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Walrus Movements in Smith Sound: A Canada–Greenland Shared Stock

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ABSTRACT. Fifty of 58 walruses (*Odobenus rosmarus rosmarus*) instrumented with satellite-linked transmitters in four areas in eastern Smith Sound, Northwest Greenland, during May and June of 2010–13 and 2015 provided data for this study. These animals departed from the feeding banks along the Greenland coast in June–July (average 14th June), simultaneously with the disappearance of sea ice from these areas. Most of them moved to Canadian waters in western Smith Sound. The most frequently used summering grounds were along the coasts of Ellesmere Island: on the eastern coast, the area around Alexandra Fiord, Buchanan Bay, and Flagler Bay (west of Kane Basin) and Talbot Inlet farther south, and on the southern coast, Craig Harbour. This distribution of tagged walruses is consistent with prior understanding of walrus movements in summer. In addition, however, nine tracks of these tagged animals entered western Jones Sound and four entered the Penny Strait-Lancaster Sound area, crossing two putative stock boundaries. Since these 13 tracks were made by 12 animals, one walrus entered both areas. It is possible that some of the tracked walruses used terrestrial haul-out sites in the largely ice-free areas of Jones Sound and Lancaster Sound for short periods during the summer, though this cannot be confirmed with certainty. The return migration from western Smith Sound to the wintering area in eastern Smith Sound takes place in October. The tracked walrus showed high affinity to coastal areas, while walruses moving between Greenland and Canada also used offshore areas in Smith Sound. This study demonstrates that the walrus population that winters along the northwestern coast of Greenland is shared more widely in Canada than previously thought and should be managed accordingly.

Key words: Canadian High Arctic; haulout; North Water polynya; Northwest Greenland; satellite tracking; seasonal migration; shared stock

RÉSUMÉ. En mai et juin 2010 à 2013 et 2015, 50 des 58 morses (*Odobenus rosmarus rosmarus*) munis d'émetteurs liés à des satellites dans quatre régions à l'est du détroit de Smith, au nord-ouest du Groenland, ont permis de recueillir des données pour cette étude. Ces animaux ont quitté les aires d'alimentation le long de la côte du Groenland aux mois de juin et juillet (en moyenne le 14 juin), au même moment que la disparition de la glace marine de ces régions. La plupart des animaux se sont déplacés vers les eaux canadiennes dans l'ouest du détroit de Smith. Les aires d'été les plus souvent utilisées étaient celles situées le long des côtes de l'île d'Ellesmere : sur la côte est, la région autour du fjord Alexandra, la baie Buchanan et la baie Flagler (à l'ouest du bassin Kane) et le passage Talbot plus au sud, et sur le littoral sud du village Craig Harbour. Cette distribution des morses munis d'émetteurs correspond aux déplacements de morses déjà constatés en été. Toutefois, neuf signaux provenant d'animaux munis d'émetteurs sont entrés dans la partie ouest du détroit de Jones et quatre sont entrés par les détroits de Penny et de Lancaster, traversant les limites de deux aires de stocks présumés. Puisque ces 13 signaux ont été émis par 12 animaux, un morse est entré dans les deux régions. Il se peut que certains des morses suivis aient emprunté la portion terrestre qui entoure les échoueries dans les régions en grande partie dépourvues de glace des détroits de Jones et de Lancaster pendant de courtes périodes durant l'été, mais il est impossible de le confirmer avec certitude. La migration de retour de l'ouest du détroit de Smith vers l'aire d'hivernage dans l'est du détroit de Smith a lieu en octobre. Les morses suivis ont montré une grande affinité pour les zones côtières, tandis que les morses qui se déplaçaient entre le Groenland et le Canada empruntaient également les zones extracôtières du détroit de Smith. Cette étude démontre que la population de morses qui hiverne le long de la côte nord-ouest du Groenland est plus importante au Canada qu'on ne le pensait auparavant et devrait être gérée en conséquence.

Mots clés : Extrême-Arctique canadien; échouerie; polynie des eaux du Nord; nord-ouest du Groenland; repérage par satellite; migration saisonnière; stock partagé

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INTRODUCTION

Smith Sound in northern Baffin Bay is a narrow waterway (40 km) between Canada and Greenland. In winter, this area is largely covered in sea ice, but it does contain a recurrent polynya, the so-called North Water Polynya, which is a highly productive, open-water area that is a key habitat for marine mammals and seabirds. This region has provided the resource base for a thriving maritime hunting culture for at least 4000 years (Schledermann, 1980, 1990), and the walrus (*Odobenus rosmarus*) remains one of the most important game species harvested in this region (Vibe, 1950; Born, 1987).

Walruses are found during fall, winter, and spring in eastern Smith Sound, where the modern human population of the region is also concentrated. During the summer months, however, walruses are absent from this part of Smith Sound. It has long been thought that the walruses leave Smith Sound in late spring and undertake large-scale counter-clockwise migrations within Baffin Bay, returning to Smith Sound in the early fall (Freuchen, 1921; Vibe, 1950). More recently, it has been proposed that walruses in Smith Sound belong to a population that extends widely into the Canadian High Arctic, and that animals in this area are genetically separated from walruses occurring farther south in West Greenland and along the east coast of Baffin Island (Shafer et al., 2014). Stewart (2008) proposed that walruses in Smith Sound and adjacent areas be subdivided for management purposes into three stocks (Baffin Bay, West Jones Sound, and Penny Strait-Lancaster Sound) on the basis of lead isotope ratios and genetics (mtDNA). One of Stewart's objectives was to generate testable hypotheses, including hypotheses regarding the extent of exchange of breeding animals between wintering areas in Jones Sound and Lancaster Sound and Northwest Greenland. In this paper, we seek to address Stewart's hypotheses with direct observations of the seasonal movements of walruses in Smith Sound and adjoining regions collected via satellite tracking of individual animals (e.g., Jay et al., 2006; Lydersen et al., 2008).

MATERIAL AND METHODS

During May and June in 2010–13 and 2015, we instrumented 58 walrus with satellite-linked transmitters in the eastern part of Smith Sound, NW Greenland in four different areas: Etah, Murchison Sound, south of Kiatak and Wolstenholme Fjord (Fig. 1; see online Appendix 1: Table S1 for details regarding the animals and the duration of records). The tags consisted of an external transmitter and an internal anchor (Fig. 2). The transmitter was mounted on a flexible base plate that could turn around the anchor's shaft. Tag design varied slightly over the course of the study, but the transmitters were SPOT5, MK10, or SPLASH tags (all made by Wildlife Computers, Redmond, USA). The anchor consisted of a 6 cm stainless steel rod with a sharp, fixed harpoon head that penetrated the skin of the walrus. The head of the harpoon was equipped with barbs to delay its migration out through the skin. The distal part of the steel rod had a cylindrical plug used to hold the tag during the deployment. We used traditional hand-held harpoons to deploy the tags and modified the harpoon tip to hold the tag until the anchor was embedded under the walrus skin. We targeted tag placement in the middle of the back, close to the neck; however, in several cases placed the tags in other parts of the body. The 2 m long harpoons were usually thrust at the walrus, but were also occasionally thrown at shorter distances (< 1 m from the tip of the harpoon to the walrus).

