Diving behavior of the Atlantic walrus in high Arctic Greenland and Canada

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A R T I C L E   I N F O

A B S T R A C T

Investigations of diving behavior of the Atlantic walrus (Odobenus rosmarus rosmarus) in the high Arctic Greenland and Canada are important for understanding behavioral adaptations and area utilization of this Arctic benthic feeder. Furthermore, such information along with estimations of annual consumption and carrying capacity of walruses are needed in management decisions of this utilized species. Satellite-linked transmitters deployed on 27 walruses from 2010 to 2013 provided data for investigations of diving behavior in three pre-defined main areas: NW Greenland, Smith Sound and NE Canada. Sub-areas within each main area were also compared. Depth of dives, dive rates, time at depth of dives, haul-out periods and vertical speeds were estimated. Majority of dives targeted depths from 10 to 100 m, which corresponds to the distribution of walrus preferred food items. Four dives to depths > 500 m occurred and are the deepest ever documented for a walrus. Dive rates and time at depth of dives were significantly different between sub-areas (p < 0.0001), whereas haul-out periods were not (p = 0.072). Mean vertical speeds to destination depths ranged from 1.0 m s^{-1} (95% CI: 0.8–1.2) to 1.8 m s^{-1} (95% CI: 1.0–2.6). Based on dive rates, time at depth, haul-out and percentage of feeding dives Alexandra Fjord and Princess Mary Bay in NE Canada and Carey Island in NW Greenland were identified as the most important areas for walrus feeding during summer. Walrus predation on the standing bivalve biomass in NW Greenland (within 5–100 m of depth) was estimated to 3.2% annually based on assessments of mean biomass of walrus preferred prey items. From a simple relationship between available shallow water habitat, current population size (n = 2544) and walrus pre-exploitation population sizes it is furthermore proposed that the carrying capacity in the Smith Sound region does not exceed 5000 walruses.

1. Introduction

The warming of the Arctic and changes in Arctic marine biota in response to climate change are well documented (Wassmann et al., 2011). Atlantic walruses (Odobenus rosmarus rosmarus) are benthic feeders. They occur north of the Arctic Circle for most of the year and depend on the Arctic ecosystem for all aspects of life (Laidre et al., 2008). Understanding diving behavior and area utilization of this Arctic marine mammal is essential for assessing how vital behaviors change when animals are exposed to environmental stressors and to ensure correct management decisions in the light of a changing environment.

Smith Sound, located between Northwest (NW) Greenland and the Canadian high Arctic, attracts large numbers of marine top-predators most of which are only in the area during the open water season where they primarily feed in the pelagic part of the food web (Heide-Jørgensen et al., 2013). The Atlantic walrus is one of few marine mammals that remain when a recurring polynya – the North Water –

forms during winter in Smith Sound. During winter and spring, variable and usually small amounts of, open water can be found in the coastal areas adjacent to the North Water. In contrast to the summer visitors, the walruses depend on benthic prey where bivalve molluscs constitute most of their diet (Vibe, 1950). The walruses feed mainly in shallow waters (< 100 m) where they can reach the seabed and prey on molluscs (Fay and Burns, 1988; Jay et al., 2001). However, shallow water habitats, where the majority of bivalves are found, constitute only a minor part of the Arctic in this region. A recent study (Lowther et al., 2015) documented that walruses near Svalbard are capable of diving to great depths (461.9 m) and in theory can stay submerged for extended periods of time (max. 57 min) (Schreer and Kovacs, 1997). In light of the environmental changes occurring rapidly in Arctic regions and new information on walrus diving capacity it seems prudent to assess the walruses utilization of this high Arctic region through documentation of diving habits.

Vibe (1950) described walrus foraging banks in NW Greenland

ranging from the south-eastern part of Smith Sound to Kane Basin that constitute the northern boundary of walrus distribution. Except for the work of Vibe, there is little information on benthic communities and walrus consumption rates in this region. In the Bering and Chukchi seas (i.e. Beringia), Pacific walruses (*O. r. divergens*) annually consume an estimated 3 million metric tons of benthic biomass (Ray et al., 2006). Ray et al. (2006) found that the annual to long-term bioturbation from walrus feeding activity resulted in significant, large-scale changes in sediment and biological community structure. Furthermore, nutrients locked in the sediment were redistributed to the water column by about two orders of magnitude over large areas. Walruses have also been observed to eat seals and birds in addition to benthic prey (Lowry and Fay, 1984; Fay and Sease, 1990; Fox et al., 2010; Mallory et al., 2004; Lovvorn et al., 2010) but only a few observations of seal remains in the stomachs of walruses from the Smith Sound have been documented (Vibe, 1950).

The walruses in the Smith Sound region (defined as Smith Sound, coast and fjord systems in NW Greenland and coast, bays and inlets in eastern Canadian High Arctic) belong to the Baffin Bay walrus stock (Stewart, 2008). They stay from October to June in NW Greenland. In early to mid June, they cross Smith Sound and stay in shallow bays and inlets of the eastern part of Ellesmere Island, Jones Sound and south of Devon Island during summer (Heide-Jørgensen et al., 2017). Heide-Jørgensen et al. (2017) found that most frequently used summering areas were the Alexandra Fjord/Buchanan Bay/Flagler Bay area, Talbot Inlet and Craig Harbour along the coast of Ellesmere Island.

This study investigated the diving behavior of walruses of the Baffin Bay stock by using satellite transmitters specialized to provide positions and data on diving. Study objectives were to answer the following questions: 1) what are the characteristics of the diving behavior of walruses in the Smith Sound region, and 2) can important feeding areas and consumption rates of walrus in the Smith Sound region be identified using available data.

2. Materials and methods

2.1. Definition of study areas

Smith Sound is located in northern Baffin Bay between NW Greenland and the eastern part of the Canadian high Arctic (76˚N to 79˚N and 70˚W to 80˚W). Walruses cross Smith Sound from NW Greenland in June to summer in the eastern part of the Canadian high Arctic (Heide-Jørgensen et al., 2017). They return to Greenland in October. Based on this seasonal distribution three main areas of walrus occupancy were defined (Fig. 1): NW Greenland, including the coast, fjords and inlets, up to 30 km from the coastline (approximately 76˚N to 79˚N and 69˚W to 73˚W); the eastern part of the Canadian high Arctic, called NE Canada throughout, including the east coast, fjords and inlets of Ellesmere Island up to 30 km off the coast, Kane Basin, Pim Island, Jones Sound, Coburg Island and coastal areas south and east of Devon Island (approximately 74˚N to 80˚N and 75˚W to 92˚W); and Smith Sound defined as the deep offshore area between NW Greenland and NE Canada, not overlapping the former two main areas. The three main areas were further divided into several sub-areas and termed the Smith Sound region. The sub-area of Alexandra Fjord includes fjords on Ellesmere Island between 78.76˚N and 79.22˚N.

2.2. Field operations

During May–June 2010–2013 and 2015, 51 walruses were instrumented with satellite-linked transmitters in NW Greenland. Walruses were located and tagged at four different locations (Etah, Murchison Sound, south of Kiatak, and in Wolstenholme Fjord) (Fig. 1). Description of the tags and deployments methods is provided in Heide-Jørgensen et al. (2017). Of the 51 tags 27 (deployed from 2010 to 2013) were of the type Mk10 that in addition to positions also provided

summarized data on the diving behavior of the walruses. Of the 27 Mk10 tags, 26 tags transmitted data and 21 provided diving data in several consecutive days. The 21 tags were deployed on 13 females, 3 males and 5 walruses with no information on sex. The tags were programmed to transmit at different intervals during the five years with deployments. In 2010–2011 the tags were programmed to transmit every day between 8:00 and 20:00 local time in June and every fourth day the rest of the year. This setting failed in July 2010 and no positions were obtained for that month. The same setting was used in 2012 except that the tags were allowed to transmit every day in August. In 2013 and 2015 all tags were programmed to transmit every fourth day independent of month. The sex of tagged walruses was determined from sexually dimorphic features (Fay, 1982) or the presence of a calf close to an adult female. If sex could not be determined using these methods, the sex of the animal was classified as unknown.

