ALFRED-WEGENER-INSTITUT
HELMHOLTZ-ZENTRUM FÜR POLAR-
UND MEERESFORSCHUNG

Universität Bremen

# The Future Arctic Biosphere

## Environmental Drivers of Change in Arctic Benthic Biota

Dissertation zur Erlangung des Grades eines
Doktors der Naturwissenschaften
- Dr. rer. nat. -

Fachbereich 2 Biologie/Chemie

vorgelegt von

**Renate Degen**

Universität Bremen, Mai 2015

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## Environmental Drivers of Change in Arctic Benthic Biota

## Umweltveränderungen in der Arktis - Wie werden sich benthische Ökosysteme entwickeln?

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*“There is nothing permanent except change.”*

Heracleitus of Ephesus

# Summary

Arctic ecosystems are facing unprecedented changes today. Annual surface temperatures increased almost twice the rate than the global average, and both sea ice thickness and extent decreased drastically, reaching a record low in summer 2012. Sea ice is the main structuring force in the Arctic environment as it modulates water column stratification and light intensities, and subsequently also pelagic and benthic production. Changes in sea ice conditions accordingly will lead to unforeseeable changes and consequences for the entire arctic ecosystem. This situation stresses the need for more information to enable us to predict upcoming scenarios. However, studies that link benthic production patterns to ecosystem processes on large spatial scales are still scarce, and baseline data from which change could be identified are lacking. Studies that focus on the ecological functioning of Arctic benthic communities are equally rare.

The aim of this thesis is to fill knowledge gaps of macro- and megabenthic community dynamics on the Barents Sea shelf and the adjacent Eurasian deep sea by means of an integrated approach. Benthic secondary production was estimated for the first time on Arctic shelf-wide scale and in the Arctic deep sea. Environmental drivers significantly explaining the observed patterns were identified by using geostatistical modeling and multivariate statistics. A biological trait approach was applied to estimate and compare the ecological functioning of Arctic benthos between shelf, slope and basin communities and between datasets from 1991 and 2012. A thorough literature review supported the discussion of our results and expected future scenarios in a wider context.

The results of this study showed significantly higher benthic secondary production in the northeastern, seasonally ice covered region of the Barents Sea shelf than in the permanently ice-free southwestern areas. In the deep-sea areas a significant decrease of secondary production with increasing water depth was apparent, but also with distance from the marginal ice zone. The major conclusion of this thesis is that food input and the tight pelagic-benthic coupling in the marginal ice zone are explaining the observed patterns. As ongoing warming drags the productive sea ice edge closer towards the North Pole, we expect shelf food webs to shift from a state favoring the benthic production towards one favoring the pelagic food web. Regions in the central Arctic could on the other hand benefit from increased food input associated with the approaching ice edge. The comparison of macrobenthic functioning at stations from the central Arctic sampled recently with stations sampled 20 years ago indicates that functional changes are already happening.

The present thesis provides for the first time estimates of Arctic macro-and megabenthic secondary production on a shelf- and basin-wide scale and contributes to a better understanding of Arctic benthic energy flow and ecosystem functioning. Results presented here provide a valuable input into prospective Arctic food web models and will help to improve our predictions of the future Arctic biosphere.

# Zusammenfassung

Das arktische Ökosystem steht heute noch nie da gewesenen Veränderungen gegenüber. Im Vergleich zum globalen Durchschnitt ist die durchschnittliche Jahrestemperatur in der Arktis beinahe um das Doppelte angestiegen, und sowohl Dicke als auch Ausdehnung des arktischen Meereises sind drastisch zurückgegangen. Das Meereis ist der zentralen Faktor im arktischen Ökosystem, da es die Lichtbedingungen und die Stratifizierung im Oberflächenwasser reguliert, und dadurch auch die pelagische, sowie in weiterer Folge auch die benthische Produktion. Änderungen der Eisbedingungen führen demnach zu Veränderungen im gesamten arktischen Ökosystem, deren weitreichende Konsequenzen heute noch schwer abzuschätzen sind. Diese Situation unterstreicht die Notwendigkeit von Datenerhebungen als Basis zu denen Veränderungen in Bezug gesetzt werden könnten und für genauere Zukunftsvorhersagen. Dennoch sind großräumige Studien benthischer Produktionsmuster und ihrer zugrunde liegenden Umweltfaktoren selten. Ähnlich rar sind Studien, welche sich mit den funktionellen Merkmalen (im Englischen „functional traits“) arktisch benthischer Gemeinschaften beschäftigen.

Das Ziel dieser Doktorarbeit ist Wissenslücken über makro- und megabenthische Gemeinschaften und deren Dynamik auf dem Barentssee Schelf und in den angrenzenden Tiefseegebieten zu füllen. Benthische Sekundärproduktion wurde zum ersten Mal in einem großflächigen Ansatz ermittelt und die erklärenden Umweltfaktoren mittels geostatistischer Methoden und multivariater Statistik bestimmt. Mittels „Biological Trait Analysis“, einer biologischen Merkmalsanalyse, wurden erstmals ökologische Funktionen zwischen benthischen Gemeinschaften von arktischen Schelf-, Hang- und Tiefseegebieten, sowie zwischen Datensätzen aus den Jahren 1991 und 2012 verglichen. Gründliche Literaturrecherche ermöglichte und unterstütze die Diskussion der Ergebnisse und möglicher Zukunftsszenarien in einem weiteren Kontext.

Die hier ermittelten Ergebnisse zeigen eine signifikant höhere benthische Sekundärproduktion in den nordöstlichen, saisonal eisbedeckten Regionen des Barentssee Schelfs, als in den permanent eisfreien Gebieten der südlichen Barents

See. In den angrenzenden Tiefseegebieten wurde ein signifikanter Abfall der benthischen Sekundärproduktion mit zunehmender Tiefe, aber auch mit zunehmender Entfernung von der Eisrandzone festgestellt. Die zentrale Schlussfolgerung lautet, dass der höhere Nahrungseintrag und die enge pelagisch-benthische Kopplung an der Eisrandzone die beobachteten Muster erklären. Da die laufende Erwärmung der Arktis die produktive Eisrandzone immer weiter nach Norden zieht, erwarten wir, dass sich die Nahrungsnetze des arktischen Schelfs von einem benthisch-dominierten Zustand mehr in Richtung eines pelagisch-dominierten Zustandes verändern werden. Die Gebiete der zentralen Arktis hingegen könnten von den erhöhten Nahrungseinträgen durch die sich nähernde Eisgrenze profitieren Der Vergleich zwischen makrobenthischen Gemeinschaften der zentralen Arktis von 1991 und 2012 deutet darauf hin, dass funktionelle Veränderungen bereits stattgefunden haben.

Die vorliegende Doktorarbeit liefert erste großflächige Analysen der arktischen makro- und megabenthischen Sekundärproduktion und trägt damit zu einem besseren Verständnis der arktischen Energieflüsse und Ökosystemfunktionen bei. Die hier präsentierten Ergebnisse bilden einen wertvollen Beitrag zur Modellierung von arktischen Nahrungsnetzen und werden zur Vorhersage exakterer Zukunftsszenarien beitragen.

# Content

# 1 Introduction

## 1.1 Benthic ecosystems

The sea floor represents one of the largest, but least explored habitats on earth (Kaiser et al. 2005). Zoobenthic organisms (here further referred to as benthos) are animals inhabiting the sea bottom from the intertidal zone down to the deep-sea basins and trenches. Apart from taxonomic and phylogenetic classification, benthic fauna is traditionally divided into four compartments or size classes: microbenthos (<0.06 mm), meiobenthos (0.06–1 mm), macrobenthos (>1 mm) and megabenthos (visible on seabed photographs or videos) (Gulliksen et al. 2009). Further common classifications of benthos relate to its motility (sessile to mobile), habitat (epifauna or infauna), trophic status (herbivore, carnivore or omnivore) or feeding type (grazer, suspension feeder, surface or sub-surface deposit feeder, predator or scavenger).

### 1.1.2 Role of benthos in marine ecosystems

All benthic compartments are involved in important ecological functions, ranging from processes structuring the local habitat to biogeochemical processes that affect the entire marine carbon budget, and accordingly also the global carbon budget (Fig. 1). Humanity benefits - directly or indirectly - from all these functions, in this context termed *ecosystem services* (Daily 1997).

*Secondary structures*

Epifauna, i.e. larger animals inhabiting the sediment surface (Gage & Tyler 1991), can create secondary structures that serve as living space for a variety of associated species and provide protection from environmental stress and/or predation (Bruno & Bertness 2001; Cochrane et al. 2009). Infauna can fulfill the same function within the sediment by creating three-dimensional structures and channels. Such contributions to local heterogeneity of the seabed have been shown to enhance biodiversity (Bruno et al. 2003). The most prominent examples are tropical coral reefs. Scleractinian corals can modify ecosystems on landscape-level and play an important role in sediment stabilization, prevention of coastal erosion and provide protection from storms and rising sea levels (Ferrario et al. 2014).

*Bioturbation*

Bioturbation, i.e. the biogenic modification of sediments through particle reworking and burrow ventilation (Queirós et al. 2013), can enhance sediment re-suspension and several biogeochemical processes like oxygenation/oxygen consumption and remineralization of sequestered carbon and nutrients (Cochrane et al. 2012 and references therein; Bonaglia et al. 2014). It can further promote biogeochemical heterogeneity within the sediment, thus stimulating microbial activity, in turn again enhancing mineralization (Kristensen 1988; Gage & Tyler 1991; Smith et al. 2008).

*Carbon cycle*

The carbon that reaches the ocean floor is processed in three ways: One part is buried in the sediment and sequestered from the atmosphere for probably millions of years (Klages et al. 2004). Although this process is of highest societal interest regarding the increasing levels of atmospheric $CO_2$, it represents only a small fraction of the overall carbon reaching the ocean floor (approximately 0.2 PgC $y^{-1}$) (Ciais et al. 2013; IPCC report). A larger part is remineralized by the benthos into $CO_2$, dissolved organic carbon (DOC) and nutrients, which are re-mixed into the hydrosphere (Klages et al. 2004). The remaining carbon is stored in the benthic biomass and available as food source for higher trophic levels. This third part of stored carbon can be channeled back into the pelagic food chain, thus contributing to overall marine energy flow (Fig. 1 and 2).

*Human interest*

Humanity benefits from all the previously mentioned functions of benthic communities and even more could be listed, but the most prominent human interest relates to fisheries production (Petersen & Lubchenco 1997). Several benthic organisms are of high commercial importance (e.g. crabs, lobsters, shrimps, scallops, mussels, oysters), or gain commercial importance by serving as prey for commercially important demersal fish (e.g. sole, plaice, cod).

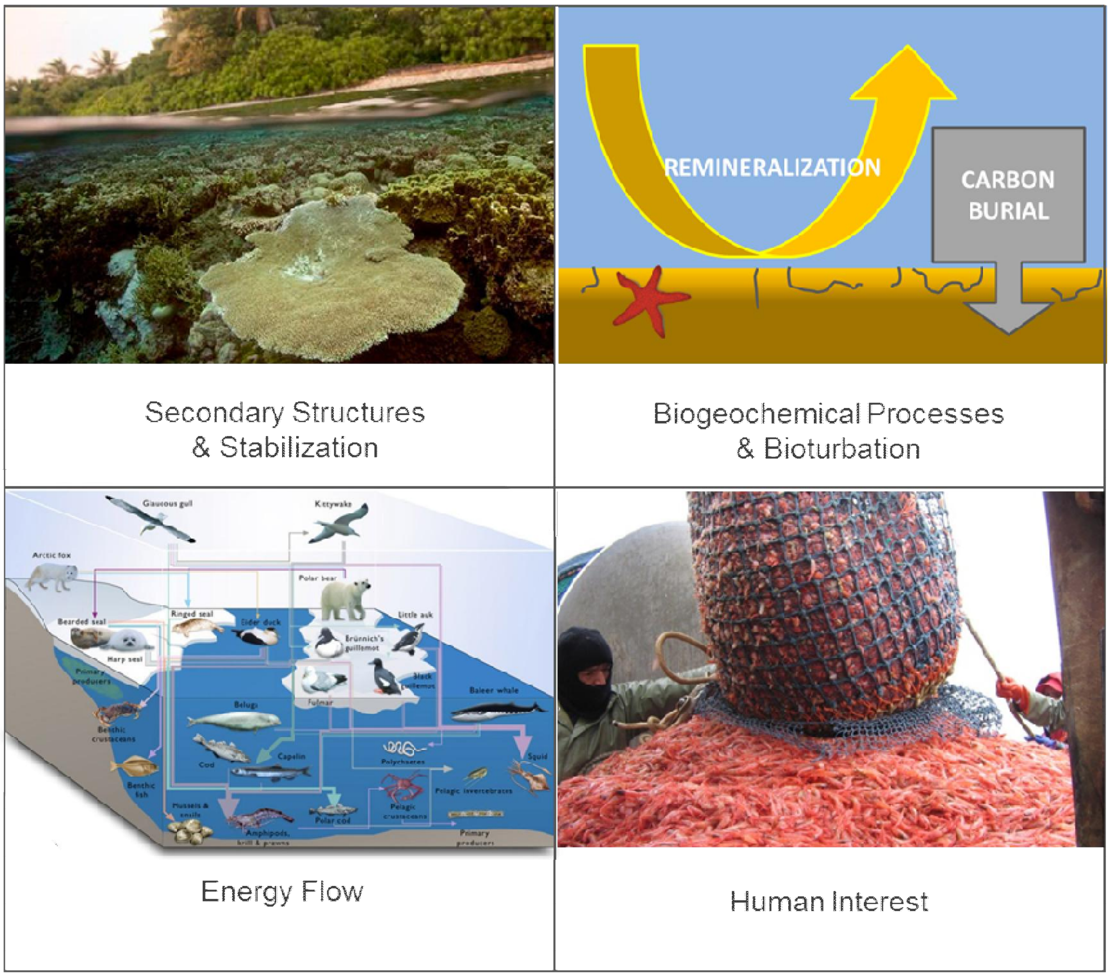

**Fig. 1** Examples for the role of benthos in the marine ecosystem. Images from N. Hall (up left), ACIA 2004 (down left) and NOAA (down right).

### 1.1.3 Factors structuring benthic communities

Food input is reported to be the main driver of distribution and biomass of all benthic compartments on a large scale perspective (Rowe 1971; Pearson & Rosenberg 1978; Piepenburg 2005). Several factors, i.e. surface production, water depth, distance from shore, width of the continental shelve, water column assimilation efficiency and latitude determine the benthic community structure, all of them related to the amount and quality of food reaching the seafloor (Gage & Tyler 1991).

At local scales other factors like seabed attributes, predation and/or disturbance, environmental stability, competition and hydrodynamics can explain benthic community patterns (Pearson & Rosenberg 1978; Grebmeier et al. 1989;

Piepenburg 2005). In particular, hydrodynamics play an important role in community function, with feeding types shifting towards suspension feeders in dynamic areas, and towards deposit feeders in more stagnant and therefore depositional areas (Feder et al. 2005). Grebmeier et al. (1989) showed that, together with food supply, sediment heterogeneity and temperature are the major regulating factors in benthic community structure.

## 1.2 Arctic benthic ecosystems

In several characteristics Arctic benthic ecosystems are not differing from non-polar marine realms. The main difference in the Arctic ecosystem though, affecting also the benthos, is the strong seasonality in solar radiation and nutrient availability as well as the long-lasting sea-ice cover (Carmack & Wassmann 2006). The Arctic ice cap consists of a permanent sea ice cover in the central Arctic (about 6 x $10^6$ km² in summer) and a surrounding seasonally moving marginal ice zone (MIZ) (about 15 x $10^6$ km² in winter) that reaches as far south as 44° N (IPCC 2013). This sea ice cover is the main factor structuring Arctic ecosystems, as it controls pelagic and benthic production through modulating water column stratification and light fields (Bluhm & Gradinger 2008). The productive season starts at the end of the polar night, with sunlight triggering the ice-edge bloom which moves along with the seasonal ice-melt in pole-ward direction (Wassmann et al. 2011b). These episodic pulses of pelagic and ice-related organic carbon form the most important food supply to the benthos below the euphotic zone, which relies in its nutrition entirely on horizontal or lateral input from productive layers (Carmack and Wassman 2006). Although phytoplankton constitutes the bulk of overall primary production, ice algae can contribute up to 25 %, potentially even more in the central Arctic (Gosselin et al. 1997; Wassmann et al. 2006; von Quillfeldt et al. 2009). Furthermore, ice algal blooms occur earlier in the season than phytoplankton blooms, hence providing an important early-season supply of very fresh organic material (Carroll & Ambrose 2012).

Despite the mentioned environmental constraints in the Arctic, benthic abundance and biomass can be very high. This is explained by the efficient energy transfer from the water column to the sea floor, i.e. the tight pelagic-benthic coupling on Arctic shelves (Petersen & Curtis 1980, Grebmeier and Barry 1991). Due to the large proportion of shallow shelf seas in the Arctic Ocean (Fig. 4), the benthic food web is considered to be of relatively more importance than at lower latitudes (Gulliksen et al 2009). Accordingly, also the proportion of benthic production relative to primary productivity has been hypothesized to be greater at high latitudes (Brey and Clarke 1993; Grebmeier et al. 2006a). However, studies that focus on benthic secondary production in the Arctic are scarce and restricted to shallow shelf areas (see 1.2.1). Benthic secondary production corresponds to the newly formed biomass per unit of area an time (mostly given in g C $m^{-2}$ $y^{-1}$) (Brey 2001). It provides important ecological information, as it depicts exactly that quantity of energy that is available as food for the next trophic level in the food web (Fig. 2).

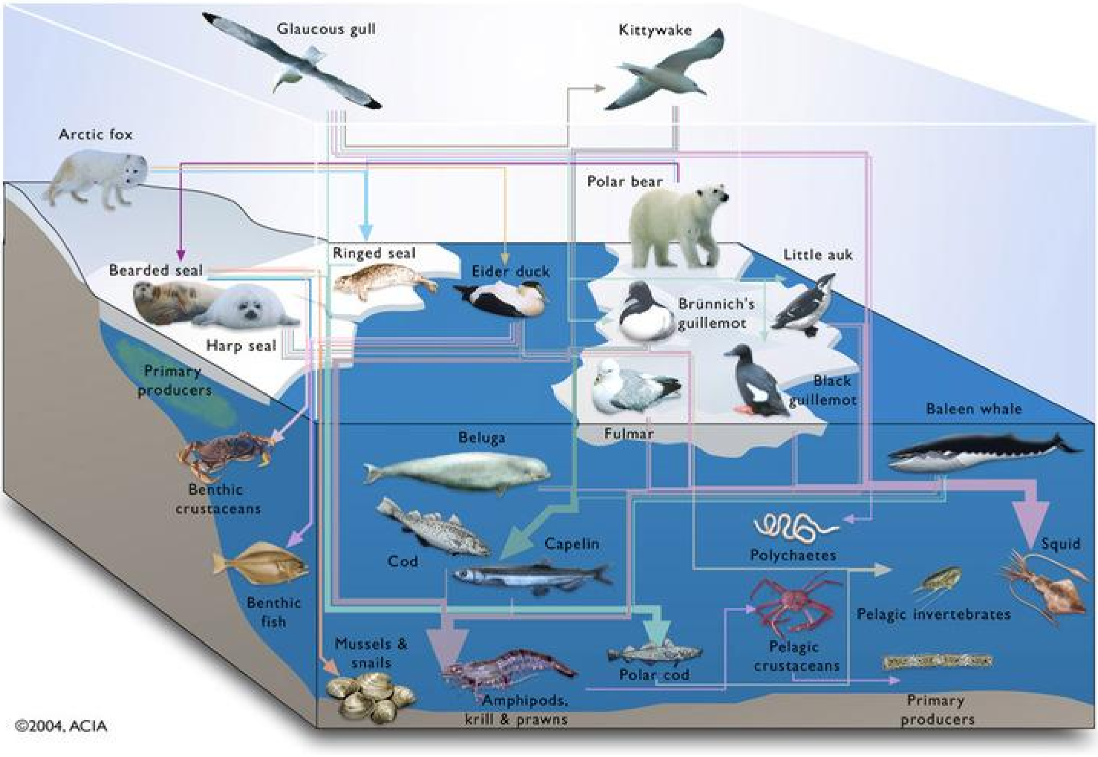

**Fig. 2** Arctic marine food web. ACIA 2004.

### 1.2.1 Arctic Shelves

Continental shelves extend from the low water mark on the shoreline down to an average depth of 200 m (Fig. 3). The ecology is strongly influenced by physical processes such as waves, tides, currents, erosion and input from the adjacent land mass; processes that generate a great diversity of ecosystems and habitats on regional and local scale (Kaiser et al. 2005). Arctic shelves are additionally characterized by a pronounced seasonality in solar radiation, nutrient availability and sea ice cover as well as by temperatures close to the freezing point (Carmack and Wassmann 2006). The Southern Chukchi Sea, the Bering Shelf and the Barents Sea (Fig. 4) are Arctic shelves exhibiting complex food webs and some of the highest densities of benthic invertebrate fauna in the world's Oceans (Grebmeier et al. 1989, 2006a). These rich benthic communities support a variety of upper tropic level consumers, ranging from commercially important fish stocks up to marine mammals (Carmack and Wassmann 2006; Gulliksen et al 2009). The benthic production is fueled by high pelagic primary production and by the episodic flux of organic matter linked to the brief passage of the ice-edge blooms during the seasonal ice melt (Carmack and Wassman 2006).

Macro- and megafauna generally contribute more to overall benthic biomass (>50 %) in shallow water than meiofauna and nanobiota, while this pattern is reversed in deeper areas (Gage & Tyler 1991). The previously described heterogeneity of Arctic shelf habitats is mirrored in the diversity of macrobenthic living and feeding habits. Hard substrata in areas of moderate current can be inhabited by rich epifauna assemblages of sessile particle or suspension feeders and mobile predators or grazers. In deeper or sheltered areas finer sediments can accumulate and harbor communities of burrowing deposit or suspension feeding infauna and fewer sessile filter feeders or mobile scavengers (Grebmeier et al. 1989; Feder et al. 2005; Kaiser et al. 2005).

Megafauna is highly abundant on Arctic shelves and represents an important pathway of the benthic carbon and energy flow (Clough et al. 2005; Piepenburg 2005; Renaud et al. 2007). Although this importance of macro- and megabenthic secondary production on Arctic shelves is widely recognized, the few existing studies set focus only on one taxonomic group (e.g. Highsmith & Coyle 1990) or are rather small scaled (Kedra et al. 2013). Studies that analyze patterns of total community macro- and megabenthic secondary production on a large scale are lacking completely.

### 1.2.2 Arctic Basins

Beyond the shelf break (>200 m water depth) the continental shelf slopes down towards the deep Arctic Basin with average water depths of 4000 m (Jakobsson et al. 2008) (Fig. 3). The Arctic basin is separated by the Lomonosov Ridge into the Amerasian and the Eurasian part. The first is further separated into the Makarov Basin and the Canadian Basin and the latter is separated by the Gakkel Ridge system into the Nansen and the Amundsen Basin (Fig. 4). To a vast extent the deep sea floor can be depicted as a mostly stable, soft bottom habitat, characterized by consistent physical conditions (cold, dark, high pressure) and food limitation (Kaiser et al 2005). The central Arctic Ocean is characterized by extreme limitations in solar radiation and nutrient availability, permanent ice cover and temperatures always close to the freezing point (Piepenburg 2005). Accordingly, overall surface productivity is very low, resulting in low food fluxes to the benthos (Klages et al. 2004; Fahl & Nöthig 2007; Wassmann et al. 2010). Technical equipment and logistics have significantly improved in the last years, nevertheless, sampling great depths in remote areas with dense sea ice cover and during Arctic winter remains challenging (Klages et al. 2004). Consequently, the Arctic central Basins remain very poorly studied, even when compared to other deep-sea areas (Bluhm et al. 2011). The few existing studies describe the Arctic deep sea as an oligotrophic area with steep gradients in faunal abundance and biomass from the slopes to the basins, primarily driven by food availability, but overall not different from other deep-sea regions that are equally characterized by remoteness from land and low surface productivity (Gage & Tyler 1991; Bluhm et al. 2011).

In the deep sea basins Meiofauna and Nanobiota contribute significantly more to overall benthic abundance and biomass than macrofauna (Gage & Tyler 1991). While on shelves complex food webs and a variety of feeding types are reported (Grebmeier et al. 1989), benthic deep-sea communities are reported to be dominated by deposit feeders (Gage and Tyler 1991; Kröncke 1994, 1998). Exceptions can occur in areas of high bottom current flow, where suspension feeders can become prominent (Gage & Tyler 1991). At abyssal depths the proportion of sessile deposit feeders appears to shift towards mobile deposit feeders, potentially related to the fact that fewer sessile feeders are able to reach a large enough area to survive (Thistle 2003). The proportion of mobile carnivores was reported to decrease with increasing depth towards mobile opportunistic scavengers (Gage & Tyler 1991).

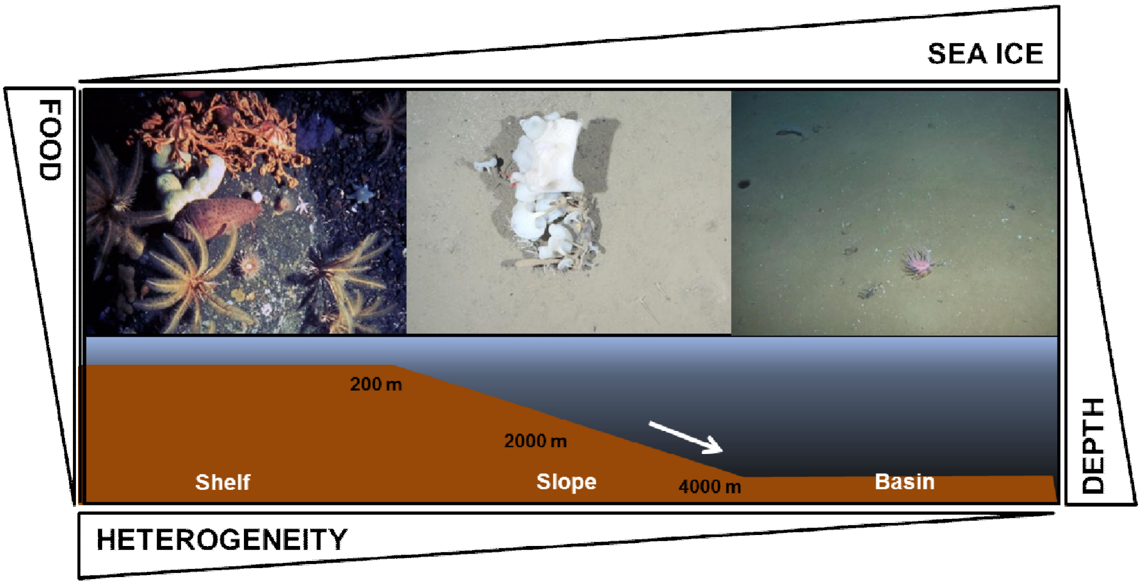

**Fig. 3** Simplified scheme of factors influencing benthic communities on Arctic shelves, slopes and basins. Triangles symbolize basic trends in food flux, sea ice concentration, water depth and habitat heterogeneity; the small arrow symbolizes bottom slope water movement. Images provided by D. Piepenburg, M. Bergmann (both AWI) and ArcOD (from left to right).

### 1.2.3 Shelf – Basin interactions

Generally, continental shelves are characterized by strong lateral exchange of matter between each other and by export to adjacent deep-sea regions. As shelves are usually much more productive than oceanic regions, this export of organic carbon across the continental margin was reported to cause enhanced activity and abundance of benthic organisms at depth (Piepenburg 2005). It was assumed that such shelf-basin interactions might be particular intense in the Arctic, which is surrounded by mostly very productive shelves like the Bering, Chukchi and Barents Sea shelves (Fig. 4). However, until today it is still not clear how significant these exports are (Piepenburg 2005).

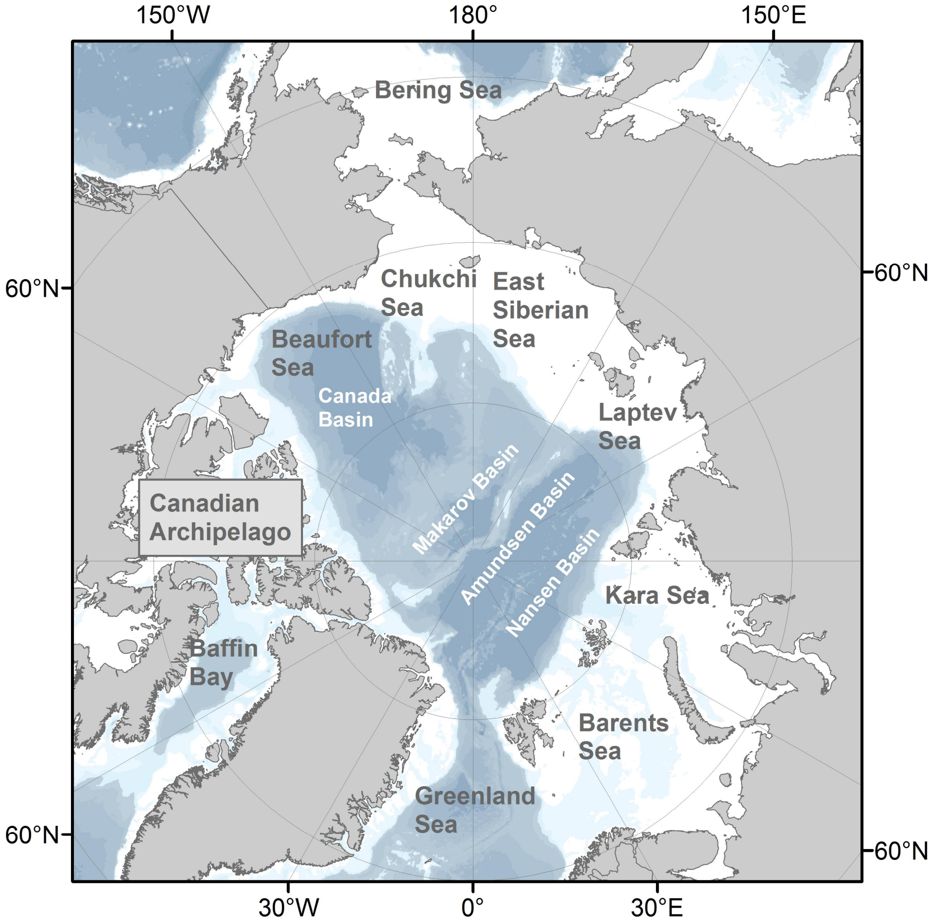

**Fig. 4** The Arctic Ocean with its shelves and Basins. Bathymetry after Amante & Eakins (2009).

## 1.3 Climate change in the Arctic

Climate change has a more pronounced impact at high northern latitudes compared to low latitudes, and annual average temperatures in the Arctic have increased almost twice the rate than the global average over the past few decades (ACIA 2004). Climate warming induces higher water temperatures, increased fluvial run-off and reduced sea-ice extent and thickness. Since the late 1970ies, the annual mean Arctic sea ice extent has decreased significantly, showing most dramatically during summers, where decreases ranging from 9.4 to 13.6 % per decade have been registered (Fig. 5) (Vaughan et al. 2013). In September 2012, a record sea ice minimum was reached, 49 % below the 1979–2000 average (NSIDC). As the Arctic sea ice is the main regulatory component controlling pelagic and benthic production (Bluhm & Gradinger 2008) (see also 1.2), this observed changes might have cascading effects through all trophic levels in the Arctic ecosystem.

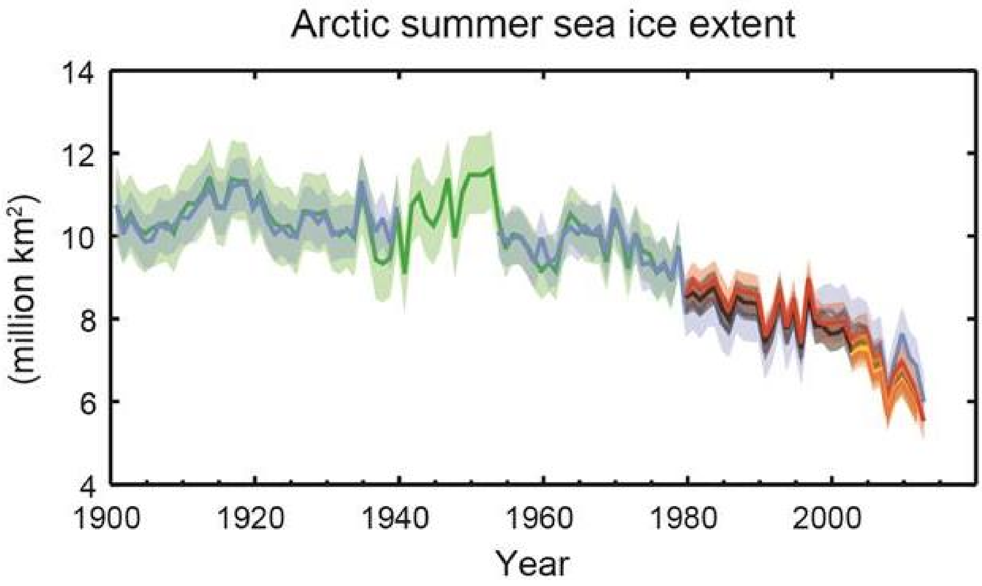

**Fig. 5** Arctic summer (July-August-September) sea-ice extent. All time-series (coloured lines indicate different data sets) show annual values, uncertainties are indicated by coloured shading (Vaughan et al. 2013, IPCC report).

### 1.3.1 Benthos as indicator of change

Benthic community parameters like species composition, biomass, diversity, and growth reflect the overlying primary production regime, hence they can be used as indicators of changes in water column processes as currently observed in the Arctic Ocean (Carroll & Ambrose 2012). But not all compartments of the benthos are responding on the same time scales. While macro- and megafauna integrate changes over longer, seasonal and annual time scales, microbenthos was reported to react on time scales of hours to days, and also meiobenthos might react very fast and is accordingly an indicator of short-term changes (Klages et al. 2004). Major obstacles are our lack of knowledge regarding the current state of the Arctic ecosystem and of the Arctic deep-sea floor in particular, and the lack of reliable baseline information (“pre-change system state”) from which change can be identified (Wassmann et al. 2011a). This holds especially true for benthic secondary production, as only a few spatially confined studies exist from Arctic shelves and none so far from the Arctic deep sea.

## 1.4 Objectives

Albeit the acknowledged importance of benthic energy flow in Arctic ecosystems, studies that link benthic production patterns to ecosystem processes on large spatial scales are still scarce (e.g. Highsmith & Coyle 1990). The principal aim of this thesis was – in the light of the substantial environmental changes observed in the Arctic – to estimate the secondary production of the macro- and megabenthic compartment of the Arctic biosphere and to employ it as an indicator of the ongoing changes. The focus is set on the benthic secondary production as it quantitatively links the pelagic and benthic energy flow and provides a suitable baseline for regional comparisons and assessment of a potential system change. The first step in achieving this goal is the estimation of benthic secondary production on shelf- and basin-wide scale and the identification of spatial and temporal patterns (1.4.1). Subsequently, the observed patterns should be linked to environmental parameters to identify the environmental drivers significantly explaining the observed patterns (1.4.2). The last objective is to identify spatial patterns also in the functioning of macrobenthic shelf, slope and basin communities and to test whether changes in functioning are already visible today (1.4.3).

The objectives raised here are investigated in the corresponding Manuscripts I–III and further discussed in the synthesis (chapter 4). The aim of Manuscript IV was a large-scale assessment of the current knowledge on the structure of Arctic marine food webs (Fig. 2) and their response to climate change, and the main outcome of this review is equally discussed in section 4.

### 1.4.1 Spatial and temporal patterns

The aim of assessing spatial patterns of benthic secondary production on the Barents Sea shelf (Manuscript I) and in the Eurasian Arctic deep sea (Manuscript

II) implied different approaches of data acquisition and processing regarding the two different environmental settings. Due to its economical importance and the relatively good accessibility, the Barents Sea shelf is among the best-studied Arctic shelves, and monitoring approaches reach back to the early 20th century. In Manuscript I a huge trawl dataset resulting from the joint Norwegian-Russian Ecosystem Survey (Michalsen et al. 2013) is analyzed. Based on this spatially inclusive and comprehensive dataset the objective of Manuscript I is to estimate for the first time megabenthic secondary production on a shelf-wide scale and to identify spatial patterns and trends. The data situation in the Arctic deep sea is strikingly different, and only few studies exist that assessed benthic abundance and biomass, both parameters necessary for the estimation of secondary production in the multiparameter ANN model used in this thesis (see 2.3). Accordingly, here an integrated approach of field work (RV POLARSTERN Expeditions ARK-XXVII/2 & ARK-XXVII/3) and data mining (see section 2.1.3) was required to increase the amount of useable data. The objective in Manuscript II is to estimate for the first time macrobenthic secondary production in the Arctic deep-sea and to identify spatial patterns and trends.

### 1.4.2 Environmental drivers

In order to understand how ongoing changes like sea ice retreat affect benthic energy flow, we have to identify the drivers behind patterns in benthic community production. The huge and dense set of benthic and environmental data on the Barents Sea shelf enables us to apply global and local regression models to examine the spatial relationship of secondary production and the environment. Accordingly the objective in Manuscript I is to identify the environmental drivers significantly explaining the observed patterns of megabenthic secondary production. The Arctic deep-sea dataset is smaller and wider distributed, preventing the application of spatial models. Accordingly stations were grouped into clusters and analyzed with multivariate statistics. The objective of Manuscript II is to identify significant differences in secondary production among stations when grouped into regional clusters and clusters related to water depth, latitude and sea ice concentration.

### 1.4.3 Changes in functioning

Secondary production is probably the most important function in benthic communities, and changes in secondary production can indicate environmental change (see 1.3.1). The biological trait analysis (BTA) is another approach to indicate environmental change (Bremner et al. 2006). It is based on a set of life history, morphological and behavioral traits to indicate ecosystem functioning, and changes in the trait composition or relative importance of traits can indicate changes in the environment (see 2.5). The objectives of Manuscript III are to compare the secondary production weighted trait composition between Arctic shelf, ridge and deep-sea basin communities and between stations samples in the year 1991 and 2012 to detect if changes in functioning are already apparent.

# 2 Materials and methods

This section gives a brief overview of the sampling methodology and the approaches used in this thesis. More detailed information can be found in the Methods section of the respective Manuscripts.

## 2.1 Data acquisition

### 2.1.1 Macrofauna sampling

For quantitative sampling of benthic macrofauna commonly benthic grabs or box corers with sample areas of 0.1–0.25 $m^2$ are used (Eleftheriou & Moore 2005). For deep-sea use the 0.25 $m^2$ USNEL box corer (Hessler and Jumars 1974) is preferred as it proved to be a reliable sample gear in obtaining deep and relatively undisturbed samples from a variety of sediments (Gage & Bett 2005) (Fig. 6a). Less commonly used gears are the nine-core multibox corer that samples an area of 0.22 $m^2$ over 2–3 $m^2$ of seafloor (Gerdes 1990) (Fig. 6b) and benthic chambers of bottom lander systems (Fig. 6c). Independently of the used gear, usually several subsamples are taken to aggregate an area of up to 0.5–0.1 $m^2$ per station, a sample size considered to be adequate for quantitative determinations of the more common species and measurements of abundance and biomass (Eleftheriou & Moore 2005). However, in Arctic deep-sea studies often smaller sample areas are accepted due to the difficulties involved sampling these remote sites, e.g. challenging sea ice and weather conditions, time constraints and the often interdisciplinary nature of the benthic research on board ship, which involves the sharing of samples among groups (Kröncke 1994, 1998).

### 2.1.2 Megafauna sampling

Dredges and trawls are used for qualitative sampling of the epifauna and megafauna (Fig. 6e). Several types of nets exist that are designed to skim over the surface of the sea bottom. Because they can cover a large area they are considered useful for collecting scarcer members of the epifauna that might be underrepresented in benthic grabs or box corers (see 2.1.1.) (Eleftheriou & McIntire 2005). The gear has to be considered as qualitative or at best semi-quantitative, as the efficiency (i.e. the numbers of animals captured in relation to those in the area swept by the net) is generally low, and it is selective for particular species (Eleftheriou & McIntire 2005).

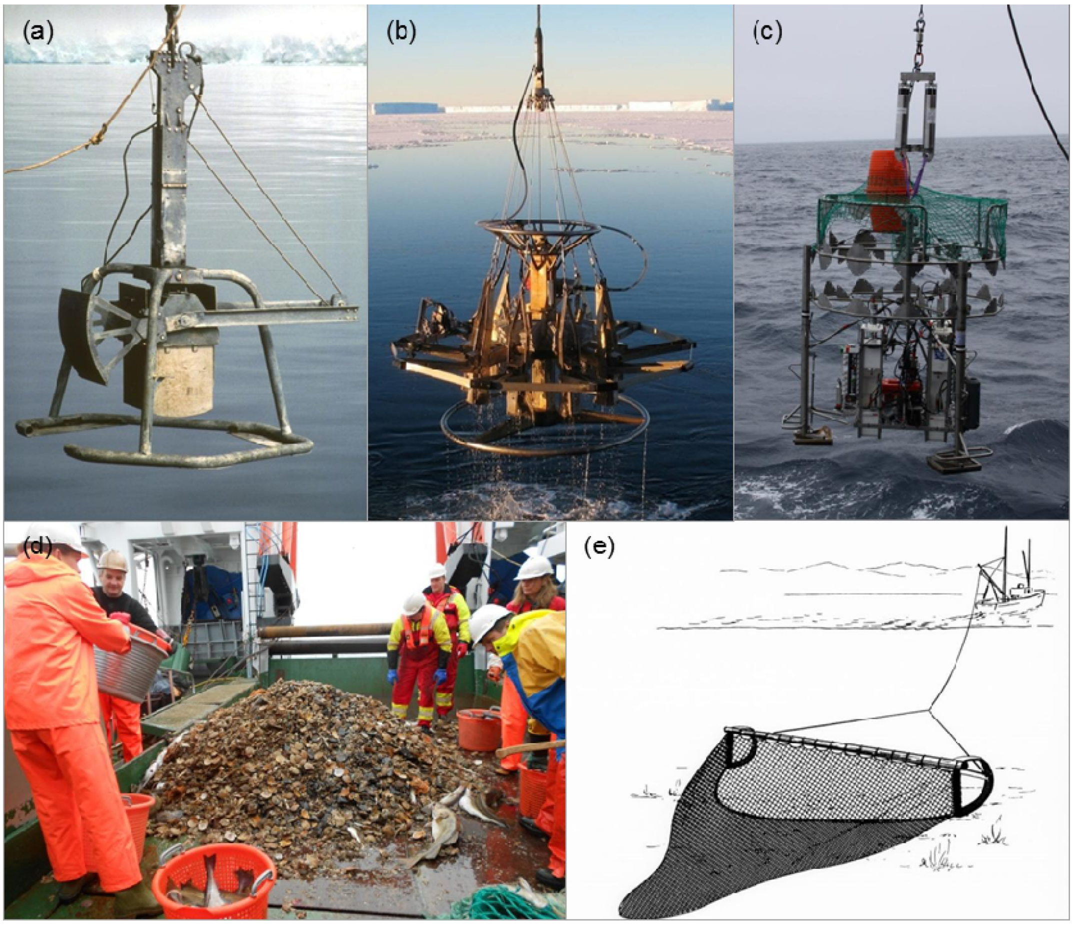

**Fig. 6**. Sampling devices used in the manuscripts I–III of this thesis. USNEL or giant box corer (a) (H. Grobe, AWI), multibox corer (b) (A. Rose, AWI), benthic lander system (d) (F. Wenzhöfer, AWI), beam trawl (NEFSC). Picture (d) shows a haul of a Campelen 1800 bottom trawl on deck of the Norwegian RV Johan Hjort.

### 2.1.3 Data mining

In the context of large scale ecological studies, data mining or data recovery refers to the effort of finding unpublished datasets and consolidating them in large databases accessible to the scientific community (Zeller et al. 2005). Such datasets might be recovered in unpublished scientific cruise data, technical reports, or any other form of grey literature (Piepenburg et al. 2011). Data mining is of high importance, as large temporal and spatial scale biological datasets are scarce, especially in the Arctic deep sea, and there is an imminent danger that such data will disappear from scientific memory (Zeller et al. 2005; Vandepitte et al. 2010). Additionally, in the light of ongoing climate warming and expanding Arctic shelf and deep-sea exploitation, there is an urgent need for baseline inventories from which change can be identified (Bluhm et al. 2011; Wassmann et al. 2011a). Consolidating data from different sources and collected for various purposes and under diverse circumstances requires standardization efforts, i.e. the harmonization of taxonomic and geographical information and of units (Vandepitte et al. 2010). Additionally, the potentially different sampling methods and further sample treatment have to be considered in subsequent analyses (see e.g. Bluhm et al. 2011).

## 2.3 Productivity (P/B) model

Secondary production of benthic communities is of special interest for ecologists as it allows direct insight into the energy flow through benthic systems and tells us how much food there is available for the next trophic level in the food web (Fig. 2). Classical methods to assess the secondary production in freshwater and marine ecosystems (cohort and size based methods) are expensive and time consuming, and in regions like the deep sea or in studies on very large scale simply not applicable (Rigler & Downing 1984; Cusson & Bourget 2005). Using empirical models bypasses the requirement of intense sampling programs needed in the classical approach, as they are based on empirical relations of production and P/B and other characteristic, but easily obtained parameters (e.g. mean body mass, bottom water temperature and water depth) (Brey 2001). Artificial Neural Network (ANN) models can learn and generalize from example data and perform slightly better than other empirical models (Brey 1996; Cusson & Bourget 2005; Dolbeth et al. 2005). The model used in the manuscripts I–III is an ANN P/B model published by Brey (2012), more detailed information about the model can be found in the method part of Manuscript II and in Brey (2012).

