

Divergent responses of *Pygoscelis* penguins reveal a common environmental driver

Jefferson T. Hinke · Kasia Salwicka ·
Susan G. Trivelpiece · George M. Watters ·
Wayne Z. Trivelpiece

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Abstract The responses of predators to environmental variability in the Antarctic Peninsula region have exhibited divergent patterns owing to variation in the geographic settings of colonies and predator life-history strategies. Five breeding colonies of *Pygoscelis* penguins from King George Island and Livingston Island, South Shetland Islands, Antarctica, were examined to (1) compare the responses of sympatric congeners to recent changes in their Antarctic ecosystem and (2) assess underlying causes for such responses. We used linear regression and correlation analyses to compare indices of abundance, recruitment, and summer breeding performance of the Adélie (*P. adeliae*), gentoo (*P. papua*), and chinstrap penguins (*P. antarctica*). Breeding colonies of Adélie and chinstrap penguins have declined by roughly 50% since the mid-1970s, and recruitment indices of Adélie penguins have declined by roughly 80%, but no such patterns are evident for gentoo penguins. Fledging success, however, has remained stable at all breeding colonies. The different trends in abundance and

recruitment indices for each species, despite generally similar indices of summer performance, suggest that winter conditions contribute to the divergent responses among the penguins. In particular, strong correlations between indices of penguin and krill recruitment suggest that penguins in the South Shetland Islands may live under an increasingly krill-limited system that has disproportionate effects on the survival of juvenile birds.

Keywords Climate change · Ecosystem monitoring · Life history · Prey availability · Recruitment · Scotia sea · Sea ice · Survival · Winter

Introduction

Reduced sea ice coverage in the Antarctic Peninsula (AP) region during winter and consequent variability of Antarctic krill (*Euphausia superba*) densities (Murphy et al. 1995; Siegel and Loeb 1995; Loeb et al. 1997; Quentin and Ross 2003) have generated interest in understanding how krill-dependent predators have responded to changes in their ecosystem (Fraser et al. 1992; Smith et al. 1999; Forcada et al. 2006). Generally, the responses of different predators have depended on prevailing physical conditions at study sites (Smith et al. 1999; Wilson et al. 2001; Jenouvrier et al. 2006) and contrasting life-history strategies (Fraser et al. 1992; Croxall et al. 2002; Rombolá et al. 2003; Lynnes et al. 2004). Explanations of trends in predator abundance typically link reproductive performance or adult survival to indices of environmental variability (Trathan et al. 1996; Croxall et al. 1999; Jenouvrier et al. 2005). Other studies suggest that the survival of juveniles has strongly affected population responses (Wilson et al. 2001; Clarke et al. 2003). Here, we compare long-term data from *Pygoscelis*

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J. T. Hinke (✉) · S. G. Trivelpiece · W. Z. Trivelpiece
Antarctic Ecosystem Research Division,
Southwest Fisheries Science Center, National Oceanic
and Atmospheric Administration, La Jolla, CA 92037, USA
e-mail: Jefferson.Hinke@noaa.gov

W. Z. Trivelpiece
e-mail: Wayne.Trivelpiece@noaa.gov

K. Salwicka
Department of Antarctic Biology,
Polish Academy of Sciences, Warsaw 02141, Poland

G. M. Watters
Protected Resources Division, NOAA/SWFSC,
Pacific Grove, CA 93950, USA

penguins colonies in the South Shetland Islands and assess underlying causes of responses to recent changes in the AP ecosystem.

Pygoscelis penguins in the AP region have tended to exhibit species- and colony-specific responses to environmental variability (e.g. Forcada et al. 2006). For example, relative to the western AP, the reproductive success of gentoo penguins (*P. papua*) at South Georgia appears more variable, largely because ocean currents do not favor krill retention there (Croxall et al. 1999; Hofmann and Murphy 2004). Additionally, divergent responses of breeder abundance and breeding success have been attributed to different environmental conditions in the winter habitats used by the *Pygoscelis* penguins (Fraser et al. 1992; Trathan et al. 1996; Lynnes et al. 2004). During winter, Adélie penguins (*P. adeliae*) are obligate inhabitants of pack ice, chinstrap penguins (*P. antarctica*) use open water habitats (Fraser et al. 1992; Wilson et al. 1998; Trivelpiece et al. 2007), and gentoo penguins are non-migratory and remain near natal colonies year-round (e.g., Tanton et al. 2004). In the South Shetland Islands, the three *Pygoscelis* species maintain adjacent breeding colonies, thus allowing a comparison of responses by species that breed under similar conditions but inhabit largely different habitats during winter.

Our work is guided by two hypotheses that integrate variation in the AP ecosystem with penguin life histories and trends in breeder abundance. First, we hypothesize that shared environmental conditions and similar requirements for habitat and food resources during the breeding season (Trivelpiece et al. 1987) ought to result in similar indices of reproductive performance at each colony in the South Shetland Islands. Consequently, different trends of abundance or recruitment between species ought to arise mainly from processes that operate in their respective wintering habitats. Our second guiding hypothesis derives from a proposed mismatch between the sea ice cycle and the krill life cycle (Fraser and Hofmann 2003) whereby large recruitment events of krill are increasingly likely to be followed by multiple years of very low krill recruitment (see also Siegel 2005). Extended intervals with poor krill recruitment have affected reproductive output of krill-dependent predators, including fur seals (*Arctocephalus gazelle*), gentoo penguins, and black-browed albatross (*Thalassarche melanophrys*) at South Georgia (Reid and Croxall 2001) and may have contributed to abrupt declines in Adélie penguins in the western AP in the early 1990s (Fraser and Hofmann 2003). Thus, we hypothesize that changes in krill abundance that accrue from cumulative predation and other mortalities between large recruitment events alter the breeding success or survival of krill-dependent predator populations. We expect breeding performance and recruitment indices of *Pygoscelis* penguins to co-vary with krill recruitment. To explore these hypotheses, we examine

patterns in penguin breeder abundance, recruitment, and summer performance indices (explained below) in relation to an index of krill recruitment.

