Oceanographic and climatic factors differentially affect reproduction performance of Antarctic skuas

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ABSTRACT: We studied how environmental conditions affect reproduction in sympatric skua species that differ in their reliance on marine resources: the exclusively marine foraging south polar skua *Catharacta maccormicki*, the terrestrially foraging brown skua *C. antarctica lonnbergi* and mixed species pairs with an intermediate diet. Egg size, clutch asymmetry and hatching dates varied between species and years without consistent patterns. In the south polar skuas, 12 to 38% of the variation in these parameters was explained by sea surface temperature, sea ice cover and local weather. In mixed species pairs and brown skuas, the influence of environmental factors on variation in clutch asymmetry and hatching date decreased to 10–29%, and no effect on egg size was found. Annual variation in offspring growth performance also differed between species with variable growth in chicks of south polar skuas and mixed species pairs, and almost uniform growth in brown skuas. Additionally, the dependency on oceanographic and climatic factors, especially local wind conditions, decreased from south polar skuas to brown skua chicks. Consistent in all species, offspring were more sensitive to environmental conditions during early stages; during the late chick stage (>33 d) chick growth was almost independent of environmental conditions. The net breeding success could not be predicted by any environmental factor in any skua species, suggesting it may not be a sensitive indicator of environmental conditions. Hence, the sensitivity of skuas to environmental conditions varied between species, with south polar skuas being more sensitive than brown skuas, and between breeding periods, with the egg parameters being more susceptible to oceanographic conditions. However, during offspring development, local climatic conditions became more important. We conclude that future climate change in the Maritime Antarctic will affect reproduction of skuas more strongly through changes in sea ice cover and sea surface temperature (and the resulting alterations to the marine food web) than through local weather conditions.

KEY WORDS: Maritime Antarctic · Sea surface temperature · Sea ice cover · *Catharacta* spp. · Breeding parameter · Chick growth · Life history

INTRODUCTION

The climate of the western Antarctic Peninsula region has undergone profound changes in the last decades, such as a 2 to 3°C increase in mean air temperatures over the last 50 yr, an earlier retreat of winter sea ice, and an increased frequency of extreme weather events (see e.g Smith & Stammerjohn 2001, Vaughan et al. 2003). These changes can have opposing effects on polar seabirds. For example, while reduced sea ice cover generally facilitates foraging of marine surface feeders, decreased winter sea ice is also associated with lower krill densities in summer (Siegel & Loeb 1995, Loeb et al. 1997). Krill *Euphausia*

spp.) comprise the key resource for almost all higher-order predators in the Antarctic, either representing the main prey for penguins, fishes and whales, or indirectly affecting top predators such as seals and skuas that prey on krill-consuming species. Because the Antarctic food web is comparatively simple (Hempel & Kerry 1990), environmental changes affecting lower food chain levels can also rapidly influence reproduction and population dynamics of top predators (Fraser & Hofmann 2003, Weimerskirch et al. 2003).

In studies of polar seabirds, oceanographic factors like sea ice cover and sea surface temperatures have been used as proxies for food accessibility and availability, as they indicate open water and areas of enhanced primary production (e.g. Ainley et al. 1998, Barbraud & Weimerskirch 2001). Furthermore, local weather conditions in summer influence the breeding success of seabirds directly via their effects on offspring growth (Busser et al. 2004).

Oceanographic and local weather conditions in the Maritime Antarctic vary remarkably between years (Smith & Stammerjohn 2001). Therefore, reliable predictions have been largely lacking on how particular environmental factors affect different episodes of reproduction and, hence, population dynamics of the respective species.

In our study we analysed the effect of oceanographic and climatic factors on reproduction of Antarctic skuas *Catharacta* spp., which are important top predators in the Antarctic marine ecosystem (Young 1994, Phillips et al. 2004). In the South Shetland Islands, western Antarctic Peninsula region, the distribution ranges of the closely related south polar skua *C. maccormicki* and brown skua *C. antarctica lonnbergi* overlap and they breed sympatrically (reviewed by Ritz et al. 2006). Additionally, both species regularly form mixed pairs comprising a south polar skua male and a brown skua female (e.g. Hahn et al. 2003). Within the area of sympatry, the skua species occupy different ecological niches separated by foraging behaviour and foraging areas. Whereas the diet of south polar skuas comprises 90 to 95% marine food, mainly pelagic fishes, brown skuas feed mainly on seabirds, their eggs and chicks, e.g. penguins, petrels and storm-petrels (Reinhardt 1997). This species-specific foraging behaviour is reflected in the diet provided to offspring of mixed species pairs with 45 to 80% marine and 18 to 50% terrestrial food (Pietz 1987, Reinhardt 1997).

The sympatric breeding but different foraging of skuas in the South Shetlands provided the unique opportunity of identifying species-specific responses to the same set of environmental factors. We used egg dimensions and chick hatching date as indicators of conditions at the beginning of the breeding period (e.g. Hiom et al. 1991) and indices of chick growth

variation for the characterisation of late-season effects (Ritz et al. 2005). Additionally we recorded the total breeding success as an overall measure of annual breeding output.

As the skua species should have similar requirements for nest initiation and incubation in spring, we expected the annual variation in egg dimensions and hatching dates to be similar across skua species. Later in the breeding season, offspring development should depend on parental foraging strategy and, thus, vary between species. In south polar skuas, offspring growth was expected to be influenced by both marine and local weather conditions, because breeding adults have to fly larger distances between nest and offshore foraging areas (Pietz 1986). This leaves offspring exposed to potentially adverse weather, and provisioning largely depends on the accessibility and availability of marine food. In contrast, chick growth of brown skuas should depend merely on local weather conditions because of their terrestrial food.

