



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

Jan Marcin WĘSŁAWSKI¹, Sławomir KWAŚNIEWSKI¹, Lech STEMPNIEWICZ²
and Katarzyna BŁACHOWIAK-SAMOŁYK¹

¹ *Instytut Oceanologii, Polska Akademia Nauk, Powstańców Warszawy 55, 81-712 Sopot, Poland*
<weslaw@iopan.gda.pl> <kwas@iopan.gda.pl> <kasiab@iopan.gda.pl>

² *Instytut Biologii, Uniwersytet Gdański, Legionów 9, 80-441 Gdańsk, Poland*
<biols@univ.gda.pl>

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

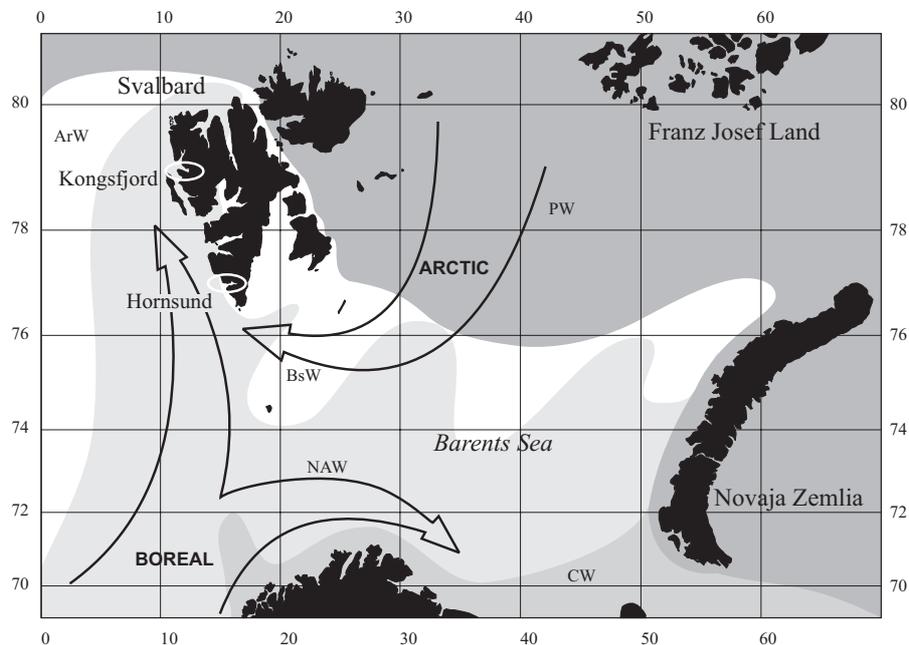


Fig. 1. The study area in European Arctic and occurrence of main water masses. Shading reflects the water masses marked as: PW – Polar Water, BsW – Barents sea Water, NAW – North Atlantic Water, CW – Coastal Water, ArW – Arctic Water.

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 in this paper 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-