Methods

Study sites

All field studies were conducted from October to March on adjacent islands in the South Shetland Islands. All three *Pygoscelis* species breed at Admiralty Bay, King George Island (62°10'S, 58°30'W); only gentoo and chinstrap penguins breed at Cape Shirreff, Livingston Island (62°28'S, 60°46'W). The penguin colonies at Admiralty Bay and Cape Shirreff have been observed continuously since the 1977–1978 and 1996–1997 austral summers, respectively. All data were collected using standard methods defined by the Convention for the Conservation of Antarctic Living Marine Resources (CCAMLR) Ecosystem Monitoring Program (CCAMLR 2004). We review relevant methods below.

Breeding colony abundance

Breeding colony sizes were estimated by counting all occupied nests in each sub-colony 1 week after peak egg laying. Only sub-colonies with ≤ 500 nests were counted, and final abundance estimates required at least three independent counts within 5% of each other. For large Adélie sub-colonies (>500 nests), abundance was estimated by multiplying the area of the large nesting area by the mean nest density of smaller sub-colonies.

Recruitment

Recruitment was based on data of first-time recaptures (visual) of banded, known-age birds in their natal colony. At Admiralty Bay, banding of age 0+ chicks (i.e., chicks hatched the year of banding) began in 1980–1981 for gentoo and chinstrap penguins and 1 year later for Adélie penguins. In 1997–1998, banding began for gentoo and chinstrap penguins at Cape Shirreff. Each year, between 200 and 2000 age 0+ chicks were banded near the base of left flipper with a single, uniquely numbered metal band. Over the duration of the banding studies, either aluminum or stainless steel bands were used. Band loss rates differ for the two tag types, and were assumed to be 21 and 6% year⁻¹ for aluminum and stainless steel bands, respectively. The loss rate for aluminum bands was determined from unpublished data held by one of the authors (WZT), while the loss rate for stainless steel bands derives from the maximum loss rate reported for king penguins by Froget et al.

(1998). We assumed that band loss rates did not differ between penguin species.

We estimated two indices of recruitment to each breeding colony. The indices are year-specific ratios of the number of birds sighted for the first time relative to the potential number of un-sighted, banded birds remaining from (1) each cohort and (2) from all cohorts combined. Numbers of un-sighted birds were estimated by accounting for band loss and previously sighted birds. The first index, hereafter, “cohort recruitment,” measures the first-time returns from a single cohort over the life of that cohort. The second index, hereafter, “total recruitment,” measures the total first-time return of birds from multiple cohorts during a given year. We placed two restrictions on the age-at-first-return data prior to calculating the cohort and total recruitment indices. First, on average, 88% of first-time returns occurred during the first 3 years of a cohort’s life. Therefore, to ensure an adequate number of returns from a single cohort, we limited our analyses to cohorts for which at least 3 years of observations are available (cohorts that were tagged prior to 2002–2003). For total recruitment, the first year with three representative cohorts was 1984–1985 and 2000–2001 for Admiralty Bay and Cape Shirreff, respectively. Second, on average, 96% of first-time returns to natal colonies were observed by age 5+. Return rates from each older cohort typically accounted for <1% of total annual returns. Given the small contribution to annual recruitment by older individuals, we did not analyze recruitment of birds aged 6+ or older. Note that our indices of recruitment may include birds that are neither reproductively mature nor successful breeders.

Indices of breeding performance

Four indices of breeding performance (nesting success, fledgling mass, diet mass, and foraging trip durations by parents) were measured to assess colony-specific responses to local conditions during the breeding season. Nesting success was measured as the number of chicks successfully raised to the crèche stage per breeding pair. Annual estimates of nesting success were made from 20 replicate sets of five randomly selected nests (100 nests total) from each of the main sub-colonies. Each nest was observed daily to determine the presence and fate of each chick. Nesting success was not measured for chinstrap penguins at Admiralty Bay.

The mass of chicks at the time of fledgling was measured for 200–300 chicks per species per year. For Adélie and chinstrap penguins, the time of fledging was determined when chicks left their natal colonies and entered the sea. During this period, the beaches were swept two to three times daily, and chicks near the water were captured and weighed with spring scales to the nearest 50 g. Unlike Adélie

and chinstrap chicks, gentoo fledglings do not leave natal colonies 'en masse' (Williams 1990; Polito and Trivelpiece, in review). Therefore, the timing of fledging for gentoo chicks was defined to be 85 days after the date of peak egg laying by gentoo penguins. This period approximates the length of time from egg laying to fledging for Adélie and chinstrap penguins.

The times spent foraging by parent Adélie penguins at Admiralty Bay and chinstrap penguins at Cape Shirreff during both the brood and crèche stages were measured with radio telemetry. Twenty to forty penguins were tagged per year at each site. Radio transmitters were attached to each penguin using the method described by Croll et al. (1996). An onshore receiving station scanned for the presence of transmitters every 15 min. We considered birds that were absent from the beach for more than 1 h to be on foraging trips.

Diet samples were collected from parent penguins throughout the rearing season. Diets were collected only after a parent returned from a foraging trip and established contact with its chick. Once contact was established, but before the stomach contents were transferred, the parent was captured and a diet sample was collected by gastric lavage (Wilson 1984). Diet samples were typically collected from four to five individuals and replicated on 5- to 8-day intervals, resulting in 20–40 collections per colony per year. The individual diets were weighed for total wet mass and sorted to identify all contents. From each diet, 50 whole krill were measured for total length to the nearest 1 mm.

