

2009

Large-scale study of Calanus in the North Atlantic Ocean: macroecological patterns and potential impacts of climate change

Helaouet, Pierre

<http://hdl.handle.net/10026.1/2656>

<http://dx.doi.org/10.24382/1301>

University of Plymouth

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

**Large-scale study of *Calanus* in the North Atlantic
Ocean: macroecological patterns and potential impacts
of climate change**

By

Pierre Helaouët

A thesis submitted to the University of Plymouth in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Marine Science and Engineering

Faculty of Science and Technology

In collaboration with:

Sir Alister Hardy Foundation for Ocean Science and CNRS France

September 2009

University of Pennsylvania
Library

70 29253918

THESIS 577.727 HGL

Large-scale study of *Calanus* in the North Atlantic Ocean: macroecological patterns and potential impacts of climate change

Pierre Helaouët

Abstract

Marine ecosystems show natural fluctuation throughout a large range of spatial and temporal scales. Despite the large amount of study devoted to the North Atlantic Ocean, drivers of those fluctuations remain unclear. By changing global climate, polluting, introducing exotic species, expanding and intensifying land uses and overharvesting biological resources, human activities have degraded the global ecosystem and drastically accelerated species extinction rates. Consequences of this human forcing become apparent in the progressive degradation of ecosystem that are used by humans (Schröter *et al.*, 2005), climate change-induced shifts in species distributions toward the poles (Parmesan *et al.*, 1999) and higher elevations (Wilson *et al.*, 2005), and in rapidly changing phenology (Edwards & Richardson, 2004). Data collected by the Continuous Plankton Recorder (CPR) constitutes, by both their temporal and biogeographical extends, one of the most useful datasets to investigate further major marine management issues as the distinction between anthropogenic, climatically forced and natural ecosystems fluctuations.

The present work is a contribution to environmental change biology focused on copepods *Calanus* species as key structural species characteristic of the North Atlantic Ocean and adjacent seas. The purpose is to (1) identify environmental factors leading to the large-scale distribution patterns of *Calanus* that occurred in the North Atlantic Ocean, and (2) to propose and investigate new methods to assess both fundamental and realised niches of a dominant species in these basins.

Most current approaches using Hutchinson concept of ecological niches to model species distribution belong to correlative or mechanistic models. A correlative approach has been developed to assess statistical relationships between the observed spatial distributions of two congeneric species and a set of environmental variables characteristic of the studied area. The method is designed to show the seasonal dynamics of environmental restriction driving observed distributions. Both *Calanus finmarchicus* and *C. helgolandicus* environmental preferences and optimum have been defined for 11 environmental parameters. A principal component analysis (PCA) has been used (1) to quantify the importance on the spatial distribution of each environmental parameter and (2) to identify the ecological niche. A numerical analysis based on Multiple Response Permutation Procedures (MRPP) was utilised to assess the breath of each niche and to compare them.

The egg production rate of *Calanus finmarchicus* has been defined to investigate the link between physiology, macroecological patterns and ecological niches. It typically assesses the fundamental niche as in opposition to the correlative approach, the model based on a fundamental biological process is more focused on the potential response of *C. finmarchicus* to environmental conditions. The simplicity of the method which used only Sea Surface Temperature (SST) allows us to use IPCC scenarios and predict a shift in distribution over the 21st century.

Table of contents

List of tables.....	vi
List of figures.....	vii
List of abbreviations.....	x
Acknowledgements.....	xi
Author's declaration.....	xii
Chapter 1. Introduction.....	1
1.A. The North Atlantic Ocean.....	2
1.B. The North Atlantic climate variability.....	4
1.C. Anthropogenic climate change.....	7
1.D. Copepods as climate change indicators in the North Atlantic Ocean.....	7
1.E. Overview of the ecological niche concepts.....	12
1.F. Goals of the study.....	14
Chapter 2. The continuous Plankton Recorder (CPR) survey.....	18
2.A. Concepts and history.....	19
2.B. Sampling and sub-sampling.....	21
2.C. Overview of statistical methods applied to CPR data.....	24
2.C.1. Descriptive methods applied to CPR data.....	24
2.C.2. Multivariate analyses.....	25
Chapter 3. Macro-ecological study of the niche of <i>Calanus finmarchicus</i> and <i>C. helgolandicus</i> in the North Atlantic Ocean and adjacent seas.....	27
3.A. Introduction.....	28
3.B. Materials and methods.....	32
3.B.1. Biological data.....	32
3.B.2. Environmental data.....	33
3.B.3. Pre-processing of the data.....	36
3.B.4. Statistical analyses.....	36
3.B.4.A. Analysis 1: Characterisation of the environmental preference and optimum of both <i>Calanus</i> species at a seasonal scale.....	38
3.B.4.B. Analysis 2: Quantification of the importance of each environmental parameter at a seasonal scale.....	38
3.B.4.C. Analysis 3: Identification of the ecological niche of both <i>Calanus</i> species at a seasonal scale.....	39
3.B.4.D. Analysis 4: Quantification and comparison of the species Hutchinson's niches.....	39
3.B.4.D.1. Rationale of the technique.....	40
3.B.4.D.3. Test of niche separation.....	45
3.B.4.E. Analysis 5. Thermal profiles of both <i>Calanus</i> as a function of the state of the North Atlantic Oscillation (NAO) and the 1987's climatological regime shift.....	47
3.B.4.F. Analysis 6. Thermal profile of both <i>Calanus</i> as a function of CPR data for daylight and dark period.....	48

3.C. Results	49
3.C.1. Spatial distribution of biological and environmental data.....	49
3.C.2. Environmental profiles	52
3.C.2.1. Monthly thermal profile	52
3.C.2.2. Others monthly profile	54
3.C.3. Quantification of the factors that influences spatial distribution of <i>Calanus</i>	58
3.C.4. Identification of the ecological niche of both <i>Calanus</i> species.....	63
3.C.5. Application of the ecological niche approach to explain the change in dominance of <i>Calanus</i> that happened in the North Sea after the 1980s regime shift	65
3.C.6. Time stability of the thermal niche of <i>Calanus</i>	66
3.D. Discussion	71
Chapter 4. Physiology, ecological niches and species distribution	78
4.A. Introduction	79
4.B. Materials and methods.....	83
4.B.1. Biological and environmental data	83
4.B.1.A. <i>Calanus finmarchicus</i>	83
4.B.1.B. Sea Surface Temperature	84
4.B.1.C. Chlorophyll <i>a</i>	85
4.B.1.D. Bathymetry	86
4.B.2.A. Estimation of the realised niche.....	86
4.B.2.B. Estimation of the optimal part of the fundamental niche.....	86
4.B.2.C. Correlations.....	88
4.B.2. Procedures and analyses	88
4.C. Results	90
4.D. Discussion	97
Chapter 5. Macroecology and macrophysiology of <i>Calanus finmarchicus</i> in the North Atlantic Ocean.....	101
5A. Introduction	102
5.B. Materials and methods.....	105
5.B.1. Studied areas.....	105
5.B.2. Biological data.....	106
5.B.3. Environmental Data.....	106
5.B.3.A. Sea Surface Temperature (SST)	106
5.B.3.B. Chlorophyll <i>a</i>	107
5.B.3.C. Bathymetry	107
5.B.3.D. Chemical data	107
5.B.3.E. Water column stability	107
5.B.4. Statistical analyses.....	108
5.B.4.A Quantification of the influence of each parameter on the spatial distribution	108
5.B.4.B. Determination of the optimal part of the fundamental niche.....	108
5.B.4.C. Spatial distribution and the fundamental niche.....	109
5.B.4.D. Determination of the realised niche	109
5.B.4.E. Projections of changes in the abundance of <i>C. finmarchicus</i>	110
5.C. Results	112
5.C.1. Influence of environmental parameters on the spatial distribution of <i>C.</i> <i>finmarchicus</i>	112

5.C.2. Spatial distribution of <i>C. finmarchicus</i> and the fundamental niche	116
5.C.3. Determination of the realised niche.....	119
5.C.4. Projections of changes in the abundance of <i>C. finmarchicus</i>	121
5.D. Discussion	123
Chapter 6. General conclusions	129
References	136
Publications	151

Helaouët, P., Beaugrand, G., 2009. Physiology, ecological niches and species distribution. *Ecosystems* 12, 1235 - 1245.

Beaugrand, G., Helaouët, P., 2008. Simple procedures to assess and compare the ecological niche of species. *Marine Ecology Progress Series* 363, 29-37.

Beaugrand, G., Lindley, J.A., Helaouët, P., Bonnet, D., 2007. Macroecological study of *Centropages typicus* in the North Atlantic Ocean. *Progress in Oceanography*. 72, 259–273.

Helaouët, P., Beaugrand, G., 2007. Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series*. 345, 147-165.

Helaouët, P., Beaugrand, G., Reid, P.C., submitted. Macroscale ecophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Global Ecology and Biogeography*.

List of tables

Table 3.1. Origin and characteristics of the environmental data used in this study.	34
Table 3.2. Fictive example showing the occurrence of three species according to 2 environmental variables.	444
Table 3.3. Results of the comparison between the breadth and position of the two ecological niches of <i>Calanus finmarchicus</i> and <i>Calanus helgolandicus</i> . “ p_{δ} ” is the probability of separation of the two ecological niche.	63
Table 4.4. Relationships between fundamental and realised niches.	92
Table 5.5: First five contributors (C1 to C5) for the first principal component (PC1) for each month.	113
Table 5.6. Annual and monthly relationships between abundance and egg production rate of <i>C. finmarchicus</i>	117

List of figures (abbreviated titles)

Figure 1.1. Pathways associated with the transformation of warm subtropical waters into colder sub-polar and polar waters in the northern North Atlantic Ocean....	3
Figure 1.2. Simplified representation of the influence of the NAO.....	6
Figure 1.3. Changes in the NAO index from 1964 to 1997	6
Figure 1.4. Main area (in grey) sampled by the Continuous Plankton Recorder survey from 1960 to 2002.....	8
Figure 1.5. Schematic representation of the <i>Calanus finmarchicus</i> life cycle.....	11
Figure 2.6. Original Hardy Continuous Plankton Recorder, 1925.....	20
Figure 2.7. The two different kind of plankton recorder used since the beginning of the study.....	20
Figure 2.8. A cross-section of the CPR, its internal mechanism and CPR body	23
Figure 3.9. Summary of the different statistical analysis performed in the chapter	37
Figure 3.10. Origin of matrices tested in this chapter	42
Figure 3.11. Hypothetical ecological niche of three species in the space of two factors	45
Figure 3.12. Spatial distribution of <i>Calanus finmarchicus</i> (a) and <i>Calanus helgolandicus</i> (b) in the North Atlantic Ocean	50
Figure 3.13. Spatial distribution of 10 parameters	51
Figure 3.14. Contour diagram of the abundance of <i>Calanus finmarchicus</i> (a) and <i>Calanus helgolandicus</i> (b) as a function of SST and months.....	53
Figure 3.15. Contour diagram of the abundance of <i>Calanus finmarchicus</i> and <i>Calanus helgolandicus</i> as a function of salinity (a), oxygen dissolved (b), chlorophyll <i>a</i> (c) and phosphate (d) and months.....	55
Figure 3.16. Contour diagram of the abundance of <i>Calanus finmarchicus</i> (a) and <i>Calanus helgolandicus</i> (b) as a function of bathymetry and months.....	57
Figure 3.17. Results from a standardised principal component analysis performed on environmental data. (a) Normalised eigenvector 1 and 2	59
Figure 3.18. Results from a standardised principal component analysis performed on environmental data. (a) Normalised eigenvector 2 and 3	61

Figure 3.19. Results from a standardised principal component analysis performed on environmental data. (a) Normalised eigenvector 1 and 3	62
Figure 3.20. Representation of the ecological niche (sense Hutchinson) using the first three principal components.	64
Figure 3.21. Contour diagram representing the proportion of <i>C. helgolandicus</i> on total <i>Calanus</i>	66
Figure 3.22. Contour diagram of the abundance of <i>Calanus finmarchicus</i> and <i>Calanus helgolandicus</i> as a function of the state of the NAO	68
Figure 3.23. Contour diagram of the abundance of <i>Calanus finmarchicus</i> and <i>Calanus helgolandicus</i> as a function of the regime shift	69
Figure 3.24. Contour diagram of the abundance of <i>Calanus finmarchicus</i> and <i>Calanus helgolandicus</i> as a function of daylight or dark periods	70
Figure 3.25. Diagram showing the influence of the different abiotic variable on two <i>Calanus</i> species.....	72
Figure 4.26. Response curve illustrating the effects of an environmental factor (X) on the species abundance (Y)	81
Figure 4.27. Sketch diagram summarising the different steps and analyses performed in this study	89
Figure 4.28. a. Spatial distribution of <i>C. finmarchicus</i> for the period 1960-2005. b. Spatial distribution of EPR	91
Figure 4.29. Decadal changes in the spatial distribution in the abundance of <i>C. finmarchicus</i> and egg production rate.....	94
Figure 4.30. a. Spatial distribution of egg production rate of <i>C. finmarchicus</i> b. Projected spatial distribution of egg production rate for the period 2050-205996	
Figure 5.31. Spatial distribution of <i>Calanus finmarchicus</i> in the North Atlantic Ocean	105
Figure 5.32. Example of distribution of 4 parameters used in the Principal Component Analysis.....	114
Figure 5.33. Results from a standardised PCA performed on normalised environmental data. (a) Normalised eigenvector 1 and 2	115
Figure 5.34. Monthly spatial distribution of both abundance and egg production rate of <i>Calanus finmarchicus</i>	118
Figure 5.35. Abundanceand PEPR of <i>Calanus finmarchicus</i> as a function of both categorised abundances of diatoms and SSTs for the whole area	120

Figure 5.36. Projection of annual SSTs for the coldest (in blue) and warmest (in red) years of the three decades (2010-2019, 2050-2059 and 2090-2099)122

List of abbreviations

AMO – Atlantic Multidecadal oscillation	4
AO-GCM – Atmosphere-Ocean General Circulation Model	84
ARCT – Atlantic Arctic Province	8
BAT – Bathymetry	59
CHL – Chlorophyll <i>a</i>	59
CPR – Continuous Plankton Recorder	15
COADS – Comprehensive Ocean-Atmosphere Data Set	33
CTD – Conductivity Temperature Depth	35
CVB – coefficient of variation of the Bathymetry	59
ECHAM4 – European Centre of HAMbourg	84
ENSO – El Niño-Southern Oscillation	4
EPR – Egg Production Rate	87
GEBCO – General Bathymetric Chart of the Oceans	34
GFST – Gulf Stream Province	8
GHG – GreenHouse Gas	7
GSNW – Gulf Stream North Wall	1
IPCC – Intergovernmental Panel on Climate Change	16
MBT – Mechanical BathyThermograph	35
MLD – Mixed Layer Depth	35
MOC – Meridional Overturning Circulation	2
MRPP – Multiple Response Permutation Procedures	40
NAC – North Atlantic Current	2
NADR – North Atlantic Drift Province	8
NADW – North Atlantic Deep Water	2
NAO – North Atlantic Oscillation	1
NASA – National Aeronautics and Space Administration	35
NAST – North Atlantic Subtropical Gyral Province	8
NECS – Northeast Atlantic Shelves Province	8
NIT – Nitrate	59
NODC – National Oceanographic Data Center	33
NWCS – Northwest Atlantic Shelves Province	8
OGCM – Ocean General Circulation Models	75
PCA – Principal Component Analysis	25
PEPR – Potential Egg Production Rate	88
PHO – Phosphate	59
RC – Relative Contribution	58
SAHFOS – Sir Alister Hardy Foundation for Ocean Science	15
SDM – Species Distribution Model	12
SeaWIFS – Sea-viewing Wide Field-of-view Sensor	35
SAL – Salinity	59
SARC – Atlantic Subarctic Province	8
SIL – Silicate	59
SLP – Sea Level Pressure	4
SST – Sea Surface temperature	5
TUR – Turbulence	59
WOA1 – World Ocean Atlas 2001	33
WOCE – World Ocean Circulation Experiment	35
XBT – eXpendable BathyThermograph	35

Acknowledgements

I wish to thank Dr S. Votier and Dr A. Hirst for examining this thesis.

I am very grateful to my director of studies Prof. Martin Attrill for his support and advices. Many thanks for your help during the PhD.

I also thank my two supervisors Dr. Gregory Beaugrand and Dr. Chris Reid for their support over the three years I spent between Wimereux and Plymouth.

I would like to thank Eur-Oceans for its financial support.

Thanks to all past and present SAHFOS teams without whom this work would not have been possible.

I thank Dr Martin Edwards for his advice and his time. I am thankful to Jean Nyman, Marion Smith and Linda Horsfield for their patience when I was barely able to speak English. All of you helped me to deal with the administration, my bank, my landlord and so many other things. Thanks to David Johns and Abby for your friendship over the three years in SHAFOS.

Je voudrais également remercier de tout mon cœur toutes les personnes qui ont été la pour moi durant ma thèse. Merci à eux de m'avoir soutenu pendant les moments difficiles. Cette thèse n'aurait pas pu être menée à bien sans vous, donc merci encore à vous tous :

Les Wimereusiens : Clément, Dr. David « D », Maud, Gaétan, ...

Les Plymouthien : Damien, Jo, Kirsty, Lise, Maria, Niall, Taimour, Vale, ...

Merci à ma seule et unique collocatrice, Laure. Je n'oublierai pas les trois années passées ensemble. Merci de tout ce que tu as fait pour moi, tu as été royale jusqu'au bout.

Evidement, je tiens à remercier ma famille. Mes parents qui m'ont toujours poussé à faire ce que j'aimais et qui à chaque instant m'ont apporté leur soutien.

Merci à ma sœur Marie et à mon beau frère Fred pour tous les petits moments passés ensemble. J'ai également une pensée pour mes grand-mères.

Enfin je voudrais remercier Marie. Pour tout ce qu'elle m'a apporté et m'apportera dans le futur.

Merci encore à vous tous, cette thèse est aussi la votre.

Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

This study was financed with the aid of a studentship from the EUR-OCEANS (WP6-SYSNO-1050) and carried out in collaboration with the Sir Alister Hardy Foundation for Ocean Science.

Relevant scientific seminars and conferences were regularly attended at which work was often presented; external institutions were visited for consultation purposes and several papers prepared for publication.

Publications 2005-2008:

1. Beaugrand, G., Lindley, J.A., **Helaouët, P.**, Bonnet, D., 2007. Macroecological study of *Centropages typicus* in the North Atlantic Ocean. *Progress in Oceanography* 72, 259–273.
2. **Helaouët, P.**, Beaugrand, G., 2007. Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series*. 345, 147-165. This paper is part of the chapter 3.
3. Beaugrand, G., **Helaouët, P.**, 2008. Simple procedures to assess and compare the ecological niche of species. *Marine Ecology Progress Series* 363, 29-37. This paper is part of the chapter 3.
4. **Helaouët, P.**, Beaugrand, G., 2009. Physiology, ecological niches and species distribution. *Ecosystems* 12, 1235-1267. This paper is part of the chapter 4.
5. **Helaouët, P.**, Beaugrand, G., Reid, P.C., submitted. Macroscale ecophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Global ecology and Biogeography*. This paper is part of the chapter 5.

Presentation and Conferences Attended:

Helaouët, P. 2009. 3rd GLOBEC Open Science Meeting “Marine ecosystems: from function to prediction”, Victoria, British Columbia, Canada, 22-26 June 2009 (presentation).

Helaouët, P. 2007. Marine institute conference “Understanding marine systems”, University of Plymouth, England, 17th December 2007 (presentation).

Helaouët, P. 2007. Habitat modelling of marine populations. IPIMAR, Lisbon, Portugal, 2-13 July 2007 (presentation).

Helaouët, P. 2007. EUR-OCEANS annual PIs meeting in Glyfada, Greece, 25-26 April 2007 (presentation).

Helaouët, P. 2006. Towards ecosystem oceanography: Identification and modelling of controls in marine ecosystems. Dragerup field station, Dragerup, Danmark, 18-28 June 2006 (presentation)

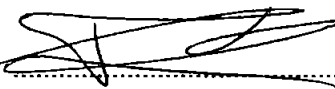
Helaouët, P., Johns, D. 2006. NCOF Development workshop 12-15 June 2006 (poster)

Helaouët, P. 2006. EUR-Oceans annuals Pls meeting in Barcelona, Spain, 15-16 March 2006 (poster)

External Contacts:

Word count of main body of thesis: 26190

Signed



Date

12.7.10

Chapter 1

Introduction

Climate variability in the North Atlantic Ocean is primarily forced by the atmospheric variability related to the state of the North Atlantic Oscillation (NAO) or the latitudinal displacement of the Gulf Stream North Wall (GSNW). Recently, some authors provided evidence for an anthropogenic influence related to global warming (Levitus *et al.*, 2005). These changes are expected to affect the state, the structure and the functioning of ecosystems of the North Atlantic Ocean and its adjacent seas.

Chapter 1: Introduction

1.A. The North Atlantic Ocean

The Atlantic Ocean is the second largest ocean in the world (Tomczak & Godfrey, 2003). When all adjacent seas are included, the Atlantic Ocean covers $107 \times 10^6 \text{ km}^2$ (about a fifth of the Earth's surface) with a total meridional extent of more than 21,000 km from the Arctic to the Antarctic (Tomczak & Godfrey, 2003). The North Atlantic Meridional Overturning Circulation (MOC) transfers warm upper waters from the tropical region to the polar region and returns cold deep waters southward (Garrison, 2004). This feature has a special role in the regulation of weather and climate over the North Atlantic Ocean and a capital function in the global ocean circulation (Stenseth *et al.*, 2004). As part of the MOC, the Gulf Stream (composed by the Florida Current, the Gulf Stream extension and the Gulf Stream proper) plays an important role in the transfer of heat in the North Atlantic Ocean (Tomczak & Godfrey, 2003). The Gulf Stream proper is a western-intensified current, largely driven by wind stress, which flows across the open ocean. It separates in the region east of 50°W (referred as the Gulf Stream extension) near the Newfoundland Rise (also called Grand Banks) into two branches giving the North Atlantic Current (NAC) flowing towards Scotland and the Azores Current, which is part of the subtropical gyre, streaming to the west (Tomczak & Godfrey, 2003). The NAC is mostly driven by thermohaline circulation carrying warm water northeast across the Atlantic Ocean along the boundary between the Subpolar and the Subtropical gyre (Stenseth *et al.*, 2004). The inflows reach the Nordic seas (Greenland, Iceland and Norwegian Seas) and the Labrador Sea, where they are subject to deep convection and vigorous mixing (Fig. 1.1; Stenseth *et al.*, 2004). Through these processes, the North Atlantic Deep Water (NADW) is formed, constituting the lower southward-flowing part of the MOC (Talley *et al.*, 2003). There is evidence for a link between the MOC and abrupt changes in surface climate during the Earth history even if

the exact mechanisms involved remain unclear (Clark *et al.*, 2002). To date no consistent evidence for a trend in the mean strength of the MOC has been found over the modern instrumental record (Intergovernmental Panel on Climate Change, 2007a).

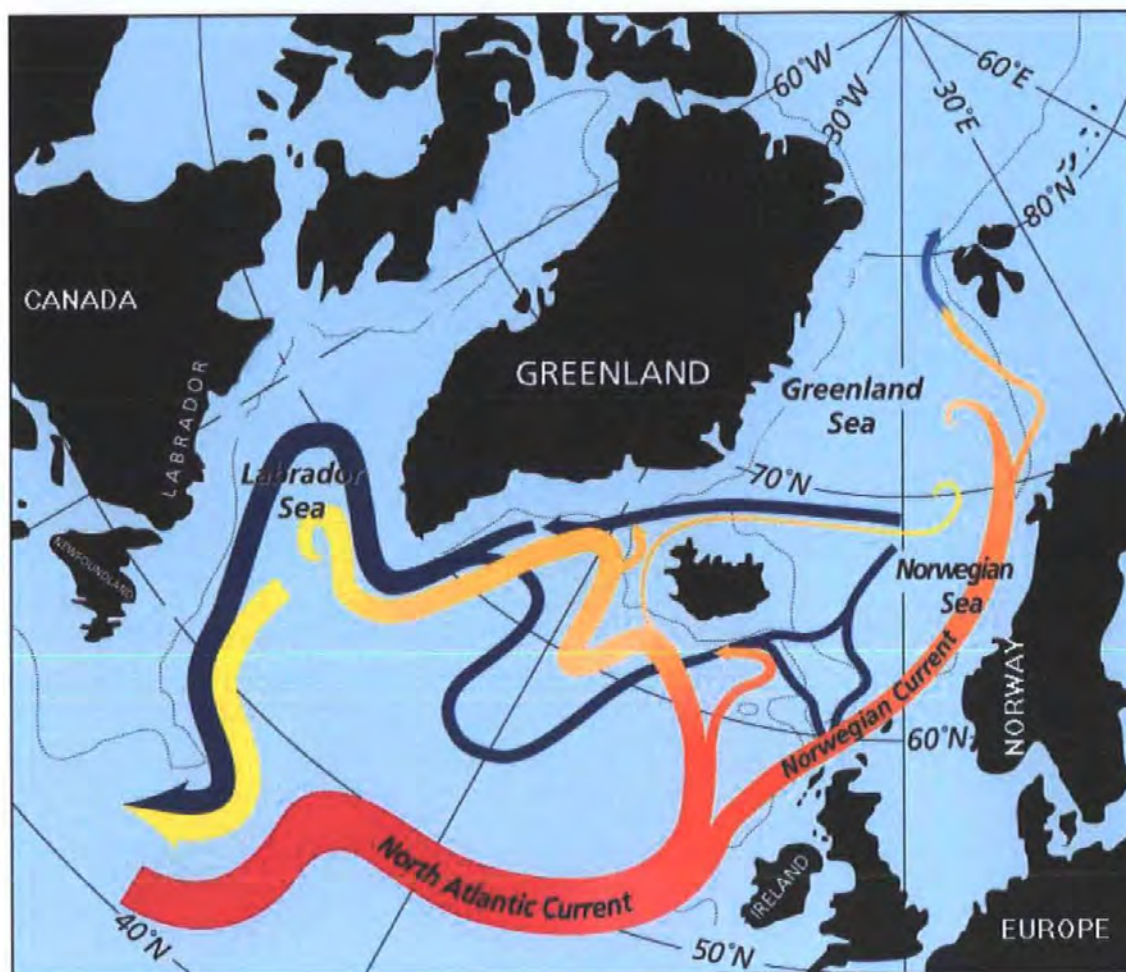


Figure 1.1. Pathways associated with the transformation of warm subtropical waters into colder sub-polar and polar waters in the northern North Atlantic Ocean. (source: <http://www.gsf.nasa.gov/topstory/2004/0415gyre.html>)

1.B. The North Atlantic climate variability

The climate of the North Atlantic Ocean displays a high variability which occurs at a large range of timescales (Stenseth *et al.*, 2004). Multidecadal variations in sea surface temperature in the North Atlantic have been identified (Schlesinger & Ramankutty, 1994). It has also been shown that global climate models dealing with external factors such as greenhouse gases and solar variations cannot explain entirely the multidecadal Atlantic variability (Andronova & Schlesinger, 2000), suggesting that this variability is more likely to arise from internal actions of the climate system. The Atlantic Multidecadal Oscillation (AMO) identified by Kerr (2000) has been linked with several climatic features such as the multidecadal variations in the summertime climate of both North America and Western Europe (Sutton & Hodson, 2005), and the Western Hemisphere rainfall and hurricanes in the United States (Goldenberg *et al.*, 2001; McCabe *et al.*, 2004). However, the evidence for an Atlantic link is derived from observations showing correlation rather than causality (Sutton & Hodson, 2005). Therefore, understanding whether AMO-related changes are responsible for the observed variations in the North Atlantic climate is still an ongoing debate with climatologists.

The major driving climatic force in the north Atlantic has been identified as the North Atlantic Oscillation (NAO) discovered by Walker (1924) at the same time as the El Niño Southern Oscillation (ENSO; Van Loon & Rogers, 1978; Rogers, 1984; Hurrell *et al.*, 2001). An index of its activity has been defined and is generally measured as the difference in normalised Sea Level Pressures (SLP) between Ponta Delgadas (Azores) and Akureyri (Iceland) in the winter season (December to February) (Rogers, 1984). A high and positive value in the winter NAO index reflects a higher than usual pressure difference between the subpolar and subtropical Atlantic (Fig. 1.2.a). This augments the

influence of westerly winds, which increase temperature in the western part of Europe while an inverse pattern occurs on the eastern coast of Canada. When the NAO index is negative, this pressure difference is reduced and wind circulation changes over Europe (Northerly wind increases) which decreases winter temperature in Western Europe (Fig. 1.2.b). The oscillation presents a cyclic variability with different periods of 2.1, 8 and 24 years and a multi-decadal signal (Fig. 1.3; Cook *et al.*, 1998). Changes in the NAO index may affect the characteristics of the North Atlantic current system and the horizontal flow of the upper ocean through the alteration of the oceanic heat transport and therefore influence marine ecosystems (Dickson & Turrell, 2000).

The cyclic variability of the NAO exerts a dominant influence on winter-time temperatures across the North hemisphere and therefore on the North Atlantic Ocean Sea Surface Temperatures (SST). In the same way, the Gulf Stream undergoes long-term changes of latitude. The latitudinal position of the north wall of the Gulf Stream (GSNW) has been used as an indicator of climatic fluctuations over the North Atlantic (Taylor, 1995). The NAO and the GSNW displacement, as two strong signals of large-scale hydro-climatic variations, are probably connected through atmosphere-ocean interaction (e.g. Ottersen & Stenseth, 2001). As stated by Planque (1996), they probably play an important role but at different time-scales, since both interannual and interdecadal fluctuations in surface ocean conditions in the North Atlantic are largely governed by wind-induced changes in the sea-air energy fluxes. They can be considered as a major source of hydro-climatologic variability in the North Atlantic Ocean and may therefore have a profound influence on a large variety of biological processes (Stenseth *et al.*, 2004). Small but persistent changes in climate can have an impact on ecosystems. These changes occur naturally like, for example, in the case of ice ages and interglacial

periods. However, the 20th century highlights the possibility of climate changes through human activity.

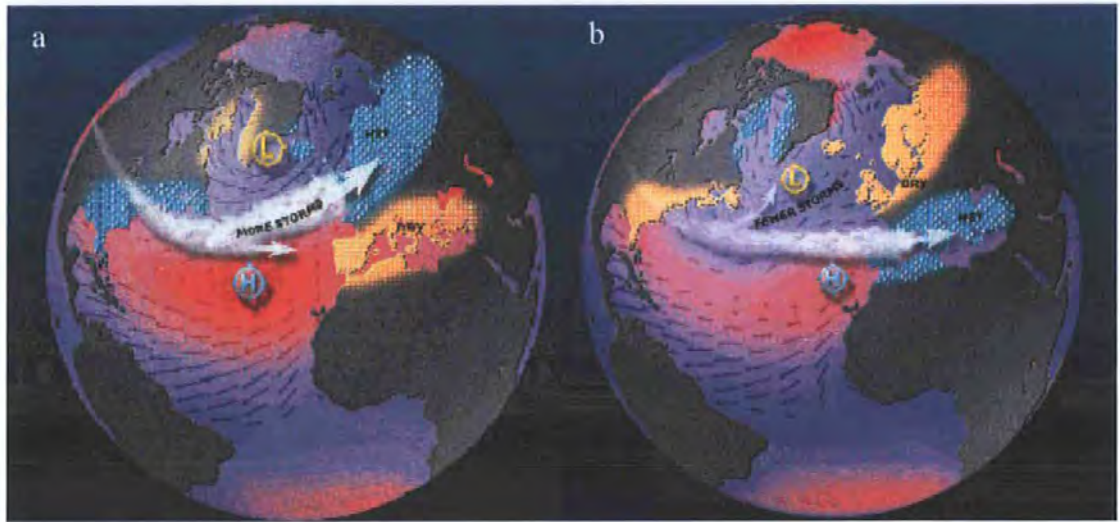


Figure 1.2. Simplified representation of the influence of the NAO in the North Atlantic Ocean during (a) a positive and (b) a negative index phase. Source <http://www.Ideo.columbia.edu/NAO> created by Ian Bell and maintained by Martin Visbeck.

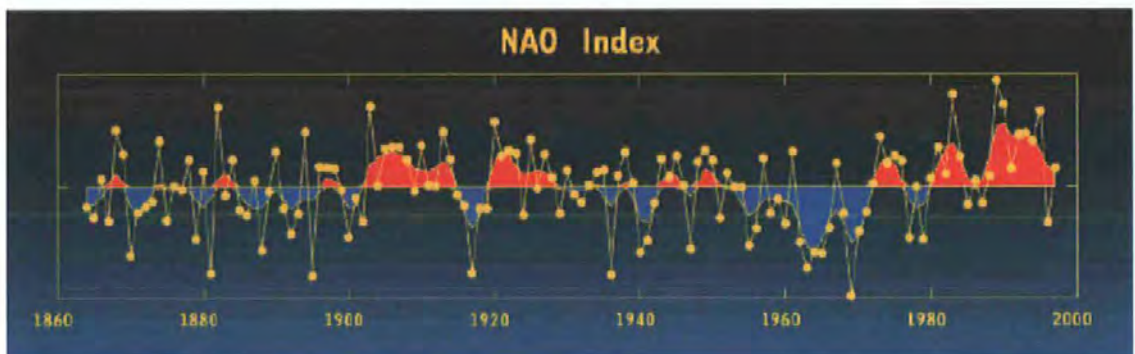


Figure 1.3. Changes in the NAO index from 1964 to 1997. Extreme positive events are in red while extreme negative events are represented in blue. Source <http://www.Ideo.columbia.edu/NAO> created by Ian bell and maintained by Martin Visbeck.

1.C. Anthropogenic climate change

The climate system can be defined as the interactions between the atmosphere, land surface, cryosphere, hydrosphere and biosphere (Intergovernmental Panel on Climate Change, 2007b). The climate system evolves through time due to its own internal dynamics and due to changes in external factors (also called forcings). The global mean surface temperatures have risen by $0.74^{\circ}\text{C} \pm 0.18^{\circ}\text{C}$ when estimated by a linear trend over the last 100 years (1906-2005) and one part of this increase has been linked to a rise in the concentration of some greenhouse gases (GHGs) such as carbon dioxide and methane (Intergovernmental Panel on Climate Change, 2007a). By 2100, most projections of human-induced climate change fall into ranges of about 1.3 to almost 4.5°C increase in annual global mean surface temperature compared to the period 1961-1990 (Intergovernmental Panel on Climate Change, 2001). Levitus *et al.* (2001) suggest that the ocean heat content constitutes the major component of the variability of the total heat balance of the Earth. Both structure and functioning of ocean ecosystems are linked to climatic conditions which are expected to change with a changing climate. The potential response of ocean ecosystems to climatic variability has become more documented (Intergovernmental Panel on Climate Change, 2007b).

1.D. Copepods as climate change indicators in the North Atlantic

Ocean

There are many cycles existing among most of the chemical elements present within an ecosystem. Some of them are cycling back and forth between organisms and their physical environment and are therefore called biogeochemical cycles (Nybakken, 2001). The large-scale patterns of biogeochemical process in pelagic oceanic environments results from ocean climate, mostly from the seasonal cycles of vertical stability of the water column, nutrient supply, and intensity of illumination (Longhurst, 1995). Based

on that statement, the North Atlantic Ocean has been divided into four biomes called the Atlantic Coastal Biome, the Atlantic Polar Biome, the Atlantic Trade-Winds Biome and, the Atlantic Westerly Winds Biome, each divided into a number of provinces (Fig. 1.4; Longhurst, 1998). Their ecological characteristics have been reviewed in Longhurst (1998) and some complementary descriptions added in Beaugrand *et al.* (2001) and Beaugrand *et al.* (2002a) for the northern part of the North Atlantic Ocean and its adjacent seas. Also, large-scale variability of climate (e.g. both AMO and NAO) may temporarily rearrange the occurrence of provinces by changing the position of their borders. Recent studies have provided evidence of climate modifying benthic and pelagic ecosystems from plankton to fish to higher trophic levels. The impact of climate change has been particularly well documented for copepods (Roemmich & McGowan, 1995).

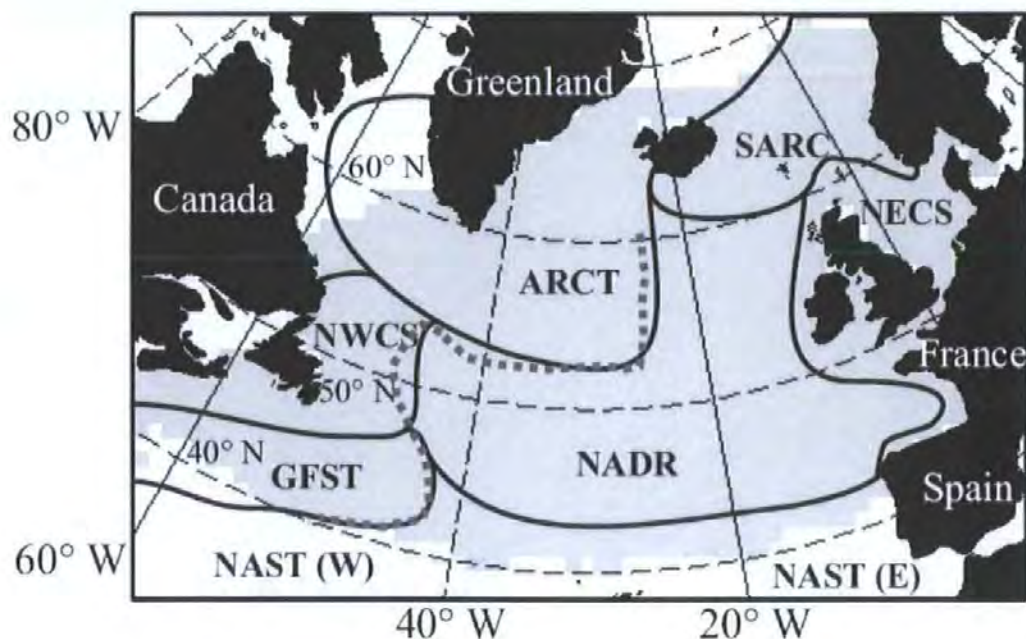


Figure 1.4. Main area (in grey) sampled by the Continuous Plankton Recorder survey from 1960 to 2002. Provinces as defined recently by Longhurst (1998) are indicated. Atlantic Polar Biome. SARC: Atlantic Subarctic Province. ARCT: Atlantic Arctic Province. Atlantic Westerly Winds Biome. NADR: North Atlantic Drift Province. NAST: North Atlantic Subtropical Gyral Province (West (W) and Eastern (E) part). GFST: Gulf Stream Province. Atlantic Coastal Biome. NECS: Northeast Atlantic Shelves Province. NWCS: Northwest Atlantic Shelves Province. The grey dash line represents the Oceanic Polar Front. (from Beaugrand *et al.* 2001).

Copepods constitute a key trophic group, having a central role in the trophodynamics of pelagic ecosystems. These zooplankton organisms transfer energy from phytoplankton to higher trophic levels (Mauchline, 1998) and are often important in the diet of at least one developmental stage of some economically important fish species such as cod (*Gadus morhua*), herring (*Clupea harengus*) or mackerel (*Scomber scombrus*) (Sundby, 2000; Beaugrand *et al.*, 2003a; Orlova, 2005; Skreslet *et al.*, 2005). They also represent a high proportion of the carbon biomass in the mesozooplankton, generally increasing with latitude (e.g. 33% in the Atlantic Trade Wind Biome, 53% for the Atlantic Westerlies Wind Biome and 69% in the Arctic Ocean, (Longhurst, 1998)). In the North Atlantic, the mesozooplankton are largely dominated by copepods and among them by the genus *Calanus* which constitutes a major resource to higher trophic levels and a potential important grazer for phytoplankton. Members of this genus are among the largest copepods and can contribute as much as 90% of the dry weight of the mesozooplankton in some regions such as the North Sea and the Celtic Sea (Bonnet, 2005 and references therein). The copepod genus *Calanus* is widely distributed over the global ocean and, consequently, is found in almost all marine environments, from tropical to arctic regions. Among other things, the life cycle of some *Calanus* species in the North Atlantic Ocean is characterised by periods of dormancy called overwintering (Marshall & Orr, 1955) during the winter at a particular depth, this depth varies geographically (Heath *et al.*, 1999a). Despite a number of studies focused on overwintering, it remains unclear whether this phenomenon is motivated to reduce predation risk and/or to diminish the respiration costs (e.g. Hirche, 1991; Miller *et al.*, 1991; Hirche, 1996; Kaartvedt, 1996).

Due to *Calanus finmarchicus*' place in the food web (e.g. Aksnes & Blindheim, 1996) and its importance as a prey for a large range of exploited fish (e.g. such as cod (Lynch

et al., 2001)), its wide distribution (e.g. Conover, 1988) together with high abundance often dominating the mesoplanktonic biomass (Heath *et al.*, 2000), it constitutes a key structural species. *C. finmarchicus* is a mainly omnivorous calanoid copepod (Mauchline, 1998) which, before becoming adult (CVI), will develop through six naupliar (NI to NVI) and five copepodite stages (CI to CV; Fig. 1.5). This species produces at least one generation per year in spring, most often followed by one or two more before the autumn (Conover, 1988) with a development time mainly linked with temperature (Campbell, 2001). Biogeographical studies necessitate dealing with the climate complexity, and associated biogeochemical cycles, as well as with the complexity of organisms' life cycles. This constrains most modelling studies to choose a strategic simplification (Speirs *et al.*, 2006) by, for instance, ignoring the horizontal transport of the studied organisms (Carlotti & Radach, 1996). In this work, the ecological niche concepts were used to integrate all those sources of complexity in a common framework.

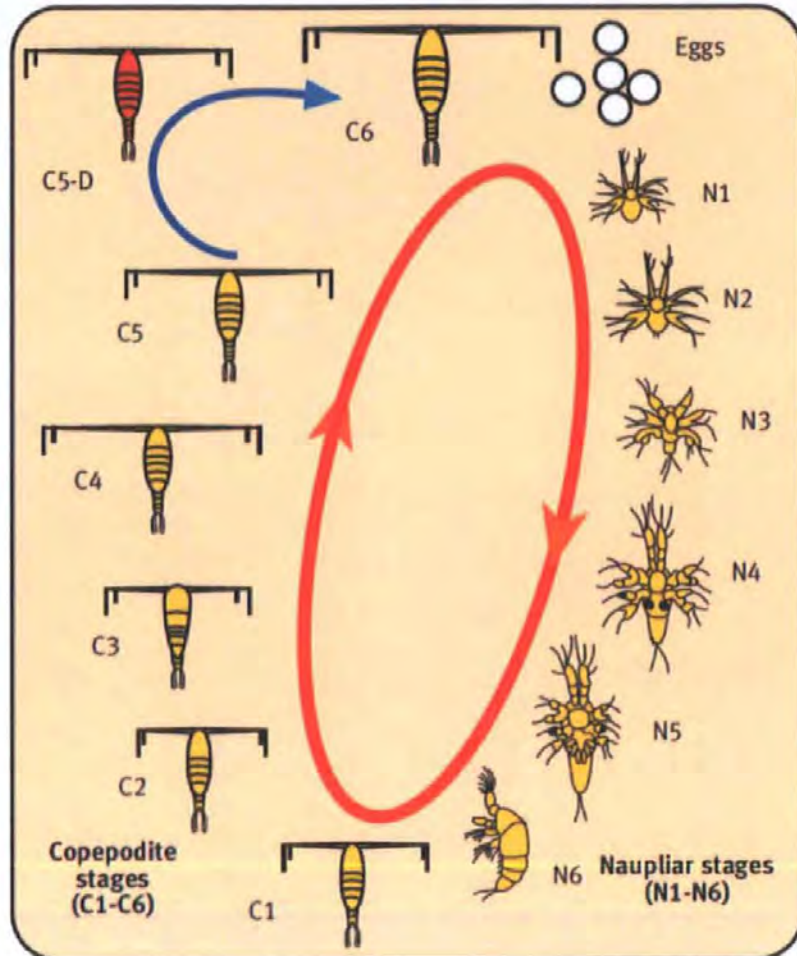


Figure 1.5. Schematic representation of the *Calanus finmarchicus* life cycle. The eggs hatch into nauplii which develop through 6 moult stages (N1-N6) and then 5 copepodite stages (C1-C5) before becoming adults (C6). At certain times of year, stage 5 copepodites may enter a dormant state (C5-D) in which they may remain for many months before awakening and developing into adults. (From <http://www.marlab.ac.uk/FRS.Web/Uploads/Documents/ME02Zooplankton>).

1.E. Overview of the ecological niche concepts

By controlling the quantity of nutrients available (e.g. vertical mixing, upwelling), keeping individuals constituting a population together in the suitable place (e.g. Ekman convergence cells, lack of turbulences for the dispersion) or by driving the capability for an organism to colonise new environments (e.g. larvae dispersal), climate variability greatly influences the dynamics of both spatial and temporal patterns of species distribution (Stenseth *et al.*, 2004). Many external forces occurring at different scales (from micro- to mega-scale) influence the variability of marine ecosystems. Therefore, identifying the main variables that drives the temporal variability of biological processes is complex (Araújo & Guisan, 2006).

Species Distribution Models (SDMs) are models that relate observations of species over a period of time to various attributes of the environment (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). SDMs are characterised by their reliance on the ecological niche concept (Guisan & Zimmermann, 2000). Many definitions of the ecological niche have been proposed (Grinnell, 1917; Elton, 1927; Hutchinson, 1957; Macarthur, 1958; Levin, 1970; Odum, 1971). Consequently, two different ways to conceptualise the ecological niche are often made. The first one is based on “functional” criteria while the second one is related to the concept of “habitat”.

Many definitions of habitat exist in the literature. The simplest is probably proposed by Morrison *et al.* (1998) which states that the habitat is “a place where an animal lives”. Here the habitat is defined as a physical description of area where species lives. A habitat is usually described using abiotic and biotic features known to be important for an organism but it is not necessary to take into account the mechanistic links occurring between the parameters and the organism’s fitness (Kearney, 2006). A habitat can exist

without reference to a species. For example, it is possible to define a typical Martian habitat without taking into account any Martian species.

For Odum (1971) “the ecological niche of an organism depends on where it lives and on what it does”. By extension, the habitat becomes the organism's address and the niche its profession. This definition is close to Elton (1927) ecological niche concept. This author compared the niche to the function of an organism in the community. This concept is therefore related to the location of the species within the food web and includes how the biomass and energy are distributed among the different trophic levels.

Grinnell (1917) defined the niche as all the areas where an individual species can live if conditions are suitable for life. Grinnell's original explanation of the niche is aligned with the first ecological definition based on the ecological requirements and have therefore the same roots as the Hutchinson's (1957) definition. Hutchinson defined the niche of a species as the field of tolerance of the species to the principal factors of the environment. The niche can be represented in Euclidean space, with as many dimensions as there are factors, like a “n-dimensional hypervolume”. When a few numbers of parameters are used, the niche of two species can still overlap. Adding the number of factors allows the relative importance of the overlapping to be reduced, leading possibly to the complete separation of the niche of two species (i.e. Gause's competitive exclusion principle (Gause, 1934)). A niche is not a place but more like a summary of the organism requirements and tolerance. Therefore, each habitat might provide many potential niches but according to Hutchinson's definition, only species have niches, not environments.

For the last 40 years, the niche concept has been refined. The distinction between fundamental and realised niche can be made in the Hutchinsonian framework. First, according to Gause's competitive exclusion principle (Gause, 1934), a species will not utilise its entire fundamental niche, but rather the realised niche actually occupied by the species which will be smaller, only consisting of parts of the fundamental niche where the species is competitively dominant. But species not only respond to variation in the environment, they also change the environment in which they occur. Then the distinction between two cases can be made. The first case is when species interact directly with each other (e.g. predator-prey interactions or inter-specific territorial interactions) and the second case is for species interacting indirectly by jointly influencing the environments. Second, Pulliam (2000) propose to differentiate source habitats, where local reproduction exceeds local mortality from sink habitats where local mortality exceeds local reproduction. A habitat could be qualified as "sink-habitat" when the conditions (biotic or abiotic) are not suitable or sufficient for a species to complete its own life history. In a source-sink situation, a species can be expected to frequently occur outside the boundaries of its fundamental niche if the frequency of the immigration (dispersal) permits to maintain a large number of individuals in place despite the environmental factors. The result is that the realised niche can be larger than the fundamental one.

1.F. Goals of the study

Understanding the influence of climate on oceanic species distribution is crucial to fundamental and applied research in biogeography, ecology and wildlife management (Araújo & Guisan, 2006). Plankton play an important role in biogeochemical cycles and in the functioning of marine ecosystems. Because of their ability to integrate a wide range of hydrometeorological forcing it has been stressed that changes in the

composition and abundance of plankton species may act as indicators of climate change. The main aim of this work is to use information provided by the Continuous Plankton Recorder (CPR) survey combined with environmental databases to understand, assess and predict the potential impact of climate change in the pelagic ecosystems of the North Atlantic Ocean, focusing on the subarctic species *Calanus finmarchicus*.

All the ecological questions addressed in this work necessitate long-term information on both the physics and the biology of the North Atlantic Ocean. While physical data are generally widely available, biological information on the spatial, seasonal and decadal distribution of species are extremely rare. The Sir Alister Hardy Foundation for Ocean Science (SAHFOS) have been collecting plankton samples in the North Atlantic Ocean for more than 60 years using Continuous Plankton Recorders (CPR) which provides one of the biggest and most useful database of the world.

The first chapter constitutes a general introduction to this work. The objectives were:

- (1) To present the North Atlantic Ocean and its climate variability.
- (2) To describe the role of Copepods in this Ocean.
- (3) To introduce the concept of ecological niches.

The second chapter is focused on the Continuous Plankton Recorder survey conducted by the Sir Alister Hardy Foundation for Ocean Science. The objectives were:

- (1) To present the origin of the CPR concept.
- (2) To describe the sampling method and thereby to highlight both strength and weakness of the method.
- (3) To present some statistical analyses applicable on the CPR database.

The third chapter is focused on the determination of the environmental optimum level of both *Calanus finmarchicus* and *C. helgolandicus* regarding 11 environmental parameters selected regarding their potential influence on the spatial distribution of both species (Helaouët & Beaugrand, 2007; Beaugrand & Helaouët, 2008). The objectives were:

- (1) To quantify the influence of each parameter on the spatial distribution of both *Calanus* species at a decadal scale.
- (2) To identify and to calculate the breadth of realised niches of both *Calanus finmarchicus* and *C. helgolandicus*.
- (3) To provide a baseline to forecast the potential modifications in the abundance and spatial distributions of the two species expected with global climate change.

The fourth chapter is focused on the relationship between both fundamental and realised niche of *C. finmarchicus* at a macroecological level (Helaouët & Beaugrand, 2009). The objectives were:

- (1) To provide a new method to assess the fundamental niche and to compare it with the realised one.
- (2) To combine results from the niches comparison with IPCC scenarios of temperature to assess the potential changes in the spatial distribution of the species that might occur during the 21st century.
- (3) To investigate the potential implications of those changes for lower and upper trophic levels and some biogeochemical cycles.

The fifth and last chapter is focused on the impact of climate on *C. finmarchicus* abundance and egg production rate at a seasonal scale (Helaouët *et al.*, submitted). The objectives were:

- (1) To refine at a macroecological scale the main abiotic factors impacting the spatial distribution of *Calanus finmarchicus* in the North Atlantic Ocean.
- (2) To assess changes in the explicative power of those drivers at a seasonal scale.
- (3) To investigate the potential changes in the abundance of *C. finmarchicus* in some key regions by using a joint macroecological and ecophysiological methods based on the concept of the niche of Hutchinson (1957).

Chapter 2

The continuous Plankton Recorder (CPR) survey

If the biogeochemical processes are altered by climate changes, major shifts in the planktonic population structure can be expected (Angel *et al.*, 2007). The CPR survey account for the world's largest dataset to address major hypotheses on the structure and functioning of the North Atlantic plankton ecosystem related to climate changes.

Chapter2: The continuous Plankton Recorder (CPR) survey

2.A. Concepts and history

The Continuous Plankton Recorder survey (CPRs) is a large-scale plankton monitoring program. The CPR (the recorder) was towed for the first time during the “Discovery” expedition in the Antarctic in 1925-1927 over 1300 miles (Hardy, 1926). Since 1931 the CPR has been used on regular routes in the North Sea (Hardy, 1939). Since 1991, the CPR survey and the dataset have been managed by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). Now the CPR survey is the largest multi-decadal plankton monitoring programme in the world. The data on the near-surface abundance of phyto- and zooplankton are available monthly from 1946 and at the end of 2006, this dataset amounts to 2,542,580 positive entries, counted for 519 phyto- and zooplankton taxa, many of which are identified to the species level. The list of the species is consultable on the SAHFOS website (<http://www.sahfos.org/>). CPR data have become increasingly important as a baseline to assess impacts of global change on pelagic ecosystems. This is an important set of tools for all those concerned with biodiversity loss, climate change, eutrophication, pollution, harmful algal blooms and sustainable fisheries (Brander *et al.*, 2003).

After the prototype device, two new kinds of recorder have been deployed (Fig. 2.6). The first one is called the “diving plane” which was used until 1975-1980 then it was replaced by a new version, “box-tail”, with a greater stability at higher speed (Fig. 2.7). It has been shown that all the different changes have not affected the time-series (Hays & Warner, 1993; Hays, 1994; Warner & Hays, 1994; Batten *et al.*, 2003; Reid *et al.*, 2003a; Jonas *et al.*, 2004).



Figure 2.6. Original Hardy Continuous Plankton Recorder, 1925 (source: Andy Bleck).

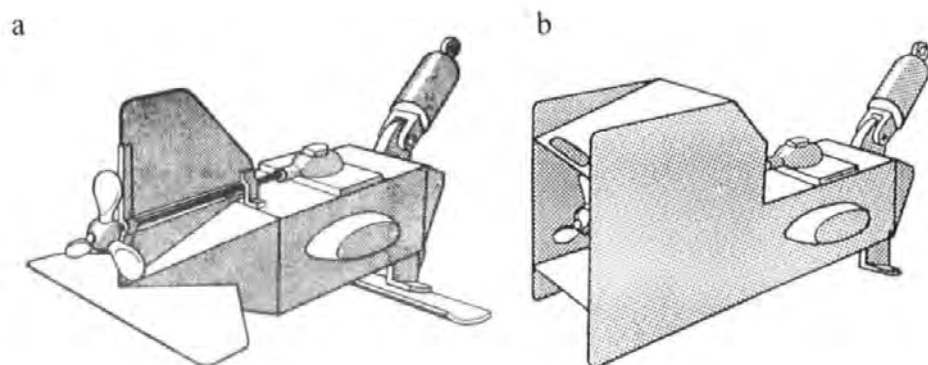


Figure 2.7. The two different kind of plankton recorder used since the beginning of the study. The first one (a) is the “diving plane” and the second one (b) is “the box-tail”.

2.B. Sampling and sub-sampling

The CPR is towed behind ships of opportunity on their normal trading routes at their conventional operating speeds (15–20 knots) without any scientists on board. A fixed sub-surface depth (a standard depth of 7 m) was chosen to give the most consistent results in the relatively shallow North Sea (Hays & Warner, 1993). Water enters the CPR through a square aperture 1.27 cm 1.27 cm (1.61 cm²) (Fig. 2.8) down an expanding tunnel, which effectively reduces the water pressure to minimise damage to the captured plankton, and exits through the rear of the device (Fig. 2.8). The movement of the water past the CPR turns an external propeller at the rear of the device that operates a drive shaft and gear system, which advances the silk filtering mesh. Plankton in the water are filtered onto this constantly moving band of silk. The filtering silk meets a second band of covering silk, effectively sandwiching the plankton, and is then wound onto a spool in a storage tank containing formalin. The mesh size of the silk is 270 µm in order to give an adequate representation of copepods, cladocera, pteropods, and chaetognaths, but also to give an indication of blooms of large phytoplankton, while reducing clogging by small phytoplankton cells (Hardy, 1939). Despite the relatively large size of the mesh, small phytoplankton are still retained on the silk.

After towing, the CPR is returned to the laboratory and the silk is removed from the storage tank. The silk is divided into samples corresponding to 10 nautical miles (18.5 km) of towing (equivalent to about 3 m³ of sea water filtered assuming 100% filtration efficiency; Jonas *et al.*, 2004). Positions and times of each sample are estimated with the knowledge of the start and the end of each tow as well as possible changes in the direction and the speed of the ship. The identification and plankton counting is realised in four steps:

2.B.1. Step 1. It consists of an estimation of the colour of the silk in order to give an index (called greenness index) of concentration of chlorophyll in the environment. There are four different categories of colour (no colour, very pale green, pale green and green).

These four levels of the phytoplankton colour index (PCI) represent the amount of phytoplankton pigment on the silk and have been assigned numerical values on a ratio scale based on acetone extracts using spectrophotometric methods (Colebrook & Robinson, 1965).

2.B.2. Step 2. Phytoplankton are identified and counted to species level when it is possible. More than 200 phytoplanktonic species or taxa are identified. Subsampling of the silk is processed by selected 20 fields under a x400 magnification (295µm diameter view) on one of the diagonals of the silk. These 20 fields amount to 1/10,000 of the area of the filtering silk. Abundance of each phytoplankton taxonomic category is determined by counting the number of fields in which each taxon is detected. This has been derived from the Poisson distribution, which assumes organisms are randomly distributed on the silk (Colebrook, 1960).

The methodology of the step 1 and step 2 have been unchanged since 1958.

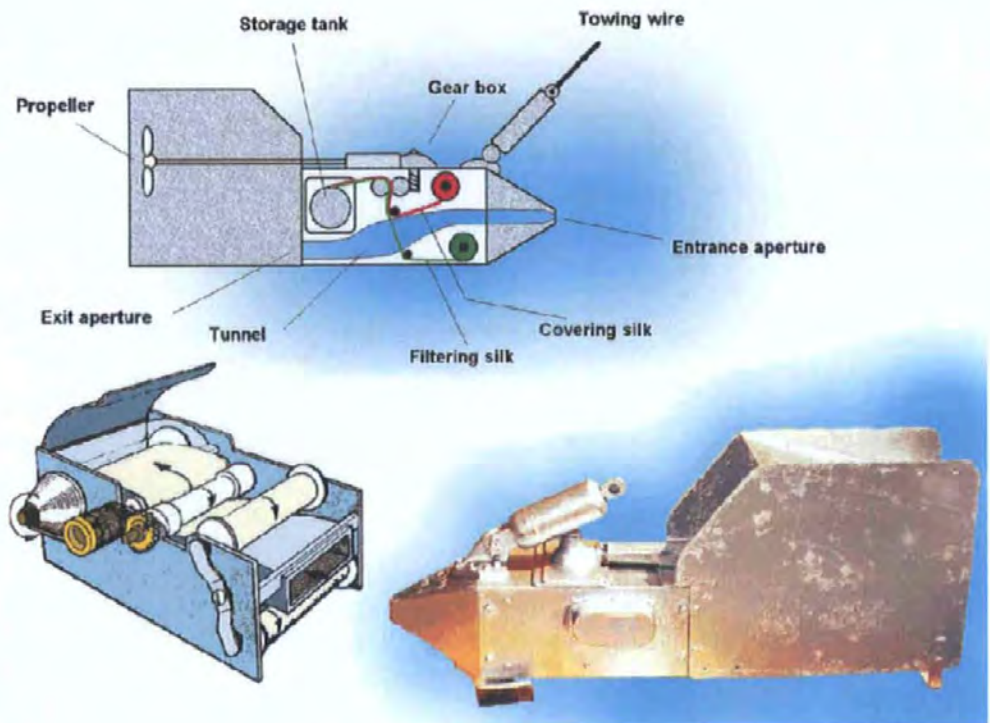


Figure 2.8. A cross-section of the CPR, its internal mechanism and CPR body.

2.B.3. Step 3. This consists of an examination of zooplankton that are generally smaller than 2 mm. Over 70 species or taxa are identified at this stage. Five fields (2.06 mm diameter view) on one of the diagonals of both filtering and covering silks are studied under a x45 magnification. It assumes retained organisms are uniformly distributed on the silk. This procedure examines 1/50 of the silk.

2.B.4. Step 4. This consists of an identification of the zooplankton greater than *Metridia lucens* stage V in size (>2 mm total length: (Rae, 1952)). More than 150 species or taxa are identified at this step. A category system is used to count the zooplankton in order to reduce the time of the analysis. The method is described in details in Colebrook (1960), Colebrook & Robinson (1965) and Warner & Hays (1994).

Quality control checks are carried out at all stages of the analysis and the data processing. If high variations are detected between two samples related in space or time, an analyst is asked to re-analyse the sample.

2.C. Overview of statistical methods applied to CPR data

2.C.1. Descriptive methods applied to CPR data

Until the middle of the 70's, investigations of CPR data were carried out using graphs, contour diagrams and maps while most statistical analyses were restricted to one dimension. This led rapidly to good progress in describing the biogeography of species around United Kingdom (Lucas, 1940; Colebrook *et al.*, 1961a; Robinson, 1961) such as the coastal distribution of *Centropages hamatus* and *Ceratium fusus* (Colebrook *et al.*, 1961b). This way of investigating CPR results is still used nowadays, although the multivariate statistics have increased drastically the quantity of information extracted

from CPR dataset (Beaugrand *et al.*, 2003b). The aim of this section is not to provide a thorough description of all statistics methods used in ecology with CPR data but rather to show the range of applications the use of modern statistics provides.

2.C.2. Multivariate analyses

After this descriptive period, it appeared that the huge quantity of multidimensional information provided by the survey had to be sorted and reduced. Methods of ordination in reduced space have been applied extensively to CPR data. Their aim being to represent the relationships between objects and observations by reducing the number of dimension (Legendre & Legendre, 1998). Standardised Principal Component analysis (PCA) was applied for the first time by Colebrook (1964) to investigate patterns of variability of 22 taxa around United Kingdom using eigenvectors. The author showed the separation of the 22 taxa into 5 species associations (northern and southern oceanic, northern and southern intermediate, and neretic) and specified that their location were partially explained by the synergistic effects of temperature, seasonal variability of the temperature and salinity. PCA (e.g. Colebrook, 1964; Colebrook, 1978; Colebrook, 1982; Reid *et al.*, 1998; Reid & Beaugrand, 2002), three-mode PCA (e.g. Jolliffe, 1986; Beaugrand *et al.*, 2000; Edwards, 2000) and non-metric multidimensional scaling (e.g. Kruskal, 1964; Lindley, 1987; Lindley & Williams, 1994) are perfect examples of ordination in reduced space applied to the data set.

Another way to describe relationships between objects or descriptors was to investigate rearrangement of an association matrix. For example Colebrook (1969) used the method “seriation” to examine geographical similarities in the interannual variability of *Temora longicornis* in the North Sea. This opened the way to cluster analyses which are new

powerful multivariate tool using almost any distance or similarity matrix between objects or descriptors. This method can fit with the type of data (e.g. quantitative, semi-quantitative or qualitative data) and nature (abundance or presence/absence) by changing the coefficient of association.

Over the years, the CPR data have been used in many biogeographical studies (Beaugrand *et al.* 2003b and references therein), generating the deployment of numerous statistical analyses (Beaugrand *et al.* 2003b). In this work, the standardised principal component analysis has been used to extract the relevant information in many tables derived from the CPR dataset. PCAs are unconstrained ordination using Euclidian distance and are mostly used to visualise multidimensional dataset (by reducing the number of dimensions). PCAs are also a good way to remove correlations (in the new table, constituted by two axes, points have a null correlation), to reduce the inherent variability that occurs in most biological dataset (considering that removed axis are noisy) and to classify data in clusters. All those features make together the PCA an accurate tool to investigate the macroecology using CPR data.

Chapter 3

Macro-ecological study of the niche of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas

The present chapter is constituted by the following two papers:

Helaouët, P., Beaugrand, G., 2007. Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. Marine Ecology Progress Series. 345, 147-165.

Beaugrand, G., Helaouët, P., 2008. Simple procedures to assess and compare the ecological niche of species. Marine Ecology Progress Series 363, 29-37.

Global climate change is expected to modify the spatial distribution of marine organisms. However, projections of future changes should be based on robust information on the ecological niche of species. This paper presents a macroecological study of the environmental tolerance and ecological niche (sense Hutchinson, i.e. the field of tolerance of a species to the principal factors of its environment) of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. Biological data were collected by the Continuous Plankton Recorder (CPR) survey, which samples plankton in the North Atlantic and adjacent seas at a standard depth of 7 m. 11 parameters were chosen including bathymetry, temperature, salinity, nutrients, mixed-layer depth and an index of turbulence compiled from wind data and chlorophyll *a* concentrations (used herein as an index of available food). The environmental window and the optimum level were determined for both species and for each abiotic factor and chlorophyll *a* concentration. The most important parameters that influenced abundance and spatial distribution were temperature and its correlates such as oxygen and nutrients. Bathymetry and other water-column-related factors also played an important role. The ecological niche of *C. finmarchicus* was larger than that of *C. helgolandicus* and both niches were significantly separated. Our results have important implications in the context of global climate change. As temperature (and to some extent stratification) is predicted to continue to rise in the North Atlantic sector, changes in the spatial distribution of these 2 *Calanus* species can be expected. Application of this approach to the 1980s North Sea regime shift provides evidence that changes in sea temperature alone could have triggered the substantial and rapid changes identified in the dynamic regimes of these ecosystems. *C. finmarchicus* appears to be a good indicator of the Atlantic Polar Biome (mainly the Atlantic Subarctic and Arctic provinces) while *C. helgolandicus* is an indicator of more temperate waters (Atlantic Westerly Winds Biome) in regions characterised by more pronounced spatial changes in bathymetry.

Chapter 3: Macro-ecological study of the niche of *Calanus*

***finmarchicus* and *C. helgolandicus* in the North Atlantic**

Ocean and adjacent seas

3.A. Introduction

Understanding the consequences of variability in climate on pelagic ecosystems requires a clear identification of the factors driving variability in the abundance of each species and the parameters or processes that control their geographical distribution. Biogeographical studies are essential and provide a baseline for evaluation of the impact of climate on ecosystems (Longhurst, 1998; Beaugrand, 2003).

The high nutrient supply in the temperate and subpolar part of the North Atlantic Ocean results in high planktonic production (Ducklow & Harris, 1993; Longhurst, 1998). This region is influenced by the North Atlantic Current which transfers energy and heat from the SW oceanic region of Newfoundland to the NE part of the North Atlantic Ocean (Krauss, 1986). This current also has a profound impact on plankton diversity (Beaugrand *et al.*, 2001). The North Atlantic Ocean is divided into 3 biomes: called the Atlantic Polar Biome, the Atlantic Westerly Winds Biome and the Atlantic Coastal Biome, each divided into a number of provinces (Fig. 1.4; Longhurst, 1998). Their ecological characteristics have been recently reviewed by Longhurst (1998) and some complementary descriptions have been added by Beaugrand *et al.* (2001) and Beaugrand *et al.* (2002b) for the northern part of the North Atlantic Ocean and its adjacent seas.

Copepods constitute a key trophic group, with a central role in the trophodynamics of pelagic ecosystems. These planktonic organisms transfer energy from the phytoplankton to higher trophic levels (Mauchline, 1998) and are often important in the diet of at least 1 developmental stage of economically important fish species such as cod, herring or mackerel (Sundby, 2000; Orlova, 2005; Skreslet *et al.*, 2005). Copepods represent a high proportion of the carbon biomass in the mesozooplankton, generally increasing with higher latitude (e.g. 33% for the Atlantic Trade Wind Biome, 53% for the Atlantic Westerly Winds Biome and 69% for the Arctic Ocean, (Longhurst, 1998)). Members of the genus *Calanus* are amongst the largest copepods and can comprise as much as 90% of the dry weight of the mesozooplankton in regions such as the North Sea and the Celtic Sea (Bonnet (2005) and references therein). The congeneric calanoid copepod species *C. finmarchicus* and *C. helgolandicus* have been well studied (e.g. Planque & Fromentin, 1996; Bonnet, 2005). They are morphologically so similar that they were not distinguished until 1958 in the Continuous Plankton Recorder (CPR) survey (Planque & Fromentin, 1996). However, their spatial distribution differs significantly (Beaugrand, 2004a). *C. finmarchicus* is mainly located in the Atlantic Polar Biome north of the Oceanic Polar Front (Dietrich, 1964; Beaugrand, 2004a; Fig. 1.4) while the pseudo-oceanic species *C. helgolandicus* occurs in more temperate waters south of the Oceanic Polar Front, mostly located above European shelf-edge in the Atlantic between 40° and 60°N (Beaugrand, 2004a; Bonnet, 2005). In regions (e.g. the North Sea) where they occur together, the 2 species generally have different seasonal timing (Beaugrand, 2003). Some studies have also reported different depth of occurrence at the same location (Bonnet (2005) and references therein).