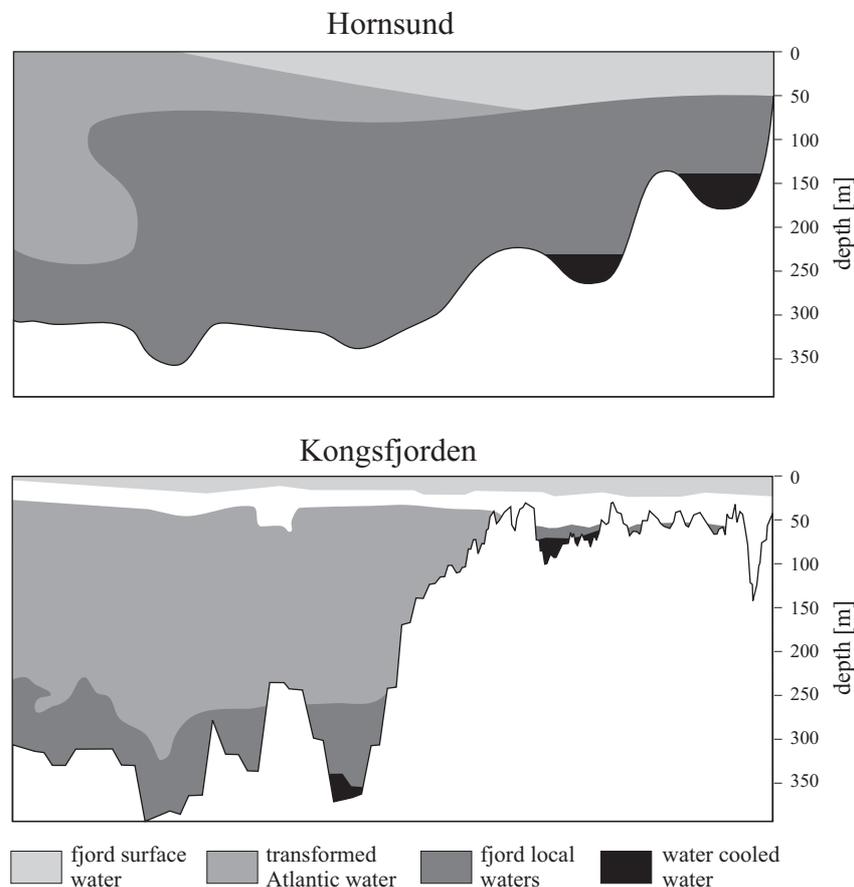


Fig. 2. The cross section of two fjords showing the distribution of water masses in Hornsund and Kongsfjord during summer (hydrology after Beszczyńska-Möller and Walczowski (2003); www.iopan.gda.pl).

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 Kwaśniewski (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 with 200 µm 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>nanseni</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 Kongs-fjord	energy cont. Hornsund [kJ/m ³]	energy cont. Kongs fjord [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 compressa</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

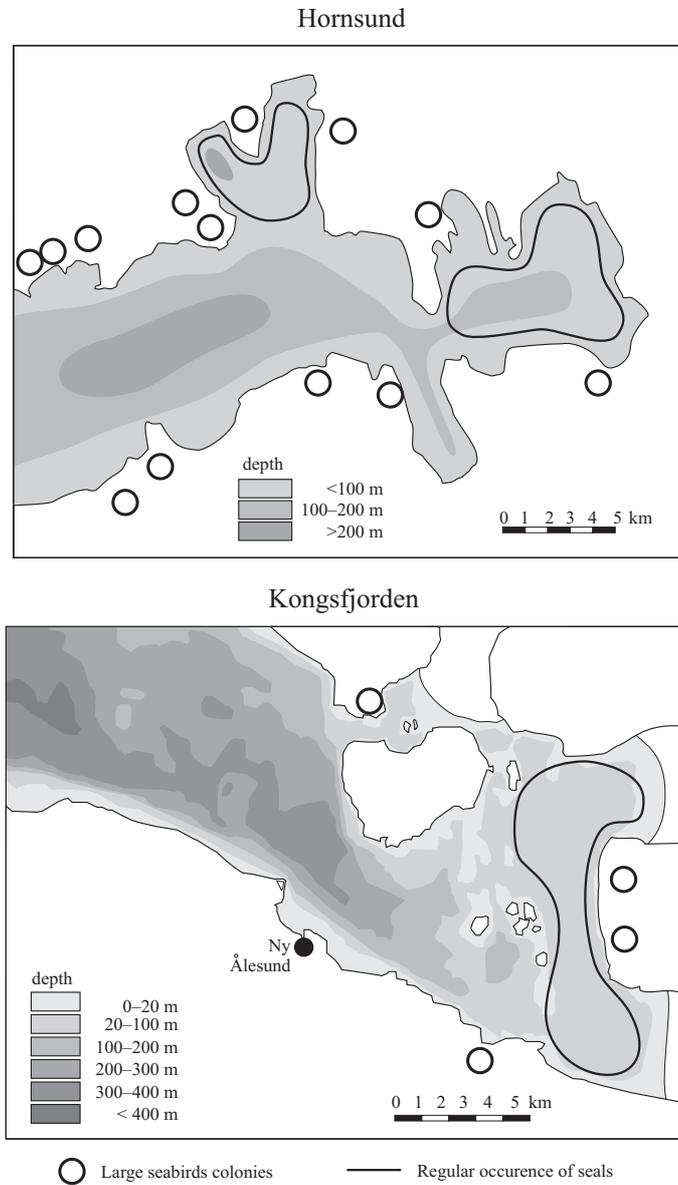


Fig. 3. The occurrence of top predators in Hornsund and Kongsfjorden during summer.