Statistical analysis

We used simple linear regressions to test for the presence of trends in abundance, recruitment, and summer performance. We also computed correlations between these indices using Pearson product-moment correlations. To compare recruitment indices with krill lengths (from the diet samples), we also calculated correlation coefficients at lags ranging from +3 to –3 years, the range of ages within which the majority of juvenile penguins first return to natal colonies. Correlations at negative lags suggest that the recruitment of penguins was related to krill sizes in the past, while positive lags suggest that penguin recruitment was related to krill sizes in the future. To compare krill sizes with the indices of breeding performance, we calculated correlations at lag 0 only. For the graphical display, the summer performance indices were normalized to have a mean of 0 and a standard deviation of 1 (standard normal deviates). The data used for our analyses are available from the one of the authors (WZT) upon request.

Note that some of the time series analyzed here are relatively short (<10 years) and often contain years with missing

observations. Thus, interpretation of the reported trends and correlations should be viewed cautiously. To account for multiple comparisons in our correlation analyses, we also use Bonferroni corrections for significance reporting; however, our interpretation of the results relies on the bulk direction and magnitude of each group of correlations, and not entirely on the statistical significance of individual correlations. Finally, we note that many of the data series may be better modeled with non-linear or step-change models. However, our main emphasis is to compare trends across species, and we contend that the simple linear regressions and correlative analyses adequately capture the basic patterns within these data.

Results

Breeding colony abundances

The abundance of breeding Adélie and chinstrap penguins declined at both study sites; this was not the case for gentoo penguins. At Admiralty Bay, declines in the abundances of both Adélie (-182 pairs year $^{-1}$, $F_{1,25} = 40.7$, $P < 0.01$) and chinstrap (-132 pairs year $^{-1}$, $F_{1,25} = 167$, $P < 0.01$) penguins began in the early 1980s (Fig. 1). The abundance of chinstrap penguins at Cape Shirreff has declined since the late 1990s (-418 pairs year $^{-1}$, $F_{1,6} = 58.5$, $P < 0.01$) (Fig. 1), with a rate of decrease similar to that observed for Adélie penguins at Admiralty Bay during this period (Fig. 1). There were no trends in the abundances of gentoo penguins at Admiralty Bay (-9 year $^{-1}$, $F_{1,25} = 0.89$, $P = 0.36$) and Cape Shirreff (-13 year $^{-1}$, $F_{1,6} = 0.61$, $P = 0.46$).

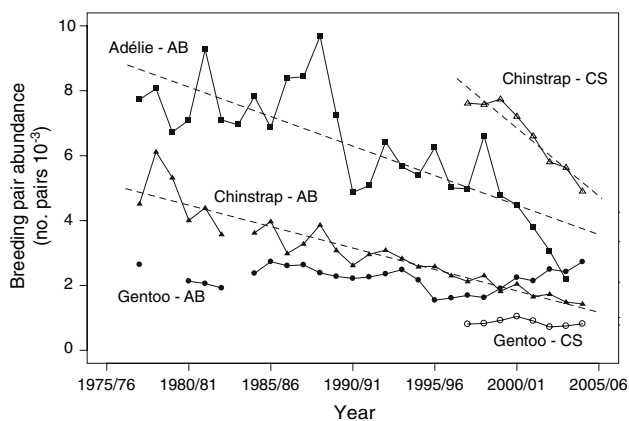


Fig. 1 Number of breeding pairs of Adélie (filled square), gentoo (filled and open circles) and chinstrap (filled and open triangles) penguins at Admiralty Bay (AB, filled symbols), King George Island and Cape Shirreff (CS, open symbols) Livingston Island, South Shetland Islands, Antarctica from 1977 to 2004. Linear regressions with significant, non-zero slopes are plotted as dashed lines

Recruitment indices

Patterns in cohort recruitment were complex (Fig. 2). On average, cohort recruitment of Adélie penguins at Admiralty Bay declined over the study period ($F_{1,19} = 65.3$, $P < 0.01$), with a peak recruitment from the 1984–1985 cohort and minima from the 1998–1999 and 2000–2001 cohorts. Cohort recruitment of chinstrap penguins at Admiralty Bay increased during the early 1980s, peaked in 1985–1986, and declined thereafter (at a rate similar to that for Adélie penguins). Nevertheless, there was not an overall trend in cohort recruitment of chinstrap penguins at Admiralty Bay ($F_{1,10} = 1.96$, $P = 0.2$). Cohort recruitment of gentoo penguins at Admiralty Bay did not trend ($F_{1,20} = 0.04$, $P = 0.84$), but large cohorts were recruited in 1983–1984 and 1998–1999 (Fig. 2). Cohort recruitments of all three species at Admiralty Bay were uncorrelated (Table 1). Cohort recruitment of chinstrap penguins at Cape Shirreff did not trend ($F_{1,4} = 0.18$, $P = 0.7$, Fig. 2), but was positively correlated with that of Adélie penguins at Admiralty Bay ($r = 0.82$, $t_4 = 2.9$, $P = 0.05$; Table 1). Similarly, cohort recruitment of gentoo penguins at Cape Shirreff did not trend ($F_{1,3} = 0.6$, $P = 0.5$; Fig. 2) but was positively correlated with gentoo recruitment at Admiralty Bay ($r = 0.61$, $t_3 = 1.3$, $P = 0.28$; Table 1).

Patterns in total recruitment were simpler. Total recruitment of Adélie penguins at Admiralty Bay declined significantly ($F_{1,19} = 19.8$, $P < 0.01$), with the largest change occurring between 1988–1989 and 1990–1991 (Fig. 2). Total recruitment at all other penguin colonies did not trend (Fig. 2). Total recruitments of gentoo penguins at both study sites were positively correlated ($r = 0.89$, $t_3 = 3.2$, $P = 0.05$; Table 1), owing to strong returns in 2000–2001 and 2002–2003 (Fig. 2). There were no other notable correlations in total recruitment (Table 1).

