



Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords

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Abstract: The food and foraging strategy of fifteen species of seabirds and sea mammals from two high Arctic fjords were analysed. One of the fjords, Kongsfjord, is strongly influenced by warm waters from the Atlantic, while Hornsund is of a more Arctic character. Prey species in the Atlantic waters were more diverse (82 species and 16 functional groups) compared to those of Arctic waters (67 prey species and 14 functional groups). The consumption of top predators from Hornsund in the peak season of July was estimated at $2.86 \cdot 10^6$ MJ, while that in Kongsfjord was $1.35 \cdot 10^6$ MJ. For the analysed function of the ecosystem (the transfer of energy to the top trophic levels) the specific character of prey species is of key importance and not the diversity, abundance or biomass *per se*. Lower species diversity and biomass in Arctic waters is compensated for by the occurrence of larger individuals of these species, which permits top predators to prey directly on lower trophic levels.

Key words: Arctic, climate change, food web, ecosystem function.

Introduction

The functions of ecosystem are considered a feasible measure of biodiversity importance (Palmer *et al.* 1997; Emmerson and Raffaelli 2000; Emmerson *et al.* 2001; Loreau *et al.* 2001; Duffy 2002). Functions analysed by the above investigators include primary and secondary productivity, nutrient fluxes, carbon fixation, organic matter mineralization and suspension removal. These functions are also considered ecosystem services – those that might be valued by man (Snelgrove *et al.* 2004). So far there have been no experimental or direct observational data on the links between biodiversity and marine ecosystem function (Karl *et al.* 2001; Bolam *et al.* 2002). Most of the cited authors state that there are particular roles of

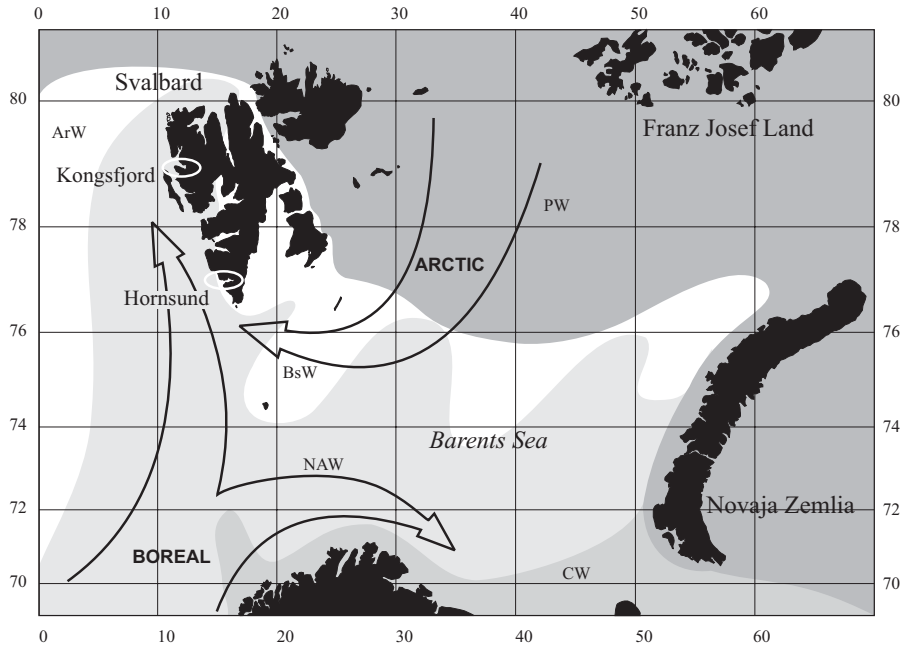


Fig. 1. The study area in European Arctic and occurrence of main water masses. Shading reflects the water masses marked as: PW – Polar Water, BsW – Barents sea Water, NAW – North Atlantic Water, CW – Coastal Water, ArW – Arctic Water.

the species which are significant in maintaining key ecosystem functions, and not the biodiversity (or species richness) or biomass *per se*. However, the role of biodiversity might be very complex and hidden in the presence of different functional groups (Bolam *et al.* 2002).

The present study compares two similar marine ecosystems from the high Arctic. The first, Kongsfjord (79°N), is supplied with Atlantic waters from the West Spitsbergen Current (Figs 1 and 2) and is potentially rich with pelagic and benthic fauna of Northern Atlantic origin (Hop *et al.* 2002; Svendsen *et al.* 2002). The second, Hornsund fjord (77°N), is under the influence of mixed local waters (Swerpel 1985) that carry a reduced, predominantly Arctic species pool (Węśławski *et al.* 1999; Gulliksen *et al.* 1999).

The energy transfer to the top trophic levels (seabirds and sea mammals) was designated here as the indicative ecosystem function. Food web studies from both fjords are relatively numerous and include vertebrate stomach analysis (Węśławski and Kuliński 1987, Lydersen *et al.* 1989; Węśławski *et al.* 1994), the energetics of food consumption and marine food intake assessments (Stempniewicz and Węśławski 1992, Mehlum and Gabrielsen 1993, 1995). Despite the fact that the dominant species in the examined food web are not numerous (polar cod – *Boreogadus saida*, three species of copepods – *Calanus*, three species of euphausiids – *Thysanoessa*, two species of pelagic amphipods – *Themisto*), the vari-

