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Redefining Walrus Stocks in Canada

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ABSTRACT. Defining management units is basic to the sound management of resources. Walrus (*Odobenus rosmarus rosmarus*) are hunted throughout their range in Canada and are subject to other human activities requiring management decisions. Current management units are based on a comprehensive review and a stock assessment completed in the mid 1990s. Between 1993 and 2004, satellite-linked radio tags provided information on the movements of walrus in Canada's High Arctic. These data were incorporated with other information that has become available since 1995 to reassess walrus management units in Canada. Tagging data and other information suggest that some finer discrimination of walrus populations is needed as a precautionary approach and to formulate testable hypotheses. Specifically, the previous North Water/Baffin Bay walrus stock may be considered to be three stocks: Baffin Bay, west Jones Sound, and Penny Strait-Lancaster Sound stocks. The Foxe Basin population appears to comprise two stocks (North Foxe Basin and Central Foxe Basin) rather than one. Previously suspected subdivisions in the Hudson Bay-Davis Strait population are substantiated by isotopic evidence although sampling on a finer geographic scale is required before this stock can be partitioned. There is new evidence to support the previously postulated separation of the walrus in the Southern and Eastern Hudson Bay stock from all others, but no evidence to warrant subdivision.

Key words: walrus, *Odobenus rosmarus*, satellite tag, genetic, isotope, contaminant

RÉSUMÉ. La définition des unités de gestion est fondamentale à la bonne gestion des ressources. Le morse (*Odobenus rosmarus rosmarus*) est chassé dans son aire d'extension au Canada, en plus d'être assujetti à d'autres activités humaines nécessitant des décisions en matière de gestion. Les unités de gestion actuelles sont fondées sur l'examen exhaustif et l'évaluation des groupes effectués vers le milieu des années 1990. Entre 1993 et 2004, des étiquettes radio par satellite ont fourni des renseignements sur les mouvements du morse dans le Grand Nord du Canada. Ces données ont été intégrées à d'autres informations disponibles depuis 1995 dans le but de réévaluer les unités de gestion du morse au Canada. Les données obtenues grâce aux étiquettes et d'autres informations laissent croire qu'il y a lieu d'avoir une discrimination plus raffinée des populations de morse en tant qu'approche de précaution et de formuler des hypothèses pouvant être mises à l'épreuve. Plus précisément, l'ancien groupe de morses des eaux du Nord et de la baie de Baffin peut être considéré comme trois groupes, soit les groupes de la baie de Baffin, du détroit Jones de l'ouest et des détroits de Penny et de Lancaster. Par ailleurs, la population du bassin Foxe semble comprendre deux groupes (le bassin Foxe du nord et le bassin Foxe du centre) au lieu d'un seul groupe. Les sous-divisions dont on se doutait auparavant pour ce qui est de la population de la baie d'Hudson et du détroit de Davis sont corroborées par des preuves isotopiques, quoiqu'un échantillonnage plus perfectionné s'avère nécessaire à l'échelle géographique avant que ce groupe ne puisse faire l'objet d'une répartition. Il y a de nouvelles preuves permettant de soutenir l'ancienne séparation hypothétique des groupes de morses dans le sud et l'est de la baie d'Hudson par rapport à tous les autres groupes, mais aucune preuve ne vient justifier une sous-division.

Mots clés : morse, *Odobenus rosmarus*, étiquette par satellite, génétique, isotope, contaminant

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INTRODUCTION

In fisheries science, management units are often referred to as stocks, and managing organizations (e.g., DFO, 2001; NMFS, 2001) carry out stock assessments to determine stock status. Atlantic walrus (*Odobenus rosmarus rosmarus*) in Canada are the subject of such stock status assessments (DFO, 2000).

Historically, walrus occupied Canadian waters from Nova Scotia to perhaps 85˚ N and from the boundary with Greenland to roughly 100˚ W, but their range now is less extensive and more discontinuous (Born et al., 1995). Walrus breed in winter, between January and April (Born et al., 1995; Stewart and Fay, 2001), in restricted areas of open water or polynyas (Finley and Renaud, 1980; Stirling et al., 1981). Within their summer range, walrus are segregated by age and sex (Born et al., 1995), with mature males forming separate groups. In many areas, walrus haul out onto land to rest, but they also rest on floating ice.

Here I consider management units of walrus in Canada as the foundation for making management decisions affecting hunting and other human activities. I start by

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reviewing conceptual aspects of defining management units and then examine the stock structure proposed by Born et al. (1995) that has been applied to recent walrus assessments (DFO, 2000). On the basis of isotopic profiles, Outridge et al. (2003) indicated that some of the stocks proposed by Born et al. (1995) should be further subdivided. I review published data on distribution, hunting availability, isotope and contaminant profiles, body size, and genetic data, as well as new data from walrus fitted with satellite-linked radio tags.

What is a Stock?

The concept of "stock" is common in fisheries management for making intraspecific subdivisions (usually focusing on the question "Which animals are taken where by whom?") to assist managers in making allocation decisions. But, while the term is prevalent in the literature, the concept of "stock" is not defined rigorously. Outside of fisheries, the word "stock" generally refers to the base from which other groups derive. Thus "stock" is analogous to the stem of a tree rather than its branches, an interpretation constant since at least the 14th century (Booke, 1981). In fisheries, "stock" has been used to delimit groups of fish, from systematic to management units (Booke, 1981).

The Fish and Agriculture Organization of the United Nations considered "stock" and "population" to be synonymous (Jefferson et al., 1993). The evolutionarily significant unit applied to Pacific salmon (*Oncorhynchus* spp.) stock issues was defined as (1) a population that is reproductively isolated and (2) an important part of the species evolutionary legacy (Waples, 1991). Waldman (2005:11) concluded that the first criterion, i.e., a population, is "essentially the definition of a stock." Secor (2005), however, cautioned against this interpretation and considered a stock to be a specific portion of a population in which anthropogenic activity influences population productivity. Two groups may not have different evolutionary potential, but still require management decisions at a lower taxonomic level (Taylor, 1997; Taylor and Dizon, 1999). I consider "stock" to be a subpopulation designation.

For operational purposes, Royce (1972) defined a stock as a management unit, a group of animals capable of independent exploitation or management. "Stock" is therefore defined by its interaction with humans: the segment of the fish population considered with respect to actual or potential utilization (Ricker, 1975).

The operational definition of stock based on anthropogenic interaction has at least three influential consequences. First, the delineation of the stock is dependant on the nature of the interaction. For example, trophy-sized male walrus, the object of sport hunts, may be a different stock than the part of the same population that supports the subsistence hunt in the same area. Trophies are selected on the basis of absolute size, and as long as the number of big males removed does not reduce the productivity of the population (surplus male hypothesis, but see Harris et al., 2002; Singer and Zeigenfuss, 2002), the number of animals available for subsistence hunting will not change. The edible walrus products of trophy-kills return to the subsistence consumers, so the sport hunt is not considered additive. This concept, a familiar one in wildlife management, is evidenced in different hunting seasons or bag limits for males and females of a species in one hunting district. However, the term "stock" is used infrequently by wildlife managers, who tend to get by with "demes" and "populations" (see for example Novaks et al., 1987; Harris et al., 2002).

Second, with respect to removals by hunting, the interaction basis for defining stocks means that if one has biological information on every landed walrus at a community, one has the definition of that hunted stock (except for killed and lost animals) at that location. Statistical differences in one or more parameters between harvests mean they are different stocks, or different harvest stocks (Waldman, 2005). Offsetting this advantage is the first influential consequence: sampling by biologists taking biopsies, for example, is an interaction quite different from hunting and may not accurately represent the intraspecific group that will enter the harvest stock.

Third, the perception of "stock" depends on the character set used to differentiate it (Ihssen et al., 1981; Waldman, 2005). Genetic data provide insights into population identity reflecting not only current distribution, but also ancestral patterns that may not relate to existing conditions (Swain et al., 2005; Waldman, 2005). Moreover, selective removal can alter gene flow and enhance population differentiation (Harris et al., 2002), and comparison of neutral genetic markers may not reflect locally adaptive traits or differences (Swain et al., 2005). Population parameters, behaviour, morphology, and meristics, to name a few methods, all present different views of the group being studied. Contaminant profiles and stable isotope signals used to identify stocks indicate that one group of animals lived its life—sampled its environment—differently than the other group (Outridge and Stewart, 1999; Innes et al., 2002; Outridge et al., 2003; Campana, 2005). These are real stock differences; removing animals at one locale characterized by certain chemicals may not affect the number of animals at another locale with different chemical profiles. Clayton (1981) advocated the use of multiple tests employing different types of data, noting that a difference in one type of data was sufficient to differentiate stocks. "A stock is a stock," according to Waldman (2005:12), if a marker discriminates it from other stocks. It is incumbent upon biologists to understand those differences in the context of population structure and ecology. Accepting differences regardless of the nature of the marker also tends to err on the side of conservation: erroneously identifying more stocks than exist is more protective than erroneously pooling stocks that are in fact different (Taylor, 1997; Taylor and Dizon, 1999). Conversely, negative results are not conclusive because other techniques may reveal differences (Waldman, 2005; Wirgin and Waldman, 2005).

