# The contiguous domains of Arctic Ocean advection: trails of life and death

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*0. Abstract*

The central Arctic Ocean is not isolated, but tightly connected to the northern Pacific and Atlantic oceans. Advection of nutrient-, detritus- and plankton-rich waters into the Arctic Ocean forms lengthy contiguous domains that connect subarctic with the arctic biota, supporting both primary production and higher trophic level consumers. In turn, the Arctic influences the physical, chemical and biological oceanography of adjacent subarctic waters through southward fluxes. However, exports of biomass out of the Arctic Ocean into both the Pacific and Atlantic oceans are thought to be far smaller than the northward influx. Thus, Arctic Ocean ecosystems are net biomass beneficiaries through advection. The biotic impact of Atlantic- and Pacific-origin taxa in arctic waters depends on the total supply of allochthonously-produced biomass, their ability to survive as adults and their (unsuccessful) reproduction in the new environment. Thus, advective transport can be thought of as trails of life and death in the Arctic Ocean. Through direct and indirect (mammal stomachs, models) observations this overview presents information about the advection and fate of zooplankton in the Arctic Ocean, now and in the future. The main zooplankton organisms subjected to advection into and inside the Arctic Ocean are a) oceanic expatriates of boreal Atlantic and Pacific origin, b) oceanic Arctic residents and c) neritic Arctic expatriates. As compared to the Pacific gateway the advective supply of zooplankton biomass through the Atlantic gateways is 2-3 times higher. Advection characterises how the main planktonic organisms interact along the contiguous domains and shows how the subarctic production regimes fuel life in the Arctic Ocean. The main differences in the advective regimes through the Pacific and Atlantic gateways are presented. The Arctic Ocean is, at least in some regions, a net heterotrophic ocean that – during the foreseeable global warming trend – will more and more rely on an increasing local primary production while the advection of zooplankton, as revealed by models, will cease.

*1. Introduction*

The recent awareness of rapid climate change in the Arctic Ocean (AO, basically defined as the sea region north of 70°N, north of the Bering Strait, the northern Chukchi Sea, the White Sea and the southern Canadian Archipelago, see Fig. 1) has resulted in increased attention to the oceanography of the high north. Warming of the Arctic is taking place 2-3 times faster than global rates (Trenberth et al., 2007). Sea-ice cover has decreased more than 10% per decade with two-thirds of sea-ice volume lost since the 1980s (Duarte et al., 2012b, Naam, 2012). Copious amounts of methane and detrital carbon are being released by melting permafrost (Schuur, 2013, Whiteman et al., 2013). These changes affect the biophysical, political and economic systems of the Northern Hemisphere (e.g., Gramling, 2015), and their ecosystems are increasingly being challenged by tipping elements[1] (e.g., Duarte et al., 2012a, Wassmann and Lenton, 2012). These facts no longer make the Arctic as remote and disconnected to the Pacific and Atlantic oceans as the Mercator projections used in early oceanography textbooks suggested. We now appreciate how tightly linked the AO is with the circulation of water masses in the Northern Hemisphere (Yamamoto-Kawai et al., 2006, Carmack et al., 2010, Wassmann, 2011).

The influence of global warming on Arctic ecosystems is inevitable (Jeffries et al., 2013). For example, boreal species such as the blue mussel have arrived at Svalbard after an absence of several thousand years (Berge et al., 2005) and the Atlantic hyperid amphipod, *Themisto compressa,* have expanded its range into arctic waters (Kraft et al., 2013). Many fish species in arctic seas have recently shifted hundreds of km northward (Mueter and Litzow, 2008, Fossheim et al. 2015). Even tropical and subtropical species have travelled thousands of kilometres on Atlantic currents to end up north of Svalbard under warming conditions (Bjørkelund et al., 2012). As arctic waters continue to warm, and as global climate change causes shifts in the large-scale circulation patterns (Overpeck et al., 1997), such events are expected to increase in frequency. How then are water masses advected into the AO, where a staggering half of the surface area is comprised of continental shelves (Jakobson et al., 2004)? And

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[1] Large-scale processes (or processes components) of the Earth system that may pass a tipping point, such as the melt of Greenlandic ice sheet, Arctic sea ice loss, permafrost and Tundra loss and Atlantic deep-water formation

what are the implications of such advection for the arctic marine life and biogeochemistry, now and in the future? Considering that the AO is not well studied compared to the adjoining oceans (Wassmann et al., 2011), these are demanding questions.

Climate change in the AO implies range shifts of biota over large spatial and temporal scales. Teleconnection indices, such as the North Atlantic Oscillation (Dickson and Østerhus, 2007) or the Arctic Oscillation (Thompson and Wallace, 1998) explain some fraction of the variance observed in AO ecosystems (Overland et al., 2012). The variance of physical forcing cascades through coupled physical/biological systems to smaller scales affecting biogeochemical cycling and biota (Carmack and McLaughlin, 2011). Additional or alternative approaches to time-series analyses are those of macroecology and biogeography (e.g., Ekman, 1953, Li, 2002, Bluhm et al., 2011), which examine patterns in species distribution and abundance to determine relationships between abiotic and biotic factors. Due to demanding logistics, sampling across the full set of scales linking climate to biota is seldom accomplished. It is thus useful to consider what biogeographic scales come closest to matching and connecting with those of the climate system. Here it is useful to think in terms of *contiguous domains*; that is, physical habitats with common salient characteristics – by geography, state or transport processes - that are internally linked in space, time or both (Carmack and Wassmann, 2006, Carmack and McLaughlin, 2011). It is within these contiguous domains that the ecological processes associated with advection are made manifest.

In the AO at least five climate-linked, contiguous domains have been identified[2] (cf. Carmack and McLaughlin, 2002, Bluhm et al., 2015). Here with our attention towards the role of advection into the AO, we restrict our focus to *the pan-Arctic shelf-break and margin domain* that extends around the AO, and to its connection to the adjacent Atlantic and Pacific oceans (Fig. 1). Advection affects arctic marine ecology in two fundamental ways. First, nutrients or biomass produced elsewhere are carried by currents to a new location where

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[2] The seasonal ice zone (summer openings), the riverine coastal domain, the pan-arctic shelf-break and margin domain (circumpolar boundary current), the Pacific Arctic Domain, and the Atlantic Arctic Domain.

they may result in production or be consumed by other organisms. Secondly, biomass may be concentrated by flow structures (e.g., eddies, convergent fronts, boundary currents) at local or regional scales thus becoming more readily accessible to higher-level predators such as fish and marine mammals. While there is an import of particulate organic carbon into the AO an export of dissolved inorganic carbon across the main Arctic Ocean gateways, mainly into the North Atlantic takes place (MacGilchrist et al., 2014).

One of the most prominent features of the AO is its strong and persistent connection to the Pacific and, in particular, to the Atlantic Ocean. This is distinctly reflected through the advective processes that transfer Atlantic Water into the AO via eastern Fram Strait, the Barents and Kara seas, and Pacific waters via Bering Strait and the Chukchi Sea into the AO interior. Arctic waters, comprised of Atlantic, Pacific and freshwater components, then exit mainly through western Fram Strait and the Canadian Arctic Archipelago (Falck et al., 2005, Schauer et al., 2008, Shadwick et al., 2011; Fig. 3). The water advected into the AO not only transports significant amounts of nutrients and detritus, but also large quantities of phyto- and zooplankton. This biotic and geochemical supply then supports both primary production and higher trophic level´s consumers within the AO. Biogenic exports out of the Arctic into both the Pacific and Atlantic oceans are thought to be far smaller than the northward influx (Popova et al., 2013, but see Torres-Valdes et al., 2012 for indications of net nutrient export from the Arctic Ocean (e.g. by transformed Polar Water of Pacific origin that leaves over the Arctic outflow shelves), making the ecosystems of the AO a net beneficiary of biomass advection.

The biotic impact of Atlantic- and Pacific-origin taxa in arctic waters is two-fold. It depends on their ability to survive and reproduce in the new environment. Some species will die as soon as they encounter a physical environment different from their origin and serve simply as a passive source of organic carbon. As the consequence, their numbers decline due to attrition and reproductive/recruitment failure.

Here we review the role of water mass advection and frontal zones for the AO ecosystems. We then look at the spreading of organisms with water masses while trying to estimate how much biomass is advected into the AO. Ultimately

we critically evaluate the state of the art of quantifying advection to and from the region and assess the role of advection for the ecology of the AO, now and in the future.

*2. The role of the Arctic Ocean in the oceanic circulation of the Northern Hemisphere*

The position of the AO between the Pacific and Atlantic oceans is unique (Fig. 2). The top central part of the Northern Hemisphere is covered by sea ice that is now being subjected to rapid global warming (Trenberth et al., 2009) and rapid decline (Duarte et al., 2012b, Carstensen et al., 2012).  The seasonal ice zone and the Polar Vortex are surrounded by the cyclonic winds that provide moisture (mostly from the south, e.g., Serreze et al., 1995) for precipitation to the adjoining watersheds, and thus runoff to the AO (Carmack and McLaughlin, 2011). Salinity-driven vertical stratification in the AO and the subsequent southward spreading of melt water are significant for the time development of and total primary production.  However, the advection of Pacific and Atlantic waters into the AO is neither equal nor symmetric (Carmack et al., 2006).  While Atlantic Water spreads throughout the entire AO, subducting below the Polar Water (modified water from the Bering Strait inflow), the Pacific Water is mostly confined to the Canadian Basin.  Pacific waters enter the AO through Bering Strait and exit both through the Canadian Arctic Archipelago, down the Baffin and Labrador shelves and onto the Grand Banks (Jones et al., 2003) and also through Fram Strait along the East Greenland shelf and margin (Falck et al., 2005).  Within the Amerasian Basin they provide an additional halocline layer at depths 60-220 m between the surface layer and the Atlantic Water, making this region much more strongly stratified than the Eurasian Basin (McLaughlin et al., 1996, Bluhm et al., this issue).  Further, mixing of these outflow waters with deep-water formed in the adjacent Nordic and Labrador seas connects the AO circulation with the rest of the world ocean (in ways not fully understood).

There are three major regions where advection into the AO occurs (Fig. 3); through the eastern Fram Strait north of Spitsbergen and around the Yermak Plateau (Schauer et al., 2008), through the northern Kara Sea region via the eastern St. Anna Trough as a bathymetry-controlled boundary current (Schauer

et al., 2002, Pnyushkov et al., 2015), and through Bering Strait following three main pathways across the Chukchi shelf (Woodgate et al., 2012). These inflow regions connect to the main outflow region, the western Fram Strait, through cyclonic, boundary current flows around the Canada/Makarov and Amundsen/Nansen basins and the Transpolar Drift. Inflow into the AO takes place through passages with rather different topography. Fram Strait is wide, deep and has an adjacent shelf that influences the physical and biological components of water entering the AO north of Svalbard (e.g., Cottier et al., 2005, Nilsen et al., 2006, Aaboe et al., 2009). The two-branched inflow of warm and saline Atlantic Water to the AO is the major contributor of oceanic heat to the arctic climate system (Schauer et al., 2002, Smedsrud et al. 2013). However, while the Atlantic Water entering the AO through Fram Strait retains a large part of its heat as it flows along the AO continental slope [and adjacent northern Barents Sea (Lind and Ingvaldsen, 2012)], the branch flowing through the shallow Barents Sea releases a substantial amount of heat to the atmosphere (Lien et al., 2013). The region towards the St. Anna Trough (> 500 m) in the wide eastern Barents Sea is about 250 m deep and narrower than Fram Strait (Schauer et al., 2002). The Bering Strait is about 50 m deep and only 80 km wide at its narrowest, with vast shallow areas both south and north of the strait (Woodgate et al., 2012).

The currents in the Arctic are often associated with oceanfronts that separate different water masses (Fig. 4). One type of front occurs at the offshore edge of coastal buoyancy currents, e.g., Siberian Coastal Current Front or the Norwegian Coastal Current Front (Fig. 4). These fronts divide shelf waters from deep offshore waters with largely distinct biological communities. In the production season, such fronts often tend to be areas of higher zooplankton concentrations, caused by upwelling-induced primary production. Although cross-front mixing is limited, some does occur. For example, baroclinic instabilities caused by shear associated with strong along-front currents can lead to large meanders at the front and ultimately the formation of anticyclonic eddies that separate from the front. These eddies can advect nutrients and phytoplankton production as well as organisms such as zooplankton and

ichthyoplankton from the shelves to the deep ocean (Watanabe and Hasumi, 2009, Watanabe et al., 2012).