## 2.4 GIS

A Geographical Information System or GIS is a computerized data management system used to visualize, question, analyze, and interpret large datasets in order to understand spatial relationships, patterns, and trends (ESRI 2011). Data are georeferenced to the coordinates of a particular projection system, allowing spatially congruent placement of features and the analysis of spatial relationships between the mapped features. Examples of spatial statistics used in benthic ecology include the identification of statistically significant clusters (e.g. Hotspot Analysis), the assessment of overall spatial patterns (e.g. Spatial Autocorrelation) and the modeling of relationships (e.g. Geographically Weighted Regression). Here we used all previously mentioned tools in Manuscript I, in Manuscript II-IV we used GIS to map and visualize data distribution (ESRI 2011, ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute).

## 2.5 The biological trait analysis (BTA)

The biological trait analysis describes the contribution of a suite of ecological characteristics (i.e. life history, morphological and behavioral traits) to species' abundance or biomass patterns (Bremner et al. 2006; Darr et al. 2014). As there are strong links between functional traits and ecosystem processes, this approach is both valid to describe the ecological functioning of benthic communities and to detect changes in functioning related to changes or gradients in the environment (Bremner et al. 2006, Van der Linden et al. 2012). Here we used this approach for the first time with a dataset of macrobenthic secondary production from an Arctic shelf and the adjacent deep sea region. Further details on the BTA can be found in the method section of Manuscript III.

*(References of chapters 1 and 2 provided in chapter 5)*

# 3 Manuscripts

The following section provides an overview of the four manuscripts that constitute the core of this thesis and explains the contribution of co-authors. Information about the respective publication status is provided.

*Manuscript I*

**Higher Benthic Secondary Production in the Northern, Seasonally Ice-Covered Barents Sea**

Renate Degen, Lis Lindal Jørgensen, Pavel Lyubin, Ingrid Ellingsen, Hendrik Pehlke and Thomas Brey.

RD performed study design, data standardization, data mining, P/B modeling, GIS techniques and further data analysis and writing of the manuscript. LLJ and PL provided the trawl dataset (raw data) from the joint Norwegian-Russian Ecyosystem Survey (IMR-PINRO) from the years 2008 and 2009. IE provided NPP data. HP programmed an R code for downloading and extracting sea ice cover satellite images, calculating relevant statistical sea ice parameters and for storing the data in a GIS compatible format. TB supervised the writing of the manuscript.

The manuscript will be submitted to *Global Ecology and Biogeography*

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*Manuscript II*

**Patterns and Trends of Macrobenthic Abundance, Biomass and Production in the Deep Arctic Ocean**

Renate Degen, Andrey Vedenin, Manuela Gusky, Antje Boetius and Thomas Brey.

RD performed study design, field work, taxonomic identification, data mining, data standardization, P/B modeling, data analysis and writing of the manuscript. AV contributed the dataset ARK-XXVII/2 (HAUSGARTEN). MG assisted in taxonomic identification and data mining. AB and TB supervised the writing of the manuscript.

The manuscript is in press at *Polar Research*.

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*Manuscript III*

**Changes in Functioning of Arctic Macrozoobenthos**

Renate Degen and Thomas Brey.

RD performed study design, field work, data mining, building of a functional trait database (see Appendix chapter 7), BTA, further data analysis and writing of the manuscript. TB supervised the writing of the manuscript.

*Manuscript in preparation.*

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*Manuscript IV*

**Status and trends in the structure of Arctic benthic food webs**

Monika Kędra, Charlotte Moritz, Emily S. Choy, Carmen David, **Renate Degen**, Steven Duerksen, Ingrid Ellingsen, Barbara Górska, Jacqueline M. Grebmeier, Dubrava Kirievskaya, Dick van Oevelen, Kasia Piwosz, Annette Samuelsen and Jan Marcin Węsławski

This literature review is an output of the first joint Arctic in Rapid Transition (ART) and Association of Polar Early Career Scientists science workshop, in Sopot, Poland, October 2012. RD contributed to manuscript writing, figure design (Fig.1), proof reading and to the editing process. MK was lead author and responsible for consolidating the input of the other co-authors. CM contributed most of the gaps & recommendations section. Other co-authors contributed to a varying extent.

The manuscript is published in *Polar Research*.

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# Manuscript I

## Higher Benthic Secondary Production in the Northern, Seasonally Ice-Covered Barents Sea

Renate Degen[1], Lis Lindal Jørgensen[2], Pavel Lyubin[3], Ingrid Ellingsen[4], Hendrik Pehlke[1] and Thomas Brey[1]

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Submitted to *Global Ecology and Biogeography*

## Abstract

The Barents Sea is one of the most productive Arctic shelf regions in terms of pelagic primary and secondary production. A significant share of the overall energy flow is channeled through the benthic compartment towards top predators. Megabenthos is acknowledged to play a major role in this process, but quantitative data are lacking so far. Based on a unique dataset from the joint Norwegian-Russian Ecosystem survey we estimated for the first time megabenthic secondary production on the entire Barents Sea shelf. Contradictory to the generally inverse correlation of sea ice cover and primary production, we found significantly higher secondary production of benthic megafauna in the northeastern, seasonally ice-covered regions of the Barents Sea, than in the permanently ice-free southwest. The observed pattern indicates tight pelagic-benthic coupling in the realm of the productive seasonal ice zone. Ongoing decrease of winter sea ice extent and the associated pole-ward movement of the seasonal ice-edge point towards a strong decline of benthic secondary production in the northeastern Barents Sea in the future.

**Keywords**

Benthos, Megafauna, Pelagic-benthic coupling, MIZ, GWR, Geostatistic

## Introduction

Benthic secondary production constitutes an important pathway of energy flow on Arctic shelves. Accordingly, it is of particular ecological and economical interest in the Barents Sea, which holds one of the world oceans´ richest fisheries (Wassmann et al. 2006b). The Barents Sea ecosystem is characterized by the antagonistic interplay of polar and Atlantic water masses, and by a seasonal ice cover. However, the ongoing rapid retreat of sea ice raises questions concerning its current and future productivity. The joint Norwegian-Russian Ecosystem Survey (Michalsen et al. 2013) produced a huge dataset on megabenthos that covers the entire Barents Sea. This dataset is unique in spatial coverage and resolution and thus allows for the first time to model megabenthic secondary production for an entire Arctic shelf.

Macrozoobenthos of Arctic shelves is a significant player in benthic carbon cycling and serves as food for a variety of higher trophic level commercially important species like cod or halibut (Clough et al. 2005; Renaud et al. 2007). Especially the abundant megafauna represents an important compartment of benthic energy flow (Piepenburg et al. 1995). While the macrobenthic fauna (i.e. size class of animals < 1-2 cm, usually sampled with grabs or box cores) of the Barents Sea has been studied extensively in the last century (Cochrane et al. 2009 and references therein), significantly less information is available on benthic megafauna (animals of a size visible on pictures or caught via bottom trawling). Moreover, little is known about Barents Sea benthic secondary production, despite the general awareness of the benthic compartment’s role in energy flow and food web (Piepenburg et al. 1995; Cochrane et al. 2009). So far just one study (Kedra et al. 2013) deals with benthic secondary production, compared to the numerous publications on primary production and pelagic secondary production (Sakshaug et al. 2009; Dalpadado et al. 2014). Kedra et al. (2013) estimated benthic infauna and epifauna secondary production on the Spitsbergen bank to amount to ~2 g C $m^{-2}$ $y^{-1}$ and ~22 g C $m^{-2}$ $y^{-1}$ respectively. The first systematic large-scale study on Barents Sea megafauna results from the joint Norwegian-Russian Ecosystem Survey (Michalsen et al. 2013) and was published recently (Anisimova et al. 2010; Jørgensen et al. 2014). Jørgensen et al. 2014 provide the first explicit, large scale analysis of Barents Sea megafauna community composition and distribution patterns and identified a northern and a southern megafauna assemblage. The border between these coincides quite well with the Polar Front, but as it is defined by the encounter of cold and warm bottom water it is hence termed the “Benthic Polar Front” (Fig.1) (Jørgensen et al. 2014). The northern assemblage shows more taxa, higher abundance and higher biomass than the southern assemblage (Jørgensen et al. 2014).

Generally food input is seen as the main driver of benthic fauna distribution and biomass at large, regional scales, while seabed attributes explain patterns more significantly at local scales (Pearson & Rosenberg 1978; Piepenburg 2005). Arctic shelves communities have been found to reflect the primary production regime of the overlying water column in terms of biomass, abundance and production, suggesting a tight pelagic-benthic coupling (Tamelander et al. 2006). This holds true for the Barents Sea macrofauna, too, which shows areas of highest biomass in those areas that are predicted to have the highest primary production (Wassmann et al. 2006b). Zenkevich (1963) pointed out that in the Barents Sea highest benthic biomass correlates inversely with water temperature, presumably related to the fact that areas of coolest water coincide with the areas of most active mixing, and subsequent upwelling (Zenkevich 1963). However, studies that link benthic production patterns to ecosystem processes on large spatial scales are scarce (e.g. Highsmith & Coyle 1990), this is even more the case for benthic megafauna. Currently, we are quite ignorant of regional patterns in megafauna production on the Barents Sea shelf and of their environmental drivers. Consequently we are not able to develop reliable future scenarios for this rapidly changing ecosystem.

Here we analyze for the first time megabenthic community production for an entire Arctic shelf, i.e. the Barents Sea. We estimated secondary production by means of a species-based empirical model (Brey 2012) and use a global regression model to identify significant drivers of the observed production pattern. Owing to the substantial regional variations of environmental conditions (water depth, temperature, salinity, sediment structure, and sea ice concentration) and human impact (commercial trawling); we apply a Geographically Weighted Regression (GWR) model to examine the relationship of secondary production and the environment in space (Fotheringham et al. 2002). To our knowledge this is the first time such geo-statistical techniques are used to map and spatially analyze marine benthic secondary production.

In brief we aim to (1) estimate total and major group secondary production (P) of megafauna for the entire Barents Sea shelf, (2) identify regional patterns, (3) identify the significant environmental drivers behind the observed patterns and (4) analyze their regionally varying relationship to P.

## Methods

### Study area

The Barents Sea is the deepest of all circum-Arctic shelf seas with depths down to 500 m in the western troughs (Jakobsson et al. 2004). Generally the bathymetry is characterized by several shallow shelf banks that are segregated by a complex pattern of deeper depressions (>200 m), the average depth is 230 m (Piepenburg et al. 1995; Ingvaldsen & Loeng 2009). The Barents Sea covers an area of 1.6 million km² and is surrounded by the Arctic Ocean in the north, the island Novaya Zemlya in the east, the Norwegian and Russian mainland in the south, and the Norwegian Sea and Fram Strait in the west (Ozhigin et al. 2011) (Fig. 1). Three main water masses characterize the Barents Sea (see Fig 1): nutrient rich Atlantic water (AW) with temperatures >3° C and salinity of >35 and coastal water with temperatures in a wider range and salinity <34.7 enter the Barents Sea in the south-west, and Arctic water (ArW) with temperatures <0° C (core temp. <-1.5) and salinity of 34.4-34.7 enters the shelf between Svalbard and Franz Josef Land, between Franz Josef Land and Novaya Zemlya, and via a small inflow from the Kara Sea south of Novaya Zemlya (Ingvaldsen & Loeng 2009). A Polar Front (grey line in Fig. 2) separates the warm AW from the cold ArW respectively the permanently ice-free areas in the south-west from the seasonally ice-covered north-eastern areas (Loeng et al. 1997). Regarding bottom temperature the front runs slightly different and is termed the “Benthic Polar Front”, separating a northern from a southern fauna assemblage (Jørgensen et al. 2014) (dashed grey line in Fig. 1). Sediment structure on the shelf is heterogeneous, fine mud dominates deeper areas and coarser substrates are found in shallower areas with stronger currents (Jørgensen et al. 2014). Current speed on the Barents shelf is moderate, with highest values of >0.25 m/s in the Norwegian Coastal Current, but just ±0.1 m/s in the western outflow (Ingvaldsen & Loeng 2009). Pelagic primary production is highest in the southwestern regions influenced of nutrient rich AW with values >100 g C $m^{-2}$ $y^{-1}$ and supposedly lowest in the seasonally ice covered northeast (Wassmann et al. 2006b), though information on annual rates of sea-ice associated production is still insufficient. Trawling impact on the benthos is highest in the areas harboring rich accessible fish stocks, i.e. the ice-free southern areas in particular (Ljubin et al. 2011), but reliable geo-referenced information of trawling pressure for the entire Barents Sea is lacking currently.

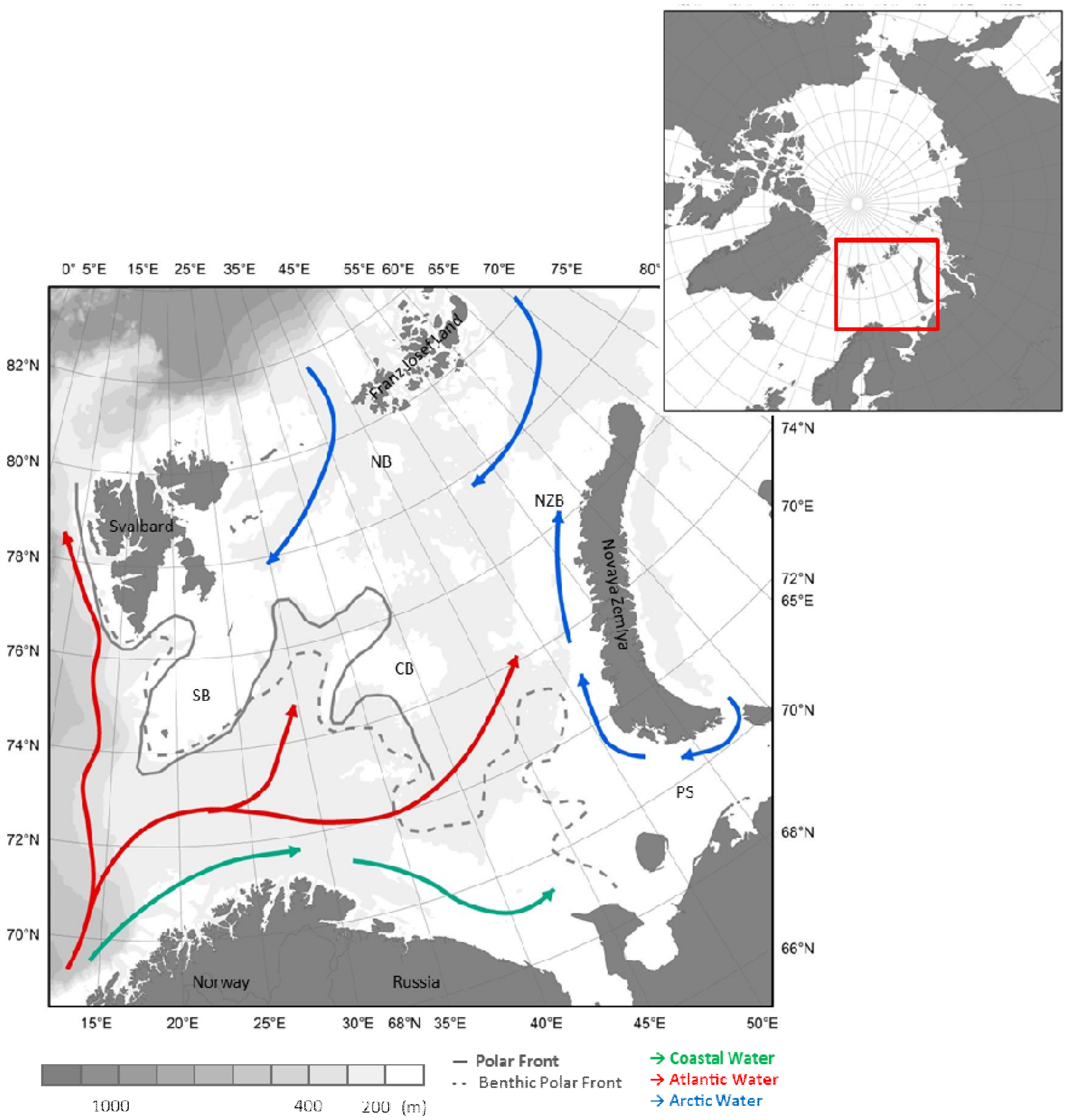


**Fig. 1** Barents Sea bathymetry and scheme of the main water masses. The approximate position of the Polar Front and the Benthic Polar Front is indicated by a grey and a dashed grey line. Bathymetry is based on the IBCAO basemap (http://www.ibcao.org). Abbreviations in alphabetical order: BIC – Bear Island Channel, CB – Central Bank, HID – Hopen Island Deep, KI – Kolguyev Island, NB – North Bank, NZB – Novaya Zemlya Bank, PS – Pechora Sea, SB – Spitsbergen Bank.

## Fauna dataset

Benthic megafauna abundance and biomass data were derived via the joint Norwegian-Russian Ecosystem Survey (Michalsen et al. 2013). The dataset of 398 bottom trawl stations presented in this study was compiled by experts on three Norwegian and one Russian research vessel in August to October 2008 and August to October 2009. Samples were taken with a Campelen 1800 bottom trawl, towed for 15 min at 3 knots. The standard distance between stations was 65 km. On board ship the benthic megafauna was separated from the fish and shrimp catch, identified on species level, counted and wet-weight biomass was measured with electronical scales. For more information on the joint Norwegian-Russian Ecosystem Survey, the used gear and the exact sampling protocol see Michalsen et al. 2013 and Jørgensen et al. 2014.

## Environmental dataset

Water depth (m) was estimated with a Seabird CTD at each sampling station. Mean annual bottom temperature (° C), salinity (psu) and currents speed (m $s^{-1}$) was derived from a numerical ocean model (Lien et al. 2014). The standard deviation of mean sea ice concentration (%) of the period 2001-2008 was estimated from monthly average sea ice concentration maps provided by NORMAP (10 km grid, http://normap.met.no) via an algorithm in R software. Mean New Primary Production (g C $m^{-2}$ $y^{-1}$) for the period 2001-2008 was derived from the SINMOD model (see Wassmann et al. 2006a). New production is a measure of the maximum harvestable production or export production from the system (Wassmann et al. 2006a). We presume that – as invertebrate megafauna are on average long-lived – the integration of the previous eight years to be appropriate. Sediment types are characterized by six classes based on the classification scheme of Vinogradova & Litvin (1960), with class 1 being sand, class 2 silty sand, class 3 sandy silt, class 4 mud, class 5 clay-silt and class 6 being clay. There is insufficient information on sediments in the Spitsbergen area hence we estimated the sediment class for several stations based on information from environmentally comparable example stations. As geo-referenced information on trawling pressure in the Barents Sea is lacking, we categorized the trawling intensity information provided in the illustrations of Lyubin et al. (2011) into four classes with 1 = no trawling, 2 = low trawling, 3 = intermediate trawling and 4 = high trawling pressure. Table 1 provides minimum, maximum and mean of the environmental parameters considered in this study.

**Table 1**: Environmental parameters longitude (°W), latitude (°N), water depth (m), temperature (°C), salinity (psu), standard deviation of mean sea ice concentration from 2001-2008 (%) and New Primary Production (NPP, g C $m^{-2}$ $y^{-1}$).

| | Long. | Lat. | Depth | Temp. | Salinity | Current | Sea Ice | NPP |
|---|---|---|---|---|---|---|---|---|
| Min | 8.90 | 68.47 | 20.00 | -1.49 | 33.34 | 0.00 | 0.00 | 20.23 |
| Max | 75.88 | 82.05 | 485.00 | 5.92 | 35.03 | 0.16 | 39.43 | 93.77 |
| Mean | 35.59 | 74.51 | 248.28 | 1.55 | 34.85 | 0.03 | 15.18 | 65.78 |

## Estimating Production and P/B

The secondary production (P) of Barents Sea megafauna was estimated with an empirical ANN model (for detailed information on the model see Brey 2012, for another application in Arctic regions see Nilsen et al. 2006 and Degen et al. in press). The model is implemented in an excel spreadsheet and can be freely assessed via http://www.thomas-brey/science/virtualhandbook. Abundance and biomass data – previously given as individuals and biomass (g wet weight) per 15 min haul – were recalculated to $m^{-2}$ by assuming an average trawled area of 18000 $m^2$ (Anisimova et al. 2010). As mean body mass (M) in Joule is the main model input parameter, biomass was divided by abundance for each species and station and converted to Joule using the conversion factor database of Brey et al. (2012, database version 4, www.thomas-brey.de/science/virtualhandbook). Further model input parameters are bottom temperature (K), water depth (m), five taxonomic categories (Mollusca, Annelida, Crustacea, Insecta, Echinodermata), seven lifestyle categories (infauna, sessile, crawler, facultative swimmer, herbivore, omnivore, carnivore), four environmental categories (lake, river, marine, subtidal), and a marker for exploitation. All categorical variables were binary (0 or 1). The necessary ecological information for each species was extracted from literature and online resources (see supplement S1 for a list of sources). Species that did not belong to any of the five taxonomic categories of the model were grouped by the category their body form resembled to most. The output of the model is population P/B ratio ($y^{-1}$), including upper and lower 95% confidence limits. Population P was calculated by multiplying the P/B ratio with population biomass, previously converted to g C $m^{-2}$ $y^{-1}$. Total community P was calculated by adding up all population values per station. Production per phylum was calculated for Annelida, Arthropoda, Cnidaria, Echinodermata, Mollusca and Porifera. The phyla Brachyopoda, Bryozoa, Cephalorhyncha, Chordata, Echiura, Nemertea, Platyhelminthes and Sipuncula occurred in very low abundances (<0.1 Ind. $m^{-2}$) and biomasses (<5 mg C $m^{-2}$) and were added up in the group “Others”.

### Geostatistical Analysis

P, P/B, NPP, trawling pressure, water depth, temperature, salinity, current speed, standard deviation of mean sea ice concentration and sediment structure were projected spatially using a GIS environment (ESRI 2011, ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). The WGS 1984 Stereographic North Pole projection was used. The data distribution was visually inspected (scatterplot) and outliers (2 stations) were eliminated from the dataset. All analytical methods applied can be found in the spatial statistics toolbox of ArcGIS. Grouping analysis based on bottom temperature was used to separate the dataset into a south-western (SW) and a north-eastern (NE) group. Hotspot analysis (Getis-Ord Gi*) was used to identify regions of significantly higher P and P/B. This method identifies statistically significant hotspots, i.e. regions where stations with high (or low) values cluster together. The global regression model Ordinary Least Squares (OLS) was used to determine the environmental parameters significantly correlated to the observed patterns of P and P/B. The independent input variables in the OLS model were water depth, temperature, salinity, current speed, sea ice concentration, NPP, trawling pressure, and sediment structure. The significant variables were consequently used as input in the GWR model. GWR accounts for the spatial variability of input data by incorporating spatially varying relationships in the regression analysis (Fotheringham et al. 2002) and was used to visualize the regionally varying relationships between P, P/B and the explaining variables. This model is appropriate when more than 100 features (here sample stations) are available, no binary outcomes are predicted and a projected coordinate system is used. All skewed input data were previously transformed to approach normal distribution. Salinity data had to be grouped in classes because transformation did not reduce skewness sufficiently. The graphical output of the GWR model are maps of correlation coefficients with hot-to-cold rendering indicating regional variation in the relationship of the dependent and the independent variables. The models were tested to fulfill all required assumptions necessary to guarantee a reliable model output. Moran's I. was used to test for potential spatial autocorrelation of the regression residuals.

### Further statistics

ANOVA was conducted to test for significant differences between the group SW and the group NE (previously identified with grouping analysis in GIS) using the JMP® software package, Version *10.0* by SAS Institute Inc., Cary, NC, 1989-2007.

## Results

### Total community P and P/B

Total community production per station ranged from 0.015 mg C $m^{-2}$ $y^{-1}$ to 105 mg C $m^{-2}$ $y^{-1}$ (Table 2; Fig. 2a). The grouping analysis based on bottom temperature separates the dataset into a north-eastern (NE) and a south-western (SW) part (R2=0.70). Production was significantly higher in the NE part than in the SW part (F=106.27; p<0.0001). The hotspot analysis performed on boxcox transformed P data identified four hotspots in the northern region and three coldspots in the south and northwest (Fig. 3). The largest hotspot area is located west of Novaya Zemlya, the hotspot with highest local benthic production is located SW of Franz-Josef-Land (North Bank). Another hotspot is located on the southern slope of Novaya Zemlya and the smallest resides in the central Barents Sea (Hopen Island Deep and western slopes of the Central Bank). The largest coldspot is in the southwestern Barents Sea, the area of Atlantic water inflow. The two other and much smaller coldspots are located northwest of Spitsbergen and in the southeast, west of Kolguyev Island. Total community productivity (P/B) ranged from 0.038 to 0.841 (Table 2a; Fig. 2b). P/B was not found to be significantly different between the SW and the NE region (F=3.00; p=0.084). The hotspot analysis identified one large hotspot in the central Barents Sea and two smaller hotspots northwest of Spitsbergen and in the southwest deep Bear Island Channel (Fig. 3b).

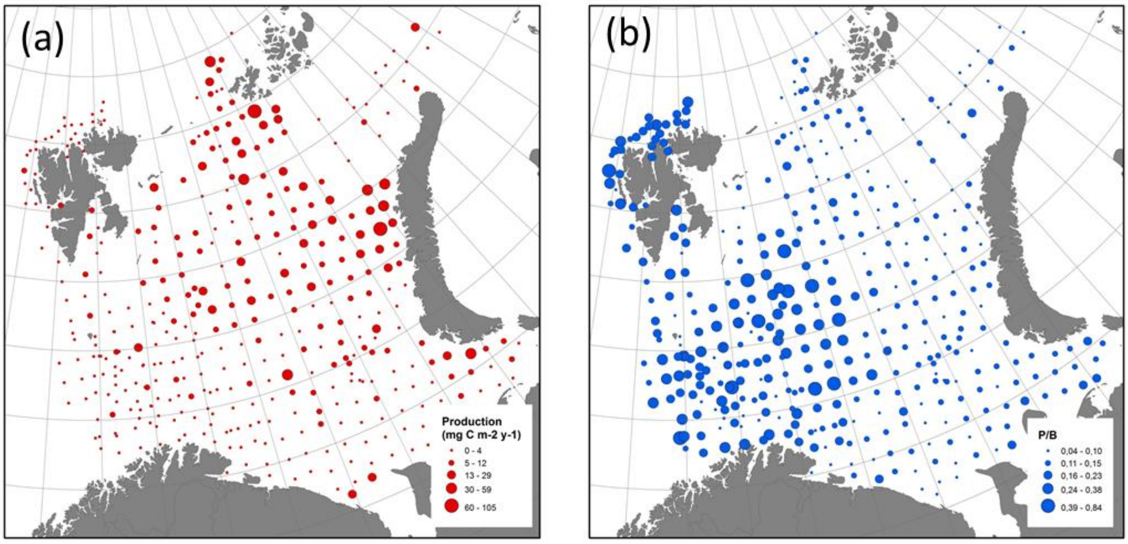


**Fig. 2** Total community production (P) (mg C $m^{-2}$ $y^{-1}$) (a) and productivity (P/B) ($y^{-1}$) (b).

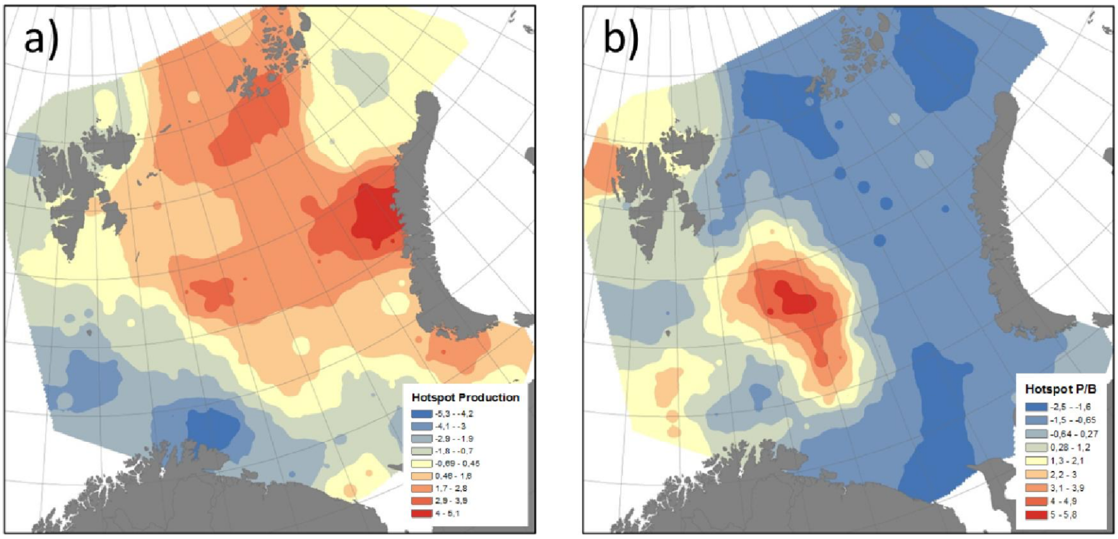


**Fig. 3** Interpolated (Inverse Distance Weighting method) standard-deviation of G* scores of the Hotspot analysis of total community P (a) and P/B (b). Red color indicates significantly higher values than the mean; blue indicates significantly lower values than the mean.

### Major Group P and P/B

Echinodermata clearly dominate the megabenthic production in the Barents Sea by contributing 50% to the total production, followed by Arthropoda (18%), Annelida (12%), and Mollusca (7%). Cnidaria, Porifera and all other taxa contribute below 5% (Fig. 4). The overall pattern of P is mainly shaped by Echinodermata and Arthropoda, with both showing clear hotspots in the northern Barents Sea in the western area of Franz Josef Land and in the SE Barents Sea. Arthropods have a third hotspot on the Novaya Zemlya bank. Highest productivity was found in the phyla Annelida (mean 0.61), Arthropoda (0.20) and Mollusca (0.17). Annelida have productivity hotspots in the southwest Barents Sea, north of Spitsbergen and north of Novaya Zemlja, Arthropods have a hotspot in the southwestern Barents Sea, north of Novaya Zemlja and in the Pechora Sea, and Mollusca have a P/B hotspot in the southwestern and southern Barents Sea and in the Pechora Sea. The figures of results per major group can be found in the supplementary material (S1), detailed information about regional megafauna community composition can be found in Jørgensen et al. (2014).

**Table 2** Min., max., and mean of total community abundance (Ind. m-2), biomass (mg C m-2), secondary production (mg C m-2 y-1), and productivity (P/B) and per major taxonomic group. The group "Others" includes taxa occurring in very low numbers (<0.1 Ind. m-2) and biomass (<5 mg C m-2), i.e. Brachiopoda. Bryozoa. Cephalorhyncha. Echiura. Nemertea. Platyhelminthes and Sipuncula. Highest mean values for P and P/B are highlighted in bold.

| | | Abundanc (Ind. $m^{-2}$) | Biomass (mg C $m^{-2}$) | Production (mg C $m^{-2}$ $y^{-1}$) | P/B ($y^{-1}$) |
|---|---|---|---|---|---|
| Total | min | 0.00 | 0.08 | 0.01 | 0.04 |
| | max | 3.12 | 950.09 | 104.87 | 0.84 |
| | mean | 0.11 | 45.16 | 5.32 | 0.15 |
| Annelida | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 1.26 | 57.96 | 33.62 | 1.49 |
| | mean | 0.02 | 0.79 | 0.65 | 0.61 |
| Arthropoda | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 0.29 | 139.83 | 15.37 | 0.73 |
| | mean | 0.01 | 6.49 | 0.94 | 0.20 |
| Chordata | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 0.48 | 19.45 | 2.89 | 0.41 |
| | mean | <0.01 | 0.27 | 0.04 | 0.07 |
| Cnidaria | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 0.41 | 261.62 | 21.01 | 0.49 |
| | mean | 0.01 | 3.06 | 0.26 | 0.12 |
| Echinodermata | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 2.98 | 762.91 | 81.14 | 0.44 |
| | mean | 0.06 | 27.60 | 2.68 | 0.14 |
| Mollusca | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 0.17 | 210.53 | 33.70 | 0.46 |
| | mean | 0.01 | 2.24 | 0.37 | 0.17 |
| Porifera | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 0.17 | 267.41 | 12.90 | 0.39 |
| | mean | <0.01 | 3.74 | 0.23 | 0.07 |
| Others | min | 0.00 | 0.00 | 0.00 | 0.00 |
| | max | 0.09 | 80.08 | 11.42 | 0.09 |
| | mean | <0.01 | 0.17 | 0.02 | <0.01 |

## Global model (OLS)

The Ordinary Least Squares (OLS) model for secondary production fitted the data with $R^2$=0.41 and a corrected Akaike Information Criteria AICc=1800.12. The AICc is a measure of the relative quality of a statistical model for a given dataset;

accordingly it can be used to compare OLS and GWR models based on the same input parameters. The OLS model identified 6 parameters that explained the observed production patterns significantly (table 3). The P/B OLS model had a model fit of $R^2=0.15$ and an AICc=-1114.12 and identified four parameters to significantly explain the variance in the P/B data (table 3). Here a significant Jarque-Bera statistic ($p=0.0036$) indicated severe model bias.

**Table 3** Results of the Ordinary Least Squares (OLS) and Geographically Weighted Regression (GWR) models for total community P and P/B. Significant parameters ($p<0.05$) are highlighted in bold.

| OLS | | | | |
|---|---|---|---|---|
| | Production | | P/B | |
| | Coefficient | p | Coefficient | p |
| Depth (m) | -0.002 | 0.1778 | 0.000 | 0.2785 |
| Temperature (°C) | -0.835 | <0.0001 | 0.005 | 0.0457 |
| Salinity (class) | 0.947 | <0.0001 | 0.001 | 0.7534 |
| Current Speed (m $s^{-1}$) | -46.990 | 0.0112 | 1.293 | 0.0069 |
| Sea Ice Concentration (Stdv.) | 1.138 | 0.0048 | 0.028 | 0.0079 |
| NPP (mg C $m^{-2}$ $y^{-1}$) | -0.034 | 0.0082 | 0.002 | <0.0001 |
| Trawling Pressure | 0.320 | 0.0015 | -0.006 | 0.0144 |
| Sediment (class) | 0.118 | 0.3961 | 0.005 | 0.1853 |
| | | | | |
| $R^2$ | 0.415 | | 0.151 | |
| AICc | 1800.112 | | -1114.108 | |

| GWR | | |
|---|---|---|
| | Production | P/B |
| $R^2$ | 0.734 | 0.527 |
| AICc | 88.402 | -59.511 |

### Local model (GWR)

The GWR model for production based on the six parameters identified with OLS (table 3) displayed an overall model fit of $R^2=0.73$ and an AICc=88.40. The GWR model for productivity P/B based on the four parameters identified with OLS had an overall model fit of $R^2=0.53$ and AICc=-59.51. The higher $R^2$ value and the distinct difference in AICc between the OLS and the GWR models indicate that GWR is the appropriate model for the production dataset. The spatial distribution of stations with highest model fit is shown in Fig. 4. The six significant correlation coefficients identified with GWR (shown in Fig. 5 a-f) highlight the regionally varying relationships of production and the environment. As the GWR model of P/B is based on potentially biased assumptions from the OLS model, it should be interpreted cautiously. Consequently we restrain from interpreting spatial P/B patterns and model output in this study.

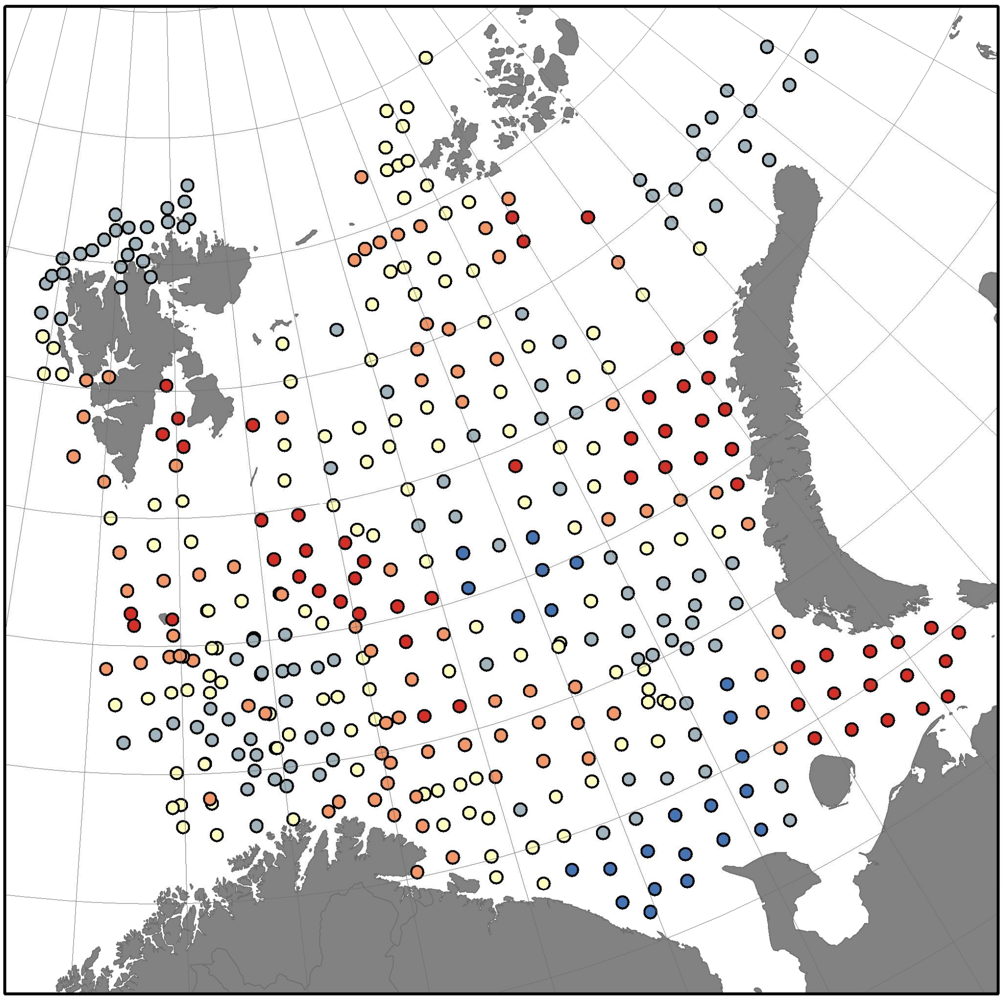
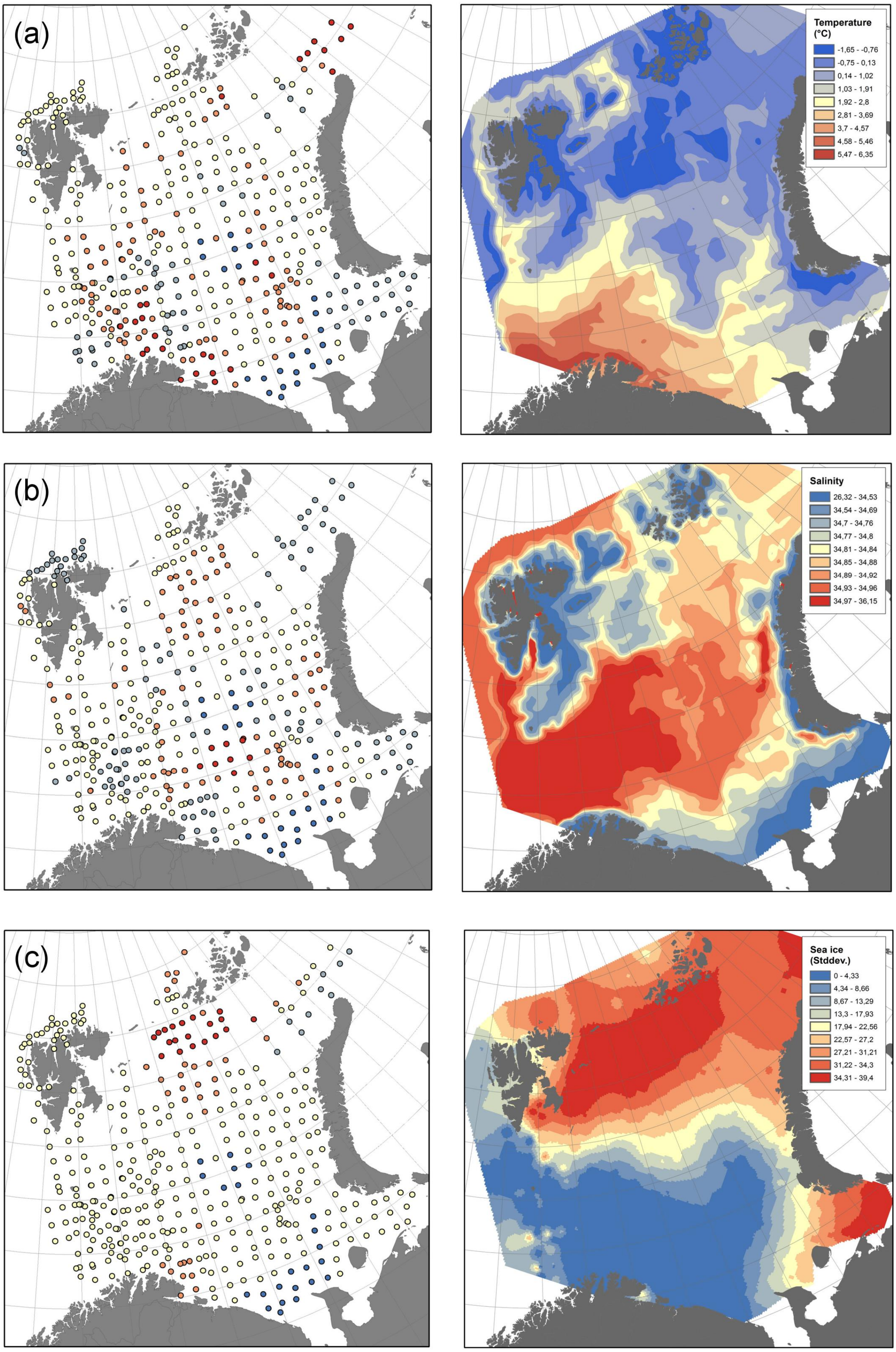


**Fig. 4** Mapped $R^2$ values from the GWR model of P. Dark red points indicate areas with highest model fit ($R^2$ values 0.62-0.82).


(a)
Temperature (°C)
-1,65 - -0,76
-0,75 - 0,13
0,14 - 1,02
1,03 - 1,91
1,92 - 2,8
2,81 - 3,69
3,7 - 4,57
4,58 - 5,46
5,47 - 6,35
(b)
Salinity
26,32 - 34,53
34,54 - 34,69
34,7 - 34,76
34,77 - 34,8
34,81 - 34,84
34,85 - 34,88
34,89 - 34,92
34,93 - 34,96
34,97 - 36,15
(c)
Sea ice (Stddev.)
0 - 4,33
4,34 - 8,66
8,67 - 13,29
13,3 - 17,93
17,94 - 22,56
22,57 - 27,2
27,21 - 31,21
31,22 - 34,3
34,31 - 39,4

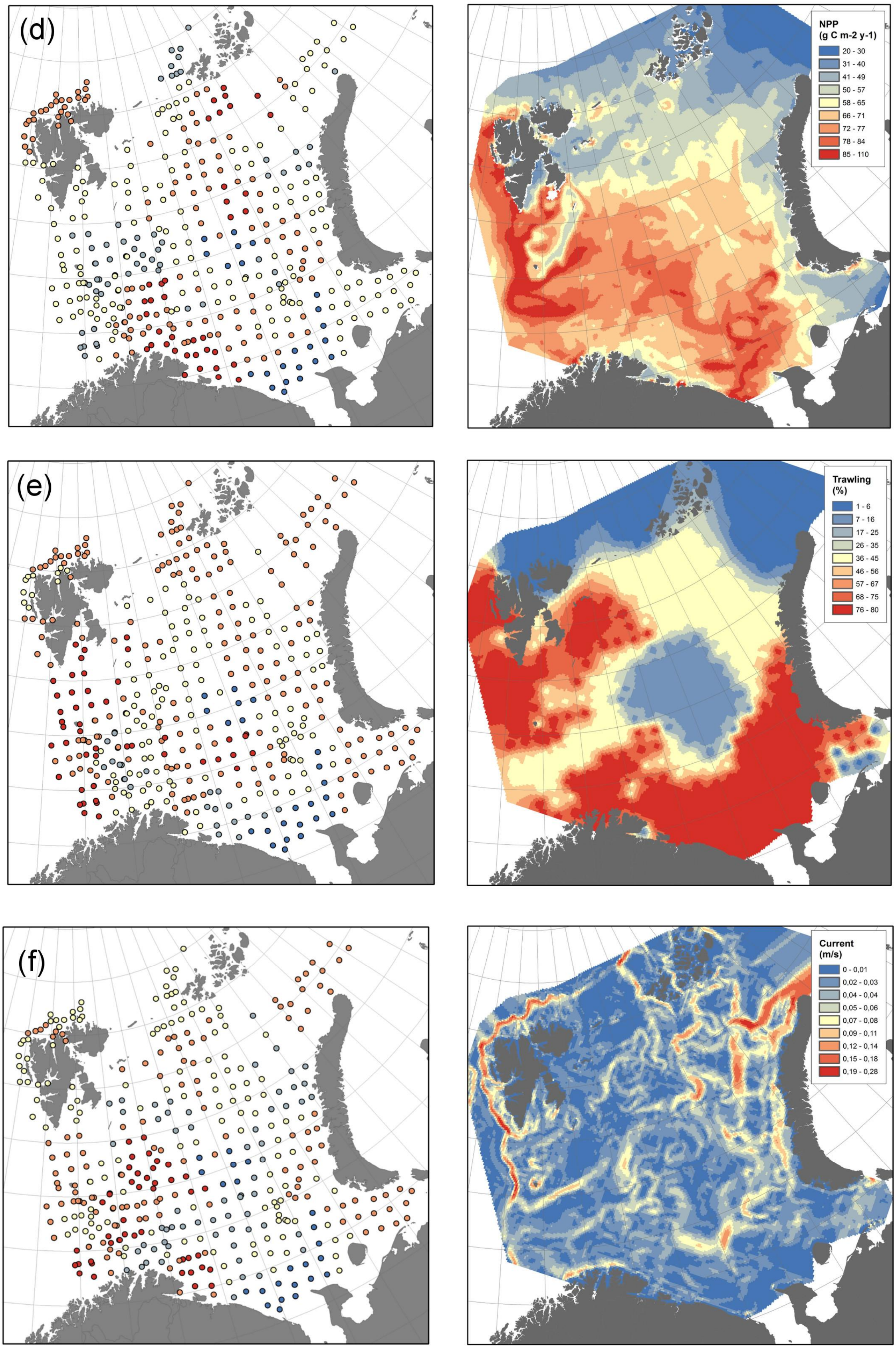


**Fig. 5** Correlation coefficients derived from the GWR production model for the six significant parameters bottom temperature (a), salinity (b), sea ice concentration (Standard Deviation) (c), NPP (d), trawling pressure (e) and current speed (f). Red circles indicate significant positive correlation;

blue circles indicate significant negative correlation of P and the respective parameter. The maps on the right show the interpolated (IDW) environmental parameters, with red areas indicating high, blue indicating low, and yellow indicating intermediate values.