Indices of breeding performance

Patterns in fledging rates, fledgling masses, and indices of parental provisioning to chicks were similar for Adélie and chinstrap penguins but often different for gentoo penguins. The number of chicks fledged per nest increased for gentoo penguins at Admiralty Bay ($F_{1,22} = 13.9$, $P < 0.01$), but there was no evidence of such trends at all other colonies (Fig. 3). Nevertheless, fledging rates at all colonies were positively correlated, suggesting that annual effects on reproductive performance were similar across species (Table 2). Fledgling masses declined at all colonies, with strong trends at Admiralty Bay for Adélie ($F_{1,22} = 28.6$, $P < 0.01$) and chinstrap ($F_{1,12} = 7.1$, $P = 0.02$) penguins and at Cape Shirreff for chinstraps ($F_{1,7} = 11.4$, $P = 0.01$, Fig. 3). Apparent declines in gentoo fledgling masses were not significant at Admiralty Bay ($F_{1,6} = 0.5$, $P = 0.5$) and

Fig. 2 Cohort and total recruitment based on first-time sightings of banded birds in their natal colony for Adélie, gentoo, and chinstrap penguin colonies at Admiralty Bay and gentoo and chinstrap penguin colonies at Cape Shirreff. Cohort recruitment indices indicate recruitment from an individual cohort. Total recruitment indices indicate recruitment from multiple cohorts in single year. Linear regressions with significant, non-zero slopes are plotted as dashed lines

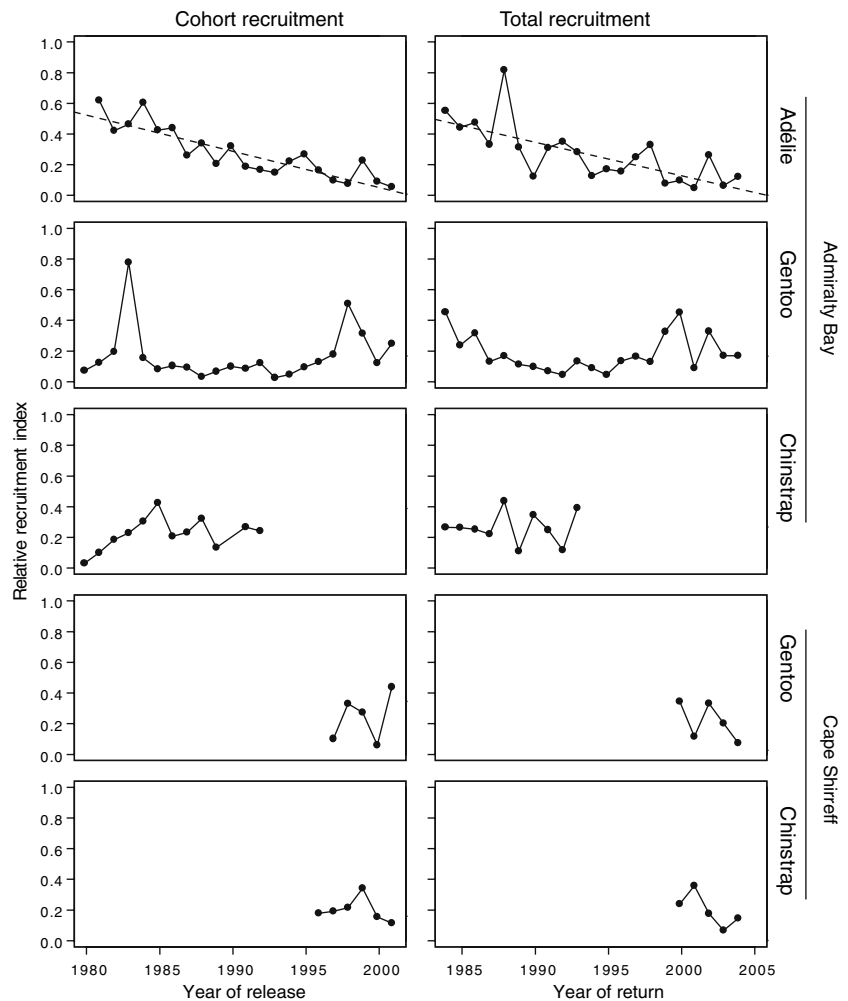


Table 1 Pair-wise correlation coefficients (*r*) of recruitment for five penguin colonies in the South Shetland Islands

Field site	Species	Admiralty Bay			Cape Shirreff	
		Adélie	Gentoo	Chinstrap	Gentoo	Chinstrap
Admiralty Bay	Adélie	–	0.05	–0.04	–0.11	0.82 ^a
	Gentoo	0.16	–	–0.01	0.61	0.39
	Chinstrap	0.33	0.15	–	NA	NA
Cape Shirreff	Gentoo	0.51	0.89 ^a	NA	–	–0.04
	Chinstrap	–0.22	–0.07	NA	–0.07	–

Values above the diagonal are the correlation coefficients for the cohort recruitment indices. The values below the diagonal are correlation coefficients for the total recruitment indices. Correlations followed by an “a” are significant at the $\alpha = 0.05$ level. Correlations that could not be determined because of non-overlapping time series are denoted by NA

Cape Shirreff ($F_{1,6} = 1.1$, $P = 0.33$). Fledging masses of Adélie and chinstrap penguins at Admiralty Bay were positively correlated ($r = 0.73$, $t_{12} = 3.7$, $P < 0.01$; Table 2). Fledging masses of gentoo penguins were positively correlated with those of chinstrap but not Adélie penguins (Table 2). There were no trends in total diet masses (Fig. 3), but diet masses at all colonies were positively correlated (Table 2). Similarly, there were no trends in foraging trip

durations for Adélie penguins at Admiralty Bay and chinstrap penguins at Cape Shirreff (Fig. 3), but trip durations during the brood and crèche periods were positively correlated across species and colonies (Table 3).