The tags were programmed to transmit for 12 h (0800 to 2000 local time), at different intervals in the various years of the study. In 2010–11, they transmitted every day in June and every fourth day for the rest of the year. In 2012 the setting was the same, except that tags also transmitted every day in August. In 2013 and 2015, the tags were set to transmit every fourth day throughout the whole year.

Transportation to field sites was facilitated by small skiffs operated by experienced walrus hunters from Qaanaaq, Northwest (NW) Greenland, who also deployed the tags. We observed walruses from promontories, icebergs, or the boats that were used to search the four tagging areas. Most were tagged from the boats while they were resting on sea ice, but some were tagged in the water. Occasionally, walruses were located far into the pack ice and tagging was done by walking across the ice to the animals. Tags were deployed on available walruses and deployment success did not appear to vary among age and sex classes. When possible, sex of the walruses was determined visually on the basis of tusk morphology and the presence of calves.

Locations of the walrus were estimated by the Argos satellite data processing system, using the Kalman filtering algorithm. The location accuracies were rated according to the standard Argos location codes (LC) 3–0, A, and B (CLS America, 2008). More than 70% of the location estimates ($n = 37\,000$) were of low and uncertain positional accuracy (quality 0, A, or B). To guard against falsely assigning the presence or absence of tracked walrus at known coastal haul-out sites, we considered only standard-quality locations when examining the use of specific coastal haul-outs. Duration of the stay at specific localities was determined from all positions, and weighted averages of the duration of stay at the localities were determined using the duration of the entire tracking period in days for each walrus as weight.

In order to create track lines for a subsample of the instrumented walruses, we calculated daily average positions for all standard-quality locations (LC > 0), and if no standard-quality locations were available, we used low-quality locations (LC = 0, A, and B).

Rate of movement per hour was calculated for the tags deployed in 2015, the year for which the largest sample of tagged walruses with the most consistent programming was

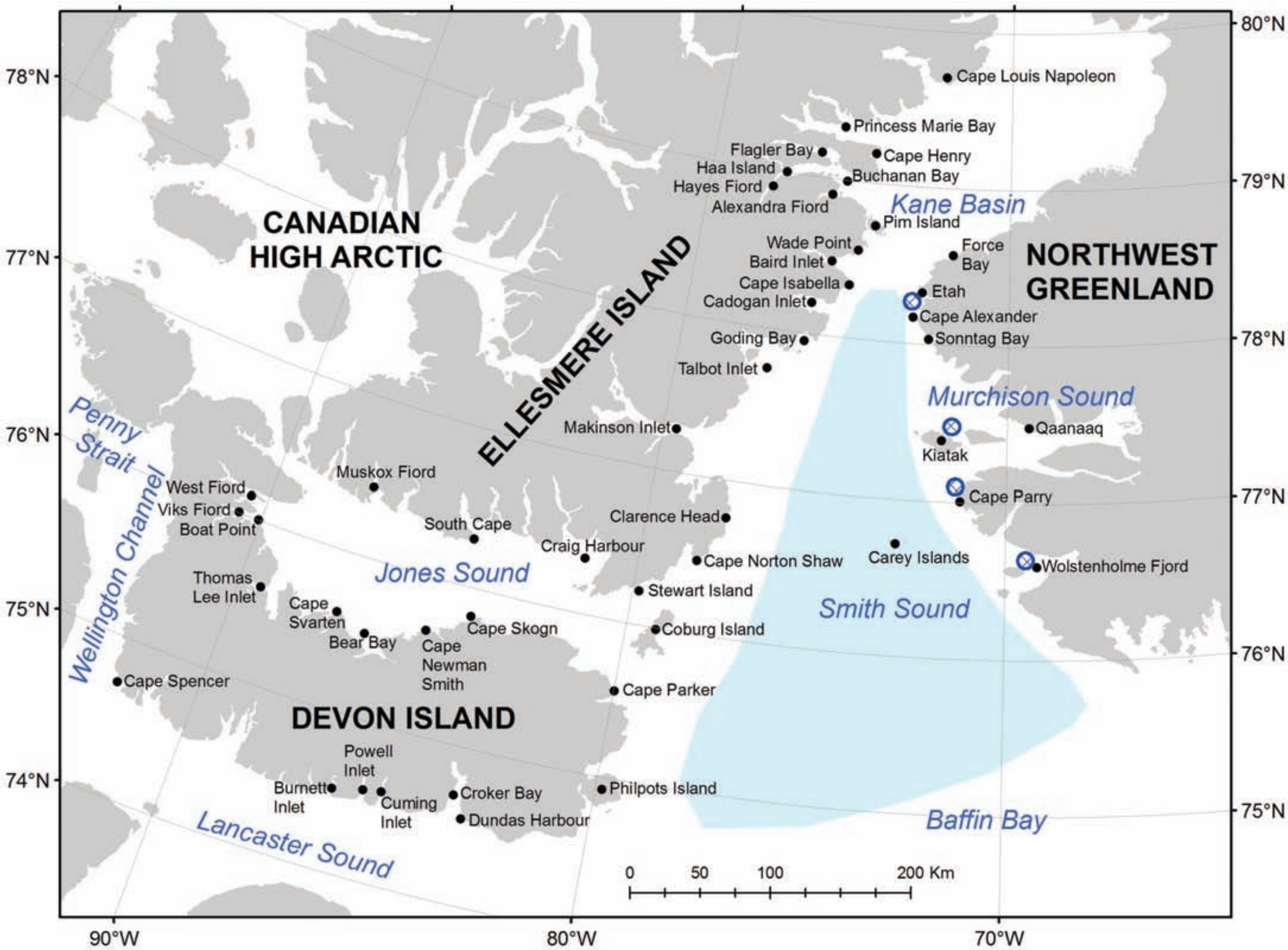

FIG. 1. Map of the study area with locality names mentioned in the text. Blue rings indicate tagging sites close to Etah, in Murchison Sound, between Kiatak and Cape Parry, and in Wolstenholme Fjord. The shaded area approximates the extent of the North Water Polynya in March (Yackel et al., 2001).

available. Movement distances were calculated for standard quality locations obtained in two intervals, 0.5 – 5 h, and 0.5 – 24 h, following Dietz et al. (2014).

All the walruses were tagged in the area denoted by Stewart (2008) as belonging to the Baffin Bay stock. To test hypotheses about stock boundaries, we used 85˚ W to mark the transition into the West Jones Sound (WJS) stock area. Stewart (2008) did not specify a demarcation line between the Baffin Bay stock and the Penny Strait-Lancaster Sound (PS-LS) stock; however, we used 80˚ W, 75˚ N at Philpots Island as a threshold.