## Discussion

### Methodical remarks

Data from trawl samples are generally considered semi-quantitative and gross estimates (Eleftheriou & Moore 2005). However, when trawling is carried out consistently over a large number of stations, like in the joint Norwegian-Russian Ecosystem Survey (Michalsen et al. 2013), relative spatial patterns can be identified (Anisimova et al. 2010). In this study we accordingly do not present estimated secondary production per station and in detail, but rather focus on the regional differences and relations.

### Patterns of megabenthic secondary production

Secondary production of Barents Sea megafauna is significantly higher in the north-eastern seasonally ice-covered areas than in the permanently ice-free south-western areas (p<0.0001).

We detected four hotspots of megabenthic secondary production: the area west of and on the southern slope of Novaya Zemlya, the region southwest of Franz-Josef-Land, and a smaller hotspot in the central Barents Sea. These regions of high megafauna production correspond approximately to the hot spots of benthic biomass reported in previous studies (Wassmann et al. 2006b). Regarding the contribution of major taxonomic groups to overall benthic secondary production we found echinoderms clearly dominating, followed by arthropods and annelids (table 2). The overall biomass pattern in the Barents Sea is reportedly vice versa, molluscs (predominantly bivalves) dominate before echinoderms (Wassmann et al. 2006b).

## Drivers of megabenthic secondary production

At large regional scales, food input is reported to be the main driver of distribution and biomass of benthos, and of benthic production accordingly (Grebmeier et al. 1988, Piepenburg 2005). Arctic benthic biomass hotspots sharply coincide with areas of highest primary production and with ice edge areas (Denisenko 2002, Wassmann et al. 2006b). We used New Primary Production (NPP) (Wassmann et al. 2006a) as a proxy of food input to the benthos in our regression model and expected a positive correlation with megabenthic production, i.e. high P values in areas of high NPP. However, we found a reversed pattern: P is related to NPP negatively ($p=0.0082$), and P is significantly higher in regions that are seasonally sea ice covered and reported to be of distinctly lower pelagic primary production (Wassmann et al. 2006b). Furthermore, we found P to be negatively correlated to bottom water temperature ($p<0.0001$), positively to salinity ($p<0.0001$) and positively to the standard deviation of sea ice concentration ($p=0.0048$). All these factors relate to some extent to the marginal ice zone (MIZ). Temperature relates to MIZ because in the Barents Sea the maximum extent of colder Arctic water masses respectively the Polar Front often coincides with the sea ice extent in winter or early spring (Wassmann et al. 2006b). Salinity effects on P were found to be significant in areas where strong mixing between Atlantic and Arctic water masses occurs, i.e. along the Polar Front (Wassmann et al. 2006b). And the standard deviation of sea ice concentration is an obvious proxy for the MIZ.

The bulk of the total annual primary production of the northern and northeastern Barents Sea takes place in the MIZ (Piepenburg et al. 1995). Spring ice melt gives rise to a nutrient rich euphotic zone that supports a distinct phytoplankton bloom in the MIZ which moves constantly pole-ward while receding from its winter position at the Polar Front (Piepenburg et al. 1995; Wassmann et al. 2006a). Tamelander et al. (2006) analyzed the pelagic-benthic coupling in the Barents Sea MIZ during summer and detected tight coupling between surface production and the benthic community over relatively small scales. Additionally they detected a high degree of heterogeneity, determined by water mass properties like local upwelling and primary production regimes. Our benthic secondary production estimates reflect this patchiness (Fig. 2), there are four significant hotspots and high variability between stations that are on average just 65 km apart (Fig. 3). We further investigate the strength of the pelagic-benthic coupling in the northern seasonally ice-covered region compared to the ice-free southern regions by means of an “inverse” approximation. The ratio of mean secondary production (P) to mean NPP (0.003:76 g C $m^{-2}$ $y^{-1}$) in the southern region is 0.00004, in the northern region it is 0.00016 (0.008:50 g C $m^{-2}$ $y^{-1}$). This distinctly higher ratio in the north indicates that here either a larger part of NPP is channeled to the benthos (i.e. tighter pelagic-benthic coupling), or there is further NPP not accounted for so far. Kedra et al. (2013) estimated a benthic carbon demand of up to 70 g C $m^{-2}$ $y^{-1}$ to sustain the mean epibenthic production of ~22 g $m^{-2}$ $y^{-1}$ at the Spitsbergen bank. As this region was a coldspot in our study we might have to consider a significantly higher benthic carbon demand in the regions south and west of Novaya Zemlya or SW of Franz-Josef-Land, which we identified as hotspots of benthic production (Fig. 3a). The mean estimated NPP for this regions is 50 g C $m^{-2}$ $y^{-1}$, if we add a suggested contribution of ice algae primary production of max 25% (Wassmann et al. 2006b) we would reach around 60 g C $m^{-2}$ $y^{-1}$, not enough to fulfill a carbon demand of potentially much more than 70 g C $m^{-2}$ $y^{-1}$. We assume that in this regions sea ice production might be considerably higher than previously anticipated. Additionally there might be a substantial contribution of advected material originating from pelagic production or shallower macroalgae areas.

Apart from the parameters that are related to the MIZ, we further detected a significant negative correlation between P and current speed ($p=0.0112$) and a positive correlation between P and trawling pressure ($p=0.0015$). The former can be related to the fact that regions with high current speed often are dominated by filter feeders like bivalves that contributed little to overall P. The positive correlation to trawling pressure probably relates to the fact that long term bottom trawling changes the age and size spectrum of benthic communities from long-lived, large sized individuals to short lived, smaller sized individuals and species. As P/B is inversely related to body size, this shift increases community P/B and most likely community P, too (see e.g. Callaway et al. 2007).

### Regional varying relationships

Overall our geo-statistical approach shows that the tight pelagic-benthic coupling along the productive, seasonally moving ice-edge is of crucial importance for Barents Sea megabenthic production. The geographically weighted approach (GWR) enables us further to investigate the regional variation in the correlation between P and environmental parameters (Fig. 5a-f). Here we want to focus on salinity (Fig. 5b) and on sea ice concentration (Fig. 5c). Salinity is correlated positively to P in a regional band resembling the position of the Benthic Polar Front (Fig. 1, Fig. 5b), thus indicating the relevance of mixed water masses along the MIZ for benthic production. The standard deviation of sea ice concentration shows the highest positive correlation with P in the central north of the Barents Sea, the region where the highest P values were observed in this study (Fig 5c). This may point towards the importance of sea ice algae for benthic secondary production in this region, as ice-algal contribution was reported to be proportionally more important in areas where sea-ice retreats later in the year (Gosselin et al. 1997). Either way, our findings highlight the effectiveness of GWR in identifying areas of particular relationships between environmental and ecological features that should be studied in more detail.

## Conclusions

We found significantly higher benthic production in the northern, seasonal ice-covered Barents Sea than in the southern, ice-free region. Although annual primary production is reported to be generally lower in the north, the tighter pelagic-benthic coupling along the MIZ facilitates higher secondary production than in the south. Additionally, a higher contribution of sea ice associated primary production and advection processes are to be considered. These novel insights into the patterns of benthic secondary production and its relationships to different environmental parameters will facilitate the improvement of regional carbon flux models. Regarding the continuous warming and a subsequent pole-ward moving MIZ, our findings indicate that future benthic production might be significantly impoverished. This prospect, which will have cascading effects on all levels of the Barents Sea ecosystem, stresses the importance of continuous integrated monitoring programs like the joint Norwegian-Russian Ecosystem Survey that will provide the information required for sound scientific advice to ecosystem management.

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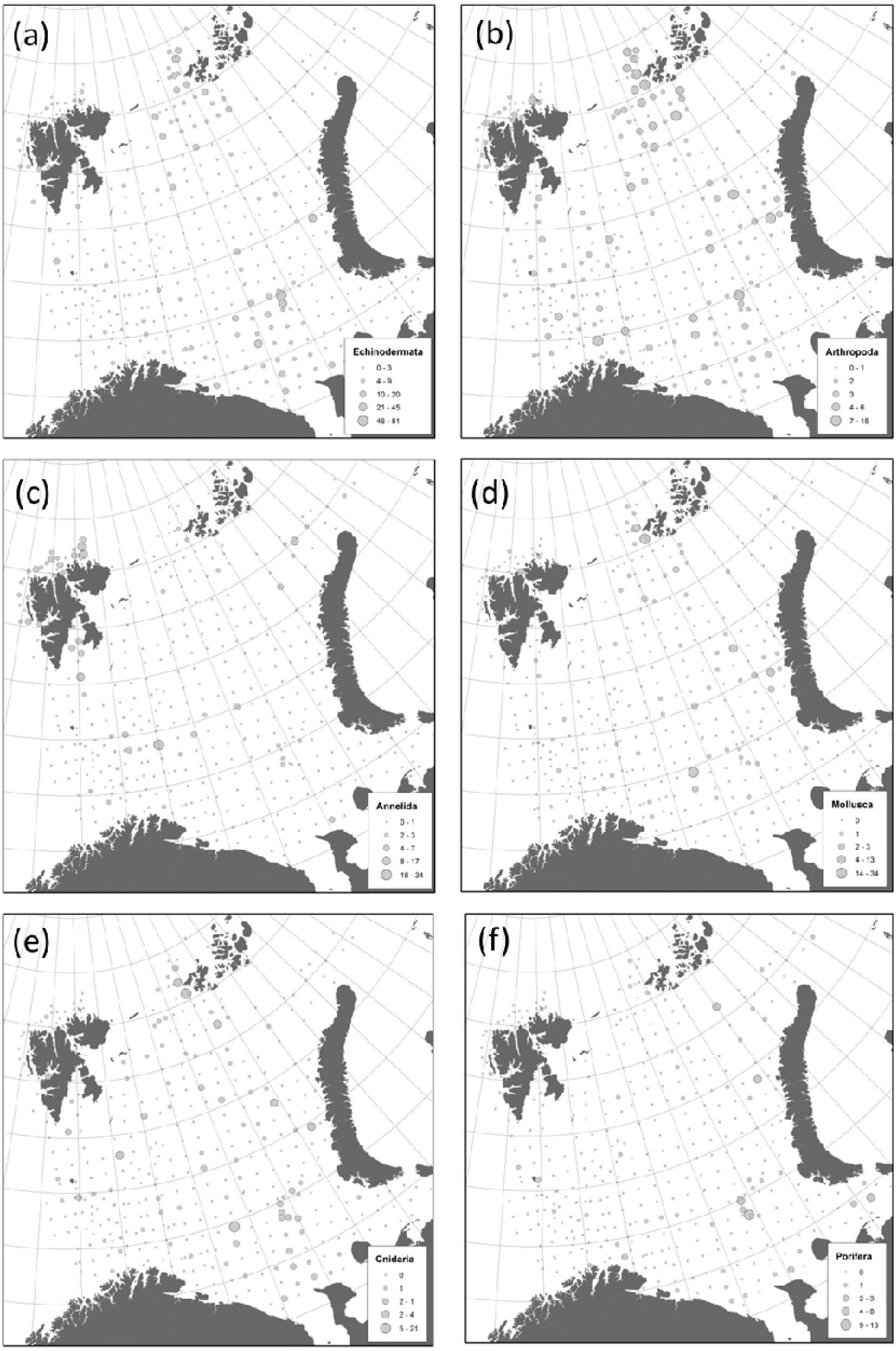
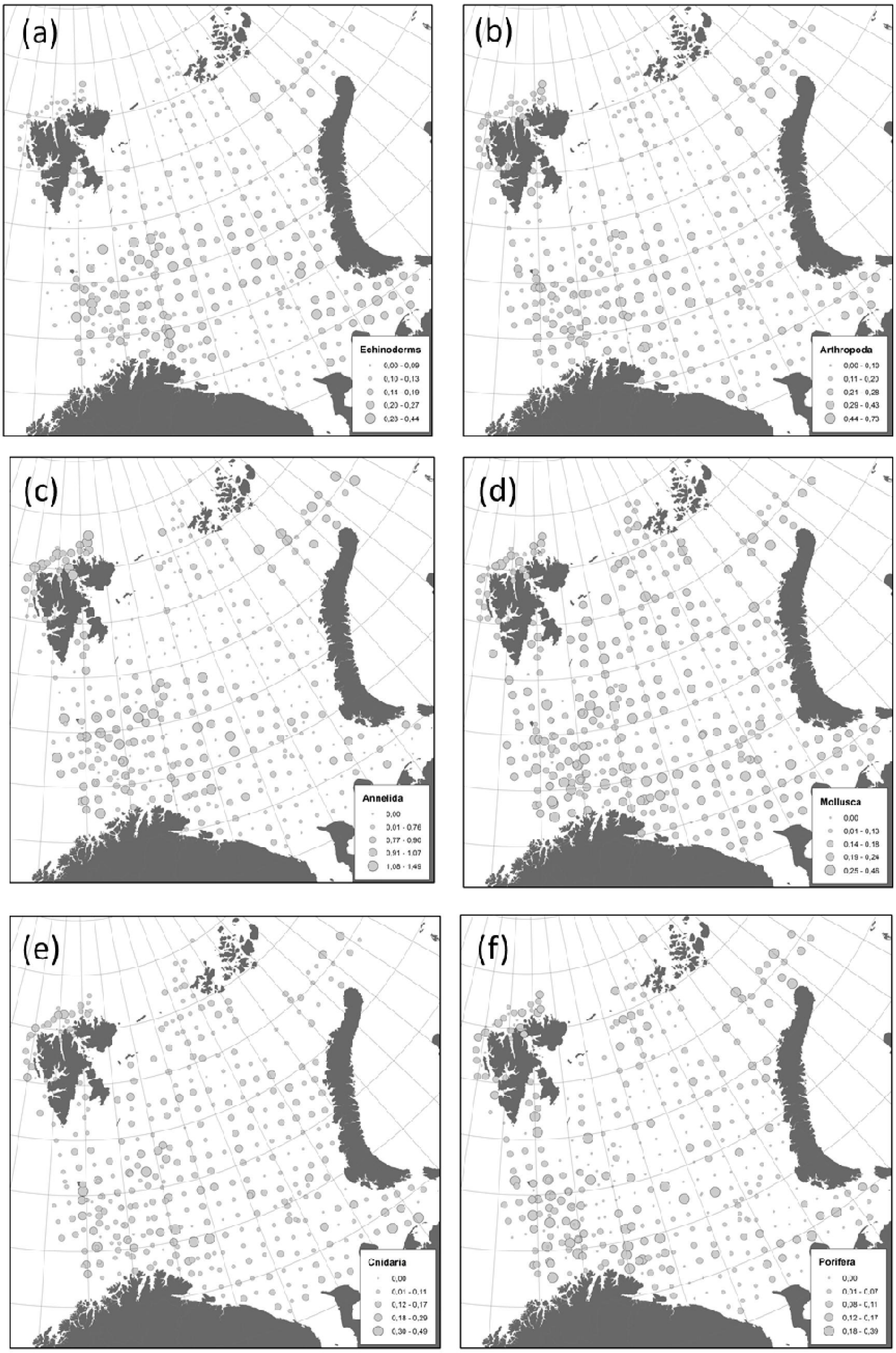
# Supplementary material

**S1** Production (P) (mg C m-2 y-1) of the major taxonomic groups Echinodermata (a), Arthropoda (b), Annelida (c), Mollusca (d), Cnidaria (e) and Porifera (f).



**S2** Productivity (P/B) ($y^{-1}$).of the major taxonomic groups Echinodermata (a), Arthropoda (b), Annelida (c), Mollusca (d), Cnidaria (e) and Porifera (f).



# Manuscript II

## Patterns and trends of macrobenthic abundance, biomass and production in the deep Arctic Ocean

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## Abstract

Little is known on the distribution and dynamics of macrobenthic communities of the deep Arctic Ocean. The few previous studies report low standing stocks and confirm a gradient with declining biomass from the slopes down to the basins as commonly reported for deep-sea benthos. In this study we have investigated regional differences of faunal abundance and biomass, and made for the first time ever estimates of deep Arctic community production by using a multi-parameter Artificial Neural Network model. The underlying dataset combines data from recent field studies with published and unpublished data from the past 20 years, to analyze the influence of water depth, geographical latitude and sea ice concentration on Arctic benthic communities. We were able to confirm the previously described negative relationship of macrofauna standing stock with water depth in the Arctic deep sea, whilst also detecting substantial regional differences. Furthermore, abundance, biomass and production decreased significantly with increasing sea ice extent (towards higher latitudes) down to values <200 ind m$^{-2}$, < 65 mg C m$^{-2}$ and <73 mg C m$^{-2}$ y$^{-1}$, respectively. In contrast, stations under the seasonal ice zone regime showed much higher standing stock and production (up to 2500 mg C m$^{-2}$ y$^{-1}$), even at depths down to 3700 m. We conclude that particle flux is the key factor structuring benthic communities in the deep Arctic Ocean, explaining both the low values in the ice-covered Arctic basins and the higher values in the seasonal ice zone.

### Keywords

Deep sea, benthos, macroinvertebrate, carbon flux

## Introduction

The density and biomass of marine benthic macrofauna generally decreases with increasing water depth, distance from land, and with decreasing latitude from polar and temperate towards tropical latitudes (Gage and Tyler 1991; Levin and Gooday 2003; Wei et al. 2010). The driving force behind this pattern is the decrease in food input, depending on the regionally varying surface production and the assimilation efficiency in the water column (Gage and Tyler 1991; Levin and Gooday 2003 and references therein). Following Thiel (1975) the low food concentration in the deep sea leads to a higher share of smaller organisms in total community metabolism (“size structure hypothesis”), an observation corroborated also in more recent studies that found a decrease in mean body mass or size with increasing water depth (McClain et al. 2006; Rex et al. 2006, Wei et al. 2010). Additional to food availability also substrate characteristics and hydrodynamic processes are important factors structuring benthic communities (Rosenberg 1995). Accordingly deposit-feeding organisms are reported to dominate areas of reduced flow like the abyssal plains, while suspension feeders are prominent in areas with high bottom current flow as on continental slopes or mid-ocean ridges (Gage & Tyler 1991; Thistle 2003).

Compared to standing stock, only little is known about patterns of benthic secondary production (P) and productivity (P/B) in the deep sea. The production to biomass (P/B) ratio represents the rate of biomass turnover and is inversely related to life span (Benke 2012). Populations whose size structure is dominated by small, fast growing organisms will show a higher P/B ratio than one consisting of older and slower growing adults (Gage & Tyler 1991). Secondary production (P) corresponds to the newly formed biomass per unit of area and time and depicts – contrary to pure measurements of biomass – exactly that quantity of energy that is available as food for the next trophic level (Brey 2001). Thus secondary production constitutes the quantitative base of energy flow in benthic food webs and is as such an essential variable for ecosystem models. The few existing studies on deep-sea benthic production report a negative correlation with water depth and low values of 0.1-0.2 g C $m^{-2}$ $y^{-1}$ at depths below 1500 m (Gage 1991; Brey & Gerdes 1998; Cusson & Bourget 2005). Benthic community P/B ratios of 0.49 $y^{-1}$

(Gage 1991) and 0.55 $y^{-1}$ (Brey & Gerdes 1998) are reported from 2900 m depth in the Rockall Trough (North Atlantic) and in the Weddell Sea. While two studies detected a negative correlation of P/B ratios with water depth (Brey and Gerdes 1993; Cusson & Bourget 2005), no significant correlation was found by Brey & Gerdes in 1998. All the previously mentioned studies detected a positive relation of P/B with temperature.

Today, even less information than from the deep-sea in general is available about the Arctic deep sea benthic communities. This is due to the logistical challenges of sampling the remote, seasonally or permanently ice-covered Arctic basins. Bluhm et al. (2011) found a significant negative correlation of macrobenthic abundance and biomass with water depth and latitude. Based on a thorough literature review they summarized the Arctic deep sea to be an oligotrophic area with steep gradients in faunal abundance and biomass from the slopes to the basins, but with overall density and biomass comparable to other deep-sea areas. Due to the permanent ice cover in the central Arctic surface productivity and associated fluxes are low and previous studies detected extremely small abundances, <200 individuals $m^{-2}$ and biomasses, <0.2 g carbon (C) $m^{-2}$ (Klages et al. 2004; MacDonald et al. 2010; Bluhm et al. 2011). Nevertheless, comparably low values of 100 individuals $m^{-2}$ and 0.5 g wet biomass $m^{-2}$ have been reported from deep-sea regions equally characterized by remoteness from land and low surface productivity, namely the central North Pacific, the Sargasso Sea and the Porcupine Abyssal Plain (Gage and Tyler 1991).

The recent substantial decrease in ice cover of the Arctic Ocean (Arrigo et al. 2008) has fueled speculation as to the future of its productivity and related changes in community structure and distribution. The shift from an Arctic Ocean that is covered with a thick layer of multi year ice (MYI) in the center, and surrounded by a seasonal ice zone (SIZ), to a system with a mostly seasonal ice zone is already happening (Notz 2009). Arctic marine ecosystems are expected to change accordingly (Wassmann et al. 2011). Currently, neither the direction nor mode of these ecological developments is understood sufficiently to predict forthcoming changes in Arctic marine ecosystem functions, goods and services. One major obstacle is our lack of knowledge regarding the current system state, as quite often there is no reliable baseline information (“pre-change system state") from which change can be identified (Wassmann et al. 2011). As the changes in sea-ice cover and surface productivity are ongoing, it is highly important to increase efforts in establishing such baseline information, including the synthesis of previously unpublished data. Here, we focus on the Arctic deep-sea macrozoobenthos. Deep-water benthic communities are depicted as good indicators of change as they are on average more stationary and long-lived compared to pelagic communities and rely in their nutrition almost entirely on the organic flux from euphotic layers. Hence they reflect changes in surface layer production in their own dynamics (Sibuet et al. 1989; Gage and Tyler 1991).

We compiled data on macrozoobenthic communities sampled during expeditions of RV Polarstern between 1990-1997 and in 2012, to the deep Fram Strait and the Central Arctic (Fig. 1; Table 1) and estimated benthic productivity (P/B) and secondary production (P) by applying the empirical ANN model developed by Brey (2012). Based on this dataset we tested patterns previously reported (i.e. decrease of standing crop with depth and latitude, decrease of mean body mass with depth, distribution patterns of feeding types), and investigated additional drivers of macrozoobenthic community patterns. In order to identify the major spatial patterns in the dataset we grouped the sample stations into regional and latitudinal clusters, depth zones, and zones of different sea ice concentration and tested this groups for significant differences in their community properties abundance, biomass, mean body mass (M), secondary production (P), productivity (P/B) and feeding structure. Only few estimates on total macrobenthic secondary production exist from deep-sea regions (Gage 1991; Brey and Gerdes 1998) and high latitudes (Nilsen et al. 2006; Kedra et al. 2013), but none are available yet from the Central Arctic deep sea. Our first estimates of benthic secondary production in the Arctic deep sea can serve as an initial baseline for comparisons on a regional and basin wide scale to help understanding and predicting upcoming changes in the Arctic Ocean.

Briefly, the main hypotheses tested were: 1) a negative relationship of macrobenthic standing stock (N, B) and production (P) with increasing water depth; 2) an increase of community P/B with depth as a consequence of mean body mass (M) decreasing with depth; 3) a regional variation and a negative relationship of macrobenthic standing stock (N, B) and production (P) with increasing latitude and sea ice coverage; 4) a dominance of deposit feeding organisms in the basins but more evenly distributed feeding structures on the slopes and ridges.

## Methods

### Study area and dataset

The study area ranges from the seasonally ice covered Eastern Fram Strait (78° N) up to the permanently ice covered central Arctic Ocean at 90° N. In the NW-Spitsbergen and Fram Strait region water depths down to 5600 m are reached at its deepest site, the Molloy Hole (Soltwedel et al. 2005). Inflow of warm Atlantic water that enters the Arctic Ocean via the West Spitsbergen Current (WSC) explains that the southern stations are only seasonally ice-covered. Eastward the WSC splits up into the Svalbard Branch and the Yermak Branch, both affecting the sea ice conditions on the Yermak Plateau. This shallow, marginal plateau, located between 80 and 82° N northwest of Spitsbergen, ranges from 500-800 m on the crest down to 3000 m as it merges into the Nansen Basin (Soltwedel et al. 2000). Northwards the Nansen and the Amundsen Basin adjoin with average depths of 4000 m and most areas permanently covered with sea ice. The two basins are separated by the Gakkel Ridge, a slow spreading ridge system rising up to 1000 m below sea level (Jakobsson et al. 2012). The Amundsen Basin is limited by the Lomonosov Ridge, which rises 3000 m above the abyssal plains and separates the Eurasian from the Amerasian Basin (Kristoffersen et al. 2007). The Makarov Basin, flanking the Lomonosov Ridge from the opposite side is the only region from the Amerasian part of the Arctic included in this study. The western Amundsen Basin merges into the steep slopes of the Morris Jesup Rise, which reaches up to 1000 m below sea level and then transitions into the Greenland slope (Jakobsson et al. 2012) (for detailed station information see table 2 and S1).

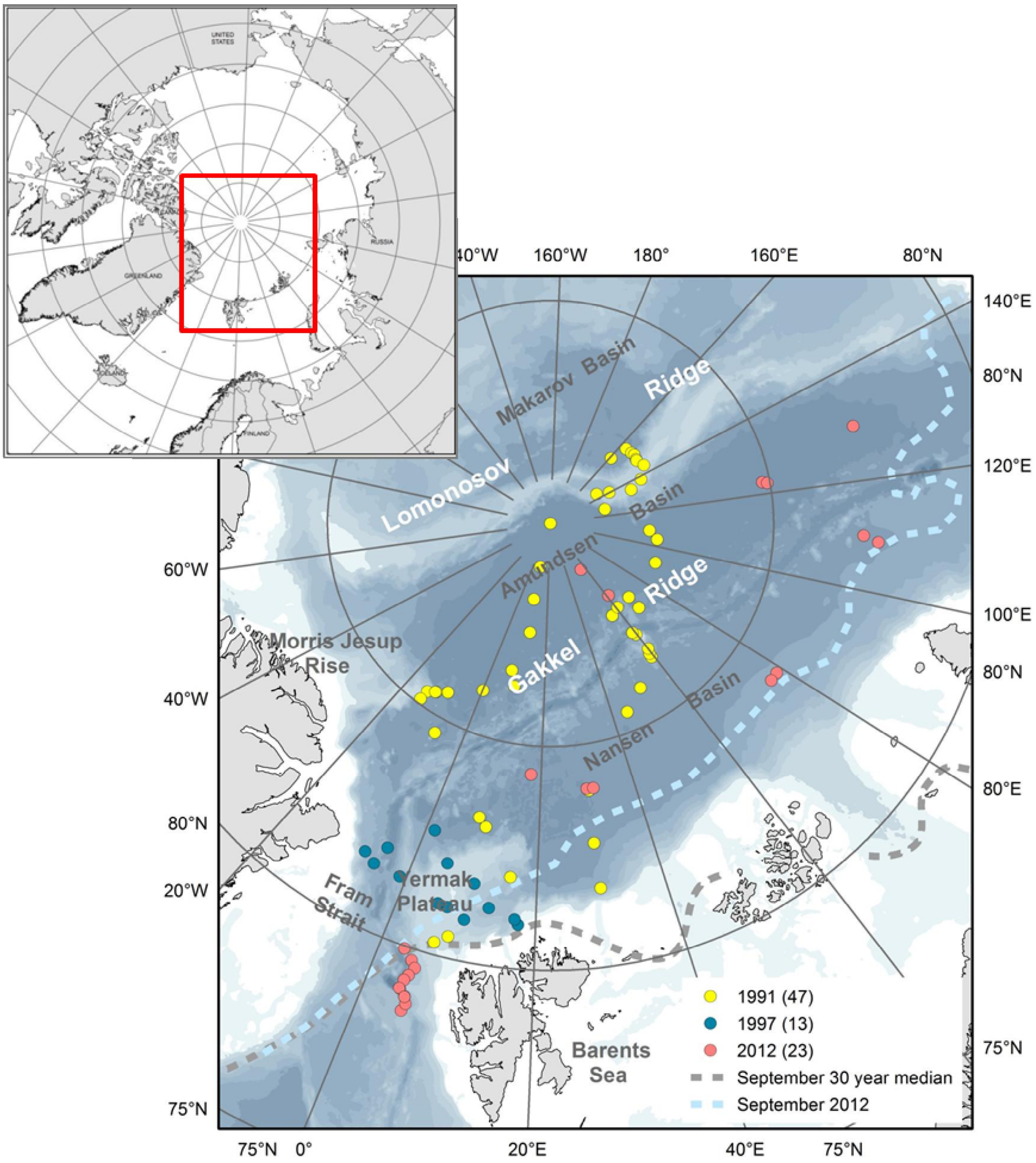

**Fig. 1**: Sample stations (yellow – stations from 1991, blue – stations from 1997, red – stations from 2012; number of stations in brackets) and September sea-ice extent (blue line – 2012 sea ice minimum; grey line – 1981-2011 median sea ice extent).

The dataset used for this study (http://doi.pangaea.de/10.1594/PANGAEA.828348; Fig. 1) constitutes a compilation of AWI Arctic macrozoobenthos data (PANABIO – pan-Arctic database of benthic biota - project, in progress) selected using the following criteria: 1) abundance and biomass data available on species level, 2) comparable sampling and sample treatment (comparable sampling device and sample area and sieving of samples with 250 µm or 500 µm sieve sizes) to keep comparison errors to a minimum and 3) data distributed along a transect from the Fram Strait (78° N) to the Central Arctic (90° N) with a focus on the Eurasian basins. The samples were taken during several RV POLARSTERN cruises between 1991 and 2012 (Table 1). Data from the cruise ARK-VIII/3 in 1991 (Fütterer 1991; 47 stations from northern Svalbard, Yermak Plateau, Morris Jesup Rise and Arctic Ridges and Basins) were published by Kröncke (1994 and 1998) and samples from cruise ARK-XXVII/2 (11 stations from the longtime deep-sea observatory “Hausgarten”, hereby referred to as group “NW-Spitsbergen”) by Soltwedel 2013. Data from ARK-XXVII/3 in 2012 (Boetius 2013a; 5 and 7 stations, Nansen and Amundsen Basin) as well as samples from the cruise ARK-XIII/2 in 1997 (Stein and Fahl 1997; 23 stations, Yermak Plateau, Fram Strait) are provided in this study (Table 1; Fig. 1).

**Table 1**: Overview of stations sampled with RV Polarstern used for this study. More detailed station information (coordinates, date, water depth) are provided in S 1. BL = Bottom Lander. MG = Multigrab.

| Expedition | Year | Gear | Region | Reference |
|---|---|---|---|---|
| ARK-VIII/3 | 1991 | Giant Box Corer (0.25 m-2) | N-Svalbard, Yermak Plateau, Nansen and Amundsen Basin, Gakkel and Lomonosov Ridge, Morris Jesup Rise | Kröncke (1994, 1998) |
| ARK-XIII/2 | 1997 | Giant Box Corer (0.25 m-2) | Fram Strait, Yermak Plateau | this study |
| ARK-XXVII/2 | 2012 | Giant Box Corer (0.25 m-2) | Fram Strait / NW Spitsbergen, "HAUSGARTEN" | Vedenin et al. (unpubl. ms.) |
| ARK-XXVII/3_BL | 2012 | Bottom Lander Chambers (3 x 0.04 m-2) | Nansen Basin, Amundsen Basin | this study |
| ARK-XXVII/3_MG | 2012 | Multigrab (9 x 0.024 m-2) | Nansen Basin, Amundsen Basin | Vedenin et al. (in press) |

## Sampling procedure

Giant box corers of 0.25 $m^2$ surface area (USNEL-type) were used for sampling benthic macrofauna on ARK-VIII/3 (see Kröncke 1994, 1998), ARK-XIII/2 and ARK-XXVII/2. Up to 7 subsamples of 0.02 $m^2$ were taken per box core on ARK-

VIII/3 and ARK-XIII/2. The total surface of a box core was sampled in ARK-XXVII/2 (Soltwedel 2013). On ARK-XXVII/3 samples were taken with a Multigrab (9 x 0.024 $m^2$) and benthic chambers of a Bottom Lander system (3 x 0.04 $m^2$). Single chambers from Lander and Multigrab deployments were treated like replicate subsamples of box corers from other cruises. The samples from ARK-VIII/3 and ARK-XXVII/2 were washed over 500 µm sieves (top 14 cm), the samples from ARK-XIII/2 with 250 µm sieves (top 2 cm) and 500 µm sieves (2 to max. 20 cm) and samples from ARK-XXVII/3 only with 250 µm sieves (top 10 cm). All samples were stored in 4% (at ARK-XXVII/2 10%) Borax-buffered Formalin.

In the respective home laboratories macroinvertebrates were counted, weighed (wet weight) and identified to the lowest possible taxonomic level. Generally all metazoan animals retained on a sieve with 250 or 500 µm mesh size were included in the analysis, only significantly larger animals belonging to the size class “megafauna” (>2 cm) were excluded.  We are aware that estimates of macrofauna distribution are affected by the gear design, sampling area, sample depth and sieve mesh sizes (Wei et al. 2010). Especially abundance estimates seem to be more affected by differing sieve mesh sizes than biomass estimates (Shirayama & Horikoshi 1989; Romero-Wetzel & Gerlach 1991; Gage et al. 2002). Gage et al. (2002) showed that 95% of the biomass retained on a sieve with 250 µm mesh size could still be retained on a much coarser sieve of 1 mm mesh size, while about 40% of abundance would be lost when switching from a 250 µm sieve to a sieve with only 500 µm mesh size. Due to this effect we have to consider an underestimation of abundances by 500 µm samples. Sample area and depth of sample horizon are thought to have comparatively less impact on both abundance and biomass (Gage et al. 2002; Hammerstrom et al. 2010). To exclude potential effects of sampling procedure on our results we performed a three-way ANOVA of the factors sieve size, sample area, and year of sampling on the residuals of an ANOVA of abundance ($p=0.97$) and biomass ($p=0.80$) vs. regions (see also “Statistical Analysis” and “Results” part). The ARK-VIII/3 dataset was provided as the median of all subsamples / station (Kröncke 1994, 1998) while the remaining dataset consists of mean values / station. No significant “median/mean-effect” was detected by an *a priori* pairwise test mean vs. median across all ARK-XXVII/3_BL stations ($p=0.708$).

## Data Harmonization

All geographical coordinates were converted to decimal degree. The station data were plotted on a modified polar stereographic IBCAO base map (http://www.ibcao.org; Jakobsson et al. 2012) in the WGS84 coordinate system using ESRI ArcGIS 10.1.

The taxonomic name of each species was matched with the World Register of Marine Species (WoRMS) as first authority and also with the Integrated Taxonomic Information Service (ITIS) for reasons of comparability with other datasets. When abundance and biomass data were not already provided per m² from the start they were recalculated to individuals and g wet mass (WM) per $m^2$. A complete list of species taxonomy, abundance, biomass and production can be found in the Open Access library PANGAEA (http://doi.pangaea.de/10.1594/PANGAEA.828348).

## Environmental data

Water depth refers to the recorded depth at the time the sampling device was deployed at the seafloor; bottom water temperature (°C) data were compiled using the Open Access library PANGAEA (http://www.pangaea.de). If temperature was not measured during sampling we used data from nearby CTD stations from the same cruise. If no such data were available we searched for the spatially and temporally closest measurement available from other cruises. This approach is reasonable as the seasonal variations in bottom water temperature from stations below 800 m depth are negligible (Langehaug et al. 2012). Information about sea ice concentration (%) per station was extracted from GeoTiff pictures of sea ice concentration for the respective year and month (25 km raster cells). Sea-ice maps used for the cruises from 2012 were provided by the Institute of Environmental Physics University of Bremen (www.iup.uni-bremen.de). For stations sampled before 2002 the pictures used were provided by NISDC (http://nsidc.org/).

## The P/B model

Estimation of benthic production was performed using the empirical ANN model developed by Brey (2012). The difference and advantage of an “artificial neural network” (ANN) model compared to other empirical models which are based on multiple linear regression is that it can model complex, nonlinear and non-continuous relationships between independent and dependent variables by learning and generalizing from example data (Brey et al. 2012). The P/B model used here is based on an initial database of 1258 datasets, each providing information on annual production P, biomass B, mean body mass M, annual P/B ratio, taxonomy and ecology per species as well as the applied methods. The final model (which is implemented in an excel spread sheet and can be assessed via http://www.thomas-brey/science/virtualhandbook (Brey 2001)) consists of three continuous and 17 categorical input parameters: mean body mass (log(M), [J]), temperature (1/T, [K]), water depth (log(D), [m]), five taxonomic categories (Mollusca, Annelida, Crustacea, Insecta, Echinodermata), seven lifestyle categories (infauna, sessile, crawler, facultative swimmer, herbivore, omnivore, carnivore), four environmental categories (lake, river, marine, subtidal), and a marker for exploitation.

All categorical variables were binary (0 or 1). The necessary ecological information for each species was extracted from literature and online resources (see paragraph below and supplementary material S 3 for details). Mean body mass (M) was calculated for each species by dividing biomass by abundance. Biomass data were previously converted to Joule, using the conversion factor (CF) database of Brey (2012, database version 4, www.thomas-brey.de/science/virtualhandbook). When no CF was found for a certain species the CF of the next higher taxonomical level was used. Species that did not belong to any of the five taxonomic categories of the model were grouped by the category their body form resembled to most. Accordingly we grouped Porifera, Tunicata, Cnidaria and Bryozoa by category Mollusca, and Sipuncula, Nemertea, Entoprocta and Cephalorhyncha were grouped by category Annelida. The exploitation marker indicates whether a species is commercially exploited and was set to zero for each species in this study. Model output is population P/B ratio ($y^{-1}$), including upper and lower 95% confidence limits; population P was calculated by multiplying the P/B ratio with population biomass and community P by adding up all population values. For further details on the model see Brey (2012).

### Functional Traits

Information about life style, motility and alimentation type needed as input into the P/B model (see before) was obtained from literature and through web search engines like WoRMS (www.marinespecies.org), MARLIN (www.marlin.ac.uk) and the Marine Species Identification Portal (http://species-identification.org/). When no information was found for a certain species the next taxonomic level was tried until reliable information was found.  A list of used sources is included in the supplementary material S3 (mainly for the two most prominent taxonomic groups in this study, the Annelida and Arthropoda).

For the analysis of the trophic group structure of macrozoobenthic communities the feeding types were assessed from the same sources as above and assigned to one of the four groups carnivore/predator/scavenger, filter- and suspension feeder, interface feeder or deposit feeder (combining surface and subsurface deposit feeders).

### GIS

For mapping benthic abundance, biomass and production ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute was used. Shapefiles containing the georeferenced sea ice extent from 2013 and a 30 years mean were provided by NSIDC (http://nsidc.org/data/; Fetterer et al. 2002).

### Statistical Analyses

We tested for differences in abundance, biomass, mean body mass (M), production (P), productivity (P/B) and feeding structure between (i) regions (NW-Spitsbergen, Fram Strait, Yermak Plateau, Nansen Basin, Gakkel Ridge, Amundsen Basin, Lomonosov Ridge, Morris Yesup Rise), (ii) sea ice zone (i.e. sea ice concentration in month of sampling) (“ice free” – sea ice concentration < 10%;

marginal ice zone “MIZ” - pack-ice with concentrations between 10-80%; “ice covered” – sea ice concentration between > 80%), (iii) depth zone (upper slope < 1500 m, lower slope 1500-3000 m, and Basin > 3000 m) and (iv) latitudinal zone (78-80°, 80-82°, 82-84°, 84-86°, 86-88°, 88-90° N). The SIMPROF approach was used to test if the environmental parameters (water depth, temperature, sea ice concentration, longitude, latitude) significantly differ between the compared regions and thus justify the applied regional clustering. As P/B and M are known to be largely influenced by temperature we tested for a correlation of temperature with P/B and M and also for regional differences in bottom temperature. Statistical approaches included regression, ANOVA, multi-way ANOVA, ANCOVA and Post Hoc Tests (Student's t) using the JMP® software package, Version *10.0* by SAS Institute Inc., Cary, NC, 1989-2007. Due to limited number of samples we performed one-way ANOVAs and ANCOVAs with water depth used as co-variable to test for significant differences between stations (grouped by regions, latitudes and sea ice concentration) after eliminating the generally acknowledged impact of depth on benthic communities. As depth and temperature are co-varying in the Arctic Ocean, we performed an ANOVA on the residuals of a temperature versus depth regression to test for temperature differences among regions. The region Makarov Basin was excluded from the statistical comparison of regions due to the minor sample size of only two stations, all other regions contained 4 – 20 stations (Table 2). To exclude potentially distorting effects of sampling procedure (i.e. sieve size, sample area, year of sampling) on our regional comparison we performed a 3-way ANOVA of these factors on the residuals of an ANOVA of abundance vs. depth and biomass vs. depth. Data from regions that were sampled in 1991 and 2012 (Nansen Basin, and Amundsen Basin) were additionally tested with ANCOVA for an effect of time. Data were transformed using power (Box-Cox) and log transformation. ANOSIM was used to test for differences in the relative contribution of different feeding types to overall biomass and production. SIMPROF and ANOSIM were performed with PRIMER Version 6; Clarke, KR, Gorley, RN, 2006.

## Results

### Effects of environment and sampling procedure

The SIMPROF test based on latitude, longitude, temperature and sea ice concentration found eight significantly different groups ($p< 0.001$) that correspond to the 9 regional groups except for the two Makarov Basin stations which were grouped together with Lomonosov Ridge stations. Temperature differed significantly between regions (ANOVA with the residuals of a temperature vs. depth regression; $F=2.17$; $p=0.0449$).

The 3-way ANOVA of the residuals of an ANOVA of abundance per regions ($F=20.81$; $p=0.001$) and biomass per regions ($F=9.96$; $p=0.001$) on the factors sieve size, sample area, and year of sampling did not find them explaining any variance in abundance ($F=0.25$; $p=0.97$) and biomass data ($F=0.54$; $p=0.8022$). The a priori pairwise test of median vs. mean abundances did not detect significant differences for the ARK-XXVII/3 stations ($F=0.15$; $p=0.708$). ANCOVA with depth as co-variable found abundance and biomass in Nansen Basin significantly higher in 1991 compared to 2012 ($F=11.52$; $p=0.007$ and $F=5.44$; $p=0.042$), but in Amundsen Basin significantly higher in 2012 compared to 1991 ($F=6.58$; $p=0.021$ and $F=11.13$; $p=0.004$).

