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An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast

David G. Ainley,[1] H. T. Harvey and Associates Ecological Consultants, Los Gatos, California 95032, U.S.A.; **Michelle A. Larue**, Department of Earth Sciences, University of Minnesota, Minneapolis, Minnesota 55455, U.S.A.; **Ian Stirling**, Department of Biological Science, University of Alberta, Edmonton, Alberta TG6 2E9, Canada and Wildlife Research Division, Science and Technology Branch, Environment Canada, 5320 122 Street, Edmonton, Alberta T6H 3S5, Canada; **Sharon Stammerjohn**, Institute of Arctic and Alpine Studies, University of Colorado at Boulder, Boulder, Colorado 80309, U.S.A.; **Donald B. Siniff**, Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108, U.S.A.

Abstract

Ground counts during 1959–1968 compared with counts using high resolution (0.6 m^2) satellite imagery during 2008–2012 indicated many fewer Weddell seals (*Leptonychotes weddellii*) at two major molting areas in the western Ross Sea: Edisto Inlet-Moubray Bay, northern Victoria Land, and McMurdo Sound, southern Victoria Land. Breeding seals have largely disappeared from Edisto-Moubray, though the breeding population in McMurdo Sound appears to have recovered from harvest in the 1960s. The timing of decline, or perhaps spreading (lower numbers of seals in more places), is unknown but appears unrelated to changes in sea ice conditions. We analyzed both historic and satellite-derived ice data confirming a large expansion of *pack ice* mostly offshore of the Ross Sea, and not over the continental shelf (main Weddell seal habitat), and a thinning of *fast ice* along Victoria Land (conceivably beneficial to seals). Timing of fast ice presence and extent in coves and bays along Victoria Land, remains the same. The reduction in numbers is consistent with an altered food web, the reasons for which are complex. In the context of a recent industrial fishery targeting a seal prey species, a large-scale seal monitoring program is required to increase understanding of seal population changes.

Key words: Antarctic toothfish, climate change, fast ice, fishery effects, population change, Ross Sea, sea ice, *Leptonychotes weddellii*, Weddell seal.

Much has been written recently about trends in populations of Antarctic sea ice-obligate species, principally penguins, in relation to changes in sea ice extent and timing of its breakup and formation (*e.g.*, Jenouvrier *et al.* 2005, Ducklow *et al.* 2007, Montes-Hugo *et al.* 2009, Ainley *et al.* 2010*a*). Some studies have also addressed decadal changes in food supply, mostly but not entirely in conjunction with documented climate changes (*e.g.*, Ainley and Blight 2009, Schofield *et al.*

[1]Corresponding author (e-mail: dainley@penguinscience.com).

2010, Trivelpiece *et al.* 2011, Lynch *et al.* 2012). In contrast to penguins, few long-term studies of populations of Antarctic seals exist and fewer still have tested for possible trends in abundance in relation to long-term climate-related changes (for decadal-scale changes see Testa *et al.* 1991, Chambert *et al.* 2012). Furthermore, understanding population trends of Antarctic pinniped species and subpopulations has been complicated by variable recoveries from unsustainable harvesting in the past (*e.g.*, Testa and Siniff 1987, Trathan *et al.* 2012).

Hall *et al.* (2006) reported the disappearance of southern elephant seals (*Mirounga leonina*), a sea-ice tolerant species, from the Ross Sea since the 1970s, ascribing it to climate change. However, others have interpreted the trend as a consequence of severe reductions since the 1980s of breeding populations at subantarctic breeding sites, such as at Macquarie Island in the Pacific sector (*cf.* Hindell *et al.* 1994, Ainley and Blight 2009). The result would be reduced density-dependent pressure for elephant seals to seasonally expand their marine feeding habitat as far away as the Ross Sea, thousands of kilometers south. In the case of the sea ice obligate Weddell seal (*Leptonychotes weddellii*), Siniff *et al.* (2008) reported a long term decrease in numbers at Anvers Island, Antarctic Peninsula, monitored during 1973–2002, after which the species has become quite uncommon coincident with the disappearance of sea ice. Weddell seals remain farther south (Costa *et al.* 2010, Pitman 2011), however, where the sea ice season is still sufficiently long (Stammerjohn *et al.* 2012). Lake *et al.* (2008) reported no long-term trends in counts of Weddell seals at a much higher latitude site, Vestfold Hills, East Antarctica, during 1973–2000. In that area, there has been a notable but localized decrease in the length of the ice season (2–3 d/yr from 1979–1980 to 2009–2010) in Prydz Bay (offshore of Vestfold Hills), which stands in contrast to an increase of similar magnitude just to the west in the Cape Darnley region (Massom *et al.* 2013). However, in general, fast ice extent in a number of locations has increased slightly, presumably to the benefit of Weddell seals, in the southeast Indian Ocean sector of East Antarctica (20°E–90°E) during the last decade (Fraser *et al.* 2012). Another long time series of Weddell seal population trends and dynamics, which has also been challenged by intensive harvest in the past, is that for eastern McMurdo Sound, southern Victoria Land, from the 1960s to the present, as discussed below.

The Weddell seal requires areas of fast ice that remain in place for several months each year, from freeze-up in autumn to at least early summer. During this period, the seals self-maintain breathing holes in the ice along tide cracks of headlands, islands, and glacier fronts by abrading the sea ice with their upper canine teeth in order to access the ocean for food and air for breathing while remaining in the water (Stirling 1969*b*). A reduction in the availability of tide cracks leads to fewer seals hauling out to give birth in a region as well as to molt (Stirling and Greenwood 1972, Siniff *et al.* 2008). During late October to early November, seals use the fast ice adjacent to the tide cracks for pupping and during December–January for molting, after which, the adults usually stay with the remaining fast ice for as long as it is present. If there is no ice, they haul out on beaches laid bare by the disappearance of sea ice or in areas along the coast where buckling of glacial ice or ice shelves creates accessible low spots (see fig. 3 in Siniff *et al.* 2008). As shore ice disappears seasonally, the seals move into the pack ice, moving back as close to the coast as possible only when the coastal ice refreezes.

The longest time series of population data gathered on an ice-breeding seal in the Antarctic is from the Weddell seals in eastern McMurdo Sound, the highest known concentration of this species and the most southerly in Antarctica. Here environmental factors have been linked to population fluctuations (Siniff *et al.* 2008, Chambert *et al*. 2012, Garrott *et al*. 2012). Short-term climate phenomena, such as El Niño-Southern Oscillation (ENSO), affect demographic parameters such as incidence of pupping by established breeding adults (can vary annually by 20%), pupping by first-time breeders, pup growth, and over-winter survival of adult females (see also Testa *et al*. 1991). Whether the ENSO effect is through altered sea ice or the food web is not known.

Unfortunately the capacity to detect longer-term, climate-related variations in that eastern McMurdo Sound time series is confounded by the killing of a large number of seals to support humans and their dogs at various periods including "heroic expeditions" of the early 20th century, but more importantly again from 1956 to 1984 by the New Zealand (NZ) and USA Antarctic programs (Fig. 1). The harvest was directed mainly at molting animals and, ultimately, >2,200 seals were taken by the NZ program between 1956 and 1984. The largest numbers (600) were taken during the first 4 yr (Stirling 1971). The take by the USA program was small, about 20 seals, between December 1955 and December 1959 (Backus 1956, Testa and Siniff 1987, D. Baker[2]).

