

SEVENTH FRAMEWORK PROGRAMME THEME 6 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 3.1 Report on the biogeographic regimes of the North Atlantic and the dynamics to climate change

Authors: Claudia Castellani, Priscilla Licandro (SAHFOS)

Due date of deliverable: 1 May 2012

Actual submission date:

Organisation name of the lead contractor of this deliverable: SAHFOS

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

Dissemination Level

PU	Public	X
PP	Restricted to other programme participants (including the Commission)	
RE	Restricted to a group specified by the consortium (including the Commission)	
CO	Confidential, only for members of the consortium (including the Commission)	

Task 3.1: Retrospective analysis of the spatial distribution of key species. This task will assemble datasets and perform retrospective analysis of past and present patterns of biogeography and meso–basin-scale processes in the North Atlantic and shelf seas using data from T1.3.3, T1.3.4 and T1.3.5. Furthermore, we will include the database developed during the TASC project (Trans-Atlantic Study of Calanus) containing data mainly for the northeastern North Atlantic waters, presently being held at IMR, and collaborate with US and Canadian scientists to access datasets for the northwestern North Atlantic (see attached US and Canadian support letters for their commitments and companion proposals). The retrospective analysis will focus on geospatial and long term variations of distribution, abundance, taxonomic compositions, population genetics and rates of key species of copepods, jellyfish and euphausiids over the basin-scale.

In order to foster the development of an International Strategy for the assembly of oceanographic, ecosystem and biogeochemical data we will carry out a workshop together with WP1, 2, 4 and 5 and international collaborators in the US and Canada as well as relevant individuals from the International Council for the Exploration of the Sea to establish the format and complementary data (taxonomy, population genetics, sizes, spatial position and environmental indices such as temperature, salinity, chl a, depth, and topographical features) needed to develop predictive habitat models for key ecologically and biogeochemically important species. One of the focus areas will include further development of standards, methods and protocols for archiving genetic, rate, taxonomic, optical and acoustic data used to characterize planktonic, nekton and fish populations, biomass and distributions.

All above feed directly to WP1, and will be exploited in T3.5, T4.1, T.6.2, and T.6.3 and T 8.3
Responsible: SAHFOS ; Participants IMR; MRI-HAFRO; BUC
Start: month 1, end month 20;

Deliverable 3.1: Report on the biogeographic regimes of the North Atlantic and the dynamics to climate change

Executive Summary:

An analysis of the recent spatial distribution of key zooplankton species in the North Atlantic using CPR data has shown that these taxa are characterised by very different patterns in distribution. The key taxa considered here are the planktonic copepods *Calanus finmarchicus*, *C. helgolandicus*, *C. hyperboreus*, *Pseudocalanus* spp. and *Oithona* spp, the planktonic gastropod Thecosomata species, the Euphausida spp, and the gelatinous zooplankton in the phylum Cnidaria. These taxa are representative of the most important mesozooplankton groups in the northern North Atlantic based on their abundance and on the roles they play within food webs and biogeochemical cycles. Here we discuss how these patterns are the result of very different physiological, life history and ecological characteristics for each taxa. The conclusions of the present study complement recent results summarized in an ICES Report on CPR biogeography by Licandro et al (2011) that based on the analysis of time-series has revealed that important changes have occurred in the abundance, distribution, community structure, and population dynamics of several of these key plankton species. These changes appear to be linked to changes in regional climate, caused predominately by the warming of air and SSTs, and associated changes in hydrodynamics. This report also concludes that anthropogenic pressures (e.g. fishing) may also affect the community composition and abundance of plankton and may act synergistically with the climate. Changes in phytoplankton and zooplankton communities at the bottom of the marine pelagic foodweb may affect higher trophic levels (e.g. fish, seabirds), because the synchrony between predator and prey (match –mismatch) plays an important role (bottom – up control of the marine pelagic environment) in the successful recruitment of top predators, such as fish, seabirds, and mammals. The poor recruitment of several fish species of commercial interest and the low seabird breeding productivity recorded in recent years in some North Atlantic regions are associated with changes in plankton biomass and in the seasonal timing of plankton production. The conclusions of the present study also make a key contribution to a chapter arising from the WP3 activities on “species biogeography and ecological niches” for the first EURO-BASIN Special Issue in the journal *Progress in Oceanography*, on state of the art North Atlantic Ecosystem Research (*Milestone 57*; manuscripts in review).

Relevance to the project & potential policy impact:

The deliverable does not directly contribute to policy, however it builds on North Atlantic Ecosystem assessment performed for the International Council for Exploration of the Sea, and lays the groundwork for synthesis in WorkPackage 8, where recommendations for ocean management will be formulated.