2.3. Area and dive data

Positions of the walruses were obtained from the Argos satellite data processing system with Kalman filtering algorithm, and the accuracy of positions was classified by Argos location codes (LC) 3–0, A and B (CLS America, 2007). More than 70% of the positions obtained ($n = 37,000$) from the walruses were of low or uncertain positional accuracy (quality 0, A or B). Filtering of positions and tracks of the walruses are presented in Heide-Jørgensen et al. (2017).

The Mk10 tags provided data on the number and depth of dives (*DOD*) and the time-at-depth (*TAD*, in %) in predetermined bins. The setup of the bins for *TAD* was 0, 0– < 2, 2– < 20, 20– < 50, 50– < 100, 100– < 150, 150– < 200, 200– < 300, 300– < 400, 400– < 500, 500– < 600 m and the same for *DOD* except that the first bin was 0–10 m, second bin 10–20 m and the rest as *TAD*. Data on *DOD* and *TAD* were collected in four 6-h periods across each day and summarized into histograms. Only 6-h periods with information on both *DOD* and *TAD* were used in the analysis. Intervals between surfacing's were not considered dives unless a depth of > 2 m was recorded. Time spent within a depth category with a duration of < 1 s may have been missed because of the short temporal resolution. Data on the maximum depth (m) of dives (*MAX* dives) within 24 h were also collected. Dive data were transmitted in segments when the walruses surfaced, and were re-assembled using Wildlife Computers software packages (SATPAK). *MAX* dives were included on every 20th transmission and the temporal coverage is therefore much below the high priority transmissions of *DOD* and *TAD* with more missing data for the *MAX* dataset than for the other datasets.

2.4. Vertical speeds (m s^{-1})

The rates of ascent and descent of dives could occasionally be calculated if the deepest destination depth bin was isolated from the previous transit bins by one or more bin(s) without dives (Heide-Jørgensen and Dietz, 1995). The isolated destination depth bin provided the number of dives that went through the transit bins and the transit bins provided the incremented amount of time spent passing through the transit bins. Vertical speeds to destination depths bin ($\overline{S}_j$ where j = depth bin) were calculated based on a model developed in Heide-Jørgensen et al. (1998):

$$\text{Vertical speed } (\overline{S}_j) = N_j * D / (\textstyle\sum TAD/2) \tag{1}$$

where N_j is the number of dives to an isolated destination depth bin, D is the vertical distance (in m) across the transit depth bins to the isolated destination depth, and ΣTAD is the sum of time-at-depth measurements (in s) through the transit depth bins. The ΣTAD is divided by two because it includes both ascent and descent times. Average vertical speeds ($\overline{S}_j$) were calculated for all dives to each isolated depth bin for walruses tagged between 2010 and 2013. The vertical speeds were used
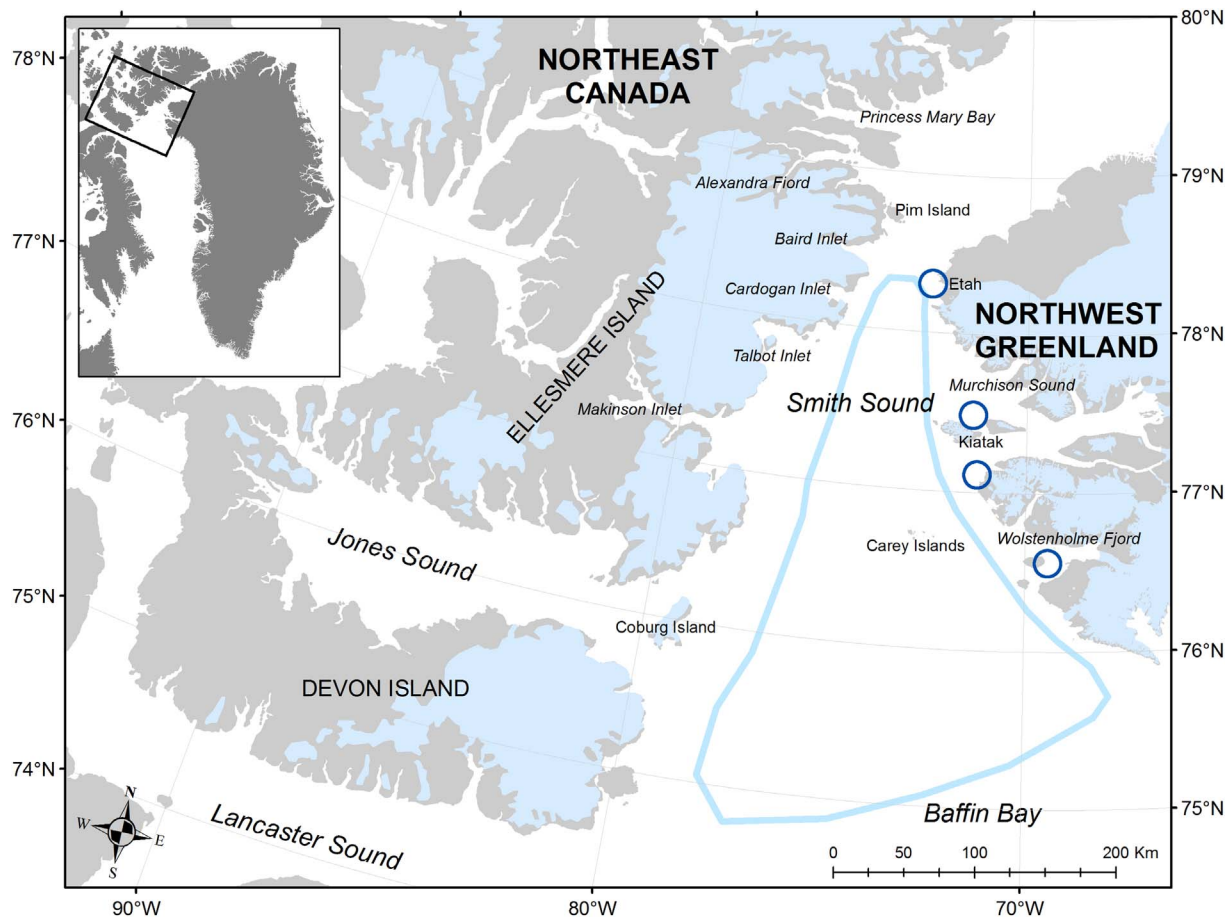
Fig. 1. Map of the study area with locality names mentioned in the text. The area marked with the blue line indicates the approximate extent of the North Water. Walruses were tagged at Etah, Murchison Sound, south of Kiatak, and in Wolstenholme Fjord.

to calculate the total time required to reach target depths and return to the surface, as well as total time spent transiting through different depth bins to reach a destination depth. Vertical transit speeds (m s^{-1}) were assumed to be constant from the surface to the destination depth.

2.5. Time spent in the last destination depth bin and travel time

Time spent in the last destination depth bin in minutes per dive ($\overline{B_j}$ where j = depth bin) for samples of 6-h periods (21,600 s) was calculated using model (2):

Time spent in last destination depth bin ($\overline{B_j}$)

$$= (((TAD/N_j)/100)*21,600 \text{ s})/60 \text{ s} \tag{2}$$

where *TAD* is % time and N_j is the number of dives to depth bin j.

Travel time to destination depth bin in minutes per dive ($\overline{T_j}$ where j = depth bin) was estimated using model (3):

Travel time ($\overline{T_j}$) $= ((2*D_i)/S_j)/60 \text{ s}$ (3)

where *D* is the vertical distance (in m) and S_j is vertical speed in m s^{-1}.

2.6. Depth of seabed at walrus habitats

Bathymetric contours based on 1° resolution data were obtained from the General Bathymetric Chart of the Oceans (GEBCO, 2015). The data is stored in a format that utilizes 30 arc-seconds of longitude and latitude to register cell values. Although the GEBCO grid is presented at one-minute intervals of latitude and longitude, this does not imply that knowledge is available on seabed depth at this resolution – the depth in most one-minute squares of the world's oceans has yet to be measured.

Hence, several cell values are extrapolated over greater distances to measured depths. Positive depth values were discarded.

2.7. Walrus consumption and predation on the standing bivalve biomass

Estimation of walrus consumption per year in NW Greenland was based on method II in Born and Acquarone (2007). In the calculation, consumption rates of 4.2–6.2% of total body weight per day (Fay, 1982) together with data on asymptotic growth in body mass of Atlantic walrus (extracted from Fig. 2 in Knutsen and Born, 1994) and walrus annual occurrence in NW Greenland (Heide-Jørgensen et al., 2017) were used. Monte Carlo simulations were used for the calculations where parameter values were randomly selected from sampling distributions that best described their uncertainty (Manly, 2002).

