1   The North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life history

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Abstract

Here we present a new, pan-Atlantic compilation and analysis of data on *C. finmarchicus* abundance,

demography, dormancy, egg production and mortality in relation to basin-scale patterns of temperature,

phytoplankton biomass, circulation and other environmental characteristics in the context of

understanding factors determining the distribution and abundance of *C. finmarchicus* across its North

Atlantic habitat. A number of themes emerge: (1) the south-to-north transport of plankton in the

northeast Atlantic contrasts with north-to-south transport in the western North Atlantic, which has

implications for understanding population responses of *C. finmarchicus* to climate forcing, (2)

recruitment to the youngest copepodite stages occurs during or just after the phytoplankton bloom in

the east whereas it occurs after the bloom at many western sites, with up to 3.5 months difference in

recruitment timing, (3) the deep basin and gyre of the southern Norwegian Sea is the centre of

production and overwintering of *C. finmarchicus,* upon which the surrounding waters depend, whereas,

in the Labrador/Irminger Seas production mainly occurs along the margins, such that the deep basins

serve as collection areas and refugia for the overwintering populations, rather than as centres of

production, (4) the western North Atlantic marginal seas have an important role in sustaining high *C.*

finmarchicus abundance on the nearby coastal shelves, (5) differences in mean temperature and

chlorophyll concentration between the western and eastern North Atlantic are reflected in regional

differences in female body size and egg production, (6) regional differences in functional responses of

egg production rate may reflect genetic differences between western and eastern populations, (7)

dormancy duration is generally shorter in the deep waters adjacent to the lower latitude western North

Atlantic shelves than in the east, (8) there are differences in stage-specific daily mortality rates between

eastern and western shelves and basins, but the survival trajectories for cohort development from CI to

CV are similar, and (9) early life stage survival is much lower in regions where *C. finmarchicus* is

1   found with its congeners, *C. glacialis* and/or *C. hyperboreus*. This compilation and analysis provides

2   new knowledge for evaluation and parameterisation of population models of *C. finmarchicus* and their

3   responses to climate change in the North Atlantic. The strengths and weaknesses of modeling

4   approaches, including a statistical approach based on ecological niche theory and a dynamical approach

5   based on knowledge of spatial population dynamics and life history, are discussed, as well as needs for

6   further research.

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1. Introduction

The northern North Atlantic Ocean is characterized by its circulation and water mass distribution, its extensive latitudinal expanse (from roughly 40 to 75°N) and topography, and its seasonally and geographically varying wide ranges of temperature, salinity and light conditions, which provide a variety of habitats for its biota. Regional differences in physical features lead to differences in the timing and intensity of the annual cycles of primary production, and in the distributions, abundances and seasonal cycles of planktonic grazers and their predators. The distribution of any zooplankton species in the North Atlantic is the manifestation of its ability to maintain itself within this range of conditions, from suboptimal to optimal, that constitute its habitat.

One approach to understanding the distribution of a species is to examine and define its ecological niche in terms of its range of tolerance based on a series of environmental factors (e.g. Helaouët and Beaugrand, 2009). Advances in statistical and numerical techniques, such as generalized linear models (GLM) and geographic information systems (GIS), have been applied to quantify species distributions, in species distribution models (Elith and Leathwick, 2009), habitat distribution models (Guisan and Zimmerman, 2000) and habitat suitability models (e.g. Hirzel et al., 2002). Extrapolation to future distribution patterns resulting from habitat change, however, confronts the statistical and ecological assumptions of these models (Elith and Leathwick, 2009). To gain predictive insight into the consequences of habitat change on the abundance of a species and on shifts in its range and biogeographic boundaries, it is also necessary to understand, at the species level, processes determining population dynamics and life history in relation to environmental changes that affect both physiological and behavioural responses and dispersal patterns. This information can be integrated into complex

1   process models (e.g. Korzukhin et al., 1996) in the marine realm by means of coupled physical-

2   biological models (e.g. de Young et al., 2010).

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4   The planktonic copepod, *Calanus finmarchicus*, is one of the most important multicellular

5   zooplankton species in the northern North Atlantic, based on its abundance and role in food webs and

6   biogeochemical cycles. It is the subject of a book (Marshall and Orr, revised edition, 1972) and over

7   1000 research articles since its publication. It has been the target species of several previous basin-scale

8   research programs, including investigation of *C. finmarchicus* migrations between oceanic and shelf

9   seas off Northwest Europe (ICOS: e.g. Heath et al., 1999), Trans-Atlantic Studies of *Calanus*

10   *finmarchicus* (TASC: e.g. Tande and Miller, 2000), the Global Ocean Ecosystem Dynamics program

11   (GLOBEC: e.g. Gifford et al., 2010), and the ongoing EURO-BASIN program. From the basin-wide

12   programs, in combination with local time series measurements and Continuous Plankton Recorder

13   (CPR) surveys, a tremendous source of information and knowledge of *C. finmarchicus* distribution and

14   life history traits has emerged. Basin scale themes such as the past, present and possible future

15   distribution of *C. finmarchicus*, based on observations and inferences from statistical and process

16   models (Planque and Fromentin, 1996; Speirs et al., 2005, 2006; Helaouët and Beaugrand, 2007, 2009;

17   Reygondeau and Beaugrand, 2011) have been investigated. In addition, process and modeling studies

18   have studied *C. finmarchicus* phenology, grazing, egg production, over-wintering strategy, mortality

19   and role in carbon flux budgets (e.g. Aksnes and Blindheim, 1996; Heath et al., 2000, 2004; Ohman et

20   al. 2004; Melle et al., 2004; Broms and Melle 2007; Stenevik et al., 2007; Johnson et al., 2008; Broms

21   et al., 2009; Bagoeien et al., 2012; Head et al., 2013a; Hjollo et al., 2013). We review this knowledge

22   of *C. finmarchicus* life history and its North Atlantic habitat in the following section. We then compile,

23   for the first time, the across-basin data sets and provide a synthesis of previously reported and new

24   information on spatially and seasonally resolved demography and life history strategies related to

1   seasonal cycles, development, reproduction, dormancy and mortality across the North Atlantic. We

2   use this information to identify the factors involved in determining distribution and abundance of *C.*

3   *finmarchicus*, including the important question of connectivity between basin and shelf populations on

4   both sides of the North Atlantic. We consider whether genetic differences between populations in the

5   northeast and northwest/central North Atlantic lead to differences in physiological and ecological

6   responses to changes in environmental conditions. Our overall objective is to provide parameter values

7   and new knowledge of *C. finmarchicus* life history characteristics on a North Atlantic basin scale and,

8   thus to further the development of habitat and basin-scale dynamic models that can be used to predict

9   the effects of climate change on *C. finmarchicus* populations.

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11 *1.1. The North Atlantic habitat*

12   Ocean circulation is fundamental to the dynamics of a planktonic species' habitat. The North

13 Atlantic surface circulation system is made up of a series of gyres, encircled by strong boundary

14 currents (Fig. 1a). In the west, the Northwest Atlantic Subpolar Gyre, commonly referred to as the

15 Subpolar Gyre, includes the Labrador and Irminger Seas and is defined by bathymetry to the north and

16 the North Atlantic Current to the south. In the east, the Southern Norwegian Sea Gyre, a cyclonic gyre

17 over the Norwegian Basin of the southern Norwegian Sea, is bounded by bathymetry to the north and

18 by the North Atlantic Current to the south. These two gyres are interconnected, however, and together

19 can be regarded as one basin-scale North Atlantic Subpolar Gyre system, throughout which organisms,

20 including plankton, can be broadly distributed over appropriate time scales, but which nevertheless

21 shows regional differences in ecological characteristics due to the responses of individual species to

22 local conditions.

23

1   The Gulf Stream System transports warm and saline water from west to east in the North

2   Atlantic at a latitude of about 40^0N in the west (e.g. Reverdin et al., 2003). At about 54^0W, the Gulf

3   Stream splits into two branches, a northern branch connected to the North Atlantic Current and a

4   southern branch connected to the Azores Current. The Azores Current and the southward flowing

5   Canary Current limit the Subtropical Gyre to the north and east. The North Atlantic Current flows to

6   the northeast, with branches flowing into the Icelandic basin and Irminger Sea before the main body

7   enters the Norwegian Sea as the Norwegian Atlantic Current. Thus, the Northeast Atlantic is strongly

8   influenced by northward flowing warm and saline water. Warmer water of Atlantic origin also

9   circulates clockwise around Iceland. Cold Arctic water enters the system from the Arctic Ocean

10   through the Fram Straight as the East Greenland Current and east of Baffin Island as the Baffin Island

11   Current. North of Iceland, the East Icelandic Current separates from the East Greenland Current,

12   bringing Arctic water eastward into the western Norwegian Sea. The East Greenland Current itself

13   continues southward and meets the warmer Atlantic water of the Irminger Current, with both turning

14   around the southern tip of Greenland and entering the Labrador Sea. This northwesterly flow has a cold

15   water shelf component (the West Greenland Current) and a warmer, deeper offshore component

16   (identified as the Irminger Current), which provides a major warm water input to the Labrador Sea. The

17   main sources of water to the Labrador Shelf and Slope are the outflows from the Arctic via Hudson

18   Strait and the Baffin Island Current, and the branch of the slope water current that follows the

19   bathymetry westward across the mouth of Davis Strait. These water masses mix off Hudson Strait

20   together forming the inshore (shelf) and offshore (slope) branches of the Labrador Current moving

21   southwards. Part of the inshore branch enters the Gulf of St. Lawrence through the Strait of Belle Isle,

22   and part continues on to the Newfoundland Shelf and turns around the southeast tip of Newfoundland.

23   A substantial portion of the offshore branch turns to the northeast at the Tail of the Grand Bank to join

24   the North Atlantic Current, but a portion also flows around the Tail of the Grand Bank and along the

edge of the Scotian Shelf and Georges Bank (Fratantoni and MacCartney, 2010; Loder et al., 1998).

Cross-shelf transport of slope water at the Laurentian Channel, Scotian Gulf, and Northeast Channel

influences the deep water properties of the Gulf of St. Lawrence, western Scotian Shelf, and Gulf of

Maine, and variability in the slope water source, e.g. cold Labrador Slope water vs. warm Atlantic

slope water, can drive substantial changes in deep water temperatures on the western Scotian shelf and

in the northwest Atlantic marginal seas (Bugden,1991; Petrie and Drinkwater, 1993; Gilbert et al.,

2005). In contrast to the northeast Atlantic, the western Atlantic shelf and slope waters are therefore

strongly influenced by southerly flowing cold and low salinity water of Arctic origin. As we discuss

later, this contrast in physical regime has implications for understanding east-west differences in effects

of climate forcing on species distribution.

The topography of the North Atlantic is characterised by several deep basins: the Labrador Sea

basin, the Iceland basin and Irminger Sea, the Norwegian Sea basin in the southern Norwegian Sea, the

Lofoten basin in the Northern Norwegian Sea and the Greenland Sea basin. More or less well defined

cyclonic gyres are located over these deep basins, which thus offer reduced dispersal for animals within

the gyres and possibilities for deep overwintering or deep diurnal migration. In addition to these deep

basins are the Norwegian deep fjords (up to 1,300 m deep) and basins or troughs (200-400 m depth) in

the northwest Atlantic marginal seas (Gulf of Maine and Gulf of St. Lawrence).

The geographical pattern of seas surface temperature (SST) in the North Atlantic is strongly

influenced by the Gulf Stream and North Atlantic Current, resulting in a southwest to northeast

orientation of isotherms (Fig. 1a, 2a). Because the same SST is found much farther south in the west

than in the east, with very different seasonal and diurnal light regimes, habitats that have similar annual

average temperatures in the western and eastern North Atlantic can have biologically quite different

1 conditions. For example, Georges Bank has, on average, temperatures similar to those in the southern

2 Norwegian Sea, but because it is much farther south, light levels in winter are typically sufficient to

3 support primary production. By contrast, on the eastern side of the Atlantic, although temperatures

4 remain relatively high during winter, phytoplankton production ceases, whereas in summer during the

5 growth season, the midnight sun and long days prevail. In addition, in the west cool water

6 temperatures, caused by cold winters and the influence of Arctic waters, allow for the presence of the

7 same visually guided predators much farther south than in the northeast Atlantic.

8

9 　　　The North Atlantic pattern of primary production (PP) is strongly related to light conditions and

10 SST, but also to nutrient supply, and to mechanisms of water column vertical stabilisation and grazing.

11 The northeast Atlantic is a typical spring bloom system, although the seasonal cycle of PP differs

12 between deep basins and shelves. In the deep Norwegian Sea basin the pattern of seasonal

13 phytoplankton production has been shown to comply with Sverdrup's concept of critical depth

14 (Sverdrup, 1953), although newer publications indicate that the controlling mechanisms may be more

15 complex or at least regionally different (e.g. Behrenfeld, 2010; Mahavedan et al., 2012). According to

16 the critical depth concept, production will occur when the mixing depth of algal cells is less than a

17 critical depth such that net production is positive. This usually occurs in March-April and the bloom

18 starts in May-June when the pycnocline approaches the upper 30-40 m (Rey, 2004; Bagoeien et al.,

19 2012; Zhai et al., 2012). The timing of the bloom may vary by more than a month among years (Rey,

20 2004) and the chlorophyll concentration of the upper mixed layer is on average less than 3 mg m^{-3}

21 (Bagoeien et al., 2012). On the Norwegian shelf the water column is permanently stratified by a near

22 surface layer of fresh (light) coastal water or is restricted by shallow bottom depths, so that pre-bloom

23 production and blooms tend to start earlier and to some extent are more intense, providing relatively

24 high chlorophyll concentrations in the water column (Rey, 2004). During the bloom diatoms are the

1   main algal group (Rey, 2004). The post-bloom period lasts until September and is characterised by

2   flagellates, utilising re-cycled nutrients. It has been suggested that pre-bloom levels of phytoplankton

3   are lower than might be expected in the Norwegian Sea due to the grazing activity of the large

4   overwintering population of *Calanus finmarchicus*, which returns to the surface at this time, and that

5   the intensity of the spring bloom itself is kept low by grazing by the offspring of the overwintered *C.*

6   *finmarchicus* (Rey, 2004).

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8   In the Irminger Sea, spatial variability in the timing and magnitude of the spring bloom is

9   considerable, reflecting differences in the seasonal timing of stratification of the surface waters

10   (Henson et al., 2006, Waniek and Holliday, 2006, Gudmundsson et al., 2009; Mahavedan et al., 2012;

11   Zhai et al., 2012). On the Iceland and Greenland shelves fringing the Irminger Sea, the growth of

12   phytoplankton usually starts in late April culminating in June and July, whereas in the central region of

13   the Irminger Sea growth usually starts in early May with a maximum in June. As in the northeast

14   Atlantic, timing of the start of the bloom is patchy and may vary interannually by as much as one

15   month, influenced by storms and mixed layer eddy restratification (Mahavedan et al., 2012).

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17   In the northwest Atlantic regions, the timing of spring bloom initiation generally varies with

18   latitude, but there can be substantial departures from this trend among shelf areas due to local or

19   regional processes (O'Reilly and Zetlin, 1998; Platt et al., 2010). Spring and fall blooms tend to start

20   earlier in shallow water, and spring blooms tend to be longer in shallow water (O'Reilly et al., 1987).

21   Interannual variability in bloom timing can be high in the northwest Atlantic (Thomas et al., 2003; Platt

22   et al., 2010). In the Gulf of Maine/Georges Bank region, the spring bloom starts earliest in the shallow

23   coastal areas (January – March), later over Georges Bank (March – April), and latest in the deep basins

24   of the Gulf of Maine and over the shelf edge (April – May) (O'Reilly et al., 1987). On the western and

1   eastern Scotian Shelf, the spring bloom starts in March or April and peaks after about a month, while in

2   the Scotian Slope waters it starts in February or March and peaks in May (Zhai et al., 2011). In the

3   Gulf of St. Lawrence, the spring bloom is earlier in the northeast and southern Gulf (April – May) than

4   in the lower St. Lawrence Estuary (June – July) (reviewed by Zhi-Ping et al., 2010). On the Grand

5   Bank and Flemish Cap, the spring bloom starts in late March or April and peaks after about a month,

6   while on the Labrador Shelf it starts in May (Fuentes-Yaco et al., 2007). The spring bloom starts

7   relatively late (April – June) in the central Labrador Sea, but slightly earlier (April – May) in the

8   northern Labrador Sea, where early stratification is driven by offshore flow of relatively freshwater

9   from the West Greenland Shelf (Frajka-Williams and Rhines, 2010). Estimates of annual primary

10   production from satellite ocean colour and temperature from 1998 – 2004 indicate that the highest

11   offshore production in the northwest Atlantic occurs on Georges Bank and in the outflow from the

12   Hudson Strait (ca. 275 – 325 gC m^{-2} y^{-1}), while the lowest production occurs in the Labrador slope

13   waters (ca. 150 gC m^{-2} y^{-1}) and southern Labrador Sea (ca. 175 – 200 gC m^{-2} y^{-1}) (Carla Caverhill, pers.

14   comm., Platt et al., 2008).

