SEVENTH FRAMEWORK PROGRAMME THEME 7 Environment

Collaborative project (Large-scale Integrating Project)

Project no: 246 933
Project Acronym: EURO-BASIN
Project title: European Basin-scale Analysis, Synthesis and Integration

**Deliverable 3.4 Map the distribution of key biogeo-chemical groups in parallel with trophodynamic studies: related to food web interactions**

Contributors: Webjoern Melle (IMR), C. Castellani (SAHFOS), P. Licandro (SAHFOS), C. Broms (IMR)

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Start date of project: 31.12.2010    Duration: 48 months
Project Coordinator: Michael St John, DTU Aqua

Project co-funded by the European Commission within the Seventh Framework Programme,
Theme 6 Environment

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**Executive Summary:**

Critical for understanding the population dynamics of key ecosystem players is determining the habitats that contribute to the maintenance of their populations during ontogeny. In order to develop a predictive understanding of the development of these populations in the future Task 3.2 have during field programmes and collation of historic data identified the habitats utilized by key biogeochemical and ecosystem players. Future projections of the occurrence of these habitats will be performed in WP 6 enabling the potential dynamics of these species to be assessed in WP8. Activities have included dedicated cruises as well as cruises of opportunity where EURO-BASIN partners and collaborators have modified existing programmes and contributed data from local ongoing activities in order to provide key species distributional data.

This report summarises the biogeography of the key species; *Calanus finmarchicus*, *C. helgolandicus*, *C. hyperboreus*, *Oithona* spp. *Pseudocalanus* spp., *Thecosomata*, *Euphausia* and *Cnidaria* in the North Atlantic based on CPR data (this is a contribution from SAHFOS). In addition the work with the WP3 special issue article has made available to us an extensive distributional and demographic data set on *C. finmarchicus*, combining data from Canadian, European and US sources. Biogeography of key species are presented as distributional maps including SST, Colour Index, area and site temperatures and chlorophyll. Euro-Basin partners IMR and MRI-HAFRO contributed with time series data on *C. finmarchicus*. In addition *C. finmarchicus* data have been obtained from US and Canadian collaborators, historic European data sets as well as the sub-contractor at the Faroes. The *C. finmarchicus* data set has been analysed and described in the manuscript to the Special Issue of Progress in Oceanography entitled “The North Atlantic Ocean as habitat for *Calanus finmarchicus*: environmental factors and life history traits”, lead by IMR (Melle et al submitted). The analyses and writing have been performed with authors coming from both sides of the Atlantic. Data from more than 20 time series sites across the North Atlantic was collated and analyzed with respect to total abundance, phenology, mortality and dormancy initiation and end. Measurements of egg production and female size with accompanying temperature and chlorophyll data across the northern North Atlantic were compiled and analysed, however, that is not part of the present deliverable report.

The main conclusions are:

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 found with its congeners, *C. glacialis* and/or *C. hyperboreus*. The maps show the distribution of key species.

**Relevance to the project & potential policy impact:**

Deliverable 3.4 will provide information to tasks T2.1, T2.5, T4.3, T5.3, and key species distributions in selected habitats of the North Atlantic to T7.2, as well as to WP8 Ocean Management. The biogeography outlined for the basin on past and present data will be used for model validation in T6.3.5.

**Access to Data (where relevant):**
The raw data discussed is archived in www.pangaea.de and published as a peer-reviewed data publication in *Earth System Science Data Journal*, via Task T3.1 Retrospective analysis of the spatial distribution of key species (gritted CPR data).
Report:

Map the distribution of key biogeo-chemical groups in parallel with trophodynamic studies: related to food web interactions

Webjørn Melle¹, Claudia Castellani², Priscilla Licandro², Cecilie Broms¹, and all co-authors of Melle et al. submitted.

¹ IMR (Norway)
² SAHFOS (United Kingdom)

1. Introduction

As habitat for zooplankton, the northern North Atlantic Ocean is characterized by its circulation and water mass distribution, its topography, its extensive latitudinal expanse (from roughly 40 to more than 70°N) and its seasonally and geographically varying wide ranges of temperature, salinity and light. These physical features lead in turn to regional differences in the timing and intensity of the annual cycles of primary production, and in the distributions, abundances and seasonal cycles of planktonic and nektonic predators.

The distribution of any zooplankton species in the North Atlantic is a manifestation of its ability to maintain itself within this range of conditions, from suboptimal to optimal, that constitute its habitat. One approach to determining 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 liner models (GLM) and geographic information systems (GIS) have been applied to quantify species distributions, for example 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 behavioral responses and dispersal patterns. This information can be integrated into complex process models (e.g. Korzukhin et al., 1996), in the marine realm by means of coupled physical-biological modeling (e.g. de Young et al., 2010).