In all years, the diet of each species at each colony was dominated by krill. Krill comprised 98, 96, and 94%, respectively, of Adélie, chinstrap, and gentoo diet mass at Admiralty Bay, and 99 and 70%, respectively, of chin-

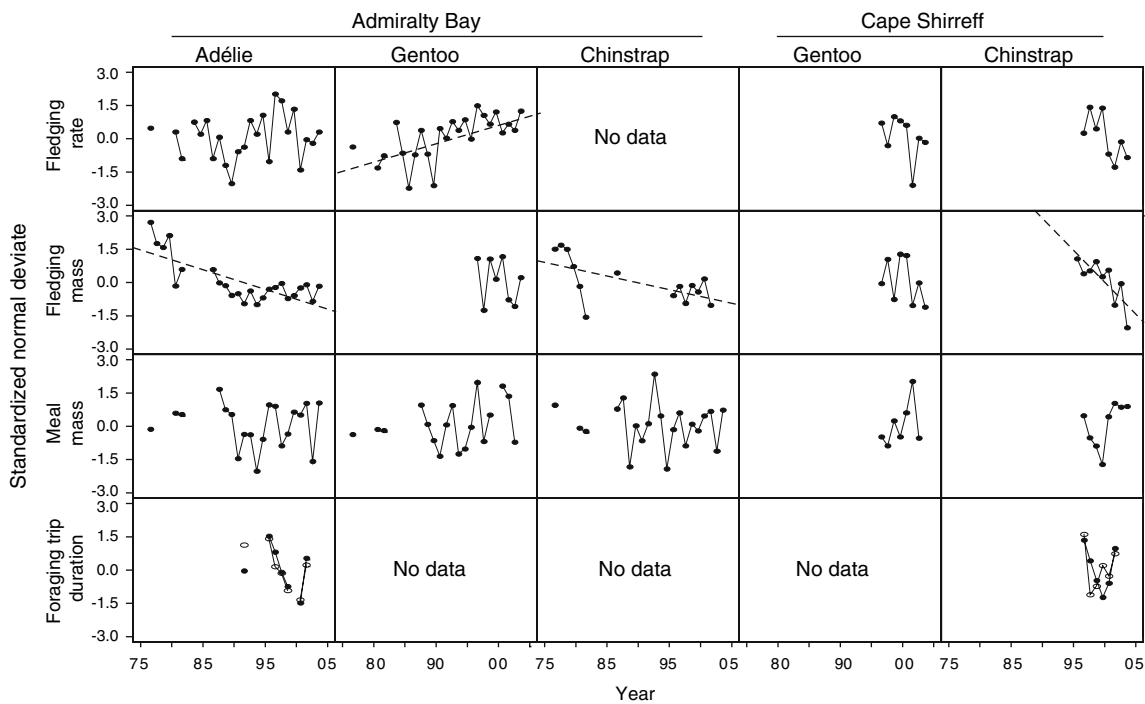


Fig. 3 Standardized normal deviates (mean = 0, SD = 1) for summer performance indices of mean fledging rates, fledgling mass, meal mass, and foraging trip durations from the brood (filled circle) and crèche (open circle) stages of Adélie, gentoo, and chinstrap penguins at Admi-

rality Bay and Cape Shirreff from 1977 to 2004. Years are abbreviated to the final two digits. *No data* indicates that data necessary to compute this index were not collected. Linear regressions with significant, non-zero slopes are plotted as *dashed lines*

Table 2 Pair-wise correlation coefficients (*r*) for the indices of fledging rates, fledgling masses, and diet masses for five *Pygoscelis* penguin colonies in the South Shetland Islands

Index	Location	Species	Admiralty Bay		Cape Shirreff	
			Adélie	Gentoo	Chinstrap	Gentoo
Fledging rate	Admiralty Bay	Gentoo	0.53 ^b			
		Chinstrap	NA	NA		
	Cape Shirreff	Gentoo	0.14	0.14	NA	
		Chinstrap	0.69	0.40	NA	0.52
Fledging mass	Admiralty Bay	Gentoo	-0.08			
		Chinstrap	0.73 ^b	0.95 ^b		
	Cape Shirreff	Gentoo	0	0	0.23	
		Chinstrap	-0.30	0.27	0.52	0.60
Diet mass	Admiralty Bay	Gentoo	0.67 ^b			
		Chinstrap	0.26	0.54 ^a		
	Cape Shirreff	Gentoo	0.53	0.52	0.67	
		Chinstrap	0.13	0.31	0.31	0.45

Correlations followed by an “a” are significant at the $\alpha = 0.05$ level and those followed by a “b” are significant using Bonferroni corrections. Correlations that could not be calculated because of missing data are denoted by NA

strap and gentoo penguins diet mass at Cape Shirreff. Various fish, amphipod, and other Euphausiid species comprised the remainder of the diet (data not shown). We focus the remainder of our analysis on the primary diet item, krill. The mean length of krill in the diets of breeding penguins was cyclical, with diets from all five penguin colonies showing maxima in 1995–1996 and 2000–2001 followed by minima 1–2 years later (Fig. I4). Few indices of breeding performance were correlated with the

mean sizes of krill in the diet (Table 4). Fledging rates and fledgling masses at all colonies showed neither consistent nor strong correlations with krill sizes (Table 4). Diet masses delivered to chicks of all penguin species were negatively correlated with mean krill sizes (Table 4), significantly so for gentoo penguins at Admiralty Bay ($r = -0.76$, $t_{11} = -4.0$, $P < 0.01$). Foraging trip durations were negatively related to mean krill sizes (Table 4).