Allowing that a stock may not be a self-replicating unit, it becomes important to understand the indirect effects mediated through interbreeding among stocks at the population level, where a population is an intraspecific group more likely to interbreed than to breed with members of another group (Pianka, 1988). Also inherent in this perspective is the separation in time and place that allows site-specific differences to accumulate and persist over time. Simultaneous hunts in separated parts of a walrus population's range may mean there are two stocks, but the distinction requires additional evidence of philopatry to those areas.

The population structure is the fundamental aspect of living resources (Secor, 2005). Population reproductive isolation is often achieved through geographic separation, which was an underlying consideration in the separation of walrus stocks described by Born et al. (1995). The geographic distribution of animals, as opposed to genetic or chemical stock-identifying markers, is something that can be seen in real time. Indeed, aside from trophy walrus, few walrus stocks could be discerned outside of the laboratory. So, if the stock is not a complete, self-sustaining unit but rather a distributional branch of a larger, interbreeding population, managers must return to the population structure and consider both the local group (stock) and the population that supports it (Secor, 2005).

Here I adopt Secor's (2005) definition that a stock is a specific part of a population impacted by human activity in a way that affects population productivity, with Ricker's (1975) caveat to include potential utilization. Therefore, I refer to walrus populations in Canada and assume they are best represented by wintering aggregations when breeding occurs (e.g., Sjare and Stirling, 1996). More widely dispersed aggregations or herds in the open-water season are expected to be segregated by age and sex, with at least female philopatry (Andersen and Born, 2000). Various parts of a population may be removed, sampled, or otherwise impacted at one or more location, and I refer to those aggregations as stocks. This conceptual framework parallels that used for "harvest stocks" of beluga (*Delphinapteras leucas*) by Innes et al. (2002) and of walrus by Outridge et al. (2003), except for the inclusion of summering herds that are not known to be exposed to hunting. It is a model similar to that proposed by Andersen and Born (2000) except that I consider separate breeding groups of walrus to be populations instead of subpopulations.

The final conceptual consideration is the degree of physical separation between two putative stocks. Stock distinctiveness is most easily envisaged when there is a large geographic separation, for example between Foxe Basin and south Hudson Bay walrus. But walrus were once more widely distributed in Canada, and current geographic isolation may be an artefact: isolated groups may be the end points of a once-contiguous distribution characterized not by geographic isolation, but by a cline of differences (Mayr, 1970; Royce, 1972; Gaskin, 1982). Evidence of clinal variation of genotypic and phenotypic characteristics, in which adjacent localities are not statistically different but at some increasing distance (cline width) two samples do differ significantly, may not be apparent outwardly, but is critical to sound management (Taylor and Dizon, 1999). Cline width is often estimated as the distance at which the frequency of the less common marker falls to 20% and the more common marker rises to 80% (Owen and Baker, 2001), or the 20/80 rule (May et al., 1975). Conceivably, with sufficient sampling, it may be possible to measure clinal widths in walrus for management purposes or to reveal structure within a continuous distribution using more powerful statistical techniques (Hoffman et al., 2006). For now, the concept of clinal variation is useful in interpreting the limited information available.

The Hypothesis

Born et al. (1995) identified four putative stocks of walrus in Canada (Fig. 1): North Water (Baffin Bay–Eastern Canadian Arctic); Foxe Basin; Northern Hudson Bay–Hudson Strait–Southeastern Baffin Island–Northern Labrador; and Southern and Eastern Hudson Bay. For brevity, and to base the names, as much as possible, on the relevant water bodies, I use these stock names: Baffin Bay (BB), Foxe Basin (FB), Hudson Bay-Davis Strait (HBDS), and Southern and Eastern Hudson Bay (SEHB). I test these hypothesized stock delineations using new information from satellite-linked radio tags that track movements of individuals and from published data. Born et al. (1995) identified a fifth stock, the West Greenland stock, which is discussed as an adjunct to the HBDS stock.

METHODS

A study area in the western reaches of Jones and Lancaster sounds was selected in which to test, using satellite telemetry, the hypothesis that walrus from Canada were also being hunted in Greenland. In consultation with local communities, terrestrial haulout sites distant from main hunting areas were selected for walrus tagging.

Males and females without calves were selected for attachment of satellite tags. A selected walrus was approached within ~20 m, and an immobilizing drug was administered by a pressurized dart propelled by a CO_2 rifle (Dan-Inject®) (Lanthier et al., 1999). Different immobilizing agents were used over the years (Table 1); the narcotics etorphine and carfentanil (Lanthier et al., 1999) were replaced, first with medetomidine-zolazepam-tiletamine (MZT), then with medetomidine-ketamine (MK) (R.E.A. Stewart and C. Lanthier, unpubl. data). Narcotics were reversed with naltrexone (Lanthier et al., 1999), and the other drugs, with atipamezole.

When the darted walrus was immobilized, neighbouring walrus were displaced to a safe distance by slowly approaching the herd. A satellite-linked transmitter/data collection tag was attached to a tusk with a bonding agent such

FIG. 1. Range of putative walrus stocks in Canada (redrawn from Fig. 3 of Born et al., 1995): 1 Foxe Basin; 2 Southern and Eastern Hudson Bay; 3 Northern Hudson Bay–Hudson Strait–Southeastern Baffin Island–Northern Labrador; and 5 North Water (Baffin Bay-Eastern Canadian Arctic). The numbering used by Born et al. (1995) has been retained (#4 – West Greenland, is outside Canada and has not been labeled).

as epoxy or Ray-Crete® and stainless steel bands. Tag design varied over the course of the study (Fig. 2, Table 1), but all tags except number 11270 (Telonics) were built by Wildlife Computers. Location data were restricted to ARGOS location quality (LQ) 0, 1, 2, and 3, defined by ARGOS as having precision radii of greater than 1500 m, less than 1500 m, less than 500 m, and less than 250 m, respectively (Service Argos, 2007). For each day (local time), the highest LQ was used. If there were several uplinks of maximum LQ in one day, they were averaged for a daily location. LQ 0 data may contain large location errors. LQ 0 data that were more than 1500 m inland were removed from the data set. After generating daily averages, days for which LQ 0 data were the best available were compared to LQ 1–3 data for improbably rapid movement. Location data of quality 1 or better when locations were 24 ± 1 h apart were used to establish a distance criterion (40 km/24 h, see Results). If a daily average LQ 0 location exceeded the distance criterion, the individual data points in the average were examined and extreme values removed until the daily average met the distance criterion or until there were no data for that day.

Relevant tag data are available only for the Baffin Bay stock. The literature was reviewed to obtain other data that might be useful in examining stock definitions for this and other stocks in Canada. Data included, but were not limited to, contaminant levels or signatures, isotopic profiles, disease occurrence or prevalence, and genetic composition. Stock definitions may also reflect the distribution of the human interaction with the stock, and I considered the distribution of approximately 1200 kill sites for walrus harvested between 1996 and 2001 (Priest and Usher, 2004: CD-ROM inclusion). None of the data available sampled the entire range of a putative stock, so the analysis compared point sources of information to determine similarities with or differences from other point sources.

RESULTS AND DISCUSSION

Eighteen tags were deployed between 1993 and 2004 (Table 1). Eleven tags were deployed in fiords on southwest Devon Island, Grinnell Peninsula (Devon Island),

TABLE 1. Tag history of 18 satellite-linked radio tags deployed on walrus between 1993 and 2004. Data are separated into two general areas (Jones Sound and Penny Strait/Lancaster Sound).

Deployed			PTT				Transmission		
Date	Site	Latitude/Longitude	No.	Type[1]	Walrus Sex	Immobilizing Agent[2]	Final Date	Duration[3]	Days with LQ ≥ 0
10/08/93	Brooman Pt	75° 31′/97° 23′	2509	W1	M	etorphine	30/08/93	20	17
11/08/93	Brooman Pt	75° 31′/97° 23′	2500	W1	M	etorphine	16/08/93	5	0
12/08/93	Brooman Pt	75° 31′/97° 23′	2508	W1	M	etorphine	08/09/93	27	15
13/08/93	Brooman Pt	75° 31′/97° 23′	2511	W1	M	carfentanil	13/08/93	0	1
13/08/93	Brooman Pt	75° 31′/97° 23′	2512	W1	M	carfentanil	17/08/93	4	1
14/08/93	Brooman Pt	75° 31′/97° 23′	2514	W1	M	carfentanil	16/08/93	2	5
15/08/93	Brooman Pt	75° 31′/97° 23′	11270	T1	M	carfentanil	28/08/93	13	7
25/08/01	Ryder Inlet	74° 50′/88° 33′	2511	W1	M	MK	27/09/01	33	3
11/08/03	Barrow Harbour	76° 32′/96° 02′	2511	W3	F	MK	31/08/03	20	14
19/08/03	Kearney Cove	74° 43′/90° 48′	3303	W3	M	MK	01/09/03	13	12
19/08/03	Kearney Cove	74° 43′/90° 48′	8198	W2	M	MK	19/08/03	0	0
25/08/98	Goose Fiord, S	76° 28′/88° 25′	2500	W1	M	MZT	25/09/98	31	24
24/08/99	Goose Fiord, N	76° 37′/88° 31′	8199	W2	M	MZT	15/11/99	83	36
25/08/01	Goose Fiord, N	76° 37′/88° 31′	2514	W1	F	MK	10/10/01	46	16
26/08/01	Goose Fiord, S	76° 28′/88° 25′	8199	W2	F	MK	13/10/01	48	29
24/08/04	Norfolk Inlet	76° 30′/91° 18′	49503	W3	F	MK	25/11/04	93	53
24/08/04	Goose Fiord, S	76° 28′/88° 25′	49504	W3	M	MK	13/11/04	81	36
25/08/04	Goose Fiord, S	76° 28′/88° 25′	2511	W3	F	MK	25/11/04	92	41

[1] Tag type and dimensions as in Figure 2.