Walrus annual predation on the standing bivalve biomass in NW Greenland was estimated using a combination of data on walrus consumption per year in NW Greenland, information on bivalve biomass m^{-2} from Vibe (1950) and seabed depths per km in NW Greenland in the categories 0– < 20, 20– < 50, 50– < 100, 100– < 150, 150– < 200 m obtained from GEBCO.

2.8. Statistical analysis

Values of *MAX* dives were natural log-transformed to achieve homogeneity of variance and an approximate normal distribution. The log-transformed *MAX* dives and the *TAD* were analysed with linear mixed effects models depending on area, with a random effect of animal. The *TAD* analysis further depended on two bins; whether the *TAD* was spent above or below 20 m depth. The random effect of animal was
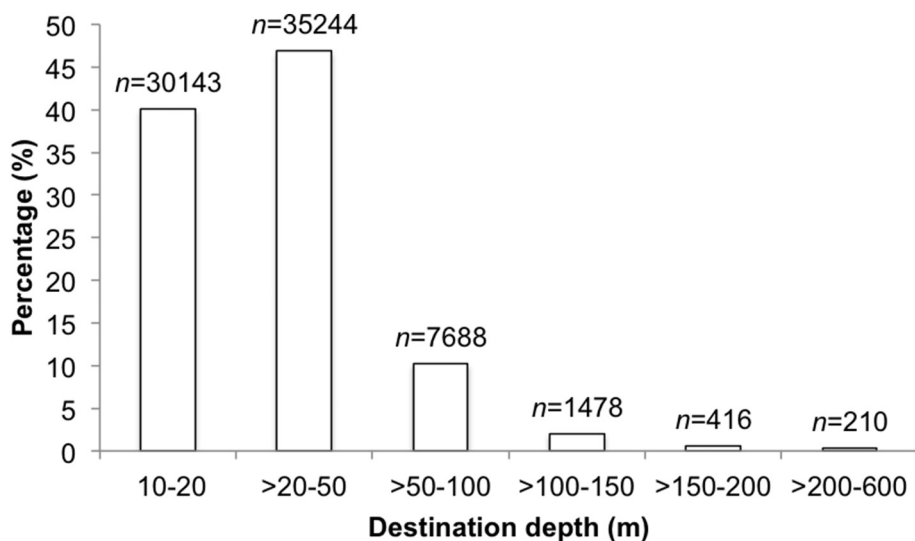
Fig. 2. Histogram of the percentage distribution of dives to destination depth ($N = 75,179$). n represents the number of dives in each category. Destination depths > 200 m were merged: bin 200–300; $n = 155$; bin 300–400; $n = 44$; bin 400–500; $n = 7$; bin 500–600; $n = 4$.

in this case allowed to interact with the bin, correcting for each animal having more propensity of diving close to the surface or at deeper depths. *DOD* was count data and analysed with a Poisson regression (for number of dives ≥ 20 m and exclusive the 6-h periods with no diving activity), where the log-mean depended linearly on area, with a random effect of animal. Percentages of haul-out periods were analysed with a logistic regression, where the log-odds depended linearly on area, with a random effect of animal. The random effect introduces a positive correlation between measurements from the same animal (and bin in the case of *TAD*), while measurements from different animals are independent. Likelihood ratio tests were applied to assess statistical significance. The procedures lmer and glmer from the package lme4 (version 1.1.13) in R (version 3.4.0; R Core Team, 2016) were used.

3. Results

3.1. Number of dives (DOD)

The majority of all dives (≥ 10 m) were to depths of 10–100 m (97%; $n = 73,075$; 23 walruses) (Fig. 2). Several dives went deeper than 200 m ($n = 210$), but they only constituted a minor part of the total number of dives (0.28%). Deepest dives were achieved by two females reaching depths > 400 m ($n = 7$) and > 500 m ($n = 4$). All four dives > 500 m and six of the seven dives > 400 m were recorded in Smith Sound whereas one dive > 400 m was recorded in NW Greenland.

3.2. Dive rate, TAD and haul-out time

The mean dive rate (number of dives ≥ 20 m h^{-1}) for walruses (n) in the main area of NW Greenland was 2.2 (95% CI: 1.6–3.2; $n = 19$), Smith Sound 1.4 (95% CI: 1.0–2.0; $n = 19$), and NE Canada 2.4 (95% CI: 1.7–3.4; $n = 21$) (Table 1). Sub-areas with highest dive rates per hour were Carey Islands (7.3; $n = 1$), Alexandra Fjord (3.5; $n = 5$) and Princess Mary Bay (3.4; $n = 3$). Sub-areas with lowest dive rates per hour were Makinson Inlet (1.1; $n = 3$), Talbot Inlet (1.2; $n = 8$) and Kiatak (1.33; $n = 5$) (Table 1).

Time spent at depths (*TAD*) ≥ 20 m for the three main areas was 21.0% (95% CI: 16.2–25.8) for NW Greenland, 14.3% (95% CI: 9.7–18.9) for Smith Sound and 24.3% (95% CI: 20.5–28.2) for NE Greenland. At the sub-areas *TAD* for all depths bins > 0 m ranged from approximately 58% at Kane Basin to 85% at Carey Islands. Walruses at all sub-areas spent between 4.9% (95% CI: 0–18.2; $n = 3$) and 36.7% (95% CI: 30.4–43.0; $n = 5$) of their time at depths ≥ 20 m and between 34.2% (95% CI: 28.8–39.6; $n = 5$) and 68.8 (95% CI: 55.8–81.7; $n = 3$)

Table 1
Sub-areas, number of walruses, mean dive rate per hour, haul-out periods and 95% confidence intervals.

Sub-area	n walruses	Mean dive rate per hour (≥ 20 m)	95% CI	Haul-out periods (%)	95% CI
Alexandra Fjord	5	3.5	2.5–5.0	22.5	16.6–29.8
Baird and Cadogan Inlet	11	2.5	1.7–3.5	11.2	7.3–16.7
Carey Islands	1	7.3	5.1–10.5	24.9	13.4–41.3
Coburg Island	6	2.4	1.7–3.4	15.5	10.2–22.7
Etah	10	2.0	1.4–2.9	16.3	9.2–27.1
Jones Sound	4	2.6	1.8–3.7	17.1	11.3–24.9
Kane Basin	2	1.9	1.3–2.7	16.2	6.3–35.5
Kiatak	5	1.3	0.9–2.0	17.6	7.2–37.0
Makinson Inlet	3	1.1	0.7–1.5	4.7	0.6–27.4
Murchison Sound	9	2.0	1.4–2.8	11.5	7.1–18.1
Pim Island	9	2.8	2.0–4.0	10.0	5.3–18.2
Princess Mary Bay	3	3.4	2.4–4.8	19.6	11.4–31.5
Smith Sound	21	1.8	1.3–2.5	16.6	13.4–20.3
Talbot Inlet	8	1.2	0.8–1.7	14.7	10.9–19.6

of their time at depths $> 0- < 20$ m. At Makinson Inlet and Talbot Inlet walruses spent $< 10\%$ of their time at depths ≥ 20 m whereas $> 30\%$ were spent at Alexandra Fjord, Carey Islands and Princess Mary Bay. At Makinson Inlet, Talbot Inlet and Kiatak $> 60\%$ was spent at depths $> 0- < 20$ m. Alexandra Fjord, Kane Basin and Princess Mary Bay accounted for least time spent at those depths ($< 42\%$).

Dive rate and *TAD* was found to be statistically different between sub-areas compared to a model with only main area ($p < 0.0001$), as was between main areas compared to a model with no area effect ($p < 0.0001$).