1. Introduction

Marine zooplankton plays an essential role within food-webs and in biogeochemical cycles by providing a trophic link between the phytoplankton and higher predators such as fish and by transporting the carbon ingested from the upper ocean to the deep ocean, where it is sequestered for hundreds to thousands of years. Given the ecological and economic importance of zooplankton, it is essential to understand and predict which environmental factors determine the spatial distribution of key species and how these taxa are likely to respond to climate change. This is a complex problem but recent research suggests that

zooplankton is very sensitive to climate-induced change in the physical and chemical properties of the upper ocean, and that their responses have implications for the recruitment of larval fish, sea-birds and mammals (Edwards, 2009; Licandro et al 2011). Hence, the aim of the task and resulting deliverable was to investigate the recent (2000-2009) spatial distribution patterns, based on Continuous Plankton Recorder (CPR) observations (e.g. Beaugrand, 2004) for key zooplankton taxa in the northern North Atlantic Ocean in relation to changes in hydrography, sea surface temperature (SST) and phytoplankton biomass.

2. Material and methods

2.1. Data set

The data for the key species and for the phytoplankton colour index (PCI) were obtained from the CPR data base. 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 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 fixed to a final concentration of 4% formalin into a tank within the CPR body. On return to the laboratory, the silk roll is unwound and cut into sections corresponding to 10 nautical miles (approx. 3 m³ 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 2000-2009 were gridded using the inverse-distance interpolation method (Isaaks & 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. $\log_{10}(x+1)$). We use the Phytoplankton Colour Index (PCI), which is a visual assessment of the greenness of the silk, as an indicator of the distribution of total phytoplankton biomass across the Atlantic basin (Batten et al. 2003; Richardson et al., 2006). Sea surface temperature (SST) data for the North Atlantic Basin during 2000-2009 were obtained from the Hadley Center (UK Met-Office).

3. Results

3.1. Basin scale habitat characteristics: hydrography and chlorophyll-a

Ocean circulation systems are fundamental in defining species' habitats. The North Atlantic surface circulation system is made up of a series of gyres, encircled by strong boundary currents (Fig.1). The Gulf Stream System transports warm and saline water from west to east in the North Atlantic at about 40°N (e.g. Reverdin et al. 2003).

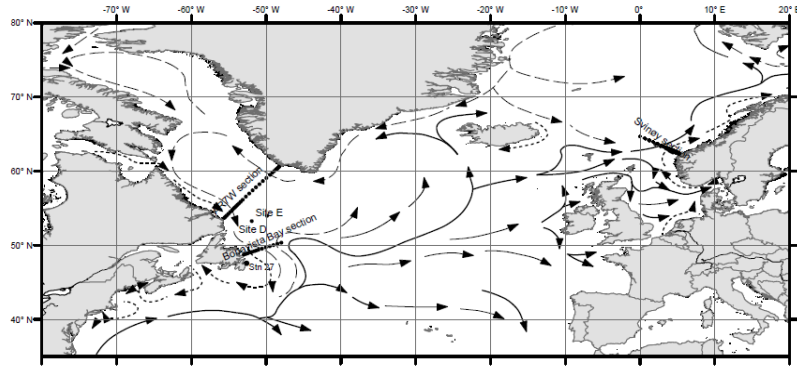


Figure 1: Main pattern of currents in the North Atlantic basin

At about 54°W, the Gulf Stream splits into two branches, a northern branch connected to the North Atlantic Current and a southern branch connected to the Azores Current. The Azores Current and the southward flowing Canary Current limit the Subtropical Gyre to the north and east. The North Atlantic Current flows northeastwardly, with branches flowing into the Icelandic basin and Irminger Sea before the main body enters the Norwegian Sea as the Norwegian Atlantic Current. Thus, the Northeast Atlantic is strongly influenced by northward flowing warm and saline water.