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16   *1.2. Calanus finmarchicus*

17   The copepod *Calanus finmarchicus* is the main contributor to mesozooplankton biomass

18   throughout the North Atlantic. Population centres, defined as regions where overwintering populations

19   exceed 15,000 m^{-2}, have been identified in the Labrador Sea, northern Irminger Basin, northern Iceland

20   Basin, Faroe-Shetland Channel, eastern Norwegian Sea and Norwegian Trench (Heath et al., 2004).

21   Based on this criterion, slope waters off the Grand Bank of Newfoundland, the Laurentian Channel of

22   the Gulf of Saint Lawrence, deep basins in the Gulf of Maine, and slope waters of the western Scotian

23   Shelf are also population centres (Plourde et al, 2001; Head and Pepin, 2008; Maps et al., 2012). *C.*

24   *finmarchicus* makes up >80% of large copepods by abundance in the central Labrador Sea in spring

1 and summer (Head et al., 2003, sampled with a 200 μm mesh net, which in this cold region catches all

2 *Calanus* copepodite stages), about 40-70 % of the mesozooplankton community on Flemish Cap, east

3 of the Grand Bank of Newfoundland (Anderson, 1990, sampled with 333-505 μm mesh nets, which

4 excludes the youngest copepodite stages as well as smaller copepod species) , and 40-90% of the

5 zooplankton community by abundance in waters around Iceland in summer (Gislason and Astthorsson,

6 2000, sampled with a 200-μm mesh net which here excludes some of the smaller stages) . There are

7 apparently two major overwintering areas, which serve as population reservoirs and distribution

8 centres , in the two subpolar gyres; one in the Labrador/Irminger Seas and the other in the southern

9 Norwegian Sea (Conover, 1988; Planque et al., 1997; Head et al., 2003; Melle et al., 2004; Heath et al.,

10 2008; Broms et al., 2009). These cyclonic gyres are centred over deep ocean basins, so that they can

11 retain populations as they are overwintering at depth, a necessity for *C. finmarchicus* to close its life

12 cycle both spatially and inter-annually (Heath et al., 2004; Heath et al., 2008). From these distribution

13 centres *C. finmarchicus* is transported to the surrounding shelves and shallow seas (*e.g.* the Labrador,

14 Newfoundland shelves; North and Barents seas) and ultimately to more distant regions (*e.g.* Scotian

15 Shelf, Gulf of Maine) (Speirs et al., 2006; Heath et al., 2008). There is evidence from genetic analysis

16 that there are two to four distinct *C. finmarchicus* populations, with greatest differences occurring

17 between the northwest/central North Atlantic and northeast Atlantic (Unal and Bucklin, 2010). Toward

18 the Arctic domain, *C. finmarchicus* co-occurs with its larger congeners, *C. hyperboreus* and *C.*

19 *glacialis*, while in the southeast it co-occurs with the temperate water species, *C. helgolandicus*

20 (Conover, 1988; Hirche, 1991; Head et al., 2003; Melle et al., 2004; Bonnet et al., 2005; Hop et al.,

21 2006; Broms et al., 2009).

22

23   Throughout its biogeographic range, *C. finmarchicus* is a dominant grazer and the main prey

24 for numerous planktivorous fish, including herring, mackerel, capelin and young blue whiting and

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1   salmon (e.g. Dalpadado et al., 2000; Darbyson et al., 2003; Dommasnes et al., 2004; Skjoldal, 2004;

2   Overholtz and Link, 2007; Smith and Link, 2010; Langøy et al., 2012). The larvae of many fish species

3   also feed, sometimes almost exclusively, on the eggs and nauplii of *C. finmarchicus*, and copepodite

4   stages are important food for the juvenile fish in shelf and shallow sea nursery areas (Runge and de

5   Lafontaine, 1996; Heath and Lough, 2007).

6

7   During its life cycle from egg to adult (females, CVIF and males, CVIM), *C. finmarchicus* pass

8   through six nauplius (NI-NVI) and five copepodite stages (CI-CV). The first two naupliar stages do not

9   feed. The life cycle of *C. finmarchicus* is annual in its main distributional area (Conover, 1988; Heath

10   et al., 2000a; Irigoien, 2000; Hirche et al., 2001; McLaren et al., 2001; Heath et al., 2008, Broms et al.

11   2009; Bagoeien et al., 2012; Head et al., 2013b). In regions influenced by Arctic outflow, however,

12   where water temperatures are low, development rates are reduced and young copepodites (CI-CIII) are

13   found among the older overwintering stages (Broms and Melle, 2007; Heath et al., 2008), suggesting

14   that there is either a multiannual life cycle or an inability to reach stages that can survive the winter

15   within the first season, leading to expatriation (Melle and Skjoldal, 1998). Although there is only one

16   generation per year within the main distributional area within the subpolar gyre (*e.g.* Labrador Sea,

17   Northern Norwegian Sea) farther south (*e.g.* Georges Bank) there may be up to three generations per

18   year (Irigoien, 2000; Hirche et al., 2001; McLaren et al., 2001; Plourde et al., 2001; Head et al.,

19   2013b). The number of generations may vary among years at the same location (Irigoien, 2000) and in

20   some areas (*e.g.* Newfoundland Shelf) distinct generations are not evident.

21

22   The main overwintering stage is the pre-adult CV (Conover, 1988). In the deep basins, *C.*

23   *finmarchicus* CVs spend most of the year at depths below 400-1000 m (Heath et al., 2000b, 2004;

24   Melle et al., 2004). In the northern Norwegian Sea, overwintering *C. finmarchicus* are most abundant

1　between about 600 and 1200 m, at temperatures less than 2 °C (Edvardsen et al., 2006). In the Iceland

2　Basin, overwintering *C. finmarchicus* reside between about 400 m and the bottom (> 2000 m) at

3　temperatures about 3-8 °C, while in the Irminger Basin, they reside between about 200 and 1800 m at

4　temperatures of 3-6 °C (Gislason and Astthorsson, 2000). In the northwest Atlantic, overwintering *C.*

5　*finmarchicus* occupy a broad and spatially variable depth range, in temperatures ranging from 1 to 10

6　°C (Head and Pepin, 2008). Overwintering depths are shallowest in Gulf of Maine basins, the

7　Laurentian Channel and in eastern Scotian slope waters (ca. 100 – 400 m) and deeper in western

8　Scotian slope water (400 – 950 m) and in Newfoundland slope waters (400 – 1500 m). In the western

9　part of the central Labrador Sea overwintering depths are variable, but generally <1000 m, while in the

10　eastern Labrador Sea near the Greenland shelf, *C. finmarchicus* overwinters at greater depths, similar to

11　those in the Irminger Sea, (Head and Pepin, 2008). Individual *C. finmarchicus* enter dormancy in

12　summer and fall (Hirche, 1996a), carrying with them lipid stores that make up most of their body

13　weight. These lipid stores sustain metabolism during overwintering and subsequent molting and partial

14　development of gonads in mid-late winter (Rey-Rassat et al., 2002). Dormant copepodites are

15　characterized by reduced metabolism and arrested or slowed development (Saumweber and Durbin,

16　2006). In many locations there is evidence that fourth stage copepodites (CIVs) enter dormancy, with

17　higher proportions of dormant CIV copepodites observed in the northeast Atlantic than in the northwest

18　Atlantic (Heath et al., 2004; Melle et al., 2004; Head and Pepin, 2008). The implications of CIV

19　dormancy have not been rigorously examined, although it is unlikely that CIVs can molt to CVs

20　without feeding since they are significantly smaller. The descent to overwintering depths at Weather

21　Station India occurred during at least two pulses towards the end of each of two cohorts (Irigoien,

22　2000), whereas elsewhere individuals from different generations may descend over several months

23　(e.g. Johnson et al., 2008).

24

1   Arousal from the winter diapause generally occurs in mid-late winter, when most CVs leave

2   dormancy, molt into adults and mate upon returning to the surface (e.g. Melle et al., 2004). Females

3   then lay eggs in response to food levels, for which chlorophyll a concentration is a useful proxy (Runge

4   et al., 2006). The arctic species, *Calanus hyperboreus*, uses internal body stores including lipids to

5   produce eggs without any external food supply (Conover, 1988), but the extent to which internal body

6   stores contribute to egg production for *C. finmarchicus* is still unresolved. In many populations, not all

7   CVs from the new year's generation enter dormancy; some molt on to adulthood, so that reproduction

8   can occur throughout the year (e.g. Durbin et al., 1997; Heath et al., 2008).

9

10   In the Norwegian Sea, studies have demonstrated that spawning occurs at relatively low food

11   concentrations and low individual rates before the spring bloom. However, population egg production

12   rates were higher during the pre-bloom period than during the bloom itself, due to the higher

13   abundance of females (Niehoff et al., 1999; Richardson et al., 1999; Stenevik et al. 2007; Debes et al.,

14   2008). Regional differences in the timing and intensity of *C. finmarchicus* reproduction have been

15   observed (e.g., Plourde et al., 2001; Runge et al., 2006; Stenevik et al. 2007; Head et al., 2013a; Head

16   et al. 2013b), reflecting regional variations in the timing and intensity of spring blooms. These results

17   are mainly based on individual studies that have usually been limited to one or a few regions; whether

18   responses of females to environmental conditions can be generalized throughout the North Atlantic has

19   not been addressed.

20

21   The maximum abundance of CIs of the first generation has often been observed to occur during

22   the peak of bloom or just after (Hirche et al., 2001; Melle et al., 2004; Bagoeien et al., 2012), and these

23   CIs must have arisen from eggs spawned before the bloom. On the other hand, during the pre-bloom

24   period, mortality rates are thought to be high due to starvation of first feeding nauplii and/or predation

1   on eggs during the pre-bloom phase, which may include predation by the females themselves (e.g.

2   Ohman and Hirche, 2001; Plourde et al., 2001; Heath et al., 2008). The CIs-CIIIs are found exclusively

3   in the upper mixed layer or in the pycnocline, if a subsurface chlorophyll maximum develops during

4   the post-bloom phase (Melle and Skjoldal, 1989; Irigoien, 2000; Melle et al., 2004).

5

6   Mortality and survival are key parameters in *Calanus finmarchicus* population dynamics. In the

7   early stages (eggs, nauplii) they are especially important in determining overall recruitment success

8   (i.e., Ohman and Hirche, 2001; Ohman et al., 2002; Plourde et al., 2009a, 2009b). Survivorship of *C.*

9   *finmarchicus* is mainly governed by temperature, food availability and/or con-specific abundance,

10   which results in marked seasonal and regional differences in stage-specific mortality patterns (Ohman

11   and Hirche, 2001; Ohman et al., 2002; Ohman et al., 2004; Heath et al., 2008; Plourde et al., 2009b). In

12   the northwest Atlantic, the integration of stage-specific daily mortality rates over the entire cohort

13   developmental period revealed significant differences in survival trajectories among seasons and sub-

14   areas, associated with differences in environmental conditions (Plourde et al., 2009b). The use of

15   mortality formulations corresponding to different sets of environmental conditions have enabled

16   modeling of region-specific *C. finmarchicus* population dynamics, a significant step forward in basin-

17   wide biological modeling for the species (Runge et al., 2005; Neuheimer et al., 2010; Maps et al.,

18   2010; Maps et al., 2011).

19

20   In the Norwegian Sea studies of predation mortality for C. *finmarchicus* copepodite stages have

21   been conducted to evaluate feeding conditions for pelagic fish stocks and to investigate top down

22   *versus* bottom up processes in the ecosystem. Analysis of stomach samples have shown herring,

23   mackerel and young blue whiting to be important predators on *Calanus finmarchicus* copepodites

24   (Dalpadado et al. 2000; Gislason and Astthorsson, 2002; Prokopchuk and Sentyabov, 2006).

1   Consumption by herring has been estimated at about 20-100 % of the annual *C. finmarchicus*

2   production (Dommasnes et al. 2000; Skjoldal et al. 2004; Utne et al. 2012). Other potential predatory

3   taxa in the Norwegian Sea are krill, amphipods, cnidarians, chaetognaths, large copepods and

4   mesopelagic fishes. For these taxa reliable estimates of biomass, diet and stomach evacuation rates are

5   generally not known, making their predatory impact hard to estimate. Nevertheless, it seems clear that

6   these taxa may also be important predators of *C. finmarchicus* copepodites (Melle et al. 2004; Skjoldal

7   et al. 2004).

8

9   **2. Materials and methods**

10

11   *2.1. Hydrography and chlorophyll measurements and analyses*

12   CTD probes were used to collect hydrographic data (temperature and salinity) at all sampling

13   stations (Fig 1b, c). Water samples for measurements of chlorophyll-a concentration were collected

14   using water bottles on a rosette on the CTD or on a hydro-wire. At most sites the hydrographic and

15   chlorophyll samples were taken in concert with the zooplankton net samples. CTD profiling depths and

16   water bottle depths varied among sampling sites. Methodologies for determination of chlorophyll a

17   concentrations are described in publications or can be retrieved from the data provider associated with

18   each station as shown in Tables 1 and 2. Temperatures (^{0}C) were averaged over various depth ranges,

19   while chlorophyll concentrations were either integrated (mg m^{-2}) or averaged (mg m^{-3}) over various

20   depth ranges, as indicated in figure captions. At each site where time series measurements were made,

21   temperatures and chlorophyll concentrations were first averaged over 2-week periods within a given

22   year and then over the 2-week periods for all years.

23

1   The basin scale distribution of Sea Surface Temperature (SST, ºC) was calculated from data

2   available from the British Atmospheric Data Centre (BADC); [HadISST 1.1 dataset

3   (http://badc.nerc.ac.uk/home/)]. Monthly SST records (1 degree by 1 degree) or the years 2000-2009

4   were firstly averaged by year and then used to produce the overall average SST map for the period of

5   reference.

6

7   *2.2. Mapping of* Calanus finmarchicus *distribution at the basin scale*

8   The CPR survey is an upper layer plankton monitoring program that has regularly collected

9   samples (ideally at monthly intervals) in the North Atlantic and adjacent seas since 1946 (Warner and

10   Hays, 1994). Water from approximately 6 m depth (Batten et al., 2003a) enters the CPR through a

11   small aperture at the front of the sampler and travels down a tunnel where it pass through a silk filtering

12   mesh of 270 μm before exiting at the back of the CPR. The plankton filtered on the silk is analysed in

13   sections corresponding to 10 nautical miles (approx. 3 m^3 of seawater filtered) and the plankton

14   microscopically identified (Jonas et al., 2004). In the present study we used the CPR data to investigate

15   the current basin scale distribution of *C. finmarchicus* (CV-CVI). Monthly data collected between 2000

16   and 2009 were gridded using the inverse-distance interpolation method (Isaaks and Srivastava, 1989),

17   in which the interpolated values were the nodes of a 2 degree by 2 degree grid. The resulting twelve

18   monthly matrices were then averaged within the year and the data log-transformed (i.e. $\log_{10}(x+1)$).

19   The Phytoplankton Colour Index (PCI), which is a visual assessment of the greenness of the silk, is

20   used as an indicator of the distribution of total phytoplankton biomass across the Atlantic basin (Batten

21   et al., 2003b; Richardson et al., 2006).

22

23   *2.3. Seasonal dynamics of Calanus finmarchicus*

Seasonal abundance cycles of *Calanus finmarchicus* were derived from samples taken at sites across the North Atlantic (Table 1, Fig. 1b). The sampling sites include both coastal and oceanic stations and vary from relatively cold to warm water locations. Sampling frequency also differs among sites; the more easily accessed coastal sites were generally visited more frequently than the offshore sites. An overview of sampling sites characteristics, sampling gear and methods is provided in Table 1. Temperatures and chlorophyll concentrations are provided for all sites and details on depth ranges and units are given in Appendix figures 1-6.

2.4. Dormancy

Dormancy timing was calculated using metrics developed by Johnson et al. (2008). Briefly, entry to dormancy was determined as the date when the CV portion of the total composition of the copepodites and adults comprised 50% of the overall maximum CV proportion, calculated using all years of data at a station. In other words, if the maximum CV proportion was 90% at a given station, the date at which the proportion of CVs was greater than 45% of the total number of copepodites and adults would be the dormancy start date. The end of dormancy was calculated as the first date at which adults constituted more than 10% of all copepodites and adults in a given year for three consecutive dates. This was done to alleviate spurious estimates of dormancy end that may result from transient increases in the proportion of adults in the population.

Data (see Table 1) were gathered from the AZMP dataset (Johnson et al., 2008; Pepin, Plourde, Johnson, Head, pers. comm; http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html), the TASC time series dataset (Heath et al., 2000a: http://tasc.imr.no/tasc/reserved/cruiseact/timeseries.htm), the Svinoy Section and Station M datasets

1 (Melle, pers. comm.) and the Gulf of Maine PULSE and REACH time series datasets (Runge, pers

2 comm.).

3

4 *2.5. Egg production*

5   Observations of egg production rates (EPR) for female *Calanus finmarchicus* were compared

6 for different regions of the North Atlantic (Fig. 1c). The regions were diverse in size and sampling

7 frequency, ranging from a fixed time series station in the Lower St Lawrence Estuary, off Rimouski

8 (RIM), where nearly 200 experiments were carried out between May and December from 1994 to 2006

9 (RIM), to a large-scale survey in the Northern Norwegian Sea (NNWS), where about 50 experiments

10 were carried out between April and June from 2002 to 2004 (NNWS). For this analysis the stations

11 were grouped mostly along geographic lines, with only limited attention being paid to oceanographic

12 features. There is some overlap between regions, however, where stations were sometimes kept

13 together when they were sampled on the same cruise. As well, although not shown in Fig. 1c, some

14 stations other than RIM were occupied more than once during different years and/or in different

15 seasons. An inventory of the experiments used in this synthesis and of the data contributors is

16 presented in Table 2. Some of the data included here have appeared in published papers and the

17 citations are included. Previously unpublished data were also provided by C. Broms, E. Gaard, A.