The estimated percentage of 6-h periods without dives (haul-out periods) was 14.5% for NW Greenland (95% CI: 10.7–19.6; $n = 19$), 16.4% for Smith Sound (95% CI: 12.4–21.5; $n = 19$) and 15.7% for NE Canada (95% CI: 13.1–18.7; $n = 21$). Sub-areas with highest percentage of haul-out periods were Carey Islands (24.9%; $n = 1$), Alexandra Fjord (22.5%; $n = 5$), and Princess Mary Bay (19.6%; $n = 3$). Sub-areas with lowest percentage haul-out periods were Makinson Inlet (4.7%; $n = 3$), Pim Island (10.0%; $n = 9$) and Baird and Cadogan Inlets (11.2%; $n = 11$) (Table 1). Neither sub-area ($p = 0.072$) nor main area ($p = 0.79$) were statistical significant. The estimated mean percentage of haul-out periods was 15.6% (95% CI: 13.3–18.4) for all areas.

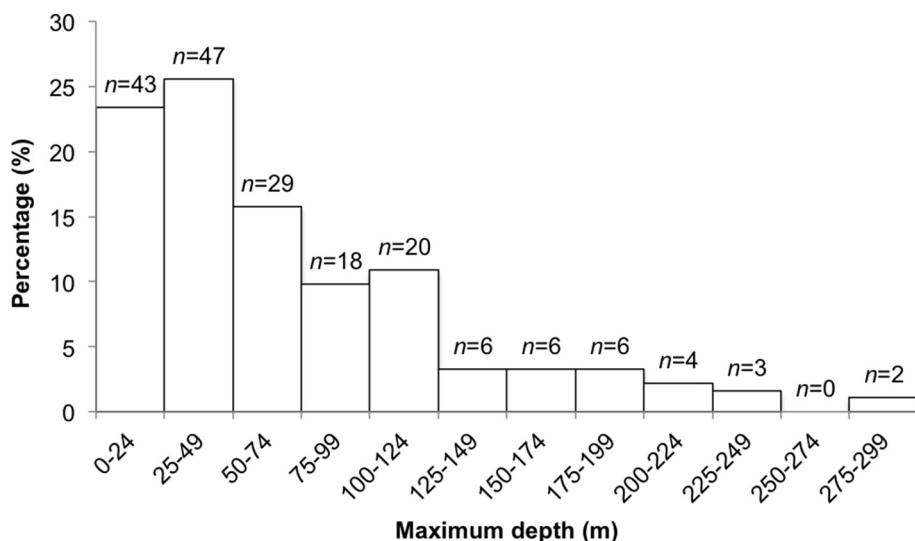### 3.3. Daily maximum depths of dives (MAX dives)

MAX dives was significantly different between the three main areas (p = 0.0263) whereas it was not significantly different between sub-areas (p = 0.262). The geometric mean of the *MAX* dives (recorded during 24 h; *n* = 184; 26 walruses) for the three main areas was 27.7 m (95% CI: 17.6–43.5; *n* = 19) for NW Greenland, 57.0 m (95% CI: 38.0–85.6; *n* = 22) for Smith Sound, and 49.8 m (95% CI: 38.9–63.5; *n* = 143) for NE Canada.

MAX dives < 100 m accounted for 74% of all *MAX* dives (*n* = 137) (Fig. 3). All *MAX* dives > 150 m were recorded in Smith Sound (*n* = 15) or at Coburg Island (*n* = 5) except for one recorded in Alexandra Fjord (176 m) (Fig. 4). The deepest *MAX* dives recorded were 294 m and 276 m and were performed by females while the *MAX* dive record for a male was 234 m. The only subadult in the dataset, estimated to be 2–3 years old, had a *MAX* dive of 112 m but dived to depths of 150–200 m according to the binned *DOD* data. A female with a calf dived to 166 m, whether the calf dived with her or stayed behind is not known. In general the *MAX* dives did not reach the seabed in the three areas and nearly all *MAX* dives were exceeded by the binned *DOD* data. The mean seabed depth at the *MAX* dive positions (*n* = 108) was 528 m for NW Greenland, 353 m for offshore Smith Sound and 224 m for NE Canada. The *MAX* dives on average reached 30% (SD 27) of the actual distance to the seabed, with only ~6% (*n* = 6) reaching the seabed

(relative distance 90–100%) (Fig. 5).

3.4. Depth of the seabed at positions of dives and extent of shallow water areas

Depth of the seabed at positions of dives was deepest at the sub-areas of Kiatak, Etah, south of Devon Island (including a few positions in Lancaster Sound) and offshore Smith Sound (Fig. 6). The shallowest sub-areas included the fjords and inlets of the east coast of Ellesmere Island (Princess Mary Bay, Alexandra Fjord, Baird and Cadogan inlet and Makinson inlet). Shallow water (0–200 m; Fig. 7) in the three main areas covered a total of 39,160 km². The NW Greenland part constituted 8881 km^{-2} from 0 to 200 m and 3962 km^{-2} from 5 to 100 m of depth.

3.5. Vertical speed, time spent in the last destination depth bin and travel time

Vertical speeds could be calculated to eight destination depths: 50, 100, 150, 200, 300, 400, 500 and 600 m (*n* = 21 walruses). Mean vertical speeds ranged from 1.0 (95% CI: 0.8–1.2) to 1.8 m s^{-1} (95% CI: 1.0–2.5). Vertical speeds to destination depth bins were statistically different compared to a model with only an intercept (p < 0.00224) (Table 2). The random effect of animals is also listed in Table 2. The
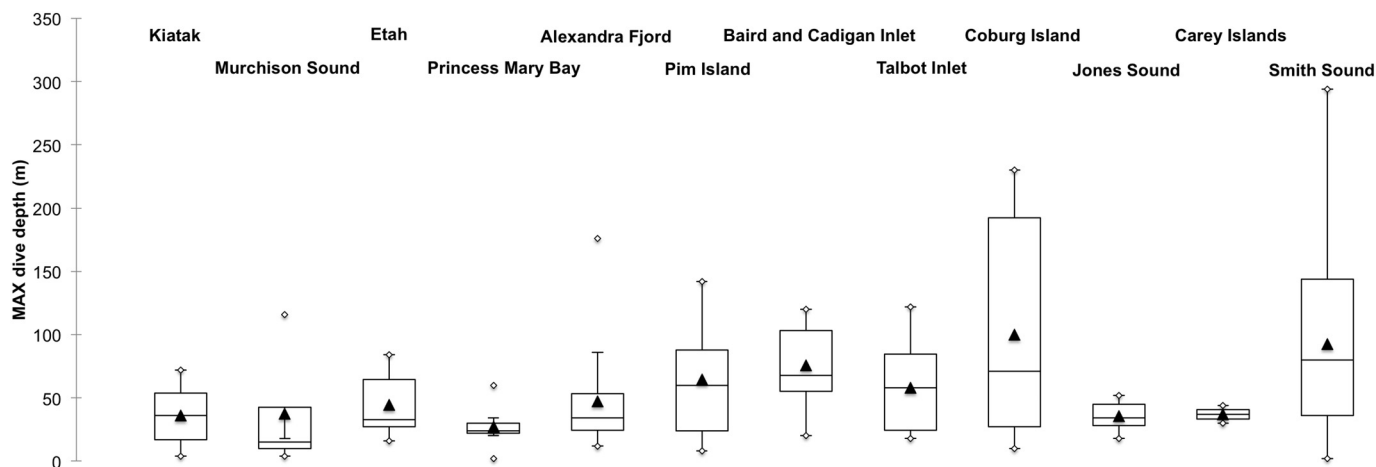