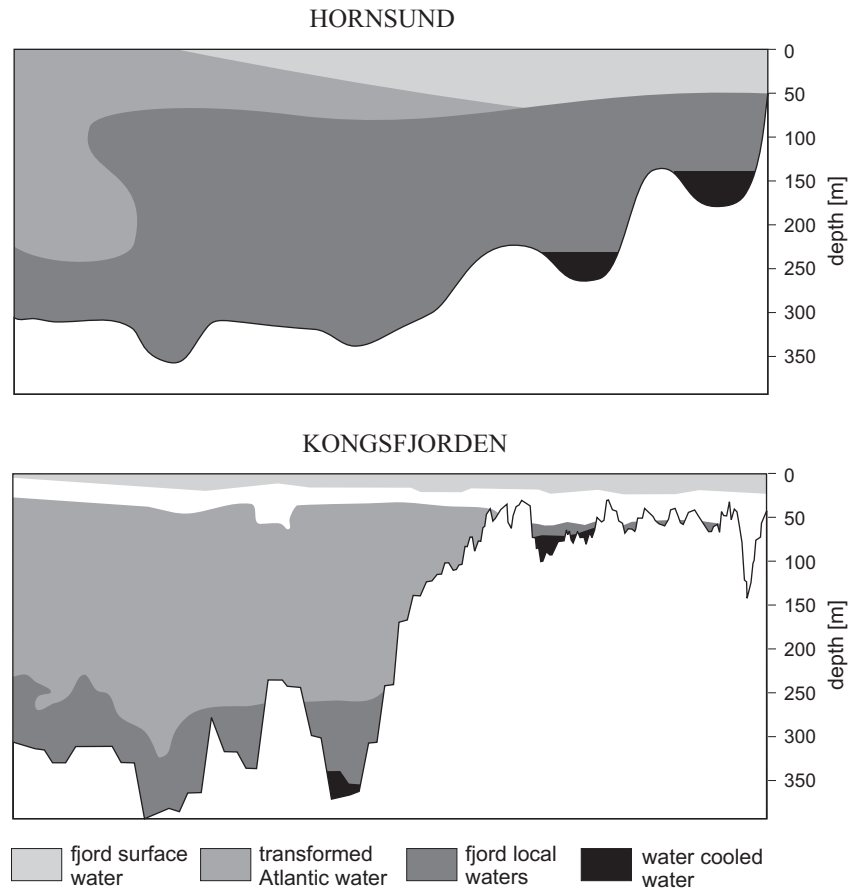


Fig. 2. The cross section of two fjords showing the distribution of water masses in Hornsund and Kongsfjord during summer (hydrology after Beszczyńska-Möller and Walczowski (2003); www.iopan.gda.pl).

ety of food items consumed is high, with a large proportion of rare and accessory species consumed (Lydersen *et al.* 1989; Węśławski *et al.* 1994).

The productivity of large areas of the sub-Arctic (the Arctic Norwegian Sea and West Spitsbergen) is relatively high (primary production of 80–120 g C/m² year in coastal waters: Eilertsen *et al.* 1989; Sakshaug *et al.* 1992). There are no reasons to expect major differences in primary productivity between Hornsund and Kongsfjord since primary production is highly seasonal, mainly local, and associated with fast ice, ice edge and coastal, mixed waters (Eilertsen *et al.* 1989; Wiktor 1999). On the other hand, a large part of zooplankton production and biomass is advected into the study area (Kwaśniewski *et al.* 2003; Edvardsen *et al.* 2003).

A recent examination of extensive data on seabird marine food from the North Atlantic indicates that the species-rich, productive Norwegian Sea (boreal area) supports 1.8 million pairs of seabirds, while the equally productive but spe-

Table 1
 Characteristics of top predators considered in present study. Data on predator abundance and consumption of prey (MJ – mega joules) was adopted from sources cited in the text. Individual consumption is presented as amount of energy needed by mean individual in the course of July.

Predator	Mean body mass [kg]	mean individual consumption in July [MJ]	number of ind. in Kongsfjord	number of ind. in Hornsund	Kongsfjord July consumption [MJ]	Hornsund July consumption [MJ]
Arctic tern (<i>Sterna paradisaea</i>)	0.1	7	3000	2000	21000	14000
Little auk (<i>Alle alle</i>)	0.2	14	2000	100000	28000	1400000
Black guillemot (<i>Cepphus grylle</i>)	0.4	14	200	1000	2800	14000
Kittiwake (<i>Rissa tridactyla</i>)	0.4	22	10400	10000	228800	220000
Puffin (<i>Fratercula arctica</i>)	0.5	17	50	100	850	1700
Fulmar (<i>Fulmarus glacialis</i>)	0.7	24	2000	10000	48000	240000
Brunnich's guillemot (<i>Uria lomvia</i>)	0.8	31	3400	10000	105400	310000
Common eider (<i>Somateria mollissima</i>)	1.8	81	8000	4000	648000	324000
Glaucous gull (<i>Larus hyperboreus</i>)	1.8	68	200	700	13600	47600
Ringed seal (<i>Pusa hispida</i>)	40	176	400	400	70400	70400
Harbour seal (<i>Phoca vitulina</i>)	70	520	15		7800	0
Bearded seal (<i>Erignathus barbatus</i>)	200	1162	100	100	116200	116200
Walrus (<i>Odobenus rosmarus</i>)	800	812	5		4060	0
White whale (<i>Delphinapterus leucas</i>)	800	811	50	50	40550	40550
Minky whale (<i>Balaenoptera acutorostrata</i>)	5000	3206	5	5	16030	16030
total July consumption (MJ)*10 ⁶			1.35*10 ⁶	2.86*10 ⁶	1.4	2.8

cies-poor Barents Sea (Arctic area) provides food for 6 million pairs of seabirds (Barret *et al.* 2002). An examination of sea-mammal consumption suggests the same pattern since polar areas are typically depicted as areas of mass sea mammal occurrence (Hunt 1991; Sakshaug *et al.* 1992; Mehlum *et al.* 1998).

Similar to the Barents and Norwegian seas, the two fjords (Arctic Hornsund and boreal Kongsfjord) model generally the two climatic/biogeographic provinces on a small scale. This work is based on the reexamination of the extensive data collected by present authors and mostly published before in different context. We are presenting a discussion paper, with the new concept of the relations between biodiversity, climate and ecosystem function. This concept says that Arctic system, with lower prey biomass and diversity, supports more top predators in comparison to the more diversified and biomass-rich boreal system. This problem is approached by the comparison of data from the Arctic influenced Hornsund and the Atlantic influenced Kongsfjord.