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 and benthic organisms characteristic of the partic-

ular 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 of prey 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.

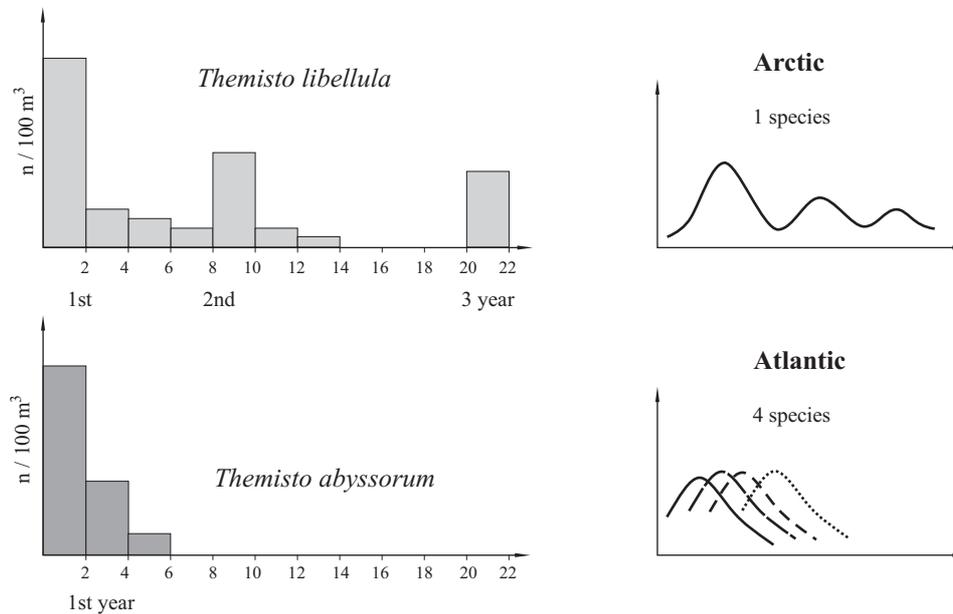


Fig. 4. Size separation of annual cohorts in a population of long living pelagic species *T. libellula* versus uniform size frequency in population of annual species *T. abyssorum*. Ideograms present the size frequency in population of single perennial species (Arctic), versus the size frequency in sample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

This is typical of the free-moving crustaceans in Svalbard (Węstawski 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 (Węstawski 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 2 mm to 8 mm (Koszteyn *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; Koszteyn *et al.* 1995). Its population consists of three separate annual cohorts of different feeding ecology 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).