18 Gislason, E. Head and S. Jónasdóttir.

19

20   Egg production in *C. finmarchicus* occurs in spawning bouts, which are of relatively short

21 duration and may occur once or more per day (Marshall and Orr, 1972; Hirche, 1996b). While there is

22 evidence for diel spawning periodicity in the sea (Runge, 1987; Runge and de Lafontaine, 1996),

23 females incubated in dishes for the first 24 h after capture do not always show a consistent night time

24 release of eggs, as they did for *Calanus pacificus* (Runge and Plourde, 1996; Head et al., in prep).

1   Because of the potential for diel egg-laying behaviour, the vast majority of egg production experiments

2   have been carried out by incubating freshly caught females for 24 h. It has been shown that female

3   *Calanus* that are kept and fed *in vitro* and then transferred to an incubation chamber lay the same

4   number of eggs over the next 24 h whether or not they are fed (Plourde and Runge, 1993; Laabir et al.,

5   1995). Thus, it has been assumed that average egg production rates of freshly caught females are the

6   same during the 24 h following capture as they would have been *in situ* (Runge and Roff, 2000). In

7   this study we include only results from such 24 h incubation experiments, and we term the eggs laid

8   during these 24 h periods "clutches", even though they may originate from more than one spawning

9   bout, and the number of eggs laid by one female during a 24 h period as the clutch size (CS). In most

10   experiments 20-30 females were incubated individually in separate chambers, and the proportion of

11   females that laid eggs over 24 h is referred to as the "spawning frequency" (SF), which is here

12   expressed as a percentage per day. Egg production rates (EPRs) reported here were calculated by

13   individual contributing investigators either simply as the sum of all of the eggs produced in an

14   experiment divided by the number of females incubated and the average incubation time (generally 1

15   day), or as the average of the EPRs calculated for each experimental female individually, which takes

16   account of differences in incubation times for individual females. For the WGBB most experiments

17   were carried out using prolonged incubation periods (*e.g.* 36-48 h), often with relatively few females

18   (~10). For several of the analyses carried out here it was necessary to include the results of these

19   prolonged incubations.

20

21   As batches of eggs are released into the water column *in situ*, they may hatch and develop, or

22   they may be consumed by local predators, including female *C. finmarchicus* themselves, which are

23   sometimes the most abundant potential predators (Basedow and Tande, 2006). To avoid cannibalism,

24   incubations are generally set up so as to minimise contact between the females and the eggs they are

1   laying. This has been done by the investigators contributing to this work using one of five techniques

2   (see Table 2). In Method A females are incubated individually in 45-50 ml of seawater in 6-10 cm

3   diameter petri dishes. The eggs sink rapidly to the bottom surface, where they are unlikely to be caught

4   up in the females' feeding currents. Method B involves incubating females individually in similar but

5   smaller "Multi-well" chambers, which have a volume capacity of 10-15 ml. In Method C females are

6   placed individually (or in groups of 2 or 3) in cylinders, fitted with mesh screens on the bottom, which

7   are suspended in beakers of 400-600 ml capacity (Gislason, 2005). The eggs sink through the mesh

8   and are thus separated from the females. Method D represents a modification of Method C, in which

9   there is flow of seawater through the chamber (White and Roman, 1992). Finally, in Method E,

10 individual (or groups of 2 or 3) females are incubated in bottles or beakers (up to 1 l capacity), without

11 screening (Jónasdóttir et al., 2005). For Method E the vessels are kept upright and it is assumed that

12 the eggs will sink out and become unavailable to the females relatively rapidly.

13

14   There have been relatively few comparisons of these different experimental methods. Cabal et

15 al., (1997) found that female *C. finmarchicus* from the Labrador Sea incubated individually in 50 ml

16 petri dishes (Method A) or 80 ml bottles (Method E) produced similar numbers of eggs after 3 days,

17 although only three experiments were done and over the first 24 h CSs were larger for Method A.

18 They also found that over 24 to 72 h periods groups of females in screened cylinders within large

19 volume chambers (Method C) gave higher egg production rates than did those in chambers without

20 screens (Method E). Runge and Roff (2000) reported egg laying in dishes (Method A) yielded similar

21 egg production rates to those for groups of 10-15 females incubated in 1.5 l screened beakers (Method

22 C). However, the beaker egg production estimates declined dramatically relative to dish estimates in

23 rough weather, presumably due to increased mixing in beakers and therefore higher loss due to

24 cannibalism. More recently, Plourde and Joly (2008) found that suspending a mesh screen within petri

1   dishes 2 mm above the bottom made no difference to the number of eggs produced by female *C.*

2   *finmarchicus* over 24 h, although it did increase the number of eggs recovered from *Metridia longa*

3   females, which could be seen swimming actively and sweeping the bottom with their mouthparts in the

4   unscreened dishes. In the Northeast Atlantic, at Ocean Weather Station M (included in our Southern

5   Norwegian Sea (SNWS) region), B. Niehoff (pers. comm.) found that females incubated for 24 h in

6   Multi-wells (Method B) had similar CSs to those incubated according to Method C. None of these

7   studies compared all methods and the fact that the NW Atlantic groups have used Method A, while the

8   central and NE Atlantic groups have used mainly Methods C, D or E introduces a question as to

9   whether methodological differences might have contributed to the differences found among the CSs

10   and EPRs in the different regions. Such an analysis is not possible based on the data currently

11   available, however, and the topic will not be considered further in this work, although it merits further

12   attention.

13

14   Another point on which investigators differed is how they dealt with small clutches. For the

15   Georges Bank (GB), Rimouski station (RIM) and Scotian Shelf (SS) regions and for the Labrador Sea

16   (LS) data provided by R. Campbell, clutches of <6 eggs were routinely not included in the datasets on

17   CSs, since they were regarded as being the result of interrupted spawning events. These small clutches

18   were apparently very rare (J. Runge, pers. comm.) and indeed for the LS data reported by Head et al.

19   (2013a) clutches of <6 eggs accounted for only 32 of the 1324 clutches observed, i.e. 2%. For regions

20   farther east, however, the proportions of clutches of <6 eggs were generally larger, between 13%

21   (SNWS) and 33% (Northern Norwegian Sea, NNWS). Because of this difference in data reporting,

22   CSs of <6 eggs were excluded from the calculations of average CSs for all regions. Small clutches

23   were, however, included by all investigators in their calculations of EPRs.

24

1   Previous studies of egg production have shown a significant link between clutch size and

2   female size (Runge and Plourde, 1996; Campbell and Head, 2000; Jónasdóttir et al., 2005; Runge et al.,

3   2006) and most of the datasets provided for this work included measurements of the prosome lengths

4   for each individually incubated female for each egg production experiment, along with each

5   corresponding individual clutch size (Table 3). One exception to this was in the SNWS region (data

6   from Ocean Weather Station M), for which average female prosome lengths were determined for

7   groups of females that had not been used in experiments, but that had been collected on the same day.

8   In addition, there were no measurements of prosome lengths for some data from the region "Between

9   Scotland and Iceland" (BIS)   and the SNWS and NNWS regions. As well, prosome lengths were not

10   measured for all clutch sizes enumerated at RIM.

11

12   Egg production rates for the experiments carried out within a given region were averaged

13   seasonally (Table 2). The rationale for the grouping of months into seasons within each region was

14   based partly on observations of seasonal cycles of temperature and chlorophyll concentration, partly on

15   what could be ascertained from the literature about the timing of the appearance of females at the

16   surface after over-wintering, and partly on the availability of data. The spring months cover the period

17   when water temperatures are increasing, when the spring bloom is starting or is in progress, when

18   diatoms dominate the female diet and when the overwintered (G0) generation of females is abundant in

19   the surface layers. Spring is the time when community egg production rates, although maybe not

20   individual rates, are expected to be highest. In summer, temperatures are higher, the bloom may still be

21   in progress, but the female diet may be more varied, and some females of the new year's generation

22   may be present. In autumn and winter relatively few females are in the near surface layers and

23   phytoplankton levels are generally low (see Section 3.3 below).

24

1   Observations of *in situ* temperature and chlorophyll concentration were made at nearly all

2   experimental stations. The original aim had been to use *in situ* temperatures from 5 m and chlorophyll

3   concentrations integrated to 30 m in this study. Not all data were provided in this form, however. For

4   example, in some datasets temperature data were surface values or 0-10 m or 0-20 m averages and

5   chlorophyll concentrations were sometimes values integrated to 50 m. In Fig. 3 the data were

6   standardized to a comparable format by assuming that surface, 0-10 m or 0-20 m average temperatures

7   were the same as 5 m temperatures, and that the chlorophyll concentrations were uniform throughout

8   the 0-50 m depth range. These assumptions are likely to be most appropriate in spring and winter,

9   when mixed layers are relatively deep.

10

11   *2.6. Mortality and survival estimation*

12   Data were obtained from sampling programs in different regions of the northeast Atlantic and

13   northwest Atlantic, for which there is sampling at fixed stations sampled at least once a month

14   (sometimes 3-4 times a week, e.g., Station M) or along sections once or a few times per year (Table 1,

15   Fig. 1b). In the northwest Atlantic suitable data were collected in the Gulf of Maine (GoM), on the

16   Scotian Shelf (SS) and the Newfoundland Shelf (NLS), in the Gulf of St Lawrence (GSL) and in the

17   Labrador Sea (LS). In the northeast Atlantic appropriate data were available in areas to the south and

18   north of Iceland (the former including Station India), to the north of the Faroe Islands, in the

19   Norwegian Sea (NWS), and in the Skagerrak (Table 1). Data collected during the TASC and MarProd

20   programmes were also included (Heath et al. 2000a, 2008). Sampling in the northeast Atlantic (with the

21   exception of TASC and MarProd) and in the Labrador Sea targeted the active part of the *C.*

22   *finmarchicus* population, with sampling in the near-surface layers (different depth ranges at different

23   sites) whereas sampling in the GoM and in the AZMP region (SS, GSL, NLS) in the northwest Atlantic

24   was over the entire water column, potentially including dormant individuals at depth (Table 1). This

1 difference had to be accounted for before using the VLT method (see below). Because several of the

2 programs did not sample the diapausing component of the population, mortality and survival during the

3 overwintering period were not addressed. Temperature and chlorophyll a biomass were estimated for

4 the region-specific surface layer, which was generally shallower on the northwest Atlantic shelves than

5 in other regions.

6 We adopted the approach of Plourde et al. (2009b) using the Vertical Life Table (VLT) method to

7 estimate mortality and survival for the following stage pairs Egg-CI (which actually includes all of the

8 naupliar stages), CI-CII, CIII-CIV, CIV-CV, CV-CVI. The VLT uses the ratio in abundance of

9 adjacent stages, except for eggs, for which female population egg production rate is used rather than

10 abundance. This method is thought to be relatively robust except in highly dynamic or advective

11 environments (Ohman, 2012; Gentleman et al., 2012). In order to minimize biases due advection and

12 insufficient sampling, which are likely to induce violations to the assumptions associated with VLT, we

13 averaged stage abundances and environmental data for each month at fixed stations (e.g. Halifax 2) or

14 along transects (AZMP) or for oceanographic domains (*e.g.* LS, NWS, Arctic vs. sub-arctic waters)

15 sampled during each survey. This approach resulted in more robust input data, reducing the proportion

16 of discontinuous stage structures (stage abundance = 0) or negative mortality estimates that may be

17 caused by patchy plankton distributions or violations of the VLT assumptions (Plourde et al., 2009b).

18 Thus, our meta-analysis was based on replicates of robust averaged stage abundances and

19 environmental data. Only the data collected in Icelandic waters were not averaged because they were

20 collected over only two years. Overall, our data set includes 1233 monthly or transect/regional

21 averages (total n = 1334, including Icelandic data), and *C. finmarchicus* shows markedly different

22 phenology across its distributional range (see Fig. Appendix 1-6).We established a common metric to

23 define phases of the population dynamics so that we could compare *C. finmarchicus* populations at the

24 same stage of their seasonal cycles (pre-growth, growth and post-growth periods, see Plourde et al.,

1 2009b), and limit potential biases in our large scale analysis (Gentleman et al., 2012). We chose to

2 restrict our analysis to the population growth period because all development stages should be actively

3 developing and because several sampling programs target the active component of the population in the

4 surface layer, both factors being optimal for the use of the VLT method (Table 1) (Plourde et al.,

5 2009b). We estimated egg production rates per female (EPR) using functional relationships between

6 EPR and chlorophyll a that have been reported for each region (Gislason, 2005; Runge et al., 2006;

7 Plourde and Joly, 2008; Head et al., 2013a). EPRs were then combined with the monthly climatology

8 for CVIf abundance for each region (location) to calculate the population EPR per square metre. The

9 region-specific population growth period was defined as months with the population EPR was greater

10 than 0.15 of its regional seasonal maximum. Using this metric, the population growth period was, for

11 example, from January to August on the SS and from May to September off southern Iceland (not

12 shown). Overall, 57% of all data were collected during the population growth period (n= 757).

13   As in Plourde et al. (2009b), we used the developmental parameters of Corkett et al. (1986) to

14 estimate stage-specific development times (DT) in regions with relatively cold (<6°C) near-surface

15 temperatures during the population growth period, and those of Campbell et al. (2001) for regions that

16 were relatively warm (>6°C). We chose 6°C because this represents the lower limit of the optimal

17 thermal habitat for $C.$ $finmarchicus$ (Helaouët and Beaugrand, 2007). In the northwest Atlantic, only

18 the GoM was considered to be a warm habitat, while in the central and northeast Atlantic Corkett's

19 parameters were used for transects/regions located in Arctic water masses north of Iceland, the Faroe

20 Islands and on the part of the Svinoy section where near-surface temperatures were <6°C.

21   Because our dataset was large, we were able to statistically exclude mortality and survival data that

22 gave unrealistic results which indicated violations of the assumptions and conditions for the application

23 of the VLT method (Plourde et al., 2009b). Based on the cumulative percentile distribution of all

28

1   mortality and survival values, we determined that mortality values lower than the 5th percentile and

2   survival values greater than the 85th percentile were anomalous, and therefore excluding mortality rates

3   < -0.20 d^{-1} and survival >2. Application of this procedure allowed us to objectively exclude between

4   0% (Egg-CI) and 20% (CI-CII, CII-CIII) of the mortality values (depending on the location), and

5   between 5% and 35% of survival values.

6   The data originated from sampling programs with different sampling strategies and from regions

7   showing markedly different environmental conditions (temperature, food), both being potential vectors

8   of bias in estimating stage-specific abundance and development time (stage duration, DT) and using

9   VLT (Ohman, 2012; Gentleman et al., 2012). We standardized the data in order to minimize these

10   potential biases. Here, we summarize these operations and their rationale as follows:

11   • We corrected the data for the presence of overwintering stages in the GoM, GSL, on the SS and

12   NLS (northwest Atlantic), which could cause problems with the mortality estimates in stage pairs

13   CIV-CV and CV-CVI (Plourde et al., 2009b). We adapted the seasonal climatology in the activity

14   index (proportion of abundance in 0-100m/0-bottom) at RIM in the GSL based on the phenology

15   (timing of diapause) in different regions (Plourde, unpublished data, Johnson et al., 2008). This

16   correction had a stronger impact during the early and late phases of the population growth period

17   by decreasing the observed CIV-VI abundance. This adjustment made the abundances of late

18   development stages in the GoM and AZMP comparable with those found in the LS and in the

19   northeast Atlantic where sampling, which was in the upper 0-100 or 0-200 m, and which would

20   have excluded most of the overwintering stages (Østvedt, 1955; Gislason and Astthorsson, 2000;

21   Gislason et al., 2000; Heath et al., 2000b, Melle et al., 2004).

22   • Sampling the 0-50 m layer along the line off northern Faroe Island and in the Skagerrak likely

23   underestimated total *C. finmarchicus* abundance, especially the late development stages CV and

1   CVI (Gaard and Hansen, 2000). This bias would probably have been even more important later on

2   during the population growth period, when surface temperatures are higher (Williams, 1985;

3   Bonnet et al., 2005; Jónasdóttir and Koski, 2011). Thus, at these locations, we excluded mortality

4   and survival values of stage pairs for the following stages: egg-CI CIV-CV and CV-CVI.

5   • We found differences in temperature regimes and phytoplankton biomass among sampling sites

6   and regions, both parameters being important in the determination of DT for most stages in *C.*

7   *finmarchicus* (Campbell et al., 2001). In the absence of stage-specific parameters for the effect of

8   food limitation on DT, we transposed to *C. finmarchicus* results of an exhaustive study of the

9   effect of food and temperature on development and growth of *C. pacificus* (Vidal, 1980). This

10   study, which included temperatures representative of the whole distributional range of *C. pacificus*

11   (8°C, 12°C, 16°C), showed that the effect of food limitation on DT increased with temperature and

12   developmental stage. We applied these results to *C. finmarchicus*, separating its temperature range

13   into three categories: $<6^{o}$C, $6-11^{o}$C, $>11^{o}$C. These temperature limits were chosen because based

14   on CPR observations (Helaouët and Beaugrand, 2007) that the optimal thermal habitat for *C.*

15   *finmarchicus* CV-CVI in the North Atlantic is at surface temperatures between 6 and 11°C .

16   Overall, the impact of this food limitation formulation was greater at chlorophyll *a* concentrations

17   of <25 mg m^{-2} in the upper 0-50 m (or 0.5 mg m^{-3}) and at temperatures above 6°C. This effect was

18   therefore more prominent in the northeast Atlantic where conditions during the population growth

19   period were generally warmer (greater proportion of temperatures $>6^{o}$C) (Fig. 17). The northeast

20   Atlantic also showed a greater proportion of stations with chlorophyll a concentrations <20 mg m^{-}

21   ^{2}, while concentrations >100 mg m^{-2} were more frequently observed in the northwest Atlantic.