Not all fronts in the Arctic and subarctic exhibit eddy formation. Some fronts have strong horizontal gradients in temperature and salinity but relatively weak density gradients owing to density compensation of the temperature and salinity characteristics of the two adjacent water masses (e.g., the Polar Front in the Barents Sea (Fer and Drinkwater, 2014); the West Spitsbergen Current Front (Saloranta and Svendsen, 2001); and the deep front between the Arctic and Atlantic waters at the entrance to Fram Strait (May and Kelly, 2001). Eddy activity tends to be weak and little phytoplankton enhancement occurs at such fronts (Erga et al., 2014a,b, Børsheim and Drinkwater, 2014). Weak cross-front advection occurs in the vicinity of such fronts.

Large shifts in frontal locations are often evidence of changes in advection, e.g., prior to the 1990s, the boundary separating Arctic and Pacific waters laid over the Lomonosov Ridge, but by 1995 the boundary had shifted towards the Alpha-Mendeleyev Ridge (McLaughlin et al., 1996, 2004, Morison et al., 2000, see stippled line in Fig. 4) and has remained there (Kwok and Morison, 2011). The shift in frontal location was caused by increased advection of Atlantic Water into the Makarov Basin (Karcher and Oberhuber, 2002, Steele and Ermold, 2007). Another example is the Polar Front in the Barents Sea that shifts farther to the northeast with increased Atlantic inflow (Loeng, 1991). It may be expected that the Barents Sea Polar Front moves significantly northwards to the northern slopes of the Barents Sea during the course of this century (Fig. 5 A, C).

The function of the inflow shelves is completely different from that of the interior and outflow shelves and they have differing ecological functions, behaving more like 'plug flow'[3] chemostats than continuously-stirred reactors governed by spring bloom dynamics (Carmack and Wassmann, 2006). Incoming waters from the Atlantic (western Spitsbergen and Barents Sea) and Pacific (Bering and Chukchi seas), rich in nutrients and detritus, but also large quantities of phyto- and zooplankton (seasonally), are modified by physical and biogeochemical processes during transit. Atlantic waters (or locally modified waters in the eastern Barents Sea) subsequently subduct below surface waters

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[3] In plug flow there is no boundary layer adjacent to the inner wall of the pipe

along the shelf break or in the St. Anna Trough and influence property distributions downstream within the Arctic Basin (Carmack and Wassmann, 2006). The outflow shelves allow arctic waters back into the North Atlantic (Nordic and Labrador seas), mainly via the east coast of Greenland and less so through the topographically complex Canadian Archipelago. The surface waters of the outflow are strongly stratified and relatively nutrient-poor (e.g., Mauritzen et al., 2011). Their plankton communities reflect the low productivity of the AO interior. The outflow shelves are not simple gates or channels, as transit times across the shelves are long enough for thermohaline and biogeochemical changes to occur *en route* during passage (cf. McLaughlin et al., 2004).

This overall picture demonstrates that the exchange of the AO waters with the Atlantic and Pacific oceans is dissimilar. The North Atlantic Current transports 5-8 Sv of water into the AO characterized with salinity of ~35 and divides into two main branches: the Fram Strait and the Barents Sea branches (Rudels et al., 1994, Carmack et al., 2006). At about 1 Sv with a salinity of 31-33, the Pacific inflow through Bering Strait is far smaller in volume and fresher than the Atlantic inflow (Woodgate et al., 2012). Volume-wise most of the advection into and out of the AO, therefore, takes place in the European Arctic Corridor (Fram Strait to northeastern Kara Sea) and in particular through the central Barents Sea (Rudels et al., 2002, Smedsrud et al., 2013) and in Fram Strait (Schauer et al., 2008, Beszczynska-Möller et al., 2012). More precise estimates of the magnitude and variability of Atlantic water advection into the AO remain elusive. While the volume fluxes into the Barents Sea and out of the St. Anna Trough are roughly estimated to be 2.3 and 1.8 Sv, respectively (Gammelsrød et al., 2009, Smedsrud et al., 2013), the lack of long-term investigations regarding the complex recycling of Atlantic water across the northern Fram Strait prevents accurate estimates (Mauritzen et al., 2011).

The advective inflows and outflows create a "cyclonic" thermohaline circulation regime within the AO that is modulated through wind forcing by the overlying atmospheric pressure distributions that characterize the Arctic Oscillation. The period 1979-1988 corresponds to negative (more anti-cyclonic) Arctic Oscillation indices, whereas the period 1989-2006 corresponds to positive (more cyclonic) and neutral Arctic Oscillation indices (e.g., Steele et al., 2004).

During the former period, observations indicate that the circulation featured a stronger Beaufort Gyre with the Transpolar Drift more aligned with the Lomonosov Ridge (McLaughlin et al., 1996). Now, with sea ice mobile (e.g., Gascard et al., 2008) and in retreat (Wadhams, 2012), the wind is more effective in spinning up the Beaufort Gyre (McLaughlin et al., 2011). At the depth range of the core of Atlantic Water, approximately 100-800 m, the main circulation feature is the Arctic Circumpolar Boundary Current, which follows cyclonically along the AO continental slopes (Rudels et al., 2000, Polyakov et al., 2013, Pnyushkov et al., 2015). This is the fastest oceanic current in the deep AO, with annual mean velocities up to 0.1 m s$^{-1}$, based upon models and observations (Aksenov et al., 2011). The boundary flow is relatively stable in the Nansen, Amundsen and Makarov basins, but exhibits large variability in strength and flow direction upon encountering the Chukchi Borderland complex in the Canada Basin (high-resolution simulations and observational data; Karcher et al., 2007, 2012, Aksenov et al., 2011). Within the boundary current the advective inflow of Atlantic Water and associated organisms, starting from Fram Strait, can reach the base of the Lomonosov Ridge in less than a year based on the mean flow (Rudels et al., 2002). The spread of water entering the Arctic from the Bering Sea is important for the advection of plankton organisms, heat transport and stratification, but the impact along the boundary current expanse is much smaller compared to the European Arctic Corridor, in part because the cyclonic boundary current is opposed by the overlying anticyclonic Beaufort Gyre.

Little is known about the advection of nutrients in to the AO. Numerical experiments by Popova et al. (2013) show clearly how advection of nutrients along with the bottom water (partly influenced by brine formation) from the Atlantic and Pacific oceans are advected through the Barents Sea and Bering Strait, respectively, into the central AO in a matter of 1-3 years (Fig. 6). These time scales are in the same range as that of advected zooplankton. From these regions nutrients are advected along with the boundary currents, while major Siberian rivers inject additional nutrients to the shelves that are quickly taken up in the innermost sections of the shelf (e.g., Hirche et al., 2006, Schmidt et al., 2006, Flint et al., 2010). The advective timescales linking subsurface layers of the central AO with the nutrient rich Pacific and Atlantic waters through the AO do

not exceed 15-20 years, while the advective supply of shelf nutrients to the deep AO occurs on the timescale of about 5 years (Fig. 6).

*3. Advection of zooplankton: Atlantic and Pacific expatriates*

Advection from the Atlantic and Pacific oceans determines the stock and structure of zooplankton communities in many parts of the AO (Hirche and Mumm 1992, Mumm, 1993, Kosobokova and Hirche, 2000, 2009, Kosobokova et al., 2011). The oceanographic and ecological dynamics in the European section of the pan-Arctic shelf-break and marginal domain shape the conditions zooplankton encounter upon their advection (Cottier et al., 2005, Nilsen et al., 2006, Willis et al., 2006, Kwasniewski et al., 2012), just as they do east of a trench north of Alaska, Barrow Canyon (Ashjian et al., 2003, Nelson et al., 2009). Recent studies speculate that the biomass of the Atlantic plankton advected into the Eurasian Basin of the AO is greater than the input of Pacific plankton into the Canadian Basin (Hopcroft et al. 2010, Kosobokova et al., 2011, Kosobokova 2012, Nelson et al., 2014). This biomass input difference (for the most recent estimate, see part 6) is driven by the almost 10-fold greater volume transport from the Atlantic and lack of substantive topographic barriers that reduce survival of advected animals as occurs on the Pacific side (see part 2). As a result, Atlantic zooplankton contributes substantively to both the number of species and the zooplankton biomass found in the Eurasian Basin (Kosobokova, 2012).

In the following paragraphs we focus upon mesozooplankton species that are of particular significance in the flux of biomass from the Atlantic and Pacific oceans into the AO. Prominent in this group are the Atlantic copepod species *Calanus finmarchicus,* and the boreal/arctic species *C. glacialis*, most commonly identified based upon morphology, colour and size. Recently, it has been suggested that traditional morphological delineation of species alone may not work well for *C. finmarchicus* and *C. glacialis* in enclosed fjords near the margins of the latter´s range (Gabrielsen et al., 2012), or that hybridization may be common between these species (Parent et al., 2012). If these observations hold true widely, they could confound studies and models that consider the life history and biogeochemical cycling differences of these two species (e.g.,

Wassmann et al., 2006b, part 5). Nonetheless, in the present review, results are based upon the traditional morphological identification most widely accepted by the scientific community.

3.1. Atlantic epi- and mesopelagic zooplankton expatriates

The survival and spatial distribution of Atlantic zooplankton taxa in the AO largely depends upon their tolerance and ability to acclimate to environmental conditions such as temperature, food supply, salinity, sea ice, etc. Many of the Atlantic zooplankters are known to die shortly after entering the AO proper (Kosobokova, 2012, Nelson et al., 2014). For example, the temperate copepods *Paracalanus parvus*, *Metridia lucens, Pleuromamma robusta,* and *Rhincalanus nasutus* have been registered in the AO close to Fram Strait, but never farther east (Dunbar and Harding, 1968, Blachowiak-Samolyk et al., 2007, Kosobokova et al., 2011). Absence in the eastward regions clearly indicates rapid extirpation once they enter arctic waters. Even the arctic *Calanus* species may meet survival challenges after passing the Atlantic gateway. This includes the Sofiadjupet, a small oceanic basin located at the southern edge of the AO north of Svalbard, where 94% of *Calanus* at depth (between 300 and 2000 m) were found dead in winter (Daase et al., 2013b).

Other species advected with Atlantic Water in the boundary current penetrate further east into the Eurasian Basin. These are the pelagic polychaetes *Tomopteris septentrionalis*, the euphausiids *Thysanoessa longicaudata*, *Meganyctiphanes norvegica,* the copepods *Oithona atlantica, Paraeuchaeta norvegica,* and the siphonophore *Gilia reticulata*, demonstrating their higher tolerance of arctic conditions (Table 1). All these species have been repeatedly registered in low numbers over the Eurasian continental slope within the range of the Atlantic Boundary Current (Rudels et al., 1994, Schauer et al., 1997, 2002, Kosobokova, 2012). None of them, however, have yet been found in the Canada Basin (Kosobokova and Hopcroft, 2010, Kosobokova et al., 2011, Gagaev and Kosobokova, 2012, Nelson et al., 2014). They appear to be unable to reproduce in the AO, or at least not at rates sufficient to offset their mortality; thus, under present conditions, they are functionally sterile expatriates (Ekman, 1953).

The copepod *C. finmarchicus* is one of the most numerous zooplankton species in the northern North Atlantic, and is the most notable example of a sterile Atlantic expatriate in the AO (Jaschnov, 1970, Hirche and Kosobokova, 2007). *C. finmarchicus* are continuously advected in high numbers into the AO, but loose the ability to reproduce soon after entering the Arctic Basin for reasons not completely understood, although temperature and/or food issues play important roles (Hirche and Kosobokova, 2007). Observations of *C. finmarchicus* distribution in the region including the northern shelves of the Eurasian Arctic Seas, continental slope and the deep inner Eurasian and Canadian Basin (Fig. 7), show that the species is mainly confined to the core of the Atlantic inflow moving eastward with the boundary current along the Eurasian continental slope (Fig. 2). Populations of *C. finmarchicus* within this area consist almost exclusively of late-stage copepodids CIV, CV and adult females (Kosobokova and Hirche, 2000, Hirche and Kosobokova, 2007. Kosobokova, 2012). The complete absence of younger developmental stages gives a clear signal of their reproductive failure, a fact confirmed by examination of gonadal development in females and by egg production experiments (Hirche and Kosobokova, 2007).