[2] MZT = medetomidine-zolazepam-tiletamine, MK = medetomidine-ketamine.

[3] Duration is the day of final transmission minus the deployment date.

and at Brooman Point (Bathurst Island). Seven were deployed in Norfolk Inlet and Goose Fiord adjacent to western Jones Sound (Fig. 3).

There were 16 pairs (7 walrus in 5 years) of tag locations of LQ ≥ 1 approximately 24 h (23.8 ± 0.6, mean + 1 SE) apart. The average distance these tagged walrus moved was 10.8 ± 10.7 km/24 h. The maximum distance moved was 37.8 km in 24 h. Another tagged walrus (2511 in 2003) left a haulout and moved 32.4 km in 14 h, 4.7 km the next day, then 31.0 km to an occupied haulout the third day. Based on this animal and the maximum movement recorded in 24 h, I used 40 km sea distance, multiplied by the number of days for longer periods, to determine if the LQ 0 position was improbably far from adjacent positions. Of the 18 tags deployed, 16 provided at least one location. A total of 1337 locations of LQ ≥ 0 generated 310 daily locations over a maximum of 93 days. Tag data are discussed further in the stock-by-stock analysis that follows. In addition to other studies reviewed in the next sections, I also examined the incidence of diseases that may have been instructive for postulating population separations. Antibodies to canine distemper virus, phocine distemper virus, canine adenovirus, and influenza A antibodies (Duignan et al., 1994; Nielsen et al., 1996, 2000, 2001a; Philippa et al., 2004) did not reveal location differences. Brucella antibodies were not found in small collections of walrus from Grise Fiord (n = 5), Resolute Bay (n = 4) and Nunavik (n = 4), all of the Baffin Bay stock, but were found in Foxe Basin at low frequency (3.2%, n = 157, Nielsen et al., 2001b). Generally, incidence of antibodies was not useful in discerning stock differences.

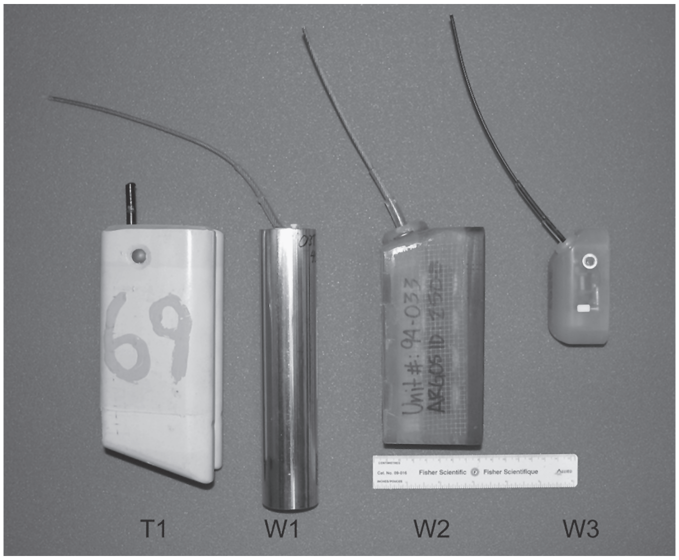

FIG. 2. Satellite radio tags used in this study with the surface contacting the walrus tusk to the right. Left to right: tags from Telonics (T1: 18.7 × 4 × 7.9 cm [length × width × depth], 1503 g) and Wildlife Computers (W1: 19.5 × 4 cm, 612 g; W2: 15 × 5.5 × 7 cm, 772–783 g; W3: 8.8 × 4.9 × 3.7 cm, 194 g) deployed on walrus.

Baffin Bay

Wintering areas (Fig. 4) occur in the Cardigan Strait-Fram Sound area at the west end of Jones Sound, around Dundas Island (Born et al., 1995; COSEWIC, 2006), the floe edges of Jones and Lancaster sounds, and in the North Water polynya between approximately 69° and 77° N on the Greenland coast (Born et al., 1995). The degree of separation among wintering areas is not known. Andersen

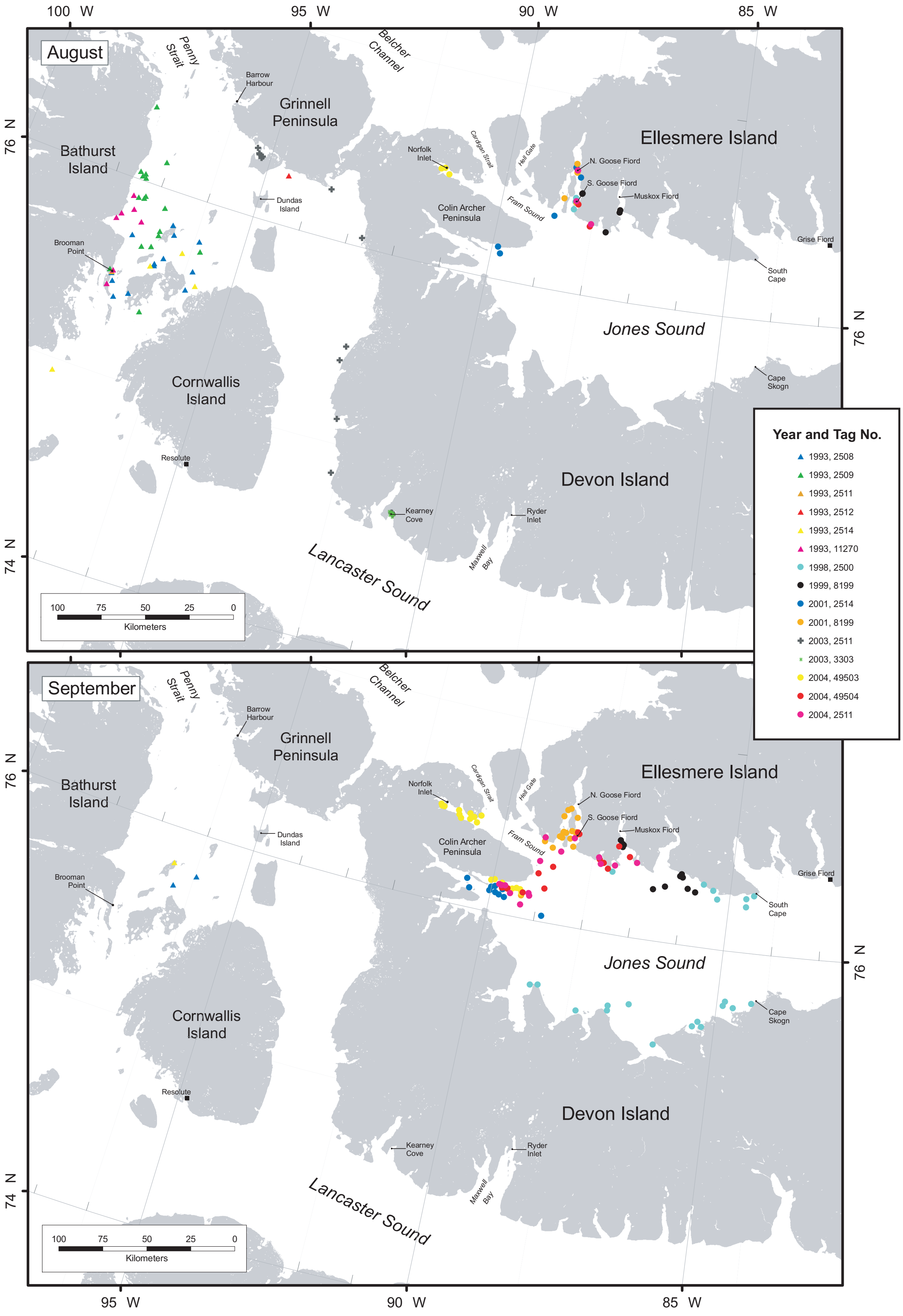

FIG. 3. Sites where satellite tags were deployed on walrus in 1993 and in 1998–2004, as well as daily locations (LQ ≥ 0) for 16 tags that returned data. See Table 1 for the number of tags deployed at each site. This panel: August and September locations.