Materials and methods

The general hydrology of waters of Svalbard archipelago (Fig. 1) is adopted from papers by Loeng (1991) and Koszteyn *et al.* (1995). The hydrology of two examined fjords is presented after the www.iopan.gda.pl/projects/biodaf data collected by Agnieszka Beszczyńska-Möller and Waldemar Walczowski, from the summer r/v *Oceania* cruises (Fig. 2). The CTD measurements were collected from undulated Seabird Sonde and partly presented in the paper by Beszczyńska-Möller *et al.* (1997).

The data on zooplankton density come from papers by Koszteyn and waśniewski (1989), Węśławski *et al.* (1991a), Koszteyn *et al.* (1995) and Kwaśniewski *et al.* (2003). Zooplankton samples have been collected with the use of WP-2 nets of 200 mm mesh size and closing device, hauled vertically in three discrete layers of the upper 100m (surface water, mixing zone and below pycnocline). Table 2 presents only zooplankton data (the species known as prey items of seabirds and seals) from 0–50 m layer only, averaged for 1 m³. Individual values of plankton species biomass were derived from the authors' measurements, unless otherwise cited from the papers of Mumm (1991) and Karnovsky *et al.* (2003). Biomass is presented in wet weight of preserved specimens, and the data on the energy of specific species were taken from Szaniawska and Wołowicz (1986) and Węśławski and Kwaśniewski (1990). The energy content, expressed in kJ/m³, was obtained by multiplying the individual species energy value by its relative abundance arbitrarily assigned for each species (1 – for present, 2 – for rather abundant, 3 – for very abundant) based on the authors' own data from the area. Each prey species was assigned to specific functional group defined as a combination of mobility mode and feeding type (Table 2).

The occurrence of specific species of benthic animals (seabirds and sea mammals prey species only, Table 3) was taken from the authors' own observations, some of which were published in Włodarska *et al.* (1998, 2001). The sessile benthos density class have been assessed from Van Veen grab samples, while the density of motile benthic animals (shrimps, carrion feeding amphipods) have been assessed from light epibenthic sledge trawls (unpublished own data). Among the mobile benthos the species density varied within the same order of magnitude in both fjords; only *Pandalus borealis* and demersal fishes had a higher coefficient in Kongsfjord, which distinctly emphasizes their more common occurrence in this fjord as compared to Hornsund. The data on biology of individual benthic species come from year-round field observations partly published by Węśławski and Legeżyńska (2002). Each prey species was assigned to specific functional group, defined as a combination of mobility type and feeding mode (Table 3).

The energy demand (consumption) for individual predator species was adopted from Hop *et al.* (2002), where radiochemical methods were the main technique used. The population size of predators from Kongsfjord was taken from Hop *et al.* (*op.cit.*), based on census of seal breeding pairs and direct counts of other animals.

Table 2
Pelagic prey items taken by seabirds and sea mammals in upper 50m. (Explanations: C1 – CV copepodit stages; F– females, M – males; relative abundance expressed as: 1 – present, 2 – rather abundant, 3– very abundant; functional groups defined as combination of mobility type and feeding type – symbols for mobility: gs – good swimmer, ms – moderate swimmer, s – sympagic, mp – mesopelagic; symbols for feeding type: h – herbivore, sc – small carnivore, lc – large carnivore).

taxon over 3 mm length	density class [ind/m ³]	indiv.ww [mg]	energy content [kJ/g]	functional group	relative abundance Hornsund	relative abundance Kongsfjord	energy cont. Hornsund [kJ/m ³]	energy cont. Kongsfjord [kJ/m ³]
POLYCHAETA								
<i>Nereis virens</i>	1	60	18	gs–lc	1	1	1.1	1.1
CRUSTACEA								
<i>Calanus finmarchicus</i> , CV–VIM	1000	0.8	25	ms–h	1	3	20.2	60.6
<i>Calanus glacialis</i> , CV	1000	1	17.4	ms–h	3	2	51.1	34.1
<i>Calanus glacialis</i> , CVIF	1000	1.2	16	ms–h	3	2	59.9	39.9
<i>Calanus glacialis</i> , CVIM	1000	1.2	16	ms–h	3	2	59.9	39.9
<i>Calanus hyperboreus</i> , CIII	1000	0.8	25	ms–h	1	2	20.2	40.4
<i>Calanus hyperboreus</i> , CIV	1000	1	17.4	ms–h	1	2	17.0	34.1
<i>Calanus hyperboreus</i> , CV	1000	1.2	16	ms–h	1	2	20.0	39.9
<i>Calanus hyperboreus</i> , CVIF	1000	2.3	16.7	ms–h	1	2	38.0	75.9
<i>Erythropus erythropthalma</i>	1	2	17	ms–sc	1	2	0.0	0.1
<i>Eualus gaimardi</i> , larvae	10	2	17	ms–h	1	2	0.3	0.7
<i>Eupagurus pubescens</i> , zoea	10	1.2	16	ms–h	1	2	0.2	0.4
<i>Gammarus wilkitzkii</i>	1	11.2	17	s–sc	2		0.4	
<i>Heterorhabdus norvegicus</i> , CIV–CVI	10	0.8	25	ms–h		1		0.2
<i>Hyas</i> sp., megalopa	1	1	20	ms–h		1		0.02
<i>Hyas</i> sp., zoea	1	0.8	20	ms–h	1	2	0.02	0.03
<i>Hyperia medusarum</i>	1	3.8	15.6	ms–sc		1		0.1
<i>Lebbeus polaris</i> , larvae	10	2	17	ms–h	1	1	0.3	0.3
<i>Meganyctiphanes norvegica</i>	1	50	20	gs–h		1		1.0
<i>Metridia longa</i> , CVI	10	0.8	25	ms–h	1	2	0.2	0.4
<i>Mysis oculata</i>	1	24	21	ms–sc	3	2	1.5	1.0
<i>Onisimus</i> sp. <i>nansenii</i>	1	10	15	s–sc	1		0.2	
<i>Pareuchaeta norvegica</i> , CIV	1	0.8	25	ms–sc		1		0.02

Table 2 – continued.