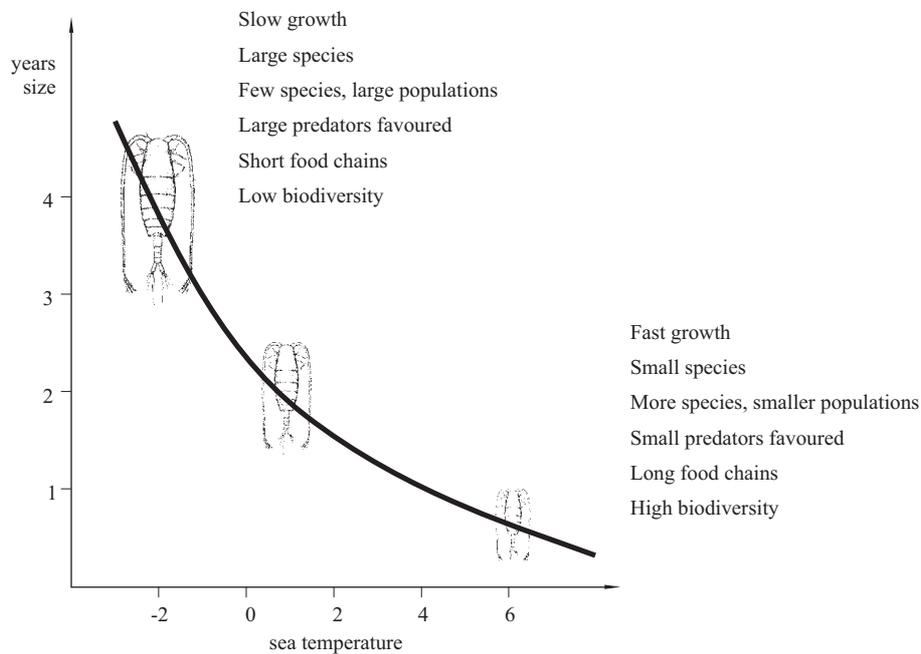


Fig. 5. The relation between sea temperature, poikilotherms growth, life span and biodiversity from Arctic to boreal conditions.

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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References

- ANKER-NILSSEN T., BAKKEN V., STØRM H., GOLOVKIN A.N., BIANKI V.V. and TATARINKOVA I.P. 2000. The status of marine birds breeding in the Barents Sea region. *Norsk Polarinstittutt Rapport* 113: 1–213.
- BARRETT R.T., ANKER-NILSSEN T., GABRIELSEN G.W. and CHAPDELAINE G. 2002. Food consumption by seabirds in Norwegian waters. *ICES Journal of Marine Science* 59: 43–57.
- BARRETT R.T., BAKKEN V. and KRASNOV Y. 1997. The diets of common and Brunnich's guillemots *Uria aalga* and *Uria lomvia* in the Barents Sea. *Polar Research* 16: 73–84.
- BEAUGRAND G., REID P.C., IBANEZ F., LINDLAY J.A. and EDWARDS M. 2002. Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science* 296: 168–170.
- BESZCZYŃSKA-MÖLLER A., WĘSŁAWSKI J.M., WALCZOWSKI W. and ZAJĄCZKOWSKI M. 1997. Estimation of glacial meltwater discharge into Svalbard coastal waters. *Oceanologia* 39: 289–298.
- BLACKER R.W. 1957. Benthic animals as indicators of hydrological conditions and climatic changes in Svalbard waters. *Fisheries Investigations* 2: 1–49.
- BOLAM S.G., FERNANDES T.F. and HUXHAM M. 2002. Diversity, biomass and ecosystem processes in the marine benthos. *Ecological Monographs* 72: 599–615.
- BRATTEGARD T. and HOLTHE T. 1997. *Distribution of marine benthic macro-organisms in Norway. A tabulated catalogue*. Research Report for DN 1997-1, Trondheim: 1–409.
- CHAPELLE G. and PECK L.S. 1999. Polar gigantism dictated by oxygen availability. *Nature* 399: 114–115.
- CLARKE A. 1979. On living in cold water: K strategies in Antarctic benthos. *Marine Biology* 55: 111–119.
- CLARKE A. 1991. What is polar adaptation and how we should measure it? *American Zoologist* 3: 81–92.