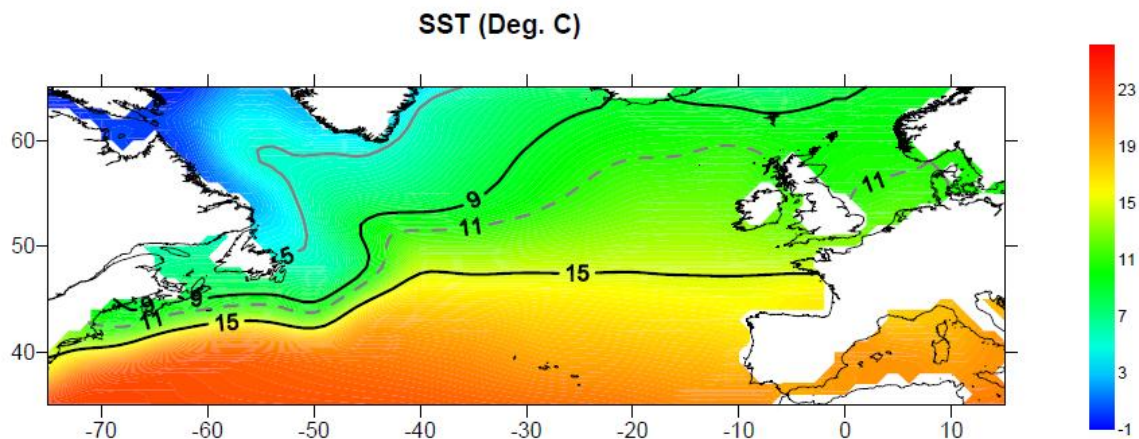


Figure 2: Basin scale distribution of the mean sea surface temperature (SST, °C) for the time interval 2000-09.

The geographical pattern of seas surface temperature (SST) in the North Atlantic is strongly influenced by the Gulf Stream and North Atlantic Current (Fig. 2). The pattern of annually averaged SST (Fig. 2) shows clearly the demarcation of the northern North Atlantic, above the 15°C surface isotherm at approximately 40° latitude (south of Long Island, New York) in the west and rising to about 47° latitude in the east (south of Brittany, France). The coldest surface temperatures occur in the Labrador Sea and off the east coast of Greenland. The 11-15 °C annual average temperature occurs in a narrow band from southern New England to Long Island in the west, then, corresponding to the northeasterly drift of the Gulf Stream, expands northward to include a large area of the deep North Atlantic basin south of Iceland, the North Sea, and coastal shelves of Great Britain (Fig. 2).

Phytoplankton Colour Index

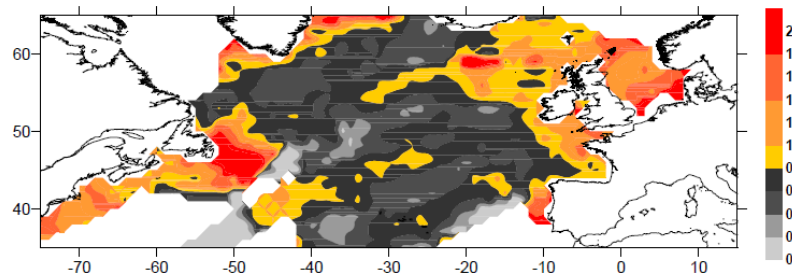


Figure 3: Basin scale distribution of the mean abundance of Phytoplankton Colour Index (PCI) for the time interval 2000-09.

The annual phytoplankton colour index (PCI, Fig.3), a relative index of phytoplankton biomass as sampled by the silk mesh in the CPR, shows no obvious correspondence with the annual pattern of SST (Fig. 1). It indicates that the areas of highest phytoplankton biomass occur at the shelf margins, including the Gulf of Maine, Grand Banks, North Sea and shelf north and west of the British Isles. Higher phytoplankton biomass is also indicated in the Denmark Strait and deep water south of Iceland. In general, surface phytoplankton biomass is lower in the deep, central North Atlantic basin.

3.2. Distribution of the key species

Figures 4 - 11 show the spatial distribution of the log-transformed mean annual abundance (and presence/absence for the Cnidaria) of the selected taxa between 2000- 2009. Overall the plots show a remarkable difference among the distribution of the different taxa. The abundance of the boreal species *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 the northern regions (Fig.4).

C. finmarchicus

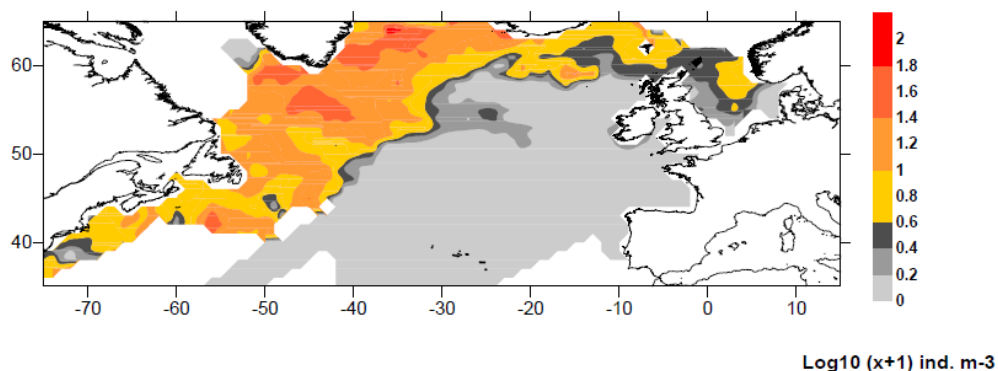


Figure 4: Basin scale distribution of the mean abundance of the copepod *C. finmarchicus* for 2000-09

