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Greenland whales and walrus in the Svalbard food web before and after exploitation*

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Abstract

Between 1600 and 1900 two numerous and ecologically important large marine mammals were extirpated in the Svalbard archipelago. These were the pelagic-feeding Greenland whale (*Balaena mysticetus*) and the benthic-feeding walrus (*Odobenus rosmarus rosmarus*), the initial stocks of which prior to exploitation are estimated to have numbered approximately 46 000 and 25 000 animals respectively. Their annual food consumption at that time is estimated to have been some 4 million tons of plankton and 0.4 million tons of benthic organisms. Assuming that the primary and secondary production of the shelf/coastal ecosystem in the 16th century (before the peak of the Little Ice Age) was similar to that of the present

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day, the authors have concluded that a major shift in the food web must have occurred after the Greenland whales and walrus were eliminated. Planktonivorous seabirds and polar cod (*Boreogadus saida*) very probably took advantage of the extirpation of the Greenland whales, while eiders (*Somateria mollissima*) and bearded seals (*Erignathus barbatus*) benefited from the walrus's extinction. In turn, the increased amount of pelagic fish provided food for piscivorous alcid and gulls, and may have given rise to the huge present-day seabird colonies on Svalbard.

1. Introduction

In general, marine mammals and seabirds are believed to be food-limited (Valiela 1995). One example is the serious depletion of the Antarctic baleen whale stocks to a fifth of their initial numbers, which created a surplus in krill production from the 1930s to the 1960s. This, in turn, stimulated an increase in the seal and penguin populations (Sladen 1964, Laws 1985, Croxall *et al.* 1988). In the northern hemisphere's Barents Sea marine mammals are estimated to be the principal consumers of fish (Joiris 1992, Sakshaug *et al.* 1992, 1994, Joiris *et al.* 1996). Similar studies of the Bering Sea (Fay *et al.* 1977), Lancaster Sound (Welch *et al.* 1992) and Antarctica (Huntley *et al.* 1991, Rakusa-Suszczewski 1992) illustrate the importance of marine mammals as a link in the carbon cycle through both food consumption and exhaustion of CO₂ directly into the atmosphere (Huntley *et al.* 1991, Banse 1995). The exploitation of marine mammals in the Svalbard coastal waters started in 1596, only 15 years after the discovery of the archipelago. The hunting of Greenland whales (*Balaena mysticetus*) began in 1611 at Spitsbergen, the largest island of the archipelago. This had been preceded by the hunting of walrus (*Odobenus rosmarus rosmarus*) on Bjornoya. Between 1604 and 1611 approximately 3000 walrus were killed on this small island. In later years hunting decreased and the last walrus was killed there in 1866; the species has never appeared there again (Perry 1967). Since 1669 whaling has been well documented, which has allowed for the back calculation of original stocks (Hacquebord & Leinenga 1994). Although several historical sources exist (Perry 1967, Lono 1972, Gjertz & Wiig 1994, Born *et al.* 1995), walrus hunting is not as well documented. Both species were severely depleted in the area. Whaling was coastal until 1650, at which time it gradually became more and more offshore (Conway 1906). Practically speaking, the last Greenland whales from the Spitsbergen stock were caught before 1850 (Vibe 1967, Jonsgard 1980), although single animals were hunted as late as 1932 (Reeves 1980). The last large walrus hunt on west Spitsbergen took place at the turn of the century, while drastically reduced hunting was continued on northeastern Svalbard (Conway 1906, Lono 1972, Stora 1987). The east Atlantic Greenland whales survived in separate stocks in the northern Kara Sea, probably

numbering fewer than 100 individuals (de Korte & Belikov 1995, Lydersen & Wiig 1995). Except for single, stray animals, Greenland whales are not observed in the Svalbard area today (Jonsgard 1980, Mehlum 1990). Walruses from the initial east Atlantic stock were estimated to number between 70 000 and 80 000 animals, but were reduced to 1200–1300 individuals by 1934 (Fedoseev 1976). This species also survived in an isolated group in the northern Kara Sea until 1952, when international protection allowed them to replenish their numbers to at least 2000 animals in the joint Svalbard and Franz Josef Land populations (Born *et al.* 1995). Virtually absent on Spitsbergen since 1870, walruses from Franz Josef Land reappeared in Svalbard in 1970 and today close to 1000 animals can be observed there (Gjertz & Wiig 1994, Born *et al.* 1995). The extensive and rapid exploitation of these two large marine mammals began just before the culmination of the Little Ice Age (1650–1850), a period of cooling in the North Atlantic which had a pronounced impact on the environment, economy and historical events (Hacquebord 1987, Grove 1990). It has been presumed that changes in environmental conditions along with intensive exploitation accelerated the extermination of Arctic marine mammals (Vibe 1967, Hacquebord 1984).