The number of seals that molt on the fast ice in eastern McMurdo Sound during late December–late January usually doubled the number seen during the pupping season, due to an addition of nonbreeders, which previously were excluded by territorial behavior of adults, as well as breeders from unknown breeding colonies elsewhere in the region (*e.g.*, reaching 2,960 in 1964; Smith 1965, Stirling 1971; Fig. 1). During the spring and early summer very few Weddell seals remain in those portions of the Ross Sea covered by drifting pack ice (Ainley 1985, Ballard *et al.* 2012). In the fast ice area where most of the seals were actually killed, from Cape Armitage to Pram Point (southernmost coast of Ross Island; Area A in Smith 1965), as many as 945 seals hauled out in January but numbers dropped as the seal kill took its toll (only 400 hauled out by 1967: Stirling 1971; mean for 1956–1967 = 758 ± 206 SD). The number of molting seals in western McMurdo Sound is unknown but estimated to be about 2,000 (Stirling 1969*c*).

In regard to the main McMurdo Sound breeding population, which is found in Erebus Bay of the southeastern Sound during October–November (20 km north of Cape Armitage; Areas C–G in Smith 1965), when the seal-kill was halted (in 1984) population size, as indexed by number of pups, had declined from a maximum of 767 pups in 1967 (a decade after the harvest began) to 375–475 pups by 1980 (Testa and Siniff 1987; Fig. 1). Initially (1956) the total number of seals, males and females, in this breeding population was estimated to be ~1,400 by Smith (1965) (females outnumber males >2:1; Testa and Siniff 1987). As of 2009 ~900 females were present during the pupping season (Chambert *et al.* 2012), and as many as ~1,000 in most recent years.[3] Stirling (1971) hypothesized that the harvest led to increased production of pups per female owing to fewer negative effects of territoriality due to lower densities and a decrease in age of females giving birth to their first pup. After a significant decrease in the number of seals killed for dog food, he proposed that the population apparently was able to compensate for the subsequently lower harvest rate. Pup counts have increased during the past few years, with numbers reaching ~600, and

[2]Personal communication from D. Baker, U.S. Navy dog-handler (retired), 20 March 2014.

[3]Personal communication from J. Rotella, Department of Ecology, Montana State University, Bozeman, Montana 59717, U.S.A., 15 May 2014.

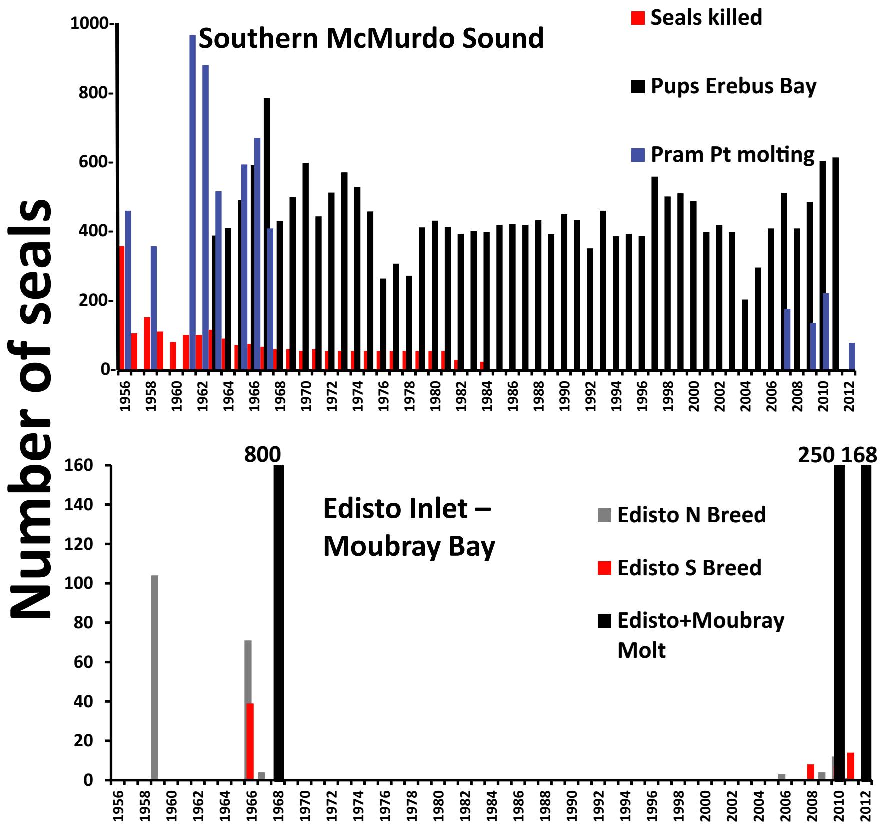

Figure 1. Number of Weddell seals in the two study areas, 1956–2012: early counts done on the ground (ice), later counts by satellite imagery. Erebus Bay breeding population estimated by counts of pups in November; counts of molting seals in vicinity of Pram Point were within Area A of Smith (1965); Edistro North and South areas are shown in Figure 2. Data are from Stirling 1969*c*, 1971; Testa and Siniff 1987, Cameron and Siniff 2004, Chambert *et al*. 2012, and this study.

thus comparable to the late 1960s (Cameron and Siniff 2004, *cf.* Chambert *et al.* 2012). Besides the eastern Sound, a low number of seals haul out for pupping at tide cracks along shorelines of the western Sound, where the fast ice is more or less permanent and thick (*e.g.,* 55 seals at Dunlop Island vicinity in mid-November 2007; Siniff and Ainley 2008). Unlike the breeding numbers in southern McMurdo Sound, molting numbers have not recovered (see Results).

Herein, we report the results of Weddell seal censuses of two extensive fast ice areas of the Victoria Land coast using high-resolution satellite imagery, from 2006 to 2012: southeastern McMurdo Sound in the south and Moubray Bay, including Edisto Inlet, in the north. These estimates are compared to ice-level and aerial counts conducted during the 1950s–1960s. The northern study area consists of waters between Cape Hallett, where a joint USA-NZ research station existed from 1957 to 1973, and Cape Roget (Fig. 2). The southern study area of molting seals consists of south-

