



Ecology of krill in Icelandic waters

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Ecology of krill in Icelandic waters

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Abstract

Krill are an important component of the Icelandic marine ecosystem. Given their important ecological niche, as conveyors of biological production between phytoplankton and higher trophic levels, fluctuations in krill abundance can have large impacts on the dynamics of species at higher trophic levels. For this reason, understanding their population dynamics is of great importance. This thesis aims to contribute new insights into the biology of krill and their ecological role in the Icelandic marine ecosystem. The thesis is based on four scientific publications, three of which are published. One manuscript examines seasonal and long-term changes of krill in the North Atlantic (**Paper I**). The results show a significant decreasing trend in annual mean abundance of krill from 1958 to 2007 in the oceanic waters south and southwest of Iceland. It is hypothesized that a weakened temporal synchrony between the development of young euphausiids and the phytoplankton bloom influenced by recent climate warming may have led to the observed decrease in krill abundance. Two manuscripts assess krill abundance, distribution and development, in relation to environmental variables and phytoplankton spring bloom dynamics around Iceland (**Papers II and III**). Krill abundance was closely associated with abiotic factors (mainly temperature, salinity and bottom depth) and biotic factors (phytoplankton concentration and the onset of the phytoplankton bloom). Hydrographic conditions are important for growth and development. For instance, krill eggs and larvae were much more abundant in the warmer waters south of Iceland than in the colder waters off the north coast in May 2013. Adults were also most abundant in the warm water. *Meganyctiphanes norvegica* dominated in the Atlantic water in south and west of Iceland, whereas *Thysanoessa inermis* was found more evenly distributed around the island, while the highest values were also observed in the southwest for this species. The fourth paper evaluates the effect of temperature on physiological rates of *M. norvegica* (**Paper IV**). It is shown that temperature influences the physiological rates of *M. norvegica*; with increasing temperature, both egestion and mortality rates increased. Moulting frequency increased with temperature.

Útdráttur

Ljósáta er mikilvæg í vistkerfi Íslandsmiða. Vegna þess að stór hluti af frumframleiðslu svifþörunga berst til efri fæðuþrepa um ljósátu er líklegt að breytingar í stofnstærðum ljósátustofna segi til sín í vexti og viðgangi dýra sem eru ofar í fæðukeðjunni. Rannsóknir á vistfræði ljósátu eru því mikilvægar. Rannsóknin byggir á þremur ritrýndum greinum og einni sem liggur fyrir í handriti. Fyrsta greinin fjallar um árstíða- og langtímabreytingar ljósátu suðvestur, suður og suðaustur af landinu í tengslum við umhverfisþætti og svifgróður (**Grein I**). Niðurstöðurnar sýndu að á árunum 1958 til 2007 minnkuðu ljósátustofnar suður og suðvestur af landinu. Í ritgerðinni er líkum leitt að því, að hlýnun sjávar á umræddu tímabili hafi valdið því að vorvöxtur plöntusvifs var tiltölulega seint á ferðinni sem aftur kann að hafa valdið því að það dró úr vexti ljósátu. Tvær greinar lýsa útbreiðslu, magni og aldurssamsetningu ljósátu umhverfis Ísland að vorlagi í tengslum við umhverfisþætti og vorvöxt plöntusvifs (**Greinar II og III**). Niðurstöðurnar sýndu að magn ljósátu tengist bæði ólífrænum þáttum (aðallega hita, seltu og botndýpi) og lífrænum (einkum magni og tímasetningu vorvaxtar svifgróðurs). Útbreiðsla sjógerða við landið hefur þannig mikil áhrif á vöxt og viðgang ljósátu. Til dæmis voru ljósátuegg og -lirfur mun algengari í hlýsjónum suður og vestur af landinu en í kaldari sjó fyrir norðan og norðaustan í maí 2013. Fullorðin dýr voru einnig algengust í hlýsjónum. Þannig var stærsta ljósátutegundin, náttlampi (*Meganyctiphanes norvegica*), algengust í hlýsjónum fyrir sunnan og vestan. Augnsíli (*Thysanoessa inermis*) var hins vegar tiltölulega algengt allt í kringum land, en einsog náttlampi fannst mest af því í hlýsjónum fyrir sunnan og vestan. Í fjórðu greininni er gerð grein fyrir niðurstöðum rannsókna þar sem náttlampi var alinn við mismunandi hitastig í tilraunastöð Hafrannsóknastofnunar að Stað við Grindavík (**Grein IV**). Hitastig reyndist hafa mikil áhrif á úrgangslausun og dánartölu dýranna. Tíðni skelskipta jókst með auknu hitastigi.

To my daughter, Diana
and
in memory of my uncle
Antonio Giesta (1971-2013).

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List of Original Publications

- Paper I:** Silva T., Gislason A., Licandro P., Marteinsdóttir G., Ferreira A. S. A., Gudmundsson K. and Astthorsson O. S. 2014. Long-term changes of euphausiids in shelf and oceanic habitats southwest, south and southeast of Iceland. *Journal of Plankton Research*, 36: 1262–1278.
- Paper II:** Silva T., Gislason A., Astthorsson O. S. and Marteinsdóttir G. 2016. Abundance and distribution of early life stages of krill around Iceland during spring. *Marine Biology Research*, 12: 864–873.
- Paper III:** Silva T., Gislason A., Astthorsson O. S. and Marteinsdóttir G. 2017. Distribution pattern, maturity and population structure of *Meganyctiphanes norvegica* and *Thysanoessa inermis* around Iceland in spring. *PLoS ONE*, 12 (11): e0187360.
- Paper IV:** Silva T., Gislason A. and Astthorsson O. S. 2018. Effects of temperature on growth, egestion and mortality of *Meganyctiphanes norvegica* south of Iceland. Manuscript.

Published manuscripts not included in the thesis:

- Gislason A. and Silva T. 2012. Abundance, composition, and development of zooplankton in the Subarctic Iceland Sea in 2006, 2007, and 2008. *ICES Journal of Marine Science*, 69: 1263–1276.
- Víkingsson G. A., Pike D. G., Schleimer A., Valdimarsson H., Gunnlaugsson T., Silva T., Elvarsson B. P., Mikkelsen B., Øien N., Desportes G., Bogason V., Hammond P. 2015. Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Frontiers in Ecology Evolution*, 3: 1–18.

Abbreviations

BL	Body Length
CE	Catch Efficiency
chl <i>a</i>	Chlorophyll <i>a</i>
CL	Carapace Length
CPR	Continuous Plankton Recorder
DTU Aqua	Technical University of Denmark: National Institute of Aquatic Resources
EURO-BASIN	European Union Basin-scale Analysis, Synthesis and Integration
GAM	Generalized Additive Model
Isa	Isafjord-deep
MARICE	Marine Academic Research in Iceland
MFRI	Marine and Freshwater Research Institute
MRI	Marine Research Institute
NAO	North Atlantic Oscillation
NASC	Nautical Area Scattering Coefficient
OPB	Onset of Phytoplankton Spring Bloom
SAHFOS	Sir Alister Hardy Foundation for Ocean Science
SST	Sea Surface Temperature
TL	Total Length
WP2	Working Party 2 – Vertical plankton net

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1 Introduction

1.1 Rationale and background studies

The Icelandic marine ecosystem is one of the world's most productive ocean regions (Longhurst et al., 1995; Lutz et al., 2007; Zhai et al., 2012). The ocean around Iceland comprises approximately 87% of the total Icelandic territory. Fisheries have been a key source of revenue for the Icelandic economy for centuries and continue to be of vital importance at present (Astthorsson and Vilhjálmsson, 2002; Sigurdardóttir et al., 2016). For example, in 2015 the marine sector accounted for ~8% of the Icelandic Gross Domestic Product, with revenues from the export of goods estimated at ~800 000 € (Sigurdardóttir et al., 2016). As one of the world's leading fishing nations, Icelanders have sought to conduct the fishery in a sustainable manner. To successfully manage fisheries and to protect both the exploited and non-exploited species, an ecosystem-based fisheries management is required (Grumbine, 1994; Pikitch et al., 2004). Even though scientists have collected extensive data on the most important exploited species and Iceland has performed well in the implementation of ecosystem-based fisheries management (Pitcher et al., 2009), lack of data on keystone species, such as krill, may hinder the efficiency of such management schemes (Pikitch et al., 2004; Ballesteros et al., 2017). Thus, before an ecosystem-based fisheries management approach can be fully and effectively implemented, comprehensive knowledge of the biology of keystone species in the ecosystem is essential.

The North Atlantic Ocean, including Icelandic waters, is a region with profound variations in environment and ocean climate. Sea surface temperatures in the North Atlantic Ocean have changed rapidly than in other sea areas (Belkin, 2009). As a consequence, shifts of several plankton and fish species have been observed (Edwards and Richardson, 2004; Reid and Valdés, 2011; Zhai et al., 2013), as have large and rapid biogeographical northward shifts in calanoid copepods ($\sim 23 \text{ km year}^{-1}$, Gregory et al., 2009), Atlantic fishes (Astthorsson et al., 2007, 2012; Drinkwater, 2005; Valdimarsson et al., 2012) and baleen whales toward Icelandic waters (Vikingsson et al., 2015).

Since the early 1960s, monitoring of the abundance, biomass and composition of zooplankton has been carried out around Iceland (Astthorsson et al., 1983). Most of these studies have focused on the abundant copepod *Calanus finmarchicus* (Gislason and Astthorsson, 2000; Gislason et al., 2000; Astthorsson and Gislason, 2003). Krill, on the other hand, have received far less attention. Therefore, there is limited information on the large-scale distribution of krill in Icelandic waters. While mesozooplankton, like *C. finmarchicus*, can be caught with relatively simple and inexpensive gear (e.g. WP2 nets), sampling of krill at appropriate spatiotemporal scales is logistically and financially much more challenging. This is because adult krill are fast swimmers that can escape traditional plankton nets relatively easily (Brinton, 1967; Mathew, 1988). Therefore specially designed gears and acoustic assessments are needed for quantitative sampling of the adult stages (Everson, 2000).

Krill are an important component of North Atlantic Ocean ecosystems in terms of biomass (Saetre and Skjoldal, 2004; Tarling, 2010b). And within the Icelandic Exclusive Economic Zone, they make up the third largest biotic component in terms of annual mean wet biomass (~5 million tonnes) (Astthorsson et al., 2007). In comparison, the mean annual biomass of the most abundant copepod, *C. finmarchicus*, is ~7 million tonnes (Astthorsson et al., 2007). The ecological role of krill is manifested in many ways. They can aggregate in large schools and their grazing impact on the daily phytoplankton standing stock can be substantial (e.g. Pakhomov et al., 2002). They are food for many commercially important species, like herring, cod, capelin, saithe and redfish (Astthorsson and Gislason, 1997b; Sigurjónsson and Víkingsson, 1997; Björnsson, 1999; Sigurjónsson et al., 2000; Gislason and Astthorsson, 2002; Jaworski and Ragnarsson, 2006; Pálsson and Björnsson, 2011; Pétursdóttir et al., 2008, 2012; Víkingsson et al., 2014; Óskarsson et al., 2016). Additionally, krill play a major role in marine biogeochemical cycles, contributing to the vertical carbon flux by feeding on phytoplankton in the upper layers and releasing large fast-sinking faecal pellets at greater depths (Riser et al., 2002; Michels et al., 2008). The role of krill in carbon sequestration has been shown in several studies, for instance in the Southern Ocean (Pakhomov et al., 2002; Michels et al., 2008; Ruiz-Halpern et al., 2011) and in the Barents Sea (Riser et al., 2002). Similar to several other zooplankton species, krill may also serve as ecological indicators of climate change. The boreal species, *Meganyctiphanes norvegica*, has for instance been used as an ecological indicator for particular water masses (Beaugrand et al., 2003; Buchholz et al., 2010; Eriksen and Dalpadado, 2011). Furthermore, krill can synthesize vitamin A in larger concentrations than many other invertebrates (Fisher et al., 1952; Fisher and Goldie, 1959; Mauchline and Fisher, 1969). Beaugrand et al. (2003) suggested that the high energy content and vitamin A concentrations of krill could be of importance for fish recruitment, as fish cannot synthesize vitamin A and are dependent on acquiring it in their food.