Differences in the spatial or/and temporal patterns of variability in both species of *Calanus* suggest different responses to environmental variability. It is therefore

important to identify their environmental preference (window or tolerance interval) and their environmental optimum level. When the preference of more than one factor has been determined, the ecological niche (sense Hutchinson (1957)) can be calculated (i.e. the field of tolerance of a species to the principal factors characteristics of its environment). The niche can be represented in a Euclidean space with as many dimensions as factors considered. When a few numbers of parameters are used, the niche of 2 species may overlap. Increasing the number of factors reduces the relative importance of such overlap and often enables the complete niche separation (Gause competitive exclusion hypothesis (Gause, 1934)). Abiotic parameters are related to both geographical (e.g. topography) and water-column factors (e.g. nutrient concentration) which influence directly the physiology (e.g. growth, development and mortality rates (Carlotti *et al.*, 1993) or reproduction of a species (Hall, 2002; Halsband-Lenk, 2002)). This study investigated abiotic environment and chlorophyll *a* concentration (as an index of available food), which makes the Hutchinson ecological niche a more suitable concept, often preferred in this type of work (e.g. Pulliam, 2000; Guisan & Thuiller, 2005).

Despite the large number of studies on the biology and ecology of both *C. finmarchicus* and *C. helgolandicus* (e.g. Carlotti *et al.*, 1993; Hirst & Batten, 1998; Heath *et al.*, 1999a; Bonnet, 2005) many gaps in our knowledge remain. Herein we employ a macroecological approach using large data sets of 11 abiotic parameters and data from the CPR survey to (1) determine the environmental preference and optimum level of both species for each environmental parameter, (2) quantify the influence of each parameter on both species, (3) identify and (4) calculate the breadth of their ecological niches. The temporal stability of the temperature profiles of both species is also investigated. A baseline is provided for use in forecasting modifications in the

abundance and spatial distributions of the 2 species expected with global climate change.

3.B. Materials and methods

3.B.1. Biological data

Data on the abundance of *Calanus finmarchicus* and *C. helgolandicus* were provided by CPR survey, a large-scale plankton monitoring programme initiated by Sir Alister Hardy in 1931. The CPR is a robust instrument designed for use by seamen on commercial ships. Management and maintenance of the survey have been carried out by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) since 1991. CPR instruments are towed at a depth of 7 m (Reid *et al.*, 2003a) and the survey has monitored plankton ecosystems at this depth only (Batten *et al.*, 2003). Therefore, it might be dangerous to infer the Hutchinson ecological niche from a single depth. However, calanoid copepods migrate vertically (Daro, 1985) and because CPR sampling is carried out during day and night, it is unlikely that this process influenced too much the measurement of the Hutchinson ecological niche in this study.

Water enters through an inlet aperture of 1.61 cm² and passes through a 270 µm silk filtering mesh (Batten *et al.* 2003). Individuals greater than 2 mm such as copepodite stages CV and CVI of *C. finmarchicus* and *C. helgolandicus* are then removed from both the filtering and covering silk. Generally, all individuals are counted, but for particularly dense samples a sub-sample is taken (Batten *et al.* 2003). Data used in this study correspond to copepodite stages CV and CVI. Despite the near surface sampling, studies have shown that sampling gives a satisfactory picture of the epipelagic zone (Batten *et al.* 2003). This programme has made it possible to obtain one of the greatest databases on marine plankton. Currently, about 200,000 samples have been analyzed, each giving information on the presence and/or the abundance of more than 400

plankton species every month since 1946 in both the temperate and subpolar region of the North Atlantic Ocean.

3.B.2. Environmental data

The zone investigated in this study extended from 99.5°W to 19.5°E of longitude and 29.5°N to 69.5°N of latitude. Eleven environmental factors were chosen (Table 3.1). Sea Surface Temperature (SST) was essential to take into account because of its recognized influence on plankton (e.g. Reid & Edwards, 2001). An indicator of the water turbulence (induced by wind) was used because it has been shown that the effect of wind, by its impact on the water column stability, influences plankton populations (Heath *et al.*, 1999a). The index of turbulence and SST originated from the Comprehensive Ocean-Atmosphere Dataset (COADS) and was downloaded from the internet site of the National Oceanographic Data Center (NODC) (Woodruff *et al.*, 1987). This centre manages acquisition, controls quality and ensures the long-term safeguarding of the data.

Salinity also constitutes an important limiting factor for many species. This parameter, as well as silicates, phosphates, nitrates and dissolved oxygen were downloaded from the World Ocean Atlas 2001 (WOA1) database. Values corresponded to a depth of 10m.

Table 3.1. Origin and characteristics of the environmental data used in this study.

Data	Source	Spatial Resolution	Type	Units	Data Number (in million)
Biotic	Sir Alister Hardy Foundation for Ocean Science	(no grid)	Each month for 1946-2002	Individual number	0.2 per species
Sea Surface Temperature	National Oceanographic Data Center (COADS)	260.5°E to 29.5°E 69.5°N to 30.5°N each 1° degree	Monthly mean 1960-2002	°C	33.5
Wind-induced turbulence index	National Oceanographic Data Center (COADS)	260.5°E to 29.5°E 69.5°N to 30.5°N each 1° degree	Monthly mean 1960-2002	m ³ .s ⁻³	33.5
Salinity	World Ocean Atlas 2001	99.5°W to 19.5E 89.5°N to 10.5°N each 1° degree	Monthly mean (climatology)	psu	2.8
Silicate	World Ocean Atlas 2001	99.5°W to 19.5E 89.5°N to 10.5°N each 1° degree	Monthly mean (climatology)	μmol.l ⁻¹	2.8
Phosphate	World Ocean Atlas 2001	99.5°W to 19.5E 89.5°N to 10.5°N each 1° degree	Monthly mean (climatology)	μmol.l ⁻¹	2.8
Nitrate	World Ocean Atlas 2001	99.5°W to 19.5E 89.5°N to 10.5°N each 1° degree	Monthly mean (climatology)	μmol.l ⁻¹	2.8
Oxygene dissolved	World Ocean Atlas 2001	99.5°W to 19.5E 89.5°N to 10.5°N each 1° degree	Monthly mean (climatology)	ml.l ⁻¹	2.8
Bathymetry	General Bathymetric Chart of the Oceans	80°W to 20°E 90°N to 10°N each 0.4° degree	Monthly mean (climatology)	m	27.4
Spatial variability in the bathymetry	General Bathymetric Chart of the Oceans	99.5°W to 19.5°E 69.5°N to 29.5°N each 1° degree	Monthly mean (climatology)	m	0.058
Chlorophyll	Sea-viewing Wide Field-of-view Sensor (SeaWiFS)	100°W to 30°E 70°N to 40°N each 0.5° degree	Monthly mean 1997-2002	mg.m ⁻³	18.8
Mixed Layer Depth	World Ocean Circulation Experiment	179.5°W to 179.5°E 89.5°N to 89.5°S each 1° degree	Monthly mean 1941-2002	m	0.8

Bathymetry was selected because it has been suggested that this parameter influences the distribution of some copepod species (Beaugrand *et al.*, 2001). Bathymetry data originate from the database General Bathymetric Chart of the Oceans (GEBCO). The spatial variability in the bathymetry was assessed over the studied area. In a geographical cell of 1° latitude and 1° longitude, the average and standard deviation of

bathymetry data were first calculated (225 data per geographical cell). Then, the coefficient of variation (CVB) was calculated as follows:

$$CV_B = \frac{S_B}{m_B} \quad (1)$$

with m_B being the average and s_B the standard deviation of the bathymetry in each geographical cell. A high variability in the bathymetry occurred generally over continental slope regions.

Chlorophyll *a* is a potentially influential parameter because the two selected species are mainly herbivorous (Mauchline, 1998). However as Kleppel (1993) showed and Mauchline (1998) stressed, the dietary requirements of copepods change from the first nauplii stage to the adult stage and are likely to vary at both diel and seasonal scales. Furthermore, it is likely that both *Calanus* species also feed on the microzooplankton (Mauchline, 1998). Therefore, the chlorophyll *a* value should only be considered as an index of food availability. Chlorophyll *a* values originated from the programme and satellite Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from the National Aeronautics and Space Administration (NASA).

The Mixed Layer Depth (MLD) is another indicator of water column stability. Contrary to the index of turbulence, this parameter is built from vertical profiles of temperature and salinity. Mixed layer depth data come from a compilation of about 4.5 million profiles gathered by National Oceanographic Data Center (NODC) and World Ocean Circulation Experiment (WOCE). These profiles are the result of the analysis of data from 1941 to 2002 and originate from various measuring instruments like conductivity-temperature-depth (CTD), mechanical bathythermograph (MBT) or expendable bathythermograph (XBT).

3.B.3. Pre-processing of the data

The first stage of the analysis consisted of the homogenisation both environmental and biological variables. The abiotic databases were different by their dimension, grid or organisation (see Table 3.1). All original data tables were converted into three types of matrix: (1) matrices (2.48 millions data points) with data for each month and year for the period 1960-2002 (temperature, wind stress); (2) matrices (57600 data points) with data for each month (nutrients, oxygen, chlorophyll *a*, mixed layer depth) based on the average of time periods ranging from 5 to 43 years; (3) matrices (4800 data points) without information on time (bathymetry and spatial variability in the bathymetry). The three types of environmental grids were used to regularise biological data so that no spatial interpolation was made. An arithmetic mean was calculated when the number of data for a given location and time period was greater than 1.

3.B.4. Statistical analyses

Figure 3.9 summarises the different statistical analyses performed in this study.

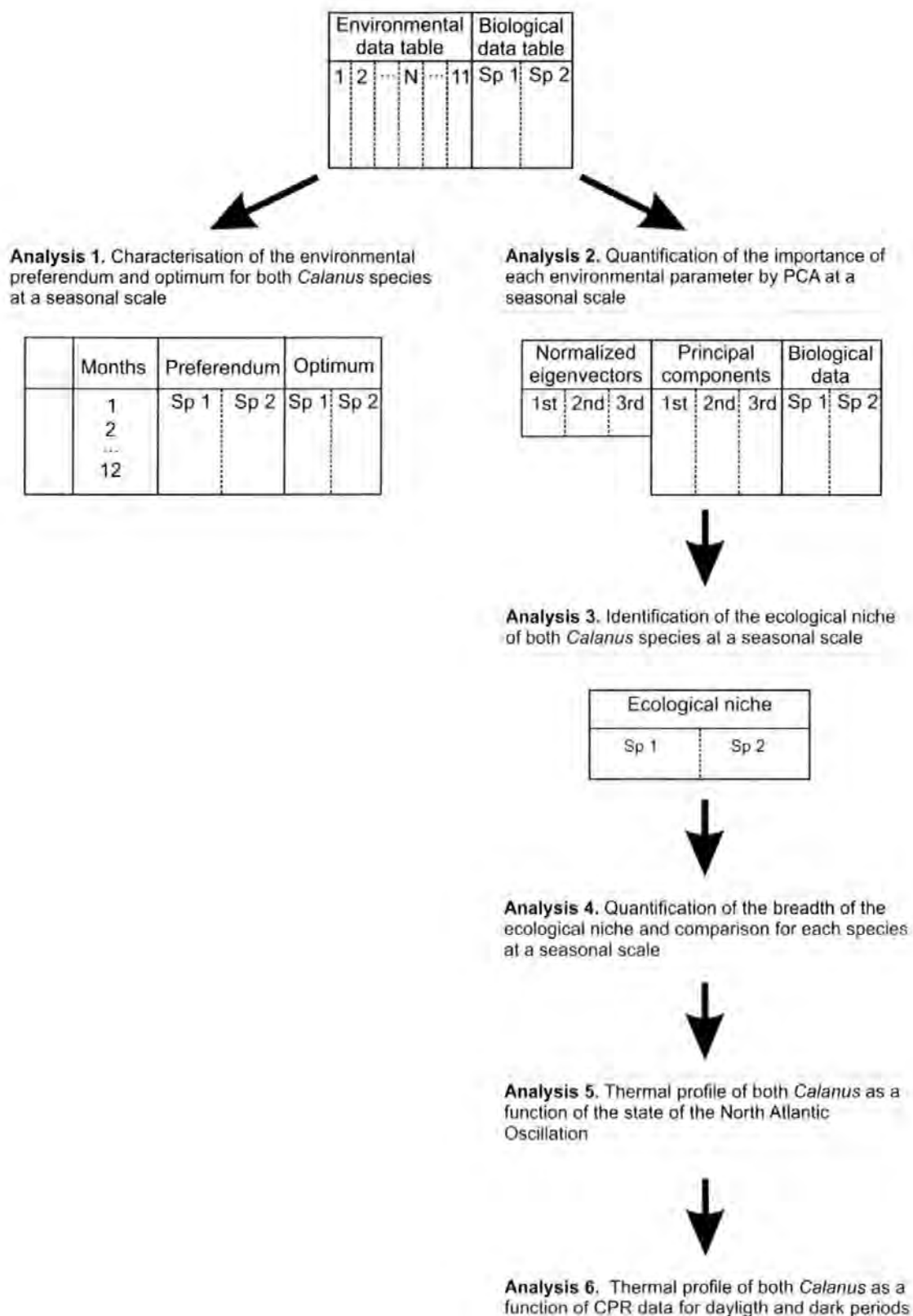


Figure 3.9. Summary of the different statistical analysis performed in the chapter.

3.B.4.A. Analysis 1: Characterisation of the environmental preference and optimum of both *Calanus* species at a seasonal scale

The preference of each *Calanus* species was identified for every environmental variable (a total of 22 environmental profiles, 2 species x 11 environmental parameters). A profile was a contour diagram of a matrix 12 months x n environmental categories. To determine the number of environmental categories, the minimum and maximum values were first calculated. Then, intervals were chosen by trial and error, being a compromise between the resolution of the profile and the number of missing data that rose when the resolution increased. The profile matrix was assessed by averaging abundance data for each month and environmental category. Abundance data were log-transformed ($\log_{10}(x+1)$) to limit the influence of extreme values.

3.B.4.B. Analysis 2: Quantification of the importance of each environmental parameter at a seasonal scale

A Principal Components Analysis (PCA) was used to quantify the influence of each abiotic factor and chlorophyll *a* concentration (used here as an index of available food) on the spatial and seasonal changes in *Calanus* abundance at the scale of North Atlantic Ocean (Fig. 3.9). An algorithm that took into consideration missing data was utilised for the calculation of the eigenvectors (Bouvier, 1977). This method of ordination made possible to summarise multivariate information in a reduced number of dimensions: the principal components (Jolliffe, 1986). The normalised eigenvectors allowed the identification of the variables that contribute the most to the principal components. The PCA was calculated on the table (120 longitudes x 40 latitudes x 12 months) x 11 environmental variables. The spatial grid had a resolution of 1° longitude and 1° latitude. This table was centred and reduced prior to the application of the analysis to remove any effect of scale between environmental variables.

3.B.4.C. Analysis 3: Identification of the ecological niche of both *Calanus* species at a seasonal scale

To identify the ecological niche of both species, we used the first three principal components. The concept of ecological niche utilised in this study was the one of Hutchinson (1957) which states that the niche is the field of tolerance of a species to the principal factors of the environment. The concept is refined here while holding of the recent improvements discussed by Frontier *et al.* (2004). In particular, our analysis takes into account that some factors are not independent but covary either positively or negatively. The use of principal components decreases the effect of multicollinearity in the data (Legendre & Legendre, 1998). We repeated the procedure used in Analysis 1 to map the ecological niche of both *Calanus* species as a function of principal components (linear combination of environmental factors).

3.B.4.D. Analysis 4: Quantification and comparison of the species Hutchinson's niches

Quantification and comparison of the Hutchinson's niches for both *Calanus* were performed for 4 different categories of abundance. The first category was based on all presence data. The value of the 11 environmental variables was retained when an individual (of *C. finmarchicus* or *C. helgolandicus*) was recorded in a geographical cell that belongs to the environmental grid of 1° x 1° (from 99.5°W to 19.5°E of longitude and 29.5°N to 69.5°N of latitude). A total of 24 subsets was determined (12 months x 2 species). A similar procedure was applied for three other categories. The second category gathered *Calanus* data greater than the first quartile, the third category was for *Calanus* data greater than the median and the fourth category contained *Calanus* data superior to the third quartile. The breadth of the niche becomes lower from category 1 to

category 4. Indeed, this latter category goes towards the centre of the niche. The quartiles and the median were assessed from the biological data table (see Fig. 3.9). Therefore, the quantification and the comparison of the Hutchinson's niche for both *Calanus* were made for $24 \times 4 = 96$ subsets.

To assess and compare the Hutchinson's niche of both *Calanus* species, a numerical analysis based on Multiple Response Permutation Procedures (MRPP) was utilised (Mielke, 1981; Zimmerman, 1985). MRPP has been often applied with Split Moving Window Boundary analysis (Webster, 1973) to detect discontinuities in time series (Cornelius & Reynolds, 1991). For example, this method was applied to detect the substantial and rapid changes called regime shift (Reid & Edwards, 2001) that occurred in North Sea plankton ecosystems (Beaugrand, 2004a). The method quantifies the breadth of the niche of the two species of *Calanus* and tests if their niches are statistically different. First, the quantification of the niche was made by calculating the mean Euclidean distance for each subset based on the 11 environmental parameters. The higher the mean Euclidean value, the greater the Hutchinson's niche. Second for a given month and category, a weighted mean of the Euclidean distance of both species niche is calculated (for a given month and category). Then, the weighted distance is tested by permutations of one of the original subset. A number of 10,000 permutations was selected. For each simulation, the weighted distance was recalculated and the probability that the separation of the niche of *C. finmarchicus* and *C. helgolandicus* be significant was given by the number of times the recalculated weighted distance was inferior to the observed one. A full description of the method is performed below with a simple fictive example.

3.B.4.D.1. Rationale of the technique

Let $X(m,p)$ be the matrix of p environmental variables with the m environmental categories. Each cell of X represents the centre of the interval of an environmental variable (Fig. 3.10). Let $C(p,1)$ be the vector that contains the total number of category for each of the p variables. The number of rows m in X is given by:

$$m = \prod_{i=1}^p c_i \quad (1)$$

Let $Y(m,s)$ be the vector with m abundance or presence/absence values corresponding to the m environmental categories for the s species (Fig. 3.10). Missing data are often present in the matrix and correspond to an environmental category that was not sampled. The amount of missing data increases with the number of environmental variables (and therefore m). Only rows of X for which the species was detected (or belong to a certain category of abundance) are considered in the calculation. Therefore, the number of rows n to be tested often varies between species (and $n \leq m$, Fig. 3.10).

The analyses were used based on occurrence data (all environmental data for which species are >0 , case 1, Fig. 3.10). For example, the data point for a temperature class centred on 10°C , a salinity class of 34.75 and a spatial bathymetry variability class of -45 was considered as abundance data for *C. finmarchicus* was superior to 0 in these environmental intervals. This was not so for *C. helgolandicus*. The procedures were also used for abundance data $>$ first quartile (case 2), data $>$ median (case 3), data $>$ third quartile (case 4). The first quartile, the median and third quartile were assessed for each species from matrix Y . Figure 3.10 illustrates reshaping and building of the matrices used in the analyses.

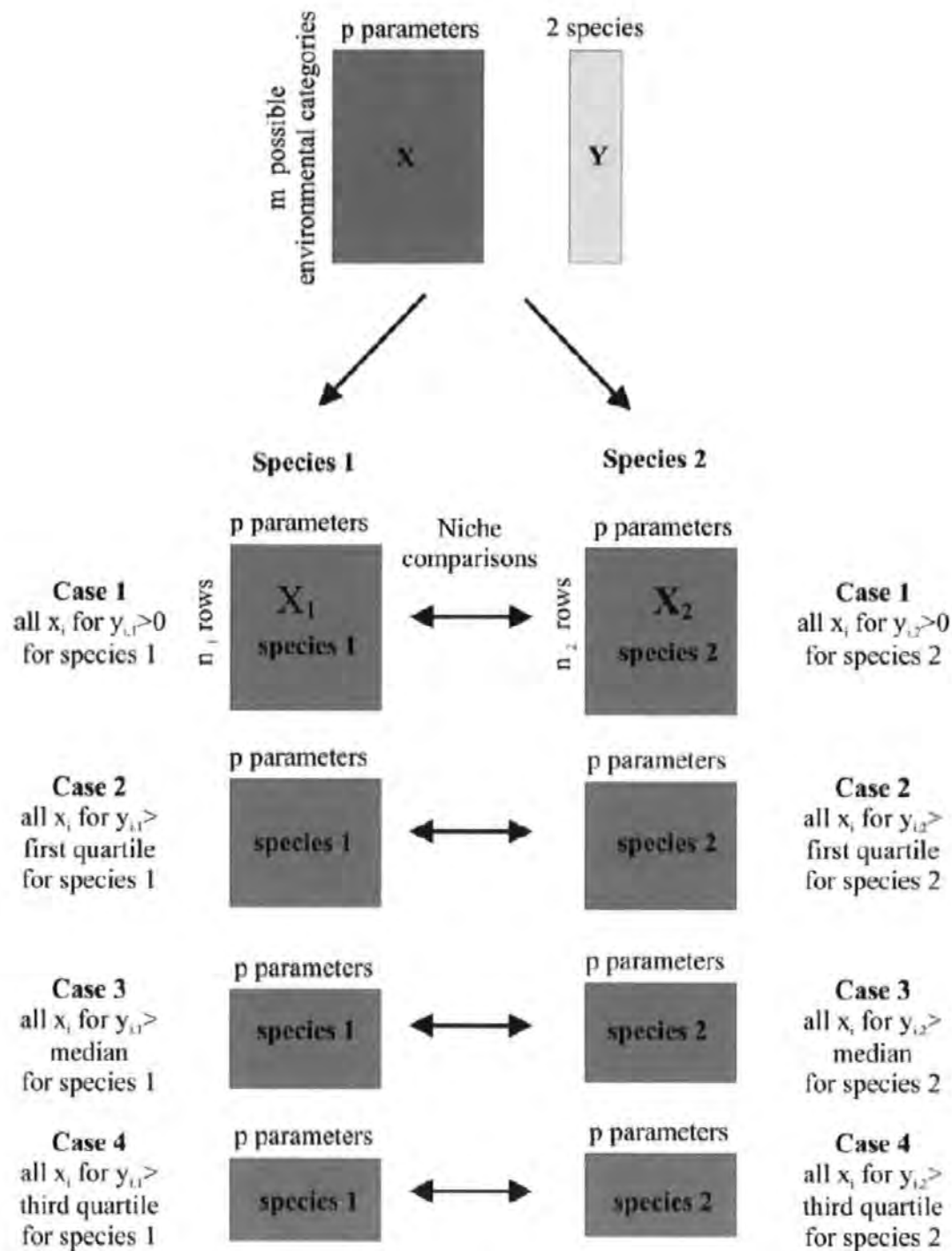


Figure 3.10. Origin of matrices tested in this chapter. Comparisons between species niche were performed for each case.

3.B.4.D.2. Assessment of the niche breadth

For each species and case (Fig. 3.10.), the breadth of the ecological niche is assessed by calculating the Euclidean distance between all possible pairs of points. The Euclidean distance between the rows and in the matrix $j \times k \times X$ (i.e. n rows that represent the environmental categories in which the species is either >0 , or $>\text{first quartile}$, or $>\text{median}$, or $>\text{third quartile}$ according to the different cases and p columns representing the number of environmental variables) is calculated as follows:

$$d(x_j, x_k) = \sqrt{\sum_{i=1}^p (x_{j,i} - x_{k,i})^2} \quad (2)$$

With p the number of environmental variables. The total number of Euclidean distances g to be calculated for a species (and a case) is:

$$g = n(n-1)/2 \quad (3)$$

With n the number of rows in X. Calculations are illustrated with a simple example (Table 3.2 and Fig. 3.12). In this example n=3 for species 1. Therefore, three Euclidean distances should be calculated (g=3, Table 2). Calculations give $d_{(x1,x2)}=2.236$, $d_{(x1,x3)}=2.000$ and $d_{(x2,x3)}=2.236$.

Then for each case and species, the mean Euclidean distance ε is calculated to assess the breadth of the ecological niche:

$$\varepsilon = \frac{\sum_{i=1}^g d_i}{g} \quad (4)$$

Table 3.2. Fictive example showing the occurrence of three species according to 2 environmental variables.

Species 1		Species 2		Species 3	
Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
Untransformed data					
1	1	4	4	1	2
2	3	5	2	3	3
3	1	5	5	6	5
-	-	7	4	7	1

With g the total number of Euclidean distances calculated from X. In the example (Table 3.2, Fig. 3.11), $\varepsilon = \frac{2.236 + 2.000 + 2.236}{3} = 2.157$ for species 1, $\varepsilon=2.452$ for species 2, $\varepsilon=4.392$ for species 3. Therefore, the breadth of the ecological niche (only based on 2 factors here) is greater for species 3, then species 2 and species 1 (Fig. 3.11).

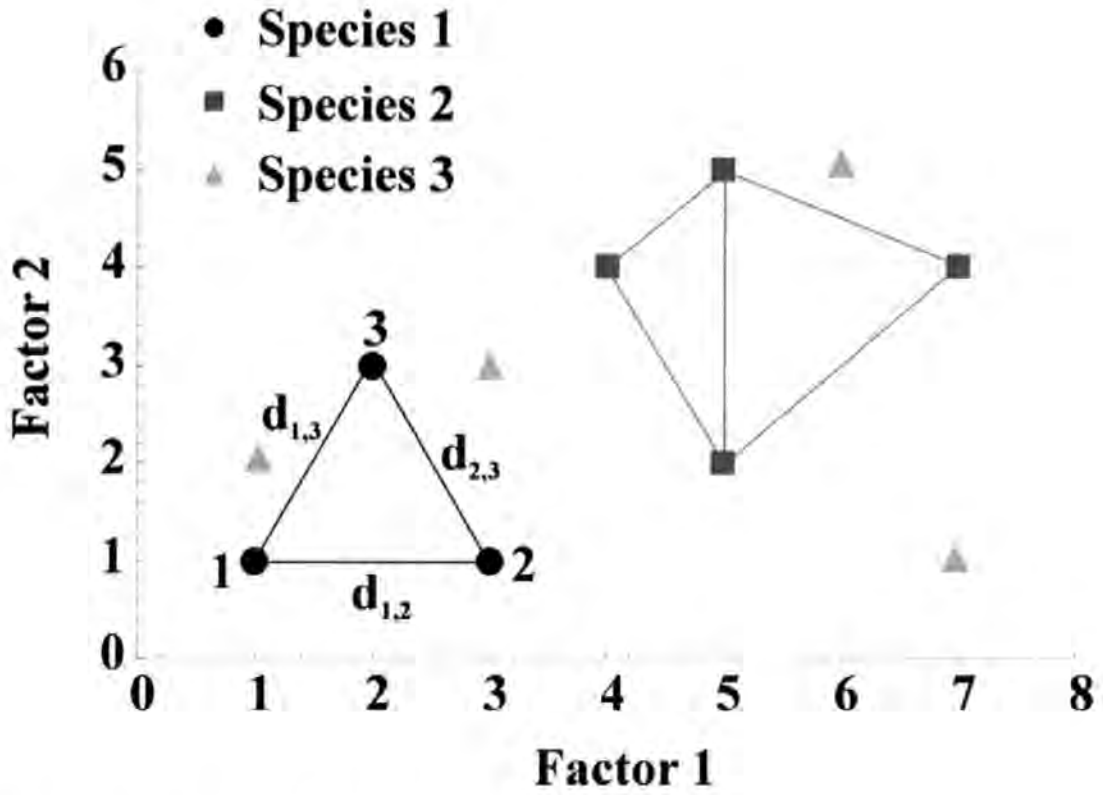


Figure 3.11. Hypothetical ecological niche (sensu Hutchinson) of three species in the space of two factors. All possible Euclidean distances are indicated for species 1 and 2. Data are presented in Table 2.

3.B.4.D.3. Test of niche separation

The following non-parametrical technique known as Multiple Response Permutation Procedures (MRPP test (Mielke, 1981; Zimmerman, 1985)) can then be applied to test if the species have different ecological niches. Test δ between species 1 and 2 (2 species) and a given case is calculated as being the weighted mean of the values ϵ :

$$\delta_{1,2} = \frac{g_1 \epsilon_1 + g_2 \epsilon_2}{g_1 + g_2} (5)$$

With g_1 and g_2 the total number of Euclidean distances calculated for species 1 (matrix X_1) and species 2 (matrix X_2), respectively (see Fig. 3.10). ε_1 and ε_2 are the mean Euclidean distances for species 1 and 2, respectively.

The probability value of the MRPP statistics is assessed by permutations (Zimmerman, 1985). For comparison of the ecological niche of two species (e.g. species 1 and 2), the number of possible permutations $PE_{1,2}$ is:

$$PE_{1,2} = \frac{(g_1 + g_2)!}{g_1! \cdot g_2!} \quad (6)$$

In the example, $PE_{1,2}=35$ permutations, $PE_{1,3}=35$ permutations, $PE_{2,3}=70$ permutations.

The probability $p_{1,2}$ (e.g. species 1 and 2) is assessed by calculating the following ratio:

$$p_{1,2} = \frac{K_{\delta_{1,2}^s < \delta_{1,2}}}{PE_{1,2}} \quad (7)$$

With $K_{\delta_{1,2}^s < \delta_{1,2}}$ being the number of recalculated or simulated $\delta_{1,2}$ (e.g. species 1 and 2), called $\delta_{1,2}^s$, found to be inferior to the observed $\delta_{1,2}$ after permutation.

In the fictive example (Table 3.2, Fig. 3.11), values of $\delta_{1,2}= 2.3260$ and $p_{1,2} = 0.0286$. Therefore, the ecological niche of species 1 and 2 are significantly different. $\delta_{1,3}= 3.4342$ and $p_{1,3} = 0.2857$ and $\delta_{2,3}= 3.4221$; $p_{2,3} = 0.6286$ so that the niches do not significantly differ between species 1 and 3 and species 2 and 3. The number of possible permutations is important to have an idea on the robustness of the probability. In the

example, it is relatively low. When the number of occurrence point starts to be moderately high, the test becomes rapidly robust. For example, a species with 10 occurrences and another with 15 lead to 2.85 million possible permutations. When the number of possible permutations is too high, it is not possible to do all calculations and Berry & Mielke (1983) proposed to use the Pearson type III distribution. However in that case, only the Euclidean distance can be applied. We propose to use a finite number of permutations. A minimum number of 10,000 permutations is generally recommended to stabilise the probability for tests based on random permutations such as the Mantel's test (Jackson & Somers, 1989). This way of assessing the probability enables the use of any distance or similarity measures. This assumption works as long as there is no substantial difference in the number of occurrence (or abundance values > first quartile, median or third quartiles) for each species. Environmental data were standardized prior to the calculation of Euclidean distances so that each environmental variable had the same weight in the analysis.

3.B.4.E. Analysis 5. Thermal profiles of both *Calanus* as a function of the state of the North Atlantic Oscillation (NAO) and the 1987's climatological regime shift

One important issue was to know whether the Hutchinson's niche was constant at a decadal scale and whether it was influenced by climate variability during the period of investigation (1958-2002). In such case, the species could be able to acclimatise quickly with climate change. To test this issue, we calculated the thermal profile of both *Calanus* for negative NAO (NAO index < -1), medium NAO ($-1 \leq \text{NAO index} \leq 1$) and positive NAO (NAO index > 1). Thermal profiles were calculated according to a procedure identical to Analysis 1. To examine the potential impact of the regime shift in the North Sea (Beaugrand, 2004b), thermal profiles were also assessed for years prior and after 1987.

3.B.4.F. Analysis 6. Thermal profile of both *Calanus* as a function of CPR data for daylight and dark period

Changes in the depth distribution of *Calanus* through time could bias our assessment of the Hutchinson's niche as the CPR survey samples at a standard depth of about 7 m. To evaluate if this process could have significantly affected our results, we assessed the thermal profile (see analysis 1) of both *Calanus* for CPR samples collected during daylight (CPR samples collected between 10.00 and 16.00) and dark periods (CPR samples collected between 22.00 and 4.00) (Beaugrand *et al.*, 2001; see their Fig. 1)

3.C. Results

3.C.1. *Spatial distribution of biological and environmental data*

Figure 3.12 shows the mean spatial distribution of *C. finmarchicus* and *C. helgolandicus* for the period 1958-2002. The spatial distribution of *C. finmarchicus* (Fig. 3.12a) was located north of the Oceanic Polar Front (Dietrich, 1964) with two main centres of distribution south of the Labrador Sea and in oceanic regions south and west of Norway (Fig. 3.12a). The figure suggests that the species is an indicator of the Atlantic Polar Biome and especially the Atlantic Arctic Province and the Atlantic Subarctic Province as defined by (Longhurst, 1998). The spatial distribution of *C. helgolandicus* was different (Fig. 3.12b), being mainly centred along the shelf-edge in temperate regions. Figure 3.13 presents the mean values of the environmental parameters in the North Atlantic Ocean. Temperature is an important driver for *C. finmarchicus* while it has probably a more limited role for *C. helgolandicus* (Fig. 3.13a).

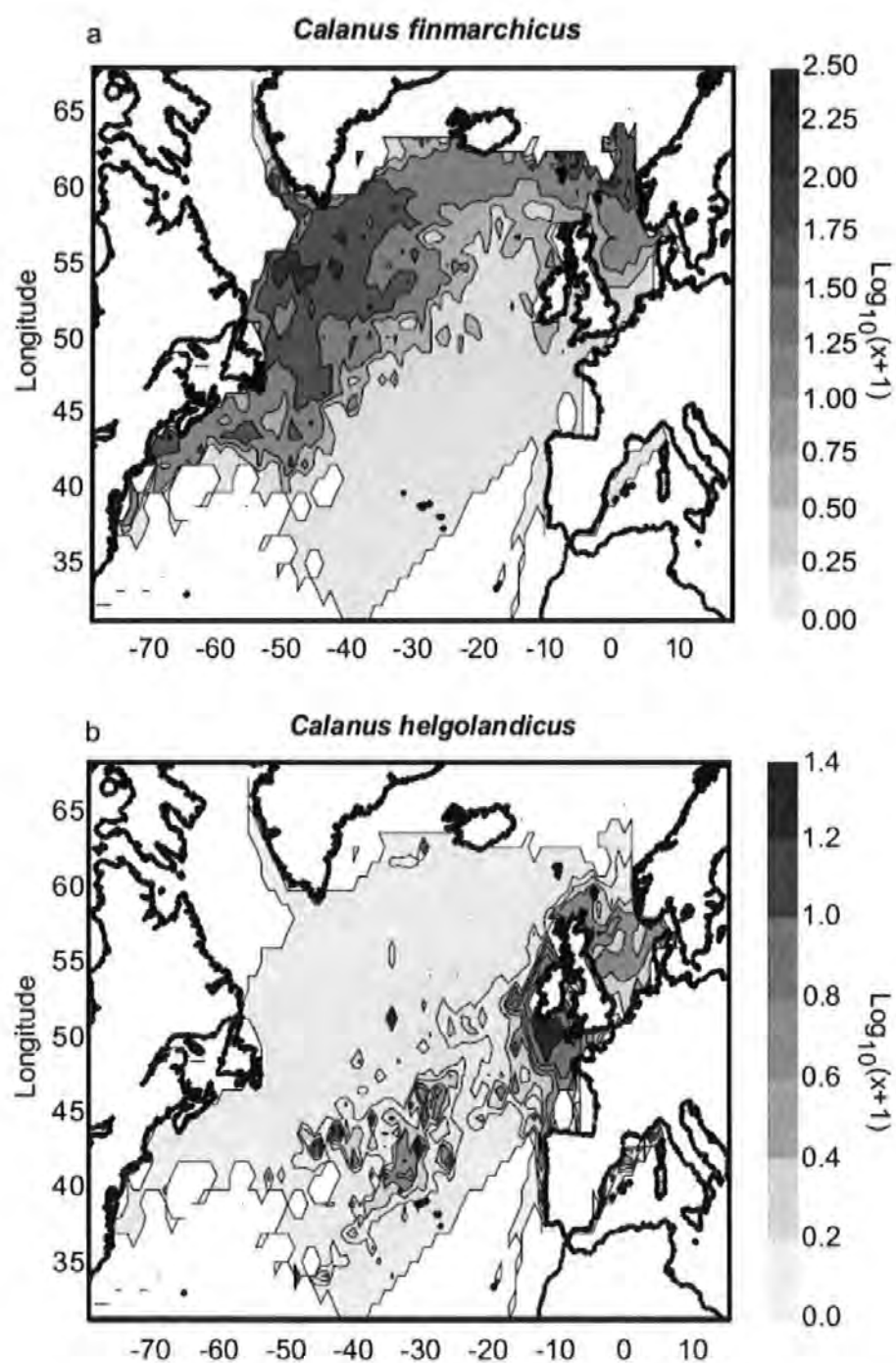


Figure 3.12. Spatial distribution of *Calanus finmarchicus* (a) and *Calanus helgolandicus* (b) in the North Atlantic Ocean. No interpolation was made.

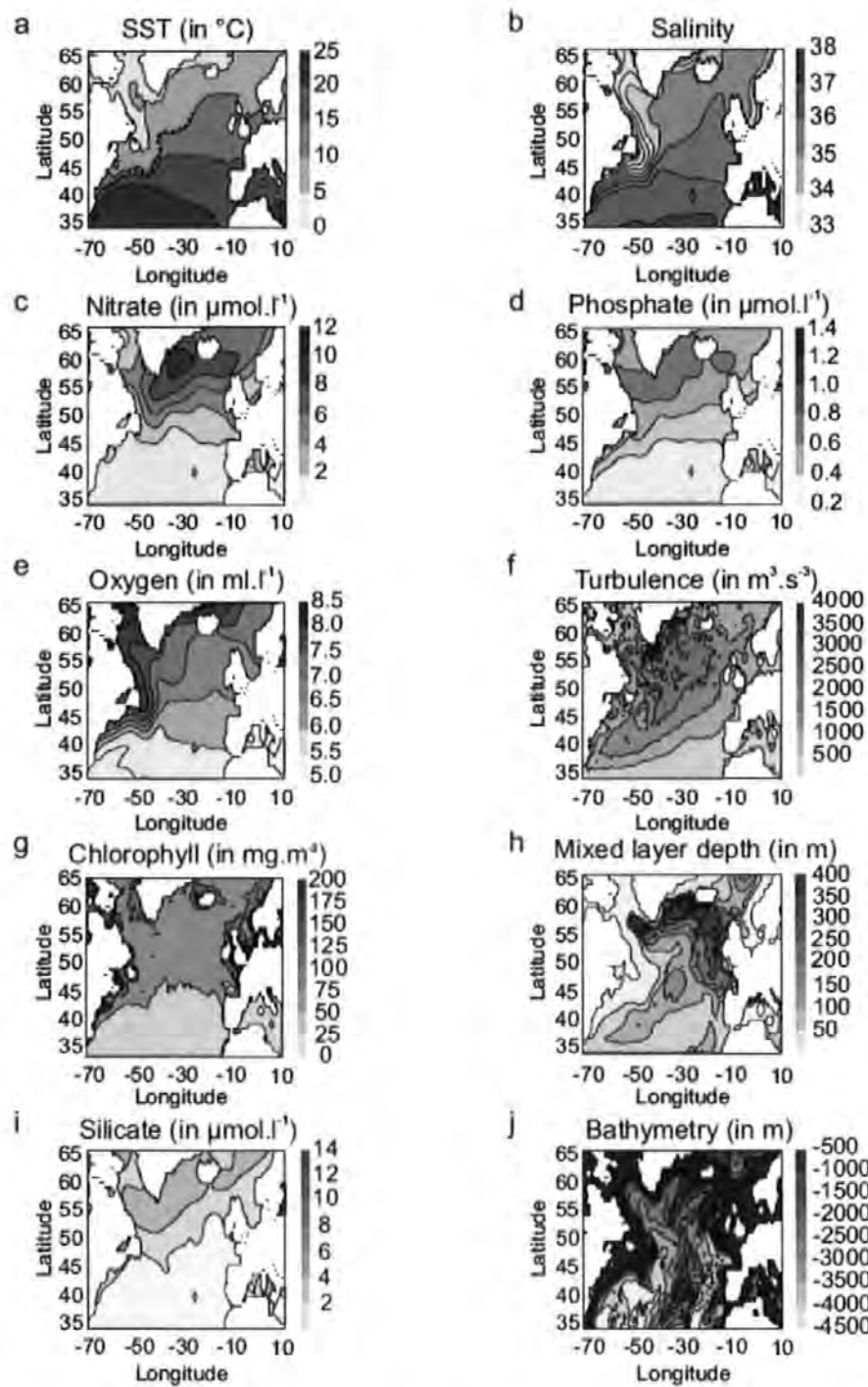


Figure 3.13. Spatial distribution of mean SST (a), salinity (b), nitrate (c), phosphate (d), oxygen dissolved (e), turbulence (f), chlorophyll *a* (g), mixed layer depth (h), silicate (i) and bathymetry (j). The location of the Oceanic Polar Front is superimposed in panel (a).

3.C.2. Environmental profiles

3.C.2.1. Monthly thermal profile

Figure 3.14 shows both the thermal profile of *C. finmarchicus* (Fig. 3.14a) and *C. helgolandicus* (Fig. 3.14b) for each month. *C. finmarchicus* had its maximal abundance between April and September for temperature ranging from 6 to 10°C. The species *C. helgolandicus* had a tolerance range between 11°C and 16°C especially in spring (Fig. 3.14b). A remarkable feature was that for both *Calanus* species the optimum varied seasonally. The two species had a clear distinct thermal preference. The interval of tolerance of *C. finmarchicus* was greater than the one of its congeneric species. Figure 3.14c shows the mean abundance of *C. finmarchicus* and *C. helgolandicus* by categories of temperature. The complementarity in the distribution of the two species was speaking fluently. These results show that a temperature change in a region with an annual thermal regime of about 10°C could trigger a shift from a system dominated by *C. finmarchicus* to a system dominated by *C. helgolandicus*.

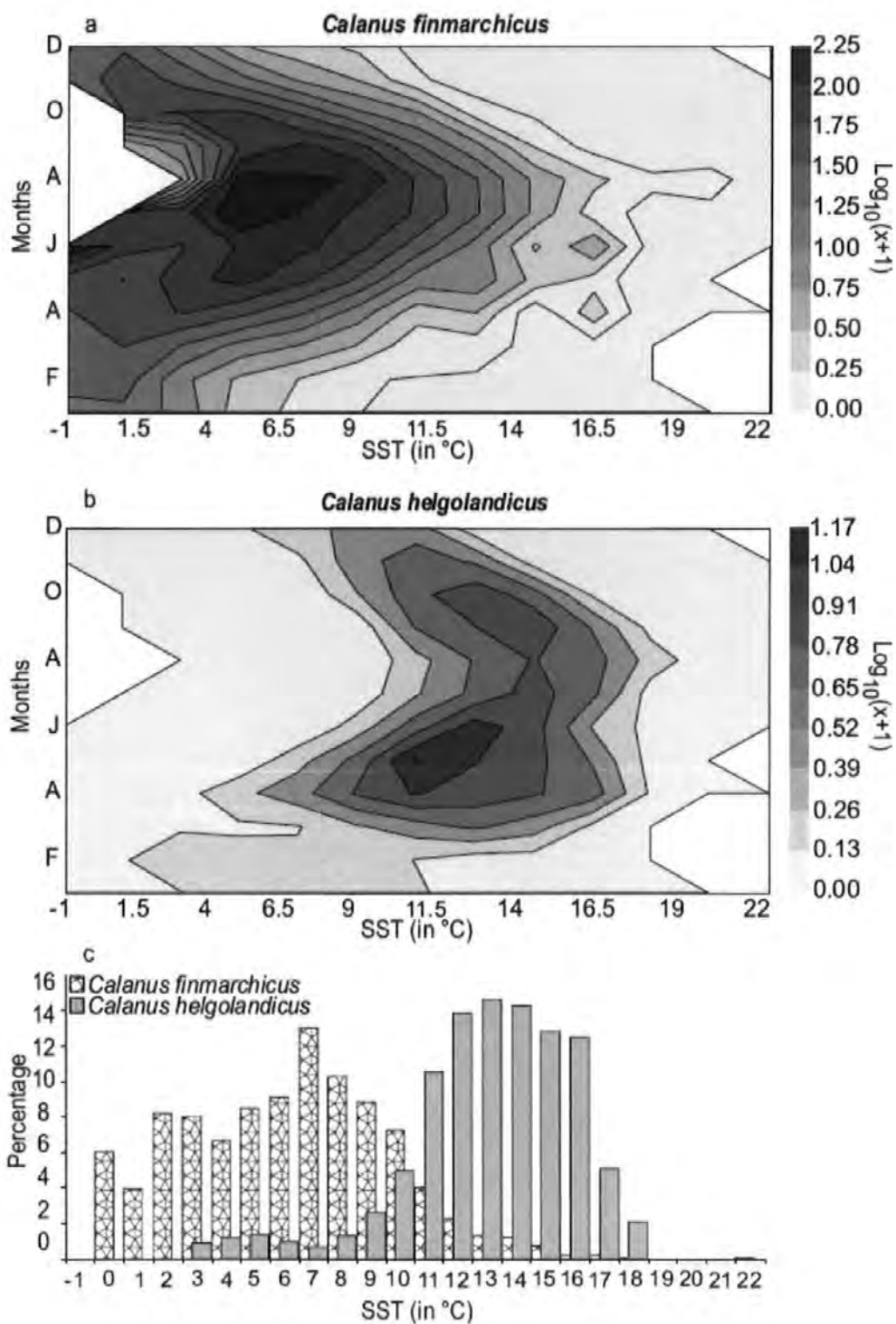


Figure 3.14. Contour diagram of the abundance (in decimal logarithm) of *Calanus finmarchicus* (a) and *Calanus helgolandicus* (b) as a function of SST and months. Histogram that represents the relative average abundance of both *Calanus* (expressed as a percentage) by categories of SST is also represented (c).

3.C.2.2. Others monthly profile

Figure 3.15 presents other environmental profiles. Salinity profiles separated well the two *Calanus* (Fig. 3.15a). *C. finmarchicus* had its maximal abundance for salinity values between 33.8 and 35 for spring and summer months. The salinity optimum was higher for *C. helgolandicus* (35-35.5). Dissolved oxygen also distinguished the 2 *Calanus* (Fig. 3.15b). Abundance of *C. finmarchicus* was maximal for values ranging from 6.4 ml.l⁻¹ to 7.3 ml.l⁻¹. *C. helgolandicus* was found in water with less oxygen (5.9 ml.l⁻¹ to 6.6 ml.l⁻¹). The chlorophyll *a* concentration did not allow a complete distinction between the species (Fig. 3.15c). Nutrients were also examined. Figure 3.15d shows an example of profile for phosphate. Higher abundance of *C. finmarchicus* corresponded to values of phosphate concentration between 0.2 µmol.l⁻¹ and 0.8 µmol.l⁻¹. For *C. helgolandicus*, the optimum was found between 0.1 µmol.l⁻¹ and 0.3 µmol.l⁻¹. As in the case of salinity and temperature, high abundance of *C. helgolandicus* was located in a more restricted tolerance range and time interval. Other nutrient profiles (not shown; nitrate and silicate) showed that *C. finmarchicus* was found in waters with more nutrients than its congeneric species. *C. finmarchicus* was located in waters with a higher index of turbulence than *C. helgolandicus* (not shown). Similar results were found with mixed layer depth (not shown).

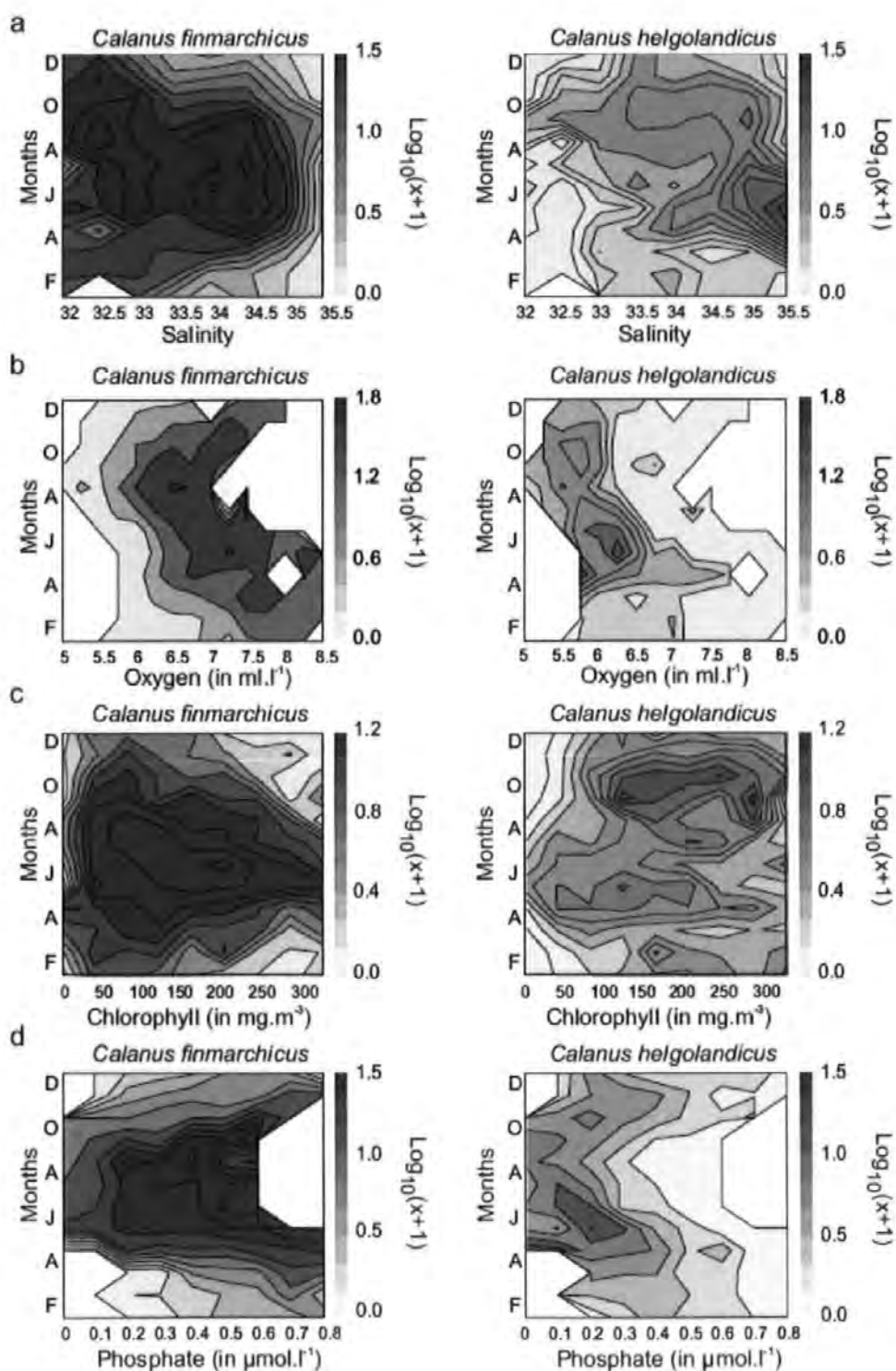


Figure 3.15. Contour diagram of the abundance (in decimal logarithm) of *Calanus finmarchicus* and *Calanus helgolandicus* as a function of salinity (a), oxygen dissolved (b), chlorophyll *a* (c) and phosphate (d) and months.

The species *C. finmarchicus* was mainly abundant at depth ranging from 269 m to 3513 m but can be found in regions with low bathymetry (Fig. 3.16a). The species was primarily found in regions with low to medium spatial variability in bathymetry. *C. helgolandicus* was more often found in regions characterised by a bathymetry between 82 m and 1216 m despite the fact that a second mode was detected at depth > 4000 m (Fig. 3.16b). This last mode was probably related to expatriate individuals in the region near to the Bay of Biscay (see Fig. 3.12b). The species was identified in regions characterised by a higher spatial variability in bathymetry, which reinforces the fact that *C. helgolandicus* is often called pseudo-oceanic (i.e. can be found in both neritic and oceanic regions but is mainly abundant above the shelf-edge).

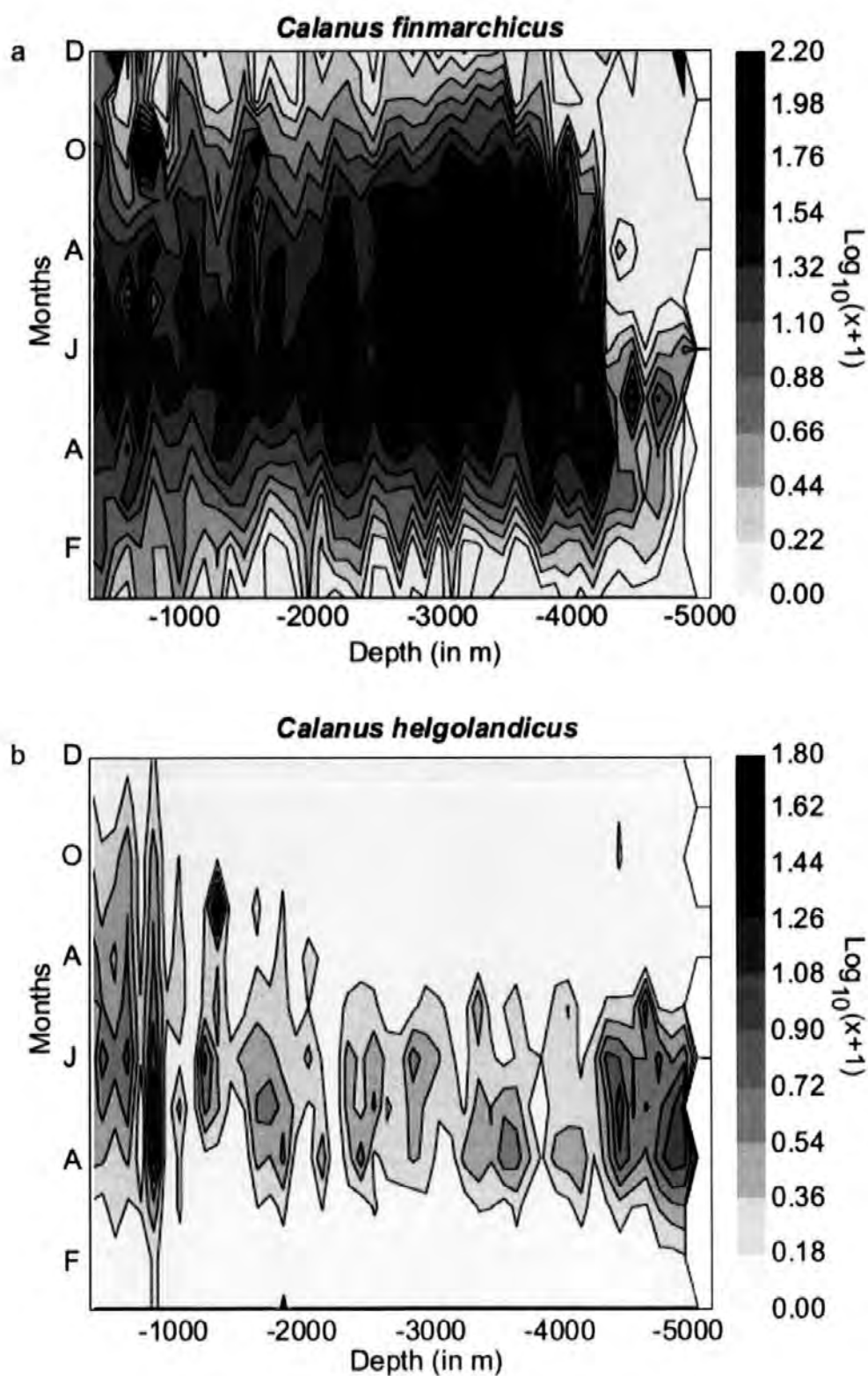


Figure 3.16. Contour diagram of the abundance (in decimal logarithm) of *Calanus finmarchicus* (a) and *Calanus helgolandicus* (b) as a function of bathymetry and months.

3.C.3. Quantification of the factors that influences spatial distribution of *Calanus*

A PCA was applied on the table 12 months-4800 geographical squares x 11 variables. The first axis explained 43.6% of the total variance, the second 21.4%, the third 8.9% and the fourth 7.2%. The calculation of the equiprobability (noted $E = \left(\frac{1}{N}\right) \times 100$ with N the number of variables) indicated that all axes with a variance of more than 9.1% can be considered to be significant. Therefore, only the first three normalised eigenvectors and principal components (representing 73.9% of the total variance) were retained. Figure 3.17 shows the scatter plot of the first two normalised eigenvectors and mapping of the first principal component. Variables such as temperature (Relative Contribution RC = 82%); phosphate (RC = 75.1%), oxygen (RC = 73.8%), silicate (RC = 62.9%) and nitrate (RC = 54.7%) contributed greatly to the first component. Temperature was correlated negatively with the above factors (Fig. 3.17a). Mapping of the first principal component identified a northward change from March to August and then an opposite movement from September to December (Fig. 3.17b). The Oceanic Polar Front (Dietrich 1964) was clearly identified (for the location of the Oceanic Polar Front, see Fig. 1.4 and Fig. 3.13a). An asymmetry in the seasonal changes of the physical-chemical parameters was detected. The northern limit of the western part of the Atlantic basin remained relatively constant at a monthly scale while in the eastern part the seasonal northward movement was much more pronounced. The influence of bathymetry on this first principal component was not detected.

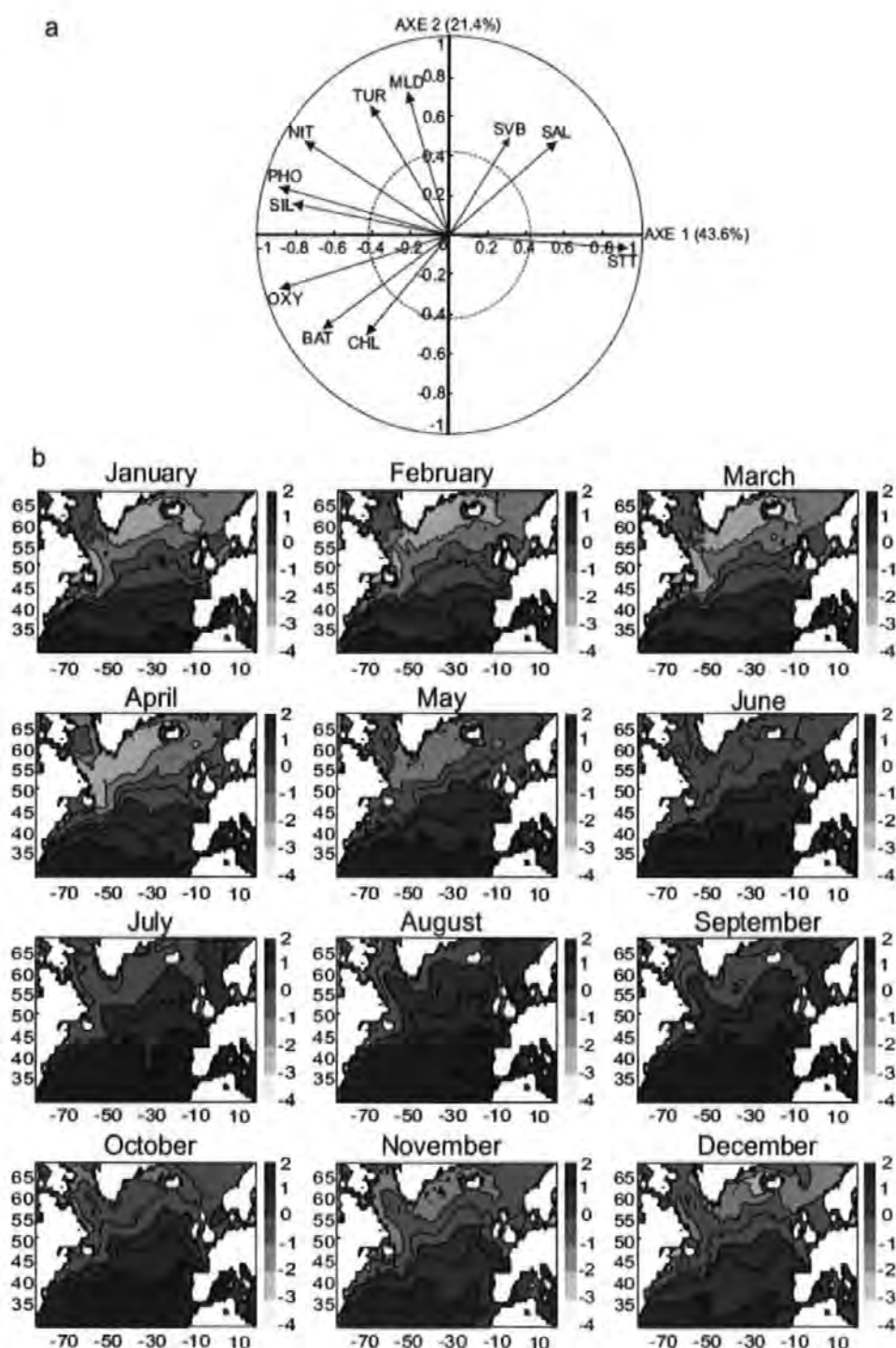


Figure 3.17. Results from a standardised principal component analysis performed on environmental data. (a) Normalised eigenvector 1 and 2 (65%). Circle of correlation and circle of regime descriptor contribution ($C=0.43$) are also displayed. (b) Spatial and monthly changes of the first principal component (43.6% of the total variance). SST: sea surface temperature; SAL: salinity; NIT: nitrate; PHO: phosphate; TUR: turbulence rating; CHL: chlorophyll *a*; MLD: mixed layer depth; SIL: silicate; BAT: bathymetry; CVB: variation of bathymetry.

Figure 3.18 shows the scatter plot of the second and third normalised eigenvectors and maps of the seasonal changes in the second principal component at a seasonal scale. Variables that contributed mostly to the second principal component was mixed layer depth (RC = 51.1%), the index of turbulence (RC = 43.7%), and to a lesser extent chlorophyll *a* concentration (RC = 27.1%), the index of spatial variability in bathymetry (RC = 23.2%) and average bathymetry (RC = 22.9%). Mapping of seasonal changes in the second principal component (Fig. 3.18b) shows the importance of parameters related to structure of the water column and the stable-biotope component (geographically stable, e.g. variables related to bathymetry). The effect of the structure of the water column was especially strong in the Atlantic Arctic Biome.

Figure 3.19a shows that the main parameter related to the third principal component was primarily the index of spatial variability in bathymetry (RC = 42.4%) so that the third principal component (Fig 3.19b) highlighted directly the bathymetry of the region.

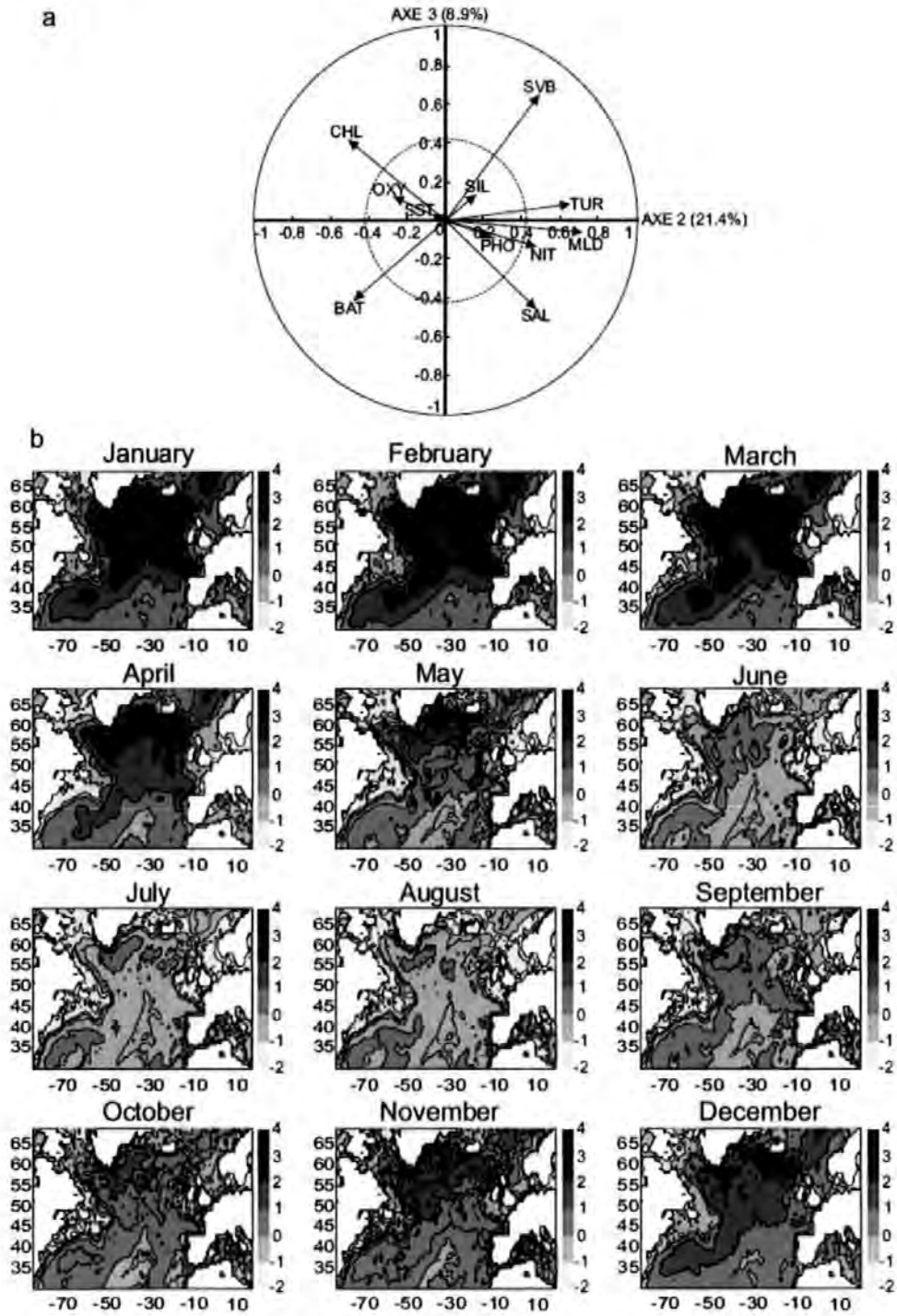


Figure 3.18. Results from a standardised principal component analysis performed on environmental data. (a) Normalised eigenvector 2 and 3 (30.3%). Circle of correlation and circle of regime descriptor contribution ($C=0.43$) are also displayed. (b) Spatial and monthly changes of the second principal component (21.4% of the total variance). SST: sea surface temperature; SAL: salinity; NIT: nitrate; PHO: phosphate; TUR: turbulence rating; CHL: chlorophyll a ; MLD: mixed layer depth; SIL: silicate; BAT: bathymetry; CVB: variation of bathymetry.