In the present report we present recent spatial distribution patterns, based on Continuous Plankton Recorder observations (Beaugrand, 2004) for key meso- and macrozooplankton taxa in the northern North Atlantic Ocean. A full listing of zooplankton species diversity from CPR samples is provided by the Continuous Plankton Recorder Survey Team (2004). The
key zooplankton taxa considered here are the copepods *Calanus finmarchicus*, *C. helgolandicus*, *C. hyperboreus*, *Pseudocalanus* spp. and *Oithona* spp, the gastropod *Thecosomata* species, the euphausid species, and the gelatinous zooplankton in the phylum Cnidaria. These taxa are representative of the most important multicellular zooplankton groups in the northern North Atlantic based on their abundance and on the roles they play within food webs and biogeochemical cycles. We discuss how these patterns are the result of very different physiological, life history and ecological characteristics for each taxon.

We then focus on perhaps the most ecologically significant, and certainly the most-studied, of all of the zooplankton species in the North Atlantic, the copepod *Calanus finmarchicus*. *C. finmarchicus* is the subject of over 1000 research articles since the revised edition of Marshall and Orr’s book (1972) and it has been the target species of several previous basin-scale research programs, including Investigations of *C. finmarchicus* migrations between oceanic and shelf seas off Northwest Europe (ICOS: e.g. Heath et al., 1999), Trans-Atlantic Studies of *Calanus finmarchicus* (TASC: e.g. Tande and Miller, 2000) and the Global Ocean Ecosystem Dynamics program (GLOBEC: e.g. Gifford et al., 2010), as well as the ongoing EURO-BASIN program. We provide a synthesis of *C. finmarchicus* distribution across its North Atlantic habitat based on net data collected at more than 20 sites, provided by Canadian, European and US collaborators (Melle et al. submitted).

### 2. Material and Methods

#### 2.1. Hydrography and chlorophyll measurements and analyses

CTD probes were used to collect hydrographic data (temperature and salinity) at all sampling stations (Fig 1b, c). Water samples for measurements of chlorophyll-a concentration were collected using water bottles on a rosette on the CTD or on a hydro-wire. At most sites the hydrographic and chlorophyll samples were taken in concert with the zooplankton net samples. CTD profiling depths and water bottle depths varied among sampling sites. Temperatures (°C) were averaged over various depth ranges, while chlorophyll concentrations were either integrated (mg m⁻²) or averaged (mg m⁻³) over various depth ranges.

The basin scale distribution of Sea Surface Temperature (SST, °C) was calculated from data available from the British Atmospheric Data Centre (BADC); [HadISST 1.1 dataset (http://badc.nerc.ac.uk/home/)]. Monthly SST records (1 degree by 1 degree) or the years 2000-2009 were firstly averaged by year and then used to produce the overall average SST map for the period of reference.

#### 2.2. Mapping of key species

The CPR survey is an upper layer plankton monitoring program that has regularly collected samples, at monthly intervals, in the North Atlantic and adjacent seas since 1946 (Warner and Hays, 1994). Water from approximately 6 m depth (Batten et al., 2003a) enters the CPR through a small aperture at the front of the sampler and travels down a tunnel where it passes through a silk filtering mesh of 270 μm before exiting at the back of the CPR. The plankton
filtered on the silk is analyzed in sections corresponding to 10 nautical miles (approx. 3 m$^3$ of seawater filtered) and the plankton microscopically identified (Jonas et al., 2004). In the present study we used the CPR data to investigate the current basin scale distribution of *C. finmarchicus* (CV-CVI), *C. helgolandicus* (CV-CVI), *C. hyperboreus* (CV-CVI), *Pseudocalanus* spp. (CVI), *Oithona* spp. (CI-CVI), total euphausiida, total pteropoda and the presence/absence of Cnidaria. Monthly data collected between 2000 and 2009 were gridded using the inverse-distance interpolation method (Isaaks and Srivastava, 1989), in which the interpolated values were the nodes of a 2 degree by 2 degree grid. The resulting twelve monthly matrices were then averaged within the year and the data log-transformed (i.e. log$_{10}$ ($x+1$)). The Phytoplankton Colour Index (PCI), which is a visual assessment of the greenness of the silk, is used as an indicator of the distribution of total phytoplankton biomass across the Atlantic basin (Batten et al., 2003b; Richardson et al., 2006).

### 2.3. Distribution of *Calanus finmarchicus* based on net data

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 generally more easily accessed coastal sites were visited more frequently than the offshore sites. An overview of sampling sites characteristics, sampling gear and methods is provided in Table 1. Abundance data of *C. finmarchicus* by developmental stages were averaged over 14 days periods within years and then over years within the same periods. Sampling depths were usually 200, 100 or 50m (Table 1). No corrections were attempted with regard to differences in sampling depth. We comment, though, on extreme values possibly related to sampling depth throughout the report.
Table 1. Metadata for *Calanus finmarchicus* sampling stations and transects in the North Atlantic analyzed in this study. *C. finmarchicus* abundances together with temperature and chlorophyll including details on units and sampling depths are shown in Appendix figures A1-A6.

