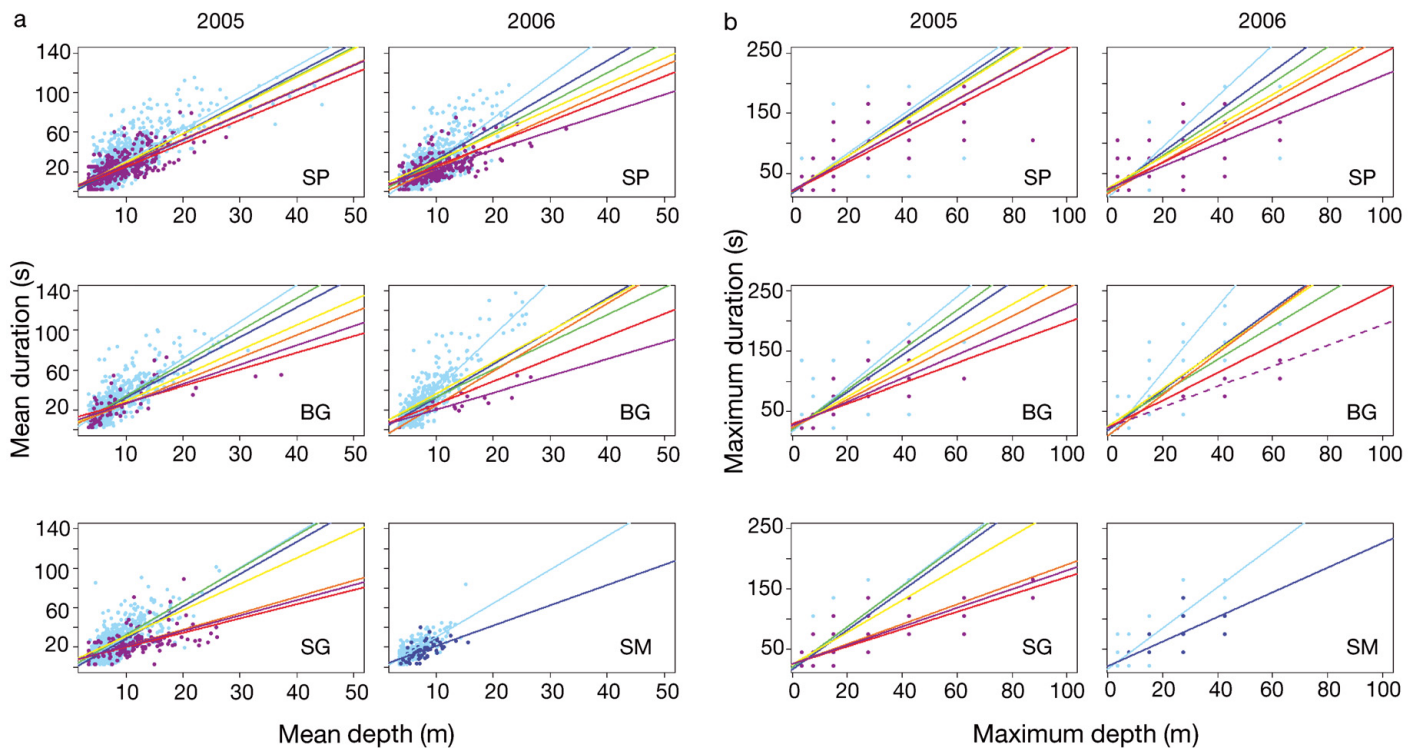


Fig. 7. Relationship between: (a) mean depth (m) and dive duration (s) and (b) maximum depth (m) and dive duration (s), by site (see Table 1 for site abbreviations) and year in relation to months since departure. (Mean depth and dive duration recorded over 6 h periods.) Scatter-plots of the first (light blue) and last months (7+, purple) post-departure are shown. Lines are coloured by months since departure—1: light blue; 2: blue; 3: green; 4: yellow; 5: orange; 6: red; 7+: purple (purple dashed line for BG 2006 in (b) is not significant, so represents a trend line). SP: St Paul Island; BG: Bogoslov Island; SG: St George Island; SM: San Miguel