In this paper the authors attempt to reconstruct the principal components of the historical marine food web of the Svalbard coastal waters and to discuss the possible consequences of the disappearance of important components from the marine ecosystem of Svalbard waters.

2. Materials and methods

The Svalbard shelf and its coastal waters is situated on the boundary between the Arctic and sub-Arctic marine zoogeographical zones, and in the confluence zone of Atlantic and Arctic waters (Fig. 1). This area belongs to the very productive yet high (77–80°N) latitudes (Eilertsen *et al.* 1989, Sakshaug *et al.* 1992). The following assumptions were made for this study:

- the present-day food and feeding behaviour of the west Atlantic Greenland whale and east Canadian walrus are no different from those of the historical Svalbard populations;
- the present-day relationships between environmental, climatic and hydrographic factors, and marine primary and secondary productivity do not differ from those of the past;
- the present-day individual bioenergetics and energy requirements of the Greenland whale and walrus are no different from those of the past;
- both species fed in coastal waters no deeper than 200 metres.

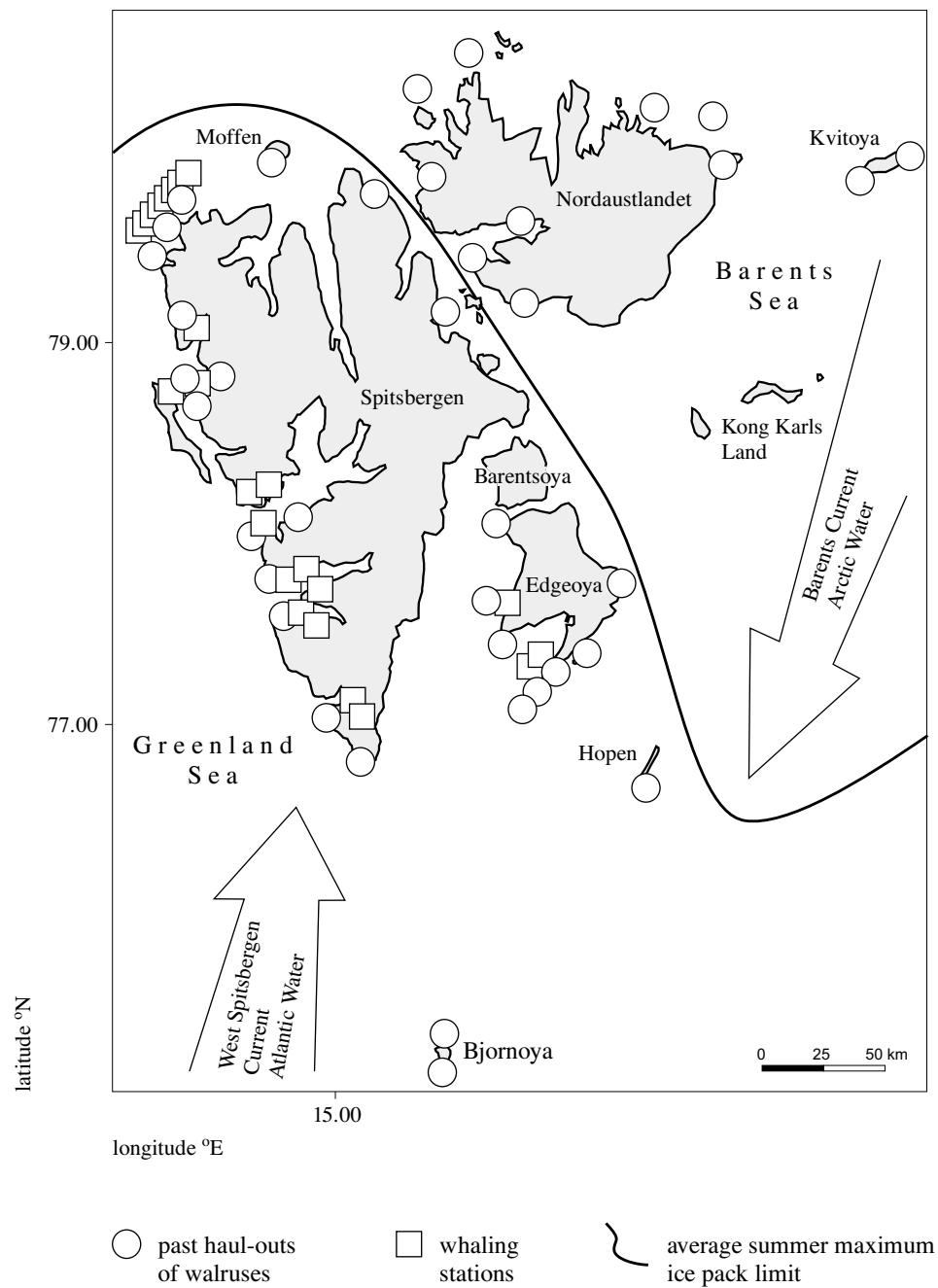


Fig. 1. Area covered by the present study; the locations of walrus hauls, seasonal and permanent whaling stations are marked (compilation from Hacquebord 1987, Krawczyk & Węśławski 1987, Gjertz & Wiig 1994)

The size of the initial stock of the Greenland whale was back-calculated from archival reports and estimated to number 46 000 individuals (Hacquebord & Leinenga 1994). Earlier estimations gave no fewer than 24 000 animals in the Svalbard (Spitsbergen) stock (Mitchell & Reeves 1981). Numerous papers address the indirect methods of Greenland whale assessment (de Jong 1983, Breiwick 1983, Breiwick & Mitchell 1983, Reeves *et al.* 1983). The estimate presented in the present paper is based on the thorough international archival research presented in Hacquebord & Leinenga (1994). In the present paper the size of the initial walrus stock on Spitsbergen is assumed to have been 25 000 animals. Assuming that the initial walrus stock on Franz Josef Land was 6000–12 500 animals (Gjertz & Wiig 1998), that the area of Svalbard is much larger and that there were numerous haul-outs (Fig. 1), the estimation given here seems reasonable. The Greenland whale population structure and length-weight relationships were taken from Burns *et al.* (1993), who reported that the population consisted of 4% calves, 48% adolescents and 48% adults. The rough proportions of the walrus population was assumed to be 15% calves, 40% immature individuals and 45% adults (based on a 25-year life span, maturation at 10 years of age and a 2–3 year interval between births – after King (1983).

