









Skin in the game: Epidermal molt as a driver of long-distance migration in whales

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Abstract

Long-distance migration in whales has historically been described as an annual, round-trip movement between high-latitude, summer feeding grounds, and low-latitude, winter breeding areas, but there is no consensus about why whales travel to the tropics to breed. Between January 2009 and February 2016, we satellite-tagged 62 antarctic killer whales (*Orcinus orca*) of four different ecotypes, of which at least three made short-term (6–8 weeks), long-distance (maximum 11,000 km, round trip), essentially nonstop, migrations to warm waters (SST 20°C–24°C), and back. We previously suggested that antarctic killer whales could conserve body heat in sub-freezing (to –1.9°C) waters by reducing blood flow to their skin, but that this might preclude normal (i.e., continuous) epidermal molt, and necessitate periodic trips to warm waters for routine skin maintenance (“skin molt migration,” SMM). In contrast to the century-old “feeding/breeding” migration paradigm, but consistent with a “feeding/molting” hypothesis, the current study provides additional evidence that deferred skin molt could be the main driver of long-distance migration for antarctic killer whales. Furthermore, we argue that for all whales that forage in polar latitudes and migrate to tropical waters, SMM might also allow them to exploit rich prey resources in a physiologically challenging environment and maintain healthy skin.

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KEYWORDS

Antarctica, diatoms, killer whale, *Orcinus orca*, satellite tagging, skin molt, whale migration

1 | INTRODUCTION

1.1 | Why do whales migrate?

Baleen whales undertake the longest-known migrations of any mammal: gray whales (*Eschrichtius robustus*) complete round trips of 15,000–25,000 km, and an individual humpback whale (*Megaptera novaeangliae*) traveled at least 18,840 km (Swartz, 2018; Robbins, Dalla Rosa, & Allen, 2011; respectively). Surprisingly, and despite what must be a compelling reason(s), why whales travel these vast distances is still unknown.

Historically, large whale migration has been described as an annual, round-trip movement between high-latitude, summer feeding grounds, and low-latitude, winter breeding areas—a “feeding/breeding” paradigm that has held sway for over a century (e.g., Chittleborough, 1958; Geijer, Notarbortolo de Sciara, & Panigada, 2016; Jonsgård, 1966; Kellogg, 1929; Lillie, 1915; Lockyer & Brown, 1981; Mackintosh, 1965; Matthews, 1937; Norris, 1967; Stern & Friedlaender, 2018; Stevick, McConnell, & Hammond, 2002). It has long been recognized that whales migrate to high latitudes during summer to forage on seasonally abundant prey, but why they then migrate thousands of kilometers to winter and breed in low latitudes, where feeding opportunities are generally scarce or nonexistent, has remained a mystery (e.g., Berta, Sumich, & Kovacs, 2015; Clapham, 2001; Corkeron & Connor, 1999; Lavigne, Innes, Worthy, & Edwards, 1990; Stern & Friedlaender, 2018; Stevick et al., 2002).

Over the years, numerous hypotheses have been proposed to explain whale migration to low latitudes. Foremost has been the putative growth and survivorship benefits that accrue to calves born in warm waters. Although the “calf thermoregulation” hypothesis has long been the most popular explanation (e.g., Clapham, 2001; Dawbin, 1966; Mackintosh, 1965; Norris, 1967; Rasmussen et al., 2007; Whitehead & Moore, 1982), others have not been persuaded (e.g., Corkeron & Connor, 1999; Elsner, 1999; Evans, 1987; Gaskin, 1982; Stern & Friedlaender, 2018; Stevick et al., 2002). As Bowen and Siniff (1999) and other skeptics have pointed out, bowhead whales (*Balaena mysticetus*) live year-round and calve in the Arctic and subarctic, and several other, much smaller, odontocete and pinniped species also live and breed in arctic and antarctic waters—thermoregulation in polar latitudes should not pose an insurmountable physiological challenge to the newborn calves of large whales.

As a variant on the calf thermoregulation hypothesis, Brodie (1975) suggested that adult rorquals could optimize their own energy budgets by relocating to warm waters during winter when polar areas are colder and prey scarcer. Additional support for this hypothesis came from Kshatriya and Blake (1988) who used energetic models and data from antarctic blue whales and fin whales (*Balaenoptera musculus* and *B. physalus*, respectively). However, Lavigne et al. (1990) reestimated the lower critical temperature of blue whales and suggested that not only was it likely that large whales are thermoneutral in antarctic waters, but their main thermoregulatory challenge probably involved dissipating body heat when they were in the tropics (see also Hokkanen, 1990; Norris, 1967; Ryg et al., 1993; Watts, Hansen, & Lavigne, 1993).

Other explanations for whale migration have included suggestions that the warm waters could be important for conception (Gaskin, 1982); a holdover from a time before drifting continents moved traditional feeding and breeding areas farther apart (Evans, 1987; Lipps & Mitchell, 1976), or a response to shifts in oceanographic conditions between glacial maxima (Sumich, 2014). Payne (1995) listed a buffet of possible explanations, including whales tracking prey resources that could be more abundant at lower latitudes during the winter; whales needing to shed barnacles, which tend to fall off in warm waters, or mothers seeking shallow water to protect their calves from attacks by large sharks or killer whales (*Orcinus orca*).

After countering nearly all the above arguments, Corkeron and Connor (1999) and Connor and Corkeron (2001) concluded that baleen whales might indeed migrate to the tropics to reduce the risk of killer whale predation on their calves. Although killer whales are, in fact, much less common in lower latitudes (Forney & Wade, 2006), Clapham (2001) and Rasmussen et al. (2007) nevertheless discounted the killer whale predation argument in favor of the calf thermoregulation hypothesis (but see Clapham, 2017). This lack of consensus over the years might have been a clue that whales were making these long-distance migrations for some other reason(s).

1.2 | Killer whale movements and migration

Historically, killer whales were not known to undertake long-distance migrations. More recently, however, individuals from two different groups in the eastern North Pacific were documented traveling minimum (straight-line) distances of 2,660 and 4,435 km based on photo-identification matches (Goley & Straley, 1994; Dahlheim et al., 2008; respectively), and 1,333 km (straight line) and 3,839 km ("path" distance; i.e., not straight line) based on satellite-tracking data (Reisinger, Keith, Andrews, & de Bruyn, 2015; Matkin et al., 2012; respectively). However, these movements occurred almost entirely within mid-latitudes (i.e., between 30° and 60°), and it is not known if these were actual migrations or just the normal ranging of a large, apex predator. On the other hand, Matthews, Luque, Petersen, Andrews, and Ferguson (2011) satellite-tracked a killer whale at the onset of winter in the eastern Canadian Arctic as it moved from Lancaster Sound, southward, into the central North Atlantic. Before the tag stopped transmitting, the whale had traveled at consistently high speeds (average 6.6 km/hr, maximum 10.5) and covered a minimum latitudinal range of 38° (from 75°N to 37°N), with a minimum one-way distance of 5,400 km on a meandering path. Although the authors did not document a return trip, another whale that was present during the tagging was photographed 4 years later, near the original tagging site.¹

In antarctic waters, it was previously assumed, without much evidence, that killer whales were migratory, with timing and movement patterns assumed to be like those of baleen whales (e.g., Budylenko, 1981; Mikhalev, Ivashin, Savusin, & Zelenaya, 1981). For example, Kasamatsu and Joyce (1995) analyzed 12 seasons of cetacean survey data from cruises conducted in antarctic waters by the International Whaling Commission (IWC), and they concluded that most killer whales migrated to antarctic waters in early January and left by late February. During the IWC cruises, however, research vessels surveyed only as far south as the pack ice edge (e.g., Branch & Butterworth, 2001) and rarely ventured into the ice (RLP, personal observation), which is habitat for many, if not most, antarctic killer whales (Pitman & Durban, 2012; Pitman & Ensor, 2003; Thiele & Gill, 1999; see also figure 12 in Kasamatsu & Joyce, 1995).

Another potential impediment to understanding movements of antarctic killer whales is that five different ecotypes have now been described from the Southern Ocean based on differences in morphology, habitat, prey preferences, and foraging behaviors (ecotypes A, B1, B2, C, and D; Durban, Fearnbach, Burrows, Ylitalo, & Pitman, 2016; Pitman & Ensor, 2003; Pitman et al., 2011). Two of these types (A and D) occur predominantly in open waters, two others (B1 and C) forage almost exclusively among sea ice, and the remaining type (B2) is intermediate. The validity of these ecotypes has been confirmed by genetic analyses (Foote et al., 2016; LeDuc, Robertson, & Pitman, 2008; Morin et al., 2015), but the degree to which this ecotypic variation might shape the movement and residency patterns of antarctic killer whales is currently unknown.

Initial evidence for long-distance movements by antarctic killer whales came from photographs taken at sea of the distinctive B and C ecotypes in lower latitudes. This included sightings of both types off New Zealand (Pitman & Ensor, 2003; Visser, 1999), and an unidentified "antarctic type" killer whale (i.e., type B or C; see Discussion) at 28°31'S, 145°46'W, approximately 350 km south of Tahiti (Pitman & Ensor, 2003). In addition, type C has also been photographed off New South Wales, Australia, and an unidentified type B has been photographed off Western Australia.² Moreover, photographs of virtually every group of killer whales from antarctic waters that we have seen, including all five of the ecotypes mentioned above, have included individuals with the distinctive bite wounds of cookiecutter sharks (*Isistius* spp.; RLP, JWD, and HF, personal observation). From this, we infer that all killer whales that

occur in antarctic waters probably spend at least some time in deep, warm waters where these small, mid-water sharks normally occur (see Dwyer & Visser, 2011).

The first unambiguous documentation of long-distance migration by individual antarctic killer whales came from types B1 and B2 satellite-tagged on the western side of the Antarctic Peninsula (Durban & Pitman, 2012). Whales with transmitting tags departed the Peninsula area between 4 February and 20 April (different years) and traveled north to at least 30°S, at the edge of the tropics in the western South Atlantic; before turning around and returning to Antarctica almost immediately. They covered 9,400 km round trip, at high speed (average 5–10 km/hr; maximum at least 12), and one individual returned to within 40 km of where it was tagged, within a relatively short period (42 days). Because these were high-speed, round trips of relatively short duration (weeks, versus months for large whales), it was considered unlikely that these migrations were for breeding or feeding purposes. Instead, Durban and Pitman (2012) noted that individual killer whales in Antarctica were often covered with a conspicuous yellow diatom film, but at other times, the same individual whales were “clean.” To explain this, they hypothesized that killer whales might conserve body heat in subfreezing (to -1.9°C) antarctic waters by reducing blood flow to their outer skin, which would preclude normal skin growth and sloughing, thus allowing diatoms to accumulate. Killer whales might then be obliged to make periodic trips to warm waters to molt their skin; they would shed diatoms in the process and appear clean when they returned to antarctic waters (Durban & Pitman, 2012). This was referred to as “physiological maintenance migration,” and it was suggested that, because all whales accumulated diatoms in antarctic waters, skin molt could form the basis for long-distance, latitudinal migration for whales that forage in higher latitudes (Durban & Pitman, 2012).

Regardless of the impetus for it, whale migration is a major biological phenomenon. For the individual whale, it represents a significant investment of time and energy. On a global scale, prior to large-scale removals by commercial whaling, it entailed hundreds of thousands of large whales annually traveling thousands of kilometers—a vast resource conversion and redistribution in the world ocean (Croll, Kudela, & Tershy, 2006; Estes, Heithaus, McCauley, Rahser, & Worm, 2016; Laws, 1977; Roman et al., 2014). The unparalleled scale and biological significance of this event, spanning from the individual whale to the entire ocean biome, underscores the importance of trying to understand why whales migrate.

In this paper, we use updated satellite-tagging results to describe and compare the migration patterns of four different ecotypes of antarctic killer whales (types A, B1, B2, and C). These findings provide additional support for the hypothesis of Durban and Pitman (2012) that killer whales do not migrate to low latitudes primarily to breed (or feed) but, instead, to molt their skin. We also discuss at length how this might be a plausible explanation for long-distance migration by all whales.

2 | METHODS

We conducted photo-identification studies (all years) and satellite-tagging (various years; Table 1) of killer whales in coastal waters of Antarctica in two separate areas: adjacent to the Western Antarctic Peninsula (WAP), including the northwestern Weddell Sea (visited annually during austral summer from 2008–2009 to 2016–2017) and in the western Ross Sea, including McMurdo Sound (77.5°S , 165.0°E ; visited intermittently between 2001–2002 and 2014–2015) and Terra Nova Bay (74.8°S , 164.5°E ; during 2003–2004 and 2014–2015; Figure 1).

For our tagging studies, we deployed two different types of tags: SPOT5 (location only) and SPLASH/MK-10 (location plus time/depth profiles; Wildlife Computers, Redmond, WA). We attached tags to the dorsal fins of killer whales using a 150 lb. draw-weight, recurve crossbow, firing bolts at ranges of 5–25 m. The floating bolt detached from the tag after contact with the whale, leaving the tag attached by two, 6.5 cm titanium barbs. As part of our photo-identification studies, we compiled catalogs of individually identified killer whales from the western Ross Sea (McMurdo Sound and Terra Nova Bay; Pitman, Fearnbach, & Durban, 2018) and the WAP (Fearnbach et al., 2019). We also photographed whales as they were being tagged, which allowed us to document interannual site fidelity. In

TABLE 1 Summarized results of individual killer whales satellite tagged in Antarctica, 2009–2016.