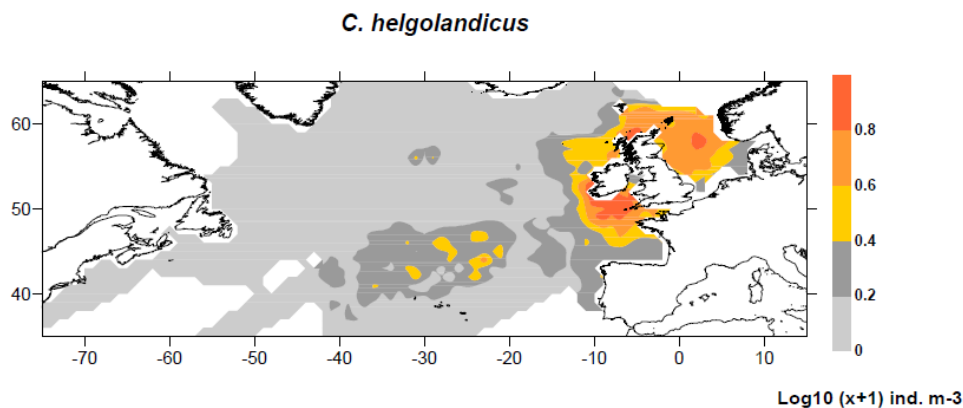


Figure 5: Basin scale distribution of the mean abundance of the copepod *C. helgolandicus* for 2000-09

In contrast, *C. helgolandicus* is mainly found on the shelf regions around the British Isles, particularly on the southern part of the eastern Atlantic and the North Sea (Fig.5).

Compared to its congeneric species, *C. hyperboreus* is found at lower concentrations and appears to be more abundant off Newfoundland, the Labrador Sea and the Irminger Basin (Fig.6). The small copepod species *Pseudocalanus* spp. is mainly distributed on the shelf areas of both the eastern and western Atlantic (Fig.7). In contrast, Fig. 8 shows that the small cyclopoid copepod *Oithona* spp. has a wider basin scale distribution with high concentrations south of Iceland, in the Irminger Basin and on the Grand Banks region off Newfoundland. The Thecosomata also show a wide scale basin distribution although these taxa appear to be more abundant on the shelf regions around the British Isle and the northern North Sea, the Irminger Basin and south of Greenland (Fig.9). The 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 Cnidaria presence is mainly in the Irminger Basin, off Ireland and in the southern and eastern part of the North Atlantic basin (Fig.11).

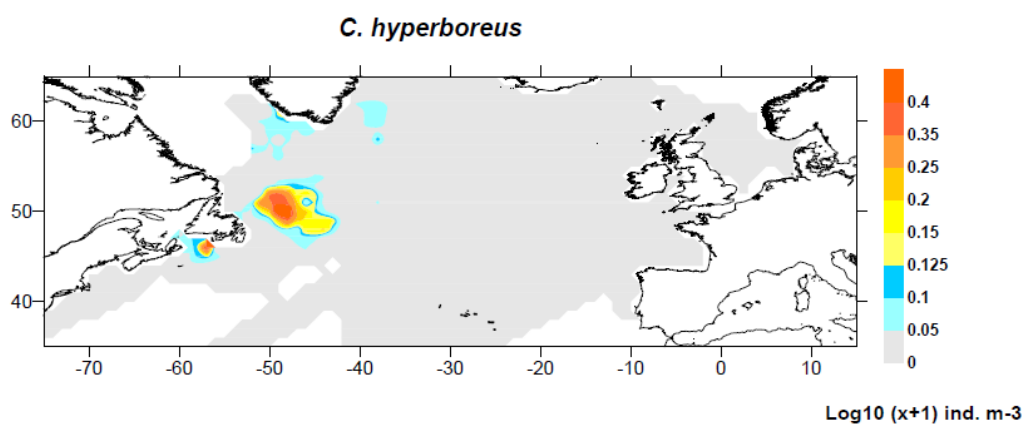


Figure 6: Basin scale distribution of the mean abundance of the copepod *C. hyperboreus* for 2000-09

Pseudocalanus spp.