### Abundance

Mean abundance (individuals (ind.) $m^{-2}$) per region varied between 10 (Gakkel Ridge) and 1053 ind. $m^{-2}$ (Yermak Plateau) (Table 2; Fig. 2). The highest abundance by far was found at Yermak Plateau at a water depth of 517 m (4136 ind. $m^{-2}$). Stations from NW-Spitsbergen, Morris Jesup Rise and Fram Strait showed relatively high average abundances of 552, 410 and 326 ind. $m^{-2}$, respectively. All other regions showed lower mean abundances that ranged between 10 and 203 ind. $m^{-2}$. The lowest abundances were found at the stations in the central Arctic with means of 90 ind. $m^{-2}$ and lowest counts of 0 ind. $m^{-2}$ in Amundsen Basin and at Gakkel Ridge (Table 2). Because water depth was found to have a significant effect on abundances (ANOVA, $F=41.53$; $p<0.0001$, Table 3) it was accordingly used as a co-variable in ANCOVAs to test for differences between stations grouped by regions, latitudes and sea ice concentration (Table 3, Fig. 7). Abundance (ind. $m^{-2}$) was significantly different between the different regions (F=9.99; p<0.0001), latitudinal zones (F=12.46; p<0.0001) and areas of different sea ice concentration (F=10.52; p=0.0005) (Fig. 4). The Post Hoc Tests (Student's t) grouped the regions with highest abundance values per $m^2$, i.e. NW-Spitsbergen and Yermak Plateau (mean abundance per station 552 and 1053 ind. $m^2$) as significantly different from the regions with stations in greater depths and higher latitudes (i.e. Nansen Basin, Amundsen Basin, Lomonosov Ridge and Morris Jesup Rise; with average abundances between 61 and 410 ind. $m^{-2}$). The Gakkel Ridge stations were also significantly different from all the other stations as they showed the lowest abundances (zero abundance in four of five stations and one station with 50 ind. $m^{-2}$. Regarding latitude, abundance was significantly higher between 78-82° N compared to 82-90° N, whereas the stations between 86-88° N showed significantly lower values than all the other stations. The northernmost stations between 88-90° N were ranked third highest, although not significantly different from the stations between 82-86° N. When stations were grouped according to percentage of sea ice concentration with water depth as co-variable, the stations in the group “ice free” and “MIZ” did not show significantly different abundances, but were both grouped as significantly different from the group “ice covered” (F=10.52; p<0.0001) (Table 3, Fig. 7). Regarding the major taxonomic groups Annelida were by far the most prominent group ranging from 21% at Lomonosov Ridge up to 68% at NW-Spitsbergen (Fig. 3). The second dominant taxonomic group was Arthropoda with ranges of 25-50% at Gakkel Ridge, Makarov Basin, Amundsen Basin and Fram Strait, but lower contributions in all other regions (1-20%). Porifera were the third most prominent group with a high share of 27-54% at Lomonosov Ridge, Makarov Basin and Morris Jesup Rise and lower contributions of 0-14% in the other regions. Mollusca had a higher share of the total community with 22% only at NW-Spitsbergen. They grouped with all other phyla (Bryozoa, Cephalorhyncha, Chordata, Cnidaria, Echinoidea, Entoprocta, Nematoda, Nemertea and Sipuncula) in the lower range of 0-14% at other regions (Fig. 3, S2).

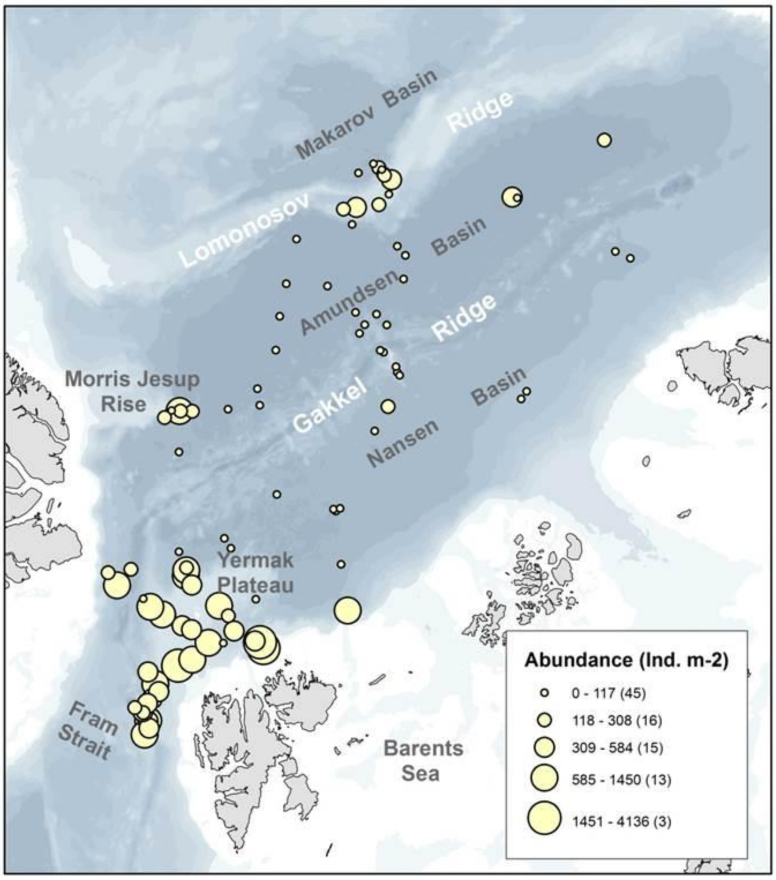

**Fig. 2** Macrobenthic abundance (ind. $m^{-2}$).

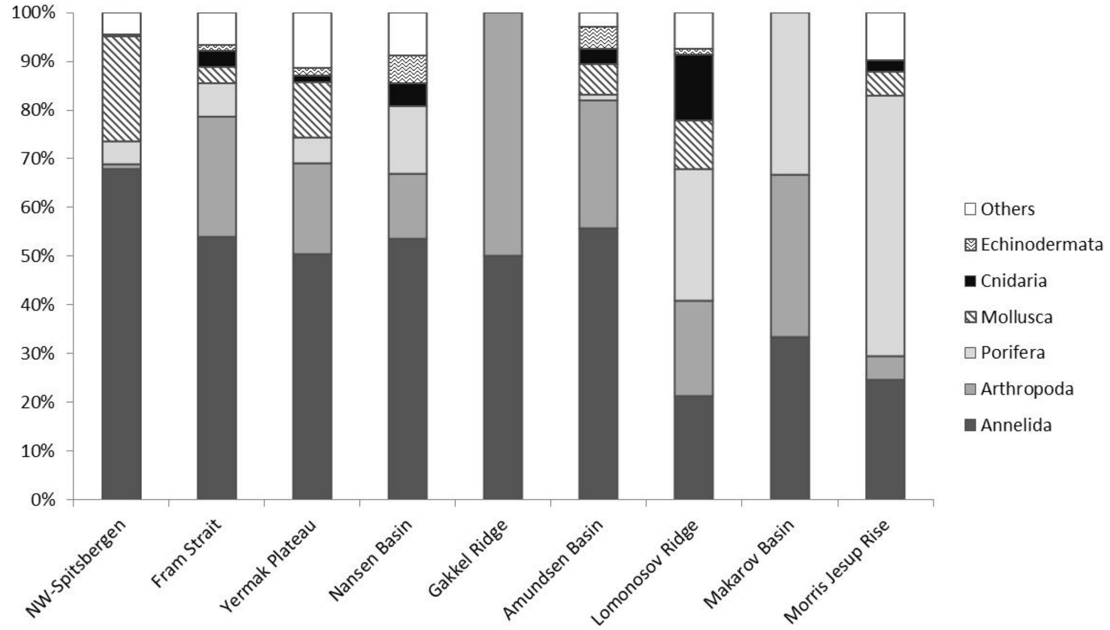

**Fig. 3** Relative abundance of major groups Annelida, Arthropoda, Porifera, Mollusca, Cnidaria and Echinodermata. The group "Others" combines Bryozoa, Cephalorhyncha, Chordata, Entoprocta, Nematoda, Nemertea and Sipuncula.

## Biomass

Mean biomass per region ranged from 2 mg C m-2 at Gakkel Ridge up to 410 mg C m-2 at Yermak Plateau (Table 2). Highest biomass by far was found at Yermak Plateau and Nansen Basin stations (max. 2009 and 3026 mg C m-2), while all other regions showed low mean biomass ranging between 2 and 65 mg C m-2. Because water depth was found to have a significant effect on biomass (ANOVA, F=19.55; p<0.0001, Table 3) it was used as co-variable in the following ANCOVAs (Table 3, Fig. 7). ANCOVAs detected significant differences in biomass between regions (F=5.07; p<0.0001) (Table 3; Fig. 7). Post Hoc tests grouped the stations from Yermak Plateau (mean biomass 410 mg C m-2) to be significantly different to those of Amundsen Basin, Morris Jesup Rise and Gakkel Ridge. No significant difference was detected to stations from NW-Spitsbergen, Fram Strait, Nansen Basin and Lomonosov Ridge. Also regarding latitudes, a significant difference was found between stations (F=5.53; p=0.0002). Here the stations between 80° and 82° N were found to be significantly higher in biomass than all the stations of the areas 82-84, 84-86 and 86-88° N, but were not found to be significantly different from the southernmost (78-80° N) and northernmost (88-90° N) stations. Comparing stations by sea ice concentration showed significantly higher biomasses for the stations in the group “MIZ” (F=3.11; p=0.0496) compared to the group “ice covered”. The group “ice free” was not significantly different from the other two groups (Table 3; Fig. 7). Annelids contributed most to community biomass at Morris Jesup Rise (86%) and NW-Spitsbergen (74%), and between 10 and 60% elsewhere (Fig. 4). Arthropoda contributed 58% of the biomass in Amundsen Basin, 40% at Gakkel Ridge and 34% in Fram Strait, but only between 0–17% in all other regions. Echinoderms dominated biomass in Nansen Basin (66%), but showed rather low percentages at all other regions (0–12%). Porifera dominated the community biomass in Makarov Basin (60%) and contributed a lot in Fram Strait (45%), at Lomonosov Ridge (32%) and Nansen Basin (21%). Mollusca showed relevant shares of 29% at Lomonosov Ridge, in other regions they contributed ≤4%. All other groups did not contribute significantly to community biomass and ranged between 0-10% in all regions (Fig. 4; S2). Regarding trophic structure, deposit feeders were the dominant group, while interface feeders had significantly lower biomasses (F=14.61; p<0.0001). Deposit feeders had a much higher share with 66% of total biomass at Nansen Basin and 4–60% in the other regions except Makarov Basin. Carnivores/Predators/Scavengers contributed most at Morris Jesup Rise (84%) and Amundsen Basin (67%). Filter feeders dominated the biomass at Makarov Basin (60%) and Lomonosov Ridge (53%) (S5). ANOSIM did not detect differences in the relative contribution of different feeding types between any of the tested groups (depth, latitude, sea ice, and region) (Global R<0.20).

**Fig. 4** Relative biomass of major groups Annelida, Arthropoda, Porifera, Mollusca, Cnidaria and Echinodermata. The group "Others" combines Bryozoa, Cephalorhyncha, Chordata, Entoprocta, Nematoda, Nemertea and Sipuncula.

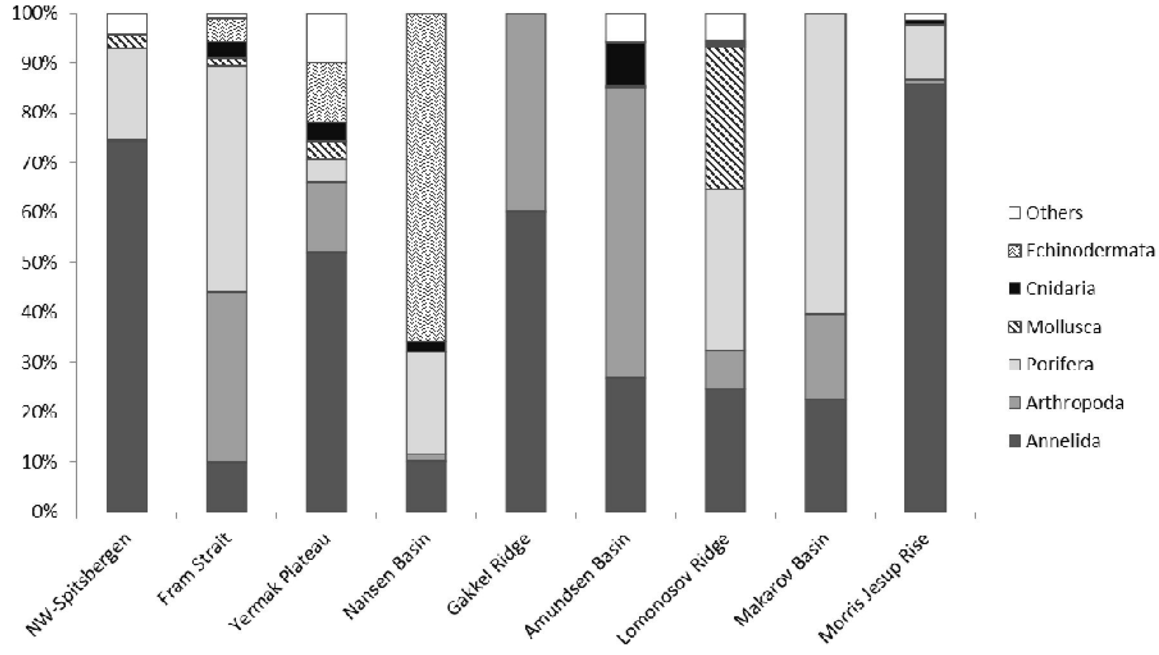

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**Table 2** Number of sample stations, depth range, number of species and major taxonomical groups and the mean, minimum and maximum parameters abundance (individuals m$^{-2}$), biomass (mg C m$^{-2}$) and production (mg C m$^{-2}$ y$^{-1}$).

| Stations | Stations | Depth (m) | Species | Major Groups | Abundance (Ind m$^{-2}$) | | | Biomass (mg C m$^{-2}$) | | | Production (mg C m$^{-2}$ y$^{-1}$) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | mean | min | max | mean | min | max | mean | min | max |
| Fram Strait / NW Spitzbergen | 11 | 2340 - 2740 | 23 | 7 | 586 | 248 | 976 | 8 | 3 | 19 | 12 | 5 | 29 |
| Fram Strait | 4 | 2530 - 4130 | 22 | 6 | 767 | 275 | 1739 | 667 | 110 | 2206 | 466 | 66 | 1394 |
| Yermak Plateau | 13 | 520 - 2530 | 180 | 12 | 2737 | 100 | 7323 | 1620 | 5 | 4689 | 1401 | 9 | 3706 |
| Nansen Basin | 15 | 2650 - 4050 | 46 | 9 | 153 | 6 | 800 | 339 | < 1 | 3026 | 164 | < 1 | 1585 |
| Gakkel Ridge | 5 | 1790 - 4420 | 2 | 2 | 10 | 0 | 50 | 2 | 0 | 8 | 2 | 0 | 12 |
| Amundsen Basin | 20 | 3400 - 4480 | 36 | 7 | 63 | 0 | 346 | 49 | 0 | 492 | 33 | 0 | 247 |
| Lomonosov Ridge | 10 | 1020 - 3840 | 27 | 8 | 203 | 75 | 450 | 65 | 26 | 126 | 73 | 42 | 130 |
| Makarov Basin | 2 | 4000 - 4010 | 4 | 3 | 75 | 50 | 100 | 23 | 10 | 35 | 29 | 8 | 51 |

## Mean body mass (M)

Mean body mass of the stations from Nansen Basin, Lomonosov Ridge and Yermak Plateau with values between 0.4-2.5 mg C were significantly higher than at NW-Spitsbergen, Morris Jesup Rise and Gakkel Ridge with values of 0.03-0.1 mg C (F=3.12; p=0.0028). While no significant differences in mean body mass were found within the different water depths (F=0.73; p=0.4835) and sea ice zones (F=1.87; p=1398), we detected significant differences between latitudinal zones (F=2.83; p=0.0207). Post Hoc tests ranked the groups 86-88° N and 78-80° N to be significantly lower than the groups 88-90° N, 80-82° N and 82-84° N. M was not significantly related to bottom water temperature (F=0.01; p=0.9144).

## Secondary production (P)

Mean macrobenthic secondary production was lowest at Gakkel Ridge with 2 mg C $m^{-2}$ $y^{-1}$ and highest at Yermak Plateau with 385 mg C $m^{-2}$ $y^{-1}$ (Table 2; Fig. 5). The highest production per station was found at Yermak Plateau (reaching up to 2534 mg C $m^{-2}$ $y^{-1}$), followed by Nansen Basin with values reaching 1585 mg C $m^{-2}$ $y^{-1}$. The production at NW-Spitsbergen and Lomonosov Ridge was rather similar with means of 70 and 73 mg C $m^{-2}$ $y^{-1}$ respectively. All other regions ranged in their means between 2 and 46 mg C $m^{-2}$ $y^{-1}$. Because water depth was found to have also a significant effect on production (ANOVA, F=25.88; p<0.0001, Table 3) it was used again as co-variable in ANCOVAs (Table 3, Fig. 7). ANCOVAs showed that there were significant differences between regions (F=5.32; p<0.0001) (Table 3). Post Hoc tests grouped the regions with highest mean production (Yermak Plateau, NW-Spitsbergen and Lomonosov Ridge) and the stations with lowest production (Morris Yesup Rise and Gakkel Ridge) to be significantly different from each other. Also when grouped by latitude, significant differences were found by ANCOVA (F=5.95; p<0.0001). Post Hoc tests revealed that the benthic secondary production from stations between 80–82° N, 78-80° N and 88-90° N was significantly higher than in the groups between 84-88° N. Comparison of stations grouped after their sea ice concentration showed as well significant differences in production (F=4.25; p=0.0173). Like for biomass, Post Hoc tests showed significantly higher benthic production in the group “MIZ” (mean 0.5 g C $m^{-2}$ $y^{-1}$) compared to group “ice covered” (mean 0.06 g C $m^{-2}$ $y^{-1}$) (Table 3; Fig. 7). Annelids contributed most to the overall production at NW-Spitsbergen (73%), at Morris Jesup Rise (67%), at Yermak Plateau and Gakkel Ridge (both 64%) and at Amundsen Basin (51%) (Fig. 6; S2). At the other regions they contributed between 14 and 25% to the overall production. Porifera were the most productive group at Makarov Basin (70%), Nansen Basin (49%) and Lomonosov Ridge (47%). Arthropoda contributed 45% at Fram Strait, 39% at Amundsen Basin and 36% at Gakkel Ridge, but only between 0 and 16% in all other regions. All other groups contributed much less to the overall production. Echinoderms contributed 23% to the overall production at Nansen Basin but only between 0-6% in other regions. Molluscs only showed a higher percentage at Lomonosov Ridge (12%) but ranged at all other stations between 0 and 3%. Suspension feeders had the largest share in production, while deposit feeders showed the significantly lowest values (F=30.22; p<0.0001). Regarding the three depth zones, suspension feeders contributed most in the group “lower slope” (50%) and comparably less to the group “upper slope” (17%) and “basins” (24%). At a regional scale, filter- and suspension feeders contributed most to production at Makarov Basin (70%), Nansen Basin (64%) and Lomonosov Ridge (55%), predators at Morris Jesup Rise (65%), deposit feeders at Gakkel Ridge (64%), Amundsen Basin (50%) and Yermak Plateau (48%), and interface feeders at NW Spitsbergen (42%) (Fig. 8). ANOSIM did not detect differences in the relative contribution of different feeding types in any of the categories tested (depth, latitude, sea ice, region) (Global R always <0.20).

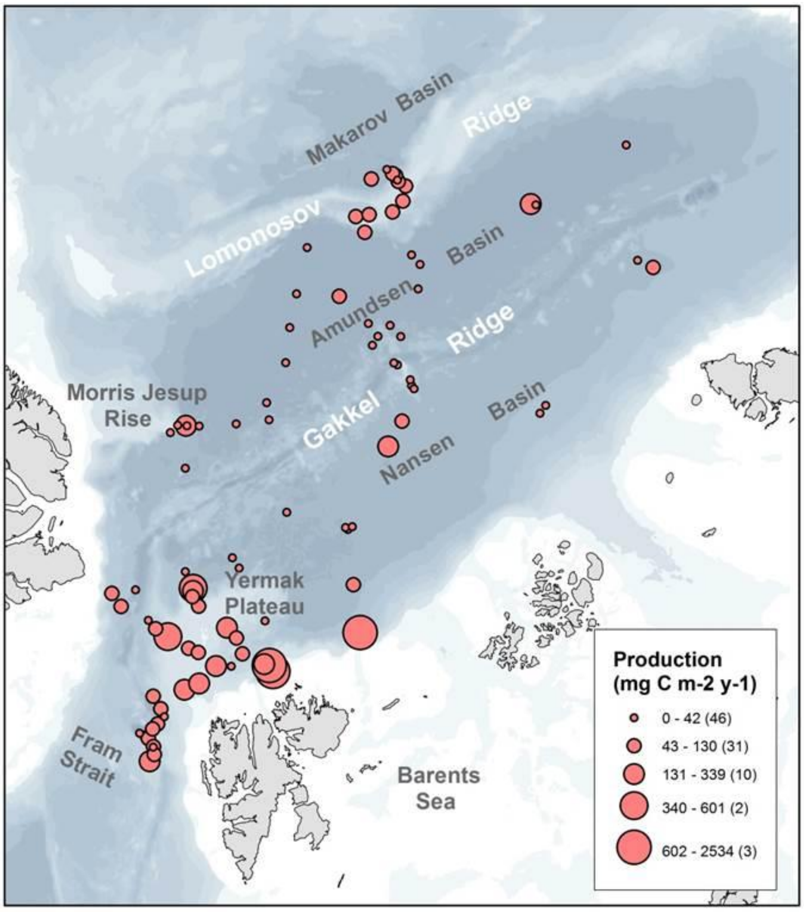

**Fig. 5** Macrobenthic secondary production (mg C $m^{-2}$ $y^{-1}$).

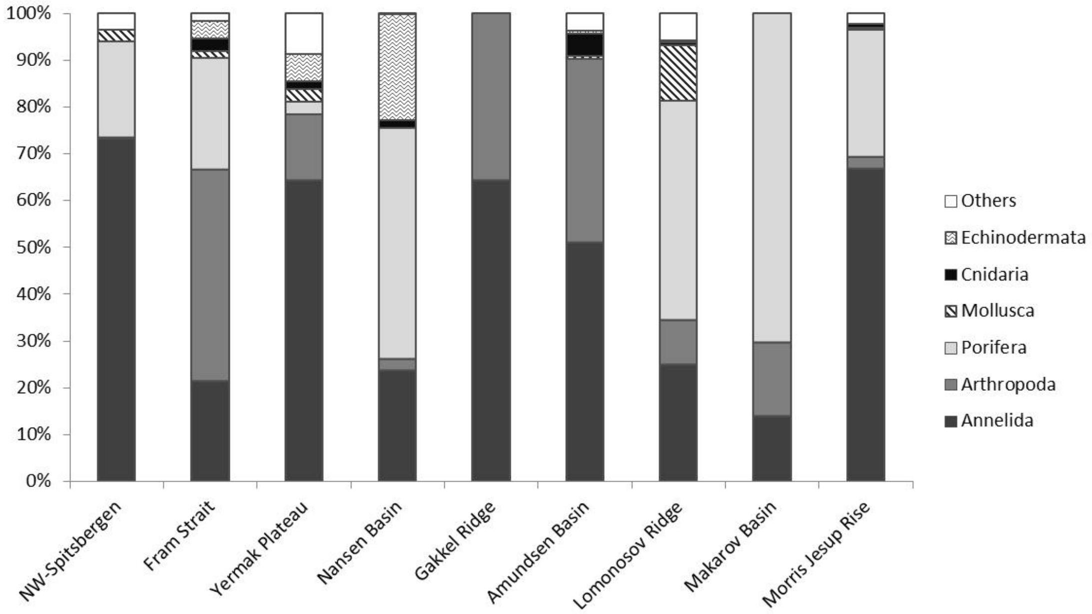

**Fig. 6** Relative production of major groups Annelida, Arthropoda, Porifera, Mollusca, Cnidaria and Echinodermata. The group “Others” combines Bryozoa, Cephalorhyncha, Chordata, Entoprocta, Nematoda, Nemertea and Sipuncula.

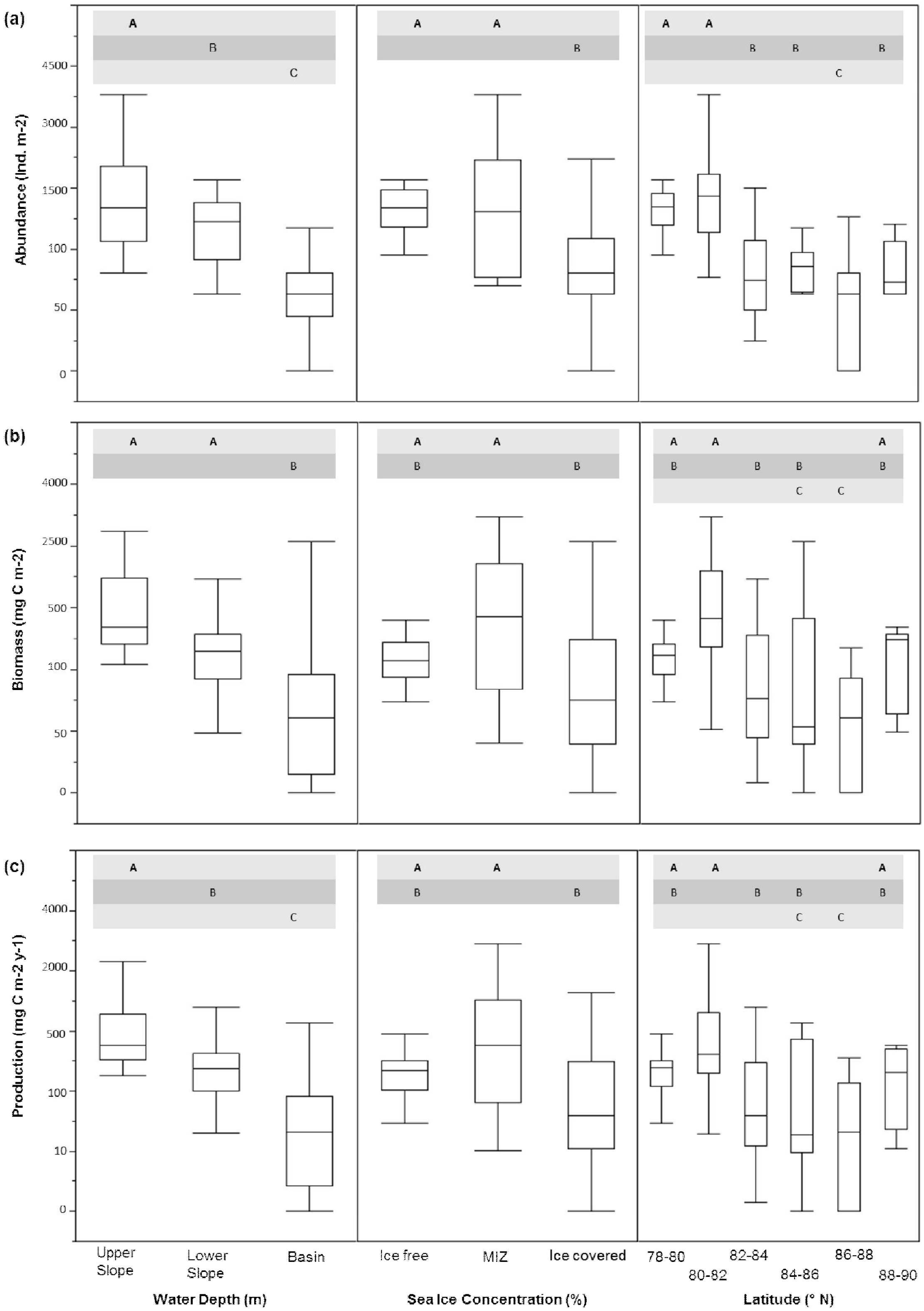

**Fig. 7** Comparison of macrobenthic abundance (a), biomass (b) and production (c) between depth zones (upper slope, lower slope, basin), sea ice zones (Ice free, MIZ, Ice covered) and latitudinal bands (78-80°, 80-82°, 82-84°, 84-86°, 86-88°, 88-90° N) in a box-plot (min, max and mean). Letters above bars indicate significant differences between groups as identified by ANOVA (Depth Zone) and ANCOVA with depth as co-variable (Sea Ice Zone, Latitude) and (Student's t) Post Hoc test on differences between means. Plots are based on transformed (Box-Cox) data

to meet ANOVA/ANCOVA preconditions; the y-axis shows the corresponding non-transformed raw data (making the scale non-linear).

**Table 3** Differences in macrofaunal abundance, biomass and estimated production between regions (see Table 2, Fig. 1 and Fig. 2), latitudinal bands (78-80°, 80-82°, 82-84°, 84-86°, 86-88°, 88-90° N) and areas differing in sea ice concentration (ice free < 10%, MIZ, ice covered > 80%) as identified by one-way ANCOVA with water depth as covariate. Differences between depth ranges (upper slope < 1500 m, lower slope 1500 – 3000 m, basin > 3000 m) were tested with ANOVAs.

| | F | p |
|---|---|---|
| **Region** | | |
| Abundance | 9.99 | <0.0001 |
| Biomass | 5.07 | 0.0001 |
| Production | 5.32 | <0.0001 |
| **Latitude** | | |
| Abundance | 12.46 | <0.0001 |
| Biomass | 5.53 | 0.0002 |
| Production | 5.95 | <0.0001 |
| **Sea Ice Concentration** | | |
| Abundance | 10.52 | <0.0001 |
| Biomass | 3.11 | 0.0496 |
| Production | 4.25 | 0.0173 |
| **Depth** | | |
| Abundance | 41.53 | <0.0001 |
| Biomass | 19.55 | <0.0001 |
| Production | 25.88 | <0.0001 |

## Productivity (P/B)

Production to biomass ratios (P/B) ranged from 0.14–2.22 and were highest at Morris Jesup Rise, Lomonosov Ridge, and NW-Spitsbergen with means per region ranging from 1.17-1.42 $y^{-1}$. Gakkel Ridge was the region with the significantly (F=3.13; p=0.0057) lowest P/B ratio (mean=0.29 $y^{-1}$). ANOVA and ANCOVA did not detect differences in P/B between depth zones (F=1.34; p=0.265), latitude zones (F=1.56; p=0.1690) and zones of different sea ice concentration (F=1.15; p=0.3212). Among major taxonomic groups Porifera and Arthropoda had highest mean ratios of 1.28 and 1.25 $y^{-1}$. Regarding trophic structure, deposit and suspension feeders showed significantly higher ratios than interface feeders and predators (F=2.96; p=0.03). P/B was significantly positively related to bottom water temperature (F=10.01; p=0.002), but not to mean body mass (M) (F=3.28; p=0.0733).

## Discussion

Macrofauna standing stock and secondary production in the Arctic deep-sea decrease with increasing water depth. In addition, we detected significant regional differences for all studied community properties (abundance, biomass, mean body mass, secondary production and P/B). Stations in the vicinity of the highly productive marginal ice zone (MIZ) (latitudes 80-82° N) showed secondary production levels comparable to shallower regions and lower latitudes (Table 4). In the permanently ice-covered central Arctic Amundsen Basin, mean macrobenthic production was estimated to be as low as 25 mg C $m^{-2}$ $y^{-1}$ (Table 2). Assuming an average production-to-consumption ratio (P/C) of macrofauna of about 0.2 (0.239 ± 0.190, N = 97; unpublished data collection of T. Brey), this production would require a particulate organic carbon (POC) input of at least 165 mg C $m^{-2}$ $y^{-1}$ for the macrofaunal consumption only, which is presumably 20% of all benthic size classes including bacteria (Piepenburg et al. 1995). Based on the assumption that < 10% of surface primary production reaches the deep-sea floor (Bauerfeind et al. 2009), a gross primary production (GPP) of around 8 g C $m^{-2}$ $y^{-1}$ would be sufficient to cover this benthic demand. This number is well in the range of reported GPP estimates of 1-25 g C $m^{-2}$ $y^{-1}$ for the central Arctic (Wassmann et al. 2010). Sufficiently high POC fluxes of >1 g C $m^{-2}$ $y^{-1}$ were also recorded via sediment traps situated at 1550 m of depth (Fahl & Nöthig 2007). In contrast to the Central Arctic stations we estimated a mean secondary production of 385 mg C $m^{-2}$ $y^{-1}$ at the Yermak Plateau. Taking into account that at shallower depths (mean 1500 m) a higher percentage of GPP can reach the seafloor, a GPP of approximately 30-90 g C $m^{-2}$ $y^{-1}$ would be required to enable the estimated community production. In the Arctic such a high primary productivity can be found regionally along the highly productive seasonal ice zone (SIZ) and in productive shelf areas like in the Barents Sea (Klages et al. 2004; Wassmann et al. 2010), which are both in the vicinity of and most likely affecting our sample stations. We conclude that particle flux induced by vertical and lateral transport processes is the key factor structuring benthic communities in the deep Arctic Ocean, explaining both the very low values in the ice-covered Arctic Basins and the higher values in the seasonal ice zone.

### Depth-related patterns

Our study confirms the trends shown earlier (Gage & Tyler 1991; Klages et al. 2004; Bluhm et al. 2011): Significantly lower mean abundances and biomasses are found in the deep basins compared to the upper slopes adjacent to the large Arctic shelves (F=41.53; p<0.0001; respectively F=19.55; p<0.0001; Table 3; Fig. 7). Mean abundance at the upper slope below 1500 m water depth ranges between 100 and 4130 ind. m$^{-2}$ (table 2; Fig. 3), consistent with abundances summarized in Bluhm et al. 2011 and Budaeva et al. 2008, and comparable to or even higher than abundances at lower latitudes from previous studies at similar depth ranges (see e.g. Levin and Gooday 2003). Estimated benthic production was shown to follow the same pattern, i.e. significant differences between shallower and deeper stations (F=25.88; p<0.0001) (table 2; Fig. 7). This corroborates the pattern of community production decreasing exponentially with water depth, as reported previously by Brey & Gerdes (1998) for a combined dataset from Antarctic, Arctic and non-polar regions and by Cusson & Bourget (2005) who analyzed global patterns of community production.

Extreme food limitation as found in the deep sea creates selection pressure towards smaller body sizes (Thiel 1975; Wei et al. 2010). Smaller size often coincides with a higher growth rate and thus a higher production to biomass (P/B) ratio (Brown et al. 2004). Accordingly, mean body mass (M) should decrease and community P/B should increase with increasing water depth (Peters 1983). However, M and P/B ratios did not significantly relate to water depth (F=0.73; p=0.4835 and F=1.34; p=0.265), in accordance with Polloni et al. (1979) who did not find a decline in mean macrofaunal organism size from 400–4000 m. Distinctly larger body size seems to be restricted to very shallow (neritic or coastal) waters. Accordingly, datasets that exclude the upper 500 m like in this study may not show depth effects on mean body mass, and models that include shallow depths may overstate the depth effect in the deep sea (Wei et al. 2010). On the other hand, Kaariainen & Bett (2006) found clear evidence of smaller body size in the deep sea when evaluating body size accumulation curves, stressing the need for size structure analysis. While no correlation of P/B ratios and water depth was found here, Cusson & Bourget (2005) even found a negative relation of P/B with water depth (and a positive relation to temperature), and presume that certain life history traits may explain patterns in P/B ratios better than environmental variables.

**Table 4** Mean community Production (P) (g C m-2 y-1) and productivity (P/B) values found in literature, ordered after increasing water depth (m). When originally given in other units, data was converted to carbon using conversion factors from the database of Brey (2012, database version 4, www.thomas-brey.de/science/virtualhandbook).

| Region | Latitude | Water Depth | P | P/B | Authors |
|---|---|---|---|---|---|
| Wadden Sea Tidal Flat (DE) | 54° N | 1 | 8-234 | 0.4-1.8 | Asmus (1987) |
| North East Coast (GB) | 54° N | 15 | 1.97-4.25 | 0.9-1.7 | Rees (1983) |
| Laizhou Bay and Bohai Sea (CN) | 37-39° N | 20-25 | 2.25-3.47 | 0.9-1.2 | Hua et al. (2010) |
| New York Bight (US) | 40° N | 25 | 8.3 | 1.4 | Steimle (1985) |
| Phangnga Bay (TH) | 8°N | 30-50 | 1.6 | 5 | Petersen & Curtis (1980) |
| Bay of Fundy (CAN) | 45° N | 0-70 | 9-18 | - | Wildish et al. 1986 |
| North Sea | 51-57° N | 0-100 | 0.6- > 20 | 0.7-2.5 | Duinevald et al. (1991) |
| Sørfjord (NO) | 69° N | 18-128 | 4.74 | 0.4 | Nilsen et al. (2006) |
| Continental Shelf (GB) | 50° N | 10-137 | 0.4-3.8 | 1.2-1.9 | Bolam et al. (2010) |
| Barents Sea Bank (Infauna) | 75-76 °N | 40-150 | 0.2-5.3 | - | Kedra et al. (2013) |
| Southern Plateau (NZ) | 50° S | 750 | 0.25 | 1 | Bradford-Grieve et al. (2003) |
| Global study | 77° S-69° N | 0-930 | < 0.01-1869 | < 0.1-36.7 | Cusson & Bourget (2005) |
| Magellan Region (CL) | 48-56° S | 8-1140 | 0.4-1.1 | 0.2-0.3 | Thatje &Mutschke (1999) |
| Weddell Sea (Antarctica) | 69-78 °S | 200-2900 | 0.12-4.83 | 0.2-0.6 | Brey & Gerdes (1998) |
| Rockall Trough (NE-Atlantic) | 54° N | 2900 | 0.122 | 0.5 | Gage (1991) |
| Arctic Deep Sea (MIZ) | 80-82 ° N | 500-3500 | < 0.01-2.5 | 0.5-1.8 | this study |
| Arctic Deep Sea (North) | 82-90° N | 500-5400 | < 0.01-0.6 | 0.1-2.2 | this study |

## Regional patterns

Here we detected significant regional differences – beyond those caused by water depth – for all studied community properties (abundance, biomass, mean body mass, secondary production and P/B). The regions Yermak Plateau and NW-Spitsbergen (latter only in abundance) showed significantly higher values than the regions in higher latitudes (i.e. Amundsen Basin and Gakkel Ridge) (Table 3; Fig. 5). This pattern is corroborated when stations were grouped by latitude (significantly higher values at “80–82° N” and for abundance at “78-80° N) or by ice zone (significantly higher values in the group “MIZ”) (Table 3; Fig. 7). The generally higher values at Yermak Plateau might be explained by the vicinity to the highly productive Barents and Spitsbergen Shelves and the high primary production in this region (gross primary production GPP 30-100 g C $m^{-2}$ $y^{-1}$ (Wassmann et al. 2010). The high GPP is supported by Atlantic water supply and the fertile conditions generally found along the MIZ (Sakshaug 2004), which covers a large fraction of Northern Fram Strait (Sakshaug 2004; Wassmann et al. 2010). Along ice edges POC fluxes of >300 mg C $m^{-2}$ $d^{-1}$ are recorded, greatly exceeding those found in open water (intermediate export fluxes 12-27 mg $m^{-2}$ $d^{-1}$) (Klages et al. 2004). The estimated benthic production in the group MIZ (highest value 2.5 g C $m^{-2}$ $y^{-1}$, mean 0.5 g C $m^{-2}$ $y^{-1}$; depth of 500-3500 m) is in the lower range of but still comparable to benthic production estimates from the shallow Barents Sea Bank (0.02-5.3 g C $m^{-2}$ $y^{-1}$) in depths between 40 and 150 m (Kedra et al. 2013; Table 4), and to shallow areas from temperate regions like the UK Continental Shelf with means ranging from 0.4–3.8 g C $m^{-2}$ $y^{-1}$ (Bolam et al. 2010; Table 4). Regarding regional groups, the highest mean production was found at Yermak Plateau with 385 mg C $m^{-2}$ $y^{-1}$. The values from the second most productive area (Nansen Basin, mean production of 138 mg C $m^{-2}$ $y^{-1}$) from depths between 3000-4000 m are – although covered with sea ice throughout most of the year – comparable to values reported from the Rockall Trough in the NE-Atlantic (122 mg C $m^{-2}$ $y^{-1}$) in depths of 2900 m (Gage 1991). These comparisons indicate that benthic communities from the Arctic deep-sea can be comparable in production to other regions, if they are in the vicinity to the highly productive seasonal ice zone and the continental shelf. The third most productive areas are the southernmost stations in NW-Spitsbergen and the northernmost stations on the Lomonosov Ridge (70 and 73 mg C $m^{-2}$ $y^{-1}$). While the stations NW of Spitsbergen benefit from the conditions mentioned previously, the stations in the high north are far from any input from the marginal ice zone and the productive shelf areas. We assume that benthic production at the Lomonosov Ridge could be fueled by organic matter that gets transported with sea ice along the Transpolar Drift, enhancing export via seasonal melting processes. The stations far off the seasonal ice edge, e.g. in Amundsen or Makarov Basin or on the Gakkel

Ridge, show as low production as anticipated for the most oligotrophic deep-sea regions, as primary production under the permanent ice cover is very low (1-25 g C $m^{-2}$ $y^{-1}$) (Wassmann et al. 2010). Recent studies have found indications for much higher carbon fluxes associated with sea-ice minima in 2007 (Lalande et al. 2009) and 2012 (Boetius et al. 2013 b), and the rapid export of sea-ice algae to the seafloor. Our results corroborate these observations, as the significantly higher benthic biomass in the Central and Eastern Amundsen Basin in 2012 compared to 1991 (F=11.13; p=0.004) may indicate an increase in vertical flux over these two decades. However, there are just five samples from 2012 and these were not taken in exactly the same area of Amundsen Basin as in 1991. Hence, this finding should not be over-interpreted; distinctly higher sampling effort is required to produce more reliable data. Nevertheless, ongoing decline in sea-ice cover and thickness in the central basins are likely to cause future changes in macrozoobenthos abundance, biomass and production.

While we found no correlations of mean body mass (M) and productivity (P/B) with water depth, we did detect significant regional differences (F=3.12; p=0.0028; F=3.13; p=0.0057). Highest P/B ratios were found in the region Morris Jesup Rise, ranging from 0.8–2.2 $y^{-1}$. The most important factors influencing the community P/B ratio are body mass, temperature and food (Brey and Clarke 1993 and references therein). Overall we found no correlation of P/B ratios with mean body mass M (F=3.28; p=0.0733), but we did detect a positive relation of P/B to temperature (F=10.01; p=0.002). However, as the temperature difference among regions is small, and the region with the highest P/B values (Morris Jesup Rise) is not the one with the highest temperatures (Lomonosov Ridge), we assume that additional drivers have to be considered. The third proposed explanatory factor, food input, is quite difficult to determine in the ice-covered Arctic Ocean. We presume the highest food fluxes to be in areas influenced by the MIZ and close to shelf regions, i.e. those regions where we found the highest secondary production. But unlike production, P/B ratios where highest in the northern most regions under permanent sea ice (i.e. Morris Jesup Rise and Lomonosov Ridge), where low POC fluxes of >1 g C $m^{-2}$ $y^{-1}$ were measured (Fahl & Nöthig 2007). To summarize, although we found a correlation of P/B with temperature, none of the usual drivers of P/B (mean body mass, temperature and food input) could satisfyingly explain the observed regional pattern. This may partially be due to the high degree of inter-correlation between temperature, depth, and food input in the Arctic deep-sea hampering statistical analysis.

### Patterns in feeding structure

Structure and function of benthic communities can be analyzed beyond the assessment of basic community parameters, by dividing organisms in groups with shared behavioral traits or with shared resource bases (Cochrane et al. 2012). Here we analyzed feeding mechanisms, as they are one of the central determinants of marine ecosystem structure (Bremner et al. 2003), and information can be found in literature or be inferred from feeding or mouth structures (S 3). Cusson & Bourget (2005) found highest secondary production for suspension feeders and highest P/B ratios for omnivores and predators. They explain this result by the fact that this feeding guild is dominated by annelids and arthropods with short life span, small body mass and high mobility, all factors assumed to enhance the metabolic rate and as such also P/B ratios. The effect of mobility on P/B ratios is discussed controversially though. On one hand motile species potentially use more energy for respiration than for growth, leading to lower P/B rations. On the other hand mobility enables access to higher quality food, which might lead to higher P/B ratios. This is an important factor especially in the Arctic deep sea, where food falls like carcasses or ice-algae deposits (Boetius et al. 2013b) form an important source of nutrition. However, we found suspension feeders to contribute most to overall production ($F=30.22$; $p<0.0001$), while deposit and suspension feeders displayed higher P/B ratios than interface feeders and predators ($F=2.96$; $p=0.03$). This result might be explained by the fact that highly mobile predators and scavengers are underrepresented in our study, as in the deep sea this group is predominantly represented in the megafauna size class (Gage & Tyler 1991).

Physical dynamics play an important role in determining trophic community structure, with fauna shifting to suspension feeders in hydrographically dynamic areas and deposit feeders in depositional areas (Rosenberg 1995). Accordingly, deep-sea areas with reduced flow and with low amount and low quality food input such as abyssal plains are dominated by deposit feeders, while suspension feeders are abundant in areas with high bottom current flow as on continental slopes or mid-ocean ridges (Gage & Tyler 1991; Thistle 2003). Our findings confirm this general view; deposit feeders contribute most to overall production in the Amundsen Basin (50%), and suspension feeders at the Lomonosov Ridge (55%). However, other regions show a less clear pattern. In the Nansen Basin suspension feeders contributed 64% and deposit feeders only 24% to overall production. Highest production in the Nansen Basin was found at the stations on the lower Barents Sea and Yermak Plateau slope (Fig. 5), presumably benefitting from bottom current flows and food advection from the Barents Sea shelf. Generally, when stations were grouped into three depth zones (upper slope, lower slope, basin), the highest contribution of suspension feeders was found in the group “lower slope” (50%). The region with highest secondary production (Yermak Plateau) shows a more even distribution of feeding types than the low productivity regions (Gakkel Ridge, Amundsen Basin) (Fig. 8). This indicates a complex benthic food web well adapted to handle the high POC input found along the MIZ in the vicinity to the productive continental shelf. Although certain patterns are apparent, the ANOSIM analysis failed to detect significant differences in the relative contribution of different feeding types between regions, depth zones, latitudinal zones and areas of different sea ice concentration. Bremner et al. (2003) could show that the biological trait analysis (BTA) provides more information on the ecological functions of benthic communities than taxonomical or trophic group approaches. Accordingly the BTA might be a more suitable approach here, but our knowledge about behavioral and life history traits of deep-sea taxa is currently still limited.