Killer whale ecotype	Tag type	Tag #	Tagging location ^a	Sex	Age ^b	Argos start date	Argos end date	Span of transmission days	Number of transmission days	Number of days in Antarctic waters pre-migration ^c	Migration departure date	Mean speed on feeding ground (km/hr)	Mean speed during migration (km/hr)	Mean dive depth on feeding ground (m)	Mean dive depth during migration (m)	Max. dive depth on feeding ground (m)	Max. dive depth during migration (m)	Latitude of turnaround point (°S)	Geodesic distance to turnaround point (km)	Path distance to turnaround point (km)	Sea surface temperature at turnaround point (°C)	Duration of full migration (days)	Full migration: time to turnaround point x 2 (days)	Incomplete migration: time to turnaround point x 2 (days)
A	SPOT	93240	WAP	U	J	16-02-2010	02-04-2010	46	39	-45.0	-	3.9	-	-	-	-	-	-	-	-	-	-	-	-
A	SPOT	99223	WAP	F	A	24-02-2010	13-03-2010	18	18	-17.0	-	4.8	-	-	-	-	-	-	-	-	-	-	-	-
A	SPLASH	126260	WAP	F	A	01-02-2013	26-04-2013	85	33	34.4	07-03-2013	3.5	-	40.5	36.0	616	380	34.9	3,427.8	-	17.5	-	-	99.3
A	SPOT	126266	WAP	F	A	01-02-2013	04-04-2013	63	42	35.4	08-03-2013	3.9	4.8	-	-	-	-	-	-	-	-	-	-	-
A	SPLASH	126261	WAP	M	A	01-02-2013	12-03-2013	40	24	-39.0	-	3.3	-	42.8	-	648	-	-	-	-	-	-	-	-
A	SPOT	126269	WAP	U	SA	04-12-2013	12-04-2014	130	80	109.3	23-03-2014	4.6	6.2	-	-	-	-	-	-	-	-	-	-	-
A	SPOT	129718	WAP	U	SA	04-12-2013	02-04-2014	120	64	27.5	31-12-2013	4.6	5.1	-	-	-	-	36.0	2,807.1	3,656.5	22.3	59.2	58.4	-
A	SPLASH	143493	WAP	U	SA	04-12-2014	28-01-2015	56	26	-55.0	-	3.0	-	46.8	-	308	-	-	-	-	-	-	-	-
A	SPOT	143498	WAP	F	A	04-12-2014	21-12-2014	18	18	-17.0	-	5.3	-	-	-	-	-	-	-	-	-	-	-	-
A	SPOT	143500	WAP	M	A	04-12-2014	28-01-2015	56	37	-55.0	-	4.3	-	-	-	-	-	-	-	-	-	-	-	-
B1	SPOT	88702	WAP	F	A	15-01-2009	02-02-2009	19	19	-18.0	-	1.8	-	-	-	-	-	-	-	-	-	-	-	-
B1	SPOT	88703	WAP	F	A	15-01-2009	31-01-2009	17	17	12.2	28-01-2009	4.5	9.8	-	-	-	-	-	-	-	-	-	-	-
B1	SPOT	88707	WAP	F	A	24-01-2009	13-02-2009	21	21	10.2	04-02-2009	4.4	8.8	-	-	-	-	-	-	-	-	-	-	-
B1	SPOT	103877	WAP	M	A	13-01-2011	31-01-2011	19	19	-18.0	-	2.8	-	-	-	-	-	-	-	-	-	-	-	-
B1	SPOT	103874	WAP	F	A	13-01-2011	25-02-2011	44	42	22.0	04-02-2011	2.9	7.6	-	-	-	-	-	3,559.9 ^d	3,710.4 ^d	22.0 ^d	-	-	-
B1	SPOT	103876	WAP	F	A	24-01-2011	14-02-2011	22	22	-21.0	-	4.2	-	-	-	-	-	-	-	-	-	-	-	-
B1	SPLASH	126264	WAP	M	A	17-02-2013	27-02-2013	11	11	-10.0	-	4.2	-	42.5	-	712	-	-	-	-	-	-	-	-
B1	SPLASH	143495	WAP	F	A	12-02-2015	04-03-2015	21	18	-20.0	-	3.7	-	36.1	-	552	-	-	-	-	-	-	-	-
B2	SPOT	88701	WAP	F	A	08-01-2009	16-01-2009	9	9	-8.0	-	3.6	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPOT	99220	WAP	M	SA	13-02-2010	24-02-2010	12	12	-11.0	-	4.4	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPOT	99221	WAP	U	SA	13-02-2010	21-05-2010	98	65	66.2	21-04-2010	3.0	8.6	-	-	-	-	30.0	3,868.1	4,087.5	23.3	-	-	37.1
B2	SPOT	99222	WAP	F	A	14-02-2010	01-06-2010	108	70	65.3	20-04-2010	3.2	8.6	-	-	-	-	30.3	3,887.4	4,092.9	23.0	39.5	39.2	-
B2	SPOT	103879	WAP	F	A	15-01-2011	16-04-2011	92	66	78.3	04-04-2011	3.5	9.9	-	-	-	-	-	-	-	-	-	-	-
B2	SPOT	103878	WAP	F	A	15-01-2011	22-04-2011	98	69	78.2	04-04-2011	3.6	8.7	-	-	-	-	29.8	3,665.6	3,844.2	24.2	-	-	36.8
B2	SPOT	113552	WAP	F	SA	10-01-2012	31-01-2012	22	22	-21.0	-	3.1	-	-	-	-	-	-	-	-	-	-	-	-

(Continues)

TABLE 1 (Continued)

Killer whale ecotype	Tag type	Tag #	Tagging location ^a	Sex	Age ^b	Argos start date	Argos end date	Span of transmission days	Number of transmission days	Number of days in Antarctic waters	Pre-migration ^c	Migration departure date	Mean speed on feeding ground (km/hr)	Mean speed during migration (km/hr)	Mean dive depth on feeding ground (m)	Mean dive depth during migration (m)	Max. dive depth on feeding ground (m)	Max. dive depth during migration (m)	Latitude of turnaround point (°S)	Geodesic distance to turnaround point (km)	Path distance to turnaround point (km)	Sea surface temperature at turnaround point (°C)	Duration of full migration (days)	Full migration: time to turnaround point x 2 (days)	Incomplete migration: time to turnaround point x 2 (days)
B2	SPOT	113555	WAP	F	A	24-01-2012	29-02-2012	37	37	-36.0	-	-	4.1	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPLASH	113558	WAP	F	A	24-01-2012	08-02-2012	16	16	-15.0	-	-	4.0	104.7	600	-	-	-	-	-	-	-	-	-	-
B2	SPLASH	126259	WAP	F	A	11-01-2013	22-03-2013	71	31	-70.0	-	-	2.1	106.2	696	-	-	-	-	-	-	-	-	-	-
B2	SPOT	126265	WAP	F	A	15-01-2013	22-03-2013	67	44	-66.0	-	-	2.9	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPOT	126267	WAP	F	A	07-02-2013	17-03-2013	39	29	-38.0	-	-	2.8	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPOT	126268	WAP	F	A	08-02-2013	13-03-2013	34	27	-33.0	-	-	2.9	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPLASH	126258	WAP	M	A	08-02-2013	06-05-2013	88	22	-87.0	-	-	1.4	138.1	568	-	-	-	-	-	-	-	-	-	-
B2	SPOT	134371	WAP	F	A	14-12-2013	10-04-2014	118	70	116.6	10-04-2014	2.8	7.9	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPLASH	134558	WAP	F	A	02-02-2014	12-03-2014	39	20	-38.0	-	-	2.5	168.5	600	-	-	-	-	-	-	-	-	-	-
B2	SPOT	129717	WAP	F	A	02-02-2014	25-05-2014	113	65	71.8	15-04-2014	2.9	8.4	-	-	-	-	-	30.9	3810.1	3982.3	22.8	39.4	36.4	-
B2	SPLASH	134559	WAP	F	A	03-02-2014	01-04-2014	58	23	-57.0	-	-	2.1	132.0	632	-	-	-	-	-	-	-	-	-	-
B2	SPLASH	134560	WAP	F	A	11-02-2014	16-04-2014	65	18	-64.0	-	-	1.5	80.9	552	-	-	-	-	-	-	-	-	-	-
B2	SPOT	143497	WAP	M	SA	17-12-2014	12-05-2015	147	80	-146.0	-	-	2.9	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPOT	143501	WAP	F	A	12-02-2015	17-03-2015	34	25	-33.0	-	-	2.6	-	-	-	-	-	-	-	-	-	-	-	-
B2	SPOT	129722	WAP	F	A	23-02-2016	04-08-2016	164	83	16.1	11-03-2016	2.5	-	-	-	-	-	-	32.0	3518.1	-	-	36.9	40.0	-
B2 ^e	SPOT	129722	WAP	F	A	23-02-2016	04-08-2016	164	83	71.1	27-06-2016	3.4	-	-	-	-	-	-	28.4	3775.3	-	-	-	-	40.0
C	SPLASH	113561	WRS/MS	F	A	22-12-2012	02-01-2013	12	12	-11.0	-	-	4.0	138.2	632	-	-	-	-	-	-	-	-	-	-
C	SPOT	119495	WRS/MS	F	A	26-12-2012	25-03-2013	90	56	73.5	09-03-2013	2.5	8.2	-	-	-	-	182	-	-	-	-	-	-	-
C	SPLASH	113560	WRS/MS	M	SA	26-12-2012	26-03-2013	91	36	74.8	11-03-2013	1.9	8.4	89.7	38.3	-	-	-	-	-	-	-	-	-	-
C	SPLASH	121382	WRS/MS	M	A	26-12-2012	26-03-2013	91	35	74.7	11-03-2013	1.9	8.4	132.2	33.4	640	292	-	-	-	-	-	-	-	-
C	SPLASH	121384	WRS/MS	M	A	26-12-2012	15-04-2013	111	39	74.7	11-03-2013	1.9	7.3	99.7	42.5	688	202	-	-	4.778.6	4911.2	20.9	-	-	51.7
C	SPOT	108422	WRS/MS	F	A	26-12-2012	01-03-2013	66	47	-65.0	-	-	2.6	-	-	-	-	-	35.1	-	-	-	-	-	-
C	SPOT	113556	WRS/MS	M	A	26-12-2012	18-04-2013	114	67	81.1	17-03-2013	2.7	-	-	-	-	-	-	-	4.707.1	-	19.9	-	-	55.6
C	SPOT	143834	WRS/TNB	M	A	14-01-2015	02-02-2015	20	20	11.3	25-01-2015	4.2	10.8	-	-	-	-	-	31.7	-	-	-	-	-	-
C	SPOT	143833	WRS/TNB	M	A	14-01-2015	16-02-2015	34	27	11.3	25-01-2015	4.2	9.4	-	-	-	-	-	-	4.624.3	4.896.8	21.6	-	-	41.6

TABLE 1 (Continued)

Killer whale ecotype	Tag type	Tag #	Tagging location ^a	Sex	Age ^b	Argos start date	Argos end date	Span of transmission days	Number of transmission days	Number of days in Antarctic waters pre-migration ^c	Migration departure date	Mean speed on feeding ground (km/hr)	Mean speed during migration (km/hr)	Mean dive depth on feeding ground (m)	Mean dive depth during migration (m)	Max. dive depth on feeding ground (m)	Max. dive depth during migration (m)	Latitude of turnaround point (°S)	Geodesic distance to turnaround point (km)	Path distance to turnaround point (km)	Sea surface temperature at turnaround point (°C)	Duration of full migration (days)	Full migration: time to turnaround point x 2 (days)	Incomplete migration: time to turnaround point x 2 (days)	
C	SPOT	134373	WRS/IMS	M	A	14-01-2015	28-01-2015	15	15	-14.0	-	3.9	-	-	-	-	-	-	-	-	-	-	-	-	
C	SPOT	129716	WRS/IMS	M	A	14-01-2015	28-01-2015	15	15	-14.0	-	3.0	-	-	-	-	-	30.3	-	-	-	-	-	-	
C	SPOT	134375	WRS/IMS	M	A	15-01-2015	23-04-2015	99	60	61.7	18-03-2015	2.4	8.5	-	-	-	-	-	5,353.8	5,794.1	22.4	-	-	48.6	
C	SPLASH	134369	WRS/IMS	M	A	15-01-2015	01-02-2015	18	18	-17.0	-	3.2	-	117.6	-	696	-	-	-	-	-	-	-	-	-
C	SPLASH	134368	WRS/IMS	M	A	15-01-2015	31-01-2015	17	17	-16.0	-	3.6	-	111.5	-	584	-	31.7	-	-	-	-	-	-	-
C	SPLASH	143823	WRS/TNB	M	A	15-01-2015	24-02-2015	41	28	9.6	25-01-2015	4.2	8.7	-	-	-	-	31.3	4,627.1	4,967.0	21.6	-	-	-	
C	SPOT	143831	WRS/TNB	M	A	15-01-2015	19-02-2015	36	28	9.6	25-01-2015	4.6	9.3	-	-	-	-	31.3	4,669.8	4,986.5	21.8	-	-	-	
C	SPOT	143828	WRS/TNB	F	A	15-01-2015	17-02-2015	34	27	9.5	25-01-2015	4.2	9.5	-	-	-	-	33.9	4,667.2	4,972.4	21.9	-	-	-	
C	SPLASH	143824	WRS/TNB	M	A	18-01-2015	12-02-2015	26	25	6.6	25-01-2015	4.7	10.7	-	-	-	-	-	4,391.5	4,656.7	20.4	-	-	-	
C	SPLASH	143825	WRS/TNB	F	A	18-01-2015	07-02-2015	21	21	6.5	25-01-2015	4.7	11.1	-	-	-	-	-	-	-	-	-	-	-	
C	SPOT	143830	WRS/TNB	M	A	22-01-2015	12-02-2015	22	21	2.6	25-01-2015	7.3	10.7	-	-	-	-	32.1	-	-	-	-	-	-	
C	SPOT	143832	WRS/TNB	M	A	25-01-2015	10-03-2015	45	32	17.6	11-02-2015	3.5	8.1	-	-	-	-	-	4,661.0	4,859.5	22.4	-	-	49.4	
C	SPLASH	143826	WRS/TNB	M	A	26-01-2015	24-02-2015	30	27	15.8	11-02-2015	3.8	9.2	-	-	-	-	-	4,596.0	4,895.8	-	-	-	-	

^aWAP - Western Antarctic Peninsula; WRS - Western Ross Sea; MS - McMurdo Sound; TNB - Terra Nova Bay.

^bA - adult; SA - subadult; J - juvenile; U - unknown.

^cNegative values are number of days in Antarctic waters for whales that did not initiate migration before their tags stopped transmitting; positive values are for whales that initiated migration while still transmitting.

^dThis is at the northernmost point, which may not have been turnaround point.

^eThis is the second migration of the same whale immediately above.

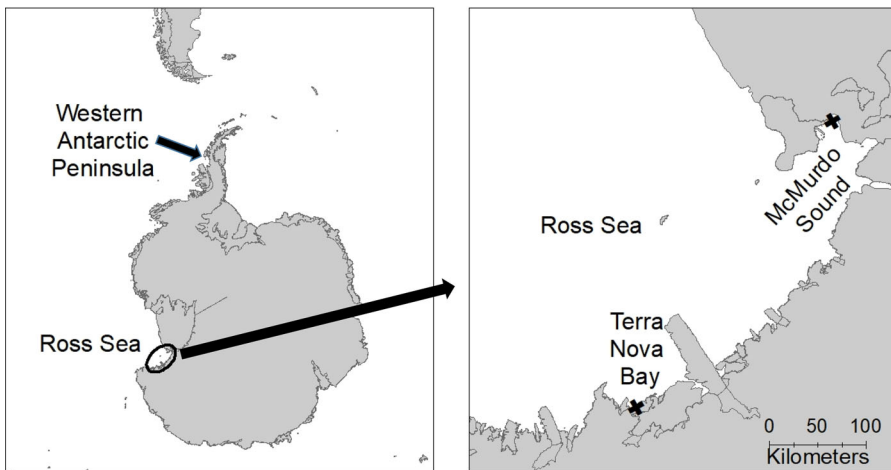


FIGURE 1 Our two killer whale study areas in Antarctica: the Western Antarctic Peninsula and the western Ross Sea (including McMurdo Sound and Terra Nova Bay).

some cases, we attempted to conserve battery life and extend transmission days by duty-cycling transmissions, in which case the span of transmission days was greater than the number of transmission days; both are presented in Table 1 where applicable. Tags were programmed to transmit 400–600 times during 12–24 hr/day and timed to coincide with passes of Argos satellites; duty cycling was programmed to begin after 3–6 weeks, transmitting 1 day on and either 1 or 4 days off. Further details of our tagging and photo-identification methods are provided by Pitman et al. (2018) and Fearnbach et al. (2019).