RESULTS

Tagging caused all of the walrus to leave the ice and go into the water. But they did not always leave the area after the operation. Sometimes they simply stayed at the surface close to the tagging boats for up to 30 min.

Eight tags did not provide any data, but 50 of the tags provided locations for more than three days for 19 females, 17 males, and 14 walruses of unknown sex. The average tag longevity was 68 days (SD = 47, range 3 – 278 days) for the 50 functioning tags (see online Appendix 1: Table S1). No tag or group of tags differed in functional longevity from what would be expected in a single pool of variance ($p < 0.05$, Bartlett's test of homoscedasticity).

Most females were tagged in the area south of Kiatak (63%), which is also where half of the females with calves were tagged (n = 3 in this region, six pairs in total). A female with a calf was tagged in each of the other areas, but females with calves were generally rare in Wolstenholme Fjord (1 out of 15 tagged walruses).

The average departure date from the Greenland coast was 14 June (n = 49, SD = 9, range: 25 May to 8 July). We found no differences among the four tagging areas (ANOVA $p > 0.75$), nor did we find that females with calves left at a different time than other females (t-test, $p = 0.15$).

The mean hourly rate of movement of 16 walruses tagged in 2015 was 2.3 km (SD = 1.7) for the interval of 0.5 – 5 h between positions. An ANCOVA (with day and time as covariates, $r^2 = 0.09$) revealed no significant

FIG. 2. Above: Satellite transmitter mounted on a hunter's harpoon. Below: Tagging of two walruses.

difference between individual walruses ($p > 0.05$, Tukeys post hoc tests) and no significant effect of date on the rate of movement ($p > 0.06$). Mean hourly movement for the interval of 0.5–24 h between locations was 1.9 km (SD = 0.65).

Tagged females with calves either went to Alexandra Fiord (n = 5) or to Cape Svarten in western Jones Sound (n = 1). Half of the walruses tagged in Wolstenholme Fjord (9 of 18 tracked walruses), as well as four of the 14 walruses tagged south of Kiatak, visited the Carey Islands in Smith Sound, even though they did not stay there for long (mean = 3 days). Apart from visiting the Carey Islands, the walruses spent little time in the offshore areas of Smith Sound or farther south.

All walruses tracked for more than three days (n = 50) moved west and crossed Smith Sound into Canada, and all but one made this crossing by 1 July. At least 28 localities in coastal areas of Ellesmere and Devon Islands were visited by one or more of the tracked walruses during the summer and early fall (Fig. 3), and we identified three primary areas of summer occupancy.

The summer distribution of the walruses was generally associated with the tagging site. Most walruses tagged in the north at Etah went northwest for summering, whereas most tagged walruses from Wolstenholme Fjord went southwest (Table 1). However, this segregation was incomplete, as some walruses from Etah (8%) also moved to the southwest, and some from Wolstenholme Fjord went north.

We determined the relative importance of regions used in the summer on the basis of observed frequency and duration of use by tracked walruses. The most visited locality, and most used in terms of time, was a fjord complex on the eastern coast of Ellesmere Island, consisting of Alexandra Fiord, Buchanan Bay, and Flagler Bay (Figs. 3 and 4). Walruses tagged at Etah and in Murchison Sound spent 42% and 13% (weighted average), respectively, of their tracking period in this fjord complex, and those tagged at the other two localities also visited this area. Talbot Inlet/Goding Bay was the second most frequently visited locality. It was also visited by walruses from all areas, but seemed to be visited particularly often by walruses tagged south of Kiatak, which on average spent 24% of their time there.

The third most important summering area in terms of numbers of animals and time spent was Craig Harbour. It was visited mainly by animals tagged in Wolstenholme Fjord (56% of the tags; 23% of their time). In addition, 15% of tagged walruses from Murchison Inlet and 21% of those from south of Kiatak also moved to Craig Harbour.

Nine tagged walruses moved into Stewart's proposed WJS stock range, three as far west as 90˚ W (Figs. 4 and 5). They had been tagged either south of Kiatak (21%), or in Wolstenholme Fjord (17%) or Murchison Inlet (15%). No walrus tagged from Etah went into the WJS stock area. Four walrus (22%) tagged in Wolstenholme Fjord moved into Stewart's proposed PS-LS stock range. One of these moved into the WJS area mid-summer and is included in the nine tracks there, as well. Overall, 12 (24%) of the tags that transmitted more than three days moved into an adjacent stock area and two additional walruses were tracked near the edge of the WJS area (South Cape and Cape Skogn). On the other hand, none moved into Stewart's proposed Hudson Bay-Davis Strait-West Greenland stock range in the Canadian Subarctic.

The tagged walruses that entered the WJS and PS-LS stock ranges approached known terrestrial haul-out sites (Fig. 4, Stewart et al., 2014b), but only a few (n = 4) were tracked to within 5 km of the haul-outs, and they spent little time (< 4 d) in those areas.

Nine tracked walruses transmitted long enough to show that they stayed along the coasts of Ellesmere and Devon Islands through September. Three tags on two females and one male transmitted long enough to document their return migration from eastern Ellesmere Island (Alexandra Fiord and Pim Island) to their original tagging area on the Greenland coast (north of Kiatak), where they arrived between 3 and 27 October. A fourth walrus remained in Jones Sound (Cape Skogn) as late as 3 November.

TABLE 1. Directional dispersal to three regions of northern Canada of walruses tagged in four areas in Northwest Greenland. One animal entered both the PS-LS and WJS areas. There are therefore 13 tracks from 12 walruses.

Tagging sites in Northwest Greenland	# of walruses	Destination N (Cadogan Inlet and farther N)	Destination W (Cape Norton Shaw to Goding Bay)	Destination SW (S and W of Stewart Island)	Tracks entering WJS area	Tracks entering PS-LS area
Etah	12	75%	33%	8%	0	0
Murchison Sound	6	100%	50%	17%	1	0
South of Kiatak	14	29%	64%	36%	4	0
Wolstenholme Fjord	18	6%	67%	72%	4	4
				Total	9	4

DISCUSSION

Tag Performance

Eight (14%) of the 58 tags deployed did not report any data. The reported battery voltage remained within operational bounds (2.9 – 3.7 V) for the 50 transmitters that transmitted, so tag failure of the other 10 tags is not likely due to low battery voltage. In some few cases when walruses were tagged in the water, the tags might not have struck the animal at all and been lost in the water. The most likely cause of these failed deployments was improper attachment of the anchor under the skin of the walrus. It cannot be ruled out that perhaps some of these walruses ripped the tags out right after the instrumentation.