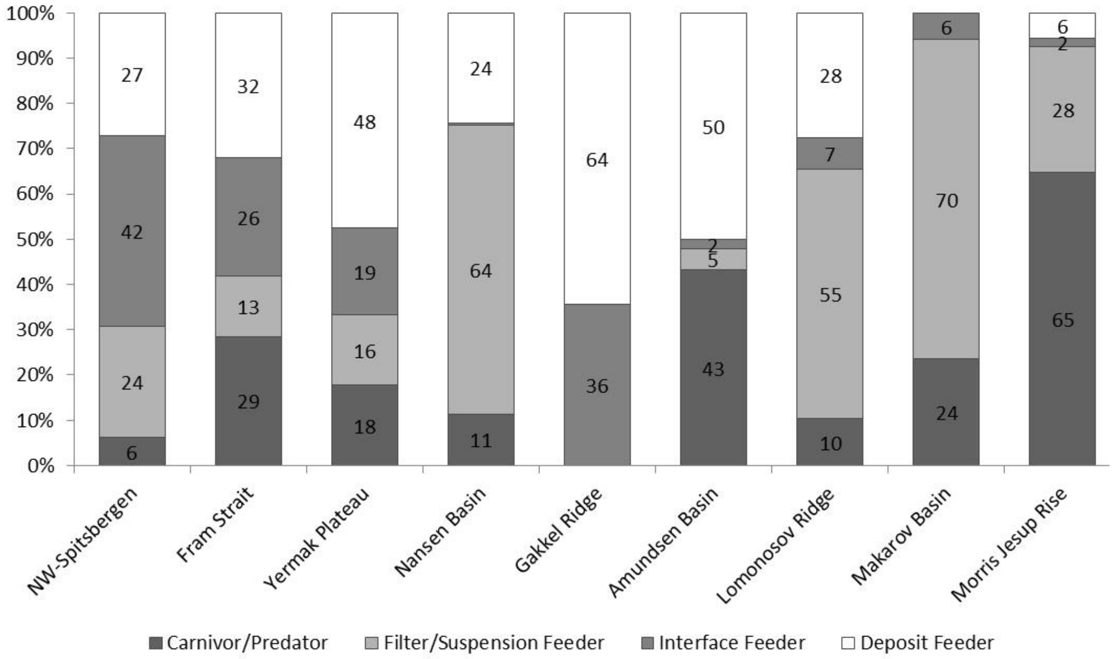

**Fig. 8** Macrofauna feeding types (%) based on production data per region.

## Outlook

This study is a first step in providing baseline data of macrobenthic community parameters in the Arctic deep sea based on a data synthesis covering the years 1990-2012 and different regions of the Arctic deep-sea slopes and basins. A major limitation to assessing changes in the Arctic deep-sea ecosystem status remains the poor spatial and temporal resolution of sampling. In light of the observed climatic changes and the rapid decrease of sea ice volume and cover, it is important to collect more data at higher spatial resolution now. Furthermore, quality control procedures, such as standardized study design (i.e. sample size, sample depth and sieve mesh size) should be implemented. We support the recommendations already stated in previous large scale studies on deep-sea macrozoobenthos (e.g. Bluhm et al. 2011), to apply consistent sampling sizes and to use sieves with 250 µm mesh size as a standard, to account for the small body sizes of deep-sea taxa. We further want to stress the importance of geo-referenced data archives and international efforts to synthesize available data, to improve our understanding of current and future changes in the Arctic Ocean ecosystem.

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## Supplementary Material

**S1** List of stations including coordinates, region, date of sampling and water depth.

| Expedition | Station | Long | Lat | Region | Date | Depht (m) |
|---|---|---|---|---|---|---|
| ARK-VIII/3 | PS2157-7 | 29,99 | 81,75 | Nansen Basin | 06.08.1991 | 2950 |
| ARK-VIII/3 | PS2158-1 | 29,93 | 82,78 | Nansen Basin | 07.08.1991 | 3800 |
| ARK-VIII/3 | PS2159-7 | 30,34 | 83,95 | Nansen Basin | 09.08.1991 | 3950 |
| ARK-VIII/3 | PS2161-5 | 44,30 | 85,44 | Nansen Basin | 11.08.1991 | 4005 |
| ARK-VIII/3 | PS2162-1 | 50,83 | 85,79 | Nansen Basin | 12.08.1991 | 3981 |
| ARK-VIII/3 | PS2163-5 | 59,23 | 86,24 | Gakkel Ridge | 13.08.1991 | 3047 |
| ARK-VIII/3 | PS2164-7 | 59,29 | 86,33 | Gakkel Ridge | 14.08.1991 | 2035 |
| ARK-VIII/3 | PS2165-6 | 60,07 | 86,44 | Gakkel Ridge | 14.08.1991 | 1794 |
| ARK-VIII/3 | PS2166-4 | 59,76 | 86,86 | Gakkel Ridge | 15.08.1991 | 3636 |
| ARK-VIII/3 | PS2167-4 | 59,07 | 86,93 | Gakkel Ridge | 15.08.1991 | 4425 |
| ARK-VIII/3 | PS2168-4 | 55,93 | 87,51 | Amundsen Basin | 17.08.1991 | 3845 |
| ARK-VIII/3 | PS2170-1 | 60,77 | 87,59 | Amundsen Basin | 18.08.1991 | 4226 |
| ARK-VIII/3 | PS2171-1 | 68,98 | 87,59 | Amundsen Basin | 19.08.1991 | 4384 |
| ARK-VIII/3 | PS2172-5 | 68,54 | 87,26 | Amundsen Basin | 20.08.1991 | 4478 |
| ARK-VIII/3 | PS2174-7 | 91,69 | 87,48 | Amundsen Basin | 22.08.1991 | 4427 |
| ARK-VIII/3 | PS2175-6 | 103,68 | 87,58 | Amundsen Basin | 23.08.1991 | 4413 |
| ARK-VIII/3 | PS2176-7 | 108,14 | 87,77 | Amundsen Basin | 25.08.1991 | 4364 |
| ARK-VIII/3 | PS2177-7 | 134,89 | 88,03 | Lomonosov Ridge | 27.08.1991 | 1388 |
| ARK-VIII/3 | PS2178-6 | 159,17 | 88,00 | Makarov Basin | 29.08.1991 | 4009 |
| ARK-VIII/3 | PS2179-4 | 138,09 | 87,74 | Lomonosov Ridge | 30.08.1991 | 1230 |
| ARK-VIII/3 | PS2180-1 | 156,68 | 87,63 | Makarov Basin | 31.08.1991 | 4005 |
| ARK-VIII/3 | PS2181-1 | 153,06 | 87,60 | Lomonosov Ridge | 31.08.1991 | 3112 |
| ARK-VIII/3 | PS2182-6 | 151,35 | 87,57 | Lomonosov Ridge | 01.09.1991 | 2609 |
| ARK-VIII/3 | PS2183-5 | 148,92 | 87,60 | Lomonosov Ridge | 01.09.1991 | 2031 |
| ARK-VIII/3 | PS2184-4 | 148,20 | 87,61 | Lomonosov Ridge | 01.09.1991 | 1654 |
| ARK-VIII/3 | PS2185-3 | 144,17 | 87,53 | Lomonosov Ridge | 02.09.1991 | 1073 |
| ARK-VIII/3 | PS2186-6 | 140,18 | 88,51 | Lomonosov Ridge | 04.09.1991 | 1867 |
| ARK-VIII/3 | PS2187-6 | 126,99 | 88,73 | Lomonosov Ridge | 05.09.1991 | 3844 |
| ARK-VIII/3 | PS2189-6 | 144,67 | 88,77 | Lomonosov Ridge | 06.09.1991 | 1018 |
| ARK-VIII/3 | PS2190-6 | 0,00 | 90,00 | Amundsen Basin | 07.09.1991 | 4273 |
| ARK-VIII/3 | PS2191-4 | 9,01 | 88,99 | Amundsen Basin | 09.09.1991 | 4348 |
| ARK-VIII/3 | PS2192-1 | 9,86 | 88,26 | Amundsen Basin | 10.09.1991 | 4375 |
| ARK-VIII/3 | PS2193-2 | 11,48 | 87,51 | Amundsen Basin | 10.09.1991 | 4399 |

| Expedition | Station | Long | Lat | Region | Date | Depht (m) |
|---|---|---|---|---|---|---|
| ARK-VIII/3 | PS2195-4 | 9,62 | 86,25 | Amundsen Basin | 12.09.1991 | 3793 |
| ARK-VIII/3 | PS2196-2 | 0,17 | 85,96 | Amundsen Basin | 13.09.1991 | 3958 |
| ARK-VIII/3 | PS2198-1 | -9,06 | 85,56 | Morris Jesup Rise | 15.09.1991 | 3820 |
| ARK-VIII/3 | PS2199-5 | -11,91 | 85,43 | Morris Jesup Rise | 15.09.1991 | 1789 |
| ARK-VIII/3 | PS2200-3 | -14,02 | 85,33 | Morris Jesup Rise | 16.09.1991 | 1073 |
| ARK-VIII/3 | PS2201-2 | -12,14 | 85,42 | Morris Jesup Rise | 17.09.1991 | 1353 |
| ARK-VIII/3 | PS2202-11 | -14,37 | 85,11 | Morris Jesup Rise | 18.09.1991 | 1081 |
| ARK-VIII/3 | PS2205-7 | -6,77 | 84,64 | Amundsen Basin | 21.09.1991 | 4283 |
| ARK-VIII/3 | PS2209-3 | 8,57 | 83,23 | Nansen Basin | 26.09.1991 | 4046 |
| ARK-VIII/3 | PS2210-1 | 10,12 | 83,05 | Nansen Basin | 27.09.1991 | 3949 |
| ARK-VIII/3 | PS2212-1 | 15,67 | 82,02 | Yermak Plateau | 29.09.1991 | 2531 |
| ARK-VIII/3 | PS2213-1 | 8,21 | 80,47 | Yermak Plateau | 30.09.1991 | 897 |
| ARK-VIII/3 | PS2214-1 | 6,63 | 80,27 | Yermak Plateau | 01.10.1991 | 552 |
| ARK-XIII/2 | PS2830-6 | 17,49 | 80,98 | Yermak Plateau | 04.07.1997 | 517 |
| ARK-XIII/2 | PS2831-5 | 16,97 | 81,09 | Yermak Plateau | 04.07.1997 | 942 |
| ARK-XIII/2 | PS2832-12 | 16,22 | 81,11 | Yermak Plateau | 05.07.1997 | 2065 |
| ARK-XIII/2 | PS2833-5 | 11,83 | 80,97 | Yermak Plateau | 06.07.1997 | 1964 |
| ARK-XIII/2 | PS2834-6 | 9,82 | 80,92 | Yermak Plateau | 08.07.1997 | 1001 |
| ARK-XIII/2 | PS2835-5 | 7,07 | 81,10 | Yermak Plateau | 10.07.1997 | 847 |
| ARK-XIII/2 | PS2836-6 | 5,65 | 81,13 | Yermak Plateau | 11.07.1997 | 657 |
| ARK-XIII/2 | PS2837-6 | 2,42 | 81,23 | Yermak Plateau | 12.07.1997 | 1028 |
| ARK-XIII/2 | PS2838-9 | 0,44 | 81,29 | Yermak Plateau | 14.07.1997 | 2325 |
| ARK-XIII/2 | PS2839-5 | -0,97 | 81,40 | Fram Strait | 14.07.1997 | 2926 |
| ARK-XIII/2 | PS2840-4 | -5,31 | 81,42 | Fram Strait | 15.07.1997 | 3524 |
| ARK-XIII/2 | PS2843-2 | -7,35 | 81,57 | Fram Strait | 17.07.1997 | 2526 |
| ARK-XIII/2 | PS2847-3 | -4,54 | 81,87 | Fram Strait | 18.07.1997 | 4130 |
| ARK-XIII/2 | PS2849-7 | 1,50 | 82,65 | Nansen Basin | 21.07.1997 | 3247 |
| ARK-XIII/2 | PS2851-2 | 3,62 | 82,38 | Yermak Plateau | 23.07.1997 | 2927 |
| ARK-XIII/2 | PS2853-9 | 3,71 | 82,32 | Yermak Plateau | 24.07.1997 | 2008 |
| ARK-XIII/2 | PS2854-2 | 3,90 | 82,20 | Yermak Plateau | 25.07.1997 | 1805 |
| ARK-XIII/2 | PS2855-7 | 5,29 | 82,05 | Yermak Plateau | 26.07.1997 | 1454 |
| ARK-XIII/2 | PS2859-10 | 10,19 | 81,75 | Yermak Plateau | 29.07.1997 | 1180 |
| ARK-XIII/2 | PS2860-7 | 11,85 | 81,58 | Yermak Plateau | 30.07.1997 | 2032 |
| ARK-XIII/2 | PS2861-11 | 13,05 | 81,27 | Yermak Plateau | 31.07.1997 | 2309 |
| ARK-XIII/2 | PS2868-5 | 3,10 | 79,11 | NW Spitsbergen | 04.08.1997 | 5416 |
| ARK-XXVII/2 | PS80/165-9 | 4,18 | 79,07 | NW Spitsbergen | 16.07.2012 | 2465,5 |
| ARK-XXVII/2 | PS80/174-1 | 4,99 | 78,93 | NW Spitsbergen | 19.07.2012 | 2609,2 |

| Expedition | Station | Long | Lat | Region | Date | Depht (m) |
|---|---|---|---|---|---|---|
| ARK-XXVII/2 | PS80/177-1 | 5,33 | 78,78 | NW Spitsbergen | 20.07.2012 | 2469,5 |
| ARK-XXVII/2 | PS80/185-6 | 4,51 | 79,74 | NW Spitsbergen | 23.07.2012 | 2668 |
| ARK-XXVII/2 | PS80/186-4 | 3,17 | 79,94 | NW Spitsbergen | 24.07.2012 | 2513,1 |
| ARK-XXVII/2 | PS80/188-4 | 5,17 | 79,60 | NW Spitsbergen | 25.07.2012 | 2741,8 |
| ARK-XXVII/2 | PS80/191-3 | 4,69 | 79,41 | NW Spitsbergen | 26.07.2012 | 2505,7 |
| ARK-XXVII/2 | PS80/194-3 | 4,33 | 79,28 | NW Spitsbergen | 26.07.2012 | 2363,5 |
| ARK-XXVII/2 | PS80/195-3 | 4,10 | 79,08 | NW Spitsbergen | 27.07.2012 | 2458,3 |
| ARK-XXVII/2 | PS80/197-1 | 5,00 | 78,92 | NW Spitsbergen | 27.07.2012 | 2594,4 |
| ARK-XXVII/3_BL | PS80/0236 | 78,67 | 83,92 | Nansen Basin | 14.08.2012 | 3462,8 |
| ARK-XXVII/3_BL | PS80/0251-3 | 108,87 | 82,64 | Nansen Basin | 19.08.2012 | 3560,7 |
| ARK-XXVII/3_BL | PS80/0334 | 123,18 | 85,16 | Amundsen Basin | 07.09.2012 | 4354 |
| ARK-XXVII/3_BL | PS80/0371-1 | 55,67 | 88,76 | Amundsen Basin | 23.09.2012 | 4369,1 |
| ARK-XXVII/3_BL | PS80/221 | 29,92 | 84,00 | Nansen Basin | 08.08.2012 | 4014,2 |
| ARK-XXVII/3_MG | PS80/229 | 31,32 | 84,00 | Nansen Basin | 10.08.2012 | 4008,3 |
| ARK-XXVII/3_MG | PS80/241 | 76,71 | 83,93 | Nansen Basin | 15.08.2012 | 3431,8 |
| ARK-XXVII/3_MG | PS80/262 | 109,92 | 82,98 | Nansen Basin | 21.08.2012 | 3601,4 |
| ARK-XXVII/3_MG | PS80/278 | 129,95 | 82,88 | Amundsen Basin | 25.08.2012 | 4166,9 |
| ARK-XXVII/3_MG | PS80/339 | 122,74 | 85,06 | Amundsen Basin | 08.09.2012 | 4351,8 |
| ARK-XXVII/3_MG | PS80/355 | 61,01 | 87,93 | Amundsen Basin | 19.09.2012 | 4380,7 |
| ARK-XXVII/3_MG | PS80/368 | 17,72 | 84,36 | Nansen Basin | 23.09.2012 | 4023,5 |

**S2** Mean macrobenthic abundance, biomass and production per m$^2$ and region per major taxonomic group Annelida (1), Arthropoda (2), Bryozoa (3), Cephalorhyncha (4), Chordata (5), Cnidaria (6), Echinodermata (7), Entoprocta (8). Mollusca (9), Nematoda (10), Nemertea (11), Porifera (12) and Sipuncula (13).

| | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abundance (Ind. m$^{-2}$) | | | | | | | | | | | | | |
| NW Spitzbergen | 374 | 6 | 0 | 0 | 0 | 2 | 0 | 0 | 119 | 7 | 12 | 26 | 6 |
| Fram Strait | 176 | 81 | 0 | 0 | 0 | 11 | 4 | 0 | 11 | 22 | 0 | 22 | 0 |
| Yermak Plateau | 529 | 197 | 10 | 1 | 0 | 15 | 17 | <1 | 120 | 60 | 6 | 55 | 41 |
| Nansen Basin | 59 | 15 | <1 | 0 | 7 | 5 | 6 | 0 | 0 | 2 | <1 | 15 | 0 |
| Gakkel Ridge | 5 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Amundsen Basin | 34 | 16 | 2 | 0 | 0 | 2 | 3 | 0 | 4 | 0 | 0 | <1 | 0 |
| Lomonosov Ridge | 43 | 40 | 0 | 0 | 0 | 28 | 3 | 0 | 20 | 13 | 0 | 55 | 3 |
| Makarov Basin | 25 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 |
| Morris Jesup Rise | 100 | 20 | 0 | 0 | 0 | 10 | 0 | 0 | 20 | 10 | 10 | 220 | 20 |
| Biomass (mg C m$^{-2}$) | | | | | | | | | | | | | |
| NW Spitzbergen | 45 | <1 | 0 | 0 | 0 | <1 | 0 | 0 | 2 | <1 | 1 | 11 | 1 |
| Fram Strait | 5 | 17 | 0 | 0 | 0 | 2 | 2 | 0 | <1 | <1 | 0 | 22 | 0 |
| Yermak Plateau | 213 | 58 | 9 | <1 | 0 | 15 | 50 | <1 | 15 | 25 | <1 | 18 | 5 |
| Nansen Basin | 33 | 4 | <1 | 0 | <1 | 6 | 211 | 0 | 0 | 0 | <1 | 66 | 0 |
| Gakkel Ridge | <1 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Amundsen Basin | 11 | 23 | 2 | 0 | 0 | 3 | <1 | 0 | <1 | 0 | 0 | 0 | 0 |
| Lomonosov Ridge | 16 | 5 | 0 | 0 | 0 | <1 | <1 | 0 | 19 | 3 | 0 | 21 | <1 |
| Makarov Basin | 5 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 0 |
| Morris Jesup Rise | 42 | <1 | 0 | 0 | 0 | <1 | 0 | 0 | <1 | <1 | <1 | 5 | <1 |
| Production (mg C m$^{-2}$ y$^{-1}$) | | | | | | | | | | | | | |
| NW Spitzbergen | 52 | <1 | 0 | 0 | 0 | <1 | 0 | 0 | 2 | <1 | 1 | 14 | 1 |
| Fram Strait | 8 | 18 | 0 | 0 | 0 | 1 | 1 | 0 | <1 | <1 | 0 | 9 | 0 |
| Yermak Plateau | 247 | 54 | 4 | <1 | 0 | 6 | 23 | <1 | 10 | 21 | <1 | 11 | 7 |
| Nansen Basin | 33 | 4 | <1 | 0 | <1 | 2 | 31 | 0 | 0 | 0 | <1 | 68 | 0 |
| Gakkel Ridge | 1 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Amundsen Basin | 13 | 10 | <1 | 0 | 0 | 1 | <1 | 0 | <1 | 0 | 0 | <1 | 0 |
| Lomonosov Ridge | 18 | 7 | 0 | 0 | 0 | <1 | <1 | 0 | 9 | 3 | 0 | 35 | <1 |
| Makarov Basin | 4 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 | 0 |
| Morris Jesup Rise | 30 | 1 | 0 | 0 | 0 | <1 | 0 | 0 | <1 | <1 | <1 | 12 | <1 |

**S3** Literature and web sources used in research for taxonomic and functional trait information. Since online platforms were repeatedly visited during a longer time period in 2013 no accessed date is included in the reference.

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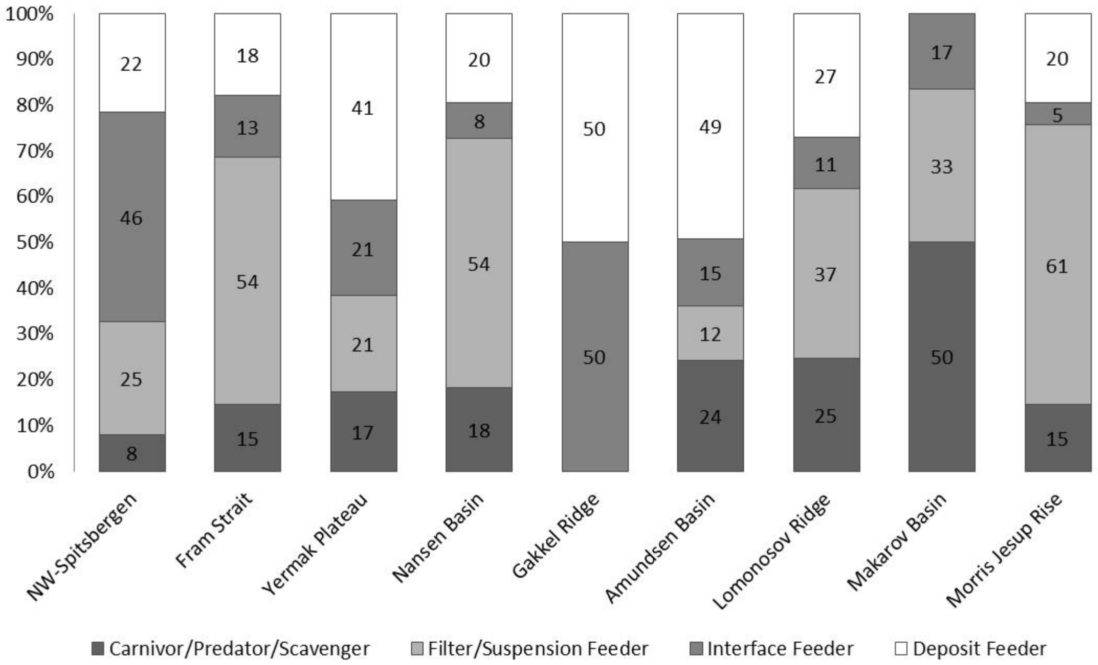
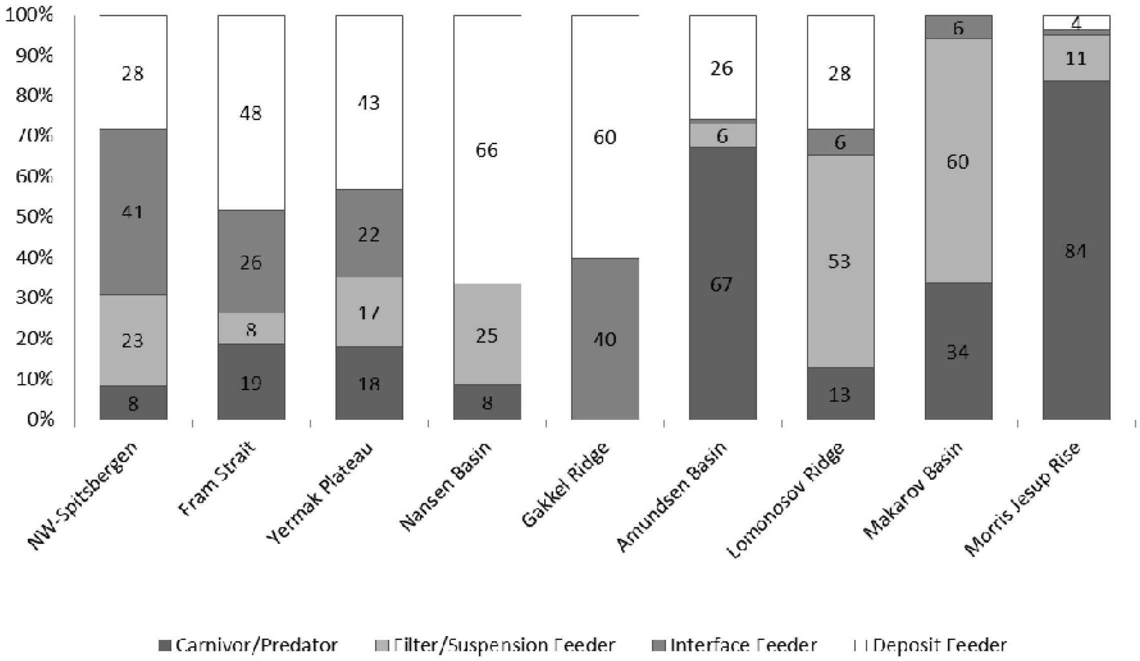
**S 4** Macrofauna feeding types (%) based on abundance data.



**S5** Macrofauna feeding types (%) based on biomass data.



# Manuscript III

## Changes in Functioning of Arctic Macrozoobenthos

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Manuscript in preparation.

## Abstract

The shift towards a seasonally ice-free Arctic Ocean raises questions related to the future of productivity and functioning of Arctic ecosystems. We use biological trait analysis (BTA) to study macrobenthic functions and responses based on two datasets from 1991 and 2012, ranging from the northern Barents Sea shelf down to the deep Amundsen Basin. Life history, morphological and behavioral characteristics (= traits) were weighed with secondary production (mg C $m^{-2}$ $y^{-1}$) and used to indicate ecological functioning. The composition of relevant traits in terms of secondary production and the functional diversity were compared between regions and between the years 1991 and 2012. Our results showed that the traits living habit, bioturbation, body form and morphology contribute most to differences among regions and that there was a substantial change in trait composition and secondary production between 1991 and 2012. We conclude that food input is the main structuring force in benthic communities. The shift of the marginal ice zone (MIZ) and the corresponding modification of export processed are likely causes of the observed changes in benthic ecosystem functioning.

### Keywords

BTA, traits, secondary production, FCA, functional diversity, climate change

## Introduction

The ongoing retreat of Arctic sea ice and the prospect of a seasonally ice-free Arctic Ocean by the year 2040 (Polyakov et al. 2010) fuels speculations about future productivity and functioning of the whole Arctic ecosystem. Benthic communities mirror long term changes of pelagic production in their own dynamics; accordingly we can use them as bioindicators of pelagic change (Pearson & Rosenberg 1978). Knowledge on the structural variability of Arctic benthos is rather limited (Bluhm et al. 2011 and references therein, Degen et al. in press), but information on functional variability is lacking almost completely so far (Bolam et al. 2014). Functional characteristics or ‘traits’ include the interactions of organisms with each other and with their physical and chemical environments. Their distribution may be directly related to the mechanisms structuring the ecosystem. Consequently, a change in the trait composition of a community mirrors changes in the structure of the respective ecosystem (Bremner et al. 2006).

Biological trait analysis (BTA) uses a series of life history, morphological and behavioral characteristics of species present in assemblages to indicate ecological functioning (Statzner et al. 1994, Bremner et al. 2006). As the method is based on characteristics shared by different taxa and not by taxonomy, it is a valuable tool for measuring ecosystem structure independent of biogeographical location. Integral part of the BTA is the estimation of the functional diversity (FD), i.e. the diversity of species traits in an ecosystem. This index – an analog to taxonomic diversity indices – considers also the functional redundancy, an important property of ecosystem stability (Díaz and Cabido 2001; Petchey and Gaston 2006; van der Linden 2012). Originating in freshwater science, the BTA has been successfully applied in various marine systems, especially due to the cutting-edge work of Julie Bremner (see Bremner et al. 2003, 2006). The approach was applied to detect differences in ecosystem functioning between regions (Bremner et al. 2006; Bolam et al. 2014), along environmental gradients (van der Linden 2012; Darr et al. 2014; Törnroos et al. in press) and to assess effects of pollution, fishing or climate change (Bremner et al 2003; Tillin et al 2006; Neumann and Kröncke 2010) on marine benthic communities. Previous studies used either abundance or biomass data for weighing functional traits, but no study so far used secondary production weighted traits. Study areas range from very shallow estuaries (van der Linden et al. 2012) over costal waters (Darr et al. 2014) to entire shelf sees (Bolam et al. 2014), but so far the BTA was never applied on benthic communities in water depths below 500 m or in Arctic regions beyond 75° N.

Here we use the BTA for the first time to study benthic ecosystem functioning in the Eurasian part of the Arctic Ocean and along a gradient of increasing depth and latitude. As biological trait composition was shown to be stable over regional and continental scales (Bremner et al. 2006) we use the same set of 11 traits along a transect from the shallow Barents Sea shelf down to the deep Amundsen Basin. We regard secondary production the most important benthic function; accordingly the analysis is based on secondary production weighted traits. We use fuzzy correspondence analysis (FCA) to explore differences between regions and stations and to identify the traits that contribute most to the differences in functioning between the regions. We further estimate functional diversity (FD) by calculating the Rao's quadratic entropy (RQE). RQE is the most common multivariate index in BTA as it considers functional richness, functional evenness and functional divergence (van der Linden et al. 2012).

In brief our aim is to (1) compare the production weighted trait composition and the functional diversity of Arctic shelf, ridge and deep-sea basin communities, and (2) compare the trait composition and functional diversity between Nansen and Amundsen Basin sampled in 1991 and 2012.

## Methods

### Study area

The study area ranges from the seasonally ice-covered northern Barents Sea shelf around 80° N up to the permanently ice-covered central Arctic Ocean around 90° N and spans across the entire Eurasian Basin from 7° E to 70° E (Fig. 1). The Barents Sea is among the most productive subarctic shelves, with reported values of mean primary production of ±80 g C $m^{-2}$ $y^{-1}$ (Wassmann et al. 2006). Water depth in the sampled region ranges from 80-260 m. Primary production in the central Arctic was reported to be significantly lower at 1-25 g C $m^{-2}$ $y^{-1}$

(Wassmann et al. 2010). The depth range sampled is 3000-4000 m in the Nansen Basin, 3800-4400 m in the Amundsen Basin and 1000-3800 m on the Lomonosov Ridge.

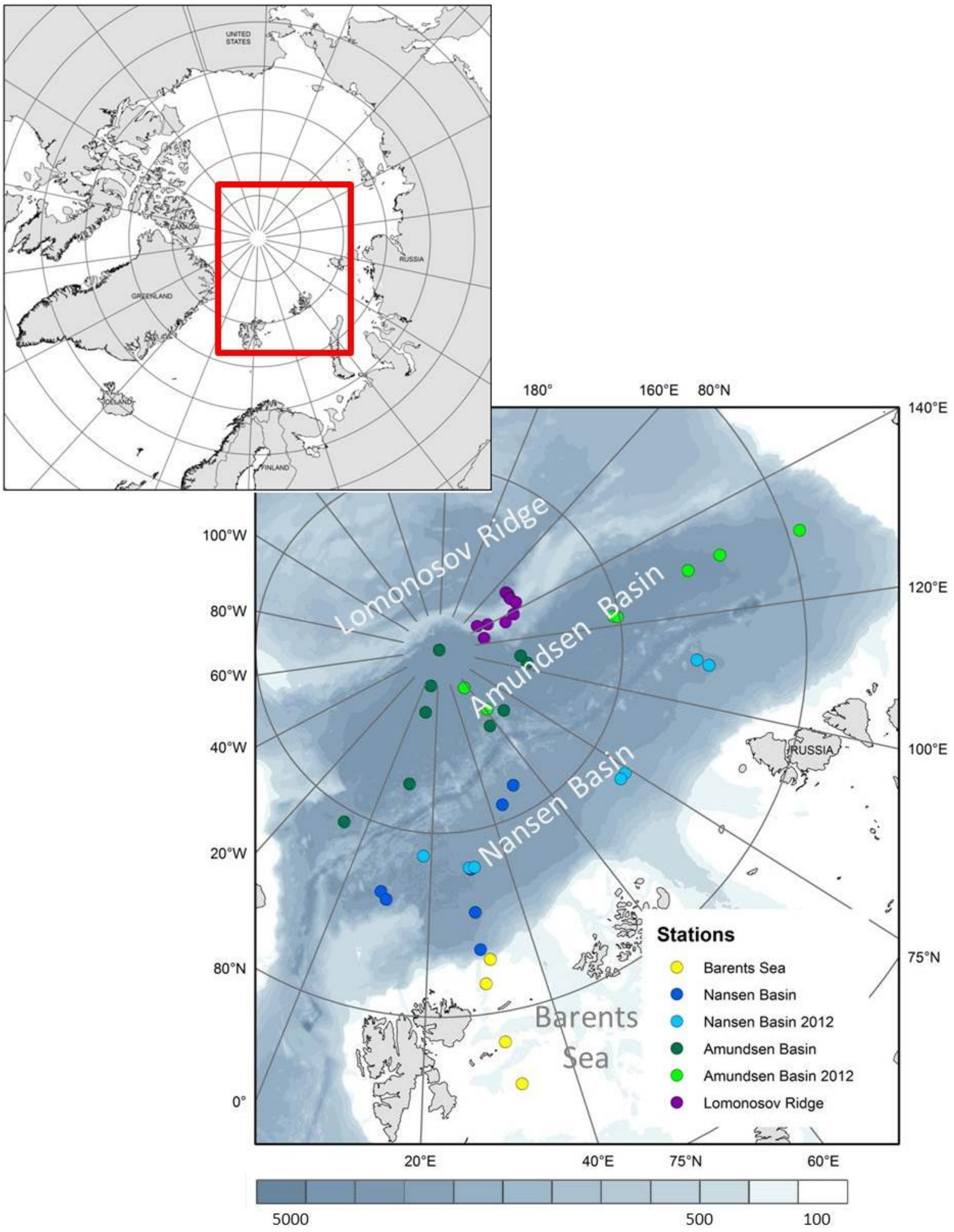

**Fig. 1** Study area and sampling stations.

## Dataset

In 1991 samples were taken with a giant box corer of 0.25 $m^2$ surface area during the RV POLARSTERN cruises ARK-VIII/2 (Rachor & Hempel 1992) and ARK-VIII/3 (Fütterer 1992). Barents Sea data (four stations) were published by Kendall (1996), data from Nansen Basin, Amundsen Basin and Lomonosov Ridge (7, 9 and 10 stations) by Kröncke (1994, 1998) (table 1). The 14 samples from the cruise ARK-XXVII/3 (2012, Boetius et al. 2013) were taken with a multigrab (9 x 0.024 $m^2$) and with benthic chambers of a Bottom Lander system (3 x 0.04 $m^2$) and published in Degen et al. (in press).

**Table 1** Study area: Region, mean coordinates, mean water depth, number of stations and Expedition. For detailed station information see supplementary material (S1).

| Region | Longitude °W (decimal) | Latitude °N (decimal) | Depth (m) | Stations | Expedition |
|---|---|---|---|---|---|
| Barents Sea | 31.55 | 79.86 | 167 | 4 | ARK-VIII/2 |
| Nansen Basin | 29.16 | 83.71 | 3812 | 7 | ARK-VIII/3 |
| Amundsen Basin | 39.83 | 87.62 | 4231 | 9 | ARK-VIII/3 |
| Lomonosov Ridge | 143.05 | 87.97 | 1983 | 10 | ARK-VIII/3 |
| Nansen Basin 2012 | 64.73 | 83.69 | 3729 | 7 | ARK-XXVII/3 |
| Amundsen Basin 2012 | 107.72 | 84.48 | 4152 | 7 | ARK-XXVII/3 |

## Benthic secondary production

Macrobenthic secondary production (mg C $m^{-2}$ $y^{-1}$) on the Barents Sea shelf was estimated with an empirical ANN model (Brey 2012). Production data from Nansen Basin, Amundsen Basin and Lomonosov Ridge were previously estimated and published in Degen et al. (in press). For detailed explanation of the model see Brey (2012), for the application with Arctic macrobenthos see Degen et al. (in press). We used ANOVA to test on differences in secondary production between regions and between 1991 and 2012.

## The biological trait approach (BTA)

### Functional traits

We considered 11 different traits for our study that relate to life history (adult size, larval development), morphology (body form, morphology) and behavior (habitat, living habit, mobility, movement, feeding habit, alimentation, bioturbation) (table 2). The 11 traits were divided into 39 subcategories or trait modalities that display the organism's strategy more in detail. If not specified otherwise, all modalities relate to adult stages. Trait information was gathered via literature and various internet sites and databases. A detailed list of sources is provided in the supplement (S2). Table 2 displays the traits in detail.

**Table 2** Functional traits, trait modalities and abbreviations used in this study.

| Trait | Abbreviation | Modality |
|---|---|---|
| Life history | | |
| *Size* | S 1 | < 5 mm |
| | S 2 | 5 - 20 mm |
| | S 3 | > 20 mm |
| *Larval Development* | LD1 | benthic |
| | LD2 | pelagic |
| Morphology | | |
| *Body Form* | BF1 | flat |
| | BF2 | mound |
| | BF3 | erect |
| *Morphology* | Mor1 | soft |
| | Mor2 | tunic |
| | Mor3 | exoskeleton |
| | Mor4 | crustose |
| | Mor5 | cushion |
| | Mor6 | stalked |
| Behavior | | |
| *Habitat* | H 1 | infauna |
| | H 2 | epifauna |
| *Living Habit* | LH1 | attached |
| | LH2 | tube dweller |
| | LH3 | burrow (channel) dweller |
| | LH4 | motile tube/case |
| | LH5 | free |
| *Mobility* | Mob1 | sessile |
| | Mob2 | semi-motile |
| | Mob3 | motile |
| *Movement* | Mov1 | no movement |
| | Mov2 | burrower |
| | Mov3 | crawler |
| | Mov4 | facultative swimmer |
| *Feeding Habit* | FH1 | suspension Feeder |
| | FH2 | deposit Feeder |
| | FH3 | grazer |
| | FH4 | scavenger |
| | FH5 | predator |
| *Alimentation Type* | AT1 | omnivor |
| | AT2 | carnivor |

| | | |
|---|---|---|
| *Bioturbation* | BT1 | surface mixing |
| | BT2 | deeper mixing |
| | BT3 | transport |
| | BT4 | none |

## Matrices & Fuzzy coding

The biological trait approach as used here requires three different numerical matrices: (1) the secondary production of each taxon per station (matrix 'taxa by stations'), the biological traits of the taxa (matrix 'taxa by traits'), and a combination of the previous two, the production weighted biological traits per station (matrix 'traits per station') (Bremner et al. 2003, van der Linden et al. 2012). The 'taxa by traits' matrix is designed following the 'fuzzy coding' approach (Chevenet et al. 1994). Herewith, each trait modality is valued 0, 1, 2, or 3 in each taxon, with 0 indicating no affinity and 3 indicating highest affinity. Where trait information was not available for a taxon, the mean trait profile of all other taxa at that station was given, so the respective taxon could not distort the result in any direction (Statzner and Beche 2010). The fuzzy coded 'taxa by trait' matrix is included in the appendix. The 'traits by station' matrix is constructed by multiplying the trait modality values of every taxon ('taxa by traits' matrix) with the secondary production of the respective taxon at this station ('taxon by stations' matrix).

## Fuzzy Correspondence Analysis (FCA)

The fuzzy correspondence analysis (FCA) is a form of correspondence analysis (CA) appropriate for fuzzy coded biological trait data (Chevenet et al. 1994, Theodorou et al. 2007). FCA will identify the traits most relevant for the observed differences between regions (or times) and is performed on a contingency table of the 'traits by stations' matrix. Like a classical CA the FCA creates orthogonal components (FCA plot) and a set of scores for each item in the table. The eigenvalues are indicating the total variance on each axis, and can be used to select the number of axes that describe the structure of the data best and should be studied in detail (Chevenet et al. 1994). The correlation ratios tell us how much of the variance of a certain trait are explained by a given axis and can be used to order the relevance of traits for the various axes (Chevenet et al. 1994). We performed FCA (a) on pooled station data per region (Barents Sea, Nansen Basin, Amundsen Basin, Lomonosov Ridge, Nansen Basin 2012 and Amundsen Basin 2012) and (b) on all 44 stations.

### Functional Diversity Index (FDI)

Rao's quadratic entropy index (RQE) was used to estimate the functional diversity FD (RAO 1982; Champely and Chessel 2002), i.e. the diversity of species traits in the different Arctic regions. The RQE index is most commonly used to calculate FD as it takes functional richness, functional evenness and functional divergence into account (van der Linden et al. 2014). This approach requires two tables as input; here it is performed on the ‘taxa by traits’ matrix and the “taxa by stations” matrix. We used ANOVA to test for differences in RQE between regions.

### Used Software

For all analysis R-2.12.2 open-source software (R Development Core Team, 2011), with ‘ade4’ (version 1.4-17; Chessel et al. 2004) was used. The ‘ade4’ package can be downloaded via http://cran.r-project.org/web/packages/ade4/ade4.pdf.

## Results

### Number of taxa & traits

The overall number of trait modalities in this study was 39; the overall number of taxa occurring was 188. Highest numbers of species per station occurred in the Barents Sea shelf where altogether 130 taxa expressed 38 functional trait modalities. The trait modality Mor6 (“stalked”) did not occur in the Barents Sea samples (see table 2 for all following abbreviations). The samples from Nansen and Amundsen Basin included 14 and 12 taxa that expressed 36 trait modalities. The trait modalities LH4 (“motile tube/case”) and FH3 (“grazer”) did not occur in the basins. The samples from Lomonosov Ridge contained 27 taxa that expressed 37 functional trait modalities. At Lomonosov Ridge the traits Mor4 (“crustose”), Mor5 (“cushion”) and LH4 (“motile tube/case”) did not occur. The species numbers from the 2012 samples increased compared to the 1991 samples in Nansen Basin to 16 and in Amundsen Basin to 32, while the type and number of expressed traits (36) stayed the same (Table 3).

Table 3 Number of taxa and functional traits per region and mean secondary production (mg C m-2 y-1)

| Region | Number Taxa | Number of Trait modalities | Production (mg C $m^{-2}$ $y^{-1}$) |
|---|---|---|---|
| Barents Sea | 130 | 38 | 3834.27 |
| Nansen Basin | 14 | 36 | 279.57 |
| Amundsen Basin | 12 | 36 | 9.41 |
| Lomonosov Ridge | 27 | 37 | 73.45 |
| Nansen Basin 2012 | 16 | 36 | 16.22 |
| Amundsen Basin 2012 | 32 | 36 | 91.94 |

### Secondary production

Secondary production decreased significantly from the Barents Sea shelf (> 6 g C $m^{-2}$ $y^{-1}$) towards the deep-sea basins (<2 mg C $m^{-2}$ $y^{-1}$; F=5.95, p<0.0001) (Fig. 2) (see S1 for exact results per station). Secondary production was significantly higher in the Barents Sea and significantly lower in the Amundsen Basin compared to the Nansen Basin and at the Lomonosov Ridge (post hoc test). Secondary production in Nansen Basin did not differ between 1991 and 2012 (F=2.6647, p=0.1285), while in Amundsen Basin production was significantly higher in 2012 than in 1991 (F=7.0802; 0.0058).

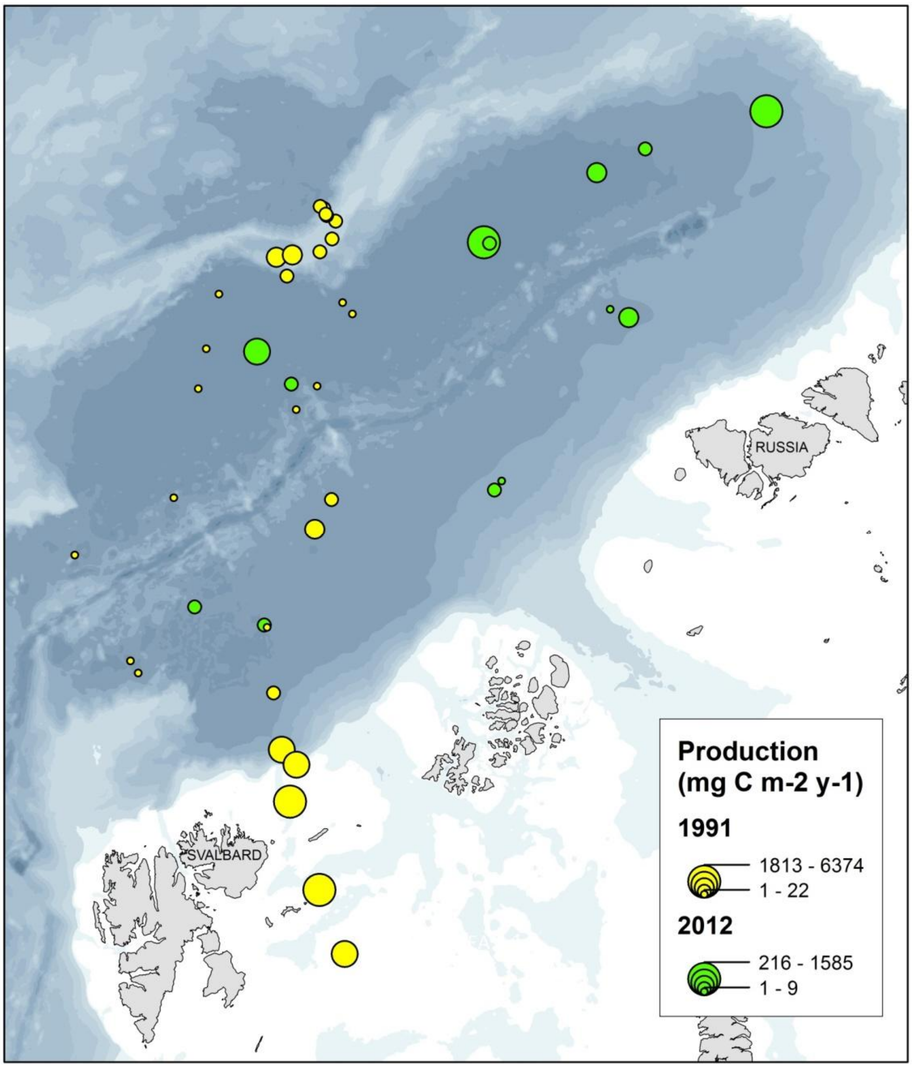

**Fig. 2** Patterns of secondary production (mg C $m^{-2}$ $y^{-1}$) in 1991 (yellow) and 2012 (green) (note the different scale range between 1991 and 2012).