Fig. 4. Box plot of the geographical distribution in summer, May–October, of daily maximum depth of dives from 26 walrus tagged in NW Greenland in 2010–2013. Mean values are represented by a black triangle. The error bars represent the 95% confidence intervals. Maximum and minimum values of dives are represented by a dot, the 25th and the 75th percentile are illustrated by the empty boxes and the median is represented by the black line.
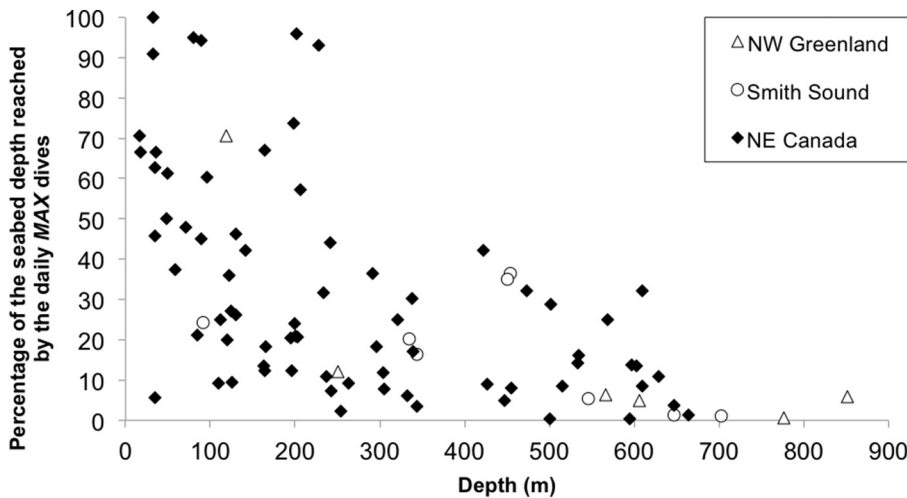
Fig. 5. Percentage of the seabed depth reached by the daily *MAX* dives during summer for 21 walrus. Positions were categorized into three main areas: NW Greenland (*n* = 6), Smith Sound (*n* = 8) and NE Canada (*n* = 73). Only dives with a positive distance to the seabed are shown.

individual vertical speeds for the 21 walruses are thus given by the estimates in the table for the individual bins plus the random effect, i.e. the eight vertical speeds for the eight different end destination depths (50 m–600 m) for walrus no. 20158 are 1.4, 1.6, 1.1, 1.4, 1.9, 1.9, 1.6, 1.6. Mean travel times (descend and ascend combined) to destination bins ranged from 1.3 min (50 m) to 13.2 min (600 m).

3.6. Estimation of walrus consumption of bivalves in NW Greenland

Using Monte Carlo simulations (10,000 trials; Table S1) it was estimated, that mean amount of shell-free (SF) bivalve wet weight (WW) consumed in NW Greenland is 17,420 tons year^{-1} (95% CI: 5534–22,954; SD 6065). This corresponds to mean consumption per walrus per day of ~28 kg (95% CI: 9–37 kg). The estimates were based on consumption rates of 4.2–6.2% of total walrus body mass (Fay, 1982), mean mass of males of 834 kg (95% CI: 716.9–951.9 kg), females of 630 kg (95% CI: 555.0–705.0) and subadults of 350 kg, and a population of 2544 walruses (95% CI: 1513–4279) (Heide-Jørgensen et al., 2016) that stay in the NW Greenland part of Smith Sound for 243.31 days year^{-1} (~15. October–15. June) (Heide-Jørgensen et al., 2017).

3.7. Impact of walrus predation on the bivalves in NW Greenland

Walrus annual predation on the standing bivalve biomass in NW Greenland was estimated to be 3.2%. Calculations were based on mean

biomass of 137.7 g WW m^{-2} (95% CI: 56.25–219.08) of the species *Mya* sp., *Hiatella* sp., *Serripes* sp. and *Ciliatocardium ciliatum* (Vibe, 1950) and assuming main predation to occur within 5–100 m of depth, where bivalve biomass is highest. Using the mean estimate from Born and Acquarone (2007) of total annual production of *Mya* and *Hiatella* of 7.9 g SF WW m^{-2} year^{-1}, it was estimated that the walrus population in NW Greenland consume ~56% of the annual production of these two bivalves at depths from 5 to 100 m.

4. Discussion

Walruses from the Baffin Bay stock move from Greenland to Canada in June and even though they prefer coastal areas they are, in the absence of terrestrial haul-out sites, dependent on fast-ice or drifting ice pans for hauling out (Heide-Jørgensen et al., 2017). There are no terrestrial haul-out sites in Smith Sound and this, together with the general logistical challenges with working at high latitudes, makes it difficult to obtain detailed dive information from walruses in this area. Retrievable data-loggers that collect high resolution dive data are unlikely to provide information for longer periods (> 2 days) and the only feasible option for examining diving behavior and area utilization by walruses in the Smith Sound region is through remote instrumentations with satellite transmitters that relay compressed information on diving characteristics. This is hovever suboptimal as complete dive profiles are not obtained and the data collection is restricted by the pre-determined choices of diving characteristics.
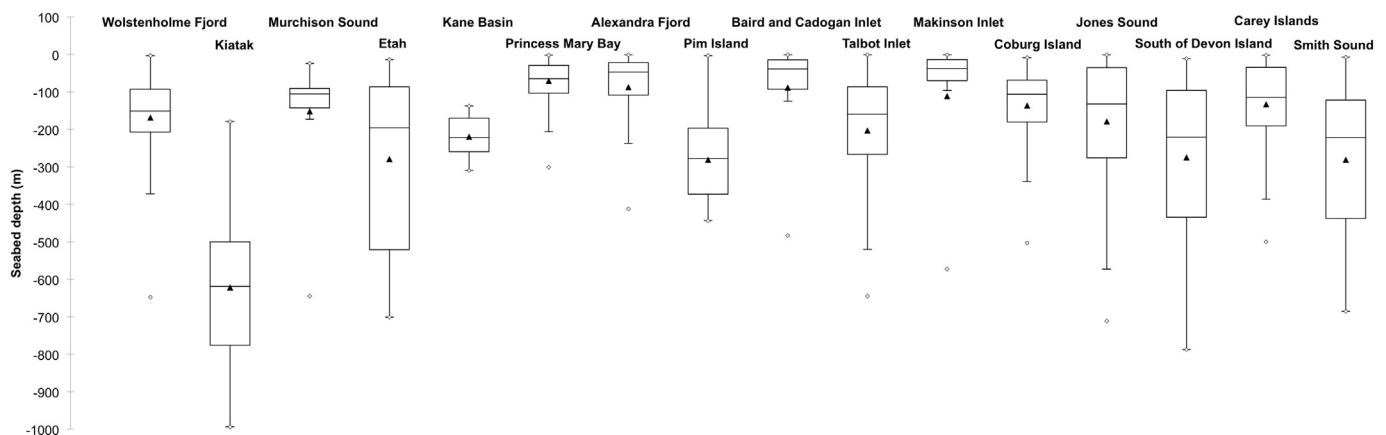

Fig. 6. Seabed depth in meters at the walrus positions in the Smith Sound region (*n* = 26 walruses). Mean values are represented by a black triangle. The error bars represent the 95% confidence intervals. Maximum and minimum values of dives are represented by a dot, the 25th and the 75th percentile are illustrated by the empty boxes and the median is represented by the black line.
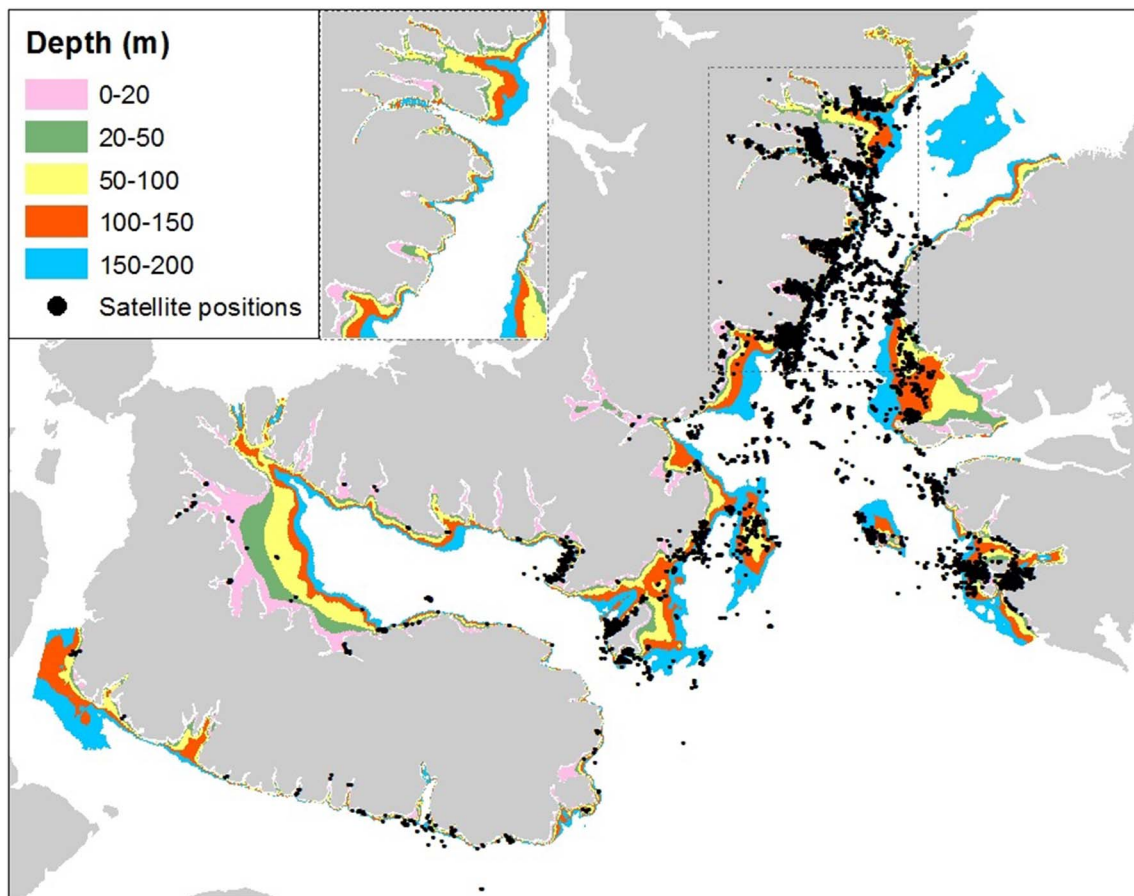
Fig. 7. Satellite positions plotted on a map showing seabed depth categories from 0 to 200 m in the Smith Sound region (NW Greenland, Smith Sound and NE Canada). The two boxes marked with a dashed line show coastlines with and without satellite positions. White areas indicate waters deeper than 200 m.