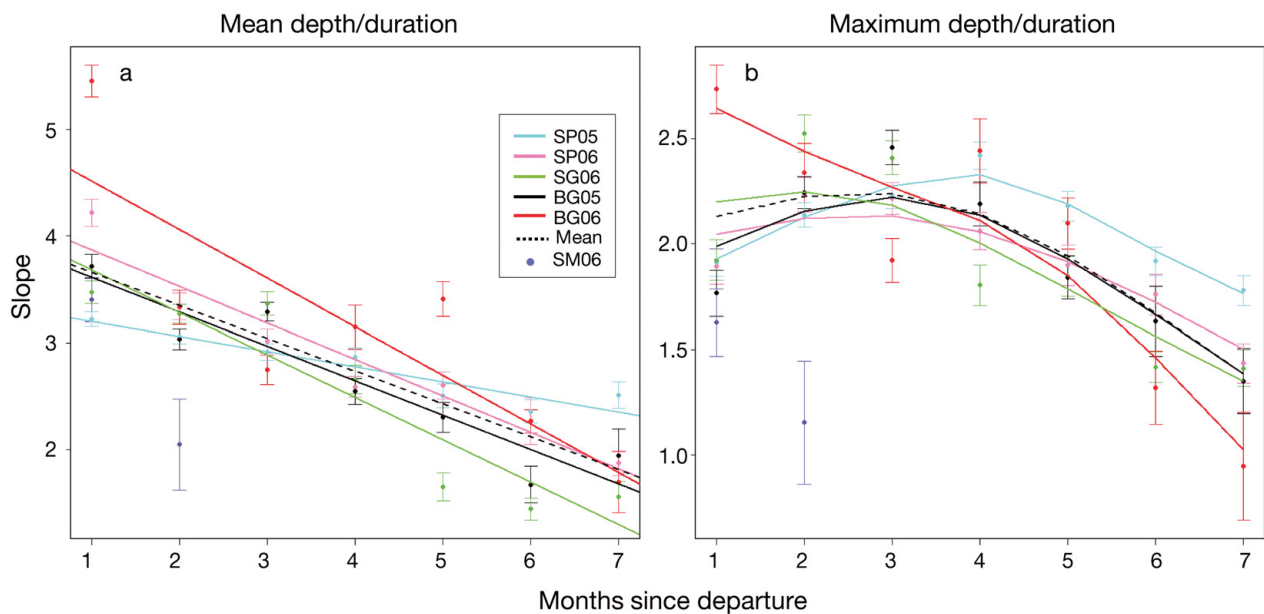


Fig. 8. *Callorhinus ursinus*. Regression coefficients for: (a) mean depth and mean duration and (b) maximum depth and maximum duration relationships by site and year in relation to months since departure. SP: St Paul Island; SG: St George Island; BG: Bogoslov Island; SM: San Miguel; 05: 2005; 06: 2006

(Table 3). Pups also dived deeper at dawn and dusk than during daytime periods (Table 3, Fig. 3).

The lunar illumination fraction (L) positively influenced mean and maximum dive depth and duration during night and crepuscular periods (Tables 2 & 3, Fig. 9). L and days since departure (D) factors also featured consistently in the highest ranked mixed models (Tables 2 & S5), in addition to sex and site effects. Pup sex as a single fixed-factor model ranked poorly ($\omega\text{AIC} < 0.1$; Table 2), however, there were complex and significant interactions between sex and lunar illumination fraction and days since departure (D in Table 2). Mixed models indicate that during periods of increasing illumination, male pups tended to dive deeper, longer and less frequently (all behavioural response variables) than female pups (Table S5). The sex–D interaction term, however, indicated that, relative to males, female pups increased average diving capability at a faster rate with respect to D (e.g. females had a larger change in maximum dive duration for a given post-departure period). L and D also consistently appeared in high-ranking mixed models for twilight behavioural response variables (Table S5).

Dive frequency generally decreased with increasing L, indicating that pups dived less frequently, more deeply and for longer periods during the full moon than during the new moon (Fig. 9, Table 3). Comparisons of diving behaviour in relation to L, between years and sites (see Fig. 9), also revealed variability between and within sites in both years. For pups from SP in 2005/2006, for example, lunar periodicity was detectable in the data during the second month at sea, while in 2006/2007 this did not occur until 4 mo at sea when the magnitude of the response was almost double (30 m cf. 15 m). Distinct between-year variability is also evident in terms of mean depth and dive frequency attained (Fig. 9). For example, SP pups dived to average depths of 20 to 30 m in February/March 2007 and only to 15 m in 2006.

DISCUSSION

Both physiological constraints and key environmental factors such as lunar phase and time of day exert considerable influence on the developing dive behaviour of *Callorhinus ursinus* pups during their first 6 to 8 mo at sea.