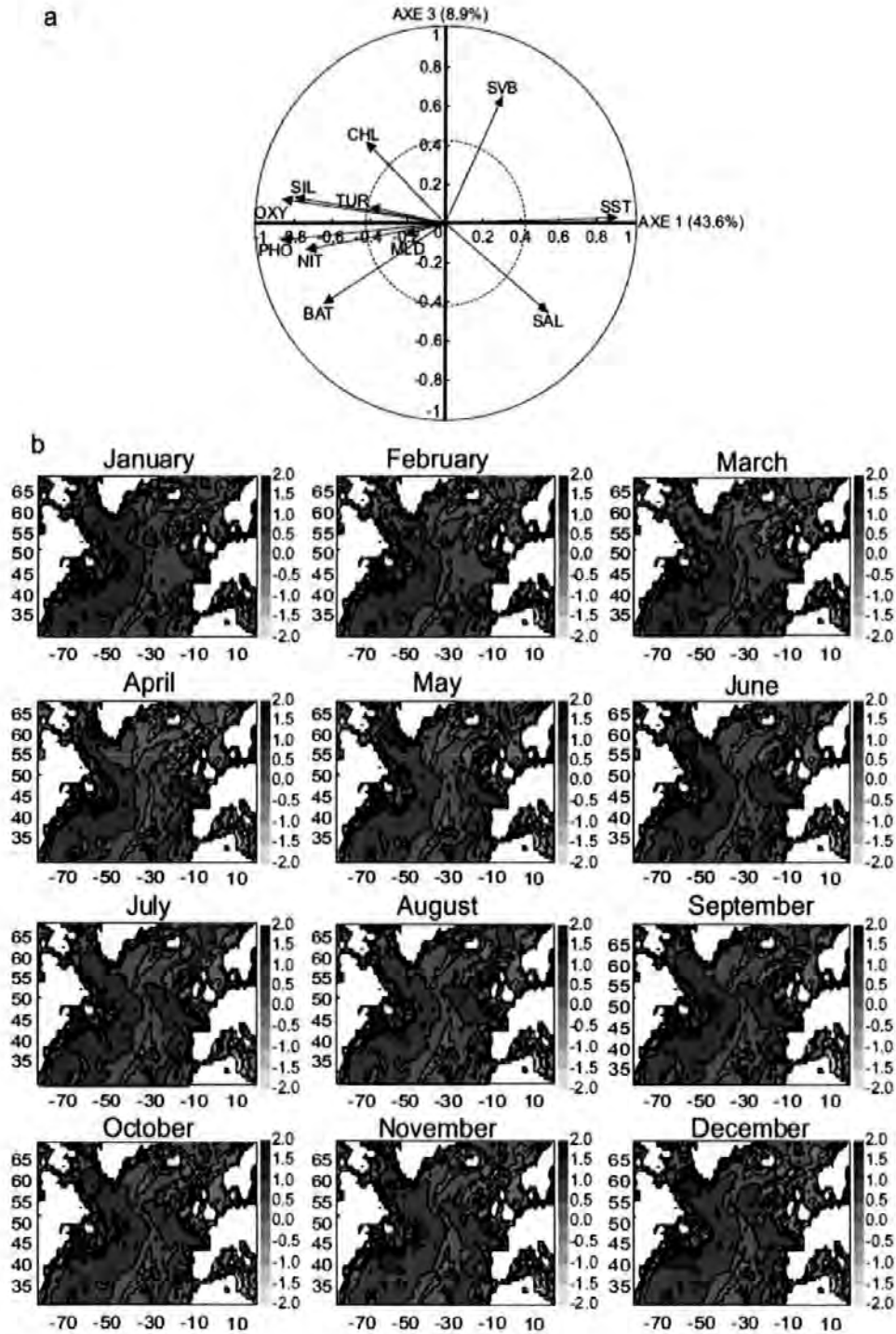


Figure 3.19. Results from a standardised principal component analysis performed on environmental data. (a) Normalised eigenvector 1 and 3 (52.5%). Circle of correlation and circle of regime descriptor contribution ($C=0.43$) are also displayed. (b) Spatial and monthly changes of the third principal component (8.9% of the total variance). SST: sea surface temperature; SAL: salinity; NIT: nitrate; PHO: phosphate; TUR: turbulence rating; CHL: chlorophyll a ; MLD: mixed layer depth; SIL: silicate; BAT: bathymetry; CVB: variation of bathymetry.

3.C.4. Identification of the ecological niche of both *Calanus* species

Using the first three principal components, a representation of the ecological niche (sense Hutchinson 1957) can be outlined (Fig. 3.20). The figure suggests that the ecological niche of both *Calanus* species was well separated. The graphical examination is confirmed by the MRPP-based test, which indicated a statistically significant separation of the niche for every month and category of abundance (Table 3.3). Quantification of the breadth of the niche further indicated that the niche breadth of *C. finmarchicus* was overall larger (e.g. niche breadth index = 8.2 for January) than the one of its congeneric species (e.g. niche breadth index = 7.4 for January) when the estimation was based on presence data and whatever the month. When higher categories of abundance were considered, few exceptions were detected corresponding to the main seasonal maximum of *Calanus* species. These exceptions might be related to the positive relationship between dispersal and abundance for the two species.

Table 3.3. Results of the comparison between the breadth and position of the two ecological niches of *Calanus finmarchicus* and *Calanus helgolandicus*. “ p_{δ} ” is the probability of separation of the two ecological niche.

months	cat 1 (>0%)			cat 2 (>25%)			cat 3 (>50%)			cat 4 (>75%)		
	breadth Cfin	breadth Chel	p_{δ}	breadth Cfin	breadth Chel	p_{δ}	breadth Cfin	breadth Chel	p_{δ}	breadth Cfin	breadth Chel	p_{δ}
January	8.15	7.36	<0.01	8.11	7.01	<0.01	7.97	6.46	<0.01	6.88	6.64	<0.01
February	8.46	7.37	<0.01	8.39	7.21	<0.01	8.55	6.52	<0.01	7.14	5.94	<0.01
March	8.84	7.55	<0.01	8.95	7.19	<0.01	9.22	6.97	<0.01	8.97	6.57	<0.01
April	8.68	7.87	<0.01	8.32	7.44	<0.01	8.65	6.91	<0.01	8.55	6.66	<0.01
May	7.95	7.38	<0.01	7.42	6.93	<0.01	7.19	6.51	<0.01	7.46	5.92	<0.01
June	7.34	6.36	<0.01	7.12	6.01	<0.01	6.85	5.69	<0.01	6.82	5.26	<0.01
July	7.49	6.37	<0.01	7.12	5.92	<0.01	6.51	5.74	<0.01	5.83	5.17	<0.01
August	6.97	5.85	<0.01	6.44	5.92	<0.01	5.85	6.17	<0.01	5.14	5.93	<0.01
September	7.30	6.32	<0.01	6.71	6.08	<0.01	6.17	6.21	<0.01	5.47	6.05	<0.01
October	7.75	6.75	<0.01	7.65	6.68	<0.01	7.36	7.05	<0.01	7.61	6.66	<0.01
November	7.82	6.56	<0.01	8.09	6.48	<0.01	8.31	5.68	<0.01	8.45	5.19	<0.01
December	7.74	6.55	<0.01	7.75	6.62	<0.01	7.45	6.12	<0.01	6.42	5.52	<0.01

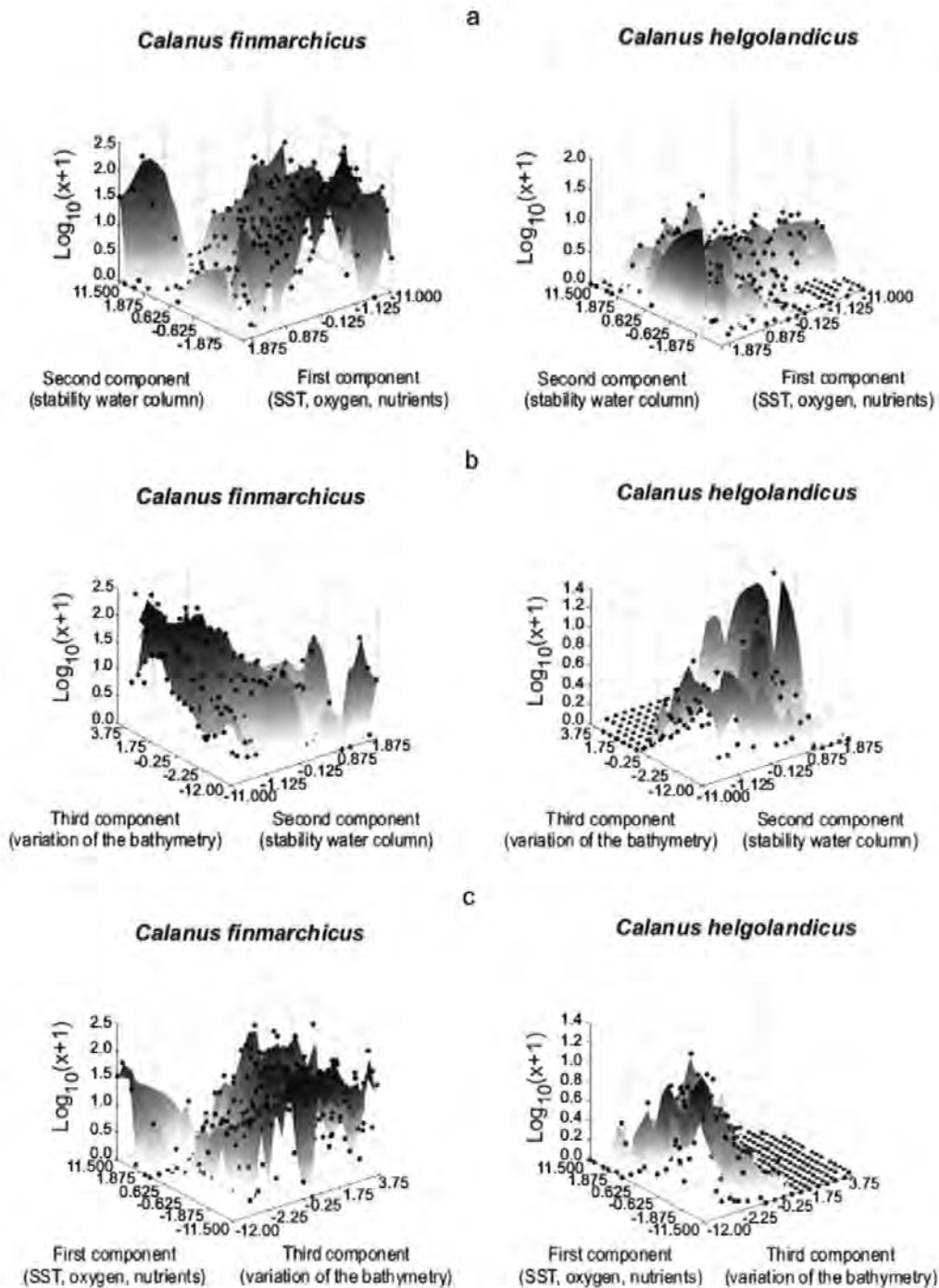


Figure 3.20. Representation of the ecological niche (sense Hutchinson) using the first three principal components. (a). Abundance of both *Calanus* as a function of the first and the second principal components. (b). Abundance of both *Calanus* as a function of the second and the third principal components. (c). Abundance of both *Calanus* as a function of the first and the third principal components.

3.C.5. Application of the ecological niche approach to explain the change in dominance of Calanus that happened in the North Sea after the 1980s regime shift

Temperature was the most important environmental parameter according to PCA results. This parameter separated well the two species. Figure 3.21 shows changes in the proportion of *C. helgolandicus* on total *Calanus* (*C. finmarchicus* and *C. helgolandicus*) as a function of temperature. The location of the line below which 10% of *Calanus* identified by the CPR survey were *C. helgolandicus* varied monthly. The figure shows that a change in *Calanus* dominance (from 10 to 60% of *C. helgolandicus*) occurs when temperature increases by 1.5-3°C during the reproductive season. Superimposed on the contour diagram, minimal and maximal temperatures in the North Sea for the period 1958-2002 demonstrate that this magnitude of temperature changes was indeed observed. This diagram explains by temperature alone (related to increase in atmospheric temperature, advection change or water mass location) the change in *Calanus* dominance that happened in the North Sea during the regime shift (Reid et al. 2003b). Cold temperatures were nearly exclusively found prior to the shift while warmer temperatures (with the exception of the negative NAO year in 1996) were mainly observed after the shift (Beaugrand 2004b).

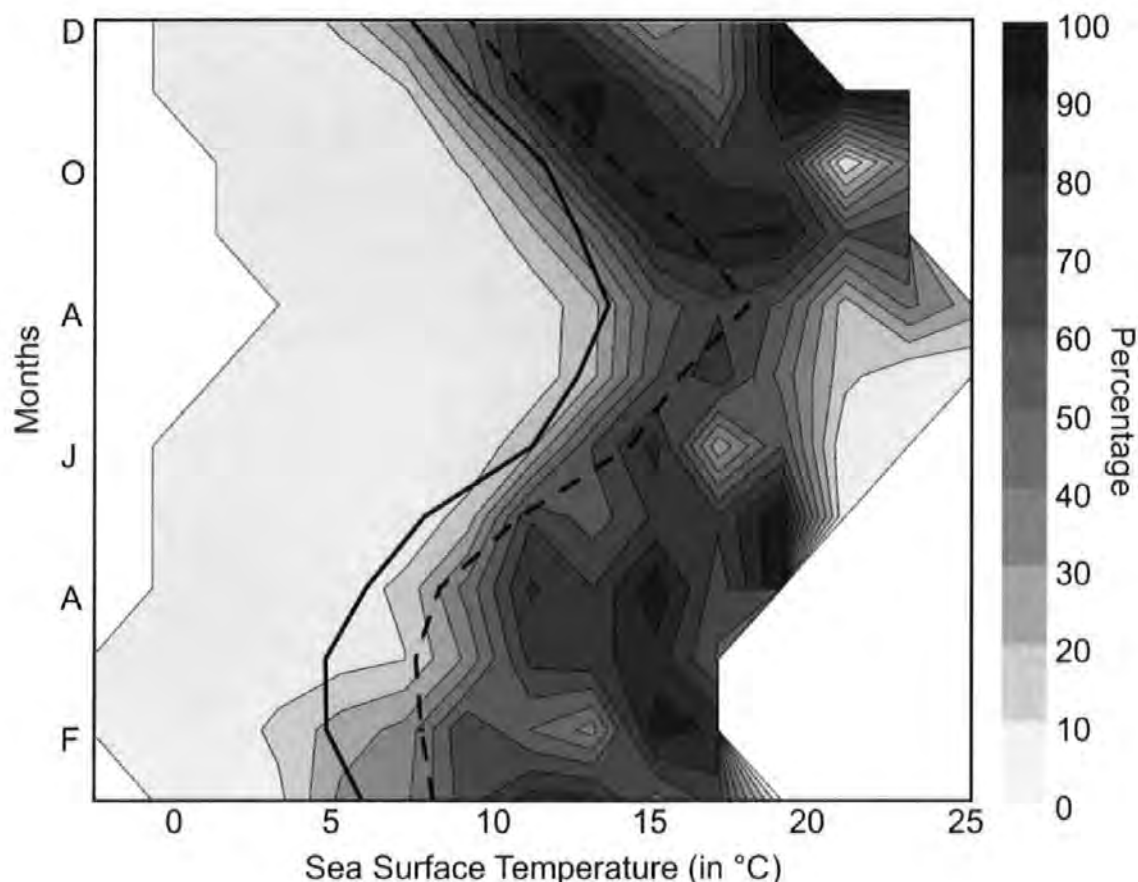


Figure 3.21. Contour diagram representing the proportion of *C. helgolandicus* on total *Calanus* (*C. finmarchicus* and *C. helgolandicus*). Values are expressed in percentage. Both minimum (black line) and maximum (dash line) monthly SST for the North Sea are superimposed.

3.C.6. Time stability of the thermal niche of *Calanus*

Figure 3.22 shows that depending upon the state of the North Atlantic Oscillation, the thermal niche of both *Calanus* did not change ($r = 0.79$; $p < 0.01$; $n = 133$ for *C. finmarchicus* and $r = 0.77$; $p < 0.01$; $n = 128$ for *C. helgolandicus*). Beaugrand (2004b) stressed that the timing of the shift varied according to species, trophic levels and the spatial centre of distribution of organisms. However, the selection of different time periods did not affect the results. Similar results are found for periods before and after the 1980's regime shift (Fig. 3.23) ($r = 0.88$; $p < 0.01$; $n = 135$ for *C. finmarchicus* and $r = 0.92$; $p < 0.01$; $n = 135$ for *C. helgolandicus*).

Figure 3.24 shows the stability of the thermal niche of *Calanus* at the diel scale. No significant change between the thermal niche between daylight and dark period was identified ($r = 0.76$; $p < 0.01$; $n = 142$ for *C. finmarchicus* and $r = 0.94$; $p < 0.01$; $n = 142$ for *C. helgolandicus*). This analysis suggests that possible year-to-year changes in the depth distribution of the *Calanus* species are unlikely to have biased our assessment of the Hutchinson's niche for the two *Calanus*.

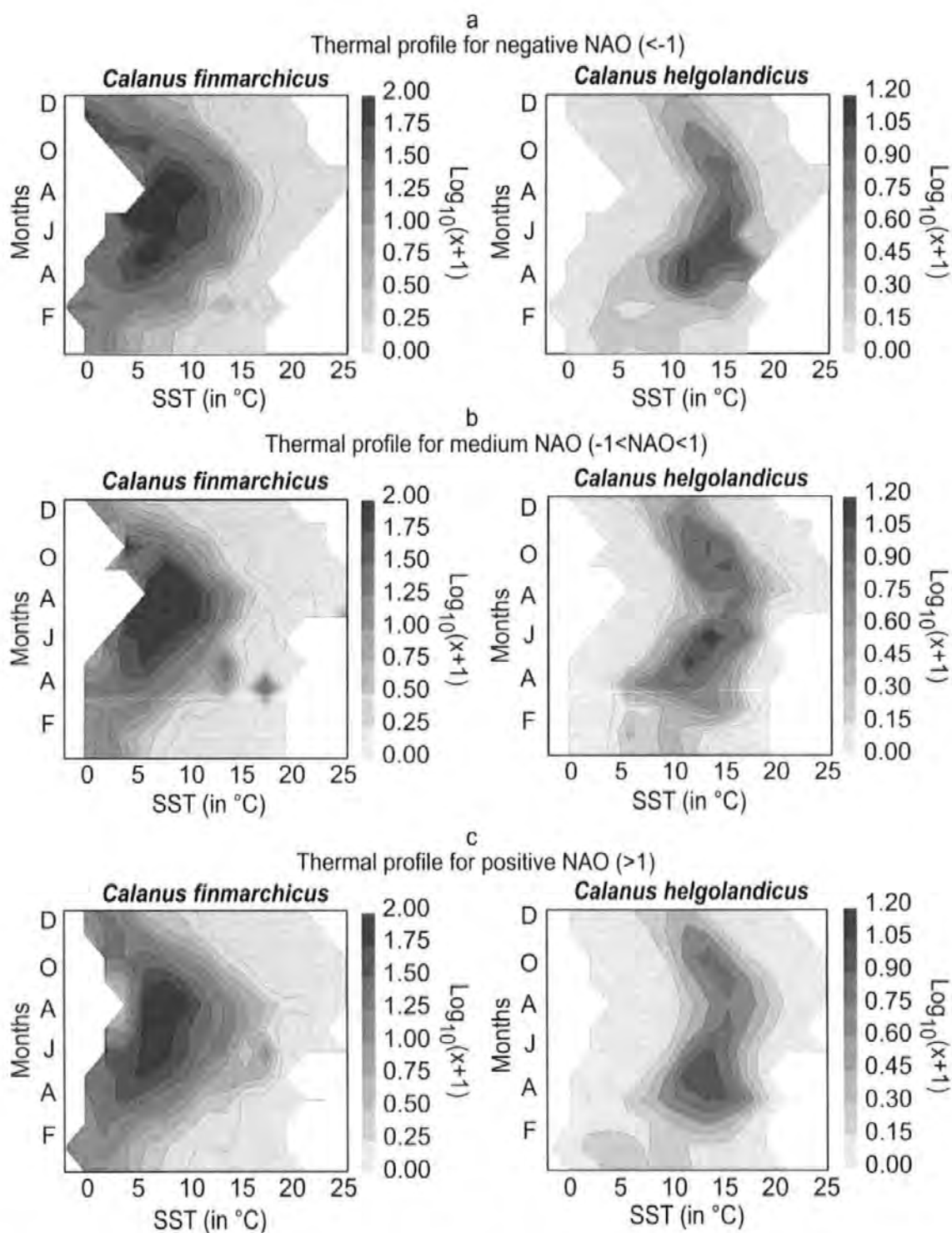


Figure 3.22. Contour diagram of the abundance (in decimal logarithm) of *Calanus finmarchicus* and *Calanus helgolandicus* as a function of the state of the North Atlantic. (a). For a value of the NAO index <-1 . (b). For a value of the $-1 < \text{NAO index} < 1$. (c). For a value of the NAO index >1 .

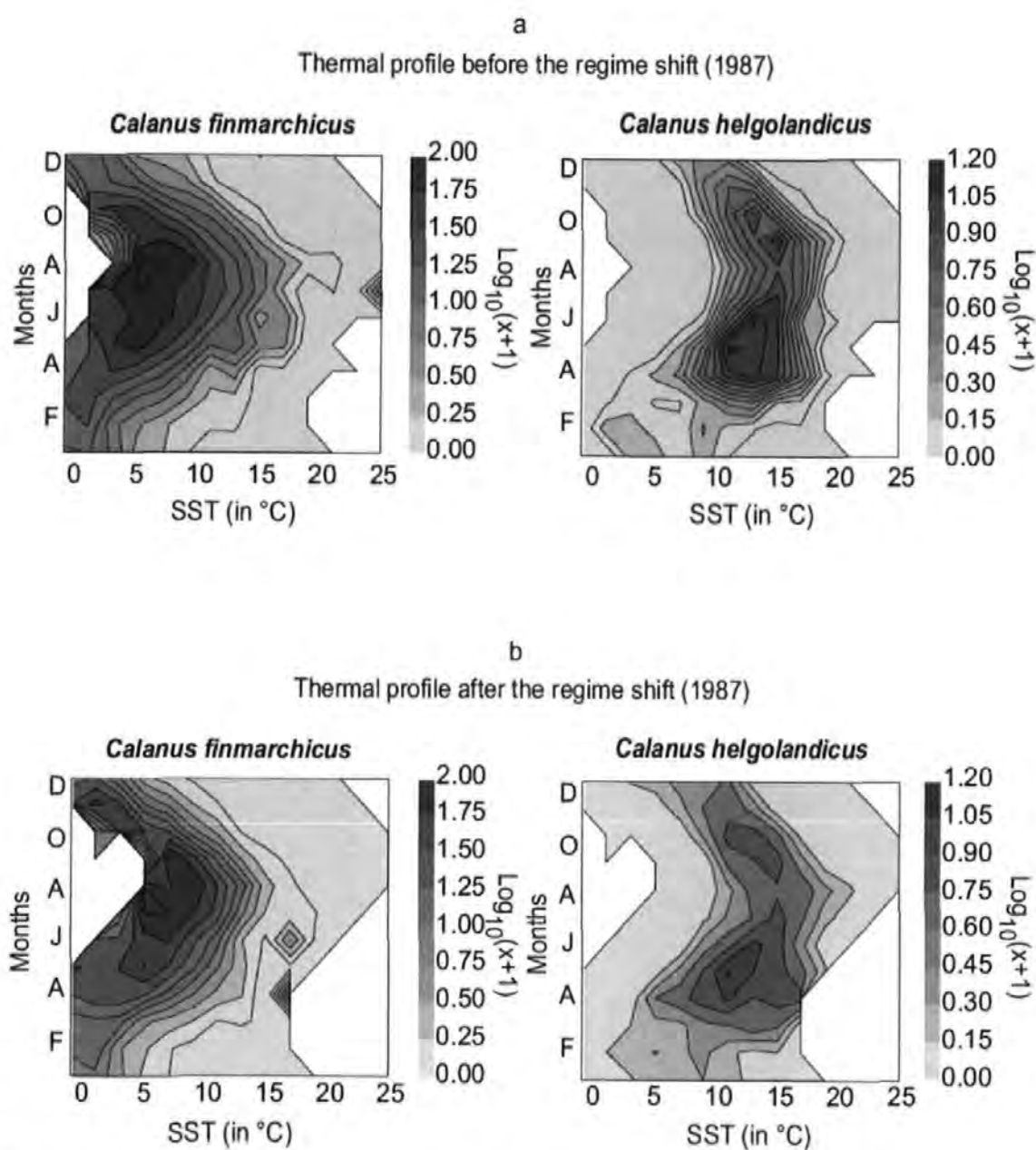


Figure 3.23. Contour diagram of the abundance (in decimal logarithm) of *Calanus finmarchicus* and *Calanus helgolandicus* as a function of the state of the North Atlantic. (a). For a period before the 1980's regime shift. (b). For a period after the 1980's regime shift.

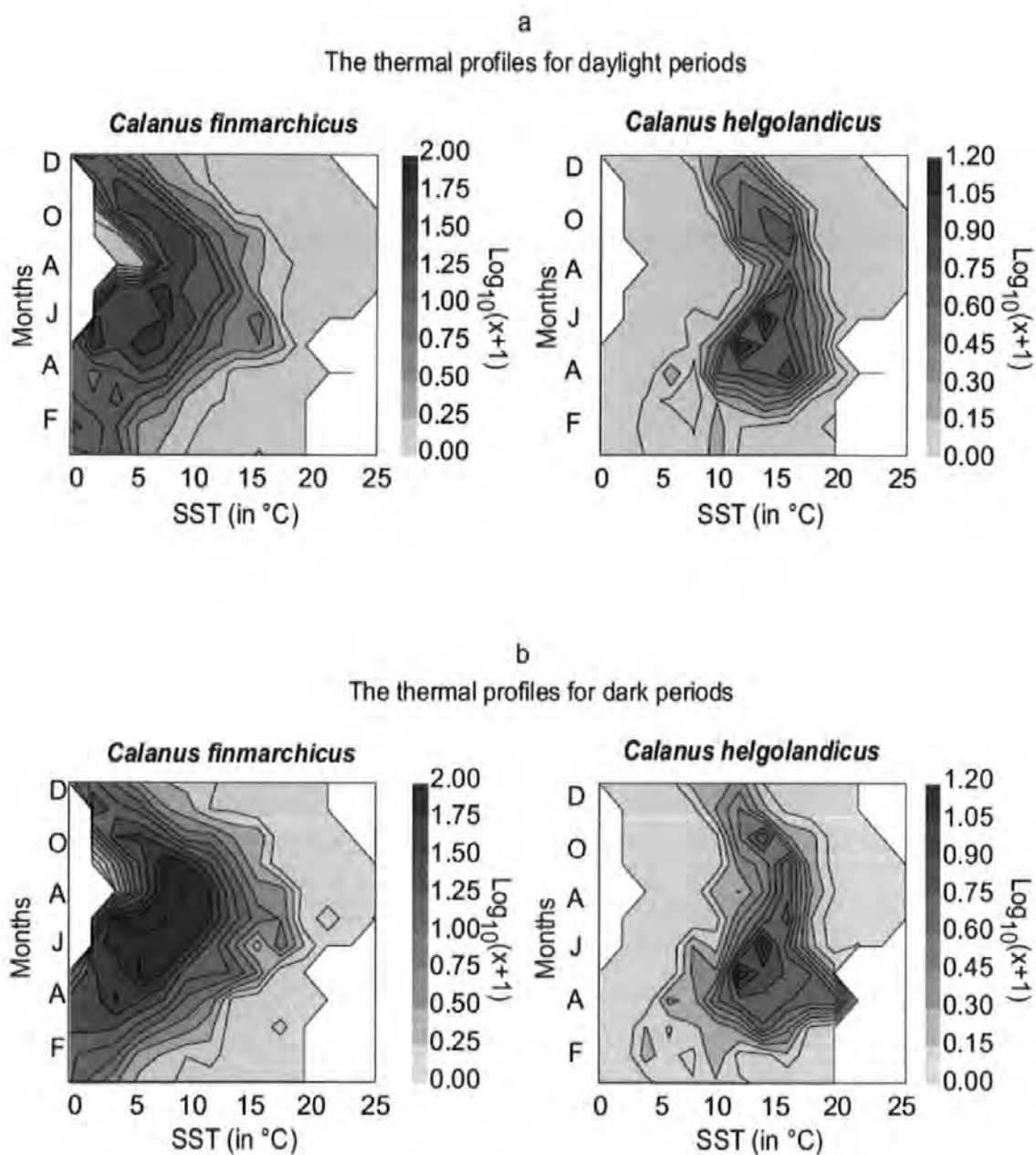


Figure 3.24. Contour diagram of the abundance (in decimal logarithm) of *Calanus finmarchicus* and *Calanus helgolandicus* as a function of the state of the North Atlantic. (a). For daylight period (10 to 16 o'clock). (b). For dark period (22 to 4 o'clock).

3.D. Discussion

This chapter has shown that the (Hutchinson) ecological niches of *C. finmarchicus* and *C. helgolandicus* are significantly separated despite the similar morphology of the species (Fleminger & Hulsemann 1977; Bucklin et al. 1995). The niche of *C. helgolandicus* is smaller than its congeneric species with few exceptions for higher abundance categories mainly when *C. helgolandicus* has its seasonal maximum in abundance. These exceptions are probably related to the positive relationships between abundance and dispersal in the pelagic realm (Beaugrand et al. 2001). Figure 3.25 summarises the different environmental optimums of both *Calanus* found in the present study. The subarctic species *C. finmarchicus* has a broader tolerance interval than its congeneric species and is therefore able to support larger environmental variations (Fig. 3.25). This species is adapted to a cold oceanic environment, with high mixing during the winter time and more nutrients, silicates, oxygen and is therefore indicative of the Atlantic Arctic Biome and especially the Atlantic Arctic and Subarctic provinces defined by Longhurst (1998) (see also Fig. 1.4). Its congeneric species *C. helgolandicus* is more adapted to temperate waters found in the Atlantic Westerly Winds Biome (Longhurst 1998) although mainly present along shelf-edges (regions with higher spatial variation in bathymetry). Provinces of this biome have typically higher temperature, less nutrients, silicates and oxygen (Longhurst 1998).

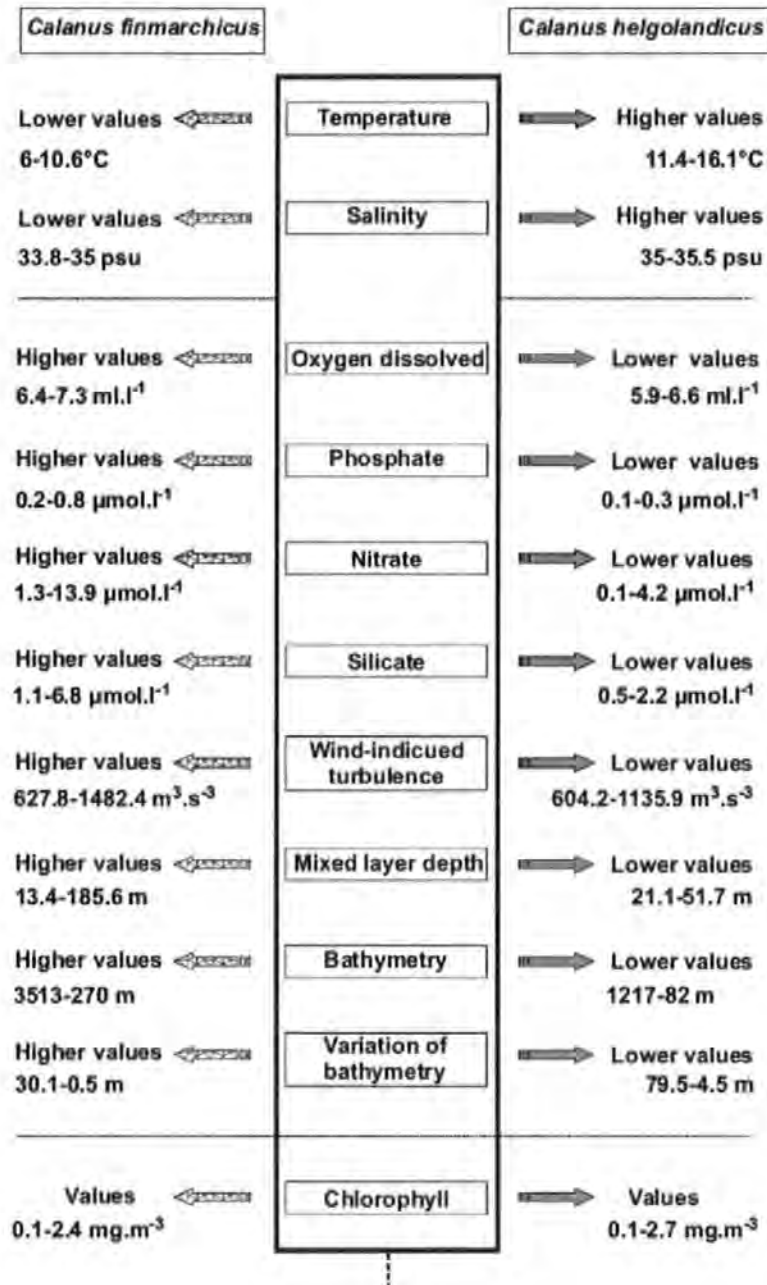


Figure 3.25. Diagram showing the influence of the different abiotic variable on two *Calanus* species. Environmental preferences were determined using the first and the ninth deciles for each environmental parameters for which *Calanus* species were superior to the first quartile. It can be seen from the diagram that *Calanus helgolandicus* is the species indicative of the Westerly Wind Biome for regions above the shelf edge (e.g. regions with high spatial variability in bathymetry) while *Calanus finmarchicus* is indicative of the Arctic biome (especially subarctic and Arctic Atlantic province, Longhurst (1998).

Temperature appears to be the factor that mostly influences the spatial distribution of the two species. This parameter was highly correlated to the first principal component. Many authors have highlighted the importance of this parameter for the physiology, the biological cycle and the ecology of copepods (Mauchline 1998, Halsband-Lenk et al. 2002, Lindley & Reid 2002). Beaugrand et al. (2001) have shown the close link between the spatial distribution in copepod diversity and temperature. Currie (1991) suggested that this parameter was the principal factor explaining the difference in diversity between the equator and the poles. This factor influences growth, development and reproduction of many plankton species (Halsband-Lenk et al. 2002).

Temperature covaries negatively with nutrients and oxygen concentration so that a change in temperature is accompanied by a change in nutrient and oxygen concentration over the study area. These relationships hold because when temperature increases, biological production augments, thus consuming nutrients (Russel-Hunter 1970). Furthermore, when temperature increases, stratification is strengthened limiting nutrient input from deeper waters (Beaugrand et al. 2001). The relationship between temperature and oxygen is related to the physical link between oxygen solubility and temperature (Millero et al. 2002). Therefore, we believe that the main driver is temperature and not its covariates although it is possible that nutrients and oxygen also play a role especially through food web interactions (Legendre & Rassoulzadegan 1995). Indeed Legendre & Rassoulzadegan (1995) showed that by altering nutrient concentration, changes in phytoplankton composition can impact higher trophic levels.

Structure of the water column indicated by the wind-induced turbulence index and mixed layer depth is also an important factor. It appears that *C. finmarchicus* is mainly located in oceanic regions with lower stratification than *C. helgolandicus*. Structure of

the water column is likely to have a substantial influence on zooplankton distribution, life strategy and population dynamics (Longhurst 1998; Heath et al. 1999b). A negative relationship between stratification and zooplankton biomass has been reported for the Californian coast by Roemmich & McGowan (1995). They suggested that a longer stratification period, as well as stronger stratification, might hamper the inter-change of nutrients from deeper to surface waters, limiting phytoplankton growth and ultimately food for higher trophic levels.

Bathymetry also influences, to a lesser extent than temperature, the spatial distribution of the two species. Indeed, *C. helgolandicus* is mainly centred over areas between 0 and 500 m of depth whereas *C. finmarchicus* is generally present in deeper areas. These results confirm previous work that classified *C. finmarchicus* as being primarily an oceanic species and *C. helgolandicus* as being a pseudo-oceanic species (Fleminger & Hulsemann 1977; Beaugrand et al. 2001, Bonnet et al. 2005). Bathymetry is especially important for *C. helgolandicus* (Beaugrand 2004a, Bonnet et al. 2005). Fleminger & Hulsemann (1977, their Fig. 5) proposed a map of the spatial distribution of both *Calanus* studied in this work. Our results are similar and differences noted for *C. finmarchicus* are mainly related to the use of presence data by Fleminger & Hulsemann (1977) while abundance data were utilised in the present study. Furthermore, 45 years of sampling are now available while Fleminger & Hulsemann (1977) based their synthesis on 17 years of CPR sampling.

Identification and quantification of environmental factors involved in the spatial regulation and ecological niche of *C. finmarchicus* and *C. helgolandicus* may enable the calculation of habitat suitability maps (Pulliam 2000). The fact that temperature is an important controlling factor of the spatial distribution of *C. finmarchicus* and *C.*

helgolandicus has significant implications in the context of global climate change. Indeed, temperature is one of the parameters which will be the most affected (Intergovernmental Panel on Climate Change 2001). Moreover, temperature is the most accessible parameter in the various scenarios suggested by the Intergovernmental Panel on Climate Change (2001). This makes possible the realisation of scenarios of changes in the spatial distribution of *C. finmarchicus* and *C. helgolandicus*. Forecasting the distribution of *C. finmarchicus* and *C. helgolandicus* with Ocean General Circulation Models (OGCM) outputs is of great interest because these *Calanus* species are key-structural species of pelagic ecosystems in the North Atlantic and adjacent seas. These species have a significant role in the life cycle of many exploited fishes. For example, Beaugrand et al. (2003) recently showed the importance of *C. finmarchicus* for the survival of larval cod in the North Sea. A positive correlation between cod recruitment and the abundance of *C. finmarchicus* was detected. The relation was opposite with *C. helgolandicus*. Mechanisms proposed were based on the "match/mismatch" hypothesis (Cushing 1997). *C. finmarchicus* was abundant in the North Sea prior to the 1980s regime shift. As this species has its seasonal maximum in spring, it ensured a great availability of prey for cod larvae (period of occurrence from March to August). *C. finmarchicus* decreased during the 1980s while its congeneric species increased. This change in dominance reduced the availability of *Calanus* prey in spring because *C. helgolandicus* has its seasonal maximum in autumn at a time when cod larvae feed on larger prey such as euphausiids or other fish.

A remarkable feature in our study is that the environmental optimum of *Calanus* species varies seasonally for all abiotic parameters. These seasonal fluctuations might be influenced by the spatial variability in the seasonality of both species (Planque et al. 1997). For *C. finmarchicus*, seasonal fluctuations could be related to large-scale

differences in the timing of the ontogenetic vertical migration. Another hypothesis could be related to the differential sensitivity of the mean developmental stage of *Calanus* population to temperature. This has been observed in some experiments (Harris et al. 2000).

The use of this ecological niche approach has allowed an explanation of the shift in *Calanus* dominance to be outlined. Reid et al. (2003b) showed a substantial and sustained reduction in the percentage of *C. finmarchicus* on total *Calanus* in the North Sea. While in 1962, *C. finmarchicus* represented 80% of the *Calanus* in the North Sea, *C. helgolandicus* composed 80% of *Calanus* identified by the CPR survey in 2000. As seen in Figure 3.21, the dominance of *Calanus* in the North Sea is highly sensitive to temperature, especially in spring and summer. We demonstrate that the shift in dominance could have been triggered by temperature changes alone in the North Sea. Sea surface temperature changes are likely to be related to the rise in air temperature (Beaugrand 2004b) over the region and changes in advection recently discussed in Reid et al. (2003b). These authors reported that when the NAO was positive, the strength of the European shelf-edge current, which flows northwards, increased and that oceanic inflow into the northern part of the North Sea was strengthened. During the cold regime in the North Sea prior to 1980, this region was at the boundary between a subarctic biome and a more temperate biome (Longhurst 1998). As *C. finmarchicus* is indicative of the Atlantic Arctic biome, the change in the proportion of *Calanus* in the North Sea may indicate that the subarctic biome has moved northwards. This has been recently suggested by Beaugrand (2004b). A northward movement of plankton has been detected using calanoid copepods in the northeastern part of the North Atlantic (Beaugrand et al. 2002) and a similar shift has been found for fish (Perry et al. 2005).

This chapter has shown that the concept of the Hutchinson ecological niche is useful and some authors even stressed that it remains poorly utilised by ecologists. However, it is important to remember that in the present study, we have assessed the realised niche, not the fundamental niche of *Calanus*. Hutchinson (1957) made this distinction and stated that the realised niche should always be smaller than the fundamental niche as species interactions eliminate individuals from favourable biotope. However, Pulliam (2000) recently showed that when dispersal is high, the realised niche can be larger than the fundamental. This is probably the case here as the oceanic pelagic realm is continuous, three-dimensional and without geographical barriers which make biogeographical regions less well-defined than in the terrestrial realm. One way to assess the fundamental niche would be to base the assessment of the species niche from a physiological model such as the one described in Pulliam (2000).

Chapter 4

Physiology, ecological niches and species distribution

The present chapter is constituted by the following paper:

Helaouët, P., Beaugrand, G., 2009. Physiology, ecological niches and species distribution. *Ecosystems* 12, 1235-1267.

While many studies have debated on theoretical links between physiology, ecological niches and species distribution, few studies have provided evidence for a tight empirical coupling between these concepts at a macroecological scale. We used a physiological model to assess the fundamental niche of a key-structural marine species. We found a close relationship between its fundamental and realised niche. The relationship remains constant at both biogeographical and decadal scales, showing that changes in environmental forcing propagate from the physiological to the macroecological level. A substantial shift is detected in the North Atlantic and projections of range shift using IPCC scenarios suggest a poleward movement of the species of one degree of latitude per decade for the 21st century. The shift in the spatial distribution of this species reveals a pronounced alteration of polar pelagic ecosystems with likely implications for lower and upper trophic levels and some biogeochemical cycles.

Chapter 4: Physiology, ecological niches and species distribution

4.A. Introduction

Biogeographical studies necessitate having a reasonable knowledge of the ecological niche, defined here as the range of tolerance of a species when several environmental factors are taken simultaneously (Hutchinson, 1957). Hutchinson (1957) conceptualised this notion with the so-called *n*-dimensional hypervolume, in which *n* ideally corresponds to all environmental factors. This concept is a powerful tool against which researchers can better assess potential effects of global change on species distribution (Beaugrand & Helaouët, 2008). Indeed, the concept of ecological niche has been extensively used to understand and model anthropogenic impacts such as the introduction of exotic species and pollution on species distribution (Peterson, 2003). Determining the contribution of different environmental factors is achieved from knowledge of the distribution of species with field observations that can be related to environmental predictor variables (Guisan & Thuiller, 2005). Different techniques exist, depending on species data, which can simply be presence data (e.g. ecological niche factor analysis (Hirzel *et al.*, 2002)), presence-absence data (e.g. generalised additive models (Hirzel *et al.*, 2006)) or abundance data based on field sampling (e.g. all regression analyses (Legendre & Legendre, 1998)). However these techniques can only estimate the realised niche since they are based on observational data. Pulliam (2000) proposed a new type of model to explain and assess differences between fundamental and realised niches. As stated by Hutchinson (1957), his work indicates that the realised niche is smaller when factors reducing survival such as competition predominate. However, Pulliam (2000) also provided evidence that the realised niche can be greater than the fundamental one when dispersal is high.

The fundamental niche represents the response of all physiological processes of a species to the synergistic effects of environmental factors (Fig. 4.26). Only optimal conditions generate high abundances and allow for successful reproduction. When the environment becomes less favourable, this affects consecutively the reproduction, growth and feeding (Fig. 4.26). Extreme conditions become critical and may eventually affect survival (Schmidt-Nielsen, 1990). Ideally, any study that attempts to predict the habitat of a species based on the knowledge of the environment should use both fundamental and realised niches. Past studies have largely focussed on the realised niche (e.g. Hirzel *et al.*, 2002; Helaouët & Beaugrand, 2007) while estimation of the fundamental niche has been neglected. However, comparison of both niches can provide important insights on biological mechanisms (e.g. competition or predation) that structure a population.

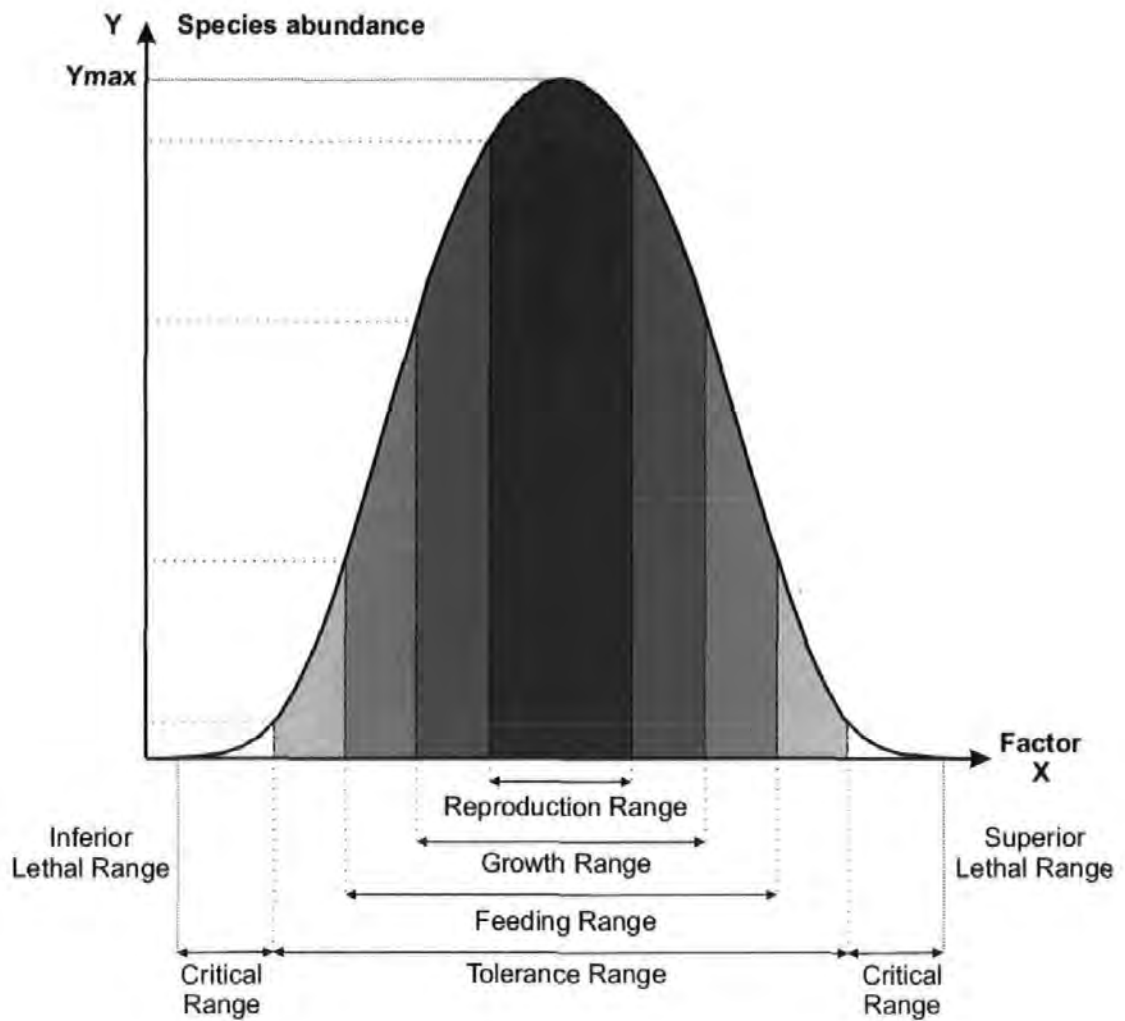


Figure 4.26. Response curve illustrating the effects of an environmental factor (X) on the species abundance (Y). Extremes values of X are lethal; less extreme values prevent feeding and then growth; only optimal conditions allow reproduction.

Climate change affects the structure, the dynamics and the functioning of marine ecosystems through many physical and biological processes (Reid & Beaugrand, 2002). Changes in the state of the climate system may also unbalance the location of boundaries between major biogeographical systems (Lomolino *et al.*, 2006). Key-structural species are useful to track such changes in the ecosystem state and location. Understanding the spatial distribution of these species has become an important issue in marine ecology (Helaouët & Beaugrand, 2007). *Calanus finmarchicus* is a key-structural marine zooplankton copepod species in the North Atlantic Ocean and is among the most studied copepods in this area (e.g. Heath *et al.*, 2000). This mainly herbivorous species plays an important role in transferring primary production to higher trophic levels in the food web (Mauchline, 1998). Indeed, it has been suggested that the species is a key element for the larval survival of some commercially important fish species such as the Atlantic cod (Beaugrand *et al.*, 2003a). The species also modulates the abundance of phytoplankton through changing grazing pressure (Carlotti & Radach, 1996). Assessing future changes in the spatial distribution of the species is a prerequisite to anticipate ecosystem changes but should be based on the joint assessment of the fundamental and the realised niches.

In this chapter, we assess both the fundamental and realised niches of *C. finmarchicus* and provide evidence for a close correspondence of the two niches at a macroecological level. The concomitant spatial and temporal changes seen in physiology and biogeography are constant at the decadal scale which makes it possible to propose projections of the spatial distribution of the copepod as a function of different scenarios of changes in temperature established by the (Intergovernmental Panel on Climate Change, 2007b). Our study shows that the temperature rise observed and projected by atmosphere-ocean general circulation models over the North Atlantic sector propagates

from the physiological to macroecological level. Implications of the result for ecological niche modelling are discussed and potential consequences of the change in this key-structural species for ecosystem structure and functioning outlined.

4.B. Materials and methods

The area covered by this study extended from 99.5°W to 19.5°E of longitude and 29.5°N to 69.5°N of latitude thereby covering all the North Atlantic Ocean and adjacent seas.

4.B.1. Biological and environmental data

4.B.1.A. Calanus finmarchicus

Data on the abundance of adult *Calanus finmarchicus* (copepodite CV and CVI) were provided by the Continuous Plankton Recorder (CPR) survey. The CPR survey is a large-scale plankton monitoring programme managed and maintained by the English laboratory Sir Alister Hardy Foundation for Ocean Science (SAHFOS) since 1991. The sampler is towed at a constant depth of ~ 7 m (Reid *et al.*, 2003a). Despite the near surface sampling, the sampling gives a satisfactory picture of the epipelagic zone (Batten *et al.*, 2003). Water enters through an inlet aperture of 1.61 cm² and passes through a 270 µm silk filtering mesh (Batten *et al.*, 2003). Individuals greater than 2 mm such as adult copepodite stages CV and CVI of *C. finmarchicus* are then removed from both the filtering and covering silk. Generally, all individuals are counted, but for particularly dense samples a sub-sample can be realised (Batten *et al.*, 2003). We created gridded data (from 99.5°W to 19.5°E of longitude and 29.5°N to 69.5°N of latitude with a spatial resolution of 1° latitude x 1° longitude) averaging the abundance of *C. finmarchicus* for the whole sampling period 1960-2005. The climatology of the

abundance of *C. finmarchicus* for each decade of the period 1960-2005 (1960s, 1970s, 1980s, 1990s) and for the most recent period 2000-2005 was based on interpolated data. Interpolation was made to maximise the number of values and thereby increase the quality of model comparison. Interpolation was realised using the inverse squared distance method (Lam, 1983) with a search radius of 250 km (about 135 miles) using a technique applied by Beaugrand *et al.* (2001).

4.B.1.B. Sea Surface Temperature

Temperature (as Sea Surface Temperature) was selected as this parameter strongly influences the abundance and spatial distribution of marine ectotherms (Schmidt-Nielsen, 1990; Mauchline, 1998). Sea Surface Temperature (SST) data come from the Comprehensive Ocean-Atmosphere Data Set (COADS) and were downloaded from the internet site of the National Oceanographic Data Center (NODC), which manages acquisition, control quality and ensures the long-term safeguarding of the data (Woodruff *et al.*, 1987). To perform all analyses, we created two different kinds of SST climatology. The first climatology was based on the averaging of 45 years (1960-2005), the second one was the result of the average of each decade for the period 1960-1999 (1960s, 1970s, 1980s, 1990s) and the most recent period 2000-2005.

To evaluate the potential impact of changes in SST on spatial distribution, data (1990-2100) from the ECHAM 4 (EC for European Centre and HAM for Hambourg) model were utilised. This Atmosphere-Ocean General Circulation Model (AO-GCM) has a horizontal resolution of 2.8° latitude and 2.8° of longitude (Roeckner *et al.*, 1996). The present data were selected by the Intergovernmental Panel on Climate Change (2007b) based on criteria among which are physical plausibility and consistency with global projections. Data are projections of monthly skin temperature equivalent above the sea

to SST (<http://ipcc-ddc.cru.uea.ac.uk>). Data used here are modelled data based on scenario A2 (concentration of carbon dioxide of 856 ppm by 2100) and B2 (concentration of carbon dioxide of 621 ppm by 2100) (Intergovernmental Panel on Climate Change, 2007b). In scenario A2, the increase of CO₂ has a rate similar to current observed data (Intergovernmental Panel on Climate Change, 2007b). The scenarios A2 and B2 are based on a world population of 15.1 and 10.4 billion people by 2100, respectively. Data were recommended by Intergovernmental Panel on Climate Change on the basis of physical plausibility and consistency with global projections. Data are projections of monthly skin temperature equivalent above the sea to SST (<http://ipcc-ddc.cru.uea.ac.uk>). A decadal mean was calculated for the 2050s and 2090s.

4.B.1.C. Chlorophyll *a*

Phytoplankton concentration is also an important parameter to explain changes in the spatial distribution and abundance of *C. finmarchicus*. Therefore chlorophyll *a* data were selected. These data originated from the programme and satellite Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from the National Aeronautics and Space Administration (NASA). Chlorophyll *a* data were converted into food concentrations (F) using Equation 1 (Hirche & Kwasniewski, 1997):

$$F_{t,s} = r \times C_{t,s} \quad (1)$$

With $F_{t,s}$ the food concentrations (in $\mu\text{g.l}^{-1}$) at time *t* and location *s* and $C_{t,s}$ the quantity of chlorophyll *a* (in $\mu\text{g.l}^{-1}$) at time *t* and location *s* using a carbon:chlorophyll ratio *r* of 40 (Hirche & Kwasniewski, 1997). A climatology of food concentration was calculated,

based on the period 1997-2005. This implicitly assumes that the period is representative of 1960-2005, which is, for the selected spatial scale, a reasonable assumption.

4.B.1.D. Bathymetry

Spatial distribution of *C. finmarchicus* in the area is influenced by bathymetry (Helaouët & Beaugrand, 2007), the species being rarely detected when the water column becomes shallow (Continuous Plankton Recorder Survey Team, 2004; Helaouët & Beaugrand, 2007). We used bathymetry data to restrict our calculations in areas deeper than 50m. This threshold was fixed after examination of the spatial distribution of *C. finmarchicus* (Beaugrand, 2004a; Helaouët & Beaugrand, 2007). Bathymetry data originated from the database General Bathymetric Chart of the Oceans (GEBCO).

4.B.2.A. Estimation of the realised niche

The realised niche was inferred from the calculation of the spatial distribution of adult *C. finmarchicus* (CV and CVI) for the whole sampling period 1960-2005. As already mentioned in the introduction, the realised niche represents the fundamental niche modified by factors such as dispersal that increase the width of the niche or factors such as competition that, on the contrary, tighten it.

4.B.2.B. Estimation of the optimal part of the fundamental niche

Many studies have revealed that reproduction is maximal when the species is at its optimal part of the fundamental niche (Hirche, 1990). We used this physiological property as a proxy to determine the central part of the fundamental niche of *C. finmarchicus* (see Fig. 4.26). When the optimal part of the fundamental niche is reached, the species must have its maximum abundance. Potential egg production rate

(EPR) at time t and location s ($E_{t,s}$, in Eggs.female⁻¹.d⁻¹) was therefore calculated based on information on temperature and food concentration (Heath *et al.*, 2000):

$$E_{t,s} = p_1 (F_{t,s} - F_h)^{p_2} p_3 10^{\frac{p_4 - ((T_{t,s} - T_{opt}) p_5)^2}{100}} \quad (2)$$

With $T_{t,s}$ the sea surface temperature (in °C) at time t and location s and T_{opt} , the temperature optimum. The latter, which determines the maximum value of egg production, was taken from Heath *et al.* (2000), who fixed its value to 6°C. $F_{t,s}$ is food concentration (in µg.l⁻¹) at time t and location s (see Equation 1). Parameter F_h is the food concentration below which no egg production is expected. This parameter was fixed to 8 µg.l⁻¹ by Richardson *et al.* (1999). Other parameters from p_1 to p_5 were estimated by non linear least square regression and were taken from Hirche and others (1997) ($p_1 = 6.2$; $p_2 = 0.48$; $p_3 = 0.14$; $p_4 = 60$; $p_5 = 1.9$). It is clear from Equation 2 that this model is only valid in situations when $F_{t,s} \geq F_h$. Therefore, when food concentration was inferior to 8 µg.l⁻¹, value of EPR was set to 0.

The possibility to use or forecast egg production of *C. finmarchicus* is limited by the difficulty to obtain chlorophyll *a* data. Therefore, we simplified equation (2) by fixing food concentration ($F_{t,s}$) to its optimal value. The optimal value (21.79 µg.l⁻¹) was determined by fitting equation 2 to potential EPR versus temperature (climatology based on the period 1960-2005). When $F_{t,s} = 21.79$ µg.l⁻¹, Equation (2) becomes:

$$E_{t,s} = 3.06 \times 10^{\frac{p_4 - ((T_{t,s} - T_{opt}) p_5)^2}{100}} \quad (3)$$

It should be noted that when EPR is calculated using equation 3, it becomes the potential egg production rate (PEPR) since it is not representing the number of eggs expected but more the potential of production.

4.B.2.C. Correlations

The Pearson coefficient of correlation was calculated to examine the relationship between the realised (spatial distribution of *C. finmarchicus*) and the optimal part of the fundamental niche (PEPR) for different time periods (Fig. 4.27). To evaluate the impact of spatial autocorrelation when correlation was calculated between maps, the minimum degree of freedom needed to have a significant correlation ($p = 0.01$) and corresponding to the observed correlation value was assessed.

4.B.2. Procedures and analyses

Figure 4.27 summarises the different analyses performed in this study.

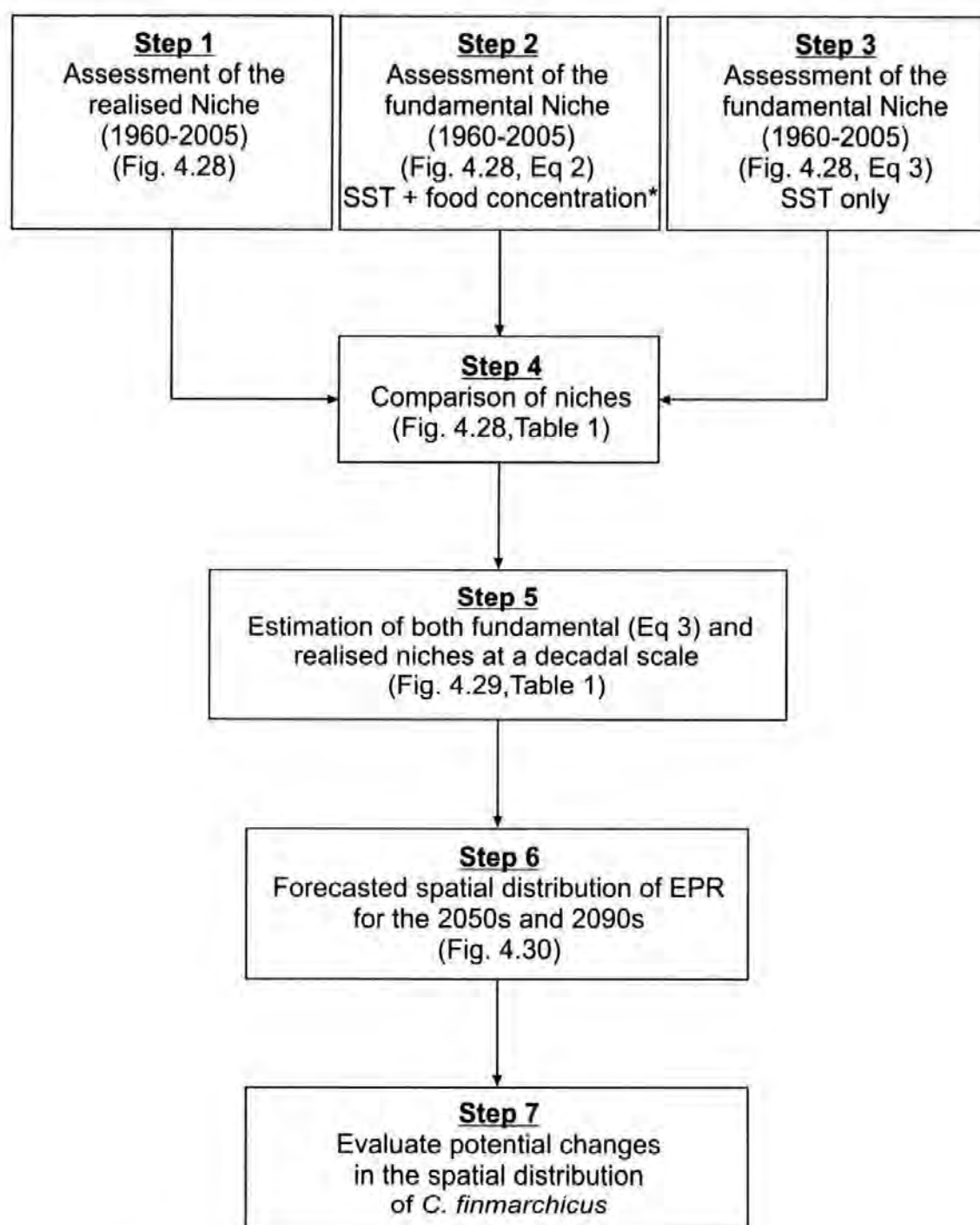


Figure 4.27. Sketch diagram summarising the different steps and analyses performed in this study. * The climatology of food concentration is based on chlorophyll *a* data, only available for the period 1997-2005.

4.C. Results

Analyses confirm that *C. finmarchicus* is a subarctic species, mostly abundant north of the Oceanic Polar Front (Dietrich, 1964) (Fig. 4.28a). Its realised niche shows an optimum range around 6°C but abundance remains high between 2.5°C and 9.5°C. This optimum corresponds to the temperature where egg production rate, determined in laboratory experiments, is maximal (Hirche and others 1997). Spatial distribution of EPR closely matches the spatial distribution of the abundance ($r = 0.71$ for all marine regions and $r = 0.81$ for regions deeper than 50m, Fig. 4.28a-b, Table 4.4), confirming that the abundance of the species is proportional to its potential EPR. These results suggest a strong correspondence between physiology and the biogeography of the species.

The central part of the fundamental niche is narrower than the realised niche as it is inferred from EPR (Fig. 4.28.c-d). The adjustment of the model by non-linear least square fitting is best when food concentration ($F_{t,s}$ in Eq 2) is fixed to 21.79 $\mu\text{g.l}^{-1}$. This value allowed us to simplify Eq 2 (see Eq 3 in Materials and Methods). Correlation between the two ways of assessing EPR (from Eq 2 and 3) is high and range from $r = 0.89$ ($p < 0.001$, Table 4.4) when all marine regions are considered to $r = 0.93$ ($p < 0.001$) when only regions deeper than 50m are included in the analysis. This result suggests that food concentration is not so limiting in the regions of interest, probably because chlorophyll *a* covaries well with temperature ($r = -0.71$; $p < 0.001$; $n = 3148$; $nf = 19$). Such a simplified model, depending only upon temperature, is an advantage because good quality data on chlorophyll *a* are restricted to years after 1997 and also because chlorophyll *a* data assessed from biogeochemical models have large uncertainties.

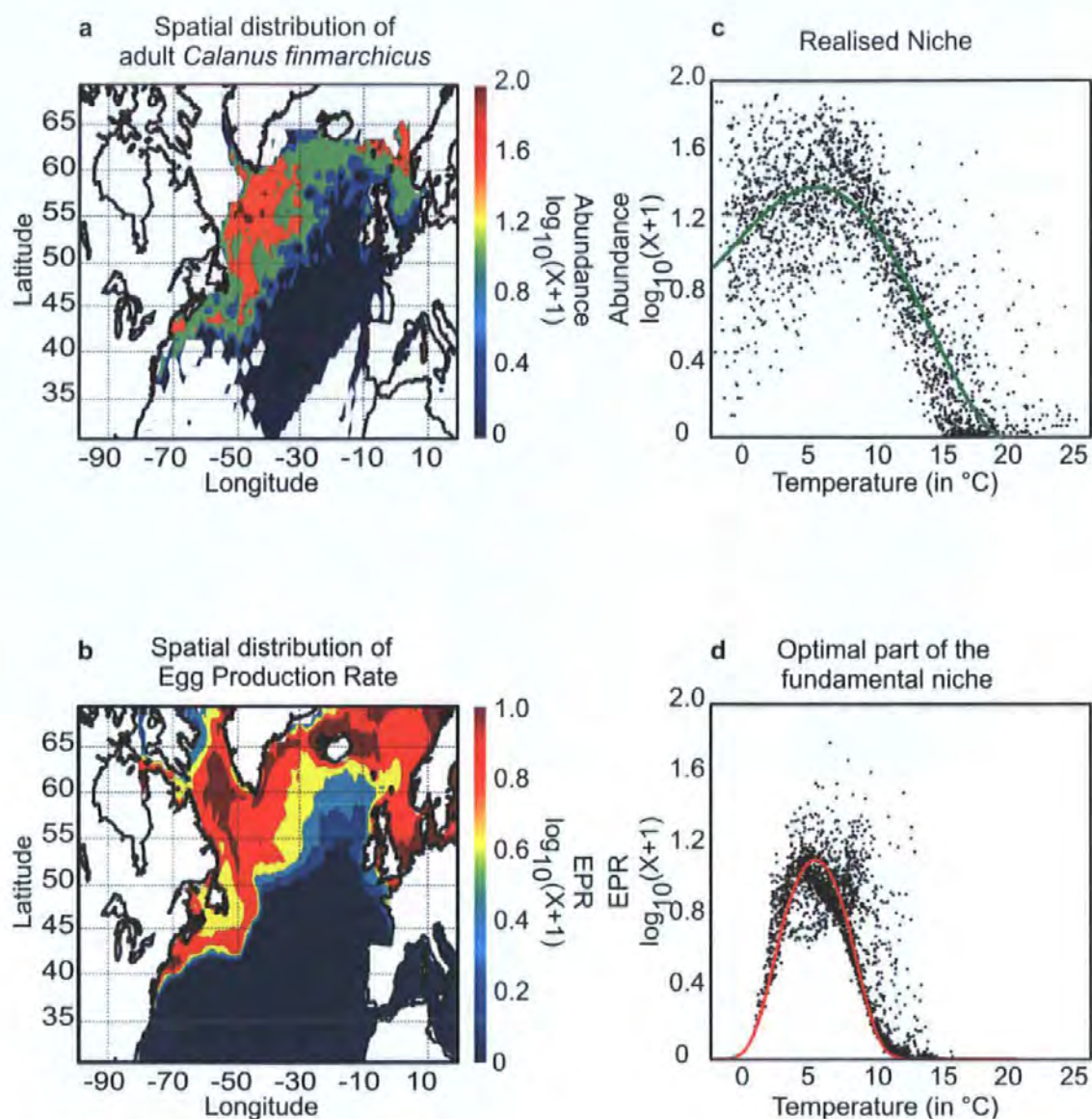


Figure 4.28. a. Spatial distribution of *C. finmarchicus* for the period 1960-2005. b. Spatial distribution of EPR calculated from Eq 2 and using temperature data for the period 1960-2005 and a climatology of food concentration based on chlorophyll *a* data for the period 1997-2005. The reproduction potential is high in the whole North Sea while the species rarely occurs in the shallow part of this sea. c. Abundance as a function of temperature (mean SST regime). Data are from Fig. 4.28a. The bold green line, reflecting the realised niche was calculated from a polynomial regression of order 5. d. Potential Egg production Rate (PEPR) as a function of temperature. Data are from Fig. 4.28b. The bold red line was calculated by adjusting $F_{t,s}$ in Eq. 2 as a function of data, using least square fitting.