Overall breeding success is unlikely to be affected by a single environmental factor if different environmental factors influence reproductive performance period specifically. However, we expected that in accordance with their different feeding habits, reproduction of south polar skuas and brown skuas would depend on oceanographic and local climatic factors, respectively. This could be confirmed by the intermediate position of the mixed species pairs.

MATERIALS AND METHODS

Study site and population. The study sites were 2 neighbouring ice-free areas, Fildes Peninsula and Potter Peninsula, on King George Island (62° S, 58° W) in the Maritime Antarctic. King George Island belongs to the South Shetland Island group. This group is separated from the Antarctic Peninsula by the approximately 100 km wide Bransfield Strait. The climate on the island is characterised by high precipitation (approx. 700 mm yr^{-1}) and strong westerly winds; storms with maximum wind speeds >100 km h^{-1} are typical. Mean summer temperatures (January and February) and winter temperatures (July and August) are 1.5 and –6.5°C, respectively; the snowmelt normally starts at the end of October. During the winter months, the adjacent sea is covered with fast sea ice until October or November, with a high interannual variability of ice cover extent and duration.

We analysed data of the breeding performance on Antarctic skuas *Catharacta* spp. on Fildes Peninsula and Potter Peninsula in the austral summers of 1983–84 to 2003–04. The breeding grounds are approx. 15 km apart; exchanges of individuals between the sites

occur regularly (S. Hahn et al. pers. obs.). The skua breeding populations on Fildes Peninsula (Potter Peninsula) consists, on average, of 170 (50) pairs of south polar skuas *C. maccormicki* (SPS), 70 (30) pairs of brown skuas *C. antarctica lonnbergi* (BS), and 25 (10) mixed species pairs (MSP). All individuals were identified to species level by plumage coloration and body size differences. MSP consist of SPS males and BS females (Hahn et al. 2003). SPS, BS and MSP are henceforth referred to as 'skua forms'. The data set includes the breeding seasons of 1984, 1985, 1987, 1988 (Fildes Peninsula) and 1994 to 1995 and 1999 to 2004 (Potter Peninsula). The year refers to the time of chick fledging, e.g. 1984 denote the austral summer of 1983 to 1984. Skuas breeding in the Antarctic are migratory birds, which only attend their breeding sites during the reproduction period. Hence, the abiotic winter conditions at the breeding areas should influence the annual breeding performance of the birds indirectly, e.g. by different dates of snowmelt or sea ice break-up. In our study we focused on 2 different periods of skua reproduction: the pre-incubation period from October to November, and the chick-rearing period from January to March. The incubation period (December) was not considered in the analysis, because we assumed that neither egg parameters nor chick growth were influenced by this period.

Breeding parameters. *Egg measurements and hatching date:* Clutch size, egg dimensions (length and breadth, ±0.1 mm) and egg mass (±1 g) were measured for each nest. Egg size was calculated as egg size (cm^3) = $0.00048 \times$ length $\times$ breadth^2 (after Coulson 1963). We incorporated only first-egg data into the analysis of egg size. If clutches contained 2 eggs, we calculated clutch asymmetry (CA) as size of second egg divided by size of first egg (Catry & Furness 1997). Hatching dates were either observed directly or calculated using hatching date–egg density relationships: 50 and 90% errors of estimation were 1.4 and < 4 d, respectively (formulas for BS + MSP: Hahn & Peter 2003, SPS: M. S. Ritz unpubl. data). We considered only the hatching date of the first chick per clutch as the second chick invariably hatches 1 to 3 d later. Years containing only 1 data point were excluded (BS in 1984, MSP in 1988). Hatching dates are given as days from 1 December (e.g. 1 January = Day 32) and were square-root transformed to conform to normal distribution. For all skua forms and breeding parameters, we calculated a long-term mean over all study years and the annual deviations as the difference between annual and long-term mean.

Chick growth performance: Skua chicks were weighed at irregular intervals during their growth period; to avoid handling effects the minimum interval length was 4 d. For each skua form, a growth curve was calculated for body mass as $A / \{1 + \exp [k \times (x - t0)]\}$,

where A = asymptotic size, k = growth constant and $t0$ = age at the inflection point of the sigmoid model. We included all chicks, irrespective of hatching order and survival to fledging. The goodness of fit of the models was $r^2 = 0.96$ (df = 1125) for SPS, $r^2 = 0.95$ (df = 613) for MSP and $r^2 = 0.94$ (df = 1409) for BS. Individual chick growth performance was expressed as the proportional deviation from the predicted body mass at a given age. An average value was calculated if more than 2 data points per chick were available. The growth variability between skua forms and between years was quantified by an average value for each chick for the complete growth period from the age of 10 d to fledging or death, called the 'entire stage model'. Furthermore, we repeated the analyses of chick growth performances for the chick stages 'early' (Days 10 to 21), 'middle' (Days 22 to 33) and 'late' (Days 34 to fledging). All growth data of chicks younger than 10 d were excluded because of lack of variance homogeneity.

Breeding success: For each skua form we calculated an annual average breeding success as the number of chicks fledged per nest.

Environmental factors. We calculated the impact of maritime factors that may indirectly affect skua reproduction via food (namely regional and local sea ice conditions) as proxies for accessibility of maritime food, and sea surface temperatures as a proxy for food availability (Ainley et al. 1998, Prézèlin et al. 2004). Direct effects on skua offspring and adults were measured by local weather conditions, characterised by air temperature, precipitation and wind speed.