22   Under these conditions, the DT for CIVs at temperature in the $6-11^{o}$C range with a chlorophyll *a*

23   concentration <20 mg m^{-2} would be 3-4 times longer than under non-limiting food conditions.

1   This adjustment diminished the proportion and amplitude of negative mortality estimates for

2   several stage pairs.

3   • Different temperature regimes might also affect the size of *C. finmarchicus*, which could

4   influence the sampling efficiency for CI, CII and CIII, depending on the net mesh size (Nichols

5   and Thompson, 1991). We used field data collected in the GSL and on SS to establish a

6   relationship between prosome length (PL) of early stages and surface temperature (Plourde, Head,

7   unpublished). PL of both stages decreased significantly with increasing temperature. We used this

8   relationship to predict PL from surface temperature in our data set, determining a minimal PL

9   above which increasing temperature had no effect (Conway, 2006; Plourde, unpublished). PL was

10   then used to estimate the prosome width necessary to estimate sampling efficiency (Nichols and

11   Thompson, 1991; Conway, 2006). Again, the bias was likely more important in warmer

12   conditions late in the growth period, *i.e.* generally in the northeast Atlantic. For example, the

13   sampling efficiency for CI and CII with a 200-µm mesh rapidly diminishes between 4-12°C, with

14   less than 75% and 50% of CI and CII being sampled at temperatures equal to or higher than 12°C

15   (no effect on CIII). This adjustment reduced the proportion and amplitude of negative mortality

16   estimates in early stages pairs (CI-CII, CII-CIII), and the absolute mortality for the egg to CI

17   transition.

18   Non-parametric statistical tests (Mann-Whitney to contrast between two groups; Kruskal-Wallis

19   for more than two groups;) were used to contrast mortality and survival estimates among different

20   groups (see text below). We used non-linear regression models to describe the relationships between

21   mortality estimates in all stage pairs and temperature, and linear multiple regression models to describe

22   the relationships between mortality in early stages (egg-CI) and temperature, phytoplankton biomass

23   and CVI female (CVIf) abundance.

1   We contrasted stage-specific mortality and survival among offshore (>1000 m, deep basins) and

2   shelf (<1000 m) domains in the northeast and northwest Atlantic regions. We note, however, that the

3   offshore domain (n = 44) was under-represented relative to the shelf (n= 357) in the northwest Atlantic,

4   whereas both domains were reasonably covered in the northeast Atlantic (offshore = 146, shelf = 210).

5   Late stages of sub-arctic and temperate *Calanus* species and other suspension feeding copepods

6   can ingest their own eggs and nauplii at high rates (see Landry, 1981; Bonnet et al., 2004; Basedow

7   and Tande, 2006), with sizeable consequences on the recruitment patterns (i.e., Ohman and Hirche,

8   2001; Ohman et al., 2008; Plourde et al., 2009a). Feeding experiments have shown that the large arctic

9   species *C. hyperboreus* can clear up to $5 \, l \, d^{-1}$ when fed with *C. finmarchicus* eggs at realistic field

10   concentrations (Plourde unpublished data), suggesting a potential for a high impact of arctic *Calanus*

11   species on *C. finmarchicus* population dynamics. Therefore, we contrasted stage-specific mortality and

12   survival of *C. finmarchicus* in different 'habitats' defined on the basis of local temperature and on the

13   likelihood of high abundance of *C. glacialis* and *C. hyperboreus* in the surface waters, both indicative

14   of regions being under the influence of cold arctic water. In the northwest Atlantic *C. hyperboreus* and

15   *C. glacialis* are generally abundant on the shelves and slopes of the Labrador Sea, on the NLS, in the

16   GSL and part of the SS (Head et al., 1999, 2003; Plourde et al., 2003). In the central and northeast

17   Atlantic, these species are important in the arctic/polar waters off the north coast of Iceland and the

18   Faroe Islands and in the northwestern Norwegian Sea (Astthorsson and Gislason, 2003; Broms et al.,

19   2009; Gislason et al., 2009). These arctic species are generally active in the surface layer from mid-

20   winter (SS) or early spring (GSL, NLS) to June (SS) or July (GSL, NLS), the end of their active phase

21   in surface waters corresponding roughly to when temperatures reach 6°C (Plourde et al., 2009; Head

22   and Pepin, 2010; Plourde, unpublished). In the northeast Atlantic, *C. hyperboreus* and *C. glacialis* are

23   present in surface waters from April to July, a pattern similar to the one observed for the GSL and NLS

24   (Hirche, 1997; Melle and Skjoldal, 1998; Astthorsson and Gislason, 2003). In this analysis, we

1 therefore combined these spatial and seasonal patterns to classify our data into the following 'habitats':

2 1) 'habitats' with temperatures <6°C with high (n= 235) or low (n= 150) likelihood for *C. finmarchicus*

3 to co-occur with *C. hyperboreus* and *C. glacialis*, and 2) 'habitats' with low abundance of *C.*

4 *hyperboreus* and *C. glacialis* with temperatures 6-11°C (n= 272) or 11-16°C (n= 97). Given the

5 importance of mortality and survival during the egg and naupliar stages in determining the overall

6 cohort development success (Plourde et al., 2009b), this analysis primarily focused on stage pair Egg-

7 CI.

8   Results for all stage pairs were integrated into survival trajectories specific to each region or

9 'habitat' as in Plourde et al. (2009b). We used the average population EPR during the population

10 growth period across all study sites in the North Atlantic (50,000 eggs m^{-2} d^{-1}) to normalize the survival

11 trajectories to a common scale to allow for regional/habitats comparisons. This comparison is not

12 intended to provide actual predictions of survival *in situ*, but is rather a way of showing the effects of

13 varying mortality values under idealised (*i.e.* unchanging) conditions.

14

15 **3. Results**

16

17 *3.1. Basin scale habitat characteristics: hydrography and chlorophyll*

18   The 15°C surface isotherm, from approximately 40° latitude (south of Long Island, New York) in

19 the west and at about 47° latitude in the east (south of Brittany, France), delimits the southern edge of

20 the northern North Atlantic (Fig. 2a). The coldest surface temperatures occur in the Labrador Sea and

21 off the east coast of Greenland. The 11-15 °C annual average surface temperature occurs in a narrow

22 band between southern New England and Long Island in the west, expanding in the drift path of the

1   Gulf Stream, to include a large area of the deep North Atlantic basin south of Iceland, the North Sea,

2   and coastal shelves of Great Britain.

3

4   The annual phytoplankton colour index (i.e. PCI, Fig. 2b), a relative index of phytoplankton

5   biomass as sampled by the silk mesh in the CPR, shows no obvious correspondence with the annual

6   pattern of sea surface temperature in the northern North Atlantic. Instead, it indicates that the areas of

7   highest phytoplankton biomass occur at the shelf margins, including the Gulf of Maine, Grand Bank,

8   North Sea and the shelf north and west of the British Isles. Higher phytoplankton biomass is also

9   indicated in Denmark Strait. In general, surface phytoplankton biomass is lower in the deep, central

10   North Atlantic basin, with the exception of the deep water south of Iceland.

11

12   Phytoplankton data from the *Calanus* sampling stations generally corroborate the annual patterns of

13   PCI shown in the CPR data, although they indicate that phytoplankton biomass is lower in the

14   northeast Atlantic than in the northwest, except in the northern Norwegian Sea. Two independent

15   regional analyses of the environmental data were carried out. For the first, surface layer averaged

16   temperature and chlorophyll a biomass during the *C. finmarchicus* population growth period (Fig. 3)

17   were calculated for the stations used in the analyses of mortality and survival. Surface layer

18   temperatures were significantly higher in the northeast Atlantic than in the northwest (Mann-Whitney

19   test, $p < 0.0001$), but similar in offshore and shelf habitats within the northeast and northwest Atlantic

20   habitats (Mann-Whitney test, $p > 0.05$). On the other hand, chlorophyll *a* biomass was greater in both

21   offshore and shelf habitats in the northwest Atlantic than in the northeast (Kruskal-Wallis test,

22   $p < 0.0001$). For the second analysis, near surface temperatures and integrated chlorophyll standing

23   stocks (0-30 m) were calculated by season using data from stations where *C. finmarchicus* egg

24   production rates were measured (Fig. 4). Average 5 m temperatures were highest in summer within

1   each region, and in all seasons and regions they were generally between 4 and 10°C although they were

2   below 4°C four regions: the Scotian Shelf (SS), Labrador Sea (LS) and West Greenland Baffin Bay

3   (WGBB) in spring, and Rimouski (RIM) in winter, and above 10°C at one station the North Sea (NS)

4   in summer and autumn. Most regions were not sampled in every season, but where data are available,

5   integrated chlorophyll concentrations were highest in spring or summer, with the spring months

6   coinciding with the early to mid-bloom period, and the summer months to the mid- to post bloom

7   period. The highest average springtime chlorophyll concentration was near Iceland, north of 65°C

8   (ICE(N)) where the average 0-30 m value was 4.6 mg m^{-3}, the lowest was in the southern Norwegian

9   Sea region, where it was 1.1 mg m^{-3}. Chlorophyll concentrations were generally low in autumn and

10   winter. The Georges Bank (GB) region, located relatively far south with high winter light levels, was

11   anomalous in that integrated chlorophyll concentrations were relatively high in winter (Jan-Feb).

12

13   *3.2. Distribution of* Calanus finmarchicus *by CPR sampling*

14   The spatial distribution of the log-transformed mean annual abundance for *Calanus*

15   *finmarchicus* from CPR collections between 2000 and 2009 is shown in Figure 5. The abundance of *C.*

16   *finmarchicus* is highest in the western part of the Atlantic basin particularly off the Scotian Shelf, the

17   southern Labrador Sea, south of Greenland and in the Irminger Basin. The data show lower abundance

18   in the eastern Atlantic, where it is restricted mainly to northern regions.

19

20   *3.3. Seasonal dynamics of Calanus finmarchicus in relation to chlorophyll and temperature*

21   Detailed descriptions of the seasonal cycle and associated environmental variables at the

22   sampling stations compiled in Table 1 are provided in the appendix (Figs. A1- A6). Here we explore

23   general demographic patterns (abundance, recruitment timing and dormancy timing) of *C. finmarchicus*

24   populations across the North Atlantic.

1

2   Two indices of abundance at the study sites across the North Atlantic were calculated. The

3   annual maximum abundance of all copepodite stages combined (Fig. 6) was highest (135-265 x 10^3 m$^-$

4   ^{2}) at the southern and eastern Norwegian Sea, southern Iceland shelf and eastern Labrador Sea stations.

5   Differences in abundance could not be simply explained by location on shelves or over deep ocean

6   basins. The relatively high abundance observed at Foinaven is likely due to the fact that here sampling

7   was down to the bottom (500 m), where dormant copepodites would have been captured. The autumn

8   and winter mean annual maximum abundance of stage CV (Fig. 7) shows much higher abundances (on

9   average 10-30 x 10^3 m^{-2}) along the western North Atlantic shelves and at a Norwegian fjord station.

10 Abundances in Wilkinson Basin in the Gulf of Maine are notably higher than at any other shelf site and

11 are similar to abundances of stage CV found at depth in the Norwegian and Irminger Seas (Heath et al.,

12 2004). These high shelf abundances represent overwintering stage CVs in areas where the sea is deep

13 enough to allow overwintering to occur. Other sites in the central and eastern Atlantic are either too

14 shallow (e.g. Arendal, Stonehaven) for overwintering, or are very deep (e.g. Station Mike), in which

15 case the overwintering stage CVs were deeper than the depths sampled at sites used in this study. Data

16 from the overwintering period in the Labrador Sea are not shown here, but there individuals would

17 have been at depths greater 0-100 m, which is the depth range that was used for the Labrador Sea data

18 presented here (Head and Pepin, 2008; Head et al. 2013b).

19

20   Maximum abundances of *Calanus finmarchicus* showed a positive relationship with the annual

21 maximum temperature in the surface layer (see axes labels in Appendix Figs. 1-6 for actual depth range

22 of temperature measurements, Fig. 8). Maximum temperature gives a measure of habitat suitability if

23 there is an upper temperature limit above which population growth, reproduction or survival are

24 hampered. Abundances of *C. finmarchicus* peaked where maximum temperatures were around 12-13

36

1 ^{0}C (Fig. 8). Abundances were both high and low at higher maximum temperatures and invariably low

2 at lower maximum temperatures. If the very near shore and shallow stations of the North Sea and

3 Faroes are excluded, the maximum abundance of *C. finmarchicus* increased exponentially for all

4 maximum temperatures measured at the sites included here.

5

6   The timing of recruitment to stages CI-III of the first generation (G1) was investigated by

7 plotting the time of maximum abundance of CI-CIII versus the maximum annual water temperature in

8 the surface layer and the time of maximum chlorophyll concentration (Fig. 9). At all sites, except at the

9 Faroese and Rimouski stations, maximum number of CI-CIII occurred during or after the peak in

10 chlorophyll concentration. There was a weak positive correlation between the times of occurrence of

11 the chlorophyll and CI-CIII maxima (Fig. 9) and a strong, positive relationship between temperature

12 and the timing of recruitment to CI-CIII, so that recruitment at the western North Atlantic sites was up

13 to 3.5 months later than at the eastern Atlantic sites. The sites that showed delayed timing of CI-CIII

14 recruitment relative to the timing of the bloom (sites in upper left corner of Fig. 9, upper panel), were

15 sites with low temperatures, suggesting that low temperature may cause a mismatch between *C.*

16 *finmarchicus* recruitment and the bloom (Broms et al. 2009) (but see also section 3.6 for potential

17 effects of *Calanus* congeners on survival of *C. finmarchicus* early stages). There was no apparent

18 relationship between temperature and the timing of the bloom (not shown).

19

20 *3.4. Dormancy*

21   Considerable variability in the timing of dormancy across the range of *C. finmarchicus* has been

22 recorded (e.g. Planque et al., 1997; Hind et al., 2000; Johnson et al., 2008). Using the dormancy timing

23 metrics described by Johnson et al. (2008), we calculated dormancy entry and exit dates of *C.*

24 *finmarchicus* for 15 time series data sets throughout the North Atlantic (Fig. 10 a, b). In general, the

1 start date of dormancy was more variable than the end date, and the northwest Atlantic had more

2 variability in timing than the northeast Atlantic over similar spatial scales. The dormancy metrics

3 indicated that *C. finmarchicus* enters dormancy later at the northwest Atlantic sites but that the timing

4 of arousal occurs over a relatively short period in late winter (20-60 d) across all stations. In the

5 northwest Atlantic, the major exceptions are the Rimouski and Shediac stations in the Gulf of St.

6 Lawrence, but these may be skewed by the absence of sampling in late winter due to the presence of

7 ice cover. In the northeast Atlantic, the very late exits from dormancy at Foinhaven and Vestfjorden

8 (10 and 15 in Fig. 10) are likely due to local effects on the calculation of dormancy exit times,

9 involving the possible inclusion of a high number copepodites that may have been *C. helgolandicus* or

10 the short length of the time series (<2 yr). Inclusion of *C. helgolandicus* will be a general problem in

11 time series from the North Sea and south of the Norwegian Sea, unless *C. helgolandicus* have been

12 identified (Bonnet et al. 2005). Around Iceland and farther west the numbers of *C. helgolandicus* are

13 small. The data suggest that duration of dormancy, from time of entry to time of exit, is shorter in the

14 western North Atlantic than in the eastern North Atlantic. Our estimate of the median duration of

15 dormancy is 200 d in the northwest Atlantic and 250 d in the northeast Atlantic (270 d if two outliers,

16 Iceland and Faroes, are excluded). There are no time series with sufficient temporal resolution to make

17 these calculations in the middle of the Atlantic (e.g. in the Irminger and Labrador Seas).

18

19

20 *3.5. Egg production*

21 Broad-scale regional differences in egg production rate (EPR), clutch size (CS), spawning

22 frequency (SF) and prosome length (PL) were examined by averaging all observations carried out

23 within a given region during a given season (Fig 11). Average female egg production rates were

24 generally highest in spring and summer within regions, and the spring and summer rates were generally

1   higher west of the Irminger Sea (in the GB, SS, RIM and LS regions)[1] and in the ICE(N) region than in

2   the Irminger Sea (IRM) or farther east. One exception to this east-west pattern was the WGBB region,

3   where rates were lower than in other western regions, particularly in spring, when chlorophyll

4   concentrations were very high and temperatures, very low (Fig. 4). Egg production rates were

5   relatively high in winter on GB, but no females laid eggs in experiments carried out during winter in

6   the RIM, IRM and SNWS regions. Average experimental clutch sizes were highest at RIM and in the

7   LS. Spawning frequencies were generally lower in autumn and winter than in spring and summer, but

8   relatively high for GB and NNWS (73% d^{-1} and 78% d^{-1}) in winter and low (13% d^{-1}) for SNWS in

9   summer. The highest average female prosome lengths were in the SS, RIM, LS and IRM regions and

10   the lowest, in the North Sea (NS).