Table 4.4. Relationships between fundamental and realised niches. Pearson correlation coefficients calculated between maps of EPR estimated from Eq 2 (E) and PEPR from Eq 3 (E*), abundance (Ab) for the period 1960-2005 (see Fig. 4.28) and at a decadal scale (see Fig. 4.29). Abundance data were transformed ($\log_{10}(\text{Ab}+1)$) prior to the calculation of correlation. ‘nf’ denotes the degree of freedom needed to have a significant correlation at $p = 0.01$. This was calculated to evaluate the strength of the correlation and to take into account that data are spatially autocorrelated. For example, when $\text{nf} = 10$ and $n = 3000$, this indicates that the correlation remains significant even when 10/3000 geographical pixels are kept (0.33% of the 3000 pixels).

All regions	correlation	probability	degree of freedom (n)	degree of freedom (nf)
E / E*	0.89	< 0.001	3144	10
E / Ab	0.71	< 0.001	1697	18
E* / Ab	0.79	< 0.001	1698	14
Regions >50m				
E / E*	0.93	< 0.001	2757	8
E / Ab	0.81	< 0.001	1618	13
E* / Ab	0.82	< 0.001	1618	13
Decadal analysis				
E* / Ab (1960-1969)	0.62	< 0.001	1567	25
E* / Ab (1970-1979)	0.74	< 0.001	1528	17
E* / Ab (1980-1989)	0.82	< 0.001	1227	13
E* / Ab (1990-1999)	0.79	< 0.001	1189	14
E* / Ab (2000-2005)	0.79	< 0.001	1358	14

At a decadal scale, spatial distribution of the abundance of *C. finmarchicus* also closely corresponds to EPR (Fig. 4.29). Correlations ranged from 0.62 in the 1960s to 0.82 in the 1980s (Table 4.4). It is interesting to note that correlations are fairly constant (with no observed trend) and that EPR explains between 38.44% and 67.24% of the variation in the abundance of *C. finmarchicus*. A concomitant northwards movement of the species and EPR is observed in the north-eastern part of the North Atlantic Ocean after the 1980s (Fig. 4.29). The reduction in the abundance of the species detected in the North Sea after 1990 is clearly explained by PEPR. A reduction is also detected over the eastern Scotian Shelf.

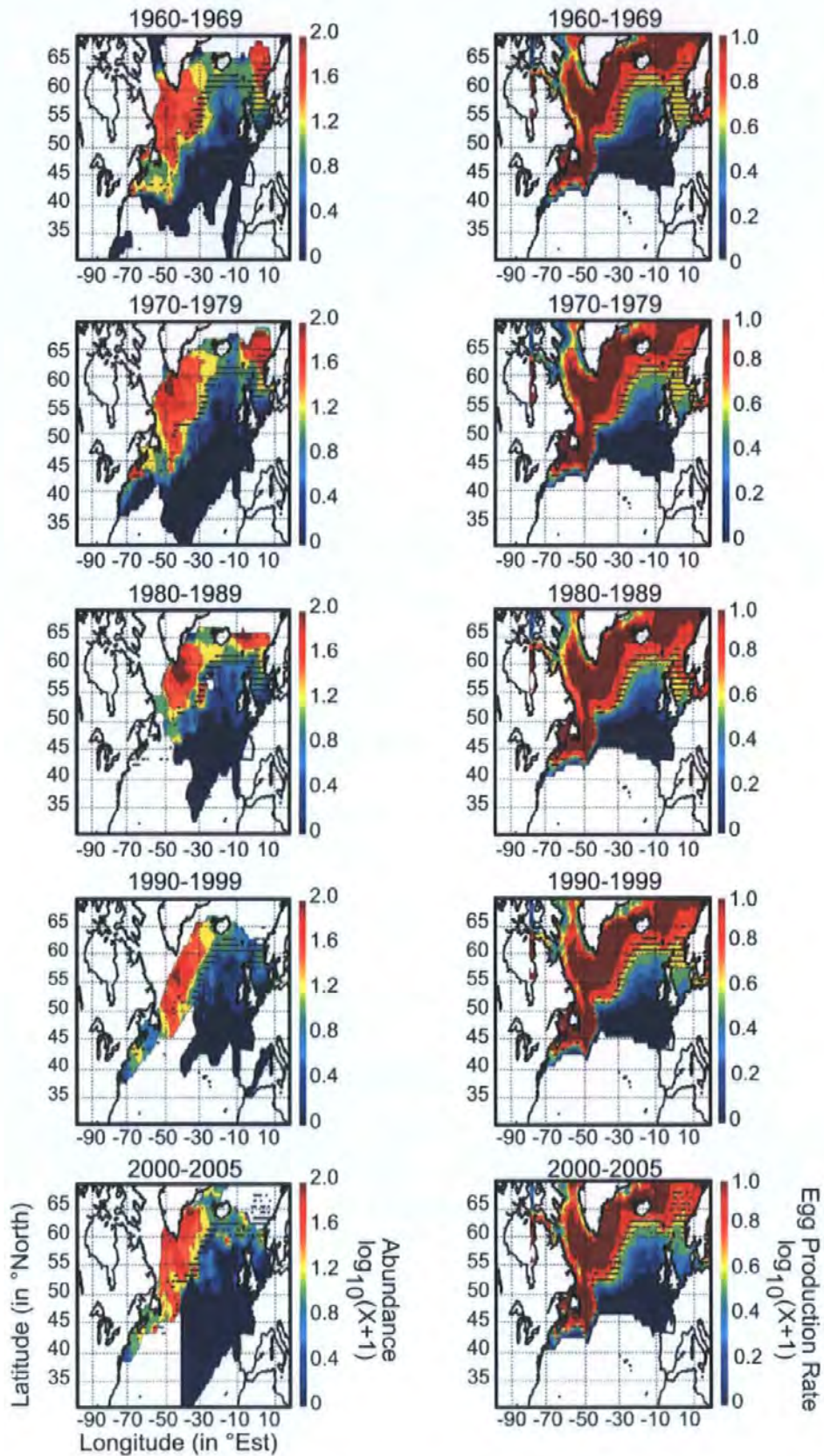


Figure 4.29. Decadal changes in the spatial distribution in the abundance of *C. finmarchicus* (in left) and egg production rate (in right). Abundances are extrapolated using to improve the number of values and thus increase the quality of model comparison. The isotherm 9-10°C is represented by asterisks (Beaugrand *et al.*, 2008).

The close correspondence in the spatial distribution of both abundance and PEPR and thereby both fundamental and realised niches as well as the constancy of the correlation at the decadal scale together make it reasonable to use PEPR as a proxy to forecast the spatial distribution of *C. finmarchicus*, utilising scenario of temperature changes from AO-GCMs (here ECHAM 4 data using the moderate scenarios A2 and B2). This way of forecasting the spatial distribution of the species is currently neglected and more emphasis is needed on the estimation of the likely distribution from the realised niche. Mapping of forecasted PEPR for the 2050s and the 2090s shows a pronounced biogeographical change in the north-eastern part of the North Atlantic Ocean (Fig. 4.30b-c). In the North Sea, the species could disappear at the end of the 21st century (Fig. 4.30c). Changes are observed on the western side of the Atlantic. Although our analysis is limited in spatial resolution, decrease in the abundance of *C. finmarchicus* could be observed over George Bank and Newfoundland.

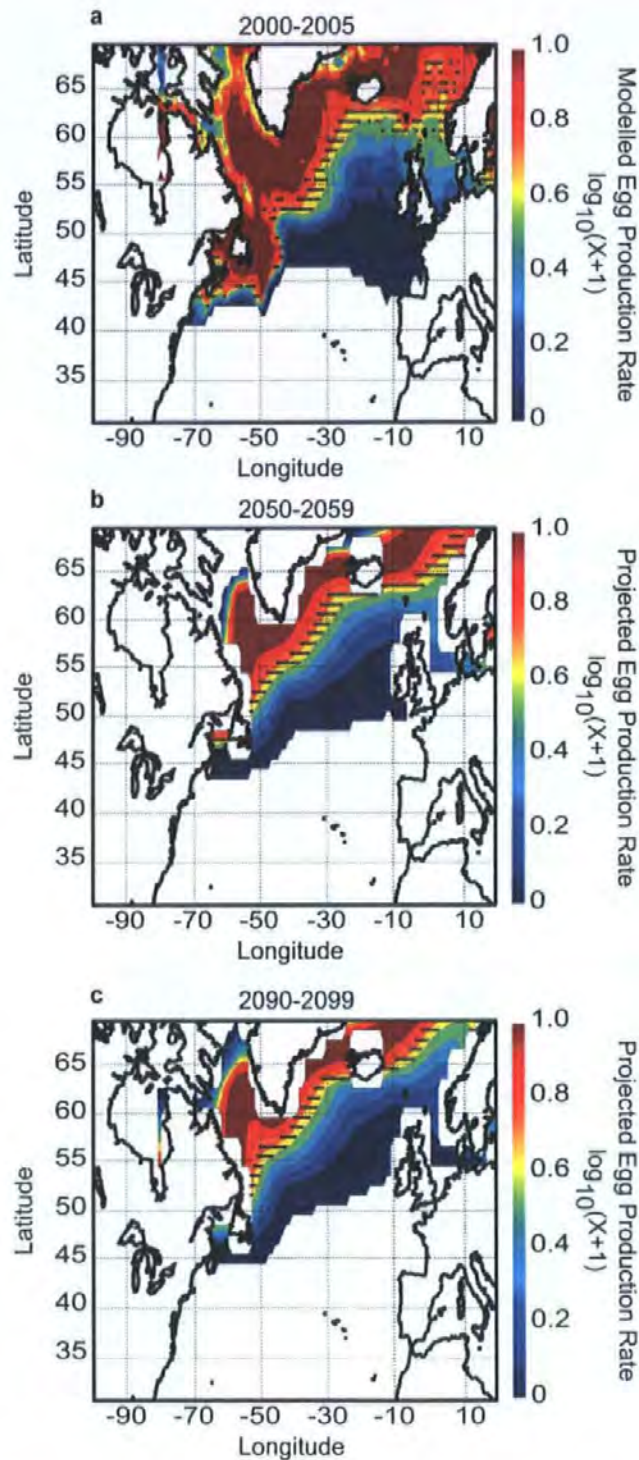


Figure 4.30. a. Spatial distribution of egg production rate of *C. finmarchicus* based on observed SST data for the period 2000-2005. b. Projected spatial distribution of egg production rate based on scenario A2 of SST change for the period 2050-2059. The egg production rate is used here as a proxy to evaluate future changes in spatial distribution of the abundance of *C. finmarchicus* with global climate change. c. Projected spatial distribution of egg production rate based on scenario A2 of SST change for the period 2090-2099. Scenario B2, which gives very similar results, is not presented. The isotherm 9-10°C is represented by asterisks (Beaugrand *et al.* 2008).

4.D. Discussion

This study provides compelling evidence, at a macroecological scale, that the spatial distribution of a species (here a marine pelagic species) is constrained by the influence of temperature on its physiology (e.g. Huggett, 2004). A close relationship has been found between the fundamental and the realised niche (i.e. its optimal part) of *C. finmarchicus* which was evident when egg production rates and spatial distributions were mapped together at both bioclimatological and decadal scales (Fig. 4.28 and 4.29, Table 4.4). Our results demonstrate that the species is generally present in regions where it can reproduce and that a high level of abundance is detected in places where reproduction is maximal. This correspondence between physiology and spatial distribution was expected from the ecological niche theory (e.g. Leibold, 1995; Guisan & Thuiller, 2005; Begon *et al.*, 2006) illustrated in figure 4.26 and some authors also stressed this relationship from laboratory experiments (Parmesan (2005) and references therein). To our best knowledge, such results have never been established on actual data.

Foundations of niche modelling are intimately linked to the Hutchinson's fundamental and realised niche concepts and most modellers subscribe to this framework (Guisan & Thuiller, 2005; Araújo & Guisan (2006) and references therein)). Despite that some authors argue that ecological niche models based on observed data provide an approximation of the fundamental niche (e.g. Soberon & Peterson, 2005), many more consider that niche models provide a spatial representation of the realised niche (e.g. (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003). Chase & Leibold (2003) suggest dropping the Hutchinson's concept and provided a major revision of the niche theory. They defined the niche as the environmental conditions that allow a species to

keep the population growth rate positive or null (besides both immigration and emigration). Our results do suggest however that the combined use of both fundamental and realised niches enables a better understanding of the environmental conditions that allows the growth of the population (Chase & Leibold, 2003).

Two hypotheses can be proposed to explain the correlation between potential egg production and abundance observed in this study. First although dispersal is generally considered to be high in the pelagic realm (Longhurst, 1998), hydro-dynamical features might behave as a barrier and prevent migration. Indeed, the spatial distribution of *C. finmarchicus* clearly matches the subpolar gyre and is limited by the Oceanic Polar Front (Dietrich, 1964) and associated oceanic currents (Krauss, 1986; Helaouët & Beaugrand, 2007). Second, the link between egg production and spatial distribution may be explained by the fact that an expatriated population is unlikely to persist and therefore to be detected at the scale of our study. Pulliam (2000) stressed that a population may persist as long as the immigration rate from source regions nearby is sufficient. Dispersion from source habitats (region where local reproduction exceeds mortality; Pulliam (1988)) seems to be rapidly counteracted by mortality related to physiological stress, which might in turn be worsened by interspecific competition, parasitism and predation in sink habitats (regions where mortality exceeds local reproduction (Pulliam, 1988)).

Our results show that *C. finmarchicus* could be abundant in the North Sea as the model forecasts high reproductive potential. This paradox has already been noted by Heath *et al.* (1999a). The species is not observed throughout the year because it typically requires bathymetry > 500 m to overwinter in diapause (Hirche, 1996). The North Sea is thought to be invaded each spring by adults from deeper oceanic regions (Heath *et al.*, 1999a).

Not only the magnitude of the spring invasion has reduced due to a warming of the Norwegian Sea Deep Water (Heath *et al.*, 1999a), but our results also suggest that the potential for this remaining population to reproduce and grow during the season has been considerably reduced. Year-to-year changes between the abundance of *C. finmarchicus* and modelled egg production rate in this region are highly correlated ($r = 0.66$, $p < 0.001$, 45 years). The parallelism between decadal changes in both egg production and abundance (see Fig. 4.29) indicates that a reduction of offspring quickly propagates to the level of species population. The concomitant changes between level of abundance and egg production rate suggests that an approach based on physiological rule combined with biogeographical information enables better projections of change in spatial distribution to be made (Parmesan 2005). Overall we found a very close link between abundance and potential PEPR. However, at a regional scale, local hydrodynamics may have a strong influence such as the volume of Norwegian Sea Deep Water and its influence on spring invasion (Heath *et al.* 1999a) on the eastern side of the North Atlantic or the influence of the state of the NAO and its impact on Labrador Sea Water (Greene, 2003).

Modelled sea surface temperature (SST) data from the ocean-atmosphere general circulation model (ECHAM4 scenarios A2 and B2) and observed sea surface temperature (COADS) data are highly positively correlated in the area covered by this study, showing that we can be confident in the use of the two scenarios of changes in SST for our projection of spatial patterns in egg production rate (Beaugrand *et al.*, 2008). Modelled changes in egg production rate for the period 2050-2059 and 2090-2099 show a substantial poleward movement of the species of about one degree of latitude per decade (Fig. 4.30). Regions characterised by high abundance and high reproduction rate, observed (Fig. 4.29) or modelled (Fig. 4.30), are just below the

isotherm 9-10°C. This isotherm represents a biogeographical boundary between the Atlantic Arctic and Atlantic Westerly Winds Biome (*sensu* Longhurst, 1998) (Beaugrand *et al.*, 2008). Beaugrand *et al.* (2008) linked a change in the location of this boundary to abrupt ecosystem shift affecting the food web from phytoplankton to zooplankton to fish. As a key structural species (Planque & Batten, 2000; Speirs *et al.*, 2004), *C. finmarchicus* is one of the most abundant copepods in subarctic waters of the North Atlantic Ocean (Conover, 1988). This species transfers energy from phytoplankton to upper trophic levels (Mauchline, 1998) and represents a key-prey for at least some stages of exploited fish (e.g. cod (Sundby, 2000)). Its biogeographical movement might therefore reveal major ecosystem changes that will propagate northwards if climate warming continues (Intergovernmental Panel on Climate Change, 2007b). The expected changes in the abundance of the species might impact the trophodynamics of the pelagic ecosystems, altering predator-prey relationships (Cushing, 1997) and some biogeochemical cycles (Beaugrand, 2009).

Current knowledge of the spatial distribution of species is limited in the pelagic realm, which cover 71% of the earth surface. By establishing a link between physiology, ecological niches and species distribution, our study opens a new way to predict potential response of species and ecosystems to global climate change. Further investigations of regions and species for which information on physiology and distributional pattern are known would enable to generalise this link to other realms. Such a validation might bring new empirical evidence to the ongoing debate on the redefinition of the fundamental and realised niches (Araújo & Guisan, 2006).

Chapter 5

Macroecology and macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean

The present chapter is constituted by the following paper (in submission):

Helaouët, P., Beaugrand, G., Reid, P.C., submitted. *Macroscale ecophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. Global ecology and Biogeography.*

Both structure and functioning of pelagic mid and high-latitude ecosystems are influenced by the dynamics of copepod populations. Among copepods, the species *Calanus finmarchicus* exerts a central role in the trophodynamics of subarctic ecosystems in the North Atlantic Ocean. The species *C. finmarchicus*, along with all other copepods, permanently adjusts to spatial and temporal variability in their environment. To keep their critical developmental phases (e.g. production of eggs) tuned to the environment a species can attempt to adjust by modifying the timing of its life cycle. Changes in phenology constitute the first type of response of a species to changes in environmental forcing. Here, we combined a macroecological and a physiological approach to investigate how the environment controls the phenology of *C. finmarchicus* as well as its biogeographical distribution. Both approaches are based on the ecological niche concept (sensu Hutchinson). The macroecological approach was used to identify the principal factors explaining the biogeographical distribution of the species. While the realised niche was inferred from the spatial distribution, the physiological approach allows the fundamental niche to be assessed by investigating the link between egg production rate and sea surface temperature. Results indicate that the main drivers of the spatial distribution remain stable throughout the year and chlorophyll *a* has a gradual influence from spring to autumn. The seasonal comparison of both niches together reveals their entanglement and highlights the particularity of the North Sea where difference between niches is obvious.

Chapter 5: Macroecology and macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean

5A. Introduction

Understanding how the environment controls the spatial distribution of a species is crucial for issues ranging from climate change projections to endangered species to resource management (Sanchez-Cordero *et al.*, 2005). Consequently, a significant part of the research in ecology has focused on the identification and the quantification of processes that link a species to its habitat (Lomolino *et al.*, 2006). Although a number of methodological difficulties remain (e.g. spatial autocorrelation, a paucity of training set, minimal consideration of species interaction), results obtained in many cases provide important information to model the spatial distribution of species and explain how it may interact with the environment in a changing world (Araújo & Luoto, 2007; Bigg *et al.*, 2008).

To assess potential impacts of climate change on species, a number of models have been developed for plants (e.g. Guisan & Thuiller, 2005) and animals (e.g. Hirzel *et al.*, 2002). Most of them have focussed on the identification of a bioclimate envelope (or climate space) (e.g. Pearson *et al.*, 2002), on the correlation between species distribution and environmental variables (e.g. Helaouët & Beaugrand, 2007) or on a physiological response to climate variations (e.g. Guisan & Zimmermann, 2000; Bigg *et al.*, 2008; Helaouët & Beaugrand, 2009). These models provide an estimation of ecological requirements of the species and are therefore linked to the ecological niche concept. Hutchinson (1957) defined the ecological niche as representing the range of tolerance of a species when all environmental factors are taken simultaneously which includes notions of interspecific competition and dispersal (Hutchinson, 1957). This led to the

distinction of two concepts, the realised and the fundamental niche that symbolise the two different ways of defining the entire ecological properties of a species.

Plankton represent an important functional unit of marine pelagic ecosystems. This group provides half of global primary production (Falkowski *et al.*, 1998) and exerts a central role in some biogeochemical cycles (Roemmich & Mcgowan, 1995; Beaugrand, 2009). Both plankton composition and abundance are strongly influenced by hydro-climatic change often originating from natural variability. Much covariation between climate variations and the plankton abundance and composition have been identified (Beaugrand *et al.*, 2003a). Climate change alters the phenology of organisms, modifies the distribution of species and changes the composition of assemblages (Edwards & Richardson, 2004; Beaugrand *et al.*, 2009). By impacting plankton, climate variations drive the quantity of energy available in the marine system as well as its transfer through the food chain (Kirby *et al.*, 2009).

Calanus finmarchicus is one of the most studied copepods. The species is found preferentially in the Atlantic Arctic biome north of the Oceanic Polar Front (Longhurst, 1998), one of the most productive areas of the world (Sarmiento *et al.*, 2004). As a key player of the secondary production, the species has an important role in the trophodynamics of subarctic Atlantic ecosystems (Beaugrand *et al.*, 2003a), entering for example in the diet of some exploited species (e.g. the larval stage of the Atlantic cod (Beaugrand *et al.*, 2003a)). Thereby, a drastic decrease in the abundance of *C. finmarchicus* could have strong impact on both the structure and functioning of the ecosystems of the region (Reid *et al.*, 2003b).

The investigation of the relationship between both realised and fundamental niches of *C. finmarchicus* is a prerequisite for a better understanding of the spatial distribution of the species in the North Atlantic Ocean and adjacent seas. The aim of the study was (1) to quantify at a macroecological scale the main abiotic factors impacting the spatial distribution of *Calanus finmarchicus* in the North Atlantic Ocean, (2) to assess changes in the explicative power of those drivers at a seasonal scale and (3) to investigate potential changes in the abundance of *C. finmarchicus* in some key regions by using joint macroecological and ecophysiological methods based on the niche concept of Hutchinson (1957).

5.B. Materials and methods

5.B.1. Studied areas

The zone investigated in the first part of the study extends from 99.5°W to 19.5°E of longitude and 29.5°N to 69.5°N of latitude and is considered representative of the North Atlantic Ocean. A focus was also made on the “Subarctic Gyre” within 55.5°W to 35.5°W longitude and from 50.5°N to 60.5°N latitude and the North Sea enclosed by 4.5°W to 10.5°E longitude and 50.5°N to 60.5°N latitude (Fig. 5.31).

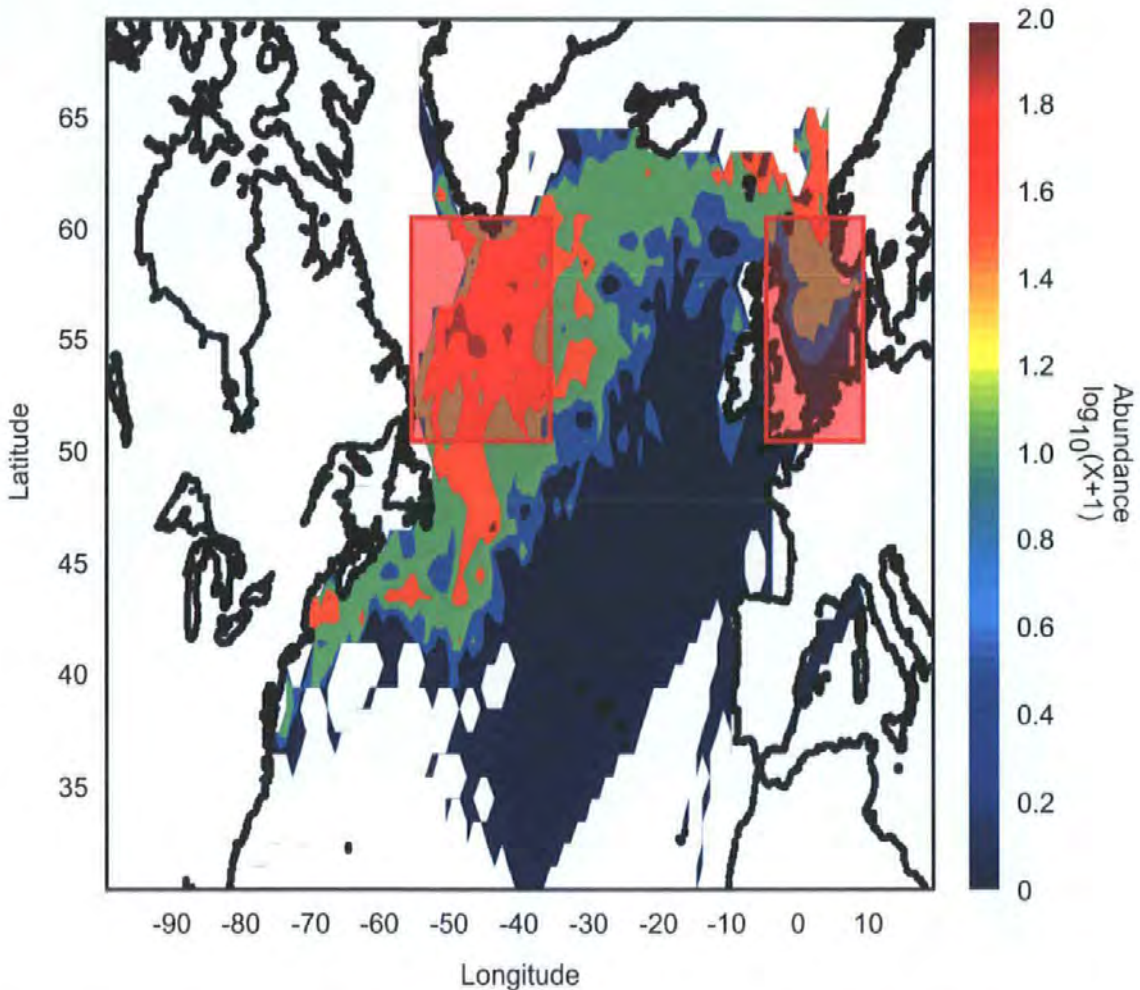


Figure 5.31. Spatial distribution of *Calanus finmarchicus* in the North Atlantic Ocean (no interpolation made). Areas representing the Subarctic Gyre and the North Sea are superimposed (in red).

5.B.2. Biological data

Data on the abundance of both *Calanus finmarchicus* and total diatoms were provided by the CPR survey (Batten *et al.*, 2003). Only data for adult *C. finmarchicus* were used to build a monthly climatology based on the average of data from 1960 to 2002. “Diatoms” represent the aggregation of 59 genera.

5.B.3. Environmental Data

All environmental data had a spatial resolution of 1° longitude and 1° latitude and were used because of their recognised influence, either direct or indirect, on the spatial distribution of *C. finmarchicus* (Helaouët & Beaugrand (2007) and references therein). We obtained a monthly climatology for each parameter (matrix 120 x 40 x 12 geographical cells for the North Atlantic).

5.B.3.A. Sea Surface Temperature (SST)

Sea surface temperature originated from the Comprehensive Ocean-Atmosphere Data Set (COADS) and was downloaded from the National Oceanographic Data Centre (NODC) (Woodruff *et al.*, 1987). A climatology was built using monthly means from 1960 to 2002. The potential impact of changes in SST on spatial distribution was evaluated using data from the ECHAM 4 (EC for European Centre and HAM for Hamburg) model for three time periods (2010-2019; 2050-2059; 2090-2099). Data used here are modelled data based on scenario A2 (concentration of carbon dioxide of 856 ppm by 2100). Data based on IPCC scenario B2 (concentration of carbon dioxide of 621 ppm by 2100) were also used but are not presented due to the similarity of the results with A2.

5.B.3.B. Chlorophyll a

Chlorophyll a values came from the programme and satellite Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from the National Aeronautics and Space Administration (NASA). A climatology based on monthly means from 1997 to 2002 was used. Chlorophyll a is used here as an index of food availability and can be therefore considered as an environmental factor.

5.B.3.C. Bathymetry

Bathymetry data originated from the database General Bathymetric Chart of the Oceans (GEBCO). The spatial variability in the bathymetry was from (Helaouët & Beaugrand, 2007). A high variability in bathymetry is generally characteristic of continental slope regions.

5.B.3.D. Chemical data

Salinity constitutes an important limiting factor for many marine species (Kinne, 1964). Climatology of this parameter as well as those for silicate, phosphate, nitrate and dissolved oxygen were downloaded from the World Ocean Atlas 2001 (WOA1) database. Values were selected at 10m depth to fit with the characteristics of the CPR sampling method.

5.B.3.E. Water column stability

Most of the abrupt ecological changes occur across a few ten-metre depth constituting the epipelagic zone (Longhurst, 1998). Both mixed layer depth (MLD) and wind induced turbulence have been used as indicators of water column stability. The wind-induced turbulence index originated from the Comprehensive Ocean-Atmosphere Data

Set (COADS) and was downloaded from the internet site of the National Oceanographic Data Center (NODC) (Woodruff *et al.*, 1987).

5.B.4. Statistical analyses

5.B.4.A Quantification of the influence of each parameter on the spatial distribution

A total of 13 Principal Component Analyses (PCAs) were carried out. First PCA was applied on the annual climatology of the 11 environmental parameters to determine the correlation between all environmental parameters and *C. finmarchicus*, added in the analysis as a supplementary variable. Twelve separate PCAs were applied to evaluate the monthly changes in the contribution of the environmental parameters to the first 3 principal components (adding again *C. finmarchicus* as a supplementary variable). These analyses were conducted to help characterise the realised niche. An important assumption when using a PCA is the multinormality of the data. This assumption was checked using a test of normality for every parameter and when needed, the normalising procedure called “Omnibus” was used on the data (Legendre & Legendre, 1998). This macroecological approach allows the influence of abiotic parameters to be identified and quantified.

5.B.4.B. Determination of the optimal part of the fundamental niche

An ecophysiological approach based on an assessment of the Potential Egg Production Rate (PEPR) of *C. finmarchicus* was used to estimate the central part of its fundamental niche (Helaouët & Beaugrand, 2009). Assuming that reproduction is maximal when the species is within the optimal part of its fundamental niche (Helaouët & Beaugrand, 2009), PEPR at time t and location s ($P_{t,s}$, in Eggs.female⁻¹.d⁻¹) was calculated from an

adaptation of the equation of Heath *et al.* (2000) to calculate this information based only on SST (Helaouët & Beaugrand, 2009).

$$P_{t,s} = 3.06 \times 10^{\frac{A - ((T_{t,s} - T_{opt})B)^2}{100}} \quad (2)$$

With $T_{t,s}$ the sea surface temperature (in °C) at time t (ranging from 1960 to 2002 for each month) and location s . T_{opt} is the temperature optimum (6°C). Parameters A and B are respectively equal to 60 and 1.9 (Heath *et al.*, 2000).

5.B.4.C. Spatial distribution and the fundamental niche

The realised niche represents the fundamental niche modified by factors such as dispersal that increase the breadth of the niche or factors such as competition that, on the contrary, tighten it (Hutchinson, 1957; Pulliam, 2000). A Pearson coefficient of correlation was calculated to examine relationships between the spatial distribution of *C. finmarchicus* (i.e. the realised niche) and the potential egg production rate (optimal part of the fundamental niche) for each month as well as for the entire year. The minimum degree of freedom needed to have a significant correlation ($p = 0.01$) and corresponding to the observed correlation value was assessed to evaluate the potential impact of spatial autocorrelation when correlation was calculated between maps (Beaugrand *et al.*, 2008). A conservative probability threshold was chosen ($p = 0.01$) to again consider that the data are spatially autocorrelated.

5.B.4.D. Determination of the realised niche

We consider that the observed spatial distribution of a species is constrained by both abiotic and biotic factors, which include interspecific relationships and dispersal. The entire distribution of *C. finmarchicus* represents the synergistic outcome of all factors and may be considered as a spatial representation of the realised niche (Helaouët &

Beaugrand, 2009). As results from the PCAs indicated that temperature and chlorophyll *a* were important parameters, we projected the n-dimensional realised niche on a 2-dimensional diagram using monthly sea surface temperature and an index of the monthly abundance of total diatoms inferred from the CPR survey (see Fig. 5.35). To determine the number of environmental categories, the minimum and maximum values were first calculated and intervals were chosen by trial and error. We used categories instead of information on abundance to take into account the specificity of phytoplankton counting by the CPR survey (Colebrook, 1960) that limits the number of small values. The abundance of diatoms was converted into 5 categories: 1 (absence); 2 ($1 - 10^4$); 3 ($10^4 - 10^5$); 4 ($10^5 - 10^6$); 5 ($10^6 - 10^7$). SST was categorised using a step of 1°C between -2°C and 25°C. The coldest and warmest years of the time period (1960 – 2002) were determined in both the North Sea (coldest year = 1963 and warmest year = 2002) and the Subarctic Gyre (coldest year = 1972 and warmest year = 2001). The abundance and PEPR of *C. finmarchicus* were calculated for these two years and these two regions for each category of diatoms and SST on a monthly basis and projected on the realised niche.

5.B.4.E. Projections of changes in the abundance of C. finmarchicus

First, a reduction of the two-dimensional (diatoms and SST) realised niche based on data of the period 1960-2002 was performed to keep only intervals of annual SST as information on future abundance in diatoms was obviously not available. The resulting data had information on abundance of *C. finmarchicus* for each degree of annual SST between -2°C and 22°C. To assess the thermal limits of the realised niche, two percentiles were then calculated on the cumulated abundance (e.g. the 95th and 99th percentiles) of *C. finmarchicus* and the associated SST was identified by linear interpolation. Therefore, the two temperatures indicated the annual SST from which the

abundance of the species became inferior to 5% and 1%, respectively. Second, projected annual SSTs using Scenario A2 were superimposed for three decades in both the Subarctic Gyre and the North Sea. For each region, the coldest and warmest years were identified for each of the three decades 2010-2019, 2050-2059 and 2090-2099. Third, the standardised values of PEPR were also calculated in the Subarctic Gyre and in the North Sea using Equation 2 and the calculated average SST for the three time periods.

5.C. Results

5.C.1. Influence of environmental parameters on the spatial distribution of *C. finmarchicus*

All of the 11 environmental parameters were normalised by using the “Omnibus” transformation. A graphical control of a subset of 4 variables showed the normality of the data after applying the method (Fig. 5.32). A first PCA was applied on the two-way table with a total of 57,600 rows (120 longitudes x 40 latitudes x 12 months) and 11 columns corresponding to the environmental variables. The examination of the first two normalised eigenvectors (69.8 % of the total variance) showed that variables such as SST and salinity were positively related to the first principal component, while nutrients, chlorophyll *a*, bathymetry and dissolved oxygen contributed negatively. The mixed layer depth and the wind-induced turbulence were positively linked to the second principal component (Fig. 5.33a-b) and the coefficient of variation in the bathymetry was positively related to axis 3 (Fig. 5.33b; 7.5 % of the total variance). The analysis showed negative relationships between the mean spatial distribution of *C. finmarchicus* and the spatial pattern in SST and salinity, a positive link with nutrients, chlorophyll *a*, bathymetry and oxygen. No clear link was found between bathymetry, the structure of the water column and *C. finmarchicus*.

A standardised PCA was applied on the table (120 longitudes x 40 latitudes) x 11 environmental variables for each month to evaluate the seasonal changes in the relative contribution of the main drivers to the spatial distribution of *C. finmarchicus*. The first five most important contributors of the first principal component are summarised for each month (Table 5.5). *Calanus finmarchicus*, added to each analysis as a supplementary variable, was only related (negatively) to the first principal component

(Table 5.5) showing a range of correlations between -0.46 in December and -0.70 in June. Results showed that the first principal component was generally dominated by SST (first contributor) and oxygen concentration (second contributor). The contribution of the concentration of chlorophyll *a* was more important between May and October with a maximum in September (Table 5.5). Parameters that contributed most to the first principal component and thus the spatial distribution were temperature (and its correlates dissolved oxygen and nutrients) and chlorophyll *a*. The second principal component was mainly dominated by parameters representing the structure of the water column: MLD, the wind-induced turbulence and occasionally the spatial variation in the bathymetry.

Table 5.5: First five contributors (C1 to C5) for the first principal component (PC1) for each month. SST: sea surface temperature; SAL: salinity; NIT: nitrate; PHO: phosphate; TUR: turbulence rating; CHL: chlorophyll *a*; MLD: mixed layer depth; SIL: silicate; BAT: bathymetry; CVB: variation of bathymetry; OXY: oxygen dissolved. The sign of the relationship between each descriptor and the principal component is also given.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
r	-0.50	-0.53	-0.62	-0.65	-0.69	-0.70	-0.65	-0.57	-0.58	-0.59	-0.56	-0.46
PC1	C1	+SST	-OXY	+SST	+SST	+SST	-OXY	+SST	+SST	+SST	+SST	+SST
	C2	-OXY	+SST	-OXY	-OXY	-OXY	+SST	-OXY	-CHL	-OXY	-OXY	-OXY
	C3	-PHO	+SAL	+SAL	+SAL	-CHL	-CHL	-CHL	-OXY	-CHL	-PHO	+SAL
	C4	+SAL	-PHO	-PHO	-PHO	+SAL	+SAL	-PHO	+SAL	+SAL	-PHO	-PHO
	C5	-SIL	-SIL	-SIL	-SIL	-PHO	-PHO	+SAL	-PHO	-PHO	+SAL	-CHL

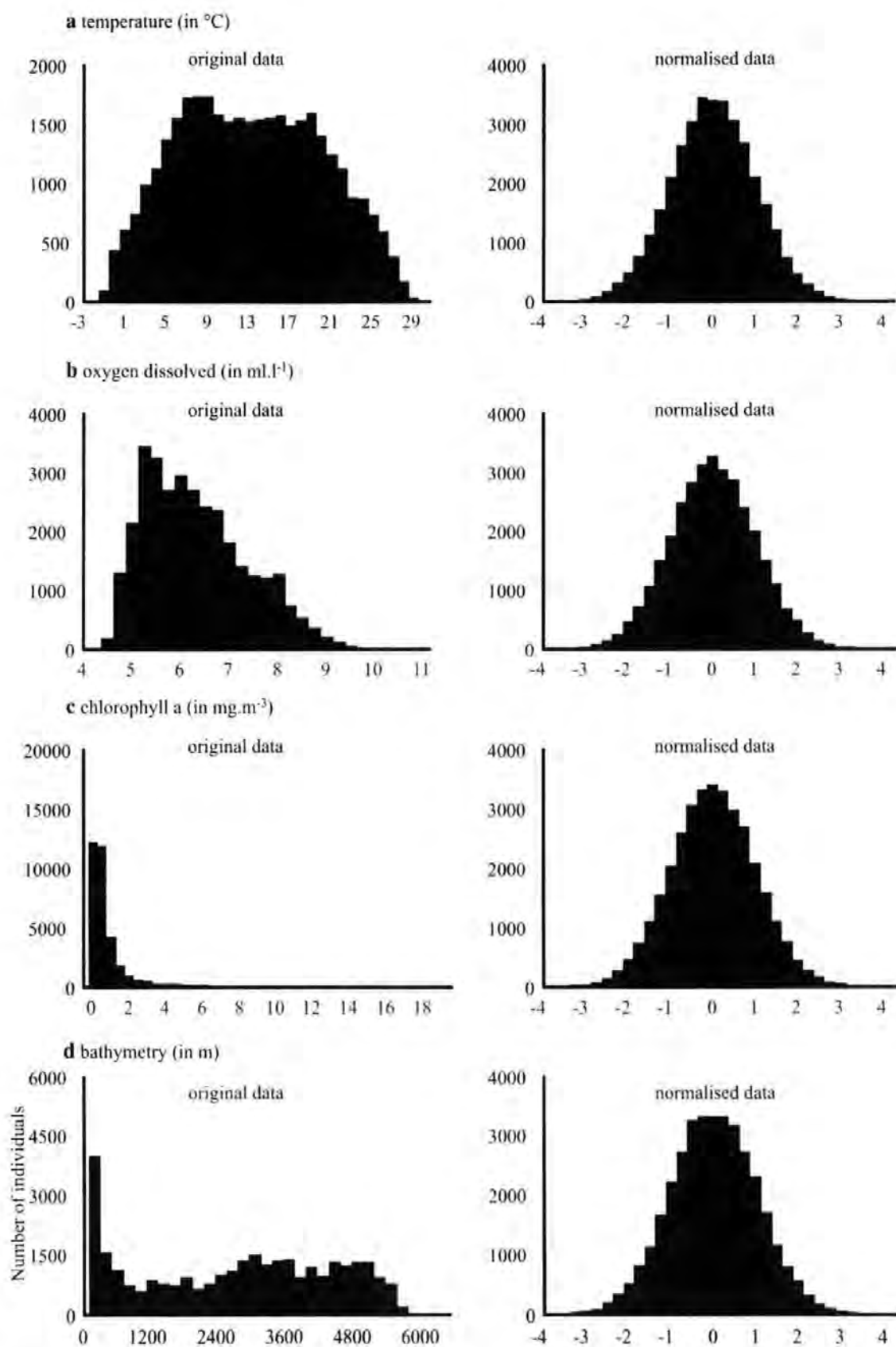


Figure 5.32. Example of distribution of 4 parameters used in the Principal Component Analysis, before (left) and after (right) the normalising procedure “Omnibus”. (a) temperature, (b) dissolved oxygen, (c) chlorophyll *a*, (d) bathymetry.

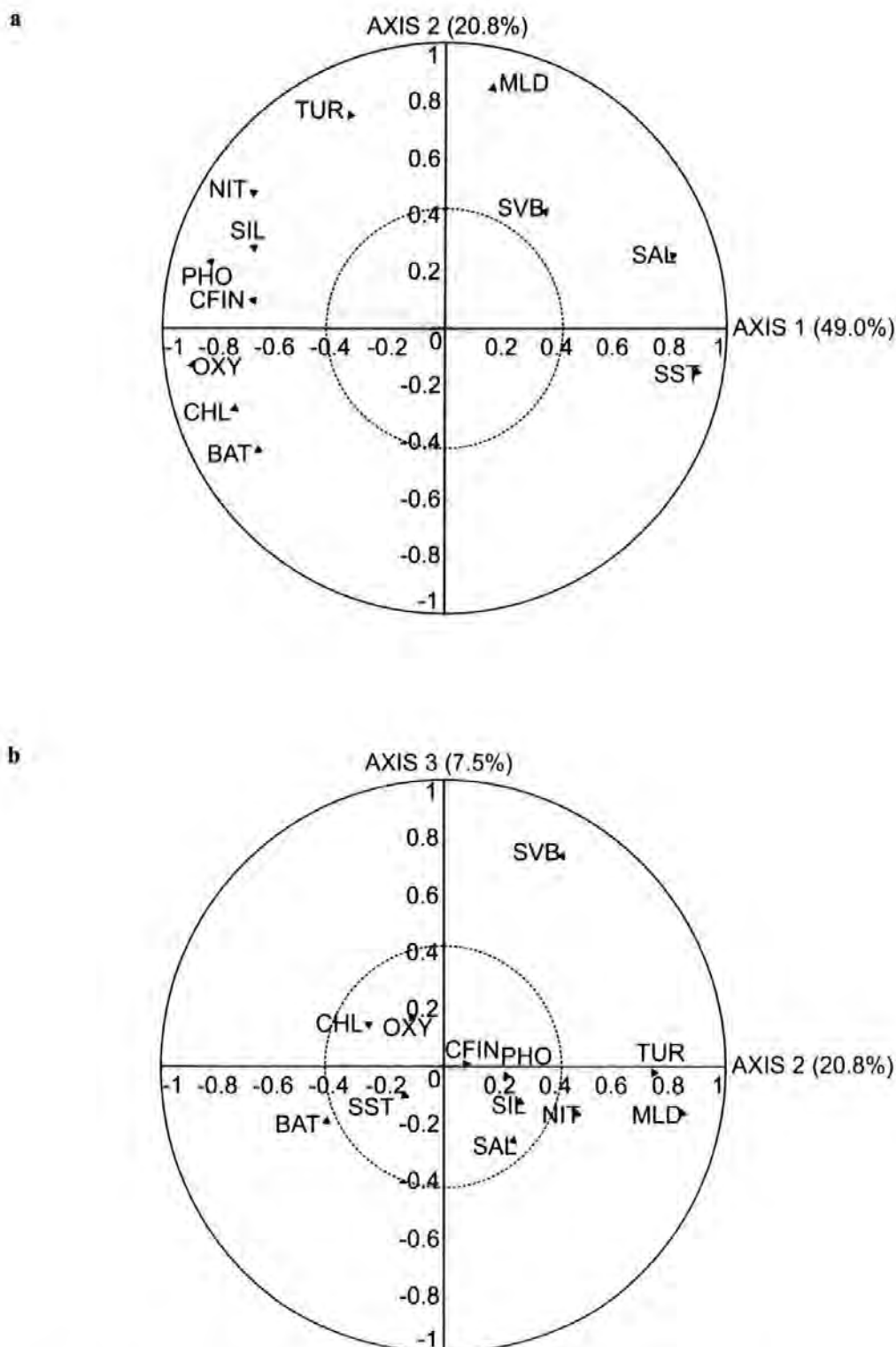


Figure 5.33. Results from a standardised PCA performed on normalised environmental data. (a) Normalised eigenvector 1 and 2 (69.8%). (b) Normalised eigenvector 2 and 3 (28.3%). Circle of correlation (radius = 1) and circle of regime descriptor contribution (radius = $E = 0.43$) are also displayed. SST: sea surface temperature; SAL: salinity; NIT: nitrate; PHO: phosphate; TUR: turbulence rating; CHL: chlorophyll *a*; MLD: mixed layer depth; SIL: silicate; BAT: bathymetry; CVB: variation of bathymetry; OXY: oxygen dissolved; CFIN: *C. finmarchicus*

5.C.2. Spatial distribution of *C. finmarchicus* and the fundamental niche

The assessment of the optimal part of the fundamental niche was based on the calculation of PEPR (see Materials and Methods). On an annual basis, the spatial distribution of PEPR closely matched the spatial distribution of the abundance of *C. finmarchicus* ($r = 0.78$, Table 5.6). This result highlights the close correspondence between the physiological constraints and the geographical pattern in the abundance of this species.

The seasonal changes in the spatial distribution of both abundance and PEPR of *C. finmarchicus* were examined for four selected months (January, April, July and October) (Fig. 5.34). In January, *C. finmarchicus* was mainly located in the western part of the North Atlantic Ocean along the American shelves between 70°W and 40°W of longitude and 40°N and 50°N of latitude. The species was almost absent at the surface in the eastern part (Fig. 5.34a). On the contrary, the physiological model forecasted a high PEPR in the entire area located north of the Oceanic Polar Front (Fig. 5.34b) leading to a significant but small correlation between the maps ($r = 0.25$, Table 5.6). In April, the spatial distribution of the abundance covered almost all regions north of the Oceanic Polar Front (Fig. 5.34c). The figure also showed a rise in the abundance level of the species off the Norwegian coasts and in the northern part of the North Sea. The relationship between abundances and PEPR increased ($r = 0.69$, Table 5.6). In July, abundances continued to increase in the western and eastern parts of the area and especially in the Subarctic Gyre, corresponding to the main core of the spatial distribution of the species (Fig. 5.34e). There was a pronounced decrease in PEPR values in the south-western and the north-eastern regions of the North Atlantic Ocean. This diminution in PEPR, associated with a rise in the abundance of the species,

produced a low correlation with abundance in comparison to the previous month ($r = 0.52$, Table 5.6). In October, abundances diminished over the whole area (Fig. 5.34g) while estimated PEPR remained stable (Fig. 5.34h). This contributed to an increase in the correlation between the spatial distribution of *C. finmarchicus* and its fundamental niche ($r = 0.74$, Table 5.6)

Table 5.6. Annual and monthly relationships between abundance and egg production rate of *C. finmarchicus*. Pearson correlation coefficients calculated between maps of abundance and egg production rate (Eggs.female⁻¹.d⁻¹) for the period 1960-2005. Abundance data were transformed (log₁₀(Ab+1)) prior to the calculation of the coefficient of correlation. “nf” denotes the degree of freedom needed to have a significant correlation at $p = 0.01$. This was calculated to evaluate the strength of the correlation as data are spatially autocorrelated. For example, when $n = 3000$ and $nf = 10$, this indicates that the correlation remains significant even when ~0.33% of geographical pixels are retained (Beaugrand *et al.*, 2008).

Month	correlation probability		degree of freedom (n)	minimum degree of freedom (nf,p=0.01)
January	0.25	< 0.001	1144	171
February	0.20	< 0.001	1050	268
March	0.40	< 0.001	1144	65
April	0.69	< 0.001	1131	20
May	0.69	< 0.001	1094	20
June	0.57	< 0.001	1164	30
July	0.52	< 0.001	1090	38
August	0.43	< 0.001	1166	56
September	0.55	< 0.001	1176	34
October	0.74	< 0.001	1156	17
November	0.60	< 0.001	1150	27
December	0.32	< 0.001	1112	101
Annual	0.78	< 0.001	1698	14

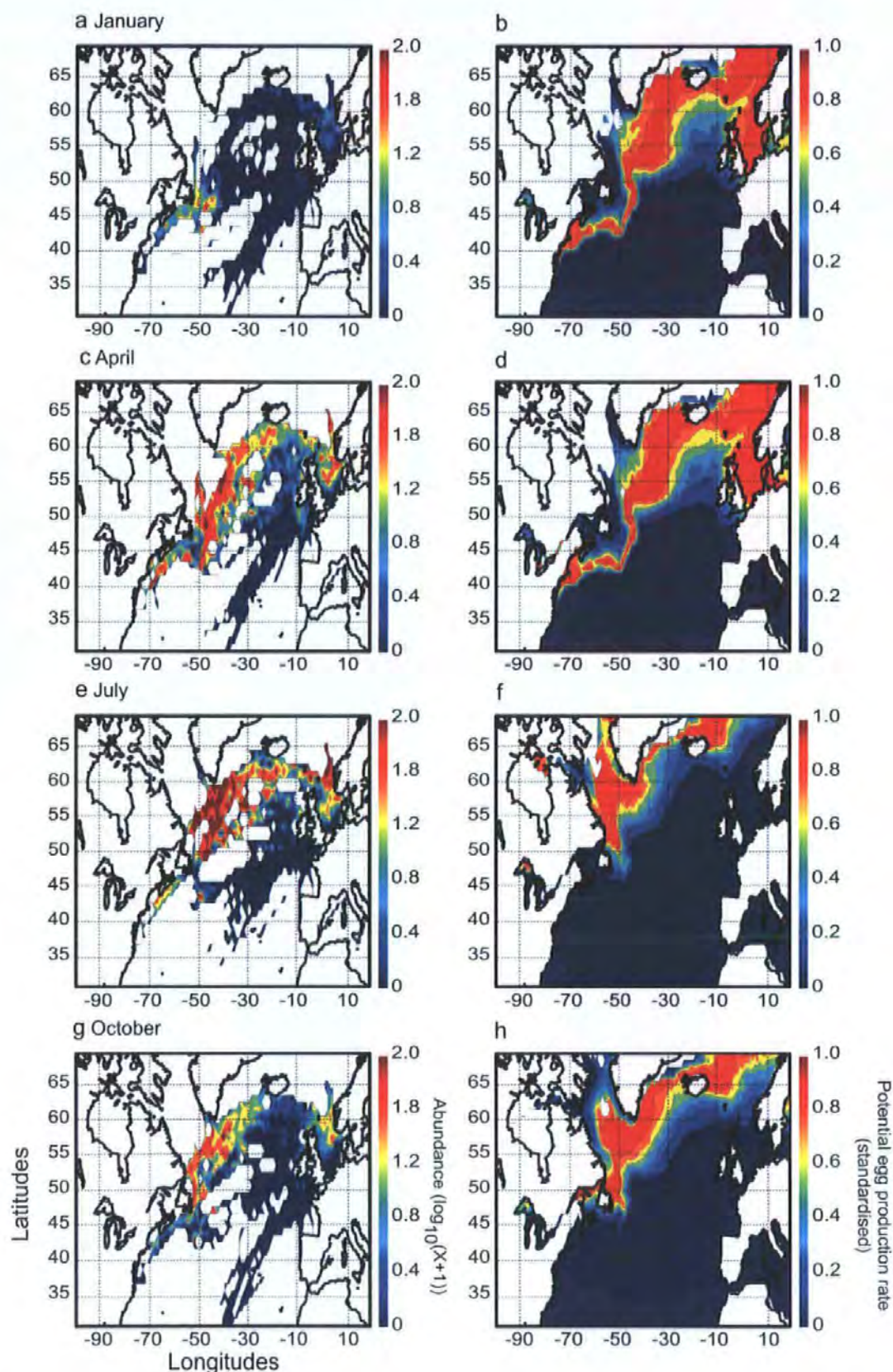


Figure 5.34. Monthly spatial distribution of both abundance (left; $\log(X+1)$) and egg production rate (right; standardised) of *Calanus finmarchicus* in the North Atlantic Ocean for the period 1960-2005. No interpolation was made. (a-b) January. (c-d) April. (e-f) July. (g-h) October.

5.C.3. Determination of the realised niche

Results from both the annual and monthly PCAs suggested that temperature and food concentration (chlorophyll *a*) were important limiting factors of the spatial distribution of *C. finmarchicus*. The realised niche was mapped by projecting the abundance of *C. finmarchicus* on a two-dimensional diagram as a function of SST and the abundance of total diatoms (Fig. 5.35). The seasonal trajectories in both the abundance of *C. finmarchicus* and PEPR of the coldest and warmest years in the Subarctic Gyre and the North Sea were superimposed on the realised niche.

In the Subarctic Gyre, seasonal changes in the abundance and PEPR of *C. finmarchicus* were similar and appeared to be confined to the optimal part of the realised niche (Fig. 5.35a-b). Both the abundance and PEPR of the species were elevated, corroborating the assumption that the area was located in the central part of the realised niche. During the period 1960-2002, the environmental conditions (temperature and food conditions) in the Subarctic Gyre remained inside the realised niche. Indeed, variations in SST between the coldest (1973) and the warmest (2001) year had a little impact on the capacity of the species to produce eggs and to be abundant.

Results were different in the North Sea (Fig. 5.35c-d). The species was not located in the centre of its realised niche and its abundance was generally less than in the Subarctic Gyre. During the coldest year (1964), the species remained inside its niche with its maximum abundance in July, reaching only temporarily its edge in August. During the warmest year (2002), the species reached its seasonal maximum in May and was outside its niche during four months between June and September (Fig. 5.35c). The examination

of the seasonal pattern in PEPR indicated a potential strong physiological stress. These reduced considerably the period of seasonal growth (Fig. 5.35d).

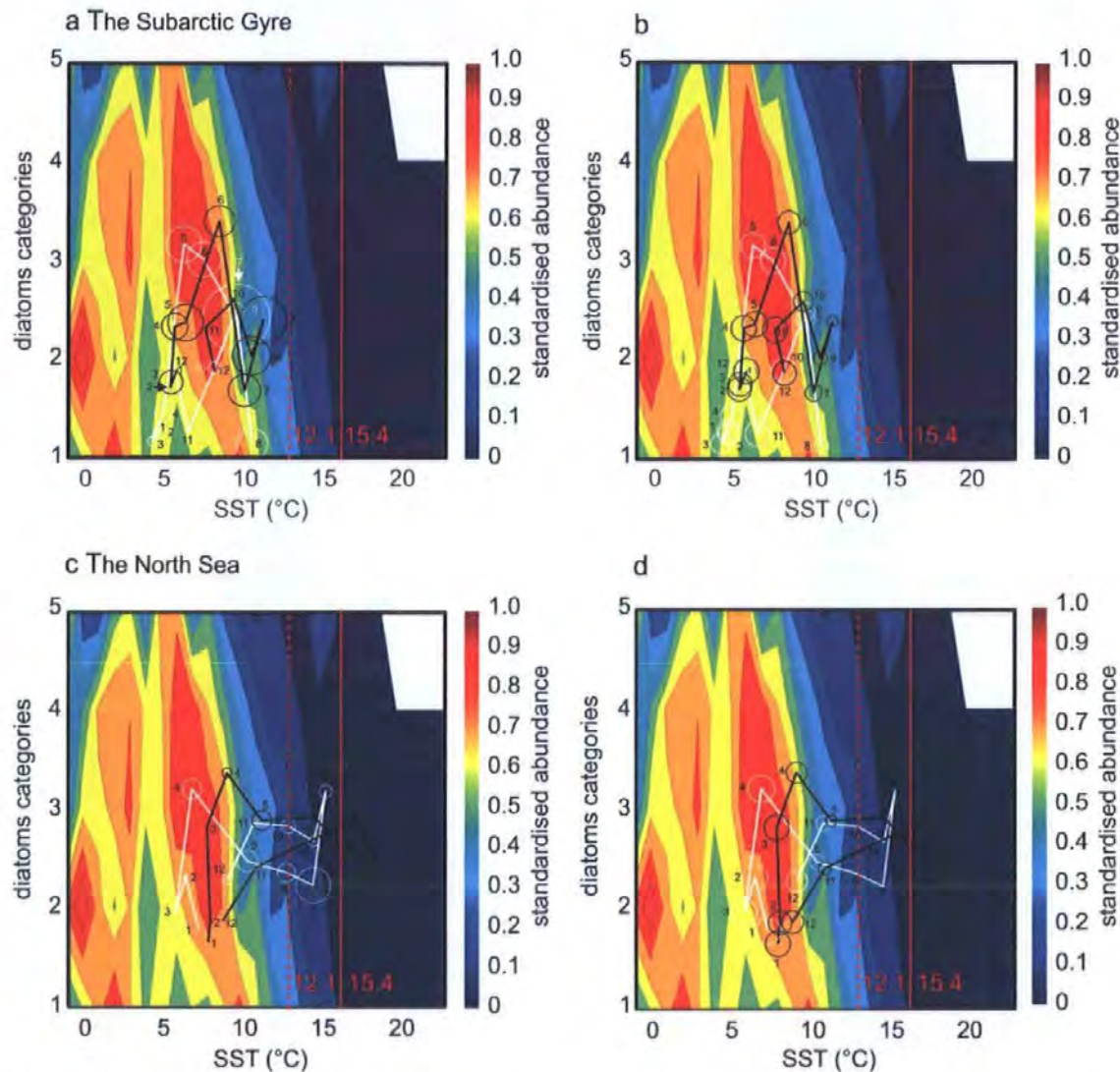


Figure 5.35. Abundance of *Calanus finmarchicus* (standardised between 0 and 1) as a function of both categorised abundances of diatoms and SSTs for the whole area. Thermal limits of the realised niche corresponding to the 95th (dashed red line) and 99th (red line) percentiles calculated on the cumulated abundance are superimposed. (a-c; circles) abundances of the species for the coldest (in white; 1973 for the Subarctic Gyre and 1964 for the North Sea) and the warmest (in black; 2002 for the Subarctic Gyre and 2001 for the North Sea) year of the whole time period (1960-2002) are represented in function of SSTs and abundances of diatoms. (b-d; circles) PEPR of the species are represented as a function of SSTs only for both the coldest and the warmest year of the time period

5.C.4. Projections of changes in the abundance of *C. finmarchicus*

The thermal limits of the realised niche were 12.1°C (95th percentile) and 15.4°C (99th percentile; Fig. 5.36a-b). In the Subarctic Gyre, the coldest years for the three time periods were respectively 2012, 2057 and 2090 whereas the warmest years were 2019, 2054 and 2099 (Fig. 5.36a). Projections for the next decade suggest that the area will meet the species requirements. By the middle and the end of this century, the species might start to experience some degree of physiological stress in summer during warm years. However, if annual SST follows Scenario A2, the species will never reach the limit of its niche (Fig. 5.36a).

In the North Sea, the coldest years for the three time periods were respectively 2014, 2057 and 2092 while the warmest years were 2011, 2050 and 2098 (Fig. 5.36b). In this region for the next few decades, the species is likely to experience a high degree of physiological stress in both cold and warm years during the summer months of the year (Fig. 5.36b). By the middle of this century in a warm year, the species may reach the limit of its thermal niche. By the end of the century, the species might for most of the time be in a state of physiological stress and might even cross the edge of its niche for several months a year (Fig. 5.36b).

Based on projected SST (Scenario A2), the estimation of PEPR in the Subarctic Gyre for the 2010s, 2050s and 2090s suggests a modest reduction in the potential production of eggs (Fig. 5.36c). This might not have an effect on the persistence of populations of *C. finmarchicus* in this region but might reduce the size of the populations. In the North Sea, the decrease in PEPR is likely to be pronounced. By the end of the century, the

potential for the production of eggs of *C. finmarchicus* might be greatly reduced if temperature changes follow Scenario A2 (Fig. 5.36d).

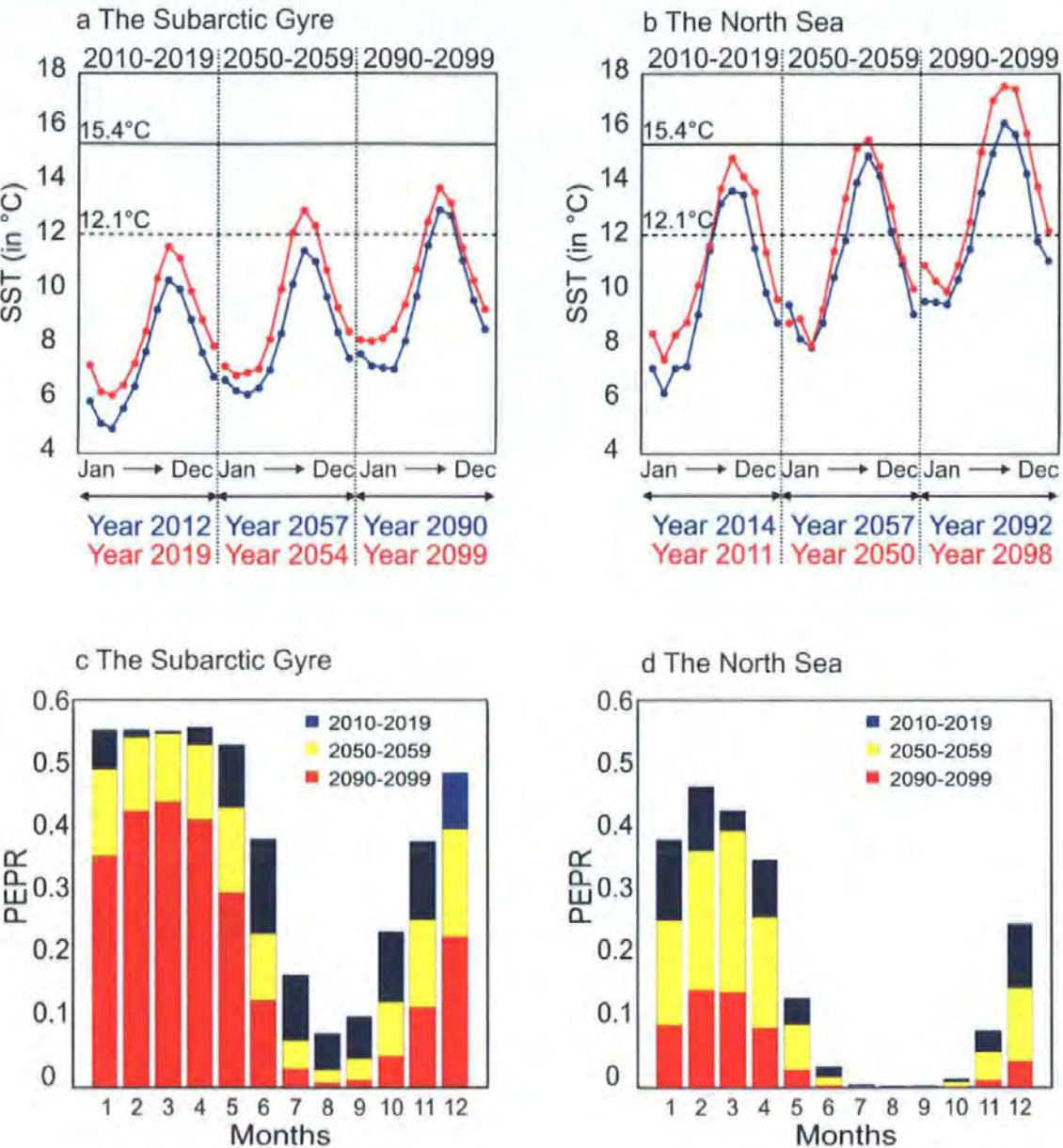


Figure 5.36. Projection of annual SSTs for the coldest (in blue) and warmest (in red) years of the three decades (2010-2019, 2050-2059 and 2090-2099) using scenario A2 in (a) the Subarctic Gyre and (b) the North Sea. Thermal limits of *C. finmarchicus*'s realised niche corresponding to the 95th (dashed line) and 99th (line) percentiles calculated on the cumulated abundance are superimposed. Monthly PEPR of the species are represented as a function of averaged SSTs for the three decades 2010-2019, 2050-2059 and 2090-2099 using scenario A2 in (c) the Subarctic Gyre and (d) the North Sea.

5.D. Discussion

The concept of Hutchinson's (1957) n -dimensional hypervolume constitutes an essential tool in macroecology to help understand the way a species experiences its environment. The fundamental niche represents the range of tolerance of a species when several environmental factors are simultaneously taken into account (Hutchinson, 1957). Successful reproduction occurs at the centre of the fundamental niche (i.e. when environmental conditions are optimal, (Helaouët & Beaugrand, 2009)). The fundamental niche is genetically and physiologically determined whereas the realised niche is additionally constrained by interspecific relationships (Pulliam, 2000). Here, the realised niche was evaluated by projecting the spatial distribution of the species in an Euclidean space as a function of a few key environmental parameters. A prerequisite was to identify and quantify the main environmental drivers of the spatial distribution of the species and these were identified by applying a standardised Principal Component Analysis (PCA).

The original equation used to calculate EPR took into account the quantity of food available using chlorophyll a as an index (Heath *et al.*, 2000). We chose however, to remove the effect of food in the model for several reasons. First, correlations found between the spatial distribution of abundance and PEPR on a monthly basis were lower than when temperature was exclusively considered (Table 2). Second, the influence of temperature was much more pronounced than our indicator of food abundance when the realised niche of *C. finmarchicus* was mapped as a function of these two parameters (Fig. 5.35). Third, temperature and chlorophyll a covaried negatively and are therefore not independent ($r = -0.63$; $p < 0.001$; $n = 30711$). Fourth, the equation that enables the calculation of EPR from both temperature and chlorophyll a can sometimes be

undetermined mathematically when the concentration of chlorophyll *a* is low (Helaouët & Beaugrand, 2009). Finally, information on chlorophyll *a* is likely to be projected by biogeochemical models with a higher degree of uncertainty than temperature (Buitenhuis *et al.*, 2006).

Sea surface temperature and to a lesser extent its correlates oxygen and nutrients appeared to be the most conspicuous factors driving the spatial distribution of *C. finmarchicus* in the North Atlantic Ocean at both annual (Fig. 5.33) and monthly scales (Table 5.5). It is well known that temperature exerts an influence on most physiological processes and biological rates (Cossins & Bowler, 1987; Brown *et al.*, 2004) and some studies have shown that this parameter affects growth (Huntley, 1992), development (Carlotti *et al.*, 1993) and the egg production rate of *C. finmarchicus* (Hirche *et al.*, 1997; Heath *et al.*, 2000)). While the choice to select SST as the first dimension to assess the realised niche was therefore straightforward, the selection of the second dimension was more complicated. Indeed, our study indicates that other factors also influence *C. finmarchicus*. Correlates of temperature (e.g. nutrients, oxygen) were other important controlling factors. Furthermore, bathymetry and salinity emerged more clearly than in our previous studies (Helaouët & Beaugrand, 2007; Beaugrand & Helaouët, 2008). The concentration of chlorophyll *a* was highly positively correlated with the abundance of *C. finmarchicus*. However, its relationship was more evident during the reproductive season. Hirche & Kwasniewski (1997) suggested that egg production of *C. finmarchicus* was significantly affected by low food concentration and low phytoplankton quality. Feeding conditions do indeed have a severe effect on the oocyte maturation process and therefore on reproduction (Niehoff, 2004). Chlorophyll *a* is however, not the best proxy to characterise the spatial distribution of *C. finmarchicus*. Many studies have reported that the species is a major grazer of diatoms (e.g. Castellani

et al., 2008). Koski & Riser (2006) showed that late copepodite stages of *C. finmarchicus* constantly selected for diatoms since ingestion and faecal pellet production rates were higher feeding on diatoms. Therefore, we chose to characterise the realised niche by using SST and an index reflecting the concentration of diatoms in the field.