Given the important ecological role of krill as conveyors of matter and energy between phytoplankton and higher trophic levels (Astthorsson et al., 2007), it is clearly of interest to study their biology and ecological role in marine systems. The lack of data and monitoring on krill has been stated as an issue that needs to be addressed in the North Atlantic Ocean by researchers and advisory bodies alike (e.g. ICES (2012) and Mitra et al. (2014)).

Krill biology and distribution have been studied in the northeastern North Atlantic Ocean (Einarsson, 1945; Mauchline and Fisher, 1969; Mauchline, 1980; Siegel, 2000a, 2000b). Recent focus has been on krill ecology in the Barents Sea (Dalpadado and Ikeda, 1989; Dalpadado et al., 2008b), Norwegian waters (Saetre and Skjoldal, 2004; Dalpadado, 2006) and in the Greenland Sea (Agersted and Nielsen, 2014; Tegllhus et al., 2015). Several studies on krill in the North Atlantic Ocean were conducted in the late 1980s based on samples taken within the surface layers (~7 m) by Continuous Plankton Recorders (CPR) on commercial ships (Lindley, 1978a, 1982, 1977, 1978b) or by using plankton nets and pelagic trawls (Mauchline and Fisher, 1969; Mauchline, 1980; Siegel, 2000a, 2000b). Only a few recent investigations have surveyed the whole water column, near the mid-Atlantic ridge (Letessier et al., 2011) and in the Irminger Sea (Saunders et al., 2007, 2013).

Paulsen (1909) was the first to record the occurrence and distribution of krill in Icelandic waters. Later, Stephensen (1938) gave an overview of the biology and distribution of krill species around Iceland. A milestone study of the distribution and ecology of krill around the island and in adjacent areas was done by Einarsson (1945). Einarsson's (1945) illustrations on the developmental stages of key species are still referred to by taxonomists. The latest ecological studies were carried out in the 1990s. These mainly aimed at elucidating the

distribution and life cycles of the species in the subarctic environment north of Iceland (Astthorsson and Gislason, 1997a; Astthorsson and Pálsson, 1987), in a fjord on the northwestern peninsula (Astthorsson, 1990; Astthorsson and Gislason, 1992) and in the Atlantic water southwest of the country (Gislason and Astthorsson, 1995). Skúladóttir et al. (2009) presented the results of long-term investigations on the abundance of krill in the waters north and east of Iceland collected using a “minibag” on a shrimp trawl.

1.2 The Icelandic marine ecosystem

1.2.1 Hydrography

Iceland is a surface manifestation of a system of submarine ridges in the North Atlantic Ocean: the Reykjanes Ridge, the Greenland-Iceland Ridge, the Iceland-Faroe Ridge and the Kolbeinsey Ridge (Figure 1.1). The seafloor features around Iceland are known to influence the flow of ocean currents and the distribution of water masses around the island (Stefánsson, 1962; Malmberg and Kristmannsson, 1992; Hansen and Østerhus, 2000; Malmberg, 2004; Jónsson and Valdimarsson, 2004, 2005; Jónsson, 2007; Valdimarsson et al., 2012; Logemann et al., 2013).

The main surface currents around Iceland are the Irminger Current, the North Icelandic Irminger Current and the East Icelandic Current (Stefánsson, 1962; Malmberg and Kristmannsson, 1992; Hansen and Østerhus, 2000; Malmberg, 2004; Jónsson and Valdimarsson, 2004, 2005; Jónsson, 2007; Valdimarsson et al., 2012; Logemann et al., 2013). The Irminger Current flows from the North Atlantic Current towards the south coast of Iceland and then westwards and northwards along the west coast. Off the west coast, it divides into two branches: a large branch flows towards east Greenland, and a smaller branch continues towards the north of Iceland, this branch is known as the North Icelandic Irminger Current (Figure 1.1). This current mixes with Arctic water from the East Greenland Current to form the East Icelandic Current that flows southeastwards along the east coast (Hansen and Østerhus, 2000; Jónsson and Valdimarsson, 2004). A coastal current circulates clockwise around Iceland, driven primarily by freshwater runoff including glacial discharge during the summer months (Ólafsson et al., 2008; Logemann et al., 2013).

Based on the hydrographic characteristics, the waters around Iceland can be divided into three main regions (Astthorsson and Gislason, 1995; Valdimarsson and Malmberg, 1999; Beare et al., 2000; Gislason, 2005; Astthorsson et al., 2007). First, the **Atlantic region** off the south and west coasts of Iceland with warm ($>6^{\circ}\text{C}$) and saline (>35 PSU) waters. Second, the **Atlantic-Arctic mixture region** off the north coast of Iceland, characterized by temperatures between -1 and 4°C and salinities between 34.6 and 34.9. Third, the **Arctic region** off the northeast and east coasts, characterized by relatively cold ($<0^{\circ}\text{C}$) and less saline (<34.5) waters. The variations in abiotic conditions between these three hydrographic domains affect phytoplankton phenology and production (Zhai et al., 2012) and secondary production (Astthorsson and Gislason, 1995; Beare et al., 2000; Gislason, 2005). In this thesis, the ecology of krill will be discussed in the context of this division.

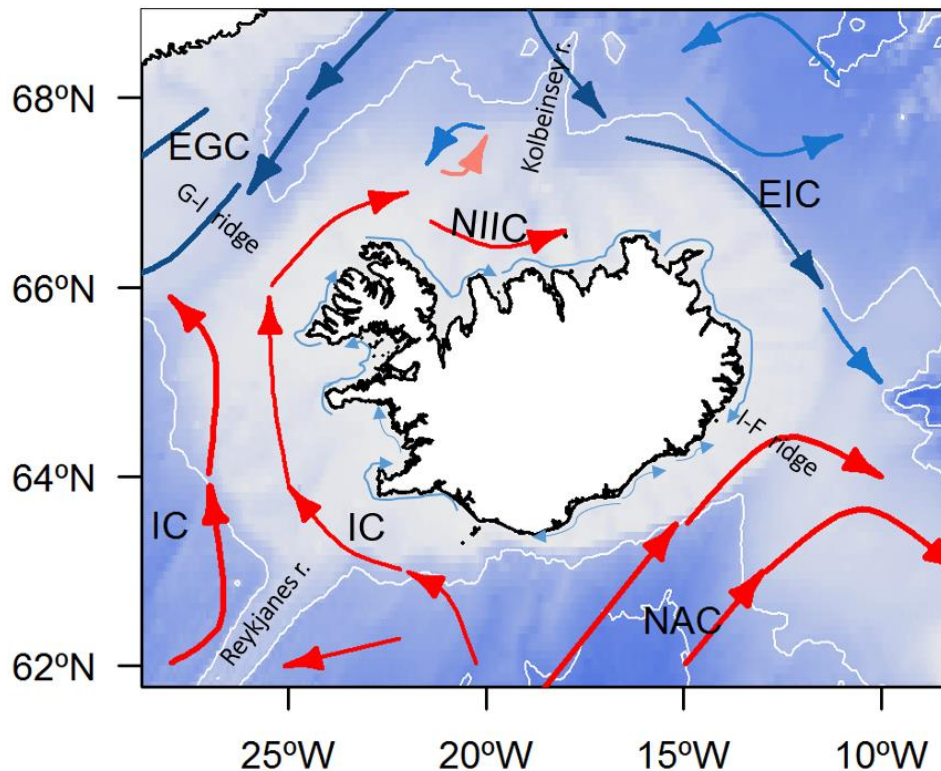


Figure 1.1 Main surface currents around Iceland, adapted from Valdimarsson and Malmberg (1999) and Valdimarsson et al. (2012). NAC: North Atlantic Current; IC: Irminger Current; NIIC: North Icelandic Irminger Current; EGC: East Greenland Current and EIC: East Iceland Current. Arrows close to Iceland in light blue indicate the coastal current. The Reykjanes, Greenland-Iceland (G-I), Iceland-Faroe (I-F) and Kolbeinsey Ridges are also indicated. Line shows isobath of 1000 m.

1.2.2 Phytoplankton and spring bloom dynamics

As stated above (section 1.1), Iceland is situated in one of the most productive oceanic areas in the world (Longhurst et al., 1995). The average annual primary production of the waters around Iceland has been estimated as $\sim 200 \text{ g C m}^{-2} \text{ year}^{-1}$ (Thórdardóttir and Gudmundsson, 1998; Zhai et al., 2012). The shelf waters off the south coast are more productive ($\sim 309 \text{ g C m}^{-2} \text{ year}^{-1}$) than the waters off the north ($\sim 251 \text{ g C m}^{-2} \text{ year}^{-1}$) and east ($\sim 179 \text{ g C m}^{-2} \text{ year}^{-1}$) coasts (Thórdardóttir and Gudmundsson, 1998; Zhai et al., 2012).

As in most shelf seas (Degerlund and Eilertsen, 2010; Simpson and Sharples, 2012), large phytoplankton cells, mainly diatoms such as *Thalassiosira* spp. and *Chaetoreceros* spp., dominate the phytoplankton spring bloom in Icelandic shelf waters when nutrients are not limiting growth (Thórdardóttir, 1986; Thórdardóttir and Gudmundsson, 1998). In the summer months, dinoflagellates, such as *Ceratium* spp. and *Protoperidinium* spp., tend to dominate (Thórdardóttir and Gudmundsson, 1998). Occasionally blooms of *Phaeocystis pouchetii* are observed over the northern shelf during summer (Thórdardóttir and Gudmundsson, 1998).

The phytoplankton spring bloom usually starts between late March and early April and reaches a peak in May (Thórdardóttir, 1986; Gudmundsson, 1998). The onset of the

phytoplankton spring bloom is strongly correlated with the mixed layer depth and the photosynthetically available radiation (McGinty, 2016). The bloom tends to start earlier and last for a longer period off the southwest coast of Iceland, where Atlantic water prevails, than in other regions (Thórdardóttir, 1986; Gudmundsson, 1998; Zhai et al., 2012). The timing and duration of the phytoplankton spring bloom off the southwest coast of Iceland is influenced by the freshwater runoff, wind regime and zooplankton grazing (Thórdardóttir, 1986).

1.2.3 Biology of krill

Krill are found in the marine environment worldwide (Mauchline and Fisher, 1969; Mauchline, 1980). There are around 87 species of krill in the world's oceans (Mauchline, 1980; Horton et al., 2017). Most species inhabit the epipelagic zone, while a few (19 species) are meso- or bathypelagic (Mauchline and Fisher, 1969; Mauchline, 1980). The highest abundances are generally found in polar and subpolar regions (Mauchline and Fisher, 1969).

Ocean currents can easily transport krill larvae and juveniles (i.e. categorized as plankton), while adult krill can swim against weak ocean currents (3-18 cm s⁻¹) (Sawdling et al., 2005). The ability of adult krill to swim against weak currents may facilitate retention in particular areas (Nicol and Endo, 1997). These swimming capabilities have led some authors to classify krill as micronekton rather than plankton (Mauchline, 1980; Nicol and Endo, 1997; Lancraft et al., 2004; Eriksen et al., 2016).

Harvesting

The largest krill species, the Antarctic krill *Euphausia superba*, is one of the most studied and by far the most harvested krill species in the world (Everson, 2000). In 2016, around 260 thousand tonnes of Antarctic krill were caught in the Southern Ocean (CCAMLR, 2016). In the North Atlantic Ocean, primarily in the Gulf of St. Lawrence and over the Scotian Shelf, a small krill fishery targeting *M. norvegica*, *Thysanoessa inermis* and *T. raschii* operated around the 1990s (Nicol and Endo, 1997; Nicol and Foster, 2003). The potential of harvesting krill has been investigated in the Irminger Sea (Lamhauge et al., 2008) and in Ísafjord-deep (Gislason et al., 2013), and harvesting of krill has been introduced in Ísafjord-deep recently (Gislason, A. personal communication, 2018).

Reproduction, life cycle and feeding

The mating season of Atlantic and subarctic krill species begins in late winter with males transferring spermatophores to females (Ross and Quetin, 1997). Spawning activity commences the following spring, with multiple spawning events occurring throughout the spawning season (Cuzin-Roudy, 1993). The start and duration of the spawning activity are quite variable within and between species and between regions (Astthorsson, 1990; Ross and Quetin, 1997), while generally synchronized with the phytoplankton spring bloom (Astthorsson, 1990; Dalpadado and Skjoldal, 1991; Dalpadado, 2006; Pinchuk and Coyle, 2008).