Despite its reproductive failure, *Calanus finmarchicus* contributes strongly to zooplankton abundance and biomass over the Eurasian continental slope within the range of the Atlantic Boundary Current (Kosobokova and Hirche, 2009, Kosobokova, 2012). In the region northeast of Svalbard, where the Fram Strait branch of Atlantic inflow enters the AO (Rudels et al., 1994, Schauer et al., 2002), it may contribute up to 40% of the overall zooplankton biomass (Kosobokova, 2012). North of St. Anna and Voronin Troughs where the Barents Sea branch enters the AO (Schauer et al., 2002) it contributes up to 30% (Kosobokova, 2012). Farther east, *C. finmarchicus* abundance and biomass decrease dramatically; north of the New Siberian Islands its contribution is 5% or less. After entering the AO *C. finmarchicus* exists with "one foot in the grave" as these doomed zooplankters travel deeper into the arctic along the "death trail" at the perimeter of the AO (see Fig. 7).

Only a few *C. finmarchicus* specimens make it as far as the western Makarov Basin to the region immediately east of the Lomonosov Ridge (Johnson, 1963, Kosobokova, 1981, Thibault et al., 1999, Kosobokova and Hirche, 2000).

They reach only the western region of the Makarov Basin that can have Atlantic inflow (Rudels et al., 1994 Schauer et al., 2002). Observations of *C. finmarchicus* found in the western Makarov Basin in 1994-1998 are in good agreement with observations of simultaneous Atlantic Water inflow into that basin (Carmack et al., 1998, Shimada et al., 2004, McLaughlin et al., 2009), but further advection is hampered by the slow transport of Atlantic water, combined with the sterility and single-year life cycle of *C. finmarchicus*. In the more distant regions of the Canada Basin not directly affected by the Atlantic inflow, *C. finmarchicus* is absent.

3.2 Pacific epi- and mesopelagic zooplankton expatriates

Northward transport through Bering Strait averages about 1 Sv, but the flow is highly seasonal ranging from 0.4 Sv in winter to 1.2 Sv during the ice-free season (Woodgate et al., 2005). The volume of northward flow through Bering Strait has increased in recent years by as much as 50% (Woodgate et al., 2012), which undoubtedly has influenced the advection of biota and nutrients into the AO. In summer, the Chukchi Sea Shelf zooplankton is primarily Pacific in character (Springer et al., 1989, Hopcroft et al., 2010); the influence of the Pacific zooplankton fades as the Pacific Water travels northward and is progressively transformed by arctic conditions, interaction with the Siberian Coastal Current, and the waters of the Chukchi Sea shelf, and eventually, waters of the Arctic Basin (Grebmeier et al., 1995, Pickart et al., 2010). By late summer what is left of the Pacific zooplankton influx reaches the boundaries of the Chukchi Sea as far east as Wrangel Island (Hopcroft et al., 2010), and the shelf break of the northeast Chukchi Sea (Lane et al., 2008 Nelson et al., 2009), although bowhead whale stomach contents suggest Pacific-derived euphausiids sometimes reach the eastern Beaufort Sea (see part 4). In the winter, the Chukchi Sea Shelf becomes completely ice-covered and transitions back to being more arctic-like in faunal character.

An early estimate suggested that annually up to 1.8 million tons of zooplankton DW (dry weight) are transported through Bering Strait into the Chukchi Sea in high-biomass years and that the influx was highly variable such that transport was two to five-fold lower during low-biomass years (Springer et

al., 1989). Such estimates are inherently limited in that they are derived from data gathered only during the productive ice-free summer and we have limited quantitative understanding of zooplankton standing stock and transport during the winter. Nonetheless, the majority of biomass moves through Bering Strait in the summer and fall, so the use of data collected during this period may still produce a useful estimate. If we take the cross-sectional area of the Strait as 4.25 $km^2$ with an annual average flow of 1.1 Sv (Woodgate et al., 2012), in combination with an average zooplankton biomass of about 50 mg DW $m^{-3}$ (Hopcroft et al., 2010, Matsuno et al., 2011, Questel et al., 2013), we obtain an annual estimate of 1.75 million tons of zooplankton DW (~0.8 tons carbon) advected into the AO from the Pacific Ocean, well within the range of Springer et al. (1989). This zooplankton biomass, along with the accompanying detritus and phytoplankton, drives the high productivity of the Chukchi Sea (e.g., Grebmeier et al., 1995, Plourde et al., 2005).

Unlike the situation regarding northward transport from the Atlantic Ocean into the AO, flow from the Pacific Ocean is tightly constrained due to the narrow and shallow Bering Strait gateway. The strait forces the convergence of three distinct northward-flowing water masses all of which carry distinctive assemblages of zooplankton (Springer et al., 1989 Hopcroft et al., 2010 Eisner et al., 2013) and have distinct water properties, nutrient concentration (Coachman et al., 1975), and phytoplankton (Springer and McRoy, 1993, Lee et al., 2007). Both interannual and long-term variation in climate (i.e. the 50% increased flow through Bering Strait noted by Woodgate et al., 2012) can affect the relative rates of transport of these three water masses, and hence the composition, distribution, and abundance of Pacific zooplankton and their predators in the Chukchi Sea (Questel et al., 2013).

Among these three water masses, the cold, salty, nutrient-rich Anadyr Water originates at the Bering Sea shelf break and enters Bering Strait from the west and carries the distinctive oceanic copepods *Neocalanus plumchrus*, *N. flemingeri*, *N. cristatus*, *Metridia pacifica* and *Eucalanus bungii*, as well the neritic copepods *Calanus glacialis* and *C. marshallae.* Anadyr Water is also assumed to be a major source of krill (*Thysanoessa* spp.) advected into the Pacific arctic region (Berline et al., 2008). Nutrient-rich Anadyr Water is the major driver of

primary and secondary production in the northern Bering and southern Chukchi seas (Springer and McRoy, 1993).  The Alaskan Coastal water, which is the warmest and freshest of the three water masses, enters the strait from the east. A euryhaline contingent of zooplankters is found in this water, notably *Acartia longerimis, A. hudsonica, Centropages abdominalis, Pseudocalanus* spp*., Oithona similis,* marine cladocerans and large numbers of meroplankton (Springer et al., 1989, Hopcroft et al. 2010). Bering Shelf water has properties intermediate to those of Anadyr and Alaskan Coastal waters, and enters Bering Strait between these two other water masses.  The Bering Shelf zooplankton fauna is largely neritic and less distinctive than that of the Anadyr or Alaska Coastal water. The zooplankton community of the Bering Shelf water is notable for containing relatively high numbers of meroplankton, the copepods *Oithona similis, Pseudocalanus* sp., and *Metridia pacifica* plus a large biomass of *Calanus marshallae* and/or *C. glacialis* (Springer et al., 1989, Hopcroft et al., 2010). Genetic results suggest that most of the Bering Shelf *Calanus* biomass is *C. glacialis* (R.J. Nelson, unpublished).

Bering Strait is the "doorway of death" for many Pacific zooplankters but is the start of a lifeline for predators and scavengers within the AO. The pathways and the rate of transformation of the three water masses passing through Bering Strait shape the death trail of Pacific zooplankters leading into the Arctic. Anadyr and Bering Shelf waters blend shortly after passing through Bering Strait and are thereafter referred to as Bering Sea Water (Coachman et al., 1975); this blending phenomenon could be a major cause of Pacific zooplankton morbidity and mortality.  In contrast, the Alaskan Coastal water remains distinct as it travels along the coast of Alaska (Coachman et al., 1975) where it is reinforced by freshwater discharge and can still be detected east of Point Barrow, the northernmost point of Alaska (Nikolopoulos and Pickart, 2008; Fig. 8A).

The majority of Bering Sea water travels northward over the Chukchi Shelf (Windsor and Chapman, 2002) and is channelled through three channels between the Chukchi Sea and the AO, Herald Valley, the Central Channel and Barrow Canyon (Weingartner et al., 2005).  All of these routes follow the shelf break of the Chukchi and Beaufort seas eastward into the Canada Basin (Pickart

et al., 2005, 2010; Fig. 8A). The distribution of Pacific zooplankters such as *Metridia pacifica, Neocalanus cristatus, N. plumchrus/flemingeri,* and *Eucalanus bungii* in the AO reflect these pathways of transport (Fig. 8A-D). Analysis of the 16S ribosomal RNA gene of *C. glacialis* shows a haplotypic distribution pattern that also follows the influx of Pacific Water into the Arctic (Nelson et al. 2009). *Neocalanus* species appear to be the least successful at surviving in deep water and are restricted to the shelf, while *M. pacifica* and *E. bungii* have been reported far into the basin (Brodsky and Nikitin, 1955, Johnson, 1963, Dunbar and Harding, 1968, Ashjian et al., 2003, Kosobokova and Hopcroft, 2010, Nelson et al., 2014); Pacific Water eddies which are observed throughout the western Canada Basin (Manley and Hunkins, 1985, D'Asaro, 1988, Watanabe and Hasumi, 2009) are in part responsible for this transport (see also Llinas et al., 2009).

Most of the biomass of Pacific mesozooplankton advected through Bering Strait appears not to make it out of the Chukchi Sea (Ashjian et al. 2003, Lane et al 2008, Kosobokova and Hopcroft 2010), but recently, it has been suggested that much of the euphausiid population present in the US sector of the Beaufort Sea is advected from the Bering Sea (Berline et al., 2008, see also part 4). Based on current speeds in the Chukchi Sea (see Woodgate et al., 2005) and Canada Basin (see Timmermans et al., 2008) the large oceanic Pacific zooplankters found in the Beaufort Sea or Canada Basin probably have survived at least one arctic winter, as they are unlikely to have been produced in the AO (E.A. Ershova, R.R. Hopcroft and K.N. Kosobokova, unpublished data). As an alternative, eddies could carry zooplankters from the shelf into the basins (Watanabe and Hasumi, 2009), which presumably could happen on shorter time scales than the mean currents and would not necessarily require the zooplankters to have survived a winter. The smaller neritic Pacific zooplankton species are seldom reported outside the Chukchi Sea (Hopcroft et al. 2010, Nelson et al., 2014). Long-lived Pacific scyphozoans such as *Cyanea* and *Chrysaora* are sometimes found in arctic waters but the majority of non-crustacean taxa, such as hydromedusae that are observed in the Chukchi Sea and beyond are arctic in their faunal affinity (Questel et al., 2013). Because of the huge numbers of Pacific zooplankters advected annually into the Arctic, there is high potential for northward range expansions and ecological transformation under warmer conditions (see

Occhipinti-Ambrogi 2007). In recent decades however, there has been no documented reproductive establishment of a Pacific expatriate in the Arctic. The persistence of at least seasonal sub-zero temperatures will likely remain a substantial barrier for most species.

3.3 Arctic neritic zooplankton expatriates

In addition to the Atlantic and Pacific epipelagic and midwater expatriates, Arctic shelf species can represent a source of allochthonous nutrients and organic carbon to the central basins (Table 1). Although normally trapped by shelf-break fronts, Arctic shelf species can be advected off the shelf, including by eddies. Although many of them are ecologically important over the shelves (i.e. *Parasagitta elegans*, *Pseudocalanus* spp. and *Acartia* spp.), their contribution to abundance and biomass in the deep AO is negligible. A striking exception from this rule is the large, and lipid-rich calanoid copepod *Calanus glacialis* (Kosobokova and Hirche, 2001, 2009, Auel and Hagen, 2002, Ashjian et al., 2003, Kosobokova and Hopcroft, 2010, Kosobokova et al., 2011). Often considered a shelf species, it appears to be successful along the entire AO shelf break and boundary currents (see Fig. 9, 11B) and is common far into the Arctic basins (e.g., Olli et al., 2007); it appears however that in the waters of the deep Arctic basins *C. glacialis* reproduction may be largely unsuccessful (Kosobokova and Hirche, 2001, Ashjian et al., 2003).