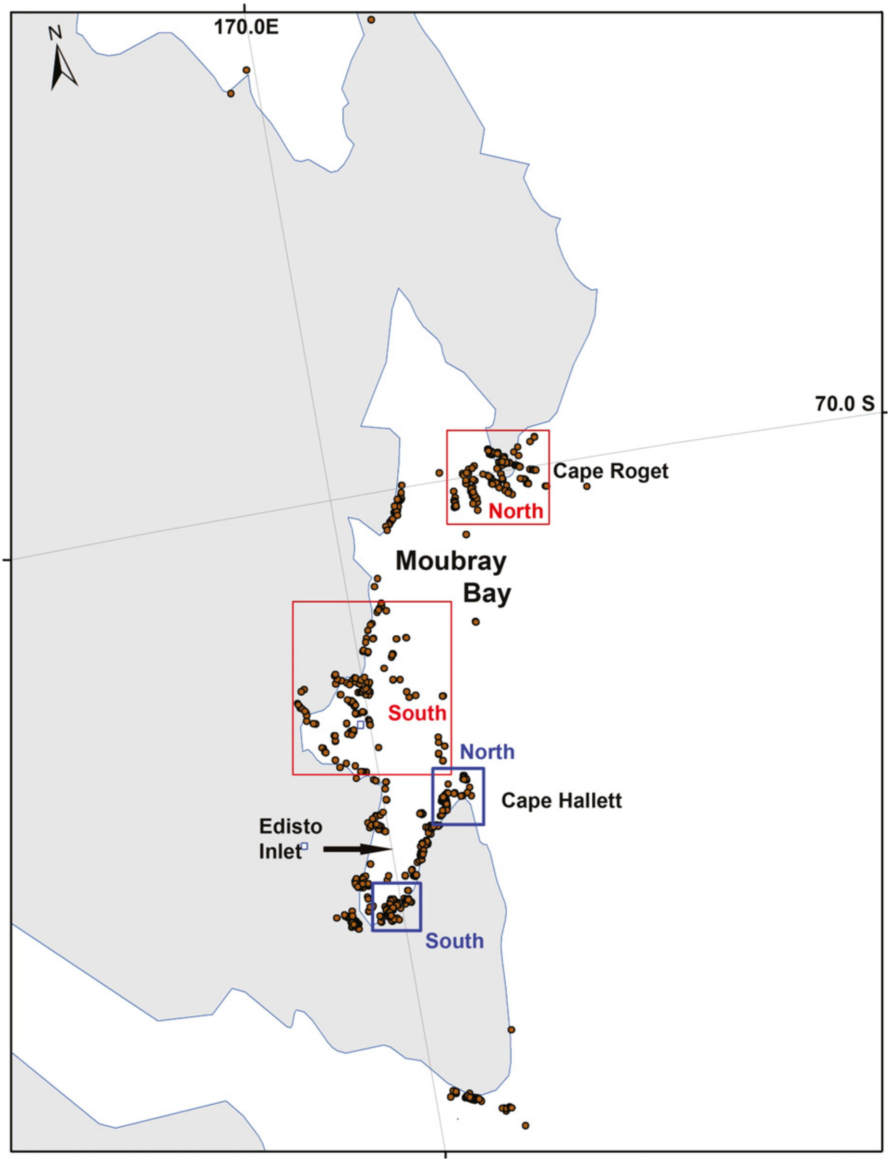

Figure 2. Study area showing census boxes in Moubray Bay (red) and Edisto Inlet (blue); see Table 1. Yellow dots represent the total detections of seals by high resolution satellite without deference to month or year as detected, 2006–2012.

eastern McMurdo Sound, including Erebus Bay and the coast between Cape Armitage and Scott Base (see above, Smith 1965).

We examine possible causes for the changes in numbers observed at these historic haul out sites examining both the physical characteristics of sea ice, as well as

Weddell seal counts. Initially, we hypothesized that overall population trends were due to changes in the seasonal fast ice dynamics, which appears to have resulted in the disappearance of Weddell seals at Anvers Island, western Antarctic Peninsula (Siniff *et al.* 2008). We provide possible explanations for why that hypothesis was rejected and suggest two, not necessarily mutually exclusive, alternate hypotheses.

Methods

Seal Counts

Our northern study area comprised ~355 km^2 of Edisto Inlet and Moubray Bay (Fig. 2), which lie between Cape Hallett (72°19′S, 170°12′E) and Cape Roget (71°59′S, 170°31′E), about 625 km north of McMurdo Sound and 100 km south of Cape Adare, the northernmost point of Victoria Land. The southern study area was in southern McMurdo Sound (see map in Smith 1965: Area A is molting area, C–G is Erebus Bay breeding area). McMurdo Sound in total includes waters south of a line from Cape Roberts (77°02′S, 163°12′E) on the mainland coast across to Cape Bird (77°10′S, 166°41′E) on Ross Island. The portion north of Cape Royds (20 km south of Cape Bird) is usually free of fast ice while the portion to the south and along the mainland coast is mainly covered by fast ice well into January. The Moubray Bay and McMurdo Sound areas are the two major locations of almost year-round fast ice in the western Ross Sea, constituting prime habitat for Weddell seals; in both areas there are far more molting seals present in late summer than there are pupping and breeding in spring (even factoring in weanlings), illustrating the demographic "pull" of these two areas of persistent fast ice.

During the early years, counts of seals in Edisto Inlet/Moubray Bay were done directly, driving a snow-cat from Hallett Station, beginning mid-morning, closely paralleling the coastal tide crack and checking for tagged seals whenever any seal was encountered (all untagged seals tagged as encountered) . Thus, counts were done in the late morning to early afternoon, the drive to return to Station before evening taking considerable time. Some of the counts were done by helicopter survey, with numbers corrected for diel haul-out patterns—if they were not made during the period of maximum haul-out—by approximating a qualitative extrapolation from the curves in Stirling (1969*c*, fig. 2; see Table 1). Counts of molting seals in southern McMurdo Sound during recent years were made by taking telephotos from the same vantage point used by Smith (1965, see his map), *i.e.*, on slope above Scott Base (~200 m asl). These were taken at mid-day, same as satellite imagery (see below; hence, no specific correction necessary to derive a rough comparison).

For the years 2006–2007 to 2011–2012, we acquired cloud-free, high-resolution (0.6 m^2) satellite images (*i.e.*, DigitalGlobe and GeoEye platforms) of our study areas that were captured during mid-day November–January. The Moubray Bay area is typically cloudy which made the acquisition of suitable images difficult. This situation forced us to divide the Edisto/Moubray study area into segments (see details below), because often one portion but not the other was cloud free; a marine cloud layer covers much of the open water of the Ross Sea almost always during spring–summer (DGA, personal observations). This was not an issue for McMurdo Sound, where the weather is "continental" rather than "marine" and cloud free days during spring–summer are frequent. Local times of Moubray images acquired were between 1000 and 1100. Aerial photos taken in mid-January 2008 (Pram Point) and early December 2009 (Edisto)

Table 1. Comparison of counts among years for Edisto Inlet and Moubray Bay, northern Victoria Land; see Figure 2 for location of various census areas, denoted as "boxes" ("entire" can include more than just adding north + south boxes; ND = no data). Pupping season = November counts; molting season = January counts. Ground counts in early to middle part of the day; * indicates count from helicopter usually in afternoon, not requiring correction for time of day.

	Year	Number adult/ subadult seals	Source	Notes
Pupping season				
Edisto Inlet North	1959	104	B. Reid *in* Stirling (1969*c*)	Inlet ice covered
	1966	71	Stirling (1969*c*)	Inlet ice covered
	1967	4	IS, personal observation	Inlet ice covered
	2006	3	This study	Inlet ice covered
	2007	ND		Too cloudy
	2008	ND		Too cloudy
	2009	4	This study	Inlet ice covered
	2010	12	This study	Inlet ice covered
	2011	1	This study	Inlet ice covered
Edisto Inlet South	1966	39	IS, personal observation	Inlet ice covered
	1967	0	IS, personal observation	Inlet ice covered
	2006	ND		Too cloudy
	2007	ND		Too cloudy
	2008	8	This study	Inlet ice covered
	2009	0	This study	Inlet ice covered
	2010	7	This study	Inlet ice covered
	2011	14	This study	Inlet ice covered
Edisto Inlet entire	1966	106	Stirling (1969*c*)	Inlet ice covered
Moubray North	2008	32	This study	Ice covered
	2009	ND		Too cloudy
	2010	49	This study	Ice covered
	2011	36	This study	Ice covered
Moubray South	2008	42	This study	Ice covered
	2009	ND		Too cloudy
	2010	20	This study	Ice covered
	2011 (3)	14, 24, 36	This study	Ice covered
Molting season				
Edisto Inlet				
N box only	1964	220 (daily maximum)	Müller-Schwarze (1965)	Inlet ice covered
Entire Inlet	1967	600*	Stirling (1969*c*)	Outer ⅔ Inlet ice free
Entire Inlet	1968	460*	Stirling (1969*c*)	Outer ⅓ Inlet ice free
N + S boxes	2010	124	This study	Inlet ice covered
N box only	2011	68	This study	Inlet ice covered
N + S boxes	2012	114	This study	Inlet ice covered

(Continued)

Table 1. (Continued)

	Year	Number adult/ subadult seals	Source	Notes
Moubray Bay	1965	650*	Stirling (1969*c*)	Ice covered
	1968	52*	Stirling (1969*c*)	Open water prevalent
	2011	ND		Too cloudy
	2012	54	This study	Ice covered
Edisto + Moubray	1968	800	Stirling (1969*c*, corrected)	Ice covered
	2010	189	This study	Ice covered
	2011	ND		Too cloudy
	2012	168	This study	⅔ open water

were used to roughly ground-truth counts made from satellite imagery during those years if at equivalent times of day. See also LaRue *et al.* (2011) for a study in which satellite and ground counts were compared, finding up to 88% agreement even in, as in the present study, "correction" for different timing of counts was approximate, *i.e.*, within a certain window of several hours. Given that an adult Weddell seal occupies a space ~2–3 m^2 and the satellite image pixels were ~0.6 m^2 it is not difficult to understand why high resolution satellite imagery is effective in detecting these seals, especially against white background (see also McMahon *et al*. 2014).