The joint approach, based on both the realised and the fundamental niches together, was complementary. Correlations between the spatial distribution of abundance (representative of the realised niche) and PEPR (representative of the fundamental niche) were remarkably high from spring to autumn, but decreased during the winter months (Table 5.6, Fig. 5.34). This decrease was mostly related to the fact that the ecophysiological model did not consider the overwintering stage of *C. finmarchicus* at depths ranging from 500m to 2500m (Hirche, 1996). The examination of the seasonal pattern exhibited by the species in the North Sea (Fig. 5.35) showed that regions or time periods with a high level of abundance were characterised by high reproduction (Helaouët & Beaugrand, 2009). The niches were characterised by a well-defined optimum separated from the rest of the niche by a pronounced gradient between 8°C and 12°C within which abundance and PEPR decreased rapidly to a level inferior to 5% of the total abundance of the species (see Fig. 5.35). Beaugrand *et al.* (2008) found a high local biological variance in areas characterised by annual SST ranging from 9°C to 12°C with a peak of variability between 9°C and 10°C. It is important to note that the boundary observed by these authors on the basis of the examination of three trophic levels, coincided with that of *C. finmarchicus* at the physiological (i.e. PEPR) and the macroecological level (i.e. abundance). At these scales, the species was mostly associated with lower temperature and salinity, deeper bathymetry and higher chlorophyll *a* concentration, values that are characteristic of the Subarctic Gyre

(Longhurst, 1998). This explains why the species is often considered as an indicator of this ecological province (Beaugrand *et al.*, 2003a).

The joint macroecological and macrophysiological approaches used here represent a tool against which long-term decadal and future changes in *C. finmarchicus* can be better assessed and anticipated. The impact of climate change on marine ecosystems is now well documented (Intergovernmental Panel on Climate Change, 2007b). Recent studies have emphasised that these systems will potentially respond rapidly to climate warming (Weijerman *et al.*, 2005; Beaugrand *et al.*, 2009). However, recent studies indicate that the sensitivity of marine ecosystems to climate change is not constant spatially (Beaugrand *et al.*, 2008). Some regions, called vulnerability hotspots (i.e. regional discontinuities characterized by high biological variance), may react quickly to climate change while others will remain virtually unchanged. Our approach will help to develop a better understanding of this phenomenon. In the subarctic gyre, climate change and its effect on SST will have only a limited impact on *C. finmarchicus* (Fig. 5.35 and 5.36). The modest variations in both abundance and PEPR of *C. finmarchicus* between a cold and a warm year suggest that the species will not be affected by climate until the end of this century when some degree of physiological stress may be evident. As an important component of the trophodynamics (Longhurst, 1998), it is therefore unlikely that the North Atlantic Drift Province (*sensu* Longhurst, 1998) will be severely affected this century. The position of *C. finmarchicus* at the optimum of its ecological niche may temper the effect of variation in SST on the trophodynamics of the ecosystem.

The North Sea has recently experienced substantial changes in ecosystem state (Reid *et al.*, 2001; Weijerman *et al.*, 2005). One of the major changes that has been documented

has been a pronounced decline in the abundance of *C. finmarchicus*. In 1962, the species represented 80% of the total *Calanus* whereas it represented only 20% of the genus by the beginning of the 2000s (Reid *et al.*, 2003b). Our approach explains well the pattern of change and indicates that the phenomenon is unlikely to reverse in the next few decades. The pattern of change might, in contrast, be reinforced. At the end of the century, *C. finmarchicus* could be outside its thermal preference for 8 months in a warm year and 5 months during a cold year (Fig. 5.36). The physiological stress induced by rising temperature is expected to affect consecutively: reproduction, growth, feeding and ultimately the survival of the individuals (Schmidt-Nielsen, 1990; Helaouët & Beaugrand, 2009).

Our approach does not consider explicitly (mathematically) some characteristics of the life cycle of the species. Although *C. finmarchicus* is ecologically important in shelf regions such as the North Sea (Beaugrand *et al.*, 2003a; Skreslet *et al.*, 2005), it does not overwinter there in substantial numbers (Hirche, 1996), but is believed to re-invade in spring after overwintering in deeper water (Heath *et al.*, 1999a). The north-eastern part of the North Sea, including the western side of the Norwegian Trench, is the only part of this area where the majority of copepodite survives from the overwintering rather than the first generation of offspring (Heath *et al.*, 1999a). A deep reduction of the volume of the Norwegian Sea Deep Water has been reported (Heath *et al.*, 1999a). The reduction of this cold water mass may have also contributed to reduce the abundance of this species (Reid *et al.*, 2003b). Another phenomenon could also reinforce the reduction of *C. finmarchicus*. Hátún *et al.* (2009) have recently documented major ecosystem changes, seen from phytoplankton to blue whiting to pilot whales in the north-east Atlantic and the North Sea. The changes that have been correlated with a contraction of the Subarctic Gyre, that modulates the amount of warm-

water advected in the North East Atlantic and the North Sea (Hátún *et al.*, 2009). Such large-scale influences may strongly impact the abundance of the species. They often manifest themselves by affecting SST, which is included in our model.

Consequences of rising temperature extend from phenological to biogeographical changes to modifications in dominance of key-structural species (Edwards & Richardson, 2004; Intergovernmental Panel on Climate Change, 2007b). Changes in abundance of *C. finmarchicus* may affect ecosystems (Reid *et al.*, 2003b; Helaouët & Beaugrand, 2007), altering the diet of exploited fish (e.g. the Atlantic Cod (Beaugrand *et al.*, 2003a)), modifying the flow of energy in ecosystems and the strength of the biological carbon pump (Beaugrand, 2009). Our approach based on the Hutchinson concept of the ecological niche has enabled patterns of changes observed for this key-structural species to be better understood and may allow future changes to be better anticipated.

Chapter 6

General conclusions

Overall, the results of this macroecological study suggest that the distribution of species of the genus *Calanus* might be deeply impacted by climate change and consequently might lead to major changes in the trophodynamics of the North Atlantic ecosystems. Both dynamic and spatial variability of a species result from the synergistic response, at different temporal and spatial scales of a large quantity of biological processes, to the dynamic of the environment. To understand and assess the potential impact of climate change on species, communities, and ecosystems, it is necessary to break up the overall biological responses to climate following different categories of time and space. By focusing on macroecological patterns of key-structural species, the approach used in this study allows investigating separately some features characteristic of a species (e.g. thermal windows, egg production rate) but also to integrate their synergistic effects in a common framework: the ecological niche. More precisely, this study gives some clarifications on the relationship existing between a species and its environment which has led to the definition of new methods to understand and assess the potential impact of climate change on key-structural species of the North Atlantic Ocean.

Chapter 6: General conclusions

Changes in the abundance, diversity and composition of plankton in marine pelagic ecosystems may have pronounced consequences for higher trophic levels and therefore have to be investigated. Interpretation of both temporal and spatial variability of a planktonic species' abundance is complex; mainly because of the difficulty to identify the main variables that drive species' dynamics. The climatic envelope approach is designed to determine the range of environmental conditions able to sustain species development. This statistical method constitutes a key tool in identifying a potential limiting factor driving the chorology of a species which can explain its presence or absence from an area (e.g. Green *et al.*, 2008; Duncan *et al.*, 2009). Nevertheless, the description of the variability of a species feature (e.g. the variability of its abundance) regarding an environmental parameter only becomes functional when the influence of this parameter has been previously quantified. Both qualification and quantification of the importance of environmental parameters on the spatial distribution of a species can be investigated by coupling Principal Component Analyses (PCAs) and bioclimatic envelopes within a macroecological approach (Chapter 3; Helaouët & Beaugrand, 2007).

Despite the similarity of their morphology, *C. finmarchicus* and *C. helgolandicus* present differences in their spatial variability suggesting some differential responses to environmental variability (Bucklin, 1995). The macroecological approach shows that both environmental window and optimum level, calculated as a function of important environmental parameters, allow the two species to be distinguished (Chapter 3; Helaouët & Beaugrand, 2007). It also specifies that the main parameter explaining the spatial distribution of both *C. finmarchicus* and *C. helgolandicus* is SST. Even more

interesting, is the fact that this result holds true through a broad range of time scales (from the seasonal to the annual to the decadal) (Chapter 4; Helaouët & Beaugrand, 2009; Chapter 5; Helaouët *et al.*, submitted). This stability of the thermal profile over a large period of time, and the predominance of SST in the structure of *Calanus* species constitute a major conclusion of this study.

Thermal profiles of both species show clearly how a raise of SST will alter differently these two species. By favouring a warm temperate species such as *C. helgolandicus* at the expense of a polar key-structural species like *C. finmarchicus*, changes in SST can unbalance the dynamic of an ecosystem and therefore trigger major changes in key components of the food web such as the seasonal successions of dominant species (Beaugrand *et al.*, 2002b), predator-prey relationships (Beaugrand & Reid, 2003), and recruitment of exploited species, eventually leading to negative socio-economic impacts (e.g. fisheries). For instance, the macroecological approach suggests that the regime shift that occurred in the late 1980s in the North Sea (e.g. Reid *et al.*, 2003b; Beaugrand, 2004b) can be explained by a change of dominance in the zooplankton community triggered solely by a raise of SST.

Living organisms integrate and amplify the temperature signal through their biological processes which explains why looking at changes in the biology can allow an early detection of changes in an hydro-climatic forcing signal such as a raise of SST (Taylor *et al.*, 2002). The main reason in explaining the structuring power of the temperature is that most of the physiological processes, and therefore associated biological rates, are dependent on temperature (Cossins & Bowler, 1987) and are most often described in terms of Q10. However, temperature has many covariates (concentration of oxygen dissolved, quantity of nutrients) (Legendre, 1995) and has therefore some indirect

effects that cannot be investigated using environmental windows only. While climatic envelopes inform on the behaviour of a species regarding one parameter, the calculation of the niche of a species allows taking into account the synergistic aspect of the environment impact (Chapter 3; Helaouët & Beaugrand, 2007).

Hutchison made a distinction within his theory between the realised and the fundamental niche (Hutchinson, 1957). In summary, the realised niche represents the outcome of the combined effects of the environment (both biotic and abiotic) on the spatial distribution of a species while the fundamental niche can be defined as the response of all physiological processes of a species to the synergistic effects of environmental factors. By definition, the realised niche is representative of the requirements of a species regarding its environment and is therefore crucial in developing our understanding in biogeographical research (Hutchinson, 1957). Performed on a large dataset, the principal component analysis constitutes a powerful tool to identify the realised niche since it allows the reduction of all parameters that are available in a reduced number of dimensions. The synthesis of n-parameters in two or three dimensions constitutes a simple way to assess, compare and represent the realised niches of several species. Applied on both *C. finmarchicus* and *C. helgolandicus* the method provides a new set of information and opens a new field of investigation. For instance the method indicates that both realised niches are completely separated; confirming that the potential response of both species to climate change might be different. The method also highlights that *C. finmarchicus* is able to support larger environmental variations than *C. helgolandicus* since the realised niche breadth of *C. finmarchicus* is overall larger than the one of its congeneric species.

Theoretically, the spatial distribution of a species should be linked to its physiology. Indeed, the capacity of an organism to fulfil its biological functions, and therefore to sustain itself within a given habitat, is mainly dictated by its physiology. Using complex equations, a number of models have tried to recreate the spatial dynamic of the distribution of species. This usually leads to the definition of accurate but complex models which need a large amount of time to be set up and are rarely able to be applied at different time- and space scales. SST appears to be not only the main parameter able to act on the spatial distribution and the dynamic of key-structural species such as *C. finmarchicus* and *C. helgolandicus*, but it also appears to drive the reproductive rate (Heath *et al.*, 2000). Based on an equation calculating the Potential Egg Production Rate (PEPR) using SST only, an ecophysiological model provides clear evidence of a strong link between the fundamental and the realised niche. This link is an integral part of the theory since the ecological niche concept as defined by Hutchinson precisely states that the realised niche is nothing more than the fundamental niche for which factors such as dispersal and competition are integrated. The concomitant spatial changes seen in physiology (fundamental niche) and biogeography (realised niche) are constant at a monthly, annual and decadal scales allowing us to propose projections of the spatial distribution of the copepod as a function of different scenarios of changes in temperature established by the Intergovernmental Panel on Climate Change (2007b). This study provides for the first time evidence of the link between physiology, ecological niches and species distribution. The method is applicable to a diverse number of species since it requests only, besides some data on the spatial distribution, an equation linking the production of offspring to temperature. The comparison of both niches gives the rare opportunity to glimpse phenomenon such as competition at a macroecological scale.

Despite its usefulness, the realised niche concept of Hutchinson has been poorly utilised by ecologists; mainly because of some conceptual, biotic and algorithmic uncertainties (Araújo & Guisan, 2006). However, the last decade has shown a renewal of interest for applied biogeography using niche concepts improving the sampling methods, model definition and model evaluation (e.g. Chase & Leibold, 2003; Soberon & Peterson, 2005; Kearney, 2006; Bahn & McGill, 2007). The aim of this study was to provide some new tools to investigate the relationship between species and the environment within an ecosystem by integrating different fields such as physiology, biology and ecology into a common conceptual framework. The domain of application of this method appears to be large and this study highlights only a part of its potential extent. For instance, Gause's competitive exclusion hypothesis states that in competition between species that seek the same ecological niche, one species survives while the other expires under a given set of environmental parameters (Gause, 1934). The method can, therefore, be used to better understand the potential consequences of the arrival of an invasive species by comparing its realised niche with the one of a native species.

In this work the niche-based approach has been specifically designed on CPR data but it can also be performed on any kind of datasets (the quality of results being linked with the quantity of observations). Both the assessment and comparison of a large number of ecological niches may provide a new insight into ecosystems functioning. The next step will be to apply the macroecological approach on a larger number of species using CPR database and other sources of data: for instance in the Pacific Ocean (using the Pacific CPR survey) and in the southern Ocean (using the Southern Ocean PCR Survey). At the same time, the physiology of some copepod species will be investigated to develop the ecophysiological approach. Afterwards, this interdisciplinary approach (macroecology and ecophysiology) will also be widened by adding the genetic information which seeks to

understand the process of inheritance. Recently, studies combining genetic, oceanographic, behavioural and modelling approaches have provided new insights into the spatial ecology of marine populations (e.g. Selkoe *et al.*, 2008). It appears from results obtained that molecular tools perform at their best when integrated with other data and approaches, in particular regarding larval migrations, dispersal and “source-sink” population dynamics (Neigel, 2002; Jones *et al.*, 2005). However, data analyses compiling different kinds of data are complex and the necessity of using preliminary exploratory analyses to visualise all the different datasets appears clear. The aim of this kind of analysis (e.g. GUESS: The Graph Exploration System (Raymond & Hosie, 2009)) is to recognise and explore the structure in data in order to identify some patterns (Raymond & Hosie, 2009). They are especially useful to examine network structures and processes across a number of different disciplines and therefore can facilitate the analytical integration of an overall ecosystem with the dynamics of its individual elements (e.g. hydrodynamic, ecological niches, inter- and intra-specific relationships, genetic markers).

References

References

- Aksnes, D. L. & Blindheim, J. (1996) Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. *Ophelia*, **44**, 7-28.
- Andronova, N. G. & Schlesinger, M. E. (2000) Causes of global temperature changes during the 19th and 20th centuries. *Geophysical Research Letters*, **27**, 2137–2140.
- Angel, M. V., Blachowiak-Samolyk, K., Drapun, I. & Castillo, R. (2007) Changes in the composition of planktonic ostracod populations across a range of latitudes in the North-east Atlantic. *Progress in Oceanography*, **73**, 60-78.
- Araújo, M. B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677-1688.
- Araújo, M. B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology & Biogeography*, **16**, 743-753.
- Bahn, V. & McGill, B. J. (2007) Can niche-based distribution models outperform spatial interpolation? *Global Ecology & Biogeography*, **16**, 733-742.
- Batten, S. D., Clark, R., Flinkman, J., Hays, G., John, E., John, A. W. G., Jonas, T., Lindley, J. A., Stevens, D. P. & Walne, A. (2003) CPR sampling: the technical background, materials, and methods, consistency and comparability. *Progress in Oceanography*, **58**, 193-215.
- Beaugrand, G. (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydro-climatic environment. *Fisheries Oceanography*, **12**, 270-283.
- Beaugrand, G. (2004a) Continuous Plankton Records: a plankton atlas of the North Atlantic Ocean (1958-1999): I. Introduction and methodology. (1 ed. by G. Beaugrand & M. Edwards & A. Jones & D. Stevens). Marine Ecology Progress Series.
- Beaugrand, G. (2004b) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, **60**, 245-262.
- Beaugrand, G. (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Research II*, **56**, 656-673.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S. & Reid, P. C. (2003a) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661-664.
- Beaugrand, G., Edwards, M., Brander, K., Luczak, C. & Ibanez, F. (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters*, **11**, 1157-1168.

- Beaugrand, G. & Helaouët, P. (2008) Simple procedures to assess and compare the ecological niche of species. *Marine Ecology Progress Series*, **363**, 29-37.
- Beaugrand, G., Ibañez, F. & Lindley, J. A. (2001) Geographical distribution and seasonal and diel changes of the diversity of calanoid copepods in the North Atlantic and North Sea. *Marine Ecology Progress Series*, **219**, 205-219.
- Beaugrand, G., Ibañez, F. & Lindley, J. A. (2003b) An overview of statistical methods applied to the CPR data. *Progress in Oceanography*, **58**, 235-262.
- Beaugrand, G., Ibañez, F., Lindley, J. A. & Reid, P. C. (2002a) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Marine Ecology Progress Series*, **232**, 179-195.
- Beaugrand, G., Ibañez, F. & Reid, P. C. (2000) Long-term and seasonal fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Marine Ecology Progress Series*, **200**, 93-102.
- Beaugrand, G., Luczak, C. & Edwards, M. (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biology*, in press.
- Beaugrand, G. & Reid, P. C. (2003) Long-term changes in phytoplankton, zooplankton and salmon linked to climate change. *Global Change Biology*, **9**, 801-817.
- Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A. & Edwards, M. (2002b) Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692-1694.
- Begon, M., Townsend, C. R. & Harper, J. L. (2006) *Ecology. From individuals to ecosystems*, 4 edn. Blackwell Publishing, Bath.
- Berry, K. J. & Mielke, P. W. (1983) Computation of finite population parameters and approximate probability values for multi-response permutation procedures (MRPP). *Communications in Statistics - Simulation and Computation B*, **12**, 83-107.
- Bigg, G. R., Cunningham, C. W., Ottersen, G., Pogson, G. H., Wadley, M. R. & Williamson, P. (2008) Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. *Proceedings of the Royal Society of London, B*, **275**, 163-172.
- Bonnet, D., Ridchardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., Ceballos, S., Diekman, R., López-Urrutia, A., Valdes, L., Carlotti, F., Molinero, J-C., Weikert, H., Greve, W., Lucic, D., Albaina, A., Yahia, N-D., Umani, S-F., Miranda, A., Dos Santos, A., Cook, K., Robinson, S., Fernandez De Puellas, M-L. (2005) An overview of *Calanus helgolandicus* ecology in European waters. *Progress in Oceanography*, **65**, 1-53.

- Bouvier, A. (1977) Programme ACPM. Analyse des composantes principales avec des donnees manquantes., CNRA. Laboratoire de biometrie, Document 77/17, Jouy en Josas.
- Brander, K., Blom, G., Borges, M. F., Erzini, K., Henderson, G., Mackensie, B. R., Mendes, H., Ribeiro, J., Santos, A. M. P. & Toresen, R. (2003) Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? *ICES Marine Science Symposium*, **219**, 261-270.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.
- Bucklin, A., Frost, B.W., Kocher, T.D. (1995) Molecular systematics of six *Calanus* and three Metridia species (Calanoida: Copepoda). *Marine biology*, **121**, 655-664.
- Buitenhuis, E., Le Quéré, C., Aumont, O., Beaugrand, G., Bunker, A., Hirst, A., Ikeda, T., O'Brien, T., Piontkovski, S. & Straile, D. (2006) Biogeochemical fluxes through mesozooplankton. *Global Biogeochemical Cycles*, **20**, doi:2010.1029/2005GB002511.
- Campbell, R. G., Wagner, M.M., Teegarden, G.J., Boudreau, C.A., Durbin, E.G. (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series*, **221**, 161-183.
- Carlotti, F., Krause, M. & Radach, G. (1993) Growth and development of *Calanus finmarchicus* related to the influence of temperature: Experimental results and conceptual model. *Limnology and Oceanography*, **38**, 1125-1134.
- Carlotti, F. & Radach, G. (1996) Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model. *Limnology and Oceanography*, **41**, 522-539.
- Castellani, C., Irigoien, X., Mayor, D. J., Harris, R. P. & Wilson, D. (2008) Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. *Journal of Plankton Research*, **30**, 1095-1116.
- Chase, J. M. & Leibold, M. A. (2003) *Ecological niches – linking classical and contemporary approaches*, 1 edn. The University of Chicago Press, Chicago, IL.
- Clark, P. U., Pisias, N. G., Stocker, T. F. & Weaver, A. J. (2002) The role of the thermohaline circulation in abrupt climate change. *Nature*, **415**, 863-869.
- Colebrook, J. M. (1960) Continuous Plankton Records: methods of analysis, 1950-59. *Bulletins of Marine Ecology*, **41**, 51-54.
- Colebrook, J. M. (1964) Continuous Plankton Records: a principal component analysis of the geographical distribution of zooplankton. *Bulletins of Marine Ecology*, **6**, 78-100.

- Colebrook, J. M. (1969) Variability in plankton. *Progress in Oceanography*, **5**, 115-125.
- Colebrook, J. M. (1978) Continuous Plankton Records: zooplankton and environment, north-east Atlantic and North Sea, 1948-1975. *Oceanologica Acta*, **1**, 9-23.
- Colebrook, J. M. (1982) Continuous Plankton Records: persistence in time-series and the population dynamics of *Pseudocalanus elongatus* and *Acartia clausi*. *Marine Biology*, **66**, 289-294.
- Colebrook, J. M., Glover, R. S. & Robinson, G. A. (1961a) Contribution towards a plankton atlas of the North-Eastern Atlantic and the North Sea. General introduction. *Bulletins of Marine Ecology*, **5**, 67-80.
- Colebrook, J. M., Jhon, D. E. & Brown, W. W. (1961b) Contribution towards a plankton atlas of the North-Eastern Atlantic and the North Sea. Part II: Copepoda. *Bulletins of Marine Ecology*, **5**, 90-97.
- Colebrook, J. M. & Robinson, G. A. (1965) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the northeastern Atlantic and the North Sea. *Bulletins of Marine Ecology*, **6**, 123-139.
- Conover, R. J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia*, **167/168**, 127-142.
- Continuous Plankton Recorder Survey Team. (2004) *Continuous Plankton Records: Plankton atlas of the North Atlantic Ocean (1958-1999): II. Biogeographical charts*, edn. Marine Ecology Progress Series.
- Cook, E. R., D'arrigo, R. D. & Briffa, K. R. (1998) A reconstruction of the North Atlantic Oscillation using tree-ring chronologies from North America and Europe. *The Holocene*, **8**, 9-17.
- Cornelius, J. M. & Reynolds, J. F. (1991) On determining the statistical significance of discontinuities within ordered ecological data. *Ecology*, **72**, 2057-2070.
- Cossins, A. H. & Bowler, K. (1987) *Temperature Biology of Animals*, 1 edn. Chapman and Hall, New York.
- Cushing, D. H. (1997) *Towards a science of recruitment in fish populations*, 1 edn. Ecology Institute, Oldendorf/Luhe.
- Daro, M. H. (1985) Feeding rhythms and vertical distribution of marine copepods. *Bulletin of Marine Science*, **37**, 487-497.
- Dickson, R. R. & Turrell, W. R. (2000) The NAO: the dominant atmospheric process affecting oceanic variability in home, middle and distant waters of european atlantic salmon. *The ocean life of Atlantic salmon. Environmental and biological factors influencing survival* (ed. by D. Mills), pp 92-115. Fishing News Books, Bodmin.

- Dietrich, G. (1964) Oceanic polar front survey. *Research Geophysic*, **2**, 291-308.
- Ducklow, H. W. & Harris, R. P. (1993) Introduction to the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Research II*, **40**, 1-8.
- Duncan, R. P., Cassey, P. & Blackburn, T. M. (2009) Do climate envelope models transfer? A manipulative test using dung beetle introductions. *Proceedings of the royal society B*, **267**, 1449-1457.
- Edwards, M. (2000) Large-scale temporal and spatial patterns of marine phytoplankton and climate variability in the North Atlantic., pp 243. University of Plymouth, Plymouth.
- Edwards, M. & Richardson, A. J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881-884.
- Elton, C. (1927) *Animal ecology*, edn. Sidgwick and Jackson, London, England.
- Falkowski, P. G., Barber, R. T. & Smetacek, V. (1998) Biogeochemical controls and feedbacks on ocean primary production. *Science*, **281**, 200-206.
- Frontier, S., Pichot-Viale, D., Leprêtre, A., Davoult, D. & Luczak, C. (2004) *Ecosystèmes. Structure, fonctionnement et évolution*, 3 edn. Dunod, Paris.
- Garrison, T. (2004) *Oceanography: an invitation to marine science*, 5 edn. Cengage Learning, Stamford.
- Gause, G. F. (1934) *The struggle for existence*, 1 edn. Williams and Wilkins, Baltimore.
- Goldenberg, S. B., Landsea, C. W., Mestas-Núñez, A. M. & Gray, W. M. (2001) The Recent increase in Atlantic hurricane activity: Causes and implications. *Science*, **293**, 474-479.
- Green, R. E., Collingham, Y. C., Willis, S. G., Gregory, R. D., Smith, K. W. & Huntley, B. (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology letters*, **4**, 599-602.
- Greene, C. H., Pershing, A.J., Consersi, A., Planque, B., Hannah, C., Sameoto, D., Head, E., Smith, P.C., Reid, P.C., Jossi, J., Mountain, D., Ben Eld, M.C., Wiebe, P.H., Durbin, E. (2003) Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Progress in Oceanography*, **58**, 310-312.
- Grinnell, J. (1917) The niche-relations of the California thrasher. *Auk*, **34**, 427-433.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009.
- Guisan, A. & Zimmermann, N. E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147-186.

- Hall, C. J., Burns, C.W. (2002) Effects of temperature and salinity on the survival and egg production of *Gladioferens pectinatus* Brady (Copepoda: Calanoida). *Estuarine, Coastal and Shelf Science*, **55**, 557-564.
- Halsband-Lenk, C., Hirche, H-J., Carlotti, F. (2002) Temperature impact on reproduction and development of congener copepod populations. *Journal of experimental marine biology and ecology*, **271**, 121-153.
- Hardy, A. C. (1926) A new method of plankton research. *Nature*, **118**, 630.
- Hardy, A. C. (1939) Ecological investigations with the Continuous Plankton Recorder: object, plan, methods. *Hull Bulletins of Marine Ecology*, **1**, 1-57.
- Hátún, H., Payne, M. R., Beaugrand, G., Reid, P. C., Sandø, A. B., Drange, H., Hansen, B., Jacobsen, J. A. & Bloch, D. (2009) Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography*, **80**, 149-162.
- Hays, G. C. (1994) Mesh selection and filtration efficiency of the Continuous Plankton Recorder. *Journal of Plankton Research*, **16**, 403-412.
- Hays, G. C. & Warner, A. J. (1993) Consistency of towing speed and sampling depth for the Continuous Plankton Recorder. *Journal of the Marine Biological Association of the U. K.*, **73**, 967-970.
- Heath, M. R., Astthorsson, O. S., Dunn, J., Ellertsen, B., Gaard, E., Gislason, A., Gurney, W. S. C., Hind, A. T., Irigoien, X., Melle, W., Niehoff, B., Olsen, K., Skreslet, S. & Tande, K. S. (2000) Comparative analysis of *Calanus finmarchicus* demography at locations around the Northeast Atlantic. *ICES Journal of Marine Science*, **57**, 1562-1580.
- Heath, M. R., Backhaus, J. O., Richardson, K., Mckenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gallego, A., Hainbucher, D., Hay, S., Jonasdottir, S., Madden, H., Mardaljevic, J. & Schacht, A. (1999a) Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fisheries Oceanography*, **8**, 163-176.
- Heath, M. R., Beare, D. J., Dunn, J., Fraser, J. G., Hay, S. J. & Turrell, W. R. (1999b) Monitoring the effects of climate change - overwintering abundance of *Calanus finmarchicus* in the Faroe-Shetland Channel. Fisheries Research Services.
- Helaouët, P. & Beaugrand, G. (2007) Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series*, **345**, 147-165.
- Helaouët, P. & Beaugrand, G. (2009) Physiology, ecological niches and species distribution. *Ecosystems*, **12**, 1235-1267.

- Helaouët, P., Beaugrand, G. & Reid, P. C. (submitted) Macroscale ecophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Global Ecology and Biogeography*.
- Hirche, H.-J. (1990) Egg production of *Calanus finmarchicus* at low temperature. *Marine biology*, **106**, 53-58.
- Hirche, H.-J. (1991) Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biology*, **11**, 351-362.
- Hirche, H.-J. (1996) Diapause in the marine copepod, *Calanus finmarchicus*: a review. *Ophelia*, **44**, 129-143.
- Hirche, H.-J. & Kwasniewski, S. (1997) Distribution, reproduction and development of *Calanus* species in the northeast Atlantic in relation to environmental conditions. *Journal of Marine Systems*, **10**, 299-317.
- Hirche, H.-J., Meyer, U. & Niehoff, B. (1997) Egg production of *Calanus finmarchicus*-effect of temperature, food and season. *Marine Biology*, **127**, 609-620.
- Hirst, A. G. & Batten, S. D. (1998) Long-term changes in the diel vertical migration behaviour of *Calanus finmarchicus* in the North Sea are unrelated to fish predation. *Marine Ecology Progress Series*, **171**, 307-310.
- Hirzel, A. H., Hausser, J., Chessel, D. & Perrin, N. (2002) Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology*, **83**, 2027-2036.
- Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, **199**, 142-152.
- Huggett, R. J. (2004) *Fundamentals of biogeography*, 2 edn. Routledge, London.
- Huntley, M. E., Lopez, M.D.G. (1992) Temperature-dependent production of marine copepods: a global synthesis. *The American Naturalist*, **140**, 201-242.
- Hurrell, J. W., Yochanan, K. & Visbeck, M. (2001) The North Atlantic Oscillation. *Science*, **291**, 603-605.
- Hutchinson, G. E. (1957) *A treatise on limnology*, 1 edn. John Wiley & Sons., New York.
- Intergovernmental Panel on Climate Change, W. G. I. (2001) *Climate change 2001. The scientific basis*, 1 edn. Cambridge University Press, Cambridge.
- Intergovernmental Panel on Climate Change, W. G. II. (2007a) *Climate Change 2007. Impacts, Adaptation and Vulnerability*, 1 edn. Cambridge University Press, Cambridge.

- Intergovernmental Panel on Climate Change, W. G. I. (2007b) *Climate change 2007. The physical science basis*, 1 edn. Cambridge University Press, Cambridge.
- Jackson, D. A. & Somers, K. M. (1989) Are probability estimates from the permutation model of Mantel's test stable? *Canadian J. Zool.*, **67**, 766-769.
- Jolliffe, I. T. (1986) *Principal Component Analysis*, 1 edn. Springer-Verlag New York Inc., New York.
- Jonas, T. D., Walne, A., Beaugrand, G., Gregory, L. & Hays, G. C. (2004) The volume of water filtered by a CPR: the effect of ship speed. *Journal of Plankton Research*, **26**, 1499-1506.
- Jones, G. P., Planes, S. & Thorrold, S. R. (2005) Coral reef fish larvae settle close to home. *Current Biology*, **15**, 1314-1318.
- Kaartvedt, S. (1996) Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. *Ophelia*, **44**, 145-156.
- Kearney, M. (2006) Habitat, environment and niche: what are we modelling? *Oikos*, **115**, 186-191.
- Kerr, R. A. (2000) A North Atlantic climate pacemaker for the centuries. *Science*, **288**, 1984-1986.
- Kinne, O. (1964) The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. *Oceanography and Marine Biology: an Annual Review*, **2**, 281-339.
- Kirby, R. R., Beaugrand, G. & Lindley, J. A. (2009) Synergistic Effects of Climate and Fishing in a Marine Ecosystem. *Ecosystems*, In press.
- Kleppel, G. S. (1993) On the diets of calanoid copepods. *Marine Ecology Progress Series*, **99**, 183-195.
- Koski, M. & Riser, C. W. (2006) Post-bloom feeding of *Calanus finmarchicus* copepodites: Selection for autotrophic versus heterotrophic prey. *Marine Biology Research*, **2**, 109-119.
- Krauss, W. (1986) The North Atlantic current. *Journal of geophysical research*, **91**, 5061-5074.
- Kruskal, J. B. (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, **29**, 1-27.
- Lam, N. S. N. (1983) Spatial interpolation methods: a review. *The American cartographer*, **10**, 129-149.
- Legendre, L., Rassoulzadegan, F. (1995) Plankton and nutrient dynamics in marine waters. *Ophelia*, **41**, 153-172.

- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2 edn. Elsevier Science B.V., The Netherlands.
- Leibold, M. A. (1995) Niche concept revisited: Mechanistic models and community context. *Ecology*, **76**, 1371-1382.
- Levin, S. A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist*, **104**, 413-423.
- Levitus, S., Antonov, J. & Boyer, T. (2005) Warming of the world ocean, 1955-2003. *Geophysical Research Letters*, **32**, doi:10.1029/2004GL021592.
- Levitus, S., Antonov, J. I., Wang, J., Delworth, T. L., Dixon, K. W. & Broccoli, A. I. (2001) Anthropogenic warming of Earth's climate system. *Science*, **292**, 267-270.
- Lindley, J. A. (1987) Continuous Plankton Records: the geographical distribution and seasonal cycles of Decapod Crustacean larvae and pelagic post-larvae in the north-eastern Atlantic Ocean and the North Sea, 1981-3. *Journal of the Marine Biological Association of the U. K.*, **67**, 145-167.
- Lindley, J. A. & Williams, R. (1994) Relating plankton assemblages to environmental variables using instruments towed by ships-of-opportunity. *Marine Ecology Progress Series*, **107**, 245-262.
- Lomolino, M. V., Riddle, B. R. & Brown, J. H. (2006) *Biogeography*, 3 edn., Sunderland.
- Longhurst, A. (1995) Seasonal cycles of pelagic production and consumption. *Progress in Oceanography*, **36**, 77-167.
- Longhurst, A. (1998) *Ecological geography of the Sea*, 1 edn. Academic Press, London.
- Lucas, C. E. (1940) Ecological investigations with the Continuous Plankton Recorder : the phytoplankton in the southern North Sea, 1932-1937. *Hull Bulletins of Marine Ecology*, **1**, 73-170.
- Lynch, D. R., Lewis, C. V. W. & Werner, F. E. (2001) Can Georges Bank larval cod survive on a calanoid diet? *Deep-Sea Research II*, **48**, 609-630.
- Macarthur, R. H. (1958) Population ecology of some warblers of Northeastern coniferous forests. *ecology*, **39**, 599-619.
- Marshall, S. M. & Orr, A. P. (1955) *The biology of a Marine Copepod, Calanus finmarchicus (Gunnerus)*, 1 edn. Oliver & Boyd, London.
- Mauchline, J. (1998) *The biology of calanoid copepods*, 1 edn. Academic Press, San Diego.

- Mccabe, G. J., Palecki, M. A. & Betancourt, J. L. (2004) Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences*, **101**, 4136-4141.
- Mielke, P. W., Berry, K.B., Brier, G.W. (1981) Application of multi-response permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. *Monthly Weather Review*, **109**, 120-126.
- Miller, C. B., Cowles, T. J., Wiebe, P. H., Copley, N. J. & Grigg, H. (1991) Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. *Marine Ecology Progress Series*, **72**, 79-91.
- Morrison, M. L., Marcot, B. G. & Mannan, R. W. (1998) *Wildlife-Habitat Relationships: Concepts and Applications*, 2 edn. The University of Wisconsin Press, Madison, Wisconsin, USA.
- Neigel, J. E. (2002) Is FST obsolete? *Conservation Genetics*, **3**, 167-173.
- Niehoff, B. (2004) The effect of food limitation on gonad development and egg production of the planktonic copepod *Calanus finmarchicus*. *Journal of Experimental Marine Biology and Ecology*, **307**, 237-259.
- Nybakken, J. W. (2001) *Marine Biology: an Ecological Approach*, 5 edn. Benjamin Cummings, San Francisco.
- Odum, E. P. (1971) *Fundamentals of ecology*, 1 edn. Saunders, Philadelphia.
- Orlova, E. L., Boitsov, V.D., Dolgov, A.V., Rudneva, G.B., Nesterova, V.N. (2005) The relationship between plankton, capelin, and cod under different temperature conditions. *ICES Journal of Marine Science*, **62**, 1281-1292.
- Ottersen, G. & Stenseth, N. C. (2001) Atlantic climate governs oceanographic and ecological variability in the Barents Sea. *Limnology and Oceanography*, **46**, 1774-1780.
- Parmesan, C. (2005) *Biotic Response: Range and abundance changes.*, 1 edn. Yale University Press, New Haven, CT.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.
- Pearson, R. G. & Dawson, T. P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography*, **12**, 361-371.
- Pearson, R. G., Dawson, T. P., Berry, P. M. & Harrison, P. A. (2002) SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological Modelling*, **154**, 289-300.

- Peterson, A. T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly review of Biology*, **78**, 419-433.
- Planque, B. (1996) Spatial and temporal fluctuations in *Calanus* populations sampled by the Continuous Plankton Recorder. pp 131. Pierre et Marie Curie, Paris VI, France.
- Planque, B. & Batten, S. D. (2000) *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES Journal of Marine Science*, **57**, 1528-1535.
- Planque, B. & Fromentin, J.-M. (1996) *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series*, **134**, 111-118.
- Pulliam, H. R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652-661.
- Pulliam, H. R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349-361.
- Rae, K. M. (1952) Continuous Plankton Records: explanation and methods, 1946-1949. *Hull Bulletins of Marine Ecology*, **3**, 135-155.
- Raymond, B. & Hosie, G. (2009) Network-based exploration and visualisation of ecological data. *Ecological Modelling*, **220**, 673-683.
- Reid, P. C. & Beaugrand, G. (2002) Interregional biological responses in the North Atlantic to hydrometeorological forcing. *Changing states of the Large Marine Ecosystems of the North Atlantic* (ed. by K. Sherman & H.-R. Skjoldal), pp 27-48. Elsevier Science, Amsterdam.
- Reid, P. C., Borges, M. & Svenden, E. (2001) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research*, **50**, 163-171.
- Reid, P. C., Colebrook, J. M., Matthews, J. B. L., Aiken, J., Barnard, R., Batten, S. D., Beaugrand, G., Buckland, C., Edwards, M., Finlayson, J., Gregory, L., Halliday, N., John, A. W. G., Johns, D., Johnson, A. D., Jonas, T., Lindley, J. A., Nyman, J., Pritchard, P., Richardson, A. J., Saxby, R. E., Sidey, J., Smith, M. A., Stevens, D. P., Tranter, P., Walne, A., Wootton, M., Wotton, C. O. M. & Wright, J. C. (2003a) The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. *Progress in Oceanography*, **58**, 117-173.
- Reid, P. C. & Edwards, M. (2001) Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana Maritima*, **32**, 107-115.
- Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M. & Stevens, D. (2003b) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography*, **12**, 260-269.

- Reid, P. C., Planque, B. & Edwards, M. (1998) Is variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? *Fisheries Oceanography*, **7**, 282-288.
- Richardson, K., Jonasdottir, S. H., Hay, S. J. & Christoffersen, A. (1999) *Calanus finmarchicus* egg production and food availability in the Faroe-Shetland Channel and northern North Sea: October-March. *Fisheries Oceanography*, **8**, 153-162.
- Robinson, M. A. (1961) Contribution towards a plankton atlas of the North-Eastern Atlantic and the North Sea. Part I: phytoplankton. *Bulletins of Marine Ecology*, **5**, 81-89.
- Roeckner, E., Arpe, K., Bengtsson, L., Christoph, M., Claussen, M., Dumenil, L., Esch, M., Giorgetta, M., Schlese, U. & Schulzweida, U. (1996) *The atmospheric general circulation model ECHAM-4: Model description and simulation of present-day climate*, 1 edn. Max-Planck Institut für Meteorologie, Hamburg.
- Roemmich, D. & Mcgowan, J. (1995) Climatic warming and the decline of zooplankton in the California current. *Science*, **267**, 1324-1326.
- Rogers, J. C. (1984) The association between the North Atlantic Oscillation and the Southern Oscillation in the northern hemisphere. *Monthly Weather Review*, **112**, 1999-2015.
- Sanchez-Cordero, V., Cirelli, V., Mungia, M. & Sarkar, S. (2005) Place prioritization for biodiversity representation using species' ecological niche modeling. *Biodiversity Informatics*, **2**, 11-23.
- Sarmiento, J. L., Slater, R., Barber, R., Bopp, L., Doney, S. C., Hirst, A. C., Kleypas, J., Matear, R., Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S. A. & Stouffer, R. (2004) Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles*, **18**, 1-23.
- Schlesinger, M. E. & Ramankutty, N. (1994) An oscillation in the global climate system of period 65-70 years. *Nature*, **367**, 723-726.
- Schmidt-Nielsen, K. (1990) *Animal physiology: adaptation and environment*, 4 edn. Cambridge University Press, New York.
- Schröter, D., Cramer, W., Leemans, R., . , Prentice, C., Araújo, M. B., Nigel W. Arnell, Bondeau, A., Bugmann, H., Carter, T. C., Gracia, C. A., De La Vega-Leinert, A. C., Erhard, M., Ewert, F., Glendining, M., House, J. I., Kankaanpää, S., Klein, R. J. T., Lavorel, S., Lindner, M., Metzger, M. J., Meyer, J., Mitchell, T. D., Reginster, I., Rounsevell, M., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M. T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S. & Zierl, B. (2005) Ecosystem Service Supply and Vulnerability to Global Change in Europe. *Science*, **310**.

- Selkoe, K. A., Henzler, C. M. & Gaines, S. D. (2008) Seascape genetics and the spatial ecology of marine populations. *FISH and FISHERIES*, **9**, 363-377.
- Skreslet, S., Borja, A., Bugliaro, L., Hansen, G., Meerkotter, R., Olsen, K. & Verdebout, J. (2005) Some effects of ultraviolet radiation and climate on the reproduction of *Calanus finmarchicus* (Copepoda) and year class formation in Arcto-Norwegian cod (*Gadus morhua*). *ICES Journal of Marine Science*, **62**, 1293-1300.
- Soberon, J. & Peterson, A. T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1-10.
- Speirs, D., Gurney, W. S. C., Holmes, S. J., Heath, M. R., Wood, S. N., Clarke, E. D., Harms, I. H., Hirche, H.-J. & Mckenzie, E. (2004) Understanding demography in an advective environment: modelling *Calanus finmarchicus* in the Norwegian Sea. *Journal of Animal Ecology*, **73**, 897-910.
- Speirs, D. C., Gurney, W. S. C., Heath, M. R., Horbelt, W., Wood, S. N. & De Cuevas, B. A. (2006) Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. *Marine Ecology Progress Series*, **313**, 173-192.
- Stenseth, N. C., Ottersen, G., Hurrell, J. W. & Belgrano, A. (2004) *Marine ecosystems and climate variation. The North Atlantic. A comparative perspective.*, 1 edn. Oxford University Press.
- Sundby, S. (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, **85**, 277-298.
- Sutton, R. T. & Hodson, L. R. (2005) Atlantic forcing of North American and European summer climate. *Science*, **309**, 115-118.
- Talley, L. D., Reid, J. L. & Robbins, P. E. (2003) Data-based meridional overturning streamfunctions for the global ocean. *J. Clim*, **16**, 3213-3226.
- Taylor, A. H. (1995) North-South shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. *ICES Journal of Marine Sciences*, **52**, 711-721.
- Taylor, A. H., Allen, J. I. & Clark, P. A. (2002) Extraction of a weak climatic signal by an ecosystem. *Nature*, **416**, 629-632.
- Tomczak, M. & Godfrey, J. S. (2003) *Regional Oceanography: an Introduction*, 2 nd. Pergamon Press, New York.
- Van Loon, H. & Rogers, J. C. (1978) The seesaw in winter temperatures between Greenland and northern Europe. I. General description. *Monthly Weather Review*, **106**, 296-310.
- Walker, G. T. (1924) Correlations in seasonal variations of weather. *Mem. Indian Meteor. Dept.*, **24**, 275-332.

- Warner, A. J. & Hays, G. C. (1994) Sampling by the Continuous Plankton Recorder survey. *Progress in Oceanography*, **34**, 237-256.
- Webster, R. (1973) Automatic soil-boundary location from transect data. *Journal of the International Association of Mathematical Geology*, **5**, 27-37.
- Weijerman, M., Lindeboom, H. & Zuur, A. F. (2005) Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Marine Ecology Progress Series*, **298**, 21-39.
- Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Marínez, D., Agudo, R. & Monserrat, V. J. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**.
- Woodruff, S., Slutz, R., Jenne, R. & Steurer, P. (1987) A comprehensive ocean-atmosphere dataset. *Bulletin of the American meteorological society*, **68**, 1239-1250.
- Zimmerman, G. M., Goetz, H.P., Mielke, W. (1985) Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology*, **66**, 606-611.

Publications



Macroecological study of *Centropages typicus* in the North Atlantic Ocean

G. Beaugrand^{a,*}, J.A. Lindley^b, P. Helaouet^{a,b}, D. Bonnet^c

^a CNRS, UMR 8013 ELICO, Université des Sciences et Technologies de Lille 1, BP 80, 28 Avenue Foch, 62930 Wimereux, France

^b Sir Alister Hardy Foundation for Ocean Science, Citadel Hill, The Laboratory, Plymouth PL1 2PB, England, United Kingdom

^c Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, England, United Kingdom

Available online 13 January 2007

Abstract

Centropages typicus is a temperate neritic-coastal species of the North Atlantic Oceans, generally found between the latitudes of the Mediterranean and the Norwegian Sea. Therefore, the species experiences a large number of environments and adjusts its life cycle in response to changes in key abiotic parameters such as temperature. Using data from the Continuous Plankton Recorder (CPR) survey, we review the macroecology of *C. typicus* and factors that influence its spatial distribution, phenology and year-to-year to decadal variability. The ecological preferences are identified and quantified. Mechanisms that allow the species to occur in such different environments are discussed and hypotheses are proposed as to how the species adapts to its environment. We show that temperature and both quantity and quality of phytoplankton are important factors explaining the space and time variability of *C. typicus*. These results show that *C. typicus* will not respond only to temperature increase in the region but also to changes in phytoplankton abundance, structure and composition and timing of occurrence. Methods such as a decision tree can help to forecast expected changes in the distribution of this species with hydro-climatic forcing.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Macroecology; North Atlantic Ocean; *Centropages typicus*; CPR survey; Statistical analyses

1. Introduction

Centropages typicus is a temperate, neritic-coastal, calanoid copepod that can be found from the Mediterranean Sea to latitudes as far as the Norwegian Sea (Sars, 1903; Rose, 1933; The CPR survey team, 2004). Therefore, this species experiences a wide range of environmental factors that can potentially affect its physiology, reproductive biology, life history and relationships with other species (i.e. competition) (Halsband-Lenk et al., 2001, 2002). Although some workers have investigated the biology of this species (Dagg, 1977; Halsband-Lenk et al., 2001, 2002), knowledge about its spatial distribution and its variability

* Corresponding author.

E-mail address: Gregory.Beaugrand@univ-lille1.fr (G. Beaugrand).

at both seasonal and year-to-year scales remains poor at the scale of the North Atlantic Ocean (Halsband and Hirche, 2001).

The Continuous Plankton Recorder (CPR) survey provides a unique source of information to improve understanding of spatial and temporal changes in the abundance of many planktonic species and the factors that control them (Reid et al., 2003; Beaugrand et al., 2001). Haury and McGowan (1998) stated “most time series studies are spatially restricted and tell little about biogeography, while spatially extensive, temporally restricted studies describe a static biogeography with few hints about the dynamic factors regulating species patterns”. This problem, that is common to many monitoring programmes, is not found with the CPR survey at the scale of the North Atlantic basin. Indeed, this survey allows many temporal and spatial scales to be examined, ranging from diel to decadal variability (Hays, 1995; Fromentin and Planque, 1996; Lindley and Batten, 2002) and extending from a small region in the sea to the whole northern part of the North Atlantic Ocean (Planque and Ibañez, 1997; Beaugrand et al., 2002).

This invaluable information has been taken into consideration throughout this study to draw a more dynamic picture of the spatial and temporal changes in the abundance of *Centropages typicus*. Specifically, the objectives of this study are (1) to describe the spatial distribution of *Centropages typicus*, (2) to examine temporal changes in its spatial distribution at both seasonal and year-to-year scales and (3) to evaluate the impact of temperature on the spatial distribution of the species. Comparison will be made with the congeneric, more continental species *Centropages hamatus*.

2. Materials and methods

2.1. Biological data

Data on the abundance of genus *Centropages* come from the CPR survey. The Continuous Plankton Recorder (CPR) survey is an upper layer, plankton monitoring programme that has regularly collected samples, at monthly intervals, in the North Atlantic and the North Sea since 1946 (Warner and Hays, 1994). Despite the near surface sampling (6.5 m; Hays and Warner, 1993), studies have shown that this machine gives a satisfactory picture of the epipelagic zone (Williams and Lindley, 1980; Lindley and Williams, 1980; Batten et al., 1999). The CPR was first used during the ‘Discovery’ expedition to the Antarctic Ocean in 1925–1927. Then, from 1931, it was regularly deployed along certain routes in the North Sea. The original idea was to use a similar methodology to that of meteorology to investigate causes and effects of changes in the abundance of marine plankton and to relate them to varying hydro-climatic conditions and catches of pelagic fishes such as herring (Hardy, 1939). As the number of sampled years has increased, it has become possible to study changes in the abundance and composition of species through time. Since the start of the programme, the survey has accumulated a large amount of data. Information about the abundance of more than 450 species or taxa has been gathered from about 200,000 CPR samples collected up to 2004, which represents 90 million data-points. More details about methods and contents this data set were described by Reid et al. (2003), Batten et al. (2003) and Jonas et al. (2004). In the present study, data on *Centropages* and the phytoplankton colour index (a CPR-derived index of chlorophyll concentration in the marine environment) were utilised. *Centropages* is a genus that has generally a vertical position in the water column above 50 m (Fragopoulou and Lykakis, 1990; Alcaraz et al., this issue; Irigoien et al., 2004) and diel vertical migration may be observed (Hays et al., 1996) or not (Visser et al., 2001), but see Alcaraz et al. (this issue). Therefore, monitoring of the genus *Centropages* is not strongly affected by the constant depth of sampling used by the CPR survey.

2.2. Sea surface temperature (SST) data

Sea surface temperature (SST) data were taken from the British Atmospheric Data Centre ([http://badc.nerac.ac.uk/home/index.html](http://badc.nerc.ac.uk/home/index.html); HadISST1, Hadley Centre, Met Office). This dataset based on in situ historical marine observations and satellite data (advanced very high resolution radiometer) represents one of the most extensive collections of surface marine data available that covers most regions of the world (Rayner et al., 2003). Data are organised in 1° longitude and 1° latitude boxes and are available for every month of the period 1958–2002.

2.3. Spatial interpolation of data on *Centropages typicus*

Data on the abundance of *Centropages typicus* were spatially interpolated for each month of the period 1958–2002 (a total of 191,028 analysed CPR samples) using the inverse squared distance method (Lam, 1983). This method is simpler than kriging and gives similar results when the radius of interpolation is rela-

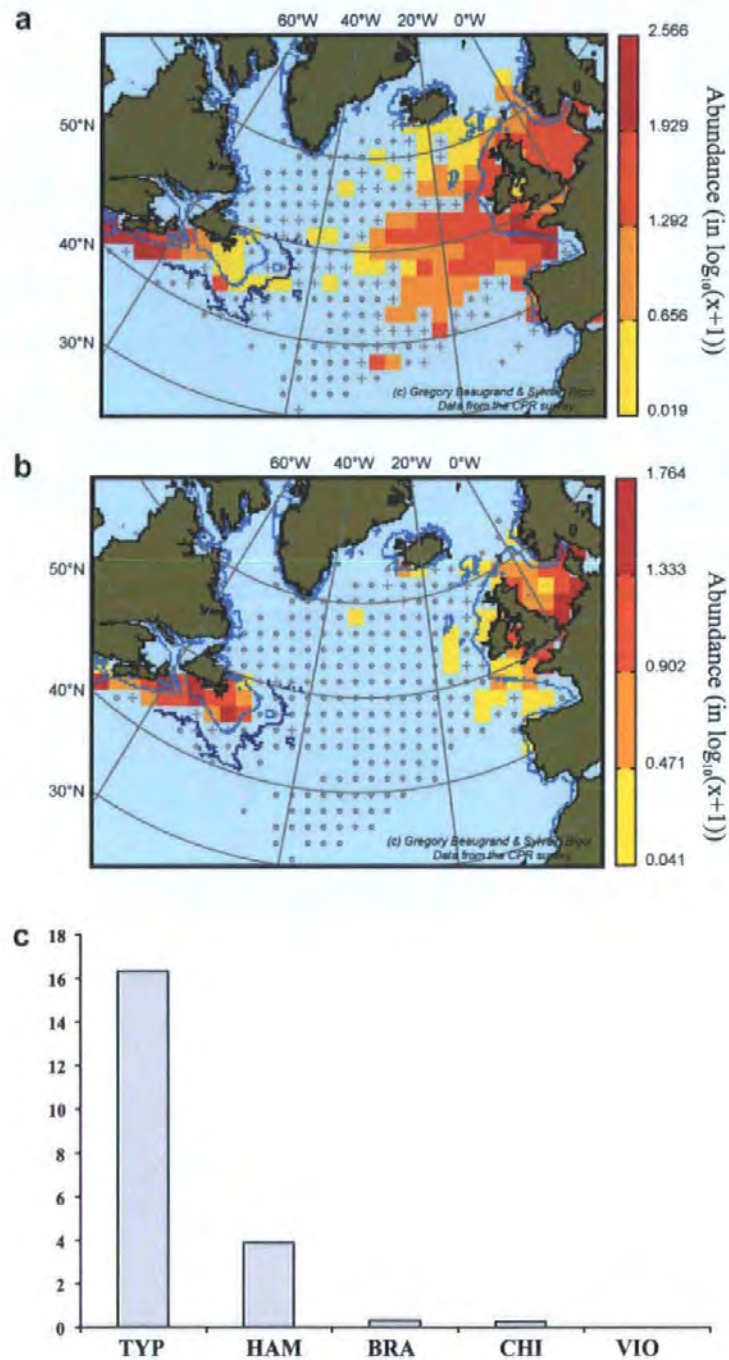


Fig. 1. Spatial distribution and abundance patterns of two species of the genus *Centropages* inferred from the CPR survey. (a) *Centropages typicus* (TYP). (b) *C. hamatus* (HAM). (c) Proportion of species of the genus *Centropages* found in CPR data for the period 1958–2002. BRA, *C. bradyi*; CHI, *C. chierchiae*; VIO, *C. violaceus*.

tively small (i.e. <250 nautical miles) (Beaugrand et al., 2000). Spatial interpolation performed on the CPR data, where the distribution of samples is far from random, has to be realised with extreme caution. In all cases, spatial interpolations were carefully checked by (1) plotting directly the samples for a fixed level of abundance and (2) using a simple mean in fixed regular squares of a grid. After interpolation, the matrix of 3519 geographical squares \times 540 time periods (12 months \times 45 years) was built. To examine the seasonal variability of *C. typicus*, an average of all years was calculated for each month (matrix of 3519 geographical squares \times 12 months), and to study the year-to-year variability of *C. typicus*, an average of all months was realised (matrix of 3519 geographical squares \times 45 years). Similar matrices were constructed for sea surface temperature (SST) data.

2.4. Analysis of the seasonal variability in the spatial distribution of *Centropages typicus*

A spatialised principal component analysis (PCA) was used to examine the seasonal variability in the spatial distribution of *C. typicus*. This analysis was applied on the original matrix of 3519 geographical squares (69 longitudes \times 51 latitudes) \times 12 months for the period 1958–2002. Eigenvectors and principal components were calculated from a correlation matrix of 3519 \times 3519 geographical squares. Eigenvectors were first calculated using the following formula:

$$(S - \lambda_k I)u_k = 0$$

where S being the dispersion matrix (here a correlation matrix), λ_k the k eigenvalues, I the unit matrix and u_k the matrix of the k eigenvectors. Then, principal components (also called component scores) P were calculated by:

$$P = XU$$

where U is the matrix of eigenvectors and X the matrix of standardised observations.

This analysis allows spatial and temporal changes to be taken into account in a single procedure. Maps of eigenvectors show where the main patterns of temporal variability (represented by principal components) occur. Such analyses have been conducted in Planque (1996) and Beaugrand et al. (2001). The original matrix

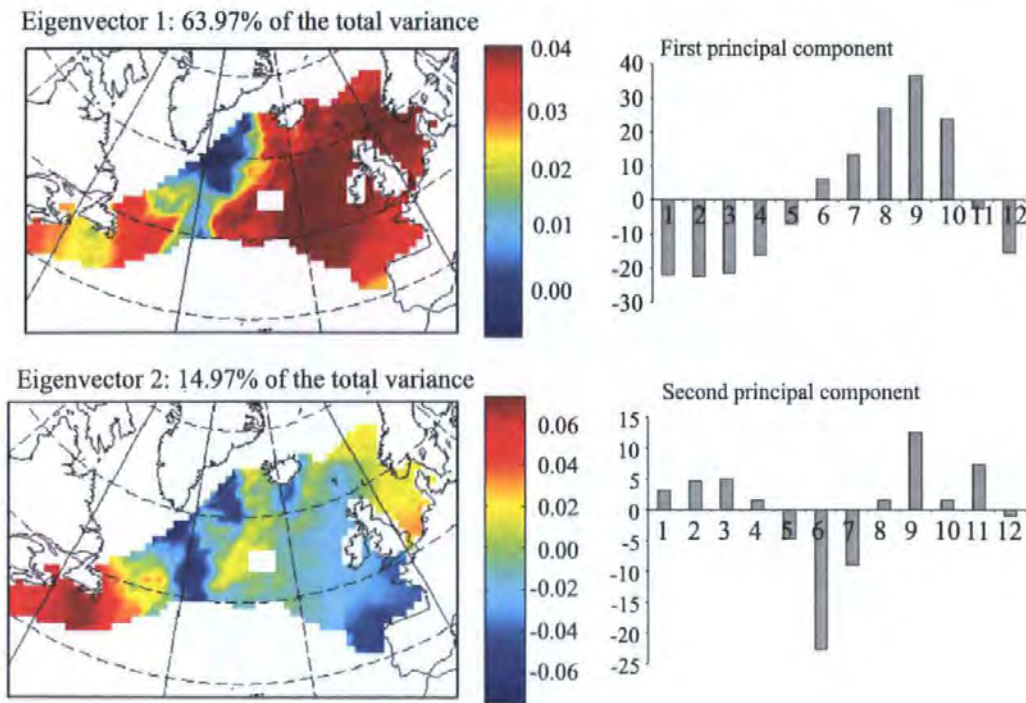


Fig. 2. Spatialised PCA applied at a seasonal scale. First and second eigenvectors (left) and corresponding principal components.

was then reassessed using the first five eigenvectors and principal components in a way similar to Beaugrand et al. (2001).

$$Xp_{3519,12} = P_{3519,5}U'_{12,5}$$

Xp being the reassessed matrix from the first five principal components p and eigenvectors U . This analysis also allows a clear examination of the seasonal cycle as expressed by the first five axes. Each principal component is constrained to be orthogonal, whilst there is no reason this should be the case in the ocean ecosystem. Reassessing the matrix enabled us to confront our interpretation of the seasonal changes inferred from the principal components.

2.5. Analysis of the year-to-year variability in the spatial distribution of *Centropages typicus*

A similar spatialised PCA was applied on the original matrix of 3519 geographical pixels \times 45 years (1958–2002). The Pearson linear correlation coefficient was used to assess the relationships between long-term changes in the principal components and temperature. Probabilities of significance (p_{ACF}) of coefficients of correlation were calculated, taking into consideration the temporal autocorrelation. A Box–Jenkins (Box and Jenkins, 1976) autocorrelation function, as modified by Chatfield (1996), was used to assess the temporal dependence of years. The Chelton (1984) formula was applied to adjust the degrees of freedom.

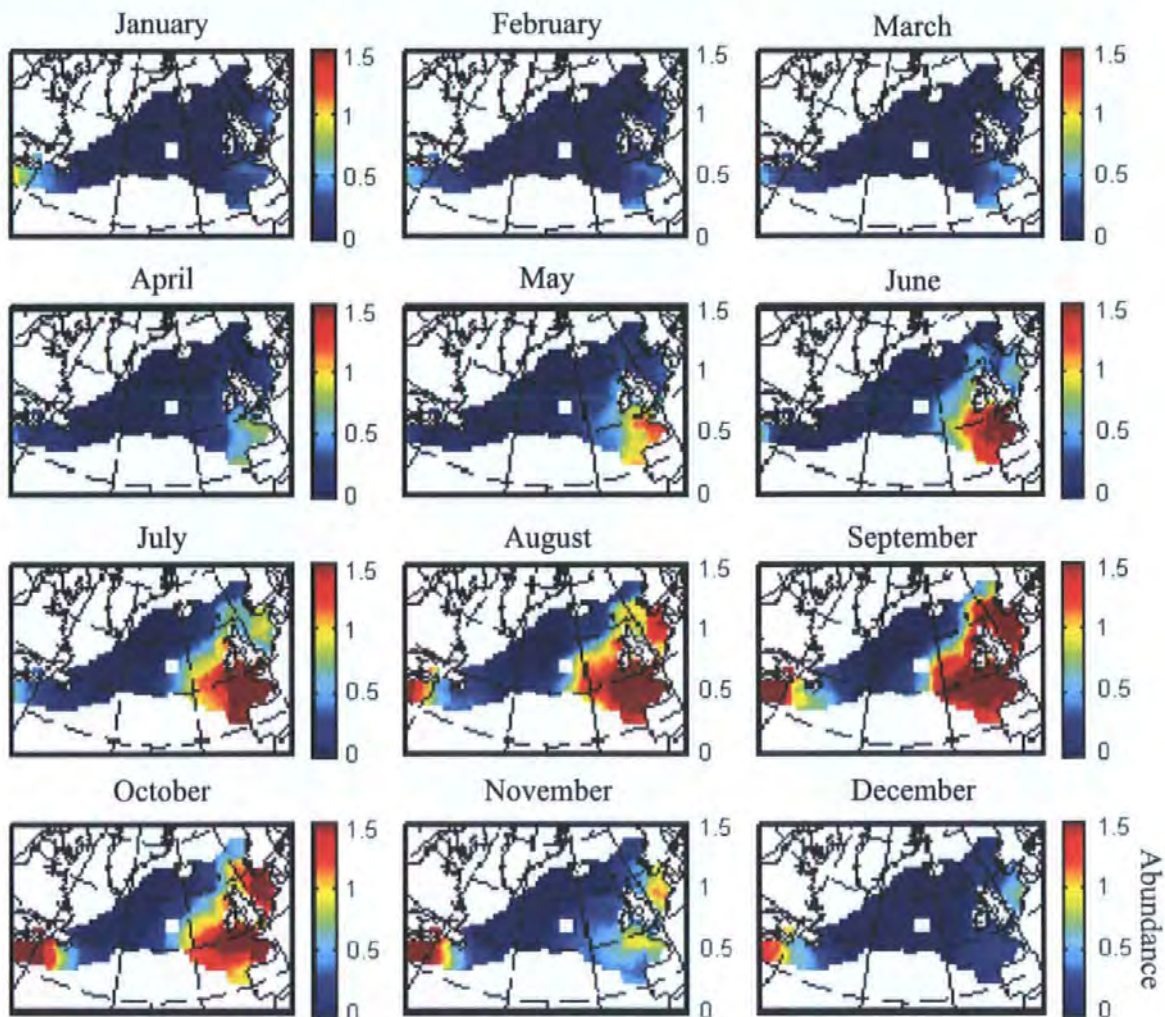


Fig. 3. Modelled seasonal cycle of *C. typicus* from the first 5 eigenvectors and principal components (93.21% of the total variance).

2.6. Spatial changes in the phenology of *C. typicus*

To investigate spatial changes in the phenology of *C. typicus*, the slope between each monthly observation of the abundance of the species was assessed for each geographical cell. The same analysis was conducted for SST data. Then, correlations between monthly changes in the slope of the abundance of the species and SST were calculated with no lag and a one-month lag (lagged temperature).

The length of the season was assessed by doing the following calculations:

- 1. Calculation of the first and third quartile of the annual abundance (using the 12 months) of *C. typicus* in each geographical cell.
- 2. Identification of the months corresponding to the quartiles. Linear interpolation was performed between the two nearest months using the following formula when the difference between the value of the nearest month and the value of the first quartile ($M_i - Q_1$) was positive:

$$M_{Q1} = M_i - \frac{M_i - Q_1}{M_i - M_{i-1}}$$

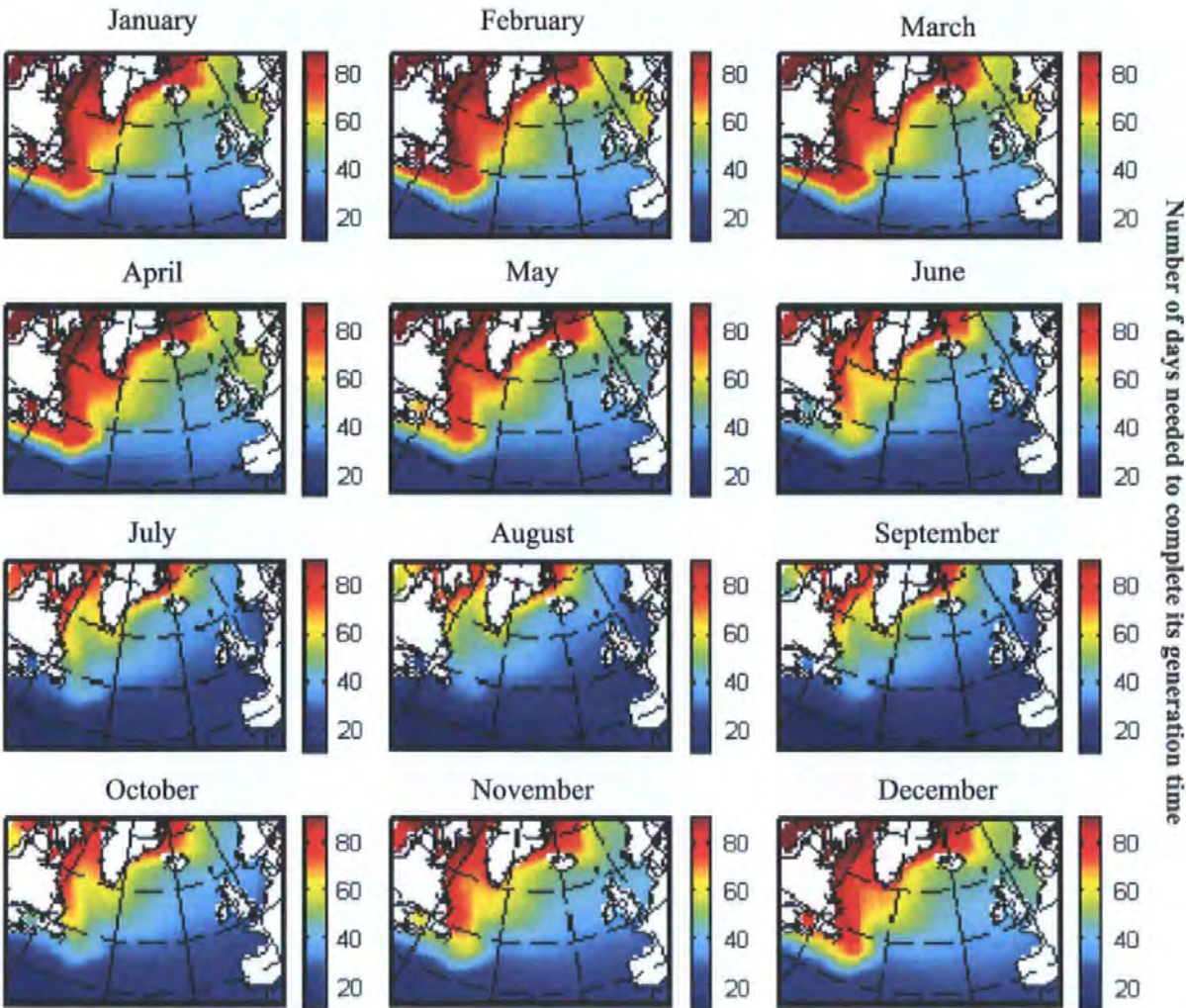


Fig. 4. Correlations between seasonal changes (change from one month to another) in the abundance of *C. typicus* and temperature with no (a) and a lag of one month (b). The symbol + indicates that a correlation is significant at the level of probability of 0.1. Geographical squares with an annual abundance of *C. typicus* <0.45 (in log₁₀(x + 1)) were removed from the analysis.