taxon over 3 mm length	density class [ind/m ³]	indiv.ww [mg]	energy content [kJ/g]	functional group	relative abundance Hornsund	relative abundance Kongsfjord	energy cont. Hornsund [kJ/m ³]	energy cont. Kongsfjord [kJ/m ³]
<i>Pareuchaeta norvegica</i> , CV	1	1.2	16	ms-sc		1		0.02
<i>Pleuromamma robusta</i>	1	0.8	25	ms-h		1		0.02
<i>Sabinea septemcarinata</i> , larvae	10	2	17	ms-h	1	2	0.3	0.7
<i>Stilomysis grandis</i>	1	30	21	ms-sc		1		0.6
<i>Themisto abyssorum</i>	10	5.4	18.4	ms-sc	1	2	1	2.0
<i>Themisto gaudichaudi</i>	1	4	17	ms-sc		1		0.1
<i>Themisto libellula</i>	10	8	17	s-sc	3	2	4.1	2.7
<i>Themisto sp juveniles</i>	10	1	16	ms-sc	2	3	0.3	0.5
<i>Thysanoessa inermis</i>	1	16.5	17	gs-h	1	3	0.3	0.8
<i>Thysanoessa longicaudata</i>	1	40	17	gs-h		1		0.7
<i>Thysanoessa rashii</i>	1	40	17	gs-h		1		0.7
<i>Thysanoessa sp.</i> , furciliae	1	2.9	15.9	ms-h		1		0.1
<i>Thysanoessa sp.</i> , calyptopis	1	2	15	ms-h		1		0.03
MOLLUSCA								
<i>Clione limacina</i>	10	40	16	ms-sc	3	2	19.2	12.8
<i>Limacina helicina</i>	1	0.8	25	ms-h	2	2	0.04	0.04
<i>Limacina retrovesa</i>	1	0.4	23.6	ms-h		1		0.01
CHAETOGNATHA								
<i>Eukhronia hamata</i>	1	3.8	15.6	ms-sc	1	2	0.1	0.1
<i>Sagitta elegans</i>	10	11.2	17	ms-sc	3	2	5.7	3.8
TUNICATA								
<i>Fritillaria borealis</i>	1	0.1	25.7	ms-h		2		0
<i>Oikopleura vanhoeffeni</i>	1	0.1	25.7	ms-h		1		0
PISCES								
<i>Bentosema glaciale</i>	1	100	24	mp-sc		1		2.4
<i>Boreogadus saida</i>	1	400	24.2	gs-ls	3	2	29.0	19.4
<i>Boreogadus saida</i> , larvae	1	4	20	ms-sc	3	2	0.2	0.2
<i>Gadus morrhua</i>	1	400	24	gs-ls		2		19.2
<i>Mallotus villosus</i>	1	400	24	gs-lc		1		9.6
<i>Sebastes mentela</i> , larvae	1	200	21	gs-sc		1		4.2
number of species					29	47		
mean relative energy content kJ/m³					351	448		
number of functional groups					5	7		
number of species per functional group					6	7		

Table 3

Benthic prey items taken by seabirds and sea mammals. Functional groups defined as combination of mobility and feeding type. Frequency of occurrence expressed as 1 – present, 2 – common, 3 – abundant. Symbols for mobility: dm – discretely motile, m – motile, s – sedentary. Explanations: symbols for feeding type: f – filtrator, lcf – large carrion feeder, scf – small carrion feeder, df – detritus feeder, sc – small carnivore, c – carnivore, h – herbivore.

taxon over 3 mm length	density class [ind/m ³]	indiv.ww [g]	energy content [kJ/g]	functional group	relative abundance Hornsund	relative abundance Kongs-fjord	energy cont. Hornsund [kJ/m ³]	energy cont. Kongs fjord [kJ/m ³]
CRUSTACEA								
<i>Ampelisca macrocephala</i>	10	0.08	14	dm-f	1	2	11	22
<i>Anonyx laticoxae</i>	1	0.1	15	m-lcf	1	1	2	2
<i>Anonyx nugax</i>	10	0.15	15	m-lcf	1	1	23	23
<i>Anonyx sarsi</i>	10	0.08	15	m-lcf	2	2	24	24
<i>Atylus carinatus</i>	1	0.08	14	m-df	1	1	1	1
<i>Caprella septentrionalis</i>	10	0.03	13	dm-df	1	2	4	8
<i>Diastylis goodsiri</i>	10	0.08	13	dm-df	1		10	0
<i>Eualus gaimardi</i>	1	0.25	17	m-sc	1	1	4	4
<i>Eudorella emarginata</i>	10	0.03	13	dm-df		2	0	8
<i>Eupagurus pubescens</i>	1	0.4	14	dm-lcf	1	1	6	6
<i>Gammarellus homari</i>	10	0.1	16	m-df	2	2	32	32
<i>Gammarus oceanicus</i>	100	0.05	15	m-df	1	2	75	150
<i>Gammarus setosus</i>	100	0.05	15	m-df	2	1	150	75
<i>Halirages fulvocinctus</i>	1	0.03	14	m-df	1	2	0	1
<i>Hyas araneus</i>	1	0.5	14	m-c	1	1	7	7
<i>Ischyrocerus</i> spp.	10	0.01	13	m-h	1	2	1	3
<i>Lebbeus polaris</i>	1	0.25	16	m-scf	1	2	4	8
<i>Onisimus caricus</i>	10	0.05	15	m-lcf	1	1	8	8
<i>Onisimus edwardsi</i>	100	0.03	15	m-scf	1	2	45	90
<i>Onisimus littoralis</i>	100	0.03	15	m-scf	1	2	45	90
<i>Orchomenella minuta</i>	10	0.01	15	m-scf	1	1	2	2
<i>Pandalus borealis</i>	10	0.5	16	m-sc		3	0	240
<i>Sabinea septemcarinata</i>	1	0.25	16	m-sc	2	1	8	4
<i>Sclerocrangon boreas</i>	1	0.5	16	m-sc		1	0	8
<i>Sclerocrangon ferox</i>	1	0.25	16	m-sc	1		4	0
<i>Spirontocaris spinus</i>	1	0.25	16	m-sc	1	2	4	8
<i>Spirontocaris turgida</i>	1	0.25	16	m-sc		2	0	8
<i>Stegocephalus inflatus</i>	1	0.08	15	m-df		1	0	1.2
<i>Synidotea nodulosa</i>	10	0.03	14	m-df	1	1	4	4
<i>Weyprechtia pinguis</i>	1	0.13	15	m-df		1	0	2
MOLLUSCA								
<i>Buccinum undatum</i>	1	0.5	16	dm-c	1	2	8	16
<i>Chlamys islandicus</i>	10	0.5	16	s-f		1	0	80
<i>Ciliatocardium ciliatum</i>	1	0.25	16	s-df	1	1	4	4