Plankton density and biomass data were collected from 1989 to 1995 in the coastal waters of Spitsbergen and have been published partially by Koszteyn & Kwaśniewski 1989, Węśławski & Kwaśniewski 1990, Timofeev 1993, Węśławski 1993, Koszteyn *et al.* 1995. Energy values of major food taxa were measured using the bomb calorimetry method by Monika Normant at the University of Gdańsk. Benthos density and biomass data were collected from 1991 to 1996 and have been published partially in Węśławski (1993) and Węśławski *et al.* (1994a). Large bivalves (*Mya*, *Ciliatocardium*, *Serripes*, *Chlamys*) as well as decapod crustaceans (*Sabinea*, *Sclerocrangon*) were considered to be walrus prey according to the reports by Fay *et al.* (1977) and Gjertz & Wiig (1992). Estimations of Bivalvia and Decapoda biomass and production were taken from Welch *et al.* (1992) and Węśławski (1993), Schmid (1996). The production/biomass (P/B) relationship was taken from Petersen (1989) and Welch *et al.* (1992), which report Bivalvia P/B ratios as 0.1 to 0.18 and Decapoda P/B ratios as 0.3. Furthermore, the following relationship was taken between organic carbon (C), dry weight (d.w.) and wet weight (w.w.): 0.1 g C = 0.25 g d.w. = 1 kcal = 4.184 J. The dry weight for Bivalvia was 43% of the wet weight (shells included) and for Crustacea it was 25% (data taken from Welch & Martin-Bergmann (1990), Schmid (1996) and the authors' own data). For Decapoda 0.8 kJ g⁻¹ w.w. was taken as the mean energy value,

while for Bivalvia it was $3.6 \text{ kJ g}^{-1} \text{ w.w.}$ (Welch & Martin-Bergmann 1990). Data on seabird density and feeding comes from Stempniewicz & Węśławski (1992), Mehlum & Gabrielsen (1993), Węśławski *et al.* (1994b), Mehlum *et al.* (1996). The daily food consumption of walrus was given as 5.7% of its body mass, and is a compromise between the 1.5% and 10% reported by Lavigne (1987), Welch *et al.* (1992), and Joiris *et al.* (1996). Greenland whale energy requirement estimations range from 4 to 6 $\text{kcal kg}^{-1} \text{ day}^{-1}$ (Lowry 1993); Frost & Lowry (1984) put the daily food requirement at 1–4% of the whale's body weight, while we took 1.5% as a conservative value.

