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Extreme weather events influence dispersal of naive northern fur seals

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Since 1975, northern fur seal (*Callorhinus ursinus*) numbers at the Pribilof Islands (PI) in the Bering Sea have declined rapidly for unknown reasons. Migratory dispersal and habitat choice may affect first-year survivorship, thereby contributing to this decline. We compared migratory behaviour of 166 naive pups during 2 years from islands with disparate population trends (increasing: Bogoslof and San Miguel Islands; declining: PI), hypothesizing that climatic conditions at weaning may differentially affect dispersal and survival. Atmospheric conditions (Bering Sea) in autumn 2005–2006 were anomalously cold, while 2006–2007 was considerably warmer and less stormy. In 2005, pups departed earlier at all sites, and the majority of PI pups (68–85%) departed within 1 day of Arctic storms and dispersed quickly, travelling southwards through the Aleutian Islands. Tailwinds enabled faster rates of travel than headwinds, a trend not previously shown for marine mammals. Weather effects were less pronounced at Bogoslof Island (approx. 400 km further south), and, at San Miguel Island, (California) departures were more gradual, and only influenced by wind and air pressure in 2005. We suggest that increasingly variable climatic conditions at weaning, particularly timing, frequency and intensity of autumnal storms in the Bering Sea, may alter timing, direction of dispersal and potentially survival of pups.

Keywords: migration; Alaska; storms; Bering Sea

1. INTRODUCTION

Animals migrate to maximize fitness in seasonal environments (Alerstam *et al.* 2003). Migratory cues may include pre-migratory state, environmental (photoperiod, temperature, weather, celestial phase and reduced prey availability) and/or behavioural (predation risk) factors (Dingle 1996). For many marine vertebrates, these cues are little studied, particularly the effect of weather on survival, departure and dispersal patterns (Roppel *et al.* 1963). Climatic seasonality in high latitudes during the breeding season purportedly drives timing of the life cycle of northern fur seals (NFS), *Callorhinus ursinus* (Trites & Antonelis 1994). Inclement weather at the start of the breeding season may compromise growth and survival of neonates, while rapid deterioration in weather conditions in autumn coincides with the onset of winter migration (Gentry 1998). NFS undertake considerable annual migrations, with adult females travelling over 9000 km to forage along continental margins and frontal regions (Ream *et al.* 2005). Such behaviour may enable NFS to avoid metabolic costs and ephemeral prey availability associated with colder northern oceans (Donohue *et al.* 2000).

At their primary breeding site (Pribilof Islands, PI), NFS numbers are declining annually at approximately 5.8 per cent (Towell *et al.* 2006), while smaller populations at Bogoslof Island (Bering Sea) and San Miguel Island (California) have risen since the 1980s (Ream *et al.* 1999; Melin *et al.* 2007). Factors controlling these divergent population trajectories are unknown and cannot be explained by emigration from the Pribilofs alone (Towell *et al.* 2006). Both environmental (Hunt *et al.* 2002) and anthropogenic factors may contribute to declines in NFS populations, particularly if they affect juvenile survival (Lander 1979).

We examine the dispersal behaviour of naive NFS pups from all North American colonies during the critical first month at sea. We hypothesized that climatic conditions, particularly the incidence of prolonged storms (Ichihara 1974; Baker 2007), influence the timing of departure and movement patterns of pups.

