Advancing the Sea Ice Hypothesis: Trophic Interactions Among Breeding *Pygoscelis* Penguins With Divergent Population Trends Throughout the Western Antarctic Peninsula

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We evaluated annual and regional variation in the dietary niche of *Pygoscelis* penguins including the sea ice-obligate Adélie penguin (*Pygoscelis adeliae*), and sea ice-intolerant chinstrap (*Pygoscelis antarcticus*) and gentoo (*Pygoscelis papua*) penguins, three species that nest throughout the western Antarctic Peninsula (AP) to test the *sea ice trophic interaction hypothesis*, which posits that penguin breeding populations with divergent trends, i.e., declining or increasing, are reliant on differing food webs. Our study relies on values of naturally occurring carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) stable isotopes as integrated proxies of penguin food webs measured over three years at three different breeding colonies. At Anvers Island in the north, where reductions in sea ice and changes in breeding population trends among sympatric sea ice-obligate (Adélie) and sea ice-intolerant (chinstrap and gentoo) penguins have been most notable, our analyses show that all three species of *Pygoscelis* penguins became more similar isotopically over the reproductive period. By late chick-rearing at Anvers Island, crèched chicks at 5-weeks-old for all species occupied similar trophic positions. Isotopic mixing models indicated that the proportions of prey provisioned by adult penguins to 5-week-old chicks at Anvers Island were generally similar across species within years, consisting primarily of Antarctic krill (*Euphausia superba*). Crèched Adélie chicks had higher $\delta^{13}C$ and $\delta^{15}N$ values at Avian and Charcot Islands, southern breeding colonies where sea ice is more prominent and populations of Adélie penguins have increased or remain stable. Trophic position increased with latitude, while the proportions of prey provisioned by Adélie penguin adults to chicks at southern breeding colonies included species typical of high Antarctic marine food webs, especially crystal krill (*Euphausia crystallorophias*). A Bayesian metric for dietary niche width, standard ellipse area (SEA-B), indicated that *Pygoscelis* penguins with greater population changes in the north had more variability in dietary niche width than stable populations further

south. Our results lend insight on marine food web drivers of *Pygoscelis* penguin reproduction at the regional scale and question the long-standing paradigm that Antarctic krill are the only food web component critical to penguin reproductive survival in this region of the Southern Ocean.

Keywords: δ^{13}C and δ^{15}N stable isotopes, food web, *Pygoscelis* penguin, reproduction, sea ice, western Antarctic Peninsula
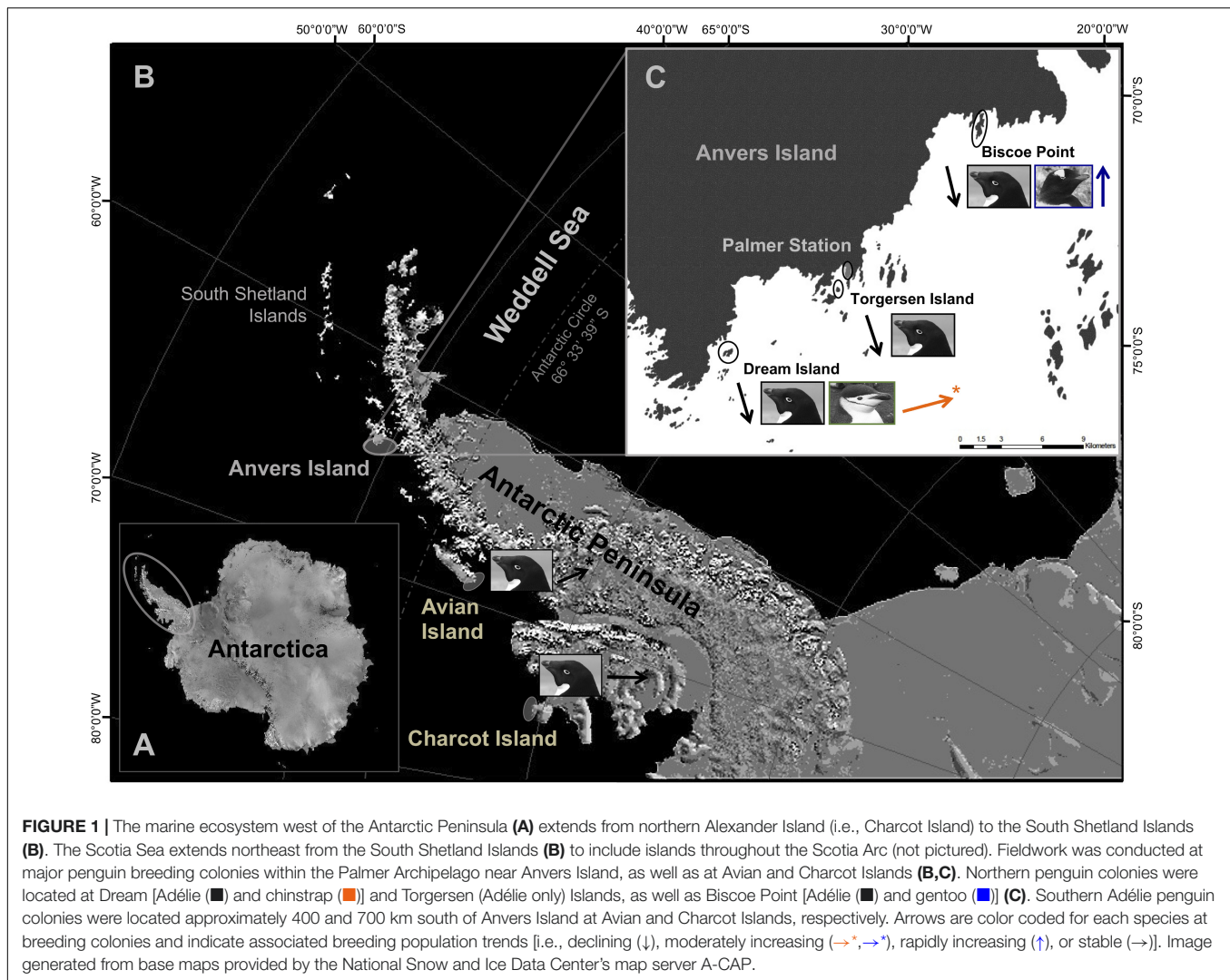
INTRODUCTION

Polar marine ecosystem studies have demonstrated broad correlations between climate-driven variation in physical oceanography and associated change in the abundance and distribution of key trophic levels including predator populations (Grebmeier et al., 2006; Ducklow et al., 2007). Although informative in terms of identifying ecosystem components involved in ecological change, the specific trophic interactions that link predator demography with variation in sea ice habitats have not been well resolved (but see Ainley et al., 2018). For example, ecological drivers of Antarctic penguin population change, i.e., *Pygoscelis* and *Aptenodytes* species (Baker et al., 2006) occurring throughout the Scotia Sea and Antarctic Peninsula (AP) regions (**Figures 1A,B**), have been classic discussions in Antarctic ecology, originally in terms of competitive release due to increases in food availability as a result of the commercial removal of baleen whales (Laws, 1977, 1985). The issue remains the focus of debate, but more recently within the context of regional climate warming (Fraser et al., 1992; Croxall et al., 2002; Forcada et al., 2006; Ducklow et al., 2007; Trathan et al., 2007, 2011; Forcada and Trathan, 2009; Bestelmeyer et al., 2011) and synergistic effects with marine resource harvesting (Ainley and Blight, 2009; Trathan and Agnew, 2010; Trivelpiece et al., 2011; McMahon et al., 2019). Fraser et al. (1992) hypothesized that climate-driven reductions in winter sea ice mediated divergent breeding population responses by chinstrap (*Pygoscelis antarcticus*) and Adélie (*Pygoscelis adeliae*) penguins by increasing or decreasing over-winter survival and subsequent recruitment of each species, respectively, given that chinstrap penguins winter in pelagic, sea ice-free regions across the Scotia Sea (Williams, 1995; Trivelpiece et al., 2007), while Adélie penguins rely on southerly distributed pack ice for winter habitat (Ainley, 2002). Although sea ice was recognized as important in mediating many trophic interactions, the physical extent of this critical winter habitat was considered the key ecological factor that allowed penguins to fully exploit their prey, particularly Antarctic krill (*Euphausia superba*) (Fraser et al., 1992). This paradigm of species' opposing life history affinities for the presence of sea ice has been invoked to explain population change, particularly at range margins, by Antarctic penguins also including gentoo (*Pygoscelis papua*) (Ducklow et al., 2007; Forcada and Trathan, 2009; but see Trivelpiece et al., 2011) and emperor (*Aptenodytes forsteri*) (Trathan et al., 2011) penguins of the western AP. However, few studies have considered this issue from an integrated food web perspective as most have exclusively focused on variability in Antarctic krill stocks as the mechanistic link between climate and sea ice change in this

region of the Southern Ocean and facets of *Pygoscelis* penguin demography that underlie breeding population change (Fraser and Hofmann, 2003; Hinke et al., 2007; Trivelpiece et al., 2011; Ducklow et al., 2013).

Here, we advance the sea ice hypothesis (see Fraser et al., 1992; Trivelpiece et al., 2011) by considering trophic interactions, over a temporal and spatial gradient in sea ice conditions, occurring among populations of all three *Pygoscelis* penguin species throughout major breeding colonies of the western AP (**Figures 1B,C**). Study populations represent species at their relative northern, core, or southern breeding distribution in the region that are characterized by long-term divergent population trends (Ducklow et al., 2007, 2013; Forcada and Trathan, 2009). We rely on values of naturally occurring carbon (^{13}C/^{12}C, δ^{13}C) and nitrogen (^{15}N/^{14}N, δ^{15}N) stable isotopes (SI), a time-integrated, biogeochemical parameter that specifically reflects assimilated prey (Deniro and Epstein, 1978, 1981; Peterson and Fry, 1987), as proxies of penguin diet. We examined variation in isotopic diet among breeding adults and their chicks of the sea ice-obligate Adélie penguin, and sea ice-intolerant chinstrap and gentoo penguins along the Palmer Archipelago, near Anvers Island (**Figures 1B,C**). Here, Adélie penguins occur at their northern breeding range margin along the western AP (Fraser et al., 1992; Polito et al., 2011a), which has contracted given extensive population declines of 80% from historical numbers (Ducklow et al., 2007, 2013) and reflects trends for the species throughout other breeding colonies of the region (Trivelpiece et al., 2011; Lynch et al., 2012). Adélie penguin breeding population declines have occurred in association with significant, long-term reductions in annual sea ice coverage within the northern seasonal sea ice zone along the western AP (Jacobs and Comiso, 1997; Ducklow et al., 2007, 2013; Stammerjohn et al., 2008, 2012). Regional environmental warming is also associated with moderate to more rapid breeding population expansions at southern range margins for sympatric nesting chinstrap and gentoo penguins near Anvers Island (Ducklow et al., 2007, 2013). Regional trends for breeding gentoo penguins generally corroborate those of our study population (Lynch et al., 2012). However, chinstrap penguins nesting near Anvers Island represent one of only several stable or increasing regional colonies among many that appear to be declining up to 60% (Carlini et al., 2009; Trivelpiece et al., 2011; Barbosa et al., 2012; Lynch et al., 2012; Strycker et al., 2020).

Annual sea ice coverage increases with higher latitude along the western AP (Ducklow et al., 2007; Stammerjohn et al., 2008). Importantly, breeding ranges of chinstrap and gentoo penguins do not extend into these sea ice-dominated regions. However, major Adélie penguin breeding colonies are located

FIGURE 1 | The marine ecosystem west of the Antarctic Peninsula **(A)** extends from northern Alexander Island (i.e., Charcot Island) to the South Shetland Islands **(B)**. The Scotia Sea extends northeast from the South Shetland Islands **(B)** to include islands throughout the Scotia Arc (not pictured). Fieldwork was conducted at major penguin breeding colonies within the Palmer Archipelago near Anvers Island, as well as at Avian and Charcot Islands **(B,C)**. Northern penguin colonies were located at Dream [Adélie (■) and chinstrap (■)] and Torgersen (Adélie only) Islands, as well as Biscoe Point [Adélie (■) and gentoo (■)] **(C)**. Southern Adélie penguin colonies were located approximately 400 and 700 km south of Anvers Island at Avian and Charcot Islands, respectively. Arrows are color coded for each species at breeding colonies and indicate associated breeding population trends [i.e., declining (↓), moderately increasing (→*,→*), rapidly increasing (↑), or stable (→)]. Image generated from base maps provided by the National Snow and Ice Data Center's map server A-CAP.

at Avian and Charcot Islands (Schofield et al., 2013) within the species core to more southern distribution along the western AP, respectively (**Figure 1B**; see also Lynch and LaRue, 2014). Here, breeding populations of Adélie penguins have increased at Avian Island (Sailley et al., 2013; W. R. Fraser unpubl. data) or appear stable at Charcot Island based on currently available census data (Henderson, 1976; W. R. Fraser unpubl. data).

Progress in understanding marine environmental drivers of *Pygoscelis* penguin demography has been hindered by a staunch focus on Antarctic krill as the only critical trophic link between penguins and sea ice variability in this region of the Southern Ocean. Thus, we evaluated annual and regional variation in isotopic diet during the reproductive period among populations of *Pygoscelis* penguins nesting throughout the western AP to test the hypothesis that breeding populations with divergent trends, i.e., declining or increasing, are reliant on differing food webs (hereafter *sea ice trophic interaction hypothesis*) as dietary variation can contribute to differences in survival and subsequent recruitment probability of chicks to their natal breeding population (e.g., Ainley et al., 2018), and ultimately

population changes (Fraser et al., 1992; Trivelpiece et al., 2011). To address this overarching hypothesis, we explored a suite of food web correlates using δ^{13}C and δ^{15}N SI metrics including (1) dietary analysis based on δ^{13}C and δ^{15}N values of penguin blood tissue throughout four stages of the reproductive period, (2) trophic position of crèched penguin chicks based on a Bayesian analysis of δ^{15}N values of chick blood tissue and a primary food web consumer (Antarctic krill), (3) Bayesian analysis of the proportion of diet items provisioned to crèched penguin chicks using mixing models based on δ^{13}C and δ^{15}N values of chick blood tissue and key penguin prey items, and finally (4) a Bayesian analysis of dietary niche width based on δ^{13}C and δ^{15}N values of crèched chick blood tissue calculated as standard ellipse area (SEA-B).