According to counts made by Müller-Schwarze (1965) in a study of circadian rhythms exhibited by the seals, peak numbers are hauled out at Cape Hallett and eastern McMurdo Sound (Siniff *et al*. 1971, Thomas and DeMaster 1983) during mid-day from about 1000 to 1400 during the pupping and breeding season (October–November). In comparison, based on hourly counts made from the same vantage point on the hillside above Scott Base (Pram Point), Smith (1965) and Stirling (1969*c*) both reported peak haul-out of molting seals in southeastern McMurdo Sound (Pram Point vicinity) between about 1500 and 1700 local time during January. Because satellite counts of Edisto-Moubray were done at approximately the same time of day as older ground counts, we had no need to correct our counts for time of day; however, those of McMurdo molting seals also obtained during mid-day were corrected.

In accord with the studies of Smith (1965) in McMurdo Sound, we assigned counts through November to the pupping population and counts in January to the molting population (hereafter, the term "population" is used only in reference to the numbers of seals present in a location and does not infer some sort of aggregation in which gene flow is restricted). As was the case in McMurdo Sound, the highest counts of seals hauled out on the ice in Edisto Inlet were obtained during the molting period in early to mid-January (see also Müller-Schwarze 1965). We loaded images into ArcGIS 10.2 (ESRI, Redlands, CA) and assessed each image for utility for counting seals as per LaRue *et al.* (2011). Then, one observer searched each image for seals at 1:2,000 scale, and placed an ArcGIS shapefile on top of each located animal. If no seals were located on an image, we created a "dummy" point to note the image had been searched.

After each image had been assessed and the seals counted, we calculated the number of animals observed per location per date. Edisto Inlet and Moubray Bay are large enough that several areas were identified where seals appeared to haul out regularly, usually in the vicinity of headlands or glacier fronts where tidal action maintains the cracks along which the seals maintain their breathing holes. We sorted seal counts in each of these areas, in part trying to accommodate frequent cloud cover, to ensure accurate spatial overlap and comparison between years (the survey "boxes" in Fig. 2). These boxes also allowed us to compensate for periods when portions but not all of the study area were obscured by clouds (see above). When possible, we also calculated the number of animals observed over the entirety of the study area per month per season (*e.g.*, November 2010) in order to create an accurate comparison to historic aerial and ground observations (*cf.* Stirling 1969*a*).

We made several assumptions for this analysis:

(1) Seals counted on fast ice are Weddell seals; no other seal species has ever been detected within the specific study areas of this project (crabeater, *Lobodon carcinophagus*, and leopard, *Hydrurga leptonyx,* seals can be found in the icebreaker channel in January).

(2) Detection probability is at or near 1 if a seal was hauled out on the fast ice at the time the satellite image was taken. We were able to conduct approximate ground truthing for both McMurdo Sound and Edisto Inlet, with results coinciding at least by order of magnitude within a season, *e.g.*, 2007 Pram Point molting season = 174 seals by satellite *vs.* 133 seals by photo count (26 Jan); 2009 Edisto North, 1 seal seen by aerial photo 29 November, four seals seen by satellite 20 December.

(3) Seals counted in November represent adults, and thus constitute the breeding population (Smith 1965). We likely could not detect pups because of their smaller size and because they often lie in body contact with their mothers. Counts by satellite, and by ground, both included young-of-the-year during late summer/molting (see below), as weanlings would have grown sufficiently to be detectable by satellite by January.

(4) Weddell seals are strongly philopatric during breeding (Stirling 1971, Cameron *et al.* 2007, Davis *et al.* 2008) and haul out at reliable locations where tidal action creates recurrent cracks within our study area. Though less well investigated, during the molting season site attractiveness might have more to do with habitat features than seal allegiance, as shown by temporary emigration (Chambert *et al.* 2012); sites appropriate for seal presence, in number, are very limited (owing to seasonal loss of fast ice) and thus usage becomes more forced by circumstances (food, avoidance of predation) than social/"habit forming."

(5) Circadian rhythms of haul out have remained consistent from the 1960s, when intensively studied in several locations (see above), to the present. The satellite images used were approximately at the same time of day as the earlier ground counts; thus corrections not necessary. Breeding counts are thought to represent maximum or near-maximum counts, given the late-morning to mid-day time frame. Aerial counts were corrected for time of day, with maximum haul-out in late afternoon (see references above). While the several studies of haul-out rhythms noted that cold, windy weather can reduce the inclination of seals to haul out, the satellite images necessarily were made with clear, sunny skies, and no evidence of snowdrift was apparent (*i.e.*, smudged items: seals, rocks, *etc.*).

(6) Seasonal population dynamics, *i.e.* pupping in October–November, followed by incursion of nonbreeding adults and subadults in mid- to late December, with molting (and peak population hauled out on sea ice) in early January, as described

by Smith (1965; also Stirling 1969*a*, *c*) for McMurdo Sound, is applicable to the Edisto-Moubray study area during the same season.

Analysis of Local and Regional Sea Ice Variability and Trends

To characterize seasonal changes in local and regional sea ice cover for the northwestern Ross Sea, coarse resolution (25 by 25km) passive microwave satellite data are available since 1979, providing a 35 yr record of variability and trends. We used the GSFC Bootstrap SMMR-SSM/I Version 2 quasi-daily time series of sea ice concentration (1979–2012; Comiso 2010) from the EOS Distributed Active Archive Center (DAAC) at the National Snow and Ice Data Center (NSIDC, University of Colorado at Boulder, CO, http://nsidc.org), augmented with SSM/I near real-time data (2013; Maslanik and Stroeve 1999), to produce a time series extending from 1979–1980 to 2012–2013. We defined four local areas in the vicinity of Moubray Bay, each consisting of one 25 by 25 km image pixel and analyzed the variability in mean monthly percent sea ice cover during the pupping and molting seasons (October–January). For context, the regional variability in yearly ice season duration is also shown and discussed. Ice season duration is defined as the length of time between first appearance of sea ice in autumn and disappearance in spring/summer at a given location (image pixel) and is discussed in further detail in Stammerjohn *et al.* (2008, 2012).

In part to compare possible changes in fast ice extent in the western Ross Sea with the findings of Fraser *et al.* (2012) for the Pacific sector of East Antarctica (90°E–160°E; Cape Adare, northern-most point of Victoria Land is at 170°E), we also report trends for McMurdo Sound (165°E) based on information from the logs of icebreakers, which annually broke a channel to McMurdo Station. Though the McMurdo Sound record dates back to 1957, we only address variation in ice thickness from 1980 to 2007 when channel breaking began on about 1 January (±5 d) of each year. However, the record of fast ice extent in McMurdo Sound from 1960 onward, overlapping the seal count data, is presented for comparison. In addition, we also discuss ice thickness using the time it took U.S. Coast Guard polar class icebreakers to make their first pass from the ice edge to the station, 1980–2007 (see also Siniff *et al.* 2008). Before 1980, two or three smaller icebreakers were used simultaneously; and after 2007, icebreakers other than polar class were used that widened the channel as they went, rather than making a first run to McMurdo Station and widening subsequently as did the polar class icebreakers. Therefore, during 2008–2013, when these icebreakers arrived in late January, we report position of the ice edge on 1 January as observed from Cape Royds where the edge was often positioned and where we had a research camp. These data are confirmed using MODIS (Moderate Resolution Imaging Spectroradiometer) images for 2008–2009 to 2011–2012.