The majority of the North Atlantic Ocean krill species, e.g. *Thysanoessa* spp. and *M. norvegica*, lay eggs freely in the surface layers (Ross and Quetin, 1997). In general, the eggs are denser than seawater, so they sink to deeper waters at a rate of 61 to 180 m d⁻¹, with faster sinking rates at higher temperatures (Mauchline and Fisher, 1969; Tarling, 2010a). The eggs then hatch in the deeper layers into the first nauplius or larval stage (Figure 1.2). The nauplii have some motile abilities allowing them to swim upwards in the water column (Tarling,

2010a). By a series of successive moults, the nauplii then develop to metanauplii and calyptopes in approximately 10 days at ~5°C (Pinchuk and Hopcroft, 2006). When the larvae have reached the calyptopis stage, they tend to be close to the surface where they start to feed on the available phytoplankton (Im and Suh, 2016; Ross and Quetin, 1991). After the second calyptopis stage, the larvae are able to conduct diel vertical migrations (Im and Suh, 2016; Mauchline and Fisher, 1969). The larvae then molt several times to reach the furcilia stage within ~29 to 60 days depending on temperature (Tarling, 2010a). Compared to the calyptopes stages, the furciliae larvae tend to feed on a more diverse diet, such as microzooplankton and small copepods in addition to phytoplankton (Im and Suh, 2016) and they also start to show schooling behavior (Hamner et al., 1989). As the animals develop further and mature from juveniles to adults (Figure 1.2), their diet shifts towards a greater inclusion of detritus (Park et al., 2011; Polito et al., 2013).

Feeding strategies vary among krill species (Mauchline, 1980; Sogawa et al., 2017). Different species in the North Atlantic and the Pacific Oceans were found to feed at different trophic levels (Agersted et al., 2014; Sogawa et al., 2017) and some species seem to have different feeding strategies depending on the time of year (Schmidt, 2010). To detect prey, krill use highly developed vision, mechanoreception, and chemoreception (Abrahamsen et al., 2010; Hamner et al., 1983). The structure of the feeding appendages and mandible sizes play an important role in the type and size of food that a krill species forages upon (Mauchline and Fisher, 1969; Mauchline, 1980; Quetin and Ross, 1985; Agersted and Nielsen, 2016). Krill may be quite opportunistic feeders, changing their feeding strategies from filter-feeding to predatory feeding based on prey availability (Agersted and Nielsen, 2016).

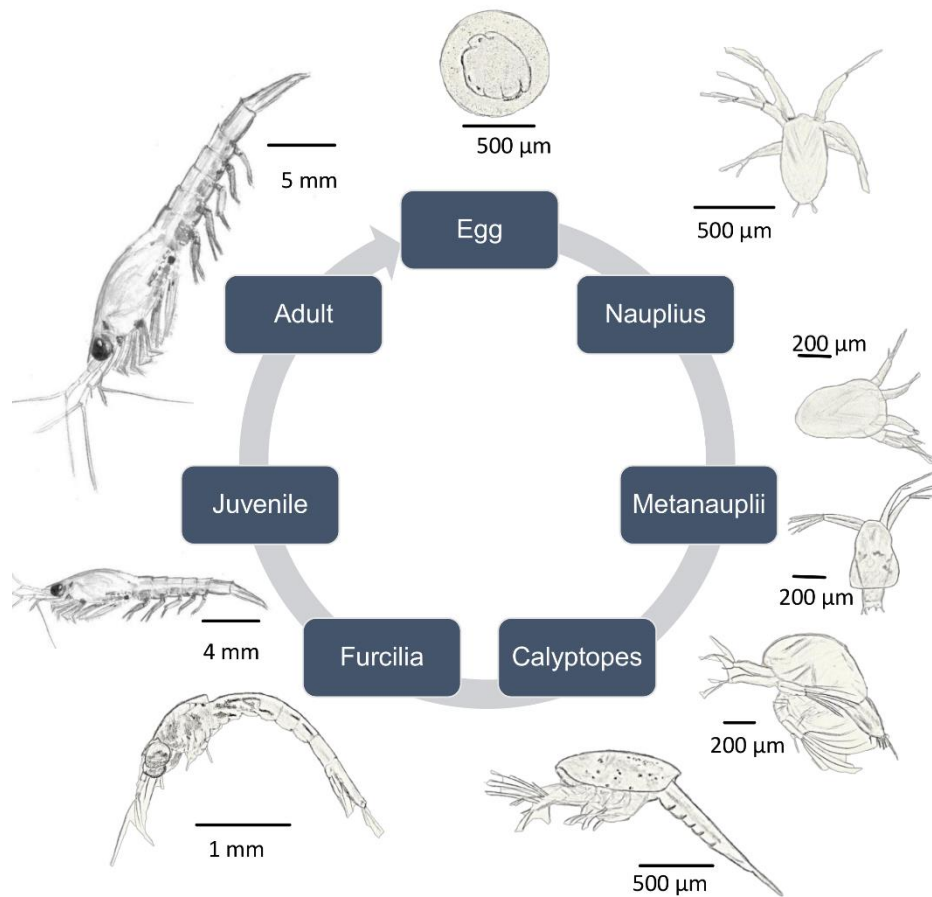


Figure 1.2 Life cycle of krill. Illustrations made by Teresa Silva.

Common krill species in Icelandic waters

Four krill species are commonly found in Icelandic waters, as well as elsewhere in the North Atlantic Ocean (Figure 1.3) (Einarsson, 1945; Mauchline and Fisher, 1969). They are *M. norvegica*, *T. inermis*, *T. longicaudata* and *T. raschii*.

The boreal species *M. norvegica* (Northern krill) is one of the most studied species of krill (Tarling, 2010b). *M. norvegica* can attain 50 mm in total size (Table 1.1) and is mostly distributed in the North Atlantic Ocean between 30°N and 80°N (Figure 1.3), as well as in the western Mediterranean (Mauchline and Fisher, 1969; Patarnello et al., 2010; Tarling, 2010a). The distribution of *M. norvegica* is restricted to a temperature range between 1.5 and 16°C (Einarsson, 1945; Saborowski and Buchholz, 2002; Spicer and Saborowski, 2010; Agersted and Nielsen, 2014; Huenerlage and Buchholz, 2015).

The subarctic-boreal species, *T. inermis*, can reach up to 32 mm in total size (Table 1.1). The species is mainly confined to the northern continental shelves of the North Atlantic and North Pacific Oceans (Einarsson, 1945; Mauchline and Fisher, 1969), but can also be found in deep waters (Lindley, 1980; OBIS, 2017). *T. inermis* cannot tolerate temperatures >12°C (Huenerlage and Buchholz, 2015), and 0°C seems to be their lower limit (Dalpadado and Skjoldal, 1991).

The oceanic species, *T. longicaudata*, is considered the most abundant krill species in the North Atlantic Ocean (Einarsson, 1945; Saunders et al., 2007). As adults the animals attain a maximum size of ~16 mm (Table 1.1). The distribution of *T. longicaudata* seems to be limited to temperatures between 3.5 and 15°C (Einarsson, 1945; Lindley, 1978a).

T. raschii is the fourth of the most common krill species found in Icelandic waters. While *M. norvegica*, *T. inermis* and *T. longicaudata* usually inhabit the open shelves or oceanic areas (Mauchline and Fisher, 1969; Saunders et al., 2007, 2013; Letessier et al., 2011), *T. raschii* is confined to the neritic zone (<200 m) of the North Atlantic and North Pacific Oceans (Einarsson, 1945; Mauchline and Fisher, 1969; Astthorsson, 1990), however, a few specimens have been found in oceanic waters (OBIS, 2017). Similar to *T. inermis*, *T. raschii* has an upper thermal tolerance of 12°C (Huenerlage and Buchholz, 2015). Adults attain a total size of ~30 mm (Einarsson, 1945).

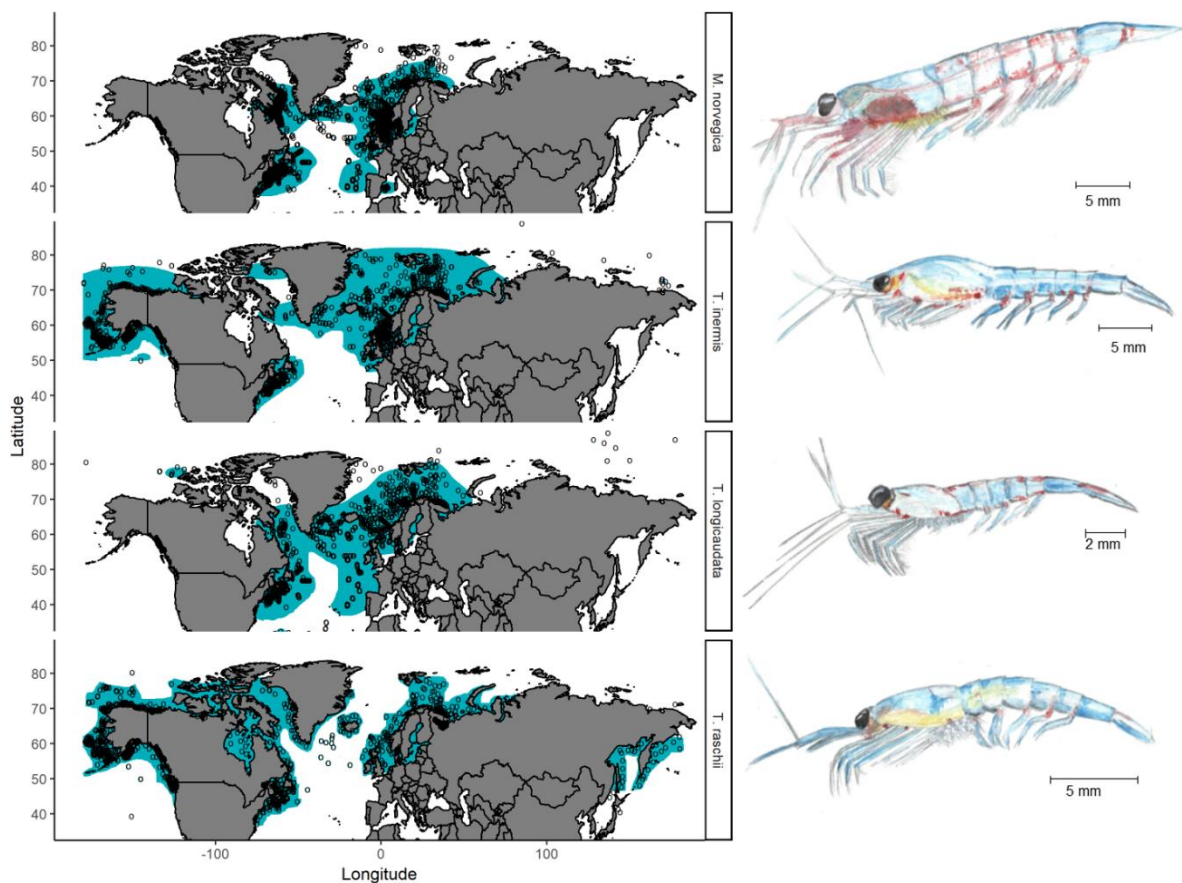


Figure 1.3 Left panel: Overall distribution of the four krill species that are most abundant in Icelandic waters (blue shading). Circles indicate the location of different records of occurrence (Mauchline and Fisher, 1969; OBIS, 2017). Right panel: Blue indicates transparency. Illustrations made by Teresa Silva.

Earlier studies have indicated that the four species have distinct habitats in Icelandic waters (Einarsson, 1945; Astthorsson and Gislason, 1997a, 1997b; Astthorsson and Pálsson, 1987; Astthorsson, 1990). *M. norvegica* is mainly restricted to the shelf break waters off the southwest coast (Einarsson, 1945), with the main spawning regions are located south and west coast over the continental slopes (Table 1.1). *T. inermis*, on the other hand, is reported to be common on the coastal banks surrounding Iceland. The main spawning activity of this species

usually occurs between April and May in the coastal waters off the north and east coasts (Einarsson, 1945). The smallest species, *T. longicaudata*, is most common in the oceanic areas surrounding Iceland, with the main spawning activity occurring in the Atlantic water in May (Table 1.1). *T. raschii* is most abundant in the fjords and coastal banks off the northwest and north coasts and was found to spawn mainly in May (Einarsson, 1945; Astthorsson, 1990).