We predicted that (1) blood tissue of adult *Pygoscelis* penguins breeding at northern colonies near Anvers Island, which integrates dietary information over approximately the previous 30–60 days given allometric turn-over rates for the cellular fraction of blood (Hobson and Clark, 1992; Bearhop et al., 2002, 2006; Cherel et al., 2007; Barquete et al., 2013), would be

isotopically distinct during primary reproductive effort (i.e., egg laying) given the differing associations each species' late winter foraging areas have with sea ice habitats (Fraser et al., 1992; Williams, 1995; Ainley, 2002; Tanton et al., 2004; Trivelpiece et al., 2007). However, we predicted that isotopic values of blood tissue of *Pygoscelis* chicks reared from these same northwestern AP colonies would become increasingly similar over the breeding season as the isotopic values of the chicks change from those reflective of egg nutrients to those of the prey provisioned to growing chicks (e.g., Sears et al., 2009) and all three species are central place foragers that rely on local prey generally dominated by Antarctic krill (Volkman et al., 1980; Fraser and Hofmann, 2003; Polito et al., 2011b; Trivelpiece et al., 2011). Conversely, we expected that Adélie penguin chicks reared from southwestern AP colonies at Avian and Charcot Islands, where winter sea ice coverage is more prominent, would have higher isotopic values relative to conspecifics reared at Anvers Island as crystal krill (*Euphausia crystallorophias*) and neritic (i.e., notothenoid) fishes that have life history affinities for the presence of sea ice are critical components of energy transfer to higher trophic levels in this region (Donnelly and Torres, 2008; W. R. Fraser unpubl. data), and have higher isotopic values relative to Antarctic krill (Polito et al., 2011b, see also **Table 1**).

The above predictions were extended to analyses of (2) trophic position, (3) the proportions of prey provisioned to older penguin chicks, and (4) dietary niche width of crèched *Pygoscelis* penguin chick blood tissue. Our focus on older chicks at 5 weeks of age for these analyses stems from the fact that these individuals are considered a demographically important group within the context of population change (Fraser and Hofmann, 2003; Hinke et al., 2007; Trivelpiece et al., 2011). We predicted that 5-week-old crèched *Pygoscelis* penguin chicks at Anvers Island would occupy similar trophic positions due to the similar reliance on local prey across species during nesting. Likewise, the proportion of diet items provisioned to crèched penguin chicks at Anvers Island were predicted to be similar across species within each season. However, crèched Adélie penguin chicks were predicted to occupy higher trophic positions at southern breeding colonies due to the reliance on prey such as crystal krill and notothenoid fishes in regions with greater sea ice coverage along the western AP. Similarly, increased proportions of prey items associated with high Antarctic marine food webs were predicted to be provisioned to penguin chicks at southern breeding colonies. Finally, we predicted that dietary niche width of crèched penguin chicks would be similar across each species breeding at Anvers Island due to a reliance on similar prey items. However, crèched Adélie penguin chicks at southern colonies were predicted to have a larger dietary niche width given the importance of higher trophic position prey in these regions to penguin predators. See **Supplementary Text 1** for specific details regarding each analysis.

MATERIALS AND METHODS

Field Methods

Pygoscelis penguins nesting on several islands within the Palmer Archipelago west of the AP near Anvers Island (**Figures 1B,C**)

were studied during the austral summers of 2007/2008, 2008/2009, and 2009/2010. Specifically, study nests were located on Biscoe Point, Torgersen, and Dream Islands (**Figure 1C**). Each study season, Adélie penguin study nests ($n = 30$) were distributed equally between the three study islands, with 10 nests located on each island. Gentoo penguin study nests ($n = 30$) were all located on Biscoe Point, while chinstrap penguin study nests ($n = 15$) were all located on Dream Island (**Figure 1C**). The reduced sample size for chinstraps was due to the overall smaller number of individuals breeding at colonies on Dream Island. During annual oceanographic research cruises aboard the A.R.S.V. *Laurence M. Gould* in January of each study year, as part of the Palmer Station Antarctica, Long-Term Ecological Research Program (PAL-LTER), we further sampled Adélie penguin chicks from colonies at Avian ($n = 25$) and Charcot ($n = 15$) Islands (**Figure 1B**).

Each season, study nests, where pairs of adults were present, were individually marked and chosen before the onset of egg laying and monitored. When study nests were found at the one-egg stage, both adults were captured to obtain blood samples for SI analysis. At the time of capture, each adult penguin was blood sampled (~1 ml) from the brachial vein. After handling, individuals at study nests were further monitored to ensure the pair reached clutch completion (i.e., two eggs). Study nests were monitored for hatch of the first egg. At day 6 and 16 post-hatch for first chicks, resulting in an approximate average nest age of 5 and 15 days given hatching asynchrony, offspring from study nests were captured, blood sampled ($\leq$~500 µl for day 5 chicks, and $\leq$~1 ml for day 15 chicks) to obtain blood samples for SI analysis, and individually marked on the side of their body (under the flipper) using a non-toxic All Weather Paintstik (i.e., cattle marker). Study nests were monitored for chick survival to 25 days, prior to crèche. At 5 weeks into chick-rearing, based on a seasonal population average hatch date for each species, older crèched chicks of all three species at colonies near Anvers Island were captured and blood sampled. Adélie penguin chicks at Avian Island were sampled on the same day Anvers Island Adélie penguin chicks were sampled. Adélie penguin chicks at Charcot Island, sampled during one season only on 25 January 2010, were handled 3 days after Anvers Island and Avian Island Adélie penguin chicks were sampled that year. Blood samples from crèched chicks (~1 ml) were taken from the brachial vein to obtain blood tissue for SI analysis. Blood samples from adults and older crèched chicks were obtained using a sterile 3 ml syringe and heparinized infusion needle. Young chicks were blood sampled from the tarsus vein using a sterile needle and heparinized capillary tubes (5-day-old chicks) or infusion needles (15-day-old chicks). All collected blood was stored in 1.5 ml microcentrifuge tubes and kept cool in the field until further processing.

Food web samples including primary prey items of penguins such as myctophid, i.e., lanternfish (*Electrona antarctica*), and notothenoid, i.e., Antarctic silverfish (*Pleuragramma antarcticum*), fishes as well as three species of euphausiids including Antarctic krill, *Thysanoessa macrura*, and crystal krill were primarily collected during a PAL-LTER oceanographic cruise in January 2009. Additional samples were obtained

TABLE 1 | Mean stable isotope [δ¹³C and δ¹⁵N ± standard deviation (SD)] values and elemental concentrations of dietary endpoints and red blood cell tissue of *Pygoscelis* penguin chicks.

Study colony and year	Dietary endpoints and consumers	Endpoint source	Sample size, prey size range (mm)	Mean $\delta^{13}C \pm SD$	Mean $\delta^{15}N \pm SD$	Elemental concentration (%C ± SD)	Elemental concentration (%N ± SD)
Anvers Island							
2007/2008	*E. superba* (krill)	08 diet	n = 5, 42–47	−26.7 ± 0.8	4.3 ± 0.4	42.7 ± 3.7	12.9 ± 1.2
	T. macrura (krill)	09 net, 10 diet	n = 14, 18–30	−27.6 ± 0.5	7.4 ± 0.4	38.5 ± 1.7	11.6 ± 0.5
	E. antarctica (fish)	11 net	n = 2, 77–80	−24.6 ± 0.5	10.2 ± 0.3	39.9 ± 4.3	12.4 ± 1.3
	P. adeliae (penguin)		n = 15	−27.7 ± 0.1	7.1 ± 0.1	51.6 ± 8.5	15.8 ± 2.4
	P. antarcticus (penguin)		n = 10	−27.5 ± 0.1	7.0 ± 0.3	49.7 ± 2.9	15.2 ± 1.0
	P. papua (penguin)		n = 15	−27.4 ± 0.3	7.8 ± 0.3	50.3 ± 4.0	15.5 ± 1.6
2008/2009	*E. superba* (krill)	09 diet, 09 net	n = 16, 30–54	−26.9 ± 0.5	4.4 ± 0.4	39.8 ± 3.9	12.3 ± 1.2
	T. macrura (krill)	09 net	n = 11, 18–30	−27.7 ± 0.5	7.4 ± 0.5	38.2 ± 1.6	11.6 ± 0.5
	E. antarctica (fish)	11 net	n = 2, 77–80	−24.6 ± 0.5	10.2 ± 0.3	39.9 ± 4.3	12.4 ± 1.3
	P. adeliae (penguin)		n = 16	−28.0 ± 0.2	7.9 ± 0.3	51.2 ± 7.7	16.1 ± 2.5
	P. antarcticus (penguin)		n = 16	−27.8 ± 0.1	8.0 ± 0.2	51.0 ± 2.5	15.9 ± 0.8
	P. papua (penguin)		n = 16	−27.5 ± 0.4	8.0 ± 0.6	51.6 ± 6.1	16.2 ± 1.9
2009/2010	*E. superba* (krill)	10 diet, 10 net	n = 20, 40–53	−26.1 ± 0.7	4.3 ± 0.7	40.6 ± 3.6	12.5 ± 1.1
	T. macrura (krill)	10 diet	n = 3, N/A	−27.1 ± 0.1	7.2 ± 0.1	39.3 ± 1.8	11.8 ± 0.6
	E. antarctica (fish)	11 net	n = 2, 77–80	−24.6 ± 0.5	10.2 ± 0.3	39.9 ± 4.3	12.4 ± 1.3
	P. adeliae (penguin)		n = 16	−26.6 ± 0.2	7.7 ± 0.2	50.5 ± 5.3	15.2 ± 1.8
	P. antarcticus (penguin)		n = 15	−26.7 ± 0.1	7.8 ± 0.2	49.6 ± 3.5	15.3 ± 1.1
	P. papua (penguin)		n = 14	−26.1 ± 0.1	7.8 ± 0.2	50.0 ± 7.2	15.7 ± 2.3
Avian Island							
2007/2008	*E. crystallorophias* (krill)	09 net, 11 net	n = 5, 27–33	−20.9 ± 1.1	8.8 ± 0.9	41.1 ± 2.2	12.7 ± 0.9
	E. superba (krill)	08 diet	n = 5, 40–48	−26.4 ± 1.1	4.6 ± 0.6	37.9 ± 4.3	11.5 ± 1.3
	T. macrura (krill)	09 net, 10 net	n = 17, 13–23	−27.1 ± 1.4	7.7 ± 0.4	37.9 ± 3.6	11.6 ± 1.0
	E. antarctica (fish)	11 net	n = 13, 54–91	−24.2 ± 0.4	10.2 ± 0.9	42.4 ± 6.7	13.9 ± 2.1
	P. antarcticum (fish)	11 net	n = 12, 85–116	−21.8 ± 0.6	12.3 ± 0.5	41.9 ± 5.1	13.2 ± 1.6
	P. adeliae (penguin)		n = 25	−26.0 ± 0.3	8.6 ± 0.2	51.6 ± 5.1	15.7 ± 1.5
2008/2009	*E. crystallorophias* (krill)	09 net	n = 2	−21.9 ± 0.9	8.8 ± 0.5	39.3 ± 2.5	11.8 ± 0.8
	E. superba (krill)	09 diet, 09 net	n = 20, 33–55	−26.5 ± 1.1	4.8 ± 0.7	40.4 ± 3.9	12.4 ± 1.2
	T. macrura (krill)	09 net	n = 10, 13–23	−28.0 ± 0.6	7.9 ± 0.3	38.7 ± 3.7	11.7 ± 1.1
	E. antarctica (fish)	11 net	n = 13, 54–91	−24.2 ± 0.4	10.2 ± 0.9	42.4 ± 6.7	13.2 ± 2.1
	P. antarcticum (fish)	11 net	n = 12, 85–116	−21.8 ± 0.6	12.3 ± 0.5	41.9 ± 5.1	13.2 ± 1.5
	P. adeliae (penguin)		n = 23	−25.6 ± 0.4	8.3 ± 0.2	50.1 ± 5.3	15.5 ± 1.6
2009/2010	*E. crystallorophias* (krill)	09 net, 11 net	n = 5, 27–33	−20.9 ± 1.1	8.8 ± 0.9	41.1 ± 2.2	12.7 ± 0.9
	E. superba (krill)	10 diet, 10 net	n = 8, 48–53	−25.8 ± 0.9	4.9 ± 0.3	39.3 ± 4.9	11.9 ± 1.4
	T. macrura (krill)	10 net	n = 7, N/A	−25.7 ± 0.8	7.3 ± 0.2	36.7 ± 3.3	11.3 ± 1.0
	E. antarctica (fish)	11 net	n = 13, 54–91	−24.2 ± 0.4	10.2 ± 0.9	42.4 ± 6.7	13.2 ± 2.1
	P. antarcticum (fish)	11 net	n = 12, 85–116	−21.8 ± 0.6	12.3 ± 0.5	41.9 ± 5.1	13.2 ± 1.6
	P. adeliae (penguin)		n = 23	−25.8 ± 0.3	8.3 ± 0.2	53.0 ± 6.4	15.7 ± 2.0
Charcot Island							
2009/2010	*E. crystallorophias* (krill)	10 net	n = 8, 24–31	−21.9 ± 0.8	8.3 ± 0.5	37.4 ± 3.7	11.6 ± 1.1
	E. superba (krill)	09 net, 11 diet, 11 net	n = 17, 40–56	−25.1 ± 2.1	5.1 ± 0.6	40.8 ± 3.7	12.5 ± 1.2
	P. antarcticum (fish)	10 net	n = 4, 78–86	−23.8 ± 0.3	11.7 ± 0.4	40.7 ± 2.2	12.9 ± 0.7
	P. adeliae (penguin)		n = 15	−23.1 ± 0.2	9.1 ± 0.2	52.2 ± 6.7	15.5 ± 2.1

Data were used in trophic position, isotopic mixing model, and isotopic niche analyses.