Tag duration in a similar study in West Greenland was on average 44 ± 34 SD days for tags similar to those used in the present study, with a maximum duration similar to that in this study (Dietz et al., 2014). With a maximum track duration of 278 d and generally higher mean duration (68 d ± 47 SD), the deployment system in this study performed better than those in previous studies using remotely deployed tags. Tags secured with stainless steel bands on the tusks of immobilized walruses had an initial failure rate of 12% and an average duration of 38 ± 31 SD days (Stewart, 2008). However, other studies have reported much longer durations of tusk-mounted tags on walruses: for example, Lydersen and Kovacs (2014) reported an average tag duration of 278 ± 32 d, with some tags transmitting data for more than a year.

Movement Rates

Short-term movements (0.5 – 5 h) were more rapid (2.3 km/h) than those measured over longer periods (0.5 – 24 h; 1.9 km/hr) and will be more affected by inaccuracy of the Argos locations. Our 24-hour traveling speeds appeared similar to those estimated by Dietz et al. (2014: 46 km/24 h or 1.9 km/h) and Stewart (2008: 40 km/24 h or 1.7 km/h), but differences in data collection negate direct comparisons. In Stewart's (2008) study, tags transmitted daily, and he used locations of quality 1 or better that were approximately 24 h apart. Dietz et al. (2014) used filtered positions from 6 – 9 day migration trips to calculate daily averages.

Terrestrial Haul-out Sites

No terrestrial haul-outs on the Greenland side of Smith Sound are known to have been used by walruses after 1900. Peary (1914) mentioned that walruses were found only on land along the Northwest Greenland coast: at Littleton Island near Etah and on the mainland shore across from the island. Vibe (1950) identified another, now abandoned, haul-out in Wolstenholme Fjord. There are no known terrestrial haul-out sites on the eastern coast of Ellesmere Island (Stewart et al., 2014a) either, but the Alexandra Fiord/Buchanan Bay/Flagler Bay-complex, and in particular Flagler Bay, is clearly an important summering area for walruses. Drifting pack ice likely provides an adequate substrate for haul-out in this area. According to Schledermann (1978, 1980), walruses arrive at Flagler Bay in the middle of June or early July. Extensive prehistoric settlements spanning 2 – 3 millennia demonstrate the importance of the walrus to settlers in this area (Schledermann and McCullough, 2003).

The tracked walruses spent 1 – 4 d close to historically known terrestrial haul-out sites in the western part of Devon Island. It could not be determined conclusively whether the walruses actually hauled out on shore at these sites, and the tracking results do not suggest that terrestrial haul-out sites in the western part of Devon Island are used for longer periods of time and by a major proportion of the walruses from Smith Sound.

Seasonal Dispersal

The walruses tracked in this study essentially abandoned the east side of Smith Sound in June, when the coastal ice disappeared, and did not return before new ice was forming in the autumn. In the period between June and October, tracked walruses primarily occupied coastal areas on the western side of Smith Sound, areas that historically have had some winter ice remaining inside fjords and bays (Barber et al., 2001). The tracked walruses spent little time in the offshore areas of the North Water Polynya (i.e., Smith Sound and Kane Basin); instead, they moved directly from one coast to the other and back.

Only three tags transmitted long enough to document the return of the walrus to the eastern side of Smith Sound in October. All three of these walruses summered on eastern Ellesmere Island. This return in October is

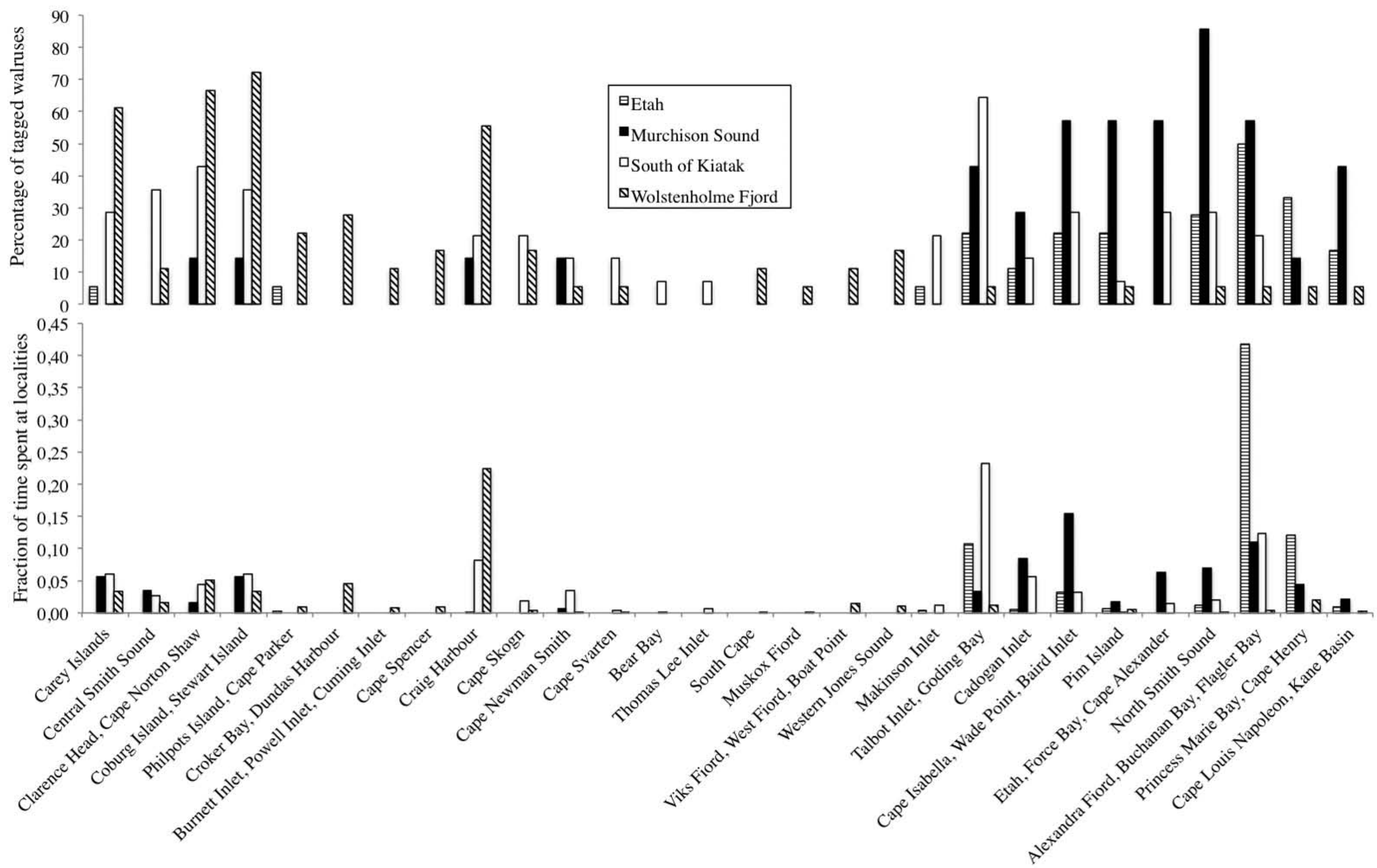

FIG. 3. Above: The percentage of the tagged walruses that moved to specific localities within Smith Sound and adjacent waters after 5 June. Below: Average time spent at the specific localities, weighted by the duration of the tracking period. (See Fig. 1 for positions of localities). Bars are coded by the area where tagging took place, and the tagging sites are not included in the list of destination localities.