## Comparison of relative trait composition per region

Except for the region Amundsen Basin that shows a higher contribution of the smallest size classes (<5 mm), there is no obvious difference in the relative contribution of modalities of the life history trait *Size* among regions and between Nansen and Amundsen Basin from 1991 and 2012. The trait *Larval Development* at Nansen Basin is clearly dominated by the modality LD2 (“pelagic”), otherwise the modalities are evenly distributed. Regarding *Morphology*, Nansen and Amundsen Basin (1991) showed a higher relative contribution of the trait modality Mor5 (“cushion”). Lomonosov Ridge and Nansen Basin 2012 showed a higher contribution of the trait modalities BF3 (“erect”) and Mor6 (“stalked”). In Amundsen Basin 2012 the trait modalities BF1 ("flat") and Mor1 ("soft") dominate compared to Amundsen Basin 1991. Regarding behavioral traits the relative contribution of the modalities of the trait *Habitat* (infauna or epifauna) are quite evenly distributed, with a higher contribution of H1 ("infauna") in the Barents Sea and in the Amundsen Basin 2012. The trait modality LH1 ("attached") is underrepresented in these regions. The highest relative contribution of the trait modality "sessile" (Mob1) and "no movement" (Mov1) is found in Nansen Basin in 2012. The *Movement* modality "facultative swimmer" (Mov4) is found to contribute more only in Amundsen Basin 2012. Regarding the trait *Feeding Habit* (FH) the modality FH1 ("suspension feeder") contributes more in Nansen Basin, Lomonosov Ridge and Nansen Basin 2012 to the overall distribution. In Nansen Basin 2012 the trait modalities FH1 ("suspension feeder") and FH2 ("deposit feeder") clearly dominate, while in the other regions modalities are more evenly distributed. Generally the trait modality AT1 ("omnivore") contributes more than the modality AT2 ("carnivore"). Regarding the trait *Bioturbation*, BT4 ("no bioturbation") is dominant in Nansen Basin, Lomonosov Ridge and Nansen Basin 2012. BT1 ("surface mixing") is dominant on the Barents Sea shelf and in Amundsen Basin, in Amundsen Basin 2012 the trait modality "transport" is dominating.

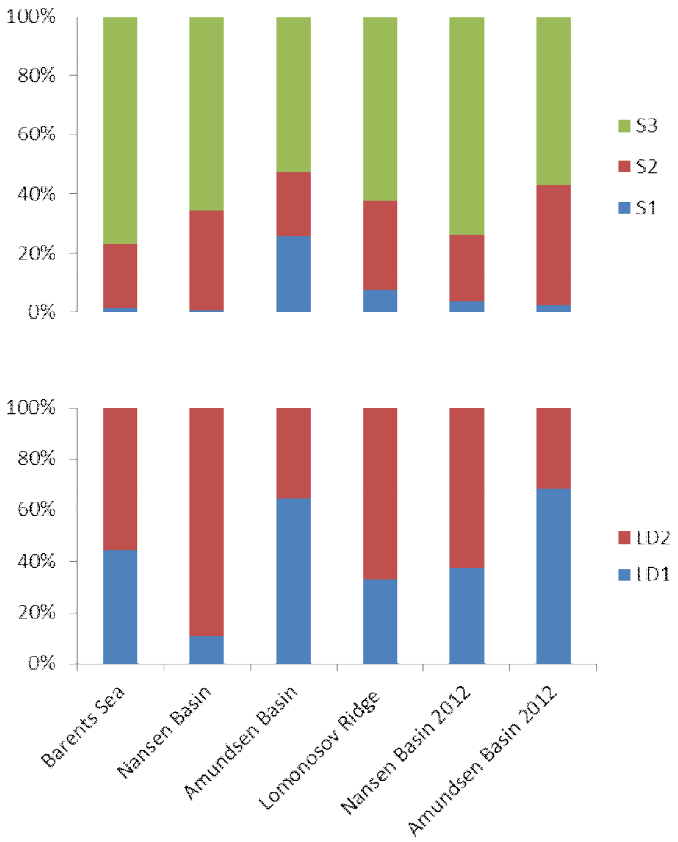

**Fig. 3** Relative contribution of life history trait modalities *Size* (<5mm, 5-20mm, >20mm) and *Larval Development* (benthic, pelagic) between the different regions (for number code see table 2).

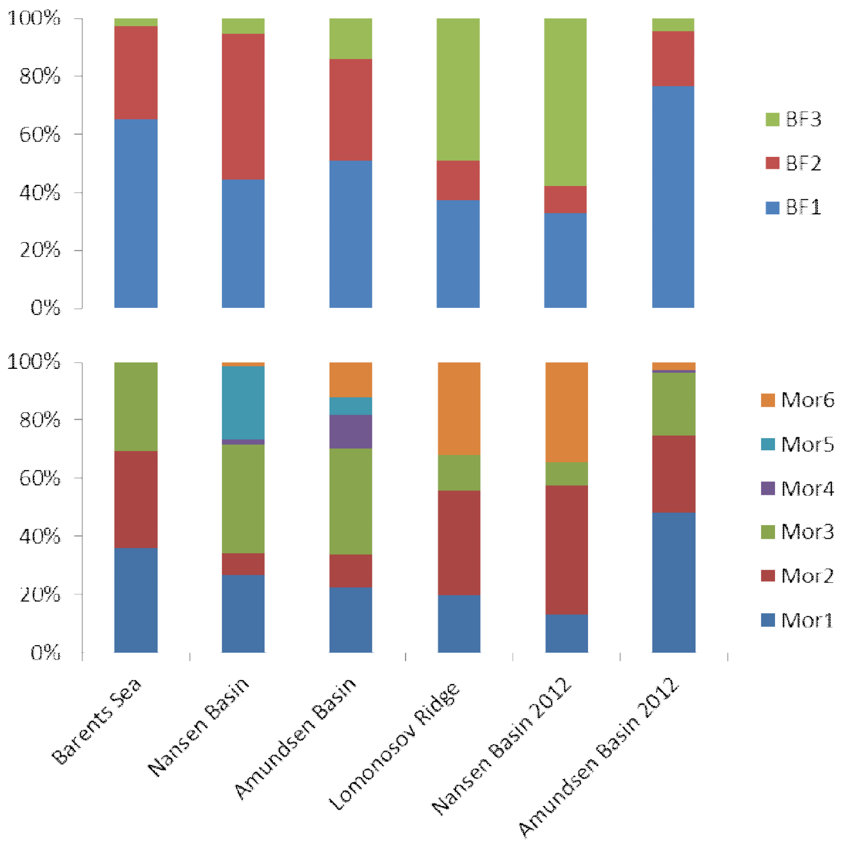

**Fig. 4** Relative contribution of morphological trait modalities Body Form (flat, mound, erect) and *Morphology* (soft, tunic, exoskeleton, crustose, cushion, stalked) (for detailed trait information see table 2).

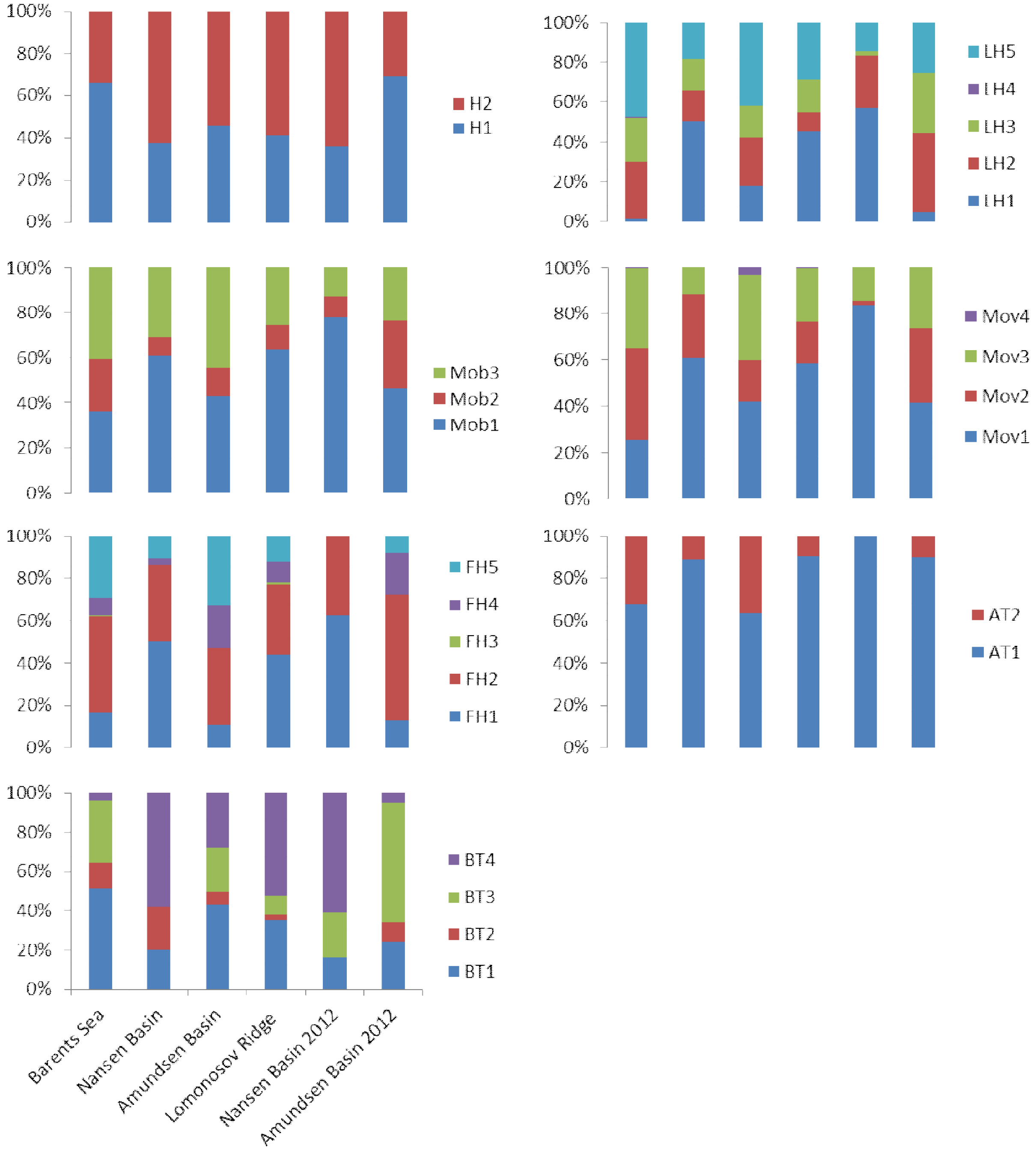

**Fig. 5** Relative contribution of behavioral trait modalities *Habitat* (infauna, epifauna), *Living Habit* (attached, tube dweller, burrow/channel dweller, motile tube/case, free), *Mobility* (sessile, semi motile, motile), *Movement* (no movement, borrower, crawler, facultative swimmer). *Feeding Habit* (suspension feeder, deposit feeder, grazer, scavenger, predator), *Alimentation Type* (herbivor, omnivore, carnivore) and *Bioturbation* (surface mixing, deeper mixing, transport, none) (for detailed trait information see table 2).

## Fuzzy correspondence analysis (FCA)

### Regions

FCA explained 26% of total variability in the regional comparison (six regions). Thereof 50% were explained by axis 1, 35% by axis 2 and 11% by axis 3. The correlation ratio reflects the contribution of each trait to the overall variability (table 4). Traits contributing most to the variation along axis 1 were *Body Form*, *Morpholog*y and *Bioturbation*, traits contributing most to the variation along axis 2 were *Bioturbation*, *Living Habit* and *Larval Development*. Fig. 6 shows the distribution of the trait categories (a) and the corresponding position of regions (b).

**Table 4** The amount of variability in the production-weighted trait data explained by the first three FCA plot axes and the correlation ratios of traits along these axes in the regional comparison.

| Traits | Ax1 (50%) | Ax2 (35%) | Ax3 (11%) |
|---|---|---|---|
| *Size* | 3 | 1 | 9 |
| *Larval development* | 0 | 15 | 0 |
| *Body form* | 34 | 13 | 1 |
| *Morphology* | 33 | 13 | 10 |
| *Habitat* | 7 | 0 | 2 |
| *Living habit* | 19 | 20 | 2 |
| *Mobility* | 13 | 6 | 2 |
| *Movement* | 20 | 2 | 3 |
| *Feeding habit* | 14 | 8 | 6 |
| *Alimentation* | 3 | 3 | 6 |
| *Bioturbation* | 24 | 23 | 5 |

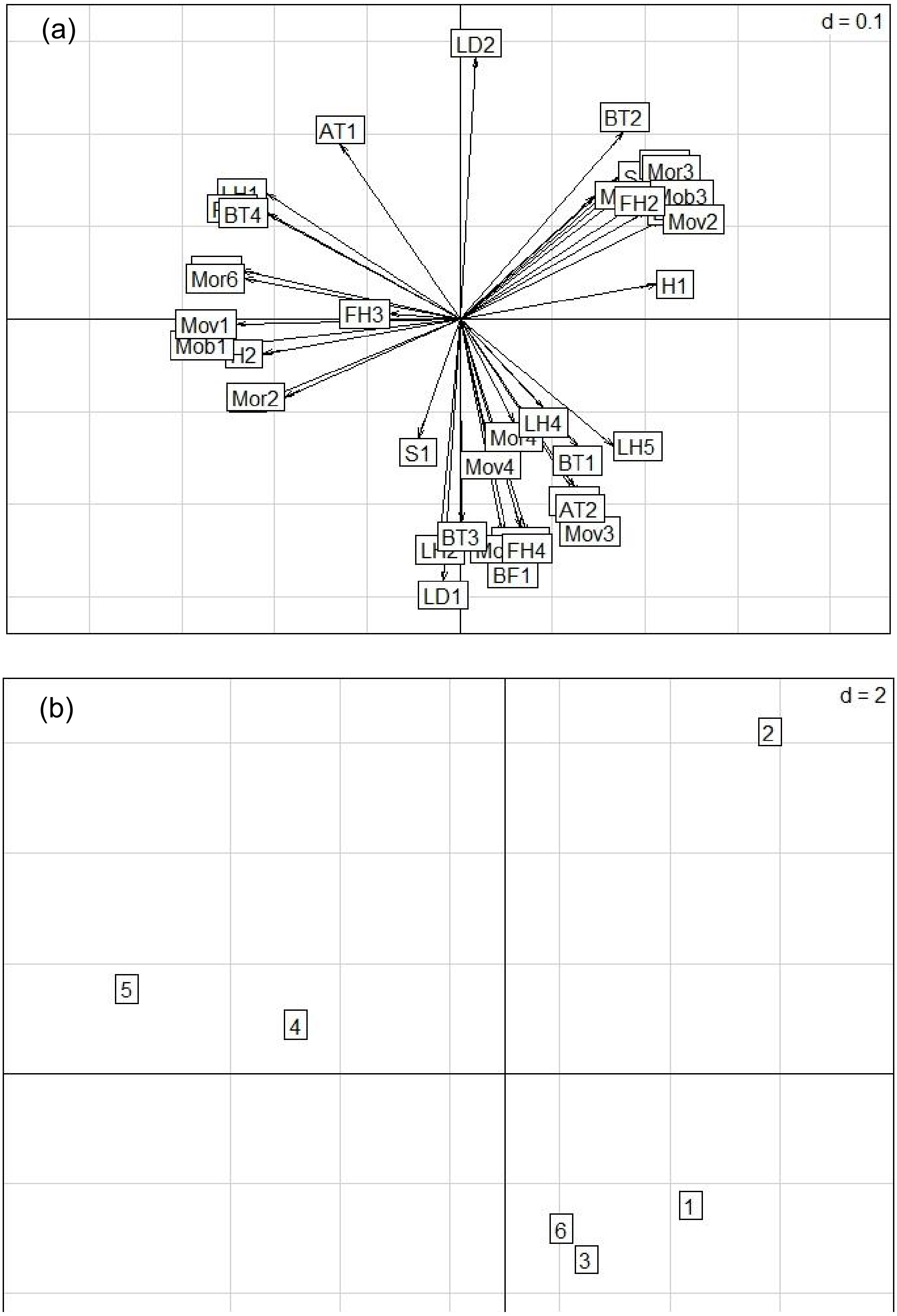

**Fig. 6** FCA plots showing the distribution of trait modalities (a) and regions (b) along the first two axes (1-Barents Sea, 2-Nansen Basin, 3-Amundsen Basin, 4-Lomonosov Ridge, 5-Nansen Basin 2012, 6-Amundsen Basin 2012) (for trait modality code see table 2).

## Stations

FCA explained 80% of total variability in the comparison of stations (44 stations). Thereof 40% were explained by axis 1, 20% by axis 2 and 17% by axis 3. Correlation ratios can be found in table 5. Traits contributing most to the variation along axis 1 were *Living Habit*, *Bioturbation*, *Body Form* and *Morphology*; traits contributing most to the variation along axis 2 were *Living Habit*, *Morphology* and *Bioturbation*. Along axis 3 *Larval Development*, *Morphology* and *Movement* contribute most to overall variation (table 5). Fig. 7 shows the distribution of the trait categories (a) and regions (b).

**Table 5** The amount of variability in the production-weighted trait data explained by the first three FCA plot axes and the correlation ratios of traits along these axes in the comparison of stations.

| Traits | Ax1 (40%) | Ax2 (20%) | Ax3 (17%) |
|---|---|---|---|
| *Size* | 2 | 17 | 13 |
| *Larval development* | 9 | 2 | 30 |
| *Body form* | 41 | 20 | 3 |
| *Morphology* | 40 | 31 | 20 |
| *Habitat* | 21 | 15 | 1 |
| *Living habit* | 57 | 37 | 14 |
| *Mobility* | 34 | 18 | 1 |
| *Movement* | 36 | 12 | 20 |
| *Feeding habit* | 32 | 11 | 5 |
| *Alimentation* | 2 | 5 | 4 |
| *Bioturbation* | 57 | 30 | 14 |

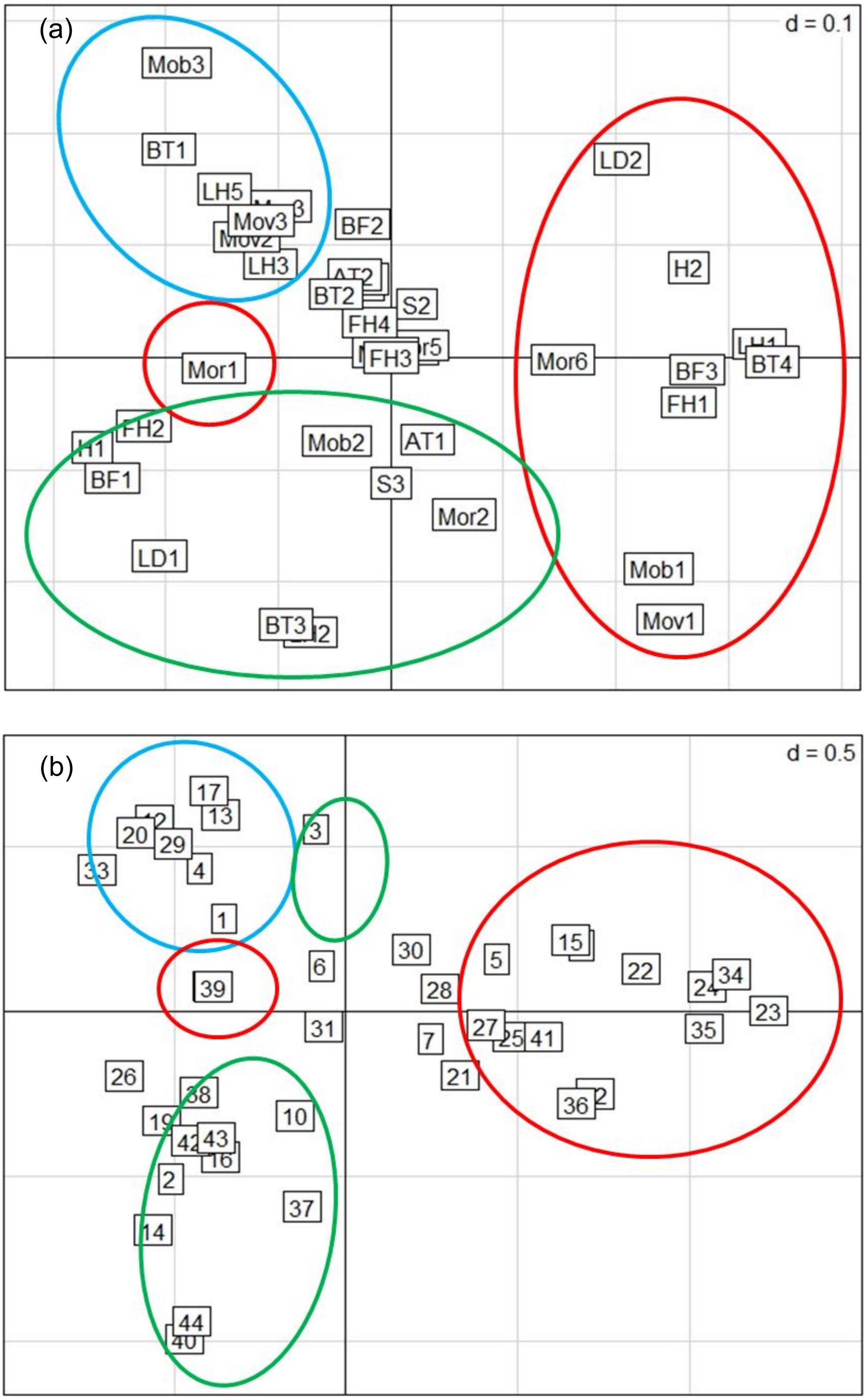

**Fig. 7** FCA plots showing the distribution of trait modalities (a) and stations (b) along the first two axes of the ordination plot. Colored circles indicate clusters of the trait modalities most important along axis 1 (red), axis 2 (green) and axis 3 (blue) and the accordingly grouped stations (for trait modality code see table 2, for station code see S1).

### Functional Diversity

The functional diversity was found to be significantly higher at Barents Sea and Lomonosov Ridge compared to Amundsen Basin (F=3.151, p=0.0418). The remaining regions Nansen Basin, Nansen Basin 2012 and Amundsen Basin 2012 were not significantly different from the previous.

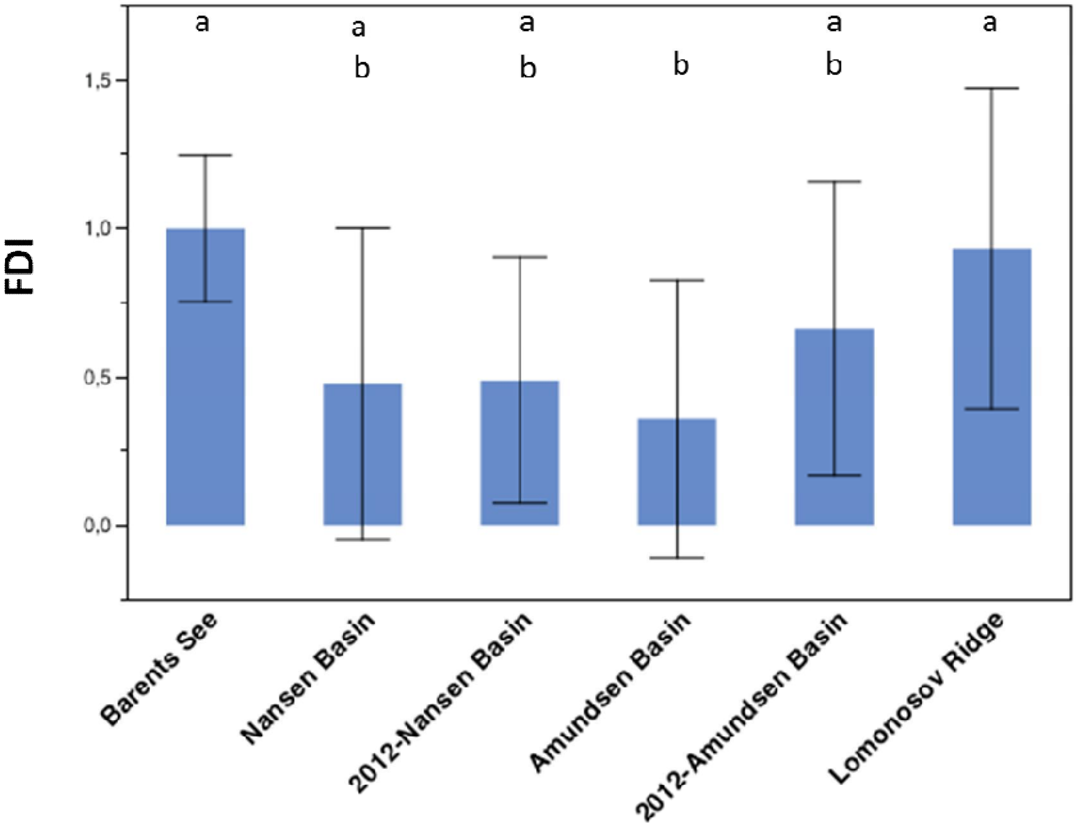

**Fig. 8** Mean Functional Diversity Index (FDI) for the regions Barents Sea, Nansen Basin, Amundsen Basin and Lomonosov Ridge in 1991 and for Nansen and Amundsen Basin in 2012. The letters above the bar charts indicate significant differences between regional groups as identified with ANOVA and Post Hoc test (Student's t) on differences between means.

## Discussion

### Patterns of benthic functioning across Arctic shelf, ridge and basin systems

Functional diversity (mean FDI=1.0), number of species (130) and secondary production (>6 g C $m^{-2}$ $y^{-1}$) were highest on the Barents Sea shelf, and decreased distinctly towards the Arctic basins (table 2, Fig. 8, S1). This trend reflects the decrease in food input to the benthos from the shallow shelf towards the deep-sea basins that is caused by the consumption of sedimenting organic matter on its passage through the water column (Gage & Tyler 1991) and by the lower primary production in the permanently ice covered central Arctic (Wassmann et al. 2010). The number of trait modalities present in the communities, however, decreased comparatively less (table 1). Regarding the relative composition of functional traits we observed clear differences between regions (Fig. 3, 4, 5). In the deep Amundsen basin smallest size classes (<5 mm) dominate the communities, while in other regions size classes are more evenly distributed (Fig. 3). This phenomenon was previously described in deep-sea regions as “dwarfism” related to the strong food limitation (Gage & Tyler 1991). Regions differ more clearly regarding morphological and behavioral traits (Fig. 4, 5). Nansen and Amundsen Basin associations show a higher share of the “cushion-shaped” morphology, while on the Lomonosov Ridge the body form “erect” and the morphology “stalked” contribute more. The latter may be indicative of more turbulence and associated particle flux in slope systems, as an erect or stalked position might be favorable for feeding under these conditions. This is also supported by the dominance of the trait modalities “suspension feeding, “no movement”, “sessile” and “no bioturbation” in this region. In the Barents Sea “infauna” dominates the macrobenthic communities, while in the other regions the trait modality “epifauna” is dominant. This could be related to the higher sedimentation rates on the shallow Barents Sea shelf that enrich surface sediment layers with organic matter to an extent that can maintain a rich infauna and bioturbating fauna. In the food depleted deeper regions the little organic matter that arrives in the sediment-water interface is mostly already consumed at the sediment surface (Gage & Tyler 1991).

The FCA identified the traits *Body Form*, *Morphology, Bioturbation* and *Living Habit* to explain most of the variance between the regions (table 4, Fig. 6). The trait modalities distributed along axis 1 are depicting a “flow or turbulence community” of attached, stalked or erect suspension feeding taxa (Fig. 6a). The traits along axis 2 depict a typical “soft bottom community” dominated by tube dwelling, sediment transport initiating infauna taxa (Fig 6a). The traits along the third axis depict an “opportunistic community” dominated by mobile, large, deposit feeding taxa (Fig. 6a). While the Lomonosov Ridge group is plotted close to the “flow or turbulence community” on axis 1, the productive Barents Sea shelf is grouped closer to the food depleted Amundsen Basin group on axis 2 (Fig 6b). Although these two regions differ strikingly in terms of secondary production (Fig. 2), they are both described as classical soft bottom habitats and share associated functional traits (Kröncke 1994, Kendal 1996).

The functional diversity, however, is significantly lower in the Amundsen Basin, while all other regions are not significantly different from each other (Fig. 8). Törnroos et al. (in press) proposed that functional diversity may be de-coupled from taxonomic richness above a certain threshold. We presume that such a threshold is crossed in the Amundsen Basin, where we detected the lowest species numbers (table 3). Low FDI and low species numbers indicate a low functional redundancy in an ecosystem (van der Linden 2012). Low redundancy again points to a low resilience against disturbance, as in the event that species are lost also a loss of function might occur (Díaz and Cabido, 2001; Loreau et al., 2001).

### Changes in benthic functioning between 1991 and 2012

Changes in benthic functioning between 1991 and 2012 are visible, although quite different in the two Arctic Basins. While the number and type of trait modalities stayed the same in both basins, the composition of traits relevant for secondary production changed in Nansen Basin only. Apparently the fauna changed from an association dominated by mobile deposit feeders towards one dominated by sessile suspension feeders. Accordingly, the region Nansen Basin 2012 is plotted closer to the Lomonosov Ridge group in the FCA ordination plot (Fig 6b). This shift towards a sessile suspension feeder community could indicate an increase in food input at least at some of the stations, making a sedentary life style possible. The groups Amundsen Basin 1991 and 2012 are plotted close together, indicating that the composition of traits relevant for production did not change. However, we detected an increase in species numbers (table 3), in functional diversity (Fig. 8) and in secondary production (table 3). The majority of stations sampled in 2012 were in the range of the marginal ice zone (MIZ), while the stations in 1991 were all under permanent sea ice cover (Fig. 9). Along the MIZ higher export rates of POC and tighter pelagic-benthic coupling are reported (Wassmann et al. 2006). The changes observed in this study indicate that the change in sea ice concentration has a direct effect on the functioning of the macrobenthic communities. However, as not all stations from 2012 are exactly in the same location than in 1991, a direct comparison is currently not possible. Future studies should aim at re-sampling those stations where historical datasets are available from.

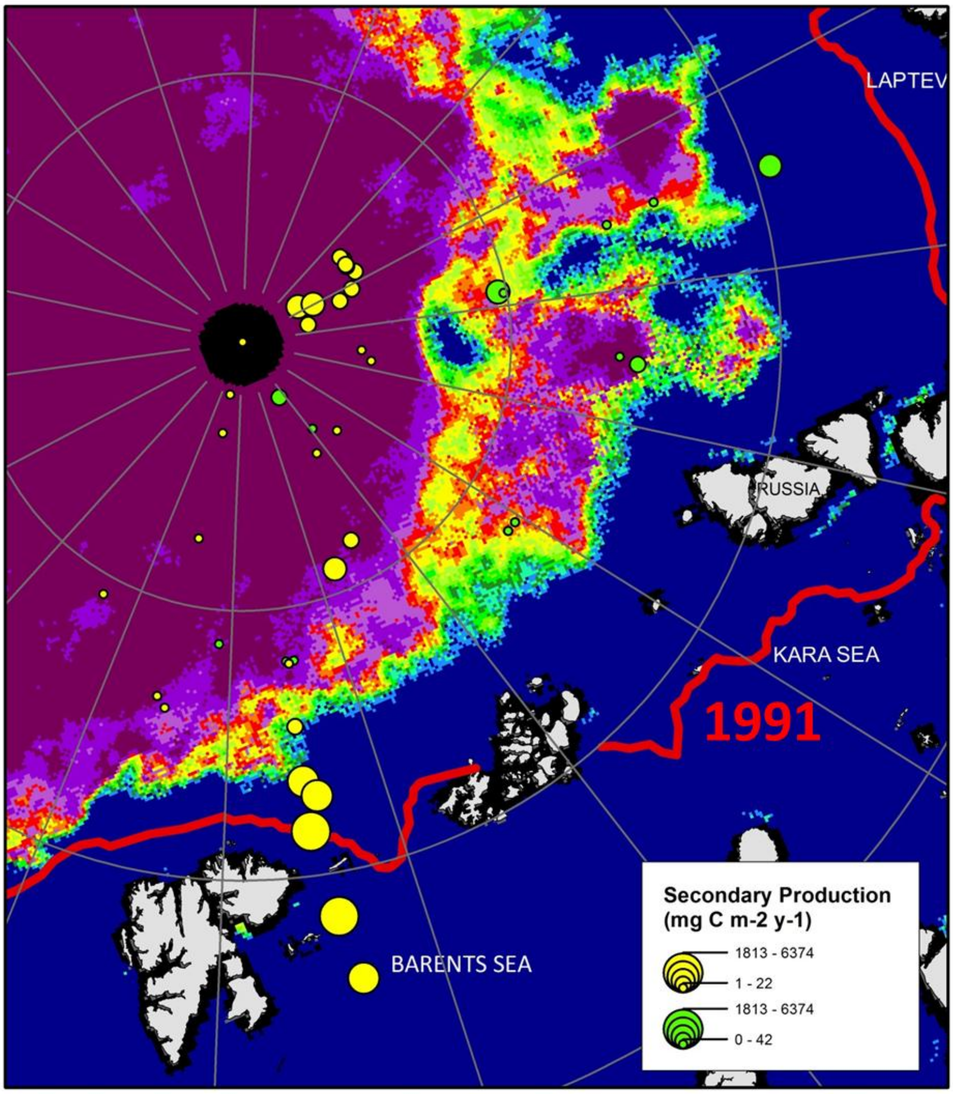

**Fig. 9** Sample stations from Nansen and Amundsen Basin in 1991 (yellow) and 2012 (green). The red line indicates the minimum sea ice extent of the year 1991. Sea ice concentration of the sea ice minimum in the year 2012 is given with dark red indicating high, and blue-green indicating very low sea ice concentration (Spreen et al. 2008).

## Summary & Outlook

Our findings indicate that BTA is an appropriate method to study benthic functioning also in Arctic and deep-sea regions. Here we detected significant changes in functioning along a spatial gradient of decreasing food supply as well as in time (1991 versus 2012) in the Nansen and the Amundsen Basin. However, the 26% share of overall variability explained in the FCA comparison of regions is rather low, indicating a high degree of within-region heterogeneity (Darr et al. 2014). The FCA performed on all stations without the regional clustering explained 80% of the data variance. This approach indicates that several stations group rather different from the regional cluster we assigned them to. We suggest that future studies should sample on smaller scales and group stations according to an *a priori* environmental clustering method that accounts for differences in water depth, bottom structure and turbulence. So far sample data from the Arctic deep sea are scarce, and as such even more valuable. To enable direct comparison to previous studies, future sampling should re-visit historical sampling sites and the corresponding classical benthic sampling design with a giant box-corer and a sieve size of 0.5 mm should be applied. The latter would enable also the reliable calculation of changes in taxonomic diversity which reacts sensitive to sampling effort and sieve size.

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# Supplementary material

**S1** Station information. “Code” is referring to the respective station in the FCA plot (Fig. 6 & 7).

| Region | Station | Code | Long | Lat | Year | Depth (m) | Production (mg C $m^{-2}$ $y^{-1}$) |
|---|---|---|---|---|---|---|---|
| Barents Sea | PS104 | 1 | 81.45 | 31.48 | 1991 | 258 | 1039.86 |
| Barents Sea | PS117 | 2 | 80.82 | 30.10 | 1991 | 193 | 6111.56 |
| Barents Sea | PS132 | 3 | 79.18 | 31.70 | 1991 | 75 | 6374.07 |
| Barents Sea | PS136 | 4 | 77.98 | 32.93 | 1991 | 143 | 1811.58 |
| Nansen Basin | PS2157 | 1 | 29.99 | 81.75 | 1991 | 2950 | 1584.66 |
| Nansen Basin | PS2158 | 2 | 29.93 | 82.78 | 1991 | 3800 | 69.46 |
| Nansen Basin | PS2159 | 3 | 30.34 | 83.95 | 1991 | 3950 | 15.44 |
| Nansen Basin | PS2161 | 4 | 44.30 | 85.44 | 1991 | 4005 | 214.78 |
| Nansen Basin | PS2162 | 5 | 50.83 | 85.79 | 1991 | 3981 | 63.80 |
| Nansen Basin | PS2209 | 6 | 8.57 | 83.23 | 1991 | 4046 | 1.08 |
| Nansen Basin | PS2210 | 7 | 10.12 | 83.05 | 1991 | 3949 | 7.78 |
| Amundsen Basin | PS2168 | 1 | 55.93 | 87.51 | 1991 | 3845 | 11.24 |
| Amundsen Basin | PS2171 | 2 | 68.98 | 87.59 | 1991 | 4384 | 9.36 |
| Amundsen Basin | PS2175 | 3 | 103.68 | 87.58 | 1991 | 4413 | 9.49 |
| Amundsen Basin | PS2176 | 4 | 108.14 | 87.77 | 1991 | 4364 | 21.91 |
| Amundsen Basin | PS2190 | 5 | 0.00 | 90.00 | 1991 | 4273 | 15.85 |
| Amundsen Basin | PS2191 | 6 | 9.01 | 88.99 | 1991 | 4348 | 5.32 |
| Amundsen Basin | PS2192 | 7 | 9.86 | 88.26 | 1991 | 4375 | 6.45 |
| Amundsen Basin | PS2195 | 8 | 9.62 | 86.25 | 1991 | 3793 | 1.08 |
| Amundsen Basin | PS2205 | 9 | -6.77 | 84.64 | 1991 | 4283 | 3.97 |
| Lomonosov Ridge | PS2177 | 1 | 134.89 | 88.03 | 1991 | 1388 | 95.96 |
| Lomonosov Ridge | PS2179 | 2 | 138.09 | 87.74 | 1991 | 1230 | 52.03 |
| Lomonosov Ridge | PS2181 | 3 | 153.06 | 87.60 | 1991 | 3112 | 45.36 |
| Lomonosov Ridge | PS2182 | 4 | 151.35 | 87.57 | 1991 | 2609 | 48.28 |
| Lomonosov Ridge | PS2183 | 5 | 148.92 | 87.60 | 1991 | 2031 | 42.07 |
| Lomonosov Ridge | PS2184 | 6 | 148.20 | 87.61 | 1991 | 1654 | 48.56 |
| Lomonosov Ridge | PS2185 | 7 | 144.17 | 87.53 | 1991 | 1073 | 88.48 |
| Lomonosov Ridge | PS2186 | 8 | 140.18 | 88.51 | 1991 | 1867 | 125.43 |
| Lomonosov Ridge | PS2187 | 9 | 126.99 | 88.73 | 1991 | 3844 | 58.69 |
| Lomonosov Ridge | PS2189 | 10 | 144.67 | 88.77 | 1991 | 1018 | 129.69 |
| 2012-Nansen Basin | PS80/0236 | 1 | 78.67 | 83.92 | 2012 | 3463 | 4.93 |

| Region | Station | Code | Long | Lat | Year | Depth (m) | Production (mg C $m^{-2}$ $y^{-1}$) |
|---|---|---|---|---|---|---|---|
| 2012-Nansen Basin | PS80/0251 | 2 | 108.87 | 82.64 | 2012 | 3561 | 58.82 |
| 2012-Nansen Basin | PS80/221 | 3 | 29.92 | 84.00 | 2012 | 4014 | 13.35 |
| 2012-Nansen Basin | PS80/229 | 4 | 31.32 | 84.00 | 2012 | 4008 | 0.31 |
| 2012-Nansen Basin | PS80/241 | 5 | 76.71 | 83.93 | 2012 | 3432 | 20.69 |
| 2012-Nansen Basin | PS80/262 | 6 | 109.92 | 82.98 | 2012 | 3601 | 5.11 |
| 2012-Nansen Basin | PS80/368 | 7 | 17.72 | 84.36 | 2012 | 4024 | 10.32 |
| 2012-Amundsen Basin | PS80/0290 | 1 | 130.60 | 79.67 | 2012 | 3400 | 214.83 |
| 2012-Amundsen Basin | PS80/0334 | 2 | 123.18 | 85.16 | 2012 | 4354 | 246.52 |
| 2012-Amundsen Basin | PS80/0371 | 3 | 55.67 | 88.76 | 2012 | 4369 | 109.28 |
| 2012-Amundsen Basin | PS80/278 | 4 | 129.95 | 82.88 | 2012 | 4167 | 37.23 |
| 2012-Amundsen Basin | PS80/326 | 5 | 130.92 | 81.93 | 2012 | 4038 | 13.25 |
| 2012-Amundsen Basin | PS80/339 | 6 | 122.74 | 85.06 | 2012 | 4352 | 10.83 |
| 2012-Amundsen Basin | PS80/355 | 7 | 61.01 | 87.93 | 2012 | 4381 | 11.62 |

**S2** Literature and web resources used on functional trait research.

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# Manuscript IV

## Status and trends in the structure of Arctic benthic food webs

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## Abstract

Ongoing climate warming is causing a dramatic loss of sea ice in the Arctic Ocean, and it is projected that the Arctic Ocean will become seasonally ice-free by 2040. Many studies of local Arctic food webs now exist, and with this review paper we aim to synthesize these into a large-scale assessment of the 35 current status of knowledge on the structure of various Arctic marine food webs and their response to climate change, and to sea-ice retreat in particular. Key drivers of ecosystem change and potential consequences for ecosystem functioning and Arctic marine food webs are identified along the sea-ice gradient, with special emphasis on the following regions: seasonally ice-free Barents and Chukchi seas, loose ice pack zone of the Polar Front and Marginal Ice Zone, and permanently sea-ice covered High Arctic. Finally, we identify knowledge gaps in different Arctic marine food webs and provide recommendations for future studies.

### Key words

Arctic; food web; climate change; sea-ice retreat; trophic transfer;
pelagic-benthic coupling.

## Introduction

The Arctic Ocean is currently experiencing significant warming of approximately three times the global average (Steele et al. 2008; Serreze et al. 2009; Polyakov et al. 2010) and, despite a very pronounced seasonality, recent winter warming far exceeds that occurring in summer (Screen & Simmonds 2010). One of the characteristic features of the Arctic Ocean is sea ice, present permanently at high latitudes and seasonally at lower latitudes in winter (Fig. 1). Presently, The most conspicuous sign of warming is the dramatic loss of sea ice (Higgins & Cassano 2009; Parkinson & Comiso 2013): its summer extent has decreased by nearly 50% over the past decade (Fig. 1), and the Arctic Ocean has undergone a regime shift from multiyear ice to largely seasonal and much thinner ice cover (Comiso 2012). The Arctic Ocean may become seasonally ice-free by as early as 2040 (Polyakov et al. 2010). Reductions in sea-ice cover are being further amplified by increased heat fluxes into the Arctic Ocean through the Bering (Woodgate et al. 2006; Woodgate et al. 2010; Woodgate et al. 2012) and Fram straits (Piechura & Walczowski 2009). This enhanced ocean temperature further delays the growth of sea ice in the fall (Steele et al. 2008). In terms of ecosystem functioning, these patterns indicate a shift towards an earlier spring transition between sea-ice-covered and sea-ice-free conditions (Grebmeier et al. 2006b; Steele et al. 2008). Therefore, in the Arctic, climate change is not only affecting the physical structures such as sea ice, but is also responsible for multiple ecological changes on ecosystem functioning, including food-web structure, stability and efficiency, especially by affecting components at the base of the food web.

The two main sources of primary production in Arctic ecosystems are sea-ice algae and phytoplankton (Søreide et al. 2006). The growth of both ice algae and phytoplankton takes place within a one to four month period during spring and summer (Søreide et al. 2006; Renaud, Carroll et al. 2008; Iken et al. 2010). The productive season starts at the end of the polar night with sunlight triggering the bloom of sea-ice algae. Ice algae, even Though they constitute only a small-to-moderate portion (<20%) of total annual primary production (Hegseth 1998; Gradinger 2009), ice algae can contribute to Arctic benthic food webs during springtime on shallow continental shelves with seasonal ice cover because they occur early and sink fast following sea-ice retreat (Hobson et al. 1995; Tamelander et al. 2006). This ice algal contribution is proportionally more important in areas where sea-ice cover lasts later in the year (Gosselin et al. 1997) but is expected to decrease with current sea-ice retreat (Leu et al. 2011). A phytoplankton spring bloom follows the ice algae bloom as the sea-ice cover melts (Leu et al. 2011). In the summer, limited nutrients support a low phytoplankton biomass (Wassmann & Reigstad 2011), with episodic bloom conditions facilitated by occasional nutrient availability (Grebmeier et al. 2006a). These phytoplankton blooms, although responsible for the bulk of annual production, are usually restricted to open waters (but see Arrigo et al. 2012; Mundy et al. 2014). In 2012, Boetius et al. (2013) also showed that sinking ice algae aggregates constitute an important food input to benthos in the Arctic basins. In addition to phytoplankton and ice algal production, microbial oceanic phototrophs can contribute up to 50% of total inorganic carbon assimilation and play a leading role in nutrient cycling (Falkowski et al. 1998). Bacterial-primary production ratios have been estimated to reach more than 240% above 81° N (Rich et al. 1997) compared to 1-143% (32±6%) in the Barents Sea (Sturluson et al. 2008). The bacterial contribution to respiration in the water column may be substantial: 3-60% in the Chukchi Sea and Canada Basin, and 25% on average in the Arctic (Kirchman et al. 2009). Moreover, bacterial activity on sinking particles, an important habitat that harbors distinct communities of Arctic bacteria (Hansell & Ducklow 2003; Hodges et al. 2005), directly affects the quantity and quality of the organic matter that reaches the sea floor. In coastal areas and interior shelves, coastal erosion, river and glacial discharge can become an important sources of terrestrial organic matter inputs that can also be further utilized in benthic food webs (Dunton et al. 2006; Dunton et al. 2012; Kędra et al. 2012; Kuliński et al. 2014).