Table 3 Pair-wise correlation coefficients (*r*) for the indices of foraging trip durations for Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis Antarctica*) penguin colonies at Admiralty Bay and Cape Shirreff, respectively

Location	Species	Adélie		Chinstrap	
		Trip	Brood	crèche	Brood
Admiralty Bay	Adélie	Crèche	0.84 ^a		
Cape Shirreff	Chinstrap	Brood	0.97 ^b	0.96 ^a	
		Crèche	0.67	0.55	0.53

Correlations followed by an “a” are significant at the $\alpha = 0.05$ level and those followed by a “b” are significant using Bonferroni corrections

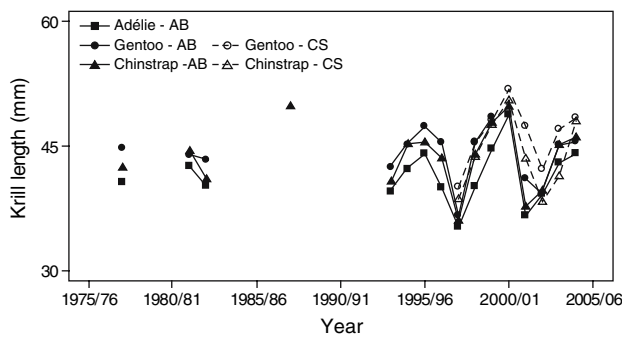


Fig. 4 Mean length of krill in the diets of parent Adélie, gentoo, and chinstrap penguins at Admiralty Bay (AB) and Cape Shirreff (CS) from 1977 to 2004

Table 4 Pearson product-moment correlation coefficients for the mean size of krill in penguin diets and fledging rate, fledge mass, meal mass, and foraging trip duration (FTD) during brood and crèche periods, respectively, for each of five penguin colonies in the South Shetland Islands

Field site	Species	Fledge rate	Fledge mass	Meal mass	FTD brood	FTD crèche
Admiralty Bay	Adélie	0.16	-0.25	-0.19	-0.13	-0.07
	Gentoo	-0.15	-0.19	-0.76 ^b	NA	NA
	Chinstrap	NA	0.13	-0.28	NA	NA
Cape Shirreff	Gentoo	0.42	0.32	-0.26	NA	NA
	Chinstrap	0.43	0.01	-0.69	-0.92 ^b	-0.56

Correlations followed by a “b” are significant using Bonferroni corrections. Correlations that could not be determined because of missing time series are denoted by NA

Mean sizes of krill in the diet were more related to recruitment (Table 5). At Admiralty Bay, cohort recruitment of Adélie penguins increased when small krill were abundant in diets 2 years after the birds fledged ($r_{lag+2} = -0.76$, $t_9 = -3.5$, $P < 0.01$; Table 5). Furthermore, total recruitment of Adélie penguins tended to increase 1 year after small krill became available as prey ($r_{lag-1} = -0.69$, $t_9 = -2.8$, $P = 0.02$). Cohort recruitment of

gentoo penguins at Admiralty Bay increased when small krill were abundant in diets 1 year before the birds fledged ($r_{lag-1} = -0.88$, $t_4 = -3.7$, $P = 0.02$; Table 5), but total recruitment at this site appeared to be independent of mean krill size (Table 5). At Cape Shirreff, cohort recruitment of gentoo penguins was independent of krill size at all lags, while total recruitment was higher in years when small krill were available ($r_{lag 0} = -0.95$, $t_2 = -4.4$, $P = 0.05$; Table 5). In contrast with all other colonies, the recruitment of chinstrap penguins at Cape Shirreff exhibited strong positive correlations with mean krill sizes (Table 5). Cohort recruitment of chinstrap penguins was relatively higher from cohorts fledged 1 year prior to maxima in the mean size of krill ($r_{lag +1} = 0.86$, $t_4 = 3.4$, $P = 0.03$), while total recruitment was highest 1 year after large krill occurred in the diet ($r_{lag-1} = 0.98$, $t_3 = 9.2$, $P < 0.01$).

Discussion

Atmospheric warming and consequent changes in sea ice conditions in the AP region (Vaughan et al. 2001) have been hypothesized to differentially affect predator populations due to different predator life-history strategies (Fraser et al. 1992; Trathan et al. 1996; Smith et al. 1999; Croxall et al. 2002) and substantially altered krill recruitment dynamics (Siegel and Loeb 1995; Fraser and Hofmann 2003). Our results support these hypotheses and further suggest that environmental effects on the recruitment of juvenile penguins to natal colonies may shape the recent trends in abundance of the *Pygoscelis* penguins in the South Shetland Islands. In general, the different patterns of abundance and recruitment for each species, despite positively correlated, non-negative trends in fledging rates at all five colonies, point to species-specific vulnerabilities during winter that contribute to differential recruitment rates. The evidence suggests that recruitment of juvenile penguins varied with respect to krill recruitment in ways that are aligned closely with the respective life-history strategies of the *Pygoscelis* penguins. We explore these connections below.

During the summer breeding season, *Pygoscelis* penguins are dependent on local food resources for the daily provisioning of chicks. With respect to the marine environment, colonies are thought to be located where local oceanic circulation or bathymetry concentrates food and promotes access to foraging areas (Fraser and Trivelpiece 1996; Trivelpiece and Fraser 1996). Such features would help provide a stable environment for provisioning chicks. The summer performance indices provide four lines of evidence that conditions at the shared colonies had similar effects on each penguin species. First, fledging rates at all colonies were positively correlated. Second, chick masses

Table 5 Pearson product-moment correlation coefficients (r) for the mean size of krill in penguin diets and the indices of cohort and total recruitment, respectively, for each of four penguin colonies in the South Shetland Islands