Table 3. *Callorhinus ursinus*. Dive parameters of migratory northern fur seal pups in relation to lunar phase (data are mean \pm SD). Sample sizes for 6 h dive periods—waxing: 3290; full: 3417; waning: 4064; new: 3654

	n	Waxing	Full	Waning	New
Mean depth (m per 6 h)					
Night	6446	8.7 \pm 5.3	12.9 \pm 9.7	8.6 \pm 5.2	7.1 \pm 2.7
Dawn	3827	9.1 \pm 4.9	11.8 \pm 8.7	10.7 \pm 7.2	9.2 \pm 5.7
Dusk	3635	11.2 \pm 7.1	11.5 \pm 7.7	9.5 \pm 5.5	9.4 \pm 4.8
Day	517	4.6 \pm 2.3	5.6 \pm 6.3	5.0 \pm 2.9	5.2 \pm 3.9
Combined	14425	9.2 \pm 5.7	11.9 \pm 8.8	9.3 \pm 5.8	8.1 \pm 4.4
Mean duration (s per 6 h)					
Night	6446	42.3 \pm 19.7	62.2 \pm 29.3	41.4 \pm 18.3	35.0 \pm 11.5
Dawn	3827	46.6 \pm 20.2	55.3 \pm 26.8	52.4 \pm 26.0	45.9 \pm 20.1
Dusk	3635	59.5 \pm 26.7	59.5 \pm 27.0	50.0 \pm 21.8	51.8 \pm 22.5
Day	517	29.1 \pm 11.3	33.2 \pm 19.4	31.3 \pm 14.9	32.5 \pm 17.6
Combined	14425	47.1 \pm 22.8	58.2 \pm 28.3	46.1 \pm 22.0	41.7 \pm 18.7
Max. depth (m per 6 h)					
Night	6446	28.1 \pm 13.5	35.8 \pm 16.3	28.3 \pm 13.6	25.1 \pm 12.8
Dawn	3827	31.3 \pm 17.3	32.5 \pm 18.5	31.0 \pm 17.8	30.4 \pm 17.0
Dusk	3635	29.6 \pm 16.0	31.7 \pm 17.0	29.4 \pm 16.1	28.9 \pm 15.2
Day	517	7.1 \pm 6.6	9.6 \pm 10.3	9.6 \pm 12.3	7.6 \pm 6.7
Combined	14425	28.6 \pm 15.7	32.5 \pm 17.8	28.8 \pm 15.7	26.8 \pm 15.0
Max. duration (s per 6 h)					
Night	6446	100.6 \pm 41.6	125.7 \pm 43.6	102.6 \pm 39.0	89.4 \pm 36.9
Dawn	3827	101.4 \pm 41.4	101.2 \pm 43.5	101.6 \pm 42.5	99.8 \pm 41.0
Dusk	3635	110.8 \pm 44.5	112.4 \pm 44.6	110.7 \pm 43.6	111.4 \pm 41.9
Day	517	36.5 \pm 20.3	44.2 \pm 31.1	43.0 \pm 32.8	42.0 \pm 26.1
Combined	14425	101.0 \pm 43.7	111.3 \pm 46.9	102.8 \pm 42.4	95.8 \pm 41.2
Mean dive frequency (per 6 h)					
Night	6446	313.0 \pm 127.7	240.9 \pm 111.6	319.8 \pm 116.5	325.4 \pm 122.9
Dawn	3827	140.0 \pm 105.7	113.9 \pm 90.3	124.9 \pm 110.6	135.9 \pm 105.9
Dusk	3635	94.4 \pm 106.9	92.9 \pm 94.9	120.2 \pm 125.7	118.9 \pm 126.1
Day	517	9.5 \pm 11.7	12.5 \pm 21.4	11.8 \pm 19.9	11.1 \pm 27.1
Combined average	14425	202.9 \pm 154.6	154.0 \pm 123.1	210.7 \pm 155.0	216.4 \pm 157.2