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<th>Sampling site</th>
<th>Site no.</th>
<th>Location</th>
<th>Latitude</th>
<th>Longitude</th>
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<th>Water mass</th>
<th>Shelf/Slope /Oceanic</th>
<th>Max. sampling depth (m)</th>
<th>Gear</th>
<th>Mesh size (µm)</th>
<th>Years</th>
<th>No. Stations</th>
<th>Analyses**</th>
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<td>-</td>
<td>-</td>
<td>Coastal/Atlantic</td>
<td>Shelf</td>
<td>Btm. or 1000</td>
<td>0.75-m Ring net</td>
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<td>1999-2009</td>
<td>108</td>
<td>M</td>
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* Number of stations out of a total of 17, based on watermass distribution

** M= Mortality, D= Dormancy, S= Seasonal dynamics
3. Results

3.1. Basin scale habitat characteristics: hydrography and chlorophyll

The 15°C surface isotherm, from approximately 40° latitude (south of Long Island, New York) in the west and at about 47° latitude in the east (south of Brittany, France), delimits the southern edge of the northern North Atlantic (Fig. 2a). The coldest surface temperatures occur in the Labrador Sea and off the east coast of Greenland. The 11-15 °C annual average surface temperature occurs in a narrow band between southern New England and Long Island in the west, expanding in the drift path of the Gulf Stream, to include a large area of the deep North Atlantic basin south of Iceland, the North Sea, and coastal shelves of Great Britain.

The annual phytoplankton colour index (Fig. 2b), a relative index of phytoplankton biomass as sampled by the silk mesh in the CPR, shows no obvious correspondence with the annual pattern of sea surface temperature in the northern North Atlantic. Instead, it indicates that the areas of highest phytoplankton biomass occur at the shelf margins, including the Gulf of Maine, Grand Banks, North Sea and the shelf north and west of the British Isles. Higher phytoplankton biomass is also indicated in Denmark Strait. In general, surface phytoplankton biomass is lower in the deep, central North Atlantic basin, with the exception of the deep water south of Iceland.

Phytoplankton data from the *Calanus* time series sampling stations generally corroborate the annual patterns of phytoplankton abundance shown in the CPR data, although they indicate that phytoplankton biomass is lower in the northeast Atlantic than in the northwest, except in the northern Norwegian Sea (Fig. 3). Surface layer temperatures were significantly higher in the northeast Atlantic than the northwest (Mann-Whitney test, p<0.0001), but similar in offshore and shelf habitats within the northeast and northwest Atlantic habitats (Mann-Whitney test, p>0.05). On the other hand, chlorophyll a biomass was greater in both offshore and shelf habitats in the northwest Atlantic (Kruskal-Wallis test, p<0.0001).

3.2. Distributions of key species

Spatial distributions of the log-transformed mean annual abundance (and presence/absence for the Cnidaria) of the selected taxa between 2000 and 2009 show notable differences among the different taxa (Figs. 4-11). The abundance of *C. finmarchicus* is highest in the western part of the Atlantic basin particularly off the Scotian Shelf, the Labrador Sea, south of Greenland and in the Irminger Basin, whereas it appears to be less abundant in the eastern Atlantic where it is restricted mainly to northern regions (Fig. 4). In contrast, *C. helgolandicus*, the warm-temperate congener of *C. finmarchicus*, is mainly found in shelf regions around the British Isles, particularly in southern areas of the eastern Atlantic and the North Sea (Fig. 5). The arctic congener, *C. hyperboreus*, is found at lower concentrations and appears to be more abundant off Newfoundland, in the southern Labrador Sea and in the Irminger Basin (Fig. 6). The very common, small cyclopoid copepod genus *Oithona* spp. has a wide basin scale distribution with highest concentrations south of Iceland, in the Irminger Basin and in the Grand Banks region off Newfoundland (Fig. 7). The small copepod species *Pseudocalanus* spp. is mainly found in shelf areas in both the eastern and western Atlantic (Fig. 8) where it is
typically among the three most common copepod taxa, along with *C. finmarchicus* and *Oithona spp*. The Thecosomata (pteropods with calcified skeletons) also show a wide scale basin distribution, although this group of taxa appears to be more abundant in the shelf regions around the British Isle and the northern North Sea, the Irminger basin and south of Greenland (Fig. 9). Euphausiida are more abundantly distributed in the northern part of the basin south of Iceland, the Irminger Basin, the Labrador Sea and off Newfoundland (Fig. 10). The presence of Cnidaria is recorded most often in the Irminger Basin, off Ireland and in the southern and eastern parts of the North Atlantic basin (Fig. 11).

