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Warming in the Arctic May Result in the Negative Effects of Increased Biodiversity

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Abstract: Warming in the European Arctic means not only sea-ice melt and temperature increase, it also means the increasing advance of Atlantic waters to high latitudes with the North Atlantic Current. Atlantic water comes from a biologically diverse marine region, and it supplies species to the relatively species-poor Arctic. The pelagic herbivores (copepods, pteropods, krill) from the relatively warm Atlantic water mass are smaller compared to the cold-water Arctic herbivore species. Top predators of the Arctic (seabirds, seals, whales) feed efficiently on these relatively large herbivores, often without any intermediate small predators between the herbivores and the top predators. The process of warming causes a switch in the food web from large, Arctic herbivores to smaller Atlantic species, thus reducing the food resources available to the top predators. In the warmer Arctic, primary production is utilized by smaller, faster-growing species. Additionally, small carnivores are becoming more diversified and numerous, which dissipates the energy flow. In this way, warming means there is higher biodiversity in the Arctic and simultaneous food shortages for the top predators.

Zusammenfassung: Eine Erwärmung der europäischen Arktis bedeutet nicht nur Zunahme der Temperatur und Schmelzen des Meereises, es bedeutet ebenfalls ein zunehmendes Eindringen atlantischer Wassermassen in hohe Breiten. Atlantische Wassermassen stammen aus biologisch anderen Meeresgebieten und importieren neue Organismen in die relativ Arten arme Arktis. Die pelagischen Herbivoren (Copepoden, Pteropoden, Krill) aus den relativ warmen Atlantischen Wassermassen sind kleiner im Vergleich zu den arktischen Kaltwasser-Herbivoren. Top-Predatoren der Arktis (Seevögel, Robben, Wale) ernähren sich effizient von diesen großen Herbivoren, häufig ohne Zwischenstufen zwischen Herbivoren und Top-Predatoren. Der Erwärmungsprozess führt zu einer Veränderung im Nahrungsgefüge von großen, arktischen Herbivoren zu kleineren atlantischen Arten, was zu einer Reduzierung der verfügbaren Nahrungsquellen für die Top-Predatoren führt. In einer wärmeren Arktis wird die Primärproduktion von kleineren, schneller wachsenden Arten genutzt. Zusätzlich werden die kleinen Karnivoren Arten reicher und zahlreicher, was den Energiefluss verändert. In dieser Hinsicht bedeutet Erwärmung der Arktis eine größere Biodiversität und gleichzeitig einen Nahrungsmangel für die Top-Predatoren.

WARMING OF THE EUROPEAN ARCTIC

Extensive reports on climate change in the Arctic (ACIA 2004) show that the European Arctic sector is probably the Northern hemisphere region that is warming the fastest, and this is associated with the increasing inflow of Atlantic waters into the Fram Strait (HOP et al. 2006, WALCZOWSKI & PIECHURA 2006). These warm waters carry Atlantic plankton and dispersal stages of benthic animals that are represented by much smaller individuals and much less rich in energy in comparison to their cold-water relatives (WĘSŁAWSKI et al. 1999, BUCHOLZ et al. 2009). Boreal, North Atlantic waters host more benthic and pelagic species (approximately 20,000 taxa; ERMS 2009) compared to the Arctic domain (about 2500 taxa in the vicinity of Svalbard (GULLIKSEN et al. 1999). The density of plankton in Atlantic waters is high (HOP et al. 2006), yet what is missing are large specimens and species that are key prey for predators. In more southern areas, the northward shift of zooplankton communities was documented in the North and Norwegian seas (BEAUGRAND et al. 2002), and for benthos in Bering Sea (GREBMEIER et al. 2006). Species distribution shifts in the European Arctic benthos were documented in detail in the late nineteenth and early twentieth centuries and in the 1950s (BLACKER 1957, PIEPENBURG 2005). Recent examples of this include the reappearance of the blue mussel *(Mytilus edulis)* on Svalbard (BERGE et al. 2005).

THE FOOD CHAIN

The common textbook notion of polar marine ecology is the "short food chain", typically illustrated as a three-step sequence from diatoms to krill to whales in Antarctic (LAWS 1985). In Arctic waters an example might be diatoms to copepods and Little auks (STEMPNIEWICZ et al. 2007) or from microplankton to pteropods then to fulmars (Fig. 1). It was recognized early on that feeding at the bottom of the food chain as close as possible to primary production provides access to vast food resources and saves energy that is lost at subsequent stages of the food web. In the marine realm, large animals feed on predators, which is a unique phenomenon that is not likely to occur among terrestrial biota. This is simply the consequence of the size of primary producers, as large green terrestrial plants can be consumed directly by large herbivores (such as undulates), which are, in turn, prey of the appropriate size for large carnivores. In ocean ecosystems the reverse relation is observed; primary producers are so small that no large herbivore can graze on them effecttively. In order to attain the size required by large animals, marine phytoplankton have to pass through a series of small herbivores and then intermediate predators. In effect, medium sized fish like cod, may be on the same food web level as lion on land. Little auks *(Alle alle),* small (150 g live weight) Arctic birds of wing are exceptionally efficient mesozooplankton predators. They feed mainly on herbivorous copepods (as small as 5 mm), which are probably the smallest marine prey taken by any seabird or sea mammal.