during seasonal diet sampling that occurred each year as part of PAL-LTER monitoring activities, as well as oceanographic cruises in January of 2010 and 2011 to increase sample sizes for some taxa. Zooplankton were sampled using oblique tows of 1 m × 1 m frame net (300 μm mesh) towed to a depth of approximately 300 m or a 2 m × 2 m frame net (700 μm mesh) towed to a depth of approximately 120 m. Food web samples were collected along PAL-LTER regional study grid lines in association with colonies at Anvers (600 – 500 lines), Avian (200 – 100 lines), and Charcot (000 to −100 lines) Islands
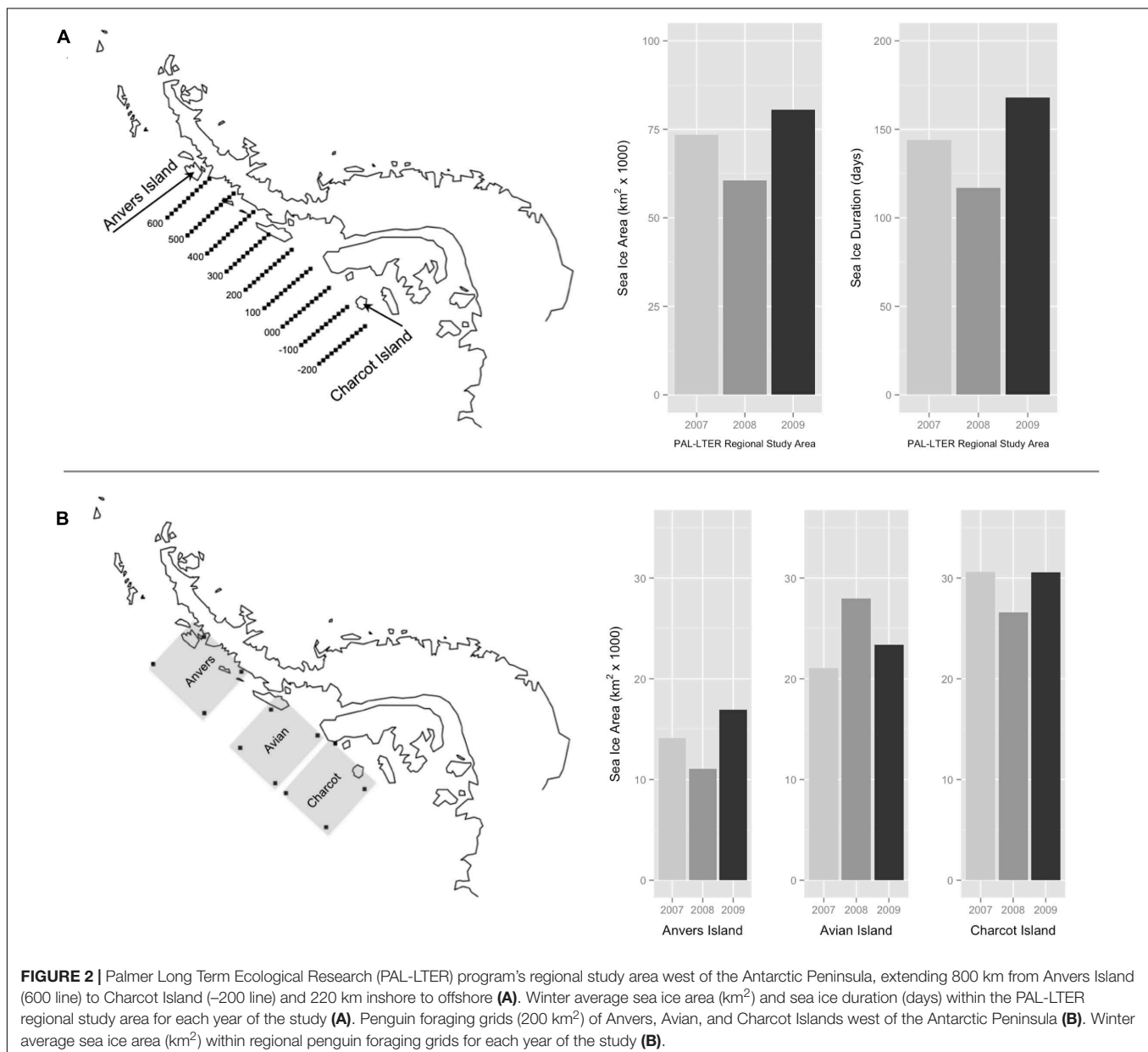
(**Figures 1B**, **2A**) to obtain a representative sample of prey items (see **Table 1**) known to be provisioned to chicks based on the general distribution of prey from traditional diet sampling (i.e., stomach lavage) of reproductive adults (see **Supplementary Table 1** for traditional diet composition of study populations, see also long-term penguin diet datasets within the PAL-LTER data system)[1]. No statistical differences were detected in the isotopic values between food web items collected via net tows versus those obtained from diet samples.

Sea ice data were based on satellite estimates of sea ice concentration (*SIC*) within two regions, (1) the PAL-LTER regional study grid (**Figure 2A**) and (2) three 200 km^2 penguin foraging grids associated with major penguin rookeries at Anvers,

Avian and Charcot Islands (**Figure 2B**). Daily and monthly time series of *SIC* were used to calculate two metrics within the PAL-LTER regional grid, (1) average winter sea ice area (km^2) representing the yearly average area of the ocean covered by winter sea ice, and (2) duration (days) representing the yearly total length of the winter sea ice season. For the 200 km^2 penguin foraging grids, the only sea ice metric calculated was average winter sea ice area within each foraging grid. Sea ice metrics were calculated using time series based on Version 2 of the Goddard Space Flight Center (GSFC) Bootstrap algorithm (Comiso, 1999) provided by the United States National Snow and Ice Data Center (NSIDC)[2], and derived based on monthly averages between the winter months of sea ice advance and retreat, and the day of

[1]https://oceaninformatics.ucsd.edu/datazoo/catalogs/pallter/datasets

[2]www.nsidc.org

FIGURE 2 | Palmer Long Term Ecological Research (PAL-LTER) program's regional study area west of the Antarctic Peninsula, extending 800 km from Anvers Island (600 line) to Charcot Island (–200 line) and 220 km inshore to offshore **(A)**. Winter average sea ice area (km^2) and sea ice duration (days) within the PAL-LTER regional study area for each year of the study **(A)**. Penguin foraging grids (200 km^2) of Anvers, Avian, and Charcot Islands west of the Antarctic Peninsula **(B)**. Winter average sea ice area (km^2) within regional penguin foraging grids for each year of the study **(B)**.

first and last appearance of sea ice within the same region and averaged for the PAL-LTER grid. These metrics are useful for describing both the winter spatial and temporal variability of Southern Ocean sea ice (Stammerjohn et al., 2008).

Laboratory Methods

Within 12 h of field collection, tubes containing whole blood were centrifuged to separate plasma and red blood cell (RBC) fractions, which were stored separately and frozen at $-80°C$. Collected food web items were also stored frozen at $-80°C$.

Samples of krill and fish were first thawed and rinsed with double-distilled water (ddH$_2$O). Samples of whole krill and fish, along with tubes containing RBCs, were allowed to dry to a consistent mass in a drying oven at $60°C$. Dried krill, fish, and RBCs were homogenized into a powder using a clean, dry mortar and pestle. Lipids of homogenized krill and fish samples were removed prior to SI analysis using a 2:1 chloroform:methanol by volume solution (Bligh and Dyer, 1959) first for 24 h, and 12 h thereafter until the solvent was clear. Lipid-free krill and fish samples were allowed to dry under the hood and subsequently in a drying oven for 24 h. Lipid-free krill were further treated with 0.1 N HCl for 24 h to remove carbonates in exoskeletons (Soreide et al., 2006) and again dried. RBC samples were not removed of lipids since the plasma portion, which tends to be more lipid-rich than RBC fractions (Bearhop et al., 2000 and references therein), was previously separated and others have shown no need to remove lipids from avian blood tissue (Bearhop et al., 2000; Cherel et al., 2005). Aliquots of lipid- and carbonate-free krill, fish and RBC samples were transferred to 8 mm × 5 mm pressed tin capsules (Elemental Microanalysis) and weighed (∼2 mg) using a microbalance. Samples were analyzed for δ^{13}C and δ^{15}N SI values using an elemental analyzer interfaced with an isotope ratio mass spectrometer at the Stable Isotope Facility, University of California, Davis. Data expressed as δ^{13}C or δ^{15}N were calculated using the following equation: δ^{13}C or δ^{15}N = $[(R_{sample}/R_{standard})-1] \times 1000$, where R_{sample} is the ratio of the heavy to light isotope for either ^{13}C/^{12}C or ^{15}N/^{14}N, and $R_{standard}$ is the heavy to light isotope ratios for international standards, Vienna PeeDee Belemnite for carbon and atmospheric N$_2$ (Air) for nitrogen. Raw δ values were normalized on a two-point scale using glutamic acid reference materials [i.e., USGS-40 (δ^{13}C$_{VPDB-LSVEC}$ = -26.39 ± 0.04‰, δ^{15}N$_{AIR}$ = -4.52 ± 0.06‰), USGS-41 (δ^{13}C$_{VPDB-LSVEC}$=+37.63 $\pm$ 0.05‰, δ^{15}N$_{AIR}$ = +47.57 $\pm$ 0.11‰)]. Based on replicates of a laboratory standard (bovine liver, n = 31), the measurement error (SD) for each run was ±0.06‰ (n = 2), ±0.03‰ (n = 6), ±0.07‰ (n = 4), ±0.04‰ (n = 8), ±0.09‰ (n = 3), ±0.09‰ (n = 6), ±0.05‰ (n = 2) for δ^{13}C. The within run measurement error for δ^{15}N was ±0.23‰ (n = 2), ±0.13‰ (n = 6), ±0.43‰ (n = 4), ±0.12‰ (n = 8), ±0.15‰ (n = 3), ±0.17‰ (n = 6), ±0.05‰ (n = 2). Across all runs, the laboratory standard measurement error was ±0.06‰ for δ^{13}C and ±0.20‰ for δ^{15}N. Measurement error based on the analysis of replicate krill samples (n = 6) collected for this study was ±0.16‰ for δ^{13}C and

±0.08‰ for δ^{15}N. Importantly, sodium heparin does not alter the stable isotope values of blood tissue (Hobson et al., 1997; Lemons et al., 2012).

Statistical Methods

Isotopic Dietary Analysis (IDA)

Statistical analyses were delineated by reproductive stage and location, and were performed in the R language environment (R Core Team, 2020). *Pygoscelis* adult and crèched chick analyses at Anvers Island (*IDA* analyses 1 and 4) employed least-squares general linear models (hereafter LM) to examine continuous variation in δ^{13}C and δ^{15}N SI values in relation to two parameters treated as main effects including (1) species and (2) year, both treated as categorical variables. An *a priori* set of five candidate models consisted of an equal-means (null) model, each predictor variable as a main effect (two models), a multiple predictor model that included both main effect parameters (one model), and an interaction model including both main effect parameters and their interaction (one model). This same candidate model set was evaluated for each isotope separately using unique datasets for each reproductive stage (*Pygoscelis* adults: n = 296 for both δ^{13}C and δ^{15}N analyses, *Pygoscelis* crèched chicks: n = 133 for both δ^{13}C and δ^{15}N analyses). For each candidate model, Akaike's Information Criterion (AICc), corrected for small sample size, in addition to ΔAICc and Akaike weight (w) values were calculated and used to compare models (Burnham and Anderson, 2002). An R^2 value was also calculated, defined as the fraction of the total variance explained by the model and given by the Multiple R-squared calculation in R (Crawley, 2007), to provide a measure of fit for each model. Inference was based on the relative support for parameters across all models and weighted parameter estimates (i.e., model averaging). Parameter estimation included calculation of model-averaged parameter estimates based on w values for all candidate models. Standard errors for parameter estimates were based on unconditional variances calculated across the same models. Parameter likelihood values were evaluated by summing w values across all models that included each parameter under consideration (Burnham and Anderson, 2002).

Adélie crèched chick analyses at Anvers, Avian, and Charcot Islands (*IDA* analysis 5) also used LM to examine continuous variation in δ^{13}C and δ^{15}N SI values in relation to two parameters treated as main effects including (1) location and (2) year, both treated as categorical variables. An *a priori* set of five candidate models considered location and year as main effects following the same model structure described above for *IDA* analyses 1 and 4. This same candidate model set was evaluated for each isotope separately (n = 132 for δ^{13}C analyses, n = 133 for δ^{15}N analyses). Again, for each candidate model, AICc, ΔAICc, and w values were calculated and used to compare models (Burnham and Anderson, 2002), as well as calculation of an R^2 value. Inference was based on model averaging with parameter estimation following that described previously.

Pygoscelis chick analyses at 5 and 15 days of age (*IDA* analyses 2 and 3) employed linear mixed effects models (hereafter LME) using the nlme package in R (Pinheiro et al., 2019) to examine

continuous variation in δ^{13}C and δ^{15}N SI values in relation to two parameters treated as fixed main effects including (1) species and (2) year, both treated as categorical variables. An *a priori* set of five candidate models consisted of an equal-means (null) model, each predictor variable as a fixed main effect (two models), a multiple predictor model that included both fixed main effect parameters (one model), and an interaction model including both fixed main effect parameters and their interaction (one model). This same candidate model set was evaluated for each isotope separately (Day 5: $n = 223$ for both δ^{13}C and δ^{15}N analyses, Day 15: $n = 202$ for both δ^{13}C and δ^{15}N analyses). A random effect of nest on intercept (random $= \sim 1|$ nest) was included in all candidate LME models to control for non-independence of data given that sibling chicks were sampled and presumably more similar in isotope values. Again, for each candidate model, AICc, ΔAICc, and w values were calculated and used to compare models (Burnham and Anderson, 2002). Inference was based on model averaging with parameter estimation following that described previously. The random effect of nest on intercept was included based on results from preliminary analyses that compared the fit (i.e., AICc value) of two models for each isotope: the most parameterized fixed effect model, both with and without, the random effect. A linear generalized least squares (GLS) model was fit without a random effect where the restricted log-likelihood was maximized (method = REML). A LME model was also fit with a random effect of nest on intercept, again maximizing the restricted log-likelihood. Both models included the same fixed main effect parameters and their interaction. For each isotope (δ^{13}C and δ^{15}N) and reproductive stage (5 or 15 days of age) it was determined that inclusion of the random effect provided a better fit to the data as AICc values were minimized for LME models.