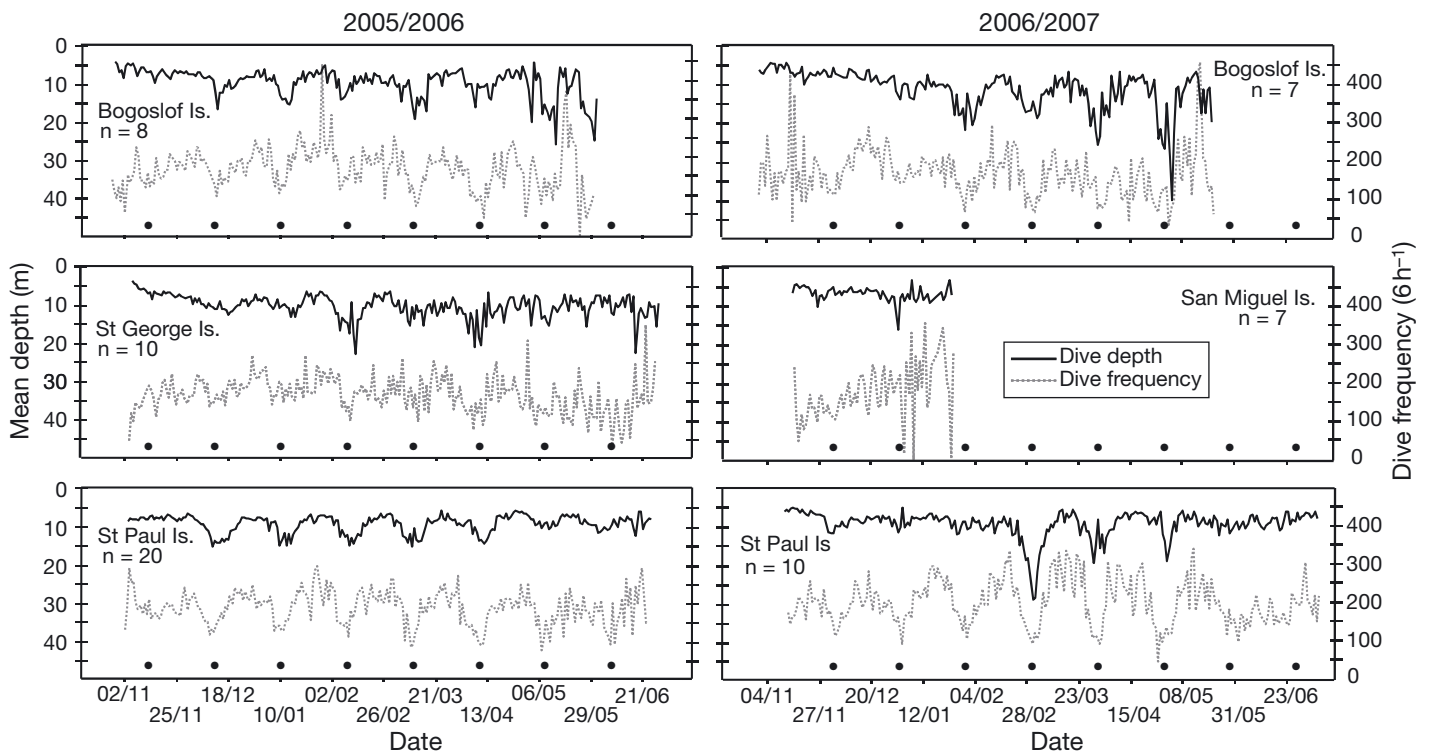


Fig. 9. *Callorhinus ursinus*. Mean dive depth (black; over 6 h periods) and mean dive frequency (grey) for northern fur seal pups in 2005/2006 (Bogoslov Is., St. George Is., St. Paul Is.) and 2006/2007 (Bogoslov Is., San Miguel Is., St. Paul Is.). Dates are dd/mm; black dots: full moon

Diving development

Prior to weaning and departure on their first winter migration, NFS pups (Baker 2007, present study) display a diving pattern of shallow and short-duration dives typical of many otariid neonates (McCafferty et al. 1998, Baker & Donohue 2000, Baylis et al. 2005, Guinet et al. 2005). In the present study, diving capability prior to weaning age and nutritional independence was influenced by both body size (mass) and condition (girth). Diving activity within 1 wk of capture indicated that lighter pups and/or pups with lower girth tended to dive deeper and for longer periods of time than heavier pups. Without further study it is difficult to say what role behavioural and/or physiological factors, such as the proportion of total body fat and buoyancy, play in this relationship. However, it is conceivable that smaller, less well-nourished pups may explore their surroundings more in search of food than their larger counterparts, perhaps developing greater diving capacity prior to weaning (see Baker & Donohue 2000).