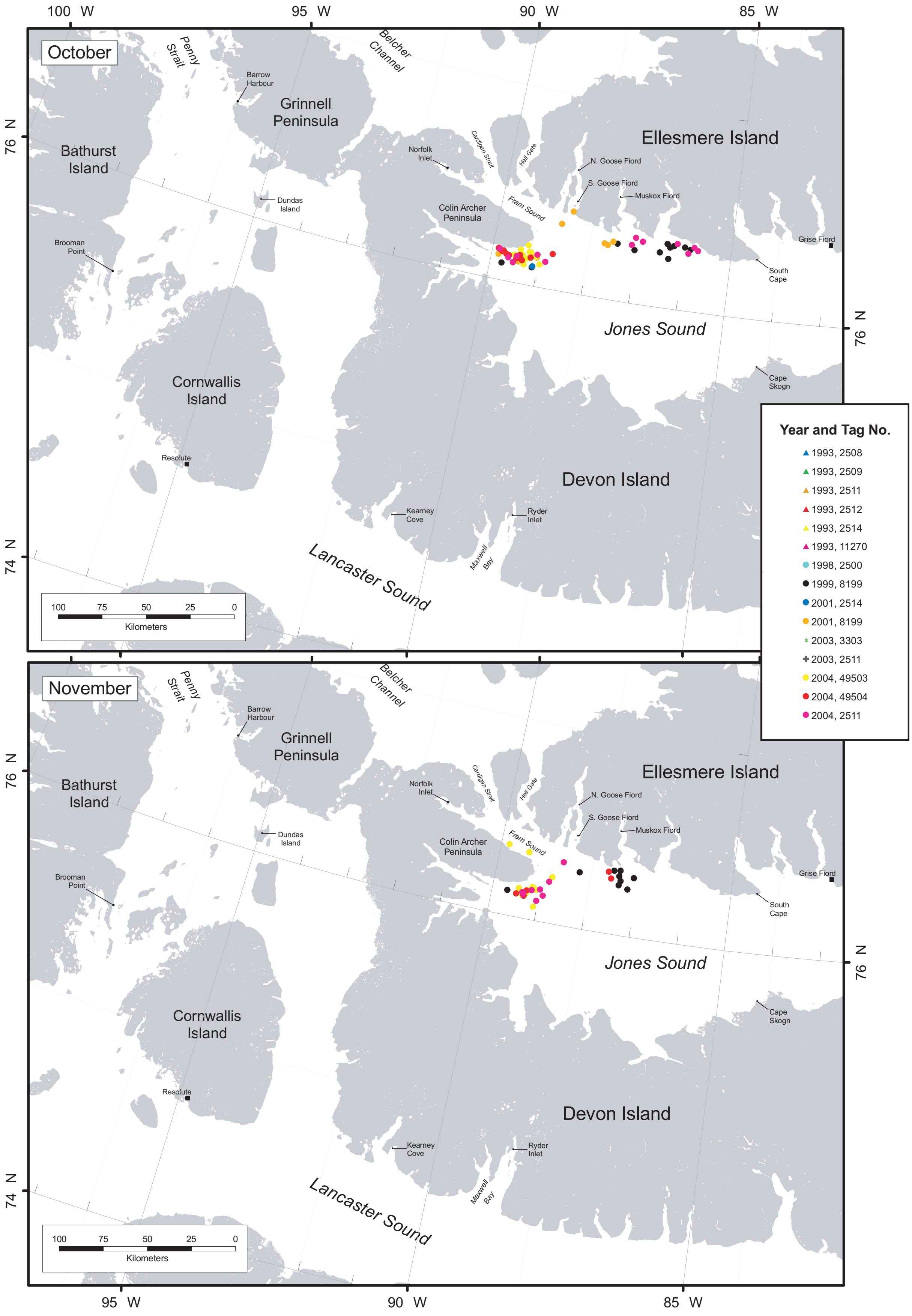

FIG. 3 cont'd. This panel: October and November locations.

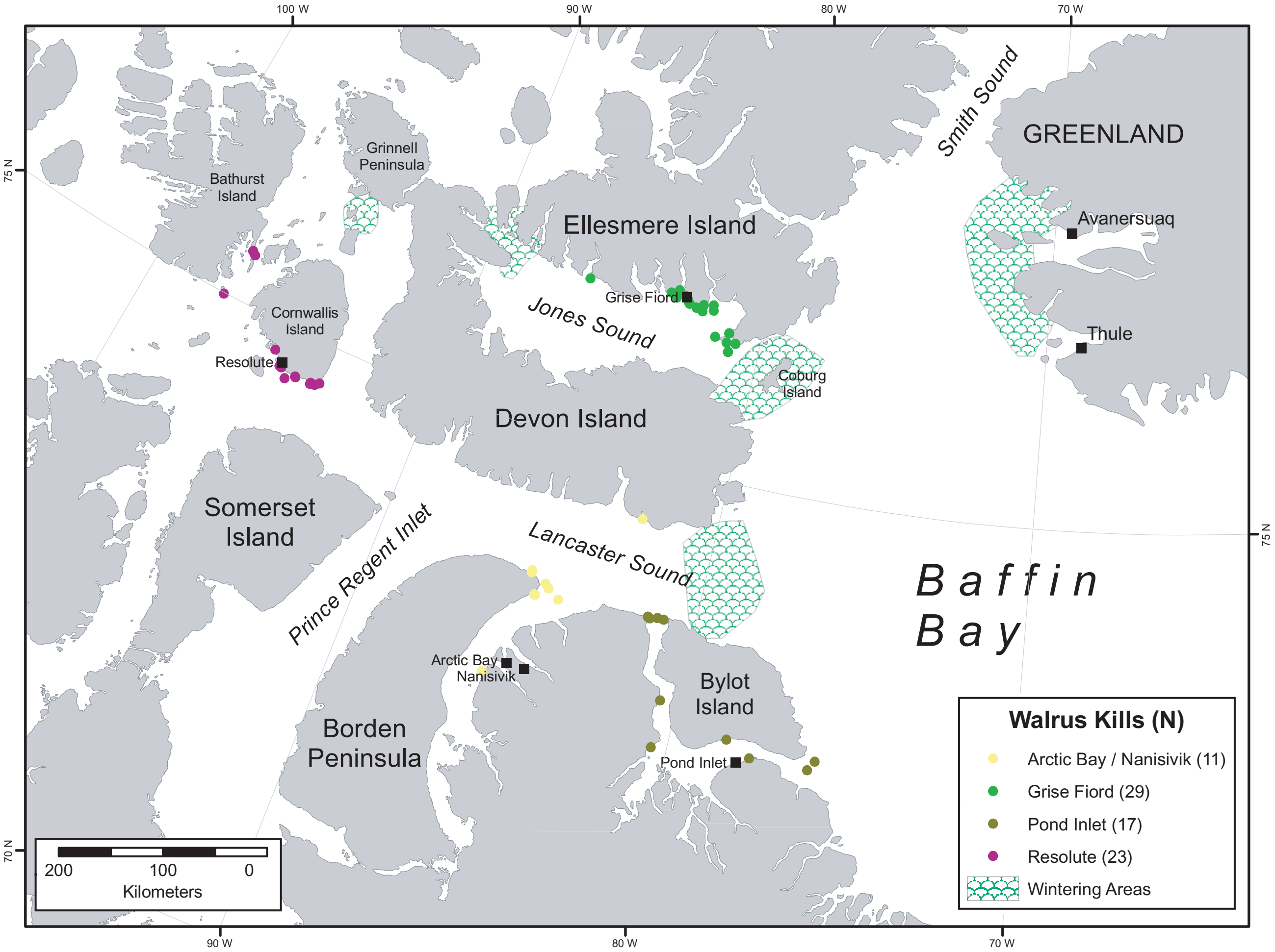

FIG. 4. High Arctic walrus harvesting locations for Grise Fiord, Resolute Bay, Pond Inlet, and Arctic Bay/Nanisivik (Priest and Usher, 2004) and wintering areas (Born et al., 1995). Each kill symbol may represent more than one animal killed; N is the number of walruses reported by each community in the Priest and Usher (2004) database.

and Born (2000) found genetic (mtDNA and microsatellite) differences between walrus landed in North Greenland and West Greenland and proposed that these two wintering groups are separate subpopulations with some male-mediated genetic exchange.