- COSTELLO M.J., EMBLOW C. and WHITE C. (eds) 2001. European Register of Marine Species. *Patrimoine naturels* 50: 463 pp.
- DALPADADO P., INGVALDSEN R. and HASSEL A. 2003. Zooplankton biomass variation in relation to climatic conditions in the Barents Sea. *Polar Biology* 26: 233–241.
- DUFFY J.E. 2002. Biodiversity and ecosystem function: the consumer connection. *OIKOS* 99: 201–219.
- DUNBAR M.J. 1957. The determinants of production in northern seas. A study on the biology of *Themisto libellula*. *Canadian Journal of Zoology* 35: 797–819.
- DUNBAR M.J. 1968. *Polar Ecosystems. Study in evolution*. Prentice Hall Inc.: 1–198.
- EDVARSDEN A., TANDE K.S. and SLAGSTAD D. 2003. The importance of advection on production of *Calanus finmarchicus* in the Atlantic part of the Barents Sea. *Sarsia* 88: 261–273.
- EILERTSEN H.C., TAASEN J.P. and WĘSŁAWSKI J.M. 1989. Phytoplankton studies in the fjords of West Spitsbergen: physical environment and production in spring and summer. *Journal of Plankton Research* 11: 1245–1260.
- EMMERSON M.C. and RAFFAELLI D.G. 2000. Detecting the effects of diversity on measures of ecosystem function: experimental design, null models and empirical observations. *OIKOS* 91: 195–203.
- EMMERSON M.C., SOLAN M., EMES C., PATERSON D.M. and RAFFAELLI D. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* 411: 73–77.
- FALK-PETERSEN S., HOPKINS C.C.E. and SARGENT J.R. 1990. Trophic relationships in the pelagic, Arctic food web. In: M. Barnes and R.N. Gibson (eds) *Trophic relationships in the marine environment*. Aberdeen University Press: 315–333.
- GJOSAETER H. 1995. Pelagic fish and ecological impact of the modern fishing industry in the Barents Sea. *Arctic* 48: 267–278.
- GRAY J.S. 2001. Marine diversity: the paradigms in patterns of species richness examined. *Scientia Marina* 65: 41–56.
- GULLIKSEN B. 1984. Under-ice fauna from Svalbard waters. *Sarsia* 69: 17–23.