11

12   Clutch size (eggs female^{-1}) increased with increasing prosome length in all regions and seasons,

13   except in the WGBB region, where the two were not related. Most points fell below a line that has

14   been suggested to define the upper limit to clutch size (CS_{max}) per unit length (Jonasdottir et al., 2005:

15   Fig. 12). One factor that contributes to variations in CS is food availability (Niehoff, 2004; Runge et

16   al., 2006; Jónasdóttir et al., 2008; Head et al., in prep.). Runge et al. (2006) reported a linear

17   relationship between CS and log transformed integrated chlorophyll concentration for females from the

18   GB region. Plots of average experimental CS *versus* integrated chlorophyll concentration (Intchl) in

19   other regions where the range of chlorophyll concentrations was large enough showed a rapid increase

20   in CS at low chlorophyll concentrations, reaching an upper limit at high concentrations (Fig. 13). The

21   degree of food limitation was investigated on a regional basis by comparing regional average values of

22   CS/CS_{max}, using the Jónasdóttir et al. (2005) relationship to estimate CS_{max}, including data from all

23   seasons, or from spring alone (Table 4). In spring, the average CS/CS_{max} values were correlated with

---

[11] For identification of acronyms, see Fig. 4.

1   average integrated chlorophyll concentrations across all regions (P<0.05), if the anomalous WGBB

2   region was omitted, although the highest CS/CS_{max} value (58% at RIM) was not in the region with the

3   highest average chlorophyll concentration (ICE(N)). Despite the effect of chlorophyll concentration on

4   CS, experimental averages for CS and PL were significantly correlated in the six of twelve regions

5   (GB, SS, RIM, LS, ICE(S), NS), although not in the others.

6

7   Relationships between experimental spawning frequency and integrated chlorophyll concentration

8   (Intchl) showed patterns similar to those shown for CS *versus* Intchl (Fig. 13), except in the WGBB.

9   CS and SF were significantly correlated in most regions including the WGBB, the exceptions being

10   ICE(S), NNWS and NS (Fig. 14). As some of the scatter might have been due to the dependency of

11   CS on female size, CS/CS_{max} values were plotted against SFs. The r^2 values for these relationships

12   were generally slightly higher than those for CS *vs*. SF, and in the NS, the correlation between

13   CS/CS_{max} and SF was significant ($r^2 = 0.12$) whereas the correlation between CS and SF was not (Fig.

14   14). Thus, females that are producing large clutches produce them more frequently and in most regions

15   these increases seem to be related to increasing food intake, due to increasing chlorophyll

16   concentration. In the WGBB region, however, the low spring temperatures may limit egg production,

17   despite the high chlorophyll concentrations (Swalethorp et al., 2011; Kjellerup et al., 2012).

18

19   Egg production rates generally increased with integrated chlorophyll concentration to a saturating

20   level (Figs. 15 and 16), showing patterns that resemble those for CS and SF *vs*. Intchl. Elsewhere (e.g.

21   Runge et al., 2006, Head et al. 2013a) the relationship between EPR and Intchl has been fitted to an

22   Ivlev function of the general form

23

24     $y = y_0 + a(1-e^{-bx})$

1

2 where y is the EPR at chlorophyll concentration x, y_0 is the EPR when the chlorophyll concentration is

3 zero (for positive y_0 values), or indicates the threshold below which EPR is zero (for negative y_0

4 values), and a and b are constants. Since spring was the only season for which there were

5 measurements in all regions, and in order to increase comparability among the datasets, only spring

6 data were used to examine the relationship between EPR and integrated chlorophyll standing stock.

7 The three parameter equation was fitted to all datasets, but in all regions a two parameter equation,

8 where y_0 was equal to zero, gave an equally good a fit to the data. There was always a great deal of

9 scatter about the Ivlev curves (Figs. 15 and 16, Table 5). The r^2 values for the Ivlev function were > 0.2

10 in two of five regions in northwest Atlantic and in two of four regions in the northeast Atlantic, but

11 <0.2 for all three regions in the central North Atlantic.

12

13   Two of the factors that might be expected to contribute to this scatter are female size and

14 temperature. Female size has a direct effect via its influence on CS, and temperature could have either

15 a direct affect, as it does on most physiological rates, or an indirect affect via its influence on female

16 size, which varies with long-term food and temperature conditions (e.g. Campbell et al., 2001). A

17 direct effect of temperature on spawning frequency has been demonstrated when groups of females

18 from a common source population are brought into the laboratory and experimental incubations are run

19 at different temperatures (Runge and Plourde, 1996; Hirche et al., 1997). In the sea, however, for

20 Georges Bank (January-June: Runge et al., 2006) and the NW Atlantic sub-polar gyre (January-June:

21 Gislason, 2005; May-June: Head et al., 2013a) there was no observable effect. In order to see whether

22 either of these factors was contributing to the variability in the expected EPR *versus* Intchl

23 relationships, the residuals (*i.e.* the EPR values observed – the EPR values predicted by the Ivlev fits)

24 were plotted against the average experimental female prosome length, or the ambient near-surface (and

41

1 experimental) temperature within each region. In three regions (GB, RIM, LS) the residuals were

2 positively correlated with prosome length, although the correlations were weak ($r^2 = 0.12$-0.20) (Table

3 6). Temperature was also positively correlated with the residuals in three regions (GB, RIM, ICE(N)),

4 but in one (IRM) there was a negative correlation, and in all cases the proportion of the variance

5 accounted for was low ($r^2 = 0.12$-0.21). Multiple regression analysis did not improve these results.

6

7   Even though temperature could not explain the scatter in the Ivlev plots, suggesting that it has no

8 substantial impact on egg production rate in most regions in spring, the very low springtime

9 temperatures in the WGBB region do appear to reduce EPRs since here, despite high chlorophyll

10 concentrations, the upper limit for EPR was 11 eggs f^{-1} d^{-1} (Table 5). As well, maximum EPRs

11 measured during summer at higher temperatures were generally much higher than those found in spring

12 at similar chlorophyll concentrations (Figs. 4 and 15).

13

14   Attempts were also made to reduce the scatter of the Ivlev plots by scaling the EPR values to

15 female size. Both EPR/PL and EPR/CS_{max} transformations were used, but neither led to any

16 appreciable increases in r^2 values for the Ivlev curve fits. Elsewhere, EPR values have been scaled to

17 female body size in terms of body carbon (C) or body nitrogen (N) content, and EPRs have been

18 expressed as % female body C (or N) d^{-1}, using literature values for egg C and N content (Runge and

19 Plourde, 1996). Runge et al. (2006) found that Ivlev curve fits to Intchl vs. EPR data, where the EPRs

20 were expressed in this way, measured between January and June, tended to maximum values of 8.5%

21 body C d^{-1} and 7.7% body N d^{-1} in the GB region. The r^2 value they report ($r^2 = 0.42$) was lower than

22 the value reported here ($r^2 = 0.47$) for EPR expressed as eggs f^{-1} d^{-1} derived using only data from April

23 and May. Head et al. (2013a), using experimental data collected between May and July in the central

24 basin of the Labrador Sea, found that scaling EPRs to female body N slightly increased the r^2 value for

1   the Ivlev fit for EPR vs. Intchl ($r^2 = 0.48$ *vs.* 0.47), while scaling to body C reduced it ($r^2 = 0.38$). These

2   curves tended towards maximum EPR values of 8.5% body C d^{-1} and 7.2% body N d^{-1}, very similar to

3   the values on GB.

4

5   For a comparison of total *C. finmarchicus* egg production across regions, it should be noted that,

6   despite variability in estimates of individual female EPRs, total population egg production rates (eggs

7   m^{-2} d^{-1}) are strongly influenced by the abundance of females, and that the contributions of the regions

8   to the North Atlantic as a whole depend on their geographical areas. Thus, the gyres of the northeast

9   (NNWS, SNWS) and the northwest (LS, IRM) Atlantic, with their high average female abundances and

10   vast areas, account for >80% of the total North Atlantic egg production of *C. finmarchicus* on a daily

11   basis in spring (Table 7). On the other hand, the duration of the spawning season is probably shorter

12   for the gyres than in coastal or more southerly regions (see dormancy duration Fig. 10) and mortality

13   rates for the egg-CI transition are also relatively high (see following section).

14

15   *3.6. Mortality and survival of Calanus finmarchicus*

16   There were significant differences in stage specific daily mortality rates among offshore and shelf

17   habitats in the northeast and northwest Atlantic (Fig. 17a). Most notably, mortality from egg to CI was

18   lower on the shelf than in the offshore in the northwest Atlantic (Kruskal-Wallis test, $p < 0.0001$),

19   whereas CIV-CV mortality was significantly greater in shelf habitats than in both oceanic basins

20   (Mann-Whitney test, $p < 0.05$). Mortality estimates for stages CV-6 also showed important variability,

21   but negative values, likely due to recruitment to and/or advection of adult stages from the

22   overwintering CV stock on the shelf in the northeast Atlantic and offshore in the northwest Atlantic,

23   precluded a more detailed analysis. No significant differences among habitats and regions (eastern vs.

24   western North Atlantic) were detected for the stage pairs CI-CII and CIII-CIV ($p < 0.05$). Daily

1   mortality rates for the egg-CI transition and the stage pairs CIV-CV and CV-CVI were positively

2   related to temperature but with relatively low coefficients of dependence, the highest being for the egg-

3   CI transition ($r^2 = 0.23$, Table 8). No significant relationship between mortality and temperature was

4   detected in the other stage pairs (Table 8).

5   Because the proportion surviving through each stage pair represents the integration of daily

6   mortality over stages, variations in survival among habitats and oceanic basins were somewhat

7   different from variations depicted for daily mortality rates (Fig. 17b). Survival from egg to CI was

8   much greater for shelf than for offshore habitats on both sides of the Atlantic (habitats; M-W,

9   p<0.0001). Overall, differences in survival were significant until the CIII-CIV stage pair, but with a

10 much lower significance level (Fig. 17b).

11   Average stage-specific recruitment rate (number m^{-2} d^{-1}) was calculated using the population birth

12 rate (PopEPR) and the proportion surviving through each stage pair for the offshore and shelf habitats

13 in the northwest and northeast Atlantic (Fig. 18). Region-specific survival trajectories of the developing

14 cohort were normalized using the same PopEPR (50,000 eggs m^{-2} d^{-1}) for all regions. Survival

15 trajectories were similar, with the notable exception of recruitment to CI offshore in the northwest

16 Atlantic (low survival) and a low survival from CII to CIV in the offshore habitat in the northeast

17 Atlantic.

18   Daily mortality rates for the egg-CI transition were generally higher in habitats colder than 6$^{\mathrm{o}}$C

19 where there was a greater likelihood for *C. finmarchicus* to co-occur with high abundances of its

20 congeners *C. hyperboreus* and *C. glacialis* in the surface layer (Mann-Whitney test, p<0.0001) (Fig.

21 19). These latter species are thought to feed on *C. finmarchicus* eggs and nauplii, since both reproduce

22 before the spring bloom, so that their offspring are abundant and feeding during the bloom when *C.*

23 *finmarchicus* are spawning. Our observations are consistent with this idea, since, egg-CI survival was

1 significantly reduced in cold waters (less than 1.5% of eggs surviving to CI), with 5-6 times lower

2 survival success than in other warmer habitats (survival from egg to CI = 5.0-6.5%) (Mann-Whitney

3 test, p<0.0001).

4 Stage-specific daily mortality rates and survival through each stage pair were integrated into

5 survival trajectories for each habitat (Fig. 20). For the same population EPR, lower survival from egg

6 to CI (above) resulted in 5-6 times lower recruitment rate to CI in the colder (<6°C) habitat, relative to

7 other habitats. This large difference in survival during early stages development and recruitment to CI

8 under the same temperature regime was reflected in the later stages as well, since overall the difference

9 in recruitment to CI (survival during early stages) determined the recruitment rate to late development

10 stages in all habitats.

11 To examine more systematically potential relationships between daily mortality rate in early stages

12 (egg-CI) and environmental factors, we applied different multiple regression models to the data either

13 from (1) regions based on the bathymetry (offshore, shelf) and large oceanic basins (northeast Atlantic,

14 northwest Atlantic) or (2) thermal habitats (<6°C, 6-11 ^{o}C, 11-16 ^{o}C) and potential abundance of *C.*

15 *hyperboreus* and *C. glacialis* (high or low) (Table 9). In regions based on bathymetry and large oceanic

16 basins, the multiple regression models were all significant and explained between 4% and 43% of the

17 variability in egg-CI mortality, with higher levels of significance in the northwest Atlantic (20% and

18 43% in shelf and offshore regions respectively: Table 9A) than in the northeast. Temperature was

19 significant on the shelf on both sides of the Atlantic, whereas egg-CI mortality was positively

20 associated with CVIf abundance for shelf and offshore regions in the northwest Atlantic, but only

21 marginally so in the offshore northeast Atlantic. The weakest levels of significance were given by the

22 multiple regression model applied to the offshore northeast Atlantic (Table 9A). In regions determined

23 using temperature conditions and potential abundance of *C. hyperboreus/C. glacialis*, the multiple

1   regression models explained a greater proportion (27%) of the variability in egg-CI mortality in

2   habitats with high abundances of arctic *Calanus* species compared with those with low abundance

3   (Table 9B). Temperature and CVIf abundance were highly significant factors in habitats with high *C.*

4   *hyperboreus/C. glacialis* abundance, while CVIf abundance had a much lower explanatory power for

5   egg-CI mortality when the abundance of *C. hyperboreus/C. glacialis* was likely to be low.

6

7   **4. Discussion**

8

9

10   *4.1. Abundance, distribution and life history characteristics of* Calanus finmarchicus *across its North*

11   *Atlantic habitat*

12   The data we have compiled here represent considerable multinational effort spanning several

13   decades. Much progress has been made in understanding *C. finmarchicus* life histories and the

14   underlying processes needed to model its population dynamics in the context of developing climate

15   change scenarios for the North Atlantic. The ocean circulation system and its associated water mass

16   characteristics exert important influences on the distribution of *C. finmarchicus*, but distribution

17   patterns are also influenced by regional differences in physiology, life history and ecological

18   characteristics. Our analysis and synthesis of the assembled datasets focuses on regional similarities

19   and differences between the northwest and northeast Atlantic with respect to processes determining the

20   distributions and abundances of shelf and basin *C. finmarchicus* populations and life history responses

21   to environmental variables.

22

23   The mean annual distribution of *C. finmarchicus* in the near surface layer, based on CPR

24   measurements alone, is mainly restricted to the northern and western North Atlantic within an area

1　delimited between the 5°C and 10°C annually-averaged sea surface isotherms (Fig. 5), in agreement

2　with previous reports of mean annual maximal abundances at SSTs of between 5 and 10°C, and critical

3　SST boundaries of 9 and 12°C (Beaugrand et al., 2008; Helaouët and Beaugrand, 2009). Overall, CPR

4　data show that *C. finmarchicus* is more abundant in the northwest Atlantic, which is cooler and where

5　the average chlorophyll standing stock is greater, than in the northeast Atlantic (see also Longhurst,

6　1998; Helaouët and Beaugrand, 2009; Helaouët et al., 2011). However, the results (presented here as

7　well as previously published observations), based on net data that includes the population epicentres

8　within the subpolar- gyres of the Norwegian and Labrador Seas (Heath et al., 2000a; 2004; 2008; Head

9　et al., 2003; Melle et al., 2004) indicate that the highest *C. finmarchicus* abundances are found north of

10　the CPR routes. This supports the idea that maximum *C. finmarchicus* abundances are found in the

11　deep basins of these seas (Fig. 6) or close to them. In the warm northeast Atlantic particularly, this

12　changes our view of *C. finmarchicus* distribution compared to the perspective from CPR data alone.

13　For this reason, since 2008, the spatial coverage of CPR monitoring has been expanded to cover the

14　core areas of *C. finmarchicus* distribution in the Norwegian Sea. We analysed temperature

15　measurements from the vertical domain of *C. finmarchicus* during the productive season and calculated

16　mean maximum temperatures for the sampling sites (Fig. 8). Net data show that maximum abundances

17　of *C. finmarchicus* in the core area of its distribution occur at sites with maximum temperatures

18　between 11 °C and 13 °C. This is slightly higher than previously reported values (Beaugrand et al.,

19　2008; Helaouët and Beaugrand, 2009). To define the temperatures ranges that are presently occupied

20　and those that are critical (*i.e.* beyond which *C. finmarchicus* is absent)*,* further analysis that includes

21　net collected data across the species distributional range is needed. Thus we conclude that habitat and

22　population dynamics modeling in the future should include data sets obtained from CPR and net hauls,

23　which complement each other in terms of sampling coverage.

24

1   The major overwintering areas for *Calanus finmarchicus* in the North Atlantic are the southern

2   Norwegian Sea and the Irminger/Labrador Sea Sub-polar Gyre (Heath et al., 2004). The 24 net

3   sampling sites included here in the analyses of demography and phenology are located at various

4   distances from these two major overwintering epicentres (Table 1, Fig. 1b). Proximity to an

5   overwintering centre has been suggested to be the main prerequisite for high abundance of *C.*

6   *finmarchicus* (e.g. Heath et al., 2000a, 2008; Speirs et al., 2004; Torgersen and Huse, 2005; Head et al.,

7   2013b) and to a large extent our observations are consistent with this notion, as the seven sites with

8   highest abundances are located within or close to the two major overwintering basins (Fig. 6). Station

9   Mike and the Svinøy section Atlantic and Arctic water regions are situated within the gyre of the

10 southern Norwegian Sea. The Svinøy coastal region is located on the Norwegian Shelf, on the eastern

11 rim of the southern Norwegian Sea deep basin, and coupled life-history/circulation models have

12 demonstrated that *C. finmarchicus* can be recruited to the shelf population from the gyre population to

13 the west (Speirs et al. 2004; Samuelsen et al. 2009). Similarly, the Westmannaey site on the southern

14 Icelandic shelf and the West Greenland shelf site on the southwestern Greenland shelf are situated

15 close to the Irminger/Labrador Seas Gyre, while the Eastern Labrador Sea site is within the gyre. The

16 overwintering female population at the central Labrador Sea site, also located within this gyre, is very

17 abundant prior to spawning but here the number of first generation copepodites is very low, indicating

18 high mortality during development and low local recruitment (Head et al., in prep).