Lag	Admiralty Bay				Cape Shirreff			
	Adélie		Gentoo		Gentoo		Chinstrap	
	Cohort	Total	Cohort	Total	Cohort	Total	Cohort	Total
3	-0.41	0.07	-0.29	0.17	-0.24	NA	-0.65	NA
2	-0.76 ^b	0.53	-0.11	-0.25	0.53	NA	0.29	-0.53
1	0.31	-0.02	0.20	-0.16	-0.24	0.66	0.86 ^a	-0.90
0	0.41	-0.43	0.08	-0.12	0.03	-0.95 ^a	0.18	0.21
-1	-0.20	-0.68 ^a	-0.88 ^a	0.29	0.08	-0.27	-0.57	0.98 ^b
-2	-0.64	0.44	-0.22	-0.31	0.26	0.87	-0.96	0.39
-3	-0.13	0.29	0.72	-0.46	NA	0.36	NA	-0.60

Correlations followed by an “a” are significant at the $\alpha = 0.05$ level and those followed by a “b” are significant using Bonferroni corrections. The lags for which insufficient data were available to measure correlations are denoted by NA. No comparison could be made for chinstrap penguins at Admiralty Bay because of non-overlapping time series

tended to decline for all species, albeit weakly for gentoo penguins. Third, food mass delivery to chicks was positively correlated at all colonies. Fourth, the mean size of krill ingested by birds at each colony was similar. Thus, these shared responses to summer conditions suggest that the observed differences in abundance and recruitment of the *Pygoscelis* penguins appear to be related to events that occur after the breeding season, i.e., winter.

Wintertime events that could lead to the different patterns in the abundance and recruitment of penguins at Admiralty Bay and Cape Shirreff could include emigration to different breeding areas, an increased frequency of decisions by adult penguins to not breed, or increased mortality rates. A lack of evidence for the former two hypotheses, discussed below, suggests that increased mortality may be the most important component of the observed demographic trends in the South Shetland Islands.

Emigration would tend to reduce colony size and recruitment rates at natal colonies, but we argue that emigration is unlikely to be an important driver in our data on two grounds. First, we have observed less than 1% emigration rates for any of our penguin species between two adjacent (<3 km), three-species colonies in Admiralty Bay that have been continuously monitored for 30 years. We regard the near-absence of movement of animals between adjacent colonies as evidence for strong site fidelity among these penguins. Further, we have no evidence to suggest that penguins from either of these monitored colonies in Admiralty Bay have moved to more distant colonies on King George Island, despite active seabird research at several of the penguin breeding colonies in this area for over two decades. Second, our data indicate that the current colonies continue to support successful breeding, and it is unclear why successful colonies would be abandoned. Recent evidence for the abandonment of natal colonies among penguins is

linked to acute disturbances such as mega-icebergs that preclude access to the colony (Kooyman et al. 2007; Shepherd et al. 2005); no such events have occurred at our study colonies. Thus, the role of emigration in the observed trends at our study colonies appears to be negligible.

The decision for penguins to breed in a given year can also be related to body condition prior to the breeding season (Trivelpiece et al. 1990; Vleck and Vleck 2002). If the resources necessary to prepare for egg laying and fasting during the incubation period are insufficient, penguins may be physiologically unable to initiate or complete a clutch. For Adélie penguins, Vleck and Vleck (2002) noted that the body mass of females that did not breed was about 90% of the mass of successful breeders. Our data cannot assess pre-breeding body condition directly, but the observed maintenance of breeding success at all colonies suggests that most adult birds remain able to fulfill their energetic requirements during winter, enabling the initiation and completion of the subsequent breeding cycle. Therefore, food availability during winter appears to have had little effect on breeding success in our study, supporting the hypothesis that winter conditions disproportionately affect juvenile penguins.

Inference from the available evidence suggests that variation in over-winter mortality rates of juveniles may provide the best explanation for the long-term patterns in breeder abundances of the *Pygoscelis* penguins at Admiralty Bay and Cape Shirreff. Increased mortality of penguins could arise directly from increased rates of predation. Leopard seals (*Hydrurga leptonyx*) are an important source of mortality at some penguin colonies (Ainely et al. 2005), and leopard seals are present at our study colonies. However, whether leopard seals preferentially hunt specific penguin species during the fledging period or if species-specific predation rates have changed is unknown. It would

thus be difficult to assess the effect of leopard seals on observed demographic trends. Therefore, based on the relationships between penguin and krill recruitment, we suggest that differential mortality among juveniles during winter may derive primarily from species-specific vulnerabilities to krill availability. These vulnerabilities may arise from at least three related causes during two winter phases. We define the first winter phase as the period during and immediately following the transition to independence for juveniles. During this phase provisioning by adults ceases, and fledgling chicks must begin feeding themselves while en route to their respective wintering habitats. The second phase occurs during the winter proper when the three species inhabit different habitats.

During the first winter phase, reduced fledgling masses and different fledging behaviors among the *Pygoscelis* penguins may have contributed to different responses in mortality rates among the juveniles. It appears reasonable to assume that the negative trend in fledgling masses observed at the study sites has resulted in reduced body conditions that may either limit the ability of juvenile penguins to successfully forage independently or decrease the amount of time available to locate and consume reliable food resources to avoid starvation (e.g., Chappell et al. 1993; Moreno et al. 1999). Second, Adélie and chinstrap chicks typically abandon their natal colonies in small groups over a short time frame (approx. 1 week) and must find suitable food resources without prior foraging experience. Fledgling gentoo penguins, in contrast, exhibit an extended transitional period to independence that can last up to 3 weeks. During this time, gentoo chicks may make repeated trips to sea while continuing to receive supplemental provisions from their parents (Williams 1990; Polito and Trivelpiece, in review). Such supplemental provisioning during a period when fledglings may learn where and how to forage near their natal colony may confer an advantage on juvenile gentoo survival that their migratory congeners lack (Polito and Trivelpiece, in review).