*4. Advection of zooplankton as reflected through marine mammal feeding*

Mammals in the AO may feed intensively upon zooplankton during spring to early autumn and investigating the stomach content can provide information about the advection and fate of zooplankton. In arctic waters, marine mammals are classified as either endemic or migratory species (Table 2), the latter spending only portions of the year there to exploit seasonally abundant prey resources (Laidre et al., 2008, 2010, Moore and Huntington, 2008). Except for the narwhal, all endemic species have a pan-Arctic distribution. Migratory species are principally comprised of baleen whales, with slightly different fauna among Pacific, West Greenland and Atlantic sectors of the AO. Their distribution

too, is concentrated in regions corresponding to locales of exceedingly high secondary and tertiary production, either locally generated or advected in.

Collectively, marine mammals require thousands of tons of biomass to sustain and grow their populations (Bowen, 1997). Prey consists primarily of mesozooplankton (e.g., euphausiids, amphipods, copepods), small pelagic fishes (e.g., polar cod, capelin, sand lance), and epi- and infaunal benthic species (e.g., clams, worms, crustacea; Bowen and Siniff, 1999). Exceptions to this include the large Greenland halibut (*Reinhardtius hippoglossoides*) sometimes targeted by narwhals and hooded seals. Many of these prey species are likely either advected directly from subarctic seas, or are themselves fed by the advection of smaller plankton, supported by phytoplankton that are dependent upon available nutrients. At local scales, marine mammals remove substantial biomass of a variety of prey types and can enhance local production through nutrient resuspension and regeneration (Roman and McCarthy, 2010). Efforts to estimate the pan-Arctic prey biomass required by marine mammals are confounded by a number of complexities, including: (i) the broad spectrum and acute seasonal and interannual variability in production of prey species, (ii) the strong spatial and temporal variability in marine mammal feeding opportunities and strategies (i.e. some engulf and some select prey), and (iii) the fact that quantitative estimates of marine mammal population sizes are few, many are antiquated and all are specific to a region (CAFF 2013).

To forage effectively baleen whales must find dense concentrations of prey, usually aggregated by physical mechanisms such as local wind forcing creating fronts aligned with bathymetric features (e.g., Okkonen et al., 2011), entrainment in tidal currents or eddies (e.g., Rogachev et al., 2008, Llinas et al., 2009) or the high trophic efficiency of the marginal ice zone (e.g., the so-called capelin front in the Barents Sea; Sakshaug and Skjoldal, 1989). Due to this reliance on dense prey assemblages, feeding whales can serve as indicators of zooplankton 'hotspots' in the AO that punctuate an otherwise contiguous advective domain (Moore et al., 2000, Laidre et al., 2012, Clarke et al., 2013). For the time being these investigations are not pan-arctic and thus no comprehensive overview over the feeding of mammals throughout the AO can be provided.

Of the two species of circumpolar whales, only bowhead feeding areas have been the focus of long-term studies offshore of Alaska, Canada and West Greenland (e.g., Ashjian et al., 2010, Walkusz et al., 2012, Laidre et al., 2010). Two populations are recognized, the Bering-Chukchi-Beaufort (BCB) stock, numbering *ca*. 17,000 whales (Givens et al., 2013), and the Eastern Canada-West Greenland (EC-WG) stock numbering *ca*. 6,500 whales (CAFF, 2013). Whales in both populations target lipid-rich copepods and/or krill, in addition to an array of other pelagic and epi-benthic prey that overwinter in the AO (Lowry et al., 2004, Laidre et al., 2010). With regard to advected prey (Fig. 10), observational and stomach-content data confirm that the BCB bowhead stock feeds on euphausiids (*Thysanoessa* spp.) along the Chukotka coast (Moore et al., 1995), near Barrow (Moore et al., 2010) and as far east as Kaktovik, Alaska (Lowry et al., 2004). These krill are likely transported into the AO through Bering Strait (Berline et al., 2008) and carried eastward in the Beaufort shelf break jet (Nikolopoulos et al., 2009) as far as the Mackenzie Shelf (Hopky et al., 1994, Lowry et al., 2004). Isotopic evidence suggests that bowheads of the EC-WG stock may also routinely feed on krill (Pomerleau et al., 2012), although the mechanism for prey delivery is unknown. In the Pacific Arctic sector, apparently also gray whales feed on advected euphausiids in the south-central Chukchi Sea (Bluhm et al., 2007), with many other upper-trophic species such as humpback whales, fin whales, seabirds (especially short-tailed shearwaters) and marine fishes also likely relying on advected krill, or on forage fishes that eat krill (e.g., capelin, cod) along the shelf-slope domain.

Available data indicate that bowhead whales north of Bering and Davis straits rely on prey reflecting different life history patterns: oceanic expatriates (e.g., krill), oceanic Arctic residents (e.g., *C. hyperboreus*) and neritic expatriates (e.g., *C. glacialis*). Delivery schemes for each type of prey (Fig. 10), include lateral transport of krill, upwelling or upward summer migration of copepods (or, feeding on overwintering *Calanus* spp. at depth, Laidre et al., 2010), and the possible role of eddies in the transport of prey fields offshore of the shelf break in the Beaufort Sea (Watanabe et al., 2012). Adult bowhead whales require roughly 500-700 kg wet weight (WW) of prey day$^{-1}$, and feed in arctic waters at least from April through October (Lowry, 1993). A simple calculation using

available estimates of population size for each stock (Laidre et al., 2015), a prey requirement of 600 kg WW day$^{-1}$ over *ca.* 7 months suggests a combined annual biomass removal of about 3 million t WW year$^{-1}$ (probably an underestimate) of which 2.1 million t WW year$^{-1}$ are consumed by the BCB stock (Lowry, 1993, Laidre et al., 2015).  Assuming that DW is 20% of WW and that 50% of DW is carbon, the total C consumption by bowheads is approximated to be 300,000 t C year$^{-1}$, which is about 1/3 of the zooplankton biomass advected through Bering Strait (see 3.2).  Thus, prey consumption by bowhead whales is a significant part of the overall C budget of coastal regions along northern Alaska.

While similar data on marine mammal prey consumption are not available from the Eurasian sector of the AO, with the exception of piscivourous minke whales in early summer in the Barents Sea (Haug et al., 2002, Smout and Lindstrøm 2007), we note that upwelling and advection of zooplankton also plays a role in the trophic dynamics of upper-trophic species both in the Barents Sea (e.g., Dalpadado and Skjoldal, 1996, Dalpadado et al., 2012) and waters north of Svalbard. Krill is a highly preferred prey for several consumers in the Barents Sea, including capelin, herring, cod (e.g., Wassmann et al., 2006a, Eriksen and Dalpadado, 2011, Orlova et al., 2013), and marine mammals (Lindstrøm et al., 2013).  Specifically, the distribution of minke, fin and humpback whales is closely associated with high densities of krill (Skern-Mauritzen et al., 2011).  According to prey availability, minke whales can switch from consumption of capelin/herring to krill (Haug et al., 2002). An increase in biomass of lipid-rich euphausiids in recent years, possibly linked to the temperature increase in the Barents Sea (Dalpadado et al., 2014), has apparently provided good feeding and growth conditions for several upper-trophic species, including capelin and young cod, although it is not clear how recent warming has impacted interactions among these taxa (Dalpadado et al., 2012, Orlova et al., 2013).

*5. How much mesozooplankton biomass is advected into the Arctic Ocean? Lessons learned from a model.*

In part 3, our knowledge on the distribution and transport of the mesozooplankton into and through the AO, as based upon net-hauls, was evaluated (Figs. 7-9). Not only do large uncertainties exist in zooplankton

concentrations that are being transported, but also the physical oceanography should be known in greater detail. These uncertainties are valid for both the Pacific and Atlantic inflow regions. While more information is available for the Barents Sea opening (Sakshaug et al., 2009) and potentially also for the over-all transport north of Svalbard (Lind and Ingvaldsen, 2012) and into the Kara Sea (e.g., Smedsrud et al., 2013), the vastness of the AO and the logistic challenges posed to obtain data may leave us no other choice but to use partially validated biophysical models to approximate advection. An individual-based modelling study has been used to look at dispersion of *Calanus* species into the central basins (Ji et al., 2012), but no biomass estimates are provided. Here we apply the SINMOD model to calculate daily average flux of zooplankton biomass crossing each model grid cell boundary of a coupled AO model (for details of the biological model, see Wassmann et al., 2006b, Slagstad et al., 2011; material and methods of the SINMOD model for the new model calculations are presented in an electronic appendix). The stored data were used to calculate depth-integrated fluxes of the two mesozooplankton species represented in the model: *Calanus finmarchicus* and *C. glacialis.* With a 20 km grid size resolution, this model does not resolve eddies that can transport plankton from the boundary currents into the central Basin of the AO. As any model, care has to be taken to interpret the specific results. While the model in hind cast mode reflects well the production dynamics in the Barents Sea and adjacent regions (e.g., Wassmann et al. 2006b, Ellingsen et al., Wassmann et al., 2010) the model extrapolates the biological model over the entire AO in order to provide some preliminary answers. In particular the projections into the future have to be interpreted with caution. They are some first attempts to answer the demanding question how the future AO will function before its present biological mode of operation is adequately known.

In the model, high production and biomass of *C. finmarchicus* is found in Atlantic water entering the AO through Fram Strait and in the southwestern Barents Sea where Atlantic water masses dominate (Fig. 11A). *C. glacialis* is found in the northern Barents Sea, Kara Sea and along the Laptev and East Siberian shelf breaks (Fig. 11B). The large biomass found in the St. Anna Trough does not necessary reflect high production, but rather advection of *C. glacialis*

from the Barents to the Kara Sea. High biomass of *C. glacialis* is also found in shelf regions in the gyre within the Greenland Sea.

A high northward flux of *C. finmarchicus* is found in the West Spitsbergen Current where the standing stock is high and the currents are strong and persistent (Fig. 12A). The model suggests major advection of *C. finmarchicus* through to Franz Josef Land, after which there is a low biomass flux towards the Siberian Shelf and along the Lomonosov Ridge. Observations usually reveal *C. finmarchicus* along the Lomonosov Ridge close to the Siberian coast (see Fig. 7) and SINMOD does indeed project *C. finmarchicus* in this region, but in low numbers. The horizontal flux of *C. glacialis* is relatively strong in the northeastern Barents Sea, but between Franz Josef Land and Novaya Zemlya most of the biomass tends to recirculate (Fig. 12B). A high zooplankton flux is observed along the eastern slope of the St. Anna Trough. This flux persists along the entire Siberian shelf. A part of *C. glacialis* advection is based upon production in the northeastern Barents Sea/Franz Josef Land/Novaya Zemlya region, while more to the east biomass transport is increasingly based upon local shelf production. We also investigated the transport of *C. finmarchicus* and *C. glacialis* towards the end of this century under climate change (Fig. 12 C, D). While *C. finmarchicus* is still advected into the AO by 2100, in particular north of Svalbard, advection along the western sections of the Siberian Shelf remains low, but is greater than predicted for the present.

Daily modelled biomass fluxes of *C. finmarchicus* and *C. glacialis* through selected AO sections (see Fig. 11A) show a strong seasonal pattern in sections of the eastern Fram Strait, northern Svalbard (Fig. 13 A, B) and northeastern Barents Sea (Fig. 13 C). Section A has a high flux of *C. finmarchicus* during late summer or autumn and fluxes of 10,000 t C d$^{-1}$ are predicted. There is also a small flux of *C. glacialis*, but it comprises only 0.02% of that of *C. finmarchicus*. In Section B the time variation of the fluxes are similar, although the peaks are smaller and the advected biomass is significantly reduced compared to Section A. The *C. glaci*alis flux increases to 0.18% of the *C. finmarchicus* flux. The section across St. Anna Trough (C) shows the largest mesozooplankton export into the AO in late autumn and early winter. Occasionally a reversal of the flux occurs. The flux is strongly dominated by *C.*

*glacialis* while the contribution by *C. finmarchicus* is insignificant. Closer to the Lomonosov Ridge (Section D), the flux of *C. glacialis* is high in late autumn and winter, but there is also interannual variability. The contribution from *C. finmarchicus* is 0.14%. In the easternmost section off the Laptev Sea (Section E) the seasonality in the *C. glacialis* flux is greatly reduced and the variability is mainly interannual. The contribution by *C. finmarchicus* is insignificant. The model supports observations as it projects advection of very limited quantities of *C. finmarchicus* into the westernmost Canadian Basin (see Fig. 7).