19

20   Total maximum abundance of *C. finmarchicus* populations at the study sites increased with

21 increasing maximum water temperature within the range of about 3-13 ^{0}C, although some locations

22 particularly in the North Sea, seem to deviate from this trend. Apart from being more distant from the

23 overwintering epicentres these locations may also be less favourably positioned with respect to

24 advection of animals from the population centres. The earliest recruitment to the young copepodite

1   stages occurred at sites with high maximum temperatures, except at some coastal sites (Figs. 8 and 9

2   upper panel), and maximum abundance of the young stages occurred during or just after the

3   phytoplankton bloom maximum (Fig. 9 lower panel). From these three relationships it is reasonable to

4   infer that if recruitment can match an early phytoplankton bloom, production of *Calanus finmarchicus*

5   populations will be improved. By contrast, *C. finmarchicus* in cold Arctic regions of the Norwegian

6   Sea and in the northwest Atlantic tend to recruit to young stages long after the bloom and abundances

7   of the species are lower there than in Atlantic water (Broms et al., 2009, Plourde et al. 2009b).

8

9   Neither high temperatures nor recruitment during early phytoplankton blooms are enough to

10   guarantee an abundant population, since some sites are characterised by high temperature and

11   agreement between recruitment and bloom time but yet have scarce populations. One explanation that

12   we have not explored by data analysis here is unevenly distributed predation pressure among the sites.

13   In the Norwegian Sea a range of different predators have been identified and both direct and

14   circumstantial evidence of predation have been given. Predation from herring on copepods which were

15   mainly *C. finmarchicus,* was estimated to be similar to the annual production of the prey (Dommasnes

16   et al. 2000), Skjoldal et al. (2004) estimated pelagic fish predation on *Calanus* to be ~30% of annual

17   production, Utne et al. (2012) using ecosystem model simulations estimated predation from pelagic

18   fish stocks at 35 mill tonnes, or 18% of the annual *C. finmarchicus* production (Hjollo et al. 2012). It

19   has also been found that *C. finmarchicus* stock size is negatively correlated to total pelagic fish stock

20   size the previous year in the Norwegian Sea (Olsen et al. 2007, Huse et al. 2012), suggesting top down

21   controls at a large scale. Additionally, predation from macroplankton predators and mesopelagic fishes

22   may greatly exceed predation from the pelagic fish stock (Skjoldal et al. 2004). In fact, when summing

23   assumed consumption of *C. finmarchicus* by all the predators the total predation loss tends to be much

24   larger than the *C. finmarchicus* production in the Norwegian Sea, strongly suggesting that predation is

1   the terminal cause of mortality there and that new estimates on production and consumption are

2   needed. We do not have similar information on *C. finmarchicus* predators in the other deep basins, but

3   the presence of large pelagic fish stocks in the Norwegian Sea is one clear difference in the predatory

4   communities between the two major overwintering deep basins in the Norwegian Sea and the

5   Labrador/Irminger Seas. However, even though *C. finmarchicus* may be more heavily grazed in the

6   Norwegian Sea, this is also the basin with the highest *C. finmarchicus* abundance. Therefore, we

7   hypothesize that the Labrador and Irminger Sea possess predatory stocks made up of

8   macrozooplankton and mesopelagic fishes that inflict considerable predation pressure on *C.*

9   *finmarchicus*.

10

11   Predation on the overwintering population is another source of mortality that needs further

12   investigation, although data from the two major overwintering basins, the southern Norwegian Sea and

13   the Labrador Sea, indicate that mortality during overwintering is low and less variable than during the

14   active phase (Head et al., in prep; Melle et al., in prep). Still, losses of almost the entire population

15   from the Norwegian shelf during winter indicate that predatory or advective losses during winter may

16   be substantial in shallower regions (Slagstad and Tande 1996, Melle et al. 2004).

17

18   Predation may shape the population distribution in the regions of marginal *C. finmarchicus*

19   productivity such as the sites with low temperature or with a mismatch to the bloom. Our mortality rate

20   calculations suggest high predation pressure on eggs and nauplii, which we suggest is by the

21   suspension feeders, *C. hyperboreus* and *C. glacialis* (in addition to cannibalism by *C. finmarchicus*

22   CVIf). This occurs because *C. hyperboreus* and *C. glacialis* have multi-year life cycles and therefore

23   are present as copepodite stages early in the spring bloom, when *C. finmarchicus* reproduction is

24   starting (Conover, 1988). Thus, during the late spring-early summer period, recruitment of *C.*

1 *finmarchicus* is suppressed and there is a delay in the timing of maximum CI-CIII abundance until well

2 after the bloom (Section 3.6, Figs. 19, 20). This interaction with arctic congeners should be more

3 prominent at sites where CI-CIII recruits peak several weeks after the bloom, such as at the Anticosti

4 Gyre, Gaspé Current, Station 27 and Labrador Shelf sites. One exception is the lower St. Lawrence

5 estuary (RIM) where the bloom is delayed relative to the adjacent Anticosti Gyre due to freshwater

6 runoff, so that it co-occurs with the relatively late CI-III peak (Fig. 9). Surface layer temperatures in

7 cold (3°C mean) and warmer habitats (10°C mean) during the population growth period should result in

8 development times from egg to N6 of 30 and 15 days respectively, representing only a two week

9 difference (Campbell et al., 2001). Therefore, differences in temperature alone cannot explain the long

10 delays (up to 3.5 months) observed between the timing of maximum in CI-CIII abundance and the

11 bloom at the cold water sites, but which is consistent with our suggestion of predation by the arctic

12 *Calanus* species.

13

14   The demographic pattern observed in the central Labrador Sea is similar to the spatial

15 demography observed within the central Irminger Basin, for which sources of overwintering

16 copepodites are hypothesized to be recruitment along the eastern and northern margins and subsurface

17 horizontal transport from the east Greenland slope and Labrador Sea (Heath et al., 2008). Recruitment

18 failure in the central Irminger Basin, likely due to high predation mortality in the early life stages

19 and/or starvation of the first feeding nauplii at persistently low food conditions, is hypothesized to

20 preclude direct descent as a major source of overwintering stage CV (Heath et al., 2008). In the central

21 Labrador Sea, food (i.e. phytoplankton) concentrations and egg production rates are higher (e.g. Fig.

22 15) than in the Irminger Basin, and early life stage mortality due to cannibalism by adult *C.*

23 *finmarchicus* and predation by *C. hyperboreus* and other as yet unrecognised predators (Head et al.,

24 2003; Head et al., in prep.) may be more important sources of recruitment failure.

1

2   The deep basin populations appear to be the main   sources of supply of *C. finmarchicus*

3   overwintering stages to the central and northeastern North Atlantic shelf populations. On-shelf

4   transport from the Norwegian Basin of overwintered adults prior to mid-summer and early life stages

5   later in the year is the primary source of *C. finmarchicus* to the relatively narrow Norwegian shelf

6   (Samuelson et al., 2009). Field and modelling studies (e.g. Heath et al., 1999; Harms et al., 2000)

7   support the hypothesis that the population of *C. finmarchicus* in the North Sea is sustained by annual

8   spring advection of late-stage individuals originating from high concentrations of stage CVs

9   overwintering in the deep Atlantic and Norwegian Sea, particularly the Faroe-Shetland Channel (Heath

10   et al., 1999). In the North Sea, the maximum abundance of *C. finmarchicus* is low (on the order of 5 x

11   10^3 ind. m^{-2}: Heath et al., 2000a; Jónasdóttir and Koski, 2011), despite relatively high egg production

12   rates (Jónasdóttir and Koski, 2011; Fig. 16). The primary factor controlling abundance in the North Sea

13   appears to be predation mortality during the early life stages (Jónasdóttir and Koski, 2011), which

14   probably also holds for the older stages, which cannot migrate vertically far enough to avoid predation,

15   because of the relatively shallow bathymetry.

16

17   Other time series sites are farther from the deep basin epicentres or have lesser degrees of direct

18   advective connection, which limits repopulation from the deep ocean overwintering sites by members

19   of the overwintering or first generations. The Arendal and the two northern Icelandic sites have long

20   transport routes from their nearest overwintering areas, the Norwegian Sea and the deep basins south of

21   Iceland (Gislason and Astthorsson, 1998; Heath et al., 2000b; Astthorsson and Gislason, 2003; See

22   Appendix and Fig. 1b), and the Faroese Shelf site is located behind a strong tidal front, within an

23   anticyclonic shelf gyre that results in a short retention time and increased dispersal of shelf plankton

24   and reduced advection of oceanic plankton onto the shelf (Debes and Eliasen, 2006). Recruitment of

G0/G1 on the Labrador/Newfoundland shelves that are adjacent to a deep overwintering area does not seem to be as effective as the recruitment to the southern Icelandic and western Norwegian shelves (Westmannaeyj and Svinøy Coast sites). This may be because the Labrador/Newfoundland shelves are broad relative to the Icelandic/Norwegian shelves and are not deep enough to sustain overwintering populations, and also because there are relatively high concentrations of *C. hyperboreus* and *C. glacialis* present in spring, which can consume *C. finmarchicus* eggs and nauplii (See Sections 3.6 and 4.2.3).

In contrast to the northeast Atlantic, the marginal seas of the northwest Atlantic (the Gulf of St. Lawrence and the Gulf of Maine) harbour local overwintering stocks, and local production is as important as advective supply from the slope water in sustaining local *C. finmarchicus* populations. Overwintering stage CVs reside at 150-175 m in the deep (300-400 m) Laurentian Channel of the Gulf of St. Lawrence and the deep basins (250-400 m) of the Gulf of Maine (Plourde et al., 2001; Johnson et al., 2008) at abundances (20-40 x 10^3 ind. m^{-2}) of the same order of magnitude as *C. finmarchicus* stocks in the deep basins (e.g. Heath et al., 2000b; Halvorsen et al., 2003). As well, a modeling investigation has indicated that the Gulf of St. Lawrence population is self-sustaining (Zakardjian et al., 2003). The roles of local production versus advective supply from the Scotian Shelf, Labrador and Atlantic slope water in maintaining the Gulf of Maine basin populations are still not determined, although there is evidence that coastal Gulf of Maine production is a significant local source (Maps et al., 2012). Nevertheless, the relatively warm overwintering temperatures in the deep Gulf of Maine reduce dormancy duration, and supply from the colder northern sources in the Gulf of St. Lawrence and distant Labrador Sea may become increasingly important to maintain the population of *C. finmarchicus* in the Gulf of Maine region under climate forcing.

1   When considering impacts of climate warming on *C. finmarchicus* distribution in the northern

2   North Atlantic, the differences in the interplay between bathymetry, advective supply and local birth

3   and mortality rates all need to be taken into account. Increasing surface layer temperature will

4   certainly be a factor at the southern geographical edge of the species range. Surprisingly, the upper

5   temperature threshold at which growth and development rates start to be constrained is not well known,

6   but is likely to be between 16-18°C (Moller et al. 2012; Runge and Preziosi, unpubl. observations).

7   Overwintering water temperature is also a factor for southern populations; for example, the warm deep

8   water temperatures in the Gulf of Maine currently appear to force *C. finmarchicus* to emerge from

9   diapause considerably earlier than it does in more northern regions (Saumweber and Durbin, 2006;

10   Johnson et al., 2008; Maps et al., 2010; Maps et al., 2012), an effect that is likely to be exacerbated as

11   water temperatures warm in future. At the moment the southern limit of the distribution of *C.*

12   *finmarchicus* in the northwest Atlantic (the Gulf of Maine/Georges Bank) is maintained by the stocks

13   overwintering in the basins in the Gulf of Maine (Miller et al. 1998) and along the shelf-slope region of

14   the Scotian Shelf (Head et al., 1999; Head and Pepin, 2008), in combination with advection from

15   upstream sources, including the surface layers of the Scotian Shelf and the Gulf of St. Lawrence (Head

16   et al., 1999) and ultimately the Labrador Sea, via the Labrador Shelf and Slope water currents (Greene

17   and Pershing, 2007; Head and Pepin, 2010). In the northeast Atlantic, however, the mean residual flow

18   is from south to north, resulting in warmer water incursions at higher latitudes. Maintenance of *C.*

19   *finmarchicus* on the northeast shelves will therefore depend on continuing advective supply from the

20   deep Norwegian Sea. For the North Sea, the southern edge of the northeast Atlantic shelf distribution,

21   advective supply is a function of the deep transport of *C. finmarchicus* from the Norwegian Sea to the

22   Faroe-Shetland Channel, together with local and regional wind fields transporting individuals into the

23   North Sea in the surface layers. The distribution of *C. finmarchicus* at its northern boundary and its

24   ability to colonise the Arctic may be constrained by the effects of less light and colder temperatures,

1 which lead to both a shorter phytoplankton growth season length and slower *C. finmarchicus*

2 development rates (Broms and Melle 2007; Broms et al. 2009; Ji et al., 2012). As well there is the

3 potential for predation on *C. finmarchicus* early life stages by its arctic congeners, *C. glacialis* and *C.*

4 *hyperboreus*. Climate change scenarios can be investigated in coupled physical-life history models for

5 shelf and offshore regions of both the northeast and northwest Atlantic, although accurate prediction of

6 future distributions will also require information on the distributions of potential predators and how

7 they respond to climate change.

8

9 *4.2. Life history responses to environmental variables*

10   Understanding the spatial population dynamics of *C. finmarchicus*, or any animal population in

11 the sea, requires the capability to quantitatively characterize birth and mortality rates, as well as

12 immigration and emigration rates. The representation of copepod life histories, including population

13 demographics, by life history models has been discussed elsewhere (e.g. Runge et al., 2005; Ji et al.,

14 2010; Neuheimer et al., 2010; see also section below). Essential to this quantitative analysis is the

15 parameterization of vital rates, including development, growth, egg production and mortality. While

16 models of *C. finmarchicus* life cycles have already shown insight into factors controlling populations at

17 both regional (e.g. Speirs et al., 2004; Samuelson et al., 2009; Maps et al., 2012) and basin scales (e.g.

18 Speirs et al., 2006; Hjollo et al. 2013), the choice of parameter values in many cases is still open to

19 considerable uncertainty (e.g. Maps et al., 2012) due to the need for more comprehensive datasets. For

20 example, the parameterization of growth rates as functions of food availability and temperature is based

21 almost exclusively on the now classic work by Campbell et al. (2001) using *C. finmarchicus* collected

22 from the Gulf of Maine in the northwest Atlantic. The extent to which the physiological responses of

23 *C. finmarchicus* captured from the northwest Atlantic are representative of those of individuals in the

24 northeast Atlantic is still an open question in light of the finding of genetic differentiation of two and

1   perhaps as many as four populations across the species' range (Unal and Bucklin 2010). Here we

2   interpret the available data on diapause timing, egg production and mortality rates in relation to habitat

3   variables in order to assess the state of our understanding of parameterization of these variables across

4   the entire basin.