There are no walrus around Avanersuaq between mid-June and mid-July, when they may travel north into Smith Sound or west into Canada (Born et al., 1995). An inductively coupled plasma mass spectrometry (ICP-MS) comparison of lead isotope ratios (^{206}Pb/^{207}Pb and ^{208}Pb/^{207}Pb) of walrus landed at Grise Fiord and Thule (Outridge et al., 2003) had ambiguous results. There were no significant differences in mean ratios (Outridge et al., 2003), but only eight samples from Grise Fiord were available. However, approximately 80% of the animals at Thule and 20% at Grise Fiord were dissimilar, and the authors concluded that they represent different stocks. This conclusion is consistent with the 20/80 rule (May et al., 1975), but the small sample size at Grise Fiord dictates caution.

Harvest records (Priest and Usher, 2004) indicate hunters from Grise Fiord take walrus near town in August, farther east in September and October, and still farther east, near Coburg Island (Fig. 4), in February to May. Hunters from Pond Inlet hunt walrus in spring at the floe edges in Milne and Pond inlets and in summer farther into these inlets. Hunters from Arctic Bay report most of their harvest from the floe edge of Admiralty Inlet, also in spring. Therefore, walrus that winter at the mouth of Lancaster Sound could be taken in summer either to the north near Grise Fiord or to the south near Arctic Bay, Pond Inlet, and Resolute Bay. The winter hunt from Grise Fiord presumably draws from the group wintering at the mouth of Jones Sound.

None of the walrus, predominantly females, tagged in Norfolk Inlet or Goose Fiord moved farther east than a line between South Cape (~84° 25′ W) on Ellesmere Island and Cape Skogn (~84°10′ W) on Devon Island. Locations in October and November, after freeze-up, were confined largely to the mouth of Muskox Fiord and off the south coast of Colin Archer Peninsula (Fig. 3). Of the 26 hunts (30 walrus landed) recorded from 1996 to 2001, only one took place west of South Cape (Priest and Usher, 2004); most were farther east, at Grise Fiord, Lee Point, and Glacier Strait (Fig. 4). Aerial reconnaissance and local knowledge also indicate that few walrus are seen between Grise Fiord and South Cape. The distribution of sightings and the tag data suggest that the walrus in western Jones Sound are a different stock than those in the eastern reaches.

Walrus tagged in western Jones Sound did not move through Hell Gate or Cardigan Strait. Exchange with Lancaster Sound walrus from Penny Strait through the Belcher Channel (Fig. 3) appears unlikely. Walrus seen north of Grinnell Peninsula in April 1977 moved west as summer progressed, rather than east towards Hell Gate and Cardigan Strait (Davis et al., 1978). This coastline is low and gradual, and the area is often ice-choked. Overall, the area appears unsuitable for walrus, although these features do not preclude passage by walrus. However, it appears to be an area of separation between a population that winters around Hell Gate and Cardigan Strait and another that winters around Dundas Island.

Walrus that summer in the Lancaster Sound area could be linked to Jones Sound and Foxe Basin stocks (next section). The one female walrus tagged in Penny Strait in August 2003 moved south to the area of Kearney Cove on southwest Devon in early September (Fig. 3). One male of a group of at least 40 males that occupied Kearney Cove at the same time was tagged and remained in that cove, also until early September. All other tags (n = 7) deployed in the areas of southwest Devon and Bathurst Island remained in that general area; none of those walrus travelled north out of Penny Strait or south into Prince Regent Inlet, although all seven tags stopped transmitting before September (Fig. 3), hence before freeze-up. There is no evidence of exchange between Penny Strait and Jones Sound around the west end of Grinnell Peninsula.

Walrus were taken by hunters from Resolute Bay in June to August (Priest and Usher, 2004). These hunters indicate walrus arrive in their hunting area (Fig. 4) from the east in spring. None of the walrus tagged (n = 5) east of Resolute Bay in August moved into the Resolute Bay hunting area that year. There is autumn movement from Penny Strait to Lancaster Sound. One adult male walrus tagged at Bathurst Island in 1993 was killed in June 1994 near Pond Inlet (Stewart, 2002). Another walrus observed at Bathurst Island in 1993 had previously been branded near Dundas Island (B. Sjare, pers. comm. 1993). There is direct exchange from Penny Strait to the mouth of Lancaster Sound, and it is possible that a walrus that summers near Cornwallis Island could winter variously at Dundas Polynya or the mouth of Lancaster Sound.

While there appears to be little or no exchange around the west end of Devon Island, potential mixing of walrus from Lancaster Sound and eastern Jones Sound is less clear. There may be differences in lead isotope ratios determined by ICP-MS between animals at Resolute Bay and those from Grise Fiord and Thule, but small sample sizes precluded statistical comparison (Outridge et al., 2003). More precise thermal ionization mass spectrometry (TIMS) analysis indicated differences between Grise Fiord and Resolute Bay samples, but these could not be compared statistically (Outridge et al., 2003). De March et al. (2002) found no differences among Grise Fiord (harvest, n = 4), Resolute Bay (harvest, n = 9), and Bathurst Island (biopsy, n = 9) samples using microsatellite frequencies and haplotypes. Subsequent microsatellite analysis of larger samples (Grise Fiord, n = 16; Resolute Bay, n = 13, R.E.A. Stewart and L. Postma, unpubl. data) agreed with de March et al. (2002). The differences in isotope ratios and lack of differences in genetic data suggest a single population divided into two stocks, but all the data are preliminary.

These combined data support subdivision of the putative Baffin Bay stock (Born et al., 1995), with the following caveats: genetic data were collected by different methods (biopsy and harvest samples); movement to the proposed wintering area near Colin Archer Peninsula is based on six tags; and females may be more philopatric than males (Andersen and Born, 2000). Adapting NAMMCO (2006) terminology, these newly defined subdivisions are: (1) the Baffin Bay stock, separated from West Greenland by genetic evidence (2) the West Jones Sound (WJS) stock, separated from the Baffin Bay by seasonal distribution and tag movements, and (3) the Penny Strait-Lancaster Sound (PS-LS) stock, separated from West Jones Sound by distribution and tag movements and from Baffin Bay by limited Pb isotope data. Such a stock structure indicates that walrus in the West Jones Sound stock have a much smaller probability of being harvested than was thought. Consequently, harvests in Lancaster Sound, at Grise Fiord, and at Avanersuaq are taken from stocks that are smaller than believed previously. Pb isotope data provide evidence of a cline within the Baffin Bay stock, but further subdivision is not yet possible.

Foxe Basin

Walrus in Foxe Basin generally winter at the floe edge around Rowley Island (Fig. 5) (COSEWIC, 2006). They move to summer areas around islands in northern Foxe Basin and are found routinely on pack ice.

Most walrus hunters in Foxe Basin are from Igloolik and Hall Beach, although hunters from Pond Inlet, Iqaluit, and Arctic Bay/Nanisivik also report landing walrus in Foxe Basin (Fig. 5). Walrus landed at Foxe Basin communities were distinguished from those landed at the HBDS communities of Akulivik, Coral Harbour, Repulse Bay, Loks Land, and Sisimiut (Fig. 6) by differences in lead isotope ratios (Outridge and Stewart, 1999; Outridge et al., 2003). Walrus taken at Akulivik also show differences in organochlorines (Muir et al., 1995). Walrus in Foxe Basin also appear to be larger than those from Hudson Bay (Garlich-Miller and Stewart, 1998). Foxe Basin walrus differ genetically from Baffin Bay walrus in haplotypes and microsatellites (Grise Fiord, Resolute Bay, Bathurst Island; de March et al., 2002) and lead isotope ratios (Grise Fiord, Resolute Bay, Thule; Outridge and Stewart, 1999; Outridge et al., 2003). Movement through Fury and Hecla Strait towards Lancaster Sound is considered unlikely (DFO, 2002).

Stewart et al. (2003) interpreted differences in lead isotope ratios of growth layer groups in the teeth of walrus