The average annual advection of *C. finmarchicus* and *C. glacialis* is estimated to be about 610 and 279 thousand t C along Section A and B, respectively (Table 3). The difference suggests recirculation in the northern Fram Strait, with about half of the northward copepod flux turning south with the East Greenland Current and not entering the AO. In addition, 628 thousand t C of *C. glacialis* are advected into the AO through Section C, implying that the total advection of C. *finmarchicus* and *C. glacialis* through the gateways of the European Arctic Corridor (907 thousand t C) is similar to the maximum total zooplankton advection through the Bering Strait (see 3.2). *Calanus* copepods are significant, however they represent only a fraction of the total advected zooplankton. Consequently the total supply of mesozooplankton through the Atlantic gateways of the AO is distinctly higher than through the Bering Strait.

For an evaluation of the zooplankton advection, we must not only calculate the biomass flux, but also its effect on local production (assimilated carbon minus respiration). The important production areas of *C. finmarchicus* are situated in the Atlantic water masses such as the West Spitsbergen Current and the southwestern Barents Sea (Fig. 14A). Areas characterized by annual respiration losses greater than carbon assimilation yield negative production. For *C. finmarchicus*, this is seen as a white and light green tongue north of the Barents Sea and along the Eurasian shelf break towards the Lomonosov Ridge (Fig. 14A). Even a small section in the West Spitsbergen Current, i.e. prior to entering the central AO, shows such negative production rates. This is due to high overwintering biomass in the region. The tongue stretching along with the boundary currents into the AO illustrates clearly the concept of death trails. The main production areas of *C. glacialis* are situated within the seasonal ice zone of

the northern Barents Sea (Fig. 14B). Negative production is detected in the St. Anna Trough and along the entire Siberian shelf break, but small negative production can be traced throughout the Canadian Basin. Thus not only *C. finmarchicus*, but – to a lesser degree - also *C. glacialis* is characterized by death trails in today's AO.

In the future, these features will change significantly due to climate warming induced increases in primary production (increase in radiation caused by the loss of ice, see also Fig. 5 B, D) and plankton metabolism (Vaquer-Sunyer et al., 2010, 2013, Alcatraz et al., 2013). Forcing SINMOD with the IPCC climate scenario A1B, large changes in the production area of *C. finmarchicus* and especially *C. glacialis* are expected towards the end of the century. Comparing a 5-year period (2091-2095) with the present climate forcing (2004-2008), the model predicts that the overall *C. finmarchicus* production decreases (Fig. 14A and C). The areas having negative production in the AO will increase; the death trails will penetrate deeper into the AO and widen. The maximum *C. glacialis* production will move towards the East Siberian and Chukchi seas, such that negative production ceases in these two regions, but continues to exist close to the Canadian Arctic Archipelago.

*6. Assessing the over-all role of advection for the ecology of the Arctic Ocean*
Advection links marine ecosystems of the AO to the Atlantic and Pacific oceans. This linkage is particularly strong close to the gateways. The waters of Northern Greenland, the central Laptev Sea, the western East Siberian Sea shelf, and central Canada Basin are most isolated from the advective influence (Fig. 3).

In order to obtain accurate information about advection into the AO, multi-annual and continuous time series are needed, but these are hard to obtain and to interpret (but see Carstensen et al., 2012). The ability of models to evaluate the role of advection was presented in part 5, but lack of observational data for comparison makes it difficult to assess their reliability. An additional approach to evaluating the impacts of advection is to track shifts in the distribution, abundance and diet of upper-trophic species, such as marine mammals. Examination of stomach contents (e.g., Moore et al., 2010, Smout and Lindstrøm, 2007) or the use of isotopic analyses (e.g., Pomerleau et al., 2012),

can supply information regarding the diet of marine mammals and thereby provide insight into prey type and distribution. Surveys of the distribution and body condition of key upper trophic level species should be standard in AO ecological research programs to provide such a top-down view (Moore et al., 2013).

Viewed through the lens of advection, AO organisms can be classified into three types: oceanic expatriates, oceanic arctic residents and neritic expatriates (Table 2). Of particular interest for the ecological understanding of the AO is the role of oceanic expatriates in the inflow regions. Some of these zooplankters are large-bodied lipid-rich species that are capable of surviving prolonged periods of transport while drawing on their internal lipid stores if unable to find adequate food (Falk-Petersen et al., 2009). Allochthonous supply of oceanic expatriates creates rich feeding grounds in the areas that are closest to the inflow sites. There, advection supports ecosystems where the biomass consumption is greater than the local primary production, i.e. the advective regions of the AO are net-heterotrophic on an annual scale, as suggested by Olli et al. (2007). This appears to make these stretches of the AO fundamentally different from most of the world's oceans.

Based upon advection estimates (Table 3), assuming that 80% of the advected zooplankton biomass comprises copepods and that 44% (41-46%) of this copepod biomass consists of *C. glacialis* and *C. finmarchicus* (Kosobokova, 2012), the annual advection of mesozooplankton through the gates of the European Arctic Corridor was calculated. In total, 2.57 million t of zooplankton C is advected and this is 3 fold greater than the advection through the Pacific gateway. The 10-fold difference in water flux between the Atlantic and Pacific gates suggests that the zooplankton concentration in the Bering Strait is high. Recent increases in the inflow through Bering Strait (Woodgate et al., 2012) may reduce the difference between the Pacific and Atlantic gateways further. The primary production in the southern Chukchi Sea is higher compared with that along the European shelf break towards the AO (Grebmeier et al., 2005, Wassmann et al., 2010). Since little of the zooplankton is exported from the shallow Chukchi Sea into the adjacent AO (see 3.2) it must be assumed that live prey is consumed there or dies when meeting the arctic environment. Benthic

and pelagic scavengers may play a pivotal role in this regard (Day et al., 2013). There is thus a basic difference between the advection into the Amerasian Arctic sector via the Chukchi Sea versus the European sector via Fram Strait and the Barents Sea shelf (Hunt et al., 2013). Therefore the influence of the advected biomass rapidly declines upon entering the Arctic in the Amerasian Arctic sector, but has a basin-scale influence in the European sector.

While primary production is expected to increase significantly along the AO shelves during this century (e.g., Wassmann et al., 2010, Slagstad et al., 2011), the advection of mesozooplankton into the AO north of Svalbard is predicted to be steady (Sections A, B; Fig. 12, Table 3). With some exceptions, the flux through St. Anna Trough (Section C) into the northern Kara Sea is predicted to decline to only 17% of the present day transport.

Along with the advection of warmer water into the AO, a northward spread of boreal and temperate life forms is anticipated as is already occurring in systems south of the AO (Renaud et al., 2015). Thus far, 32 out of 45 fish species in the Bering Sea have already shifted their centre of distribution northwards in little more than two decades (Mueter and Litzow, 2008). Similar displacements were observed for fish communities in the Barents Sea (2004-2012: 159 km for the Arctic community and 141 km for the Atlantic shallow community; Fossheim et al. 2015). Similar northward shifts have also been observed in boreal systems (Perry et al., 2005). Northward boundary shifts are far more common than southward shifts (Mueter and Litzow, 2008). The advection of warmer-water species towards the central AO transforms the contiguous pan-Arctic shelf-break and marginal domain into an ecological "battle ground". Resemblances to the geological terms transgression and regression come to mind. Pacific and Atlantic species "transgress" into the AO hitherto dominated by arctic species. They create a frontal band of territorial coexistence along the advective pathways of water. As a consequence of global warming, species such as *C. finmarchicus* will enter into the realm where *C. glacialis* has been more pervasive. Both the invaders, as well as the residents, pay a price in this confrontation.

The future displacement of *C. glacialis* by *C. finmarchicus* in the northern Barents Sea and north of Svalbard (or similar developments in the Pacific sector of the AO) is part of the faunal boundary confrontations driven by the

glaciation/deglaciation cycles that have characterised the AO for millions of years. Ice-age relicts from these confrontations (e.g., Ekman, 1953) can be found along all boreal coasts and they exemplify regression of arctic species into isolated pockets [e.g., the dominating population of *C. glacialis* in the west Norwegian Lurefjorden (Hirche and Niehoff, 1996, Eiane et al., 1999), and the White Sea (Pertsova and Kosobokova, 2003, 2010)] where the populations may have been isolated for about 10,000 years. *C. glacialis* can also stay off the shelf edge at depth where the water temperature is < 6°C, and preferentially < 4°C (Carstensen et al., 2012). Its flexibility in life history traits, as determined by temperature, ice-cover and food, makes *C. glacialis* highly successful now and in the future AO (Daase et al., 2013a). A similar situation may also be found in the northern Bering Sea region with *C. glacialis* from the remote, ice-covered Sea of Okhotsk representing a "relict" population (Safranov, 1984, Musaeva and Kolosova, 1995). In fact, genetic results support this idea as *C. glac*ialis from the Sea of Okhotsk have primarily the "arctic" haplotype of the 16S ribosomal RNA gene (Nelson et al., 2014) while Nakatsuka et al. (2002) and Nishioka et al. (2013) depicted physical mechanisms that appear to inject Sea of Okhotsk *C. glac*ialis into the western subarctic Pacific.

The boundaries between the oceanic expatriates, oceanic arctic residents and neritic expatriates, as defined above are in constant flux. The future may bring greater seasonal and long-term displacement of arctic species as well as hybridization. To be continuously informed of dominant and emerging trends in the ecology the AO, distribution and abundance of key taxa will have to be assessed frequently as the physical and biological parameters of the AO respond to climate forcing. This will also ease the validation of models such as SINMOD and provide increased confidence in projections of the future development.

*7. Summary and Outlook*

Advection is an essential mechanism that regulates the colonisation and dynamic balance of organism groups in arctic and boreal regions. The highly productive subarctic driving a seasonally ice-covered, high-productive AO rim that engirdles a low-productive AO interior creates a unique ecological scenario that differs from all other marine ecosystems. The advection of prey originating from the

subarctic into the AO produces death trails for warmer-affinity species. Likewise many arctic organisms may ultimately face their death when advected out of the AO. Simultaneously, death trails create a basis of life for those organisms that manage to survive and the provision of prey for arctic key organisms. Advection is thus literarily an issue of life and death in the AO.

The advection of Atlantic and Pacific waters exposes the AO ecosystems to a pace-making effect on seasonal, interannual and interglacial time scales. The continuity of advective fluxes into the AO boundary currents, the Transpolar Drift and the outflows from the AO, act like conveyor-belts for nutrients and biota across the Northern Hemisphere (Figs. 3, 6). Climate warming and the reduction in ice cover probably already influence today's composition and advection of water masses. Climate change may thus influence how fast the gyres spin, the magnitude of AO primary production and how much carbon and food are imported and distributed. The over-all balance determines the residence times of water and potential for biogeochemical change. When advection governs an ecosystem, moving fronts and changing currents will have a large influence. It is too early to evaluate the net effects these oceanographic changes will have in the AO of the future, but models provide some first hints (e.g., Table 3).

The frequently applied assumption that a time-series investigation of the biogeochemistry and ecology of a water column will fully resolve each depth interval (i.e. as a model does) is most often not met. In particular, within coastal and shelf waters phenomena such as estuarine circulation, advection and upwelling obviously suggest that various depth layers have specific current velocities, directions, biota and timing of development. A water column can at any time comprise different ecological time developments that – for the moment of sampling – co-occur. The water column may be best understood as a layered system where a) various strata are moving in different directions, b) certain depths intervals changes its range in space and time while c) new strata could be squeezed in between others. These complicated time-space scenarios are best summarised by the term *ecology of advection*, originally coined to address the presence of deep and open water copepods in fjords (Matthews and Heimdal 1980, Aksnes et al., 1989). As a consequence, an ecosystem investigated at a

specific location, can import/export more biomass than it produces locally. When it comes to the AO, the inflow shelf ecosystems comprise the most fertile regions inside the AO, where some of the biomass is autochthonous, while significant fractions are allochthonous (Grebmeier et al., 2006, Kosobokova and Hirche, 2010, Wassmann et al., 2010, Kosobokova, 2012). For the up-stream regions that produce the allochthonous supply the opposite is the case: they consume less biomass than they produce.