The northeast Atlantic stock of Greenland whales occurred throughout the Norwegian, Greenland and Barents Seas. Following the spring retreat of the ice pack most of these animals fed in a narrow 'whalebay' between the ice pack edge and the Svalbard coasts. Reports by Henry Hudson and Jonas Poole from 1607 and 1610–12 tell of thousands of whales seen in the entrance to the fjords (Hacquebord & Leinenga 1994). The area considered for the summer distribution of whales was the 300 000 km^2 between Bjornoya, Spitsbergen and the ice pack edge. The coastal part (between isobaths 0 and 200 m) of this area covers some 80 000 km^2 . In the first approach, the number of whales in the area was calculated on the assumption that the population of 46 000 individuals was distributed evenly throughout the summer grounds of 300 000 km^2 (1 whale per 7 km^2). Hence the coastal population would have numbered about 12 000 animals from the stock. In the second approach, it was assumed that the entire stock of whales fed along the coast, hence 46 000 whales were distributed among 80 000 km^2 (1 whale per 2 km^2). The maximum vertical extension of the whales' pelagic feeding was estimated to be 200 metres. The area considered for walrus feeding was delimited by the 100-metre isobath (Wiig *et al.* 1993) covering the Bjornoya and Svalbard shallows, which have a combined area of about 80 000 km^2 .

3. Results and discussion

Primary production and the food web of coastal Spitsbergen waters

The primary production is estimated to be $120 \text{ g C m}^{-2} \text{ year}^{-1}$ in the western Spitsbergen fjords and about $90 \text{ g C m}^{-2} \text{ year}^{-1}$ in the shelf waters of the Barents Sea (Eilertsen *et al.* 1989, Sakshaug *et al.* 1992, Węśławski 1993, authors' unpublished data). The principal pathways of present-day energy flow in the pelagial of Spitsbergen are summarised in Fig. 2. Currently, the top trophic levels in Spitsbergen waters are dominated by seabirds, which are prevalent in plankton consumption, while seals

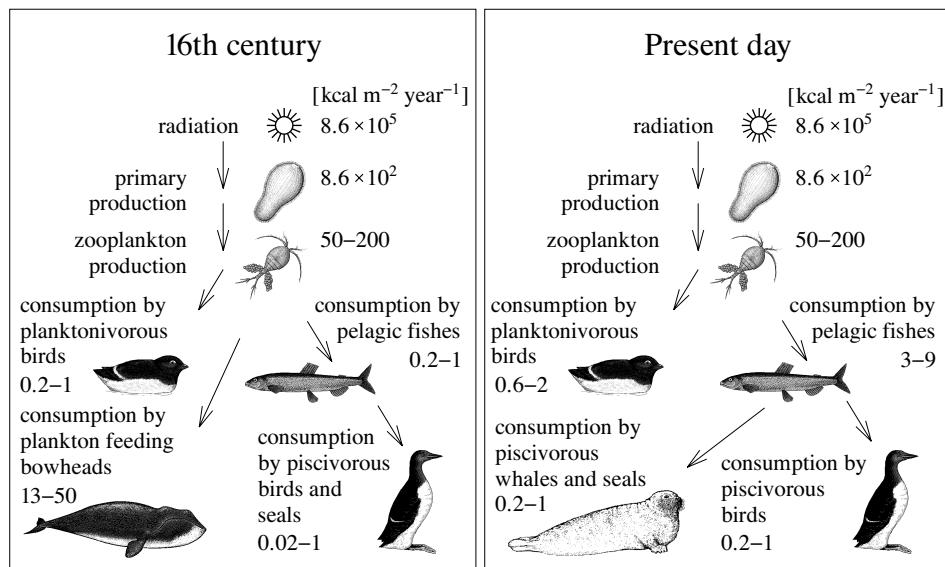


Fig. 2. Scheme of energy flow in the historical and contemporary pelagic coastal food web off Svalbard