Einarsson (1945) hypothesized that the spawning and the ontogenetic migrations of the larvae reflect the distribution of the adult animals. He suggested that *T. inermis* and *T. raschii*, spawn in the deeper waters on the shelf and *M. norvegica* near the shelf slope, and that the eggs of these species would hatch deep and the larvae undergo ontogenetic migrations to surface waters. In contrast, he hypothesized that *T. longicaudata* spawn in the upper layers and the larval development mainly takes place in the surface layers (Einarsson, 1945). However, little is known about the larval development of *T. longicaudata* (Einarsson, 1945; Mauchline, 1971; Williams and Lindley, 1982; Brinton et al., 2000), and some other studies (Mauchline and Fisher, 1969; Williams and Lindley, 1982) have shown that the spawning and development of krill species does not always follow the pattern hypothesised by Einarsson (1945). For instance, Williams and Lindley (1982) showed that *T. longicaudata* eggs were found relatively deep in the water column (100-800 m depth) and that the naupliar forms ascended to the surface after hatching. Moreover, the spawning and development of krill larvae seem to be rather complex as it is also dependent on environmental conditions (Mauchline and Fisher, 1969; Tarling, 2010a).

Little is known about the diel vertical migration of krill in Icelandic waters. The only previous study is that of Einarsson (1945), but he only studied the diel vertical migration of larval forms in the shelf regions. He showed that the larvae were mostly found in the upper layers in the water column (0- 50 m) and appeared in relatively high numbers close to the surface at night time. All four species (*M. norvegica*, *T. longicaudata*, *T. inermis* and *T. raschii*) tend to migrate to surface layers at night (0-100 m) (Einarsson, 1945; Mauchline, 1980) to feed, thereby minimizing the risk of predation (Mauchline, 1980; Kaartvedt, 2010). Both the diel light cycle and the presence of predators may affect the diel vertical migration pattern of krill. The increased light was found to cause a deeper distribution of *M. norvegica* (Mauchline, 1980; Kaartvedt, 2010), and krill have been shown to aggregate and change their vertical migratory behavior in the presence of fish schools (Onsrud et al., 2004).

Table 1.1 Size and some life history characteristics of four common krill species in Icelandic waters based on several sources (Einarsson, 1945; Mauchline, 1971; Astthorsson, 1990; Astthorsson and Gislason, 1997a; Ross and Quetin, 1997). Abbreviations are Isa: Isafford-deep and SW: southwest of Iceland.

	<i>M. norvegica</i>	<i>T. longicaudata</i>	<i>T. inermis</i>	<i>T. raschii</i>
Maximum size (mm)	50	16	32	30
Size at Maturity (mm)	18 (Isa.); 27-35 (SW)	7.5-10	14-20	15
Begin to mate	February		April	February-March
Spawning time	Feb-April (SW); March-July (North)	May	April-May	May
Size at spawning (mm)	25-35	10-16	15 (SW); 22 (North)	22
Lifespan (years)	2+	1	2+	2+

Role of krill in the food web

As pointed out above, krill play a key role in the Icelandic marine ecosystem as food source for several species, including commercially important ones. Predation from cetaceans is an important source of mortality of krill in Icelandic waters, and this is highest during the spring and summer months (Sigurjónsson and Víkingsson, 1997; Folkow et al., 2000). Annual krill consumption by cetaceans in Icelandic waters was estimated as ~3.4 million tonnes (Sigurjónsson and Víkingsson, 1997). Fin (*Balaenoptera physalus*) and sei whales (*B. borealis*) tend to feed exclusively on krill, whilst for other whale species, such as minke (*B. acutorostrata*) and humpback whales (*Megaptera novaeangliae*), krill are only a secondary prey item (Sigurjónsson and Víkingsson, 1997; Folkow et al., 2000; Víkingsson et al., 2014). Common (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are also known to supplement their main fish diet with krill (Nebel, 2011).

Krill are also a significant prey item for seabirds. Krill were found to be the third most important prey item for seabirds after capelin and sandeel (Lilliendahl and Solmundsson, 1997) in Icelandic waters and the consumption during the summer months was estimated to be ~34,000 tonnes.

Several demersal fish species have been shown to feed on krill (Björnsson, 1999; Jónsson, 1996; Jaworski and Ragnarsson, 2006; Pálsson and Björnsson, 2011). *M. norvegica* and *T. inermis* were found to be important prey of commercially important demersal fish species, including the deepwater redfish *Sebastes mentella*, redfish *S. marinus*, saithe *Pollachius virens* and cod *Gadus morhua* (Astthorsson and Pálsson, 1987; Jónsson, 1996; Jaworski and Ragnarsson, 2006; Pétursdóttir et al., 2008). Haddock (*Melanogrammus aeglefinus*), Greenland halibut (*Reinhardtius hippoglossoides*) and other species also consume krill to a varying degree (Pálsson, 1980; Jaworski and Ragnarsson, 2006; Solmundsson, 2007). The impact of demersal fish predation on *M. norvegica* and *T. inermis* was found to increase from the spring to winter months and also to increase with depth but to decrease with fish size (Pálsson, 1980; Björnsson, 1999; Jaworski and Ragnarsson, 2006; Pálsson and Björnsson, 2011).

Krill are also an important component of the diet of pelagic fishes. For instance, herring (*Clupea harengus*) prey mainly on *C. finmarchicus*, while *M. norvegica* and amphipods are also important in the summer months (Gislason and Astthorsson, 2002; Óskarsson et al., 2016). Mackerel (*Scomber scombrus*) feed primarily on *C. finmarchicus* (Óskarsson et al., 2016), while krill are found to be the second- or third most important prey item (Kvaavik, C. 2017, personal communication). Capelin (*Mallotus villosus*) feed mostly on *C. finmarchicus* (Astthorsson and Gislason, 1997b; Pétursdóttir et al., 2012) with krill being a secondary food source, mostly in the summer months (Astthorsson and Gislason, 1997b). Krill and *C. finmarchicus* are also the main food of blue whiting (*Micromesistius poutassou*) in Icelandic waters (Sveinbjörnsson et al., 1984; Pétursdóttir et al., 2012). In other parts of the North Atlantic Ocean, krill are likewise important in fish diets. Atlantic bluefin tuna (*Thunnus thynnus*) prey, to some extent, on *M. norvegica* during their autumn migrations to the Icelandic Basin (Ólafsdóttir et al., 2016). Small mesopelagic fish have also been reported to feed on krill in the North Atlantic Ocean (Gjøsæter, 1973; Gjøsæter and Kawaguchi, 1980; Sameoto, 1988; Podrazhanskaya, 1993; Bernal et al., 2015), but information from Icelandic waters is not available.

1.3 Aim of the thesis

This thesis aims to contribute to new insights into the biology of krill and their ecological role in the Icelandic marine ecosystem. For this purpose, the following research questions were addressed:

- What are the main drivers that influence the temporal changes in relative abundance of krill around Iceland? (**Paper I**)
- How do distribution patterns and population dynamics of krill differ due to the influence of phytoplankton spring bloom dynamics and water masses? (**Papers I-III**)
- How does increasing temperatures affect growth, egestion and mortality of *M. norvegica* from Icelandic waters? How much carbon would *M. norvegica* release to the seafloor southwest of Iceland? (**Paper IV**)

Therefore, the subject of **Paper I** was to study the long-term and seasonal changes in abundance of krill southwest, south and southeast of Iceland using historical data. This paper aimed to evaluate how climate and environmental variability and the onset of the phytoplankton spring bloom and biomass affected long-term changes in abundance of krill.

Papers II and **III** aimed to describe the distribution and abundance of krill around Iceland in the spring of 2013. **Paper II** related the abundance, distribution and development of the early life stages of krill (eggs, nauplii, calyptopes and furciliae) to environmental variables and phytoplankton spring bloom dynamics. **Paper III** focused on the distribution, maturity and population structure of juvenile and adult *M. norvegica* and *T. inermis*. To investigate the influence of water masses on the abundance and distribution of krill, the data were discussed in the context of the three biogeographic regions mentioned in section 1.2.1.

Paper IV aimed to estimate growth, egestion and mortality of *M. norvegica* at four temperatures (5, 8, 10 and 12°C). Data on egestion rates (**Paper IV**) together with abundance estimates of *M. norvegica* from field samples (**Paper III**) were combined and used to elucidate the role of krill in carbon sequestration within the Icelandic marine pelagic ecosystem.

2 Methods

2.1 Historical data

In **Paper I**, two different time series of krill abundance were used to assess long-term and seasonal changes of krill in Icelandic and adjacent waters (Figure 2.1). One dataset (the Icelandic spring survey) was collected by the Marine Research Institute (MRI) on a transect south of Iceland, the Selvogsbanki transect, (1990-2011). The other dataset was collected by the CPR survey covering a wider area of the northeastern North Atlantic Ocean (1958-2007).

On the Selvogsbanki transect, the zooplankton samples were collected in May-June 1990-2011 with a Hensen net (0.42 m² mouth area and 200 µm mesh size) or WP2 nets (0.25 m² mouth area and 200 µm mesh size). The plankton nets were towed from 50 m depth (or from ~2 m above the seafloor when the depth was <50 m) to the surface at a velocity of ~0.75 m s⁻¹. Volumes of water filtered was measured by HydroBios flowmeters. Data on abundance of eggs and combined larval stages (nauplii, metanauplii, calyptopes and furciliae) were used to assess long-term changes of krill along the transect. Data on temperature, salinity and chlorophyll *a* (chl *a*) were averaged for the upper layers (0-50 m) and utilized as explanatory variables.

In oceanic waters (58–66°N, -43°W–3°E), the total number of krill (furcilia, juvenile and adult krill) per cubic meter per month was estimated from day and night samples (~ 30,000 samples in all) collected by the CPR survey from 1958 to 2007 (**Paper I**). The CPR collects plankton by commercial vessels at approximately monthly intervals on standard routes at a mean depth of ~7 m.

Sea surface temperatures (SST), salinity, chl *a* and the North Atlantic Oscillation (NAO) index were used as explanatory variables. Additionally, the onset of phytoplankton spring bloom (OPB) was estimated from satellite-derived surface chl *a* concentrations (Globcolour, 1998-2011), as the first week of the year when chl *a* concentrations increased 5% above the annual median (Siegel et al., 2002; Henson et al., 2009).

Generalized additive models (GAMs) were used to analyse long-term changes in krill abundance as a function of hydrographic and biological variables (Wood, 2006). The data were characterized by many zero observations that would make the use of a Gaussian distribution inappropriate. A two-step hurdle model was therefore applied. This method combined two models: (model A) a presence/absence model fitted to all the data with a binomial error distribution and logit link function, and (model B) a separate model for the positive (non-zero) data with a gamma error distribution and log link function (Stefánsson and Pálsson, 1997; Barry and Welsh, 2002). Model A was used to analyse what explanatory variables influence krill habitat, and model B was used to determine the variables that favour an increase in krill abundance. As the different explanatory variables did not have the same temporal coverage, GAMs were limited to the period 1998 to 2007 for the CPR data and 1998 to 2011 for the Icelandic spring survey data, when records for all the environmental predictors

were available. See Method section in **Paper I** for further details on sampling and data analysis.

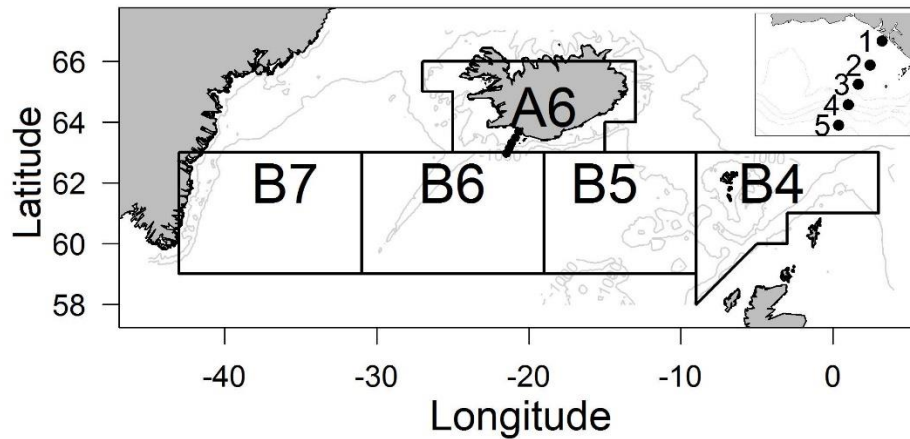


Figure 2.1 Map showing the CPR sampling areas included in the study (**Paper I**). Stations at the Selvogsbanki transect are shown by black dots (inside area A6). Grey contours show bathymetry. The inset map is an enlargement of the Selvogsbanki region with the stations indicated by numbered black dots.