Sea ice cover (SIC): We used the denoted means of sea ice extent at 60° W from October to March of each breeding season as a measurement of the regional sea ice cover (available at www.natice.noaa.gov and www.antcrc.utas.edu.au/~jacka/seaice.html). Because there were no data available for the exact area at 58° W, we calculated a monthly anomaly value of northern sea ice extent assuming related sea ice conditions at 60 and 58°. This monthly sea ice anomaly is given as An60 = mean ice extent (60°W from 1983 to 2004) – actual ice extent (60° W), e.g. a month with less-than-average sea ice cover has a negative anomaly value.

Local ice break-up: We characterised the local ice break-up at the adjacent Bransfield Strait (60° W, 62.7° S to 63.8° S) as the first month of each austral summer when 50% of the strait was free of ice (sea ice edge > 63.2° S).

Sea surface temperature (SST): We calculated a monthly average of sea surface temperatures at 62° S from the area of 62° S, 57° W to 62° S, 59° W (available at http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.ERSST/.version2/.SST/). SST ranged from −0.32 ± 0.12°C in early spring to 1.25 ± 0.27°C during the chick-rearing period.

Local weather (air temperature and precipitation): We used published data of monthly mean air temperatures (°C) and precipitation (mm) from 1984 to 2004 measured at the Russian Scientific Base Bellingshausen, Fildes Peninsula (available at www.aari.nw.ru/projects/Antarctic/default_en.asp).

Wind speed: For a smoothed average we used the monthly means (m s^{-1}) calculated from 4 measurements per day at Bellingshausen Station, Fildes Peninsula, from 1984 to 2004. Additionally, we used the 9:00 h daily measurement at the Argentinean base, Jubany (1987 to 2004: data provided by Servicio Meteorologico Nacional, Argentina), Potter Peninsula, as a more variable and 'event-based' measure of wind speed. Furthermore, we counted the monthly number of days with a wind speed >15 m s^{-1} from the Jubany data set.

Statistical methods. We compared the breeding parameters of skuas using ANOVA with skua form and year as factors. Additionally we analysed the coefficients of variation (CV) and correlation coefficients of breeding parameters to determine magnitude and direction of deviations from the long-term mean.

The impact of environmental factors on skua reproduction was analysed by multinomial linear regressions with a backward iteration procedure to exclude non-significant factors.

For the pre-incubation period (October to November), we sought to explain egg size, clutch asymmetry and hatching date by the following environmental factors: sea ice cover (SIC) at 60° W, local ice break-up and mean sea surface temperature at 62° S (SST), mean air temperatures (Temp), mean precipitation (Prec) and mean wind speed (Wind).

We analysed the influence of abiotic factors on chick growth for both the entire growth period ('entire stage model') and separately for the 3 chick stages (see above). In the entire stage regression model, we used the mean values of chick growth performance as dependent variable and the means of regional sea ice cover anomaly (SIC), local ice break-up, mean sea surface temperature (SST), average air temperatures (Temp), average wind speed (Wind) and precipitation (Prec) for the complete chick period from January to March as independent variables.

The models for the chick stages included chick growth data for 7 yr (1994 and 1999 to 2004) and the environmental factors SIC and local ice break-up, SST, monthly means of temperature, precipitation, wind speed and the number of days with wind speed >15 m s^{-1}.

Although some of the tested abiotic factors varied in a collinear way we decided to focus on original factors rather than calculating artificial factor complexes (sensu Graham 2003). In the pre-incubation period,

SIC was correlated with local ice break-up (r = 0.82, p = 0.001) and mean wind speed was correlated with air temperature (r = 0.69, p = 0.01) as well as with precipitation (r = 0.63, p = 0.02, all n = 13). In the chick-rearing period, average air temperature and SST were correlated (entire stage model, r = 0.60, p = 0.03, n = 13), whereas in the fine-tuned stage models precipitation correlated with the number of stormy days, indicating that storms in summer are almost always accompanied by precipitation (SPS: r = 0.97, n = 5, MSP: r = 0.84, n = 7, BS: r = 0.86, n = 7, all p < 0.03).

RESULTS

Egg parameters and hatching

Egg size of SPS differed significantly between study years ($F_{9,328}$ = 6.06, p = 0.001) caused by differences between 1993 and 2004 (small egg sizes) and 1994, 2001 and 2002 (years with large eggs) (post hoc Tamhane, p < 0.05, Table 1). In contrast, egg sizes of BS and MSP did not differ significantly between years (BS: $F_{11,260}$ = 1.21, p = 0.28; MSP: $F_{11,106}$ = 0.44, p = 0.94, Table 1). The annual coefficient of variation for egg size did not differ consistently between the skua forms (RM ANOVA: $F_{2,11}$ = 0.93, p = 0.41), and consequently there was no correlation (Spearman's rank correlation R_S) between the skua forms (SPS and MSP r_S = 0.59, p = 0.07, n = 10; SPS and BS r_S = –0.07, p = 0.84, n = 10; MSP and BS r_S = –0.01, p = 0.97, n = 12). These results indicate that egg sizes varied differently in the skua forms, even in MSP and BS where females belonged to the same species. Environmental factors explained 12% of egg size variation in SPS, with 11% from maritime sources: high SST and early ice break-up positively influenced egg size, whereas SIC had an adverse effect (Fig. 1A, Table 2). Local weather conditions were much less important for egg size. However, none of our environmental factors explained variation in egg size of BS or MSP (Fig. 1A, Table 2).