When the difference between the value of the nearest month and the first quartile ($M_i - Q_1$) was negative, the following formula was applied:

$$M_{Q1} = M_i + \frac{Q_1 - M_i}{M_{i+1} - M_i}$$

A similar procedure was used to identify the month M_{Q3} corresponding to the third quartile Q_3 . Then, the index of the length of the season L was assessed by:

$$L = M_{Q3} - M_{Q1}$$

This index can only work if the distribution is unimodal. This was indeed the case in all parts of the North Atlantic Ocean. The length-of-season index was then compared to the number of months with SST superior to 10–15 °C, which is generally the temperature range over which *C. typicus* can rapidly increase in abundance (Halsband-Lenk et al., 2001; Halsband and Hirche, 2001).

2.7. Characterisation of thermal window and thermal optimum of *C. typicus*

Recently a procedure has been set up by Helaouet and Beaugrand (revised Can the status of this MS be updated?) to calculate the thermic environment of a species sampled by the CPR survey. The thermic window is assessed in a zone which extends in longitude from 99.5°W to 29.5°E and in latitude from 29.5°E to 69.5°N.

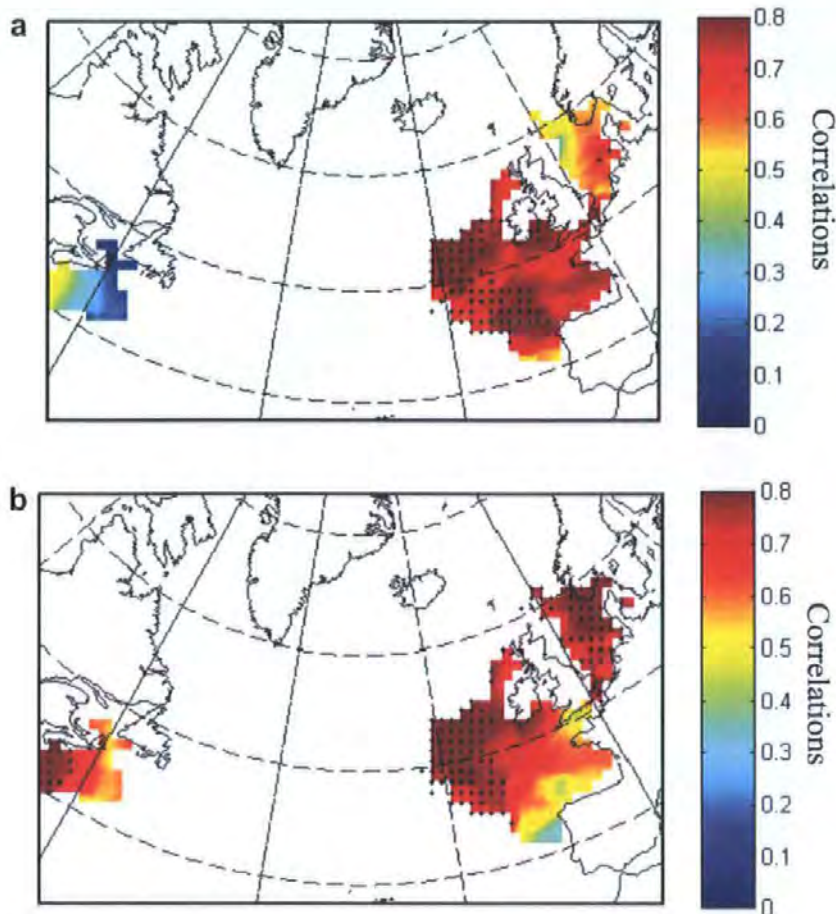


Fig. 5. Spatial changes in the development time of *C. typicus* inferred from SST. See methods. Make the scale labelling more explicit in this caption: “Number of days...”: days for what?

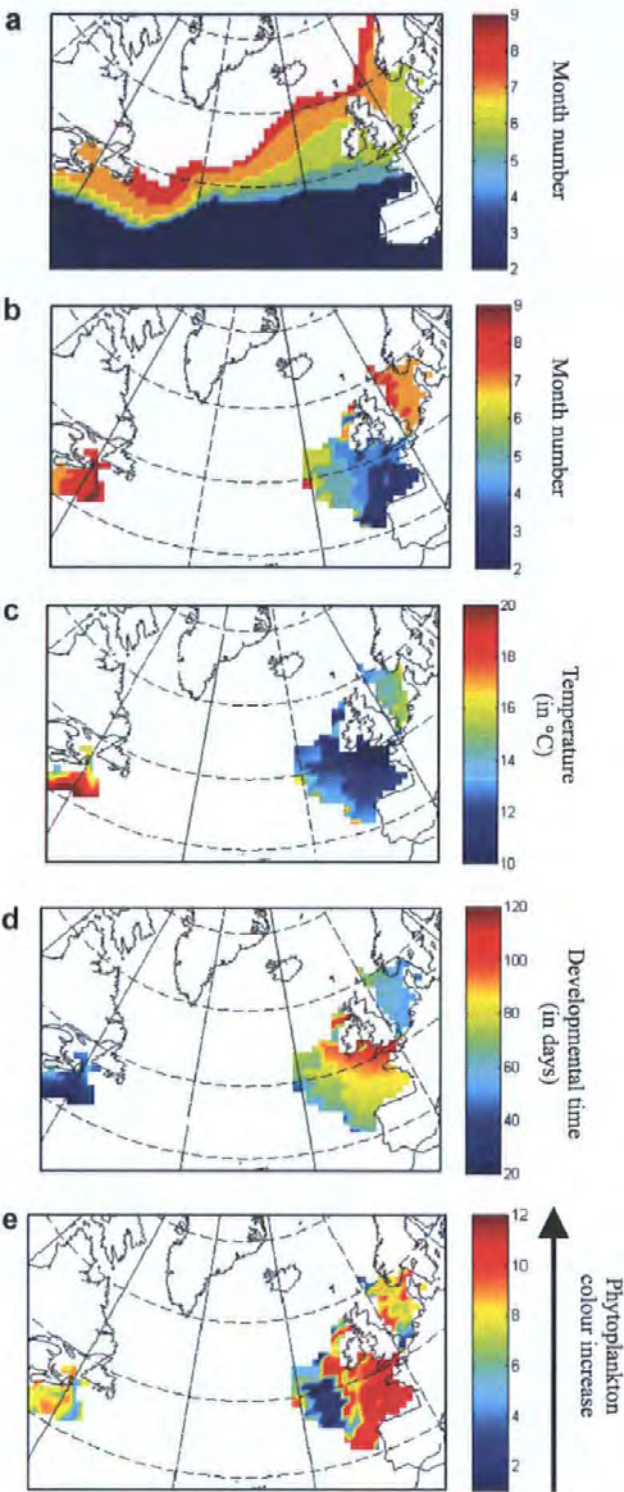


Fig. 6. Spatial changes in phenological parameters of *C. typicus* in relation to SST and the Phytoplankton Color Index. (a) First month with SST > 12 °C. (b) Month corresponding to the maximum increase in the abundance of *C. typicus*. (c) Temperature corresponding to the month of maximum increase in the abundance of *C. typicus*. (d) Development time corresponding to the month of maximum increase in the abundance of *C. typicus*. (e) Value of the phytoplankton colour index corresponding to the month of maximum increase in the abundance of *C. typicus*. Geographical squares with an annual abundance of *C. typicus* < 0.45 (in $\log_{10}(x + 1)$) were removed from the analysis.

Biological data were not interpolated but were regularised by using the physical matrix grid of SST (grid of $1^\circ \times 1^\circ$). We calculated the arithmetic mean of the abundances of the two *Centropages* species for each category of temperature (every two degrees) and each month of the time series (1958–2002). Then, we calculated the maximum value of the various averages of abundance for the whole time series. Thus we obtain the maximum average value of abundance for each category of temperature. A similar methodology was applied to identify the joint environmental window using SST and the CPR derived index of chlorophyll concentration called the phytoplankton colour index.

The development time (DT) was assessed from SST (T) using the following allometric relationships (Carroll et al., this issue):

$$DT = 89.70e^{-0.0768T}$$

All methods used in the present study were programmed using the MATLAB language.

3. Results

3.1. Mean spatial distribution of *Centropages typicus*

Fig. 1a shows the mean spatial distribution of *C. typicus* from data collected routinely by the CPR survey. *C. typicus* is by far the most abundant copepod species identified by the monitoring programme (Fig. 1). Its congeneric species *C. hamatus* is exclusively found over continental shelves although it is more abundant in

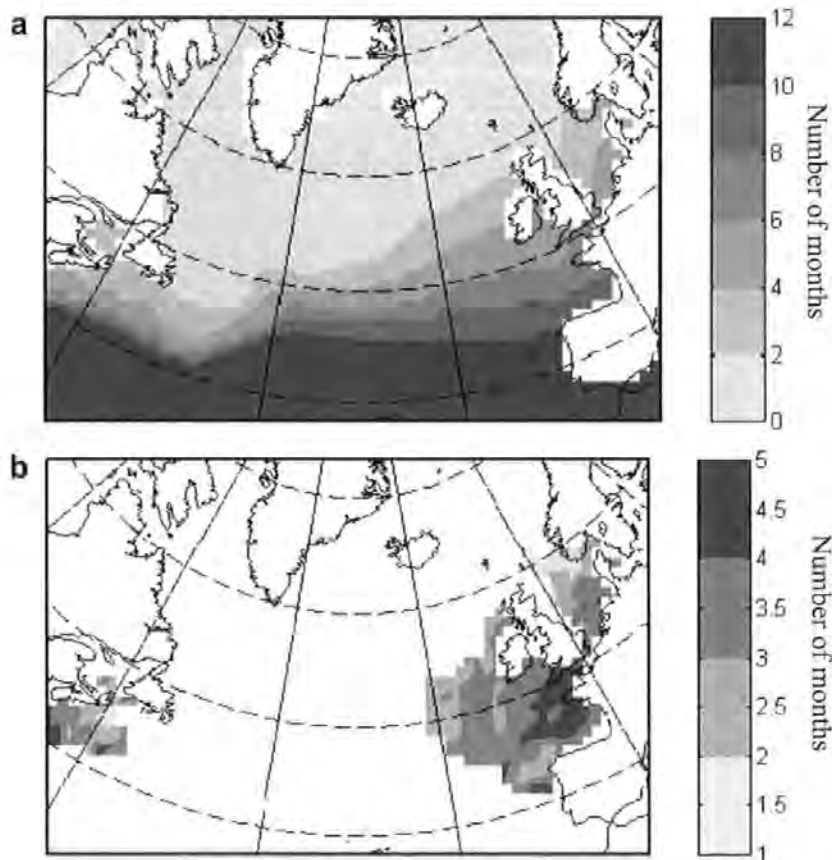


Fig. 7. The seasonal extent of *C. typicus* in relation to the number of months for which SST is $\geq 13^\circ\text{C}$. (a) Spatial changes in the number of months with SST $\geq 13^\circ\text{C}$. (b) Spatial change in the seasonal extent of *C. typicus*. Geographical squares with an annual abundance of *C. typicus* < 0.45 (in $\log_{10}(x+1)$) were removed from the analysis.

near-coastal regions (Fig. 1b). Other *Centropages* species are more rarely found in CPR samples (Fig. 1c) and are at the northern limits of their spatial distributions.

3.2. Spatial changes in the seasonal variability of *C. typicus*

A spatialised PCA was used to reveal the main seasonal cycle of *C. typicus* in the regions of the North Atlantic covered by the CPR survey. Two main patterns of variability were detected (Fig. 2). The first (63.97% of the total variance) was an increase starting during summer and ending in late autumn, especially

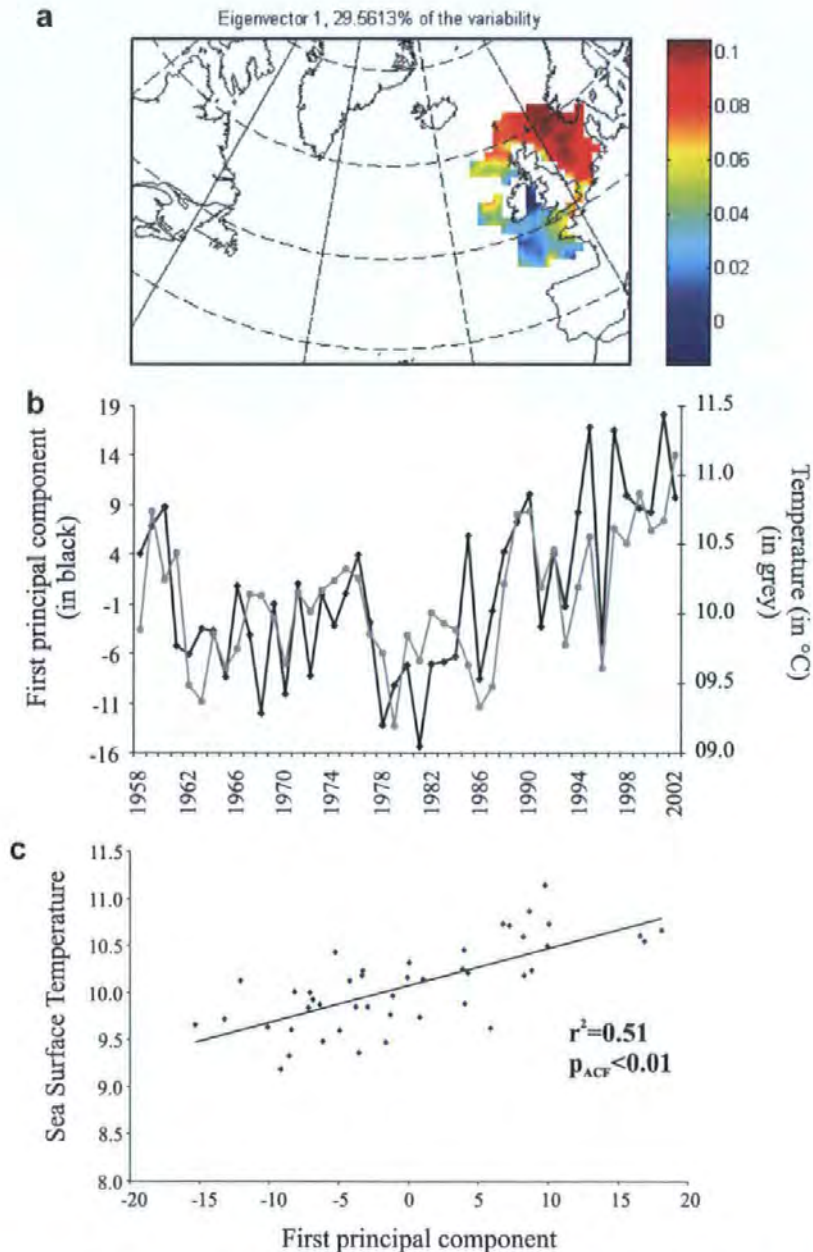


Fig. 8. Spatialised PCA applied at a year-to-year scale. (a) First eigenvector. (b) Long-term changes in the first principal component (in black) and sea surface temperature (in grey). (c) Scatterplot of temperature and the first principal component.

prevalent in regions above 50°N in the northeast Atlantic. The second (14.97% of the total variance), occurring in the western side of the Atlantic south of Nova Scotia, was characterised by a seasonal maximum in autumn and an abundance higher in winter than in the northeastern part of the Atlantic. The original matrix was reassessed using the first five eigenvectors and principal components to remove the unexplained variance (Fig. 3). The increase in abundance of *C. typicus* starts in May (?) in the south-west European basin, then spreads northwards along the European shelf-edge in June to August. In the meantime, the abundance of *C. typicus* spreads from neritic regions to oceanic regions. The increase in abundance starts in the North Sea in June but the seasonal maximum is found in August–September. On the western side of the Atlantic, the increase starts in August and the maximum is detected in October. This pattern is similar to the one observed in the North Sea, but the abundance remains high in early winter.

Temperature has an effect on the seasonal variability of *C. typicus* (Fig. 4). In the southern part of the studied area, a positive correlation between the abundance of this species and temperature is detected with and without a lag (Fig. 4), while to the north and in the western side of the Atlantic, a positive correlation is detected with a lag of one month (i.e. a change in temperature from one month to another is followed by a similar change in abundance the month after).

At first sight, this delay of one month could be explained by the time needed for this species to complete its life cycle, that is, about one month latter in the north (and in the western side of the Atlantic) than in the south (Fig. 5). Fig. 6 indeed indicates that there is a relationship between the first months with an SST >12 °C (Fig. 6a) and the month characterised by the strongest increase in the abundance of *C. typicus*. However, a close examination indicates that the delay of about one month between the south and the north is not related to the influence of temperature on development time. Temperature is warmer in the North Sea (and western side of the Atlantic) than in the south-west European basin at a time when there is the strongest increase in the abundance of *C. typicus* (Fig. 6c). Temperature is the lowest in the Celtic Sea where the annual abundance of this species is maximum. Therefore, development time based on temperature alone is quicker in the North Sea at the time the increase in abundance is maximum. This is apparently an unexpected result. When the phytoplankton colour (used here as an index of quantity of food) is plotted for months characterised by a substantial increase in abundance, it can be shown that food is generally high. This is especially true in the south-west European basin (including the Celtic Sea). So there is an advantage for this species to start the season at colder temperature. The quantity of food seems to be less important in the North Sea, but the amount of phytoplankton is elevated there in comparison to the south-west European basin.

The seasonal extent of *C. typicus* is also related positively to the number of months with SST > 13 °C (Fig. 7). The Pearson correlation coefficient is significant ($r_p = 0.44$; $p < 0.01$). However, no correction was applied to take spatial autocorrelation into account. The relationship explains a weak proportion of variance ($r^2 = 19\%$), so that other factors may also play a role such as the abundance or the quality of phytoplankton.

Long-term changes in the spatial distribution of *C. typicus* were investigated by spatialised PCA (Fig. 8). Only seas around the United Kingdom had enough data to enable the application of this numerical technique,

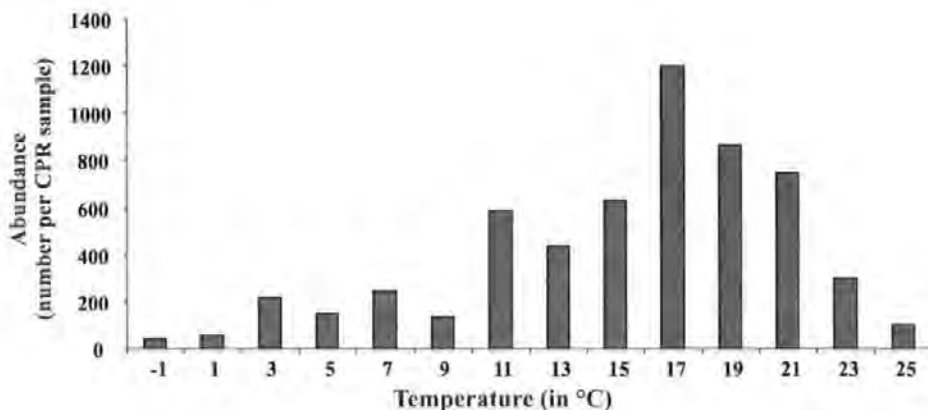


Fig. 9. Thermal preferendum of *Centropages typicus* as shown by CPR sampling.

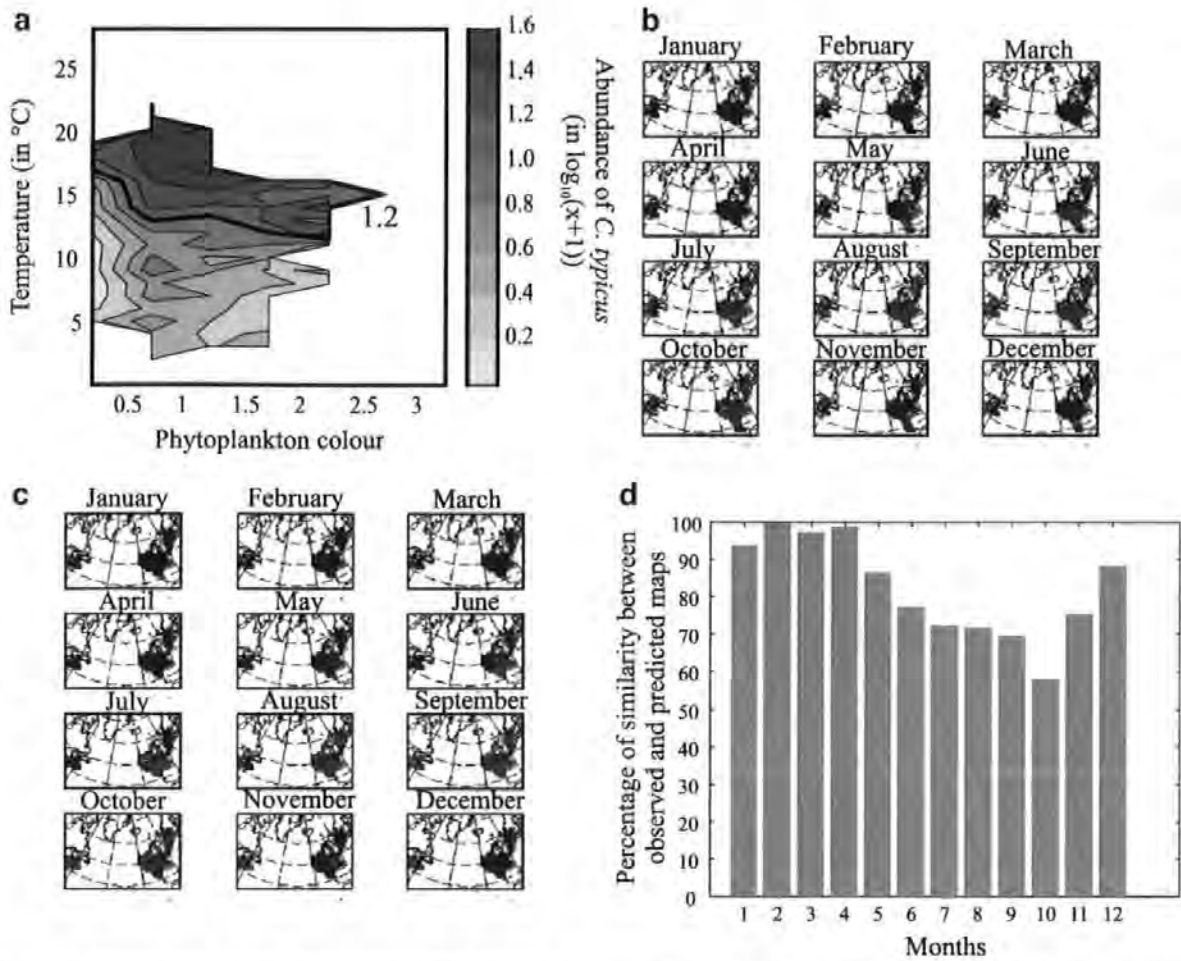


Fig. 10. (a) Environmental profile of *C. typicus* as a function of temperature and the CPR phytoplankton colour index. (b) Geographical squares with expected abundance of *C. typicus* superior to 1.2 (decimal logarithm). (c) Geographical squares with expected abundance of *C. typicus* > 1.2 (decimal logarithm). (d) Percentage of match between prediction and observation for each month.

The first eigenvector (29.56% of the total variance) shows high positive values mainly in the North Sea. The associated principal component shows a decrease until the end of the 1970s, and then an increase with clear indication of pseudo-cyclical variability (Fig. 8b). A highly significant relationship was found with sea surface temperature. About 50% of the variance in the first principal component was explained by SST (Fig. 8b and c). The thermal environmental window was characterised for *C. typicus* (Fig. 9). The analysis reveals a temperature optimum of about 17 °C.

4. Discussion and conclusions

We have characterized the macroecology of the species *C. typicus* in the North Atlantic Ocean as revealed by CPR sampling. This species occurs mainly over continental shelves and slopes, although it can also be detected in oceanic regions near continental slopes. The occurrence of this species in oceanic regions probably results from seasonal expatriation of individuals from populations living over the shelf-edge. Therefore, the spatial distribution of the species, as proposed by Rose (1933) and recently highlighted in Halsband-Lenk et al. (2002) (see their Fig. 1), can be refined for the northern part of the North Atlantic. Four main regions in the sector covered by the CPR survey can be distinguished on the basis of their seasonal variability (see Fig. 2 and 3). The southwest European basin: (1) is the region where the seasonal cycle of *C. typicus* is the

earliest (late winter-early spring). Then, the increase in abundance spreads to the Celtic Sea (2) at a time when the level of phytoplankton is high (see Fig. 7). In the North Sea (3), *C. typicus* is detected for all months of the year but has a seasonal maximum in late summer and early autumn. A similar result was found by Halsband and Hirche (2001) who investigated the seasonal variability of this species at Helgoland (southern North Sea). They identify the seasonal maximum in September–October. In the western side of the Atlantic south of Nova Scotia and Newfoundland (4), the seasonal maximum in the abundance of the species starts in autumn and remains high in early winter. In addition to this seasonal south to north movement, an inshore–offshore gradient from coast to offshore regions is also observed.

This study has revealed the impact of temperature on the seasonal variability of the species. A clear positive relationship between temperature and change in the abundance of *C. typicus* has been detected at both seasonal (Figs. 4 and 6) and year-to-year scales (Fig. 8). This has already been demonstrated at a large scale by Lindley and Reid (2002). Using CPR data in the North Sea, they identified a clear positive relationship between annual abundance of *C. typicus* and temperature. At a smaller scale, some studies also identified a close link between the reproduction cycle of the species and temperature (Halsband-Lenk et al., 2001, 2002). Parameters such as the total mortality of adult females after five days incubation, egg production rates, egg diameters and embryonic development time were all influenced by temperature (Halsband-Lenk et al., 2001, 2002). However, the present study also shows that temperature alone cannot explain all characteristics of the seasonal cycles of the species. The amount of food, investigated here by using the CPR phytoplankton colour index as a proxy for the quantity and quality of phytoplankton, also seems important. Bonnet and Carlotti (2001) have shown the influence of food on the reproduction cycle of the species. In the southwest European basin, the seasonal increase in abundance starts at a time when temperature is lower than in the North Sea. However, phytoplankton level is at its seasonal maximum (see Fig. 6). Phytoplankton level is less a limiting factor in the North Sea, and the increase in abundance occurs at a time when the level of phytoplankton is high but not the highest of the season (see Fig. 6). The strong increase in abundance occurs in late summer in the North Sea. SST is high at that time, which ensures rapid development. However, it is intriguing that the seasonal maximum in *C. typicus* occurs so late in the North Sea. If temperature alone is considered, a seasonal maximum in summer should be expected. The first hypothesis to explain the delay is related to interspecific competition of *C. typicus* with its congeneric species *C. hamatus*. The latter species has a seasonal maximum in summer and could limit the development of *C. typicus*. An alternative hypothesis can also be proposed. The spatial distribution of the species suggests that it occurs when and where food is abundant (coastal region, shelf-edge, early in spring in the southwest European basin). So this study and others in the literature (e.g. Bonnet and Carlotti, 2001) suggest that in addition to temperature, food is an important parameter. If we calculate the abundance of the species as a function of temperature and food, there is a clear environmental optimum. When we plot the geographical squares in which the abundance of *C. typicus* is expected to be above 1.2 (in decimal logarithm) from the knowledge of both temperature and phytoplankton colour index (Fig. 10c), the prediction fits well with what is observed (Fig. 10c and d). The overall match between the prediction and the observation is 82.41%. Therefore, the analysis suggests that both temperature and food are important seasonal characteristics for *C. typicus* in the North Atlantic Ocean.

Examination of the long-term changes in the abundance of *C. typicus* has revealed a strong relationship with temperature. However, the link may be direct but also indirect through the food web. Indeed, the long-term trends are also consistent with food supply being an important factor in the abundance of *C. typicus*. The downward trend in abundance until the end of the 1970s was part of a general pattern across trophic levels (Aebischer et al., 1990), as was the reversal of that trend, first noted by Colebrook (1984). The significance of food was emphasised by Lindley and Reid (2002) who proposed that a significant deviation in the early 1980s from the relationship between abundance and temperature was due to low phytoplankton levels in winter. At that time of year food is most likely to be a limiting factor for the pelagic population of *C. typicus* that can survive only for a few days without food (e.g. Dagg, 1977). Dormant eggs in sediments provide a potential buffer to short-term fluctuation in conditions. However in contrast with *C. hamatus*, which is known to produce diapausing eggs (Marcus, 1989; Marcus and Lutz, 1998), *C. typicus* has not been shown to do so, and only comparatively small number of nauplii of the latter have been hatched from sediments (Lindley et al., 1990; Lindley and Reid, 2002). The otherwise high correlation between interannual variations in abundance and temperature in the areas analysed here can be understood by the closeness of the maximum temperatures

in these areas to the optimum levels required by *C. typicus* (see Fig. 9). These results show that *C. typicus* does not answer only to temperature increase in the region but also to changes in phytoplankton abundance, composition and timing of occurrence. Methods such as the simple decision tree used in Fig. 10 can help to forecast expected changes in the distribution of this species with hydro-climatic forcing.

References

- Aebischer, N.J., Coulson, J.C., Colebrook, J.M., 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347, 753–755.
- Batten, S., Hirst, A., Hunter, J., Lampitt, R., 1999. Mesozooplankton biomass in the Celtic Sea: a first approach to comparing and combining CPR and LHP data. *J. Mar. Biol. Assoc. UK* 79, 179–181.
- Batten, S.D., Clark, R., Flinkman, J., Hays, G., John, E., John, A.W.G., Jonas, T., Lindley, J.A., Stevens, D.P., Walne, A., 2003. CPR sampling: the technical background, materials, and methods, consistency and comparability. *Prog. Oceanogr.* 58, 193–215.
- Beaugrand, G., Ibañez, F., Lindley, J.A., 2001. Geographical distribution and seasonal and diel changes of the diversity of calanoid copepods in the North Atlantic and North Sea. *Mar. Ecol. Prog. Ser.* 219, 205–219.
- Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., Edwards, M., 2002. Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692–1694.
- Beaugrand, G., Reid, P.C., Ibañez, F., Planque, P., 2000. Biodiversity of North Atlantic and North Sea calanoid copepods. *Mar. Ecol. Prog. Ser.* 204, 299–303.
- Bonnet, D., Carlotti, F., 2001. Development and egg production in *Centropages typicus* (Copepoda: Calanoida) fed different food types: a laboratory study. *Mar. Ecol. Prog. Ser.* 224, 133–148.
- Box, G.E.P., Jenkins, G.W., 1976. *Time Series Analysis: Forecasting and Control*. Holden-Day, San Francisco.
- Carlotti, C., Bonnet, D., Halsband-Lenk, C. Development and growth rates of *Centropages typicus*. *Prog. Oceanogr.*, this issue.
- Chatfield, C., 1996. *The Analysis of Time Series: An Introduction*. Chapman and Hall, London.
- Chelton, D.B., 1984. Commentary: short-term climatic variability in the northeast Pacific Ocean. In: Pearcy, W. (Ed.), *The Influence of Ocean Conditions on the Production of Salmonids in the North Pacific*. Oregon State University Press, Corvallis, pp. 87–99.
- Colebrook, J.M., 1984. Continuous plankton records: relationships between species of phytoplankton and zooplankton in the seasonal cycle. *Mar. Biol.* 83, 313–323.
- Dagg, M., 1977. Some effects of patchy food environments on copepods. *Limnol. Oceanogr.* 22, 99–107.
- Fragopoulou, N., Lykakis, J.J., 1990. Vertical distribution and nocturnal migration of zooplankton in relation to the development of the seasonal thermocline in Patraikos Gulf, Greece. *Mar. Biol.* 104, 381–388.
- Fromentin, J.-M., Planque, B., 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* 134, 111–118.
- Halsband, C., Hirche, H.-J., 2001. Reproductive cycles of dominant calanoid copepods in the North Sea. *Mar. Ecol. Prog. Ser.* 209, 219–229.
- Halsband-Lenk, C., Hirche, H.-J., Carlotti, F., 2002. Temperature impact on reproduction and development of congener copepod populations. *J. Exp. Mar. Biol. Ecol.* 271, 121–153.
- Halsband-Lenk, C., Nival, S., Carlotti, F., Hirche, H.-J., 2001. Seasonal cycles of egg production of two planktonic copepods, *Centropages typicus* and *Temora stylifera*, in the north-western Mediterranean Sea. *J. Plankton Res.* 23, 597–609.
- Hardy, A.C., 1939. Ecological investigations with the Continuous Plankton Recorder: object, plan, methods. *Hull Bull. Mar. Ecol.* 1, 1–57.
- Haury, L.R., McGowan, J.A., 1998. *Time-space Scales in Marine Biogeography*. Intergovernmental Oceanographic Commission, The Netherlands.
- Hays, G.C., 1995. Ontogenic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. *Limnol. Oceanogr.* 40, 1461–1465.
- Hays, G.C., Warner, A.J., 1993. Consistency of towing speed and sampling depth for the Continuous Plankton Recorder. *J. Mar. Biol. Assoc. UK* 73, 967–970.
- Helaouet, P., Beaugrand, G., 2007. Macroecological study of the ecological niche of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Mar. Ecol. Prog. Ser.*, in press.
- Irigoin, X., Conway, D.V.P., Harris, R.P., 2004. Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. *Mar. Ecol. Prog. Ser.* 267, 85–97.
- Jonas, T.D., Walne, A., Beaugrand, G., Gregory, L., Hays, G.C., 2004. The volume of water filtered by a CPR: the effect of ship speed. *J. Plankton Res.* 26, 1499–1506.
- Lam, N.S.N., 1983. Spatial interpolation methods: a review. *Am. Cartogr.* 10, 129–149.
- Lindley, J.A., Batten, S.D., 2002. Long-term variability in the diversity of North Sea zooplankton. *J. Mar. Biol. Assoc. UK* 82, 31–40.
- Lindley, J.A., Reid, P.C., 2002. Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Mar. Biol.* 141, 153–165.
- Lindley, J.A., Roskell, J., Warner, A.J., Halliday, N.C., Hunt, H.G., John, A.W.G., Jonas, T.D., 1990. Doliolids in the German Bight in 1989: evidence for exceptional inflow into the North Sea. *J. Mar. Biol. Assoc. UK* 70, 679–682.
- Lindley, J.A., Williams, R., 1980. Plankton of the Fladen Ground during FLEX 76 II. Population dynamics and production of *Thysanoessa inermis* (Crustacea: Euphausiacea). *Mar. Biol.* 57, 79–86.

- Marcus, N.H., 1989. Abundance in sediments and hatching requirements of eggs of *Centropages hamatus* (Copepoda: Calanoida) from the Alligator Harbor region, Florida. *Biol. Bull.* 176, 142–146.
- Marcus, N.H., Lutz, R.V., 1998. Longevity of subitaneous and diapause eggs of *Centropages hamatus* (Copepoda: Calanoida) from the northern Gulf of Mexico. *Mar. Biol.* 131, 249–257.
- Planque, B., 1996. Spatial and temporal fluctuations in *Calanus* populations sampled by the Continuous Plankton Recorder, Pierre et Marie Curie, Paris VI, pp. 131.
- Planque, B., Ibañez, F., 1997. Long-term time series in *Calanus finmarchicus* abundance – a question of space? *Oceanol. Acta* 20, 159–164.
- Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C., Kaplan, A., 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the nineteenth century. *J. Geophys. Res.* 108 (D14), 4407. doi:10.1029/2002JD00267.
- Reid, P.C., Colebrook, J.M., Matthews, J.B.L., Aiken, J., Barnard, R., Batten, S.D., Beaugrand, G., Buckland, C., Edwards, M., Finlayson, J., Gregory, L., Halliday, N., John, A.W.G., Johns, D., Johnson, A.D., Jonas, T., Lindley, J.A., Nyman, J., Pritchard, P., Richardson, A.J., Saxby, R.E., Sidey, J., Smith, M.A., Stevens, D.P., Tranter, P., Walne, A., Wootton, M., Wotton, C.O.M., Wright, J.C., 2003. The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. *Prog. Oceanogr.* 58, 117–173.
- Rose, M., 1933. Copépodes pélagiques. Librairie de la faculté des sciences, Paris.
- Sars, G.O., 1903. An Account of the Crustacea of Norway. In: *Copepoda Calanoida*, vol. 4. The Bergen Museum, Bergen, pp. 203.
- The CPR Survey Team, 2004. Continuous Plankton Records: Plankton Atlas of the North Atlantic Ocean (1958–1999). II. Biogeographical charts. In: Beaugrand, G., Edwards, M., Jones, A., Stevens, D. (Eds.), *Continuous Plankton Records: Plankton Atlas of the North Atlantic Ocean (1958–1999)*. *Mar. Ecol. Prog. Ser.*, Luhe, pp. 11–75.
- Visser, A.W., Saito, H., Saiz, E., Kjørboe, T., 2001. Observations of copepod feeding and vertical distribution under natural turbulent conditions in the North Sea. *Mar. Biol.* 138, 1011–1019.
- Warner, A.J., Hays, G.C., 1994. Sampling by the continuous plankton recorder survey. *Prog. Oceanogr.* 34, 237–256.
- Williams, R., Lindley, J.A., 1980. Plankton of the Fladen Ground during FLEX 76 I. Spring development of the plankton community. *Mar. Biol.* 57, 73–78.

Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas

Pierre Helaouët^{1,2,*}, Grégory Beaugrand¹

¹Centre National de la Recherche Scientifique (CNRS), FRE 2816 ELICO, Station Marine, BP 80, 62930 Wimereux, France

²Present address: Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

ABSTRACT: Global climate change is expected to modify the spatial distribution of marine organisms. However, projections of future changes should be based on robust information on the ecological niche of species. This paper presents a macroecological study of the environmental tolerance and ecological niche (*sensu* Hutchinson 1957, i.e. the field of tolerance of a species to the principal factors of its environment) of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. Biological data were collected by the Continuous Plankton Recorder (CPR) Survey, which samples plankton in the North Atlantic and adjacent seas at a standard depth of 7 m. Eleven parameters were chosen including bathymetry, temperature, salinity, nutrients, mixed-layer depth and an index of turbulence compiled from wind data and chlorophyll *a* concentrations (used herein as an index of available food). The environmental window and the optimum level were determined for both species and for each abiotic factor and chlorophyll concentration. The most important parameters that influenced abundance and spatial distribution were temperature and its correlates such as oxygen and nutrients. Bathymetry and other water-column-related parameters also played an important role. The ecological niche of *C. finmarchicus* was larger than that of *C. helgolandicus* and both niches were significantly separated. Our results have important implications in the context of global climate change. As temperature (and to some extent stratification) is predicted to continue to rise in the North Atlantic sector, changes in the spatial distribution of these 2 *Calanus* species can be expected. Application of this approach to the 1980s North Sea regime shift provides evidence that changes in sea temperature alone could have triggered the substantial and rapid changes identified in the dynamic regimes of these ecosystems. *C. finmarchicus* appears to be a good indicator of the Atlantic Polar Biome (mainly the Atlantic Subarctic and Arctic provinces) while *C. helgolandicus* is an indicator of more temperate waters (Atlantic Westerly Winds Biome) in regions characterised by more pronounced spatial changes in bathymetry.

KEY WORDS: Macroecological approach · Hutchinson ecological niche · Biogeography · *Calanus finmarchicus* · *Calanus helgolandicus* · North Atlantic Ocean · Continuous Plankton Recorder

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Understanding the consequences of variability in climate on pelagic ecosystems requires a clear identification of the factors driving variability in the abundance of each species and the parameters or processes that control their geographical distribution. Biogeographical studies are essential and provide a baseline for

evaluation of the impact of climate on ecosystems (Longhurst 1998, Beaugrand 2003).

The high nutrient supply in the temperate and sub-polar part of the North Atlantic Ocean results in high planktonic production (Ducklow & Harris 1993, Longhurst 1998). This region is influenced by the North Atlantic Current which transfers energy and heat from the SW oceanic region of Newfoundland to the NE

*Email: pierrehelaouet@hotmail.com

part of the North Atlantic Ocean (Krauss 1986). This current also has a profound impact on plankton diversity (Beaugrand et al. 2001). The North Atlantic Ocean is divided into 3 biomes: the Atlantic Polar Biome, the Atlantic Westerly Winds Biome and the Atlantic Coastal Biome, each divided into a number of provinces (present Fig. 1; Longhurst 1998). Their ecological characteristics have been recently reviewed by Longhurst (1998) and some complementary descriptions have been added by Beaugrand et al. (2001, 2002) for the northern part of the North Atlantic Ocean and its adjacent seas.

Copepods constitute a key trophic group, with a central role in the trophodynamics of pelagic ecosystems. These plankton organisms transfer energy from the phytoplankton to higher trophic levels (Mauchline 1998) and are often important in the diet of at least 1 developmental stage of economically important fish species such as cod, herring or mackerel (Sundby 2000, Orlova et al. 2005, Skreslet et al. 2005). Copepods represent a high proportion of the carbon biomass in the mesozooplankton, generally increasing with increasing latitude (e.g. 33% for the Atlantic Trade Wind Biome, 53% for the Atlantic Westerly Winds Biome and 69% for the Arctic Ocean, Longhurst 1998). Members of the genus *Calanus* are amongst the largest copepods and can comprise as much as 90% of the dry weight of the mesozooplankton in regions such as the North Sea and the Celtic Sea (Bonnet et al. 2005 and references therein). The congeneric calanoid copepod species *C. finmarchicus* and *C. helgolandicus*

have been well studied (e.g. Planque & Fromentin 1996, Bonnet et al. 2005). They are morphologically so similar that they were not distinguished until 1958, in the Continuous Plankton Recorder (CPR) survey (Planque & Fromentin 1996). However, their spatial distribution differs significantly (Beaugrand 2004a). *C. finmarchicus* is mainly located in the Atlantic Polar Biome north of the Oceanic Polar Front (Dietrich 1964, Beaugrand 2004a; present Fig. 1) while the pseudo-oceanic species *C. helgolandicus* occurs in more temperate waters south of the Oceanic Polar Front, mostly located above the European shelf-edge in the Atlantic between 40 and 60° N (Beaugrand 2004a, Bonnet et al. 2005). In regions where they occur together (e.g. the North Sea), the 2 species generally have different seasonal timing (Beaugrand 2003). Some studies have also reported different depth of occurrence at the same location (Bonnet et al. 2005 and references therein).

Differences in the spatial and/or temporal patterns of variability in both species of *Calanus* suggest differential responses to environmental variability. It is therefore important to identify their environmental preference (window or tolerance interval) and their optimum environmental level. When the preference of more than 1 factor has been determined, the ecological niche (sensu Hutchinson 1957) can be calculated (i.e. the field of tolerance of a species to the principal factors characteristic of its environment). The niche can be represented in Euclidean space with as many dimensions as factors considered. When a few numbers of parameters are used, the niche of 2 species may overlap. Increasing the number of factors reduces the relative importance of such overlap and often enables complete niche separation (Gause's competitive exclusion hypothesis: Gause 1934). Abiotic parameters are related to both geographic (e.g. topography) and water-column (e.g. nutrient concentration) factors which influence directly the physiology (e.g. growth, development and mortality rates, Carlotti et al. 1993) or reproduction (Hall & Burns 2002, Halsband-Lenk et al. 2002) of a species. This study investigated abiotic environment and chlorophyll *a* concentration (as an index of available food), for which the Hutchinson ecological niche is a more suitable tool, often preferred in this type of work (e.g. Pulliam 2000, Guisan & Wilfried 2005).

Despite the large number of studies on the biology and ecology of both *Calanus finmarchicus* and *C. helgolandicus* (e.g. Carlotti et al. 1993, Hirst & Batten 1998, Heath et al. 1999, Bonnet et al. 2005), many gaps in our knowledge remain. Herein we employ a macroecological approach using large data sets of 11 abiotic parameters and data from the CPR survey to (1) determine the environmental optimum level of both species for each environmental parameter, (2) quantify the influ-

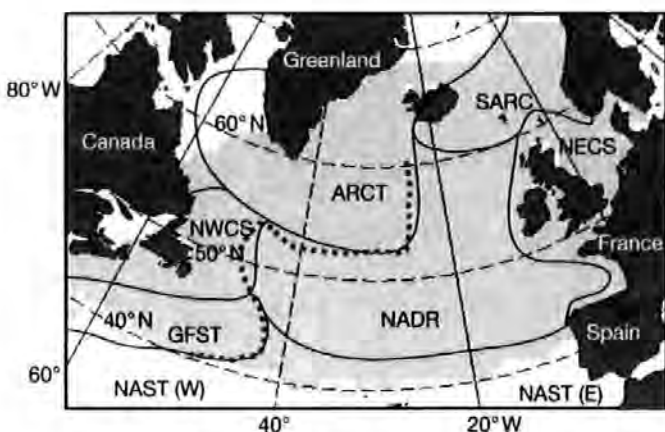


Fig. 1. Main area (light grey) sampled by the Continuous Plankton Recorder survey from 1960 to 2002, and provinces (Longhurst 1998). Atlantic Polar Biome—SARC: Atlantic subarctic province; ARCT: Atlantic arctic province. Atlantic Westerly Winds Biome—NADR: North Atlantic Drift province; NAST: North Atlantic subtropical gyral province (W and E: western and eastern parts, respectively); GFST: Gulf Stream province. Atlantic Coastal Biome—NECS: Northeast Atlantic shelves province; NWCS: Northwest Atlantic shelves province. Thick dotted line: Oceanic Polar Front

ence of each parameter on both species, (3) identify and (4) calculate the breadth of their ecological niches. The temporal stability of the temperature profiles of both species is also investigated. A baseline is provided for use in forecasting modifications in the abundance and spatial distributions of the 2 species that can be expected with global climate change.

MATERIALS AND METHODS

Biological data. Data on the abundance of *Calanus finmarchicus* and *C. helgolandicus* were provided by the CPR survey, a large-scale plankton monitoring programme initiated by Sir Alister Hardy in 1931. The CPR is a robust instrument designed for use by seamen on commercial ships. Management and maintenance of the survey have been carried out by the English laboratory (Sir Alister Hardy Foundation for Ocean Science [SAHFOS]) since 1990. CPR instruments are towed at a depth of 7 m (Reid et al. 2003a) and the survey has monitored plankton ecosystems at this depth only (Batten et al. 2003). Therefore, it might be dangerous to infer Hutchinson's ecological niche from a single depth. However, calanoid copepods migrate vertically (Daro 1985) and because CPR sampling is carried out both day and night, it is unlikely that this process greatly influenced the measurement of the Hutchinson ecological niche in this study.

Water enters the CPR through an inlet aperture of 1.61 cm² and passes through a 270 µm silk-covered filtering mesh (Batten et al. 2003). Individuals > 2 mm, such as Copepodite Stages CV and CVI of *Calanus finmarchicus* and *C. helgolandicus* are then removed from the filter and covering silk. Generally, all individuals are counted, but for particularly dense samples a sub sample is taken (Batten et al. 2003). The data used in this study correspond to Copepodite Stages CV and CVI. Studies have shown that near surface sampling provides a satisfactory representation of the epipelagic zone (Batten et al. 2003). This programme has accumulate one of the greatest databases on marine plankton worldwide. Currently, about 200 000 samples have been analysed, providing information on the presence and/or abundance of more than 400 plankton species every month since 1946 in both the temperate and sub-polar region of the North Atlantic Ocean.

Environmental data. We investigated the area from Longitude 99.5° W to 19.5° E and Latitude 29.5° to 69.5° N. Eleven parameters were chosen (Table 1). Sea surface temperature (SST) was essential as it has a well-documented effect on plankton (e.g. Reid & Edwards 2001). Wind-induced water turbulence was used as an indicator because it has been shown that wind, by its impact on water-column stability, affects

plankton populations (Heath et al. 1999). The index of turbulence and SST was acquired from the Comprehensive Ocean-Atmosphere Data Set (COADS) and was downloaded from the internet site of the National Oceanographic Data Center (NODC) (Woodruff et al. 1987), which manages acquisition, controls quality and safeguards the data.

Salinity also constitutes an important limiting factor for many species. Data on this parameter, and on silicates, phosphates, nitrates and dissolved oxygen were downloaded from the World Ocean Atlas 2001 (WOA1) database for a depth of 10 m.

Bathymetry was selected because it has been suggested that this parameter influences the distribution of some copepod species (Beaugrand et al. 2001). Bathymetry data originate from the database 'General Bathymetric Chart of the Oceans' (GEBCO). Spatial variability in bathymetry was assessed over the study area. First, the mean and SD of bathymetry data were calculated in a geographical cell of 1° latitude and 1° longitude, (225 data per geographical cell). Then, the coefficient of variation of bathymetry (CV_B) was calculated as:

$$CV_B = \frac{S_B}{m_B} \quad (1)$$

where m_B is the average and S_B the SD for bathymetry in each geographical cell. There was generally high variability in bathymetry over the continental slope regions.

Chlorophyll is a potentially influential parameter because the 2 selected species are mainly herbivorous (Mauchline 1998). However as Kleppel (1993) showed and Mauchline (1998) stressed, the dietary requirements of copepods change from the first nauplii stage to the adult stage and are likely to vary at both diel and seasonal scales. Furthermore, it is likely that both *Calanus* species also feed on microzooplankton (Mauchline 1998). Therefore, chlorophyll content should only be considered as an index of food availability. Chlorophyll values originated from the programme 'Sea-viewing Wide Field-of-view Sensor' (SeaWiFS) from the National Aeronautics and Space Administration (NASA).

The mixed-layer depth (MLD) is another indicator of water column stability. In contrast to the index of turbulence, this parameter is obtained from vertical profiles of temperature and salinity. MLD data come from a compilation of about 4.5 million profiles gathered by the NODC and World Ocean Circulation Experiment (WOCE). These profiles are the result of the analysis of data from 1941 to 2002 and originate from various measuring instruments such as the conductivity-temperature-depth (CTD) monitor, mechanical bathythermograph (MBT) or expendable bathythermograph (XBT).

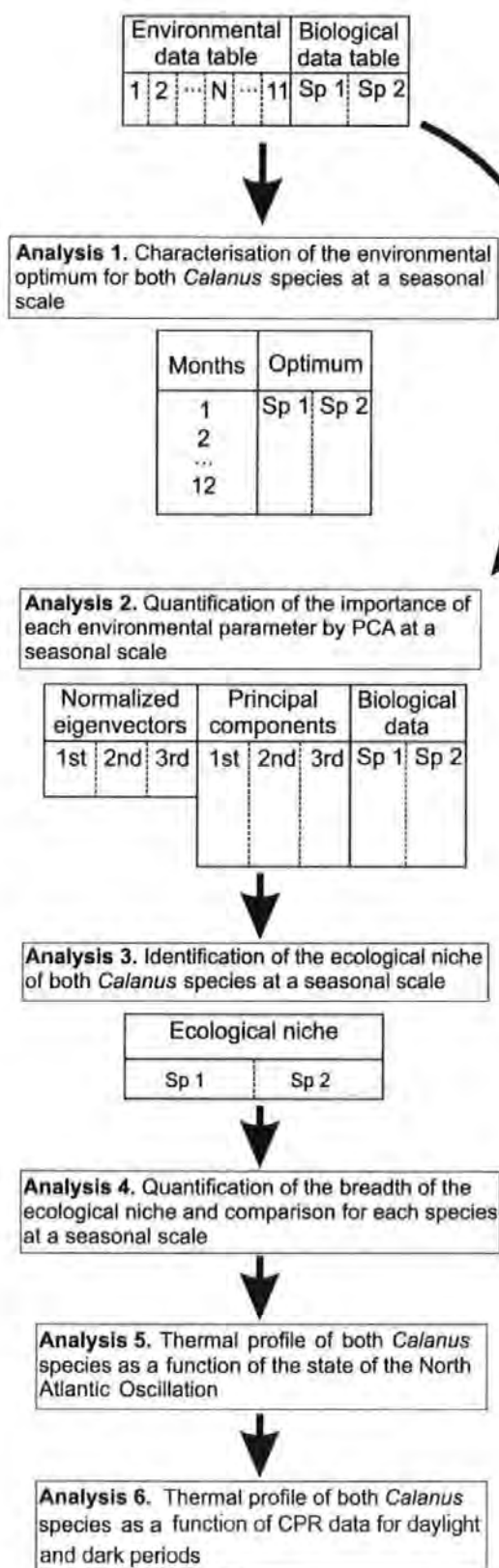
Table 1. Origin and characteristics of environmental data used in this study.

Data	Units	Spatial resolution	Type	N (× 10 ⁶)	Source
Biotic	Individual number	(no grid)	Each month for 1946–2002	0.2 per species	Sir Alister Hardy Foundation for Ocean Science
Sea surface temperature	°C	260.5° to 29.5° E 69.5° to 30.5° N (each 1°)	Monthly mean 1960–2002	33.5	National Oceanographic Data Center (COADS)
Wind-induced turbulence index	m ³ s ⁻³	260.5° to 29.5° E 69.5° to 30.5° N (each 1°)	Monthly mean 1960–2002	33.5	National Oceanographic Data Center (COADS)
Salinity		99.5° W to 19.5° E 89.5° to 10.5° N (each 1°)	Monthly mean (climatology)	2.8	World Ocean Atlas (2001)
Silicate	μmol l ⁻¹	99.5° W to 19.5° E 89.5° to 10.5° N (each 1°)	Monthly mean (climatology)	2.8	World Ocean Atlas (2001)
Phosphate	μmol l ⁻¹	99.5° W to 19.5° E 89.5° N to 10.5° N (each 1°)	Monthly mean (climatology)	2.8	World Ocean Atlas (2001)
Nitrate	μmol l ⁻¹	99.5° W to 19.5° E 89.5° to 10.5° N (each 1°)	Monthly mean (climatology)	2.8	World Ocean Atlas (2001)
Dissolved oxygen	ml l ⁻¹	99.5° W to 19.5° E 89.5° to 10.5° N (each 1°)	Monthly mean (climatology)	2.8	World Ocean Atlas (2001)
Bathymetry	m	80° W to 20° E 90° to 10° N each 0.4°	Monthly mean (climatology)	27.4	General Bathymetric Chart of the Oceans
Spatial variability in the bathymetry	m	99.5° W to 19.5° E 69.5° to 29.5° N (each 1°)	Monthly mean (climatology)	0.058	General Bathymetric Chart of the Oceans
Chlorophyll <i>a</i>	mg m ⁻³	100° W to 30° E 70° to 40° N each 0.5°	Monthly mean 1997–2002	18.8	Sea-viewing Wide Field-of-view Sensor (SeaWiFS)
Mixed-layer depth	m	179.5° W to 179.5° E 89.5° N to 89.5° S (each 1°)	Monthly mean 1941–2002	0.8	World Ocean Circulation Experiment

Pre-processing of data. The first stage of the analysis consisted of homogenising both environmental and biological variables. All original data tables were converted into 3 types of matrix: (1) matrices (2.48 million data points) with data for each month and year for the period 1960 to 2002 (temperature, wind stress); (2) matrices (57 600 data points) with data for each month (nutrients, oxygen, chlorophyll, MLD) based on the average of time periods ranging from 5 to 43 yr; (3) matrices (4800 data points) with no information on time (bathymetry and its spatial variability). The 3 types of environmental grids were used to regularise biological data, and no spatial interpolation was made. An arithmetic mean was calculated when the number of data for a given location and time period was >1.

Statistical analyses. Fig. 2 summarises the different statistical analyses performed in this study.

Analysis 1—Characterisation of environmental optima at seasonal scale: The optimum of each species was identified for each environmental variable (a total of 22 environmental profiles: 2 species × 11 environmental parameters). A profile was a contour diagram of a matrix of 12 mo × n environmental categories. To determine the number of environmental categories, the minimum and maximum values were first calculated. Then, intervals were chosen by trial and error as a compromise between the resolution of the profile and the increasing number of missing data with increasing resolution. The profile matrix was assessed by averaging abundance data for each month and environmental category. Abundance data were log-trans-



formed ($\log_{10}[x+1]$) to limit the effect of extreme values.

Analysis 2—Quantification of importance of each environmental parameter at seasonal scale: A principal components analysis (PCA) was used to quantify the influence of each abiotic factor and chlorophyll concentration (used herein as an index of available food) on spatial and seasonal changes in *Calanus* spp. abundance at the scale of the North Atlantic Ocean (Fig. 2). An algorithm that took into consideration missing data was used to calculate the eigenvectors (Bouvier 1977). This method of ordination made possible a summary of multivariate information in a reduced number of dimensions, i.e. the principal components (Jolliffe 1986). The normalised eigenvectors allowed identification of the variables contributing most to the principal components. The PCA was calculated from (120 longitudes \times 40 latitudes \times 12 mo) \times 11 environmental variables. The spatial grid had a resolution of 1° longitude and 1° latitude. This table was centred and reduced prior to application of the analysis to remove any effect of scale between environmental variables.

Analysis 3—Identification of ecological niche at seasonal scale: To identify the ecological niche of both species, we used the first 3 principal components. The concept of ecological niche used in this study is that of Hutchinson (1957) which states that the niche is the field of tolerance of a species to the principal factors of its environment. The concept has been refined here by the recent improvements discussed by Frontier et al. (2004). In particular, our analysis takes into account that some factors are not independent but covary either positively or negatively. The use of principal components decreases the effect of multicollinearity in the data (Legendre & Legendre 1998). We repeated the procedure used in Analysis 1 to map the ecological niche of both *Calanus* species as a function of principal components (linear combination of environmental factors).

Analysis 4—Quantification and comparison of Hutchinson's niches: Quantification and comparison of Hutchinson's niche for both *Calanus* species were performed for 4 different categories of abundance. The first category was based on all presence data: the value of the 11 environmental variables was retained when an individual (*C. finmarchicus* or *C. helgolandicus*) was recorded in a geographical cell within the environmental grid of 1 \times 1° (Longitude 99.5° W to 19.5° E, Latitude 29.5° N to 69.5° N); a total of 24 subsets was determined (12 mo \times 2 species). A similar procedure was applied to the other 3 categories. The second category comprised *Calanus* spp. data greater than the first quartile, the third category *Calanus* spp. data greater than the median and the fourth category data for *Calanus* spp. greater than the third quartile. The breadth of the niche thereby decreased from Category 1 to Category 4. The

Fig. 2. *Calanus finmarchicus* and *C. helgolandicus*. Summary of statistical analyses performed in this study. PCA: principal component analysis; CPR: Continuous Plankton Recorder

quartiles and median were assessed from the biological data table in Fig. 2. Therefore, the quantification and comparison of Hutchinson's niche for the 2 species used 96 (24×4) subsets.

To assess and compare Hutchinson's niche for the 2 *Calanus* species, we used a numerical analysis based on 'multiple response permutation procedures' (MRPP) and recently applied to determine the ecological niche by G. Beaugrand & P. Helaouët (unpubl. data). The method quantifies the breadth of the niche of the 2 species and tests if their niches are statistically different. First, quantification of the niche was made by calculating the mean Euclidean distance for each subset based on the 11 environmental parameters. The higher the mean Euclidean value, the greater Hutchinson's niche. Second, for a given month and category, a weighted mean of the Euclidean distance of both species niche was calculated. Then, the weighted distance was tested by permutations of original subset. A value of 10 000 permutations was selected. For each simulation, the weighted distance was recalculated and the probability that the separation of the niches of *C. finmarchicus* and *C. helgolandicus* would be significant was represented by the number of times the recalculated weighted distance was inferior to that observed.

Analysis 5—*Calanus* thermal profiles as a function of state of North Atlantic Oscillation (NAO) and 1987 regime shift: One important issue was to determine whether Hutchinson's niche was constant at a decadal scale and whether it was influenced by climate variability during the period of investigation (1958 to 2002). In the latter case, the species should be able to acclimatise quickly to climate change. To test this, we calculated the thermal profile of both species for negative NAO (NAO index < -1), medium NAO ($-1 \leq$ NAO index ≤ 1) and positive NAO (NAO index > 1). Thermal profiles were calculated according to a procedure identical to Analysis 1. To examine the potential impact of the regime shift in the North Sea (Beaugrand 2004b), thermal profiles were also assessed for years prior to and after 1987.

Analysis 6—*Calanus* thermal profiles as a function of CPR data for daylight and dark periods. Changes in the depth distribution of *Calanus* spp. through time could bias our assessment of Hutchinson's niche, as the CPR survey samples at a standard depth of about 7 m.

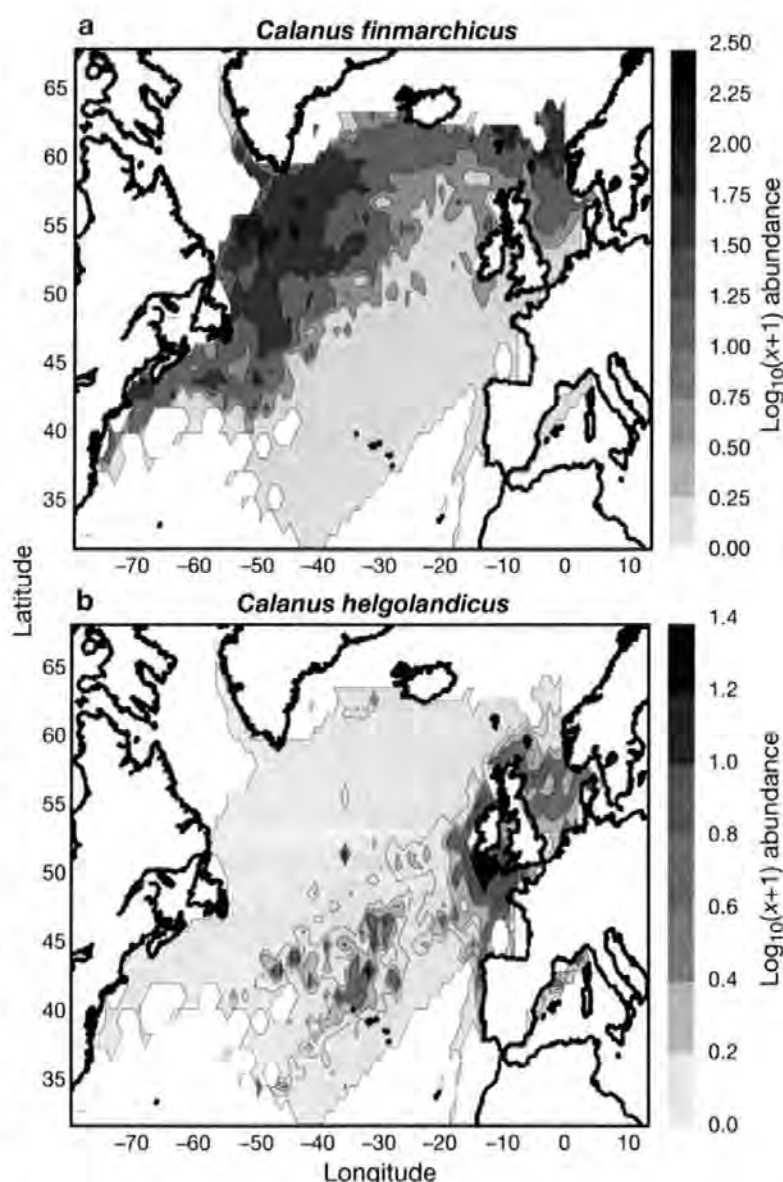


Fig. 3. (a) *Calanus finmarchicus* and (b) *C. helgolandicus*. Spatial distribution in North Atlantic Ocean. No interpolation made

To evaluate if this process could have significantly affected our results, we assessed the thermal profile (Analysis 1) of both species for CPR samples collected during daylight (CPR samples collected between 10:00 and 16:00 h) and dark (CPR samples collected between 22:00 and 04:00 h) (Beaugrand et al. 2001; their Fig. 1).

RESULTS

Spatial distribution of biological and environmental data

Fig. 3 shows the mean spatial distribution of *Calanus finmarchicus* and *C. helgolandicus* for the period 1958

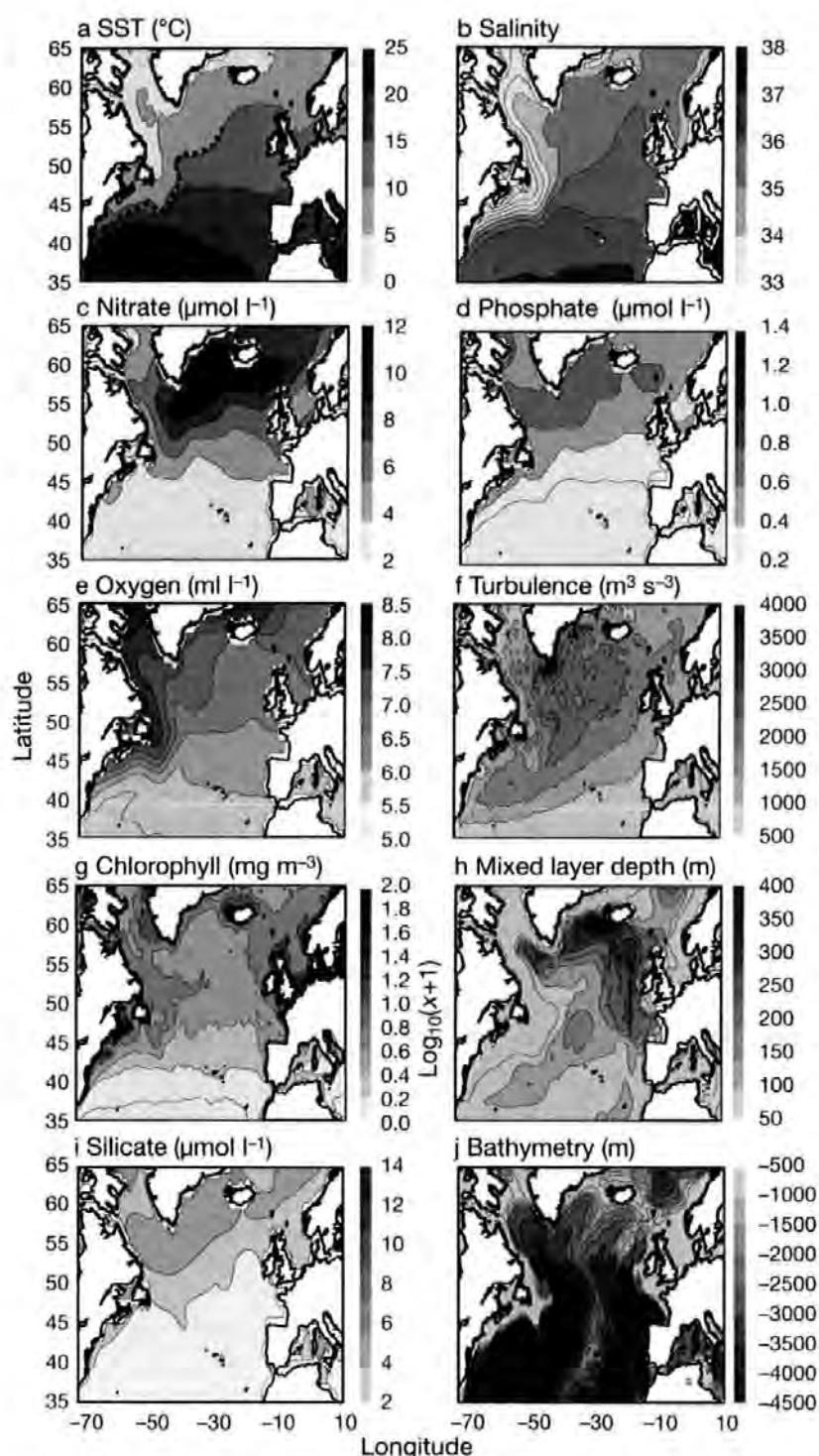


Fig. 4. Spatial distribution of (a) mean sea surface temperature (SST), (b) salinity, (c) nitrate, (d) phosphate, (e) dissolved oxygen, (f) turbulence, (g) chlorophyll *a*, (h) mixed-layer depth, (i) silicate, (j) bathymetry. Location of the Oceanic Polar Front is superimposed on (a) (thick dotted line)

to 2002. The spatial distribution of *C. finmarchicus* (Fig. 3a) was located north of the Oceanic Polar Front (Dietrich 1964) with 2 main centres of distribution south of the Labrador Sea and in oceanic regions south

and west of Norway (Fig. 3a). Fig. 3a suggests that this species is an indicator of the Atlantic Polar Biome and especially the Atlantic Arctic Province and the Atlantic Subarctic Province as defined by Longhurst (1998). The spatial distribution of *C. helgolandicus* differed (Fig. 3b), being mainly centred along the shelf-edge in temperate regions. Fig. 4 presents the mean values of the environmental parameters in the North Atlantic Ocean. Temperature is an important driving mechanism for *C. finmarchicus*, while it probably has a more limited role for *C. helgolandicus* (Fig. 4j).