Once NFS pups depart their natal sites in autumn, they show rapid increases in dive capability with increasing age and a strong shift toward nocturnal diving similar to adults (Ream et al. 2005, Baker 2007, present study). The steady monthly increases in dive

capability in terms of metres dived per second were evident at all sites (see Figs. 7 & 8), although some degree of inter-annual variability was observed. For example, the monthly spread in the mean dive depth/duration relationship for SP pups was more tightly clustered in 2005/2006 than in 2006/2007 (Fig. 7a). This is also reflected in the difference in maximum dive depth and duration with estimated age. These trends may reflect inter-annual differences in growth rates (body condition and size) and/or feeding strategies between the years. Recent research has shown, for example, that BG pups attain significantly higher growth rates and body masses prior to weaning than their SP counterparts (Iverson et al. 2007). Body mass (and length) is a reliable measure of dive capability (Kooyman 1989, Horning & Trillmich 1997), which, for pups (and offspring of other central place foragers), also reflects prey availability in proximity to the breeding site and maternal (parental) foraging efficiency (Weimerskirch et al. 1993, Staniland et al. 2007). Variability in these conditions between years and sites may account for some of the observed differences in dive capability in the present study. Further support for this theory is provided by the pups from SM. In 2006 pups weighed less than pups from other sites (see Table 1), dive records only lasted 2 mo and at least 1 emaciated animal was found dead on the Washington coast due to

starvation (authors' unpubl. data). Such events have been recorded during years of high storm activity and/or reduced prey availability due to variable oceanographic conditions both prior to weaning and post-weaning (Kenyon & Wilke 1953, DeLong & Antonelis 1991, Sydeman & Allen 1999). The diving capabilities of pups from San Miguel in 2006/2007 were considerably lower than those of larger pups from the other sites (see Figs. 7 & 8).

We have also demonstrated that both absolute diving capability, as measured by maximum dive depth and duration (Table S4) and the maximum dive depth/duration relationship (Figs. 7b & 8b) both increase concomitantly with pup age. Although NFS pups obtained a maximum depth of 175 m and 360 s duration during the first 7 to 8 mo at sea, such excursions to depth were relatively rare, and the majority of dives were <20 m depth and 2 min duration (88.8 and 94.7%). Baker (2007) highlighted a similar increase in diving capability during migration during the first 4 mo at sea with pups rarely exceeding 10 m depth (77%) and 1 min duration (81%). Developmental increases in diving capability are linked to increasing total body oxygen stores influenced by lung volume (body size), and haematocrit, haemoglobin and myoglobin levels (Fowler et al. 2007b, Spence-Bailey et al. 2007). Although published values of these parameters are not available for NFS, studies generally indicate that pup and juvenile otariids have attained from 55 to 81% of adult female mass-specific total body oxygen stores at weaning (Richmond et al. 2006, Fowler et al. 2007b, Spence-Bailey et al. 2007). Our results suggest that at 11 to 12 mo of age (7 to 8 mo post-weaning) NFS pups are capable of reaching depths regularly attained by adults (see Goebel et al. 1991, Ream et al. 2005, Baker 2007, Sterling 2009); however, sustained diving at these depths is not common and is likely a function of both reduced oxygen stores, as discussed above, and the depth of available prey during migration.

There appear to be few discernable differences in diving behaviour between male and female NFS pups up to 1 yr of age. Single-factor mixed models for pup sex ranked low for all behavioural response variables studied; however, there was some indication for all parameters that the interaction between pup sex and lunar phase was important. Male pups tended to dive deeper, for a longer duration and less frequently than female pups with an increasing lunar illumination fraction (full moon). Although NFS exhibit some of the most extreme sexual dimorphism of any mammal as adults (Badyaev 2002), divergence in body size only becomes apparent at from 4 to 5 yr of age (Trites & Bigg 1996). This may account for the limited overall intersexual differences in diving ability detected in the present study.

Lunar influences on pup diving

Ambient light levels within the water column change in accordance with lunar phase and are known to affect the vertical migration of zooplankton, predatory fish and squid species (Gilly et al. 2006). Not surprisingly, the behaviour of marine predators such as tuna (Bestley et al. 2008), sharks (Graham et al. 2006), freshwater turtles (Jensen & Das 2008), seabirds (Yamamoto et al. 2008) and marine mammals (Trillmich & Mohren 1981, Horning & Trillmich 1999), including adult NFS (Ream et al. 2005), are also correlated with lunar phase.