Clutch asymmetry varied significantly between years ($F_{11,561}$ = 21.04, p = 0.001) and there was also an interactive effect of skua form × year ($F_{18,561}$ = 2.98, p = 0.001). SPS laid more uniform clutches (0.992) than BS (0.975) or MSP (0.977), Tamhane post hoc *t*-test: SPS and BS: p = 0.001; SPS and MSP: p = 0.077; BS and MSP: p = 0.98 (Table 1). Moreover, clutch asymmetry was correlated between SPS and BS (r = 0.74, p = 0.04, n = 8), and even stronger between BS and MSP (r = 0.90, p = 0.001, n = 10). Clutch asymmetry was not related between SPS and MSP (r = 0.63, p = 0.07, n = 9).

Environmental factors explained between 23% (BS) and 38% (SPS) of the variation in clutch asymmetry in all skua forms, with a prominent role of marine factors

(Fig. 1B, Table 2). Generally, in years with low SIC and early ice break-up females laid more even clutches, irrespective of skua form. In contrast, SST was negatively related to clutch asymmetry for SPS, but positively related for BS and MSP. Local weather conditions explained 3.6, 0.4 and 2.3% of variation in clutch asymmetry in SPS, MSP and BS, respectively (Fig. 1B).

The mean hatching date varied across years and skua forms (year: $F_{12,612}$ = 15.85, p = 0.001; skua forms: $F_{2,612}$ = 4.43, p = 0.012; interaction year × forms: $F_{20,612}$ = 2.43, p = 0.001; GLM (general linear model) Type I sum of squares; see Table 1 for annual mean hatching dates). Annual mean hatching dates were not correlated between the skua forms (SPS and BS r = 0.42, p = 0.23, n = 10; SPS and MSP chicks r = 0.60, p = 0.07, n = 10; BS and MSP r = 0.59, p = 0.056, n = 11). Chicks of both SPS and MSP hatched within a shorter period (CV_{MSP} = 0.21 ± 0.12, CV_{SPS} = 0.23 ± 0.083, paired t-test: t_9 = −0.52, p = 0.62) than chicks from BS pairs (0.31 ± 0.08) (paired t-test of CVs BS – MSP: t_{10} = 3.82, p = 0.003; BS – SPS: t_9 = 3.51, p = 0.007). For both BS and SPS, chicks hatched earlier from larger eggs (SPS: r = −0.33, p = 0.001, n = 238; BS: r = −0.29, p = 0.001, n = 199), but not for MSP (r = −0.12, p = 0.29, n = 84).

Environmental factors explained 36% of hatching date variation in SPS, but only 14 and 10% in MSP and BS, respectively (Fig. 1C, Table 2). In particular, SPS chicks hatched earlier in years with high SST, little sea ice cover and early ice break-up. Less precipitation also favoured early hatching of SPS offspring. BS hatching dates were significantly delayed by extended sea ice cover, low temperatures, high wind speed and less precipitation. For MSP, late sea ice break-up and low precipitation delayed hatching (Fig. 1C, Table 2).

Chick growth and breeding success

Chick growth variation differed between the skua forms: whereas deviation from the mean growth trajectory

Table 1. *Catharacta maccormicki* and *Catharacta lonnbergi*. Reproductive parameters of south polar skua pairs, mixed species pairs and brown skua pairs at King George Island, 1984 to 2004. Egg size is given as volume of first egg (cm³) and breeding success as mean number of chicks fledged per nest. For calculation of clutch asymmetry (CA) and hatching date see 'Materials and methods'. All data for a particular year are annual means; Total range and General mean: minimum and maximum, and overall average, respectively

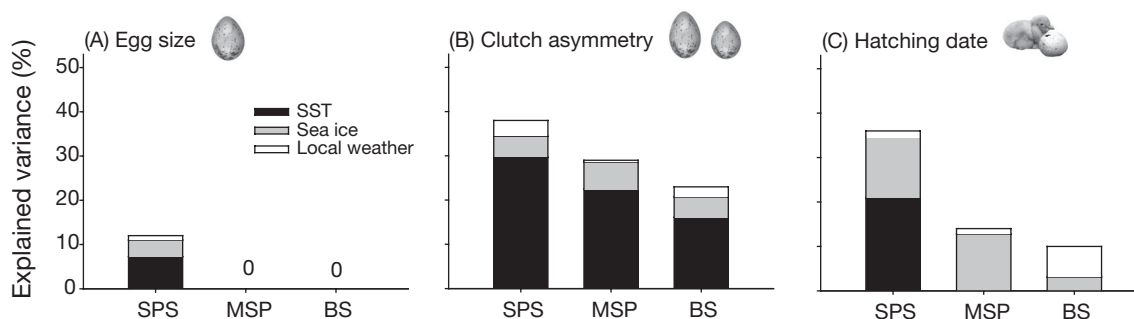| Year	South polar skua							Mixed species pairs							Brown skua						
	Egg size	n	CA	n	Hatch date	n	Breeding success	Egg size	n	CA	n	Hatch date	n	Breeding success	Egg size	n	CA	n	Hatch date	n	Breeding success
1984	82.8	7	0.958	3	44	7	1.23	91.2	3	0.994	3	38	3	1.00	100.3	2					1.27
1985	85.6	50	0.971	43	30	43	1.03	96.4	16	0.956	15	30	14	1.00	98.6	38	0.953	33	34	37	0.95
1987	83.5	4	0.949	4	32	6		94.0	4	0.964	3	46	2		95.0	22	0.969	21	38	7	
1988	86.9	8	0.959	7	31	5		92.2	1						97.7	11			43	8	
1993	82.4	27	0.972	19	32	23		91.9	7	0.996	5	34	7		98.5	17	0.966	15	24	16	
1994	88.6	43	0.941	36	31	32	0.53	96.2	12	0.933	10	31	11	0.50	97.3	28	0.950	24	32	19	0.87
1995					45	23						40	9						35	18	
1999								94.2	5	0.971	5	30	7	0.94	99.4	21	0.981	17	33	21	0.65
2000								94.5	17	1.010	13	38	13	0.94	98.1	29	0.985	24	29	21	0.70
2001	87.8	51	1.033	48	34	47	1.44	95.6	16	0.966	14	33	15	1.38	96.0	31	0.969	27	30	28	0.97
2002	87.2	63	1.041	59	31	50	0.30	96.2	14	1.044	11	27	9	0.36	98.2	34	1.032	28	28	27	0.34
2003	84.0	32	0.963	22	38	3	0.00	98.0	8	0.945	5	33	3	0.00	97.7	21	0.961	15	36	23	0.19
2004	81.1	44	0.966	24	51	38	0.62	91.4	4	0.950	3	43	5	0.60	90.0	7	0.964	4	41	12	0.57
Total range	64.7–107.7		0.760–1.159		11 Dec–17 Feb			78.7–112.8		0.839–1.111		5 Dec–29 Jan			77.9–123.7		0.873–1.105		6 Dec–8 Feb		
General mean	85.6	329	0.992	265	5 Jan	277	0.74	95.2		0.977		3 Jan		0.75	97.5		0.975		2 Jan		0.72