2. MATERIAL AND METHODS

In October/November 2005 and 2006 (table 1), pups were captured at Bogoslof (BG, 53.924° N, −168.029° W), San Miguel (SM, 34.03° N, −120.440° W), St Paul (SP, 57.108° N, −170.295° W) and St George Islands (SG, 56.562° N, −169.667° W). Extracted land-based weather parameters (SP and SG) included: daily wind speed cubed ($m^3 s^{-1}$); wind chill (C); precipitation (cm); snowfall (cm); and air pressure (hPa). Storms were defined as daily wind speeds exceeding 1500 $m^3 s^{-1}$ (i.e. 11.5 $m s^{-1}$). A known-fate survival (KFS) model was applied to departure data assessing the importance of weather parameters on probability of departure. The probability of individual pups departing on a given day, conditional on the fact that they were still ashore the previous day, was modelled analogous to daily mortality in the KFS analysis. By conditioning on presence the previous day, the KFS analysis allows staggered entry of individuals. Two other explanatory variables (i) day since October 28 (day 0) accounted for the ever-increasing tendency of pups to begin migration as energy stores decrease, and (ii) capture in the previous 3 days (tagged) tested for capture effects. The importance of explanatory variables (weather parameters, date and tagging) to the response variable (departure date) was assessed by fitting KFS models for all subsets of covariates, in each site, in 2005 and 2006. Akaike's information criteria corrected (AICc) for small samples were used for model evaluation with models ranked according to relative AICc weights (wAICc). For further methodology, see the electronic supplementary material.

3. RESULTS

Historically, November storms at SP (1943–2004) commenced on 1–19 November (mean: 7 November ± 0.8 days) with up to 13 storm days per month (5.6 ± 0.4). An average 5.4 ± 0.4 (0–13) storms occurred monthly, lasting 1.6 ± 0.9 days (1–4.3 days). In 2005, the first storm commenced on 7 November (4 days), while, in 2006, it occurred on 16 November (1 day; figure 1; electronic supplementary material, figure S1). Storm activity was greater in 2005 (6 days) compared with 2006 (3 days).

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Table 1. Tag deployment and pup departure dates, dispersal metrics during the first 4 days at sea (asterisk), storm characteristics, tag failure and potential mortality for northern fur seal pups tracked from St Paul (SP), St George (SG), Bogoslof (BG) and San Miguel (SM) islands in 2005 and 2006. (DP, dispersal concentration (low values=high dispersion).)

year	island	*n* (departed)	deploy date	median departure (range)	pup swim speed (m s^{-1})*	DP (*n*)*	Rayleigh, Z (*p*)*	first storm	*n* storm days during departure period	% departed on storm days (*n*)	% departed ±1 day of storm day	% ceased within 30 days (*n*)	*n* tag failed	% possible mortality (CI)	% Bering Sea >2 months
2005	SP	44 (44)	7 Oct–14 Nov	11 Nov 2005 (28 Oct–18 Nov 2005)	0.70±0.03	1.502 (43)	15.385 (<0.001)	7 Nov	6	40.9 (18)	68.2 (30)	29.5 (13)	5	18.1 (6.8–30)	13.6 (4.6–25)
	SG	20 (20)	6–10 Nov	10 Nov 2005 (7–14 Nov 2005)	0.75±0.02	1.24 (20)	5.595 (<0.01)	7 Nov	6	80 (16)	85 (17)	10 (2)	1	5 (0–15)	5 (0–15)
	BG	20 (18)	10–20 Oct	9 Nov 2005 (29 Oct–26 Nov 2005)	0.64±0.02	0.613 (18)	1.544 (>0.05)	8 Nov	11	44.4 (8)	72.2 (13)	5.6 (1)	0	5.6 (0–16.7)	11.1 (0–22.2)
	SM	15 (15)	11–13 Nov	26 Nov 2005 (13 Nov–3 Dec 2005)	0.45±0.02	2.988 (15)	10.888 (<0.001)	26 Nov	2	20 (3)	40 (6)	13.3 (2)	2	—	—
2006	SP	25 (24)	8–13 Nov	18 Nov 2006 (11 Nov–11 Dec 2006)	0.57±0.02	0.966 (23)	4.36 (<0.05)	16 Nov	4	33.3 (8)	45.8 (11)	4.2 (1)	0	4.2 (0–12.5)	41.7 (16.7–58.3)
	SG	18 (17)	8–12 Nov	15 Nov 2006 (10–23 Nov 2006)	0.66±0.02	1.568 (16)	6.035 (0.001)	16 Nov	4	29.4 (5)	35.3 (6)	29.4 (5)	1	23.5 (0–41.2)	11.8 (0–27.8)
	BG	15 (14)	30 Sep–7 Oct	14 Nov 2006 (28 Oct–4 Dec 2006)	0.57±0.02	0.461 (13)	1.368 (>0.05)	8 Nov	8	21.4 (3)	42.9 (6)	28.6 (4)	0	28.6 (7.1–50)	7.1 (0–21.4)
	SM	9 (9)	14 Nov	19 Nov 2006 (15 Nov–9 Dec 2006)	0.45±0.02	1.664 (9)	5.121 (<0.01)	25 Nov	1	0 (0)	0 (0)	22.2 (2)	1	11.1 (0–33.3)	—