For each analysis described above, we discuss yearly variation in penguin SI values within the context of qualitative variation in the previous winter's average sea ice coverage, i.e., low, intermediate, or high. We made no *a priori* predictions regarding relationships between penguin SI values and winter sea ice coverage as isotopic studies of the western AP marine ecosystem have not been conducted previously in this context, i.e., across several years and regions at lower and higher latitudes. In general, we expect winter sea ice to be a primary environmental driver of the prey-base encountered by penguins during the breeding season.

Trophic Position Analysis (TPA)

Trophic position of *Pygoscelis* crèched chicks at a population average of 5 weeks old was calculated for all species, locations, and years using a Bayesian model (tRophicPosition) described by Quezada-Romegialli et al. (2018) implemented in the R language environment (R Core Team, 2020). The model generally follows earlier work (Hobson and Welch, 1992; Hobson et al., 1994; Vander Zanden et al., 1997; Post, 2002) where the trophic position of a consumer can be estimated as $\lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta_n$. Values of δ^{15}N for individual RBCs of *Pygoscelis* crèched chicks at Anvers, Avian, and Charcot Islands were used for $\delta^{15}N_{consumer}$, $\delta^{15}N_{base}$ was estimated from δ^{15}N values of Antarctic krill collected annually along PAL-LTER regional study grid lines in association with breeding colonies at Anvers, Avian,

and Charcot Islands (**Table 1**), and a λ value for Antarctic krill (trophic position of the baseline) was set at 2.5 following Stowasser et al. (2012) and Schmidt and Atkinson (2016). The one Baseline model was parameterized using the trophic discrimination factors of Post (2002), i.e., 3.4 ± 0.98 SD. Seven individual *TPA* models were run for 100,000 iterations with a burn in of 20,000 iterations reflecting the need to incorporate different baseline values for year and location considered in the analysis. Trophic position models for Anvers Island included data for all three species of penguin chicks for each year of the study (*TPA* models 1–3), while models for Avian (*TPA* models 4–6), and Charcot (*TPA* model 7) Islands included only data for Adélie penguin chicks during each year. Sample sizes for penguin chick consumers and Antarctic krill baselines used in *TPA* models are reported in **Table 1**.

Isotopic Mixing Model Analysis (IMMA)

The MixSIAR package, implemented in R (Stock et al., 2018; R Core Team, 2020), was used to generate quantitative estimates of the proportion of diet items provisioned by adult penguins to 5-week-old crèched chicks of all three species at Anvers Island (*IMMA* analyses 1–3, 2007/2008: $n = 40$, 2008/2009: $n = 48$, 2009/2010: $n = 45$), and Adélie penguin chicks at Avian (*IMMA* analyses 4–6, 2007/2008: $n = 25$, 2008/2009: $n = 23$, 2009/2010: $n = 23$), and Charcot (*IMMA* analysis 7, 2009/2010: $n = 15$) Islands, for each year of the study, using dual δ^{13}C or δ^{15}N values of key prey items and chick RBCs (see **Table 1**). Within a Bayesian framework, MixSIAR functions model probability distributions by incorporating sources of variability such as that within isotopic dietary endpoints and consumers, isotopic discrimination, and elemental concentration. For all *IMMA* models, species was modeled as a fixed effect. Isotopic dietary endpoints were collected annually in association with each regional study colony to describe yearly variation in SI values of 5-week-old crèched chicks reared at those same colonies. For some years and locations, it was necessary to use a dietary endpoint collected in a different year due to difficulty in obtaining some prey species (see **Table 1**). The various dietary endpoints considered for each major study colony reflected the general distribution of dominant prey based on traditional diet sampling of reproductive adults nesting at Anvers, Avian, and Charcot Islands (W. R. Fraser unpubl. data, see **Supplementary Table 1**). Of note, long-term monitoring data collected by PAL-LTER was restricted to Adélie penguins only. The work reported here was a first effort to quantify the diet of chinstrap and gentoo penguins nesting within the PAL-LTER study area. Thus, **Supplementary Table 1** mainly reports traditional diet information for Adélie penguins. Information on gentoo penguin diets did not begin until 2010, and even later for chinstrap penguins. Mean δ^{13}C and δ^{15}N values of dietary endpoints and associated mean elemental concentrations are reported in **Table 1**. We calculated isotopic discrimination factors and associated standard deviations (SD) using data based on king penguin (*Aptenodytes patagonicus*) whole blood and a diet of Atlantic herring (*Clupea harengus*) and Icelandic capelin (*Mallotus villosus*) ($\delta13$C: -0.806 ± 0.428 SD and $\delta15$N: 2.067 ± 0.165 SD, Cherel et al., 2005). The same discrimination factors were applied to all prey types. MixSIAR

models were run under *normal* parameters with a chain length of 100,000, a burn in of 50,000, and thinned by 50 using three chains.

Isotopic Niche Analysis (INA)

Functions within the SIBER package (v2.1.5, Jackson et al., 2011) also implemented in R (R Core Team, 2020) were used to generate a Bayesian-derived metric based on the standard ellipse area (SEA-B) of δ^{13}C and δ^{15}N values of chick RBCs (see **Supplementary Figure 1**) to describe dietary niche width of penguin chicks for each species, location, and year of the study (see **Table 1** for sample sizes used in *INA* analyses 1–7). This Bayesian-derived metric is based on that described by Layman et al. (2007) for the convex hull of isotope data as an estimate of standard ellipse area. Within a Bayesian framework, SIBER functions modeled probability distributions by incorporating sources of variability such as that within the originally derived means of populations. SIBER models were run for one million iterations with a burn in of the first 50,000 iterations, and thinned by 50 using two chains.

RESULTS

Sea Ice

Sea ice metrics indicated that the austral winters preceding each study year were generally characterized by lower than average sea ice coverage, with winter 2008 being the second lowest sea ice season in the Palmer LTER record since 1979 (Stammerjohn et al., 2008, see also sea ice datasets within http://pal.lternet.edu/data/). Relative yearly variability in sea ice area and duration (**Figure 2A**) over the course of the study suggested that 2007 was an intermediate sea ice season relative to 2008 (low) and 2009 (high). Results for inter-annual variability in dietary niche of adult *Pygoscelis* penguins at the one-egg stage are discussed within the context of these qualitative differences in each year's winter sea ice season over the entire PAL-LTER regional study grid (**Figure 2A**).

Variation in average winter sea ice area across the 200 km^2 penguin foraging grids (**Figure 2B**) confirmed that in general sea ice area increased to the south during the austral winters preceding each study year (**Figure 2B**). However, this trend was not as strong during the winter of 2008 (**Figure 2B**) when sea ice area within the Avian Island penguin foraging grid (27,990 km^2) was slightly greater than that for Charcot Island (26,608 km^2). Yearly variation in average winter sea ice area within penguin foraging grids at Anvers and Charcot Islands confirmed our previous finding based on sea ice metrics calculated over the entire PAL-LTER regional study grid (**Figure 2A**) that 2007 was an intermediate winter sea ice season relative to 2008 (low) and 2009 (high). This trend was not apparent within the Avian Island penguin foraging grid (**Figure 2B**) where 2009 was an intermediate winter sea ice season relative to 2007 (low) and 2008 (high). Results for inter-annual variability in isotopic diet of 5-week-old *Pygoscelis* penguin chicks at all locations are discussed within the context of these qualitative differences in each foraging grid's winter sea ice season (**Figure 2B**).

Isotopic Dietary Analysis

Analyses of variation in δ^{13}C and δ^{15}N SI values of *Pygoscelis* adults at Anvers Island (*IDA* analysis 1, **Figures 1B,C**) resulted in only one model receiving a ΔAICc value ≤ 2 for each isotope. The most parsimonious model for each isotope was the global model that included terms for species, year, and an interaction for species × year. Both models received very high *w* values (1.00 for each isotope) and R^2 values (δ^{13}C: 0.91, δ^{15}N: 0.71, **Table 2**). All other models in the candidate set received no support. Parameter likelihoods indicated strong support for all terms in both analyses (**Table 3**). On average, adult chinstrap penguins had the highest δ^{13}C and δ^{15}N values, adult Adélie penguins were intermediate, while gentoo penguin adults had the lowest isotope values of the three species at the one-egg stage (**Figure 3A** and **Table 3**). Adult Adélie penguins had lower δ^{13}C values, and especially δ^{15}N values, following the 2008 winter of very low sea ice within the PAL-LTER regional study grid (**Figures 2A, 3A**

TABLE 2 | Candidate models describing variation in isotopic diet during the reproductive period of *Pygoscelis* penguins throughout the western Antarctic Peninsula (*IDA* analyses 1–5).

Study colony	Reproductive stage	Response variable	Model number	Explanatory variable	Number of parameters	ΔAICc	*w*	R^2
Anvers Island	Adults	δ^{13}C	5	Species + Year + Species × Year	10	0.00	1.00	0.91
		δ^{15}N	5	Species + Year + Species × Year	10	0.00	1.00	0.71
	Day 5 chicks	δ^{13}C	5	Species + Year + Species × Year	11	0.00	0.97	NA
		δ^{15}N	2	Species	5	0.00	0.45	NA
			4	Species + Year	7	1.90	0.18	NA
	Day 15 chicks	δ^{13}C	5	Species + Year + Species × Year	11	0.00	1.00	NA
		δ^{15}N	4	Species + Year	7	0.00	0.85	NA
	Week 5 chicks	δ^{13}C	5	Species + Year + Species × Year	10	0.00	0.89	0.89
		δ^{15}N	5	Species + Year + Species × Year	10	0.00	1.00	0.52
Regional Islands	Week 5 Adélie chicks	δ^{13}C	5	Location + Year + Location × Year	8	0.00	1.00	0.97
		δ^{15}N	5	Location + Year + Location × Year	8	0.00	1.00	0.86

Models presented are those determined to be most parsimonious, as well all models that received ΔAICc values ≤ 2. NA, R^2 value not available for linear mixed effects models.

TABLE 3 | Parameter estimates and likelihoods from candidate models describing variation in isotopic diet during the reproductive period of *Pygoscelis* penguins throughout the western Antarctic Peninsula (*IDA* analyses 1–5).

Study colony	Reproductive stage	Response variable	Explanatory variable	Parameter likelihood		Parameter estimate ± 1 SE	
				$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Anvers Island	Adults	$\delta^{13}C$ or $\delta^{15}N$	Intercept	1.00	1.00	−25.05 ± 0.04	9.02 ± 0.05
			Species CHPE	1.00	1.00	0.46 ± 0.07	−0.004 ± 0.09
			Species GEPE	1.00	1.00	−0.39 ± 0.06	−1.06 ± 0.07
			Year 2008/2009	1.00	1.00	−1.17 ± 0.05	−0.46 ± 0.07
			Year 2009/2010	1.00	1.00	−0.95 ± 0.05	0.01 ± 0.07
			Species CHPE × Year 2008/2009	1.00	1.00	1.13 ± 0.10	0.83 ± 0.13
			Species CHPE × Year 2009/2010	1.00	1.00	1.07 ± 0.09	0.55 ± 0.12
			Species GEPE × Year 2008/2009	1.00	1.00	−0.14 ± 0.08	0.91 ± 0.10
			Species GEPE × Year 2009/2010	1.00	1.00	0.24 ± 0.08	0.31 ± 0.10
	Day 5 chicks	$\delta^{13}C$ or $\delta^{15}N$	Intercept	1.00	1.00	−25.72 ± 0.13	8.40 ± 0.12
			Species CHPE	0.99	0.76	−0.70 ± 0.31	0.08 ± 0.24
			Species GEPE	0.99	0.76	−0.21 ± 0.19	0.20 ± 0.17
			Year 2008/2009	1.00	0.38	−1.70 ± 0.18	0.07 ± 0.12
			Year 2009/2010	1.00	0.38	−0.62 ± 0.18	−0.001 ± 0.08
			Species CHPE × Year 2008/2009	0.97	0.13	1.12 ± 0.38	0.12 ± 0.23
			Species CHPE × Year 2009/2010	0.97	0.13	1.04 ± 0.37	0.11 ± 0.20
			Species GEPE × Year 2008/2009	0.97	0.13	0.60 ± 0.25	0.004 ± 0.04
			Species GEPE × Year 2009/2010	0.97	0.13	0.72 ± 0.26	0.06 ± 0.12
	Day 15 chicks	$\delta^{13}C$ or $\delta^{15}N$	Intercept	1.00	1.00	−26.91 ± 0.07	7.35 ± 0.10
			Species CHPE	1.00	0.99	−0.74 ± 0.17	−0.04 ± 0.17
			Species GEPE	1.00	0.99	−0.10 ± 0.15	0.52 ± 0.13
			Year 2008/2009	1.00	0.99	−0.95 ± 0.11	0.49 ± 0.13
			Year 2009/2010	1.00	0.99	0.33 ± 0.11	0.19 ± 0.13
			Species CHPE × Year 2008/2009	0.99	0.15	0.70 ± 0.23	0.07 ± 0.15
			Species CHPE × Year 2009/2010	0.99	0.15	0.53 ± 0.22	0.04 ± 0.09
			Species GEPE × Year 2008/2009	0.99	0.15	0.67 ± 0.18	−0.03 ± 0.08
			Species GEPE × Year 2009/2010	0.99	0.15	0.63 ± 0.19	0.02 ± 0.06
	Week 5 chicks	$\delta^{13}C$ or $\delta^{15}N$	Intercept	1.00	1.00	−27.69 ± 0.05	7.12 ± 0.08
			Species CHPE	1.00	1.00	0.17 ± 0.09	−0.12 ± 0.13
			Species GEPE	1.00	1.00	0.31 ± 0.08	0.74 ± 0.11
			Year 2008/2009	1.00	1.00	−0.27 ± 0.08	0.74 ± 0.12
			Year 2009/2010	1.00	1.00	1.10 ± 0.08	0.56 ± 0.12
			Species CHPE × Year 2008/2009	0.89	0.99	−0.05 ± 0.10	0.26 ± 0.17
			Species CHPE × Year 2009/2010	0.89	0.99	−0.25 ± 0.11	0.23 ± 0.17
			Species GEPE × Year 2008/2009	0.89	0.99	0.12 ± 0.10	−0.63 ± 0.16
			Species GEPE × Year 2009/2010	0.89	0.99	0.11 ± 0.10	−0.59 ± 0.17
Regional Islands	Week 5 Adélie chicks	$\delta^{13}C$ or $\delta^{15}N$	Intercept	1.00	1.00	−25.99 ± 0.05	8.57 ± 0.04
			Location Anvers	1.00	1.00	−1.69 ± 0.08	−1.45 ± 0.07
			Location Charcot	1.00	1.00	2.66 ± 0.08	0.82 ± 0.07
			Year 2008/2009	1.00	1.00	0.44 ± 0.07	−0.29 ± 0.06
			Year 2009/2010	1.00	1.00	0.22 ± 0.07	−0.31 ± 0.06
			Location Anvers × Year 2008/2009	1.00	1.00	−0.71 ± 0.11	1.03 ± 0.10
			Location Anvers × Year 2009/2010	1.00	1.00	0.88 ± 0.11	0.87 ± 0.10