There were discrepancies between the *MAX* dives and the *TAD/DOD* data. Firstly, the walruses dived to considerably deeper bins according to the *TAD/DOD* data than what appeared from the more sporadically collected *MAX* dive data. Secondly, the amount of data collected from the 21 walruses varied considerably. This leads to incomparable *MAX* dive data, since animals measured frequently will typically have deeper *MAX* dives even if they follow the same distribution, because a larger sample size will represent more of the tail of the distribution. This is due to the mathematical fact that as more measurements arrive, the maximum of these will increase (a new measurement will not affect the maximum if it is smaller than the current maximum, but it will increase the maximum if it is larger).

4.1. Diving capacity and haul-out

The deepest dives observed in this study exceed records from most other areas. Jay et al. (2001) reported no dives to depths > 50 m in Alaska for Pacific walruses and Gjertz et al. (2001) found a maximum dive of 67 m near Svalbard for Atlantic walruses. Fay and Burns (1988) reported that three walruses had fresh undigested food in their stomachs when they were killed over 102–117 m deep waters in the central Bering Sea. They concluded that walrus geographical distribution is less limited by their diving ability than by the bathymetric distribution of their food. Recently dives to depths > 400 m for a male Atlantic walrus tagged on Svalbard were reported (Lowther et al., 2015). Most dives were however targeting shallower depths (< 50 m, 89%), while only 1.2% of the dives were deeper than 100 m (Lowther et al., 2015). We found similar results with most dives < 100 m (97%; < 50 m, 87%). Data from the first *DOD* destination depth bin were excluded because walruses staying near the surface can

mistakenly be registered as diving. The data presented by Lowther et al. (2015) and those obtained in this study indicate that the diving capacity of walruses has been underestimated in the past and that at least Atlantic walruses are capable of foraging at depths > 100 m and dive to much greater depths for short periods of time. Nearly 25% of dive data and the majority of dives > 300 m were found in the deep offshore areas of Smith Sound. This is surprising as bivalve biomass is assumed to be low in waters > 200 m. It seems possible that the walruses make deep dives to explore the offshore areas in their search for food.

Born and Knutsen (1997) found that male walruses in NE Greenland in August–September hauled out for ~29% of their time. Haul-out in this study was found to be considerable less (overall mean of 15.6%). Walruses in this study move between sub-areas during the summer period and are therefore not as stationary as the male walruses in NE Greenland, which possibly leave them with less time for hauling out. Also, walruses in this region need fast ice or ice floes for hauling out, and varying ice conditions with periods of limited or no ice coverage force walruses to commute to and from feeding grounds resulting in reduced haul-out time. Limited or no ice available might also result in walruses resting in water which, in our analysis, would not be considered as hauling out (where only 6-h periods without any diving activity is considered hauling out). Haul-out time and also the dive rate could therefore be somewhat underestimated in this study. Even though not statistically different some areas accounted for more haul-out time than others. The longest haul-out time was found at Alexandra Fjord, Princess Mary Bay and Carey Islands (Table 1). These three sub-areas also had the highest dive rates. Overall, the mean dive rate was significantly higher, although only slightly, in NE Canada suggesting more dives per hour at the NE Canada habitats than in NW Greenland. This could be a consequence of a patchy distribution of walrus prey or lower

Table 2

A. Mean vertical speed and travel time to destination depths for 21 walruses. B. Walrus ID no., sex of animals and random effect. Individual vertical speeds for a walrus is given by the estimates in Table A plus the random effect in Table B. A walrus diving faster than the mean vertical speed has a positive number if slower the number is negative. The total number of dives was n = 415.

A. Destination depth bin	Mean vertical speed	Travel time
50	1.3	1.3
100	1.5	2.2
150	1.0	5.0
200	1.3	5.3
300	1.8	5.7
400	1.8	7.6
500	1.5	11.4
600	1.5	13.2

B. Walrus ID no.	Sex[a]	Random effect
7934	NA	0.0005
20158	F	0.1098
20160	NA	0.0004
20165	M	− 0.0475
20167	F	− 0.0843
20169	NA	− 0.0729
20683	M	− 0.0052
20684	F	− 0.0448
20685	F	0.0235
20688	F	0.1006
46106	F	− 0.0406
46107	F	0.0316
46108	F	− 0.0093
46109	NA	− 0.0035
46113	F	− 0.0646
46115	F	− 0.0007
46116	NA	− 0.0404
46117	M	0.0436
46118	F	0.0202
46155	F	0.0502
46160	F	0.0335

[a] NA: not available.

energy food items compared to NW Greenland, forcing the walruses to make more dives to fulfill their energetic requirements. More diving in certain areas could however also be a result of rich feeding banks motivating the walruses to spent more time on feeding.

The method used in this study to estimate vertical speeds (descent and ascent combined) over long vertical distances is likely negatively biased compared to methods deployed in other studies where time-depth-recorder data with higher sampling rates and resolution were used for integrating speeds over shorter distances. Wiig et al. (1993) reported on the vertical speeds of one Atlantic walrus diving to 20 m and 55–70 m near Svalbard but did not distinguish between the two depth categories. The mean descent and ascent rates of this walrus were 0.8 m s^{-1} (SD: 0.33; range: 0.02–1.7) and 0.7 m s^{-1} (SD: 0.32; range: 0.02–0.7), respectively. Gjertz et al. (2001) reported descent and ascent velocities ranging from 0.1 ± 0.1 m s^{-1} to 0.8 ± 0.3 m s^{-1} for depths < 35 m. For Pacific walruses descent and ascent rates were similarly low (< 1 m s^{-1}) for dives down to 50 m (Jay et al., 2001). Using acoustic tracking Mouy et al. (2012) estimated that a walrus diving to 50 m in the Chukchi Sea had a descent rate of 1 m s^{-1}. All these observations from other walrus populations are lower than the mean vertical speeds (range: 1.3–1.8 m s^{-1}) to destination depths observed for walruses diving to 50 m or deeper in this study (except for mean vertical speed to destination depth bin 150 m of 1.0 m s^{-1}). The difference is probably due to shallow diving near Svalbard and Alaska. It is noteworthy that the vertical speeds did not correlate significantly with destination depth bins although vertical speeds to destination depths > 300, 400 and 600 m were higher than to the destination depths of 50–200 m. There was also no asymptotic relation between

speed and depth as shown for deep diving cetaceans (Laidre et al., 2003). It suggests that the walruses do not fully adjust their speed to the destination depth either because they do not need to or because they do not decide about the depth of the dive until late in the dive cycle.