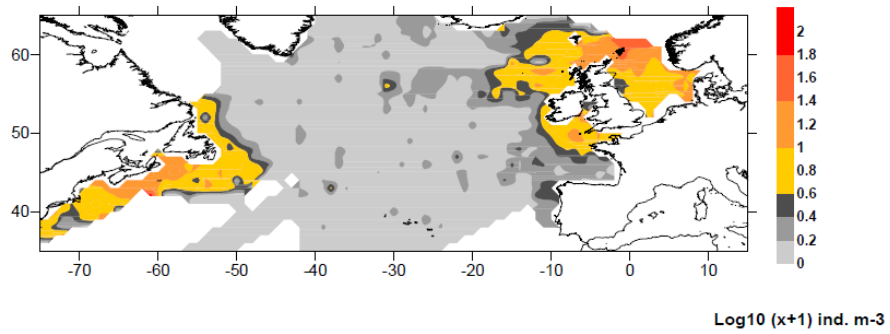


Figure 7: Basin scale distribution of the mean abundance of the copepod *Pseudocalanus spp.* for 2000-09.

Oithona spp.

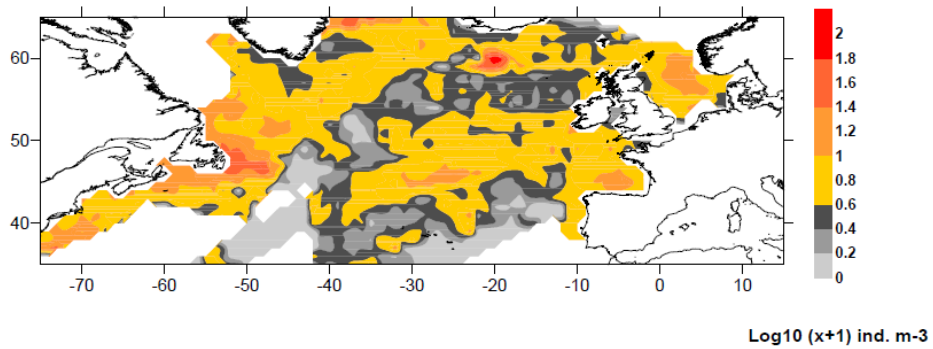


Figure 8: Basin scale distribution of the mean abundance of the copepod *Oithona spp.* for 2000-09.

Thecosomata

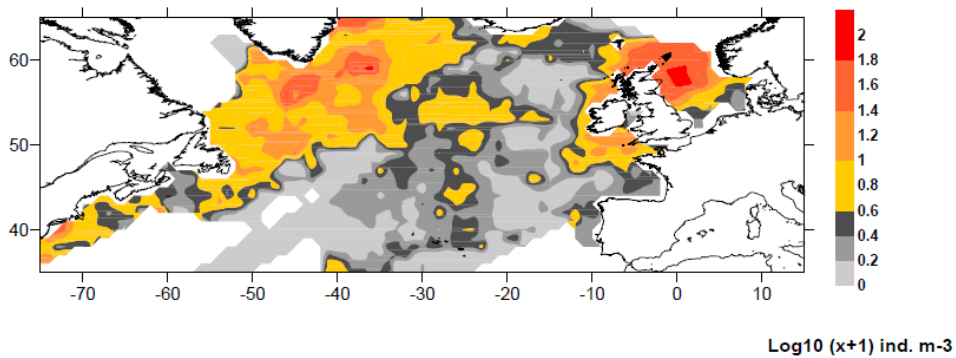


Figure 9: Basin scale distribution of the mean abundance of the Thecosomata *spp.* for 2000-09.

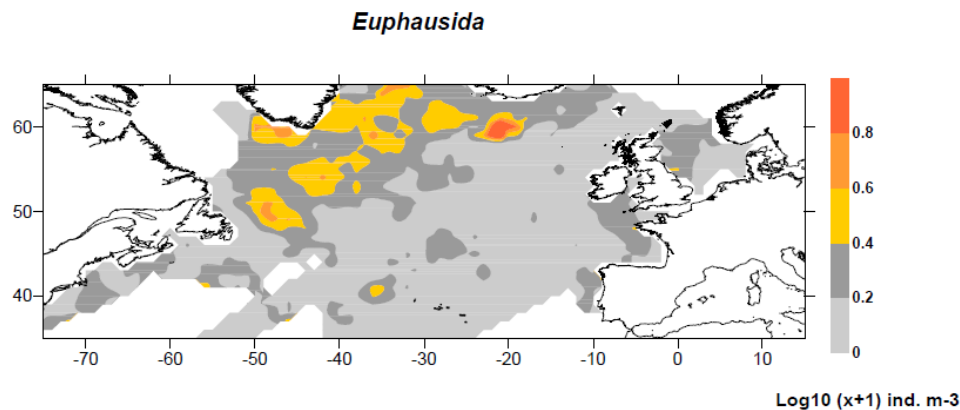


Figure 10: Basin scale distribution of the mean abundance of the *Euphausiida spp.* for 2000-09.