While the number of species at one trophic level is important to better ("complementary resource use") use of the resources (EMMERSON et al. 2001) it is not very important for the energy transfer to the next trophic level where the number of predator levels is critical. This is because there is one order of magnitude of energy lost as it passes through each level in the food chain. The size of the herbivores is also critical since the highest losses are incurred as energy passes from primary producers to grazers (Fig. 2). The larger the herbivore, the shorter the distance is to the top predator.

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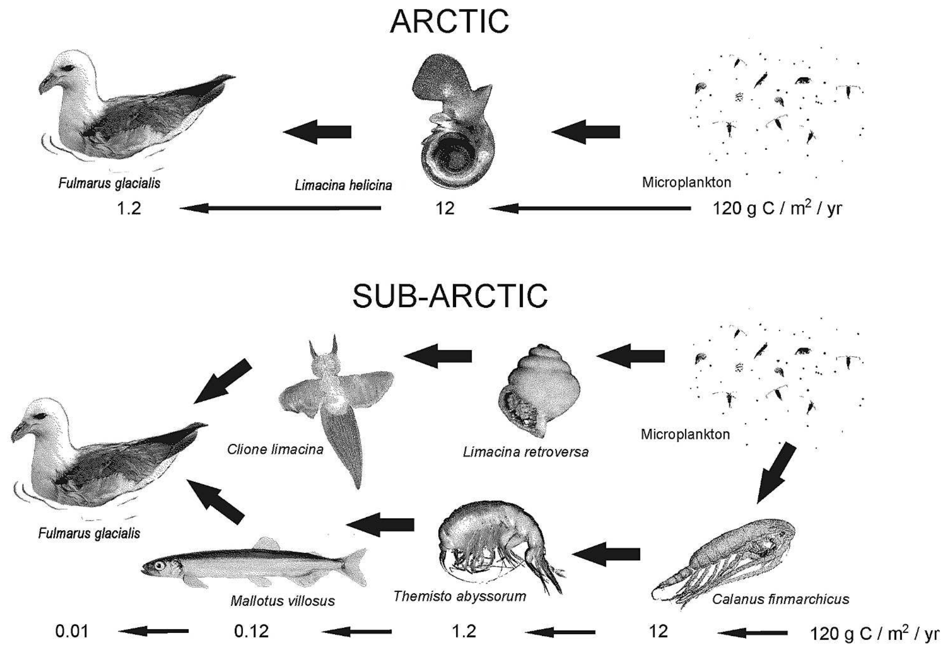

Fig. 1: Scheme of the energy flow in Arctic, efficient short food chain, versus warmed up (Sub-Arctic) situation. Organisms are not drawn to scale. Numbers at arrows indicate part of the initial primary production (120 g C m^{-2} $year^{-1}$) that reach next trophic layer.

Abb. 1: Schema des Energieflusses in kalten (arktischen) Wassermassen mit einer effizient kurzen Nahrungskette im Vergleich zur wärmeren (subarktischen) Situation. Gößendarstellung der Organismen nicht maßstäblich. Zahlenwerte zwischen den Pfeilen beschreiben den Anteil der ursprünglichen Primärproduktion von 120 mg C m^{-2} $year^{-1}$, der die nächste trophische Stufe erreicht.

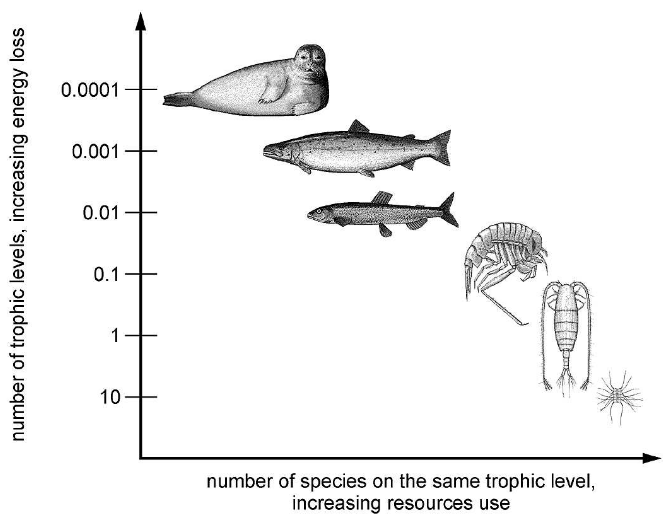

Fig. 2: Scheme of resources use and energy loss as a consequence of increasing biodiversity.