Two indices of abundance at the study sites across the North Atlantic were calculated. The annual mean of the maximum abundance of all copepodite stages combined (Figs. 12, 13) was highest (135-265 x 10^3 m^-2) at the southern and eastern Norwegian Sea, southern Iceland shelf and eastern Labrador Sea stations. Differences in abundance could not be simply explained by location on shelves or over deep ocean basins. The relatively high abundance observed at Foinaven is likely due to the fact that here sampling was down to the bottom (500 m), where dormant and vertically migrating copepodites would have been captured. The autumn and winter mean annual maximum abundance of stage CV (Fig. 14) shows much higher abundances (on average 10-30 x 10^3 m^-2) along the western North Atlantic shelves and at a Norwegian fjord station. Abundances in Wilkinson Basin in the Gulf of Maine are notably higher than at any other shelf site and are similar to abundances of stage CV found at depth in the Norwegian and Irminger Seas (Heath et al., 2004). These high shelf abundances represent overwintering stage CVs in areas where the sea is deep enough to allow overwintering to occur. Other sites in the central and eastern Atlantic are either too shallow (e.g. Arendal, Stonehaven) for overwintering, or are very deep (e.g. Station Mike), in which case the overwintering stage CVs were deeper than the depths sampled at sites used in this study. Data from the overwintering period in the Labrador Sea are not shown here, but there individuals would have been at depths greater than 0-100 m, which is the depth range that was used for the Labrador Sea data presented here (Head and Pepin, 2008; Head et al. 2013b).

Maximum abundances of *Calanus finmarchicus* showed a positive relationship with the annual maximum temperature in the surface layer (Fig. 15). Maximum temperature may represent habitat suitability if there is an upper temperature limit above which population growth, reproduction or survival are hampered. Abundances of *C. finmarchicus* peaked where maximum temperatures were around 12-13 °C (Fig. 15). Abundances were both high and low at higher maximum temperatures and invariably low at lower maximum temperatures. If the very near shore and shallow stations of the North Sea and Faroes are excluded, the maximum abundance of *C. finmarchicus* increased exponentially for all maximum temperatures measured at the sites included here.

4. Discussion

4.1. Taxon specific traits and the distribution of zooplankton in the North Atlantic habitat

The ocean circulation system and its associated water mass characteristics exert important influences on the distribution and ecology of zooplankton, but the dramatic differences in abundance and distribution that we have shown for the representative key
species suggest that distribution patterns are also influenced by differences in physiology, life history and ecological characteristics.

The mean annual distribution of *C. finmarchicus* at surface based on CPR measurements is mainly restricted to the northern and western North Atlantic within an area delimited between the 5°C and 10°C annually-averaged sea surface isotherms (Fig. 4), in agreement with previous reports of a mean annual maximal abundance at SST between 5-10°C, and critical SST boundaries of 9 and 12°C (Beaugrand et al., 2008; Helaouët and Beaugrand, 2009). Overall, *C. finmarchicus* is more abundant in the northwest Atlantic, which is cooler and where the average chlorophyll standing stock is greater than in the northeast Atlantic (see also Longhurst, 1998; Helaouët and Beaugrand, 2009, Helaouët et al., 2011). However, in the present paper we also show net data from the northeast Atlantic, north of the CPR routes, proving *C. finmarchicus* to be at least equally abundant in cold northeastern areas. In contrast, the congeneric species *C. helgolandicus* is restricted to northeastern Atlantic shelf waters and is absent from the northwest Atlantic (Fig. 5). *C. helgolandicus* is generally associated with warmer and more saline surface waters (Helaouët and Beaugrand, 2007). Differences in the spatial and temporal distribution of these two morphologically very similar sibling species are attributable to differences in their ecological niches. For instance, a recent study has shown that *C. finmarchicus* develops faster than *C. helgolandicus* at temperatures <11°C and slower at higher temperatures (Møller et al., 2012). *C. helgolandicus* is found year-round, since it supposedly does not exhibit diapause behaviour in the northeast Atlantic (but see Hirche, 1983 and Bonnet et al., 2005), unlike *C. finmarchicus*. Consistent with these observations, there are differences in the timing of the population maxima between the species, with *C. helgolandicus* usually peaking in the warmer conditions of late summer-autumn and *C. finmarchicus*, in the cooler conditions of spring (Planque and Fromentin, 1996). In addition, the limited presence of *C. helgolandicus* in oceanic areas of the North Atlantic compared to *C. finmarchicus* may be due to its lower capacity to store lipid (Lee et al., 2006), and thus its inability to endure prolonged periods without food. Despite the temporal and spatial differences in their distributions these two species do co-occur, showing that they co-exist under some conditions.

The distribution of the largest *Calanus* species, *C. hyperboreus*, in the North Atlantic is mainly associated with the arctic water outflows that are found around Greenland and on the Newfoundland Shelf and in the outflow from the Gulf of St Lawrence on to the inshore region of the Scotian Shelf (cf Figs 1 and 6). *C. hyperboreus*, which may experience recruitment failure in relatively warm Atlantic waters (Broms et al., 2009) became more abundant on the Newfoundland shelf in the 1990s than in previous decades, likely due to an increased contribution of Arctic water (Head and Sameoto, 2007; Head and Pepin, 2010; Licandro et al., 2011).