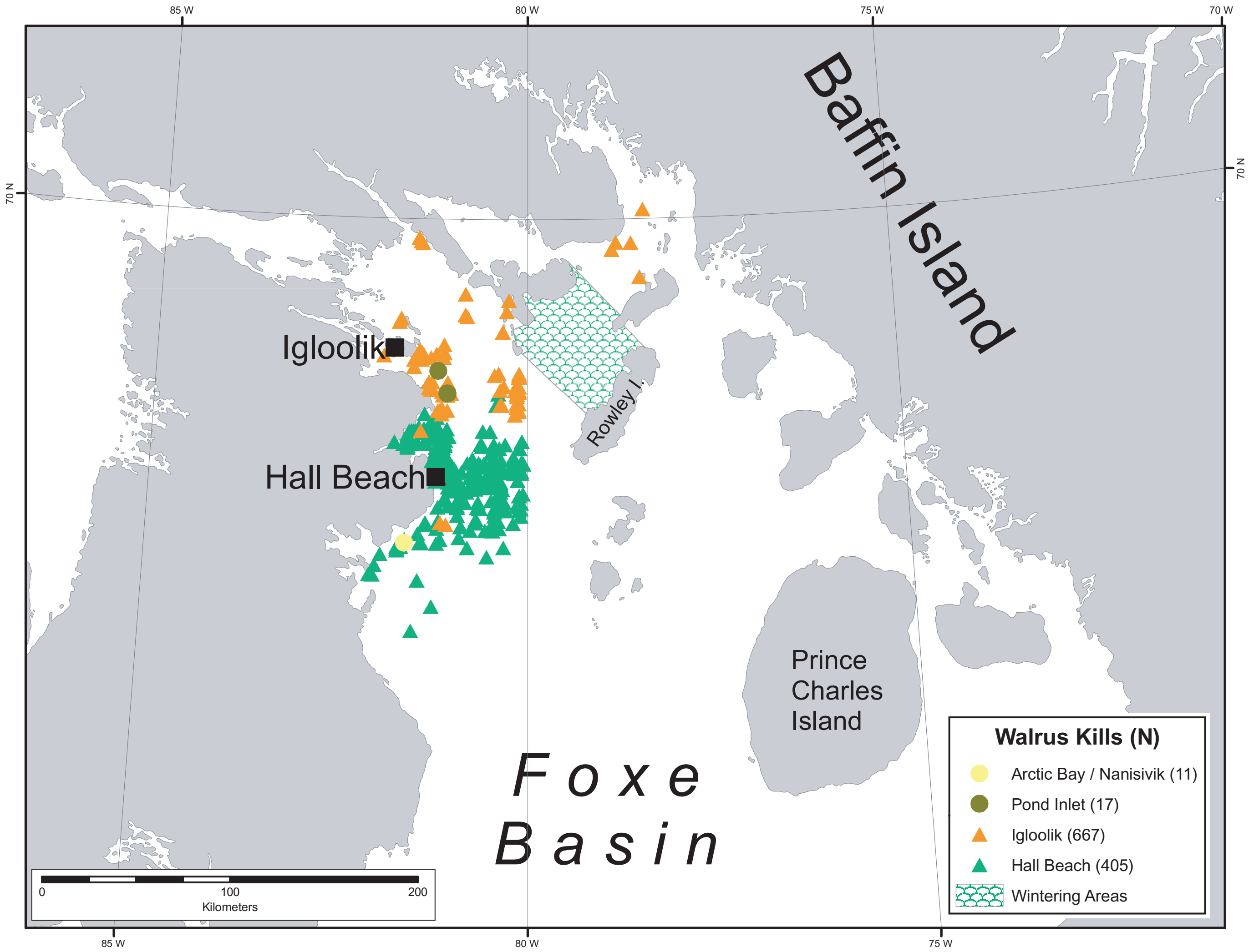

FIG. 5. Foxe Basin walrus harvesting locations for Igloolik and Hall Beach (Priest and Usher, 2004) and wintering areas (Born et al., 1995). Each kill symbol may represent more than one animal killed; N is the number of walruses reported by each community in the Priest and Usher (2004) database.

landed at Hall Beach to indicate changes in the way these male walrus sampled their isotopic environments. Although some of these layers resembled walrus teeth landed at three HBDS communities and one SEHB community, similarity does not prove congruence (Waldman, 2005). For example, walrus from east Greenland and Inukjuak on Hudson Bay have similar lead isotope ratios that reflect common geology, not common distribution (Outridge et al., 2003). Still it is plausible that some males from Foxe Basin moved into other walrus populations nearby and may have reproduced in those populations. Isotope evidence indicated that two of 11 adult males examined had left the Hall Beach area at maturation and returned some years later. Although this potential male-mediated exchange does not refute the conclusion by Born et al. (1995:9) that the Foxe Basin population is "largely isolated from other groups," it does suggest more complex interactions than expected previously.

Walrus landed by hunters at Hall Beach were not distinguishable from walrus landed at Igloolik by genetic (de March et al., 2002), heavy metal (Wagemann and Stewart, 1994), or major organochlorine data (Muir et al., 1995). But Outridge and Stewart (1999) reported differences in lead isotope ratios (^{206}Pb/^{207}Pb and ^{208}Pb/^{207}Pb) and trace elements even after removal of outliers. Peak landings at Igloolik and Hall Beach overlap in time (Priest and Usher, 2004), but are mostly separated in space (Fig. 5). Simultaneous hunting in two areas suggests two groups of walrus, but philopatry (habitual summering in one or the other area) is required for them to be considered stocks. The hunters from Igloolik take walrus mostly from the northern part of Foxe Basin, where there are areas of Palaeozoic rocks among the predominating Archean geology. The Hall Beach hunting area is underlain by older Proterozoic and Archean geology (Outridge and Stewart, 1999). The differences in isotopic signatures were thus consistent with long-term residency in different geological regimes. Inuit also identify two groups of walrus in this area on the basis of morphology and colour (DFO, 2000).

Therefore, there is evidence of stock separation within Foxe Basin. It is probable that, while landed walrus are from different stocks (the North Foxe Basin and Central

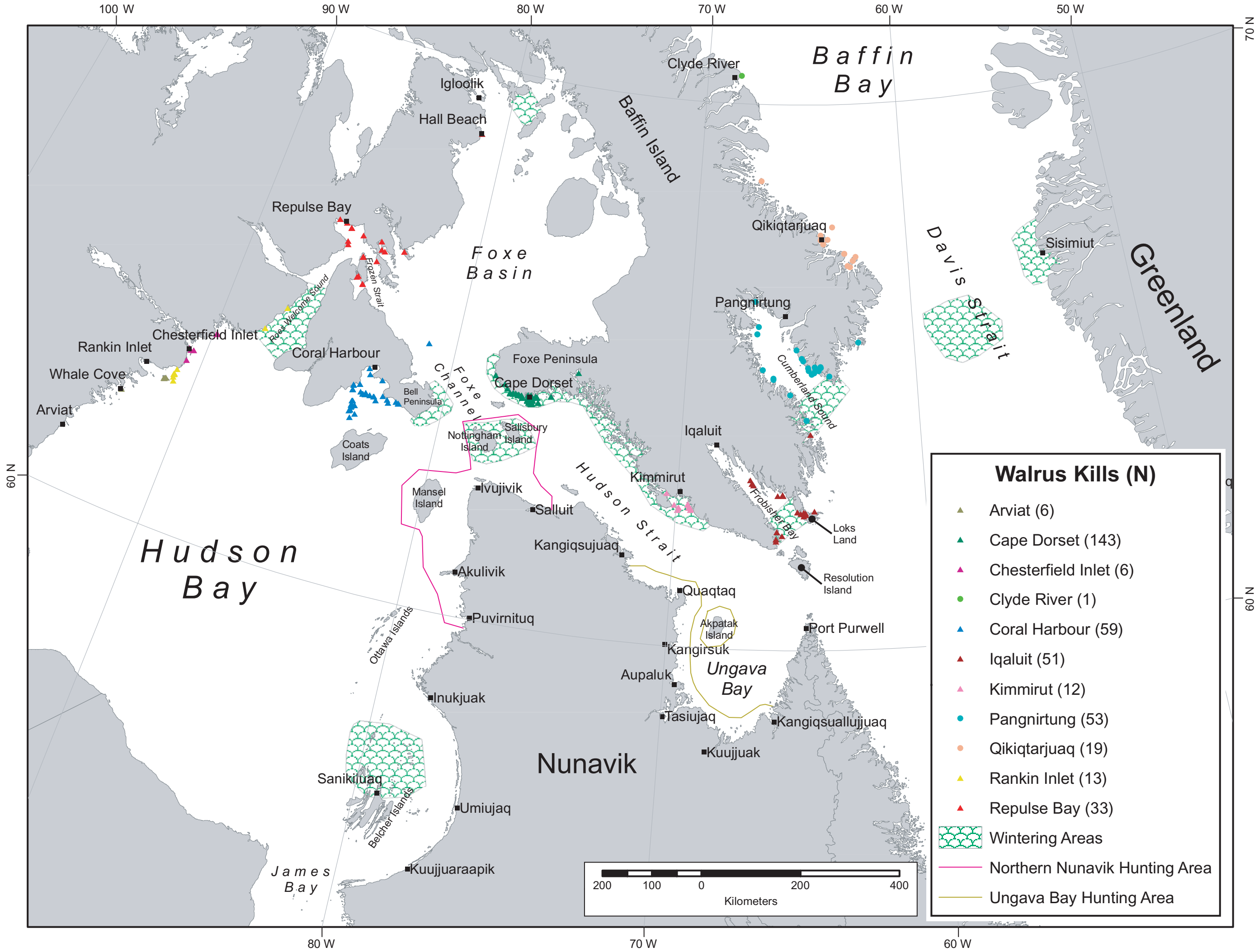

FIG. 6. Hudson Bay–Davis Strait walrus harvesting locations for Arviat, Cape Dorset, Chesterfield Inlet, Clyde River, Coral Harbour, Iqaluit, Kimmirut, Pangnirtung, Qikiqtarjuaq, Rankin Inlet, and Repulse Bay (Priest and Usher, 2004), Nunavik harvesting areas (interpreted from COSEWIC, 2006), and wintering areas (Born et al., 1995). Each kill symbol may represent more than one animal killed; N is the number of walruses reported by each community in the Priest and Usher (2004) database.