Parameter estimates [±1 standard error (SE)] are weighted averages, and standard errors are based on unconditional variances. Parameter likelihoods are Akaike weight (w) values summed across all models that include the variable. CHPE, chinstrap penguin; GEPE, gentoo penguin.

and **Supplementary Figures 2A,B**). Conversely, adult gentoo penguins had higher $\delta^{15}N$ values, but lower $\delta^{13}C$ values, following the 2008 winter of very low sea ice coverage within the PAL-LTER regional study grid (**Figures 2A**, **3A**, **Table 3**, and **Supplementary Figures 2E,F**). However, $\delta^{15}N$ values of adult

gentoo penguins were only slightly lower following the winter of 2009 with the highest sea ice coverage (**Figures 2A**, **3A**, **Table 3**, and **Supplementary Figures 2E,F**). Yearly variation in adult chinstrap penguin SI values showed no apparent relationship with over-winter sea ice conditions as adults had higher values
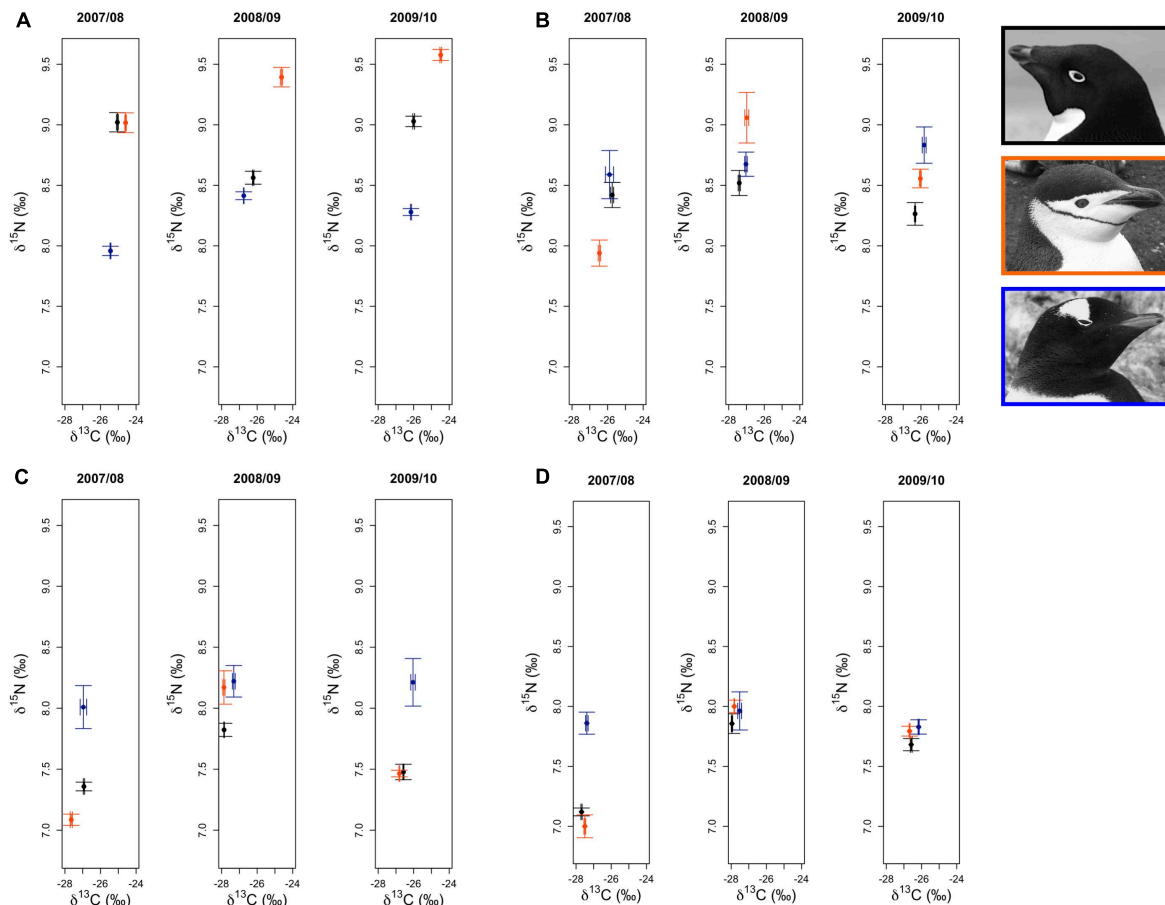
FIGURE 3 | Variation in $\delta^{13}C$ and $\delta^{15}N$ stable isotope values of Adélie (●), chinstrap (●), and gentoo (●) penguin red blood cell tissue for adults at the one-egg stage **(A)**, and their young chicks at five **(B)** and 15 **(C)** days of age, as well as older chicks at a population level age of 5 weeks **(D)**. Average isotope values (±1 standard error) for each species are presented for each year.

for both $\delta^{13}C$ and $\delta^{15}N$ in the second and third years of the study (**Figure 3A**, **Table 3**, and **Supplementary Figures 2C,D**).

Analyses of variation in $\delta^{13}C$ values of *Pygoscelis* chicks at 5 days of age reared at Anvers Island (*IDA* analysis 2, **Figures 1B,C**) resulted in only one model receiving a $\Delta AICc$ value ≤ 2. Again, the most parsimonious model was the global model that included terms for species, year, and an interaction for species × year. This model received a very high *w* value (0.97, **Table 2**). Parameter likelihoods indicated strong support for all these terms (**Table 3**). For $\delta^{15}N$ analyses of *Pygoscelis* chicks at 5 days of age, two models received $\Delta AICc$ value ≤ 2. The best-fit model included a term for species only and received more than two-times the support (*w* = 0.45) of the next best model (*w* = 0.18, **Table 2**). Parameter likelihoods indicated moderately strong support for the species term, weaker support for the year term, and no support for the interaction of species × year (**Table 3**). On average, 5-day-old Adélie and gentoo penguin chicks had similar $\delta^{13}C$ values, while chinstrap penguin chicks had lower $\delta^{13}C$ values (**Figure 3B** and **Table 3**). Gentoo penguin chicks on average had higher $\delta^{15}N$ values than the other species (**Figure 3B** and **Table 3**).

Analyses of variation in $\delta^{13}C$ values of *Pygoscelis* chicks at 15 days of age reared at Anvers Island (*IDA* analysis 3, **Figures 1B,C**) resulted in only one model receiving a $\Delta AICc$ value ≤ 2. The best-fit model was the global model that included terms for species, year, and an interaction for species × year, and received a very high *w* value (1.0, **Table 2**). Again, parameter likelihoods indicated strong support for all these terms (**Table 3**). Analyses of $\delta^{15}N$ SI values of 15-day-old *Pygoscelis* chicks resulted in only one model receiving a $\Delta AICc$ value ≤ 2. The best-fit model included terms for species and year only, and received a high *w* value (0.85, **Table 2**). Parameter likelihoods indicated strong support for both species and year terms (**Table 3**). Similar to the 5-day-old chicks, on average, 15-day-old Adélie and gentoo penguin chicks had similar $\delta^{13}C$ values, while chinstrap penguin chicks had lower $\delta^{13}C$ values (**Figure 3C** and **Table 3**). Gentoo penguin chicks on average had higher $\delta^{15}N$ values than the other species (**Figure 3C** and **Table 3**).
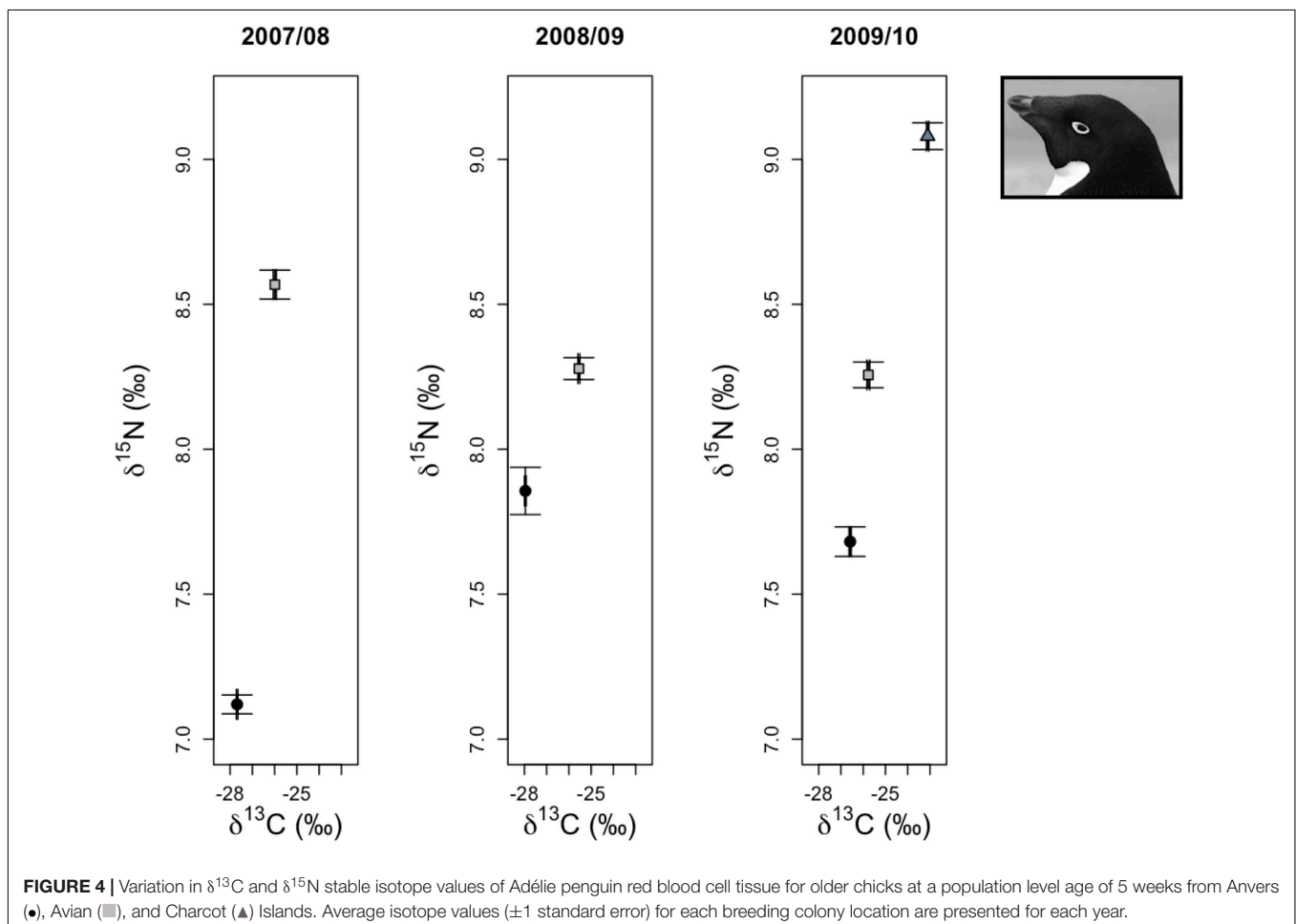
Analyses of variation in $\delta^{13}C$ and $\delta^{15}N$ values of 5-week-old *Pygoscelis* crèched chicks reared at Anvers Island (*IDA* analysis 4, **Figures 1B,C**) resulted in only one model receiving a $\Delta AICc$ value ≤ 2 for each isotope. The most parsimonious model for
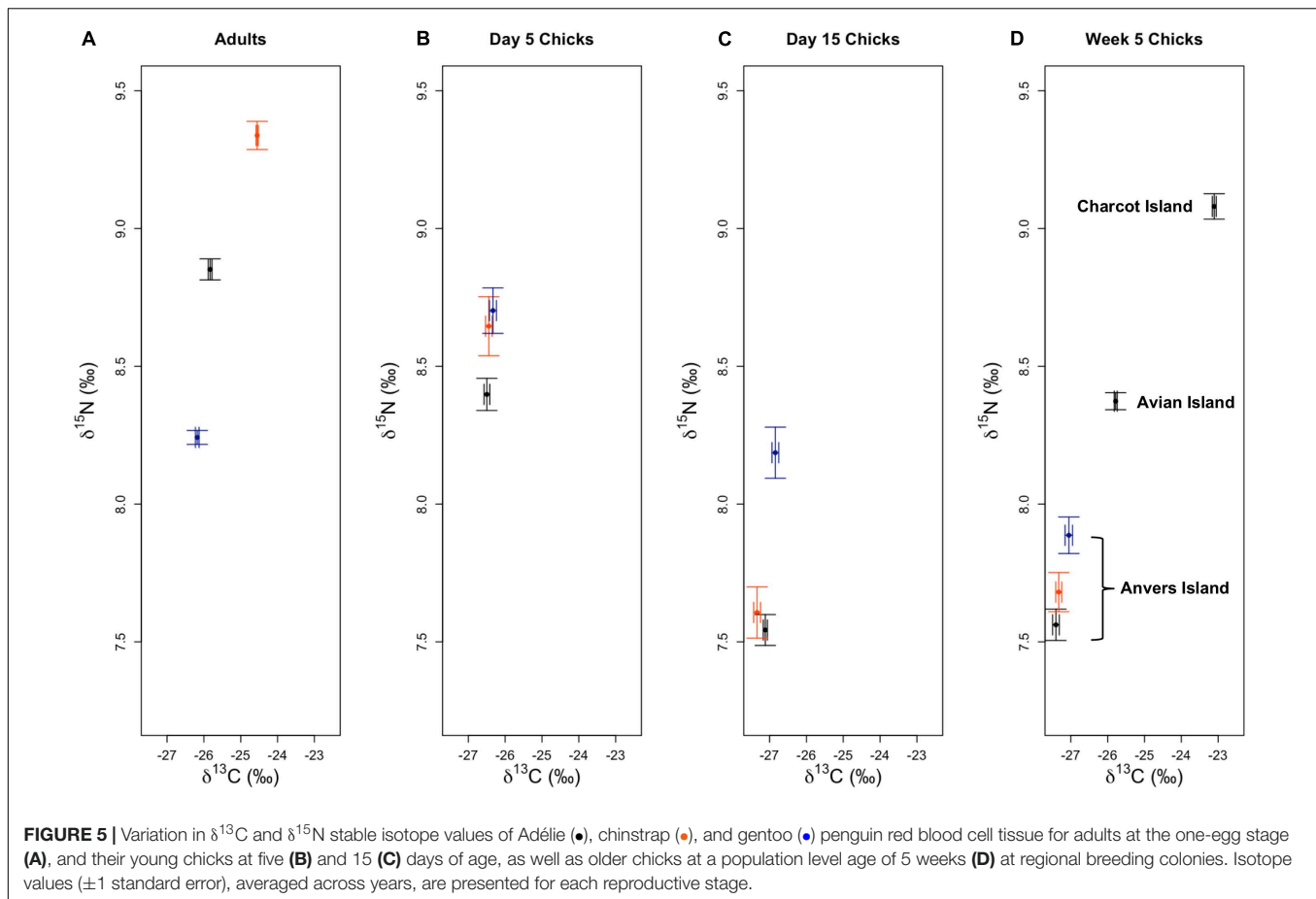
each isotope was the global model that included terms for species, year, and an interaction for species × year. Both models received very high w values (δ^{13}C: 0.89, δ^{15}N: 1.00) and R^2 values (δ^{13}C: 0.89, δ^{15}N: 0.52, **Table 2**). Parameter likelihoods indicated strong support for all terms in both analyses (**Table 3**). All species had higher δ^{13}C values in association with greater sea ice coverage within the 200 km^2 foraging grid at Anvers Island (**Figure 3D** and **Supplementary Figures 2A,C,E**). All species had similar δ^{15}N SI values during the second and third years of the study (**Figure 3D**).