in keeping with earlier published walrus arrival times at Wolstenholme Fjord and the area north of Kiatak, where they are regularly hunted by local Greenlandic hunters (Ekblaw, 1928; Vibe, 1950). Walruses can be found in these areas throughout the winter (Born et al., 1995 and references therein; Heide-Jørgensen et al., 2016). Walruses also winter on the Canadian side of Smith Sound, mainly outside the southeast coast of Ellesmere Island (Finley and Renaud, 1980; Richard et al., 1998) and, in smaller numbers, in waters around Bathurst and Cornwallis Islands (Riewe, 1976; Kiliaan and Stirling, 1978). It is not known whether walrus from NW Greenland return to Greenland each winter or remain in Canada one or more winters. Nor is it known whether a segment of the summer contingent never goes to Greenland but resides in Canada all its life.

In comparison, walrus at Svalbard and Davis Strait have been found to occupy coastal areas with haul-out substrate during summer but move far into offshore areas in winter (Freitas et al., 2009; Dietz et al., 2014). Compared to walruses in those areas, the Smith Sound walruses seem to have a higher year-round affinity for coastal areas rather than offshore areas. The strong southward-flowing current in Smith Sound (Melling et al., 2001), which moves lots of sea ice, probably makes offshore residency difficult, and the deeper waters in central Smith Sound reduce the value of this zone as a feeding area for walruses (cf. Noren et al., 2015).

The seasonal rhythm of walrus movements across Smith Sound probably reflects the regional patterns in the formation and decay of annual sea ice. The majority of the tracked walruses moved into Canadian waters along the eastern coast of Ellesmere Island, where sea ice has traditionally persisted in summer (Yackel et al., 2001). Some moved far into the central Canadian Arctic, into areas that are largely ice-free in summer. These walruses might have used well-documented terrestrial haul-outs in these areas as is common in the rest of Canada (Stewart et al., 2013, 2014b, c; Dietz et al., 2014) and around Svalbard (Freitas et al., 2009), where they rely extensively on terrestrial haul-out sites during summer. In the Bering Sea, adult male walruses use terrestrial haul-outs during summer, whereas female walruses and their young, as well as many male walruses, occupy the shallow continental shelf waters of the Chukchi Sea until all ice-based haul-out platforms are lost (Jay et al., 2012; Fischbach et al., 2016).

Sea ice extent fluctuates widely in the North Water area, but coastal areas along the western side of Smith Sound usually have had enough summer sea ice to provide haul-outs for the walruses. However, the presence of sea ice in summer depends heavily on ice formation and thickness

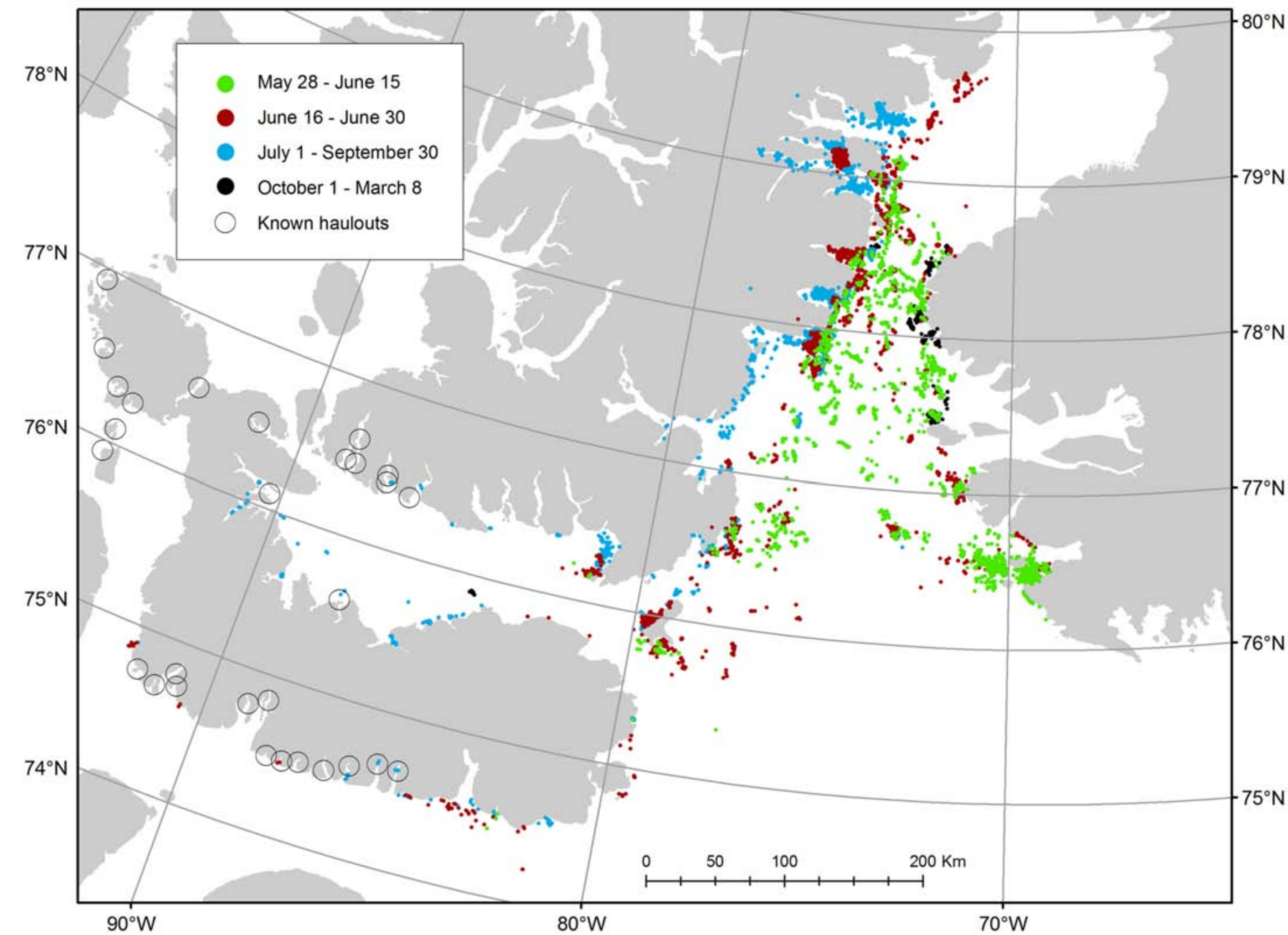

FIG. 4. Standard quality ARGOS locations from 50 walruses whose tags transmitted for more than three days. Walruses were instrumented with satellite-linked transmitters in Northwest Greenland in May or June of 2010–13 and 2015. Legend shows colors representing time periods: two-week periods starting shortly after instrumentation in Greenland; one-month periods while walruses were summering in the Canadian High Arctic; from July through September; and the winter residence period in Greenland from October through March. The open circles represent known terrestrial haul-out sites.