2.2 Sampling

A dedicated sampling to investigate the abundance and distribution of krill around Iceland was carried out during the spring of 2013 using a specially designed macrozooplankton trawl, WP2 net and acoustics. The results are presented in **Papers II** and **III**. The sampling took place as part of the hydrobiological spring survey of the MRI during 14–29 May 2013 on the R.V. *Bjarni Sæmundsson*.

A WP2 plankton net was used to collect samples of zooplankton along 14 transects running approximately perpendicular to the coast around the island (Figure 2.2). A total of 100 samples were collected in the upper layers (0–50 m) (**Paper II**). The samples were preserved at sea with 4% buffered formaldehyde and analysed afterwards in the laboratory ashore.

Paper III, describes the abundance and distribution of the most abundant krill species (*M. norvegica* and *T. inermis*) caught by the macrozooplankton trawl (27-m² mouth opening with 4 mm meshes, 6 mm stretched). A total of 26 trawl stations were taken, generally two trawl stations per transect, with one located over the shelf and the other off the shelf (Figure 2.2, open circles). Sampling took place during both day and night (19 day and 7 night stations). The trawl was towed obliquely at a speed of ~1.5–2 knots from 200 m depth to the surface or ~10 m from the seafloor when the bottom depth was <200 m. To estimate the volume of water filtered by the trawl, the mouth area was multiplied by the distance towed.

Vertical profiles of temperature, salinity and fluorescence were obtained at each station with a Sea-Bird Electronics SBE 9 CTD equipped with a fluorometer (Seapoint). Fluorescence data were converted to chl *a* (mg m⁻³) using an equation obtained during similar surveys carried out in May 2010 to 2014 (see **Paper II** for more details). The onset of the phytoplankton spring bloom (OPB) was estimated at all stations using weekly surface chl *a* data (8-day, 25 x 25 km grid) from satellite images (**Papers II** and **III**), as in **Paper I**.

Acoustic data were also collected along the survey route using Simrad EK601 echosounders (Kongsberg Maritime AS) with 38 and 120 kHz transducers, allowing the recording of the acoustic backscatter down to 300 m (Reynisson and Gislason, 2015).

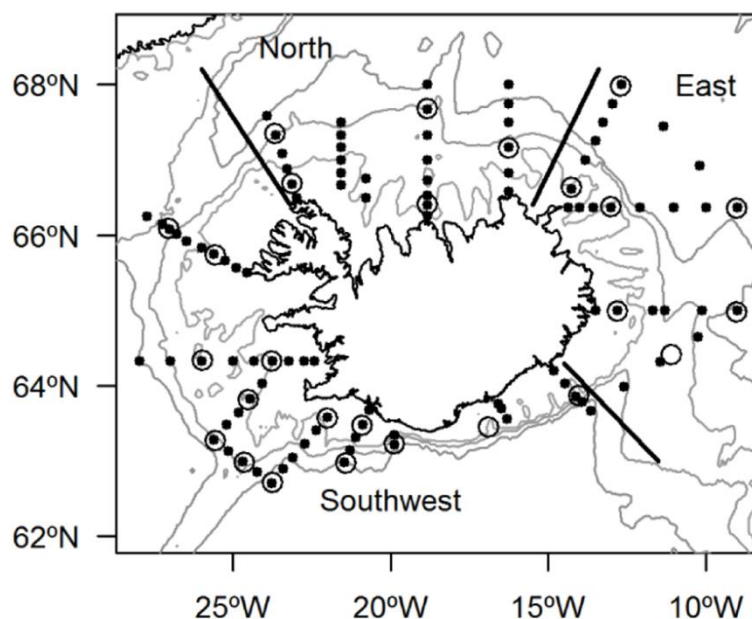


Figure 2.2 Location of stations taken during the 2013 spring cruise (**Paper II** and **III**). Dark points indicate the CTD and WP2 stations and open circles locations where the macrozooplankton trawl was deployed. Grey lines indicate isobaths of 200, 500 and 1000 m. The black lines denote the division into the main hydrographic regions: southwest, north, and east.

2.3 Analysis of samples

One of the novelties of this study was the use of automatic analysis to estimate the abundance and size of krill eggs and larvae in formalin preserved samples (**Paper II**). A total of 100 samples were digitized and analysed with ZooImage software (Grosjean and Denis, 2007). This software has performed well in similar analyses and is an efficient method time-wise for attaining information on zooplankton abundance, biomass and size-spectrum over large spatiotemporal scales (Bell and Hopcroft, 2008; Gislason and Silva, 2009; Uusitalo et al., 2016; González et al., 2017). In this study, 38 inshore and offshore samples were chosen randomly and used to build a library (i.e. training set) of the common zooplankton species in Icelandic waters during spring. In this library, special emphasis was given to the eggs, nauplii (nauplii and metanauplii combined) and calyptopes and furciliae (including also a few juveniles). Based on the library, a classifier with 81% accuracy was built using a random forest algorithm which is an accurate and widely used algorithm for this type of analysis (Bell and Hopcroft, 2008; Gislason and Silva, 2009; González et al., 2017). The abundances estimated by ZooImage were then corrected using the method of Hu and Davis (2006).

Another novel component of this work was the complementary identification to the species level of the larval of krill found in 20 WP2 samples (**Paper II**). Identification was carried out following the taxonomic keys and drawings by Einarsson (1945), Mauchline (1971) and

Brinton et al. (2000). Here, for the first time, metanauplii stages were identified at the species level using the developed key by Brinton et al. (2000). Thus, **Paper II** gives further an insight into the species composition of the larval stages in the three different water masses around Iceland.

At sea, the samples obtained by the macrozooplankton trawl (**Paper III**) were sorted into groups (krill, cnidarians, amphipods, fish and shrimp), weighed to estimate biomass and then frozen. In the laboratory, the frozen krill samples were thawed and analysed manually under a stereomicroscope, either whole or in aliquots (~1/32) obtained by a Motoda splitter and containing at least 200 individuals. All krill were counted, identified to species level, and assigned to the following maturity stages: (1) juveniles (indeterminate sex); (2) immature males or females; (3) mature males or females; (4) males with spermatophores in ejaculatory ducts or females with spermatophores attached (Einarsson, 1945; Cuzin-Roudy and Amsler, 1991; Cuzin-Roudy and Buchholz, 1999; Dalpadado et al., 2008a). Total length and carapace length were measured using a digital caliper or an ocular micrometer on a stereo microscope. Sex ratio (number males/females) was estimated at stations where at least 25 individuals of *M. norvegica* and/or *T. inermis* were sexed.

To investigate the influence of water masses on the abundance and distribution of krill, the data collected during the spring survey of 2013 (**Papers II and III**) were divided into the three biogeographic regions described in section 1.2.1: the southwest (mainly influenced by Atlantic water), the north (Atlantic–Arctic mixture) and the east (Arctic). Two-sample Kolmogorov & Smirnov tests were used to compare the population structure of krill among the three regions. Furthermore, multivariate analyses (**Paper II**) and multiple linear regressions (**Paper III**) were used to examine the relationships between explanatory variables (temperature, salinity, OPB, chl *a* and bottom depth) and abundance of krill.

2.4 Physiological rates of *M. norvegica*

M. norvegica were collected from the waters to the south of Iceland during the night from 27–28 May 2012 by oblique Bongo net tows (500 µm mesh, 0–200–0 m) using a ~2 l closed cod-end. Undamaged individuals (20–30 mm total length), were picked out from the samples and gently transferred into 40–60 l containers filled with aerated and filtered seawater (63 µm). Containers were kept in the dark at a constant temperature (~8°C) that reflected the conditions from where the individuals were sampled. The transport from harbour to the laboratory took <1 h. In the laboratory, *M. norvegica* were kept at ~7.4°C for 24–48 h in tanks with 346 l seawater, at dim light with excess concentrations of the diatom *Thalassiosira weissflogii* and brine shrimp nauplii *Artemia salina*. Individuals were acclimated gradually to the four temperatures (5, 8, 10, 12°C), were experiments on growth, mortality and faecal pellet production were run simultaneously for ~6 weeks under low light conditions with the animals being kept individually in 2.3 l containers. The seawater used in the experimental containers was initially filtered through 0.5–1 µm filters and during the experiments the animals were fed with a mixture of *T. weissflogii* (10 µg C l⁻¹ d⁻¹) and *A. salina* nauplii (60 µg C l⁻¹ d⁻¹). Every day the containers were checked for presence of moults and faecal pellets. Each *M. norvegica* was transferred gently by a spoon into a beaker with newly filtered seawater (0.5–1 µm). All the water in the container was slowly sieved through a 10 µm filter and pellets retained on the sieve were preserved in 4% acidic Lugol solution. The container was then filled with newly filtered seawater, the animal carefully placed back into it, and food added. The faecal pellets

were counted and measured from digitized images taken by camera mounted in a stereomicroscope at the highest magnification (60 or 120×). A macro in ImageJ (Schindelin et al., 2015) was created (**Paper IV**) to measure the size and volume of the faecal pellets.

2.5 Limitations

This study has some limitations that need to be pointed so that future studies can overcome or avoid them. In particular, avoidance of the plankton nets and trawls by krill represented a large source of uncertainty (**Papers I-III**). It seems evident that no single sampling method is ideal to collect all life stages of krill and therefore for the ultimate sampling one should combine several sampling techniques, such as plankton nets, large pelagic trawls, and acoustic and even optical methods (e.g. Eriksen et al. (2016)). Adult krill can detect plankton nets during the day and easily escape or evade them (Brinton, 1967). Researchers have studied krill avoidance behaviour by using strobe lights fitted to the sampling gear (Wiebe et al., 2004) or by catching them using a large greyish pelagic macrozooplankton trawl (Everson, 2000), as was done in **Paper III**. Below the main uncertainties are listed and how an attempt was made to address them in this study.

2.5.1 Catch efficiency and selectivity of nets

The catch efficiency (CE) was evaluated in **Paper I**, and here CE is revised for all gears used in this project. The calculations were done using the equation of Clutter and Anraku (1968):

$$CE = \left(\frac{\left(R - \left(\frac{K}{S_i} \right) \right)}{R} \right)^2$$

Here, R is the net radius (m), K is the avoidance parameter (i.e. the detection distance (m) multiplied by the mean krill swimming speed (m s^{-1})) and S_i is the towing speed (m s^{-1}).

Krill can swim at speeds between 1 and 3 body lengths (BL) per second (Price, 1989; Klevjer and Kaartvedt, 2003, 2006, 2011; Gaten et al., 2010), with a mean speed of $\sim 1.7 \text{ BL s}^{-1}$. The mean relative swimming speed (BL s^{-1}) was used to calculate swimming speeds in units of m s^{-1} for krill that ranged in size from 1 to 5 cm (total length). With those values, the catch efficiency of each gear type was calculated for krill ranging in size from 1 to 5 cm. The results indicate that the catch efficiency of the nets decreases with increasing body size of the animals and their ability to detect the gear.

Assuming that krill can detect the sampling gear within a distance of 0.25 m (**Paper I**), it was shown that the Hensen, WP2 and CPR gears catch $\sim 70\%$ of krill < 2 cm. Included in this size group are larval and juvenile stages of the three most common krill species in the North Atlantic Ocean (*T. longicaudata*, *T. inermis*, *M. norvegica*), as well as the adult stages of the smallest species (*T. longicaudata*). The macrozooplankton trawl used in **Paper III** shows high catch efficiency of krill of 1 to 5 cm total length ($CE > 0.97$). Evidently, all the large size groups of *T. longicaudata*, *T. inermis*, *M. norvegica* (Einarsson, 1945; Astthorsson and Gislason, 1997a; Astthorsson, 1990) were therefore caught effectively by the macrozooplankton trawl. However, the efficiency of the macrozooplankton trawl may be

limited by its ability to retain the animals in the net that is constrained by the mesh large size (see next section).

In order, to remedy the problem of low catch efficiency of adults in the Hensen and WP2 nets, only data on eggs and larvae were used in **Papers I and II**. As for the CPR, unfortunately, catch numbers included combined counts of furcilia, juvenile and adult stages (Batten et al., 2003), and therefore, it was concluded that the catch numbers could only be used as indices of temporal and spatial variability, but not as absolute abundances (**Paper I**).