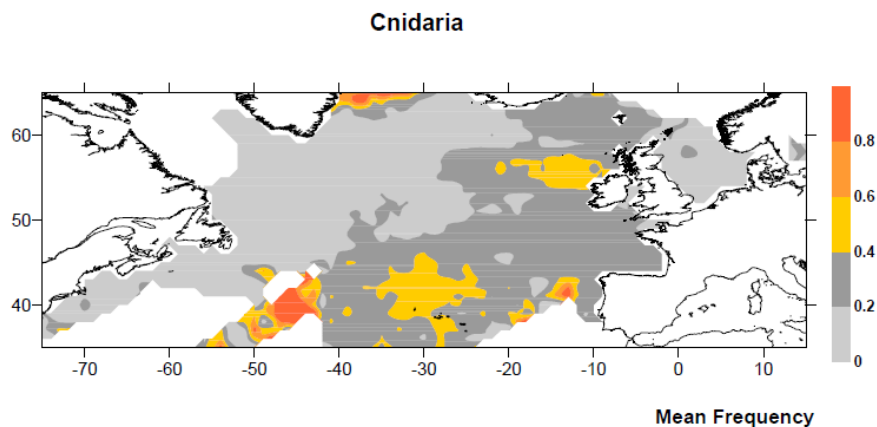


Figure 11: Basin scale distribution of the mean abundance of the *Cnidaria spp.* for 2000-09.

4. Discussion

4.1. Taxon specific traits and the distribution of zooplankton in the North Atlantic habitat in relation to hydrography and environmental conditions

While the ocean circulation system and its associated water mass characteristics exert an important influence on the distribution and ecology of zooplankton, the dramatic difference in abundance and distribution we have reported at the basin scale for the representative key species indicates that these patterns are also the result of very different physiological, life cycle and ecological characteristics of each of the taxa investigated. Figure. 4 shows that the mean annual distribution of *C. finmarchicus* is mainly restricted in the northern and western North Atlantic within an area delimited between the 5°C and 10°C annually-averaged sea surface isotherms.

This observation concurs with that reported by recent studies which have found a mean annual maxima abundance between 5°C-10°C and a critical thermal boundary between 9°C-12°C for this species in the North Atlantic (Helaouët and Beaugrand, 2009; Beaugrand

et al., 2008). Overall, *C. finmarchicus* is more abundant in the northwest Atlantic that is cooler and where average chlorophyll standing stock is greater (see also Longhurst, 1998; Helaouët and Beaugrand, 2009, Helaouët et al., 2011).

In contrast the congeneric species *C. helgolandicus* is mostly restricted to the eastern North Atlantic shelf whereas it is absent in the western North Atlantic (Fig. 5). Unlike *C. finmarchicus*, *C. helgolandicus* is generally associated with warmer and more saline waters and regions characterised by more pronounced spatial changes in bathymetry (Helaouët and Beaugrand, 2007). Thus, the difference in the spatial and temporal distribution of these two morphologically very similar sibling species has probably to be attributed to differences in their ecological niches. For instance, a recent study has shown that *C. finmarchicus* develops faster than *C. helgolandicus* below 11°C and slower above this temperature (Møller et al, 2012). *C. helgolandicus* is virtually found all year round as it is not known to undergo diapause like *C. finmarchicus*. Moreover, the seasonal difference in population maxima between these two species (i.e. *C. helgolandicus* usually peaks in late summer-autumn whereas *C. finmarchicus* peaks in spring) appears to be associated with differences in the temperature of the water column (Planque and Fromentin 1996). In addition, the limited presence of *C. helgolandicus* in oceanic areas of the North Atlantic compared to *C. finmarchicus* is probably to be attributed to the fact that *C. helgolandicus* has a lower capacity to store lipid reserves than *C. finmarchicus* (Lee et al., 2006).

Despite the temporal and spatial differences in their distribution these two species overlap where they co-occur, suggesting that these taxa are able to coexist. The distribution of the largest congeneric species *C. hyperboreus* in the North Atlantic is mainly linked with the outflow of the water from the Arctic around Greenland and in the Scotian and Newfoundland shelf regions (cf Fig.6 and Fig. 1). *C. hyperboreus*, which may experience recruitment failure in relative warm Atlantic waters (Brooms et al., 2009), since the 1990s has become more abundant than previously observed on the Newfoundland shelf in association with an increasing inflow of Arctic waters (Licandro et al., 2011).