The present contribution does not reach a comprehensive understanding of the role of advection for the oceanography of the AO, but addresses the principle processes, a number of spatial scales, and some of the players and ecosystem processes influenced by advection. Also, it hints at the potential future scenarios of advection for species distribution and biogeochemical cycling in the AO. We attempt to lay the foundation for a better interpretation of previous and future investigations by placing the AO in a more realistic time/space perspective. Thereby, a full set of scales linking climate to biota, along entire contiguous domains, may be accommodated in the future. An understanding of domain-wide responses to variance in climate should be the consequence. Within defined contiguous domains, the principles of biogeography can then be applied. Advection needs to become a topic for future marine arctic research. The physical base of the connection – let alone its biological, geochemical and biogeographic implications – is inadequately quantified at present. This lack of comprehension is a major bottleneck that compromises a domain-wide understanding of the AO. We are dealing with the most poorly known ocean of the World (Wassmann et al., 2011), but must also incorporate the AO into our understanding of the adjacent Pacific and Atlantic oceans, to which it is an integrated part.

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Table 1. List of zooplankton expatriate species advected into the Arctic Ocean basins from the adjacent areas

| Atlantic expatriates | Pacific expatriates | Neritic expatriates |
|---|---|---|
| *Calanus finmarchicus* | *Eucalanus bungii* | *Acartia longiremis* |
| *Oithona atlantica* | *Metridia pacifica* | *Drepanopus bungei* |
| *Metridia lucens* | *Neocalanus cristatus* | *Pseudocalanus acuspes* |
| *Rhincalanus nasutus* | *N. plumchrus/flemingeri* | *P. minutus* |
| *Pleuromamma robusta* | *Calanus marshallae* | *P. major* |
| *Paraeuchaeta norvegica* | | *P. newmani* |
| *Meganyctiphanes norvegica* | | *Bradyidius similis* |
| *Thysanoessa longicaudata* | | *Monstrilla sp.* |
| *Tomopteris septentrionalis* | | *Aglantha digitale* |
| *Gilia reticulata* | | *Plotocnide borealis* |
| | | *Cyanea capillata* |
| | | *Chrysaora  melanaster* |
| | | *Parasagitta elegans* |
| | | *Calanus glacialis* |

Table 2. Endemic (E) and migratory (M) marine mammals in the Arctic, primary prey, and role of advection, upwelling, eddies and pelagic-benthic coupling in prey delivery. Polar bears (E) and killer whales (M) primarily feed on mammals in the Arctic and are not included here.      *Primarily subarctic species. ** W. Greenland and Atlantic only. *** Pacific Arctic only

| Species | E/M | Primary prey | Prey delivery |
|---|---|---|---|
| Bowhead whale *Balaena mysticetus* | E | mesozooplankton (copepods, euphausiids) | advection & upwelling |
| Beluga *Delphinapterus leucas* | E | forage fishes and benthic crustaceans | advection & eddies? |
| Narwhal *Monodon monoceros* | E | deep-water & forage fishes | advection? |
| Walrus *Odobenus rosmarus* | E | benthic infauna (clams, worms) | advection & pelagic-benthic coupling |
| Ringed Seal *Phoca hispida* | E | forage fishes & benthic crustaceans | advection & upwelling |
| Bearded Seal *Erignathus barbatus* | E | benthic invertebrates & fishes | advection & pelagic-benthic coupling |
| Ribbon Seal* *Phoca fasciata* | E | forage fishes | upwelling & eddies? |
| Spotted seal* *Phoca largha* | E | forage fishes | upwelling & eddies? |
| Harp seal* *Pagophilus groenlandicus* | E | benthic invertebrates & fishes | advection & pelagic-benthic coupling |
| Hooded Seal* *Cystophora cristata* | E | deep water & forage fishes | advection? |
| Humpback whale *Megaptera novangliae* | M | euphausiids & forage fishes | advection |
| Fin whale *Balaenoptera physalus* | M | euphausiids & forage fishes | advection |
| Minke whale *Balaenoptera acutorostrata* | M | euphausiids & forage fishes | advection |
| Sei whale** *Balaenoptera borealis* | M | euphausiids & forage fishes | advection |
| Blue whale** *Balaenoptera musculus* | M | euphausiids | advection |
| Gray whale*** *Eschrichtius robustus* | M | euphausiids & benthic epi- and infauna | pelagic-benthic coupling & advection |
| Harbor porpoise** *Phocoena phocoena* | M | forage fishes & squid | advection & eddies? |

Table 3. Depth-integrated, average flux of water (Sv) and the zooplankton species *Calanus finmarchicus* (Cfin) and *C. glacialis* (Cgla) in t C d$^{-1}$ using IPCC's A1B scenario for selected 10 years periods along Sections A-E: West Spitsbergen current (A), Southern slope of Nansen Basin (B), Across the St. Anna Trough (C), Laptev Sea shelf slope (D) and Siberian Sea Shelf slope (E) (see Fig. 11A). Also indicated is the length of Sections A-E. Depth-integrated, average flux of water estimates cannot be easily compared to mass specific flux estimates provided by Mauritzen et al. (2011), Beszczynska-Möller et al. (2012) or Smedsrud et al. (2013).

| Section | 2001-2010 | | | 2046-2055 | | | 2090-2099 | | | Length of section (km) |
|---------|-------|------|------|-------|------|------|-------|------|------|------|
|  | Water | Cfin | Cgla | Water | Cfin | Cgla | Water | Cfin | Cgla |  |
| A | 6.0 | 1674 | 0 | 6.3 | 1950 | 0 | 5.8 | 1382 | 0 | 140 |
| B | 5.7 | 739 | 26 | 6.3 | 995 | 9 | 7.1 | 872 | 8 | 300 |
| C | 1.6 | 7 | 1712 | 1.7 | 131 | 656 | 1.6 | 304 | -0.1 | 180 |
| D | 10.6 | 3.6 | 3290 | 11.9 | 35 | 2695 | 13.7 | 162 | 361 | 520 |
| E | 12.2 | 0.2 | 2629 | 13.0 | 5 | 2641 | 14.3 | 40 | 909 | 360 |

Figure Legends

Fig. 1. The Arctic Ocean with its shelf seas and basins. Each comprises about 50 % of the total area. Also shown are the contiguous domains of Arctic Ocean advection: the Atlantic Arctic Domain (orange) and the Pacific Arctic Domain (red).

Fig. 2. Schematic overview showing atmospheric forcing, ice cover, water masses and topography of the Arctic Ocean. AA: Arctic Amplification (any change in net radiation balance (for example greenhouse intensification) tends to produce a larger change in temperature near the North Pole than the planetary average); MW: meridional wind maximum: WW: Westerly Winds; Q: heat exchange with the atmosphere; NSTM: Near-Surface Temperature Maximum; AW: Atlantic Water; PW: Pacific Water; DW: Deep Water. NPIW: North Pacific Intermediate Water. Also indicated is the depth of the Bering Strait and Barents Sea shelves. Redrawn from Carmack et al. (2012).

Fig. 3. The main upper ocean current patterns in the Arctic Ocean. Circulation of Pacific derived surface/subsurface water (blue) and surface/intermediate Atlantic Water (red) of the Arctic Ocean. The significance of the European Arctic Corridor for the advection of Atlantic and arctic water is obvious. The Arctic Ocean basins contain three "orbiting" water columns, which are surrounded by boundary currents and the Transpolar Drift at various depths. The Arctic Ocean is lower latitude-driven and illustrates its hemispheric dimensions dimension. Redrawn from Polyakov et al. (2013).

Fig. 4. Major fronts in the arctic and adjacent subarctic: 1. West Greenland Front (Belkin et al., 2009); 2. East Greenland Front (Johannessen, 1986); 3. Norwegian Sea Arctic Front (Blindheim, 2004); 4. Norwegian Coastal Current Front (Johannessen, 1986); 5. Barents Sea Polar Front (Johannessen, 1986); 6. Lomonosov Ridge Front (Anderson et al., 1994); 7. Alpha-Mendeleyev Ridge Front (McLaughlin et al., 1996); 8. Beaufort Shelf Front (Melling, 1993); 9. Siberian Coastal Current Front (Weingartner et al., 1999); 10. Anadyr Front

(Belkin and Cornillon, 2005); 11. Bering Shelf Front (Belkin and Cornillon, 2005); and 12. North Pacific Polar Front (Belkin and Cornillon, 2005). The stippled line indicates a shift of the front from the Lomonosov Ridge to the Alpha-Mendeleyev Ridge (see Kwok and Morison, 2011, McLaughlin et al., 1996, 2004, Morrison et al., 2000).

Fig. 5. Average position of the Polar Front in April. A & C - position as indicated by -1°C (blue) or +1°C (red) isotherms at 50 m depth, with vectors representing average currents at 50 m depth. B & D - the average Gross Primary Production (GPP, g C m$^{-2}$) for April is shown (observe the scales). A and B are the averages of the years 2000-2009 while C and D display the years 2090-2099. To force the SINMOD model (see electronic appendix) the International Panel of Climate Change (IPCC) scenario A1B was selected, providing a probable increase in mean global atmospheric temperature of close to + 4°C at the end of the century.

Fig. 6. Schematic diagram of the advective pathways of nutrient supply to the subsurface waters of the Arctic Ocean. Arrows are coloured according to the time (in years) required to reach their location from one of the three entry points. Redrawn from Popova et al. (2013)

Fig. 7. Composite figure derived from a magnitude of cruises of the number of *Calanus finmarchicus* (individuals m$^{-2}$) in the Arctic Ocean. For data sources, see Kosobokova (2012) and Schauer (2012).

Fig. 8. Observations of the expatriates *Metridia pacifica* (A), *Neocalanus cristatus* (B), *Neocalanus plumchrus* and *N. flemingeri* (C) and *Eucalanus bungii* (D) in the northern Bering Sea and adjacent pacific sector of the Arctic Ocean. The yellow circles indicate sampling sites lacking the species, while the red circles indicated observation of the indicated copepod species. Figure A shows the pathways of Pacific Water in the Arctic Ocean and upper water circulation patters, as indicated with white lines. Redrawn and modified from Nelson et al. (2014).