Limitations related to size selectivity of the macrozooplankton trawl (used in **Paper III**) were apparent due to the large mesh size (mesh size of 4 mm, 6 mm stretched). This selectivity most likely affected the abundance data of *T. longicaudata* and juveniles of the larger species (*M. norvegica* and *T. inermis*). As discussed in the Methods section in **Paper III**, it is likely that the trawl did not effectively catch krill with a total length <16 mm. This means that *T. longicaudata* were not sampled effectively because of its small size (<16 mm, maximum total length) and neither were the juveniles of *T. inermis* (~12-20 mm total length) nor *T. raschii* (~10-20 mm) (Einarsson, 1945; Astthorsson, 1990; Astthorsson and Gislason, 1997a; Saunders et al., 2007). Consequently, **Paper III** focuses on the distribution and population structure of adults of the two most abundant species caught by the macrozooplankton trawl, *M. norvegica* and *T. inermis*.

2.5.2 Influence of diel vertical migration

Krill are known to be active vertical migrants that tend to reside at shallow depths during the night and at deeper depths during the day (see e.g. Eriksen et al. (2016)). They are probably more capable of avoiding sampling gear during the daytime because of their well-developed compound eyes (Wiebe et al., 2004). In **Papers I and III**, the abundance of krill was found to be similar in the samples taken during day or night. Only one case was found where significant difference between day and night catches was found, and thus the night samples were used, as they were considered to generate more accurate estimates of krill abundance (**Paper I** for CPR area B7). No size-related net avoidance was found in the length-frequency distributions of *M. norvegica* and *T. inermis* between day and night (**Paper III**).

The macrozooplankton trawl was only deployed down to a depth of 200 m, while *M. norvegica* and *T. inermis* may inhabit depths from ~100 to 400 m during spring and summer (Einarsson, 1945; Mauchline and Fisher, 1969; Letessier et al., 2011). Thus the sampling may have missed a part of the populations. However, at most of the sampling stations the bottom depth was <200 m and therefore the whole water column was sampled. At eight offshore stations, the bottom depth was >200 m and this could have led to underestimates of krill abundance at these stations. Acoustic data collected along the survey routes were therefore analysed to explore the depth distribution of krill at these stations (Figure 2.3). The acoustic backscatter of krill was recorded down to 300 m (see Reynisson and Gislason (2015) for further details). In a few cases, krill were evident below 200 m at the deepest offshore stations (Figure 2.3) and thus it can be assumed that populations were in general sampled effectively with the macrozooplankton trawl (**Paper III**).

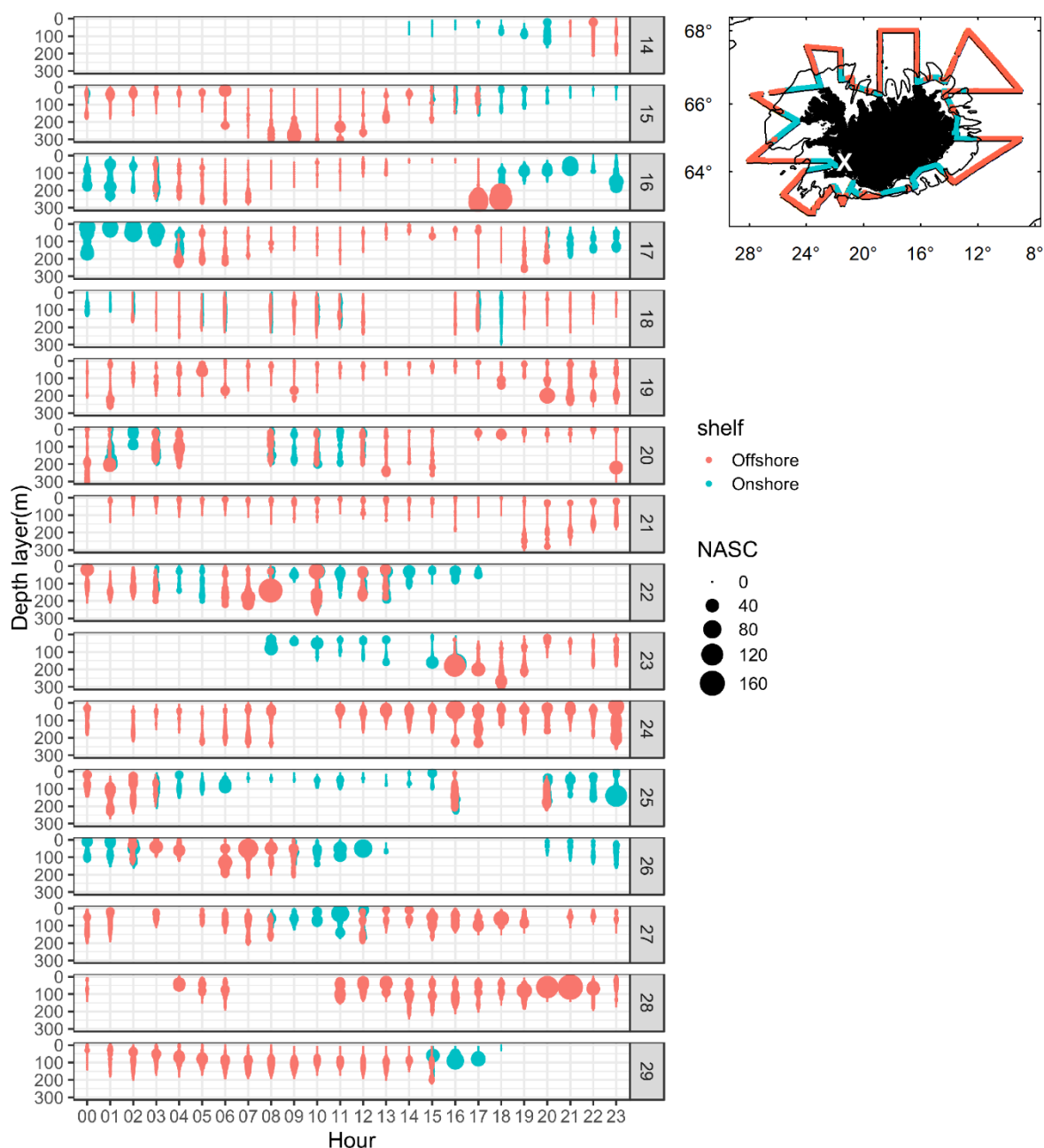


Figure 2.3 Vertical distribution of acoustic backscatter estimated to be krill around Iceland along onshore (blue) and offshore (red) transects down to 300 m depth by time of day, 14 - 29 May 2013. The size of dots indicates the average acoustic backscatter of krill (Nautical Area Backscatter Coefficient, NASC, $m^2 nm^{-2}$). The krill backscatter was estimated based on differences in backscatter at 120 and 38 kHz (Reynisson and Gislason, 2015). The map in the upper right shows the sampled locations grouped into onshore (blue) and offshore (red), and the isobath of 200 m (black). The numbers on the right side of the plots show dates of May. The research vessel started the survey off Reykjavik (marked with a cross) on the 14 of May and sailed clockwise around Iceland ending in the same harbour.

3 Results and Discussion

3.1 Temporal changes

The seasonal changes of krill in the North Atlantic Ocean are characterized by low numbers in winter and high numbers during spring and summer (**Paper I**) (Figure 3.1). The increase in numbers during spring reflects spawning and subsequent increase of 0-group animals in surface layers. The main spawning of krill tends to take place during spring with a second batch occurring in the summer (Lindley, 1978b).

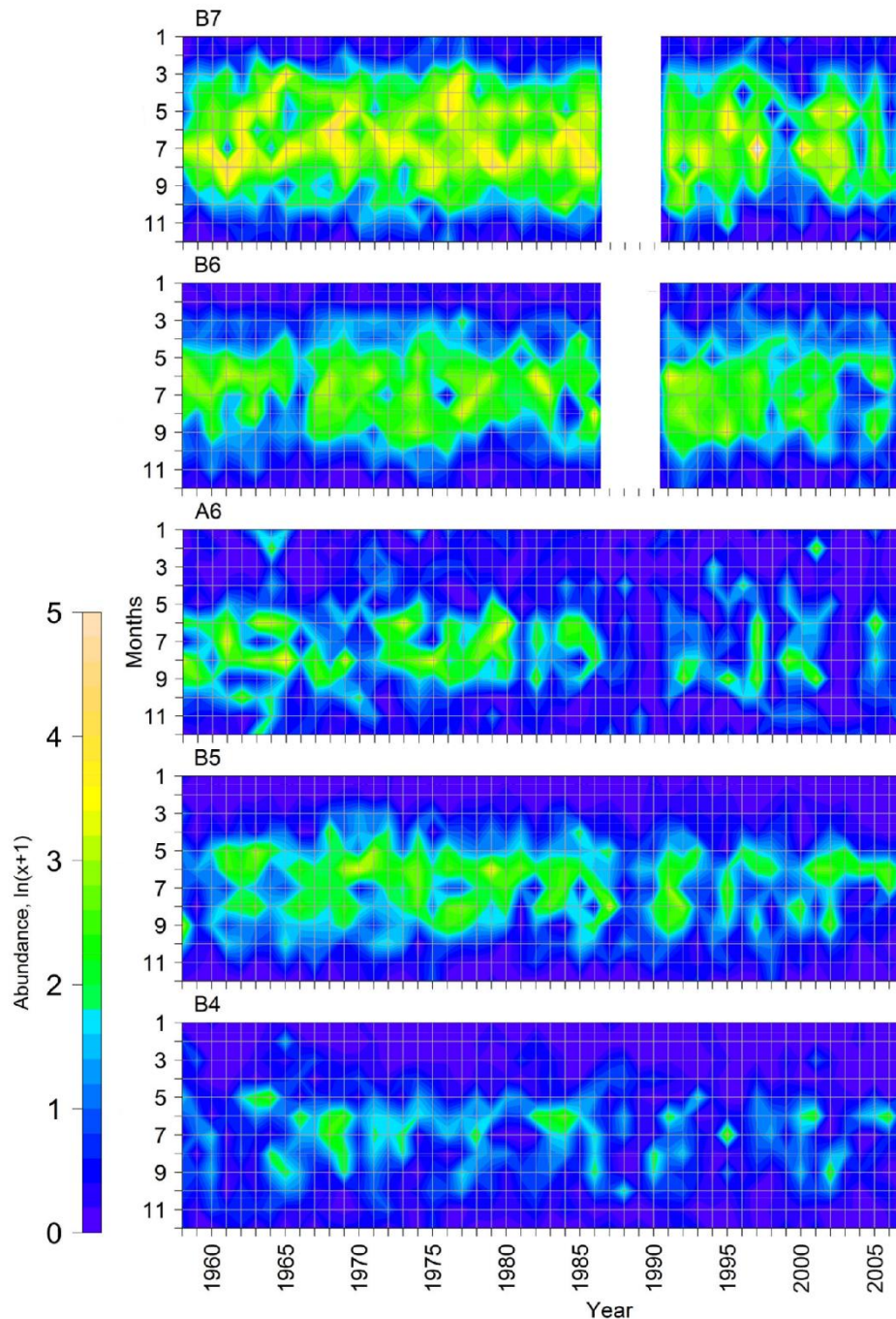


Figure 3.1 Seasonal abundance of total krill from 1958 - 2007 in CPR areas (**Paper I**). Average abundances are shown for both day and night time samples, except for area B7, where night abundances were used. For location of CPR areas refer to Figure 2.1.

The present findings show that the abundance of krill in surface layers declined from 1958 to 2007 in the oceanic waters to the south of Iceland (**Paper I**) (Figure 3.2). A similar decline in krill abundance has been reported from the North Sea and northeast Atlantic (Beaugrand and Reid, 2003; Beaugrand et al., 2003). This decline seems to persist to the present (P. Licandro, 2016, personal communication).