For tagged whales, we estimated the maximum likelihood path followed by each individual whale by fitting a continuous time correlated random walk model (CTCRW; Johnson, London, Lea, & Durban, 2008) to each track. Prior to fitting the model, we flagged potentially erroneous Argos location fixes using a speed-distance-angle filter (function *sdafilter*) from the *argosfilter* package (Freitas, Lydersen, Fedak, & Kovacs, 2008) with a maximum velocity threshold of 28 m/s (100.8 km/hr) to identify and exclude egregiously outlying points. The R package *crawl* (version 2.1; Johnson, 2013) was then used to fit CTCRW movement models, which enabled the incorporation of error ellipse information from the Argos Kalman-filter algorithm, as well as correlated random walk parameter uncertainty in estimating the maximum likelihood path of each individual through space. We generated predictions of individual tracks from CTCRW models at 30-min intervals, which enabled the calculation of speed and overall migration distances from irregularly spaced Argos location fixes. Travel speed was calculated by dividing the displacement distances between maximum likelihood predicted locations (in kilometers) by the elapsed time (0.5 hr). Displacement distances were measured from CTCRW coordinate outputs using the function *distGeo* in the *geosphere* package (Hijmans, 2017), which returned geodesic distances based on the World Geodetic Survey 1984 (WGS84) geoid model (like great circle distances but based on a nonspherical geoid). To compare dive behavior during migration and while in antarctic waters, we examined behavior log records returned by SPLASH tags. The behavior log functions of MK-10 SPLASH tags were programmed to record the maximum depth reached during each dive that exceeded 15 m in depth. Using the *crawl* continuous time correlated walk framework, we were able to predict tag locations with estimates of standard error at the times of dive mid- and end-points.

We defined the beginning of the northbound migratory phase in each track as the timestamp of the first observed Argos location fix showing movement away from antarctic waters that was followed by directionally persistent, northward movement. If migration began during a period when the tag duty cycle was off, this conservative criterion placed the beginning of migration at the start of the first duty cycle period where the tag was transmitting, rather than interpolating the beginning of migration to a time when location information was unavailable. The “turnaround point,”

separating northbound from southbound migrations, was defined as the farthest north Argos location fix, in tracks where the Argos tag continued transmitting through a partial or complete return migration towards higher latitudes. For tags that continued transmitting through a full return migration, the end of the migratory phase was defined as the last observed Argos location fix before the individual ceased directional poleward movement and became more directionally erratic following a return to antarctic waters (Durban & Pitman, 2012). Observed Argos fixes, CTCRW estimated locations, and dives recorded in SPLASH tag behavior logs were classified as either premigration, northbound migration, southbound migration, or postmigration, based on whether their timestamps fell before or after the date/time stamps corresponding to the start of northern migration, turnaround point, and/or end-point of southern migration.

We estimated sea surface temperature (SST) along CTCRW maximum likelihood tracks from an optimally interpolated SST product (OISST; Reynolds et al., 2007) based on Advanced Very High Resolution Radiometer (AVHRR) satellite SST measurements in the thermal infrared. These measurements have been further calibrated through the assimilation of in situ measurements from Argo profiling floats and surface ships. Daily global OISST layers at a $0.25^\circ \times 0.25^\circ$ resolution were downloaded from the National Centers for Environmental Information (<https://www.ncei.noaa.gov/data/sea-surface-temperature-optimum-interpolation/access/avhrr-only>) and sampled at CTCRW-estimated tag locations that temporally fell within the date stamp of each OISST layer.

3 | RESULTS

Between January 2009 and February 2016, we satellite-tagged 62 individual killer whales in antarctic waters. Of these, 30 (48%) individuals of four different ecotypes (4 type A, 3 B1, 7 B2, and 16 C) were identified as initiating northbound migrations (Table 1); presumably the other 32 individuals would also have migrated if their tags had not stopped transmitting before they departed. Three of the four ecotypes—A, B1, and B2—were tagged near the Western Antarctic Peninsula (WAP) in Western Antarctica; type Cs were tagged only in the western Ross Sea, in Eastern Antarctica (Figure 1). The median number of transmission days for all whales was 27.0 (mean 34.3; range 9–83, $n = 62$); the median span of transmission days was 39.5 (mean 54.6; range 9–164).

Tagged individuals of all four ecotypes undertook long-distance migrations to lower latitudes; Figures 2–5 show the longest migratory tracks for individuals that initiated migration for each of the different ecotypes. The migratory

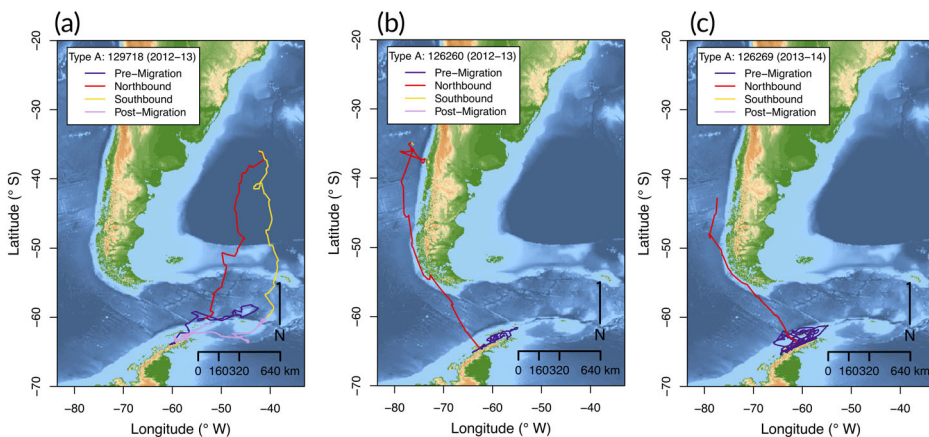


FIGURE 2 Tracks of three separate type A killer whales satellite-tagged in Western Antarctic Peninsula waters. The box in each figure indicates tag number (see Table 1) and summer tagging season (in parentheses). The background colors indicate ocean depth, with light blue areas representing shelf waters and dark blue representing deep water (>2,000 m).

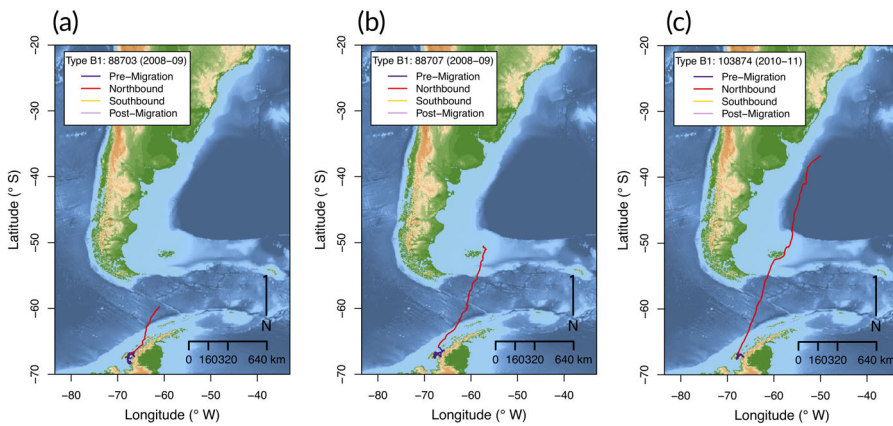


FIGURE 3 Tracks of three separate ecotype B1 killer whales satellite-tagged in Western Antarctic Peninsula waters. The box in each figure indicates tag number (see Table 1) and summer tagging season (in parentheses). The background colors indicate ocean depth, with light blue areas representing shelf waters and dark blue representing deep water (>2,000 m).

pattern of type A killer whale was demonstrably different from the other types in terms of speed and directionality and will be considered separately in some of the comments that follow. Migrating whales spent 27–109 days (mean 43.7, $n = 31$) on the antarctic feeding grounds after tagging, prior to migration. However, these are all minimum values because it is not known how long any of these individuals/groups had been in antarctic waters prior to tagging (with one exception, see below). Northbound migration departure dates for all tagged killer whales combined spanned at least 6 months, from 31 December (2013) to 27 June (2016). The latitudes of the northern turnaround points reached by individual whales of all ecotypes combined ranged from 28.4°S to 36.0°S, with a mean of 32.2°S ($n = 11$; Table 1).

Minimum geodesic distance (MGD) is the shortest distance between two points on the curved ocean surface. Mean MGD from the departure point in Antarctica to the turnaround point, for all tagged killer whale ecotypes, and using only the longest distance recorded for tagged individuals known to be in the same group, was 4,088.5 km (range 2,807.1–5,353.8, $n = 12$). The mean total distance (MTD, i.e., actual path traveled) between these two points was 4,486.4 km (range 3,656.4–5,794.1, $n = 8$). The close agreement between MGD and MTD indicates a directional progression during migrations. Moreover, most of that discrepancy between mean MGD and MTD was driven by the more meandering path of type A individuals (see below).

Tagged whales of all ecotypes traveled faster during migration than when they were foraging in antarctic waters: mean overall travel speed for individuals on the feeding grounds was 3.4 km/hr (range 1.4–7.3, $n = 63$), and during migration this increased to 8.4 km/hr (range 4.4–11.1, $n = 31$). Whales with depth profile tags all dove deeper on the feeding grounds (average of individual means 95.8 m, range 36.1–138.2; range of individual maxima 308–712, $n = 18$) compared to during migration (mean 37.5 m, range 33.4–42.5; range of individual maxima 182–380, $n = 4$).

Among the four individuals tracked through complete, round-trip migrations (1 type A, 3 B2), the time required to travel to the turnaround point differed from the time required to return to their feeding grounds in antarctic waters by an average of only 1.8 days (range –3.13–2.98 days). This close correspondence between northbound and southbound migration times allowed us to estimate total round-trip migration times for individuals that did not complete a full migration by doubling the amount of time that it took them to reach the turnaround point. The mean number of days that killer whales spent on round-trip migrations (not including type A, see below) was 43.6 (range 36.8–55.6; $n = 11$, including eight half-trips $\times 2$).

Below we summarize these findings for each of the four different killer whale ecotypes tagged in antarctic waters.

3.1 | Type A

We tagged 10 type A killer whales, all in the vicinity of the WAP; of these, four individuals from three separate groups initiated migrations including two individuals tagged in February 2013 and two in December 2013 (i.e., two separate summer seasons; Table 1, Figure 2). The span of transmission days ranged from 18 to 130 (mean 63.2; $n = 10$); the number of transmission days per whale ranged from 18 to 80 (mean 38.1). The number of days that

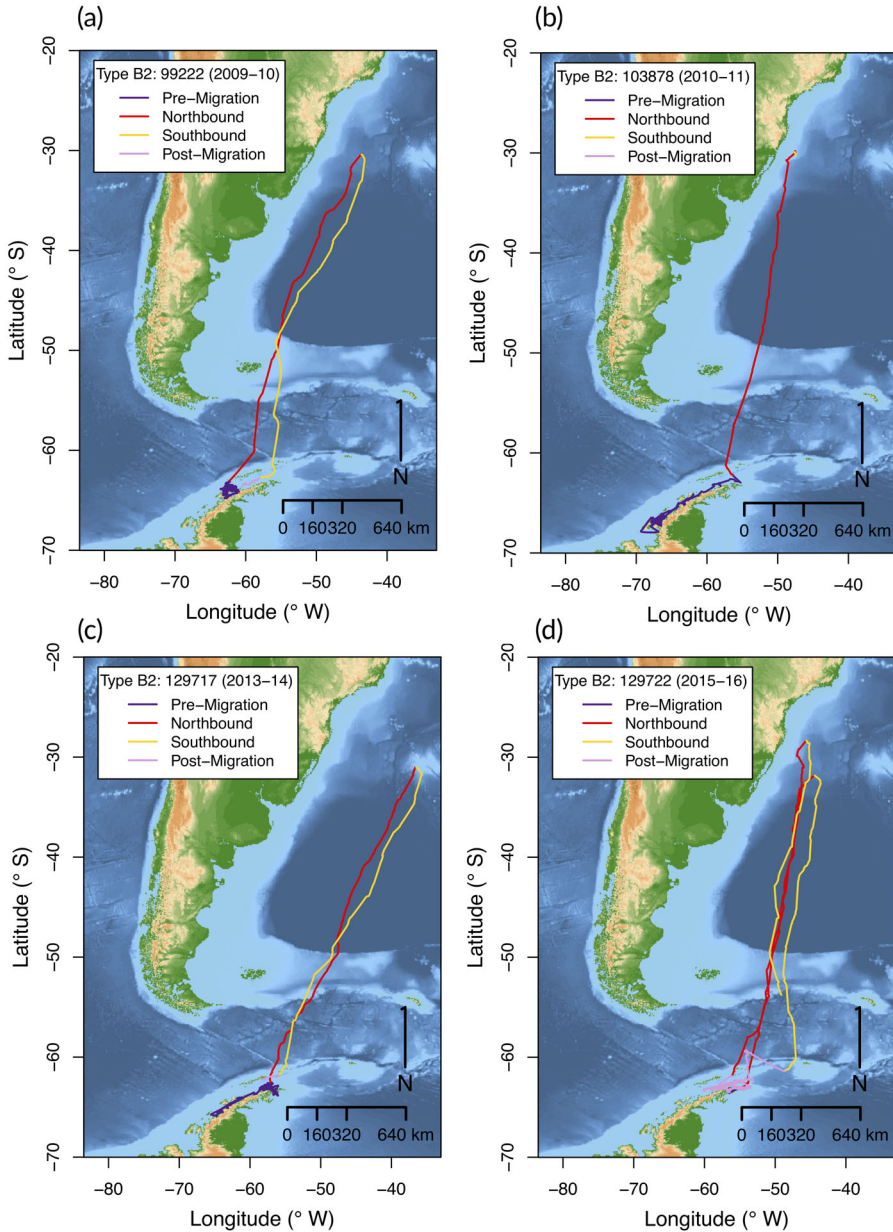


FIGURE 4 Tracks of four separate ecotype B2 killer whales satellite-tagged in Western Antarctic Peninsula waters. The box in each figure indicates tag number (see Table 1) and summer tagging season (in parentheses). The background colors indicate ocean depth, with light blue areas representing shelf waters and dark blue representing deep water (>2,000 m).

migrating whales spent on the foraging grounds after tagging and prior to migration ranged from 27.5 to 109.3, and migration departure dates ranged from 31 December (2013) to 23 March (2014). Average of mean swimming speeds on the feeding grounds was 4.1 km/hr (range of individual means 3.0–5.3, $n = 10$); average of mean travel speeds during migration was slightly higher at 5.4 km/hr (range 4.8–6.2, $n = 3$; Figure 6a). The average of mean dive depths for type A whales on the feeding grounds (43.3 m, range 40.5–46.8; range of individual maximums 308–648, $n = 3$) was slightly deeper than during migration (mean 36.0, maximum 380 m, $n = 1$; Table 1, Figure 7a), although the sample sizes were small. The turnaround latitudes for the two type A killer whales whose tags transmitted long enough to initiate southbound migrations were 36.0°S and 34.9°S. MGD (i.e., most direct route) to the turnaround point was 2,807.1 and 3,427.8 km, and MTD was 3,656 km and 5,182 km, respectively (Table 1). The relatively large discrepancies between the MGD and MTD for each of these two individuals reflected the more meandering migration routes of type A killer whales compared to types B1, B2, and C (cf. Figures 2–5). Sea surface temperatures (SST) at each of the two turnaround points was 22.3°C and 17.5°C, respectively (Table 1). Only one type A individual (Figure 2a) was tracked through a round-trip migration and it took 59.2 days. The other type A individual reached the turnaround point in an estimated 49.6 days (Figure 2b), giving an estimated round-trip duration of 99.3 days.