Table 3 – *continued.*

taxon over 3 mm length	density class [ind/m ³]	indiv.ww [g]	energy content [kJ/g]	functional group	relative abundance Hornsund	relative abundance Kongs-fjord	energy cont. Hornsund [kJ/m ³]	energy cont. Kongs fjord [kJ/m ³]
<i>Hyatella arctica</i>	10	0.25	15	s-f	1	2	38	75
<i>Margarites margaritacea</i>	10	0.03	16	dm-h	2	2	10	10
<i>Mya truncata</i>	10	0.3	15	s-df	1	1	45	45
POLYCHAETA								
<i>Bylgides sarsi</i>	1	0.13	16	m-c	1	1	2	2
ECHINODERMATA								
<i>Cucumaria frondosa</i>	1	1.25	12	dm-f	1	1	15	15
<i>Strongylocentrotus droebachiensis</i>	1	0.75	15	dm-h	1	2	11	23
PISCES								
<i>Agonus decagonus</i>	1	0.5	21	m-c	1	1	11	11
<i>Careproctus reinhardti</i>	1	0.25	21	m-c		1	0	5
<i>Eumicrotremus spinosus</i>	1	0.15	16	m-c	1	1	2	2
<i>Leptoclinus maculatus</i>	1	0.25	21	m-c	2	2	11	11
<i>Liparis liparis</i>	1	0.5	21	m-c	1	1	11	11
<i>Lycodes vahli</i>		0.5	21	m-c		2		
<i>Myoxocephalus scorpius</i>	1	0.5	17	m-c	1	1	9	9
<i>Triglops pingeli</i>	1	0.25	17	m-c	1	1	4	4
number of species					38	45		
mean relative energy content kJ/m²					652	1158		
number of functional groups					9	9		
number of species per functional group					4	5		

For Hornsund the predators density was taken from numerous seabirds counts summarized in Anker-Nielsen *et al.* (2000) and from own unpublished data (Table 1, Fig. 3).

Discussion

Climate – biogeographical settings. — It is widely believed that the earliest manifestation of global climate change will occur in the Atlantic sector of the Arctic (Marshall *et al.* 2001; Maslowski *et al.* 2001; Watson *et al.* 2001). It has even been estimated that within fifty years the ice cover in the Arctic may completely disappear (Johannessen *et al.* 1999). The Svalbard archipelago lies on the border of the sub-Arctic-boreal and high Arctic maritime province (Dunbar 1968) and experiences the effects of shifting climatic zones or biogeographical provinces. This shift was observed from the late nineteenth century (cold period) to the mid twentieth

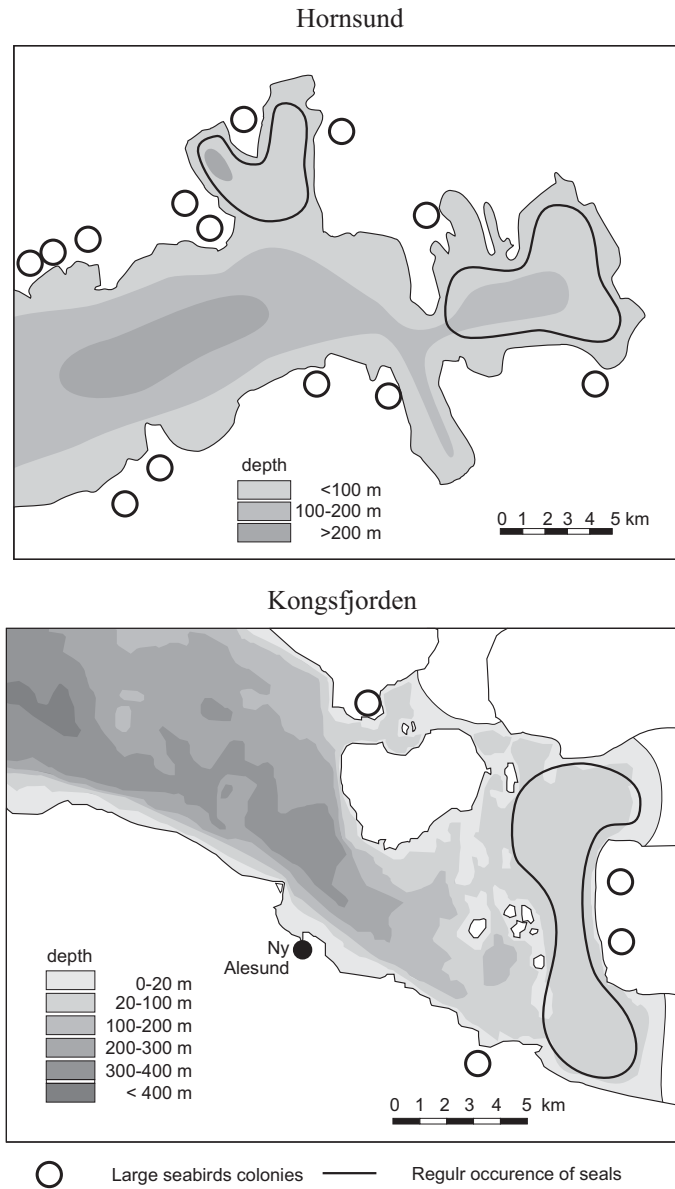


Fig. 3. The occurrence of top predators in Hornsund and Kongsfjorden during summer.