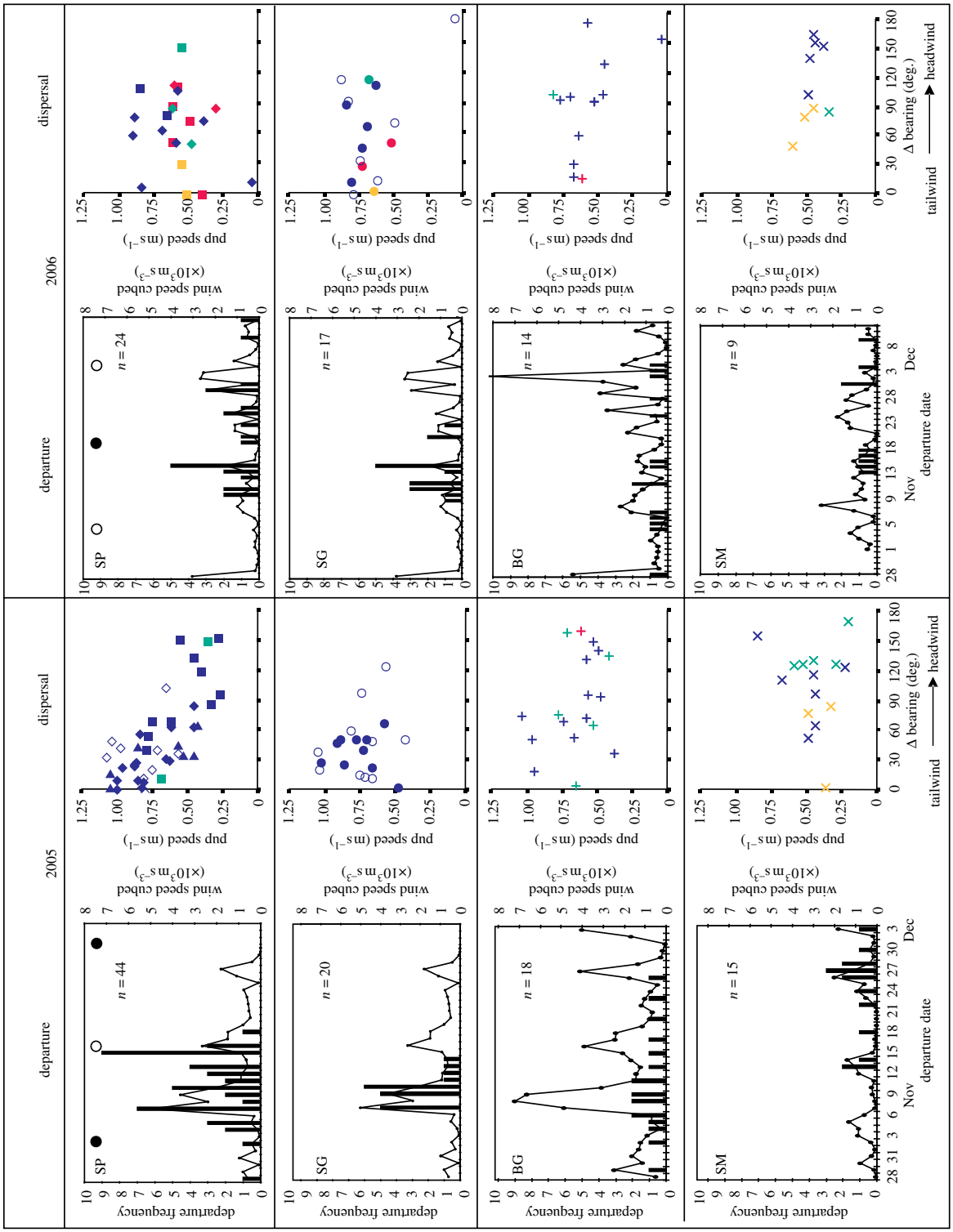

Figure 1. Wind speed ($m^3\ s^{-1}$, black line) and pup departure frequency (left, yearly panels), and pup swim speed ($m\ s^{-1}$) during 4 days post-departure at St Paul (SP), St George (SG), Bogoslof (BG) and San Miguel (SM) islands in 2005 and 2006. Wind direction (northerly (purple), westerly (green), southerly (red), easterly (yellow)) and seal rookery (SP: triangle, Polovina (E); square, Vostochni (N); filled diamond, Reef (SE); open diamond, Zapadni Reef (SW); SG: circle, Zapadni (SW, filled), North (N, open); BG: plus, Bogoslof (N); SM: cross, Adams Cove (S)). Open circle, full moon; filled circle, new moon.