Fig. 1. *Catharacta maccormicki* and *Catharacta antarctica lonnbergi*. Proportion of variance explained by environmental factors in (A) egg size, (B) clutch asymmetry and (C) hatching date of Antarctic skuas. Each factor expressed as proportional absolute value of that factor's coefficient of total explained variance. SPS: south polar skua; MSP: mixed species pairs; BS: brown skua; SST: sea surface temperature; Sea ice: local and regional sea ice cover: Local weather: local conditions of air temperature, precipitation and wind speed

Table 2. *Catharacta maccormicki* and *Catharacta antarctica lonnbergi*. Results of multinomial linear regressions, comparing influence of environmental factors on egg size, clutch asymmetry and hatching date of south polar skuas (SPS), mixed species pairs (MSP) and brown skuas (BS) at King George Island during pre-incubation periods from 1984 to 2004. SST: sea surface temperature; SIC: sea ice cover extent at 60° W; Ice break-up: first month when Bransfield Strait was 50% free of sea ice; Temp: monthly mean of temperature; Prec: precipitation. R^2 and B: quality and slope of the multinomial regression, respectively

	R^2	F	p	df1	df2	Variable	B	t	p
Egg size									
SPS	0.12	9.16	0.001	5	328	SST	212.97	2.52	0.01
						SIC	54.00	4.41	0.001
						Ice break-up	–54.92	–4.89	0.001
						Temp	15.34	2.52	0.01
						Wind	13.79	2.62	0.01
MSP	0.09	0.77	0.38	1	105	–			
BS	0.07	1.23	0.27	1	260	–			
Clutch asymmetry									
SPS	0.38	53.94	0.001	3	264	SST	–0.25	–5.79	0.001
						SIC	–0.04	–8.59	0.001
						Temp	0.03	6.77	0.001
MSP	0.29	11.37	0.001	3	86	SST	0.11	2.17	0.033
						SIC	–0.03	–4.21	0.001
						Prec	0.002	5.23	0.001
BS	0.23	21.01	0.001	3	218	SST	0.07	2.55	0.012
						Ice break-up	–0.02	–4.98	0.001
						Prec	0.01	7.83	0.001
Hatching date									
SPS	0.36	30.20	0.001	5	276	SST	–37.27	–2.57	0.011
						SIC	–13.12	–7.43	0.001
						Ice break-up	11.13	8.04	0.001
						Prec	–0.42	–5.50	0.001
						Wind	2.16	1.87	0.06
MSP	0.14	7.88	0.001	2	97	Ice break-up	2.12	2.26	0.026
						Prec	–0.20	–3.57	0.001
BS	0.10	6.31	0.001	4	236	SIC	2.93	3.09	0.002
						Temp	–2.69	–2.51	0.013
						Prec	–0.24	–3.49	0.001
						Wind	3.61	2.66	0.008

differed between years in SPS ($F_{6,227}$ = 13.48, p = 0.001) and in MSP ($F_{8,104}$ = 3.26, p = 0.002), BS chicks grew more uniformly without significant inter-annual differences ($F_{8,256}$ = 1.54, p = 0.14; Table 3). The annual deviations of the skua forms were not correlated with each other (SPS and BS: r = –0.03, p = 0.96, n = 7; SPS and MSP: r = 0.32, p = 0.48, n = 7; BS and MSP: r = 0.55, p = 0.13; n = 9), indicating species-specific effects within a particular year. Chick growth differed between skua forms mainly in the early chick stage (Table 3), but these differences disappeared in the middle stage for BS and the late stage for MSP and SPS. In the late stage, only growth performances of BS and MSP chicks were related (r = 0.92, p = 0.004, n = 8; all others p > 0.05).

In the entire stage model, sea ice conditions and local weather explained 27 and 13% of variation in offspring growth in SPS and MSP, but none of the environmental factors contributed to chick growth variation in BS (Fig. 2A, Table 4). The decreasing model fit from SPS (r^2 = 0.27) to MPS (r^2 = 0.13) to BS (r^2 = 0.02) suggests a 2-fold larger influence of environmental factors on SPS than on MSP and almost nil on BS (Table 4). Chick growth for SPS and MSP was significantly delayed in years with extended sea ice, strong wind and precipitation (the latter for SPS only). Local temperatures and SST parameters did not contribute to variance in chick growth for any skua form (Fig. 2A).