century (warm period) through the massive displacement of both benthic and pelagic marine organisms (Blacker 1957). More recently there was a cooling period in 1960–1975, and then continuous warming since the end of the 1980s (Marshall *et al.* 2001). On a shorter time scale the occasional colder or warmer years are manifested by the rapid advance of the cold Arctic water mass or the warm West Spitsbergen Current, each transporting pelagic organisms characteristic of the particular water

mass (Węśławski and Adamski 1987; Węśławski and Kwaśniewski 1990; Dalpadado *et al.* 2003). Physical phenomena, such as water mass advances, are short time events driven by complicated hydrological mesoscale features like eddies or moving fronts (Piechura and Walczowski 1995). The net volume of Atlantic water advected to Svalbard fluctuates from 5.0 to 8.7 Sv interannually (Osiński *et al.* 2003). The interannual changes in the occurrence of the key Atlantic pelagic species *Themisto abyssorum*, associated with Atlantic water inflow fluctuations, are no more dramatic at a 40% deviation from the multi-year mean (Koszteyn *et al.* 1995; Wencki 1999). However, there are reports indicating that there is a higher zooplankton biomass in the Atlantic compared to Arctic waters entering the Svalbard area (*e.g.* Skjoldal *et al.* 1992; Gjosaeter 1995). Węśławski *et al.* (1999a, b) determined the relative energy content in mesozooplankton from Atlantic waters to be 11.3 kJ/m³, while that in Arctic waters was 3.8 kJ/m³. Dalpadado *et al.* (2003) reported a higher mean biomass of zooplankton in Atlantic waters within a range of 25–30% more in comparison to that of Arctic waters. It is worth noting that the higher biomass in Arctic compared to Atlantic plankton was found in large plankton items only (samples obtained with coarse net of 0.5 mm mesh size; Karnovsky *et al.* 2003).

Diversity of respective biota. — The species diversity and distribution of fauna on the Svalbard shelf and in the fjords is relatively well known (Klekowski and Węśławski 1990; Gulliksen *et al.* 1999). The number of invertebrate species associated with the Arctic water mass (East Svalbard) is lower (700) in comparison to that (820) from the Atlantic (West coast of Svalbard); however, the sampling effort was not equal in these two areas (Gulliksen *et al.* 1999). The vast faunal reservoir in the boreal latitudes outnumbers the diversity of true Arctic species – 30.000 species in the North Atlantic (Costello *et al.* 2001) *versus* some 5000 species throughout the Arctic (Sirenko 2001). This trend is seen along the Eurasian shore; there are over 4000 species along the coast of Norway, 3245 species in the Atlantic-influenced Barents Sea, 1671 species in the Kara Sea, and only 1011 species in the purely Arctic East Siberian Sea (Brattegard and Holthe 1997; Sirenko 2001). A decline in the species richness from the boreal to the Arctic areas is not reflected in all taxonomic groups; for example, Polychaeta are represented by 263 species in Northern Norway and 251 species in Svalbard (Oug 2000). Within the Svalbard fjords, a sharp drop in species diversity is observed in the brackish, inner fjord basins subjected to massive freshwater and sediment discharge from melting glaciers (Węśławski *et al.* 1995; Zajączkowski and Legeżyńska 2001; Włodarska *et al.* 1998). Benthic and planktonic species are poorly represented in silted, inner fjord basins, although the abundance and biomass of macroplankton can be high (Węśławski *et al.* 2000).

Predators and prey. — Major populations of Arctic seabirds and mammals inhabit Hornsund and Kongsfjord (Table 1, Fig. 3). Their prey consists predominantly of pelagic and benthic crustaceans and fishes (Tables 2 and 3). The smallest prey items taken by the top predators listed in Table 2 are 0.8 mg (4 mm long) copepods

Table 4
Examples of twin species of boreal and Arctic origin

prey taxon	Arctic	boreal
genus	species	species
<i>Calanus</i> spp.	<i>glacialis</i>	<i>finmarchicus</i>
average size (mm)	6	4
ind. biomass (mg dw) – adult female	0.6	0.2
life span	3yr	1yr
<i>Themisto</i> spp.	<i>libellula</i>	<i>abyssorum</i>
average size (mm)	42	25
ind. biomass (mg dw) – adult female	65	15
life span	4yr	2yr
<i>Gammarus</i> spp.	<i>wilkitzkii</i>	<i>oceanicus</i>
average size (mm)	45	30
ind. biomass (mg dw) – adult female	150	75
life span	4yr	2.5yr

consumed massively by little auk in summer. The average size of the fish (juvenile *Boreogadus saida*) consumed by piscivorous seabirds and seals ranges from 10 to 15 cm (Węśławski *et al.* 1994). Some key prey species are closely equivalent in the two systems compared; for example, the Arctic *Calanus glacialis* is replaced in Atlantic waters by *Calanus finmarchicus* (Table 4). The Arctic calanoid species are larger and richer in energy compared to its warm water relative. This is an example of the tendency of Arctic taxa to accumulate longer fatty acid chains and store more energy in comparison to their southern relatives as was presented for euphausiids by Falk-Petersen *et al.* (1990). This difference is also related to longevity and the seasonal accumulation of the energy needed to survive winter starvation (Węśławski *et al.* 1991a). Although fishes constitute the majority of prey of top predators in the two fjords studied, fishes are not very abundant there. The main stocks of pelagic fishes are linked to the shallow shelves of the Barents and Norwegian seas (Skjoldal *et al.* 1992). The most important fish prey, polar cod (*Boreogadus saida*), is abundant in both fjords studied in Svalbard, and this might be considered a local phenomenon (Gulliksen 1984; Lønne and Gulliksen 1989).