The present study demonstrates the strong interrelationship between lunar phase (Fig. 9), illumination fraction and pup dive behaviour. Pups consistently dived deeper and made fewer dives during the full moon and the days surrounding the full moon. Such a pattern has also been noted for a smaller sample of adult female NFSs during the pelagic winter migration (Ream et al. 2005). Adult female and juvenile Galapagos fur seals *Arctocephalus galapagoensis* are also known to dive deeper, reduce diving activity and exhibit lower than average body masses during the full moon in response to the deeper location of their prey in the water column (Horning & Trillmich 1999). No measure of pup foraging success was obtained in the present study, as pups remained at sea for the duration of the study. However, given that migratory NFS pups and adults feed on squid and myctophid fish (Ream et al. 2005) that remain lower in the water column during the full moon, lunar phase likely exerts a similar cyclical pressure on foraging success of newly weaned NFS pups. The negative impacts of such reduced foraging success are likely greatest soon after weaning as pups learn to forage in a pelagic environment with limited diving capability.

Although the influence of lunar phase was particularly marked for NFS pups, the effect was somewhat variable between sites and years. During the first few months at sea, lunar effects on diving are less obvious, except for SP pups in 2005. While this pattern may be age-related, it is likely that habitat and, consequently, prey type and/or availability play a more important role. In 2005, Pribilof Island fur seals departed the Bering Sea more quickly than in 2006 (Lea et al. 2009). The earlier inception of a lunar dive signal in 2005 likely reflects pelagic foraging by pups in this year, when they were feeding off the shelf earlier in the migratory season in comparison to 2006 when pups spent a significantly longer period over the Bering Shelf (Lea et al. 2009).

Seasonal shifts in diving behaviour

Day length and movement patterns vary considerably throughout the course of the annual migration. In

November, night lasts 16 h at natal sites (~57°N), while during the spring/summer period (May) at more temperate latitudes (40°N) in the pup foraging areas (Kenyon & Wilke 1953, Baker 2007, Lea et al. unpubl. data) nights last only 9.5 h. Given the nocturnal foraging habits of fur seals, this represents a considerable reduction of potential foraging time (from 67 to 40% of the 24 h period). We may also expect considerable fluctuation in dive behaviour of pups throughout this period in response to environmental conditions independent of age, sex and lunar effects. From May onwards (10 mo of age) a reduction in mean dive depth and dive duration is evident during night and dawn periods (Table S2). While this may, in part, represent the decreasing sample size at this time (see Fig. 3, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m419p233_supp.pdf), it is likely that seasonal shifts in prey availability also contribute. In the central subtropics and mid-latitudes of the North Pacific (35 to 45°N, 150 to 180°W), a region encompassing the turning point for many pup migrations (Kenyon & Wilke 1953, Baker 2007, Lea et al. unpubl. data), the seasonal maximum (December to April) mixed layer depth (MLD) is highly variable (± 20 m) between years (Carton et al. 2008). MLD represents a vertical physical, biological boundary layer that seasonally influences marine productivity transfer to higher trophic levels (Polovina et al. 1995). Biological variation in oceanic systems is often linked to variability in the MLD (see Polovina et al. 1995), the magnitude of which is considerable (± 20 m) in regions frequented by NFS pups (Baker 2007, Lea et al. 2009) when compared with the average maximum diving depths of pups (10 to 40 m; Fig. 3). Therefore, pups remaining in pelagic waters in northern latitudes into the winter may encounter reduced prey availability, as the MLD and its associated productivity descend below their diving capabilities.

Implications and conclusions

NFS pups show considerable development in diving capability during the first 8 mo post-weaning, and, while pups are capable of diving to adult female dive depths by this age, they do so rarely and not for extended periods. Diving ontogeny post-weaning is also associated with a behavioural switch to nocturnal foraging as observed in adults (Goebel et al. 1991, Baker 2007). Consequently, those individuals in pelagic habitats are influenced significantly by lunar phase insofar as vertically migrating prey become less available to young NFS during the full moon phase (see Horning & Trillmich 1999). During the critical first 6 mo of independent foraging, this link between lunar phase and foraging success noted by Horning &

Trillmich (1999) for juvenile Galapagos fur seals may be of greater consequence for smaller NFS pups. Hindell et al. (1999) showed in their study of newly weaned southern elephant seal *Mirounga leonina* migration that dives of small pups were significantly shallower than those of larger pups. Small NFS pups operating at their physiological limits and showing reduced diving capabilities compared to those of larger pups may be at a distinct disadvantage during early migration, which coincides with a deeper winter mixed layer, as vertically migrating prey descend out of reach during the full moon.

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