Fig. 9. Composite figure derived from a magnitude of cruises of the number of *Calanus glacialis* (individuals m$^{-2}$) in the Arctic Ocean. For data sources, see Kosobokova (2012) and Schauer (2012).
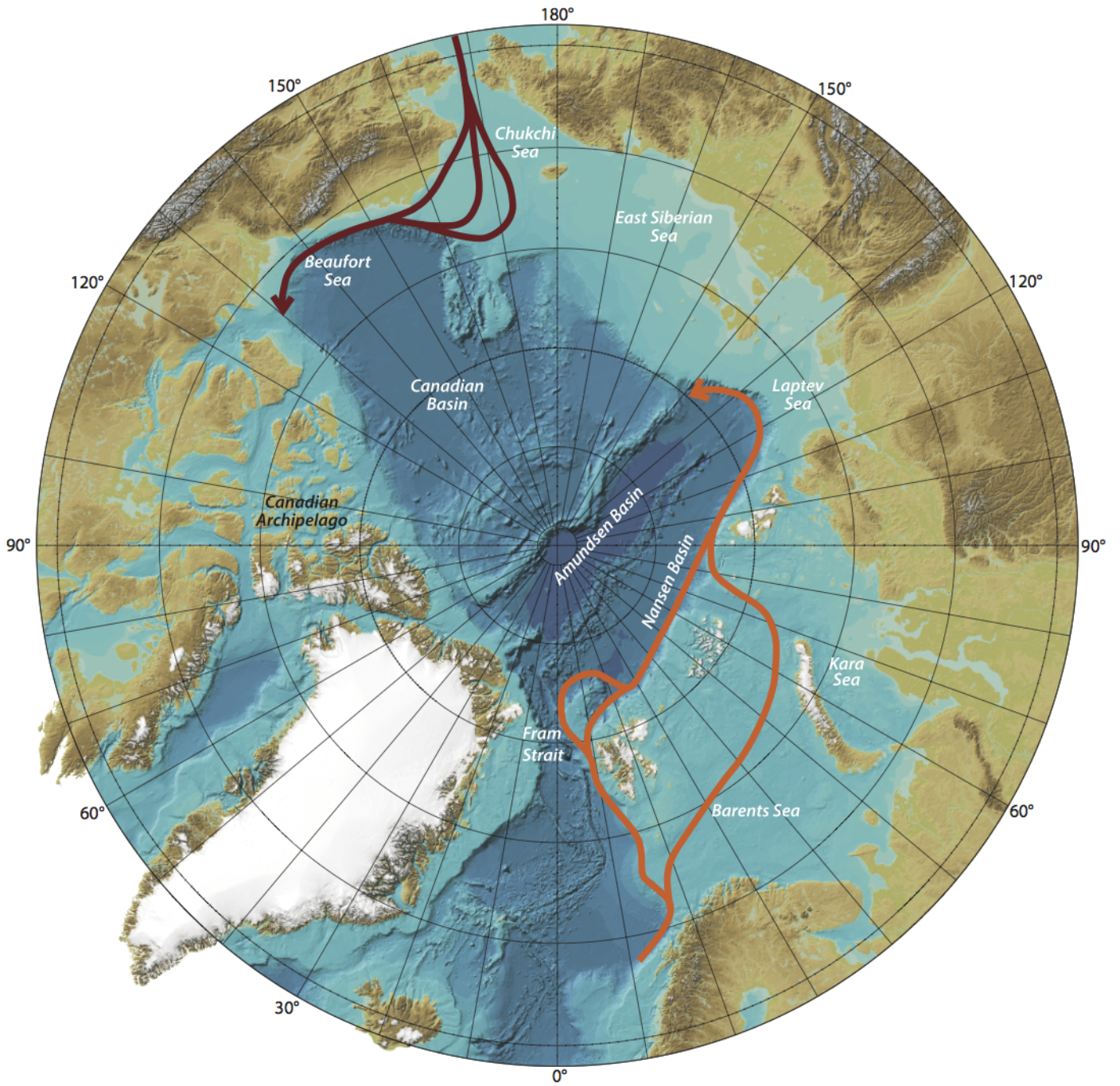
Fig. 10. Schematic of advective prey delivery for BCB (Bering-Chukchi-Beaufort) and EC-WG (Eastern Canada-West Greenland) bowhead whale populations illustrating lateral transport of euphausiids (krill) into both the Pacific Arctic (Berline, 2008) and Baffin Bay, the upwelling of copepods along the Beaufort Sea slope (Carmack and Wassmann, 2006) and the possible role of eddies in the transport of prey offshore of the shelf break in the Beaufort Sea (Watanabe et al., 2012). Supportive references from studies on whale diets are indicated by number: 1= Moore et al., 1995; 2 = Bluhm et al., 2007; 3 = Moore et al., 2012; 4 = Ashjian et al., 2010 and Moore et al., 2010; 5 = Lowry et al., 2004; 6 = Walkusz et al., 2012; 7 = Laidre et al., 2010, 2012; 8 = Pomerleau et al., 2012.

Fig. 11. Simulated annual average (2004-2008) biomass (g C m$^{-2}$) of *Calanus finmarchicus* (A) and *C. glacialis* (B). Also indicated are the positions of five cross sections for time series analysis (see Fig. 13): West Spitsbergen current (A), Southern slope of Nansen Basin (B), Across the St. Anna Trough (C), Laptev Sea shelf slope (D) and Siberian Sea Shelf slope (E).
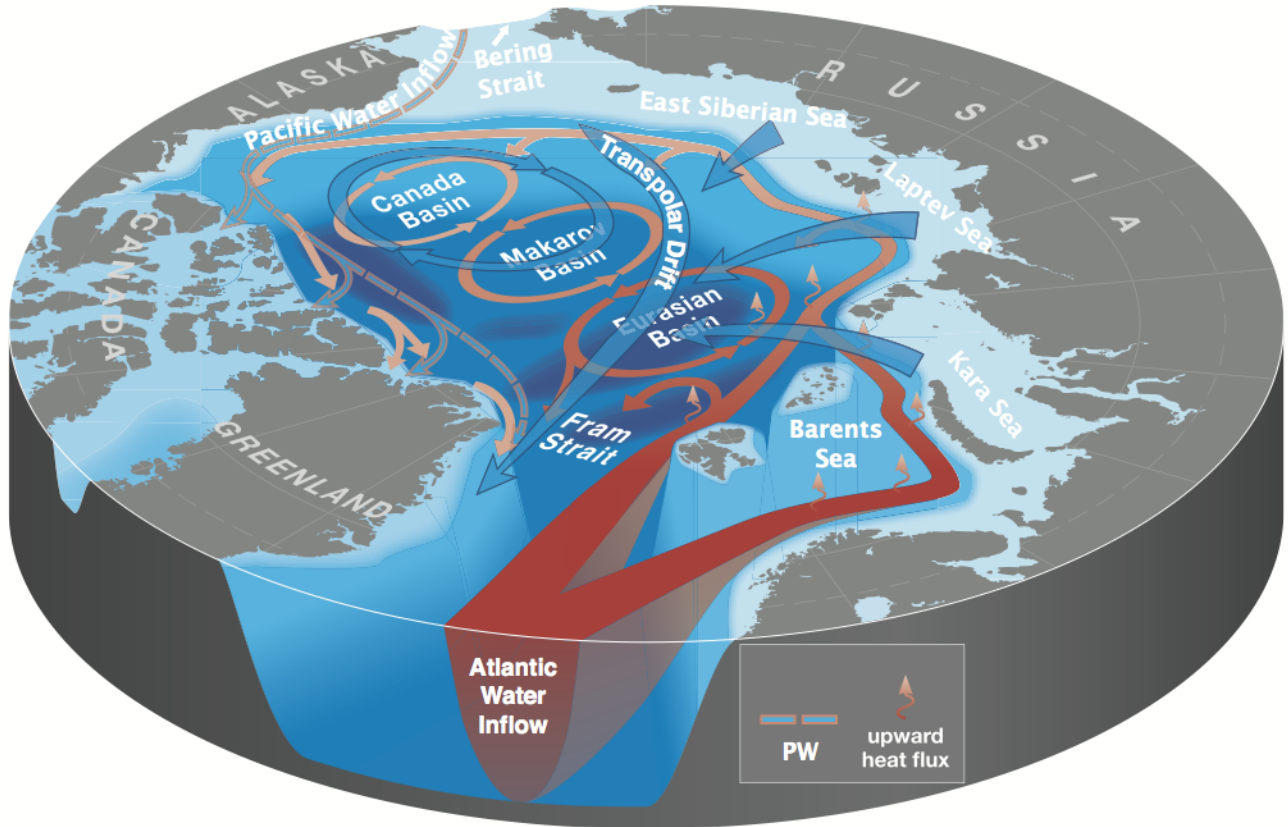
Fig. 12. Simulated annual average flux (t C km$^{-1}$ d$^{-1}$) of *Calanus finmarchicus* (A) and *C. glacialis* (B) for the period 2004-2008 and 2091-2095 (C, D), respectively. The length of the vectors represents the flux of biomass in t of carbon through the entire water column under a 1 km long section. The cut off size is 0.1 t C km$^{-1}$ d$^{-1}$.
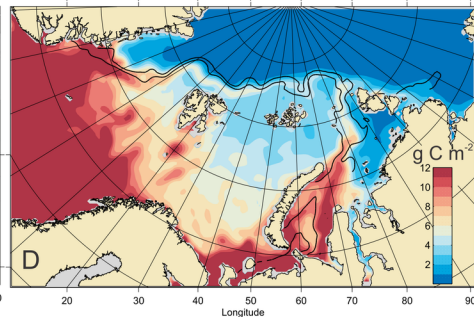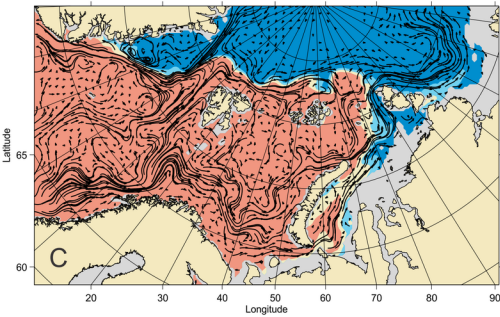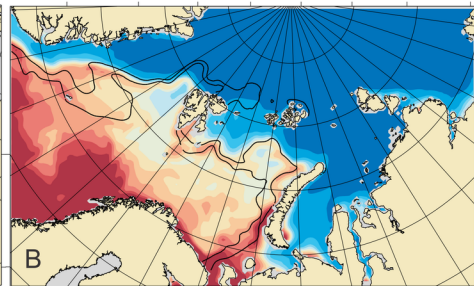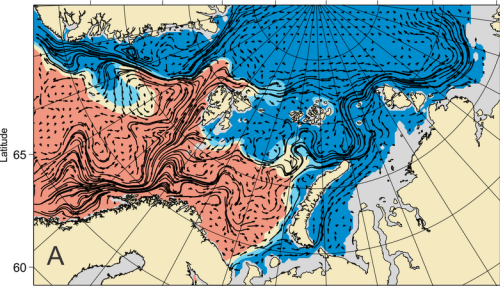
Fig. 13. Daily flux (t C d$^{-1}$) of *Calanus finmarchicus* (Cfin, black) and *C. glacialis* (Cglac, red) through the sections A-E (Fig. 11) using present climate setting (2004-2008).

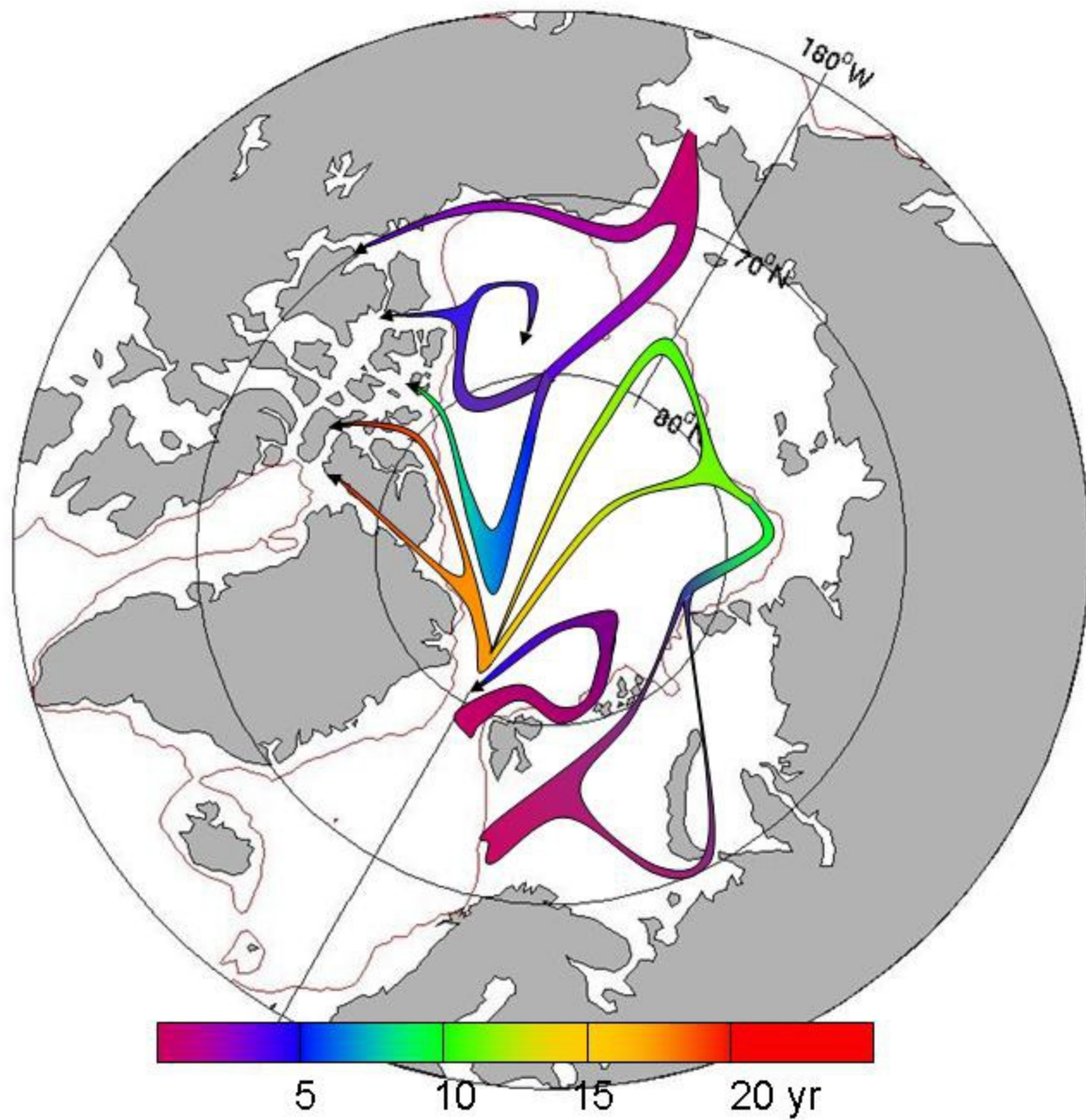Fig. 14.  Annual average (2004-2008) production (g C m$^{-2}$ y$^{-1}$) of *Calanus finmarchicus* (A) and *C. glacialis* (B) using present climate forcing. Annual average (2091-2095) production (g C m$^{-2}$ y$^{-1}$) of *C. finmarchicus* (C) and *C. glacialis* (D) using IPCC's A1B climate forcing.