The capacity to store lipid is considered to be an important adaptation for a species to enable it to cope with periods of food scarcity, for example through advection between food-rich shelf regions in spring and summer and food-limited open ocean areas in winter, where it overwinters at depth, relatively safe from predation. Compared with the distributions of the *Calanus* spp. that store large lipid reserves, the distributions of the smaller copepod species with limited or no lipid storage capacity, are usually more restricted to coastal and shelf areas. Some species, such as *Pseudocalanus* spp. and *Oithona* spp., store small lipid droplets that may confer a survival advantage compared to
other copepod species of similar size. Interestingly, *Pseudocalanus* spp. and *Oithona* spp. show very different spatial distributions. *Pseudocalanus* spp. is mainly found on the shelf areas around the British Isles and off the US coast. By contrast, *Oithona* spp. is found throughout the entire North Atlantic basin (Fig. 7 and Fig. 8). It has been suggested that the higher abundance and broader distribution of *Oithona* spp. may be result from its capacity to feed on the microbial food-web (*i.e.* omnivorously), its ability to minimise energy losses through its hop and sink swimming behaviour (Nielsen and Sabatini 1996, Castellani et al., 2005a and b), and its relatively low natural mortality rate (Eiane and Ohman, 2004). Indeed, the distribution of *Oithona* spp. shows no strong correspondence with that of phytoplankton (Fig. 8), as it can reach high concentrations offshore and over the shelf at all latitudes. In contrast, *Pseudocalanus* spp. is mainly an omnivorous filter feeder species that uses continuous swimming activity to capture its prey. Hence, this species is probably more dependent on having an abundant food supply than *Oithona* spp. and, in addition, it probably experiences higher predation rates, due to the stronger hydrodynamic signal it generates during swimming (Eiane and Ohman, 2004). These physiological and behavioural adaptations would allow *Oithona* spp to colonise open ocean areas more successfully than *Pseudocalanus* spp. and many other small copepod species.

The Thecosomata species (pteropods with calcified shells) play an important role not only within food-webs but also in the cycling of carbon and carbonate. Several species are also indicators of different water masses. In the North Atlantic these taxa are mainly concentrated on the northwest Atlantic deep water region and on the shelf of the British Isles (Fig. 9). In the northwest Atlantic the surface distribution of the Thecosomata may be limited at their southern boundary by the North Atlantic Current (NAC). Since the Thecosomata represent a species complex, interpretation of the distribution pattern will require an in-depth analysis at the individual species level.

Euphausid species are important members of the plankton community of the North Atlantic since they can account for a large proportion of the total zooplankton biomass and of the diet of many animals including fish, whales and birds (Falk et al., 1992; Dalpadado et al., 2000). Euphausids in the surface layer were most abundant in the northwest and central North Atlantic, particularly south of Greenland, south of Iceland and off the Labrador coast (Fig. 10). Euphausid standing stock appears to increase at high subarctic latitudes in colder and more productive waters, with approximately eight species making up the bulk of the biomass (Mauchline and Fisher, 1969; Lindley, 1982a). In the late 1960s Lindley (1982 a and b) investigated the distribution, population dynamics and production of the most important euphausid species based on CPR samples collected over the entire North Atlantic. A reanalysis of the most recent CPR data would be useful to investigate whether changes in hydrography that have occurred in the North Atlantic over the last two decades have affected the distribution and diversity of the euphausiid populations. There have, however, been more recent investigations of the biogeography and distribution of euphausiids along the Mid-Atlantic Ridge (Letessier et al., 2011) and in the northwest Atlantic (Endo and Wiebe, 2007). Overall, euphausiids have complex, species specific life cycles, physiology and behavioural patterns. In their review Mauchline and Fisher (1969) have reported that temperature represents one of the main determinants of euphausid species distributions, but more work is required to define the ecological niches of the different species.
In this study the Cnidaria in the surface water were particularly abundant off the Irish shelf, in the Irminger Sea and in warm oceanic waters south of 45°N (Fig. 11). Interestingly, recent studies have shown that the frequency of Cnidaria in these areas has increased over the last decade (Gibbons and Richardson, 2009; Licandro et al., 2010). Moreover, blooms of jellyfish off the northwest European shelf have become unusually persistent during winter months, with the outbreaks corresponding with a northward spread of the warm water North Atlantic Current (NAC) from mid-temperate latitudes into the northeast Atlantic (Licandro et al., 2010). Climate change scenarios suggest that the North Atlantic will continue to warm, and it seems likely that this will lead to more frequent jellyfish blooms in coastal seas where food resources are abundant. At present the distribution and diversity of the jellyfish communities in the North Atlantic are still understudied, as are the biological mechanisms controlling their population dynamics. Nevertheless, it is thought that rising temperatures, within species-specific thermal preferences, may have a positive influence on jellyfish reproduction, leading to very rapid increases in their abundance (i.e. blooms) and, perhaps, on wintertime survival rates (Boero et al., 2008).