Foxe Basin stocks), both communities rely on a single interbreeding population that is characterized by primarily local movement.

Hudson Bay–Davis Strait

Walrus are found at several widely dispersed areas in winter (Fig. 6), including Roes Welcome Sound, Foxe Channel, the north shore of Hudson Strait, pack ice in Davis Strait, and probably (based on harvest dates) the mouths of Frobisher Bay and Cumberland Sound (Orr and Rebizant, 1987; Born et al., 1995; Priest and Usher, 2004; COSEWIC, 2006). There are no data to determine whether significant numbers of walrus change wintering areas between or within years.

Cape Dorset reports landing at least a few walrus almost every month, with peaks in March and November, which is the same time when Kimmirut lands about 75% of its catch (Priest and Usher, 2004). These communities may be sampling at the level of the population (wintering aggregation) that may include multiple stocks.

Walrus in HBDS are hunted at many other communities in Nunavut and Nunavik as well, usually in the open-water season. Harvests in Nunavut tend to be close to the communities, with little overlap of hunting areas. In Nunavik, however, the hunting areas of many communities overlap (Fig. 6). Along western Hudson Bay, three communities land a few walrus every year from coastal areas between Whale Cove and Roes Welcome Sound, usually in May to September. Hunters from Repulse Bay hunt mostly in Frozen Strait, with peak harvests occurring slightly later than in communities immediately to the south (Priest and Usher, 2004). It is possible that walrus at the west end of the HBDS stock are hunted by all these communities.

The distribution of HBDS walrus stretches 1500 km from east to west, along 2500 km of coastline, so clinal variation might be expected. Outridge et al. (2003) examined the lead isotopes of walrus landed at Repulse Bay, Coral Harbour, Akulivik, Loks Land, and Sisimiut, as well as samples from FB and SEHB. They found statistical differences in ^{206}Pb/^{207}Pb ratios between Coral Harbour and both Akulivik and Sisimiut, which were not different from each other, as well as in ^{208}Pb/^{207}Pb ratios between Sisimiut and both Akulivik and Coral Harbour, which did not differ from each other. There were too few samples from intervening sites to allow statistical analysis, but there appeared to be some overlap between adjacent sites. Outridge et al. (2003) concluded that most communities were harvesting walrus that inhabited different geological areas, while noting overlap in adjacent values.

The temporal and spatial distribution of walrus harvests is consistent with Outridge et al.'s (2003) concept of local stocks that overlap each other along a cline. Peak harvests tend to occur from May to September and must reflect widespread availability. Four communities on northeast Hudson Bay report peak walrus harvests that overlap in both time (August–September, Priest and Usher, 2004) and space (Fig. 6), and share a stock. Conversely, seven communities on Ungava Bay (Fig. 6) hunt at Akpatok Island, mostly in July-August, a period concurrent with peak landings at Repulse Bay and Coral Harbour. Concurrent harvests in two locations over 800 km apart suggest different stocks.

Both Pangnirtung and Iqaluit hunters take 95% of their walrus between May and November over large areas that may overlap (Fig. 6). Some walruses are taken the rest of the year, but that does not reject the hypothesis that some walrus from southeast Baffin Island migrate to West Greenland for the winter breeding season. Those remaining in Canada may be immature animals, mature non-breeders, breeding animals that breed in both countries in different years, or animals that remain in Canada all year and that are joined seasonally by walrus from Greenland.

Walrus in the HBDS area have not been subjected to intense genetic scrutiny. Preliminary studies (NAMMCO, 2006) included the contradictory results that walrus from eastern Hudson Bay and Hudson Strait were both genetically different than walrus in West Greenland and also served as a source for West Greenland walrus. In these analyses, it was presumed that there was not an unsampled population between Hudson Strait and West Greenland (L.W. Andersen, pers. comm. 2005), but no samples from southeast Baffin Island walrus were available. A clinal model leads to two hypotheses: that southeast Baffin Island walrus will be intermediate between West Greenland and Hudson Strait walrus, and that southeast Baffin Island walrus will be the major source of immigrants to West Greenland.

Born et al. (1995) speculated there may be subunits within the HBDS range, but they noted the absence of data by which to partition this group. More recent data indicate that two groups of northern Quebec communities, one centered on Ivujivik and one in Ungava Bay (Fig. 6), share stocks with nearby communities in the group. Reviewed isotope analyses suggest that Nunavut communities harvest local animals, while the genetic studies suggest differences between animals harvested in different communities, but both types of studies were limited in geographic coverage. The range of HBDS walrus includes seven known wintering areas, and it is possible that many communities are harvesting from several stocks derived from one or a few populations (wintering aggregations). While evidence of subunits within the HBDS range has increased, it is not yet sufficient to define that substructure.

Southern and Eastern Hudson Bay

Walrus winter at the floe edges around the Sleeper and Belcher archipelagos (Fig. 7) (COSEWIC, 2006). The nearest neighbouring winter concentrations are in the HBDS population range, around Ivujivik-Nottingham-Salisbury islands and Bell Peninsula-Foxe Peninsula (Priest and Usher, 2004; COSEWIC, 2006), and they are likely separated from the SEHB population by distance and ice (Fig. 6).

Judging by information from the main hunting areas, dispersal from winter areas in the open-water season seems limited. Hunters from Sanikiluaq and Inukjuak hunt among the Sleeper and Belcher islands. Between June 1996 and May 2001, Sanikiluaq reported landing 25 walrus. Only 11 of those 25 reports included location data, but those 11 walrus were all taken at the north end of the Belcher Islands and at the Sleeper Islands (Priest and Usher, 2004). The harvest at Sanikiluaq occurs mostly in September and October (92% of 25 animals over five years, Priest and Usher, 2004). Hunters from Inukjuak hunt in the same area (Fig. 7) at about the same time. The locations of harvests reported by Kuujjuarapik and Umiujaq are unknown, but numbers may be small (Brooke, 1994, 1995).

Communities north of Inukjuak on the east side of Hudson Bay (Puvirnituq, Akulivik, Ivujivik, Salluit; Fig. 6) are thought to hunt the HBDS population. Hunters from Akulivik, the nearest community outside the SEHB area, hunt in September and October, so their hunt overlaps the Belcher-Sleeper hunt in time, but not in space as they hunt farther north, around Nottingham and Salisbury islands (Fig. 6). Walrus occupy the shoals near Cape Henrietta Maria in July-October at least, with several peak counts in September and October (COSEWIC, 2006). It is possible that some walrus that summer one year at Cape Henrietta Maria could summer in other years at the Belcher-Sleeper islands or even farther north, where they could be available to Akulivik hunters.

However, harvested walrus at Akulivik differed from those landed at Inukjuak. Muir et al. (1995) found significant differences in organochlorine concentrations and profiles in walrus landed at these two communities, which they attributed to differences in diet. Lead isotope ratios (^{208}Pb/Pb^{207}) and trace element profiles both showed significant differences between Inukjuak and Akulivik samples (Outridge and Stewart, 1999; Outridge et al., 2003). Concentrations of heavy metals appeared to differ between