in winter, and any climate-induced declines in sea ice formation will render Smith Sound less suitable for the walrus. Stewart et al. (2014a) conducted aerial surveys in the Buchanan Bay area in three summers. In two years, the bays were ice-filled, but in 2009 they were mostly ice-free (although there were still ice pans supporting walruses). In Smith Sound, only a couple of terrestrial walrus haul-outs are historically known (Vibe, 1950), and the first one documented in recent times is an observation of 2–3 walruses on the eastern end of Haa Island in Hayes Fiord (79˚0′13.52″ N, 77˚35′50.66″ W) off Buchanan Bay on 27 August 2013 (Pierre Richard, pers. comm. 2017). This recent observation may suggest that the walrus could shift from ice to land haul-outs in the future, when sea ice is expected to decrease in availability. A similar occupation of coastal haul-outs has been observed in the eastern Chukchi Sea (Fischbach et al., 2016).

Our tracked walruses demonstrate the extent and seasonal migration routes of the Baffin Bay population that occupies northern Baffin Bay (i.e., Smith Sound) and contiguous waterways. Some of those waterways in the Canadian archipelago freeze over completely in winter (Sou and Flato, 2009). As the ice forms in the fall and the North Water Polynya starts to reform, areas within the Canadian archipelago offer progressively less area with both open water and shallow depths to over-wintering walruses, who seek both food and easy access to the surface. While some small areas can support small numbers of walruses (Kiliaan and Stirling, 1978; Finley and Renaud, 1980; Born et al., 1995; Richard et al., 1998), they cannot support large numbers, and most walruses seem to migrate ahead of the North Water ice edge formation. The main coastal areas where open water over shallow banks can predictably be found are Murchison Sound and Wolstenholme Fjord in the eastern part of the North Water Polynya, where large walrus aggregations are known to occur in winter (Heide-Jørgensen et al., 2016). These aggregations remain along the Greenland coast for about 8.5–9 months of the year, which probably reflects better feeding opportunities in areas where the pack ice is looser. It is also here that the

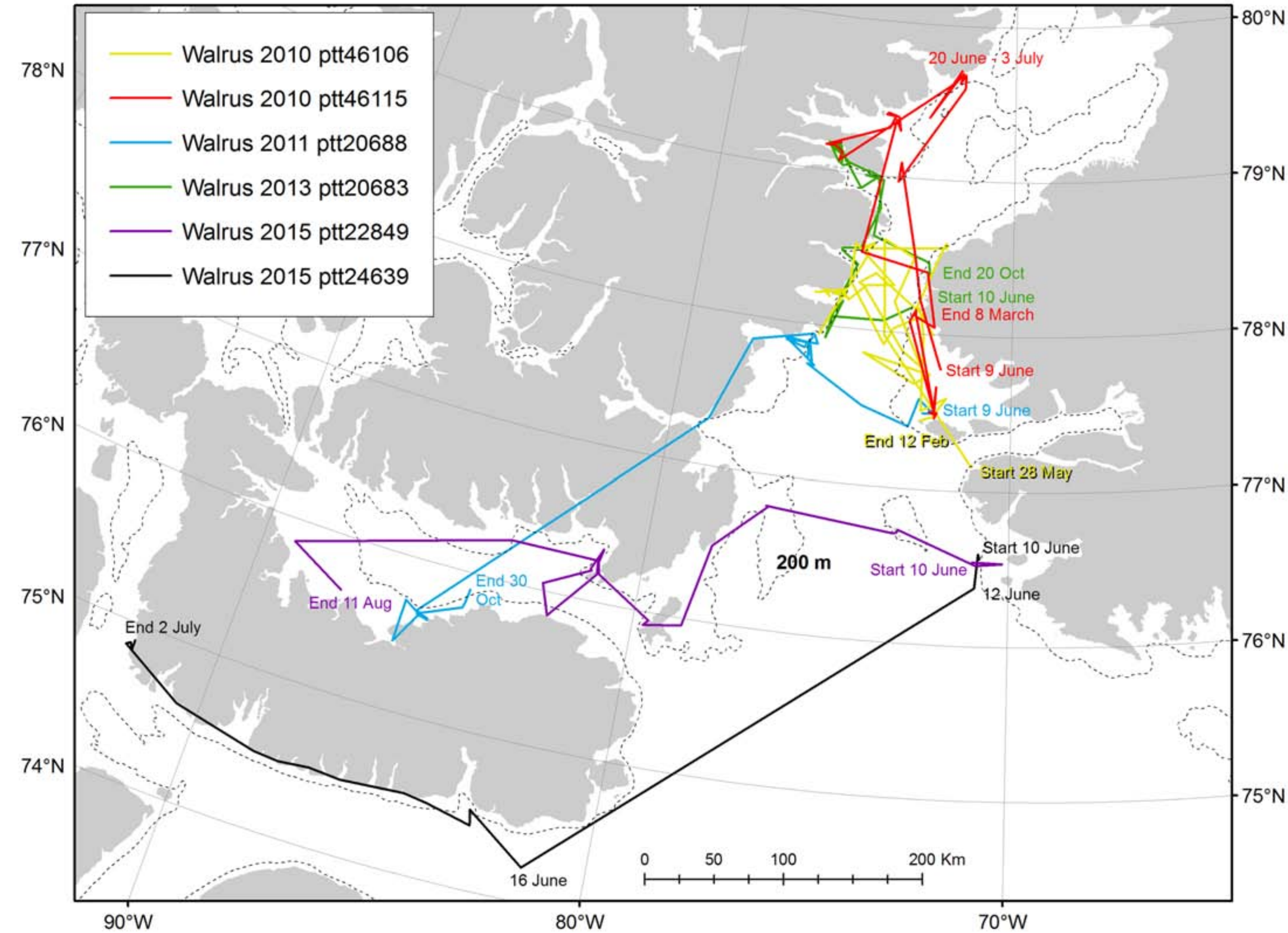

FIG. 5. Selected track lines created from average daily positions of six walruses tracked during 2010–15. Three walruses (red, yellow, and green lines) remained in Smith Sound, while the other three (blue, purple, and black) entered other stock areas. The grey dashed lines show the 200 m bathymetric contour.

highest primary production has been measured in the North Water areas (Klein et al., 2002). This high production is likely to foster high benthic productivity, including those species that are walrus prey.