Abb. 2: Schema der Resourcennutzung und Energieverlust als Konsequenz zunehmender Biodiversität.

The Arctic food web is also characterized by the important role of ice pack assemblages and strong pelago-benthic coupling (PETERSEN 1984) that favours demersal fish and benthos. The anticipated food web changes related to the warming include switches from “ice algae to benthos” to “phytoplankton to fish” energy flow (PIEPENBURG 2006, Hop et al. 2006); other features are summarized in Table 1. In historical times (XVII cent) the removal of plankton feeding Greenland whales created food surplus that was used by plankton feeding birds (WĘSŁAWSKI et al. 2000).

Size and energy distribution

Marine primary producers are almost always unified in size. There are some extremes within this group as the smallest known marine phytoplankton organism is *Protochlorococcus* at 0.5 mm, while the largest diatom cell can reach over 1 mm (VILLAREAL 1992, COURTIES et al. 1994), but all phytoplankton organisms fit into the category of microorgansisms. The polar pelagic herbivores are more diversified, from the smalllest copepods (0.5 mm - *Microcalanus*) to the 6 cm Antarctic krill (ETTERSHANK 1983). A common feature of marine invertebrates is the relation of body size/growth to the ambient temperature (Fig. 3). Biochemical and metabolic reactions are faster as temperature increases; hence, poikilothermic animals living in warm waters tend to live faster, complete the reproductive cycle in a short period, and usually produce several generation per year. As a rule, they employ the r-breeding strategy (fast development with numerous offspring). In contrast, invertebrates inhabiting cold water have slower life cycles, live longer, and employ the K-breeding strategy (less numerous offspring and slow development). It has also been demonstrated that cold-water ectotherms use energy efficiently, yet

Level of organization	Sub-Arctic (Atlantic)	Arctic
Cellular	lower C:N ratio in short living (annual) organisms	higher C:N ratio in long living (perennial) organisms
Individual	shorter fatty acid chains, lower energy reserves	longer fatty acid chains, higher energy reserves
Population	r-strategy predom. predominates, uni-modal size distribution	K-strategy predom., distinct annual size cohorts
Ecosystem	Two and more predator levels between herbivores and top predators	No or single predator between herbivores and top predators

Tab. 1: Some differences between Arctic and Sub-Arctic marine food webs (compilation from cited references and own observations).

Tab. 1: Einige Unterschiede zwischen arktischem und subarktischem Nahrungsnetz, zusammengestellt nach zitierter Literatur und eigenen Beobachtungen.

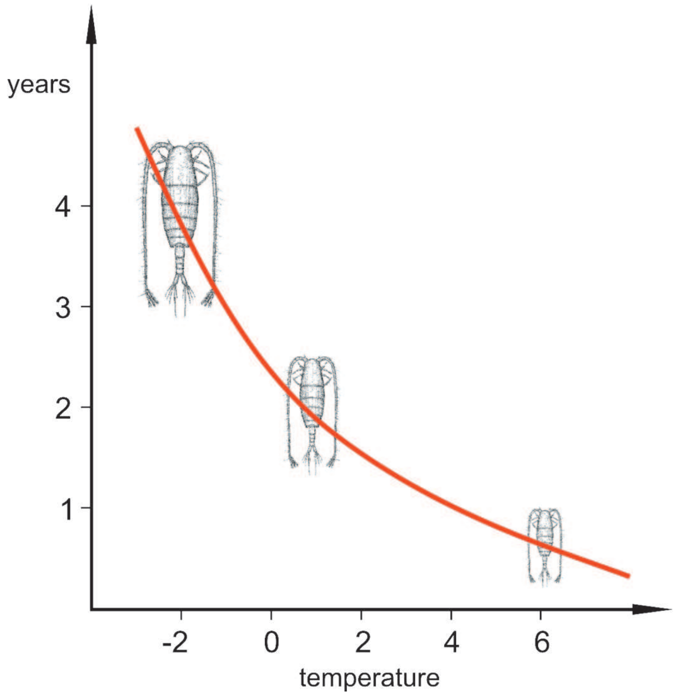

Fig. 3: Relation of invertebrate – calanoid copepods – size/age to ambient temperature.