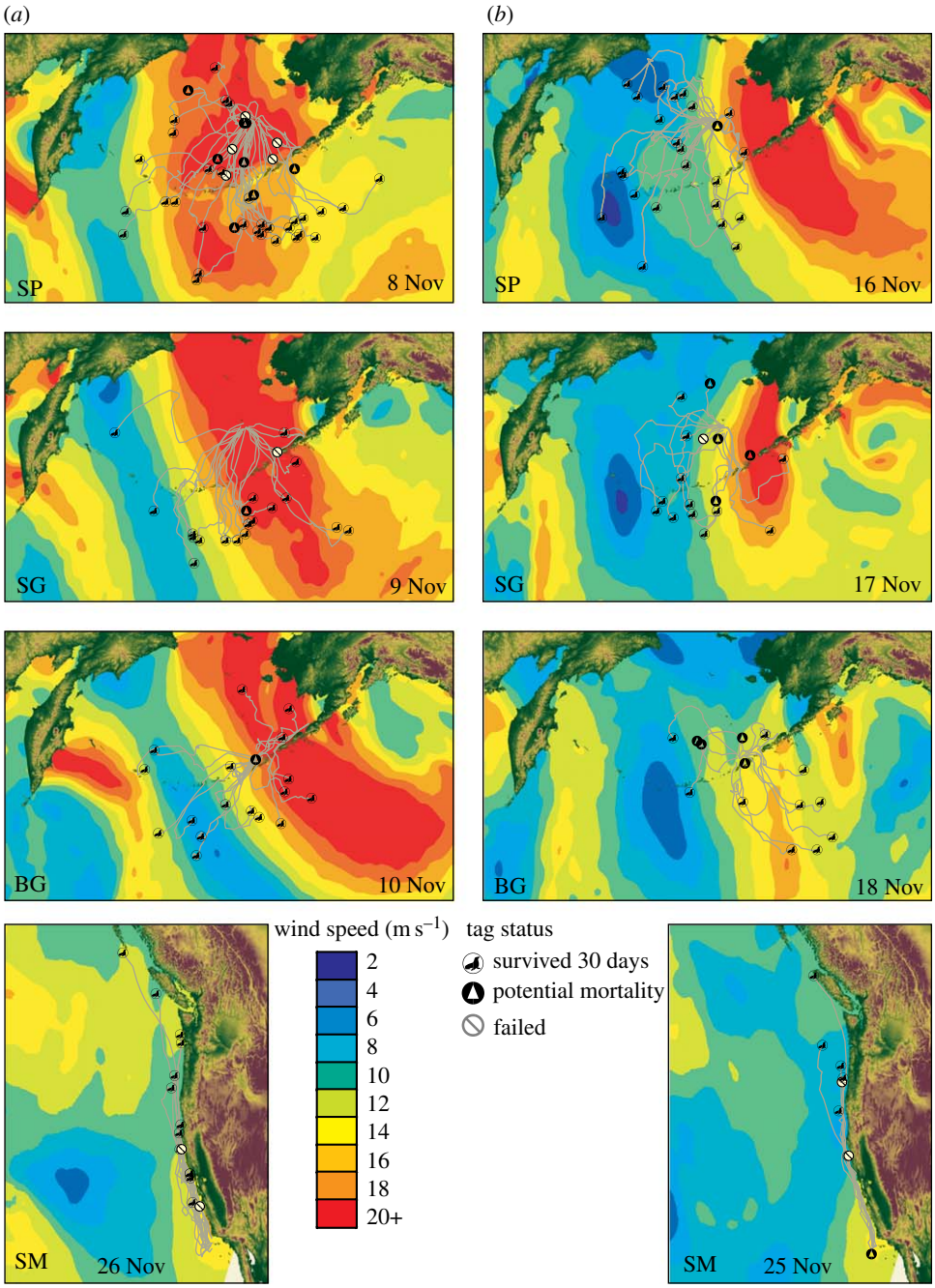

Figure 2. Post-weaning dispersal of NFS pups (*a*) 2005 ($n=97$), (*b*) 2006 ($n=64$) during the first 30 days in relation to wind velocity (m s^{-1}) for high departure days at SP, SG, BG and SM. Quickscat wind imagery highlights storm progression.

(a) *Departure timing and climatic influences*

Alaskan pups (SP, SG and BG; table 1) departed earlier than Californian (SM) pups in both years ($F_{160,3}=19.635$, $p<0.001$; table 1). Departure date was earlier in 2005 ($F_{160,1}=22.592$, $p<0.001$; table 1) and did not vary by sex. Weather at departure was a significant factor at all colonies except BG and SM in 2006 (table 2 in the electronic supplementary material). In 2005, peak SP and SG departures coincided with the onset of two strong storms (figures 1 and 2), with 41 per cent and 80 per cent of pups, respectively, departing during these events (68 and 85% within ± 1 days of storm event). At BG, 41 per cent of pups departed on stormy days (above 1500 m^3 s^{-1}) and 72 per cent within ± 1 day of these events. In 2006, conditions were considerably less stormy in the Bering Sea and departures were more gradual at SP and SG (see figure S1 and table 3 in the electronic supplementary material). Overall, BG animals departed gradually in both years with wind influencing departure date in 2005 (figure 1; table 2 in the electronic supplementary material). At SM, departure correlated with wind conditions and high pressure systems in 2005 but not in 2006 (table 3 in the electronic supplementary material).

(b) *Dispersal patterns*

During the first month at sea, Alaskan pups generally dispersed southwards, while SM animals headed north along the continental margin (figure 2). Movement was directed for SP, SG and SM pups in 2005 and 2006 (Rayleigh test; table 1; figure 2) but less concentrated at BG, than other sites (table 1). In

2006, more pups spent longer in the Bering Sea compared with 2005 (20% cf. 10%; table 1).

Rates of travel (1–4 days) varied by year ($F_{1,611}=6.539$, $p<0.05$), site ($F_{1,611}=13.252$, $p<0.01$) and sex ($F_{1,611}=13.250$, $p<0.01$) (table 1). Wind speed and direction at 1–4 days also influenced pup speed and direction (figure 1). Pups encountering tailwinds (low Δbearing) displayed higher swim speeds than those experiencing headwinds (high Δbearing). The best model, accounting for 61.2 per cent of the weight of evidence, included Δbearing, wind speed, sex and the wind speed×site interaction as fixed effects (AIC = −195.131, d.f. = 14; figure 1; electronic supplementary material, table 4), with pup nested in year as the random effect. Movement was still highly influenced by wind speed, bearing and sex at 10 days (electronic supplementary material, tables 4–6).