- GULLIKSEN B., PALERUD R., BRATTEGARD T. and SNELI J. 1999. Distribution of marine benthic macro-organisms at Svalbard (including Bear Island) and Jan Mayen. Research Report for DN 1999-4. Directorate for Nature Management, Trondheim: 1-148.
- HARGRAVE B.T. 1985. Feeding rates of abyssal scavenging amphipods (*Eurythenes gryllus*) determined *in situ* by time-lapse photography. *Deep Sea Research* 32: 443-450.
- HARTLEY C.H. and FISHER J. 1936. The marine foods of birds in an inland fjord region in West Spitzbergen. *Journal of Animal Ecology* 5: 370-389.
- HOP H., PEARSON T., HEGSETH E.N., KOVACS K.M., WIENCKE C., KWAŚNIEWSKI S., EIANE K., MEHLUM F., GULLIKSEN B., WŁODARSKA-KOWALCZUK M., LYDERSEN C., WĘŚLAWSKI J.M., COCHRANE S., GABRIELSEN G.W., LEAKEY R.J.G., LØNNE O.J., ZAJĄCZKOWSKI M., FALK-PETERSEN S., KENDALL M., WANGBERG S.A., BISCHOF K., VORONKOV A.Y., KOVALTCHOUK N.A., WIKTOR J., POLTERMANN M., DIPRISCO G. and PAPUCCI C. 2002. The marine ecosystem of Kongsfjord, Svalbard. *Polar Research* 2: 67-208.
- HUNT G.L., Jr 1991. Marine birds and ice-influenced environments of polar oceans. *Journal of Marine Systems* 2: 233-240.
- JOHANNESEN O.M., SHALINA E.V. and MILES M. 1999. Satellite evidence for an Arctic Sea Ice cover in transfer. *Science* 286: 1937-1939.
- KARL D.M., BIDIGARE R.R. and LETELIER R.M. 2001. Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: the domain shift hypothesis. *Deep Sea Research part II* 48: 1449-1470.
- KARNOVSKY N.J., KWAŚNIEWSKI S., WĘŚLAWSKI J.M., WALKUSZ W. and BESZCZYŃSKA-MÖLLER A. 2003. Foraging behaviour of little auks in a heterogenous environment. *Marine Ecology Progress Series* 253: 289-303.
- KLEKOWSKI R.Z.K. and WĘŚLAWSKI J.M. 1990. *Atlas of the marine fauna of southern Spitsbergen. Vol. I Vertebrates*. Ossolineum, Wrocław: 308 pp.
- KNOX G.A. 1994. *Ecosystem change resulting from Exploitation*. Cambridge University Press, Cambridge: 349-355.
- KOSZTEYN J. and KWAŚNIEWSKI S. 1989. Comparison of fjord and shelf mesozooplankton communities of the southern Spitsbergen region. *Rapports de Conseil Exploration de la Mer* 188: 164-169.
- KOSZTEYN J., TIMOFEEV S., WĘŚLAWSKI J.M. and MALINGA B. 1995. Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in European Arctic seas. *Polar Biology* 15: 85-92.
- KWAŚNIEWSKI S., HOP H., FALK-PETERSEN S. and PEDERSEN G. 2003. Distribution of *Calanus* species in Kongsfjord, a glacial fjord in Svalbard. *Journal of Plankton Research* 25: 1-20.
- LEGEŻYŃSKA J. 2001. Distribution patterns and feeding strategies of lysianassoid amphipods in shallow waters of an Arctic fjord. *Polish Polar Research* 22: 173-186.
- LOENG H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research* 10: 5-18.
- LØNNE O.J. and GULLIKSEN B. 1989. Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. *Polar Biology* 9: 187-191.
- LOREAU M., NAEEM S., INCHAUSTI P., BENGTSOON J., GRIME J.P., HECTOR A., HOOPER D.U., HUSTON M.A., RAFFAELLI D., SCHMID B., TILMAN D. and WARDLE D.A. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294: 804-808.
- LYDERSEN Ch., GJERTZ I. and WĘŚLAWSKI J.M. 1989. Stomach contents of autumn feeding marine vertebrates from Hornsund, Svalbard. *Polar Record* 25: 107-114.
- MARSHALL J., KUSHNER Y., BATTISTI D., CHANG P., CZAJA A., DICKSON R., HURRELL J., MCCARTNEY M., SARAVANAN R. and VISBECK M. 2001. North Atlantic climate variability; phenomena, impacts and mechanisms. *International Journal of Climatology* 21: 1863-1898.
- MASLOWSKI W., MARBLE D.C., WALCZOWSKI W. and SEMTNER A.J. 2001. On large scale shifts in the Arctic Ocean and sea ice conditions during 1979-1998. *Annales of Glaciology* 33: 345-550.