Separate tagged type A whales traveled up the eastern and western sides of the coast of South America, and tracks of at least one group (two individuals) showed an affinity for the continental shelf and slope off western South America (Figure 2b,c). The only individual tracked through an entire round-trip migration eventually returned to the same location where it was tagged prior to migration (Figure 2a). Furthermore, at least six of the tagged whales,

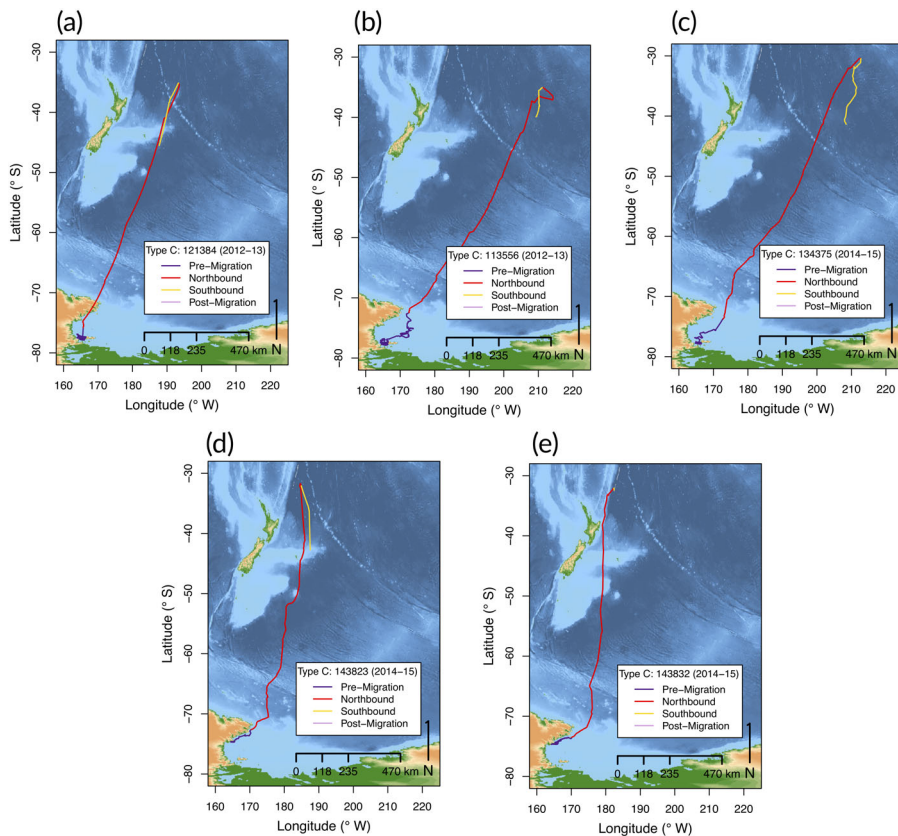


FIGURE 5 Tracks of five separate ecotype C killer whales satellite-tagged in western Ross Sea. The box in each figure indicates tag number (see Table 1) and summer tagging season (in parentheses). The background colors indicate ocean depth, with light blue areas representing shelf waters and dark blue representing deep water (>2,000 m).

including all four of the individuals that initiated migration, have been sighted again in the WAP area during subsequent years, confirming round-trip migrations and site fidelity for at least these individuals.

3.2 | Type B1

Eight type B1 killer whales from eight different groups were tagged off the WAP over four separate seasons; three individuals from three groups initiated migrations (Table 1; Figure 3). The span of transmission days for all tagged whales ranged from 11 to 44 (mean 21.8, $n = 8$); the number of individual transmission days per whale ranged from 11 to 42 (mean 21.1). The number of days that the three migrating whales spent on the foraging grounds after tagging and prior to migration was 10.2, 12.2, and 22.0; individual departure dates for those three whales were 4 February and 28 January (2009), and 4 February (2011), respectively; another whale had not departed by 4 March (2015) when its tag stopped transmitting. Mean travel speed on the feeding grounds was 3.6 km/hr (range 1.8–4.5, $n = 8$); during migration, this more than doubled to 8.7 km/hr (range 7.6–9.8, $n = 3$; Table 1, Figure 6b). Mean dive depths for two type B1 whales on the feeding grounds were 36.1 and 42.5 m, with maximum dives of 552 and 712 m; we have no dive information for this ecotype during migration (Table 1, Figure 7b). The farthest north latitude attained by a tagged B1 individual was 36.3°S (Figure 3c), and the SST there was 22.0°C (Table 1, Figure 8b). However, because this individual had not started a southbound migration when its tag stopped transmitting, it may not have reached its turnaround point. MGD to that point was 3,559.9 km; MTD was 3,710.4 km; it reached that point after 20.2 days, yielding a minimum estimate of 40.5 days for a round-trip migration.

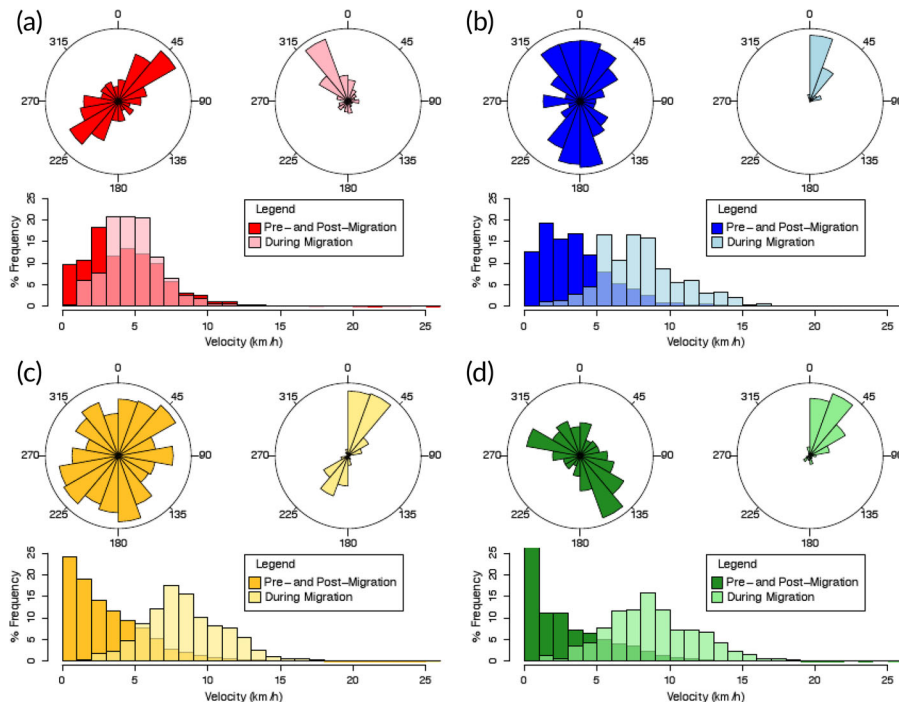


FIGURE 6 Travel direction and travel speed for four different ecotypes of killer whales that were satellite tagged during 2009–2016 and initiated migration from antarctic waters: (a) ecotype A ($n = 4$), (b) B1 ($n = 3$), (c) B2 ($n = 8$), and (d) C ($n = 16$). Shown is the travel direction and speed for each ecotype while on the foraging grounds in antarctic waters (i.e., pre- and postmigration) and during migration.

Northbound migration for B1 killer whales was directional on a course that generally ranged from 0° to 45° (Figure 6b); all tracked individuals passed east of the Falkland Islands and moved northward off the east coast of South America (Figure 3). Nearly the entire migratory route, including the area of the turnaround point, was over deep, oceanic water. At least seven of the eight tagged whales, including all three migrating individuals, were sighted again in the WAP area in subsequent seasons, thus confirming round-trip migrations and site fidelity for at least these individuals.

3.3 | Type B2

We tagged 22 type B2 killer whales off the WAP; of these, seven individuals from five separate groups initiated migrations over four separate seasons (Table 1, Figure 4). The span of transmission days for all tagged whales ranged from 9 to 164 (mean 69.5, $n = 22$); the number of transmission days per whale ranged from 9 to 83 (mean 41.0). The number of days spent on the feeding grounds in Antarctica after tagging and prior to migration ranged from 16.1 to 116.6 ($n = 8$). One individual spent 146.0 days (17 December–12 May) on the feeding grounds and did not migrate before its tag stopped transmitting. This was the longest continuous time interval that we recorded for a killer whale in antarctic waters. Another individual (Figure 4d) spent 71.1 days in antarctic waters between two migrations. This was the only complete record we have of time spent on the feeding grounds between two separate migrations, and it is currently the minimum time interval recorded for a killer whale in antarctic waters.

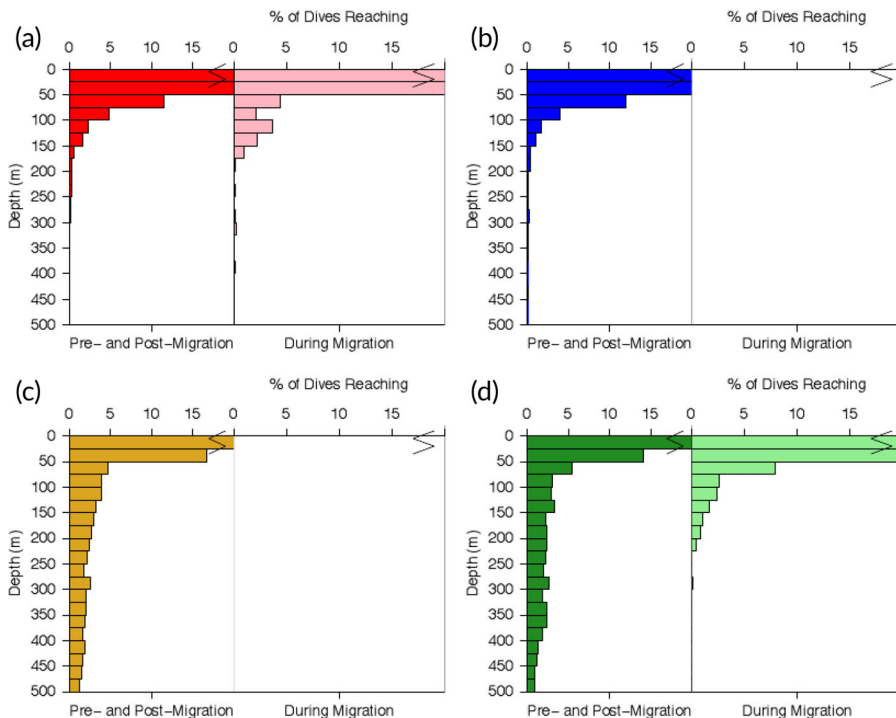


FIGURE 7 Comparisons of maximum dive depths for four ecotypes of killer whales satellite-tagged in antarctic waters during 2009–2016 for dives >15 m: (a) ecotype A ($n = 3$), (b) B1 ($n = 2$), (c) B2 ($n = 6$), and (d) C ($n = 10$). Most dives of mammal-eating forms (i.e., ecotypes A and B1) were usually <50 m, on the feeding grounds and during migration (data from migration available only for type A). For the fish-eating ecotype C (and presumably ecotype B2), dives were deeper on the feeding grounds, often >200 m, but during migration they were typically <50 m, presumably as they suspended normal feeding (no migration dive data available for B2).

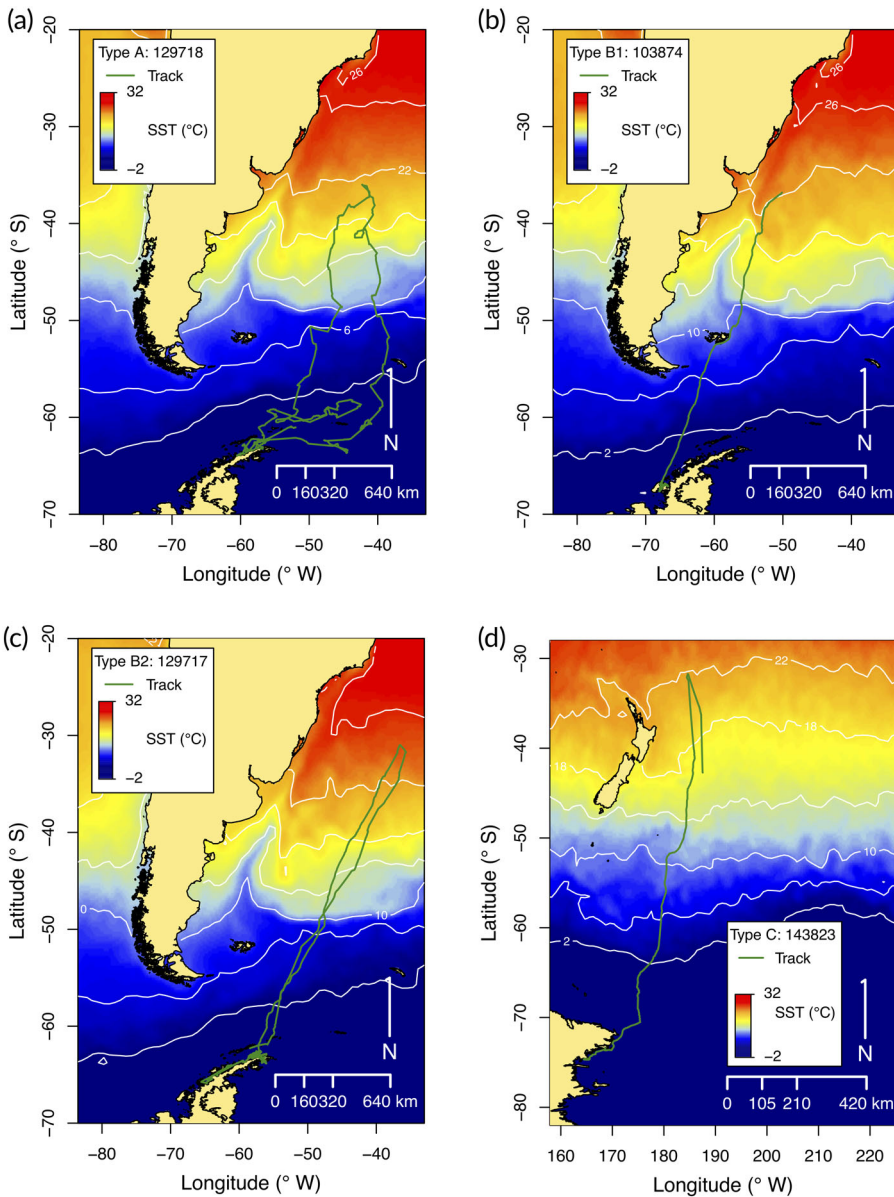


FIGURE 8 Sea surface temperatures encountered during selected migrations for selected individuals of four different ecotypes of killer whales satellite tagged in antarctic waters during 2009–2016: (a) ecotype A, (b) B1, (c) B2, and (d) C. The nearest warm water for killer whales migrating from the Antarctic Peninsula area is off the east coast of South America.