Environmental profiles

Monthly thermal profile

Fig. 5 shows the thermal profile of *Calanus finmarchicus* (Fig. 5a) and of *C. helgolandicus* (Fig. 5b) for each month. *C. finmarchicus* had its maximal abundance between April and September at temperatures ranging from 6 to 10°C. *C. helgolandicus* had a tolerance range between 11 and 16°C, especially in spring (Fig. 5b). A remarkable feature was that the optimum varied seasonally for both species. Each species had a clear distinct thermal optimum. The tolerance interval for *C. finmarchicus* was greater than that of its congener. Fig. 5c shows the mean abundance of *C. finmarchicus* and *C. helgolandicus* as a function of temperature. The complementarity in the distribution of the 2 species is significant. The results show that a temperature change in a region with an annual thermal regime of about 10°C could trigger a shift from a system dominated by *C. finmarchicus* to a system dominated by *C. helgolandicus*.

Other profiles

Fig. 6 presents further environmental profiles. Salinity profiles separated the 2 *Calanus* species well (Fig. 6a). *C. finmarchicus* had its maximal abundance at salinities between 33.8 and 35 in the spring and summer months. The salinity optimum was higher for *C. helgolandicus* (35 to 35.5). Dis-

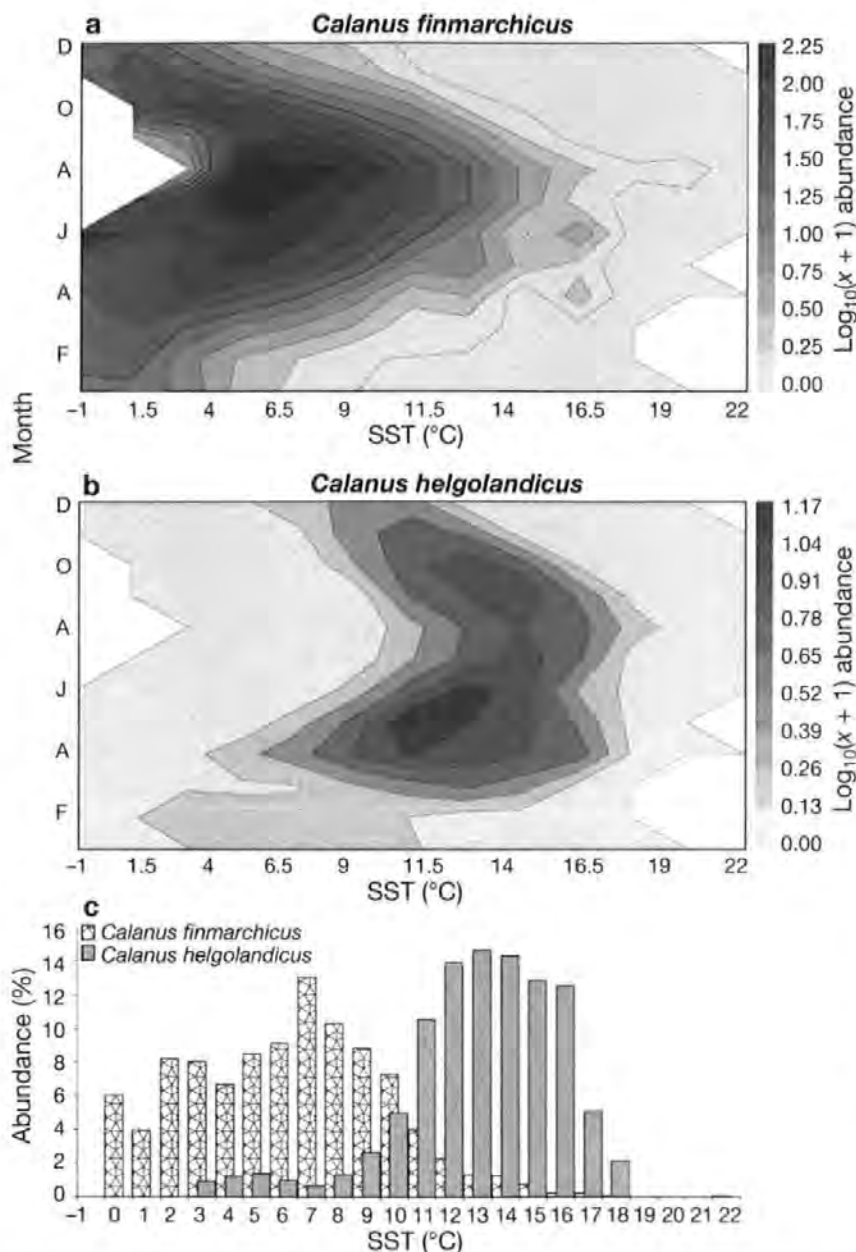


Fig. 5. *Calanus finmarchicus* and *C. helgolandicus*. (a,b) Contour diagram of abundance (decimal logarithm) as a function of SST and month of year, and (c) histogram showing percent relative average abundance as a function of SST

solved oxygen content also distinguished the 2 species (Fig. 6b). Abundance of *C. finmarchicus* was maximal at 6.4 to 7.3 ml l⁻¹, *C. helgolandicus* was found in water with less oxygen (5.9 to 6.6 ml l⁻¹). Chlorophyll *a* concentration did not completely separate the species (Fig. 6c). Nutrients were also examined. Fig. 6d shows an example of a profile for phosphate. Higher abundance of *C. finmarchicus* corresponded to phosphate concentrations between 0.2 and 0.8 μmol l⁻¹. For *C. helgolandicus*, the optimum was between 0.1 and 0.3 μmol l⁻¹. As in the case of salinity and temperature,

high abundance of *C. helgolandicus* was located in a more restricted tolerance range and time interval. Other nutrient profiles (nitrate and silicate; not shown) showed that *C. finmarchicus* occurred in waters containing more nutrients than its congener. *C. finmarchicus* was located in waters with a higher index of turbulence than *C. helgolandicus* (data not shown). Similar results were found for the mixed-layer depth (data not shown).

Calanus finmarchicus was mainly abundant at depths ranging from 269 to 3513 m, but can be found in regions of low bathymetry (Fig. 7a). The species was primarily found in regions with low to medium spatial variability in bathymetry. *C. helgolandicus* was more often found in regions characterised by a bathymetry between 82 and 1216 m, despite the fact that a second mode was detected at depths >4000 m (Fig. 7b). This last mode was probably related to expatriate individuals in the region near the Bay of Biscay (see Fig. 3b). The species was identified in regions characterised by a higher spatial variability in bathymetry, reinforcing its classification as pseudo-oceanic (i.e. occurring in both neritic and oceanic regions but is mainly abundant above the shelf-edge).

Quantification of factors influencing spatial distribution

A PCA was calculated for each variable from 4800 12-mo geographical squares × 11 variables.

The first axis explained 42.3% of the total variance, the second 20.8%, the third 9.5% and the fourth 7.2%. The calculation of equiprobability (*E*):

$$E = \left(\frac{1}{N} \right) \times 100$$

where *N* is the number of variables, indicated that all axes with a variance of more than 9.1% can be considered significant. Therefore, only the first 3 normalised eigenvectors and principal components (representing 72.6% of the total variance) were retained. Fig. 8 presents a scatterplot of the first 2 normalised eigenvectors

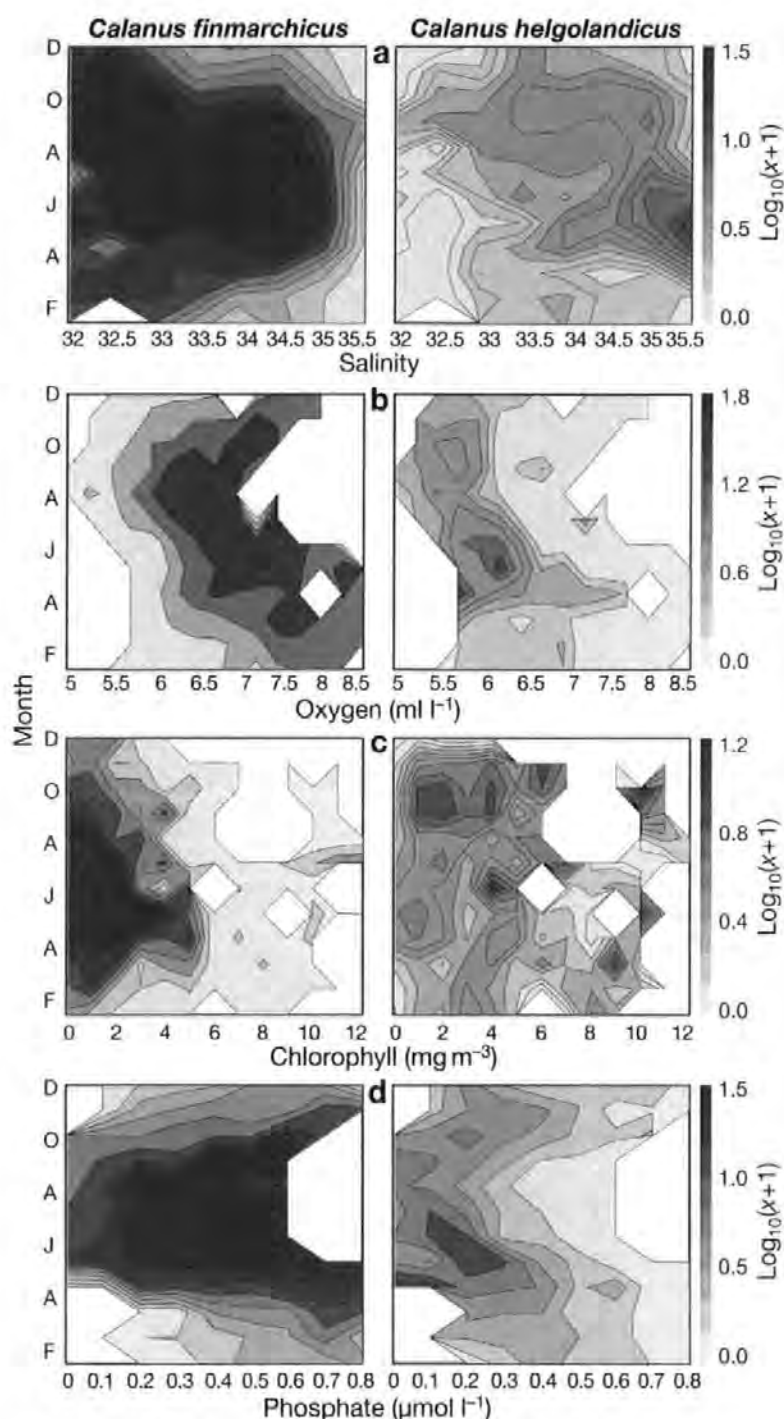


Fig. 6. *Calanus finmarchicus* and *C. helgolandicus*. Abundance (in decimal logarithm) as a function of month of year and of (a) salinity, (b) dissolved oxygen, (c) chlorophyll a, (d) phosphate

and maps of the first principal component. Variables such as temperature (relative contribution, RC = 82%); phosphate (RC = 75.1%), oxygen (RC = 73.8%), silicate (RC = 62.9%) and nitrate (RC = 54.7%) contributed greatly to the first component. Temperature was correlated negatively with the above factors (Fig. 8a). Map-

ping of the first principal component identified a northward change from March to August and then a reverse movement from September to December (Fig. 8b). The Oceanic Polar Front (Dietrich 1964) was clearly identified (for location see Fig. 1). An asymmetry in the seasonal changes of the physical-chemical parameters was detected. The northern limit of the western part of the Atlantic basin remained relatively constant at a monthly scale while in the eastern part the seasonal northward movement was much more pronounced. The influence of bathymetry on the first principal component was not detected.

Fig. 9 is a scatterplot of the second and third normalised eigenvectors and maps of the seasonal changes in the second principal component at a seasonal scale. Variables that contributed mostly to the second principal component were mixed-layer depth (RC = 51.1%), index of turbulence (RC = 43.7%) and, to a lesser extent, chlorophyll concentration (RC = 27.1%), the index of spatial variability in bathymetry (RC = 23.2%) and average bathymetry (RC = 22.9%). Mapping of seasonal changes in the second principal component (Fig. 9b) showed the importance of parameters related to water-column structure and the stable-biotope component (i.e. geographically stable, e.g. variables related to bathymetry). The effect of water-column structure was especially strong in the Atlantic Arctic Biome.

Fig. 10a shows that the main parameter related to the third principal component was primarily the index of spatial variability in bathymetry (RC = 42.4%) so that the third principal component (Fig 10b) directly highlighted the bathymetry of the region.

Identification of ecological niche

Using the first 3 principal components, a representation of the ecological niche (sensu Hutchinson 1957) is outlined in Fig. 11, which suggests that the ecological

niche of both *Calanus* species is well separated. The graphical was confirmed by the MRPP-based test, which indicated a statistically significant separation of the niche for each month and abundance category (Table 2). Quantification of the breadth of the niche further indicated that the niche breadth of *C. finmarchicus*

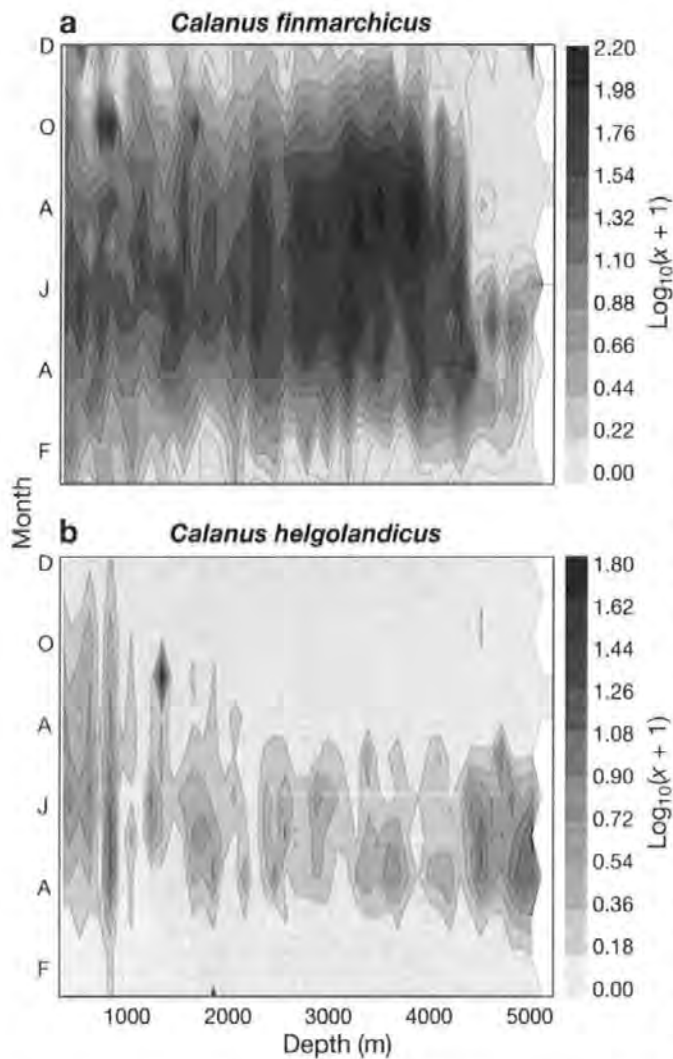


Fig. 7. (a) *Calanus finmarchicus* and (b) *C. helgolandicus*. Abundance (decimal logarithm) as a function of bathymetry and month of year

was overall larger (e.g. niche breadth index = 8.2 for January) than that of its congener (e.g. niche breadth index = 7.4 for January) when the estimation was based on presence data, whatever the month. When higher categories of abundance were considered, few exceptions were detected; these corresponded to the main seasonal maximum of the 2 species. These exceptions might be related to the positive relationship between dispersal and abundance of the 2 species.

Application of ecological niche approach to explain change in dominance

Temperature was the most important environmental parameter according to PCA results. This parameter separated the 2 species well. Fig. 12 shows changes in the proportion of *Calanus helgolandicus* as % of total *Calanus* (*C. finmarchicus* and *C. helgolandicus*) as a function of temperature. The location of the line below which 10% of *Calanus* identified by the CPR survey were *C. helgolandicus* varied monthly. Fig. 12 shows that a change in *Calanus* dominance (from 10 to 60% for *C. helgolandicus*) occurs when temperature increases by 1.5 to 3°C during the reproductive season. Superimposed on the contour diagram, the minimal and maximal temperatures in the North Sea for the period 1958 to 2002 demonstrate that this magnitude of temperature change did indeed occur. Fig. 12 explains by temperature alone (related to increase in atmospheric temperature, advection change or water mass location) the change in *Calanus* dominance that occurred in the North Sea during the regime shift (Reid et al. 2003b). Low temperatures were nearly exclusively observed prior to the shift, while higher temperatures (with the exception of the negative NAO year in 1996) were mainly observed after the shift (Beaugrand 2004b).

Table 2. Tests of comparison of breadth of *Calanus finmarchicus* (*C.fin*) and *Calanus helgolandicus* (*C.hel*). pδ: probability of separation of the 2 niches. For description of abundance categories 1 to 4 see 'Materials and methods'

Month	Category 1 (>0%)			Category 2 (>25%)			Category 3 (>50%)			Category 4 (>75%)		
	<i>C.fin</i>	<i>C.hel</i>	pδ	<i>C.fin</i>	<i>C.hel</i>	pδ	<i>C.fin</i>	<i>C.hel</i>	pδ	<i>C.fin</i>	<i>C.hel</i>	pδ
January	8.15	7.36	<0.01	8.11	7.01	<0.01	7.97	6.46	<0.01	6.88	6.64	<0.01
February	8.46	7.37	<0.01	8.39	7.21	<0.01	8.55	6.52	<0.01	7.14	5.94	<0.01
March	8.84	7.55	<0.01	8.95	7.19	<0.01	9.22	6.97	<0.01	8.97	6.57	<0.01
April	8.68	7.87	<0.01	8.32	7.44	<0.01	8.65	6.91	<0.01	8.55	6.66	<0.01
May	7.95	7.38	<0.01	7.42	6.93	<0.01	7.19	6.51	<0.01	7.46	5.92	<0.01
June	7.34	6.36	<0.01	7.12	6.01	<0.01	6.85	5.69	<0.01	6.82	5.26	<0.01
July	7.49	6.37	<0.01	7.12	5.92	<0.01	6.51	5.74	<0.01	5.83	5.17	<0.01
August	6.97	5.85	<0.01	6.44	5.92	<0.01	5.85	6.17	<0.01	5.14	5.93	<0.01
September	7.30	6.32	<0.01	6.71	6.08	<0.01	6.17	6.21	<0.01	5.47	6.05	<0.01
October	7.75	6.75	<0.01	7.65	6.68	<0.01	7.36	7.05	<0.01	7.61	6.66	<0.01
November	7.82	6.56	<0.01	8.09	6.48	<0.01	8.31	5.68	<0.01	8.45	5.19	<0.01
December	7.74	6.55	<0.01	7.75	6.62	<0.01	7.45	6.12	<0.01	6.42	5.52	<0.01

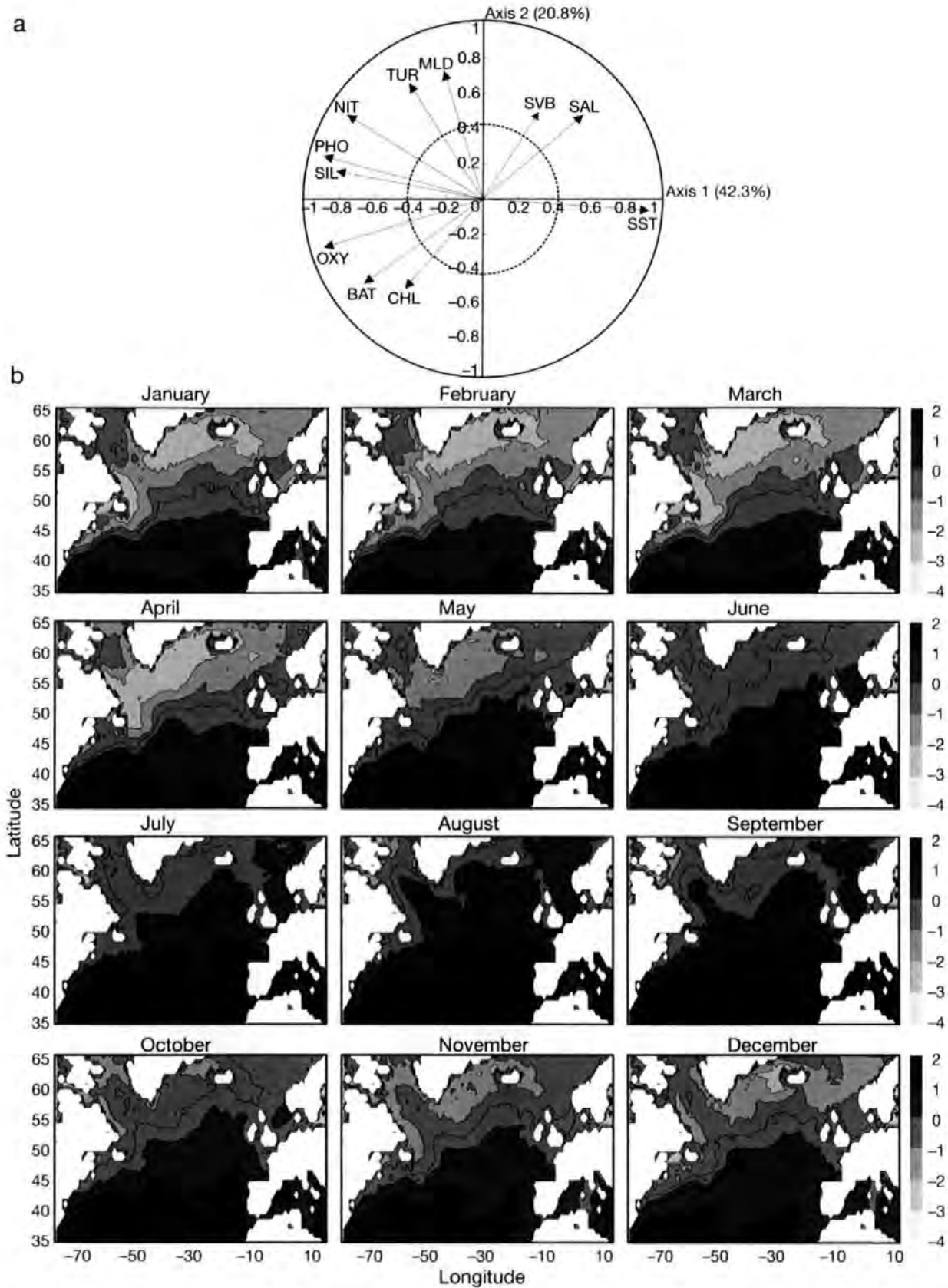


Fig. 8. Standardised principal component analysis of environmental data. (a) Normalised Eigenvectors 1 and 2 (63.1%); circles of correlation (solid) and of regime descriptor contribution (dashed, $C = 0.43$) also shown. BAT: bathymetry; CHL: chlorophyll *a*; MLD: mixed-layer depth; NIT: nitrate; OXY: oxygen; PHO: phosphate; SAL: salinity; SIL: silicate; SST: sea surface temperature; SVB: variation in bathymetry; TUR: turbulence rating. (b) Spatial and monthly changes in first principal component (42.3% of total variance)

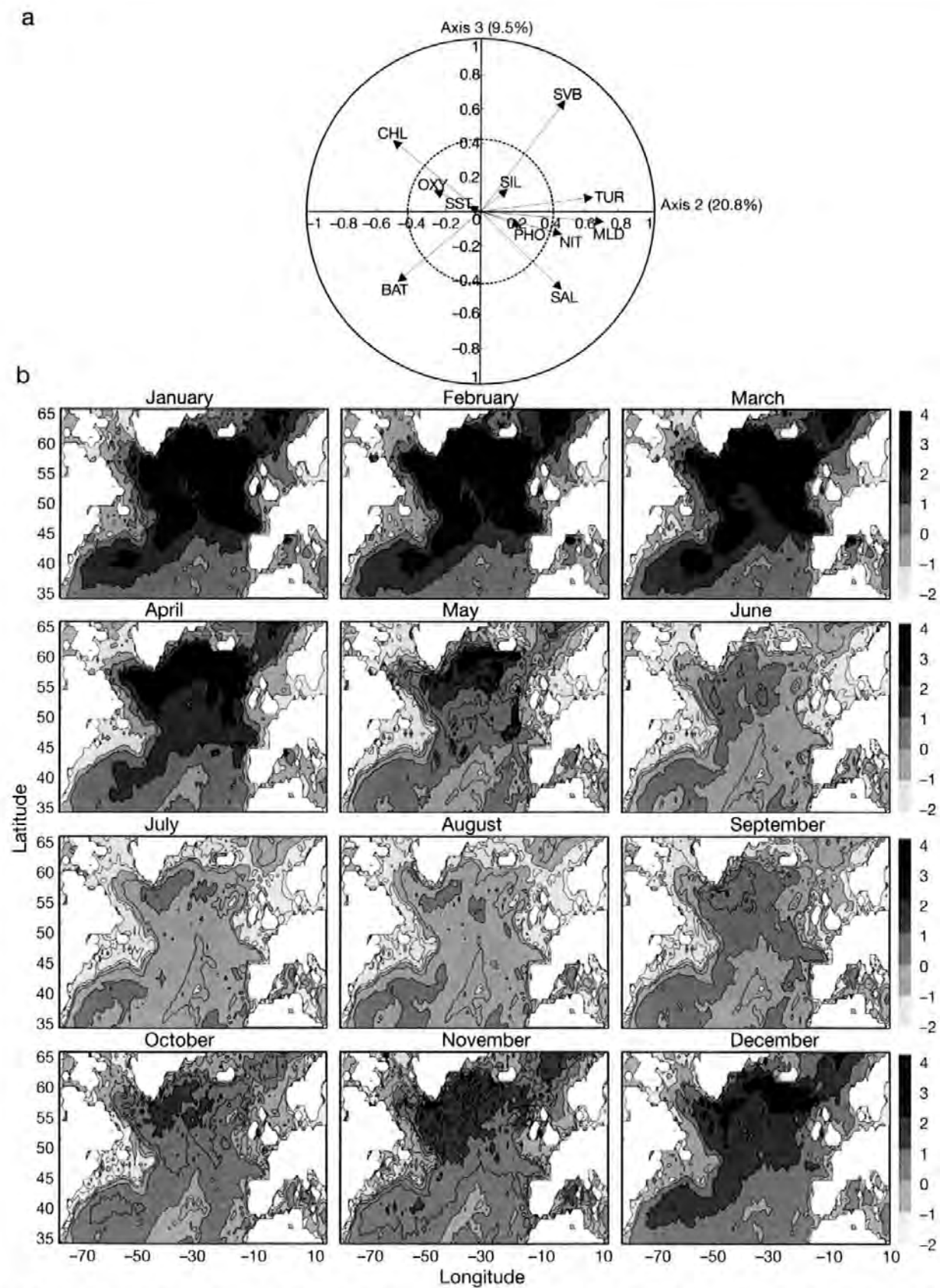


Fig. 9. Standardised principal component analysis of environmental data. (a) Normalised Eigenvectors 2 and 3 (30.3%); circles of correlation (solid) and of regime descriptor contribution (dashed, $C = 0.43$) also shown. BAT: bathymetry; CHL: chlorophyll; MLD: mixed-layer depth; NIT: nitrate; PHO: phosphate; SAL: salinity; SIL: silicate; SST: sea surface temperature; SVB: variation in bathymetry; TUR: turbulence rating. (b) Spatial and monthly changes in second principal component (20.8% of total variance)

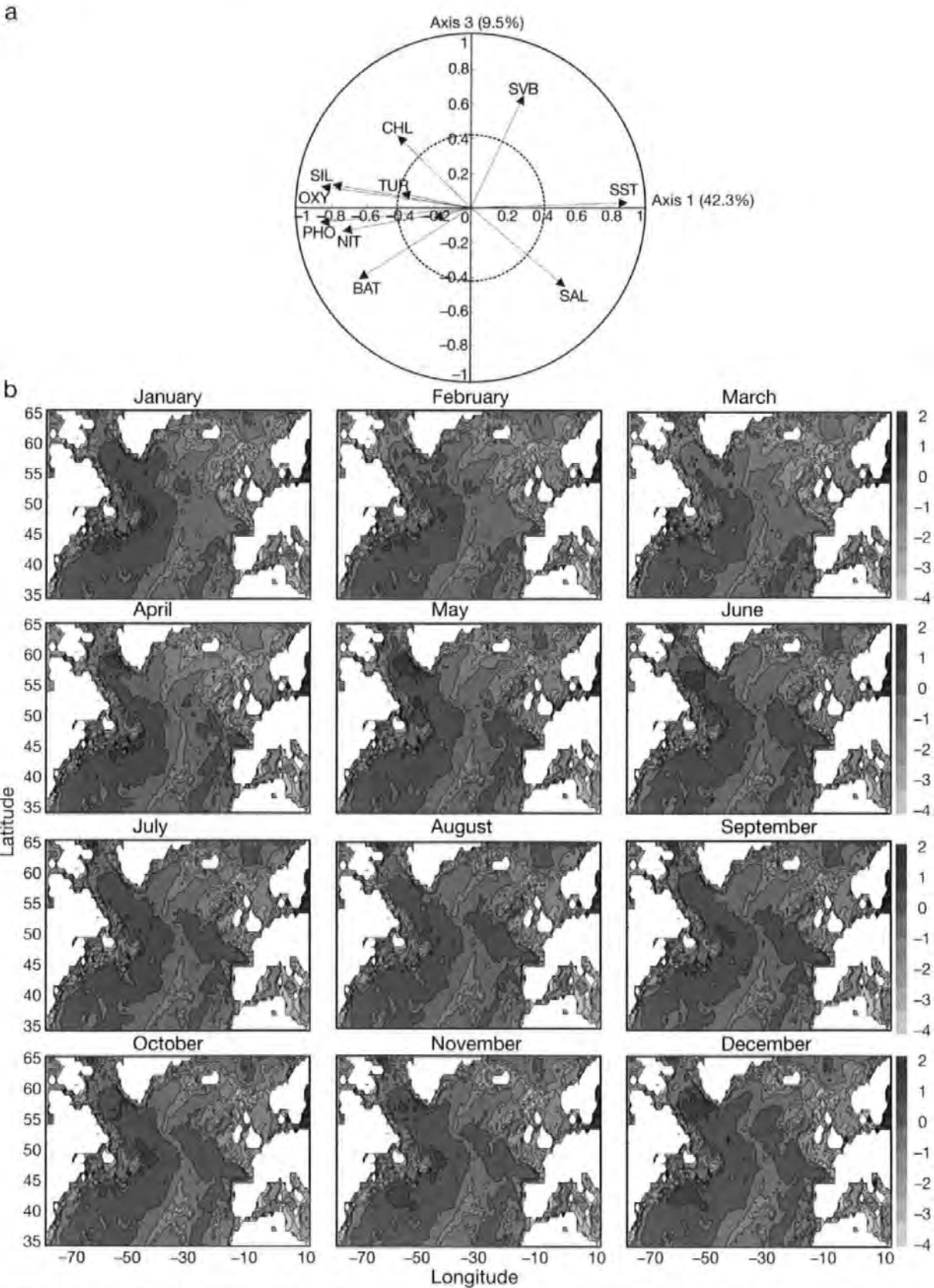


Fig. 10. Standardised principal component analysis of environmental data. (a) Normalised Eigenvectors 1 and 3 (51.8%); circles of correlation (solid) and of regime descriptor contribution (dashed, $C = 0.43$) also shown. BAT: bathymetry; CHL: chlorophyll; MLD: mixed-layer depth; NIT: nitrate; PHO: phosphate; SAL: salinity; SIL: silicate; SST: sea surface temperature; SVB: variation of bathymetry; TUR: turbulence rating. (b) Spatial and monthly changes in third principal component (9.5% of the total variance)

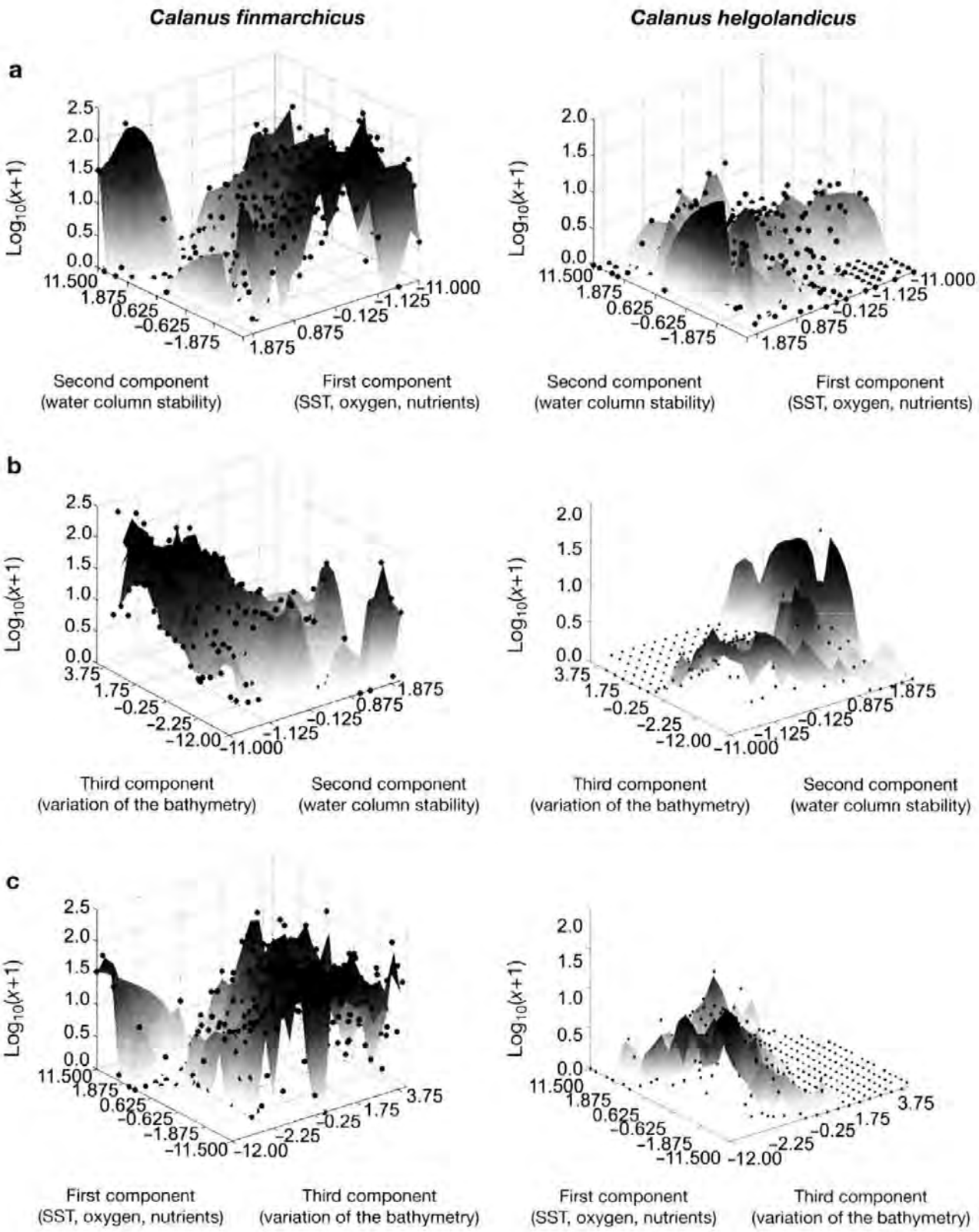


Fig. 11. *Calanus finmarchicus* and *C. helgolandicus*. Representation of the ecological niche (sensu Hutchinson 1957) using the first 3 principal components, showing abundance (indicated by shading) as a function of (a) first and second principal components (b) second and third principal components and (c) first and third principal components

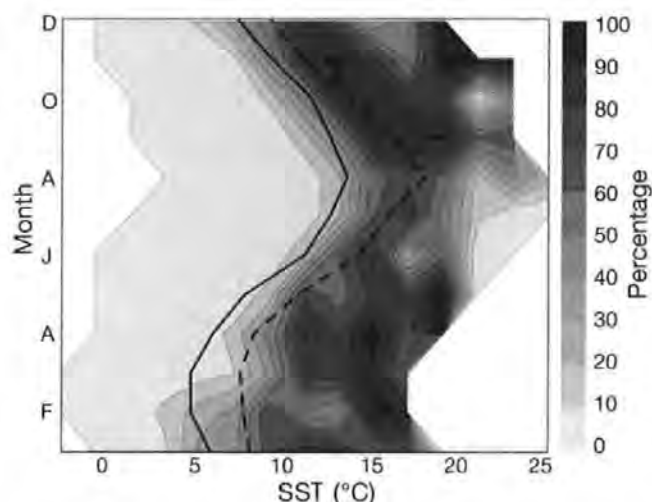


Fig. 12. *Calanus helgolandicus*. Percentage contribution to total *Calanus* (*C. finmarchicus* plus *C. helgolandicus*); minimum (solid line) and maximum (dashed line) monthly SSTs for North Sea are superimposed

Temporal stability of thermal tolerance range

Fig. 13 shows that the thermal niche of both *calanus* species changed regardless the state of the North Atlantic Oscillation ($r = 0.79$, $p < 0.01$, $n = 133$ for *C. finmarchicus*; $r = 0.77$, $p < 0.01$, $n = 128$ for *C. helgolandicus*). Beaugrand (2004b) stressed that the timing of the shift varied according to species, trophic levels and spatial centre of distribution of the individual organisms. However, the use of different time periods did not affect the results, since similar results were obtained for periods before and after the 1980s regime shift (Fig. 14) ($r = 0.88$, $p < 0.01$, $n = 135$ for *C. finmarchicus*; $r = 0.92$, $p < 0.01$, $n = 135$ for *C. helgolandicus*).

Fig. 15 shows the stability of the thermal niche of the 2 species at the diel scale. No significant change between the thermal niche between daylight and dark periods was identified ($r = 0.76$, $p < 0.01$, $n = 142$ for *Calanus finmarchicus*; $r = 0.94$, $p < 0.01$, $n = 142$ for *C. helgolandicus*). This analysis suggests that possible year-to-year changes in the depth distribution of the *Calanus* species is unlikely to have biased our assessment of Hutchinson's niche for the 2 species.

DISCUSSION

This study has shown that the (Hutchinson's) ecological niche of *Calanus finmarchicus* and that of *C. helgolandicus* are significantly separated despite the similar morphology of the species (Fleminger & Hulsemann 1977, Bucklin et al. 1995). The niche of *C. helgolandicus* is smaller than that of its congener with a few exceptions for higher abundance categories mainly when *C. helgolandicus* has its seasonal maximum in abundance. These exceptions are probably related to the positive relationships between abundance and dispersal in the pelagic realm (Beaugrand et al. 2001). Fig. 16 summarises the different environmental optima of both *Calanus* species in the present study. The subarctic species *C. finmarchicus* has a broader tolerance interval than its congener and is therefore able to support larger environmental variations (Fig. 16). This species is adapted to a cold oceanic environment, with high mixing during the winter and more nutrients, silicates, oxygen, and is therefore indicative of the Atlantic Arctic Biome and especially

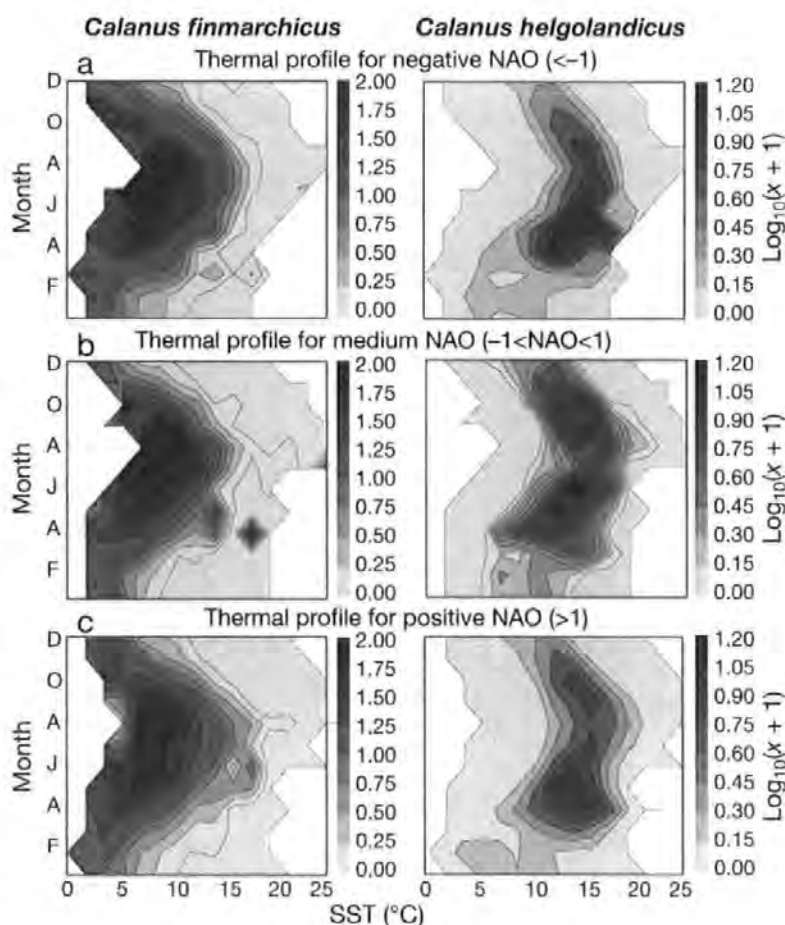


Fig. 13. *Calanus finmarchicus* and *C. helgolandicus*. Abundance (decimal logarithm) as a function of state of North Atlantic, using NAO index value of (a) <-1 , (b) $-1 < \text{NAO index} < 1$, and (c) >1

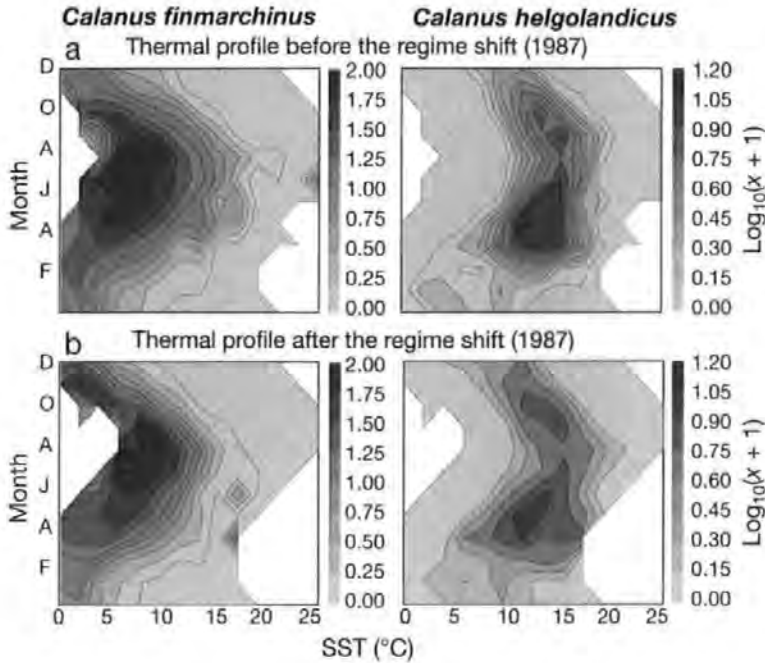


Fig. 14. *Calanus finmarchinus* and *C. helgolandicus*. Abundance (decimal logarithm) as a function of state of North Atlantic, for a period (a) before and (b) after 1980s regime shift

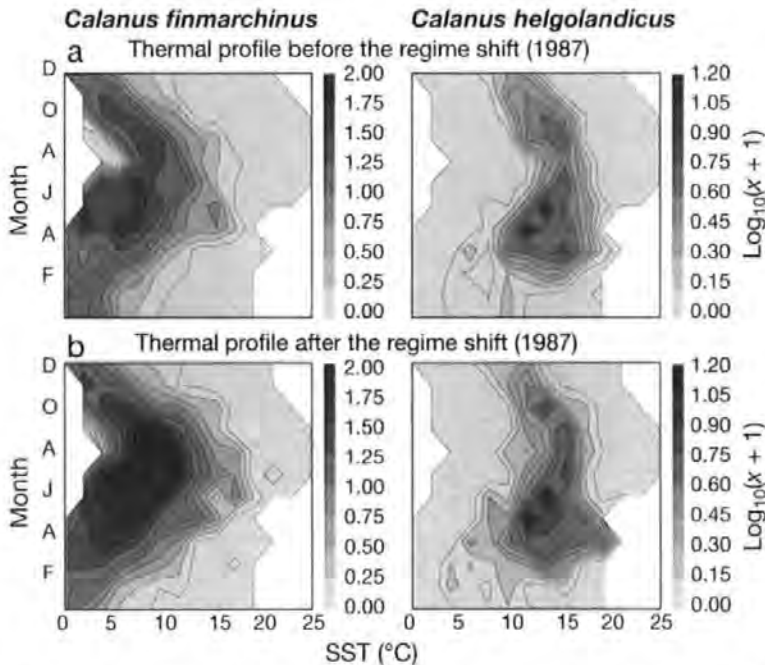


Fig. 15. *Calanus finmarchinus* and *C. helgolandicus*. Abundance (decimal logarithm) as a function of state of North Atlantic, for (a) daylight period (10:00 to 14:00 h) and (b) dark period (22:00 to 04:00 h)

the Atlantic Arctic and Subarctic provinces defined by Longhurst (1998) (see also present Fig. 1). Its congener *C. helgolandicus* is more adapted to the temperate waters in the Atlantic Westerly Winds Biome (Longhurst 1998), although it is mainly present along shelf-

edges (regions with higher spatial variation in bathymetry). Provinces of this biome have typically higher temperature and lower less of nutrients, silicates and oxygen (Longhurst 1998).

Temperature appears to be the factor that influences most of the spatial distribution of the 2 species. This parameter was highly correlated to the first principal component. A number of authors have highlighted the importance of this parameter for the physiology, the biological cycle and the ecology of copepods (Mauchline 1998, Halsband-Lenk et al. 2002, Lindley & Reid 2002). Beaugrand et al. (2001) have shown the close link between the spatial distribution in copepod diversity and temperature. Currie (1991) suggested that this parameter was the principal factor explaining the difference in diversity between the equator and the poles. Temperature influences growth, development and reproduction of many plankton species (Halsband-Lenk et al. 2002).

Temperature covaries negatively with nutrients and oxygen concentration so that a change in temperature is accompanied by a change in nutrient and oxygen concentration over the study area. These relationships hold true, because when temperature increases, biological production also increasing, thus consuming nutrients (Russel-Hunter 1970). Furthermore, when temperature increases, stratification is strengthened, limiting nutrient input from deeper waters (Beaugrand et al. 2001). The relationship between temperature and oxygen is related to the physical link between oxygen solubility and temperature (Millero et al. 2002). Therefore, we believe that the main driving mechanism is temperature and not its covariates, although it is possible that nutrients and oxygen also play a role, especially through food web interactions (Legendre & Rassoulzadegan 1995). Indeed, Legendre & Rassoulzadegan (1995) showed that by altering nutrient concentration, changes in phytoplankton composition can impact higher trophic levels.

The structure of the water column indicated by the wind-induced turbulence index and mixed-layer depth is also an important factor. It appears that *Calanus finmarchinus* is mainly located in oceanic regions with lower stratification than *C. helgolandicus*. The struc-























<i>Calanus finmarchicus</i>		<i>Calanus helgolandicus</i>
Lower values 	Temperature	 Higher values
6–10.6°C		11.4–16.1°C
Lower values 	Salinity	 Higher values
33.8–35		35–35.5
Higher values 	Oxygen dissolved	 Lower values
6.4–7.3 ml l ⁻¹		5.9–6.6 ml l ⁻¹
Higher values 	Phosphate	 Lower values
0.2–0.8 µmol l ⁻¹		0.1–0.3 µmol l ⁻¹
Higher values 	Nitrate	 Lower values
1.3–13.9 µmol l ⁻¹		0.1–4.2 µmol l ⁻¹
Higher values 	Silicate	 Lower values
1.1–6.8 µmol l ⁻¹		0.5–2.2 µmol l ⁻¹
Higher values 	Wind-induced turbulence	 Lower values
627.8–1482.4 m ³ s ⁻³		604.2–1135.9 m ³ s ⁻³
Higher values 	Mixed-layer depth	 Lower values
13.4–185.6 m		21.1–51.7 m
Higher values 	Bathymetry	 Lower values
3513–270 m		1217–82 m
Higher values 	Variation of bathymetry	 Lower values
30.1–0.5 m		79.5–4.5 m
Values 	Chlorophyll	 Values
0.1–2.4 mg m ⁻³		0.1–2.7 mg m ⁻³

Fig. 16. *Calanus finmarchicus* and *C. helgolandicus*. Influence of different abiotic variables on the 2 species. Environmental optima determined using first and ninth decile for each environmental parameter for which the relevant *Calanus* species was superior to the first quartile. It can be seen that *C. helgolandicus* is indicative of the Westerly Winds Biome for regions above the shelf edge (e.g. regions with high spatial variability in bathymetry) while *C. finmarchicus* is indicative of the Arctic biome (especially subarctic and Arctic Atlantic province; Longhurst 1998)

ture of the water column is likely to have a substantial influence on zooplankton distribution, life strategy and population dynamics (Longhurst 1998, Heath et al. 1999). A negative relationship between stratification and zooplankton biomass was reported for the Californian coast by Roemmich & McGowan (1995). They suggested that a longer stratification period, as well as stronger stratification, might hamper the interchange of nutrients from deeper to surface waters, limiting phytoplankton growth and ultimately food for higher trophic levels.

Bathymetry also influences the spatial distribution of the 2 species, although to a lesser extent than temper-

ature. Indeed, *Calanus helgolandicus* is mainly centred over areas between 0 and 500 m of depth whereas *C. finmarchicus* is generally present in deeper areas. These results confirm earlier works that classified *C. finmarchicus* as primarily an oceanic species and *C. helgolandicus* as a pseudo-oceanic species (Beaugrand et al. 2001, Bonnet et al. 2005, Fleminger & Hulsemann 1977). Bathymetry is especially important for *C. helgolandicus* (Beaugrand 2004a, Bonnet et al. 2005). Fleminger & Hulsemann (1977, their Fig. 5) proposed a map of the spatial distribution of both *Calanus* studied in this work. Our results are similar, and differences noted for *C. finmarchicus* are mainly related to the use of presence data by Fleminger & Hulsemann (1977) whereas abundance data were used in the present study. Furthermore, 45 yr of CPR sampling are now available while Fleminger & Hulsemann (1977) based their synthesis on 17 yr.

Identification and quantification of environmental factors involved in the spatial regulation and ecological niche of *Calanus finmarchicus* and *C. helgolandicus* may enable the calculation of habitat-suitability maps (Pulliam 2000). The fact that temperature is an important controlling factor of the spatial distribution of *C. finmarchicus* and *C. helgolandicus* has significant implications in the context of global climate change. Indeed, temperature is one of the parameters which will be the most affected (IPCC 2001). Moreover, temperature is the most accessible parameter in the various scenarios suggested by the IPCC (2001). This makes possible the realisation of scenarios of changes in the spatial

distribution of *C. finmarchicus* and *C. helgolandicus*. Forecasting the distribution of *C. finmarchicus* and *C. helgolandicus* with Ocean General Circulation Models (OGCMs) outputs is of great interest because these *Calanus* species are key structural species of pelagic ecosystems in the North Atlantic and adjacent seas. They have a significant role in the life cycle of many exploited fishes. For example, Beaugrand et al. (2003) recently showed the importance of *C. finmarchicus* for the survival of larval cod in the North Sea. A positive correlation between cod recruitment and the abundance of *C. finmarchicus* was detected. The relation was reversed with *C. helgolandicus*. Mechanisms pro-

posed were based on the 'match/mismatch' hypothesis (Cushing 1996). *C. finmarchicus* was abundant in the North Sea prior to the 1980s regime shift. As this species has its seasonal maximum in spring, it ensured a great availability of prey for cod larvae (period of occurrence from March to August). *C. finmarchicus* decreased during the 1980s while its congener increased. This change in dominance reduced the availability of *Calanus* prey in spring because *C. helgolandicus* has its seasonal maximum in autumn at a time when cod larvae feed on larger prey such as euphausiids or other fishes.

A remarkable feature of our study is that the environmental optimum of *Calanus* species varies seasonally for all abiotic parameters. These seasonal fluctuations might be influenced by the spatial variability in the seasonality of both species (Planque et al. 1997). For *C. finmarchicus*, seasonal fluctuations could be related to large-scale differences in the timing of ontogenetic vertical migration. Another hypothesis is that they could be related to the differential sensitivity of the mean developmental stages of *Calanus* population to temperature that has been observed in some experiments (Harris et al. 2000).

The use of this ecological niche approach has allowed an explanation of the shift in *Calanus* dominance to be outlined. Reid et al. (2003b) showed a substantial and sustained reduction in the percentage contribution of *C. finmarchicus* to total *Calanus* in the North Sea. While in 1962, *C. finmarchicus* comprised 80% of *Calanus* spp. in the North Sea, *C. helgolandicus* comprised 80% of *Calanus* identified by the CPR survey in 2000. As seen in Fig. 12, *Calanus* dominance in the North Sea is highly sensitive to temperature, especially in spring and summer. We have demonstrated that the shift in dominance could have been triggered solely by temperature changes in the North Sea. Sea surface temperature changes are likely to be related to changes in air temperature (Beaugrand 2004b) over the region and changes in advection recently discussed in Reid et al. (2003b). Reid et al. (2003b) reported that when the NAO was positive, the strength of the European shelf-edge current, which flows northwards, increased and that oceanic inflow into the northern part of the North Sea was strengthened. During the cold regime in the North Sea prior to 1980, this region was at the boundary between a subarctic biome and a more temperate biome (Longhurst 1998). As *C. finmarchicus* is indicative of the Atlantic Arctic biome, the change in the proportion of *Calanus* in the North Sea may indicate that the subarctic biome has moved northwards. This has been recently suggested by Beaugrand (2004b). A northward movement of plankton has been detected using calanoid copepods in the northeastern part of the North Atlantic

(Beaugrand et al. 2002) and a similar shift has been found for fish (Perry et al. 2005).

This study has shown the usefulness of Hutchinson's ecological niche concept, which in general has been poorly utilised by ecologists. However, it is important to note that in the present study we assessed the realised, not the fundamental, niche of *Calanus* spp. Hutchinson (1957) made this distinction and stated that the realised niche should always be smaller than the fundamental niche as species interactions eliminate individuals from favourable biotopes. However, Pulliam (2000) recently showed that when dispersal is high, the realised niche can be larger than the fundamental niche. This is probably the case here as the oceanic pelagic realm is continuous, 3-dimensional and without geographical barriers that make biogeographical regions less well-defined than in the terrestrial realm. One way to assess the fundamental niche would be to base the assessment of the species niche on a physiological model such as that described by Pulliam (2000).

Acknowledgements. We are grateful to all past and present members and supporters of the Sir Alister Hardy Foundation for Ocean Science, whose continuous efforts have allowed the establishment and maintenance of the long-term CPR data set. The survey depends on the owners, masters, and crews of the ships that tow the CPRs. The research was supported by the UK's Department for Environment, Food and Rural Affairs (DEFRA) and the European Network of Excellence EUROCEANS. This work was also supported by the French programme ZOOPNEC (Programme National d'Écologie Côtière centré sur le Zooplancton).

LITERATURE CITED

- Batten SD, Clark R, Flinkman J, Hays G and 6 others (2003) CPR sampling: the technical background, materials, and methods, consistency and comparability. *Prog Oceanogr* 58:193–215
- Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydro-climatic environment. *Fish Oceanogr* 12:270–283
- Beaugrand G (2004a) Continuous plankton records: plankton atlas of the North Atlantic Ocean (1958–1999). I. Introduction and methodology. *Mar Ecol Prog Ser Suppl* 2004:3–10
- Beaugrand G (2004b) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr* 60:245–262
- Beaugrand G, Ibañez F, Lindley JA (2001) Geographical distribution and seasonal and diel changes of the diversity of calanoid copepods in the North Atlantic and North Sea. *Mar Ecol Prog Ser* 219:205–219
- Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664
- Bonnet D, Richardson A, Harris R, Hirst A and 19 others (2005) An overview of *Calanus helgolandicus* ecology in European waters. *Prog Oceanogr* 65:1–53

- Bouvier A (1977) Programme ACPM. Analyse des composantes principales avec des données manquantes. Document 77/17, CNRA, Laboratoire de Biometrie, Jouy en Josas
- Bucklin A, Frost BW, Kocher TD (1995) Molecular systematics of six *Calanus* and three *Metridia* species (Calanoida: Copepoda). *Mar Biol* 121:655–664
- Carlotti F, Krause M, Radach G (1993) Growth and development of *Calanus finmarchicus* related to the influence of temperature: experimental results and conceptual model. *Limnol Oceanogr* 38:1125–1134
- Currie DJ (1991) Energy and large-scale patterns of animal- and plant- species richness. *Am Nat* 137:27–49
- Cushing DH (1996) Towards a science of recruitment in fish populations. In: Kinne O (ed) Excellence in ecology, Book 7. International Ecology Institute, Oldendorf/Luhe
- Daro MH (1985) Feeding rhythms and vertical distribution of marine copepods. *Bull Mar Sci* 37:487–497
- Dietrich G (1964) Oceanic polar front survey. *Res Geophys* 2: 291–308
- Ducklow HW, Harris RP (1993) Introduction to the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Res II* 40:1–8
- Fleminger A, Hulsemann K (1977) Geographical range of taxonomic divergence in North Atlantic *Calanus* (*C. helgolandicus*, *C. finmarchicus* and *C. glacialis*). *Mar Biol* 40: 233–248
- Frontier S, Pichot-Viale D, Leprêtre A, Davoult D, Luczak C (2004) Ecosystèmes: structure, fonctionnement et évolution. Dunod, Paris
- Gause GF (1934) The struggle for existence. Williams & Wilkins, Baltimore, MD
- Guisan A, Wilfried T (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8: 993–1009
- Hall CJ, Burns CW (2002) Effects of temperature and salinity on the survival and egg production of *Gadus pectoratus* Brady (Copepoda: Calanoida). *Estuar Coast Shelf Sci* 55:557–564
- Halsband-Lenk C, Hirche HJ, Carlotti F (2002) Temperature impact on reproduction and development of congener copepod populations. *J Exp Mar Biol Ecol* 271:121–153
- Harris RP, Irigoien X, Head RN, Rey C and 5 others (2000) Feeding, growth, and reproduction in the genus *Calanus*. *ICES J Mar Sci* 57:1708–1726
- Heath MR, Backhaus JO, Richardson K, McKenzie E and 11 others (1999) Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fish Oceanogr* 8 (Suppl 1):163–176
- Hirst AG, Batten SD (1998) Long-term changes in the diel vertical migration behaviour of *Calanus finmarchicus* in the North Sea are unrelated to fish predation. *Mar Ecol Prog Ser* 171:307–310
- Hutchinson GE (1957) A treatise on limnology: geography, physics, and chemistry 1. John Wiley & Sons, London
- IPCC (Intergovernmental Panel on Climate Change) (2001) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge
- Jolliffe IT (1986) Principal component analysis. Springer-Verlag, New York
- Kleppel GS (1993) On the diets of calanoid copepods. *Mar Ecol Prog Ser* 99:183–195
- Krauss W (1986) The North Atlantic current. *J Geophys Res* 91:5061–5074
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier Science BV, Amsterdam
- Legendre L, Rassoulzadegan F (1995) Plankton and nutrient dynamics in marine waters. *Ophelia* 41:153–172
- Lindley JA, Reid PC (2002) Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Mar Biol* 141:153–165
- Longhurst A (1998) Ecological geography of the sea. Academic Press, London
- Mauchline J (1998) The biology of calanoid copepods. Academic Press, San Diego, CA
- Millero FJ, Huang F, Laferriere AL (2002) Solubility of oxygen in the major sea salts as a function of concentration and temperature. *Mar Chem* 78:217–230
- Orlova EL, Boitsov VD, Dolgov AV, Rudneva GB, Nesterova VN (2005) The relationship between plankton, capelin, and cod under different temperature conditions. *ICES J Mar Sci* 62:1281–1292
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- Planque B, Fromentin JM (1996) *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Mar Ecol Prog Ser* 134:111–118
- Planque B, Hays GC, Ibañez F, Gamble JC (1997) Large scale spatial variations in the seasonal abundance of *Calanus finmarchicus*. *Deep-Sea Res I* 44:315–326
- Pulliam HR (2000) On the relationship between niche and distribution. *Ecol Lett* 3:349–361
- Reid P, Edwards M (2001) Plankton and climate. In: Steele J (ed) Encyclopaedia of sciences. Academic Press, Oxford, p 2194–2200
- Reid PC, Colebrook JM, Matthews JBL, Aiken J and 25 others (2003a) The continuous plankton recorder: concepts and history, from plankton indicator to undulating recorders. *Prog Oceanogr* 58:117–173
- Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003b) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fish Oceanogr* 12:260–269
- Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California current. *Science* 267:1324–1326
- Russell-Hunter WD (1970) Aquatic productivity. An introduction to some basic aspects of biological oceanography and limnology. Collier-Macmillan, London
- Skreslet S, Borja A, Bugliaro L, Hansen G, Meerkotter R, Olsen K, Verdebout J (2005) Some effects of ultraviolet radiation and climate on the reproduction of *Calanus finmarchicus* (Copepoda) and year class formation in Arcto-Norwegian cod (*Gadus morhua*). *ICES J Mar Sci* 62:1293–1300
- Sundby S (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* 85:277–298
- Woodruff S, Slutz R, Jenne R, Steurer P (1987) A comprehensive ocean-atmosphere dataset. *Bull Am Meteorol Soc* 68: 1239–1250

Simple procedures to assess and compare the ecological niche of species

Grégory Beaugrand^{1,*}, Pierre Helaouët^{1,2}

¹Centre National de la Recherche Scientifique (CNRS), UMR 8013 ELICO, Station Marine, BP 80, 62930 Wimereux, France

²Sir Alister Hardy Foundation for Ocean Science, The Laboratory Citadel Hill, Plymouth PL1 2PB, UK

ABSTRACT: Hutchinson's (1957; Cold Spring Harbour Symp Quant Biol 22:415–427) niche concept is being used increasingly in the context of global change, and is currently applied to many ecological issues including climate change, exotic species invasion and management of endangered species. For both the marine and terrestrial realms, there is a growing need to assess the breadth of the niches of individual species and to make comparisons among them to forecast the species' capabilities to adapt to global change. In this paper, we describe simple non-parametric multivariate procedures derived from a method originally used in climatology to (1) evaluate the breadth of the ecological niche of a species and (2) examine whether the niches are significantly separated. We first applied the statistical procedures to a simple fictive example of 3 species separated by 2 environmental factors in order to describe the technique. We then used it to quantify and compare the ecological niche of 2 key-structural marine zooplankton copepod species, *Calanus finmarchicus* and *C. helgolandicus*, in the northern part of the North Atlantic Ocean using 3 environmental factors. The test demonstrates that the niches of both species are significantly separated and that the coldwater species has a niche larger than that of its warmer-water congeneric species.

KEY WORDS: Ecological niche · Niche assessment · Statistical modeling · Macroecology

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Spatial distribution of a species is not stable in time and space (Rosenzweig 1995). It changes continually, being the result of the adjustment of the species' physiology and life cycle to both abiotic and biotic factors (Longhurst 1998). Chorology, the study of the spatial distribution of organisms and the factors involved in its control necessitates having a clear idea of the ecological niche of the species (Lacoste & Salanon 2001). Among the different definitions of the ecological niche of a species that have been proposed (e.g. Grinnell 1917, Elton 1927), the one from Hutchinson (1957) has been the most influential. Hutchinson (1957) defined the ecological niche as a multidimensional hypervolume with the factors of the environment as the axes. Contrary to the definition proposed by Grinnell (1917), the niche is a property of a species, not a property of the environment (Harmon et al. 2005). The notion of

Hutchinson (1957) is simple and represents a rigorous way of assessing the niche of a species (Pulliam 2000).

Forecasting the spatial distribution of a species has become an important issue in conservation (Austin 2002, Elith et al. 2006). Assessing the ecological niche of a species is important in terms of managing endangered species (Sanchez-Cordero et al. 2005), predicting the responses of species to global climate change (Pearson 1994, Berry et al. 2002) or assessing the potential effects of invasion of non-native species (Jackson et al. 2001). Researchers are commonly interested in (1) quantifying the breadth of the niche and (2) knowing whether the ecological niches of 2 species are distinct (e.g. Stewart et al. 2003). For up to 3 environmental factors, niche comparison can be accomplished by a simple examination of scatterplots (i.e. abundance as a function of the environmental descriptors). However, this method can lead to misinterpretation and does not numerically quantify either the

*Email: gregory.beaugrand@univ-lille1.fr

breadth of the niche of a species or the probability that the niches are separated. Austin et al. (2006) recently stressed that quantifying the niche breadths along gradients remained an unresolved scientific issue. We propose simple multivariate non-parametric procedures derived from a method originally used in climatology (Mielke et al. 1981) to (1) numerically assess species niche breadth and (2) evaluate whether the ecological niches are significantly distinct. First, we describe the technique using a simple fictive example of 3 species distinguished by 2 factors. Then, we apply the technique on 2 key structural marine zooplankton copepod species in the northern part of the North Atlantic Ocean.

MATERIALS AND METHODS

Study area and biological data. The study zone corresponds to the northern part of the North Atlantic Ocean and extends from 99.5°W to 19.5°E longitude and 29.5°N to 69.5°N latitude. Biological data were provided by the Continuous Plankton Recorder (CPR) survey; information describing this large-scale plankton monitoring programme can be found in Warner & Hays (1994), Batten et al. (2003) and Reid et al. (2003). Data for the period from 1958 to 2002 were used in the present study (Fig. 1). We applied numerical procedures to assess and compare the ecological niches of 2 marine pelagic calanoid copepods, *Calanus finmarchicus* and *C. helgolandicus*. These calanoids are key structural species in subarctic (*C. finmarchicus*) and temperate shelf-edge (*C. helgolandicus*) regions of the North Atlantic Ocean (e.g. Bonnet et al. 2005, Speirs et al. 2005).