The quality and quantity of primary production, including ice algae and phytoplankton, reaching the seafloor have a strong impact on benthic communities (Pearson & Rosenberg 1978), which further cascades through the whole food web, especially in the highly seasonal Arctic marine ecosystems. Shallow Arctic shelves in particular are currently characterized by tight pelagic–benthic coupling due to low grazing in the water column during the bloom (Grebmeier et al. 1988; Grebmeier & McRoy 1989; Renaud, Carroll et al. 2008; Tamelander et al. 2008).

This results in large export of organic matter, produced in the surface layers and descending to the seafloor and benthos (Grebmeier et al. 2006a), especially in spring, when production is far greater than zooplankton consumption (Tamelander et al. 2006). For example, almost 70% of the organic carbon produced in the water column during spring in the Pacific Arctic region reaches the seafloor (Walsh et al. 1989), supporting high biomass, abundance and diversity of benthic organisms (Grebmeier & McRoy 1989; Grebmeier et al. 2006a; Iken et al. 2010; Bluhm, Gradinger et al. 2011), which are important prey items for higher trophic level animals foraging on the seafloor, including diving sea ducks (Merginae), bearded seals (*Erignathus barbatus*), walrus (*Odobenus rosmarus*) and grey whales (*Eschrichtius robustus*) (Lovvorn et al. 2003; Grebmeier et al. 2006a; Grebmeier & Barry 2007; Grebmeier 2012). This contrasts with the summer period, when grazing of phytoplankton by zooplankton may reach up to 97% of daily water column primary production in more pelagic-oriented areas like the Barents Sea (Tamelander et al. 2006), thus limiting carbon export to the benthos. Therefore During summer, reworked organic matter consisting of zooplankton fecal pellets and carcasses, moults and bacteria, as well as phytodetritus, primarily fuels benthic food webs. Currently, Many shallow shelf Arctic systems, especially in the Pacific Arctic, have a high efficiency of energy transfer from the water column to the benthos (Ambrose & Renaud 1995). Macro- and mega-fauna appear to play a prominent role in carbon recycling (up to 30% efficiency for Arctic benthos; Clough et al. 2005; Renaud et al. 2007), but studies focusing on partitioning of carbon recycling for bacterial, meiofaunal, macrofauna and megafaunal components are rare (Piepenburg et al. 1995).

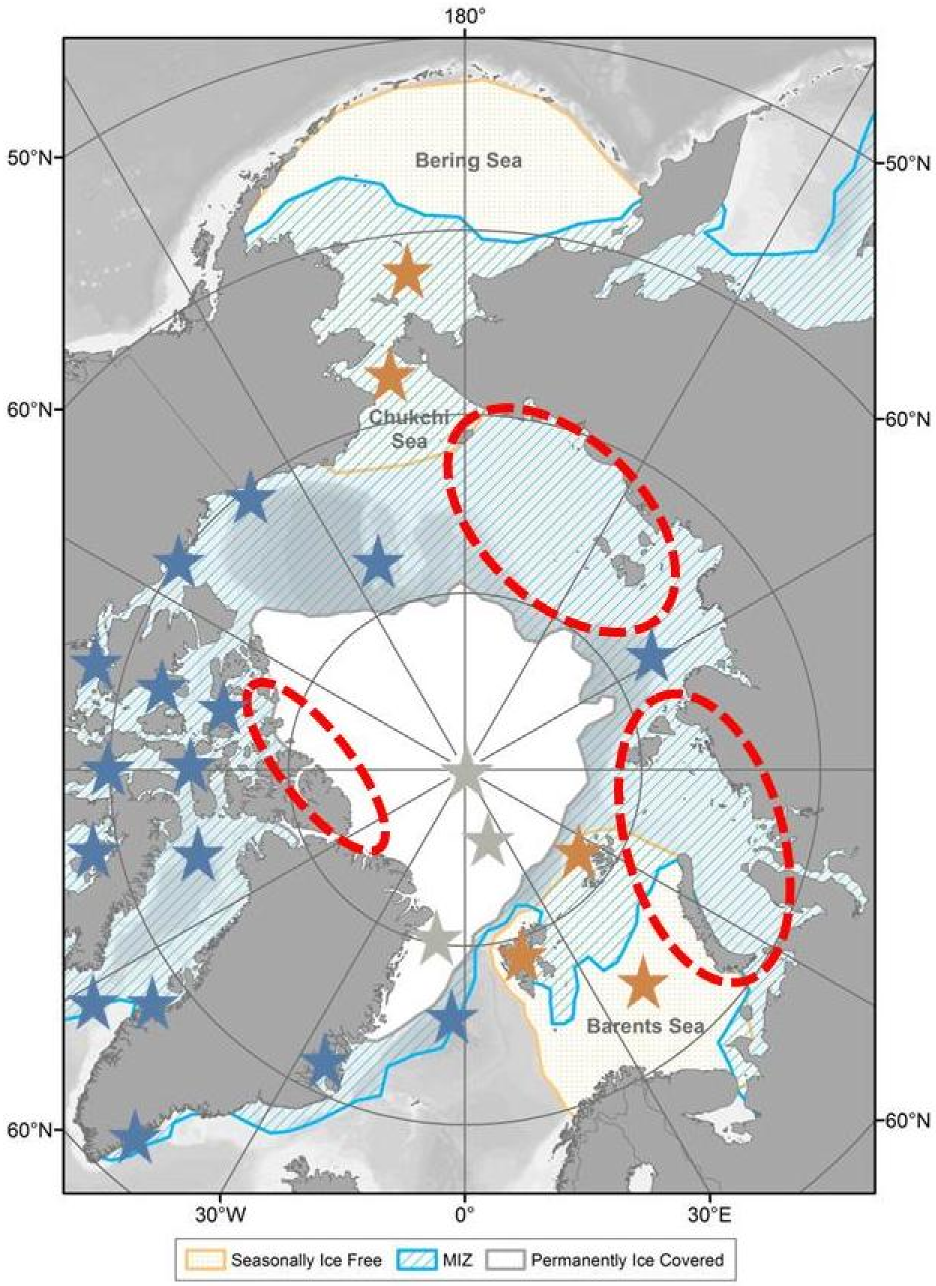

**Fig. 1** Map of the Arctic Ocean showing the minimum sea-ice extent September 2012 and the median sea-ice extent February 1981-2010 (blue line). Locations of published food-web studies and the case study areas of this review are marked with yellow (seasonally ice-free areas), blue (Marginal Ice Zone [MIZ]) and grey (permanently ice-covered High Arctic) stars. Red circles indicate areas that require more investigation. Bathymetry after Amante & Eakins (2009); sea-ice data from Fetterer et al. (2002).

Trophic transfer efficiency describes the efficiency with which energy is transferred from one trophic level to the next, in particular the relative percentage of primary production that reaches top predators (Kozlovsky 1968). Species interactions, of which many are sea-ice related in Arctic ecosystems (Fortier et al. 2002; Gradinger & Bluhm 2004; Søreide et al. 2006; Gradinger 2009), control energy and organic matter flow which determine ecological efficiencies and can limit productivity and patterns of species dominance and food-web stability (McCann 2000). In the changing Arctic Ocean, species shifts and local extinctions and invasions may occur, leading to new interactions between species that have not co-evolved (Hobbs et al. 2006). New or missing links in established food webs may lead to large energy inefficiencies, changes in energy pathways that currently support key top predators, and destabilization of food-web dynamics (Vander Zanden et al. 1999; Pauly et al. 2002). However, this process is also dependant on the level of trophic and functional redundancy in a system (Layman et al. 2007). Understanding how Arctic food webs will become structured in the future will therefore entail disentangling the factors with most impact on interspecific interactions.

The aim of this paper is to present the current status of knowledge of the structure of various Arctic marine food webs and their observed responses to ongoing climate change, in particular to sea-ice retreat. Potential changes to food-web trophic transfer efficiency are also discussed. To date, most focused studies of Arctic food webs that exist are limited in space, time or taxonomic level (e.g., Iken et al. 2005; Aydin & Mueter 2007; Bergmann et al. 2009; Megrey & Aydin 2009; Iken et al. 2010; Feder et al. 2011; Dunton et al. 2012; Whitehouse et al. 2014), and large-scale syntheses across the Arctic are generally missing. Only a few pan-Arctic reviews currently exist have been published (Carmack & Wassmann 2006; Piepenburg et al. 2011; Wassmann et al. 2011) and none has focused on species interactions and trophic pathways of food webs nor on food-web structure and with trophic transfer efficiency. To complement existing studies, this review will focus on the key drivers of ecosystem changes in the Arctic, including sea-ice decline, temperature rise and changes in stratification and the consequences for important ecosystem functions that are susceptible to change, including nutrient regeneration, primary and secondary production, pelagic–benthic coupling, structure of food webs and consequences for top predators. In particular, we aim to: (1) identify key drivers of ecosystem change and potential consequences for ecosystem functioning; (2) present different scenarios and trends in Arctic marine food webs by analysing regional ecosystem case studies located along a sea-ice gradient: the seasonally ice-free Barents Sea and Chukchi Sea, the loose ice pack Polar Front (PF) and the Marginal Ice Zone (MIZ) and the permanent ice-covered High Arctic; and (3) identify knowledge gaps existing in Arctic marine food webs, and suggest possible methods to fill these gaps and provide recommendations for future studies.

## Primary and secondary drivers of ecosystem change: potential consequences

### Key drivers of ecosystem change

The primary driver of the observed ecosystem change in high latitudes is ongoing climate change, and warming in particular (Symon et al. 2005). Increasing air temperature is the main cause of sea-ice decline, along with the secondary drivers of Arctic ecosystem change, such as increase in sea-water temperature and altered stratification (Symon et al. 2005; Stocker et al. 2013). Sea ice is a major regulating component in controlling pelagic and benthic production through modulating water-column stratification and light fields (Bluhm & Gradinger 2008; Gradinger 2009) because it controls the exchange of heat between the atmosphere and ocean and, together with snow cover, limits the penetration of light into the water column. Also, in the Arctic Ocean, the thaw–freeze cycle of sea ice and large freshwater riverine inputs result in pronounced haline stratification within the surface layer (Carmack & Wassmann 2006). Shortly after the phytoplankton spring bloom, the polar mixed layer becomes and remains nitrogen-depleted because of strong vertical stratification, which prevents replenishment during the summer season (Tremblay et al. 2008). Analysis of model data shows that when less sea ice is produced and freshwater load is increasing in the Arctic Ocean, the water column stratification becomes stronger, which decreases winter mixing (Slagstad et al. 2011), subsequently affecting nutrient distribution in the water column (Li et al. 2009; Codispodi et al. 2013; Matrai et al. 2013). In general, patterns of nutrients availability in the euphotic zone are a function of the total transport at the Barents Sea Opening and Fram Strait, through Davis Strait in the Canadian Archipelago and Bering Strait in the Pacific Arctic region, along with nutrient input from rivers, upwelling, stratification patterns and local mixing of deep water (Codispoti et al. 2013). Both major sources of nutrients in the Arctic Ocean, oceanic inputs associated with waters of Pacific and Atlantic origin, and riverine nutrient fluxes, are likely to change with accelerating climate change (Peterson et al. 2002; McClelland et al. 2006; Peterson et al. 2006; Shiklomanov & Lammers 2009). Changes in riverine freshwater runoff will likely be associated with changes in the quality and quantity of the nutrient supply, and while the loads of silicate, phosphate and dissolved and particulate organic matter are expected to increase in the future, trend in riverine nitrogen loads remain largely unknown (Frey et al. 2007; Raymond et al. 2007; Frey & McClelland 2009). Differences between nutrient transport and availability over the shelf areas and central Arctic may increase in the future: the already nutrient-depleted central Arctic Basin will likely become more oligotrophic, while shelf areas will be further enriched by increased transport of Atlantic and Pacific water masses and runoff. Biogeochemical processes and changes in adjacent basins as well as circulation changes may affect the future productivity of the Arctic Ocean.

### Primary production and its consumers

Alterations of the seasonal cycle of primary productivity at the base of the food web is one of the most important consequences of rising temperature, sea-ice retreat and changes in nutrient patterns. In general, ice algae and pelagic phytoplankton production occur sequentially during the year, with the abundance of ice algae relative to pelagic phytoplankton increasing northward coincident with greater sea-ice cover (Leu et al. 2011; Wassmann et al. 2011; Rubao et al. 2013). Although light availability and nutrients are often the prime limiting factors for primary production (Gradinger 2009; Leu et al. 2011), the timing of pelagic phytoplankton blooms is likely controlled by sea-ice retreat, whereas the timing of ice algae blooms is influenced by snow and sea-ice melt and start earlier than open water blooms. In many Arctic marginal seas, the timing of sea-ice retreat may have a strong impact on the timing of phytoplankton production, but little or no impact on the timing of ice algae peaks. Changes in the timing of maximum phytoplankton production influence the variability in time-lags between ice algal and phytoplankton production peak production (from 45 to 90 days; Ji et al. 2013). The timing of the sea-ice algal bloom is an important driver of spring secondary production as earlier ice algae bloom will export larger amounts of primary production to seafloor communities (Gradinger 1995), especially when water column grazing is low, strengthening pelagic–benthic coupling processes. Changes in timing of the pulses of ice algae and phytoplankton primary production and in the associated gap period between them will influence zooplankton grazer abundances and activities (Søreide et al. 2010; Varpe 2012). Although the timing of primary production varies greatly over time and space in different regions, systematic shifts in the timing of production and export processes have the potential to increase the frequency of mismatch between marine grazers and their food, which in turn can subsequently alter the organic matter flux to the seafloor and/or the transfer to the higher trophic levels (Rubao et al. 2013).

Because Arctic zooplankton reproduction is largely determined by the food quality of autotrophs (Müller-Navarra 2008), therefore production of lipids in sea-ice diatoms early in the season is extremely important (Falk-Petersen et al. 2009; Søreide et al. 2010). These high-energy lipid compounds are rapidly transferred through the Arctic marine food chains. Changes in the initiation and duration of the growth season, and therefore in the timing, quality and quantity of sea-ice blooms, will directly affect, among others, calanoid copepods (Ji et al. 2012), which are critical to energy transfer between lower and higher trophic levels. Diatom lipids are accumulated in large amounts by *Calanus* species and ice amphipods, and further transferred to pelagic carnivorous zooplankton and pelagic fish stocks (Scott et al. 1999; Scott et al. 2001; Auel et al. 2002). Lipid levels increase from 10 - 20 % in phytoplankton to 50 - 70 % in herbivorous zooplankton and ice fauna that then become available as nutritious prey items for upper trophic level consumers (Daase et al. 2014). Dominant Arctic zooplankton taxa, like *Calanus glacialis*, switch from a diet of ice algae in spring towards phytoplankton in late summer, while others, like the sympagic amphipod *Apherusa glacialis,* feed mainly on ice algae during early spring (Scott et al. 1999; Falk-Petersen et al. 1999;

Falk-Petersen et al. 2006). Ice-associated amphipods *Onisimus* spp. switch from ice algae in spring to an omnivorous diet by the end of productive season (Werner & Auel 2005). The young ice amphipod *Gammarus wilkitzkii* feed on ice algae, while their adults have a carnivorous diet, feeding preferentially on calanoid copepods (Scott et al. 2001; Werner et al. 2002). Although most benthic species do not feed directly on algal cells, changes in the timing and quality of bloom sedimentation (the latter additionally influenced by microbial processing) may impact those species' composition and abundances (Ambrose & Renaud 1997). Changes in the availability or abundance of ice algae or dependent zooplankton communities may cause cascading impacts on higher trophic level populations.

### Microbial processes

Earlier sea-ice melt and increased stratification of the water column will promote picophytoplankton occurrence. Because of their short generation times, microorganisms respond quickly to environmental changes and are the first to react to ongoing global changes, affecting key ecosystem functions at the base of food webs (Sarmento et al. 2010). Significant changes in microbial communities and diversity have already been observed after a sharp decline of sea-ice cover in September 2007 (between 2002 and 2010; Comeau et al. 2011). Increased carbon supply from pelagic productivity and riverine discharge coupled with increased bottom water temperature could result in higher bacterial activity and rates of bacterial cycling of carbon (Kritzberg et al. 2010; Vaquer-Sunyer et al. 2010). The decreased quality and quantity of sinking particles (Wassmann & Reigstad 2011) and usable carbon (Renaud, Morata et al. 2008) being exported to the seafloor would decrease the efficiency of food webs. Picophytoplankton is believed to be relatively inaccessible as a prey for mesozooplankton (Li et al. 2009); however some studies suggest that protozoans may constitute a larger percentage of copepod diets (Campbell et al. 2009), even up to 80-90%, during summertime, when abundances, biomass and production are dominated by pico- and nanophytoplankton (Piwosz et al. 2009; De Laender et al. 2010; Piwosz et al. 2015) and when abundances of microzooplankton are high (Kubiszyn et al. 2014). Thus, In herbivore-limited systems, copepod production is therefore closely linked with protozoan production and constitutes a direct link between the microbial loop and higher trophic levels (Campbell et al. 2009; Sherr et al. 2009; De Laender et al. 2010; Nelson et al. 2014). Still, it is likely that Arctic food webs will lengthen at their base with the increase in numbers of trophic transfers within the microbial food webs or the number of grazers in the water column, thus decreasing the amount of carbon available for the higher trophic levels in the original food chain.

Presently, there is limited knowledge of the possible impact of viruses and parasitic protists in terms of their capacity to terminate algal blooms in the Arctic is limited (Nelson et al. 2014). Viral infection has been shown to control blooms of the coccolithophore *Emiliania huxleyi* in the Northern Atlantic (Wilson et al. 2002), while parasitic protists in the order Syndiniales have been coupled with collapses of blooms of dinoflagellate species in the Mediterranean Sea (Chambouvet et al. 2008). Increased impact of algal viruses and parasites would decrease the amount of food available for pelagic and benthic grazers. How these processes affect current blooms in the Arctic Ocean remains largely unknown, but both viruses and parasitic Syndiniales have been reported from sea ice (Wells & Deming 2006; Bachy et al. 2011; Collins & Deming 2011; Comeau et al. 2013; Piwosz et al. 2013) and the water column (Howard-Jones et al. 2002; Lovejoy et al. 2006; Bachy et al. 2011; Comeau et al. 2011; Payet & Suttle 2013).

### Pelagic–benthic coupling

The initiation of sea-ice retreat is important for the timing, quality and amount of primary production (Springer et al. 1996; Hunt & Stabeno 2002), and changes in the timing of both ice algae and phytoplankton primary production may cause changes in the food webs by influencing the standing stock of zooplankton, which will in turn affect the direct, ungrazed deposition of phytoplankton (Cooper et al. 2002) and subsequently benthic species (Overland & Stabeno 2004; Grebmeier, Cooper et al. 2006; Grebmeier, Overland et al. 2006; Nelson et al. 2009; Grebmeier 2012). In areas with reduced summer sea ice, pelagic grazing pressure will be higher (Lalande et al. 2007), perhaps altering sedimentation of organic matter, resulting in more pelagic-oriented systems. With increased primary production (Arrigo et al. 2011; Arrigo et al. 2014; Palmer et al. 2014), pelagic food webs could become more productive and intercept more organic matter before it reaches the seafloor (Renaud, Carroll et al. 2008); however, nutrient limitation may halt this process. Increased grazing would reduce the export flux of carbon to the seafloor, weakening pelagic–benthic coupling processes. Studies in the Bering Sea found that with sea-ice cover the spring blooms were characterized by a higher proportion of diatoms, less recycling and greater export and, therefore, stronger pelagic–benthic coupling (Moran et al. 2012). In the case of open-water conditions, blooms were characterized by a higher proportion of dinoflagellates, greater carbon cycling in the water column and lower export to the seafloor, and consequently reduced pelagic–benthic coupling (Moran et al. 2012).

## Upper trophic levels

Changes in primary and secondary production affect upper trophic levels and are predicted to have increasing impact with climate warming (Wassmann 2006; Daufresne et al. 2009; Moore et al. 2014). Arctic marine top predators will have to face extreme changes in their habitat and forage base, including density and distributional shifts of their prey, as well as potential losses of some of their favoured lipid-rich prey species (Kovacs & Lydersen 2008; Kovacs et al. 2011). Upper trophic levels usually respond in a non-linear fashion to changes in ecosystem structure and usually the response depends on their exact position in the food web (Moore et al. 2014). Although the resilience of Arctic top predators is largely dependent on an individual's adaptive capacity, in general their resilience capacity depends largely on the region, the intensity and range of ice cover change and species characteristics (e.g. ice-obligate species are more vulnerable than ice-associated or seasonally migrant ones [Moore & Huntington 2008]). Sea-ice associated and sea-ice obligate species such as walruses and bearded seals that use sea-ice as a platform for breeding, resting and foraging activities will be most affected by changes in sea-ice cover (Laidre et al. 2008; Moore & Huntington 2008; Table 1). Reductions in prey quality have been observed to have ecosystem-wide effects, such as population crashes of Steller sea lions (*Eumetopias jubatus)* in the Gulf of Alaska (Rosen & Trites 2000) and breeding failures of seabirds in the North Sea (Wanless et al. 2005). A decline in spawning and foraging areas will affect both predators and their prey. For instance, polar cod (*Boreogadus saida*) abundance might be significantly reduced, with tremendous consequences to the entire system as this species is believed to account for up to 75% of energy transfer between zooplankton and vertebrate predators (Darnis et al. 2012). In addition to changes in resource availability, top predators will likely face increased complexity within food webs that tend to dissipate energy flow (Węsławski et al. 2009). This will likely be followed by increased competition from temperate species that are expanding northward, e.g., Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus)* (Renaud et al. 2012) and Atlantic mackerel (Scomber scombrus) (Berge et al. 2015), and increased predation from species formerly unable to access them in areas of extensive sea-ice cover, such as killer whales (*Orcinus orca*) (Higdon & Ferguson 2009), gannets following northward move of herring and mackerel (Symon et al. 2005), and fish-eating whales that are getting more abundant in the Pacific Arctic Region (Grebmeier 2012; Moore et al. 2014). Also, an increase in temperate and sub-Arctic fish migration is predicted to lead to a decrease in prey quality, since they are less lipid-rich than Arctic species (Symon et al. 2005; Hop & Gjøsæter 2013). Additionally, increased risks of disease and contaminants may also become issues (Kovacs & Lydersen 2008).

**Table 1** Circumpolar Arctic top predators, their principal food sources and estimated population sizes.

| Species | Habitat | Principal food source | Population size | Reference |
|---|---|---|---|---|
| Fulmar<br>*(Fulmarus glacialis)* | Pelagic, surface | Cephalopods, epipelagic fish, pteropods, floating carrion | 15 000 000-30 000 000 | BirdLife International 2012 |
| Spectacled eider<br>*(Somateria fischeri)* | Coastal, pelagobenthic | Benthos, crustaceans, molluscs | 330 000-390 000 | BirdLife International 2012 |
| Little auk<br>*(Alle alle)* | Coastal, pelagic | Pelagic crustaceans, copepods | 16 000 000-36 000 000 | BirdLife International 2012 |
| Ringed seal<br>*(Phoca hispida)* | Coastal, pelagobenthic, 0-100 m | Polar cod, demersal fish, large crustaceans | 2 500 000 | Miyazaki 2002 |
| Bearded seal<br>*(Erignathus barbatus)* | Coastal, benthic, 0-100 m | Demersal fish, crabs, shrimps, urchins | Unknown | Kovacs 2002 |
| Greenland seal<br>*(Phoca groenlandica)* | Pelagic, 0-100 m | Pelagic fish | 8 000 000 | Kovacs 2008 |
| Walrus<br>*(Odobenus rosmarus)* | Benthic, 0- 50 m | Large bivalves, gastropods, shrimps | Unknown | Lowry et al. 2008 |
| Minke whale<br>*(Balaenoptera acutorostrata)* | Pelagic, 0- 200 m | Large pelagic crustaceans, pteropods, pelagic fish | 182 000 | Reilly et al. 2012 |
| Bowhead<br>*(Balaena mysticetus)* | Pelagic | Pelagic crustaceans, copepods | > 10 000 | Reilly et al. 2012 |
| Eastern North Pacific grey whale<br>*(Eschrichtius robustus)* | Pelagic | Benthos, amphipods | 15 000-22 000 | Reilly et al. 2012 |
| Beluga whale<br>*(Delphinapterus leucas)* | Coastal, pelagic, estuary | Coastal and pelagic fish, crustaceans, cephalopods | >150 000 | Jefferson et al. 2012 |

### Changes in species distribution ranges mediated by temperature

Temperature has a direct impact on metabolic and physiological processes as well as on the behaviour of individual organisms (Duarte 2007; O'Connor et al. 2007). It may influence growth, survival, reproduction, phenology and recruitment success of particular species (Lewis 1996; Walther et al. 2002; Lewis 2005; Herbert et al. 2007). Therefore, spatial distributions of organisms will likely change because of differential survival and recruitment of pelagic larval stages with varying water temperatures (Sirenko & Kolutin 1992; Blanchard et al. 2010; Grebmeier 2012). Changes in phenology can lead to a decoupling of the dynamics between predator and prey that will further alter current trophic relations and communities. Some species time their reproductive efforts to match the spring algal bloom (Falk-Petersen et al. 2009), e.g., females of the copepod *Calanus glacialis* utilize the spring pulse of ice algae to initiate reproduction, allowing their young to feed on the phytoplankton bloom that occurs after the breakup (Søreide et al. 2010). Along with temperature rise and sea-ice reduction, an increase in small-sized phytoplankton cells is predicted (Li et al. 2009) as well as a decrease in individual body size coupled with an increase in proportion of juveniles (Daufresne et al. 2009). At the population level, a shift of species may be observed, e.g., large, lipid-rich zooplankton species, such as *C. glacialis* and *C. hyperboreus* are being replaced by the smaller boreal and lipid-poorer species *C. finmarchicus* (Falk-Petersen et al. 2006).

Seawater temperature rise and warmer Atlantic and Pacific waters advected northward also represent a threat to Arctic biodiversity and may further change trophic relationships and food-web structure. These changes will facilitate open-water adapted species and boreal species to expand northward and ice-adapted species to retract in range (e.g. Sirenko & Gagaev 2007; Hollowed et al. 2013), which may lead to local extinctions, especially in the case of sea-ice dependent fauna (Clarke & Harris 2003). Changes have already been observed, including a northward distributional shift of fish and invertebrates in the Bering Sea (Mueter & Litzow 2008) and in the North Atlantic (Wienerroither et al. 2011) penetration of Pacific clams into the Chukchi Sea (Sirenko & Gagaev 2007), reoccurrence of Atlantic mussels in Svalbard (Berge et al. 2005), and Pacific zooplankton northward movement into the Beaufort Sea (Nelson et al. 2009). Also, an increase in year-round resident species may occur, e.g., grey whales that usually migrate south may stay in the Bering and Chukchi seas longer because of expanded open water feeding areas and warmer water temperature (Moore & Huntington 2008).

## Sea-ice gradient: scenarios and trends

Since sea-ice retreat is probably the most critical of expected consequences of climate warming for the Arctic marine ecosystems, in this review three regional ecosystem case studies are used to conceptualize possible changes in food-web structure and efficiency along a sea-ice gradient: the seasonally ice-free Barents Sea and Chukchi Sea, the loose ice pack Polar Front (PF) and Marginal Ice Zone (MIZ) and the permanently ice-covered High Arctic (Table 2, Fig. 2a, b – current status; Fig. 2B – predicted scenarios). In general, the described scenarios refer to current or possible future conditions on the shelves. The Barents and Chukchi seas were chosen as two Arctic shelf systems food web case studies as the food webs and associated trophic relations are relatively well-studied (e.g., Iken et al. 2010; Feder et al. 2011; Renaud et al. 2011; Dunton et al. 2012; Grebmeier 2012; Kędra et al. 2012; Nelson et al. 2014; Table 2, Fig. 2). PF and MIZ are highly productive zones, which are likely to change their locations, extents and features as the ice edge retreats from the coast and continental shelves (Fig. 2). Arctic deep-sea regions represent a large part of the Arctic Ocean susceptible to change due to fast sea-ice retreat, yet only few studies of deep benthic food webs are scarce (Bergmann et al. 2009; Iken et al. 2010; van Oevelen et al. 2011; Table 2). In all three cases studies, the scale and the extent of response to climate change and sea-ice retreat remain largely unknown.

**Table 2** Number of food-web studies undertaken in the Arctic by area. Data were collected using the search terms “Arctic” and “marine” and “food web” on the Web of Science. Studies that examined the relationship between two or more trophic levels were retained. Reviews and modelling with no in situ studies were excluded.

| Area | Number of studies |
|---|---|
| Barents Sea | 18 |
| Bering Sea | 17 |
| Beaufort Sea | 44 |
| Canadian Arctic | 69 |
| Central Arctic Ocean | 7 |
| Chukchi Sea | 16 |
| Greenland Sea | 23 |
| Labrador Sea | 61 |
| Laptev Sea | 1 |
| Svalbard | 45 |
| White Sea | 1 |
| Yermak Plateau | 2 |
| Total | 327 |

### Arctic shelf: seasonally ice-free – Barents and Chukchi seas

Many Arctic shelf systems are characterized by high benthic biomass and production especially in areas of inflow of Atlantic or Pacific nutrient-rich water masses, and along the PF polar front (Carmack & Wassmann 2006; Grebmeier et al. 2006a; Renaud, Morata et al. 2008; Fig. 2a). On the south-eastern Chukchi Sea shelf, primary production can reach exceed 430 g C $m^{-2}$ $y^{-1}$ and more (Springer et al. 1996; Sakshaug 2004; Lee et al. 2007); the Barents Sea has an estimated overall average annual primary productivity of about 100 g C $m^{-2}$ $y^{-1}$ and up to 300 g C $m^{-2}$ $y^{-1}$ in shallow banks (Sakshaug et al. 2009). Typically, about 44-67% of primary production in the Barents Sea reaches the seafloor (Wassmann, Reigstad et al. 2006; Wassmann, Slagstad et al. 2006) while in the Chukchi Sea it is up to 70% (Walsh et al. 1989). Unlike the Chukchi Sea, the Barents Sea supports immense fisheries and a high density of cetaceans. Pelagic foraging piscivores and nesting seabirds are twice as abundant in the Barents Sea than in the Chukchi Sea (Hunt et al. 2013). In the Barents Sea, seasonally resident cetaceans are four to five times more abundant than in the Chukchi Sea.

On the other hand, the density of pinnipeds and benthic-foraging whale species in the Chukchi is twice that of the Barents Sea, indicative of the Chukchi Sea being more of a benthic-driven system than the Barents Sea (Hunt et al. 2013). Indeed, Chukchi soft sediment infaunal and epifaunal communities are among the most productive in the world, reaching up to 50-100 g C $m^{-2}$ or up to ca. 4 kg wet wt $m^{-2}$ (Grebmeier et al. 1988; Grebmeier et al. 2006b; Feder et al. 2007), while in the most productive areas of shallow banks in the Barents Sea the benthic fauna reaches up to 30 g C $m^{-2}$ or 1.5 kg wet wt $m^{-2}$ (Kędra et al. 2013).

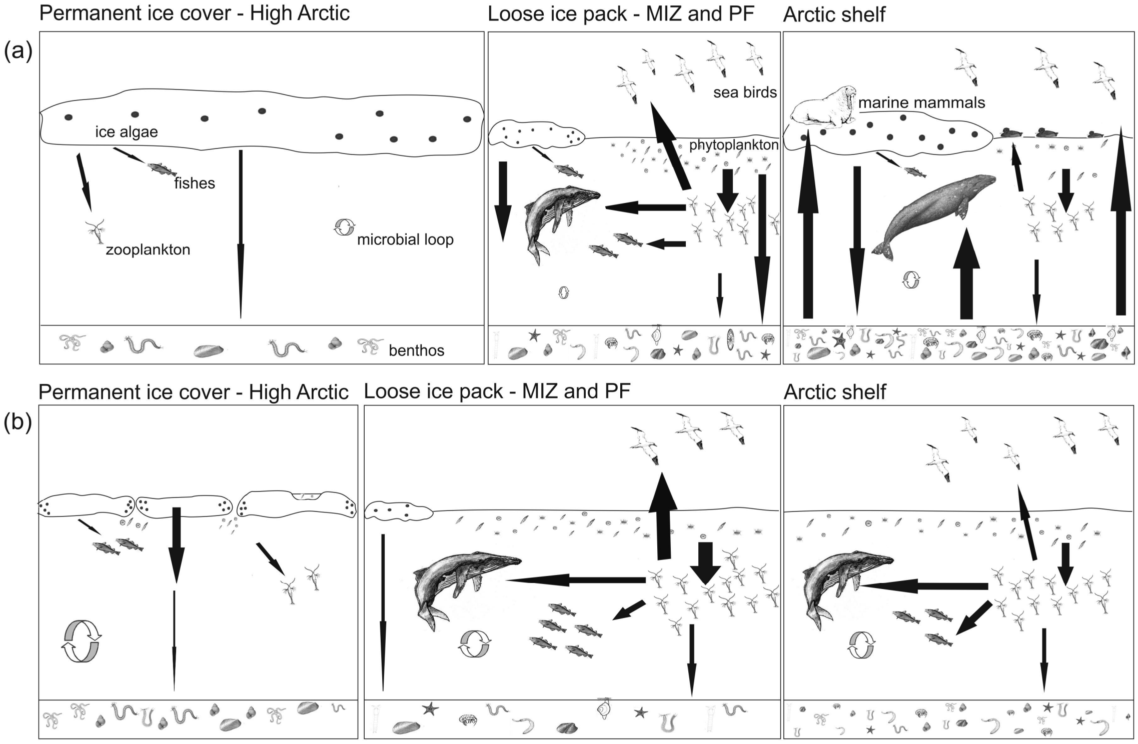

**Fig. 2** (a) Current and (b) predicted food-web scenarios for the Arctic shelf, Marginal Ice Zone (MIZ) and Polar Front (PF), and the High Arctic with permanent ice cover. The size of the picture frame for (b) reflects the predicted changes of relative contribution of each area.

Currently, the ice-edge is retreating northwards and in the near future, ice-free summers and seasonal ice cover in winter may become typical for the shelf seas (Fig. 2b). Increases in primary production and phytoplankton biomass are predicted, as well as have been measured, as a consequence of sea-ice retreat and temperature rise (Gradinger 1995; Arrigo et al. 2008; Arrigo & van Dijken 2011;

Wassmann & Reigstad 2011). Moreover, increased advection of Atlantic and Pacific waters into the Arctic Basin in the last decade (Walczowski & Piechura 2006; Woodgate et al. 2006; Piechura & Walczowski 2009; Woodgate et al. 2010; Walczowski et al. 2012) resulted in a 30% local increase of total primary productivity due to a greater proportion of smaller boreal planktonic species (Leu et al. 2011). Apart from quantitative changes in primary production, the quality and seasonality of primary production are expected to change because of the earlier onset of ice melt. Various stages of the reproductive cycle or increased activity of some Arctic benthic animals are timed to coincide with peak periods of organic matter deposition (Blake 1993; Renaud et al. 2007), so any change in seasonality, quantity or quality of food input may create a mismatch with faunal reproductive cycles (Renaud, Carroll et al. 2008). A shift from a benthic-oriented ecosystem with relatively low zooplankton stocks and strong pelagic–benthic coupling to a system dominated by pelagic food webs has already occurred in the northern Bering Sea in 1970s and 1980s (Overland & Stabeno 2004; Grebmeier et al. 2006b) and benthic productivity has been decreasing over the past two decades in the northern Bering and southern Chukchi seas (Moore et al. 2003; Grebmeier et al. 2006b; Grebmeier 2012).

### Loose ice pack—MIZ and PF

A significant feature of the recent (2007–2012) decrease in ice extent has been the retreat of the ice edge away from the coast and continental shelves. One of the more obvious impacts has been the northward expansion and widening of the MIZ, a dynamic and biologically active band of sea-ice cover adjacent to the open ocean (Strong & Rigor 2013). MIZ width is a fundamental feature for polar ecosystem functioning and climate dynamics (Wadhams 2000). It is an interfacial region that forms at the boundary of open and frozen ocean and protects the stable morphology of the inner ice from wave penetration (Squire 2007). In the MIZ, interactions between sea-ice and the open sea result in modification of the properties of the ice compared to areas deeper within the pack (Weeks 2010). Significant forcing that impacts the sea-ice in the MIZ results in varying surface roughness (Gupta et al. 2014), which affects prevalent physical and biological processes in the MIZ, such as wave dynamics (Wadhams et al. 1988; Squire et al. 1995), heat (Perovich et al. 1989), salt fluxes (McPhee et al. 2008) and floe size distribution (Lu et al. 2008). It can also create potential habitat for organisms inhabiting the ocean–ice system (e.g., Arctic cod [Fortier et al. 2006]). Properties of the MIZ relative to neighbouring ice pack can markedly affect the carbon cycle and behaviour of microorganisms and top-level predators (Dunbar & Leventer 1987; Arrigo et al. 2012). The MIZ has been a long-standing feature in many Arctic shelf seas, like in the Bering, Chukchi and Barents seas, but is a relatively new phenomenon in higher latitude regions such as the deep Beaufort Sea and Canada Basin (Shimada et al. 2006). The MIZ is advancing poleward into regions where sea-ice has become increasingly younger and thinner at the beginning of the annual melt (Strong & Rigor 2013). At the time of minimum sea-ice extent in September, the sea-ice edge is located over the deep Arctic Ocean, exposing large areas of previously permanently ice-covered waters, and MIZ-type conditions are becoming more prevalent in the High Arctic with the advancement of climate change.

Loss of sea ice will likely change the amount and characteristics of primary production in the MIZ (Bluhm & Gradinger 2008; Fig. 2b). Increased summer sea-ice melt will increase the overall extent of the MIZ over the shelves and lead to increased primary productivity (Anderson & Kaltin 2001). However, export fluxes largely depend on the coupling processes in the water column, including grazing, and therefore may not increase with warmer temperatures, especially in deep areas (Forest et al. 2010). Even if primary production increases, the fate of export fluxes will be different on Arctic shelves and over the deep Arctic Ocean (Lalande et al. 2014). It is likely that POC particulate organic carbon export will remain low above the central basins unless additional nutrients are supplied to surface waters (Codispoti et al. 2013; Lalande et al. 2014). Decreased export of diatoms, and dominance of coccolithophores was observed in Fram Strait during the warm period of 2005-07 (Bauerfeind et al. 2009; Lalande et al. 2013). Warmer water temperature also resulted in lower export fluxes of smaller zooplankton fecal pellets either due to a shift in zooplankton community composition towards small-sized zooplankton species or due to a shift in phytoplankton composition that affected grazing and fecal pellet production (Lalande et al. 2013). However, over the shelves, increased primary productivity will likely supply more food to pelagic and benthic consumers, while the low-productivity zone of the multiyear sea ice would shrink (Bluhm & Gradinger 2008). Sea-ice retreat off the shelves may result in upwelling of nutrients or planktonic prey from the basins onto the shelves (Carmack et al. 2004). Based on the inorganic carbon availability, Anderson & Kaltin (2001) proposed a possible increase of up to 50 g C $m^{-2}$ integrated over the upper 100 m of the water column across the Eurasian Basin, mainly as a result of ice loss. Nevertheless, it is the availability of nutrients, mainly nitrogen and phosphorous, that ultimately determines the total amount of primary productivity possible in any given ocean (Codispoti et al. 2013).

With reduced ice cover, ice-edge algal blooms will be displaced progressively northwards. Although benthic communities will still receive high-quality food in the short term, if the sea-ice edge retreats past the shelf break, shelf communities will no longer benefit from this early season food source (Renaud, Carroll et al. 2008) which would result in increased food input to slope and deep-sea communities (Carmack & Chapman 2003). Since it is likely that at least a part of deep-sea fauna originates from shelf species and a large overlap in taxa with Arctic shelf and deep sea taxa largely overlap currently exists (Bluhm, Ambrose et al. 2011), some shelf species would be able to dwell in the deep sea. If shelf species were unable to leave the slopes or survive in slope or deep-sea habitats, many Arctic shelf–benthos taxa could become locally extinct (Renaud, Carroll et al. 2008). Changes in under-ice community structure were noticed in the Eurasian basin in geographically close sampling locations collected within short time intervals. Habitat partitioning between sympagic and pelagic species can be abrupt, creating small-scale patterns in the surface layer community according to sea-ice habitat conditions. The difference in ice coverage was accurately mirrored by a conspicuous dominance of the ice-associated amphipod *Apherusa glacialis* in ice covered waters, versus a dominance of the pelagic amphipod *Themisto libellula* in the surface community of ice-free waters (Koszteyn et al. 1995; Hop & Pavlova 2008; David et al. 2015).

Fronts are regions characterized by narrow bands of horizontal gradients in temperature, salinity, density and biological properties that separate broader areas of different vertical structure (Mann & Lazier 1996; Belkin et al. 2003). In the Barents Sea, the Polar Front (PF) separates warmer, more saline Atlantic waters in the south from colder, less saline Arctic water in the north (Loeng 1991). Fronts can play a role in setting surface-layer properties by restratifying the surface layer (Timmermans & Winsor 2013) and thereby enhancing primary production. Fronts are known to support elevated biomasses of phytoplankton (Iverson et al. 1979), planktonic organisms (Basedow et al. 2014) and hyper-benthic communities (Dewicke et al. 2002) as well as bird and mammal aggregations (Bluhm et al. 2007). However, a recent study of the PF in the Barents Sea found no stimulatory effect on this front on primary production, and this result is attributed to this front being weak in terms of density (Erga et al. 2014). A related study found high secondary production at the PF, but also in surrounding waters (Basedow et al. 2014). Along with sea temperature rise and increased advection of Atlantic or Pacific waters into the Arctic Ocean, characteristics and location of PF are likely to change, influencing energy transfer to higher trophic levels. Northward displacement of the PF in the Barents Sea was predicted from coupled biophysical model for a B2 IPCC (Intergovernmental Panel on Climate Change) scenario (Huse & Ellingsen 2008). Simulations showed that PF displacement in the Barents Sea had impact on the distribution and spawning of capelin (*Mallotus villosus*). The model predicted increased production and large interannual variability in the Barents Sea, characteristic for the MIZ (Wassmann et al. 2010).

### Permanent ice cover—high Arctic

We have only limited knowledge of the energy flow and trophic structure of Arctic deep-sea regions. Very little is known about the linkages of the seasonal production pulse to the deep-sea communities in the High Arctic or even about the deep-sea communities themselves. Therefore, many of the assumptions made for shelf Arctic systems may not be valid for the central Arctic. The few available studies from the central Arctic report extremely low species richness and biomass (Kröncke 1994, 1998) for meiofaunal (Vanreusel et al. 2000) and macrofaunal taxa (Kröncke 1994; Clough et al. 1997; Kröncke 1998; Deubel 2000; Bluhm et al. 2005; Bluhm et al. 2011), as well as a decrease in diversity with increasing water depth (Kröncke et al. 1998). Primary productivity in the central Arctic is limited by light and nutrients. Constrained by light, sea-ice algal primary production occurs only from May to August and may be further restricted by ice thickness and snow cover (Rysgaard et al. 2001; Nicolaus et al. 2012). Nutrient supply on the other hand is constrained by stratification (Bourgain & Gascard 2011) and may not be sufficient in the central Arctic (Tremblay et al. 2008). Estimated average primary production in the ice-covered central Arctic is low, on the order of 1 to 25 g C $m^{-2}$ $year^{-1}$ (Wheeler et al. 1997; Wassmann et al. 2010), with ice algae production contributing from 0 to 80% (Gosselin et al. 1997; Wassmann et al. 2008). Bauerfeind et al. (2009) suggested very efficient processing of carbon within the water column, with <10 % of primary production reaching the seafloor in the deep sea (Fram Strait). Low primary production and export flux result in low abundance of suspension feeders in the deep basins (Kröncke et al. 1998) and a dominance of deposit feeders (van Oevelen et al. 2011). However, suspension feeders in the deep sea are known to utilize re-suspended material and directly compete with deposit feeders on the scarce food available (Lampitt et al. 1993; Iken et al. 2001). Although most benthic species in the deep sea seem to be able to cope with refractory material (van Oevelen et al. 2011), fresh phytodetritus may also arrive to the seafloor and support suspension feeders and surface deposit feeders such as cumaceans (Iken et al. 2005). Also, Boetius et al. (2013) reported fast response to *Melosira* falls of opportunistic deep-sea megafauna species, such as the holothurians *Kolga hyalina* and *Elpidia heckeri*, and the ophiurid *Ophiostriatus striatus*. Increased sediment respiration rates showed that sediment bacteria also profited from this ice-algae deposition (Boetius et al. 2013). However, infauna were probably unable to utilize ice algae as infaunal burrows and tubes were rarely seen in the under-water video footage, although they are common in other deep-sea basins with seasonally sedimenting phytoplankton blooms (Boetius et al. 2013). In the Arctic deep-sea plains, benthic communities are constrained by strong seasonality and limited food supply (Iken et al. 2005); ice algae production related to permanent sea-ice cover and export fluxes of organic matter to the sea floor are therefore important in these ecosystems. Benthic trophic pathways in the deep Arctic Ocean are longer than on the shelf region or in the temperate deep sea owing to the continuous recycling and thus isotopic enrichment of food particles in the benthic system, while a more direct link to fresh phytodetritus exists in the pelagic system (Iken et al. 2005; Bergmann et al. 2009).