Migration departure dates for type B2 killer whales ranged from 11 March (2016) to 27 June (2016), both by the same individual (Figure 4d); the remaining six individuals that initiated migration were from four separate groups and all departed in April of three separate years (2010, 2011, 2014). The average mean travel speed on the feeding grounds was 3.0 km/hr (range of individual means 1.4–4.4, $n = 23$); during migration this almost tripled, to 8.7 km/hr (range 7.9–9.9, $n = 6$; Table 1, Figure 6c). The average mean dive depth on the feeding grounds was 121.7 m (range of individual means 80.9–168.5, mean of individual maximums 608 m, range of individual maximums 552–696; $n = 6$; Table 1, Figure 7c); we have no dive depth data during migration. The latitude of the turnaround point for four

separate whales during four different seasons ranged from 28.4°S to 32.0°S, and these were recorded for the same whale during two sequential migrations in the same season (Figure 4d). SST at the turnaround point averaged 23.3°C (range 22.8–24.2, $n = 4$; Table 1, Figure 8c). Migrating whales did not appear to be heading to the same specific location (Figure 4): individual turnaround points were separated by as much as 1,052 km (Figure 4), spanning, overall, approximately 400 km of latitude and 1,048 km of longitude; an area of approximately 420,000 km². Average MGD to the turnaround point from the departure point for type B2 was 3,754.1 km (range 3,518.1–3,887.4, $n = 6$, including two trips by one individual); average MTD was 4,001.7 km (range 3,844.2–4,092.9, $n = 4$). Three round trips recorded during three different seasons took 36.9, 39.4, and 39.5 days, respectively, to complete. Three other trips when whales reached their turnaround point, but did not complete a round trip, took an estimated 36.8, 37.1, and 40.0 days, respectively, to complete the trip.

Migratory routes for type B2 were similar for all individuals. On leaving the WAP area, tagged whales traveled north on a course between 0° and 45° (Figure 6c), passing through the Scotia Sea, east of the Falkland Islands, and northward off the eastern coast of South America (Figure 4). On reaching the turnaround point, all tagged whales turned around and started travelling back toward Antarctica (Figure 4). Tagged whales remained over the continental shelf when foraging in the WAP area, but their migratory routes were almost entirely over open ocean, in deep water (>2,000 m), including their turnaround points. Tagged animals showed strong site fidelity to the foraging grounds; individuals that completed round-trip migrations ($n = 3$) returned to locations that were 13.0, 58.0, and 112.3 km, respectively, from where they began their migrations. We have not completed our catalog of the numerous WAP B2 killer whales, but to date 5 of the 22 tagged individuals have been sighted again at least once in the WAP area during subsequent seasons, including four that initiated migrations. This is evidence of site fidelity and round-trip migrations by this ecotype.

3.4 | Type C

We tagged 22 type C killer whales in the western Ross Sea, during two separate seasons. Of these, 16 individuals initiated migration while their tags were still transmitting, including 6 individuals from five groups tagged in McMurdo Sound in December 2012 and January 2015, and 10 individuals from at least two groups tagged in Terra Nova Bay in January 2015 (Table 1, Figure 5). The span of transmission days for all tagged whales ranged from 12 to 114 (mean 47.6, $n = 22$); the number of transmission days ranged from 12 to 67 (mean 30.6). The number of days that migrating whales spent on the antarctic feeding grounds after tagging and prior to migration ranged from 2.6 to 81.1 (mean 33.8, $n = 16$), although whales in McMurdo Sound spent an average of 73.4 days ($n = 6$) and those in Terra Nova Bay only 10.0 days ($n = 10$). Tagged whales from Terra Nova Bay departed on two separate days—25 January and 11 February 2015; departure dates from McMurdo Sound ranged from 9 March (2013) to 18 March (2015). The overall mean swimming speed on the feeding grounds was 3.6 km/hr (range of individual means 1.9–7.3, $n = 22$), which increased to 9.2 km/hr (range 7.3–11.1, $n = 15$) during migration (Table 1, Figure 6d).

Type C killer whales dove deeper on the feeding grounds than during migration (Table 1, Figure 7d). Overall, the mean dive depth on the feeding grounds was 114.8 m (range of individual means 89.7–138.2; mean maximum 653.3 m; range of individual maximums 584–696; $n = 6$). The overall mean of individual dive depth during migration was 38.1 m (range of individual means 33.4–42.5; mean maximum dive 225.3 m; range of individual maximums 182–292; $n = 3$, with all three animals from the same group). The latitude of the turnaround points ranged from 30.3°S to 35.1°S (mean 32.5°S, $n = 9$), and the SST at the turnaround points ranged from 19.9°C to 22.4°C (mean 21.4°C, $n = 9$; Table 1, Figure 8d). Migrating whales appeared to be headed to the same general area (i.e., northeast of New Zealand) but not to the same specific destination (Figure 5), and individual turnaround points were separated by as much as 2,894 km, spanning approximately 1,897 km of latitude and 2,894 km of longitude in an area of almost 5.5 million km². MGD to the turnaround point from where the migrations began averaged 4,707.7 km (range 4,596.0–5,353.8, $n = 10$); mean MTD was 4,993.3 km (range 4,859.5–5,794.0, $n = 9$). None of the tags transmitted

through an entire round-trip migration but, doubling the time it took five whales to reach their turnaround points, we estimated that round-trip migrations would have taken from 41.6–55.6 days. The two longest duration trips were from the more southerly McMurdo Sound, the shortest duration trip was from Terra Nova Bay.

Type C north- and southbound migration tracks were largely linear. The northbound direction in almost all cases was between 0° and 45°, and the routes, including the turnaround points, occurred almost entirely over deep, open-ocean water (Figure 5). Six of seven whales tagged in McMurdo Sound during the austral summer of 2012–2013 were subsequently sighted there in 2014–2015, including five that initiated migrations. These findings indicate that migrating type C whales made round trips and showed site fidelity to the feeding grounds even after making lengthy migrations (see also Fearnbach et al., 2019; Pitman et al., 2018).

4 | DISCUSSION

Whale migration has long been described as an annual, round-trip movement between summer foraging grounds in high latitudes and winter calving grounds in low latitudes (see Introduction). According to Matthews (1978), “We now know that the migrations are closely correlated with the two fundamental necessities of cetaceans, as indeed of all animals, those of feeding and breeding.” However, why whales travel to the tropics to breed has remained a mystery. Below, we summarize our findings on the movements and residency patterns of antarctic killer whales and offer some new insights into the nature of, and reason for, killer whale migrations. We provide additional support for the argument that antarctic killer whales migrate to lower latitudes to promote skin molt and discuss how this might apply to the migrations of other whale species as well.

4.1 | Antarctic killer whale migration

Our updated satellite-tracking results indicate that, among the four killer whale ecotypes that are known to regularly occur in antarctic waters (i.e., types A, B1, B2, and C), at least three (B1, B2, and C) undertake long-distance, high-speed, nonstop, round-trip migrations to lower latitudes. These three ecotypes comprise a mammal-eating prey specialist (B1), a fish-eater (C), and a penguin predator that is suspected to feed mainly on fish (B2; Durban et al., 2016; Pitman & Durban 2010, 2012; Pitman & Ensor, 2003; Pitman et al., 2018). Furthermore, this migratory behavior is geographically widespread in Antarctica having now been documented off the WAP (types B1 and B2), and in western Ross Sea (type C; Figure 1). It now seems likely that *all* antarctic killer whales are highly migratory, although the migratory patterns of type A killer whales (mammal-eaters that frequent open waters; Fearnbach et al., 2019; Pitman & Ensor, 2003), while broadly similar to the other ecotypes, differed in some key details and will be discussed separately below.

Antarctic killer whales performed some remarkable feats of migration. A type C killer whale from the western Ross Sea traveled 48° of latitude (from 78°S to 30°S), a round trip of over 11,000 km and the longest killer whale migration documented to date (Figure 5c). A type B2 killer whale tagged off the WAP migrated to the waters off southern Brazil and back; it then spent just 71 days in antarctic waters before repeating the same trip (Figure 4d). This is to our knowledge the only record of any animal species completing the same, long-distance, round-trip migration twice in the same year. Furthermore, these two migrations were completed within a 5.5-month period, suggesting that antarctic killer whales could, potentially, complete this migration 3–4 times per year.

These findings support the contention of Durban and Pitman (2012) that, although killer whales commonly occur in antarctic waters during summer when prey is abundant and accessible, their subsequent migrations to lower latitudes are not for purposes of feeding or breeding (except possibly type A; see below). The observed pattern of directional movement, elevated speed, decreased dive depths, and limited time spent at the northern terminus of migration argues against a hypothesis that killer whales migrate to lower latitudes for feeding. They are not spending enough time along their migratory route to obtain enough energy to offset the cost of migration. Additionally, except for type A (see

below), tagged migrants generally did not approach islands, continental shelf areas, seamounts, or other obvious topographic or oceanographic features that might have afforded enhanced feeding opportunities (Figures 3–5; cf. Reisinger et al., 2015). Instead, they traveled rapidly north and then turned abruptly around and headed south toward Antarctica (sometimes on the same track they took northward or, in most cases, just east of it; Figure 4 and Figure 5). Furthermore, all four individuals that were tracked through complete, round-trip migrations (one type A, Figure 2a; three B2s, Figure 4a,c,d) returned to the same general areas where they started their northward migrations, after being gone only about 6 weeks—a further indication that they probably did not leave antarctic waters due to a lack of prey.

Dive-depth profiles provided additional evidence that antarctic killer whales forego normal foraging behavior during migration. Mammal-eating killer whales (types A and B1) feed on air-breathing prey, and, accordingly, most of their dives were less than 50 m, both on the feeding grounds (Figure 7a,b) and during migration (Figure 7a; no dive data for type B1 during migration). In contrast, type C killer whales (fish-eaters) foraging in McMurdo Sound during the summer had an average mean dive depth of 110.0 m and regularly dove 300–500 m with a maximum of 696 m (Figure 7d). However, after they left the Sound on their northbound migration, their average mean dive depth immediately decreased to 38.0 m, with a maximum dive of 292 m (Figure 7d), as whales simultaneously increased their speed and directional coherence (Figure 6d). Although type B2 killer whales have been observed feeding only on penguins (Pitman & Durban, 2010), their dive depth profiles on the feeding ground are much more similar to the fish-eating type C killer whales than the two mammal-eaters (types A and B1; Figure 7a,b), and it appears that B2 whales are also primarily fish-eaters. Although large baleen whales are normally assumed to fast during migration to lower latitudes (Lockyer & Brown, 1981), they will feed if the opportunity arises (e.g., Andrews-Goff et al., 2018; Findlay et al., 2017; Geijer et al., 2016; Owen et al., 2017). It seems likely that killer whales, being much smaller and traveling continuously at relatively high speeds, for 6–8 weeks, would probably also take advantage of any feeding opportunities in route, but their directed tracks suggest that they normally do little or no feeding during migration.

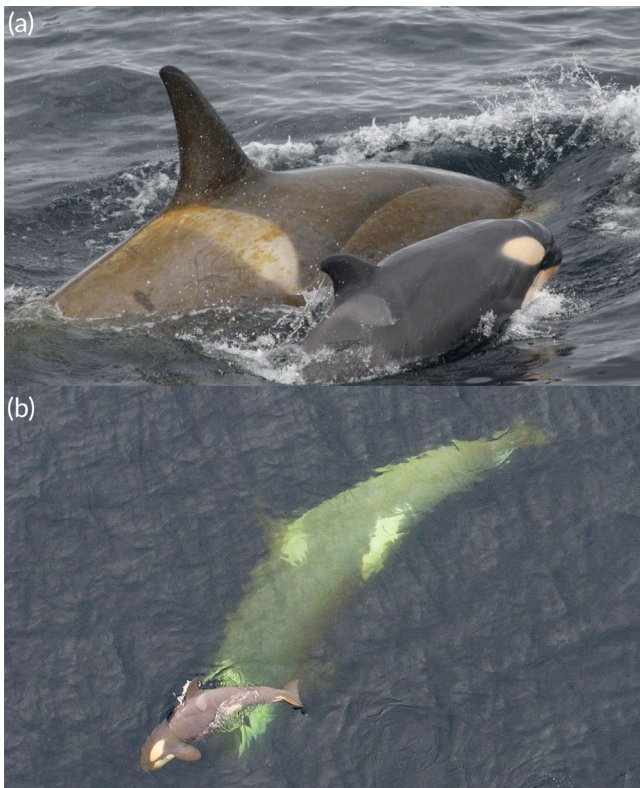


FIGURE 9 Two different female ecotype B2 killer whales with a heavy yellowish coating of diatoms all over their bodies; their newborn calves have no diatoms and we infer that they were recently born in antarctic waters (see text); (a) Wilhelmina Bay, Western Antarctic Peninsula, 14 March 2016, photo by A. Schulman-Janiger; (b) a calf with fetal folds still visible; Gerlache Strait, Western Antarctic Peninsula, 3 February 2018; photo by J. Durban and H. Fearnbach, collected from >30 m above the whales using a unmanned hexacopter, under NMFS Permit No. 19091 and Antarctic Conservation Act Permit ACA 2017–029.

It also seems unlikely that antarctic killer whales migrate to low latitudes for calving. On average, migrating killer whales, except type A, traveled 2–3 times faster than they did when they were on the feeding grounds (Figure 6). Their high-speed, almost nonstop, travel would make it difficult for a neonate calf to keep up. In addition, we also now know that killer whales are capable of successfully giving birth in antarctic waters. Gill and Thiele (1997) photographed killer whales (type C, based on their images) well within the pack ice during late winter (10 August 1995), and they cited the presence of a small calf as the first evidence of a cetacean being born in antarctic waters. Figure 9 shows two different type B2 killer whale mothers and their newborn calves photographed near the WAP in March 2016 and January 2018, respectively. Both mothers had a thick film of diatoms, but their calves were clean—clear evidence that the calves were recently born in antarctic waters, with insufficient time to accumulate diatoms (see below). Figure 9b shows a very small calf, less than a third of the length of its mother; it had a floppy dorsal fin and fetal folds and was probably no more than a few days old (JWD and HF, unpublished data). Additionally, a type C female observed at TNB on 15 January 2015 was traveling with a neonatal calf that had conspicuous fetal folds. The mother and calf appeared to be with a group that subsequently migrated northward. Birthing in antarctic waters would allow newborn calves to forgo traveling thousands of kilometers, at high speed, immediately postpartum, while living in an area where the mother has access to abundant prey resources. More observations will be needed to determine when and where most calves are born, but the evidence at hand suggests that birthing in antarctic waters is a viable, and probably desirable, option for antarctic killer whales.