4.2. Abundance, distribution and life history characteristics of Calanus finmarchicus across its North Atlantic habitat

The data we have compiled here represent considerable multinational effort spanning several decades. Much progress has been made in understanding *C. finmarchicus* life histories and the underlying processes needed to model its population dynamics in the context of developing climate change scenarios for the North Atlantic. The ocean circulation system and its associated water mass characteristics exert important influences on the distribution of *C. finmarchicus*, but distribution patterns are also influenced by regional differences in physiology, life history and ecological characteristics. Our analysis and synthesis of the assembled datasets focuses on regional similarities and differences between the northwest and northeast Atlantic with respect to processes determining the distributions and abundances of shelf and basin *C. finmarchicus* populations and life history in relation to environmental variables.

The mean annual distribution of *C. finmarchicus* in the near surface layer, based on CPR measurements alone, is mainly restricted to the northern and western North Atlantic within an area delimited between the 5°C and 10°C annually-averaged sea surface isotherms (Fig. 4), in agreement with previous reports of mean annual maximal abundances at SSTs of between 5 and 10°C, and critical SST boundaries of 9 and 12°C (Beaugrand et al., 2008; Helaouët and Beaugrand, 2009). Overall, CPR data show that *C. finmarchicus* is more abundant in the northwest Atlantic, which is cooler and where the average chlorophyll standing stock is greater, than in the northeast Atlantic (see also Longhurst, 1998; Helaouët and Beaugrand, 2009; Helaouët et al., 2011). However, the results (presented here as well as previously published observations), based on net data that includes the population epicentres within the subpolar-gyres of the Norwegian and Labrador Seas (Heath et al., 2000a; 2004; 2008; Head et al., 2003; Melle et al., 2004) indicate that the highest *C. finmarchicus* abundances are found north of the CPR routes. This supports the idea that maximum *C. finmarchicus* abundances are found in the deep basins of these seas (Figs. 12, 13) or close to them. In the warm northeast Atlantic particularly, this changes our view of *C. finmarchicus* distribution compared to the perspective from CPR data alone. For this reason, since 2008, the spatial coverage of CPR monitoring has been expanded to cover the core areas of *C. finmarchicus* distribution in the Norwegian Sea. We analysed temperature measurements from the
vertical domain of *C. finmarchicus* during the productive season and calculated mean maximum temperatures for the sampling sites (Fig. 15). Net data show that maximum abundances of *C. finmarchicus* in the core area of its distribution occur at sites with maximum temperatures between 11 °C and 13 °C. This is slightly higher than previously reported values (Beaugrand et al., 2008; Helaouët and Beaugrand, 2009). To define the temperatures ranges that are presently occupied and those that are critical (*i.e.* beyond which *C. finmarchicus* is absent), further analysis that includes net collected data across the species distributional range is needed. Thus we conclude that habitat and population dynamics modeling in the future should include data sets obtained from CPR and net hauls, which complement each other in terms of sampling coverage.

The major overwintering areas for *Calanus finmarchicus* in the North Atlantic are the southern Norwegian Sea and the Irminger/Labrador Sea Sub-polar Gyre (Heath et al., 2004). The 24 net sampling sites included here in the analyses of demography and phenology are located at various distances from these two major overwintering epicentres (Table 1, Fig. 1b). Proximity to an overwintering centre has been suggested to be the main prerequisite for high abundance of *C. finmarchicus* (*e.g.* Heath et al., 2000a, 2008; Speirs et al., 2004; Torgersen and Huse, 2005; Head et al., 2013b) and to a large extent our observations are consistent with this notion, as the seven sites with highest abundances are located within or close to the two major overwintering basins (Figs. 12, 13). Station Mike and the Svinøy section Atlantic and Arctic water regions are situated within the gyre of the southern Norwegian Sea. The Svinøy coastal region is located on the Norwegian Shelf, on the eastern rim of the southern Norwegian Sea deep basin, and coupled life-history/circulation models have demonstrated that *C. finmarchicus* can be recruited to the shelf population from the gyre population to the west (Speirs et al. 2004; Samuelsen et al. 2009). Similarly, the Westmannaey site on the southern Icelandic shelf and the West Greenland shelf site on the southwestern Greenland shelf are situated close to the Irminger/Labrador Seas Gyre, while the Eastern Labrador Sea site is within the gyre. The overwintering female population at the central Labrador Sea site, also located within this gyre, is very abundant prior to spawning but here the number of first generation copepodites is very low, indicating high mortality during development and low local recruitment (Head et al., in prep).