Table 3. *Catharacta maccormicki* and *Catharacta antarctica lonnbergi*. Statistical comparison of annual deviation from average mass growth trajectory of chicks from south polar skua pairs (SPS), from mixed species pairs (MSP) and from brown skua pairs (BS). Chick period was subdivided into early stage (10 to 21 d), middle stage (22 to 33 d) and late chick stage (>33 d)

Chick stage	F	p	df1	df2
SPS				
Early	14.94	0.001	5	160
Middle	4.83	0.001	5	154
Late	0.78	0.56	5	105
MSP				
Early	4.68	0.001	7	89
Middle	2.89	0.01	7	82
Late	1.80	0.10	7	76
BS				
Early	2.02	0.04	8	216
Middle	0.64	0.72	7	187
Late	2.03	0.05	8	141

In the stage-specific models, the model fit decreased from early, to middle, to late stage (Table 4). In the early stage, the number of days with strong wind negatively influenced chick growth of SPS and MSP, whereas high SST and high precipitation facilitated chick development in both skua forms. In BS, high precipitation delayed chick growth significantly (Fig. 2B, Table 4). In later stages, the proportion of growth variation explained by environmental factors decreased to 0–16% in the middle stage and 0–14% in the late stage. In SPS and MSP regional sea ice cover and stormy days negatively influenced chick development in the middle but not in the late stages (Fig. 2C, Table 4). For BS, no additional variation in chick growth was explained in the middle and late chick stage, indicating relative independence of chick growth from environmental factors.

The breeding success of SPS and MSP varied between years without any trend (SPS: $r^2 = 0.27$, $F_{1,6} = 1.86$, p = 0.23; MSP: $r^2 = 0.14$, $F_{1,8} = 1.15$, p = 0.32), but complete breeding failure occurred in 2003 (Table 1). In contrast, breeding success of BS declined throughout the study period (linear regression $r^2 = 0.60$, $F_{1,8} = 10.40$, p = 0.015) at a rate of 0.034 chicks yr^{-1} (± 0.011 SE), but breeding never failed completely. The annual breeding success of all skua forms was correlated (SPS – BS: r = 0.88, p = 0.008, n = 7; SPS – MSP: r = 0.99, p = 0.001, n = 7; BS - MSP: r = 0.78, p = 0.014, n = 9) indicating common factors influencing breeding success.

When skuas forms were analysed separately, breeding success of SPS and BS was not correlated with any environmental factors (SPS: n = 7, BS: n = 9, all p > 0.05). For MSP, breeding success was negatively correlated with regional sea ice extent during the chick-rearing period (MSP: r = −0.72, p = 0.03, n = 9). When the data were pooled and corrected for skua form, breeding success was positively correlated with ambient temperatures in the pre-incubation period (partial correlation: r = 0.46, p = 0.02, df = 22) and with mean wind speed during chick growth (partial correlation: r = 0.50, p = 0.01, df = 22). Regional sea ice cover during chick growth was negatively correlated with total breeding success (partial correlation: r = −0.59, p = 0.002, df = 22).

DISCUSSION

The climate of the maritime Antarctic has warmed recently, especially during winter (Smith & Stammerjohn 2001), and has strongly influenced the marine
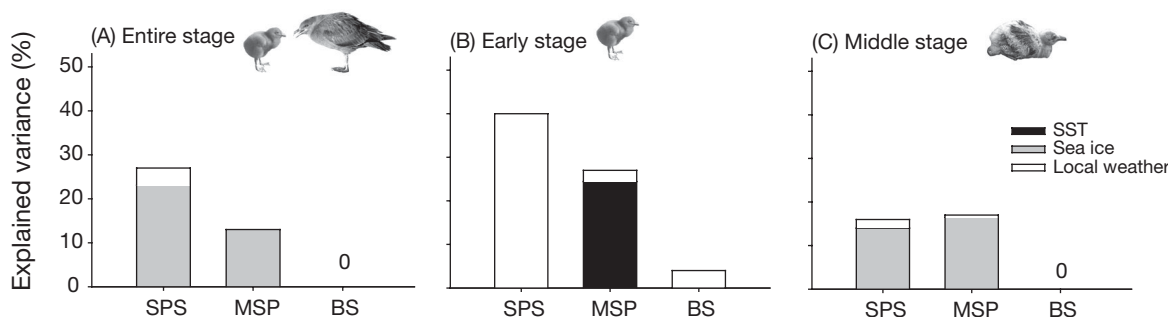

Fig. 2. *Catharacta maccormicki* and *Catharacta antarctica lonnbergi*. Proportion of variance in chick growth explained by environmental factors. (A) Entire stage model comprising entire chick growth period; (B) early stage model comprising data from 10 to 21 d old chicks; (C) middle stage model comprising data from 22 to 33 d old chicks. Each factor expressed as proportional absolute value of that factor's coefficient of total explained variance. SPS: south polar skua; MSP: mixed species pairs; BS: brown skua; SST: sea surface temperature; Sea ice: local and regional sea ice cover; Local weather: local air temperature, precipitation and wind speed

Table 4. *Catharacta maccormicki* and *Catharacta antarctica lonnbergi*. Results of multinomial linear regressions, comparing influence of environmental factors on chick growth of south polar skuas (SPS), mixed species pairs (MSP) and brown skuas (BS). Entire stage model included data of chicks from 10 d old to fledgling compared with general environmental conditions; fine-tuned models were calculated for 3 chick stages (early, middle and late) with environmental conditions adjusted to stage. SIC: sea ice cover anomaly at 60° W, Ice break-up: first month with 50% of Bransfield Strait free of sea ice; SST: sea surface temperature, Temp, Prec, Wind: means of temperatures, precipitation and wind speed, respectively; Wind n > 15: number of days with wind speed >15 m s^{-1}. R^2 and B: quality and the slope of the multinomial regression, respectively