Our results support the links between krill availability, fledgling mass, and fledgling behavior identified above. The potential effects of reduced fledgling masses and the sharp transition to independence for the migratory *Pygoscelis* penguins is most evident for the Adélie penguins, where fledgling mass, recruitment rates, and breeder abundance have declined in parallel since the early 1980s. For the chinstrap penguins, the supporting evidence is weaker, but nonetheless corroborated by declines in fledgling mass and breeder abundance, and the similar patterns of cohort recruitment for Adélie and chinstrap penguins. The responses in the gentoo colonies also support this hypothesis: chick masses, recruitment, and breeder abundance have not declined. Thus, the first few weeks of independence for fledgling Adélie and chinstrap penguins represent a potential bottleneck to recruitment.

Juvenile mortality may be further influenced by krill availability in the different habitats that *Pygoscelis* penguins use during the second winter phase. The extent to which penguin mortality is linked to krill availability depends on the composition of penguin diets. Studies conducted during the breeding season at our study colonies indicate that krill is the primary food source (>86% by mass) for all three *Pygoscelis* species (Volkman et al. 1980; Trivelpiece et al. 1987) and that these percentages have remained similarly high at both study colonies to the present. The winter composition of penguin diets from our study colonies is unknown. The available winter diet studies from other areas in the AP region indicate that *Pygoscelis* diets often contain relatively larger proportions of non-krill prey (e.g. fish, cephalopods, and other crustaceans) than during summer, but krill remain a sizable fraction of the diet. For example, Ainley et al. (1992) reported that Adélie penguin diets in the Weddell Sea contained 28% krill by mass and 98% krill by number. A study of gentoo diets during the autumn months (April–June) at Laurie Island, South Orkney Islands reported that diet composition varied inter-annually, and krill accounted for between 20 and 70% of the winter diet mass (Coria et al. 2000). Similarly, Williams (1991) and Berrow et al. (1999) reported that krill represented between 40 and 90% of diet mass among gentoo penguins during the winter at Bird Island, South Georgia. To the best of our knowledge, winter diets of chinstrap penguins have not been published. As a whole, however, the above studies do suggest that krill are an important diet item for the *Pygoscelis* penguins during winter. Furthermore, given the observed relationships between penguin and krill recruitment, it follows reasonably that changes in krill availability could affect juvenile mortality during winter.

Given that gentoo penguins remain near natal colonies throughout the year (e.g., Tanton et al. 2004), the relative stability of abundance and recruitment suggest that local krill resources have remained sufficiently stable year-round to maintain long-term stability in the gentoo colonies. However, regional declines in krill biomass and the large variability in krill recruitment in the AP region (Siegel and Loeb 1995; Loeb et al. 1997; Fraser and Hofmann 2003) suggest that krill availability may affect the mortality of the juvenile migratory *Pygoscelis* penguins during winter. In particular, the correlations between krill sizes and penguin recruitment suggest that the Adélie and chinstrap penguins have habitat-specific vulnerabilities to krill availability during winter. Adélie penguins tended to exhibit their strongest recruitment in relation to the availability of the smallest krill sizes, while chinstrap recruitment peaked in association with the largest krill. Typically, juvenile krill occur in ice-covered areas, where Adélie penguins also spend the winter. The open water distribution of chinstrap

penguins during winter (Ainley et al. 1992), however, would reduce their encounter rates with juvenile krill. Thus, the correlations between penguin recruitment and krill sizes in our data are consistent with the winter distributions of krill life-stages and the *Pygoscelis* penguins. However, in either a pack ice or pelagic habitat, an overall decline in krill density or an increased interval between the recruitment of a large cohort of krill (Siegel 2005) would tend to reduce encounter rates between penguins and krill (Fraser and Hofmann 2003; Lynnes et al. 2004). We suggest that a reduction in krill availability would increase penguin mortality during the winter. The similar patterns in recruitment of Adélie and chinstrap penguins are consistent with this hypothesis.

The role of krill recruitment on juvenile mortality among the *Pygoscelis* penguins emerges as an extension to the hypothesis of direct winter sea-ice effects on penguin abundances. Based on habitat segregation during winter, sea-ice conditions were thought to have opposite effects on the abundance of Adélie and chinstrap penguins (Fraser et al. 1992), whereby a reduction in sea-ice extent would favor the population growth rates of chinstrap penguins over Adélie penguins. However, concurrent declines in breeder abundance of Adélie and chinstrap penguins observed in the South Shetland Islands (this study) and the South Orkney Islands (Forcada et al. 2006) suggest that ice dynamics are insufficient to explain these trends alone. Fraser and Hofmann (2003) proposed that variability in the frequency of large krill recruitment events play an increasingly important role in shaping the responses of krill-dependent predators to environmental changes in the AP ecosystem, and the results from our study and others in the AP region support this view (Reid and Croxall 2001; Lynnes et al. 2004). In particular, we report evidence that the timing of large recruitment events of krill is correlated with the recruitment rates of juvenile penguins. Thus, we suggest that changes in sea-ice extent can have opposite effects on the abundance trends of a given *Pygoscelis* species (Smith et al. 1999) whereby the direction of the trend depends on the recruitment dynamics of krill. For example, a reduction in sea-ice extent may favor chinstrap penguin population growth only when krill recruitment is successful and krill are abundant. The relationships between penguin and krill recruitment suggest that penguins in the South Shetland Islands live under an increasingly krill-limited system that has disproportionate effects on the over-winter survival of juvenile birds, particularly the migratory Adélie and chinstrap penguins.

A great deal of research has been conducted to elucidate the life-history traits of the *Pygoscelis* penguins. Here, we have assessed the biological outcomes of those life-history traits when confronted with environmental changes that are occurring around the South Shetland Islands. We conclude

by suggesting that the divergent patterns of breeder abundance and juvenile recruitment rates derive from a common environmental driver, namely variability in krill recruitment. We further suggest that additional assessments of the ecology and behavior of *Pygoscelis* penguins during winter are necessary to more fully explore the effects of environmental change on these birds. The winter period encompasses up to 8 months of each year for these species, and very few data exist for this period. In particular, there is an obvious need to better gauge winter diets and dispersal patterns, particularly among juvenile penguins.

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