There are several sets of observations to suggest that killer whale occurrences in Antarctica are aseasonal and that migration could be facultative. The first is that at least some killer whales can be found in antarctic waters throughout the year. A caveat here is that our field research had a strong seasonal bias: we tagged animals only during the austral summer months (i.e., December–February; Table 1), and mean tag life was only 56.3 days. Nevertheless, based on a combination of tagging and photo-identification data, we recorded killer whales around the WAP from at least October through June (Table 1; Fearnbach et al., 2019). Further evidence of killer whale occurrences in the WAP during winter (i.e., June–August) came from a tagged B2 whale that completed a round-trip migration and returned to the WAP at the onset of winter on 1 June (2010; Figure 4a) and another B2 that nearly completed a southbound trip that would have returned it to the WAP on or about 7 August (2016; Figure 4d). Because many (and perhaps all) tagged killer whales spent at least 2 months on the foraging grounds (Table 1), these last two individuals likely would have remained in antarctic waters until at least July and September, respectively. Other evidence for winter occurrences comes from observations recorded during the relatively few winter surveys conducted in Antarctica. These include 4 July (1987), type unknown, Anvers Island, WAP (RLP personal observation); 10 August (1995), type C, fast-ice edge south of Tasmania (Gill & Thiele, 1997); and 13–16 August (1955), type B1 or B2, Carlson Island, Weddell Sea (Taylor, 1957). Plötz, Weidel, and Bersch (1991) reported three sightings of killer whales (type unknown) “roving in large open leads” in the northeastern Weddell Sea also in July and/or August (1986; exact dates unspecified). Santora (2014) reported sightings of three groups of type B (i.e., B1 or B2; mean group size: 6.0), “hanging around the Bransfield and near Elephant Island” in August 2012.³ We conclude that killer whales can be found in antarctic waters year-round, although a more complete parsing of relative abundance, by month and by ecotype, awaits further investigation.

Perhaps related to the year-round occurrence of killer whales in antarctic waters, the migration departure dates of tagged whales were protracted. This was evident both in the variable amounts of time that individual whales spent on the antarctic foraging grounds and in the wide range of their departure dates. Normally, we were unable to determine how long individual killer whales remained on their antarctic foraging grounds because, as mentioned previously, all 62 of the whales we tagged had been present for an unknown period of time prior to tagging, and among those tagged only about half (48%) initiated migration before their tags stopped transmitting. However, as mentioned previously, the one B2 individual that was tracked through two, nearly complete migrations (Figure 4d) spent 71 days in antarctic waters between migrations, while another B2 individual spent a minimum of 146 days in antarctic waters after being tagged and had not initiated migration when its tag stopped transmitting (Table 1).

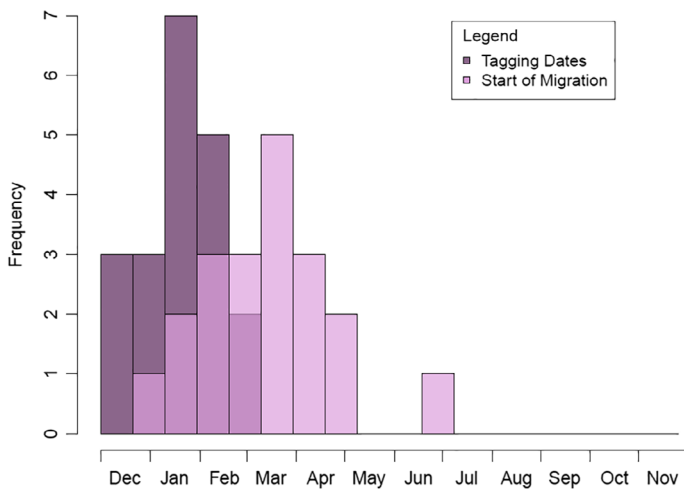


FIGURE 10 Tagging dates and migration departure dates for 22 killer whales of four different ecotypes, satellite-tagged in antarctic waters during 2009–2016. Tagging occurred from 4 December (2014) to 2 March (2016); departures were recorded from 31 December (2013) to 25 June (2016).

The variable amount of time that killer whales spent on the antarctic foraging grounds was also reflected in the wide range of migration departure dates for all tagged ecotypes combined, which spanned a minimum of almost 6 months—from 31 December (type A, Figure 2a, 2013) to 25 June (type B2, Figure 4d, 2016; Table 1, Figure 10). Again, these departure dates represent a minimum range because of the seasonal (summer) bias in our tagging efforts and a mean tag life of only 56.3 days—only one tag transmitted more than 150 days, and it recorded the latest departure date.

A wide range of migration departure dates was also recorded within individual killer whale ecotypes. Departure dates for tagged type A killer whales ranged from at least 31 December (2013) to 23 March (2014), although another whale had not departed by 2 April (2010) when its tag stopped transmitting (Table 1). A type B1 killer whale departed on 28 January (2009), and another had not departed by 4 March (2015). Departure dates for type B2 ranged from 11 March (2016) to 27 June (2016; two consecutive migrations by the same whale). Departure dates of type C killer whales from the western Ross Sea ranged from at least 25 January (2015, Terra Nova Bay) to 18 March (2015, McMurdo Sound; Table 1). As an illustration of variability in migration schedules within an ecotype, the two type Cs cited above departed 51 days apart in the same year, from locations in the Ross Sea only approximately 100 km apart. Furthermore, when the first of these two whales stopped transmitting on 24 February, it was on track to be back in Terra Nova Bay by 8 March, 10 days before the second whale departed McMurdo Sound (Table 1).

Asynchrony in migration times was also evident in the varying degrees of diatom infestation evident among different ecotypes and among different groups of the same ecotype, often on the same day, and sometimes even intermingled within the same sighting (RLP, JWD, and HF, unpublished data). All these observations taken together suggest that the migration schedules of types B1, B2, and C killer whales were flexible (perhaps facultative) and protracted—extending well beyond the austral summer (i.e., December–February). More tagging (or, possibly, intensive photo-identification studies) will be required to determine range and variability in residency times and departure dates of killer whales on antarctic feeding grounds, both within and among ecotypes, and for individual groups.

Although type A killer whales also made long-distance, round-trip migrations to lower latitudes, their tracks were notably different from the other killer whale types. Type As traveled northward on both sides of South America (Figure 2), while types B1 and B2 killer whales tagged near the WAP traveled northward only on the eastern side of the continent (Figure 3 and Figure 4), in the direction of the nearest warm water (Figure 8b,c). Compared to the other ecotypes, type As migrated at slower speeds (mean 5.4 vs. 8–9 km/hr; Table 1, Figure 6) and meandered more readily (i.e., greater difference between MTD and MGD; Figure 2), suggesting that they may have been foraging (or possibly calving) during migration. By contrast, the tracks of types B1, B2, and C killer whales were rapid and directional, with no indication of feeding. Migration by type A whales also took more time than those of types B and

C: the only type A tracked through an entire round trip took 59.2 days (Table 1; Figure 2a), almost 10 days longer than any of the other killer whale types tagged off the WAP. Another type A (Figure 2b) reached its turning point after 49.6 days; at that rate, it would have taken an estimated 99.3 days to complete its migration.

In addition to having different migratory patterns, type A killer whales differed from the other antarctic ecotypes in other ways. In general, they appeared to be less derived, behaviorally and morphologically, than the other killer whale ecotypes in Antarctica. Type A has a typical black and white killer whale color pattern, and in Antarctica, they forage only in open water, avoiding sea ice altogether (Fearnbach et al., 2019; Pitman & Ensor, 2003). In contrast, types B1, B2, and C killer whales have a distinctive, two-toned gray and white color pattern, a conspicuous dorsal cape, markedly different eye patches, and they forage extensively in and around sea ice (Durban et al., 2016; Pitman & Durban, 2012; Pitman & Ensor, 2003; Pitman et al., 2018). These “caped forms” appear to be endemic to Antarctica, and additional studies, including histology and genetic analyses (e.g., Foote et al., 2011), will be necessary to determine if they are better adapted than type A to cope with the extreme antarctic environment, and how such adaptation might contribute to observed differences in migratory patterns.

In summary, the migration schedules of antarctic killer whale ecotypes B1, B2, and C were protracted, perhaps year-round, and possibly facultative, with groups capable of making multiple, 6–8 week, round-trip migrations per year. Departure dates were highly variable among and within ecotypes, and the amount of time spent on antarctic foraging grounds for individual whales ranged from 71 days to at least 146 days, at least for type B2 killer whales. We infer that at least some of the caped forms (i.e., types B1, B2, and C) can be found year-round in Antarctica and that they are capable of calving there (at least type B2 and probably C), making it unlikely that killer whales migrate to warmer waters for breeding purposes. It is currently unknown if type A killer whale(s) give(s) birth in antarctic waters, or if they occur there during winter. Migration by type A whales appears to be longer, slower, and more meandering than the other types, perhaps due to feeding or calving. Type A killer whale(s) could be a more recent arrival to antarctic waters and therefore may be less well adapted physiologically (Foote et al., 2011). These observations provide further support for the Durban and Pitman (2012) hypothesis that most Antarctic killer whales migrate to warm waters for reasons other than feeding or breeding, which we further discuss below.

4.2 | Skin molt in cetaceans

A diverse group of vertebrates regularly undergo epidermal molt, a normal maintenance process for replacing skin, hair, and feathers (Ling, 1970, 1972). Skin and pelage molt to shed, renew, repair, and grow the outer integument is also essential to marine mammals, including cetaceans (Ling 1974, 1984; Reeb, Duffield, & Best, 2005). According to Reeb, Best, and Kidson (2007) and Reeb et al. (2005) “molting,” “ecdysis,” and “sloughing” are synonymous and refer to a seasonal or periodic skin molt, while “exfoliation” or “desquamation” refers to a more continuous process of shedding largely individual skin cells. Marine mammals provide examples of both continuous and periodic epidermal replacement. For example, among pinnipeds, otariids (fur seals and sea lions) gradually replace their hair year-round, while most phocids (true seals) haul out on land or ice as part of an annual, episodic molt cycle (Riedman, 1990). Skin molt among cetaceans has usually been described as continuous (Hicks, St. Aubin, Geraci, & Brown, 1985; Ling 1972, 1984; Reeb et al., 2005), which Ling (1974) suggested was due to whales and dolphins living in environments with little seasonal variation. This conclusion, however, fails to acknowledge that migrating whales occupy seasonal habitats with SST that can range over 30°C (e.g., from -1.9°C to 28.3°C for humpbacks; Rasmussen et al., 2007).

Historically, the one notable exception to continuous epidermal molt among cetaceans has been the annual molt of the beluga whale (*Delphinapterus leucas*). Belugas famously aggregate during summer in traditional river estuaries in the Canadian Arctic and Alaska where the water is warmer, fresher and shallower than their normal foraging habitat (e.g., Frost, Lowry, & Carroll, 1993; Smith, St. Aubin, & Hammill, 1992). In arguments very similar to those proposed for baleen whales that migrate and calve in the tropics, it was initially suggested that belugas gave birth in estuaries because the warmer water afforded increased survivorship for their calves (Sergeant, 1973; Sergeant &

Brodie, 1975), or possibly for belugas of all ages (Fraker, Gordon, McDonald, Ford, & Cambers, 1979). It was also suggested that these could be feeding aggregations (e.g., Huntington, 1999; Seaman & Burns, 1981), or that the nearshore habitat might provide mothers and calves protection from killer whales (Brodie, 1971; Caron & Smith, 1990; Smith et al., 2017).

However, despite extensive fieldwork, no calving and little or no feeding was ever observed in the estuaries (Finley, Hickie, & Davis, 1987; Smith, Hammill, & Martin, 1994; Smith et al., 1992), and, as an alternative explanation, Finley (1983) quoted an experienced Inuit hunter who stated, “Belugas go to the rivers for warmth. And like seals they moult their skins. They moult in the warm water.” It was subsequently confirmed that belugas do in fact return to estuaries as part of an annual molt cycle (Smith et al., 1992; St. Aubin et al., 1990; but see Smith et al., 2017). Perhaps as an indication of the importance of this molting process, belugas in northern Canada return to the same estuaries every year despite “heavy human predation” that has resulted in some populations being depleted and possibly extirpated (Caron & Smith, 1990; Finley, Miller, Allard, Davis, & Evans, 1982; Smith et al., 1994). Although an annual molt was previously considered unique to belugas (e.g., O’Corry-Crowe, 2018; St. Aubin et al., 1990), it has recently been reported in bowhead whales (Chernova, Shpak, Kiladze, Azarova, & Rozhnov, 2016; Fortune et al., 2017), possibly in narwhals (*Monodon monoceros*; Wagemann & Kozłowska, 2005), and it may prove to be the rule among all high-latitude cetaceans (see below).

As in pinnipeds, a warmer environment is apparently key to increasing skin cell metabolism and stimulating molt in cetaceans (Boily, 1995; Feltz & Fay, 1966). Gambell (1972) observed that sperm whales (*Physeter macrocephalus*) caught off Durban, South Africa, had fewer ectoparasites, which he suggested might be due to their higher rate of “epidermal decomposition” in the warmer waters there. Whitehead, Gordon, Mathews, and Richard (1990) reported that humpbacks, sperm whales, and gray whales all sloughed more skin in the warmer waters of their breeding grounds than in the colder waters of their feeding grounds. More specifically, they stated that sperm whales sloughed more skin in higher water temperatures (19°C–26°C), the least amount in the lowest temperatures that they sampled (14°C–18°C), and intermediate amounts at intermediate temperatures (18°C–23°C; Whitehead et al., 1990). Although belugas live and calve in cold waters (0°–7°C), the estuaries where they molt are considerably warmer (10°C–18°C; Watts, Draper, & Henrico, 1991). Bowhead whales in the western Okhotsk Sea, Russia (Chernova et al., 2016), and the eastern Canadian Arctic (Fortune et al., 2017) also move into warmer, shallow bays when they molt.

Molting requires the skin to be metabolically active. This in turn requires blood flow to the skin surface, which results in a loss of body heat, especially in a cold, aquatic environment. One way to reduce that heat loss, and maintain homeothermy, is through peripheral vasoconstriction. Although vasoconstriction reduces blood flow to the skin, it also impedes metabolism, resulting in a “conflict between thermoregulation and epidermal maintenance” (Boily, 1995). When phocid seals molt in high latitudes, they resolve this conflict by hauling out on land or ice, because the thermal conductivity and heat capacity of air is 25× and 4× lower, respectively, than that of water (Boily, 1995). However, for cetaceans in high latitudes, moving to warmer water may be the only option for reducing heat loss during skin molt.

Skin maintenance in high latitudes should present more of a challenge for cetacean calves than for adults because increased surface-area-to-volume ratio makes heat conservation more problematic for calves, while at the same time, their need for somatic growth also requires increased blood flow to the skin. These additional stressors may account for the prevalence of anomalous-looking skin conditions prevalent among killer whale calves in antarctic waters (Figure 11). Responding to the skin-molt needs of their young calves may be an important factor in determining the timing of migration for individual groups of antarctic killer whales.

4.3 | Diatoms and skin molt migration

Among the numerous species of diatoms that occur on the skin of cetaceans, *Bennettella ceticola* is by far the most common (Gerasimiuk & Zinchenko, 2012; Nemoto, 1956). It is particularly prevalent in colder waters, and cetaceans are the only known hosts (Nemoto, 1958). In Antarctica, *B. ceticola* probably occurs on all cetaceans (Hart, 1935),

FIGURE 11 Killer whale calves photographed in Antarctica showing skin conditions possibly related to their inability to molt properly in subfreezing waters. (a, b) two different ecotype Cs from McMurdo Sound; (c) ecotype B2 from Gerlache Strait, Western Antarctic Peninsula; photos by R. Pitman.



but it has been reported most commonly on rorquals, including blue, fin, sei (*Balaenoptera borealis*), antarctic minke (Figure 12), and humpback whales. Among odontocetes, diatoms (presumably *B. ceticola*) have also been recorded on sperm whales, bottlenose whales (“probably *Hyperoodon*”; Bennett, 1920), and dolphins (*Lagenorhynchus cruciger* and *Cephalorhynchus commersoni*; Best, 1969; Hart, 1935; Thomas, Leatherwood, Evans, Jehl, & Awbrey, 1981; Wilson, 1907). Diatoms have also been commonly observed on antarctic killer whale ecotypes A, B1, B2, and C (Figure 9; Durban & Pitman, 2012; Pitman & Ensor, 2003; RLP, JWD, and HF, personal observaion), and *B. ceticola* has been specifically identified on skin biopsy samples from type C killer whales in McMurdo Sound (RLP, unpublished data).