Stock Implications

The movements observed in this study were primarily west and north along the coast of Ellesmere Island or west into Jones Sound. Stewart (2008) proposed that the population of walrus in this region comprises three stocks: Baffin Bay, West Jones Sound, and Penny Strait-Lancaster Sound. Shafer et al. (2014), using microsatellite DNA, supported the separation of a West Jones Sound stock, but could not differentiate between Stewart's Baffin Bay stock and Penny Strait-Lancaster Sound stock. The population structure for the Baffin Bay population proposed by both Stewart (2008) and Shafer et al. (2014) is supported by this study. We demonstrate for the first time that walruses disperse from the eastern side of Smith Sound to the west side of Smith Sound and farther west into the Canadian Arctic Archipelago. None of the tagged walruses ventured beyond the proposed range of the Baffin Bay population (Shafer et al., 2014), that is, to areas along West Greenland south of Smith Sound or to areas south of Lancaster Sound.

However, our tracking results do not support the delineation between Stewart's Baffin Bay stock and his other proposed walrus stocks (Stewart, 2008). While most of our tracked walruses did remain in the Baffin Bay stock range (Jones Sound, east of 84˚ W, Baffin Bay, Smith Sound) as defined by Stewart (2008), 12 of them did not. Instead these animals moved farther west into either the WJS or the PS-LS stock area, and one of those walruses in fact visited both stock areas. This demonstrates that there is some overlap in the range of those three proposed stocks. However, the tracking data do not disprove the nuclear genetic differentiation of the WJS (Shafer et al., 2014). Nuclear DNA is transferred by both parents, but there are no data to determine whether walruses from Greenland that are tracked to WJS remain there through the breeding season (December through March) or return to Greenland each winter.

The possibility remains that the Baffin Bay population is further segregated into a sedentary segment that winters in small polynyas in the Canadian High Arctic and a migratory segment that moves to eastern Smith Sound for the winter, but the present study cannot address this question. Long migrations of adults with calves (Dietz et al., 2014) probably serve to transfer knowledge of migration routes across generations. One example of such migrations is a female that was accompanied by a calf when tagged and went as far west as Cape Svarten, presumably with her calf in tow.

The walrus is an important game animal for the subsistence hunt both on the Greenlandic side of the North Water and in Jones Sound in Canada (Vibe, 1950; Born, 1987; Priest and Usher, 2004). The results of the present study indicate that walruses occupying Smith, Jones, and Lancaster Sounds in summer are potentially susceptible to hunting in Northwest Greenland. Stewart (2008) attributed the walruses taken in eastern Jones Sound to this "shared stock," but thought that the walruses taken in Lancaster Sound came from a different stock. This idea would be true only if walrus harvests in Lancaster Sound were taken from a non-migratory segment of the population. Locations of tagged walruses that moved into other stock areas suggest that they may not have been exposed to hunting pressure in those areas. Hunting pressure on the WJS stock and on walruses on the south coast of Devon Island is low (7 on average between 2002 and 2011; D.B. Stewart et al., 2014), but there are no recent data on the distribution of hunts, and reported harvests appear to have declined between 1985 and 2010 (Stewart and Hamilton, 2013). However, the fact remains that some walruses that contribute to summertime population estimates in Canada (e.g., Stewart et al., 2014a) move to Greenland, where the quota is 86 per year, for the winter. Evidently walruses in Northwest Greenland and the Canadian High Arctic should be managed as a single stock, and joint assessments are needed not only to manage the hunt, but also when evaluating effects of climate changes and anthropogenic disturbances.

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APPENDIX 1

The following table is available in a supplementary file to the online version of this article at:
https://arctic.journalhosting.ucalgary.ca/arctic/indiex.php/arctic/rt/suppFiles/4661/0

TABLE S1. List of walruses tagged in Smith Sound from 2010 to 2015.

REFERENCES

Barber, D.G., Hanesiak, J.M., Chan, W., and Piwowar, J. 2001. Sea-ice and meteorological conditions in northern Baffin Bay and the North Water Polynya between 1979 and 1996. Atmosphere-Ocean 39(3):343–359.
https://doi.org/10.1080/07055900.2001.9649685

Born, E.W. 1987. Aspects of present-day maritime subsistence hunting in the Thule area, Northwest Greenland. In: Hacquebord, L., and Vaughan, R., eds. Between Greenland and America: Cross-cultural contacts and the environment in the Baffin Bay area. Works of the Arctic Centre No. 10. Groningen: Arctic Centre, University of Groningen. 109–132.

Born, E.W., Gjertz I., and Reeves, R.R. 1995. Population assessment of Atlantic walrus (*Odobenus rosmarus rosmarus* L.). Meddelelser nr. 138. Oslo: Norwegian Polar Institute. 100 p.

CLS America. 2008. ARGOS user's manual: Worldwide tracking and environmental monitoring by satellite. 14 October 2008 update. Toulouse, France: Argos/CLS.
http://www.argos-system.org/manual/index.html#home.htm

Dietz, R., Born, E.W., Stewart, R.E.A., Heide-Jørgensen, M.P., Stern, H., Rigét, F., Toudal, L., Lanthier, C., Villum Jensen, M., and Teilmann, J. 2014. Movements of walruses (*Odobenus rosmarus*) between Central West Greenland and Southeast Baffin Island, 2005-2008. NAMMCO Scientific Publications 9:53–74.
https://doi.org/10.7557/3.2605

Ekblaw, W.E. 1928. The material response of the Polar Eskimo to their far Arctic environment. Annals of the Association of American Geographers 18(1):1–24.
https://doi.org/10.1080/00045602809356904

Finley, K.J., and Renaud, W.E. 1980. Marine mammals inhabiting the Baffin Bay North Water in winter. Arctic 33(4):724–738.
https://doi.org/10.14430/arctic2592

Fischbach, A.S., Kochnev, A.A., Garlich-Miller, J.L., and Jay, C.V. 2016. Pacific walrus coastal haulout database, 1852–2016—Background report. Open-File Report 2016-1108. Anchorage, Alaska: U.S. Geological Survey. 27 p.
https://doi.org/10.3133/ofr20161108

Freitas, C., Kovacs, K.M., Ims, R.A., Fedak, M.A., and Lydersen, C. 2009. Deep into the ice: Over-wintering and habitat selection in male Atlantic walruses. Marine Ecology Progress Series 375:247–261.
https://doi.org/10.3354/meps07725

Freuchen, P. 1921. Om hvalrossens forekomst og vandringer ved Grønlands Vestkyst [Distribution and migration of walruses along the western coast of Greenland]. København: Videnskabelige Meddelelser Dansk Naturhistorisk Forening 72:237–249. Fisheries Research Board of Canada, Translation Series 2382. 14 p.