Among sites differences in population abundances can be due to unevenly distributed predation pressure. In the Norwegian Sea a range of different predators have been identified and both direct and circumstantial evidence of predation have been given. Predation from herring on copepods which were mainly *C. finmarchicus*, was estimated to be similar to the annual production of the prey (Dommasnes et al. 2000, Skjoldal et al. 2004) estimated pelagic fish predation on *Calanus* to be ~30% of annual production, Utne et al. (2012) using ecosystem model simulations estimated predation from pelagic fish stocks at 35 mill tonnes, or 18% of the annual *C. finmarchicus* production (Hjollo et al. 2012). It has also been found that *C. finmarchicus* stock size is negatively correlated to total pelagic fish stock size the previous year in the Norwegian Sea (Olsen et al. 2007, Huse et al. 2012), suggesting top down controls at a large scale. Additionally, predation from macroplankton predators and mesopelagic fishes may greatly exceed predation from the pelagic fish stock (Skjoldal et al. 2004). In fact, when summing assumed consumption of *C. finmarchicus* by all the predators the total predation loss tends to be much larger than the *C. finmarchicus* production in the Norwegian Sea, strongly suggesting that...
Predation is the terminal cause of mortality there and that new estimates on production and consumption are needed. We do not have similar information on *C. finmarchicus* predators in the other deep basins, but the presence of large pelagic fish stocks in the Norwegian Sea is one clear difference in the predatory communities between the two major overwintering deep basins in the Norwegian Sea and the Labrador/Irminger Seas. However, even though *C. finmarchicus* may be more heavily grazed in the Norwegian Sea, this is also the basin with the highest *C. finmarchicus* abundance. Therefore, we hypothesize that the Labrador and Irminger Sea possess predatory stocks made up of macrozooplankton and mesopelagic fishes that inflict considerable predation pressure on *C. finmarchicus*.

Predation on the overwintering population is another source of mortality that needs further investigation, although data from the two major overwintering basins, the southern Norwegian Sea and the Labrador Sea, indicate that mortality during overwintering is low and less variable than during the active phase (Head et al., in prep; Melle et al., in prep). Still, losses of almost the entire population from the Norwegian shelf during winter indicate that predatory or advective losses during winter may be substantial in shallower regions (Slagstad and Tande 1996, Melle et al. 2004).

Predation may shape the population distribution in the regions of marginal *C. finmarchicus* productivity such as the sites with low temperature or with a mismatch to the bloom. Our mortality rate calculations suggest high predation pressure on eggs and nauplii, which we suggest is by the suspension feeders, *C. hyperboreus* and *C. glacialis* (in addition to cannibalism by *C. finmarchicus* CVII). This occurs because *C. hyperboreus* and *C. glacialis* have multi-year life cycles and therefore are present as copepodite stages early in the spring bloom, when *C. finmarchicus* reproduction is starting (Conover, 1988). Thus, during the late spring-early summer period, recruitment of *C. finmarchicus* is suppressed and there is a delay in the timing of maximum CI-CIII abundance until well after the bloom (Section 3.6, Figs. 19, 20). This interaction with arctic congeners should be more prominent at sites where CI-CIII recruits peak several weeks after the bloom, such as at the Anticosti Gyre, Gaspé Current, Station 27 and Labrador Shelf sites. One exception is the lower St. Lawrence estuary (RIM) where the bloom is delayed relative to the adjacent Anticosti Gyre due to freshwater runoff, so that it co-occurs with the relatively late CI-III peak (Fig. 9). Surface layer temperatures in cold (3°C mean) and warmer habitats (10°C mean) during the population growth period should result in development times from egg to N6 of 30 and 15 days respectively, representing only a two week difference (Campbell et al., 2001). Therefore, differences in temperature alone cannot explain the long delays (up to 3.5 months) observed between the timing of maximum in CI-CIII abundance and the bloom at the cold water sites, but which is consistent with our suggestion of predation by the arctic *Calanus* species.

The demographic pattern observed in the central Labrador Sea is similar to the spatial demography observed within the central Irminger Basin, for which sources of overwintering copepodites are hypothesized to be recruitment along the eastern and northern margins and subsurface horizontal transport from the east Greenland slope and Labrador Sea (Heath et al., 2008). Recruitment failure in the central Irminger Basin, likely due to high predation mortality in the early life stages and/or starvation of the first feeding nauplii at persistently low food conditions, is hypothesized to preclude direct descent as a major source of overwintering stage CV (Heath et al., 2008). In the central Labrador Sea,
food (i.e. phytoplankton) concentrations and egg production rates are higher (e.g. Fig. 15) than in the Irminger Basin, and early life stage mortality due to cannibalism by adult *C. finmarchicus* and predation by *C. hyperboreus* and other as yet unrecognised predators (Head et al., 2003; Head et al., in prep.) may be more important sources of recruitment failure.