In the past, the central Arctic Ocean has been covered with multiyear ice, but the marked decline in multiyear ice (Maslanik et al. 2011) suggests that the region could be ice-free by the summer of 2040 (Polyakov et al. 2010). Moreover, according to the latest publications, the central Arctic Ocean is no longer covered with multiyear ice pack (Polyakov et al. 2012) while the remnant multiyear sea ice occurs along the north-west flank of the Canadian Arctic Archipelago, where it can drift southwards, out over the Southern Beaufort Sea and northwards (Barber et al. 2009). If we assume that areas formerly covered with thick multiyear ice will have a thinner ice cover, permitting higher primary production, we can project a higher annual primary production level due to light availability, provided nutrients are available, which may not be the case in the basins (Codispodi et al. 2013; Matrai et al. 2013). A massive under-ice bloom was reported recently from consolidated ice pack in the northern Chukchi Sea, with phytoplankton biomass beneath the ice being about fourfold greater than in open water (Arrigo et al. 2012). Similar massive blooms might be widespread in the Arctic Ocean, in relation to the lower nutrient levels available. Yet, More work is needed to determine the extent to which such blooms are controlled by thinning sea ice and proliferating melt pond fractions and how they affect marine ecosystems.

Although higher light penetration will promote ice algal growth, low level of nutrients available and progressing climate warming may also reduce the algal growing season through increased thermal or haline stratification, limiting mixing and upward nutrient transport resulting in smaller export flux to the seafloor (Carmack & Wassmann 2006; Slagstad et al. 2010). In addition, if zooplankton abundance increases as warmer Atlantic and Pacific waters are transported into the Arctic Ocean (Hirche & Kosobokova 2007), the grazing pressure will increase, leading to increased retention of organic carbon in the water column. Some studies suggest that the flux of ice-algae and ice-related particulate organic matter will decrease along with sea-ice retreat and loss of multiyear ice (Forest et al. 2010). This may lead to decreased carbon deposition at the deep seafloor to already food-limited fauna, but these shifts are not expected to be rapid (van Oevelen et al. 2011). Yet, lack of reliable baseline information makes predictions difficult and identification of change nearly impossible (Wassmann et al. 2011).

## Gaps and recommendations

Despite numerous recent studies conducted recently (Table 2, Fig. 1.), major gaps remain in the knowledge of general processes governing biodiversity, food-web structure, trophic transfer efficiency and functioning of Arctic ecosystems. Since different regions of the Arctic have received varying levels of scientific attention (Table 2, Fig. 2), these recommendations may not apply to the whole Arctic and should be treated as more general statements. Given that these processes are not yet clearly quantified, any attempt to project changes that may occur in Arctic food webs in the future, such as that suggested in this review, should be taken cautiously. Currently, Most of the predictions are qualitative and biased towards conditions on the shelves, while quantitative ones remain scarce (but see Slagstad et al. 2010, 2011; Zhang et al. 2010; Popova et al. 2012). Since a lot of changes in the Arctic food webs are expected to be driven by a shift from decreasing sea-ice algae and an increase in pelagic production, observational, experimental and modelling approaches of the present-day coupling of these two production pathways in food webs should first be implemented, and subsequently combining different scientific methods will allow for the establishment of projection methodologies for Arctic ecosystems.

To date, Large-scale studies of food webs across Arctic regions highlighting inherent differences among regions are still lacking. Although deep-sea areas are still under-sampled because of the difficulty in accessing field sites, and a consistent sampling design does not exist Arctic-wide, the lack of sampling is not the main issue. Throughout the years and thanks to scientific programmes and researchers' efforts, data on the response of different benthic communities to climate change and on food webs have increased from multiple projects. These include HAUSGARTEN, the Alfred Wegener Institute's long-term monitoring programme in Fram Strait (Soltwedel et al. 2005), with data for more than 10 years, and the Distributed Biological Observatory (DBO), an international initiative in the Pacific Arctic (Grebmeier et al. 2010), with data over 30 years, including time series from Long-term Census of the Arctic (RUSALCA) programme. While efforts to sample the Arctic Ocean must and will continue, a primary ambition should therefore be to gather, combine and analyse existing information. Such efforts have been undertaken recently regarding Arctic biodiversity (e.g., Bluhm, Ambrose et al. 2011; Gill et al. 2011; Piepenburg et al. 2011), food sources and trophic interactions, e.g., the Pacific Marine Arctic Regional Synthesis project (PacMARS), although consistent data on food webs (sensu species interactions) are still missing. Similar-format databases should be established, centralized and made easily accessible to scientists at the international level, in order to explore the issues mentioned in this review, such as the PacMARS effort. Then, to promote further consistency of data collection, a standardized data sampling protocol should be implemented when possible to facilitate data gathering and data set use. Designated sampling stations should be sampled throughout months and years to monitor seasonal and long-term changes in biodiversity (Gill et al. 2011). Apart from species identity, functional lifestyle and life-cycle traits should be recorded, which would allow detecting and monitoring changes in ecosystem functioning (Cadotte et al. 2011).

To complement field sampling and database design, empirical manipulations to be performed in situ, in several places in the Arctic, should be encouraged. Such studies should address quantitative aspects of the impact of global warming on food-web length and components, including primary production rates, grazing rates and growth rates at higher trophic levels, in order to estimate changes in trophic transfer efficiency in Arctic food webs. Also, Studies of diets relative to availability of different foods are also critical to food-web analyses, especially to predicting response to changing conditions. In situ and laboratory experiments could be complemented by use of numerical modelling. Trophic network modelling methods that are widely used in other ecosystems could be implemented in the Arctic to understand food-web structure, the effects of external threats (e.g., increased fisheries pressure, invasive species) on food-web dynamics, and to quantify energy transfers between trophic levels, in conjunction with empirical work (e.g., van Oevelen et al. 2011). Results can be subsequently used to fuel models (e.g., provide nutrient–phytoplankton–zooplankton model parameters). Since data are still lacking, this could be achieved by using well-established predesigned software able to deal with missing parameters such as Ecopath (Pauly et al. 2000), especially for fishery scenarios, and the linear inverse model package LIM in the R statistical software package (van Oevelen et al. 2010). These models have the advantage of including both pelagic and benthic compartments and are able to quantify the strength of pelagic–benthic coupling. Although such models have been implemented for some Arctic regions (e.g., Trites et al. 1999; Pedersen & Zeller 2001; Aydin et al. 2002; Dommasnes et al. 2002; Whitehouse et al. 2014), they need to be updated, integrated and compared, especially after the recent environmental changes that have occurred in the Arctic. Stability analysis methods can also be coupled with the mass-balance modelling framework to provide insights into Arctic food-web structure and intrinsic properties (Neutel et al. 2002). Such methods may comprise analyses of stable-states of population or community dynamics, and analyses of food-web properties through determination of eigenvectors, resilience and persistence levels, and equilibrium shifts. At the theoretical level, population, metapopulation, community and metacommunity dynamic models can be implemented to understand how intra- and interspecific interactions and connectivity affect diversity at different spatial scales, such as between the different Arctic regions and the surrounding oceans (Carr et al. 2011; Hardy et al. 2011). Predicted ice melt and changing hydrodynamics may alter connectivity between distant Arctic populations, in turn affecting community composition and food-web structure. Such advances could provide valuable contributions to predicting future trends of biodiversity and food-web structure in the Arctic.

Statistical modelling, particularly quantification of species–environment relationships at large scales, should be assessed once data are pooled across Arctic regions. The statistical methods developed to date and applied to different biological organisms are an efficient means to disentangle the effects of environmental gradients (both in space and time) on community structure (Dray et al. 2012). Even though these methods are often based on species, they can be applied to functional groups to assess trait–environment relationships, hence reinforcing the need to monitor species traits during field sampling. Since environmental changes in the Arctic may affect species traits, the whole ecosystem functioning may be altered, and studying functional traits is a good way to assess ecosystem functioning and trophic transfer efficiency (McGill et al. 2006; Cadotte et al. 2011).

## Conclusions: winners and losers

Currently Arctic marine ecosystems are currently subjected to accelerating climate warming and fast progressing sea-ice retreat. Although our knowledge of ecosystem functioning and processes still has significant gaps, and the scale and magnitude of climate change remain largely unknown, some qualitative predictions on the fate of Arctic marine food webs are possible. In very general terms, among the “winners” will likely be boreal species as their populations tend to follow increasing sea temperature by shifting their ranges northward (and likely losing ground in the south), and pelagic species, mainly zooplankton, whose abundance and biomass may increase with increasing water column primary production related to more and earlier open water over the Arctic shelves. Pelagic feeding animals, like some fish, marine mammals and seabirds may consequently increase in abundance. Species classified as generalists are more likely to adapt to new conditions than specialists.

Groups that will likely be among the “losers” include Arctic species, especially those that are ice-dependent, as they will be most strongly affected by rising temperatures and diminishing habitat. Benthic species may decrease in biomass with increased pelagic grazing and recycling in the water column, which may lead to reduced amount or quality of organic matter settling from the water column to the seafloor. This will affect benthic feeding marine mammals and seabirds, whose foraging areas will become less productive and prey less available. Food webs will likely lengthen at the low trophic levels, lowering trophic transfer efficiency and thereby lowering the percentage of primary production that reaches top predators. Since many species at the base of the Arctic food webs are sea-ice dependent, the stability of food webs will likely be negatively affected in areas where trophic redundancy is low. Collaborative multidisciplinary research is necessary if we are to fully understand the processes and linkages between Arctic marine environments and their associated food webs in the face of a changing North.

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# 4 Synthesis

The benthos constitutes an important component in Arctic ecosystems, and although its relevance in ecosystem functioning and energy flow is generally acknowledged, studies linking benthic production patterns to ecosystem processes on large spatial scales are scarce. However, in the light of the substantial changes Arctic ecosystems are currently undergoing, exactly such large-scale assessments are urgently needed to build reliable carbon and food web models and to predict future scenarios. The present thesis tackled this challenge by estimating macro- and megabenthic secondary production and functioning on a shelf- and basin-wide scale (4.1) and identifying the environmental drivers behind the observed patterns (4.2). Based on these results, a thorough literature review, and the comparison of ecosystem functioning in the Eurasian Arctic basin between 1991 and 2012, we discuss potential future scenarios and the role of macro- and megabenthic communities as indicators of environmental change in the Arctic (4.3). The last sub-section (4.4) is dedicated to the overall conclusions of this thesis and recommendations for future studies.

## 4.1 Spatial and temporal patterns

Secondary production of megafauna was significantly higher in the north-eastern, seasonally ice-covered regions of the Barents Sea shelf than in the south-western, permanently ice-free areas (Manuscript I). In the Arctic deep-sea adjoining the Barents Sea shelf, macrobenthic secondary production decreased with increasing water depth, following the global pattern summarized in Cusson & Bourget (2005). Additionally, we detected substantial differences among regions, with highest P on the Yermak Plateau, a shallow, marginal plateau located northwest of the Spitsbergen shelf. Stations in this area showed comparable or even higher benthic secondary production than reported from some shallower regions at lower latitudes (see MS II for details). Lowest P was found in the deep Amundsen Basin. Albeit far north and distanced from more productive regions, the secondary production on Lomonosov Ridge is slightly higher, compared to the low values at Nansen and Amundsen Basin.

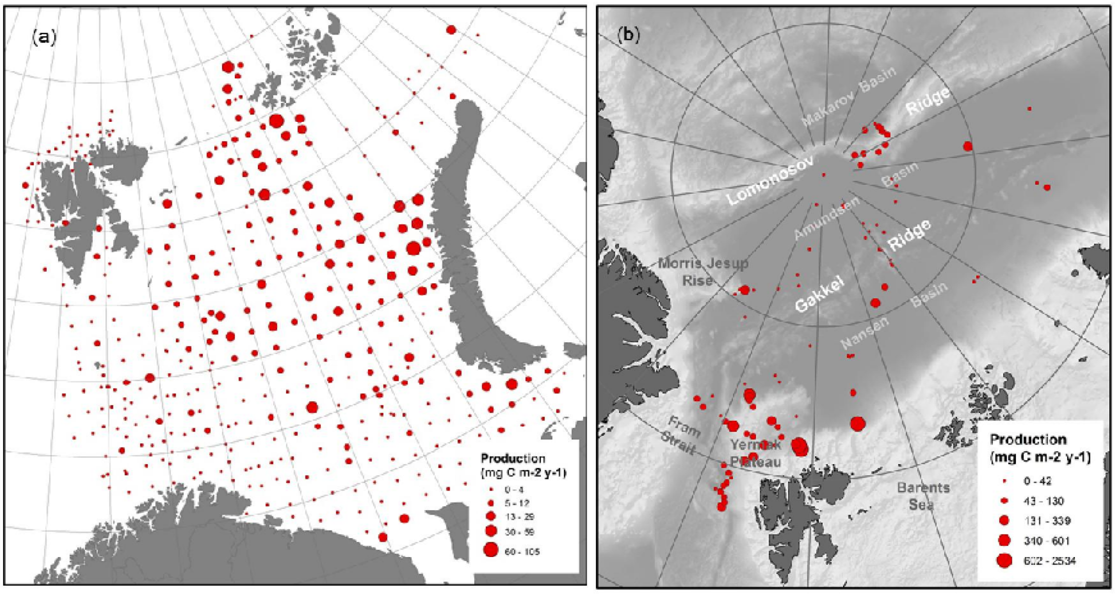

**Fig. 7** Patterns of megabenthic secondary production on the Barents Sea shelf (a) and of macrobenthic secondary production in the Arctic deep sea (b).

Significant differences in functioning were detected between shelf, slope and basin systems (Ms III). The BTA identified three characteristic communities in terms of functioning: a “flow or turbulence community” composed of sessile, stalked suspension feeders on the slope, a “soft bottom community” mainly composed of tube dwelling infauna taxa, and a “opportunistic community” dominated by large, mobile deposit feeding or scavenging taxa. High functional diversity was found on the Barents Sea shelf and on the Lomonosov Ridge, significantly lowest functional diversity was found in the deep Amundsen Basin.

In the Nansen Basin, secondary production seems to have been stable over the last decades, but the trait composition changed substantially between 1991 and 2012, with fauna shifting from a community dominated by mobile deposit feeders towards a sessile suspension feeding community. Secondary production in Amundsen Basin on the other hand was significantly higher in 2012 than in 1991, but the trait composition stayed the same.

## 4.2 Environmental drivers

On the Barents Sea shelf, six environmental parameters were identified to significantly explain the observed pattern of higher benthic secondary production: temperature, salinity, standard deviation of sea ice concentration, new primary production (NPP), trawling impact and bottom current speed. Four parameters thereof (i.e. standard deviation of sea ice concentration, temperature, salinity, and NPP) are directly related to the marginal ice zone (MIZ) (Manuscript I). We conclude that – although overall primary production is reported to be lower in the ice-covered regions (Wassmann et al. 2006) – the tight pelagic-benthic coupling along the MIZ facilitates high benthic production. The southern permanently ice-free areas, on the other hand, rather favor a pelagic food web (Tamelander et al. 2006; Carroll and Ambrose 2012). Water depth was found to be the main driver of benthic secondary production in the adjacent Arctic deep sea (Manuscript II). This difference compared to the Barents Sea shelf relates to the fact that depth gradients from 500-4500 m are implying gradients in food input to the benthic communities. This correlation is related to the higher retention and reworking of particulate organic carbon (POC) in the water column and to the fact that the deepest stations in this study are also the most distant ones from productive shelf regions, thus benefitting only little from lateral advection. Temperature on the other hand had no significant impact in the Arctic deep sea, as temperatures below a water depth of 800 m are relatively stable (Langehaug et al. 2012). But like on the shelf we identified sea ice concentration to explain the observed patterns in benthic secondary production. Significantly higher benthic secondary production was observed at stations affected by the MIZ, indicating that the influence of ice-edge related higher production and tight pelagic-benthic coupling is still visible in water depths >2000 m.

At Yermak Plateau, a deep-sea region influenced by the MIZ, we estimated a macrobenthic carbon demand that would require a gross primary production of 30–80 g C $m^{-2}$ $y^{-1}$ (see Manuscript II for details). Primary production in a comparable range is reported from productive Arctic shelf areas and regionally along the MIZ, but not from the central ice-covered Arctic, were values of <25 g C $m^{-2}$ $y^{-1}$ are expected (Klages et al. 2004, Wassmann et al. 2010). In the MIZ of the Barents Sea shelf we assume a benthic carbon demand of potentially much more than 70 g C $m^{-2}$ $y^{-1}$ (see Manuscript I and Kedra et al. 2013), although the mean new primary production estimated in these regions is only around 50 g C $m^{-2}$ $y^{-1}$ (Wassmann et al. 2006). These comparable estimates of benthic carbon demand that exceed the primary production in the MIZ of an Arctic shelf and the adjacent deep-sea basin imply that sea ice associated primary production might be considerably higher than previously anticipated. However, also advection of organic material from areas of high production has to be considered; especially the deep-sea regions bordering the productive Barents Sea shelf could benefit from such shelf-basin interactions (Piepenburg 2005; Grebmeier et al. 2006 ).

Our results of benthic secondary production from the Barents Sea shelf and the Amerasian deep-sea Basin corroborate the results of previous studies that identified food input (and tight pelagic-benthic coupling) as the main driver of benthic community structure (Piepenburg 2005). According to these results also the BTA detected changes in functioning along a spatial gradient of decreasing food supply (Manuscript III). The functional traits identified to explain most of the variances among regions were body form, morphology, bioturbation and living habit. All of these traits also relate to food input and feeding strategy of benthic taxa.

## 4.3 Future challenges

The global ocean will continue to warm during the 21st century. Year round reduction in Arctic sea ice is projected and a nearly ice-free Arctic Ocean in summer is likely before mid-century (Fig. 8) (IPCC 2015). Less ice-covered area will result in a longer productive period and in an increase in overall primary production (Arrigo et al. 2008), although due to enhanced stratification and reduced vertical mixing, surface production could become nutrient limited (Sarmiento et al. 2004; Behrenfeld et al. 2006). The associated fluxes to the benthos will be less episodic, and ice algae might loose importance also in higher latitudes (Forest et al. 2010).

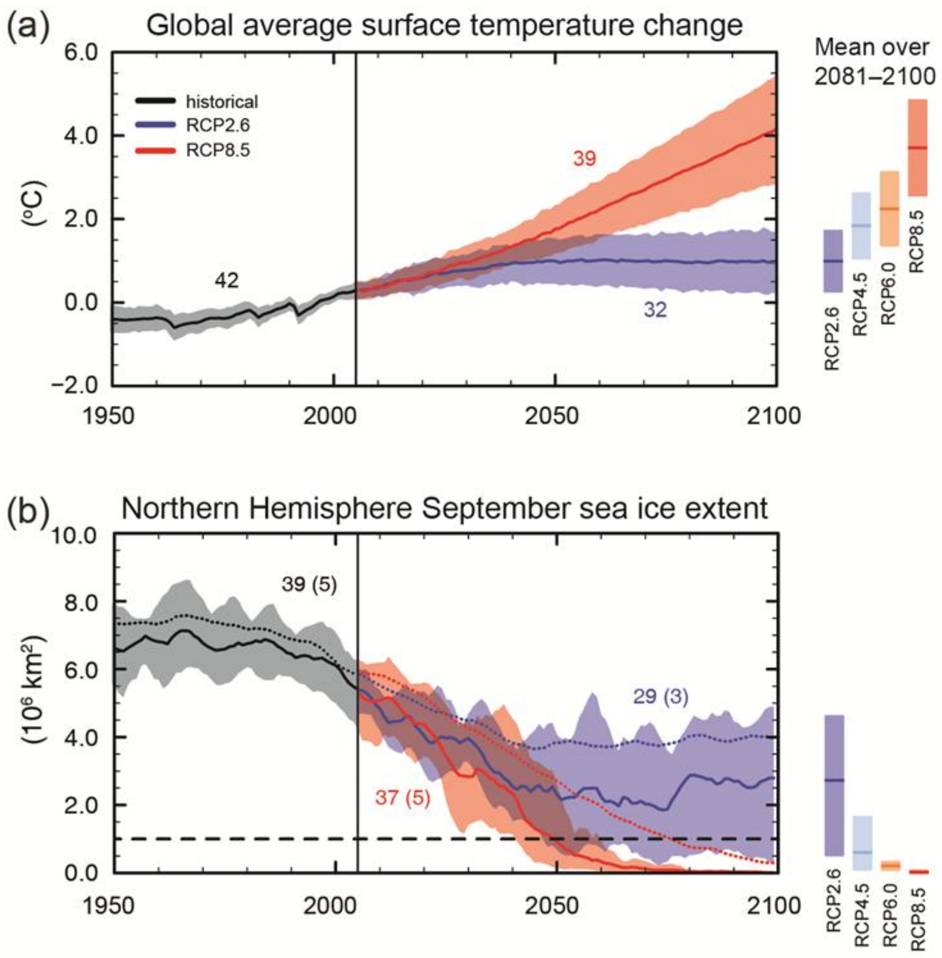

**Fig. 8** CMIP5 multi model simulated time series form 1950 to 2100 for (a) change in global annual mean surface temperature relative to 1986-2005 and (b) Northern Hemisphere September sea ice extent (5-year running mean). Time series of projections and a measure of uncertainty (shading) are shown for scenarios RCP2.6 (blue) and RCP8.5 (red). Black (grey shading) is the modelled historical evolution using historical reconstructed forcings. The mean and associated uncertainties averaged over 2081−2100 are given for all RCP scenarios as colored vertical bars. The numbers of CMIP5 models used to calculate the multi-model mean is indicated. For sea ice extent (b), the projected mean and uncertainty (minimum-maximum range) of the subset of models that most closely reproduce the climatological mean state and 1979 to 2012 trend of the Arctic sea ice is given (number of models given in brackets). For completeness, the CMIP5 multi-model mean is also indicated with dotted lines. The dashed line represents nearly ice-free conditions (i.e., when sea ice extent is less than 106 km$^2$ for at least five consecutive years) (IPCC, 2013).

Arctic shelves that had historically a food web structure more in favor of the benthic communities may begin to favor the pelagic trophic system (Gulliksen et al 2009; Carroll & Ambrose 2012) (Manuscript IV). Such a shift already occurred in the Bering Sea in the 1970ies, which changed from a benthic orientated system with tight pelagic-benthic coupling towards a system dominated by a pelagic food web; and benthic productivity has reportedly decreased since then (Grebmeier et al. 2006b). The high secondary production in areas influenced by the MIZ on the Barents Sea shelf implies that the future benthic communities will be significantly impoverished in terms of secondary production. As the benthic compartment is of crucial importance in the energy flow of Arctic shelves, these changes will have cascading effects through the entire food web. Especially benthic feeding marine mammals and seabirds will be affected and are listed among the "losers" in the future scenario of ice-free Arctic shelves (Fig. 9b).

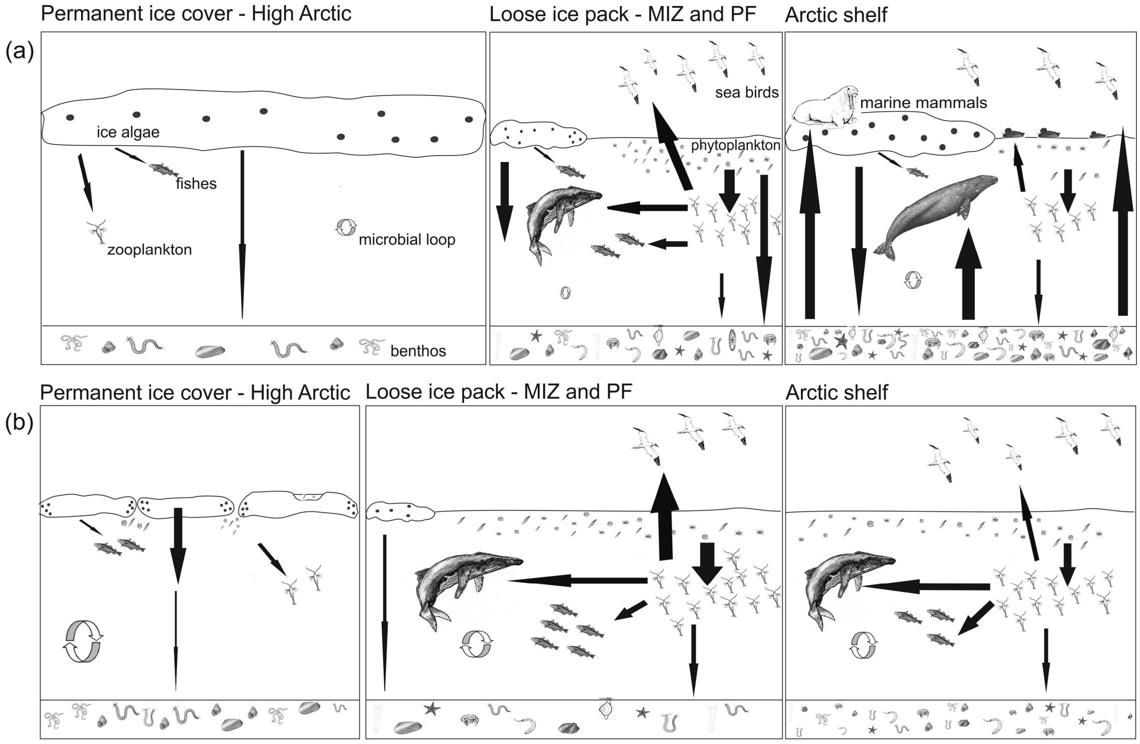

**Fig. 9** (a) Current and (b) predicted food-web scenarios for the Arctic shelf, Marginal Ice Zone (MIZ) and Polar Front (PF), and the High Arctic with permanent ice cover. The size of the picture frame for (b) reflects the predicted changes of relative contribution of each area (Kedra et al. 2015; Manuscript IV).

Benthic systems of the Arctic deep-sea on the other hand might benefit at least for some decades, as the MIZ – in previous decades not reaching the higher latitudes – now passes and assumingly supplies them with more fresh organic input (Fig. 9b). Our results support this assumption as we detected higher benthic secondary production in the Amundsen Basin 2012 compared to 1991, indicating already increased fluxes of POC to the benthos (Fig. 10). Also the functional diversity increased in Amundsen Basin 2012 – an indication for a higher functional redundancy than in 1991. The different functioning in Nansen Basin 2012 compared to 1991 equally points in that direction. The community shifted towards a sessile suspension feeding community, indicating that enough food input might be available to support a sessile life style.

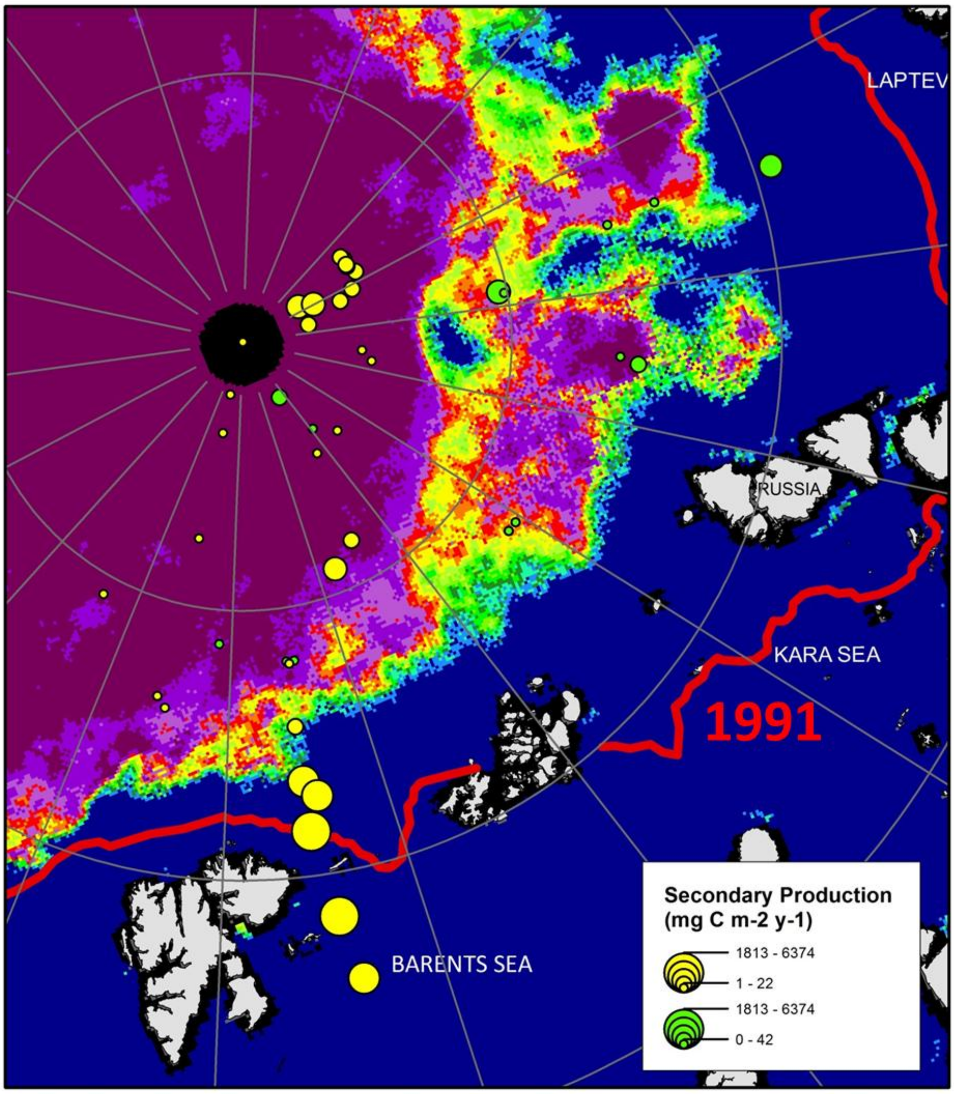

**Fig. 10** Sample stations from Nansen and Amundsen Basin in 1991 (yellow) and 2012 (green). The red line indicates the minimum sea ice extent of the year 1991. Sea ice concentration of the sea ice minimum in the year 2012 is given with dark red indicating high, and blue-green indicating very low sea ice concentration (Spreen et al. 2008) (Manuscript III).

## 4.4 Conclusions and outlook

Benthic secondary production and ecological functioning were evaluated for the first time on an Arctic shelf and basin-wide scale, contributing to a better understanding of the Arctic energy flow and providing a valuable input in prospective Arctic carbon and food web models. We detected significant differences within and between the compared regions and identified food input to be the main driver of the observed patterns in Arctic benthic systems. Due to the associated tight pelagic-benthic coupling the MIZ was identified as a zone of crucial importance for benthic energy flow, for both shelf and deep-sea systems. In the light of ongoing climate warming and sea ice decrease, Arctic shelf systems might face drastic changes, with a shift from benthos dominated food webs towards food webs more in favor of pelagic production. Deep sea benthic communities on the hand could benefit form the new proximity to the MIZ and associated food fluxes. The comparison of macrobenthic functioning at stations sampled recently with stations sampled 20 years ago indicates that functional changes are already happening.

Based on the results of this and other recent studies we can make qualitative predictions regarding the fate of Arctic benthic ecosystems, but we are still facing significant knowledge gaps. Integrated approaches are necessary to sufficiently explore energy flow through the Arctic benthic ecosystems and to predict reliable future scenarios. Such approaches include sampling of all benthic size compartments at representative locations of Arctic shelves, slopes and basins, with special emphasis on areas that are already experiencing changes in sea ice cover, e.g. the eastern Arctic Basins (see Fig. 10). A focus should be set on the use of traditional sampling gear and procedure, to ensure comparability to historic datasets. Data mining should be continued and prosecuted on a collaborative base to enhance our knowledge about the “pre-change” system state (Wassmann et al. 2011a). Here focus should be set on regions which are currently blind spots in terms in benthic research, be it due to inaccessibility of these regions (e.g. the Canadian Archipelago), or due to international data policy (e.g. the Kara Sea, East Siberian Sea) (see Manuscript IV). In addition, the methods successfully applied in this thesis, i.e. the geostatistical analysis of benthic secondary production and biological trait analysis (BTA), should be carried forward in Arctic benthic research. Especially the BTA proved to be a promising tool to highlight early changes in benthic functioning. The combined effort of comprehensive data acquisition and the methods employed here will improve our predictions of functioning and energetics of the future Arctic biosphere.

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**Web sources of Figures**

Fig. 1, Fig. 6 National Oceanic Atmospheric Administration – NOAA, Northeast Fisheries Science Center - NEFSC. http://www.nefsc.noaa.gov/.

Fig. 3 ArcOD – Arctic Ocean Diversity. www.arcodiv.org.

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# 7 Appendix

**Appendix of Mansucript III:** Fuzzy coded biological traits of Arctic macrofauna. Explanations of traits and modalities can be found in table 2, Manuscript III.

| | S | | | LD | | BF2 | | | Mor | | | | | | H | | LH | | | | | Mob | | | Mov | | | | FH | | | | | AT | | BT | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **1** | **2** | **3** | **4** |
| *Acmaea* | 0 | 2 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 2 | 3 | 0 | 0 | 0 |
| *Actiniaria* | 0 | 1 | 3 | 0 | 3 | 1 | 2 | 2 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 0 | 0 | 0 | 3 |
| *Aglaophamus malmgreni* | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 1 | 2 | 0 | 0 |
| *Akanthophoreus gracilis* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Alcyonium* | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 3 |
| *Ambasia atlantica* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 1 | 2 | 2 | 3 | 0 | 0 | 0 |
| *Ampelisca macrocephala* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 1 | 3 | 2 | 0 | 2 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Ampharete finmarchica* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Ampharetidae* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Amphilochus* | 3 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Amphipoda* | 1 | 2 | 2 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 0 | 2 | 2 | 0 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 0 |
| *Ampithoe* | 1 | 2 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Anobothrus gracilis* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Anobothrus laubieri* | 1 | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Anthozoa* | 0 | 1 | 3 | 0 | 3 | 1 | 2 | 2 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 0 | 0 | 0 | 3 |
| *Aphelochaeta* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 3 | 0 | 3 | 3 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Apistobranchus tullbergi* | 1 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 2 | 1 | 1 | 0 |
| *Aponuphis bilineata* | 0 | 0 | 3 | 3 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 3 | 1 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Aricidea* | 1 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 |
| *Aricidea suecica* | 1 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 |
| *Astarte montagui* | 0 | 3 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Asychis biceps* | 0 | 1 | 3 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Axinopsida orbiculata* | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Bathyarca* | 0 | 1 | 3 | 0 | 3 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Bathyarca glacialis* | 0 | 1 | 3 | 0 | 3 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Bivalvia* | 1 | 2 | 2 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 2 | 0 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 1 | 3 | 1 | 2 | 2 | 2 | 0 |
| *Bowerbankia* | 1 | 2 | 2 | 0 | 3 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Brachydiastylis resima* | 2 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Brada villosa* | 0 | 0 | 3 | 3 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 3 | 1 | 1 | 2 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Byblis gaimardii* | 0 | 2 | 1 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 1 | 3 | 2 | 0 | 2 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Calathura norvegica* | 0 | 3 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 |
| *Campylaspis rubicunda* | 2 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Campylaspis verrucosa* | 2 | 3 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |

| | **S** | | | **LD** | | **BF2** | | | **Mor** | | | | | | **H** | | **LH** | | | | | **Mob** | | | **Mov** | | | | **FH** | | | | | **AT** | | **BT** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **1** | **2** | **3** | **4** |
| *Capitella* | 0 | 1 | 2 | 1 | 2 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 |
| *Capitellidae* | 0 | 1 | 2 | 1 | 2 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 |
| *Caudofoveata* | 1 | 2 | 2 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 1 | 3 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Chaetoderma* | 1 | 2 | 2 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 1 | 3 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Chaetozone* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Chaetozone setosa* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Chelator* | 2 | 1 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 3 | 0 | 2 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 |
| *Chone duneri* | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 2 |
| *Cirratulidae* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Cirratulus* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Cleonardo appendiculatus* | 1 | 2 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Cossura longocirrata* | 0 | 3 | 0 | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Ctenodiscus crispatus* | 0 | 1 | 3 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 1 |
| *Cuspidaria* | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 |
| *Cylichna* | 1 | 3 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 3 | 0 | 0 | 0 |
| *Dacrydium vitreum* | 0 | 1 | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Diastylis laevis* | 1 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Diastylis lucifera* | 1 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Diastylis scorpioides* | 1 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Diastylis tumida* | 1 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Diastyloides biplicatus* | 1 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Dipolydora caulleryi* | 1 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 |
| *Dorvillea rubrovittata* | 0 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 3 | 1 | 2 | 2 | 0 | 0 | 1 |
| *Edwardsia* | 0 | 1 | 2 | 0 | 3 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 2 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 1 | 0 | 0 | 2 |
| *Elpidia glacialis glacialis* | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |
| *Elpidia heckeri* | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |
| *Ennucula tenuis* | 0 | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Eteone longa* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 3 | 0 | 0 | 0 |
| *Euchone* | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 2 |
| *Euclymene* | 0 | 0 | 3 | 3 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Eudorella truncatula* | 2 | 1 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Eurycope* | 1 | 2 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Galathowenia fragilis* | 0 | 1 | 2 | 0 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |

| | S | | | LD | | BF2 | | | Mor | | | | | | H | | LH | | | | | Mob | | | Mov | | | | FH | | | | | AT | | BT | | | |
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| | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **1** | **2** | **3** | **4** |
| *Galathowenia oculata* | 0 | 1 | 2 | 0 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |
| *Gastropoda* | 1 | 2 | 2 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 0 | 0 | 0 |
| *Gattyana cirrhosa* | 0 | 0 | 3 | 1 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 0 |
| *Geodia phlegraei* | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Glyphanostomum pallescens* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Gnathia* | 3 | 1 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Golfingia* | 0 | 1 | 3 | 0 | 3 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 |
| *Golfingia (Golfingia) margaritacea* | 0 | 1 | 3 | 0 | 3 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 |
| *Halice* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 |
| *Halice abyssi* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 |
| *Haploops* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 1 | 3 | 2 | 0 | 2 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Harpinia* | 1 | 2 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Henricia* | 0 | 0 | 3 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Hesionidae* | 0 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 3 | 2 | 0 | 0 | 1 |
| *Heteromastus filiformis* | 0 | 0 | 3 | 1 | 2 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 |
| *Hippomedon* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 3 | 0 | 2 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Hydrozoa* | 0 | 1 | 3 | 0 | 3 | 1 | 2 | 2 | 0 | 0 | 0 | 2 | 1 | 2 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 0 | 0 | 0 | 3 |
| *Ischyrocerus anguipes* | 1 | 2 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Isopoda* | 2 | 1 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Lagis koreni* | 0 | 1 | 2 | 0 | 3 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 0 | 3 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Langerhansia cornuta* | 0 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 3 | 3 | 0 | 0 | 0 |
| *Laonice* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 1 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Laonice sarsi* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 1 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Laonome kroyeri* | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 2 |
| *Leitoscoloplos* | 0 | 0 | 3 | 1 | 2 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 |
| *Leptognathia breviremis* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Leptognathiidae* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Leucon* | 3 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Leucon (Leucon) acutirostris* | 3 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Levinsenia gracilis* | 0 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 |
| *Lumbriclymene* | 0 | 0 | 3 | 3 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Lumbrineris fragilis* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 1 | 1 | 0 | 0 |
| *Lumbrineris magnidentata* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 1 | 1 | 0 | 0 |

|  | **S** |  |  | **LD** |  | **BF2** |  |  | **Mor** |  |  |  |  |  | **H** |  | **LH** |  |  |  |  | **Mob** |  |  | **Mov** |  |  |  | **FH** |  |  |  |  | **AT** |  | **BT** |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **1** | **2** | **3** | **4** |
| *Lumbrineris scopa* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 1 | 1 | 0 | 0 |
| *Lunatia* | 1 | 2 | 3 | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 0 |
| *Lysianassidae* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 3 | 1 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Lysianassoidea* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 3 | 1 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Lysippe fragilis* | 1 | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Macoma calcarea* | 0 | 0 | 3 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Magelona* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Maldane sarsi* | 0 | 0 | 3 | 3 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Melinnopsis somovi* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Melphidippidae* | 2 | 1 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 3 | 3 | 1 | 0 | 3 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Minuspio (Prionospio) cirrifera* | 0 | 2 | 2 | 0 | 3 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Munna* | 3 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Munnopsidae* | 3 | 1 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Musculus niger* | 0 | 1 | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Mya truncata* | 0 | 1 | 3 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Myriochele heeri* | 0 | 2 | 1 | 0 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |
| *Myriotrochus* | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 0 |
| *Myriotrochus rinkii* | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 3 | 1 | 0 |
| *Mysida* | 3 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 1 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Nannoniscus* | 3 | 1 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 |
| *Nematoda* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 1 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Nemertea* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 3 | 2 | 3 | 3 | 0 | 0 | 0 |
| *Nephtys ciliata* | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 1 | 2 | 0 | 0 |
| *Nephtys paradoxa* | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 1 | 2 | 0 | 0 |
| *Nicomache lumbricalis* | 0 | 0 | 3 | 3 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Nothria conchylega* | 0 | 0 | 3 | 3 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 3 | 1 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Notomastus latericeus* | 0 | 0 | 3 | 1 | 3 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 |
| *Nuculana pernula* | 0 | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Oenopota* | 0 | 3 | 1 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 3 | 0 | 0 | 0 |
| *Ophelina* | 0 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Ophelina abranchiata* | 0 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Ophelina cylindricaudata* | 0 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Ophiocten sericeum* | 0 | 1 | 3 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 2 | 0 | 3 | 0 | 2 | 0 | 0 | 1 |

| | **S** | | | **LD** | | **BF2** | | | **Mor** | | | | | | **H** | | **LH** | | | | | **Mob** | | | **Mov** | | | | **FH** | | | | | **AT** | | **BT** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **1** | **2** | **3** | **4** |
| *Ophiura* | 0 | 1 | 3 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 2 | 0 | 3 | 0 | 2 | 0 | 0 | 1 |
| *Ophiura robusta* | 0 | 1 | 3 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 2 | 0 | 3 | 0 | 2 | 0 | 0 | 1 |
| *Owenia fusiformis* | 0 | 1 | 2 | 0 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 |
| *Paraonis* | 0 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 |
| *Phascolion (Phascolion) strombus* | 0 | 2 | 2 | 0 | 3 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 |
| *Pherusa plumosa* | 0 | 0 | 3 | 3 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 3 | 1 | 1 | 2 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Philine* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 3 | 0 | 0 | 0 |
| *Pholoe inornata* | 1 | 2 | 0 | 1 | 2 | 3 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 2 | 0 | 0 | 0 |
| *Photis longicaudata* | 2 | 2 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Phyllodoce groenlandica* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 3 | 0 | 0 | 0 |
| *Poecilochaetus* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 2 | 1 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 1 | 0 |
| *Polycirrus* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Polyplacophora* | 0 | 3 | 2 | 0 | 3 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 |
| *Porifera* | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Pourtalesia jeffreysi* | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 |
| *Priapulus caudatus* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Prionospio steenstrupi* | 0 | 2 | 2 | 0 | 3 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Proclea malmgreni* | 0 | 2 | 1 | 3 | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Protis arctica* | 0 | 2 | 1 | 0 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Protomystides* | 0 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 3 | 3 | 0 | 0 | 0 |
| *Pseudosphyrapus anomalus* | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Pseudotanaidae* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Pseudotanais* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Pycnogonida* | 0 | 2 | 1 | 3 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 | 3 |
| *Radiella hemisphaerica* | 0 | 2 | 2 | 0 | 3 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Samytha sexcirrata* | 0 | 2 | 1 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Scalibregma inflatum* | 0 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 1 | 0 |
| *Scolelepis* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 1 | 2 | 0 | 2 | 2 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 1 | 3 | 0 |
| *Scopelocheirus* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 2 | 3 | 2 | 1 | 0 | 0 | 3 |
| *Siboglinidae* | 0 | 0 | 3 | 0 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Siboglinum* | 0 | 0 | 3 | 0 | 3 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Sphaerodorum* | 0 | 0 | 3 | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Sphaerodorum gracilis* | 0 | 0 | 3 | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |

| | **S** | | | **LD** | | **BF2** | | | **Mor** | | | | | | **H** | | **LH** | | | | | **Mob** | | | **Mov** | | | | **FH** | | | | | **AT** | | **BT** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **4** | **5** | **6** | **1** | **2** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **1** | **2** | **3** | **4** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **1** | **2** | **3** | **4** |
| *Spiochaetopterus typicus* | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 1 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Spiophanes kroyeri* | 0 | 1 | 3 | 0 | 3 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Stenothoidae* | 3 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 2 | 1 | 3 | 1 | 3 | 0 | 0 | 0 |
| *Stephanoscyphus* | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 3 |
| *Tanaidacea* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Tentorium semisuberites* | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Terebellidae* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Terebellides* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Terebellides stroemii* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Tharyx* | 0 | 1 | 2 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Thenea abyssorum* | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Thyasira gouldi* | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Tiron spiniferus* | 0 | 3 | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 2 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Tubificoides* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 0 | 0 |
| *Tunicata* | 0 | 1 | 2 | 0 | 3 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| *Typhlotanais finmarchicus* | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 2 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Ymerana pteropoda* | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| *Yoldiella* | 0 | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Yoldiella frigida* | 0 | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Yoldiella intermedia* | 0 | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Yoldiella lenticula* | 0 | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| *Yoldiella lucida* | 0 | 2 | 1 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |

# Erklärung gemäß § 6 (5) PromO

(vom 14. März 2007)

Name: Renate Degen
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Datum & Ort:

Ich erkläre hiermit eidesstattlich, dass ich

1. die vorliegende Doktorarbeit mit dem Titel “The Future Arctic Biosphere – Environmental Drivers of Change in Arctic Benthic Biota” ohne unerlaubte fremde Hilfe angefertigt habe,
2. keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe,
3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

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