The capacity to store lipid reserves is considered to be an important adaptation for a species to cope with periods of food scarcity in winter and to expand its area of distribution to open ocean areas where food resources are scarcer. Thus, compared to the *Calanus* spp which store large lipid reserves the distribution of smaller copepod species with limited or no lipid storage is usually restricted to coastal and shelf areas where food sources are more abundant. Some species such as *Pseudocalanus* spp. and *Oithona* spp., store small lipid droplets that likely confer a survival advantage compared to other copepod species of similar size. Interestingly, *Pseudocalanus* spp. and *Oithona* spp. show a very different basin scale distribution. *Pseudocalanus* spp. is mainly found on the eastern shelf around the British Isle and on the western shelf of the US coast, whereas *Oithona* spp. is found throughout the North Atlantic basin (Fig. 7 and Fig. 8). It has been suggested that the higher abundance and wider scale distribution of *Oithona* spp may be due to the capacity of this species to feed on the microbial food-web, to minimise its energy losses through its hop and sink swimming behaviour (Castellani et al, 2005, a & b) and because of its lower natural mortality rate compared to other copepod species (Eiane et al., 2004). Indeed *Oithona* spp distribution shows no strong dependence with phytoplankton standing stock (cf. Fig. 8 and Fig. 3), as it can reach high concentrations offshore and over the shelf across all the latitudes. In contrast *Pseudocalanus* spp. is mainly an omnivorous filter feeder species which requires continuous swimming to capture its preys. Hence, this species it is probably more dependent on food supply than *Oithona* spp. and it has higher

predation mortality due to the stronger hydrodynamic signal it generates during swimming. These physiological and behavioural adaptations allow *Oithona* spp to colonise open ocean areas more successfully than *Pseudocalanus* spp and other small copepod species. Thecosomata spp. play an important role not only within food-webs but also in the cycling of carbon and carbonate.

Several species also represent indicators of different water masses. In the North Atlantic the distribution of these taxa is mainly concentrated on the north-western part of the North Atlantic basin and on the shelf of the British Isles (Fig. 9). The pattern of distribution suggests that particularly in the western part of the North Atlantic basin the spatial distribution of the thecosomata may be delimited southward by the flow of the North Atlantic Current (NAC). In our study, however, the Thecosomata represent a species complex, hence further investigations in their pattern of distribution will require an in-depth analysis of species composition. Euphausiids spp. are an important component of the plankton community of the North Atlantic as they can account for a large proportion of the biomass and of the diet of many animals including fish, whales and birds (Dalpadado et al., 2000; Falk et al., 1992). Our study shows that Euphausiids were abundant mainly in the north-western part of the North Atlantic basin, particularly south of Greenland, south of Iceland and off the Labrador coast (Fig.10). In the North Atlantic Euphausiids standing stock increases in high latitudes in colder and more productive waters with approximately height species reported to make up the bulk of the biomass (Mauchline & Fisher 1969; Lindley 1982). In the late 1960s Lindley (1982 a and b) investigated the distribution at surface of the main Euphausiid species living in the North Atlantic, their population dynamics and production based on CPR samples at the scale of the whole North Atlantic. An update of that study would be useful to verify whether the hydro-climatic changes that have been reported in different regions of the North Atlantic in the last two decades, have affected the composition of euphausiid populations. More recent studies have investigated the biogeography and distribution of euphausiids along the Mid-Atlantic Ridge (Letessier et al., 2011) and in the Northwestern Atlantic (Endo and Wiebe, 2007). Overall, Euphausiids shows very complex and species specific life cycles, physiology and behavioural patterns. In their review Mauchline & Fisher (1969) have reported that among other factors temperature represents one of the main determinants of Euphausiids species distribution. More work, however, is required to define the ecological niche of different species.

Our study has shown that in the North Atlantic, the Cnidaria were particularly abundant off the Irish shelf, the Irminger Basin and in warm oceanic waters below 45°N (Fig.11). Interestingly, recent studies have shown that the frequency of Cnidaria in these areas has increased over the past decade (Gibbons & Richardson 2009; Licandro et al., 2010).

Moreover, a recent study has shown that the blooms of jellyfish off the Northwest European shelf have become unusually persistent during winter months and that the outbreaks correspond with a northward spread of the warm water North Atlantic Current (NAC) from mid-temperate latitudes into the Northeast Atlantic (Licandro et al., 2010). Predictions of global climate change suggest that as the North Atlantic will continue to warm we may see more frequent jellyfish blooms in coastal seas where food resources are more abundant. At present the distribution and diversity characterising the jellyfish communities in the North Atlantic basin are still understudied, as well as the biological mechanisms controlling their population dynamics. Nevertheless, rising temperature within species-specific thermal preferences, has been indicated as one of the factors that may positively influence the jellyfish reproduction, leading to a very rapid increase in their abundance and overwinter

survival rate (Boero et al., 2008).