- MEHLUM F. and GABRIELSEN G.W. 1993. The diet of high Arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. *Polar Research* 11: 1–20.
- MEHLUM F. and GABRIELSEN G.W. 1995. Energy expenditure and food consumption by seabird populations in the Barents Sea region. In: H.R. Skjoldal *et al.* (eds) *Ecology of fjords and coastal waters*. Elsevier, Amsterdam: 457–470.
- MEHLUM F., HUNT G.L., DECKER M. and NORDLUND N. 1998. Hydrographic features, cetaceans and the foraging of Thick-billed murre and other marine birds in the northwestern Barents Sea. *Arctic* 51: 243–252.
- MUMM N. 1991. On the summerly distribution of mesozooplankton in the Nansen Basin, Arctic Ocean. *Berichte zur Polarforschung* 92: 1–146.
- OSIŃSKI R., BESZCZYŃSKA-MÖLLER A. and GOSZCZKO I. 2003. ADCP – referenced geostrophic velocity and transport in the West Spitsbergen Current. *Oceanologia* 45: 425–435.
- OUG E. 2000. *The marine benthic fauna in the region of Tromsø; northern Norway, with particular reference to bristle worms (Annelida; Polychaeta)*. Norwegian College of Fishery Science, University of Tromsø, PhD thesis introduction: 31 pp.
- PALMER M.A., COVICH A.P., FINLAY B.J., GILBERT J., HYDE K., JOHNSON R., KAIRESAALOM T., LAKE S., LOVELL C. and NAIMAN R. 1997. Biodiversity and ecosystem processes in freshwater sediments. *Ambio* 26: 571–577.
- PIECHURA J. and WALCZOWSKI W. 1995. The Arctic front. Structure and dynamics. *Oceanologia* 37: 47–73.
- SAINTE-MARIE B. 1991. A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. *Hydrobiologia* 223: 189–227.
- SAKSHAUG E., BJØRGE A., GULLIKSEN B., LOENG H. and MEHLUM F. 1992. *Økosystem Barentshavet. (The Barents Sea ecosystem)*. Norwegian Research Council and Ministry of Environment: 304 pp.
- SIRENKO B.I. (ed.) 2001. List of species of free living invertebrates of Eurasian Arctic seas and adjacent deep waters. *Exploration of the fauna of the seas* 51 (59): 1–129.
- SKJOLDAL H.R., GJOSAETER H. and LOENG H. 1992. The Barents Sea ecosystem in the 1980s: ocean, climate, plankton and capelin growth. *ICES Marine Science Symposia* 195: 278–290.
- SMITH K.L. and BALDWIN R.J. 1984. Vertical distribution of the necrophagous amphipod *Eurythenes gryllus* in the North Pacific. Spatial and temporal variation. *Deep Sea Research* 31 10A: 1179–1196.
- SNELGROVE P.V.R., AUSTEN M., GAREY J.R., HAWKINS S.J., ILIFFE T., KNEIB R.T., LEVIN L.A., WĘSŁAWSKI J.M. and WHITLATCH R.B. 2004. Ecosystem Services Provided by Marine Sedimentary Biota and Their Vulnerability to Anthropogenic Disturbance. In: D.H. Wall (ed.) *SCOPE 64, Sustaining biodiversity and ecosystem services in soils and sediments*, Island Press, Washington: 275 pp.
- STEELE D.H. and STEELE V.J. 1975. Egg size and duration of embryonic development in Crustacea. *International Revue für gesellschaft Hydrobiologie* 60: 711–715.
- STEMPNIEWICZ L. 2001. *Alle alle* Little Auk. The Journal of the Birds of the Western PaleArctic. *Birds of the Western PaleArctic (BWP) Update*, vol. 3: 175–201. Oxford University Press.
- STEMPNIEWICZ L. and WĘSŁAWSKI J.M. 1992. Outline of trophic relationships in Hornsund fjord, SW Spitsbergen (with special consideration of seabirds). In: K.W. Opaliński and R.Z. Klekowski (eds) *Landscape, life world and Man in High Arctic*, Instytut Ekologii Polskiej Akademii Nauk, Warszawa: 271–298.
- STOTT F.C. 1936. The marine foods of birds in an inland fjord region in west Spitsbergen. *Journal of Animal Ecology* 5: 356–369.
- SVENDSEN H., BESZCZYŃSKA-MÖLLER A., HAGEN J.O., LEFAUCONNIER B., TVERBERG V., GERLAND S., ØRBÆK J.B., BISCHOF K., PAPUCCI C., ZAJĄCZKOWSKI M., AZZOLINI R., BRULAND O., WIENCKE C., WINTHER J.-G. and DALLMANN W. 2002. The physical environment of Kongsfjord-Krossfjorden, an Arctic fiord system in Svalbard. *Polar Research* 21: 133–166.