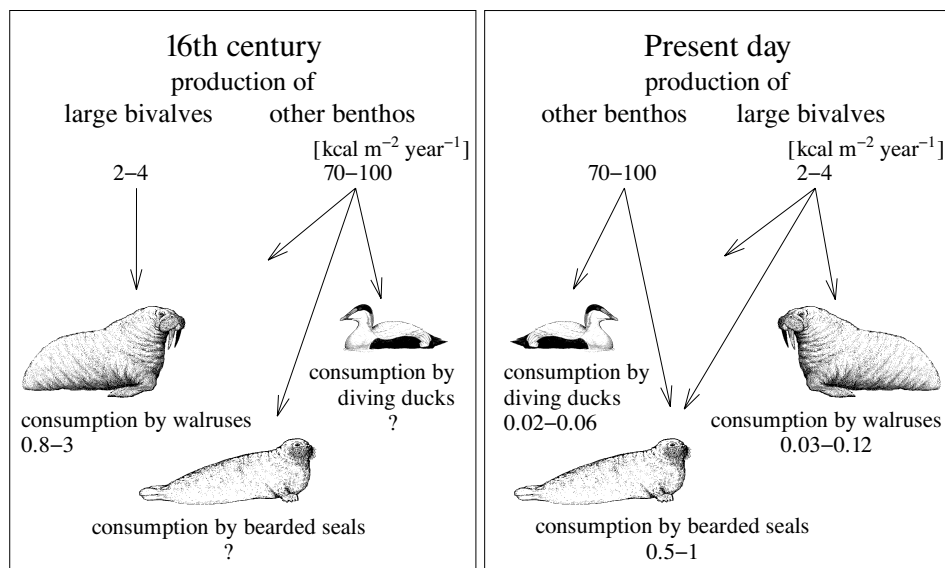


Fig. 3. Scheme of energy flow in the historical and contemporary benthic coastal food web off Svalbard

and minke whales are major fish consumers (Sakshaug *et al.* 1992, Gjosaeter 1995.) The benthic food web of shallow Spitsbergen waters is simpler (Fig. 3), with bearded seals (*Erignathus barbatus*) and diving ducks being its top consumers. Benthic feeding fish prey on smaller items and are not numerous in coastal waters (Węśławski & Kuliński 1987).

Pelagic food resources

At present the zooplankton community of the Svalbard area is dominated by the sibling species *Calanus finmarchicus* and *Calanus glacialis* in the shelf waters and by the smaller *Pseudocalanus acuspes* in the fjords (Koszteyn & Kwaśniewski 1989, Kwaśniewski 1990, Węśławski *et al.* 1991). The summer zooplankton biomass ranges from 0.1 to 5 g wet weight per m³ in the surface waters (1 g w.w. m⁻³ on average), with some 10 to 20% of the weight being contributed by macroplankton (Dalpadado & Skjoldal 1991, Węśławski 1993, authors' unpublished data). The vertical distribution of mesozooplankton in the 0–200 metre water column of the fjords and coastal waters shows that over 60% of the biomass is situated in the top 50 metres of the upper layer in summer (Węśławski 1993). The zooplankton production on the Svalbard shelf was estimated at 80–200 kcal m⁻² year⁻¹ (Sakshaug *et al.* 1992, Węśławski 1993). The value of 222 kcal m⁻² year⁻¹ given in Table 1 was obtained from the mean densities of coastal plankton.

Table 1. Pelagic food resources for Greenland whales in Svalbard coastal waters

Taxon	August mean density [indiv. m ⁻³]	Mean individual [g w.w.]	Mean energy composition [kcal g ⁻¹ d.w.]	Biomass [g d.w. (0–50 m) m ⁻²]	Biomass [g d.w. (50–200 m) m ⁻²]	Biomass [kcal (0–200 m) m ⁻²]	Production [kcal m ⁻² year ⁻¹]
copepods > 2 mm	200	0.003	5.5	7.5	3	54.6	164
amphipods	0.15	0.012	4.5	0.02	0.03	0.2	0.6
pteropods	0.5	0.056	3.6	0.35	0.53	3.2	9.5
euphausiids	0.1	0.11	5.9	0.14	0.43	3.3	10
total macroplankton				8.0	4.0	61.3	183.8