Whalers in the early 1900s were the first to recognize the significance of diatoms for interpreting the movements and nutritional status of antarctic whales, especially among the fin and blue whales that they targeted (Bennett, 1920; Hart, 1935; Mackintosh & Wheeler, 1929). Whales that were thin and clean were assumed to be recent arrivals that had been fasting in the tropics, but after about one month of feeding in antarctic waters, they began to accumulate a conspicuous yellow diatom film, which “covered perhaps the whole body within a few months” (Hart, 1935). Blue whales that acquired a heavy diatom coating on their otherwise white bellies were referred to as “sulfur-bottoms” (Bennet, 1920).

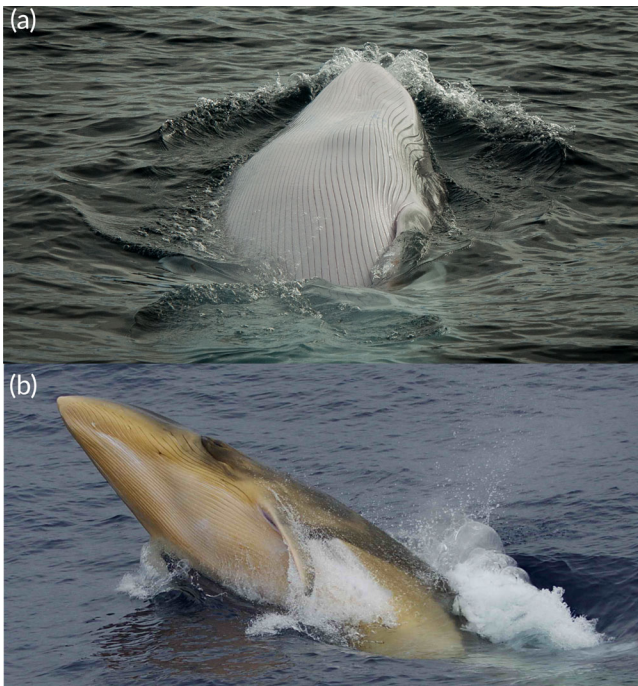


FIGURE 12 Antarctic minke whales, including: (a) an apparent recent arrival to antarctic waters from lower latitudes based on snowy white ventral surface, including throat pleats (Gerlache Strait, 21 February 2013; photo S. Hansen), and (b) an individual with a heavy infestation of diatoms on its ventral surface indicating that it has probably been in antarctic waters for at least 1 month (Drake Passage, 30 January 2012; photo by J. Durban).

Although killer whales in Antarctica are often coated with a yellow diatom film, at other times, the same individuals can be clean, without a hint of yellowing (Durban & Pitman, 2012). Hicks et al. (1985) suggested that skin molt in cetaceans limited colonization by microorganisms by providing a self-cleaning surface. Conversely, Durban and Pitman (2012) hypothesized that if killer whales conserved body heat by reducing blood flow to their skin surface; this would decrease or suspend normal skin cell proliferation, prevent sloughing, and allow diatoms to accumulate. Then, when killer whales migrated to the tropics and molted their skin, they would also shed the diatoms and return to Antarctica clean, as the early whalers had noticed for rorquals.

As noted above, it is likely that all cetaceans in antarctic waters acquire diatom films, and if, as we have suggested for killer whales, this indicates that they are not shedding their skin as they normally would, then these other species may also need to migrate to warmer waters to molt their skin. However, unlike the relatively small killer whales, large baleen whales can accumulate enough blubber during 4–6 months of intensive summer feeding in Antarctica that they can largely fast for the rest of the year (Lockyer & Brown, 1981; Mackintosh, 1965; see also Owen et al., 2017). This could allow them to synchronize their breeding cycle to coincide with a single, extended, seasonal (winter) trip to low latitudes for molting purposes. In that case, instead of whales migrating to the tropics or subtropics for calving, whales would be traveling to warm waters for skin maintenance and perhaps find it adaptive to bear their calves while they are there. The warm waters necessary for skin molt could, then, contribute to the growth and survival of their calves (e.g., Clapham, 2001; Dawbin, 1966; Norris, 1967; Rasmussen et al., 2007; Whitehead & Moore, 1982), and also allow mothers with calves to avoid areas of high killer whale density in higher latitudes (Connor & Corkeron, 2001; Corkeron & Connor, 1999; Payne, 1995). The SMM hypothesis could also help explain why non-calving individuals (i.e., prebreeders, adult males, resting females) migrate to the tropics—a question that has remained unanswered by previous explanations of whale migration (Clapham, 2000). If the SMM hypothesis is correct, the traditional paradigm of a feeding/breeding migration for large whales would perhaps be better termed a feeding/molting migration, with any increase in breeding success being viewed as a collateral benefit. It remains to be seen, however, if the existing evidence equally well supports a multifactor explanation for whale migration.

Durban and Pitman (2012) were not the first to suggest a possible link between skin molt and whale migration. Although, up until recently, belugas were thought to be the only cetacean to have an annual epidermal molt (Chernova et al., 2016), St. Aubin et al. (1990) speculated that other cetacean species that migrated seasonally between polar feeding areas and low latitude calving grounds might have a similar molt pattern. Elsner (1999) also stated that although warm water temperatures might enhance calf growth for migrating whales, “we are still left with the question of how skin growth in more mature animals immersed in cold polar waters takes place at those colder temperatures.” Annual (or periodic) molt and SMM could be the answer.

Whale migration, at least historically, was a biologically significant event on a global scale, annually transporting millions of tons of animal flesh, thousands of kilometers (Laws, 1977). Migrating whales influence local ecosystems in several ways, including as predators and prey, and as whale fall for scavengers (Croll et al., 2006; Katona & Whitehead, 1988; Pitman et al., 2015; Roman et al., 2014). To date, however, there has not been a consensus explanation for this behavior, and our suggestion that long-distance migration to warm waters is mainly for routine skin maintenance warrants further investigation. Furthermore, the proposed SMM hypothesis could have phylogeographic implications. If whales need to migrate to warm water to molt their skin, then they are likely returning to ancestral habitat (Gaskin, 1982), and, instead of being considered polar species that migrate to the tropics for molting and breeding, they might best be described as warm-water forms that migrate poleward for feeding. Histological studies that compare skin cell proliferation among different species of migratory and nonmigratory whales, sampled at high and low latitudes, throughout the year, should provide a key test of our ideas about SMM and the proposed significance of skin molt in cetacean life history.

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ENDNOTES

¹ Personal communication from Corey Matthews, Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2 N2, Canada, April 2018.

² Personal communication from David Donnelly, Killer Whales Australia, Victoria, Australia, December 2018.

³ Personal communication from Jarrod Santora, UC Santa Cruz, Santa Cruz, CA, June 2019.

REFERENCES

- Andrews-Goff, V., Bestley, S., Gales, N. J., Laverick, S. M., Paton, D., Polanowski, A. M., ... Double, M. C. (2018). Humpback whale migrations to Antarctic summer foraging grounds through the southwest Pacific Ocean. *Scientific Reports*, 8, 12333.
- Bennett, A. G. (1920). On the occurrence of diatoms on the skin of whales. *Proceedings of the Royal Society B: Biological Sciences*, 91, 352–357.
- Berta, A., Sumich, J. L., & Kovacs, K. M. (2015). *Marine mammals: Evolutionary biology* (3rd ed.). San Diego, CA: Academic Press/Elsevier.
- Best, P. B. (1969). The sperm whale (*Physeter catodon*) off the west coast of the South America. 4. Distribution and movements. *Division of Sea Fisheries Investigational Report*, 78, 1–12.
- Boily, P. (1995). Theoretical heat-flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *Journal of Theoretical Biology*, 172, 235–244.
- Bowen, W. D., & Siniff, D. B. (1999). Distribution, population biology, and feeding ecology of marine mammals. In J. E. Reynolds, III & S. A. Rommel (Eds.), *Biology of marine mammals* (pp. 423–484). Washington, DC: Smithsonian Institution Press.
- Branch, T. A., & Butterworth, D. S. (2001). Estimates of abundance south of 60°S for cetacean species sighted frequently on the 1978/79 to 1997/98 IWC/IDCR-SOWER sighting surveys. *Journal of Cetacean Research and Management*, 3, 251–270.
- Brodie, P. F. (1971). A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to Cumberland Sound, Baffin Island, population. *Journal of the Fisheries Research Board of Canada*, 28, 1309–1318.
- Brodie, P. F. (1975). Cetacean energetics, an overview of intraspecific size variation. *Ecology*, 56, 152–161.
- Budylenko, G. A. (1981). Distribution and some aspects of the biology of killer whales in the South Atlantic. *Report of the International Whaling Commission*, 31, 523–525.
- Caron, L. M. J., & Smith, T. G. (1990). Philopatry and site tenacity of belugas, *Delphinapterus leucas*, hunted by the Inuit at the Nastapoka Estuary, Eastern Hudson Bay. In T. G. Smith, D. J. St. Aubin, & J. R. Geraci (Eds.), *Advances in research on the beluga whale, Delphinapterus leucas* (Vol. 224, pp. 69–79). *Canadian Bulletin of Fisheries and Aquatic Science*.
- Chernova, O. F., Shpak, O. V., Kiladze, A. B., Azarova, V. S., & Rozhnov, V. V. (2016). Summer molting of bowhead whales *Balaena mysticetus* Linnaeus, 1758, of the Okhotsk Sea population. *Doklady Biological Sciences*, 471, 261–265.
- Chittleborough, R. G. (1958). The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). *Australian Journal of Marine and Freshwater Research*, 9, 1–18.
- Clapham, P. J. (2000). The humpback whale: Seasonal feeding and breeding in a baleen whale. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 173–196). Chicago, IL: University of Chicago Press.
- Clapham, P. J. (2001). Why do baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science*, 17, 432–436.
- Clapham, P. J. (2017). When it's right to be wrong. *Marine Mammal Science*, 33, 966–967.
- Connor, R. C., & Corkeron, P. J. (2001). Predation past and present: killer whales and baleen whale migration. *Marine Mammal Science*, 17, 436–439.
- Corkeron, P. J., & Connor, R. C. (1999). Why do baleen whales migrate? *Marine Mammal Science*, 15, 1228–1245.
- Croll, D. A., Kudela, R., & Tershy, B. R. (2006). Ecosystem impact of the decline of large whales in the North Pacific. In J. A. Estes, R. L. Brownell, Jr., D. P. DeMaster, D. F. Doak, & T. M. Williams (Eds.), *Whales, whaling and ocean ecosystems* (pp. 202–214). Berkeley, CA: University of California Press.
- Dahlheim, M. E., Schulman-Janiger, A., Black, N., Ternullo, R., Ellifrit, D., & Balcomb, K. C. (2008). Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): Occurrence, movements, and insights into feeding ecology. *Marine Mammal Science*, 24, 719–729.
- Dawbin, W. H. (1966). The seasonal migratory cycle of humpback whales. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 145–170). Berkeley, CA: University of California Press.
- Durban, J. W., & Pitman, R. L. (2012). Antarctic killer whales make rapid, round-trip movements to sub-tropical waters: Evidence for physiological maintenance migrations? *Biology Letters*, 8, 274–277.
- Durban, J. W., Fearnbach, H., Burrows, D. G., Ylitalo, G. M., & Pitman, R. L. (2016). Morphological and ecological evidence for two sympatric forms of Type B killer whale around the Antarctic Peninsula. *Polar Biology*, 40, 231–236.
- Dwyer, S. L., & Visser, I. N. (2011). Cookie cutter shark (*Isistius* sp.) bites on cetaceans, with particular reference to killer whales (*orca*) (*Orcinus orca*). *Aquatic Mammals*, 37, 111–138.
- Elsner, R. (1999). Living in water: Solutions to physiological problems. In D. A. Pabst, S. A. Rommel, & W. A. McLellan (Eds.), *Biology of marine mammals* (pp. 73–116). Washington, DC: Smithsonian Institution Press.
- Estes, J. A., Heithaus, M., McCauley, D. J., Rasher, D. B., & Worm, B. (2016). Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review Environment and Resources*, 41, 83–116.
- Evans, P. G. H. (1987). *The natural history of whales and dolphins*. London, UK: Christopher Helm.
- Fearnbach, H., Durban, J. W., Ellifrit, D. K., & Pitman, R. L. (2019). Increasing abundance of Type A killer whales (*Orcinus orca*) in the coastal waters off the Western Antarctic Peninsula. *Polar Biology*, 42, 1477–1488.