Consumption. — The energy content of prey items, individual size and availability are most important factors in their selection by predators (Table 5). Other include prey density and frequency of occurrence. Dispersed (not forming aggregations) or rare species are not key food items for top predators (Knox 1994). The diets of the fifteen seabirds and sea mammal species common in Svalbard fjords overlap partially and a few prey taxa are the key elements (Lydersen *et al.* 1989). Field metabolic rates and energy requirements are known for almost all the Svalbard predators and their seasonal energy demand has been estimated to be $2.86 \cdot 10^6$ MJ in Hornsund in July and $1.35 \cdot 10^6$ MJ in Kongsfjord at the same time (Table 1).

Table 5
Examples of habitats and niche separation among age cohorts of the same species in Arctic amphipods

Taxon	<i>Themisto libellula</i> , adults	<i>T. libellula</i> , 2nd year	<i>T. libellula</i> , 1st year
Size	30–45mm	15–30mm	5–15mm
Depth	0–50m	0–100m	0–100m
Prey	copepods	small copepods	microplankton
habitat	ice, pelagial	pelagial	pelagial
Taxon	<i>Gammarellus homari</i> , adults	<i>G. homari</i> , 2nd year	<i>G. homari</i> , juveniles
Size	30–35mm	15–30mm	5–10mm
Depth	15–30m	5–20m	0–5m
Prey	meiofauna	detritus, meiofauna	microalgae
habitat	macrophytes	macrophytes	stones, detritus, algae

Scenario of breeding strategy. — The following scenario was developed basing on the data presented above. The high diversity in the Atlantic-influenced Kongsfjord is connected with generally high macrofauna biomass, but the individual sizes of the prey species tend to be smaller. On the contrary, the lower diversity of the Arctic biota in Hornsund is associated with lower biomass, but the body size of individual species is larger. The low water temperature at high latitudes favors the *K* strategy in marine poikilotherms – slow growth, low fecundity, long life span, large size (Clarke 1979, 1991; Sainte-Marie 1991). Recent findings show that oxygen availability may have similar effects to those of temperature. In oxygen-rich conditions (often associated with cold water) amphipods attain significantly larger sizes (Chapelle and Peck 1999). Higher temperatures permit faster growth in marine poikilotherms, shorter life cycles, higher fecundity and smaller body size, *i.e.* the *r* type of strategy, as was demonstrated for North Atlantic amphipods (Steele and Steele 1975) and confirmed for Svalbard as well (Węśławski and Legeżyńska 2002). Crustacean species with wide geographic distribution tend to be smaller and have a one-year life cycle in the warmer, southern range of its occurrence, while northern populations live 2+ years and attain maximal size (Steele and Steele 1975; Van Dolah and Bird 1980; Koszteyn *et al.* 1995).

Biodiversity. — The two contrasting breeding strategies are linked to biodiversity. The *r* strategy, which combines numerous offspring and high mortality, might be linked to enhanced interspecific competition that promotes diversity on both the genetic and, consequently, species levels. The *K* strategy, with its limited number of offspring, increased survival rates, and a long life span, leads to the lower diversity. Arctic marine invertebrates with a long life span have separate, annual age cohorts (Dunbar 1957). Not only do different age groups vary in size, but they are spatially separated as well. Younger specimens inhabit shallower areas closer to shore in comparison with areas inhabited by the older size-age groups

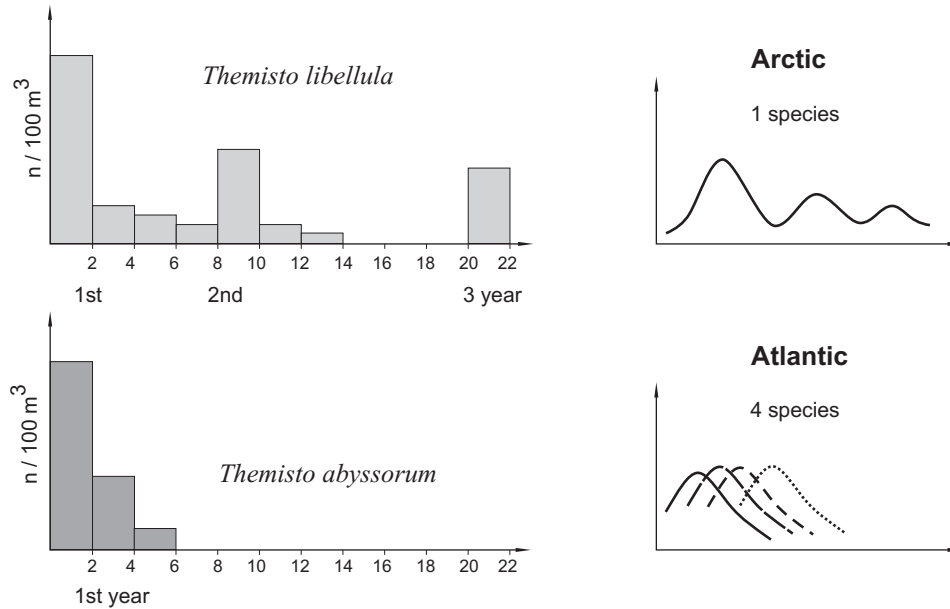


Fig. 4. Size separation of annual cohorts in a population of long living pelagic species *T. libellula* versus uniform size frequency in population of annual species *T. abyssorum*. Ideograms present the size frequency in population of single perennial species (Arctic), versus the size frequency in sample containing four different annual species (Atlantic).

(Table 6). This is typical of the free-moving crustaceans in Svalbard (Węśławski and Legeżyńska 2002). Size-age separation of individuals and ontogenic migration has been described for the very large bathypelagic amphipod *Eurythenes gryllus* (Smith and Baldwin 1984; Hargrave 1985). The different age-size amphipod cohorts feed on different food; juveniles are more herbivorous and detritophagous, while older specimens become increasingly carnivorous (Węśławski 1990; Legeżyńska 2001).

In ecological terms, the annual cohorts act as separate species. In this respect, taxonomic richness of invertebrates in high latitudes is low but it is compensated by the presence of “ecological species”. There are two pelagic hyperiids, *Themisto abyssorum* and *Themisto compressa*, in the Southern Barents and Norwegian Seas. They both have a one-year life span, and the size difference between newborn juveniles and mature adults ranges from 2mm to 8mm (Kosztajn *et al.* 1995). These species have only one Arctic counterpart, *Themisto libellula*, which lives from three to four years and attains lengths of up to 40mm (Dunbar 1957; Kosztajn *et al.* 1995). Its population consists of three separate annual cohorts that might well be regarded as three different “ecological species” (Fig. 4).