Analyses of regional variation in δ^{13}C and δ^{15}N values of 5-week-old crèched Adélie chicks reared at Anvers, Avian, and Charcot Island breeding colonies (*IDA* analysis 5, **Figure 1B**) resulted in only one model receiving a ΔAICc value ≤ 2 for each isotope. The most parsimonious model for each isotope was the global model that included terms for location, year, and an interaction for location × year. Both models received very high w values (1.00 for each isotope) and R^2 values (δ^{13}C: 0.97, δ^{15}N: 0.86, **Table 2**). Parameter likelihoods indicated strong support for all terms in both analyses (**Table 3**). Across regional colonies, crèched Adélie penguin chicks had higher δ^{13}C and δ^{15}N values at more southern colonies (**Figure 4**, **Table 3**, and **Supplementary Figures 2A,B,G,H,I,J**) with higher over-winter sea ice conditions (**Figure 2B**). This relationship between sea ice conditions and

crèched Adélie penguin δ^{13}C values was also evident across years within regions where years with higher sea ice coverage was associated with higher δ^{13}C values (**Figure 4**, **Table 3**, and **Supplementary Figures 2A,G**). Chicks provisioned at Avian Island had more similar δ^{13}C and δ^{15}N values across years than their northern conspecifics reared at Anvers Island (**Figure 4**) despite annual sea conditions that varied by approximately 7000 km^2 on average (**Figures 2A,B**).

In summary, across all reproductive stages at Anvers Island (**Figures 1B,C**), the species term was consistently selected in all best-fit models for describing variation in community level δ^{13}C and δ^{15}N values of *Pygoscelis* penguin RBC tissue (**Table 2**). Importantly, species were most different in δ^{13}C and δ^{15}N values among adults at the one-egg stage (**Figure 5**). As parents provisioned chicks from local prey found within the foraging range of Anvers Island, *Pygoscelis* chicks at 5 weeks of age were much more similar isotopically than their parents at the one-egg stage in having lower values for both δ^{13}C and δ^{15}N (**Figure 5**). Chicks at 5 and 15 days of age tracked the progressive reduction in community δ^{13}C and δ^{15}N values where chicks at 5 days of age had higher values than chicks at 15 days of age (**Figure 5**). Regional analyses of 5-week-old crèched Adélie penguin chicks reared at Anvers, Avian, and Charcot Islands (**Figure 1B**) also

FIGURE 4 | Variation in δ^{13}C and δ^{15}N stable isotope values of Adélie penguin red blood cell tissue for older chicks at a population level age of 5 weeks from Anvers (●), Avian (■), and Charcot (▲) Islands. Average isotope values (±1 standard error) for each breeding colony location are presented for each year.

FIGURE 5 | Variation in δ^13^C and δ^15^N stable isotope values of Adélie (●), chinstrap (●), and gentoo (●) penguin red blood cell tissue for adults at the one-egg stage **(A)**, and their young chicks at five **(B)** and 15 **(C)** days of age, as well as older chicks at a population level age of 5 weeks **(D)** at regional breeding colonies. Isotope values (±1 standard error), averaged across years, are presented for each reproductive stage.

demonstrated a gradient in isotopic values where Adélie penguin chicks reared from more southern colonies, which are associated with higher over-winter sea ice coverage (**Figure 2B**), had higher δ^13^C and δ^15^N values than their northern conspecifics (**Figure 5**).

Trophic Position Analysis

Median trophic position of 5-week-old *Pygoscelis* crèched chicks reared at Anvers Island (*TPA* analyses 1–3) were broadly similar across species within a year, as well as across years, as 95% credibility intervals overlapped (**Table 4**). Similarly, median trophic position of 5-week-old Adélie penguin chicks reared at Anvers, Avian, and Charcot Islands (*TPA* analyses 1–7) were broadly similar across years and regions as 95% credibility intervals overlapped (**Table 4**). Adélie and chinstrap penguin chicks at Anvers Island had more variable median trophic position values across years than gentoo penguins (Adélie: 3.34–3.53, chinstrap: 3.31–3.57, gentoo: 3.55–3.56). Adélie penguin chicks reared from southern colonies with greater sea ice coverage at Avian and Charcot Islands had slightly higher median trophic position values (3.49–3.67, **Table 4**). See also **Supplementary Figure 3**.

Isotopic Mixing Model Analysis

Bayesian mixing models estimating the proportion of diet items provisioned by adult *Pygoscelis* penguins to 5-week-old crèched

chicks reared at Anvers Island (*IMMA* analysis 1, **Figures 1B,C**) considered three main prey types (**Table 1**) including two species of krill (Antarctic krill and *T. macrura*) and the myctophid, lanternfish. Within each year, the proportion of these diet items provisioned by adults to chicks were generally similar across *Pygoscelis* species at Anvers Island, which included 56–87% of the diet each season consisting of Antarctic krill (**Figure 6A** and **Table 4**). During the first year of the study, crèched gentoo penguin chicks consumed a lower proportion of Antarctic krill (60–76%) than chinstrap (79–94%) penguin chicks (**Figure 6A** and **Table 4**). During the second year of the study characterized by lower sea ice conditions, chicks of all three species consumed greater proportions of *Thysanoessa macrura* than each species did in other years, in particular Adélie penguins, but also chinstrap penguin chicks between 2007/2008 and 2008/2009, and gentoo chicks between 2008/2009 and 2009/2010 (**Figure 6A** and **Table 4**). Smaller proportions of each species' diet consisted of lanternfish (5–25%) across all 3 years of the study. However, gentoo chicks consumed greater proportions of fish overall (15–25%), and in particular during 2009/2010 (**Figure 6A** and **Table 4**).

Five main diet items were considered in mixing models estimating the proportion of diet items provisioned by adult penguins to 5-week-old Adélie penguin chicks reared at Avian Island (*IMMA* analysis 2, **Figure 1B** and **Table 1**). Prey items

TABLE 4 | Bayesian estimates of trophic position, proportions of prey, and isotopic niche as standard ellipse area (SEA-B) and associated 95% credibility intervals (CI) for 5-week-old *Pygoscelis* penguin chicks reared at breeding colonies throughout the western Antarctic Peninsula (*TPA* models 1–7, *IMMA* models 1–7, and *INA* models 1–7).

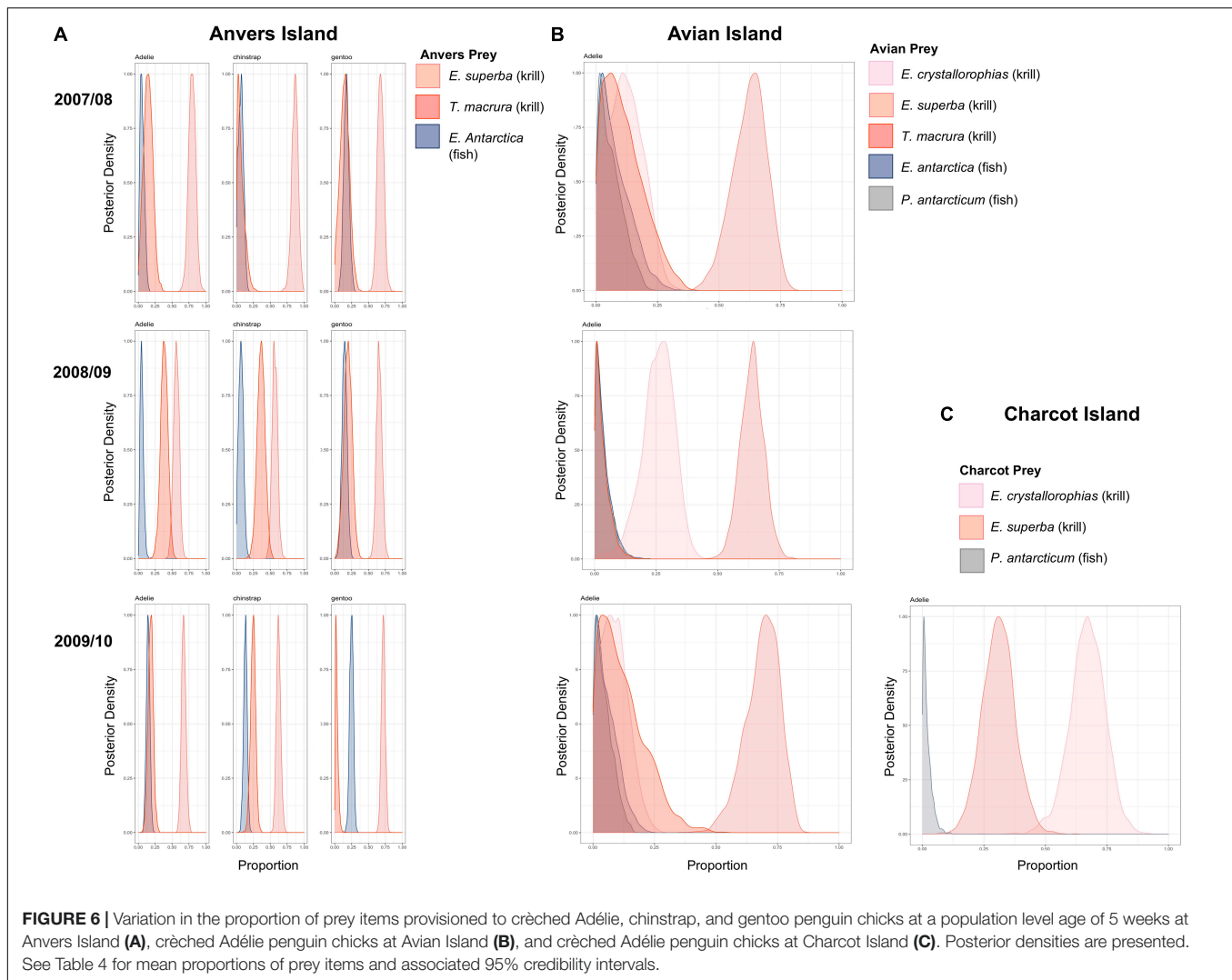| Study colony and year	Consumer	Median trophic position (lower CI, upper CI)	Mean proportion of prey items provisioned to 5-week-old chicks (lower CI, upper CI)					Mean SEA-B (lower CI, upper CI)
			E. crystallorophias (krill)	*E. superba* (krill)	*T. macrura* (krill)	*E. antarctica* (fish)	*P. antarcticum* (fish)	
Anvers Island								
2007/2008	*P. adeliae*	3.34 (3.13, 3.56)	NA	0.80 (0.71, 0.88)	0.15 (0.04, 0.25)	0.06 (0.01, 0.11)	NA	0.05 (0.03, 0.08)
	P. antarcticus	3.31 (3.09, 3.52)	NA	0.87 (0.79, 0.94)	0.07 (0.01, 0.17)	0.07 (0.01, 0.13)	NA	0.15 (0.07, 0.25)
	P. papua	3.56 (3.36, 3.78)	NA	0.68 (0.60, 0.76)	0.15 (0.03, 0.26)	0.17 (0.11, 0.24)	NA	0.27 (0.14, 0.42)
2008/2009	*P. adeliae*	3.53 (3.41, 3.65)	NA	0.56 (0.49, 0.63)	0.38 (0.30, 0.47)	0.05 (0.02, 0.10)	NA	0.17 (0.09, 0.26)
	P. antarcticus	3.57 (3.45, 3.69)	NA	0.57 (0.50, 0.63)	0.36 (0.27, 0.46)	0.07 (0.01, 0.13)	NA	0.04 (0.02, 0.07)
	P. papua	3.56 (3.41, 3.71)	NA	0.66 (0.59, 0.73)	0.20 (0.10, 0.29)	0.15 (0.09, 0.21)	NA	0.35 (0.19, 0.53)
2009/2010	*P. adeliae*	3.50 (3.38, 3.63)	NA	0.67 (0.62, 0.73)	0.18 (0.12, 0.24)	0.15 (0.10, 0.19)	NA	0.13 (0.07, 0.20)
	P. antarcticus	3.54 (3.41, 3.67)	NA	0.62 (0.57, 0.68)	0.25 (0.18, 0.30)	0.13 (0.09, 0.17)	NA	0.06 (0.03, 0.09)
	P. papua	3.55 (3.42, 3.68)	NA	0.72 (0.67, 0.77)	0.03 (0.01, 0.07)	0.25 (0.20, 0.29)	NA	0.07 (0.03, 0.10)
Avian Island								
2007/2008	*P. adeliae*	3.67 (3.31, 4.01)	0.12 (0.01, 0.24)	0.62 (0.50, 0.73)	0.11 (0.01, 0.27)	0.08 (0.01, 0.20)	0.06 (0.01, 0.16)	0.25 (0.16, 0.36)
2008/2009	*P. adeliae*	3.54 (3.41, 3.67)	0.26 (0.14, 0.35)	0.64 (0.56, 0.72)	0.03 (0.002, 0.09)	0.04 (0.001, 0.10)	0.03 (0.001, 0.10)	0.25 (0.15, 0.35)
2009/2010	*P. adeliae*	3.49 (3.38, 3.60)	0.09 (0.01, 0.19)	0.69 (0.56, 0.79)	0.12 (0.01, 0.29)	0.06 (0.004, 0.14)	0.05 (0.003, 0.11)	0.19 (0.12, 0.28)
Charcot Island								
2009/2010	*P. adeliae*	3.66 (3.52, 3.80)	0.67 (0.55, 0.78)	0.31 (0.20, 0.42)	NA	NA	0.02 (0.001, 0.06)	0.12 (0.07, 0.19)