Benthic food resources

The benthos of the Svalbard shelf is dominated by Polychaeta and Bivalvia, while in some places Echinodermata or macroscopic Foraminifera may take the leading role (Gulliksen *et al.* 1985, Węśławski 1993, Pipenburg *et al.* 1995, Holte *et al.* 1996). Walrus may feed on nearly 40 different food items; nevertheless, the bulk of their food biomass is composed of the large bivalves *Mya* spp. and *Serripes* spp., and to a lesser extent by decapod crustaceans (Fay *et al.* 1977, Gjertz & Wiig 1992, Born *et al.* 1995). In the area investigated, the production of walrus food organisms, *i.e.* Bivalvia and Decapoda, is estimated to be 80 000 tonnes d.w. per year, which makes up a biomass of about 0.8 million tonnes d.w. (Table 2). Similar biomasses ranging from 10 to 400 g w.w. m⁻² of benthos are given for other Arctic areas (Thorson 1934, Gorlich *et al.* 1987, Schmid & Pipenburg 1993, Węśławski 1993, Denisenko *et al.* 1995). Soft bottom molluscs are not abundant in the Spitsbergen region and this is why the Bivalvia biomass only occasionally reaches 200 g w.w. m⁻². Such a high bivalve biomass is typical of the hard-bottom *Chlamys islandica* beds (Denisenko & Bliznicenko 1989). Welch *et al.* (1992) report an average biomass of 70 g w.w. m⁻² for *Mya truncata* from Lancaster Sound.

Table 2. Benthic food resources for walrus in Svalbard coastal waters

Prey item	Biomass class [d.w. m ⁻²]	Area [km ²]	Biomass [tonnes d.w.]	Production [g d.w. m ⁻² year ⁻¹]	Production [kcal m ⁻² year ⁻¹]	Mean production [kcal m ⁻² year ⁻¹]	Mean biomass [g d.w. m ⁻²]
	0.5	24000	12000	0.05	0.1		
Bivalvia	5	48000	24000	0.5	1		
2 kcal g ⁻¹ d.w.	150	8000	1200000	15	30		
P/B=0.1		80000	1452000			3.63	18.2
Decapoda	10	8000	80000	3	2.4		
0.8 kcal g ⁻¹ d.w.	0.01	24000	240	0.003	0.0024		
P/B=0.3	0.1	48000	4800	0.03	0.024		
		80000	85040			0.26	1.1
total Bivalvia and Decapoda			1537040			3.89	19.21

Large portions of the food item biomass (Bivalvia and Decapoda) presented in Table 2 represent items not taken by walruses (small species, juvenile specimens). The authors' observations in the Svalbard fjords indicate that some 50% of the Bivalvia population consists of full-grown individuals.

Greenland whale and walrus consumption

There are no scientific data on the food of Greenland whales from the 17th century. However, contemporary reports, such as those by Martens, Zordrager and Scoresby cited in Hacquebord (1987), tell of 'shrimps and spiders with two wings' which refers to Copepoda, Amphipoda, Euphausiacea and Pteropoda (*Limacina helicina*). A report by Anderson, an English commander (*ca* 1660), states that 'juvenile Greenland whales emerge with kelp and "sea cucumbers" on their heads', which may suggest benthic feeding. Today, an average Greenland whale consumes about 95 tonnes of mainly pelagic food per year (Lowry 1993), which is approximately 1.5% of the body mass daily (Table 3). Considering that the historical Greenland whale population was 46 000 animals and that feeding continued for 130 days from June to September in the area investigated, it follows that the annual

Table 3. Estimates of the initial Greenland whale stock and its yearly food consumption

C a t e g o r y	Individual weight [tonnes]	Number of individuals	Biomass [tonnes]	Days of feeding	Food requirement [tonnes/day/animal]	Consumption [10 ³ tonnes/season]	Consumption [kcal m ⁻² year ⁻¹]
1st approach, 12 000 whales							
calves	6	480	2880	30	0.09	1	0.02
immatures	40	5760	230400	130	0.06	449	5.62
adults	50	5760	288000	130	0.8	599	7.49
total		12000	521280			1050	13.12
2nd approach, 46 000 whales							
calves	6	1840	11040	30	0.09	5	0.06
immatures	40	22080	883200	130	0.06	1722	21.53
adults	50	22080	1104000	130	0.8	2296	28.70
total		46000	1998240			4024	50.29

consumption must have been some 4 million tonnes of plankton. Assuming that the coastal population consisted of 12 000 animals, $13 \text{ kcal m}^{-2} \text{ year}^{-1}$ was consumed in an area of $80\,000 \text{ km}^2$, or alternatively, assuming that all the stock fed in the coastal waters, consumption must have reached $50 \text{ kcal m}^{-2} \text{ year}^{-1}$ (Table 3).