Abb. 3: Beziehung von Größe/Alter von Invertebraten (calanoide Copepoden) und der Umgebungstemperatur.

prey items	Arctic ww (mg)	Atlantic ww (mg)	Arctic ww (mg)	Atlantic ww (mg)
herbivores – suspension feeders	Benthos	Benthos	Plankton	Plankton
mean individ. weight	123	334	10,1	4,9
SD individ. weight	100	427	16,8	14,2
minimal weight	30	10	0,8	0,1
maximal weight	300	1250	60,0	50,0
carnivores				
mean individ. weight	257	238	67,2	69,0
SD individ. weight	177	191	128,5	140,2
minimal weight	10	30	2,0	0,8
maximal weight	500	500	400,0	400,0

Tab. 2: Size (individual biomass) differences in common prey items from cold (Arctic) and warmed up (Atlantic) waters of Svalbard. Data on seabirds and sea mammals prey after W_S_AWSKI et al. 1999, 2006, ww = wet weight.

Tab. 2: Größenunterschiede (individuelle Biomasse) häufiger Beute-Orga nismen aus kalten (arktischen) und erwärmten (atlantischen) Wassermassen um Spitzbergen. Daten zu Seevögeln und Säugetieren nach W_S_AWSKI et al. 1999, 2006. ww = Nassgewicht.

exhibit slower growth rates (CLARKE 1979, 2003). There are exceptions to this pattern (e.g., it was shown that oxygen is a key factor in marine invertebrates gigantism; CHAPELLE & PECK 1999), but this pattern is consistent in most pelagic ecosystems. The side effect of a long, slow life and large size is the amount of energy that is accumulated in the herbivore's body. Polar marine copepods that are able to live 4-5 years are not only very large for their taxonomic group (*Calanus hyperboreus* from Greenland Sea often reach 1 cm), they also contain high quality fats (HOP et al. 2006). In comparison, individuals of sibling copepod species from Boreal and Arctic provinces exhibit several-fold differences in weight and energy content (Fig. 3). This is what makes the difference for the predator. Studies of the diets of little auks from the area where cold and warm waters occur have shown a distinct preference by the birds for cold-water copepods (WĘSŁAWSKI et al. 1999, KARNOVSKY et al. 2003). Examples of this in other herbivores are the pteropods, which is a sea snail represented by the tiny *Limacina retrovesa* in Atlantic water and the much larger *Limacina helicina* in cold waters, and a valuable food item for a number of seabirds, seals, and whales. The analysis of the size of prey items taken by birds and mammals on Svalbard indicates a clear difference in size between Arctic (larger) and Atlantic (smaller) pelagic herbivores, while the size of carnivores are not statistically different in these two water types. Interestingly, this pattern is not recognized in benthic prey items; grazers (herbivores and deposit feeders) are larger in boreal (Atlantic) waters, compared to Arctic, while carnivores do not differ (Table 2). Explanation of this discrepancy between pelagic and benthic poikilotherms might be a strong share of two large benthic, boreal decapods in the food web *(Pandalus borealis and Sclerocrangon boreas)* collected by predators from shelf waters, while fjords food webs are dominated by amphipods – although these are large cold water species, still as a taxon even large amphipods are much smaller compared to decapods (WĘSŁAWSKI et al. 1999, 2006).

TOP PREDATORS

Large flocks of pinnipeds and huge colonies of cliff-dwelling seabirds are the icons of the Arctic. The phenomenon of exceptionally high densities of seabirds and sea mammals in polar waters is explained by the hypothesis of CAIRNS et al. (2008), which suggests that in cold waters, homoiothermic carnivores (birds and mammals) fare better energetically since the low temperature does not slow their reactions, while in warm water poikilotherms (fish) are more efficient at pursuing predators due to lower energy maintenance costs.

Studies on the seabirds from the Norwegian and Barents seas (BARRET et al. 2002) have shown that the cold water area of the Barents Sea, which is equally productive in terms of phytoplankton, hosts three times more seabirds that do the warmer waters of the Norwegian Sea (6 mln pairs in Barents and 1,8 mln pairs in Norwegian seas – op. cit.). Furthermore, the share of marine invertebrates in the seabird diets is much larger in cold areas (close to 25 %) compared to warmer areas where small fish dominate diets (for review see WĘSŁAWSKI et al. 2006).

In effect, with increasing temperature and regime shift toward a more Boreal European Arctic, the system will favor smaller predators such as pelagic fish that can prey efficiently on minute plankters (RENAUD et al. 2008). Fish are excellent, yet energetically expensive, food for large carnivores. Warming will show that the era of cheap, readily available, nutritional food for birds and marine mammals is over. The warmer waters will be very productive, but most of the energy will be transferred to small fish, as it is in the Norwegian Sea, with the predominant zooplankton consumers of herring, spratt, mackerel, and capelin. Sea birds and sea mammals will have to compete harder for food and will most likely be severely reduced in number, as they are in the Boreal regions today. This is how increased biodiversity can reduce wildlife in the most natural of ways. Other consequences of marine food web restructuring are changes introduced through the seabird colonies to the ornithogenic tundra and terrestrial ecology (STEMPNIEWICZ et al. 2007).

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