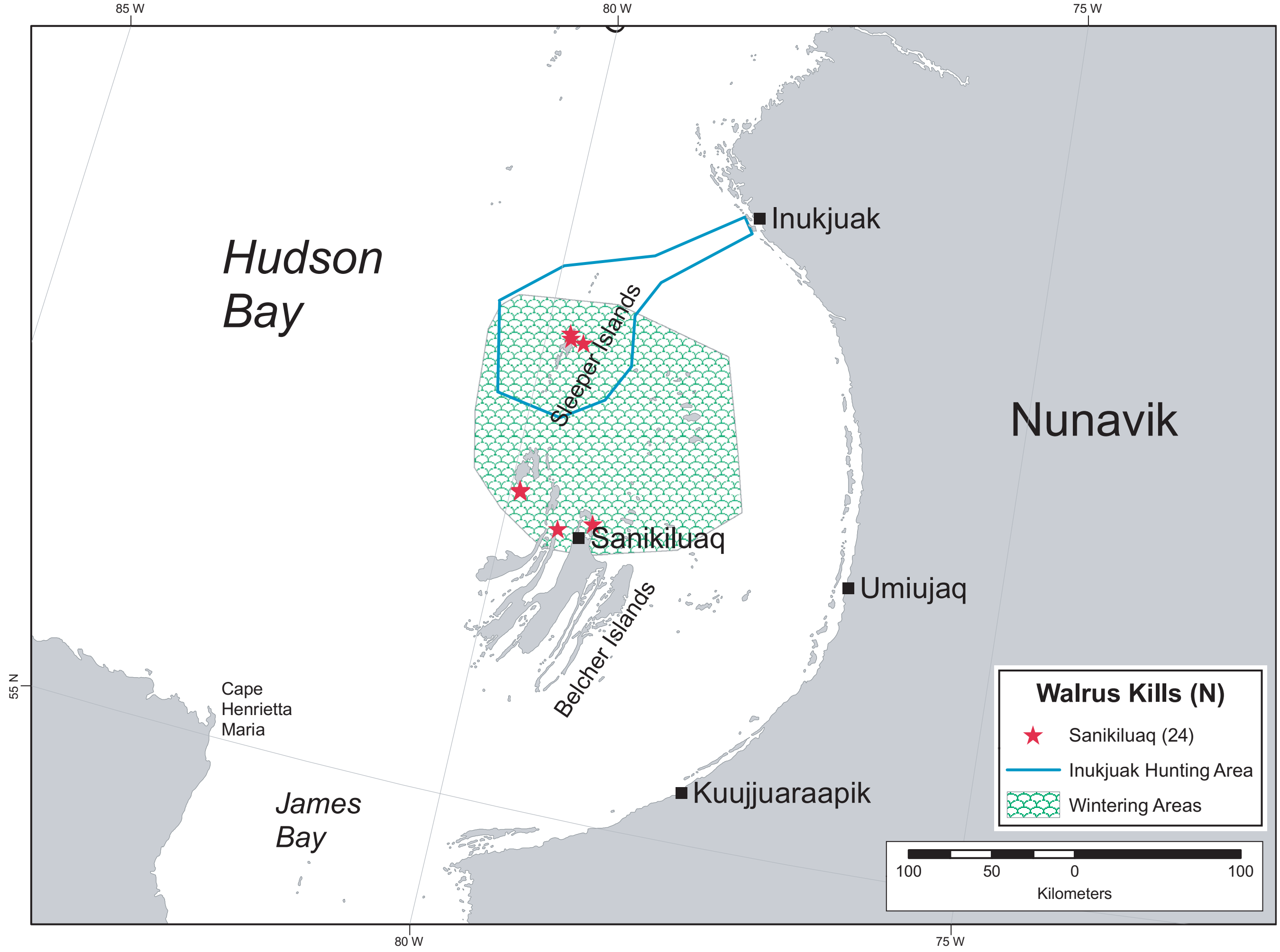

FIG. 7. Southern and Eastern Hudson Bay walrus harvesting locations for Sanikiluaq (Priest and Usher, 2004), Nunavik harvesting areas (interpreted from COSEWIC, 2006), and wintering areas (Born et al., 1995). Each kill symbol may represent more than one animal killed; N is the number of walruses reported by each community in the Priest and Usher (2004) database.

Inukjuak (Hg: 8.00 µg/g dry wt; Cd: 19.0 µg/g dry wt) and Akulivik (Hg: 4.20 µg/g dry wt; Cd: 30.0 µg/g dry wt), but sample sizes were small (9 and 4 respectively), and these differences were not statistically significant (Wagemann and Stewart, 1994).

Born et al. (1995) defined the SEHB population mostly on the basis of distribution, noting that evidence for separating it from other walrus groups in northeast Hudson Bay was not strong. Since then, new information shows significant stock differences between walrus landed at Inukjuak and at Akulivik. There are no new genetic data by which to assess the degree of interbreeding among walrus from southern and northern Hudson Bay and no new evidence to suggest subdividing this stock.

West Atlantic

Walrus were once common in the Gulf of St. Lawrence and around Nova Scotia but had been extirpated by the mid-1800s (Reeves, 1978). Five walrus were reported in the Gulf between 1992 and 1996, in four different sightings. Walrus are seen occasionally on the coast of Newfoundland (Kingsley, 1998) and Nova Scotia (Richer, 2003). Whether these observations mark recolonization of former range or random wanderings of a few individuals is unclear. Should they not be itinerant animals, the population size is small.

CONCLUSIONS

None of the new information presented here or published since the review by Born et al. (1995) refutes previous separation of stocks. It does, however, suggest further subdivision of some stocks of walrus in Canada (Table 2). Specifically, the Baffin Bay stock now appears to be three stocks: the Baffin Bay stock, the West Jones Sound stock, and the Penny Strait-Lancaster Sound stock. The Foxe Basin stock appears to be two stocks: North Foxe Basin and Central Foxe Basin. There is evidence of clinal variation in the Hudson Bay-Davis Strait stock. No changes are suggested for the SEHB stock.

TABLE 2. Summary of walrus stock revisions.

Previous Stock Designation (Born et al., 1995)	Proposed Stock Designation	Rationale	Comments
North Water (Baffin Bay-east Canadian Arctic)	West Jones Sound (WJS)	Distinguished from BB by distribution data (tags, harvest sites, survey observations, hunter observations)	Data are required to determine if this stock is a breeding population isolated from walrus wintering in east Jones Sound.
	Penny Strait–Lancaster Sound (PS–LS)	Distinguished from WJS by distribution data (tags, survey observations); Pb isotope analysis (TIMS)	Data are required to determine if this stock is also a breeding population isolated from walrus wintering in east Jones Sound and to evaluate differences between wintering areas (Dundas Polynya and east Lancaster Sound) within its range.
	Baffin Bay (BB)	Residual; Potential for further subdivisions	Pb isotope data show clinal variation between east Jones Sound and NW Greenland but sample sizes were small and new boundaries cannot be established.
Foxe Basin	Northern Foxe Basin (NFB) Southern Foxe Basin (SFB)	N and S stocks distinguished by Pb isotope ratios and distribution of harvest sites	Data are required to evaluate if these stocks form a single population.
North Hudson Bay– Hudson Strait– SE Baffin Island– N Labrador	Hudson Bay–Davis Strait (HBDS)	No change	Pb isotopes suggest clinal variation within this stock but new boundaries cannot yet be established. Data are required to assess movement of walrus between Canada and Greenland and in Canada.
Southern and Eastern Hudson Bay	Southern and Eastern Hudson Bay (SEHB)	No change	Data are required to evaluate relationships with other stocks and within the range of the SEHB stock

The new stock definitions are proposed here for three reasons. The first relates to management. It is more conservative to conclude erroneously that there are more stocks than to assume that there are fewer stocks (Taylor, 1997; Taylor and Dizon, 1999). Thus, while data that suggest subdividing stocks may be limited, it is more cautious to accept those data than to ignore them.

The second is that the recent information offers insights into the stock context of walrus populations. Walrus once had a wide and largely continuous range in Canada (Harington, 1966; Reeves, 1978) and likely were characterized by clinal variation. I suggest that females and younger animals tended to remain in more narrowly circumscribed ranges while mature males roamed among the herds and wintered in different areas over several years. Genetically different subpopulations of deer (*Odocoileus* spp.) are prevented from becoming more different by male dispersal (Harris et al., 2002). The roving male model (Suzuki et al., 1998; Stewart et al., 2003) takes this concept one step farther, in that males not only disperse from their natal area but adult males move among several breeding groups, including their natal area, over several years. Born et al. (2005) document a male walrus that returned to the same over-wintering breeding area in east Greenland in three years (1990, 2000, and 2001). Compared to the situation in Canada, these results may reflect greater fidelity to an over-wintering area or lower availability of over-wintering opportunities in east Greenland. It is possible this male over-wintered in other areas in other years.

As walrus distribution became more fragmented, female-mediated philopatry focused the population in areas of preferred habitat, including areas with less human disturbance. The roving males maintained some genetic continuity among groups, but widely separated groups became more distinct in several attributes. The roving male model was first applied to walrus by Stewart et al. (2003) to interpret different isotopic signatures at different ages in a male's life. This model is also consistent with female philopatry and moderate, male-mediated gene flow among populations (Andersen et al., 1998; Andersen and Born, 2000), and with distributional patterns seen in the High Arctic, Foxe Basin, and northern Hudson Bay to Davis Strait.

The third reason is that the newly proposed stock delineations and interpretation of the population structure of walrus in Canada generate several testable hypotheses. In Jones Sound, more data from genetics, natural markers, and tagging that cover a wider geographic distribution are required to clarify the extent of exchange of breeding animals between west and east wintering areas, with eastern Lancaster Sound, and with NW Greenland. Isotope signatures in the growth layers of teeth may indicate that an individual has wintered in different areas over the course of its life. Similarly, sampling throughout the range of the HBDS stock is required to test between the hypotheses of clinal variation (e.g., Owen and Baker, 2001) or more dramatic subdivisions within the continuous distribution of walrus (e.g., Hoffman et al., 2006). More generally, additional genetic information would test predictions that females and juveniles at summer haulouts are closely related, but males in predominantly male groups are dissimilar, and that the harvests at Igloolik and Hall Beach differ in mtDNA, but not in genomic DNA. Genetics, natural markers, and tagging could test the hypotheses that adult males occupy several wintering areas over their lives, but females occupy only one or two, and that summer distributions reflect the philopatric movements of females from wintering areas.

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ERRATUM

Stewart, R.E.A. 2008. Redefining walrus stocks in Canada. Arctic 61(3):292–308.

In Figure 6 (p. 302), please ignore the wintering area indicated in the middle of Davis Strait (ca. 65° N), which was included in error.