included all species considered by Anvers Island analyses, as well as crystal krill and the notothenoid, Antarctic silverfish. Across study years at Avian Island that were characterized by variability in winter sea ice coverage of approximately 7000 km^2 (**Figure 2B**), the proportion of various diet items consumed by crèched Adélie penguin chicks was remarkably similar, with Antarctic krill consisting of 62–69% of the diet (**Figure 6B**). Smaller proportions of the diet consisted of crystal krill (9–26%) and *T. macrura* (3–12%), while fish (lanternfish and Antarctic silverfish) again comprised smaller proportions (3–8%, **Figure 6B**).

Three main prey types were considered in mixing models estimating dietary proportions consumed by 5-week-old Adélie penguin chicks reared at Charcot Island during the breeding season of 2009/2010 only (*IMMA* analysis 3, **Figure 1B** and **Table 1**). These prey types included dominant species found within high latitude, continental-shelf regions of the Southern Ocean including Antarctic and crystal krill, as well as Antarctic silverfish. Charcot Island has the highest winter sea ice coverage within the PAL-LTER regional study grid (**Figure 2B**).

Interestingly, crystal krill comprised the largest proportion of the diet (55–78%) of the diet provisioned to Adélie penguin chicks at Charcot Island, while Antarctic krill represented 20–42% (**Figure 6C**). Antarctic silverfish again comprised only a very small proportion of the diet (up to 6%, **Figure 6C**).

Isotopic Niche Analysis

Isotopic niche analysis estimated SEA-B of crèched penguin chick RBC tissue and indicated that isotopic width was much more variable among *Pygoscelis* chicks of the northwestern AP located at Anvers Island where reductions in sea ice have been greatest, in comparison with populations farther south at Avian and Charcot Islands where sea ice coverage was greater (**Table 4**). Based on 95% credibility intervals, SEA-B of Adélie penguin chicks ranged from 3–8‰^{2} in 2007/2008, to 9–26‰^{2} in 2008/2009 and 7–20‰^{2} in 2009/2010 (**Table 4**). Similarly variable estimates of SEA-B for chinstrap (2007/2008: 7–25‰^{2}, 2008/2009: 2–7‰^{2}, 2010/2009: 3–9‰^{2}) and gentoo (2007/2008: 14–42‰^{2}, 2008/2009: 19–53‰^{2}, 2010/2009: 3–10‰^{2}) penguins were observed, however, gentoo penguins had the largest estimates of SEA-B of all

FIGURE 6 | Variation in the proportion of prey items provisioned to crèched Adélie, chinstrap, and gentoo penguin chicks at a population level age of 5 weeks at Anvers Island **(A)**, crèched Adélie penguin chicks at Avian Island **(B)**, and crèched Adélie penguin chicks at Charcot Island **(C)**. Posterior densities are presented. See Table 4 for mean proportions of prey items and associated 95% credibility intervals.

three species (**Table 4**). This result is not surprising as gentoo penguins were provisioned greater proportions of fish in their diet (**Figure 6A**) that have higher isotopic values (**Table 1**). In contrast, SEA-B of Adélie penguin chicks reared at Avian (2007/2008: 16–36‰^{2}, 2008/2009: 15–35‰^{2}, 2010/2009: 12–28‰^{2}) and Charcot (2010/2009: 7–19‰^{2}) Islands was much more consistent across years at Avian Island and both regions in 2010 (**Table 4**) although not necessarily wider than Adélie penguin chicks at Anvers Island in 2008/2009 and 2009/2010 (**Table 4**). See also **Supplementary Figure 1**.

DISCUSSION

Elucidating relationships between sea ice change and associated food web effects on penguin demography has been highlighted as a key component to understanding population responses to climate variability in the Southern Ocean (Forcada and Trathan, 2009). To this end, our study considered regional breeding population trends among western AP *Pygoscelis* penguins from

an integrated food web perspective based on variation in δ^{13}C and δ^{15}N values of penguin blood tissue measured at the individual level, as well as SI values of dominant prey. Many of our specific predictions were supported by the data. First, our analyses at Anvers Island demonstrated that over the course of the breeding season, individuals became increasingly more similar isotopically, as predicted, due to a general decrease in both δ^{13}C and δ^{15}N values of blood tissue (**Figures 5A–D**). Older chicks at 5 weeks of age near Anvers Island, the most isotopically similar breeding stage (**Figures 3D**, **5D**), also occupied generally similar trophic positions as would be expected, particularly in the second and third year of study (**Table 4**). Furthermore, isotopic mixing models indicated that the proportion of diet items provisioned by adults to older chicks reared near Anvers Island were generally similar across *Pygoscelis* species within years (**Figure 6A**). Secondly, as predicted, Adélie penguin chicks reared at regional breeding colonies had higher isotope values at more southern colonies (**Figures 4**, **5**). Within this context, trophic position values generally increased with latitude (**Table 4**), while the proportions of dietary items provisioned

by Adélie penguin adults to chicks at regional colonies were notably different, particularly at Charcot Island (**Figures 6A–C**), generally reflecting prey characteristic of a high Antarctic marine food web at more southerly colonies.

Pygoscelis Adults at Anvers Island

Adults at the one egg stage were the most isotopically distinct breeding stage, which suggests that these penguin species are foraging on different prey across the western AP or Scotia Sea during the 30–60 days prior to nest initiation in association with their preferred late winter/early spring habitat. Chinstrap penguins had the highest δ^{13}C and δ^{15}N isotope values at this stage followed by Adélie penguins, whereas gentoo penguins had the lowest δ^{13}C and δ^{15}N values among the species (**Figure 5A**). These data, coupled with previous research on our study populations demonstrating that male and female *Pygoscelis* penguins are not greatly segregated in their pre-breeding foraging niche (Gorman et al., 2014), our own field observations, and knowledge of other seabird systems suggest the possibility that adult male and female Adélie and chinstrap penguins may rely on a fish-based diet prior to egg production in association with off-shore winter habitats in sea ice-associated (Williams, 1995; Ainley, 2002) or sea ice-free regions (Trivelpiece et al., 2007), respectively. However, gentoo penguins may rely primarily on krill while wintering near-shore closer to breeding colonies (Tanton et al., 2004). Over the course of our study, depredation of *Pygoscelis* penguin eggs by brown skuas (*Catharacta antarctica*) at breeding colonies near Anvers Island revealed consistent species-specific variability across years in the color of penguin egg yolks where Adélie and chinstrap females produce pale yellow colored yolk, while gentoo females produce bright orange to red yolk (K. B. Gorman, pers. obs., see also **Supplementary Figure 4**). Research on alcids in the North Pacific Ocean has shown yolk coloration to be related to carotenoid deposition by females, including both the types and concentration of carotenoids, as a function of foraging at different tropic levels (Hipfner et al., 2010a,b). These studies confirmed marked variability in carotenoids among crustacean versus fish prey where lower trophic position crustaceans contained high concentrations of astaxanthin, while higher trophic position fish prey contained only low levels of the carotenoids astaxanthin, lutein, and zeaxanthin (Hipfner et al., 2010b). Similarly, yolk of these seabirds with a more red hue contained only astaxanthin, while yolk with a more yellow hue contained all three carotenoid types (Hipfner et al., 2010b). Inter- and intra-specific analyses showed a negative relationship between carotenoid concentration and δ^{15}N values of the yolk tissue, indicating that red colored yolks are derived from nutrients obtained at lower trophic positions with high levels of carotenoids, while yellow colored yolks are derived from higher trophic position diets with lower levels of carotenoids (Hipfner et al., 2010a,b). Similar trophic relationships may govern patterns of carotenoid allocation among *Pygoscelis* penguins, which would account for the fact that females of the two species with enriched δ^{15}N values of blood at the onset of breeding also produce eggs with pale yellow yolk. In accordance, our δ^{15}N data show forage fishes to be enriched relative to krill (**Table 1**) similar to results by Polito et al. (2011b). However, unlike Polito et al. (2011a) that

concluded female Adélie and gentoo penguins both rely on higher trophic position prey prior to breeding due to their similarity in eggshell δ^{15}N enrichment, our results suggest that adults of these two species may rely on very different prey during the 30–60 days prior to nest initiation. We caution that more detailed studies of relationships between carotenoid content and SI values of *Pygoscelis* penguin egg yolk are needed to fully support our interpretation of the specific nutrient sources used to fuel egg production. However, our data do suggest that *Pygoscelis* penguins are associated with different food webs during late winter/early spring, presumably as a function of each species preferred winter habitat. These results have important implications for understanding community variation in nutritional resources critical to the individuals that return to breed, and more specifically egg production itself.

Our study revealed important relationships between each species dietary niche during late winter/early spring and the preceding winter's average sea ice coverage (**Figure 2A** and **Supplementary Figure 2A**). Notably, foraging by Adélie penguins appeared most closely associated with sea ice variability as blood δ^{15}N values of adults were higher in years of relatively higher sea ice conditions, and lower in 2008 following the winter with the lowest sea ice conditions (**Supplementary Figure 2B**). Conversely, blood δ^{15}N values of gentoo penguins were higher following the 2008 winter of extremely low winter sea ice coverage (**Figure 3A**). Variation in blood δ^{15}N values of adult chinstrap penguins was independent of winter sea ice conditions as individuals had higher values in the last 2 years of study (**Figure 3A** and **Supplementary Figure 2F**). Interestingly, Adélie and gentoo penguins had similar responses in blood δ^{13}C values across years where individuals of both species had higher values in the second year of the study following the winter of low sea ice conditions (**Figure 3A**). Similar to the blood δ^{15}N results for adult chinstraps, blood δ^{13}C values were independent of winter sea ice conditions as individuals had similar values across the 3 years of study (**Figure 3A** and **Supplementary Figure 2C**). Our data suggest that species do hold different foraging affinities with sea ice, where Adélie penguins have higher blood δ^{15}N and δ^{13}C values in years with higher sea ice coverage, gentoo penguins had higher δ^{15}N but lower δ^{13}C values in association with higher sea ice coverage, while blood δ^{15}N and δ^{13}C values chinstrap penguins were independent of sea ice conditions (**Supplementary Figures 2A–F**; see also Gorman et al., 2014). In this context, it is possible that the higher trophic position prey, possibly fish, Adélie and chinstrap penguins appear to rely upon during late winter/early spring (**Figure 3A**) may include different communities given each species differing foraging response to sea ice variability and generally disparate wintering locations.

Previous work on pelagic fish communities of the western AP has shown that mesopelagic and neritic assemblages are typically segregated by sea ice coverage, as well as hydrographic properties (Kellerman, 1996; Donnelly and Torres, 2008). Mesopelagic fishes, including the genera *Electrona*, *Gymnoscopelus*, *Protomyctophum*, *Bathylagus*, *Cyclothone*, and *Notolepis,* typically occur in association with circumpolar deep water (CDW), a relatively warm and more saline water mass derived from the Antarctic Circumpolar Current found both at the continental shelf break, and in association with cross-shelf

submarine canyons that act as a conduit delivering CDW to more coastal regions (Kellerman, 1996; Donnelly and Torres, 2008). Conversely, notothenoids, in particular *Pleuragramma*, are found in colder and less saline coastal waters subject to sea ice formation along the western AP (Kellerman, 1996; Donnelly and Torres, 2008). The Notothenoids, which includes approximately 80 species, are critical components of energy transfer within high Antarctic continental shelf regions such as the Ross Sea, with Antarctic silverfish comprising a majority of the mid-water fish biomass (La Mesa et al., 2004). Importantly, Antarctic silverfish hold a strong affinity for the presence of sea ice (Kellerman, 1996), particularly during early life stages (Vacchi et al., 2004; Bottaro et al., 2009). Therefore, we interpret our data to suggest that adult chinstrap penguins may be relying on mesopelagic fish assemblages associated with open water habitats, while adult Adélie penguins may depend on sea ice-associated neritic assemblages during the 30–60 days prior to egg production given each species produces pale yellow colored yolk, forages at relatively high trophic positions based on $\delta^{15}N$ values of RBC tissue, but have very different foraging associations with over winter sea ice variability. Emslie et al. (2003) corroborate these ideas in studying prey remains at active chinstrap and Adélie penguin breeding colonies at King George Island where chinstraps preferred the myctophid, lanternfish, while Adélie prey remains primarily included Antarctic silverfish.