The average weight of adult walrus was estimated to be 1000 kg, with adult males averaging 1200 kg and adult females averaging 800 kg (King 1983). Other authors have estimated mean walrus weights from 500 kg (Welch *et al.* 1992) to 1000 kg (Joiris *et al.* 1996). Accepting that there were 25 000 animals whose daily food intake was 5.7% of their body weight, the walrus consumption can be estimated as ranging from between 0.25 to 0.4 million tonnes wet weight yearly prior to the arrival of man in the study area (Table 4). In the Bering Sea, the population of 150 000 to 200 000 walrus consumes between 3.3 and 4.4 million tonnes of food a year (Fay *et al.* 1977). In Lancaster Sound a pod of 1000 walrus consumes 10 500 tonnes of food annually (Welch *et al.* 1992).

Table 4. Estimates of the initial walrus stock and its consumption in Svalbard coastal waters

Walrus population	Number of individuals	Mean individual weight [tonnes]	Daily individual food intake [tonnes]	Consumption [tonnes w.w. year ⁻¹]	Consumption [kcal m ⁻² year ⁻¹]
calves	3750	0.3	0.02	23406	0.20
immatures	11250	0.8	0.05	187245	1.56
adults	10000	1	0.06	208050	1.73
total	25000			418701	3

Walrus are known to consume the siphons of *Mya* spp. while the rest of the mollusc body remains in the substrate (Welch & Martin-Bergmann 1990). This feeding method supposedly consumes only 50% of the mollusc body mass, thus the actual loss of molluscs is higher than the figure calculated from the daily walrus food ratio (Welch & Martin-Bergmann 1990).

Production versus consumption

Greenland whales

Assuming that the consumption of 46 000 animals was close to 4 million tonnes (Table 3), their intake could well have been 10% of the overall zooplankton production. This is an extremely high value for a single top consumer species. In the Beaufort Sea zooplankton consumption is divided between polar cod (*Boreogadus saida*) at 93%, Greenland whales at 5.9%, seals at 1% and seabirds at less than 0.1% (Lowry 1993). According to the literature cited previously, Greenland whales consume plankton larger than 2 mm in length, with copepods (mostly *Calanus* spp.) being the smallest prey items, and krill (up to 40 mm) being the largest. Macroplankton in Svalbard coastal waters is very patchily distributed, as is usually the case in other Arctic localities (Koszteyn *et al.* 1995). In Baffin Bay plankton concentrations varied tenfold from place to place during the Greenland whale feeding period; whales can detect food concentrations, thereby taking advantage of food patchiness (Lowry 1993, Wurzig & Clark 1993). The high consumption values obtained (Table 3) show that little macroplankton was left for other consumers. According to Lydersen *et al.* (1989), Lowry (1993) and Mehlum & Gabrielsen (1993), Greenland whales compete for macroplankton with polar cod, capelin (*Mallotus villosus*), little auks (*Alle alle*), and to some extent with kittiwakes (*Rissa tridactyla*), Brunnich's guillemots (*Uria lomvia*) and black guillemots (*Cephus grylle*). The present-day consumption of plankton-feeding seabirds in southern Spitsbergen is estimated between 0.5 and 2 kcal m⁻² year⁻¹ (Fig. 2). Mehlum & Gabrielsen (1995) give 4.9 kJ m⁻² year⁻¹ (> 1 kcal) as the mean value of seabird consumption in the Barents Sea region. Polar cod and capelin are the main plankton consumers in the area investigated. Welch *et al.* (1992) report the polar cod's share of plankton consumption in Lancaster Sound to be 90%.

Walruses

In the Bering Sea and Lancaster Sound, walruses take between 1 and 0.5% of the benthos standing crop, or about 6% of the Bivalvia production (Fay *et al.* 1977, Welch *et al.* 1992). However, a confusing figure emerges if one applies conservative estimates for walrus consumption and the upper range of benthos production in the study area. It would seem that a population of 25 000 walruses in the Spitsbergen area should take 90% of the standing crop of benthic food organisms, or close to the entire production of Bivalvia (Fig. 3, Table 4). Such a situation is ecologically impossible, so even if the walrus stock were overestimated by 100%, one of the following phenomena could be in operation:

- The production and biomass of benthos was different from that of today. Galkin (1991) reported molluscs as being especially vulnerable to long-term climate change and demonstrated that during cold periods the southern Barents Sea was inhabited by larger species with a higher biomass and lower production. This is the reverse of what happens during warm periods, when small, fast-growing Atlantic species predominate.
- Walrus were taking other food in addition to Bivalvia and Decapoda. Lowry & Fay (1984), Gjertz (1990) and Born *et al.* (1995) show that adult walrus males feed to some extent on ringed seals (*Phoca hispida*) and birds. These food items are of greater significance when benthic resources are limited.
- There are ‘hot spots’ with an extremely high benthic biomass in the area. The patchiness of marine animal distribution is a very commonly observed phenomenon, and Bivalves are often observed in shoals or beds with extremely high densities (Denisenko & Bliznicenko 1989). Nevertheless, such sites are difficult to spot using the random sampling methods employed in this study area.