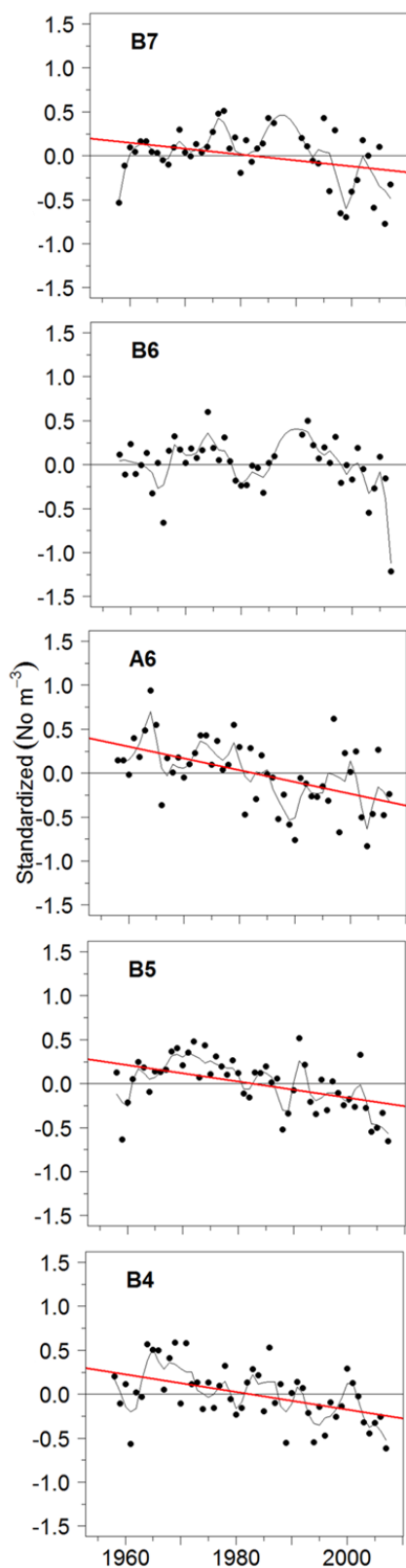


Figure 3.2 Long-term changes in abundance of total krill from 1958–2007 in CPR areas (**Paper I**). Abundances are standardized to zero mean and unit variance. The curved line is a loess smoothed curve with a span of five years. Straight red lines show regression lines significant at $p < 0.05$ level. For location of CPR areas see Figure 2.1.

In contrast to the decline of krill in the oceanic waters to the southwest, south and southeast of Iceland, the abundance of larvae increased on the shelf southwest of Iceland (Selvogsbanki transect, Figure 3.3). It was concluded (**Paper I**) that this discrepancy could be due to differences in species composition, and/or the sampling design, particularly the differences in the spatial and temporal extent of the sampling between the shelf and oceanic regions. Thus the data from the Icelandic spring survey (the Selvogsbanki transect) represent only a snapshot in time (**Papers I-III**), while the CPR data with sampling covering all seasons of the year, probably reflect better the temporal changes in krill abundance.

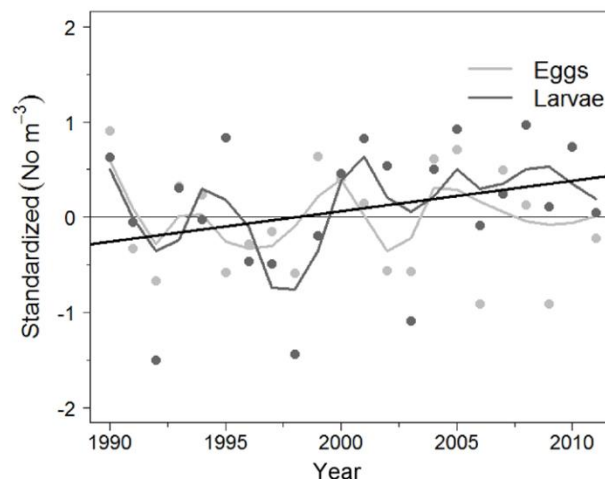


Figure 3.3 Interannual variation in the number of krill eggs (light gray) and larvae (black) on Selvogsbanki transect from 1990–2011 (**Paper I**). Abundances are based on one annual sampling at five stations in late May standardized to zero mean and unit variance. Curved line is a loess smoothed curve with a span of five years. Regression line significant at $p < 0.05$ level is shown by straight black line for larvae estimates. For location of transect see Figure 2.1.

In the oceanic waters (**Paper I**), three main environmental factors regulated krill (furciliae, juveniles and adults) presence/absence and abundances. Chl *a* concentration was the strongest predictor, followed by salinity and temperature (**Paper I**). Generally, at chl *a* $> 1.5 \text{ mg m}^{-3}$, salinities < 35.2 and temperatures $> 9^\circ\text{C}$, the probability of finding krill in high numbers increased (**Paper I**). The explanatory variables for the observed changes in krill abundance vary geographically among the CPR areas. In the west, chl *a* and bloom development were the major predictors of krill abundance, whereas in the east, temperature was the most important predictor (Table III in **Paper I**).

Krill were found to decline in the warmer years after 2000 (Figure 3.2). In years when a delay was observed in the OPB, even though chl *a* concentrations were relatively high, the abundance of krill tended to be low (**Paper I**). Based on this, it was concluded (**Paper I**) that the decline in abundance of young krill in the oceanic waters (southwest, south and southeast of Iceland) was at least partly due to a weakened temporal synchrony between the development of young krill and the phytoplankton spring bloom. It was hypothesized that the mismatch was caused by recent climatic warming.

The decline in krill abundance might also partly be due to a decreased amount of alternate prey items for krill in the North Atlantic Ocean, such as *C. finmarchicus* (Planque and Taylor, 1998; Hátún et al., 2009). Predation may also be affecting krill abundance. Thus, predation pressures by baleen whales and large pelagic fish are known to affect the sizes of krill stocks (Sigurjónsson and Víkingsson, 1997; Eriksen and Dalpadado, 2011; Orlova et al., 2015). Predation pressure may have increased due to the estimated 10% increase in fin whale numbers from 1987 to 2001 in the area between Iceland and Greenland (Víkingsson et al., 2009), as well as due to the unprecedented abundance of mackerel in the waters to the south of Iceland during the summer of recent years (Astthorsson et al., 2012). These changes may have contributed to the long-term decline of krill to the southwest, south and southeast of Iceland (Figure 3.1). A recent study on the frequency of occurrence of krill in the diet of minke whales in Icelandic waters has shown lower incidence of krill in the mid-2000s than in the early 1980s (Víkingsson et al., 2014). This recent finding may in turn be reflecting the declining number of krill in the area.

3.2 Distribution patterns and population dynamics

It was concluded that the different water masses affected distribution, development and spawning of *M. norvegica* and *T. inermis* around Iceland (**Papers II-III**). The abundance of *M. norvegica* and *T. inermis* was highest in areas where Atlantic water prevails and in the frontal regions where warm and cold waters meet to the southeast of Iceland (Figures 3.4 and 3.5).

The species composition of larvae indicates that in May the spawning of *M. norvegica* was mainly confined to the areas to the southwest and east of Iceland with a small contribution from *T. inermis* and *T. longicaudata* (Figures 3.4). Adults of *M. norvegica* was predominant in the warm water in the southwest, whilst *T. inermis* was relatively more abundant in the colder waters north and east of Iceland (Figures 3.5). These findings are in accordance with previous results, namely that *M. norvegica* is found mainly in Atlantic water and over the shelf slopes, while *T. inermis* is mainly confined to Subarctic-Arctic shelf areas and the coastal banks (Einarsson, 1945; Dalpadado and Skjoldal, 1991; Astthorsson and Gislason, 1997a; Dalpadado, 2006).

Previous studies have shown both *M. norvegica* and *T. inermis* to be opportunistic in their feeding behaviour, with the trophic position of both species being dependent on the availability of food (Falk-Petersen et al., 2000; Pétursdóttir et al., 2008, 2012; Agedsted et al., 2014). *T. inermis* have been found to feed on large diatom cells, detritus and small zooplankton, whereas *M. norvegica* additionally feeds on relative large copepods (Pétursdóttir et al., 2008, 2012). The preference for smaller zooplankton by *T. inermis* may possibly explain their more on-shelf distribution.

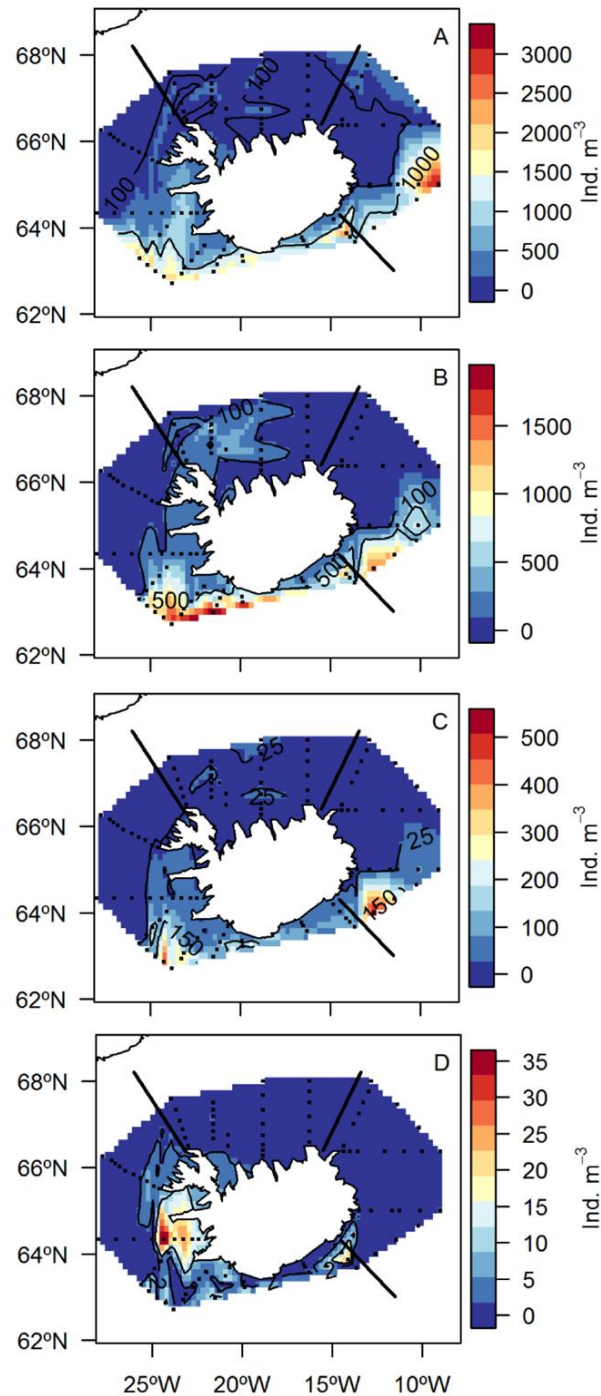


Figure 3.4 Distribution of krill eggs (A), nauplii (B), calyptopes (C) and furciliae (D) around Iceland, 14–29 May 2013 (**Paper II**). Note that the plots have different scales. The black lines denote the division into main hydrographic regions: southwest, north and east.

This study (**Papers I-III**) was carried out during a relatively warm period of the waters around Iceland (Anonymous, 2014), which likely explains why the distribution pattern found was fairly similar to that found by Einarsson (1945), whose investigation was also based on material sampled during a warm period in the North Atlantic Ocean.

This research also showed that chl *a*, temperature and bottom depth were the major drivers of the distribution and abundance of early life stages of krill (**Paper II**). Temperature and bottom depth had a major role influencing the distribution, reproduction and population structure of adults of both *M. norvegica* and *T. inermis* (**Paper III**).

As discussed in section 1.2.3, it is well known that the phytoplankton spring bloom triggers spawning of krill (Astthorsson, 1990; Dalpadado and Skjoldal, 1991; Dalpadado, 2006; Szabo and Batchelder, 2014). **Papers I-III** show that phytoplankton biomass is a key indicator of krill abundance. Further, **Papers II and III** clearly show that *T. inermis* was spawning mostly in the east, where the bloom was in the initial development phase, while *M. norvegica* was mostly spawning in the southwest, where the bloom was ending. Thus, the spawning of the two species seems to vary in the waters around Iceland. **Paper II** suggests that in the waters to the north and east of Iceland, the spawning of *T. inermis* may not take place when chl *a* concentrations are lower than 0.5 mg m^{-3} . Seasonal studies have indicated that the spawning of krill (mainly *T. inermis*) at Siglunes occurs when temperatures ranged between 3 and 4°C and chl *a* concentrations were $>2 \text{ mg m}^{-3}$ (Astthorsson and Gislason, 1997a). On Selvogsbanki, krill (mainly *M. norvegica*) started to spawn when temperatures were $\sim 7^\circ\text{C}$ and chl *a* concentrations were $>0.5 \text{ mg m}^{-3}$ (Gislason and Astthorsson, 1995). Further work should explore which temperature ranges are favourable for spawning of krill, and the potential interactions between temperature and chl *a* as triggers of spawning activity.