Continued diving to the same depths indicates foraging behavior (Wiig et al., 1993). Previous studies agree that a feeding dive (including travel time) for the Atlantic walrus lasts in the range of 6–8 min, with a mean duration of 5–6 min, at mean depth < 35 m (Born and Knutsen, 1990; Born and Knutsen, 1997; Gjertz et al., 2001; Born and Acquarone, 2007). Jay et al. (2001) found mean foraging dive duration of Pacific walruses in Alaska to last 7 min at depths < 50 m. In this study, all dives with a time spent in the last destination depth bin of ≥ 4 min were assumed to represent a feeding dive. Percentage feeding dives ≥ 4 min ranged at sub-areas from 17.6 (95% CI: 4.7–39.6) to 74.4% (95% CI: 66.3–81.5). Five sub-areas (Alexandra Fjord, Kane Basin, Murchison Sound, Carey Island and Jones Sound) had higher mean percentage of feeding dives (60%), while Makinson Inlet and Kiatak had a lower percentage (< 20%) of feeding dives. Dives ≥ 9 min also represented feeding dives and are longer than average feeding dives according to previous studies. Percentage feeding dives ≥ 9 min ranged from 0 (95% CI: 0.0–1.0) to 12.5 (95% CI: 2.2–33.8), where Kiatak and Kane Basin accounted for most of these dives (≥ 10%) and Carey Island least (0.0%). The mean percentage of feeding dives ≥ 4 min was statistically different for main (p = 0.009) and sub-areas (p < 0.0001), compared to a model with no area, but was not statistically different for dives ≥ 9 min (main area: p = 0.486; sub-areas: p = 0.163). Dive rate, haul-out time, *TAD* and percentage of feeding dives were considered for designating important feeding grounds for the Baffin Bay walrus stock. Highest dive rates, most haul-out periods and longest *TAD* ≥ 20 m was found at Alexandra Fjord, Carey Islands and Princess Mary Bay compared to the other sub-areas. Also the percentage of feeding dives was high at Alexandra Fjord, Carey Islands and Princess Mary Bay (≥ 58.8%). This indicates that walruses at these three sub-areas spent a lot of their time feeding and resting and suggests that their prey is mainly distributed deeper than 20 m. On the contrary at Kiatak, Makinson Inlet and Talbot Inlet walruses spent most of their time at depths < 20 m and their dive rate was low (≤ 1.3). The amount of feeding dives of all dives was also low at Makinson Inlet (17.6%) and Kiatak (18.8%) while approximately half of all dives were feeding dives at Talbot Inlet (47.7%). This could indicate that at least Makinson Inlet and Kiatak are not used extensively for feeding in the summer period. In their analysis of the movements of these same walruses, Heide-Jørgensen et al. (2017) found Talbot Inlet to be frequently visited by walrus in the Smith Sound region in summer and the low dive rate at shallow waters (< 20 m) in this area could also be a result of rich feeding banks. Based on our analysis of walrus diving behavior and results from Heide-Jørgensen et al. (2017) we propose that important feeding grounds for the Baffin Bay walrus stock in summer include Alexandra Fjord and Princess Mary Bay in NE Canada and that Carey Islands in Smith Sound potentially is an important feeding area and stop-over for walruses migrating from NW Greenland to NE Canada in June. Talbot Inlet could possibly also be one of the more important feeding grounds during summer. Investigations of bivalve distribution and biomass and walrus stomach content at sub-areas, however, are necessary to fully determine which areas are more important for walrus feeding. In fall, most walruses return to NW Greenland (Heide-Jørgensen et al., 2017). In particular at Murchison Sound and Wolstenholme Fjord large aggregations of walrus are found in winter which is probably a reflection of better feeding opportunities in those areas during winter and spring (Heide-Jørgensen et al., 2016).

Wiig et al. (1993) estimated an aerobic dive limit of 10.5 min for a male Atlantic walrus near Svalbard and Gjertz et al. (2001) found the longest dive duration to be 24 min also for a male walrus near Svalbard. Noren et al. (2015) calculated the aerobic dive limits (cADL) of adult walruses of both sexes not to exceed 15 min under normal conditions. An aerobic dive limit of 15 min would allow the walruses to spend

9.3 min at 300 m depth if a vertical speed of 1.8 m s^{-1} could be maintained (Table 2). At such vertical rates the walruses would have plenty of time at the bottom for feeding and even at depths > 300 m the walruses would still have time for feeding or reconnaissance for prey. Lowther et al. (2015) reported maximum dive duration of 47.1 min., which is the longest dive recorded for a wild walrus and well exceeds cADL estimated by Noren et al. (2015). However, the record supports the theoretically maximum dive duration of 57 min for adult male walruses estimated based on allometric relationships between diving capacity and body mass for pinnipeds by Schreer and Kovacs (1997). Also, Costa et al. (2001) hypothesized that while most species appear to dive well within their cADL, others appear to exceed the cADL on a regular basis. In this study maximum dive duration was 49.0 min, which is similar to the maximum dive duration reported by Lowther et al. (2015). Based on these and previous results it seems fair to assume that walruses are less restricted in their search for food by their diving abilities than by the bathymetric distribution of their preferred prey items (Fay and Burns, 1988).

Noren et al. (2015) found that a weaned 2–3 year old walrus can dive aerobically for 9–11 min and hypothesized that in a resource-limited environment independent immature walruses could be competitively disadvantaged, in terms of their diving capacity, compared to adult walruses and therefore disproportionally affected during periods of low prey availability. Here, we found that a 2–3 year old female made a relatively deep dive of 112 m (MAX dive) and several dives to the destination depth bin 150–200 m and she travelled faster than the mean vertical speed found for the other 21 walruses (Table 2). This single young walrus thus seem to have diving capabilities matching adult walruses. Her restrictions, however, could be a lowered ADL compared to adults and less experience in food searching (Noren et al., 2015). Noren et al. (2015) also argued that males would have an advantage over females when competing for food in resource-limited habitats assuming that myoglobin levels are similar between males and females. The greater body size of male walruses could provide males with an advantage over females, as found for the sexually dimorphic Northern elephant seal (Mirounga angustirostris). In this study we found no evidence of male walruses diving deeper nor for longer periods than females. On the contrary, two females made the deepest dives ever recorded for any walrus in the literature and also accounted for the fastest vertical speeds. However, we are not able to fully test the differences in male and female diving capacities due to low sample sizes. Furthermore, the walruses in this study are presumably not in a situation where they compete for food.

4.2. Walrus consumption

The Baffin Bay walrus stock consume on average ~28 kg SF WW per walrus per day (95% CI: 9–37 kg), which is considerable less than the 60 kg SF WW per walrus per day (95% CI: 42–75 kg) estimated by Born and Acquarone (2007). This estimate, however, was based on a population in NE Greenland consisting mainly of large adult males with an estimated mean total body mass of a 1000 kg and a mean per capita gross food intake of 6% of total body mass (95% CI: 4.2–7.5%). The population in the Smith Sound region consists of equal males and females, including young and subadults, with estimated total body masses between 350 and 834 kg and a food intake between 4.2 and 6.2% of total body mass (Fay, 1982). The estimate of ~28 kg SF WW per walrus per day therefore seems reasonable.

Walrus consumption per year was also estimated using an alternative method (Born and Acquarone, 2007) based on diving rate, ratio of feeding dives, walrus consumption per dive (Born et al., 2003), and walrus abundance and annual occurrence in NW Greenland (Heide-Jørgensen et al., 2016; Heide-Jørgensen et al., 2017). The point estimate of the two methods varied < 1000 ton SF WW year^{-1}, however the variance of the individual parameters of the alternative method was so large that the uncertainty around the estimate became meaningless.