References

- Batten, S.D., Walne, A.W. Edwards, M. and Groom, S.B. (2003) Phytoplankton biomass from continuous plankton recorder data: an assessment of the phytoplankton colour index. *Journal of Plankton Research* 25(7): 697-702.
- Beaugrand G. (2004) Continuous Plankton Records: Plankton Atlas of the North Atlantic ocean (1958-1999). MEPS, Supplement: 3-10, 75 p.
- Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T., Piraino, S., (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series* 356: 299–310.
- Castellani C, Irigoien X, Harris RP, Lampitt RS (2005a) Feeding and egg production of *Oithona similis* in the North Atlantic, *Mar Ecol Prog Ser*, 288: 173-182.
- Castellani C, Robinson C, Smith T, Lampitt RS (2005b) Temperature affects respiration rate of *Oithona similis*, *Marine Ecology Progress Series*, 285: 129-135.
- Dalpadado, P., Ellertsen, B., Melle, W., and Dommasnes, A. (2000) Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES Journal of Marine Science*, 57: 843–857.
- Eiane K, Ohman MD (2004) Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. *Marine Ecology Progress Series* 268:183–193.
- Endo, Y., & Wiebe, P. H. (2007) Temporal changes in euphausiid distribution and abundance in north atlantic cold-core rings in relation to the surrounding waters. *Deep Sea Research (Part I, Oceanographic Research Papers)*, 54(2): 181-202.
- Falk, K., Jensen, J., & Kampp, K. (1992) Winter diet of atlantic puffins (*Fratercula arctica*) in the northeast atlantic. *Colonial Waterbirds*, 15(2): 230-235.
- Gibbons, M. J. & Richardson, A. J. (2009) Patterns of jellyfish abundance in the North Atlantic. *Hydrobiologia*, 616: 51-65.
- Isaaks E.H. and Srivastava, R.M. (1989) *An Introduction to Applied Geostatistics*, by Edward H. Isaaks and R. Mohan Srivastava, Oxford, uk: Oxford University Press, 561 pp.
- Jonas, T. D., Walne, A., Beaugrand, G. et al. (2004) The volume filtered by a Continuous Plankton recorder sample: the effect of ship speed. *J. Plankton Res.*, 26, 1499–1506.
- Letessier, T. B., Falkenhaus, T., Debes, H., Bergstad, O. A., & Brierley, A. S. (2011) Abundance patterns and species assemblages of euphausiids associated with the mid-atlantic ridge, north atlantic. *Journal of Plankton Research*, 33(10), 1510-1525.
- Licandro P., D. V. P. Conway, M. N. Daly Yahia, M. L. Fernandez de Puellas, S. Gasparini, J. H. Hecq, P. Tranter and R. R. Kirby (2010) A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters*, 6: 688-691.
- Licandro, P., Head, E., Gislason, A., Benfield, M.C., Harvey, M., Margonski, P. and Silke, J. (2011) Overview of Trends in Plankton Communities. *ICES Coop. Res. Rep*, 310: 103-122.
- Lindley, J. A. (1982a) Continuous Plankton Records: geographical variations in numerical abundance, biomass and production of euphausiids in the north Atlantic Ocean and North Sea. *Marine Biology*, 71: 7-10.
- Lindley, J. A. (1982b) Population dynamics and production of euphausiids. III. *Meganyctiphanes norvegica* and *Nyctiphanes couchi* in the North Atlantic Ocean and the North Sea. *Marine Biology*, 66: 37-46.

Lindley, J. A. (1982c) Population dynamics and production of euphausiids. IV. *Euphausia krohni*, *Nematocelis megalops* and *Thysanoessa gregaria*, and eight rare species in the North Atlantic Ocean. *Marine Biology*, 71: 1-6.

Mauchline J. and Fisher L. R., (1969) The Biology of Euphausiids. In "Advances in Marine Biology", F. S. Russel and C. M. Yonge eds., Academic Press, London & New York, 7, 1-454.

Moller, E.F., Maar, M., Jonasdottir, S., Nielsen, T.G., Tönnesson, K., 2012. The effect of changes in temperature and food on the development of *Calanus finmarchicus* and *C. helgolandicus* populations. *Limnol. Oceanogr.* 57, 221-220.

Richardson A.J., A.W. Walne, A.W.G. John, T.D. Jonas, J.A. Lindley, D.W. Sims, D. Stevens, M. Witt (2006) Using continuous plankton recorder data, *Progress in Oceanography*, 68: 27-74.