(c) *Potential mortality*

After accounting for known tag failures (table 1), bootstrap confidence intervals (CI, 1000 iterations) indicated that potential SP mortality (i.e. unknown cause of cessation, 18%) was higher than other sites (0–6%) in 2005. In 2006, potential mortality at SP (4%) was lower than SG (24%) (and SP, 2005). Potential mortality was highest at BG (29%) in 2006, although bootstrap CI were larger owing to smaller sample size, and was generally low at SM.

4. DISCUSSION

The early migratory behaviour of NFS pups, particularly PI animals, appears to be linked to concurrent atmospheric conditions. The incidence and strength of the effect of individual weather parameters, however, were variable between years and sites. Our analyses indicate that wind speed and wind chill were most influential in predicting departure date, particularly at the PI sites in 2005, a year of higher November storm activity. Alaskan pups departed earlier during these cold, stormy conditions when storms were centred in the Gulf of Alaska, than in 2006, a factor coincident with inter-annual disparity in storm activity (figure 3 in the electronic supplementary material). Fur seals are disturbed by wind-driven rain often entering the water under such conditions (Baker & Donohue 1999). Data from previous studies at PI also suggest a relationship between storm incidence and departure with many animals departing within a day of the first November storm (Peterson 1965; Ragen *et al.* 1995; Goebel 2002; electronic supplementary material, figure S1).

At Bogoslof Island, 400 km further south, wind exerted some effect in 2005 with many pups departing within a day of storms; however, the effect was considerably weaker than for the PI. Our ability to detect a relationship at BG may have been influenced by the distance between the weather buoy and colony (time lag and reduced accuracy), or higher weaning masses at BG (Iverson *et al.* 2008) may potentially insulate pups from the effects of atmospheric weather conditions and/or an immediate requirement to feed. However, the lack of wind effects on BG pup movement during the first 4 days at sea suggests that currents and/or proximity of the Aleutian Islands may limit the influence of wind. At SM, the most southerly site, high pressure and strong winds exerted some effect on departure timing in 2005 only. SM pups also departed approximately two weeks later than Alaskan pups (PI and BG), probably as a reflection of their later median pupping dates (Gentry 1998).

The coupling of daily pup swim speed and wind speeds evident during initial dispersal highlights a new relationship between movement and the intensity and direction of winds, with tailwinds coinciding with the direction of travel enabling greater swim speeds. This finding indicates that strong northerly storm events in the Bering Sea at weaning may increase movement rates, as occurred in 2005, which is potentially advantageous in quickly shepherding younger animals along with older age classes south towards the productive Transition Zone Chlorophyll Front (Ream *et al.* 2005; Baker 2007). For those that do not disperse quickly, energy stores are limited, with Antarctic fur seal pups predicted to survive only 10–36 days at sea before succumbing to starvation (Rutishauser *et al.* 2004). Consequently, prey availability and detection ability are critical at this time. The additional 400 km to the North Pacific Ocean, coupled with increased exposure to weather in the Bering Sea, may conceivably affect PI pup survival more adversely in some years, as appears to be the case in 2005. This relationship is also probably dependent on weaning condition and, accordingly, maternal summer foraging success (Goebel 2002).

Our findings indicate that climatic factors are important not only in shaping the life history of NFS (Trites & Antonelis 1994), but also in influencing initial post-weaning behaviour (departure timing and movement rates) of pups, particularly at PI where numbers continue to decline. The increasing frequency and intensity of storms in the North Pacific Ocean (Graham & Diaz 2001) may consequently affect post-weaning behaviour and, ultimately, survival of pups at the PI.

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