Pygoscelis Chicks at Anvers Island

Chicks at day 5, 15, and 5 weeks of age at Anvers Island became increasingly isotopically similar, specifically due to a reduction in blood $\delta^{13}C$ and $\delta^{15}N$ values (**Figures 3B–D**, **5B–D**). We interpret this trend in isotopic variability over the chick stage to reflect the turnover of nutrients from those originally allocated to egg tissue during late winter/early spring, to those nutrients provisioned by parents to chicks from local foraging areas during summer (e.g., Sears et al., 2009). Interestingly, gentoo chicks appeared to have a slower rate of isotopic change as compared to Adélie or chinstrap chicks (**Figures 5B–D**). This may reflect, in part, the fact that gentoo chicks have the slowest growth rate of the three *Pygoscelis* species, broadly corresponding to their more northerly distribution (Volkman and Trivelpiece, 1980; Williams, 1995). Given the extreme similarity in 5-week-old chick isotope values across species, our data suggest that parents of all three species rely on very similar sources of nutrients to raise chicks near Anvers Island. Within this context, our trophic position analyses confirmed that older chicks do occupy generally similar trophic positions across species (**Table 4**), which appears to be due to the provisioning of similar proportions of prey items as identified by our isotopic mixing model analyses (**Figure 6A**). Only in year one did gentoo chicks appear to hold a slightly higher trophic position than the other species, which was driven by a larger proportion of *T. macrura* and *E. antarctica* being provisioned by adult gentoo penguins (**Table 4** and **Figure 6A**) that have higher $\delta^{15}N$ values relative to Antarctic krill (**Table 1**). Not surprisingly, Antarctic krill was the dominant prey species provisioned to chicks by all species during each study year (**Figure 6A**). Interspecific variability in

$\delta^{13}C$ values of penguins has been related to inshore versus offshore foraging habitats of sub-Antarctic penguins (e.g., Cherel and Hobson, 2007; Carpenter-Kling et al., 2020). We detected relatively little variation in $\delta^{13}C$ values of chicks across species within each year (**Figures 3B–D**), which would suggest that adults of all three species are foraging in similar regions while provisioning chicks during the breeding season. More recent tracking results of adult Adélie and gentoo penguins nesting near Anvers Island has confirmed that adults are generally foraging in more nearshore habitats (Pickett et al., 2018), which would explain the similar $\delta^{13}C$ values detected among chicks of all species by our study.

Associations between 5-week-old chick blood isotope values and over-winter sea ice conditions within the Anvers Island foraging grid were variable across species (**Figures 2B**, **3D**). Crèched gentoo penguin chicks showed no association between blood $\delta^{15}N$ values and the previous winter's average sea ice coverage. However, 5-week-old gentoo chicks appeared to have higher blood $\delta^{13}C$ values during years with higher sea ice coverage (i.e., 2007/2008 and 2009/2010) (**Supplementary Figure 2E**). Isotopic values of 5-week-old chinstrap chicks were higher in blood $\delta^{15}N$ during the second year of study following the winter of very low sea ice coverage in comparison with the first year (**Figure 3D**), however, this relationship was not as strong between years two and three of the study (**Figure 3D**). Similar to gentoo chicks, chinstrap penguin chicks had higher blood $\delta^{13}C$ values during years with higher sea ice coverage (**Supplementary Figure 2C**). Crèched Adélie penguin chicks showed similar trends across years as chinstrap chicks where higher blood $\delta^{15}N$ values were observed in the second year of the study (**Figures 3C,D**). Similar to the other species, 5-week-old Adélie penguin chicks had higher blood $\delta^{13}C$ values during years with higher sea ice coverage (**Supplementary Figure 2A**). We note that although our data suggest rather consistent positive relationships between blood $\delta^{13}C$ values and over-winter sea ice conditions, our dataset is limited to only 3 years of study. Further, foraging decisions by adult penguins to provisions their chicks are undoubtedly influenced by factors not measured by our study such as competition with other krill predators, or oceanographic conditions other than sea ice that might structure the availability of prey such as small- or meso-scale processes.

Isotopic mixing models indicated that Adélie and chinstrap parents provisioned their chicks greater proportions of *T. macrura* following the winter of very low sea ice coverage (**Figures 2B**, **6A**), which accounted for these species occupying a higher trophic position in year two of the study (**Table 4**). During the third year of the study, parent penguins provisioned their chicks slightly higher proportions of the myctophid, *E. antarctica*. Provisioning of *E. antarctica* during 2009/2010 appeared to have no relationship with sea ice variability as this prey item was not provisioned as readily during the first year of study characterized by similar winter sea ice conditions. It's possible the increased presence of *E. antarctica* in the summer diet during the third year of the study was related to increased CDW intrusion due to wind forcing (Martinson et al., 2008) into the Palmer Deep canyon, where penguins typically forage near Anvers Island (Kahl et al., 2010; Schofield et al., 2013).

Adélie Chicks at Regional Islands

Five-week-old Adélie penguin chicks at regional breeding colonies had increasingly higher blood $\delta^{13}C$ and $\delta^{15}N$ values at higher latitude colonies (**Figures 4**, **5**) associated with greater over-winter sea ice coverage within foraging grids (**Figure 2B**). This trend in isotopic variability was strong as it persisted across years at both Anvers and Avian Island colonies and was additionally confirmed by the 1 year of data collected at Charcot Island. Within this context, 5-week-old Adélie chicks had higher trophic position values at regional colonies in association with greater sea ice coverage (**Table 4**). Our mixing model analyses suggested that higher blood $\delta^{13}C$ and $\delta^{15}N$ values of regional Adélie chicks, particularly at Charcot Island, was primarily due to greater proportions of crystal krill being provisioned to chicks at higher latitude colonies, as opposed to greater proportions of Antarctic silverfish as we originally predicted. Like Antarctic silverfish, crystal krill are key components of high Antarctic continental shelf food webs (La Mesa et al., 2004). Therefore, it is not surprising that crystal krill are provisioned by adult Adélie penguins to chicks in greater proportions at our highest latitude study site associated with the greatest over-winter sea ice coverage (**Figure 2B**). However, the lack of a substantial fish component at Charcot Island during the final year of our study was surprising and may be related to a lack of recruitment events of Antarctic silverfish given the relatively low sea ice conditions of the previous winters since 2006 (Ducklow et al., 2013; Parker et al., 2015).

There was no strong relationship between Adélie penguin chick blood isotope values and over-winter sea ice variability within the foraging grid at Avian Island (**Figure 4**). However, there was less variability among years in chick isotope values at Avian Island than Anvers Island, which is also reflected in our results for SEA-B of penguin chicks (**Table 4**). Within this context, mixing model results indicated that across years, the proportion of prey provisioned to chicks at Avian Island was more consistent than that modeled for Anvers Island, and importantly suggest the idea that marine foraging areas may be more predictable in regions with greater over-winter sea ice coverage. Environmental predictability is critical to the evolved life history strategies of penguins (Forcada and Trathan, 2009), particularly during the breeding season given that adult penguins must maximize their foraging effort within a restricted geographic range in order to provision and protect chicks at terrestrial nesting sites. Within the northern sector of our regional study area, where changes in sea ice have been most prominent, ocean-climate variability may be impacting penguin populations by altering the predictability of prey critical for successful reproduction of adults and recruitment of chicks.

Isotopic Niche

Results for SEA-B, a proxy for dietary niche width, provided evidence that penguin breeding populations with the most dramatic changes in their population trends (i.e., those at Anvers Island) were much more variable in SEA-B across years than Adélie penguin populations farther south at Avian and Charcot Islands (**Table 4**). However, dietary niche width of Avian and

Charcot Island Adélie populations were not consistently larger than Anvers Island populations as was predicted, only for some species for a given year (Adélie penguins in 2007/2008, chinstrap penguins in 2008/2009, and chinstrap and gentoo penguins in 2009/2010). However, our data provide some intriguing evidence that variability in dietary niche width may be associated with breeding population trends for Adélie penguins along the western AP, particularly for Anvers and Avian populations.

Sea Ice Trophic Interaction Hypothesis

The data we present here lends insight on key marine food web drivers of *Pygoscelis* penguin reproduction at the regional scale along the western AP. Within the context of divergent breeding population responses among all three species occurring near Anvers Island, our most northern study site, our results question the long standing paradigm that Antarctic krill are the key food web component critical to the reproductive survival of these species in this region of the Antarctic (e.g., Fraser et al., 1992; Fraser and Hofmann, 2003; Hinke et al., 2007; Trivelpiece et al., 2011). Trivelpiece et al. (2011) argued that populations of both chinstrap and Adélie and penguins breeding at the South Shetland Islands (**Figure 1B**) are regulated by the availability of Antarctic krill, which would explain why both species appear to be declining in this region in association with reductions in krill stocks due to sea ice loss, increased pressures from krill fishery expansions, as well as recovering populations of other krill predators such as seals and whales. Demographically, the decline of these populations is considered driven by reduced survival and recruitment of young birds as breeding adults due to a reduction in krill availability that has reduced fledgling condition, which impacts energetic buffers following departure from natal colonies when young birds are learning to self-feed. While our data confirm that Antarctic krill are in fact a dominant prey item in the summer provisioning diet of both chinstrap and Adélie penguins at Anvers Island (**Figure 6A**), and therefore, undoubtedly play a major role in determining variation in fledging condition, our data also suggest that adults of these species that return to breed may rely on higher trophic position prey that we argue may be comprised of two differing communities of fish as discussed previously. Within this context, juveniles of these species may also rely on these same fish communities after the breeding season and throughout the winter months in order to survive. Therefore, an alternative hypothesis to that offered by Trivelpiece et al. (2011), specifically for the western AP populations, is that variation in the availability of critical fishes may be an important, and underappreciated, driver of juvenile survival and recruitment as breeding adults for these species. If in fact chinstrap and Adélie penguins breeding near Anvers Island are linked to mesopelagic (myctophid) and neritic (notothenoid) fish fauna during the non-breeding period, respectively, this may explain differing population trends near Anvers Island in association with regional reductions in sea ice as notothenoids such as Antarctic silverfish hold life histories tightly associated with the presence of sea ice (Kellerman, 1996; La Mesa et al., 2004; Vacchi et al., 2004; Bottaro et al., 2009), while mesopelagic fishes are typically found

in sea ice free regions in association with ACC-derived warmer water masses (Kellerman, 1996; Donnelly and Torres, 2008) – an oceanic habitat that has been enhanced by ongoing regional climate changes. Of all three species, gentoo penguins showed less variability across breeding stages in stable isotope values (**Figures 5A–D**), reflecting a more consistently available nutrient source, likely krill, important to this population's breeding effort. Dietary niche stability may partly explain why numbers of gentoo penguins have increased dramatically near Anvers Island since the mid-1990's. However, the rapid rate of increase suggests that immigration of individuals into the population is clearly an important factor as well. These issues underscore the importance of research that can address not only the spatial distribution and foraging ecology of these species outside the breeding season (e.g., Bost et al., 2009), but also carry-over or cross-seasonal effects on breeding performance (e.g., Harrison et al., 2011), as well the role of dispersal as a contributing factor in population change (e.g., Dugger et al., 2010; Clucas et al., 2014; Gorman et al., 2017).

Our results further develop an understanding of marine food web drivers of Adélie penguin reproduction during late chick-rearing at the regional scale throughout the western AP demonstrating higher latitude breeding populations, which have increased or are stable, to be reliant upon sea ice-associated food webs more characteristic of high Antarctic regions due to the greater provisioning of crystal krill to chicks (**Figures 6A–C**). Recent research reported by Ainley et al. (2018) for Adélie penguin populations of the Ross Sea confirms a link between a high Antarctic marine diet and enhanced demographic trends as chicks reared on Antarctic silverfish had a higher fledge mass and greater probability of returning to the colony as sub-adults. Further, the paleoecological record during the late Holocene suggests that Antarctic silverfish and crystal krill dominated diets of Adélie penguins during periods of colder climate and greater sea ice coverage (Emslie and McDaniel, 2002; Lorenzini et al., 2010), which generally corroborates our understanding of regional variation in the dietary niches occupied by Adélie penguins. Therefore, the onset of the historical decline of breeding Adélie penguins near Anvers Island that started in the late 1980's and early 1990's may have resulted from shifts in a high Antarctic marine food web dominated by sea ice, crystal krill and Antarctic silverfish to one more typical of sea ice-free, lower latitude regions characterized by Antarctic krill and myctophid fish assemblages.

DATA AVAILABILITY STATEMENT

Data reported here are publicly available within the PAL-LTER data system (datasets #223, 224, 225, 226, and 227): http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets. These data are additionally archived within the US LTER Network's Information System Data Portal: https://lternet.edu/using-lter-data/. Individuals interested in using these data are therefore expected to follow the US LTER Network's Data Access Policy, Requirements, and Use Agreement: http://www.lternet.

edu/policies/data-access. All datasets and associated R code are available on GitHub: https://github.com/gormankb/Gorman-et-al.-Frontiers-in-Marine-Science.

ETHICS STATEMENT

Fieldwork was conducted in accordance with Antarctic Conservation Act permits to WF, in addition to Canadian Committee on Animal Care guidelines (Simon Fraser University Animal Care Permit 890B-08 to KG and TW).

AUTHOR CONTRIBUTIONS

KG, TW, and WF conceived and designed the study. KG and KR performed fieldwork and lab analysis. KG, KR, TW, and WF contributed reagents/materials/analysis tools. KG analyzed the data and wrote the manuscript with contributions from KR, TW, and WF. All authors approved the submitted version of the manuscript.

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SUPPLEMENTARY MATERIAL

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