- SWERPEL S. 1985. The Hornsund fjord; water masses. *Polish Polar Research* 6: 475–496.
- SZANIAWSKA A. and WOŁOWICZ M. 1986. Changes in the energy content of common species from Hornsund, SW Spitsbergen. *Polar Research* 4: 85–90.
- VAN DOLAH R.F. and BIRD E. 1980. A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods. *Estuarine and Coastal Shelf Science* 11: 593–604.
- WALKUSZ W., STOREMARK K., SKAU T., GANNEFORS C. and LUNDBERG M. 2003. Zooplankton community structure; a comparison of fjords, open water and ice stations in the Svalbard area. *Polish Polar Research* 24: 149–165.
- WATSON R.T. and CORE WRITING TEAM (eds). 2001. *Climate change 2001: Synthesis report*. IPCC, Geneva: 184 pp.
- WENCKI K. 1999. Interannual variability in the occurrence of *Themisto* (Amphipoda) in the north Norwegian Sea. *Polish Polar Research* 21: 143–152.
- WĘSŁAWSKI J.M. 1990. Distribution and ecology of south Spitsbergen coastal marine Amphipoda (Crustacea). *Polskie Archiwum Hydrobiologii*. 37: 503–519.
- WĘSŁAWSKI J.M. and ADAMSKI P. 1987. Cold and warm years in South Spitsbergen coastal marine ecosystem. *Polish Polar Research* 8: 95–106.
- WĘSŁAWSKI J.M. and KULIŃSKI W. 1987. Notes on the fishes in Hornsund fjord area (Spitsbergen). *Polish Polar Research* 10: 241–250.
- WĘSŁAWSKI J.M. and KWAŚNIEWSKI S. 1990. The consequences of climate fluctuations for the food web in Svalbard coastal waters. In: M. Barnes and R.N. Gibson (eds) *Proceedings of 24th EMBS Symposium, Trophic relationships in the marine environment*. Aberdeen University Press: 315–333.
- WĘSŁAWSKI J.M. and LEGEŻYŃSKA J. 2002. Life cycles of some Arctic amphipods. *Polish Polar Research* 23: 253–264.
- WĘSŁAWSKI J.M., KWAŚNIEWSKI S. and WIKTOR J. 1991b. Winter in a Svalbard fjord ecosystem. *Arctic* 44: 115–123.
- WĘSŁAWSKI J.M., PEDERSEN G., FALK-PETERSEN S. and PORAZIŃSKI K. 2000. Entrapment of macrozooplankton in an Arctic fjord basin, Kongsfjord, Svalbard. *Oceanologia* 42: 57–69.
- WĘSŁAWSKI J.M., RYG M., SMITH T.G. and ØRITSLAND N.A. 1994. Diet of Ringed seals (*Phoca hispida*) in fjord of West Svalbard. *Arctic* 47: 109–114.
- WĘSŁAWSKI J.M., STEMPNIEWICZ L., MEHLUM F. and KWAŚNIEWSKI S. 1999b. Summer feeding strategy of the Little Auk (*Alle alle*) from Bjørnøya, Barents Sea. *Polar Biology* 21: 129–134.
- WĘSŁAWSKI J.M., JANKOWSKI A., KWAŚNIEWSKI S., SWERPEL S. and RYG M. 1991a. Summer hydrology and zooplankton in two Svalbard fjords. *Polish Polar Research* 12: 445–460.
- WĘSŁAWSKI J.M., KOSZTEYN J., KWAŚNIEWSKI S., STEMPNIEWICZ L. and MALINGA M. 1999a. Summer food resources of the little auk (*Alle alle*) in the European Arctic seas. *Polish Polar Research* 20: 387–403.
- WĘSŁAWSKI J.M., KOSZTEYN J., ZAJĄCZKOWSKI M., WIKTOR J. and KWAŚNIEWSKI S. 1995. Fresh water in Svalbard fjord ecosystems. In: H.R. Skjoldal, Hopkins C.C., Erikstad K.E. and H.P. Leinaas (eds), *Ecology of fjords and coastal waters*. Elsevier Sci. BV: 229–241.
- WIKTOR J. 1999. Early spring microplankton development under fast ice covered fjords of Svalbard, Arctic. *Oceanologia* 41: 51–72.
- WŁODARSKA-KOWALCZUK M. and WĘSŁAWSKI J.M. 2001. Impact of climate warming on Arctic benthic biodiversity: a case study of two Arctic glacial bays. *Climate Research* 18: 127–132.
- WŁODARSKA-KOWALCZUK M., WĘSŁAWSKI J.M. and KOTWICKI L. 1998. Spitsbergen glacial bays macrobenthos – a comparative study. *Polar Biology*: 20: 66–73.
- ZAJĄCZKOWSKI M. and LEGEŻYŃSKA J. 2001. Estimation of zooplankton mortality caused by an Arctic glacier outflow. *Oceanologia* 43: 341–351.

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