Results

Changes in Seal Counts

Counts along the east shore of Edisto Inlet during the pupping season of the 1960s totaled slightly more than 100 adults in 1959 and 1966 (Table 1). Compared to these early counts, those made during November 2006–2011 revealed that a one to two order of magnitude reduction in numbers of seals apparently has occurred, at all

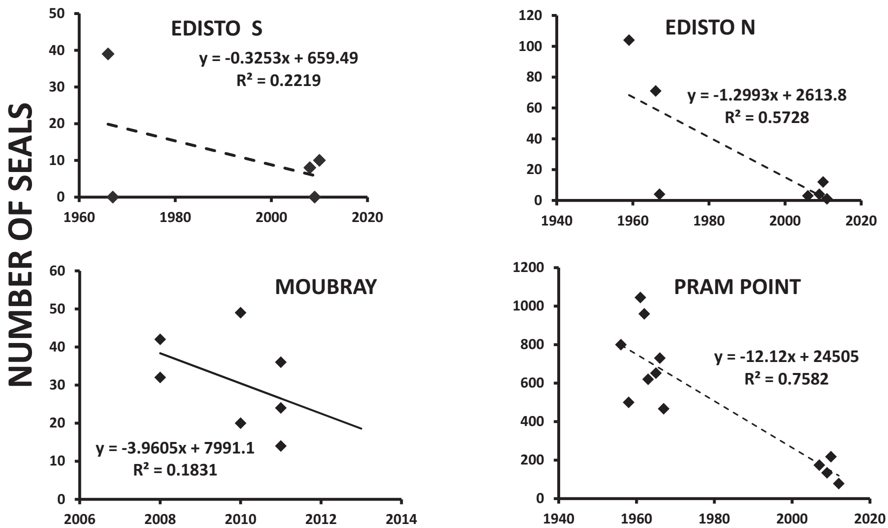

Figure 3. Comparing early ground counts with later counts made from satellite imagery, trends in numbers of seals during the pupping season at Edisto S and N, and in pupping seals based on satellite imagery alone at Moubray Bay in recent years, northern Victoria Land; and trends of molting seals counted at Pram Point, McMurdo Sound, southern Victoria Land, comparing early ground with later satellite imagery counts (see Table 1). Dashed lines indicate that we did not know what trends were apparent during intervening years.

sites (Edisto North: $y = -1.30x + 2,613.8$, $r^2 = 0.573$, $P = 0.06$; Edisto South: $y = -0.325x + 659.5$, $r^2 = 0.222$, $P = 0.42$). The trend for Moubray Bay, with data only from 2008 to 2011, was negative as well ($y = -3.96x + 7,991.1$, $r^2 = 0.183$, $P = 0.34$; Fig. 3). During both periods there was notable year-to-year variability in count totals, as was also true for seals in McMurdo Sound due to a complex of factors (summarized in Siniff *et al.* 2008, Garrott *et al.* 2012). Counts during the early years varied from 4 to 104 for Edisto North and from 0 to 39 for Edisto South, compared with 1–112 and 0–14, respectively, for the modern record.

Likewise, the peak number of seals hauled out during the molting season in Edisto Inlet-Moubray Bay was several times larger during the 1960s than has been observed in recent years (Table 1; $y = -14.758x + 29,843.3$, $r^2 = 0.995$, $P = 0.01$); for Moubray only $y = -7.628x + 15383.814$, $r^2 = 0.3663$, $P = 0.59$). Peak numbers reported in 1968 totaled at least 800 animals, compared to <200 in recent years. Similar to the better-known McMurdo Sound, areas in Edisto/Moubray where seals congregated for molting were not necessarily the same as pupping localities, in part due to seasonal change in fast ice extent although there was overlap in Edisto Inlet. Even if the recent numbers were increased by 20%–30% (*cf.* Smith 1965) to try to compensate for the possibility that they were not made at the daily peak of haul-out for that time of year, the recent totals are still far below those reported in the 1960s.

The pattern of change in the numbers of seals molting in southeastern McMurdo Sound was similar to that of Edisto-Moubray, *i.e.* a decrease from 700 to 950 seals (including those killed), averaging 758 (± 206 SD), down to <200 (mean 175 ± 60) in recent years (Fig. 1, 3; adding seals killed to number alive: $y = -12.794x + 814.4$, $r^2 = 0.786$, $P < 0.001$).

Changes in the Sea Ice Regime

Fast ice extent and the timing of freeze-up and breakup from 2008 to 2011 did not differ significantly from that in the 1960s in either Edisto Inlet-Moubray Bay or McMurdo Sound. The study areas remained covered with fast ice well into January during both observation periods, after which it usually broke out completely before refreezing in March–April (Table 2, Fig. 4). This indicates that fast ice has formed and broken out and thus has been seasonal in most years since the 1950s. By late January in 1967 and 1968, for example, ⅓–⅔ of Edisto Inlet (*i.e.,* Edisto North) was ice covered (Table 1; also in 1972 and 1973, E. Griffith[4]). In recent years, the Edisto-Moubray ice likewise has remained in place well into January throughout the study area, though in two years it began to break out near the tip of Cape Hallett (Seabee Spit) in early December (2010) and in early January (2009), but remained present inside Edisto Inlet (Edisto South) until early February (Table 2). In both eras, the ice was thick enough that large fixed-wing aircraft regularly landed on it during November (C-130s during the 1960s–1970s, when Hallett Station was operating; Basler DC-3s and Twin-Otters in recent years). The fast ice of McMurdo Sound has behaved similarly, with even larger aircraft landing throughout the period (C-130s, C-141s, C-17s), and confirmed indirectly as well by the counts of seal pups on the fast ice of Erebus Bay (Fig. 1). The only trend evident in pup counts is a decrease during the seal-kill years, followed by a slow recovery to pre-kill numbers.

The 5 yr of high-resolution MODIS observations of fast ice conditions in Edisto/Moubray were compared to the coarser resolution passive microwave observations to determine if the latter could be used as a proxy of fast ice conditions over the last 35 yr (1979 to present). Table 3 summarizes the comparison of fast ice *vs*. pack ice retreat in the Moubray Bay area for the last 5 yr. In general there is good agreement between fast ice retreat at Seabee Spit and pack ice retreat in Moubray Bay, the exception being 2010–2011, when Seabee Spit became ice free in early December, while sea ice continued to persist in Moubray Bay and vicinity until mid-January. However, fast ice inside Edisto Inlet was shown in these data to persist until early February. Thus, variability in pack ice retreat from Moubray Bay appears to be a reasonable proxy for fast ice conditions in Edisto Inlet.

Figure 5 shows time series of monthly mean sea ice concentration for the Moubray Bay vicinity for the months of October to January. October to December sea ice concentrations generally increased during the early part of the 1979–2012 period, consistent with a regional trend of increasing duration of ice cover for the greater western Ross Sea region with most of the increase evident in waters seaward of the Ross Sea continental shelf (Stammerjohn *et al.* 2012). By January (Fig. 5), in accord with patterns discussed above, there is much greater variability in monthly mean sea ice concentration in the outer part of the Bay, but with no discernible trend. In as far as pack ice variability in Moubray Bay reflecting fast ice variability in Edisto Inlet, the 35 yr time series indicates that fast ice conditions appear to have remained favorable for Weddell seals, both during pupping season (October–November) and molting season (December–January).

Similarly, fast ice extent in McMurdo Sound also shows no trend in its presence (Fig. 6) for the observational period under consideration. This apparent lack of trend appears to be consistent as far north as Cape Adare in northern-most Victoria Land (Fraser *et al.* 2012). Thus, it appears overall that the fast ice regime should have been

[4]Personal communication from E. Griffith, U.S. Navy weatherman (retired), 13 February 2014.