	R^2	F	p	df1	df2	Variable	B	t	p
Entire stage model									
SPS	0.27	16.24	0.001	5	227	SIC	−33.97	−5.58	0.001
						Ice break-up	8.38	3.46	0.001
						Prec	−0.40	−2.59	0.01
						Wind	−6.77	−2.94	0.004
MSP	0.13	15.67	0.001	1	104	SIC	−25.67	−3.96	0.001
BS	0.02	2.14	0.12	2	256	–			
Fine-tuned models									
Early chick stage									
SPS	0.40	37.20	0.001	2	112	Prec	0.85	2.59	0.01
						Wind n > 15	−14.98	−8.58	0.001
MSP	0.27	13.00	0.001	2	72	SST	38.41	4.86	0.001
						Wind n > 15	−4.04	−2.06	0.043
BS	0.04	3.53	0.03	2	174	Prec	−0.23	−2.41	0.017
Middle chick stage									
SPS	0.16	6.29	0.001	3	99	SIC	−15.02	−2.96	0.004
						Prec	−0.15	−2.07	0.04
						Wind n > 15	−1.64	−2.36	0.02
MSP	0.17	3.96	0.012	3	63	SIC	−33.91	−3.45	0.001
						Prec	0.584	2.50	0.015
BS	0.004	0.59	0.44	1	135	–			
Late chick stage									
SPS	0.01	0.67	0.42	1	74	–			
MSP	0.14	2.34	0.07	4	61	–			
BS	0.03	3.44	0.07	1	120	–			

the same sites (but with differing foraging habits), the reproduction of skuas showed (1) species-specific annual variations, (2) species-specific effects of environmental factors on reproduction, and (3) different sensitivity to environmental factors at different stages of the breeding cycle.

Breeding parameters

Egg formation is nutritionally and energetically costly to female birds (Robbins 1981). Therefore, egg size is a useful index of food availability and/or female body reserves during egg development (Hiom et al. 1991, Ratcliffe et al. 1998). Egg size in all skua forms varied annually by 4.2 to 7.7%, with no correlation between the various forms, indicating that female condition (reflected by their ability to lay large eggs) differed between years due to variations in resource availability (e.g. in terms of body reserves or local food abundance). Additionally, the investigated factors affected first-egg size only in SPS. This species is very likely to use local marine food for first egg development, since 12% of its egg size variation was explained by oceanographic factors, whereby high SST and early local ice break-up favoured large first-eggs. Surprisingly, large eggs were also associated with extended regional sea ice cover, probably an indication of a link between winter ice cover and food availability in spring, as has been found to affect krill distribution in the region (Siegel 2000). In contrast, female BS and MSP developed at least their first egg unaffected by ambient conditions at the breeding site (none of the tested environmental factors explained egg size variations in both skua forms). Thus, these females either benefited from a continuously available and plentiful local resource (i.e. penguins) or employed (partly) a capital breeding strategy and synthesised eggs from resources accumulated elsewhere (Klaassen 2003).

A similar picture of a closer relation between female BS and MSP in comparison to SPS females was given by the analysis of clutch asymmetry as a proportional measure of size of the second egg. These findings were not unexpected, since females in BS and MSP associations belong to the same species and similar con-

ecosystem from the lowest to the highest trophic levels. For example phytoplankton communities were affected by the lowered sea water salinity arising from melting glaciers (Moline et al. 2004). Likewise, species-specific changes in population size of penguins were caused by decreasing winter sea ice and food availability (Smith et al. 1999, Fraser & Hofmann 2003). Thus, the impact of the current alterations in climatic conditions differed with respect to the focal species. The predictions of its effect (e.g. on reproduction success and population dynamics) highly depend on the relevant species sensitivity to a particular environmental factor (e.g. Guinet et al. 1998, Barbraud & Weimerskirch 2001, Jenouvrier et al. 2003).

In our study we assessed the species-specific reproductive performance of Antarctic skuas and determined the effect of oceanographic and climatic factors on their breeding parameters. Although breeding at

straints for egg development are very likely. However, the production of an equally sized second egg depended to a great extent on environmental conditions, which explained 23 to 38% of variance in clutch asymmetry across all skua forms. Therefore, females would seem to have used local resources for the production of their second egg (especially sources of marine origin, since oceanographic factors were of major importance: Fig. 1B).

Hatching dates varied greatly between years, ranging from the beginning of December until mid-February. Taking a 28 to 31d incubation period (Burton 1968), the laying period starts in November with BS laying first and SPS later in the season. Eggs of SPS and MSP hatched more synchronously than those of BS — probably a direct consequence of synchrony in arrival times. Assuming a similar selection pressure for early laying in Antarctic birds, as in northern hemisphere species (Price et al. 1988), the long laying/hatching period (>2 mo) suggests considerable variation in adult condition within each skua form. Likewise, we demonstrated a specific sensitivity to environmental factors: hatching for BS pairs was less influenced by environmental factors than that for MSP and SPS pairs, the latter being strongly affected by SST, followed by sea ice conditions, but with little effect of local weather conditions (Fig. 1C). High SST and little sea ice in the pre-breeding stage favoured early egg laying and hatching whereas low temperatures and a late ice break-up delayed hatching of the chicks.