- Feltz, T. E., & Fay, F. H. (1966). Thermal requirements *in vitro* of epidermal cells from seals. *Cryobiology*, 3, 261–264.
- Finley, K. J. (1983). The estuarine habit of the beluga or white whale (*Delphinapterus leucas*). *Cetus*, 4, 4–5.
- Finley, K. J., Hickie, J. P., & Davis, R. A. (1987). Status of the beluga, *Delphinapterus leucas*. in the Beaufort Sea. *Canadian Field-Naturalist*, 101, 271–278.
- Finley, K. J., Miller, G. W., Allard, M., Davis, R. A., & Evans, C. R. (1982). The belugas (*Delphinapterus leucas*) of northern Quebec: Distribution, abundance, stock identity, catch history and management. *Canadian Technical Report, Fisheries and Aquatic Sciences*, 1123, 1–61.
- Findlay, K. P., Seakamela, S. M., Meyër, M. A., Kirkman, S. P., Barendse, J., Cade, D. E., ... Wilke, G. (2017). Humpback whale “super-groups” — A novel low-latitude feeding behaviour of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) in the Benguela Upwelling System. *PLoS ONE*, 12(3), e0172002.
- Footo, A. D., Morin, P. A., Durban, J. W., Pitman, R. L., Wade, P., Willerslev, E., ... da Fonseca, R. R. (2011). Positive selection on the killer whale mitogenome. *Biology Letters*, 7, 116–118.
- Footo, A. D., Vijay, N., Ávila-Arcos, M. C., Baird, R. W., Durban, J. W., Fumagalli, M., ... Wolf, J. B. W. (2016). Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nature Communications*, 7, 11693.
- Forney, K. A., & Wade, P. (2006). Worldwide distribution and abundance of killer whales. In J. A. Estes, R. L. Brownell, Jr., D. P. DeMaster, D. F. Doak, & T. M. Williams (Eds.), *Whales, whaling and ocean ecosystems* (pp. 145–162). Berkeley, CA: University of California Press.
- Fortune, S. M. E., Koski, W. R., Higdon, J. W., Trites, A. W., Baumgartner, M. F., & Ferguson, S. H. (2017). Evidence of molting and the function of “rock-nosing” behavior in bowhead whales in the eastern Canadian Arctic. *PLoS ONE*, 12(11), e0186156.
- Fraker, M. A., Gordon, C. D., McDonald, J. W., Ford, J. K. B., & Cambers, G. (1979). White whale (*Delphinapterus leucas*) distribution and abundance and the relationship to physical and chemical characteristics of the Mackenzie Estuary. *Canadian Fisheries and Marine Services Technical Report*, 863, 1–56.
- Freitas, C., Lydersen, C., Fedak, M. A., & Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science*, 24, 315–325.
- Frost, K. J., Lowry, L. F., & Carroll, G. (1993). Beluga whale and spotted seal use of a coastal lagoon system in the northeastern Chukchi Sea. *Arctic*, 46, 8–16.
- Gambell, R. (1972). Sperm whales off Durban. *Discovery Reports*, 35, 199–358.
- Gaskin, D. E. (1982). *The ecology of whales and dolphins*. London, UK: Heinemann.
- Geijer, C. K. A., Notarbartolo di Sciarra, G., & Panigada, S. (2016). Mysticete migration revisited: Are Mediterranean fin whales an anomaly? *Mammal Review*, 46, 284–296.
- Gerasimiuk, V. P., & Zinchenko, V. L. (2012). Diatom fouling of the little picked [sic] whales in the antarctic waters. *Hydrobiological Journal*, 48, 28–34.
- Gill, P. C., & Thiele, D. (1997). A winter sighting of killer whales (*Orcinus orca*) in Antarctic sea ice. *Polar Biology*, 17, 401–404.
- Goley, P. D., & Straley, J. M. (1994). Attack on gray whales (*Eschrichtius robustus*) in Monterey Bay, California, by killer whales (*Orcinus orca*) previously identified in Glacier Bay, Alaska. *Canadian Journal of Zoology*, 72, 1528–1530.
- Hart, J. T. (1935). On the diatoms of the skim film of whales, and their possible bearing on problems of whale movements. *Discovery Reports*, 10, 247–282.
- Hicks, B. D., St. Aubin, D. J., Geraci, J. R., & Brown, W. R. (1985). Epidermal growth in the bottlenose dolphin, *Tursiops truncatus*. *Journal of Investigative Dermatology*, 85, 60–63.
- Hijmans, R. J. (2017). Raster: Geographic data analysis and modeling. *R package version*, 2, 6–7. Available at. <http://CRAN.R-project.org/package=raster>.
- Hokkanen, J. E. I. (1990). Temperature regulation of marine mammals. *Journal of Theoretical Biology*, 145, 465–485.
- Huntington, H. P., & the communities of Buckland, Elim, Koyuk, Point Lay and Shaktoolik. (1999). Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the eastern Chukchi and northern Bering seas, Alaska. *Arctic*, 52, 49–61.
- Johnson, D. S. (2013). CRAWL: Fit continuous-time correlated random walk models to animal movement data. R package version 1.4–1. Available at <http://CRAN.R-project.org/package=crawl>
- Johnson, D. S., London, J. M., Lea, M.-A., & Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology*, 89, 1208–1215.
- Jonsgård, Å. (1966). The distribution of Balaenopteridae in the North Atlantic Ocean. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 114–124). Berkeley, CA: University of California Press.
- Kasamatsu, F., & Joyce, G. G. (1995). Current status of odontocetes in the Antarctic. *Antarctic Science*, 7, 365–379.
- Katona, S., & Whitehead, H. (1988). Are Cetacea ecologically important? *Oceanography and Marine Biology*, 26, 553–568.
- Kellogg, R. (1929). What is known of the migrations of some of the whalebone whales. *Annual Report Smithsonian Institution*, 1928, 467–494.
- Kshatriya, M., & Blake, R. W. (1988). Theoretical model of migration energetics in the blue whale, *Balaenoptera musculus*. *Journal of Theoretical Biology*, 33, 479–498.

- Lavigne, D. M., Innes, S., Worthy, G. A. J., & Edwards, E. F. (1990). Lower critical temperatures of blue whales. *Balaenoptera physalus*. *Journal of Theoretical Biology*, 44, 249–257.
- Laws, R. M. (1977). Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 279, 81–96.
- LeDuc, R. G., Robertson, K. M., & Pitman, R. L. (2008). Mitochondrial sequence divergence among Antarctic killer whale ecotypes is consistent with multiple species. *Biology Letters*, 4, 426–429.
- Lillie, D. G. (1915). Cetacea. *Natural history of the British Antarctic Terra Nova Expedition, 1910(1)*, 85–124.
- Ling, J. K. (1970). Pelage and moulting in wild mammals with special reference to aquatic forms. *Quarterly Review of Biology*, 45, 16–54.
- Ling, J. K. (1972). Adaptive functions of vertebrate molting cycles. *American Zoologist*, 12, 77–93.
- Ling, J. K. (1974). The integument of marine mammals. In R. J. Harrison (Ed.), *Functional anatomy of marine mammals* (Vol. 2, pp. 1–34). New York, NY: Academic Press.
- Ling, J. K. (1984). Epidermal cycles and molting in marine mammals. *Acta Zoologica Fennica*, 171, 23–26.
- Lipps, J. H., & Mitchell, E. (1976). Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. *Paleobiology*, 2, 147–155.
- Lockyer, C. L., & Brown, S. G. (1981). The migration of whales. In D. J. Aidley (Ed.), *Animal migration* (pp. 105–137). Cambridge, UK: Cambridge University Press.
- Mackintosh, N. A. (1965). *The stocks of whales*. London, UK: Fishing News (Books), Ltd.
- Mackintosh, N. A., & Wheeler, J. F. G. (1929). Southern blue and fin whales. *Discovery Reports*, 1, 257–540.
- Matkin, C. O., Durban, J. W., Saulitis, E. L., Andrews, R. D., Straley, J. M., Matkin, D. R., & Ellis, G. M. (2012). Contrasting abundance and residency patterns of two sympatric populations of transient killer whales (*Orcinus orca*) in the northern Gulf of Alaska. *Fishery Bulletin*, 110, 143–155.
- Matthews, C. J. D., Luque, S. P., Petersen, S. D., Andrews, R. D., & Ferguson, S. H. (2011). Satellite tagging of a killer whale (*Orcinus orca*) in the eastern Canadian Arctic documents ice avoidance and rapid, long-distance movement into the North Atlantic. *Polar Biology*, 34, 1091–1096.
- Matthews, L. H. (1937). The humpback whale, *Megaptera nodosa*. *Discovery Reports*, 17, 7–92.
- Matthews, L. H. (1978). *The natural history of the whale*. New York, NY: Columbia University Press.
- Mikhalev, Y. A., Ivashin, M. V., Savusin, V. P., & Zelenaya, F. E. (1981). The distribution and biology of killer whales in the Southern Hemisphere. *Report of the International Whaling Commission*, 31, 551–566.
- Morin, P. A., Parsons, K. M., Archer, F. I., Ávila-Arcos, M. C., Barrett-Lennard, L. G., Dalla Rosa, L., ... Foote, A. D. (2015). Geographic and temporal dynamics of a global radiation and diversification in the killer whale. *Molecular Ecology*, 24, 3964–3979.
- Nemoto, T. (1956). On the diatoms of the skin film of whales in the northern Pacific. *Scientific Reports of the Whales Research Institute, Tokyo*, 11, 97–132.
- Nemoto, T. (1958). *Cocconeis* diatoms infected on whales in the Antarctic. *Scientific Reports of the Whales Research Institute, Tokyo*, 13, 185–191.
- Norris, K. S. (1967). Some observations on the migration and orientation of marine mammals. In R. M. Storm (Ed.), *Animal orientation and migration* (pp. 101–125). Corvallis, OR: Oregon State University Press.
- O’Corry-Crowe, G. (2018). Beluga whale *Delphinapterus leucas*. In B. Würsig, J. G. M. Thewissen, & K. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 93–96). San Diego, CA: Academic Press.
- Owen, K., Kavanagh, A. S., Warren, J. D., Noad, M. J., Donnelly, D., Goldizen, A. W., & Dunlop, R. A. (2017). Potential energy gain by whales outside of the Antarctic: Prey preferences and consumption rates of migrating humpback whales (*Megaptera novaeangliae*). *Polar Biology*, 40, 277–289.
- Payne, R. (1995). *Among whales*. New York, NY: Scribner.
- Pitman, R. L., & Durban, J. W. (2010). Killer whale predation on penguins in Antarctica. *Polar Biology*, 33, 1589–1594.
- Pitman, R. L., & Durban, J. W. (2012). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal Science*, 28, 16–36.
- Pitman, R. L., & Ensor, P. (2003). Three different forms of killer whales in antarctic waters. *Journal of Cetacean Research and Management*, 5, 131–139.
- Pitman, R. L., Durban, J. W., Greenfelder, M., Guinet, C., Jorgensen, M., Olson, P. A., ... Towers, J. R. (2011). Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters. *Polar Biology*, 34, 303–306.
- Pitman, R. L., Fearnbach, H., & Durban, J. W. (2018). Abundance and population status of Ross Sea killer whales (*Orcinus orca*, type C) in McMurdo Sound, Antarctica: Evidence for impact by commercial fishing? *Polar Biology*, 41, 781–792.
- Plötz, J., Weidel, H., & Bersch, M. (1991). Winter aggregations of marine mammals and birds in the northeastern Weddell Sea pack ice. *Polar Biology*, 11, 305–309.
- Rasmussen, K., Palacios, D. M., Calambokidis, J., Saborío, M. T., Dalla Rosa, L., Secchi, E. R., ... Stone, G. S. (2007). Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. *Biology Letters*, 3, 302–305.

- Reeb, D., Best, P. B., & Kidson, S. H. (2007). Structure of the integument of southern right whales, *Eubalaena australis*. *Anatomical Record*, 290, 596–613.
- Reeb, D., Duffield, M., & Best, P. B. (2005). Evidence of postnatal ecdysis in southern right whales, *Eubalaena australis*. *Journal of Mammalogy*, 86, 131–138.
- Reisinger, R. R., Keith, M., Andrews, R. D., & de Bruyn, P. J. M. (2015). Movement and diving of killer whales (*Orcinus orca*) at a Southern Ocean archipelago. *Journal of Experimental Marine Biology and Ecology*, 473, 90–102.
- Reynolds, R. W., Smith, T. M., Liu, C., Chelton, D. B., Casey, K. S., & Schlax, M. G. (2007). Daily high-resolution blended analyses for sea surface temperature. *Journal of Climate*, 20, 5473–5496.
- Riedman, M. (1990). *The pinnipeds: Seals, sea lions, and walruses*. Berkeley, CA: University of California Press.
- Robbins, J., Dalla Rosa, L., Allen, J. M., Mattila, D. K., Secchi, E. R., Friedlaender, A. S., ... Steel, D. (2011). Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: A seasonal migration record. *Endangered Species Research*, 13, 117–121.
- Roman, J., Estes, J. A., Morissette, L., Craig, S., Costa, D., McCarthy, J., ... Smetacek, V. (2014). Whales as marine ecosystem engineers. *Frontiers in Ecology and the Environment*, 12, 377–385.
- Ryg, M., Lydersen, C., Knutsen, L. O., Børge, A., Smith, T. G., & Øritsland, N. A. (1993). Scaling of insulation in seals and whales. *Journal of Zoology, London*, 230, 193–206.
- Santora, J. A. (2014). Environmental determinants of top predator distribution within the dynamic winter pack ice zone of the northern Antarctic Peninsula. *Polar Biology*, 37, 1083–1097.
- Seaman, G. A., & Burns, J. J. (1981). Preliminary results of recent studies of belukhas in Alaska waters. *Report of the International Whaling Commission*, 31, 567–574.
- Sergeant, D. E. (1973). Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. *Journal of the Fisheries Research Board of Canada*, 30, 1065–1090.
- Sergeant, D. E., & Brodie, P. F. (1975). Identity, abundance and present status of populations of white whales, *Delphinapterus leucas*, in North America. *Journal of the Fisheries Research Board of Canada*, 32, 1047–1054.
- Smith, A. J., Higdon, J. W., Richard, P., Orr, J., Bernhardt, W., & Ferguson, S. H. (2017). Beluga whale summer habitat associations in the Nelson River estuary, western Hudson Bay, Canada. *PLoS ONE*, 12(8), e0181045.
- Smith, T. G., Hammill, M. O., & Martin, A. R. (1994). Herd composition and behavior of white whales (*Delphinapterus leucas*) in two Canadian Arctic estuaries. *Meddelelser om Grønland, Bioscience*, 39, 175–184.
- Smith, T. G., St. Aubin, D. J., & Hammill, M. O. (1992). Rubbing behaviour of belugas, *Delphinapterus leucas*, in a high Arctic estuary. *Canadian Journal of Zoology*, 70, 2405–2409.
- St. Aubin, D. J., Smith, T. G., & Geraci, J. R. (1990). Seasonal epidermal molt in beluga whales, *Delphinapterus leucas*. *Canadian Journal of Zoology*, 68, 359–367.
- Stern, S. J., & Friedlaender, A. S. (2018). Migration and movement. In B. Würsig, J. G. M. Thewissen, & K. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 602–606). San Diego, CA: Academic Press.
- Stevick, P. T., McConnell, B. J., & Hammond, P. S. (2002). Patterns of movement. In A. R. Hoelzel (Ed.), *Marine mammal biology: An evolutionary approach* (pp. 185–216). Malden, MA: Blackwell Publishing.
- Sumich, J. (2014). *E. robustus: The biology and human history of gray whales*. Corvallis, OR: Whale Cove Marine Education.
- Swartz, S. L. (2018). Gray whale *Eschrichtius robustus*. In B. Würsig, J. G. M. Thewissen, & K. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 422–428). San Diego, CA: Academic Press.
- Taylor, R. J. F. (1957). An unusual record of three species of whale being restricted to pools in Antarctic sea ice. *Proceedings of the Zoological Society of London*, 129, 325–331.
- Thiele, D., & Gill, P. C. (1999). Cetacean observations during a winter voyage into the Antarctic sea ice south of Australia. *Antarctic Science*, 11, 48–53.
- Thomas, J. A., Leatherwood, S., Evans, W. E., Jehl, J. R., Jr., & Awbrey, F. T. (1981). Ross Sea killer whale distribution, behavior, color patterns, and vocalizations. *Antarctic Journal of the United States*, 16, 157–158.
- Visser, I. N. (1999). Antarctic orca in New Zealand waters? *New Zealand Journal of Marine and Freshwater Research*, 33, 515–520.
- Wagemann, R., & Kozłowska, H. (2005). Mercury distribution in the skin of beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) from the Canadian Arctic and mercury burdens and excretion by moulting. *Science of the Total Environment*, 351–352, 333–343.
- Watts, P. D., Draper, B. A., & Henrico, J. (1991). Preferential use of warm water habitat by adult beluga whales. *Journal of Thermal Biology*, 16, 57–60.
- Watts, P., Hansen, S., & Lavigne, D. M. (1993). Models of heat loss by marine mammals: Thermoregulation below the zone of irrelevance. *Journal of Theoretical Biology*, 163, 505–525.
- Whitehead, H., & Moore, M. J. (1982). Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology*, 60, 2203–2211.

- Whitehead, H., Gordon, J., Mathews, E. A., & Richard, K. R. (1990). Obtaining skin from living sperm whales. *Marine Mammal Science*, 6, 316–326.
- Wilson, E. A. (1907). Vertebrata, Pt. 1. Mammalia (Whales and seals). In *National Antarctic Expedition 1901–1904, Natural History, Vol. 2, Zoology* (pp. 1–9). London, UK: The British Museum.

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