Table 2. A summary of fast ice patterns during recent summer seasons as seen in MODIS images for both Edisto-Moubray Bay and McMurdo Sound; NI indicates no images available.

Edisto Inlet–Moubray Bay							
	Kilometers of fast ice seaward of Cape Hallett tip						
Summer season	1 November	1 December	1 January	Ice edge Cape Hallett tip	Edge at "south" census box	Edisto Inlet no ice	Freeze up
2008–2009	NI	NI	22	22 January 2009	11 February 2009	20 February 2009	13 April 2009
2009–2010	30	8	5	8 January 2010	3 February 2010	3 February 2010	11 April 2010
2010–2011	11	8	0	11 December 2010	2 February 2011	2 February 2011	April 2011[b]
2011–2012	22	22	5	28 January 2012	7 March 2012	–[a]	15 April 2012
2012–2013	32	32	27	31 January 2013	–[a]	–[a]	30 March 2013

McMurdo Sound				
Summer season	Ice edge at Cape Royds	Erebus Bay exposed	McMurdo Sound no ice	Freeze up
2008–2009	20 January 2009	22 January 2009	14 February 2009[c]	14 April 2009
2009–2010	22 October 2009	2 January 2010	26 February 2010[c]	31 March 2010
2010–2011	1 November 2010	15 January 2011	24 February 2011	3 April 2011
2011–2012	27 October 2011	8 January 2012	21 February 2012	8 April 2012
2012–2013	1 September 2012	16 January 2013	17 February 2013	27 March 2013

[a]Ice did not break out except for a few km inward from Cape Hallett tip; small polynyas within fast ice appeared and were associated with headlands.
[b]Very cloudy weather during month; ice did appear to have frozen at some date during month.
[c]Fast ice broke south to Pram Point (southernmost tip of Ross Island) but not farther, *i.e.*, Sound not completely ice free.

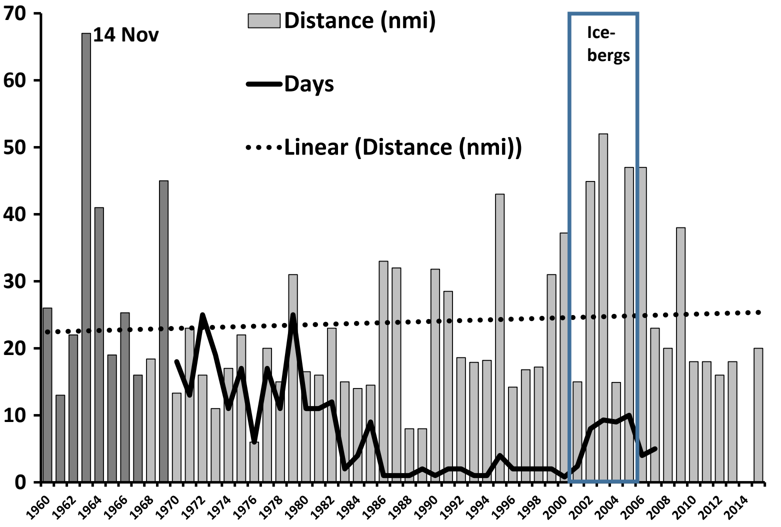

Figure 4. The extent of fast ice in McMurdo Sound on 1 January (±5 d), 1970–2013: distance from edge to Hut Point, McMurdo Station, in nautical miles. The data for 1960–1969 are also given but for reference only, as ice breaking effort (other than in 1960) began earlier, 14 November to 3 December (the period when McMurdo Sound fast ice begins to lose its outer ice). Trend line of ice extent ($y = 0.065 + 22.1$, $r^2 = 0.006$) is near flat. Light gray bars indicate years when a polar class icebreaker broke a channel through the fast ice to McMurdo Station, while in years shaded dark gray smaller icebreakers were used. Ice extent 2008–2013, when icebreakers did not arrive until late January, was measured from observations at Cape Royds, Ross Island. As a proxy to ice thickness, also shown by the dark, wavering line are number of days to make an initial pass from the edge to Hut Point; note only the line as it intersects the light gray bars when a polar class icebreaker was involved.

Table 3. A summary of fast ice break out in Edisto Inlet–Moubray Bay, based on MODIS images (fast ice edge at Cape Hallett) *vs.* SSM/I passive microwave images (ice retreat from Edisto–Moubray Bay).

Summer season	Ice edge at Cape Hallett tip	Day pack ice retreated from Moubray Bay
2008–2009	22 January 2009	31 January 2009
2009–2010	8 January 2010	2 January 2010
2010–2011	11 December 2010	17 January 2011[a]
2011–2012	28 January 2012	24 January 2012
2012–2013	31 January 2013	1 February 203

[a]Although fast ice retreated from Cape Hallett on 11 December 2010, pack ice was still present in, and offshore of, Moubray Bay until 17 January; however, sea ice concentration started to decrease on 8 December, with open pack ice conditions (~70% concentration) persisting within 25 km of Moubray Bay until 17 January 2011.

capable of facilitating the continued existence of similar and substantial numbers of Weddell seals in both Edisto/Moubray and McMurdo Sound. Furthermore, if the sea ice was thinner after the late 1980s, which appears to be the case, it might have been

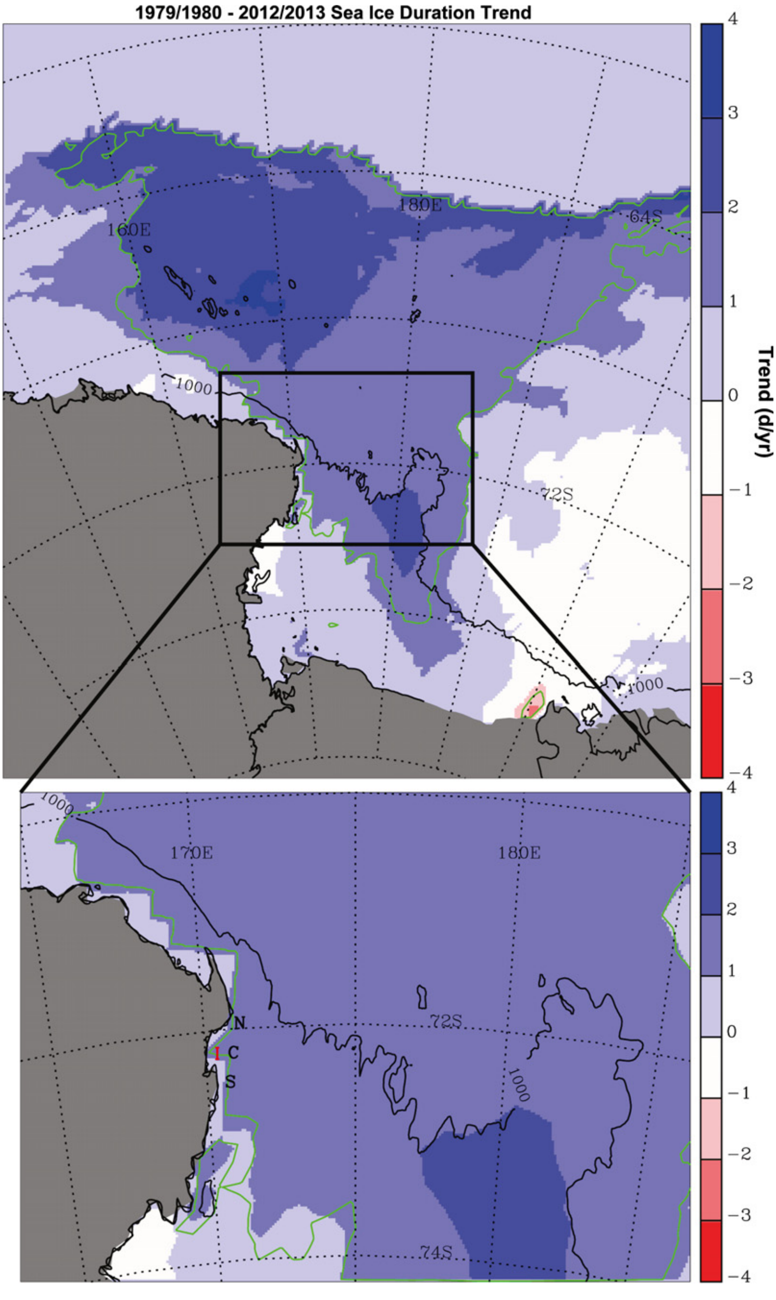

Figure 5. A (top), the area in which sea ice was assessed using coarse resolution (25 × 25 km) passive microwave satellite data to provide trends, 1979–2012; B (inset), shows the location of the four 25 × 25 km pixels from which time series of ice concentration were derived for North (N), Central (C), South (S), and Inside (I) Moubray Bay (see Fig. 2, 6).