Based on the bimodal size distributions of nauplii (**Paper II**), it was concluded that the nauplii represented more than one species. The smaller size mode belonged to *T. longicaudata*, whereas the larger mode represented *M. norvegica* and *T. inermis*. Einarsson (1945) previously pointed out that *T. longicaudata* spawns mostly in areas where Atlantic water prevails. The present study indicates that the spawning area of *T. longicaudata* is probably more extended to the north and east of Iceland than previously observed. However, the furcilia larvae found off the north coast in the present study may also have been advected to the area (Table II in **Paper II**) with the Atlantic water, as suggested by Astthorsson and Gislason (1997a).

The sex ratio (number males/females) of *M. norvegica* was significantly higher off the southwest coast than to the north and east of Iceland (**Paper III**). This difference was attributed to earlier breeding activity in the southwestern waters. In contrast, *T. inermis* showed a similar sex ratio all around Iceland, in line with the observations in other areas of the North Atlantic Ocean where the sex ratio remained constant throughout the year (Falk-Petersen and Hopkins, 1981; Dalpadado and Skjoldal, 1991).

It was concluded in **Paper III** that *M. norvegica* reached maturity at the age of 1 year and had a lifespan of 2 years all around Iceland. *T. inermis* was estimated to have a lifespan of 1 year in waters to the southwest and possibly 2 years in the north and east. Length frequency analysis showed females of both species as larger than the males. Similar gender variability was shown by Astthorsson (1990). These differences were attributed to possible differences in growth between males and females.

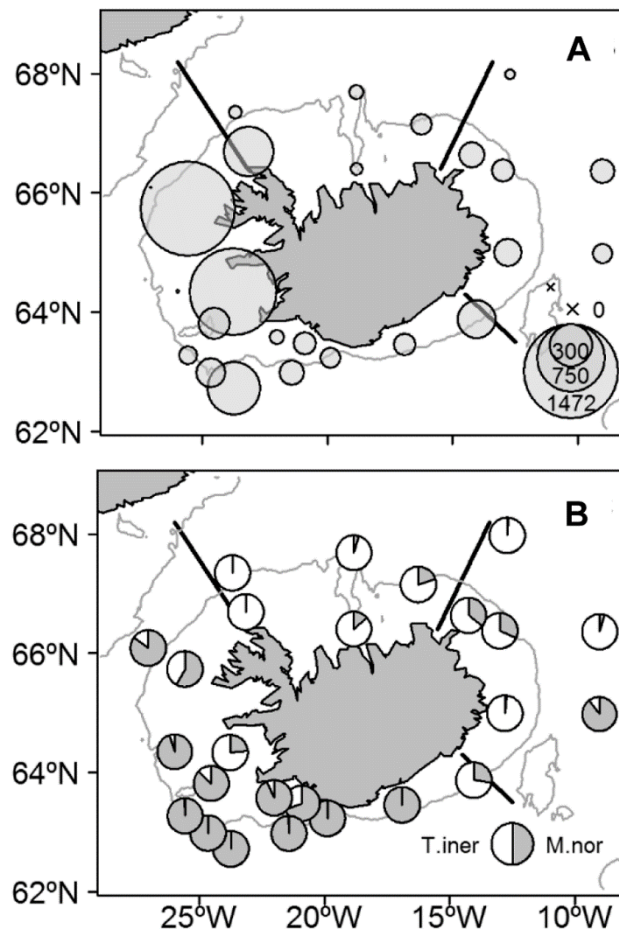


Figure 3.5. Distribution of juvenile and adult *Meganyctiphanes norvegica* and *Thysanoessa inermis* around Iceland, 14-29 May 2013 (**Paper III**). (A) Combined abundance of *M. norvegica* and *T. inermis* (individuals 1000 m⁻³). (B) Relative abundance of *M. norvegica* (*M.nor*) and *T. inermis* (*T.iner*). The grey line indicates the 400 m isobath.

3.3 Temperature effects of *M. norvegica* physiological rates

Increased temperature is well known to be metabolically costly for ectotherms (Kooijman, 2000; Sheridan and Bickford, 2011). **Paper IV** addressed the effect of different temperatures on the growth, egestion and mortality of adult *M. norvegica*. The experiments were done at temperatures ranging from 5 to 12°C, which covers the natural temperature range of *M. norvegica* in waters south of Iceland during the spring and summer months (Malmberg, 2004; Solmundsson et al., 2007; Astthorsson et al., 2012). As expected, *M. norvegica* increased their moulting frequency and egestion and mortality rates when temperature increased (**Paper IV**).

M. norvegica was found to decrease in size during the experiments. This decrease in the size was somewhat unexpected but as discussed in **Paper IV** it may have been due to food limitation (Sameoto, 1976; McClatchie, 1985; Cleary et al., 2012) and/or to a missing nutritional component(s) in the feed (e.g. McGaffin et al. (2002)). Growth in krill is dependent on high food intake and quality, as *M. norvegica* tends to grow faster when

phytoplankton and small zooplankton are abundant during spring (Tarling, 2010a). These findings are in agreement with the notion that when animals are exposed to unfavourable food conditions, they may decrease in size (shrink) to minimize somatic costs (Kooijman, 2000; Sheridan and Bickford, 2011; Meyer and Teschke, 2016). Shrinkage in krill is generally believed to be indicative of poor physiological condition due to food limitation (Shin and Nicol, 2002; Pinchuk and Hopcroft, 2007; Saunders et al., 2007; Meyer and Teschke, 2016).

Krill are known to contribute to carbon flux to the interiors of the oceans, both by diel migrations (active carbon flux) and by production of faecal pellets that sink from the euphotic layer (passive carbon flux) and into deeper layers (Youngbluth et al., 1989; Schnack-Schiel and Isla, 2005; Wassmann et al., 2006; Atkinson et al., 2012; Turner, 2015). *M. norvegica*, for instance, can produce faecal pellets, that sink relatively fast ($\sim 200 \text{ m d}^{-1}$), and supply bottom communities with large amounts of organic matter ($7\text{-}12 \text{ mg C m}^{-2} \text{ d}^{-1}$) (Youngbluth et al., 1989). By combining data on egestion rates (**Paper IV**) and abundance of *M. norvegica* (**Paper III**), it was estimated that the total amount of carbon egested within the upper 200 m (at 8°C) would be $\sim 0.2 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the waters to the southwest of Iceland during spring. This egestion was, however, low ($\sim 0.2 \text{ mg C m}^{-2} \text{ d}^{-1}$), compared to other studies (Youngbluth et al., 1989) and given that the estimated total carbon flux to the seafloor in the North Atlantic Ocean is on average $\sim 6.4 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Lutz et al., 2007). The role of krill in carbon sequestration has been addressed by several studies (Riser et al., 2002; Pakhomov et al., 2002; Michels et al., 2008; Ruiz-Halpern et al., 2011). Riser et al. (2002) showed that in the Barents Sea between 10 to $80 \text{ mg C m}^{-2} \text{ d}^{-1}$ are egested, mainly by copepods but also from krill. The contribution of fecal pellet production of Antarctic krill in the total carbon sequestration in the Southern Ocean can be up to 30 % (assuming an egestion rate of $\sim 8.143 \text{ mg C mg DW}^{-1} \text{ d}^{-1}$) (Pakhomov et al., 2002). Most likely this low estimate for the contribution of *M. norvegica* to the carbon flux to the southwest of Iceland is due to the quality of food given to the experimental animals. Further studies are needed to fully estimate the grazing impact and contribution of *M. norvegica* to the total carbon flux in the Icelandic marine environment.

4 Conclusions and Future Perspectives

The main findings of this thesis are that the distribution of krill is driven by both physical (temperature, salinity and bottom depth) and biological (biomass and development of phytoplankton) variables (**Papers I-III**). The results confirm with previous findings that krill species are confined to particular water masses and can, therefore, be used as indicators of water masses. Relatively high abundances of krill were observed in warmer and more productive waters around the island.

This dissertation is the first evaluation of long-term variability of krill in the oceanic and shelf habitats to the southwest, south and southeast of Iceland in the context of climate warming (**Paper I**). It provides new insights, namely that krill populations were declining in the oceanic habitats south of Iceland from 1958 to 2007, likely as a result of climatic changes. A significant positive effect of temperature on krill abundance was observed (**Paper I**), which may indicate that krill abundance increase with increasing temperatures. However, decreased krill densities in the CPR areas were observed during the 2000s, while sea surface temperatures increased. Based on this it is hypothesized that the warming surface waters may have resulted in a weaker temporal synchrony of developing young krill with the phytoplankton spring bloom, which in turn may have led to reduced population sizes of krill. These findings are in general agreement with studies on long-term changes of other zooplankton species (such as *C. finmarchicus*) in the open waters of the North Atlantic Ocean. They support the hypothesis that bottom-up regulation, driven by climate forcing, is a major factor affecting interannual changes in the abundance of krill (**Paper I**).

The thesis presents novel data on abundance, distribution and size distributions of krill eggs and larvae (**Paper II**) and adults (**Paper III**) around Iceland in relation to water masses and phytoplankton spring bloom dynamics. The detailed classification of the larvae into developmental stages in **Paper II** is not commonly undertaken; most studies would combine the larval stages, as was done in **Paper I**, and most taxonomists do not classify the metanauplii stages of krill to the species level on a regular basis. An important novelty of this thesis was the use of the ZooImage software to analyse a large number of zooplankton samples automatically. The results of this analysis increased understanding of the spawning locations of krill and size frequency distribution of early life stages of krill around Iceland (**Paper II**). For instance, it was determined that the spawning area of *T. longicaudata* might be more extended to the north and east of Iceland than previously observed (see Einarsson, 1945).

Paper III described the distribution, maturity and population structure of juvenile and adults of *M. norvegica* and *T. inermis*, the two most abundant species caught around Iceland by a specially designed macrozooplankton trawl. The data collected by this gear (**Paper III**) showed that warm and productive Atlantic water was an important factor affecting the distribution, development and reproduction of *M. norvegica* and *T. inermis* around the island.

Paper IV represents the first study on the growth, egestion and mortality rates of *M. norvegica* in Icelandic waters. The results showed that in conditions of low food quality, *M.*

norvegica reduced their growth. It is suggested that this may be to counterbalance for the rise in respiration and egestion costs due to increased temperatures. It was estimated in this thesis that the total amount of carbon egested by *M. norvegica* was low ($\sim 0.2 \text{ mg C m}^{-2} \text{ d}^{-1}$) compared to other studies estimates (referenced in section 3.3.) and concluded that further work is needed to corroborate this finding.

The marine ecosystem is constantly changing, and krill can be used as an important indicator of change in ocean climate. Krill also constitute a very significant part of the total zooplankton biomass in the ocean. Further studies should focus on the transfer efficiencies of mass and energy between trophic levels and the contribution of krill to the carbon flux, which may be an important step towards a better understanding of the ecosystem functioning. Such a study could be used to evaluate the role of krill in the ecosystem, and thus contribute to ecosystem-based fisheries management in Iceland.

Furthermore, monitoring of krill is therefore important but should evolve and adapt to new findings (Lindenmayer and Likens, 2009). The MFRI has recently added for the monitoring of krill to its annual spring survey for environmental conditions. The incorporation of acoustic recordings onboard research vessels during standard oceanographic surveys is an advantage. However, these surveys are mostly confined to shelf areas and the acoustic equipment used in the surveys (38 and 120 kHz transducers) can only detect krill down to 300 m. Thus, further improved technologies are required to study the abundance of krill in the whole water column.

Finally, seasonal data on krill abundance and development with high temporal resolution along with possibly laboratory studies are needed to answer a central question raised by this dissertation: what dictates the synchronization of krill spawning with the phytoplankton spring bloom? In this thesis, it is suggested that the timing of the phytoplankton spring bloom and intensity (of production), coupled with species-specific temperature thresholds may trigger the spawning of krill in Icelandic waters. This hypothesis could be addressed if seasonal studies were conducted together with dedicated laboratory feeding experiments (e.g. recreating the temperature and phytoplankton bloom conditions).

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