5

6   *4.2.1. Diapause duration and timing*

7   Our analysis of the pan-Atlantic demographic data (Figs. A1-A6) provides evidence for a longer

8   active period and shorter dormancy duration in the northwest Atlantic than in the northeast, although

9   not necessarily for a greater number of distinct "generations". An interpretation consistent with the

10   finding of higher chlorophyll concentrations and lower surface temperatures in the northwest Atlantic

11   is that the more favourable food conditions contribute to more sustained egg laying, leading to a

12   prolonged growth season, but combined with slower development this do not necessarily result in

13   more generations. For example, at the Gulf of St. Lawrence Rimouski station, prolonged summer

14   production results in a broad period of recruitment lasing several months. Seasonally late egg

15   production in the northwest Atlantic may, however, also yield an active population of early copepodites

16   constituting a "lost generation", i.e., individuals that do not enter dormancy with the bulk of the

17   population and consequently delay the metric indicating start of diapause. The presence of a fraction of

18   the population that continues to develop while most of the population enters dormancy has been

19   observed in many locations (e.g., Meise and O'Reilly, 1996), although the offspring of these

20   individuals may not survive to reproduce. Higher overwintering temperatures in the northwest

21   Atlantic, where overwintering *C. finmarchicus* experience temperatures ranging from about 1 to 10 °C,

22   with highest values in Emerald Basin on the Scotian Shelf (Head and Pepin, 2008) and in the Gulf of

23   Maine (Maps et al., 2012), likely also contribute to differences in dormancy timing and duration.

24

1   There is variability in the number of identifiable generations among sampling sites, but without

2   any distinct west-east pattern (Figs A1-A6). In the coastal Gulf of Maine stage CV emerges from

3   dormancy in late December, possibly earlier (Durbin et al., 1997; Maps et al., 2012), and 2-3

4   generations are produced over the course of a season. In contrast, upstream of the Gulf of Maine on the

5   Scotian Shelf, emergence occurs in February - March and 1-2 generations are produced (Sameoto and

6   Herman, 1990; Herman et al., 1991; McLaren et al., 2001), although production may extend into the

7   fall in some areas and some years (Head and Pepin, 2008). In the adjacent slope water, emergence from

8   dormancy also occurs in February – March, but yields only one generation (Miller et al., 1991). In the

9   Gulf of St. Lawrence and on the Newfoundland Shelf, *C. finmarchicus* generally emerges from

10   diapause in late March-early April and produces one large summer generation followed by a smaller

11   one in autumn (Plourde et al., 2001, Johnson et al., 2008, Pepin et al., 2011). In the Iceland Basin,

12   stage CVs emerge in March-April, while in the Irminger Basin, emergence begins in February

13   (Gislason and Astthorsson, 2000). In the Irminger Basin, *C. finmarchicus* mainly produces one

14   generation before entering diapause in late July or early August, but a small percentage molt to

15   adulthood and continue active development (Heath et al., 2008). On the shelf south of Iceland, 2-3

16   generations are produced, with the main population peaks in May/June and June/July (Gislason et al.,

17   2000). In the Norwegian Sea, *Calanus finmarchicus* start to emerge from dormancy in January and

18   February (Melle et al. 2004; Edvardsen et al., 2006), and there are typically one or two generations

19   annually (Petersen et al., 2000; Melle et al., 2004; Broms and Melle, 2007; Broms et al., 2009;

20   Bagoeien et al., 2012).

21

22   A qualitative assessment finds the demographic data consistent with a lipid dependent

23   mechanism (Irigoien, 2004; Johnson et al., 2008; Maps et al., 2010; 2012) to explain spatial and

24   temporal variability in dormancy timing and duration. Under this hypothesis, the food and temperature

1 conditions determine the accumulation of storage lipid in individual copepodites. Only when lipid

2 accumulates above a nominal threshold level is the signal (likely hormonal, see Tarrant et al., 2008)

3 given for that individual to prepare for diapause in stage CV. During lipid accumulation, *C.*

4 *finmarchicus* has been shown to regulate the composition of the storage lipids, biochemically altering

5 the saturation state (Clark et al., 2012). If the threshold is not attained and hence the signal not

6 received, the individual remains active and molts to adulthood. According to this hypothesis, duration

7 of dormancy is determined by the rate of storage lipid utilization, which is regulated by storage lipid

8 composition (Clark et al., 2012) and is temperature dependent (Saumweber and Durbin, 2006; Pierson

9 et al., 2013). Thus, the within-region and cross Atlantic differences in dormancy timing and duration

10 could reflect the environmental conditions experienced by individuals within each local population.

11 The warm overwintering temperatures in some areas of the northwest Atlantic may promote early

12 emergence from dormancy, for example in the Gulf of Maine (Durbin et al., 1997), where the

13 exceedingly warm (for this species) overwintering temperatures may force exit from dormancy in late

14 summer and entry into dormancy later in the fall by subsequent cohorts (Maps et al., 2012). Short

15 dormancy duration in these warm areas, and late entry in fall, may contribute to the explanation of the

16 relatively short period in late winter (days 20-60: Fig. 10) over which stage CVs emerge from

17 dormancy throughout the North Atlantic. The alternative (although not necessarily mutually exclusive)

18 hypothesis of photo-awakening (Speirs et al., 2004), in which photoperiodic cues are invoked to

19 explain synchronicity of arousal from dormancy, cannot be ruled out, however.

20

21   Future advances in understanding of dormancy timing and duration and the mechanisms to

22 explain it will require continued collection of time series data and quantitative application of the lipid

23 accumulation/metabolism hypothesis across data sets. Many of the data sets compiled here do not have

24 sufficient frequency of sample collection or length of time series to allow accurate determination of

1   dormancy timing and duration. There are fewer long-term offshore time series in the northwest Atlantic

2   than in the northeast Atlantic, and none in the middle of the basin. Further insight into dormancy

3   control will require time series observations at strategically selected stations at relatively high

4   frequency (semi-monthly to monthly) over several years (Ji et al., 2010), including biochemical and

5   perhaps genetic measurement of dormancy state in order to accurately characterise regional and

6   individual differences in timing and duration of dormancy.

7

8   *4.2.2. Reproductive rates*

9   Egg production rates (EPRs) are clearly strongly related to food availability throughout the

10   North Atlantic, but the goal of precisely predicting EPRs for *C. finmarchicus* from simple

11   environmental variables, such as chlorophyll concentration and temperature, and female size remains

12   elusive, in light of the high degree of variability reported here (e.g. Figs 15 and 16). This variability is

13   not surprising, since many other factors can also influence individual EPRs. For example, EPRs are

14   affected by food type (Marshall and Orr, 1972; Niehoff et al., 1999; Jónasdóttir et al., 2002; Niehoff,

15   2004) and although diatoms are generally dominant during spring, in some regions blooms of other

16   phytoplankton taxa, which may be inferior foods, such as the colonial prymnesiophyte *Phaeocystis*

17   spp., are common (Soreide et al., 2008). Young females that have recently molted may take several

18   days to attain reproductive maturity and until then are not reproductively active, effectively lowering

19   estimated per capita EPR (Plourde and Runge, 1993; Niehoff et al., 1999; Niehoff et al., 2002). As

20   well, during the later stages of the spring bloom old females may be less fecund (Diel and Tande, 1992;

21   Hirche et al., 1997; Head et al., 2013a; b) and may start to accumulate fat (Head et al., 2013a). At

22   stations where chlorophyll concentrations are very low, particularly in post-bloom conditions, females

23   are known to feed omnivorously (Ohman and Runge, 1994; Runge and de Lafontaine, 1996; Ohman

24   and Hirche, 2001, Levinsen et al., 2000), in which case chlorophyll concentration may not be an

1   appropriate measure of "food" concentration. Moreover, the extent to which contemporaneous

2   estimates of chlorophyll a represent female feeding history will also be a factor; in some instances (e.g.

3   patchy, advective environments such as the RIM station), chlorophyll concentrations may change

4   substantially from day to day.

5

6   Temperature undoubtedly influences EPR in laboratory studies (Hirche et al., 1997; Rey et al.,

7   1999), but the effects of changes in temperature *in situ* are not broadly predictable. For example, after

8   the effect of food had been accounted for, temperature had a positive correlation with EPRs in 3 study

9   regions (RIM, LS, ICE(N)), a negative correlation in one (IRM) and no relationship in the other 8

10   (Table 6). On the other hand, EPR_{max} for females from the WGBB region during spring, where

11   temperatures are close to $0^{o}C$, were four times lower than for those from the SS, where average

12   temperatures are only ~$2^{o}C$ higher (*c.f.* Figs. 4 and 15). Also, EPRs in the WGBB in spring were

13   substantially lower than those measured for females that were collected at *in situ* temperatures of ~$9^{o}C$

14   and switched to $0^{o}C$ (Hirche et al., 1997; Kjellerup et al., 2012) and females collected from the WGBB

15   during the spring bloom took several days to increase their EPRs when fed and incubated at higher

16   temperatures in the laboratory, implying that temperature effects may be relatively persistent. The

17   inability of *C. finmarchicus* females to produce eggs at high rates at these low temperatures may be one

18   factor limiting the species northern distribution at this time, since the periods of the year over which

19   high food concentrations co-occur with acceptably high temperatures decrease in duration with

20   increasing latitude, so that the effective reproductive and growth seasons are shorter. Indeed, it may be

21   that *C. finmarchicus* populations are not currently self-sustaining in the WGBB. This region is,

22   however, downstream of an important production area in the eastern Labrador Sea, which may serve as

23   a source of overwintering females on an annual basis.

24

1   Temperature during the spring period was negatively or positively related to female size in 7

2   study regions, and female size was positively related to egg production residuals in 3 regions (GB,

3   RIM, LS). In some regions the changes in temperature were probably associated with differences in

4   water masses among stations, and thus in the source populations for females (e.g. IRM, NNWS) of

5   varying sizes. In others, however, increasing temperatures may reflect the warming of the surface

6   layers over the spring period, and the entry of larger females, possibly from the G1 generation, into the

7   egg-laying population (e.g. GB). In addition, in stratified waters in particular, the selection of which

8   temperature accurately represents the temperature of vertically mobile females is in itself problematic.

9

10   Given the observed variability in the relationship between egg production rate and chlorophyll a

11   standing stock across regions, it is not possible at this time to identify any general parameterization of

12   egg production response to measures of food availability and temperature across the North Atlantic. In

13   some regions there is a useful fit (e.g. $r^2 > 0.2$) to an Ivlev-type relationship in spring (GB and RIM;

14   arguably also SS, LS and ICE(N)); in others (IRM, ICE (S), BIS, NNWS), there appears to be no

15   relationship with chlorophyll standing stock. It may be that each region has its own particular

16   relationship (or lack thereof), reflecting regional differences in dynamics and species composition of

17   primary producers, as well as possible physiological differences in resident *C. finmarchicus*. There is

18   evidence (Figs. 15 and 16; Table 5) for broad regional differences in maximum egg production rate

19   (35-60 eggs female^{-1} d^{-1} in the northwest Atlantic compared to 20-30 eggs female^{-1} d^{-1} in the northeast

20   Atlantic) and in critical concentrations, which range from 53-94 mg chl a m^{-2} in the upper 30 m (1.8

21   and 3.1 mg m^{-3}) in the northwest Atlantic, compared to 17-57 mg chl a m^{-2} (0.6-1.9 mg m^{-3}) in the

22   northeast Atlantic (with the exception of a very different relationship at ICE(N)). This factor of two

23   difference may reflect the generally smaller female size in the northeast Atlantic, although the average

24   prosome length of experimental females from GB was about the same as the one for experimental

1   females from the Norwegian Sea, where maximum egg production rates were lower by nearly a factor

2   of three. Alternatively, these broad regional differences in egg production characteristics may reflect

3   physiological and perhaps genetically differentiated responses to the food, light and temperature

4   regimes on the two sides of the North Atlantic. Consistent with this hypothesis is the apparent

5   divergence in conclusions with respect to the use of internal lipid stores to produce eggs prior to the

6   spring bloom; evidence for this process has been found in the northeast Atlantic (e.g. Niehoff et al.,

7   1999; Richardson et al., 1999) but not in the northwest Atlantic (e.g. Plourde and Runge, 1993; Durbin

8   et al., 2003). Production of eggs prior to the spring bloom may reflect the fact that females in the

9   northeast Atlantic are adapted to the lower food conditions (as represented by chlorophyll standing

10 stock) that are generally found there. Differences in number of eggs could to some extent be

11 compensated by egg size, which we have not measured and would reflect genetic difference between

12 the western and eastern *C. finmarchicus* populations. To our knowledge egg size has not been

13 compared among sites on a basin scale.

14

15   Analysis of prosome length-dry mass measurements for female *C. finmarchicus* also suggests

16 differences between northwest and northeast Atlantic populations. Prosome length-dry mass

17 relationships were determined for females on Georges Bank (Runge et al., 2006) and in the sea around

18 Iceland (Gislason, 2005). Based on these relationships, a 2.6 mm female should have a dry mass of

19 289 μg on Georges Bank and 165 μg off Iceland, a difference of about 40%.   The C and N contents of

20 a 2.6 mm female on Georges Bank are predicted to be 135 μg and 29 μg, respectively and a similar

21 relationship was found for females collected in the Labrador Sea (Head et al., 2013a). At Stn OWS

22 Mike (SNWS), Irigoien et al. (1998) reported a carbon content of 50 μg and nitrogen content of 12 μg

23 for females with an average PL of 2.6 mm (Niehoff et al., 1999) collected between April and June.

24 From these measurements, and using the spring EPR_{max} for the SNWS from Table 5 and literature egg

1 C and N contents (Runge and Plourde, 1996), C and N specific EPR_{max} values of 11.8 % body C d^{-1}

2 and 9.4 % body N d^{-1} can be estimated, somewhat higher than those reported for Georges Bank or the

3 Labrador Sea (8.5% and 7.2% for C and N specific rates, respectively). Similar calculations were

4 made for the SS and WGBB regions, using EPR_{max} values from Table 5 and female C and N contents

5 of 168 and 33 µg for the SS (R. Campbell, unpubl. data) and 109 and 21 µg for the WGBB (Kjellerup

6 et al., 2012). For these regions the C and N specific EPR_{max} values were 5.1% body C d^{-1} and 4.9%

7 body N d^{-1} (SS) and 2.5% body C d^{-1} and 2.3% body N d^{-1} (WGBB). *In situ* temperatures were 5-9°C

8 for GB, 3-8°C for the LS, between -1 to +6°C on the SS, and between -1.58 and +2°C in the WGBB

9 region. Thus, over four regions in the NW Atlantic, C and N specific EPR_{max} values appear to increase

10 with increasing temperature. In the NE Atlantic (SNWS), average spring temperature was similar

11 ($\sim$7°C) to those on GB and in the LS, but C and N specific EPR_{max} values were higher. Head et al.

12 (2013a) estimated a maximum C specific EPR of 5.8 % body C d^{-1} and a maximum N specific rate of

13 5.9% d^{-1} for females from a northern Norwegian fjord, using maximum observed EPRs (Diel and

14 Tande, 1992) and average female C and N contents (Tande, 1982). Here, the average temperature was

15 $\sim$5°C, so that both the maximum EPR and temperature were lower than in the SNWS. From these few

16 datasets the extent to which C and N specific EPR_{max} values are the same at similar temperatures

17 among regions, or have similar relationships with temperature, is unclear. More observations of EPRs

18 in concert with measurements of female body C and N are needed to explore this and the question of

19 physiological differences among regions and populations remains open.

20

21 *4.2.3. Mortality*

22   We have extended the VLT approach applied by Plourde et al. (2009b) to a broader

23 dataset based on several national monitoring programs in the northeast and northwest Atlantic.

24 Results for the population active growth period show a hyperbolic decrease in mortality rate from the

1 early to late life stages, with values that are generally consistent in magnitude with those determined by

2 Ohman et al. (2002). In most cases regional variations were relatively small, which is surprising given

3 the likelihood of different predator fields among regions. Mortality rates of older copepodite stages

4 (CIV-V) active in the surface layer are highest on the shelves and positively correlated with

5 temperature, suggesting there may be higher predation mortality by visually guided predators in shelf

6 ecosystems than in the deep ocean. When integrated with stage-specific development times to construct

7 development trajectories and to estimate daily recruitment, there were relatively small differences (no

8 more than a factor of two, Fig. 18) in copepodite stage-specific daily mortalities and very similar

9 survival trajectories from CI to CV across the different regions (Fig. 18, 20). In contrast to the

10 copepodite stages, differences in daily mortality rates in Egg-CI, probably mostly caused by mortality

11 in the egg and early naupliar stages (i.e., Ohman et al. 2004, Plourde et al. 2009a), appear to translate

12 into markedly different survival trajectories, particularly in cold habitats (<6$^{\mathrm{o}}$C). Here, small

13 differences in daily mortality rates of egg-CI resulted in 5-6 times lower survival rates in regions

14 where they were likely to be co-occurring with large the arctic congeners *C. hyperboreus* and *C.*

15 *glacialis* (Fig. 20). Our analysis identifies these species as potentially significant sources of mortality

16 for the early stages of *C. finmarchicus* in cold regions that are influenced by arctic water, e.g. the

17 Labrador and Newfoundland shelves. Indeed, predation by these arctic species may represent a

18 significant constraint on expansion of the species' range northward in response to warming surface

19 waters.   As evidenced by the observations of seasonal demography, predation by these arctic

20 copepodites on *C. finmarchicus* eggs and nauplii appears to have the effect of displacing the

21 recruitment window for the latter to a period either late in or after the bloom, resulting in a mismatch

22 with optimal food conditions and thus lower productivity relative to warmer regions (Fig. 8, 9). A

23 similar 'intraguild predation' interaction has been hypothesized to control copepod species succession

24 at Station India, a *C. finmarchicus* dominated system where the abundance of several small copepod

species was inversely proportional to *C. finmarchicus* abundance, which, it has been suggested, leads to

their optimal recruitment window being displaced outside the period when *C. finmarchicus* were active

in the surface layer (Irigoien and Harris, 2006).

We did not investigate mortality and survival of *C. finmarchicus* during the overwintering

period on a basin-wide scale because existing data sets were inadequate for such a study. Elsewhere,

however, estimates of mortality rates for dormant *C. finmarchicus* are generally very low ranging from

0.004 to 0.027 d^{-1}, so that overwintering mortality does not appear to be very important compared to

mortality at other times of the year. On the other hand, predation on overwintering *Calanus* may be

important in certain locations. For example Norwegian fjords, with mesopelagic fish present had

mortality rates up to three times higher (0.011-0.027 d^{-1}) than one that had only invertebrate predators

(0.008–0.009 d^{-1}; Bagoeien et al. 2001). Few estimates of overwintering mortality have been made for

deep oceanic regions although there is one that has suggested that mortality of overwintering *C.*

finmarchicus is substantially lower in Irminger Sea and Iceland Basin (0.004 d^{-1}) relative to shelf

locations, a difference mainly attributed to a reduced vertical overlap between the overwintering stock

and mesopelagic fishes such as myctophids in the deeper regions (Bagoeien et al.; 2001, McLaren et

al., 2001; Gislason et al., 2007; Pepin 2013). This limited degree of vertical overlap in the centres of

distribution of *C. finmarchicus*, could represent the expression of long-term evolutionary processes

resulting in an optimal life-cycle strategy that minimizes mortality for the species as a whole (Gislason

et al. 2007).