The deep basin populations appear to be the main sources of supply of *C. finmarchicus* overwintering stages to the central and northeastern North Atlantic shelf populations. On-shelf transport from the Norwegian Basin of overwintered adults prior to mid-summer and early life stages later in the year is the primary source of *C. finmarchicus* to the relatively narrow Norwegian shelf (Samuelson et al., 2009). Field and modelling studies (e.g. Heath et al., 1999; Harms et al., 2000) support the hypothesis that the population of *C. finmarchicus* in the North Sea is sustained by annual spring advection of late-stage individuals originating from high concentrations of stage CVs overwintering in the deep Atlantic and Norwegian Sea, particularly the Faroe-Shetland Channel (Heath et al., 1999). In the North Sea, the maximum abundance of *C. finmarchicus* is low (on the order of 5 x 10³ ind. m⁻²: Heath et al., 2000a; Jónasdóttir and Koski, 2011), despite relatively high egg production rates (Jónasdóttir and Koski, 2011; Fig. 16). The primary factor controlling abundance in the North Sea appears to be predation mortality during the early life stages (Jónasdóttir and Koski, 2011), which probably also holds for the older stages, which cannot migrate vertically far enough to avoid predation, because of the relatively shallow bathymetry.

Other time series sites are farther from the deep basin epicentres or have lesser degrees of direct advective connection, which limits repopulation from the deep ocean overwintering sites by members of the overwintering or first generations. The Arendal and the two northern Icelandic sites have long transport routes from their nearest overwintering areas, the Norwegian Sea and the deep basins south of Iceland (Gislason and Astthorsson, 1998; Heath et al., 2000b; Astthorsson and Gislason, 2003; See Appendix and Fig. 1b), and the Faroese Shelf site is located behind a strong tidal front, within an anticyclonic shelf gyre that results in a short retention time and increased dispersal of shelf plankton 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 10³ 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-sustained (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.

5. Conclusions

Our analysis of the combined distributional, demographic and physiological datasets has shown that the best approach to model the distribution of *C. finmarchicus* requires a combination of different approaches to monitoring data. While CPR data show the basin scale surface distribution of the species, CPR coverage does not include the population centres in the Norwegian Sea or the Labrador Sea; net sampling provides more targeted information on these important areas as well as on the vertical distributions of *C. finmarchicus* populations. Vertical distribution data can be crucial in identifying ambient temperatures for modeling purposes and for defining critical temperature ranges within which the species may thrive or fail to survive. A more thorough analysis using net and CPR data is recommended to explore this issue. We observed the highest population densities were within the deep basins of the Labrador and Norwegian Seas and that locations not closely connected to these deep basins by advection, had lower population densities (such as many North Sea sites). High winter mortality in shallow water regions may be why these sites need replenishment from the deep basins.

References:


Head, E.J.H., Gentleman, W.C., Harris, L.R., Ringuette, M. (In prep.) Stage-specific mortality rates for Calanus finmarchicus in the Labrador Sea


Figures:

Figure 1. (A; upper panel) The northern North Atlantic Ocean, major warm and cold water currents and important seas. (B; lower panel) Locations of demographic stations and transects listed in Table 1.
Figure 2. (A; upper panel) Annual average sea surface temperature (SST: °C). (B; lower panel) Annual average phytoplankton color index from Continuous Plankton Recorder data collected between 2000-2009.
Figure 3. (A) Surface layer average temperature (°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. Annual distribution and abundance of *Calanus finmarchicus* from Continuous Plankton Recorder data collected between 2000-2009.

Figure 5. Annual distribution and abundance of *Calanus helgolandicus* from Continuous Plankton Recorder data collected between 2000-2009.
**Figure 6.** Annual distribution and abundance of *Calanus hyperboreus* from Continuous Plankton Recorder data collected between 2000-2009.

**Figure 7.** Annual distribution and abundance of *Oithona* spp. from Continuous Plankton Recorder data collected between 2000-2009.
Figure 8. Annual distribution and abundance of *Pseudocalanus* spp. from Continuous Plankton Recorder data collected between 2000-2009.

Figure 9. Annual distribution and abundance of *Thecosomata* from Continuous Plankton Recorder data collected between 2000-2009.
Figure 10. Annual distribution and abundance of *Euphausida* from Continuous Plankton Recorder data collected between 2000-2009.

Figure 11. Annual distribution and abundance of Cnidaria from Continuous Plankton Recorder data collected between 2000-2009.
**Figure 12.** Mean annual maximum number of sum of all *Calanus finmarchicus* copepodite stages at demographic stations in the North Atlantic (Table 1; Fig. 1B). Maximum annual number of the sum of all copepodite stages is the highest abundance recorded 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 abundances is given in Table 1.
**Figure 13.** Same data as in Figure 12 plotted in a map.

**Figure 14.** 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 can not be used to compare deep ocean and shelf overwintering populations of *C. finmarchicus.*
Figure 15. 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 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.