70°N

80°N

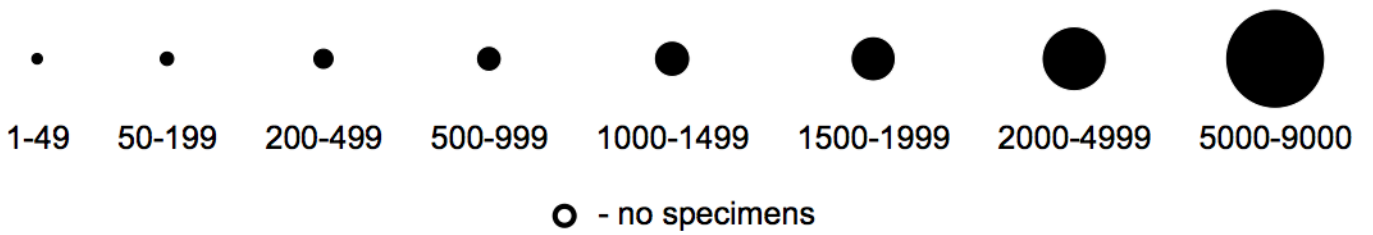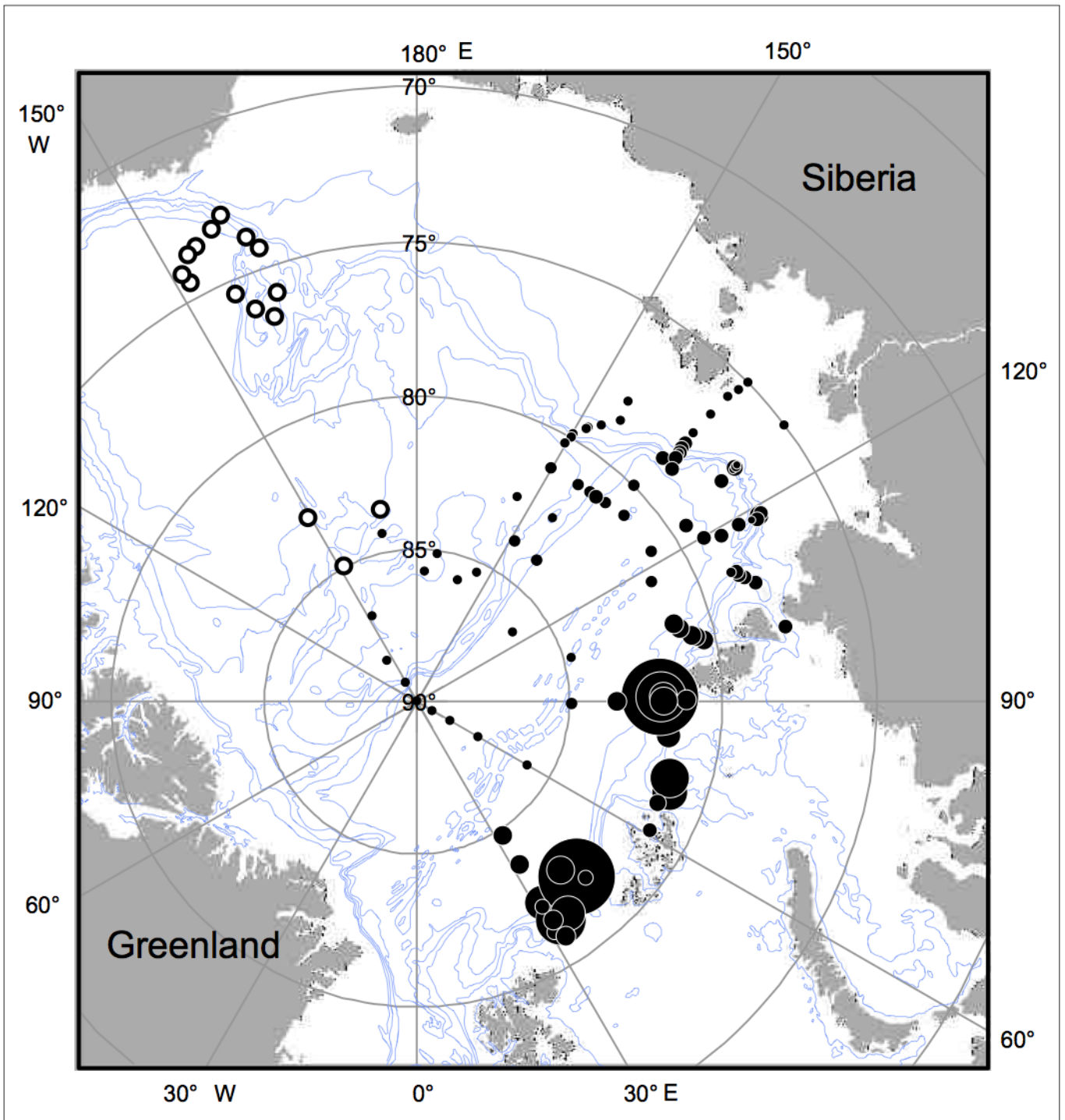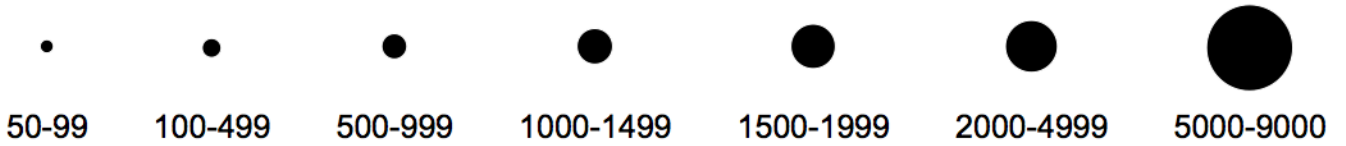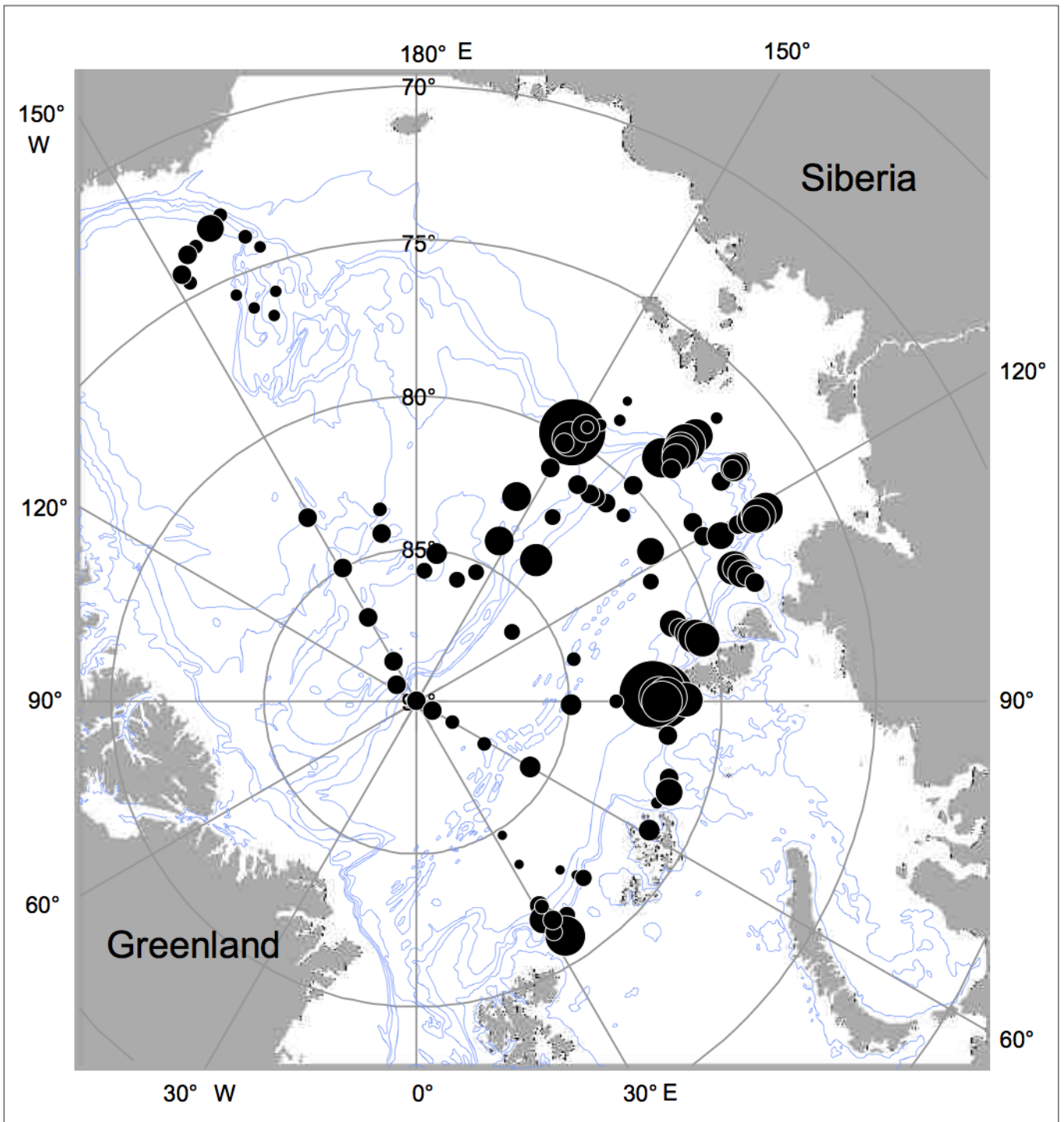5   10   15   20 yr

**1-49**    **50-199**    **200-499**    **500-999**    **1000-1499**    **1500-1999**    **2000-4999**    **5000-9000**

○ - no specimens

*Calanus finmarchicus*

150°
W

180° E

150°

70°

Siberia

75°

120°

80°

85°

120°

90°

90°

60°

Greenland

60°

30° W

0°

30° E

60°

50-99    100-499    500-999    1000-1499    1500-1999    2000-4999    5000-9000

*Calanus glacialis*

A **Metridia pacifica**

B **Neocalanus cristatus**

C **Neocalanus plumchrus+ flemingeri**

D **Eucalanus bungii**