This concept of the existence of “ecological species” in the Arctic may help to explain patterns in latitudinal diversity. The drop in marine faunal species diver-

sity from low to high latitudes (Gray 2001) is not as significant when we consider that in the Arctic, three-fold more species exist in ecological terms, *i.e.*, if all multi-annual species are recognized .

Temperature increase (or its equivalent, the Atlantic water inflow into the Arctic) not only leads to enhanced zooplankton development (Dalpadado *et al.* 2003). It is also related to the northward advance of smaller species, as was demonstrated in long-term changes in the North Sea mesozooplankton (Beaugrand *et al.* 2002).

Does increased diversity means better function or service?

Węśławski *et al.* (1999b) and Karnovsky *et al.* (2003) demonstrated that the little auk (*Alle alle*) is a selective predator that feeds only on energy-rich, Arctic species of zooplankton *Calanus* (*C. glacialis* and *C. hyperboreus*) and ignores the abundant population of smaller, energy-poor Atlantic species (*C. finmarchicus*). Arctic top predators, which have at their disposal a range of large, nutritional invertebrates, can rely on shortened food chains. For example, kittiwakes (*Rissa tridactyla*) that feed on the herbivorous Arctic planktonic sea snail, *Limacina helicina*, may not repeat this strategy in the Atlantic water mass where the local sea snail *Limacina retroversa* is twenty-fold smaller. Optimal foraging strategy does not necessarily lead to the grounds with the highest biomass and diversity. Energy-rich food might be concentrated locally along hydrological fronts or “trophic traps” in inner fjord basins. These basins, with poor biomass and low diversity, have been reported as key feeding grounds for seabirds and sea mammals because the prey items are concentrated near the surface in restricted areas of water mixing (Hartley and Fisher 1936; Stott 1936; Mehlum and Gabrielsen 1993; Mehlum *et al.* 1998; Węśławski *et al.* 2000).

The Antarctic pelagic food web is strongly dominated by a single species – the large, long-living invertebrate herbivore *Euphausia superba* (Knox 1994). The diversity of the pelagic community in the Antarctic is not very high, at least not higher than that in the Arctic (Walkusz *et al.* 2003). As in the Arctic, the Antarctic food web supports a huge number of top predators that rely heavily on krill and a shortened food chain (Knox 1994). Barrett *et al.* (2002) demonstrated that Norwegian Sea birds take only 1–5% of the invertebrate prey, while Barents seabirds consume 10–25% of this resource. Within the Arctic province, Brunnich’s guillemots (*Uria lomvia*) take more crustaceans in their northern range of occurrence in Franz Josef Land (80°N) in comparison with the population from Bjornoya (74°N) (Barret *et al.* 1997). When the little auk migrates from its wintering grounds in the Norwegian Sea, to the colonies in the Arctic, its diet shifts from fishes to copepods (Stempniewicz 2001).

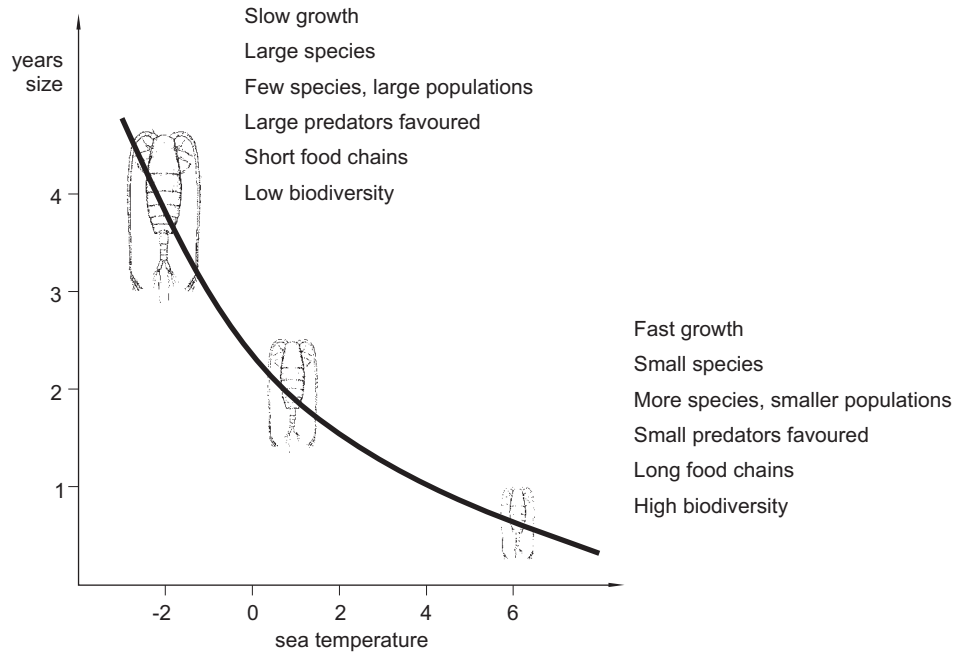


Fig. 5. The relation between sea temperature, poikilotherms growth, life span and biodiversity from Arctic to boreal conditions.

Conclusion

Being primarily piscivorous, seabirds and sea mammals in the Arctic have at their disposal a secondary, but very important and predictable, food source – large and energy-rich herbivorous invertebrates (Fig. 5). Since the boreal ecosystem lacks this reserve, if the fish stocks fail, there may be a food shortage for the top predators. The high diversity of prey, combined with smaller species size in the boreal domain, favours small predators, mainly fishes. The low species diversity in Arctic waters is linked to the larger body size and richer energy stores of the prey, and this favours large predators such as seabirds and mammals. Observed climate change may have lasting effects on the position of predators in the warming Arctic ecosystem.

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