Heide-Jørgensen, M.P., Sinding, M.-H.S., Nielsen, N.H., Rosing-Asvid, A., and Hansen, R.G. 2016. Large numbers of marine mammals winter in the North Water polynya. Polar Biology 39(9):1605–1614.
https://doi.org/10.1007/s00300-015-1885-7

Jay, C.V., Heide-Jørgensen, M.P., Fischbach, A.S., Villum Jensen, M., Tessler, D.F., and Jensen, A.V. 2006. Comparison of remotely deployed satellite radio transmitters on walruses. Marine Mammal Science 22(1):226–236.
https://doi.org/10.1111/j.1748-7692.2006.00018.x

Jay, C.V., Fischbach, A.S., and Kochnev, A.A. 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. Marine Ecology Progress Series 468:1–13.
https://doi.org/10.3354/meps10057

Kiliaan, H.P.L., and Stirling I. 1978. Observations of overwintering walruses in the eastern Canadian High Arctic. Journal of Mammalogy 59(1):197–200.
https://doi.org/10.2307/1379895

Klein, B., LeBlanc, B., Mei, Z.-P., Beret, R., Michaud, J., Mundy, C.-J., von Quillfeldt, C.H., et al. 2002. Phytoplankton biomass, production and potential export in the North Water. Deep-Sea Research Part II 49(22-23):4983–5002.
https://doi.org/10.1016/S0967-0645(02)00174-1

Lydersen, C., and Kovacs, K.M. 2014. Walrus *Odobenus rosmarus* research in Svalbard, Norway, 2000–2010. NAMMCO Scientific Publications 9:175–190.
https://doi.org/10.7557/3.2613

Lydersen, C., Aars, J., and Kovacs, K.M. 2008. Estimating the number of walruses in Svalbard from aerial surveys and behavioural data from satellite telemetry. Arctic 61(2):119–128.
https://doi.org/10.14430/arctic31

Melling, H., Gratton, Y., and Ingram, G. 2001. Ocean circulation within the North Water Polynya of Baffin Bay. Atmosphere-Ocean 39(3):301–325.
https://doi.org/10.1080/07055900.2001.9649683

Noren, S.R., Jay, C.V., Burns, J.M., and Fischbach, A.S. 2015. Rapid maturation of the muscle biochemistry that supports diving in Pacific walruses (*Odobenus rosmarus divergens*). Journal of Experimental Biology 218:3319–3329.
https://doi.org/10.1242/jeb.125757

Peary, R.E. 1914. Northward over the "Great Ice": A narrative of life and work along the shores and upon the interior ice-cap of northern Greenland in the years 1886 and 1891–1897. Vol. II. New York: Frederick A. Stokes Company. 625 p.

Priest, H., and Usher, P.J. 2004. The Nunavut Wildlife Harvest Study: Final report. Iqaluit: Nunavut Wildlife Management Board.

Richard, P.R., Orr, J.R., Dietz, R., and Dueck, L. 1998. Sightings of belugas and other marine mammals in the North Water, late March 1993. Arctic 51(1):1–4.
https://doi.org/10.14430/arctic1039

Riewe, R.R. 1976. Inuit land use in the High Arctic. In: Freeman, M.M.R., ed. Inuit land use and occupancy study, Vol. 1: Land use and occupancy. Ottawa: Department of Indian and Northern Affairs. 173–184.

Schledermann, P. 1978. Preliminary results of archaeological investigations in the Bache Peninsula region, Ellesmere Island, N.W.T. Arctic 31(4):459–474.
https://doi.org/10.14430/arctic2673

———. 1980. Polynyas and prehistoric settlement patterns. Arctic 33(2):292–302.
https://doi.org/10.14430/arctic2562

———. 1990. Crossroads to Greenland: 3000 years of prehistory in the eastern High Arctic. Komatik Series 2. Calgary, Alberta: The Arctic Institute of North America.

Schledermann, P., and McCullough, K.M. 2003. Late Thule culture developments on the central east coast of Ellesmere Island. Danish Polar Center Publication 12. Copenhagen: Sila – The Greenland Research Centre at the National Museum of Denmark and Danish Polar Center. 203 p.

Shafer, A.B.A., Davis, C.S., Coltman, D.W., and Stewart, R.E.A. 2014. Microsatellite assessment of walrus (*Odobenus rosmarus rosmarus*) stocks in Canada. NAMMCO Scientific Publications 9:15–31.
https://doi.org/10.7557/3.2607

Sou, T., and Flato, G. 2009. Sea ice in the Canadian Arctic Archipelago: Modeling the past (1950–2004) and the future (2041–60). Journal of Climate 22(8):2181–2198.
https://doi.org/10.1175/2008JCLI2335.1

Stewart, D.B., Higdon, J.W., Reeves, R.R., and Stewart, R.E.A. 2014. A catch history for Atlantic walruses (*Odobenus rosmarus rosmarus*) in the eastern Canadian Arctic. NAMMCO Scientific Publications 9:219–313.
https://doi.org/10.7557/3.3065

Stewart, R.E.A. 2008. Redefining walrus stocks in Canada. Arctic 61(3):292–308.
https://doi.org/10.14430/arctic26

Stewart, R.E.A., and Hamilton, J.W. 2013. Estimating total allowable removals for walrus (*Odobenus rosmarus rosmarus*) in Nunavut using the potential biological removal approach. Canadian Science Advisory Secretariat Research Document 2013/031. Ottawa: CSAS, Fisheries and Oceans Canada. iv + 13 p.

Stewart R.E.A., Hamilton, J.W., and Dunn, J.B. 2013. Results of Foxe Basin walrus (*Odobenus rosmarus rosmarus*) surveys: 2010–2011. Canadian Science Advisory Secretariat Research Document 2013/017. Ottawa: CSAS, Fisheries and Oceans Canada. iv + 12 p.

Stewart, R.E.A., Born, E.W., Dunn, J.B., Koski, W.R., and Ryan, A.K. 2014a. Use of multiple methods to estimate walrus (*Odobenus rosmarus rosmarus*) abundance in the Penny Strait-Lancaster Sound and West Jones Sound stocks, Canada. NAMMCO Scientific Publications 9:95–122.
https://doi.org/10.7557/3.2608

Stewart, R.E.A., Born, E.W., Dietz, R., Heide-Jørgensen, M.P., Rigét, F.F., Laidre, K., Villum Jensen, M., Knutsen, L.Ø., Fossette, S., and Dunn, J.B. 2014b. Abundance of Atlantic walrus in western Nares Strait, Baffin Bay stock, during summer. NAMMCO Scientific Publications 9:123–140.

Stewart, R.E.A., Born, E.W., Dietz, R., and Ryan, A.K. 2014c. Estimates of minimum population size for walrus around southeast Baffin Island, Nunavut. NAMMCO Scientific Publications 9:141–157.
https://doi.org/10.7557/3.2615

Vibe, C. 1950. The marine mammals and the marine fauna in the Thule District (Northwest Greenland) with observations on ice conditions in 1939–41. Meddelelser om Grønland 150(6). 115 p.

Yackel, J.J., Barber, D.G., and Papakyriakou, T.N. 2001. On the estimation of spring melt in the North Water polynya using RADARSAT-1. Atmosphere-Ocean 39(3):195–208.
https://doi.org/10.1080/07055900.2001.9649676