Generally, SST had a marked influence in annual variation of breeding onset and egg size parameters in all skua forms, which might be explained via 2 pathways. First, higher SST in polar region was often associated with less sea ice cover (White & Peterson 1996) and therefore good food accessibility for offshore foragers. Second, higher SST in the study area can be caused by upwelling of circumpolar deep water in the western Antarctic Peninsula region (Jacobs & Comiso 1997, Smith et al. 1999). The nutrient-rich water masses replenish surface waters with nutrients and hence are assumed to trigger plankton production (Prézèlin et al. 2000, 2004). The main prey of SPS are the pelagic fish species *Electrona antarctica* and *Pleuragramma antarcticum* (K. Reinhardt unpubl. data). Both fish species are zooplankton feeders (DeWitt & Hopkins 1977). An upwelling of circumpolar deep water and hence increase of zooplankton, could be associated with higher abundance of these fish species. The time scale of such an hypothesised cascade from upwelling via enhanced primary production and zooplankton abundance, to increased fish abundance and food availability for top predators is not known. Moreover, the fish preyed upon by SPS are usually 3 to

6 yr old (K. Reinhardt unpubl. data). Their abundance in the skua foraging area is more likely the result of migration rather than local breeding, but relevant data are not yet available. Hence, a link between SST and fish availability remains speculative, but should be considered in future studies.

Chick growth and breeding success

Annual differences in food availability often lead to different chick growth rates, since the amount of food provided by the parents is an important condition for offspring growth in non-precocial birds. Generally, skuas prefer easily available terrestrial food; foraging in feeding territories within seabird colonies occurrs frequently (e.g. Pietz 1987, Hahn & Peter 2003) and can enhance offspring growth (Votier et al. 2004, S. Hahn unpubl. data). We found an almost uniform chick growth pattern in terrestrially feeding BS benefiting from an always available resource. Additionally, offspring development of MSP and SPS pairs varied greatly between years. Hence, chicks of offshore-foraging parents (SPS and partly MSP) were subjected to annually variable and unpredictable marine resources. Further support comes from the species-specific susceptibility to climate conditions: growth of BS offspring was independent of climatic conditions compared to that of in MSP and SPS chicks, which was affected by sea surface temperature, sea ice cover, local temperature and wind (Ainley et al. 1990, Ritz et al. 2005). This was particularly obvious in the early chick stage and (to a lesser degree) in the middle chick stage. The decreasing sensitivity of older chicks to ambient conditions might arise from a generally enhanced ability to cope with adverse conditions, but also through higher survival probabilities of chicks from high-quality parents (Hahn & Peter 2003). However, an additional reason might be the period and frequency of absence of the parents from the nest: BS fed in adjacent seabird colonies or from food washed ashore, SPS foraged offshore (Reinhardt 1997). Foraging trip lengths thus differed markedly, with short trips for BS and longer trips of several hours for SPS (Pietz 1986). SPS have to deal with variations in fish availability and accessibility due to sea ice cover (Young 1994), strengthened by bad weather conditions such as heavy storms, which make fishing difficult (Finney et al. 1999). In the absence of their parents, young chicks are exposed to chilling and starvation; more importantly, they have no protection against predation.

The general breeding success of BS declined over our study period, while that of MSP and SPS showed no such trend. Whether the decline in BS was caused by natural factors cannot yet be answered, since it par-

alleled the banning of open garbage dumps since 1996, a former plentiful food source for skuas (Reinhardt 1997). Additionally, short-term fluctuations with a 3 to 5 yr frequency are common in Antarctic seabirds (Jenouvrier et al. 2005) and were possibly not detectable within our study period. More importantly, BS were able to raise offspring in all years, whereas the breeding success of MSP and SPS varied greatly between years, with even complete breeding failure occurring (Ritz et al. 2006). Hence, SPS and MSP again were more susceptible to changes in environmental conditions than BS. Taking into account the variety of factors that differentially affect reproduction parameters, it is not surprising that no single factor determined breeding success in the skua forms. Only pooling of the data revealed a positive effect of high ambient temperature in the pre-breeding period indicating suitable spring conditions and a general negative effect of sea ice cover for chick growth. The positive effect of wind speed on successful breeding is probably explained by frequent westerly winds which ensure plankton drift through the Bransfield Strait and thus food availability for zooplankton feeders.

CONCLUSIONS

Antarctic skuas showed annual variation in reproduction parameters depending on skua form and breeding stage, with smallest variation in egg size and large variation in hatching dates and offspring growth performance. Since up to 40% of the variation could be explained by abiotic factors, the larger part is probably attributable to biological parameters like parental age, quality, or foraging skills. However, we verified a 2-fold dependence of skua reproduction on the Antarctic environment: (1) all skuas were more affected by oceanographic conditions, i.e. SST and sea ice, than by weather conditions, but the magnitude of impact varied between skua forms, with SPS being more influenced than BS, and MSP being intermediately influenced. (2) Reproduction parameters of the early breeding season were strongly affected by oceanographic factors, whereas later in offspring development the importance of local weather conditions, especially wind, increased. These findings imply contrasting effects of potential future climate change: a further increase in air temperatures together with earlier snowmelt and shortening of ice cover period will lead to more suitable conditions for foraging during the pre-breeding period and facilitate an earlier onset of breeding for all skuas. However, the expected higher frequency of adverse-weather periods (Turner et al. 1997) could lead to worsening conditions for chick growth. Our results suggest that the effect of future climate change on skuas in the maritime Antarctic will be more strongly mediated by changes in the marine food chain caused by sea ice cover (e.g. Loeb et al. 1997, Smith et al. 1999) and sea surface temperature alterations (Prézèlin et al. 2000) than by local weather conditions.

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