The scenario

Whalers, who sometimes took more than 2000 Greenland whales each year, depleted the population in the course of the eighteenth century. In the absence of the plankton-eating Greenland whales, a large amount (up to 4 million tonnes per annum) of zooplankton thus remained free for other consumers. The pelagic fish (polar cod and capelin) and little auks may well have been the first to utilise the new surplus resources. The ice-associated polar cod feeding on *Calanus* was probably the first species to benefit from the whales’ extirpation. Further south, in the Bjornoya area, the sub-Arctic populations of capelin found abundant food resources. Increasing populations of polar cod enabled fish-eating birds like Brunnich’s and common guillemots as well as Greenland seals (*Phoca groenlandica*) and minke whales (*Balaenoptera acutorostrata*) to increase their populations too. The present-day Svalbard food web is based on the planktonivorous polar cod and capelin. Both species were able to achieve huge concentrations once the major food competitors had been eliminated. Data from the Barents Sea by Sakshaug *et al.* (1992) show the annual plankton consumption by capelin and polar cod to be 6000 terajoules (the equivalent of some 12–15 million tonnes of plankton). This means that the plankton surplus left after the whales’ extinction provided almost one third of the present-day consumption by fish in the Barents Sea. To verify this scenario, a method should be developed to establish the age of the largest seabird colonies on

Spitsbergen. If the assumption presented here holds true, the colonies of plankton-feeding birds (little auks) should be the oldest, stemming from the early 18th century, because their plankton food reproduces on an annual basis. Hence the numbers of little auks may well have increased soon after the whales' extinction. Slow-growing pelagic fish, the next link in the food chain, will have required several decades at least to build up their populations. It follows therefore that the colonies of the fish-eating Brunnich's and common guillemots, ought to be younger than the little auk sites. During Dutch archaeological excavations in northwest Spitsbergen, the seabird colony at Amsterdamoya was dated to 1012 (± 60 years). However, this carbon-14 dating could be inaccurate by a few hundred years, because an unknown part of the carbon in the sediment is of marine origin. This bird rookery was mentioned in 17th-century whalers' diaries (Hacquebord own data, van der Knaap 1985). In contrast to the present authors' 'fish and birds success' scenario, Frost & Lowry (1984), Lowry (1993) and Ross (1993) have suggested that the zooplankton surplus remaining in the Beaufort Sea and the North Atlantic after the decimation of the Greenland whales was consumed by fish as well as Greenland, hooded and ringed seals. Whichever scenario is true, the former abundance of walruses must have been a limiting factor for the bearded seals, eiders (*Somateria mollissima*) and long-tailed ducks (*Clangula hyemalis*), which were the only other animals taking the same type of food in this area. According to some reports (Hazard & Lowry 1984, Lowry 1993), Greenland whales may also occasionally feed on benthos, and so are potentially in competition with the walrus. Benthic-feeding fish (flatfish, and to some extent, cod) rely mainly on *Pandalus borealis* and polychaetes (Węśławski & Kuliński 1987, Lydersen *et al.* 1989.) The commercial fishery operates on the open shelf away from the coast (Sakshaug *et al.* 1992). Therefore, it may be assumed that the elimination of walruses left a surplus of ungrazed benthos which then became available to other consumers. The number of bearded seals is estimated at between 10 000 and 100 000 individuals in Svalbard (Lydersen & Wiig 1995); no data on their historical stock are available. Eiders were reported to be heavily depleted by egg and down collection in the early 20th century (Lovenskjold 1964), but recently the species has recovered to some 140 000 birds (Prestrud & Mehlum 1991).

The Barents Sea ecosystem and its food web is regarded as very unstable as it undergoes pronounced variations in primary productivity, zooplankton biomass and pelagic fish stocks each year. On the other hand, the marine mammals have been described as a stable element in the system (Węśławski & Adamski 1987, Węśławski & Kwaśniewski 1990, Sakshaug *et al.* 1994). One explanation of this is the flexibility of the top predators in selecting

their prey. It may be concluded that Greenland whales and walrus were the principal consumers in the pelagic and the benthic food web before the arrival of man on Svalbard. Both these large mammal species played an important part, functioning as buffers and upholding the stability of the coastal Svalbard ecosystem.

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