4.3. Estimation of the impact of walrus predation on bivalves

The estimated walrus annual removal of 3.2% of the standing bivalve biomass in NW Greenland was based on the estimate of Vibe (1950) of 137.7 g WW m^{-2} of walrus principal food species *Hiatella arctica*, *Mya truncate*, *Serripes* sp. and *Ciliatocardium ciliatum* at the walrus feeding ground in Murchison Sound (Fig. 1). Vibe points out that the two first mentioned mussels might occasionally have escaped the bottom sampler and therefore his bivalve biomass estimate must be considered an absolute minimum. The 3.2% estimate in this study could therefore be overestimated, furthermore considering that walruses eat a range of species besides the four included in Vibe's investigations (Fay, 1982; Born and Acquarone, 2007). Our estimate however is similar to that in Born and Acquarone (2007) of 2.5% for male walruses in NE Greenland and for the population of Pacific walruses in Beringia estimated to annually consume ~3% of the bivalve biomass in the area (Ray et al., 2006). Additionally, Born and Acquarone (2007) estimated predation to be ~25% of the annual production of the bivalves *Mya* sp. and *Hiatella* sp. (Sejr and Christensen, 2007) by walruses in NE Greenland. Walrus predation in NW Greenland was found to be ~56% of the annual production of these two bivalves from 5 to 100 m depths. However, as also discussed by Born and Acquarone (2007), the walruses forage on a whole range of bivalves and benthic invertebrates beside the two. When estimating walrus consumption it is important to consider, that information on distribution, density and productivity of benthos in the Arctic regions is sparse and some references are of older date (Vibe, 1950), that densities of bivalves within the same area can be extremely patchy, and that information on foraging by walruses is limited (Born et al., 1997; Ray et al., 2006). This makes our estimation of walrus consumption somewhat inaccurate. However, despite some inaccuracy in annual consumption estimates, Ray et al. (2006) concluded that the combined ecosystem effects of walrus feeding must be placed in the context of long-term, regional changes and responses. The consequences of diminishing sea ice in Beringia and thus the distribution and numbers of walruses in that area could be that the walrus' ecological role will be weakened or lost, the benthic ecosystem altered and subsistence hunters deprived a key resource (Ray et al., 2006). Based on equal percentages of walrus annual consumption of bivalve biomass in the Smith Sound region and Beringia it is hypothesized that the Atlantic walruses in NW Greenland might act locally as bioturbators at specific walrus feeding grounds as the Pacific walruses in Beringia (Ray et al., 2006). The walruses thus could play an important role in ecosystem functioning in this high Arctic area. The consequences of environmental changes caused by climate e.g. changes in sea ice regimes or anthropogenic influences like increased levels of disturbance, underwater noise or pollution could therefore be similar to that proposed for Beringia. However, multidisciplinary investigations are needed to better understand the complex ecological effects that this top predator has on the Arctic ecosystems.

In NW Greenland only a few studies have quantified benthos biomass, including density at depth. Vibe (1950) described in detail the benthos communities on walrus feeding grounds along the NW Greenland coast from northern Melville Bay to southern Kane Basin and found mean benthos biomass of 450 g m^{-2} WW at five specific walrus feeding grounds at depths from 12 to 54 m. In a more recent study Boertmann and Mosbech (2011) found great variability in infaunal bivalve biomass ranging from 23 to 1030 g WW m^{-2} (including shells and skeletons) at the entrance of the walrus feeding ground Wolstenholme Fjord. Average infaunal bivalve biomass of around 200 g WW m^{-2} at depths 0–150 m and 175 g WW m^{-2} at 150–200 m is within the range of previous observations in the area by Vibe (1939). Infaunal bivalve biomass from ~5–50 m was considerable higher (Boertmann and Mosbech, 2011). They also found that the abundance of large infaunal bivalves was highly variable but generally peaked at depths between 10 and 50 m. In general, infauna, including bivalves, is depauperate from < 5 m of depth due to variations in temperature and

salinity and seasonal presence of sea ice (Thomsen et al., 1986). Majority of dives in this study were also at depth < 100 m (97%), which is in agreement with the findings described above, showing that walruses preferred prey are concentrated at depths of < 100 m. However, walruses are capable of diving and feeding at greater depth, and although walrus prey are only found in small concentrations at depths > 200 m, it seems possibly for the walruses to forage at greater depths if necessary.

4.4. Carrying capacity of walruses in the Smith Sound region

Even though reports exist of walruses taking ringed seals (*Pusa hispida*) in NW Greenland (Vibe, 1950) and sea birds in other areas (Fox et al., 2010) large bivalves in shallow areas must be considered the primary prey in all walrus populations (Vibe, 1950; Fay et al., 1977; Jay et al., 2014).

The extent of the shallow water habitat illustrates the carrying capacity for the walrus population in the Smith Sound region. Parts of the area, and especially the localities in NE Canada, have extensive sea ice formation during winter that seasonally reduces the suitable habitat. However, large coastal areas of NW Greenland remain ice-free offering access to benthos during the 9-month's where the walruses frequent these areas (Heide-Jørgensen et al., 2016, 2017).

Although highly variable densities and productivity of benthic prey can be expected in the different walrus populations there seems to be a simple relationship between available shallow water habitat and walrus pre-exploitation population sizes (Fig. 8, Table S2). An exception is the East Greenland walrus population that even though the walruses have access to large areas with shallow water the low pre-exploitation population size is expected due the low productivity in this area (Smith et al., 1997). In this respect the East Greenland population should be regarded an outlier.

Compared to other walrus populations the population in the Smith Sound region has a relatively small shallow water area feasible for benthic feeding. It seems unlikely given the size of the available habitat that the carrying capacity in the Smith Sound region exceeds 5000 walruses also considering that for at least 6 months of the year the

walrus habitat is reduced due to the extensive ice coverage.

In conclusion the walruses in high Arctic Greenland and Canada mainly dives to depth < 100 m, which is also the main bathymetric distribution of their preferred prey items. However, walruses are capable of diving to much greater depth (> 500 m). Walruses use shallow water bays and fjord systems in NW Greenland and NE Canada for feeding during summer. Based on diving characteristics and positions of walruses Alexandra Fjord, Princess Mary Bay and Carey Islands were found to be important for feeding during summer. Investigations on bivalve distribution and biomass and walrus stomach content, however, are necessary to fully determine the most important feeding areas for the Baffin Bay walrus stock. Walrus daily consumption and annual predation on the standing stock and yearly production of bivalves was furthermore estimated and it was proposed that the carrying capacity of walruses in the Smith Sound region does not exceed 5000 animals.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2017.12.009.
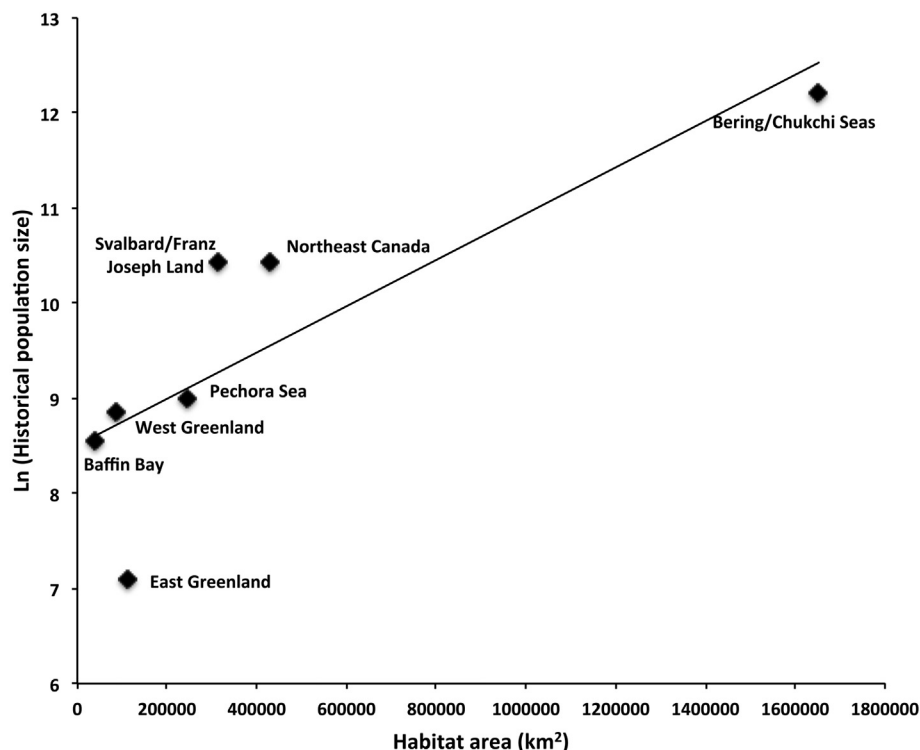

Fig. 8. Pre-exploitation abundance of walrus populations (in transformed values from Table S2) in relation to habitat areas for each population (seabed area < 200 m) in km².

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