easier for the seals to keep breathing holes open in the tide and other cracks (Fig. 6). In a reverse scenario, we can confirm that increased ice thickness during the mega-iceberg era, 2001–2006, leading to fewer cracks, in turn led to seals vacating McMurdo Sound (lower pup counts); those seals returned when the fast ice again became seasonal, offering renewed cracks, after the icebergs departed (Siniff *et al.* 2008, Chambert *et al.* 2012; Fig. 1, 4).

Discussion

Edisto Inlet-Moubray Bay and McMurdo Sound are the largest areas of fast ice that remain well into summer (through January) along the Victoria Land Coast of the Ross Sea. Both areas of extensive fast ice appear to attract (or, once attracted) large

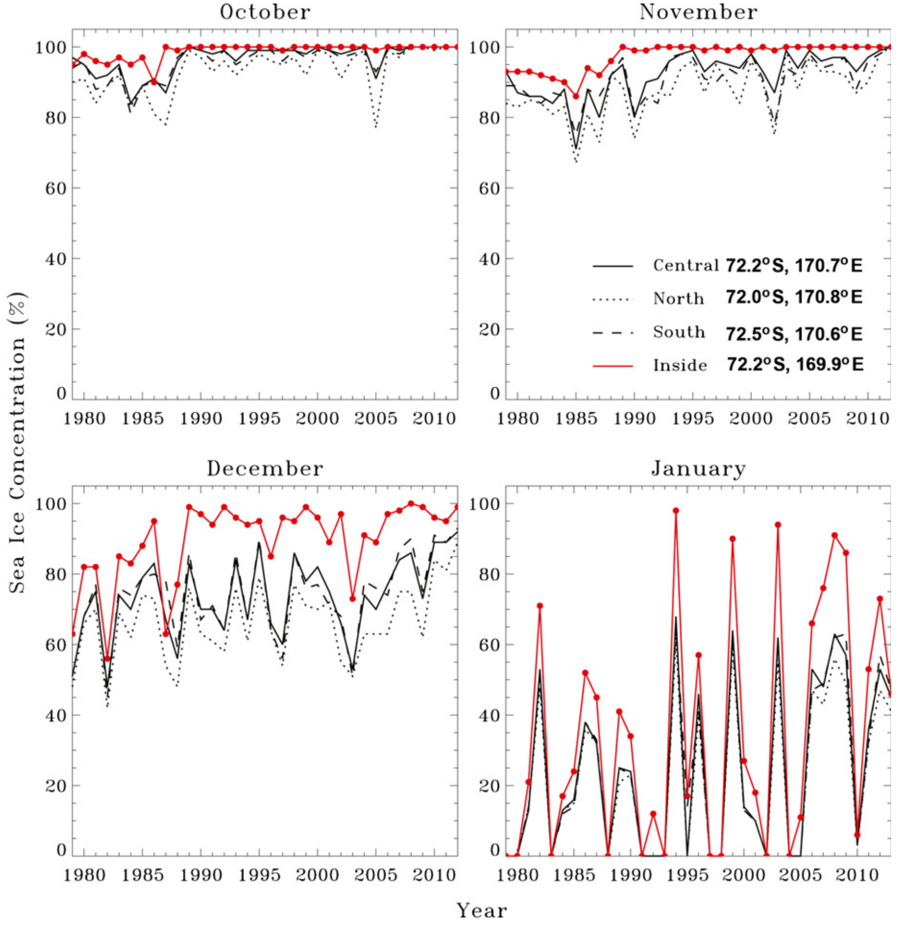

Figure 6. Time series showing percent ice cover of four areas (each one 25 × 25 km passive microwave pixel) of Moubray Bay for 4 mo of the year; October–November are pupping and December–January are seal molting periods, 1979–2012.

numbers of molting Weddell seals from outlying areas where the seals had hauled out for pupping; both areas themselves are/were also frequented by smaller numbers of breeding individuals (Stirling 1969*c*, Siniff and Ainley 2008). These haul-out patterns appear no longer to exist to the extent that they did 50 yr ago. The question is why? Initially, we hypothesized that the seasonal persistence of fast ice might have changed, especially with the increased winds that came with a regime shift in the late 1970s (Ainley *et al.* 2005). Below we discuss the several possibilities to explain the seal trends, dividing factors into physical (changed fast ice) and biological (changed food web).

We do not believe that increased disturbance, owing to the substantial increase in the human populations at Scott and McMurdo bases between the 1960s and recent years have been involved. During those intervening years the Antarctic Treaty System, especially through its Committee on Environmental Protection, has invoked guidelines prohibiting wildlife disturbance. At least at the Ross Island bases, these guidelines are very strictly enforced. Even researchers since the early censuses have needed special permits from national Antarctic programs, and for U.S. citizens from the National Marine Fisheries Service, to even approach a seal. At Hallett, the base has been vacant since the early 1980s and now is completely gone. Neither is it a strong possibility, we contend, that the seals lost the propensity to haul out in formerly preferred areas in response to periods of slaughter, disturbance, or daunting ice conditions; they immediately returned to Erebus Bay after five years of breeding (or at least hauling out) elsewhere during the B15 mega-iceberg era that brought thick fast ice to McMurdo Sound (Siniff *et al.* 2008).

Change in Fast Ice

The McMurdo and Edisto/Moubray areas still appear to provide adequate molting habitat for large numbers of Weddell seals, which probably once totaled several thousand adults but those numbers now appear significantly reduced (Stirling 1969*a*, Siniff and Ainley 2008). Apart from proximity to pupping areas, the most likely explanation for their attraction to these areas for molting, rather than to ice floes in the pack ice, is to avoid predation by type-B killer whales (*Orcinus orca*). Type-B killer whales may select for Weddell seals over other species of Antarctic seals, possibly because of greater fat content (Pitman 2011) and/or because they may be easier to catch. Predation of Weddell seals by killer whales has been observed on several occasions along the outer edge of the fast ice in McMurdo Sound during January when the edge is receding rapidly (Ainley and Ballard 2012). Once the killer whales depart in late summer, and the seals finish molt, the seals do become denizens of the Ross Sea pack ice (*cf.* Stirling 1969*c*, Ainley and Siniff 2009, Burns *et al.* 2012, Burns[5]). A possibility is that the thinner fast ice in the late season in recent years, at least since the regime shift of the late 1970s (see below), has encouraged the presence of killer whales farther into the Sound and discouraged Weddell seals concentrating as much as they did during the molt in earlier decades.

The decreasing trends in molting seal numbers in the McMurdo and Edisto/Moubray areas do not appear to have been caused by a disappearance of the seals' fast ice (or pack ice) hauling-out platform, which has reduced seal numbers in the western Antarctic Peninsula region (Siniff *et al.* 2008). As noted above (Results), the western

[5]Personal communication from J. Burns, Department of Biological Sciences, University of Alaska Anchorage, Anchorage, Alaska 99508, U.S.A., February–August 2014.