4.3. Modeling mesozooplankton distribution and abundance in the North Atlantic in the context of

climate change: statistical and spatial dynamics modeling approaches

1

2   The compilation of information reported here represents a step toward modeling the population

3 distribution and dynamics of *C. finmarchicus*, and in turn, their responses to climate change drivers

4 over the North Atlantic. In the recent years, two main modeling approaches, statistical (niche-based)

5 and dynamic (mechanistic or process-based), have been employed to improve our understanding of

6 distribution patterns in *Calanus spp.* in the northern North Atlantic.

7

8   Statistical-based modeling is based upon the ecological niche theory relating species occurrence

9 (or abundance) to environmental variables and food as predictors. This approach has been termed

10 habitat suitability (Hirzel et al., 2002), species distribution (Elith and Leathwick, 2009) or habitat

11 distribution (Guisan and Zimmermann, 2000) modelling. Although initially habitat models were

12 applied to terrestrial species (especially vascular plants, Elith and Leathwick, 2009), more recently

13 they have also been applied to a wide variety of marine species including zooplankton to provide

14 projections of future climate-driven shifts in species distributions (Beaugrand et al., 2002; Helaouët and

15 Beaugrand, 2007; 2009; Beaugrand et al., 2008; Helaouët and Beaugrand, 2009; Reygondeau and

16 Beaugrand, 2011; Helaouët et al., 2011). Most of the zooplankton studies use distance measures, in

17 contrast to the more capable generalised additive (Chust et al., 2013b) and Maximum Entropy models

18 (Provan et al., 2009). Model validation and variable selection are critical steps in order to extrapolate

19 habitat models to conditions outside of those used to generate the model, for instance for future climate

20 scenarios or other areas (e.g. Valle et al., 2011). This is especially problematic for modeling

21 consequences of future climate change. Most of the habitat modeling software (BIOCLIM (Nix, 1986),

22 Maxent (Elith et al., 2011), *dismo* R package (Hijmans and Elith, 2013), Ecological Niche Factor

23 Analysis (ENFA, Hirzel et al., 2002), BIOMOD (Thuiller et al., 2009), openModeller (Muñoz et al.,

24 2009)) were conceived to be applied for species with low spatial variation throughout the seasonal

1   cycle, such as sessile organisms, from a set of spatial layers of environmental variables. Species with

2   high seasonality such as zooplankton need to be modeled taking into account the temporal domain

3   explicitly (Chust et al., 2013b).

4

5   The coupled physical-life history modeling approach is mechanistic and mainly based upon

6   factors affecting spatial population dynamics (reproduction, mortality and migration rate). There are

7   two distinct methods for simulating the spatial dynamics of plankton, namely the Lagrangian

8   (Individual Based Models IBMs) and Eulerian approaches (reviewed in Runge et al., 2005). Several

9   models have been developed to simulate the spatial and population dynamics of *C. finmarchicus* both

10   using IBMs (e.g. Carlotti and Nival, 1992; Carlotti and Wolf, 1998; Miller et al., 1998; Hjollo et al.,

11   2012; Ji et al., 2012; Maps et al., 2012; Huse et al., submitted; Pepin et al., 2013), and Eulerian (e.g.:

12   Bryant et al., 1997; Lynch et al., 1998; Tittensor et al., 2003; Zakardjian et al., 2003; Speirs et al.,

13   2004; 2006; Slagstad and Tande, 2007; Maps et al., 2012) models. Eulerian models are numerically

14   more efficient than IBMs. On the other hand, the mechanistic process formulation of IBMs permits a

15   more detailed biological description of individuals (Grimm and Railsback, 2005; Maps et al., 2012). A

16   3-D IBM for *C. finmarchicus* in the Norwegian Sea has been developed that takes into account growth,

17   mortality, movement and reproduction of *C. finmarchicus* as well as adaptive traits, which control its

18   interaction with the environment (Hjollo et al., 2012). This model addresses the entire life cycle of *C.*

19   *finmarchicus*; the main life history features and vertical movement are emergent properties resulting

20   from many evolved generations using a genetic algorithm. A genetic algorithm procedure (Record et

21   al., 2010) has also been used in a *Calanus* IBM model to determine values for "soft parameters", for

22   which available knowledge only allows a range of values to be specified (Maps et al., 2012). Uses of

23   coupled physical-biological models in the context of understanding *C. finmarchicus* distribution and

24   abundance include identification of advective and life history factors determining biogeographical

1   boundaries (Ji et al., 2012), assessment of advection vs. local production in maintaining regional

2   abundance (Zakardjian et al., 2003; Speirs et al., 2006), investigation of sources of supply (Pepin et al.,

3   2013) and role of life history in scenarios of climate forcing (Maps et al., 2012). Variations of these

4   models will undoubtedly see application in future assessments of *C. finmarchicus* population

5   abundance in relation to ecosystem based management of fishery resources.

6

7   Compared with habitat suitability models, spatial dynamical models require extensive

8   computational resources, and can only be applied when demographical, physiological, and life traits of

9   species are well known. On the other hand, habitat modeling studies have often neglected dispersal

10   limitation and advection, even though they can play an important role in driving plankton spatial

11   distributions (Irigoien et al., 2011; Chust et al., 2013a, b). In line with taking a balanced view between

12   the importance of the role of dispersal limitation and of niche partitioning on zooplankton spatial

13   distributions (Irigoien et al., 2011, and Chust et al., 2013b), research efforts should focus on integrating

14   the two mechanisms in the modelling approach for zooplankton species, in the same way as has already

15   been done for fish and invertebrates (e.g. Cheung et al., 2009). Thus, a detailed dynamic approach to

16   understanding species distribution in relation to habitat can only be undertaken for species like *C.*

17   *finmarchicus* that are clearly of fundamental functional importance for the ecosystem, such that

18   resources can be devoted to acquiring the necessary data. As a direction of future research, a synthesis

19   of the two approaches, focusing on *C. finmarchicus*, might provide insight into the likely effects of

20   climate forcing on abundance and distribution of species in the North Atlantic. In order to obtain a

21   synoptic view of the zooplankton species community, coupling of simplified life history models to the

22   physical circulation and application of statistical habitat models is suggested.

23

24

1   *4.4 Summary, research needs and directions*

2   The great advancement in habitat suitability and life history and coupled physical-biological

3   modeling of *C. finmarchicus* populations over the past 10 years puts new demands for abundance and

4   environmental data and accurate and comprehensive parameterization of life history processes. Our

5   analysis of the combined distributional, demographic and physiological datasets has shown that the

6   best approach to model the distribution of *C. finmarchicus* requires a combination of different

7   approaches to monitoring data. While CPR data show the basin scale surface distribution of the

8   species, CPR coverage does not include the population centres in the Norwegian Sea or the Labrador

9   Sea; net sampling provides more targeted information on these important areas as well as on the

10   vertical distributions of *C. finmarchicus* populations. Vertical distribution data can be crucial in

11   identifying ambient temperatures for modelling purposes and for defining critical temperature ranges

12   within which the species may thrive or fail to survive. A more thorough analysis using net and CPR

13   data is recommended to explore this issue. We observed the highest population densities were within

14   the deep basins of the Labrador and Norwegian Seas and that locations not closely connected to these

15   deep basins by advection, had lower population densities (such as many North Sea sites). High winter

16   mortality in shallow water regions may be why these sites need replenishment from the deep basins.

17

18   Phenology associated with the *C. finmarchicus* life cycle was variable across the North Atlantic.

19   There was a 3.5 month difference in timing of the occurrence of the first generation, with the western

20   sites showing later occurrences relative to the spring phytoplankton bloom than the eastern sites. We

21   found that temperatures at which peak abundance occurred varied between 3 and 15 °C, with highest

22   population densities at about 13 °C. It is currently unclear whether the process models are able to

23   reflect these differences in timing and if they do not, we need to improve model parameterization.

24

1   Our analyses also yielded seasonal and spatial differences in stage specific mortality. Mortality

2   rates of young stages were particularly high in cold water areas, leading us to suggest significant

3   predation by the larger congeners, *C. hyperboreus* and *C. glacialis*, which are abundant in these areas

4   in spring. This hypothesis warrants a proper field investigation. In the population centres of *C.*

5   *finmarchicus* the major predators are other invertebrates (e.g. chaetognaths, euphausiids etc.),

6   mesopelagic and pelagic fish, and possibly adult females, the latter via cannibalistic feeding on their

7   own eggs and nauplii. We have cited several investigations where predation impact has been quantified

8   and related to the annual production of *C. finmarchicus*. Precise quantification of the impact of

9   predation on *C. finmarchicus* populations cannot be accomplished, however, until the population sizes

10   of the predators and prey are more accurately characterised. Due to short life spans and rapid and

11   spatially variable developmental rates of both prey and some of the predators, this cannot be solved by

12   more observations alone, but must involve the application of population dynamic models, preferably

13   with data assimilation capabilities. Representative sampling of predator stomachs and verification of

14   predation by other methods on a population scale is another largely neglected but challenging task,

15   given the complexity and costs involved. Studies on mortality during the overwintering period are also

16   needed in order to describe and understand the relative role of the physical environmental conditions

17   and different predator guilds (fishes, invertebrates) in controlling the survival success during this

18   portion of the life cycle in regions across the entire *C. finmarchicus* distribution range. Estimating

19   winter mortality in shelf areas is important in order to understand the drivers of population dynamics of

20   *C. finmarchicus* in these habitats and the importance of these overwintering populations to potential

21   predators that reside on the shelves and stay active during the winter.

22

23   There remain questions about the generality of parameterization of growth, reproduction and

24   diapause timing across the North Atlantic. Further detailed investigations of egg production rate

70

1   responses across regions are needed in order to resolve possible methodological sources for differences

2   between results obtained using females from either the northwest or the northeast Atlantic. The

3   hypothesis that apparent cross-basin differences in egg production and female body size are the

4   consequence of genetically differentiated physiological responses to habitat differences in food

5   conditions, temperature and light can be tested against the alternative: namely, that the observations

6   presented here are the consequences of differences in food and body size alone. Cross basin

7   experiments investigating growth, development and reproductive responses of *C. finmarchicus*

8   collected from both northwest and northeast Atlantic sites under identical experimental conditions

9   would provide insight, as would a careful cross-basin comparison of body size dry mass, carbon and

10   nitrogen relationships. Our quantitative understanding of timing of diapause entry and exit is still

11   rudimentary. Improved, long term and high frequency (i.e., semi-monthly to monthly) time series

12   sampling at a few selected sentinel sites for demographic analysis combined with biochemical (i.e.,

13   body mass, lipid content, RNA/DNA ratios: Wagner et al., 1998) and perhaps genetic indicators of

14   diapauses/active state would be useful for further testing of dormancy hypotheses.

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1   **Appendix: *Calanus finmarchicus* demographic patterns**

2

3   Descriptions of the data sets used to characterize demographic patterns across the North

4   Atlantic are summarized in Table 1. Here we provide detailed figures of seasonal patterns of abundance

5   by stage in relation to temperature and chlorophyll concentration at the sampling sites across the North

6   Atlantic analysed in the demographic, dormancy and mortality sections above (Figs. A1-A6). Details

7   on sampling depth of chlorophyll and temperature can be read from the axes labels.

Figure captions

Figure 1. (A) The northern North Atlantic Ocean, major warm and cold water currents and important seas. (B) Locations of demographic stations and transects listed in Table 1. (C) Locations of observations of *C. finmarchicus* egg production rates (and usually adult body size, chlorophyll a concentrations and temperature) analyzed in this study.

Figure 2. (A) Annual average sea surface temperature (SST: ^{o}C). (B) Annual average phytoplankton color index from Continuous Plankton Recorder data collected between 2000-2009.

Figure 3. (A) Surface layer average temperature (^{o}C) and (B) chlorophyll *a* biomass (mg m^{-2}) averaged over the surface 50 m in offshore and shelf habitats in the northeast (NE) and northwest (NW) Atlantic. See text for definition of different habitats. Values represent the mean ± standard error.

Figure 4. (A) Average (red horizontal line) 0-30 m integrated chlorophyll concentrations (mg m^{-2}) and (B) Surface layer (0-20 m) temperatures corresponding to regions across the North Atlantic where egg production rates were measured. Black horizontal line denotes median, vertical box boundaries show 25th and 75th percentiles, whiskers indicate 90th and 10th percentiles and filled circles 5th and 95th percentiles. The 0-30 m chlorophyll concentration for the NS in autumn was excluded because in autumn the females reside at 37 m (S. Jonasdottir).

Figure 5. Annual distribution and abundance of *Calanus finmarchicus* from Continuous Plankton Recorder data collected between 2000-2009.

Figure 6. Mean annual maximum number of sum of all *Calanus finmarchicus* copepodite stages, representing the highest abundance recorded for a single 14 day period during the year, at demographic stations in the North Atlantic (Table 1; Fig. 1B). If there is more than one year in the time series the value represents the mean of all years. Depth range for abundances is given inTable 1.

Figure 7. Average number of stage CV of *Calanus finmarchicus* from mid-October to end of February at demographic stations in the North Atlantic (Table 1; Fig. 1B). Error bars are standard errors. Note that in deep basin stations most CVs are below sampling depth and the figure cannot be used to compare deep ocean and shelf overwintering populations of *C. finmarchicus*.

Figure 8. Mean annual maximum number of sum of all copepodite stages of *Calanus finmarchicus* plotted against mean annual maximum temperature at the demographic stations in the North Atlantic (Table 1; Fig. 1B). Maximum annual temperature is the highest recorded surface layer temperature for a single 14 day period during the year. If there is more than one year in the time series this will be the mean of all years. Depth range for temperatures is given by axes labels in Appendix Figs. 1-6. Station at Foinaven excluded due to inclusion of the overwintering population by sampling to the bottom.

Figure 9. (A: upper panel) Timing of *Calanus finmarchicus* CI-CIII maximum plotted against maximum temperature (as calculated in Fig. 8), in 2-week intervals between April and mid-

August. Solid line: linear fit of time of maximum CI-CIII (Mcop) on temperature (T). Linear regression: Mcop = 18.03 − 0.70xT (R^2 = 0.56, P < 0.0001). Lower panel: Time of CI-CIII maximum versus time of chlorophyll maximum (Mchl) in 2-week intervals. Stippled line indicates 1:1 correspondence. Solid line shows linear regression of Mcop on Mchl: Mcop = 5.82 + 0.51xMchl (R^2 = 0.27, P = 0.03). Stations at the Labrador Slope, Labrador east, West Greenland, Siglunes, Langanes and Svinøy Arctic were excluded from linear regression analyses due to infrequent sampling.

Figure 10. Maps of the timing of dormancy exit (squares, upper panel) and entry (circles, lower panel) for *C. finmarchicus*. Symbol color represents day of year, with the color scale to the right of each panels. Data sources are described in Table 1 and in the text.

Figure 11. Regional averages, by season, of *C. finmarchicus* egg production rates, clutch sizes, spawning frequencies and female prosome (body) lengths. Clutch sizes and prosome lengths were determined using experimental (i.e. station) averages. Horizontal lines, boxes, whiskers and points as in Fig. 4.

Figure 12. Relationship between clutch size (CS) and female prosome length (PL) for all individuals from all seasons and all study regions of the North Atlantic (upper panel) and at two study regions, as examples, the Labrador Sea (LS, lower left panel) and the North Sea (NS, lower right panel). In all cases the line shows the clutch size upper limit for a given prosome length derived empirically by Jónasdóttir et al. (2005).

Figure 13. Relationship between integrated chlorophyll concentration and experimental average clutch size (left column) or between integrated chlorophyll concentration and spawning frequency (right column) at three exemplary study regions in the North Atlantic.

Figure 14. Relationship between spawning frequency and clutch size (left column) or spawning frequency and relative clutch size (right column) at two exemplary study regions in the North Atlantic. The lines are the linear regressions, calculated excluding points where SF = 100%.

Figure 15. Relationships between egg production rate and integrated chlorophyll concentration in the western study regions of the North Atlantic. Filled circles represent experiments carried out during spring: open circles show experiments carried out during other seasons. The curves show Ivlev functions fitted to the spring data, for which the parameters are given in Table 5. Experiments in the WGBB region were run for 24 h or longer (30-48 h). In all other regions experiments were run for 24 h.

Figure 16. Relationships between egg production rate and integrated chlorophyll concentration in the eastern study regions of the North Atlantic. Filled circles represent experiments carried out during spring: open circles show experiments carried out during other seasons. The curves show Ivlev functions fitted to the spring data, for which the parameters are given in Table 5. Experiments in all regions were run for 24 h.

Figure 17. (A) Stage-specific daily mortality rates and (B) proportion surviving through each stage pairs during population growth period of *C. finmarchicus* in offshore and shelf habitats

in the northeast (NE) and northwest (NW) Atlantic. See text for definition of different habitats. Values represent the mean ± standard error.

Figure 18. Stage-specific daily recruitment rate during population growth period of *C. finmarchicus* in offshore and shelf habitats in the northeast (NE) and northwest (NW) Atlantic. See text for definition of different habitats. Values represent the mean ± standard error.

Figure 19. Daily mortality rates in stage pair Egg-CI (A) and proportion surviving to CI (B) during the population growth period of *C. finmarchicus* in temperature habitats with high (black) or low (white) probable elevated abundance of *C. hyperboreus* and *C. glacialis*. See text for definition of different habitats. Values represent the mean ± standard error.

Figure 20. Stage-specific daily recruitment rate during population growth period of *C. finmarchicus* in thermal habitats <6$^{\mathrm{o}}$C (circles), 6-11 $^{\mathrm{o}}$C (squares), 11-16 $^{\mathrm{o}}$C (triangles) with high (black) or low (white) probable abundance of *C. hyperboreus* and *C. glacialis*. See text for definition of different habitats. Values represent the mean ± standard error.