Ross Sea fast ice regime of the 1950s–1960s appears to be much the same as it is now both at McMurdo Sound and Edisto Inlet/Moubray Bay (Fig. 4). A trend of increasing persistence of pack ice (not fast ice: Stammerjohn *et al.* 2012; Fig. 5, 6) in the larger region has been underway during recent decades and should be consistent with high numbers of seals. A short distance to the west of northern Victoria Land, fast ice has also persisted and even increased in extent slightly but measurably during the last decade (Fraser *et al.* 2012). In accord with the apparent stability of fast ice conditions in this region, Barber-Meyer *et al.* (2008) noted variable, but long-term stability in populations of emperor penguins (*Aptenodytes forsteri*) breeding at colonies that bracket Edisto Inlet-Moubray Bay, *i.e.*, at Cape Washington, Coulman Island and Cape Roget (as investigated during 1983–2005); Kooyman and Mullins (1990) provide earlier data (1958–1965) for these colonies indicating comparable colony sizes (lower for Cape Washington). Likewise, the number of emperor penguins nesting at Ross Island, other than a temporary decrease that occurred during the mega-iceberg years, increased during the 1990s and 2000s (Barber-Myers *et al.* 2008; Ainley and G. Ballard, unpublished data); before then their numbers slowly increased as the movement of the Ross Ice Shelf offered more protected and stable fast ice (*cf.* Kooyman and Mullins 1990, Kooyman *et al*. 2007). Like Weddell seals, emperor penguins require fast ice to remain in place from about May through December for purposes of raising their young; however, unlike Weddell seals, the penguins then molt in the eastern Ross Sea pack ice where the stability and large size of the floes found there is critical to their survival (Kooyman *et al.* 2000). The fact that the fast ice of McMurdo Sound (and perhaps Edisto/Moubray) has grown thinner should add to the attractiveness of the habitat in recent years, as thinner fast ice increases the propensity to form cracks conducive to Weddell seal presence (Stirling 1971, Siniff *et al*. 2008).

Change in Food Web Structure

If it is not a change in sea ice, and especially fast ice conditions, what factors could explain the observed trends in seal numbers? It is ironic that the breeding population of Erebus Bay, one of the largest for this species, has recovered following the seal kill of the 1950s–1980s, while the numbers of animals immigrating into the two major molting concentrations seasonally have all but disappeared. Two hypotheses related to the seals' trophic needs, which are not necessarily mutually exclusive, might explain the precipitous decline in abundance of Weddell seals in the former fast ice molting habitat: (1) seals during the molt are now more spread out along the Victoria Land coast between the former prime areas of McMurdo and Edisto/Moubray, compared to several decades ago because food resources are more scattered, less abundant, and thus to cope with intraspecific trophic competition molting seals move to areas where foraging success is greater; and (2), because of the changes in the distribution and abundance of food resources, there has been several years of reduced survival of subadult seals that once comprised a large proportion of those concentrating in the molting areas. The question is why?

While primary productivity in the Ross Sea has varied dramatically year-to-year, no trend is evident at least during the past two decades when adequate imagery to sense chlorophyll concentration has been available (Arrigo *et al*. 2008, Dugger *et al*. 2014). The late 1970s regime shift was physically expressed by an increase in winds, more persistence of latent heat polynyas, and likely increased over all Ross Sea productivity (a function of timing-of-opening and size of Ross Sea Polynya; Arrigo *et al.* 2002, Ainley *et al.* 2005). The shift occurred before the chlorophyll record began;

thus, no explanation is evident in that regard but increased productivity should favor the seals.

However, a major ecological factor known to have directly changed the Ross Sea during recent decades is an alteration of food availability due to two factors. First, depletion by whaling of minke whales (*Balaenoptera bonaerensis*), a potential trophic competitor of Weddell seals during the 1970s, was followed by the whales' recovery during the 1980s–1990s. Both predators feed heavily on silverfish (*Pleuragramma antarcticum*) in the Ross Sea and thus are trophic competitors. Similar to the response by Adélie penguins (*Pygoscelis adeliae*), another trophic competitor, seals should have increased and then leveled (Ainley *et al.* 2007, 2010*b*). Second, and more directly related, is the recent depletion by commercial fishing of a major prey species of the Weddell seal, the Antarctic toothfish (*Dissostichus mawsoni*; summary in Ainley and Siniff 2009). That fishery has targeted the largest fish, especially along the continental slope, from 1996 to the present (Pinkerton *et al.* 2007, CCAMLR 2013, Ainley and Pauly 2014). These large fish are the most energetically valuable to the seals, owing to their size and high fat content (see also Lenky *et al.* 2012), and to their neutral buoyancy which increases seals' access to the fish (they are in the water column not on the bottom; Ainley and Siniff 2009). The large fish have disappeared in both the science catch in McMurdo Sound (Ainley *et al.* 2012) as well as in the commercial catch in the main fishing grounds (continental slope; CCAMLR 2013). Until 2009, fishing also occurred in the deep areas along the Victoria Land coast, just south of Moubray Bay.

The nonreplacement of large fish over the shelf, with the fishery take possibly exacerbated by a regime shift that occurred during the late 1970s (Ainley *et al.* 2005), could have resulted from lower recruitment of these long-lived, late maturing fish, as noted by Ainley *et al.* (2012; see also Abrams 2014) but that influence is not likely as increased primary productivity should favor the fish (see above). The Ross Sea has had and continues to have extensive sea ice, but pack ice extent and season particularly just north of the Ross Sea shelf responded to the changing winds (Stammerjohn *et al.* 2008, 2012); water column physical properties have been changing as well (especially surface salinity; Jacobs 2006, Jacobs and Giulivi 2010). How or whether those climate-driven changes might have affected food web structure or interactions (not just the physical habitat) is not known. Penguins and benthic communities are known to have responded to the physical changes, making penguin foraging easier (less walking: Ainley *et al.* 2005); indeed Adélie penguins are now more abundant than ever (Lyver *et al.* 2014). While the penguins do not prey on adult toothfish, the penguins and seals feed heavily on toothfish prey, the Antarctic silverfish (*cf.* Eastman 1985, Burns *et al.* 1998, Ainley *et al.* 2003). If the portion of the food web that supported the Weddell seal has somehow been reduced, or the distribution of their prey changed, then the downward trends of numbers of molting seals seen in the McMurdo Sound and Edisto/Moubray areas might have been a response to processes involved in one or both of these hypotheses.

A significant portion of the molting seal populations was composed of subadults that moved seasonally into the molting areas, molting seals being a bit less site-faithful than breeders (Cameron and Siniff 2004, Stauffer *et al.* 2013). If there was a reduction of food availability, subadult seals that could no longer compete for food where adult seals dominated (see Testa *et al.* 1985, Buckley 2013) might have been forced to move elsewhere in search of food, or possibly experience lower survival if they were unsuccessful (increased exposure to killer whale predation; see above). For whatever reason, there appears to have been changes in the food web or the availability of preferred prey in recent years as satellite tracking of the seals indicates they are now searching over a much wider area and diving less efficiently during winter than they did 20 yr ago (decadal patterns corrected for instrument capabilities: Burns *et al.* 2012, Burns[5])—after the regime shift and whale recovery and just before and after initiation of the fishery. If the seals are more dispersed in their winter foraging, it is possible they might be more dispersed during the molt and the period prior to the molt when they must recover condition and avoid predation.

Conclusions

Given the patterns revealed herein, the numbers of seals breeding and molting along the Victoria Land Coast during this age of fishery exploitation of a principal prey species needs to be documented, an effort that now can be achieved using satellite remote sensing (LaRue *et al.* 2011). Seal foraging behavior, including location, should be monitored, including the neighboring populations of those breeding in McMurdo Sound.

Acknowledgments

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