Environmental data. Three environmental factors were used to assess the ecological niches of the 2 *Calanus* species. The spatial extent of the environmental data considered in the present study is shown in Fig. 1. Temperature was an essential factor because of its recognized influence on plankton (Reid & Edwards 2001a, Beaugrand & Reid 2003, Beaugrand et al. 2003). Temperature data were provided by the Comprehensive Ocean–Atmosphere Data Set (COADS; www.cdc.noaa.gov) (Woodruff et al. 1987). Salinity also constitutes an important factor for many species (Mauchline 1998). Salinity data were extracted from the 'World Ocean Atlas 2001' database (www.nodc.noaa.gov/OC5/WOA01/pr_woa01.html). Bathymetry is a factor especially influential for distribution of *C. helgolandicus*, which is considered to be a pseudo-oceanic species (i.e. a species that can be found in oceanic and neritic waters, but is mostly abundant above the shelf-edge, Beaugrand et al. 2002a). Bathymetry data came from the General Bathymetric Chart of the Oceans

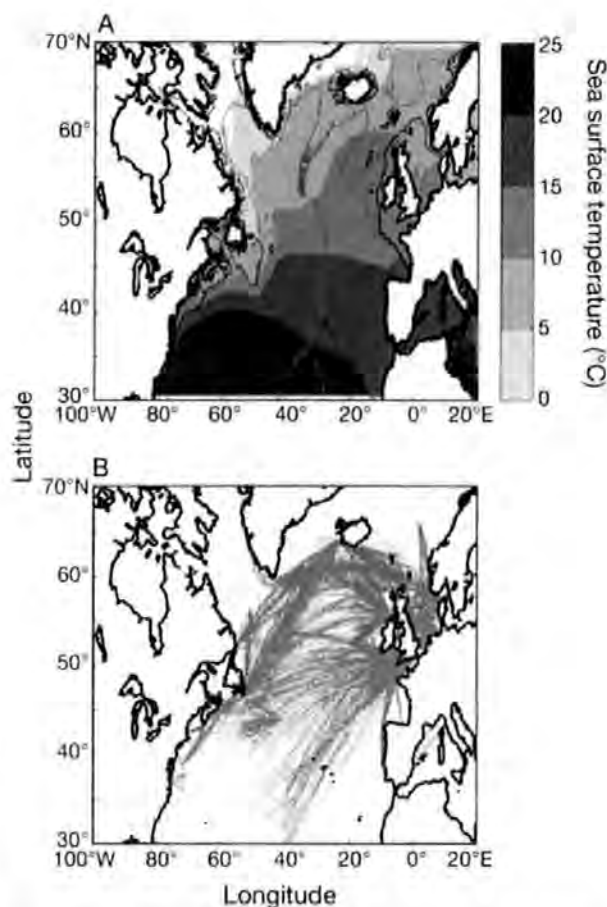


Fig. 1. (A) Spatial distribution of North Atlantic mean sea surface temperatures (grey scales), which reflect the spatial extent of environmental data used in this study. The isobaths of 200 m are also indicated. (B) Spatial distributions of the Continuous Plankton Recorder (CPR) samples for the period 1958–2002 (191 028 CPR samples, grey dots)

(GEBCO; www.bodc.ac.uk/projects/international/gebco) database and an index of spatial variability in the bathymetry was calculated. In a geographical cell of 1° latitude and 1° longitude, both the average and standard deviation of bathymetry data were first calculated (225 data per geographical cell). Then, the coefficient of variation (CV) was calculated as the percentage ratio of the standard deviation to the mean. A high variability in the bathymetry generally indicates continental slope regions (Fig. 2). The procedure is explained in more detail by Helaouët & Beaugrand (2007).

Pre-processing of data. We calculated the mean abundance of both *Calanus* species for each category of (1) temperature (every 2°C between –3°C to 35°C), (2) salinity (every 0.5 psu between <30 psu and >39.5 psu) and (3) spatial variability of the bathymetry (every 10 m between <–100 m and 0 m). The class

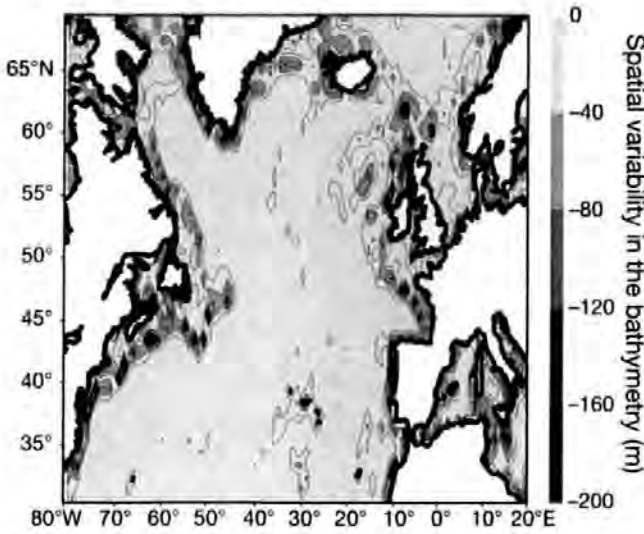


Fig. 2. Mapping of the index of spatial variability in the bathymetry (from Helaouët & Beaugrand 2007)

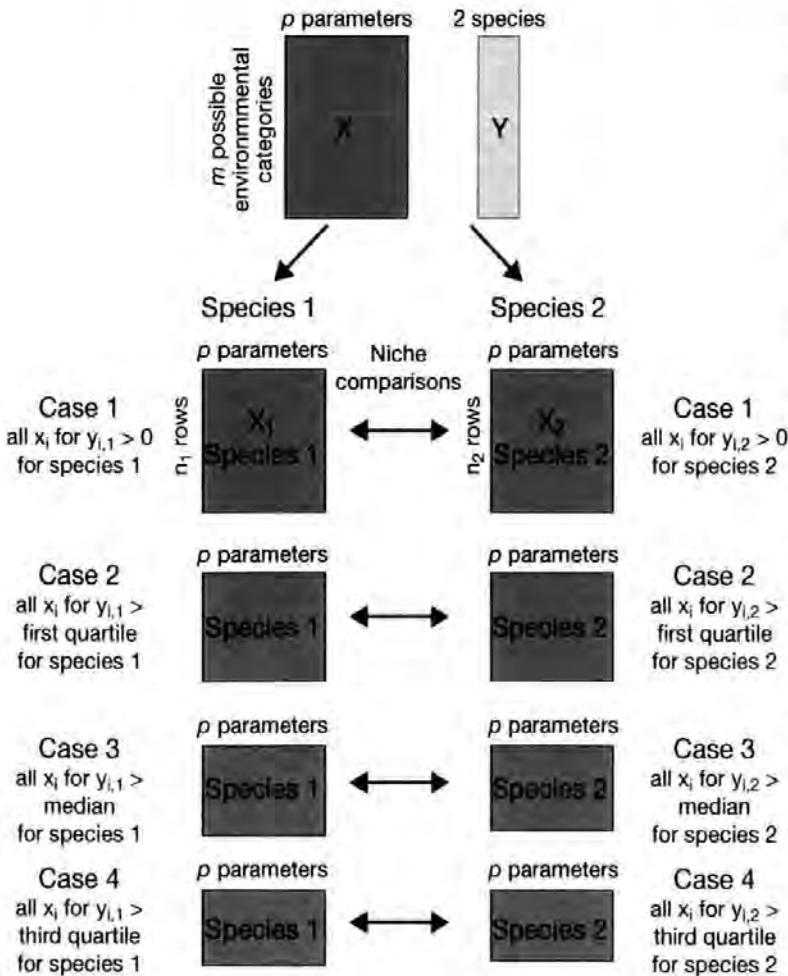


Fig. 3. Origin of matrices tested in this study. Comparisons between species niches were performed for each case

intervals of each variable were selected on the basis of the examination of the frequency histogram of each environmental factor. This stage of the analysis was performed to represent visually the ecological niche of the species and then to apply the statistical procedures described as follows.

If $X(m,p)$ is the matrix of p environmental variables with the m environmental categories, then each cell of X represents the centre of the interval of an environmental variable (Fig. 3). If $C(p,1)$ is the vector that contains the total number of category for each of the p variables, then the number of rows m in X is given by:

$$m = \prod_{i=1}^p c_i \quad (1)$$

The term $Y(m,s)$ is the vector with m abundance or presence/absence values corresponding to the m environmental categories for the s species (Fig. 3). Missing data are often present in the matrix and correspond to an environmental category that was not sampled. The amount of missing data increases with the number of environmental variables (and therefore m). Only rows of X for which the species was detected (or belong to a certain category of abundance) are considered in the calculation. Therefore, the number of rows n to be tested often varies between species (and $n \leq m$, Fig. 3).

The analyses were used based on occurrence data (all environmental data for which the abundance of species are >0 , Case 1, Fig. 3). For example, the data point for a temperature class centred on 10°C , a salinity class of 34.75 psu and a spatial bathymetry variability class of -45 , was considered as abundance data for *Calanus finmarchicus* superior to 0 in these environmental intervals. This was not the situation for *C. helgolandicus*. The procedures were also used for abundance data $>$ first quartile (Case 2), data $>$ median (Case 3), data $>$ third quartile (Case 4). The first quartile, the median and third quartile were assessed for each species from matrix Y . Reshaping and building of the matrices used in the analyses is illustrated in Fig. 3.

To assess and compare the ecological niche of 2 or more species, we propose a numerical analysis based on Multiple Response Permutation Procedures (MRPP, Mielke et al. 1981, Zimmerman et al. 1985). These procedures have been often applied with Split Moving Window Boundary ana-

lysis (Webster 1973) to detect discontinuities in time series (Cornelius & Reynolds 1991). For example, this method was applied to detect the substantial and rapid changes called regime shift (Reid & Edwards 2001b) that occurred in North Sea plankton ecosystems (Beaugrand 2004b).

Assessment of the niche breadth. For each species and case (Fig. 3), the breadth of the ecological niche was assessed by calculating the Euclidean distance between all possible pairs of points. Each environmental variable was normalized to 1 prior to the calculation of Euclidean distances. The normalization is a special kind of scaling (Legendre & Legendre 1998). Each element of the vector is divided by its length, using the Pythagorean formula. This transformation ensured that each variable had the same weight in the analysis.

The Euclidean distance (d) between the rows x_i and x_k in the matrix X (i.e. n rows that represent the environmental categories in which the species is either >0 , or $>\text{first quartile}$, or $>\text{median}$, or $>\text{third quartile}$ according to the different cases and p columns representing the number of environmental variables) is calculated as follows:

$$d(x_i, x_k) = \sqrt{\sum_{j=1}^p (x_{i,j} - x_{k,j})^2} \tag{2}$$

with p being the number of environmental variables. The total number of Euclidean distances (g) to be calculated for a species (and a case) is:

$$g = n(n-1)/2 \tag{3}$$

with n being the number of rows in matrix X . Calculations are illustrated with a simple example (Table 1, Fig. 4). No normalization was done in this example as it is fictive and we assume that the 2 variables have the same units. This is generally not the case with actual data and it is important to undertake a normalization procedure so as not to bias the results. In this example $n = 3$ for Species 1. Three Euclidean distances should be calculated ($g = 3$, Table 1). Calculations give values of $d_{(x_1, x_2)} = 2.236$, $d_{(x_1, x_3)} = 2.000$ and $d_{(x_2, x_3)} = 2.236$.

For each case and species, the mean Euclidean distance, ϵ , is then calculated to assess the breadth of the ecological niche as follows:

$$\epsilon = \frac{\sum_{i=1}^g d_i}{g} \tag{4}$$

with g being the total number of Euclidean distances calculated from X . In the example (Table 1, Fig. 4), $\epsilon = (2.236 + 2.000 + 2.236)/3 = 2.157$ for Species 1, $\epsilon = 2.452$ for Species 2 and $\epsilon = 4.392$ for Species 3. Therefore, the breadth of the ecological niche (only based on 2 factors in this example) is greater for Species 3 than for Species 2 and Species 1 (Fig. 4).

Table 1. Fictive example showing the occurrence of 3 species according to 2 environmental variables. Data are untransformed

Species 1		Species 2		Species 3	
Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
1	1	4	4	1	2
2	3	5	2	3	3
3	1	5	5	6	5
–	–	7	4	7	1

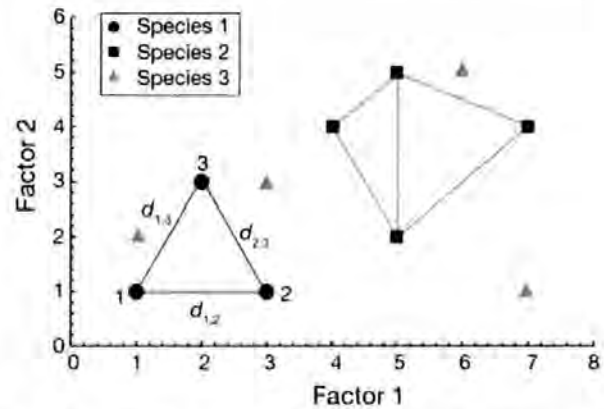


Fig. 4. Hypothetical ecological niche (sensu Hutchinson 1957) of 3 species in the space of 2 factors. All possible Euclidean distances (d) are indicated for Species 1 and 2. Data are presented in Table 1

Test of niche separation. The following non-parametrical MRPP technique can then be applied to test whether the species have different ecological niches. The test statistic δ between Species 1 and 2 (2 species) and a given case is calculated as being the weighted mean of the values for ϵ :

$$\delta_{1,2} = \frac{g_1 \epsilon_1 + g_2 \epsilon_2}{g_1 + g_2} \tag{5}$$

where g_1 and g_2 are the total number of Euclidean distances calculated for Species 1 (matrix X_1) and Species 2 (matrix X_2), respectively (see Fig. 2). The terms ϵ_1 and ϵ_2 are the mean Euclidean distances for Species 1 and 2, respectively.

The probability values of the MRPP statistics are determined by permutations (Zimmerman et al. 1985). For comparison of the ecological niche of 2 species (e.g. Species 1 and 2), the number of possible permutations, $PE_{1,2}$, is:

$$PE_{1,2} = \frac{(g_1 + g_2)!}{g_1! \times g_2!} \tag{6}$$

In the example, $PE_{1,2} = 35$ permutations, $PE_{1,3} = 35$ permutations and $PE_{2,3} = 70$ permutations. The probability $p_{1,2}$ (e.g. Species 1 and 2) is calculated from the following formula:

$$p_{1,2} = \frac{K_{\delta_{1,2}^* < \delta_{1,2}}}{PE_{1,2}} \quad (7)$$

where $K_{\delta_{1,2}^* < \delta_{1,2}}$ is the number of recalculated or simulated $\delta_{1,2}$ (e.g. Species 1 and 2), called $\delta_{1,2}^*$, found to be inferior to the observed $\delta_{1,2}$ after permutation.

In the fictive example (Table 1, Fig. 4), the calculated values are $\delta_{1,2} = 2.3260$ and $p_{1,2} = 0.0286$. Therefore, the ecological niche of Species 1 and 2 are significantly different. For Species 1 and 3, $\delta_{1,3} = 3.4342$ and $p_{1,3} = 0.2857$, and for Species 2 and 3, $\delta_{2,3} = 3.4221$ and $p_{2,3} = 0.6286$, so that the niches do not significantly differ either between Species 1 and 3 or between Species 2 and 3. The number of possible permutations is important to provide an idea of the robustness of the probability. In the example, it is relatively low. When the number of occurrence points begins to become moderately high, the test becomes rapidly robust. For example, for 2 species, one of which has 10 occurrences and the other 15, then 2.85 million permutations are possible. When the number of possible permutations is too high, it is not possible to do all calculations and Berry & Mielke (1983) proposed using the Pearson Type III distribution instead. However in that case, only the Euclidean distance can be applied. We propose to use a finite number of permutations. A minimum number of 10 000 permutations is generally recommended to stabilise the probability for tests based on random permutations such as Mantel's test (Jackson & Somers 1989). This way of assessing the probability enables the use of any distance or similarity measures. This assumption works as long as there is no substantial difference in the number of occurrences (or abundance values > first quartile, median or third quartiles), n_{si} , for each species.

RESULTS

The ecological niche for *Calanus finmarchicus* seems larger than that for *C. helgolandicus* (Fig. 5). As expected, *C. finmarchicus* has a temperature optimum lower than *C. helgolandicus*, but the former species is more eurythermal than the latter. *Calanus helgolandicus* is found at higher levels of salinity than is *C. finmarchicus* and in regions where spatial variability in the bathymetry is greater. Again, *C. finmarchicus* can tolerate higher variation in salinity than its congeneric species and is found in regions encompassing a greater diversity of bathymetry profiles (Fig. 5). The abundance patterns shown in Fig. 5 also suggest that the niches of both species are separated.

These findings are confirmed by the statistical procedures (Table 2). The procedure quantifies the breadth of the ecological niche of both *Calanus* species for sev-

Table 2. *Calanus finmarchicus* and *C. helgolandicus*. Results of the tests based on annual estimations of the abundance of both species in each category of temperature, salinity and variability of bathymetry. Case 1: all presence data, Case 2: abundance data > 1st quartile, Case 3: abundance data > median, Case 4: abundance data > 3rd quartile. Niche breadth: breadth of the ecological niche of each species. p: probability that the niches of both species are different

	Niche breadth		p
	<i>C. finmarchicus</i>	<i>C. helgolandicus</i>	
Case 1	6.6887	6.1066	<0.0001
Case 2	6.4695	5.7971	<0.0001
Case 3	6.2840	5.6667	<0.0001
Case 4	6.1522	5.3492	<0.0001

eral levels of abundance. For all degrees of abundance, the breadth of the ecological niche of the subarctic species *C. finmarchicus* (e.g. value of 6.69 based on all presence data) is higher than the breadth of the niche of its congeneric temperate pseudo-oceanic species (e.g. value of 6.11 based on all presence data). When only high abundance data are considered (i.e. data > third quartile), the separation between both species is maximum. The procedure also demonstrates that both niches are significantly separated from each other (Table 2).

DISCUSSION

These results were expected as *Calanus finmarchicus* characterizes subarctic water while its congeneric species, *C. helgolandicus*, is more indicative of temperate waters (Beaugrand et al. 2002b, Beaugrand 2003, Bonnet et al. 2005, Helaouët & Beaugrand 2007). Rapoport's rule suggests the existence of a latitudinal gradient in geographical range size and, therefore, an increased tolerance of high latitude species to environmental fluctuations (Stevens 1989). Our results conform to this ecogeographical pattern. The greater breadth of the niche of *C. finmarchicus* explains why the spatial distribution for this species is larger than for *C. helgolandicus* (Planque 1996, Beaugrand 2004a). Using the proposed procedures, quantification of the niche for species ranging from the equator to the pole could provide additional information on the validity of this long-debated pattern in ecology (Rohde et al. 1993, Colwell & Hurlt 1994, Lyons & Willig 1997, Sanders 2002).

Many methods have already been proposed to assess the ecological niche of species (for a review, see e.g. Guisan & Zimmermann 2000, see also Hölzel 2003, Elith et al. 2006). Regression techniques are often applied to characterize the relationships between a

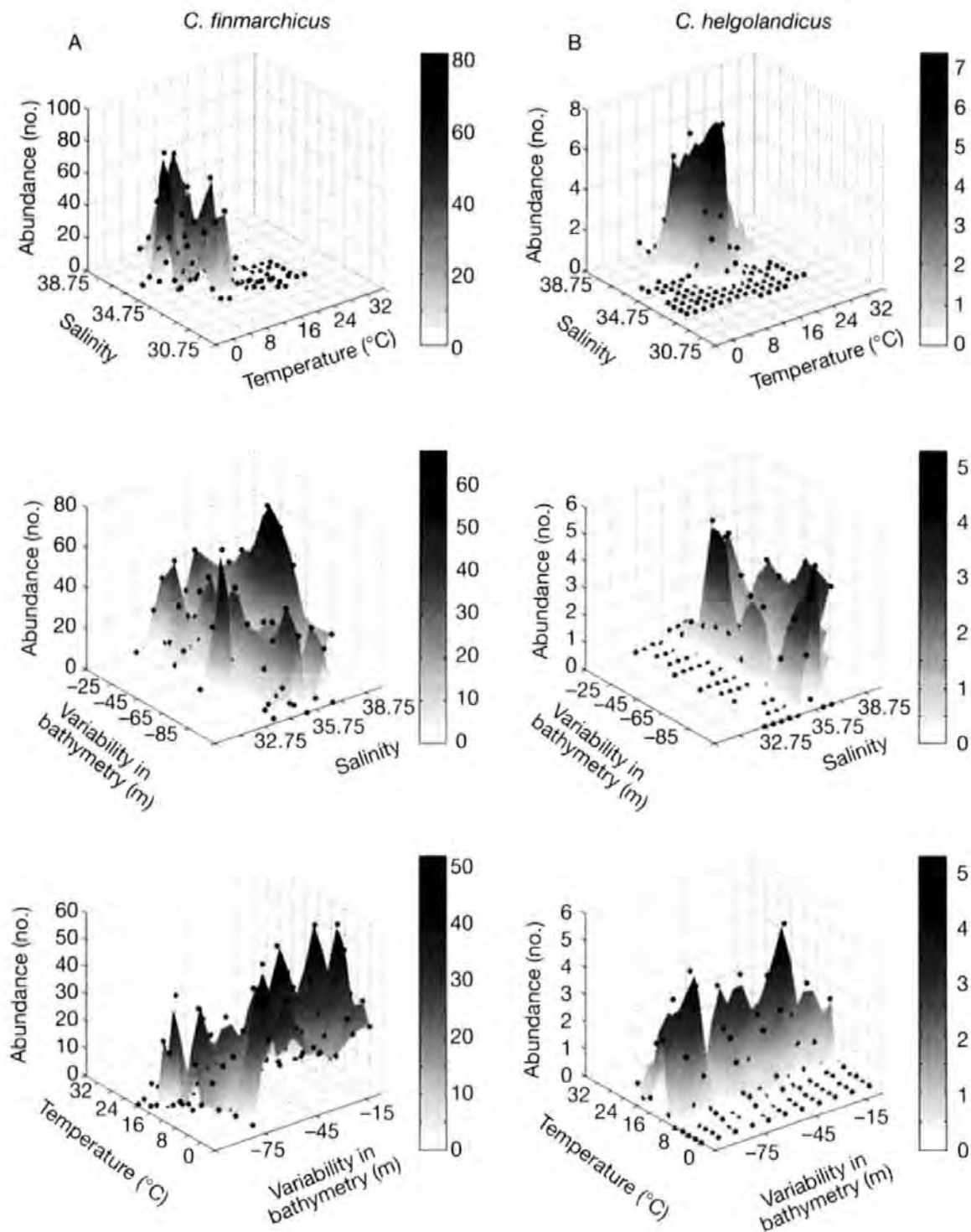


Fig. 5. Ecological niches of (A) *Calanus finmarchicus* and (B) *C. helgolandicus* based on temperature (°C), salinity (psu) and variability in the bathymetry (m). Black dots are measurements of the abundance of the species for a given environmental category and the shaded grey envelope indicates the ecological niche of the species, which was calculated by cubic polynomial interpolation

species and its environment (ter Braak & Looman 1987). Regression techniques are selected according to the characteristics of the data (i.e. quantitative or categorical) and the number of explanatory variables to be

included in the model. Generalised linear models (GLM, McCullagh & Nelder 1983) and generalised additive models (GAM, Hastie & Tibshirani 1990) have been most often used (Leathwick & Austin 2001, Hee-

gaard 2002). When more than 1 species is examined, canonical ordination techniques such as redundancy analysis (RDA) have been applied if the response of species to a change in the environment is assumed to be linear. When the response is expected to be unimodal, canonical correspondence analysis (CCA) can be computed (ter Braak 1987). Other methods such as artificial neural networks (ANN, Manel et al. 1999), regression trees and classification trees exist. Multivariate adaptive regression splines (MARS) combine regression trees with spline fitting and represent an interesting technique for modeling species distributions (Leathwick et al. 2006). Those methods, however, do not allow assessment and direct quantification of the breadth of the niche, or testing and comparison of the breadths of the ecological niches of 2 species. The outlying mean index method (OMI analysis, Dolédec et al. 2000) allows a comparison of the relative position and the breadth of the species niche. This method is especially useful when a high number of species is compared. This technique assesses the relative position of the species by calculating a marginality index, which is represented by the distance between the mean habitat conditions of a species (*sensu* Hutchinson 1957) and the average habitat conditions of the sampled region. A tolerance index that evaluates the niche breadth and a residual tolerance index that informs on the variance of the species niche not considered in the marginality axis are also computed. The niche breadth index is a measure of intra-group variance weighted by the relative abundance of the species. Our breadth niche index is simply the mean Euclidean distance based on all abiotic variables, and the procedures that allow comparisons to be tested are distribution-free. As variables are most often measured in different units, the Euclidean distance has to be calculated on transformed data. We normalized the data so that each variable has a length of 1. The Euclidean distance can be replaced by any type of distance as long as the conditions of application of the index are met (Legendre & Legendre 1998). This represents a great advantage in addition to the simplicity of the technique.

The definition of the ecological niche used in this study is that of Hutchinson (1957). This also represents what is sometimes called the environmental niche as opposed to the trophic niche (see the discussion in Guisan & Wilfried 2005). Hutchinson (1957) made the distinction between fundamental and realized niches, stating that the latter was smaller than the fundamental niche. Recently, however, Pulliam (2000) clearly demonstrated that when dispersal was high, the realized niche could be larger than the fundamental niche. Pulliam (2000) distinguished source habitats, where local reproduction is higher than local mortality, from

sink habitats, where local mortality is superior to local reproduction. Dispersal in the marine pelagic domain of the North Atlantic Ocean is high as there is no physical barrier. This is probably why marine biogeographical regions are less well identified than in the terrestrial realm (Rapoport 1994). High dispersal in the marine pelagic environment is likely to increase the breadth of the niches for *Calanus* spp. This makes the realized niches of both *Calanus* spp. probably larger than their fundamental niches (Pulliam 2000). Therefore, their ecological niches can be overestimated. Furthermore, estimation of niche breadth of both species can possibly be biased by a difference in the dispersal rate between the 2 *Calanus* spp. Dispersal is expected to be higher for *C. finmarchicus* because this oceanic species is less limited by the bathymetric factor than its congeneric species (Beaugrand et al. 2002a). One way of overcoming this problem is to assess the ecological niche using a combination of physiological and environmental variables (Pulliam 2000). The present procedures could be restarted on the outputs of such a physiological model and the results compared. The difference between the niche assessed by this method and that based on *in situ* measurements would enable an assessment of the dispersal rate of both species and could lead to an estimation of the fundamental niches of both *C. finmarchicus* and *C. helgolandicus*.

The test can be sensitive if the number of occurrence points is too different between species. In such a case, a procedure of random selection of the occurrence points can help to prevent the bias related to the estimation of the probability. Other limitations are more dependent on the theory behind the concept of ecological niche, sampling strategy and coverage (Legendre & Legendre 1998), spatial scale selection (Beaugrand & Ibañez 2002) and other potential caveats discussed recently by Guisan & Wilfried (2005). Spatial autocorrelation is an important issue in ecological niche modelling (Dormann et al. 2007). Spatial dependence or autocorrelation, related to biological or physical data, might increase the Type I error rate and lead to the incorrect rejection of the null hypothesis of no effect. In our study, data used in the test are derived from a mean abundance calculated for a given class interval using 3 variables (temperature, salinity and spatial variability in the bathymetry). Information on space is lost and the calculation of the average mixed observations located in very different places. This reduces the effect of spatial autocorrelation. We believe that the very low probabilities ($p < 0.0001$) found in this study make our conclusions robust. A special procedure of randomization could be implemented in the test to try to overcome this potential problem.

The procedures presented in this paper represent a simple and rapid way to quantify and compare the

breadth of the ecological niche of 2 species and to test whether species niches are significantly different. We used a Euclidian distance in the present paper, but virtually any measure of distance can be used (e.g. Chord distance). Such a method could be extended to compare the ecological niches of more than 2 species by correcting the probabilities of each species pair for multiple test comparisons (Sokal & Rohlf 1995). The procedure can also be reduced to the univariate case (i.e. a single environmental variable) to quantify the degree of tolerance of a species to a change in an environmental factor. The quantification of the degree of tolerance is often important in ecophysiological and global change related issues.

Acknowledgements. We are grateful to all past and present members and supporters of the Sir Alister Hardy Foundation for Ocean Science, whose continuous efforts have allowed the establishment and maintenance of the long-term CPR data set. The survey depends on the owners, masters and crews of the ships that tow the CPRs. The research was supported by the UK Department for Environment, Food and Rural Affairs (DEFRA), and the European Network of Excellence EUR-OCEANS.

LITERATURE CITED

- ▶ Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol Model* 157:101–118
- ▶ Austin MP, Belbin L, Meyers JA, Doherty MD, Luoto M (2006) Evaluation of statistical models used for predicting plant species distributions: role of artificial data and theory. *Ecol Model* 199:197–216
- ▶ Batten SD, Clark R, Flinkman J, Hays G and others (2003) CPR sampling: the technical background, materials, and methods, consistency and comparability. *Prog Oceanogr* 58:193–215
- ▶ Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydro-climatic environment. *Fish Oceanogr* 12:270–283
- Beaugrand G (2004a) Continuous plankton records: plankton atlas of the North Atlantic Ocean (1958–1999). I. Introduction and methodology. *Mar Ecol Prog Ser Suppl* 2004:3–10
- ▶ Beaugrand G (2004b) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr* 60:245–262
- ▶ Beaugrand G, Ibañez F (2002) Spatial dependence of pelagic diversity in the North Atlantic Ocean. *Mar Ecol Prog Ser* 232:197–211
- ▶ Beaugrand G, Reid PC (2003) Long-term changes in phytoplankton, zooplankton and salmon linked to climate change. *Glob Change Biol* 9:801–817
- ▶ Beaugrand G, Ibañez F, Lindley JA, Reid PC (2002a) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Mar Ecol Prog Ser* 232:179–195
- ▶ Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002b) Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- ▶ Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664
- Berry KJ, Mielke PW (1983) Computation of finite population parameters and approximate probability values for multi-response permutation procedures (MRPP). *Commun Stat B Simul* 12:83–107
- ▶ Berry PM, Dawson TP, Harrison PA, Pearson RG (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Glob Ecol Biogeogr* 11:453–462
- ▶ Bonnet D, Richardson AJ, Harris R, Hirst AG and others (2005) An overview of *Calanus helgolandicus* ecology in European waters. *Prog Oceanogr* 65:1–53
- ▶ Colwell RK, Hurtt GC (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *Am Nat* 144:570–595
- ▶ Cornelius JM, Reynolds JF (1991) On determining the statistical significance of discontinuities within ordered ecological data. *Ecology* 72:2057–2070
- Dolédéc S, Chessel D, Gimaret-Carpentier C (2000) Niche separation in community analysis: a new method. *Ecology* 81:2914–2927
- ▶ Dormann CF, McPherson JM, Araujo MB, Bivand R and others (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628
- ▶ Elith J, Graham CH, Anderson RP, Dudik M and others (2006) Novel methods improve prediction of species distributions from occurrence data. *Ecography* 29:129–151
- Elton C (1927) *Animal ecology*. Sidgwick & Jackson, London
- Grinnell J (1917) The niche-relations of the California thrasher. *Auk* 34:427–433
- ▶ Guisan A, Wilfried T (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- ▶ Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186
- ▶ Harmon LJ, Kolbe JJ, Cheverud JM, Losos JB (2005) Convergence and the multidimensional niche. *Evolution* 59:409–421
- Hastie TJ, Tibshirani RJ (1990) *Generalized additive models*. Chapman & Hall, London
- ▶ Heegaard E (2002) The outer border and central border for species–environment relationships estimated by non-parametric generalised additive models. *Ecol Model* 157:131–139
- ▶ Helauouët P, Beaugrand G (2007) Macroecological study of the niche of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Mar Ecol Prog Ser* 345:147–165
- ▶ Hölzel N (2003) Re-assessing the ecology of rare flood-meadow violets (*Viola elatior*, *V. pumila* and *V. persicifolia*) with large phytosociological data sets. *Folia Geobot* 38:281–298
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symp Quant Biol* 22:415–427
- Jackson DA, Somers KM (1989) Are probability estimates from the permutation model of Mantel's test stable? *Can J Zool* 67:766–769
- ▶ Jackson JBC, Kirby MX, Berger WH, Bjørndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Lacoste A, Salanon R (2001) *Éléments de biogéographie et d'écologie*. Nathan/HER, Paris
- Leathwick JR, Austin MP (2001) Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology* 82:2560–2573
- ▶ Leathwick JR, Elith J, Hastie T (2006) Comparative performance of generalized additive models and multivariate

- adaptive regression splines for statistical modelling of species distributions. *Ecol Model* 199:188–196
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier Science BV, Amsterdam
- Longhurst A (1998) Ecological geography of the sea. Academic Press, London
- Lyons SK, Willig MR (1997) Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos* 79:568–580
- Manel S, Dias JM, Ormerod SJ (1999) Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. *Ecol Model* 120:337–347
- Mauchline J (1998) The biology of calanoid copepods. Academic Press, San Diego, CA
- McCullagh P, Nelder JA (1983) Generalized linear models. Chapman & Hall, London
- Mielke PW, Berry KJ, Brier GW (1981) Application of multi-response permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. *Mon Weather Rev* 109:120–126
- Pearson DL (1994) Selecting indicator taxa for the quantitative assessment of biodiversity. *Philos Trans R Soc Lond B Biol Sci* 345:75–79
- Planque B (1996) Spatial and temporal fluctuations in *Calanus* populations sampled by the Continuous Plankton Recorder. PhD thesis, University of Pierre et Marie Curie, Paris VI
- Pulliam R (2000) On the relationship between niche and distribution. *Ecol Lett* 3:349–361
- Rapoport EH (1994) Remarks on marine and continental biogeography: an areographical viewpoint. *Philos Trans R Soc Lond B Biol Sci* 343:71–78
- Reid P, Edwards M (2001a) Plankton and climate. In: Steele J (ed) *Encyclopaedia of sciences*. Academic Press, Oxford, p 2194–2200
- Reid PC, Edwards M (2001b) Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenb Marit* 32:107–115
- Reid PC, Colebrook JM, Matthews JBL, Aiken J and others (2003) The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. *Prog Oceanogr* 58:117–173
- Rohde K, Heap M, Heap D (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *Am Nat* 142:1–16
- Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge
- Sanchez-Cordero V, Cirelli V, Munguia M, Sarkar S (2005) Place prioritization for biodiversity representation using species' ecological niche modeling. *Biodiversity Informatics* 2:11–23
- Sanders NJ (2002) Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography* 25: 25–32
- Sokal RR, Rohlf FJ (1995) Biometry. WH Freeman & Company, New York
- Speirs DC, Gurney WSC, Heath MR, Wood SN (2005) Modelling the basin-scale demography of *Calanus finmarchicus* in the north-east Atlantic. *Fish Oceanogr* 14:333–358
- Stevens GS (1989) The latitudinal gradient in geographic range: how so many species coexist in the tropics. *Am Nat* 133:240–256
- Stewart KM, Bowyer RT, Kie JG, Dick BL, Ben-David M (2003) Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche? *Ecoscience* 10: 297–302
- ter Braak CJF (1987) Ordination. In: Jongman RHG, ter Braak CJF, van Tongeren OFR (eds) *Data analysis in community and landscape ecology*. Pudoc, Wageningen, p 91–173
- ter Braak CJF, Looman CWN (1987) Regression. In: Jongman RHG, ter Braak CJF, van Tongeren OFR (eds) *Data analysis in community and landscape ecology*. Pudoc, Wageningen, p 27–77
- Warner AJ, Hays GC (1994) Sampling by the Continuous Plankton Recorder survey. *Prog Oceanogr* 34:237–256
- Webster R (1973) Automatic soil-boundary location from transect data. *J Int Assoc Math Geol* 5:27–37
- Woodruff S, Slutz R, Jenne R, Steurer P (1987) A comprehensive ocean-atmosphere dataset. *Bull Am Meteorol Soc* 68:1239–1250
- Zimmerman GM, Goetz H, Mielke PW (1985) Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* 66:606–611

Editorial responsibility: Otto Kinne,
Oldendorf/Luhe, Germany

Submitted: February 22, 2007; Accepted: January 14, 2008
Proofs received from author(s): June 25, 2008

Physiology, Ecological Niches and Species Distribution

Pierre Helaouët^{1,2*} and Gregory Beaugrand²

¹Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK; ²Centre National de la Recherche Scientifique (CNRS), Laboratoire d'Océanologie et de Géosciences, UMR CNRS LOG 8187, Station Marine, BP 80, 62930 Wimereux, France

ABSTRACT

Although many studies have debated the theoretical links between physiology, ecological niches and species distribution, few studies have provided evidence for a tight empirical coupling between these concepts at a macroecological scale. We used an ecophysiological model to assess the fundamental niche of a key-structural marine species. We found a close relationship between its fundamental and realized niche. The relationship remains constant at both biogeographical and decadal scales, showing that changes in environmental forcing propagate from the physiological to the macroecological level. A substantial shift in the spatial distribution is

detected in the North Atlantic and projections of range shift using IPCC scenarios suggest a poleward movement of the species of one degree of latitude per decade for the 21st century. The shift in the spatial distribution of this species reveals a pronounced alteration of polar pelagic ecosystems with likely implications for lower and upper trophic levels and some biogeochemical cycles.

Key words: fundamental niche; realized niche; physiology; spatial distribution; north Atlantic ocean; pelagic realm; *Calanus finmarchicus*.

INTRODUCTION

Biogeographical studies necessitate having a reasonable knowledge of the ecological niche, defined here as the range of tolerance of a species when several environmental factors are taken simultaneously (Hutchinson 1957). Hutchinson (1957) conceptualized this notion with the so-called *n*-dimensional hypervolume, in which *n* ideally corresponds to all the environmental factors. This concept is a powerful tool against which researchers can better assess potential effects of global change on species distribution (Beaugrand and Helaouët 2008). Indeed, the concept of ecological

niche has been extensively used to understand and model anthropogenic impacts such as the introduction of exotic species and pollution on species distribution (Peterson 2003). Determining the contribution of different environmental factors is achieved from knowledge of the distribution of species with field observations that can be related to environmental predictor variables (Guisan and Thuiller 2005). Different techniques exist, depending on species data, which can simply be presence data (for example, ecological niche factor analysis (Hirzel and others 2002)), presence-absence data (for example, generalized additive models (Hirzel and others 2006)) or abundance data based on field sampling (for example, all regression analyses (Legendre and Legendre 1998)). However, these techniques can only estimate the realized niche because they are based on observational data. Pulliam (2000) proposed a new type of model to explain and assess differences between fundamental

Received 26 June 2008; accepted 18 May 2009

Author Contributions: Pierre Helaouët and Gregory Beaugrand—conceived the project, Pierre Helaouët—performed the analyses, Gregory Beaugrand and Pierre Helaouët—co-wrote the paper.

*Corresponding author; e-mail: pierrehelaouet@hotmail.com

and realized niches. As stated by Hutchinson (1957), his study indicates that the realized niche is smaller when factors reducing survival such as competition predominate. However, Pulliam (2000) also provided evidence that the realized niche can be greater than the fundamental one when dispersal is high.

The fundamental niche represents the response of all physiological processes of a species to the synergistic effects of environmental factors (Figure 1). Only optimal conditions generate high abundances and allow for successful reproduction. When the environment becomes less favorable, this affects consecutively the reproduction, growth and feeding (Figure 1). Extreme conditions become critical and may eventually affect survival (Schmidt-Nielsen 1990). Ideally, any study that attempts to predict the habitat of a species based on the knowledge of the environment should use both fundamental and realized niches. Past studies have largely focussed on the realized niche (for example, Hirzel and others 2002; Helaouët and Beaugrand 2007) whereas estimation of the fundamental niche has been neglected. However, comparison of both niches can provide important insights on biological mechanisms (for example, competition or predation) that structure a population.

Climate change affects the structure, the dynamics and the functioning of marine ecosystems through many physical and biological processes (Reid and Beaugrand 2002). Changes in the state of the climate system may also unbalance the location of boundaries between major biogeographical systems (Lomolino and others 2006). Key-structural species are useful for tracking such changes in ecosystem state and location. Understanding the spatial distribution of key-structural species has become an important issue in marine ecology (Helaouët and Beaugrand 2007). *Calanus finmarchicus* is a key-structural marine zooplankton copepod species in the North Atlantic Ocean and is among the most studied copepods in this area (for example, Heath and others 2000). This mainly herbivorous species plays an important role in transferring primary production to higher trophic levels in the food web (Mauchline 1998). Indeed, it has been suggested that the species is a key element for the larval survival of some commercially important fish species such as the Atlantic cod (Beaugrand and others 2003). The species also modulates the abundance of phytoplankton through changing grazing pressure (Carlotti and Radach 1996). Assessing future changes in the spatial distribution of the species is a prerequisite to anticipate ecosystem changes but should be based

on the joint assessment of the fundamental and the realized niches.

In this study, we assess both the fundamental and realized niches of *C. finmarchicus* and provide evidence for a close correspondence of the two niches at a macroecological level. The concomitant spatial changes seen in physiology and biogeography are constant at a decadal scale which makes it possible to propose projections of the spatial distribution of the copepod as a function of different scenarios of changes in temperature established by the Intergovernmental Panel on Climate Change W.G.I (2007). Our study shows that the temperature rise observed and projected by atmosphere-ocean general circulation models over the North Atlantic sector propagates from the physiological to macroecological level. Implications of the result for ecological niche modelling are discussed and potential consequences of the change in this key-structural species for ecosystem structure and functioning outlined.

MATERIALS AND METHODS

The area covered by this study extended from 99.5°W to 19.5°E of longitude and from 29.5°N to 69.5°N of latitude thereby covering all the North Atlantic Ocean and adjacent seas.

Biological and Environmental Data

Calanus Finmarchicus

Data on the abundance of adult *Calanus finmarchicus* (copepodite CV and CVI) were provided by the Continuous Plankton Recorder (CPR) survey. The CPR survey is a large-scale plankton-monitoring program managed and maintained by the English laboratory of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) since 1990. The sampler is towed at a constant depth of 7 m (Reid and others 2003). Despite the near-surface sampling, the sampling gives a satisfactory picture of the epipelagic zone (Batten and others 2003). Water enters through an inlet aperture of 1.61 cm² and passes through a 270-µm silk filtering mesh (Batten and others 2003). Individuals greater than 2 mm such as adult copepodite stages CV and CVI of *C. finmarchicus* are then removed from both the filtering and covering silk. In general, all individuals are counted, however, in particularly dense samples, a sub-sample can be realized (Batten and others 2003). We created gridded data (from 99.5°W to 19.5°E of longitude and from 29.5°N to 69.5°N of latitude with a spatial resolution of 1° latitude × 1° longitude) averaging the abundance

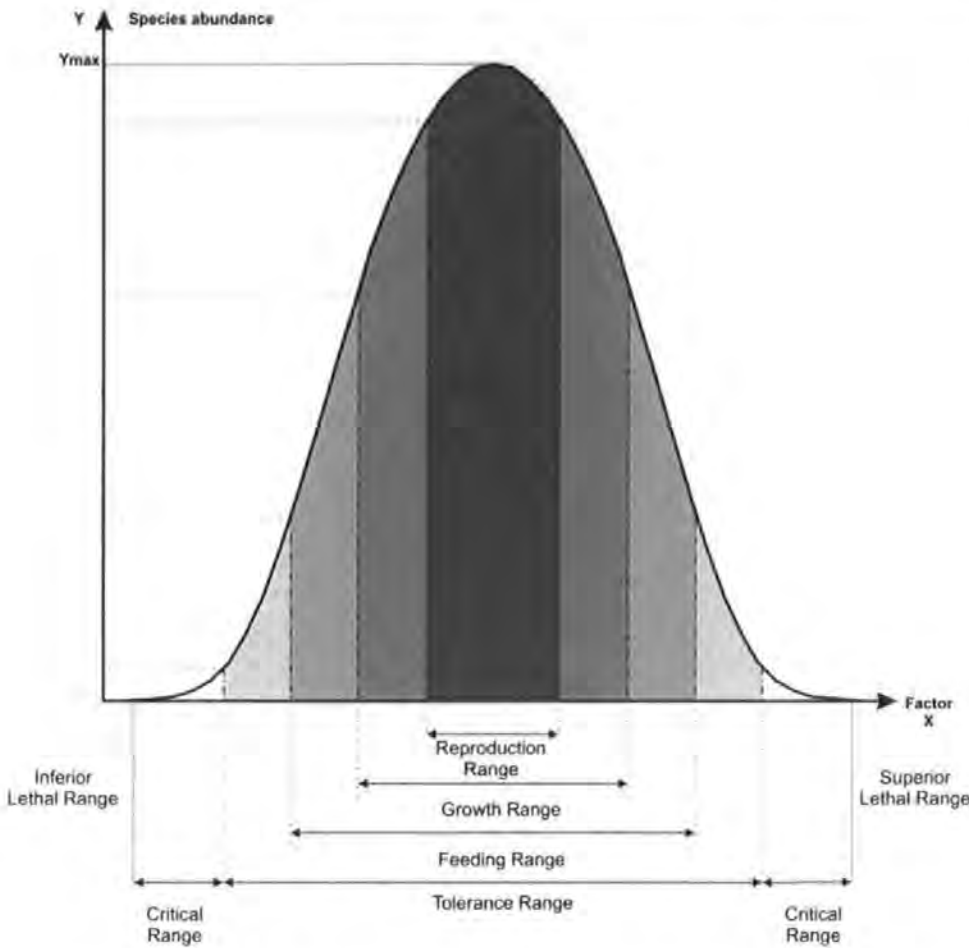


Figure 1. Response curve illustrating the effects of an environmental factor (X) on the species abundance (Y). Extremes values of X are lethal; less extreme values prevent feeding and then growth; only optimal conditions allow reproduction.

of *C. finmarchicus* for the whole sampling period 1960–2005. The climatology of the abundance of *C. finmarchicus* for each decade of the period 1960–2005 (1960s, 1970s, 1980s, 1990s) and for the most recent period 2000–2005 was based on interpolated data. Interpolation was made to maximize the number of values and thereby increase the quality of model comparison. Interpolation was realized using the inverse squared distance method (Lam 1983) with a search radius of 250 km (about 135 miles) using a technique adopted by Beaupre and others (2001).

Sea Surface Temperature

Temperature (as Sea Surface Temperature) was selected as this parameter strongly influences the abundance and spatial distribution of marine ectotherms (Schmidt-Nielsen 1990; Mauchline 1998). Sea Surface Temperature (SST) data come from the Comprehensive Ocean-Atmosphere Data Set (COADS) and were downloaded from the internet site of the National Oceanographic Data Center (NODC), which manages acquisition, con-

trols quality and ensures the long-term safeguarding of the data (Woodruff and others 1987). To perform all the analyses, we created two different kinds of SST climatology with a spatial resolution of 1° of latitude and 1° of longitude. The first climatology was based on the averaging of 45 years (1960–2005), the second one was the result of the average of each decade for the period 1960–1999 (1960s, 1970s, 1980s, 1990s), and the most recent period 2000–2005.

In order to evaluate the potential impact of changes in SST on spatial distribution, data (1990–2100) from the ECHAM 4 (EC for European Centre and HAM for Hamburg) model were utilized. This Atmosphere-Ocean General Circulation Model (AO-GCM) has a horizontal resolution of 2.8° latitude and 2.8° of longitude (Roeckner and others 1996). The data in this study were selected by the Intergovernmental Panel on Climate Change W.G.I (2007) based on criteria among which are physical plausibility and consistency with global projections. Data are projections of monthly skin temperature equivalent above the sea to SST (<http://ipcc-ddc.cru.uca.ac.uk>). Data used here are modelled

data based on scenario A2 (concentration of carbon dioxide of 856 ppm by 2100) and B2 (concentration of carbon dioxide of 621 ppm by 2100) (Intergovernmental Panel on Climate Change W.G.I 2007). In scenario A2, the increase of CO₂ has a rate similar to current observed data (Intergovernmental Panel on Climate Change W.G.I 2007). The scenarios A2 and B2 are based on a world population of 15.1 and 10.4 billion people by 2100, respectively. A decadal mean was calculated for the 2050s and 2090s.

Chlorophyll a

Phytoplankton concentration is also an important parameter to explain changes in the spatial distribution and abundance of *C. finmarchicus*. Therefore chlorophyll a data were selected. These data originated from the program and satellite Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from the National Aeronautics and Space Administration (NASA). Chlorophyll a data were converted into food concentrations (F) using equation (1) (Hirche and Kwasniewski 1997):

$$F_{t,s} = r \times C_{t,s} \quad (1)$$

with $F_{t,s}$ the food concentrations (in $\mu\text{g l}^{-1}$) at time t and location s and $C_{t,s}$ the quantity of chlorophyll a (in $\mu\text{g l}^{-1}$) at time t and location s using a carbon:chlorophyll ratio r of 40 (Hirche and Kwasniewski 1997). A climatology of food concentration was calculated, based on the period 1997–2005. This implicitly assumes that the period is representative of 1960–2005, which is, for the selected spatial scale, a reasonable assumption.

Bathymetry

The spatial distribution of *C. finmarchicus* in the area is influenced by bathymetry, the species being rarely detected when the water column becomes shallow (Helaouët and Beaugrand 2007). We used bathymetry data to restrict our calculations in areas deeper than 50 m. This threshold was fixed after examination of the spatial distribution of *C. finmarchicus* (Beaugrand 2004; Helaouët and Beaugrand 2007). Bathymetry data originated from the database General Bathymetric Chart of the Oceans (GEBCO).

Estimation of the Realized Niche

The realized niche was inferred from the calculation of the spatial distribution of adult *C. finmarchicus* (CV and CVI) for the whole sampling period, that is 1960–2005. As already mentioned in the

introduction, the realized niche represents the fundamental niche modified by factors, such as dispersal, which increase the width of the niche or factors, such as competition, which, on the contrary, tighten it.

Estimation of the Optimal Part of the Fundamental Niche

Many studies have revealed that reproduction is maximal when the species is at its optimal part of the fundamental niche (Hirche 1990). We used this physiological property as a proxy to determine the central part of the fundamental niche of *C. finmarchicus* (see Figure 1). When the optimal part of the fundamental niche is reached, the species must have its maximum abundance. Potential egg production rate (EPR) at time t and location s ($E_{t,s}$ in Eggs · female⁻¹ d⁻¹) was therefore calculated based on information on temperature and food concentration (Heath and others 2000):

$$E_{t,s} = p_1 (F_{t,s} - F_h)^{p_2} p_3 10^{\frac{p_4 ((T_{t,s} - T_{opt})/p_5)^2}{100}} \quad (2)$$

with $T_{t,s}$ the sea surface temperature (in °C) at time t and location s and T_{opt} , the temperature optimum. The latter, which determines the maximum value of egg production, was taken from Heath and others (2000), which fixed its value at 6°C. $F_{t,s}$ is food concentration (in $\mu\text{g l}^{-1}$) at time t and location s (see equation (1)). Parameter F_h is the food concentration below which no egg production is expected. This parameter was fixed at 8 $\mu\text{g l}^{-1}$ by Richardson and others (1999). Other parameters from p_1 to p_5 were estimated by non-linear least square regression and were taken from Hirche and others (1997) ($p_1 = 6.2$; $p_2 = 0.48$; $p_3 = 0.14$; $p_4 = 60$; $p_5 = 1.9$). It is clear from equation (2) that this model is only valid in situations when $F_{t,s} \geq F_h$. Therefore, when food concentration was below 8 $\mu\text{g l}^{-1}$, the value of EPR was set to 0.

The possibility to use or forecast egg production of *C. finmarchicus* is limited by the difficulty in obtaining chlorophyll a data. Therefore, we simplified equation (2) by fixing food concentration ($F_{t,s}$) to its optimal value. The optimal value of the food concentration was fixed to 21.79 $\mu\text{g l}^{-1}$ which corresponds to 0.55 $\mu\text{g l}^{-1}$ of chlorophyll a. Over the time period, 62% of the geographical cells in which *C. finmarchicus* was detected (mean abundance > 1 individual) had values above 0.55 $\mu\text{g l}^{-1}$ of chlorophyll a. This percentage varies between 51.23% and 85.51% during the period from April to September which corresponds to the reproductive season of the species. The optimal value

($21.79 \mu\text{g l}^{-1}$) was determined by fitting equation (2) to potential EPR versus temperature (climatology based on the period 1960–2005). When $F_{t,s} = 21.79 \mu\text{g l}^{-1}$, equation (2) becomes:

$$E_{t,s} = 3.06 \times 10^{\frac{p_A - ((T_{t,s} - T_{opt})p_A)^2}{100}} \quad (3)$$

It should be noted that when EPR is used alone, it means more accurately potential EPR per female and per day. The use of this indicator is based on the fact that only optimal ecological conditions allow for optimal reproduction. High potential EPR can only occur in favorable ecological conditions (see Figure 1; Schmidt-Nielsen 1990). Less suitable conditions will rapidly affect reproduction rates and more specifically egg production rate.

Correlations

The Pearson coefficient of correlation was calculated to examine the relationship between the realized (spatial distribution of *C. finmarchicus*) and the optimal part of the fundamental niche (EPR) for different time periods (Figure 2). To evaluate the impact of spatial autocorrelation when correlation was calculated between maps, the minimum degree of freedom (called *nf*) needed to have a significant correlation ($P = 0.01$) and corresponding to the observed correlation value was assessed.

Procedures and Analyses

Figure 2 summarizes the different analyses performed in this study.

RESULTS

Analyses confirm that *C. finmarchicus* is a subarctic species, mostly abundant in the north of the Oceanic Polar Front (Dietrich 1964) (Figure 3A). Its realized niche shows an optimum range around 6°C but abundance remains high between 2.5 and 9.5°C . This optimum corresponds to the temperature where egg production rate, determined in laboratory experiments, is maximal (Hirche and others 1997). Spatial distribution of EPR closely matches the spatial distribution of the abundance ($r = 0.71$ for all marine regions and $r = 0.81$ for regions deeper than 50 m, Figure 3A and B, Table 1), confirming that the abundance of the species is proportional to its potential EPR. These results suggest a strong correspondence between physiology and the spatial distribution of the species.

The central part of the fundamental niche is narrower than the realized niche as it is inferred

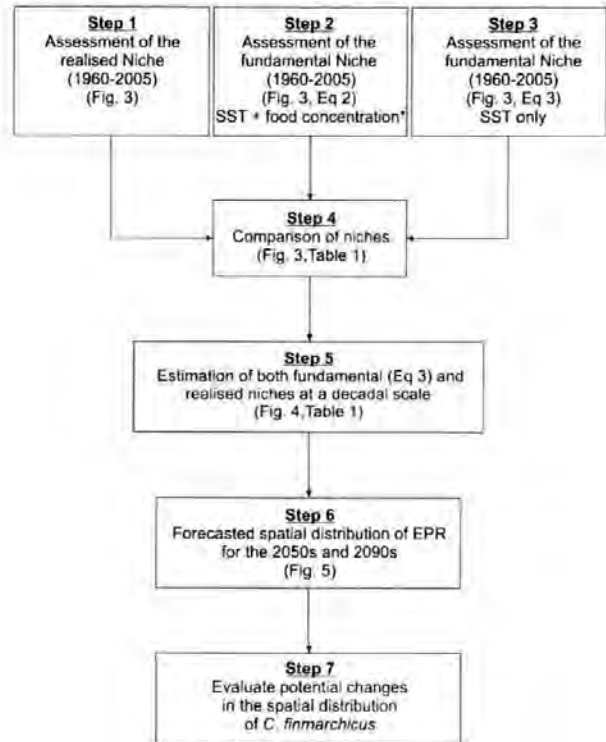


Figure 2. Sketch diagram summarizing the different steps and analyses performed in this study. * The climatology of food concentration is based on chlorophyll *a* data, only available for the period 1997–2005.

from EPR (Figure 3C and D). The adjustment of the model by non-linear least square fitting is best when food concentration ($F_{t,s}$ in equation (2)) is fixed to $21.79 \mu\text{g l}^{-1}$. This value allowed us to simplify equation (2) (see equation (3) in Materials and Methods). Correlation between the two ways of assessing EPR (from equation (2) and (3)) is high and ranges from $r = 0.89$ ($P < 0.001$, Table 1) when all marine regions are considered to $r = 0.93$ ($P < 0.001$) when only regions deeper than 50 m are included in the analysis. This result suggests that food concentration is not so limiting in the regions of interest, probably because chlorophyll covaries well with temperature ($r = -0.71$; $P < 0.001$; $n = 3148$; $nf = 19$). Such a simplified model, depending only upon temperature, is an advantage because good quality data on chlorophyll are restricted to years after 1997 and also because chlorophyll data assessed from biogeochemical models have large uncertainties.

At a decadal scale, the spatial distribution of the abundance of *C. finmarchicus* also closely corresponds to EPR (Figure 4). Correlations ranged from 0.62 in the 1960s to 0.82 in the 1980s (Table 1). It is interesting to note that correlations are fairly

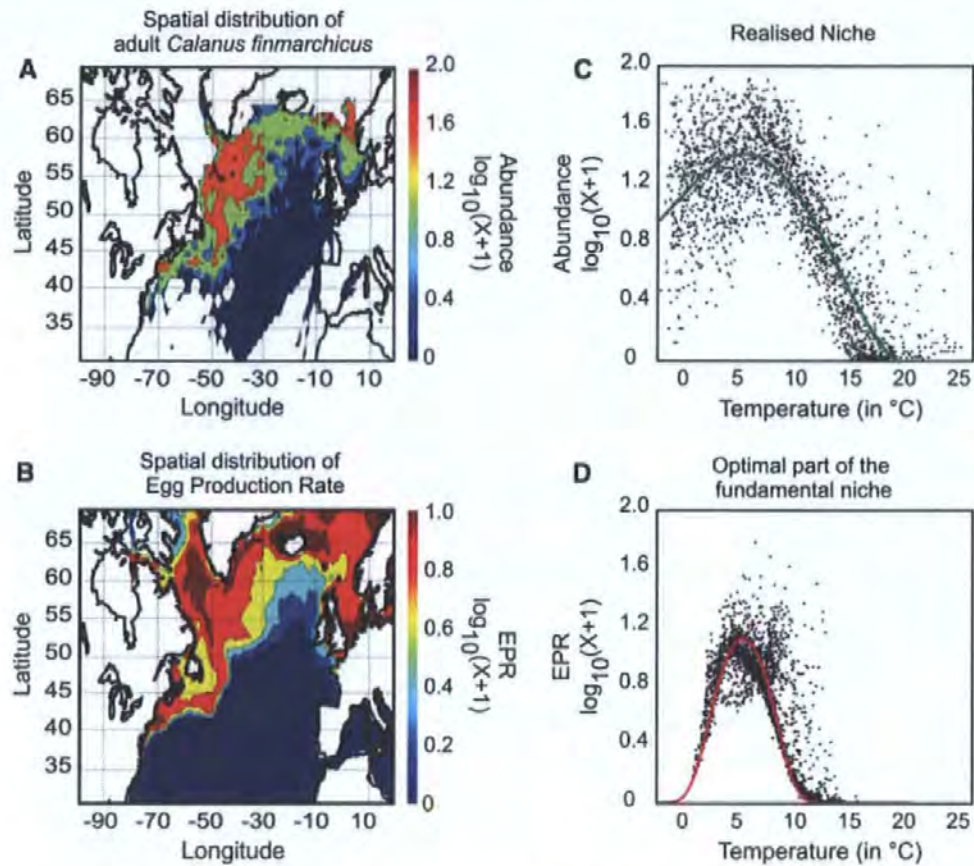


Figure 3. **A** Spatial distribution of *C. finmarchicus* for the period 1960–2005. **B** Spatial distribution of EPR calculated from equation (2) and using temperature data for the period 1960–2005 and a climatology of food concentration based on chlorophyll a data for the period 1997–2005. The reproduction potential is high in the whole North Sea although the species rarely occurs in the shallow part of this sea. **C** Abundance as a function of temperature (mean SST regime). Data are from Figure 3A. The **bold green line**, reflecting the realized niche was calculated from a polynomial regression of order 5. **D** Egg production rate (EPR) as a function of temperature. Data are from Figure 3b. The **bold red line** was calculated by adjusting $F_{T,S}$ in equation (2) as a function of data, using least square fitting.

Table 1. Relationships Between Fundamental and Realized Niches

All regions	Correlation	Probability	Degree of freedom (n)	Degree of freedom (nf)
E/E*	0.89	<0.001	3144	10
E/Ab	0.71	<0.001	1697	18
E*/Ab	0.79	<0.001	1698	14
Regions > 50 m				
E/E*	0.93	<0.001	2757	8
E/Ab	0.81	<0.001	1618	13
E*/Ab	0.82	<0.001	1618	13
Decadal analysis				
E*/Ab (1960–1969)	0.62	<0.001	1567	25
E*/Ab (1970–1979)	0.74	<0.001	1528	17
E*/Ab (1980–1989)	0.82	<0.001	1227	13
E*/Ab (1990–1999)	0.79	<0.001	1189	14
E*/Ab (2000–2005)	0.79	<0.001	1358	14

Pearson correlation coefficients calculated between maps of EPR estimated from equation (2) (E) and equation (3) (E*), abundance (Ab) for the period 1960–2005 (see Figure 3) and at a decadal scale (see Figure 4). Abundance data were transformed (log₁₀(Ab + 1)) prior to the calculation of correlation. 'nf' denotes the degree of freedom needed to have a significant correlation at P = 0.01. This was calculated to evaluate the strength of the correlation and to take into account that data are spatially autocorrelated. For example, when nf = 10 and n = 3000, this indicates that the correlation remains significant even when 10/3000 geographical pixels are kept (0.33% of the 3000 pixels).

constant (with no observed trend) and that EPR explains between 38.44% and 67.24% of the variation in the abundance of *C. finmarchicus*. A concomitant northwards movement of the species and EPR is observed in the north-eastern part of the North Atlantic Ocean after the 1980s (Figure 4). The reduction in the abundance of the species detected in the North Sea after 1990 is clearly explained by EPR. A reduction is also detected over the eastern Scotian Shelf.

The close correspondence in the spatial distribution of both abundance and EPR and thereby both fundamental and realized niches as well as the constancy of the correlation at the decadal scales together make it reasonable to use EPR as a proxy to forecast the spatial distribution of *C. finmarchicus*, utilizing a scenario of temperature changes from AO-GCMs (here ECHAM 4 data using the moderate scenarios A2 and B2). This way of forecasting the spatial distribution of the species is currently neglected and more emphasis is needed on the estimation of the likely distribution from the realized niche. Mapping of forecasted EPR for the 2050s and the 2090s shows a pronounced biogeographical change in the north-eastern part of the North Atlantic Ocean (Figure 5B and C). In the North Sea, the species could disappear at the end of the 21st century (Figure 5C). Changes are observed on the western side of the Atlantic. Although our analysis is limited in spatial resolution, a reduction in the abundance of *C. finmarchicus* is predicted over George Bank and Newfoundland.

DISCUSSION

This study provides compelling evidence, at a macroecological scale, that the spatial distribution of a species (here a marine pelagic species) is constrained by the influence of temperature on its physiology (for example, Huggett 2004). A close relationship has been found between the fundamental and the realized niche (that is, its optimal part) of *C. finmarchicus* which was evident when egg production rates and spatial distributions were mapped together at both bioclimatological and decadal scales (Figure 3 and 4, Table 1). Our results demonstrate that the species is generally present in regions where it can reproduce and that a high level of abundance is detected in places where reproduction is maximal. This correspondence between physiology and spatial distribution was expected from the ecological niche theory (for example, Leibold 1995; Guisan and Thuiller 2005; Begon and others 2006) illustrated in Figure 1 and some authors also stressed this relationship from

laboratory experiments (Parmesan 2005 and references therein).

The concept of the niche (*sensu* Hutchinson) is multidimensional. However, in this study, the emphasis was made on temperature, and the niche we assessed was mainly a thermal niche. The first reason for this is that Helaouet and Beaugrand (2007) showed that temperature was the main driver of the spatial distribution of *C. finmarchicus*. The parameter correlated well with other factors such as oxygen and nutrient concentration and to a lesser extent chlorophyll concentration. Therefore, temperature can be considered as a good proxy for other factors. The second reason is that temperature appears to be the most accessible parameter from Atmosphere-Ocean general circulation models. Our analysis showed that removing chlorophyll from the ecophysiological model did not alter the results (see Figure 4 and 5). A second parameter, the bathymetry, was identified but its impact was much less important than temperature. Bathymetry correlated well with mixed layer depth and wind-induced turbulence. Bathymetry was considered, although indirectly, by removing data at a depth below 50 m.

An ecophysiological model, originally built upon data on *C. finmarchicus* in the northeastern part of the North Atlantic Ocean, was applied in this study. Its applicability at the scale of the North Atlantic Ocean appeared to be a valid assumption (see Figure 4). There is an ongoing debate on whether or not genetic differentiation exists among the population of *C. finmarchicus* (Bucklin and others 2000; Provan and others 2008). Recent results suggest that there is no genetic difference at the scale of the North Atlantic basin, which might allow the species to track changes in available habitat in the context of global warming.

Foundations of niche modelling are intimately linked to Hutchinson's fundamental and realized niche concepts, and most modellers subscribe to this framework (Guisan and Thuiller 2005; Araújo and Guisan 2006 and references therein). Despite this general agreement, some authors argue that ecological niche models based on observed data provide an approximation of the fundamental niche (for example, Soberon and Peterson 2005). Many others workers consider that niche models provide a spatial representation of the realized niche (for example, Guisan and Zimmermann 2000; Pearson and Dawson 2003). Chase and Leibold (2003) suggest dropping Hutchinson's concept and provided a major revision of the niche theory. They defined the niche as the environmental conditions that allow a species to keep the population

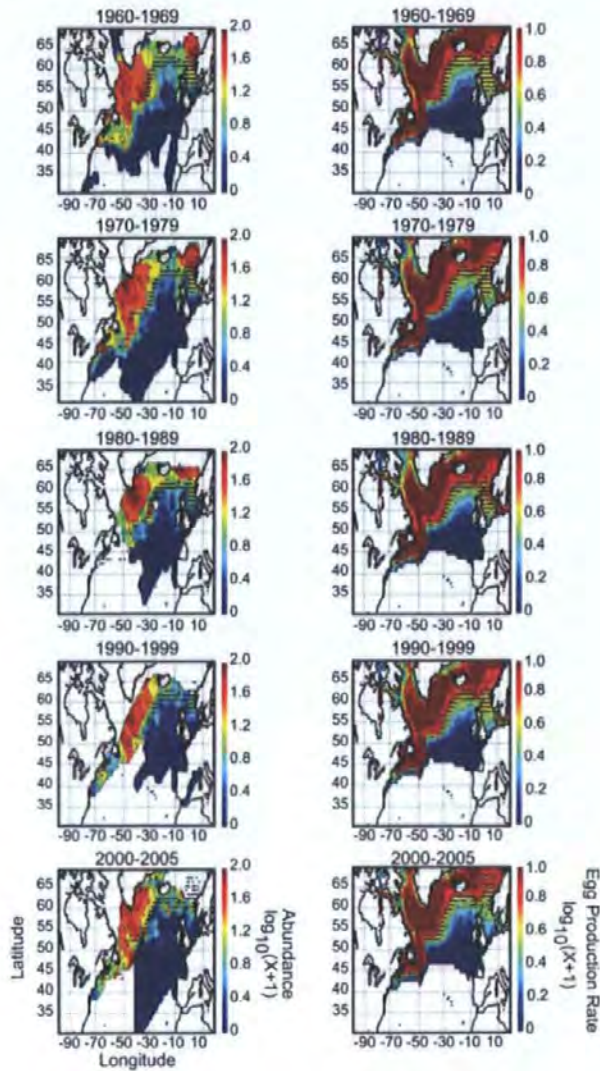


Figure 4. Decadal changes in the spatial distribution in the abundance of *C. finmarchicus* (in left) and egg production rate (in right). Abundances are extrapolated to improve the number of values and thus increase the quality of model comparison. The isotherm 9–10°C is represented by asterisks (Beaugrand and others 2008).

growth rate positive or null (besides both immigration and emigration). Our results suggest, however, that the combined use of both fundamental and realized niches enables a better understanding of the environmental conditions that allows the growth of the population (Chase and Leibold 2003).

Two hypotheses can be proposed to explain the tight coupling between egg production and abundance observed in this study. First, although dispersal is generally considered to be high in the pelagic realm (Longhurst 1998), hydrodynamical features might behave as a barrier and prevent

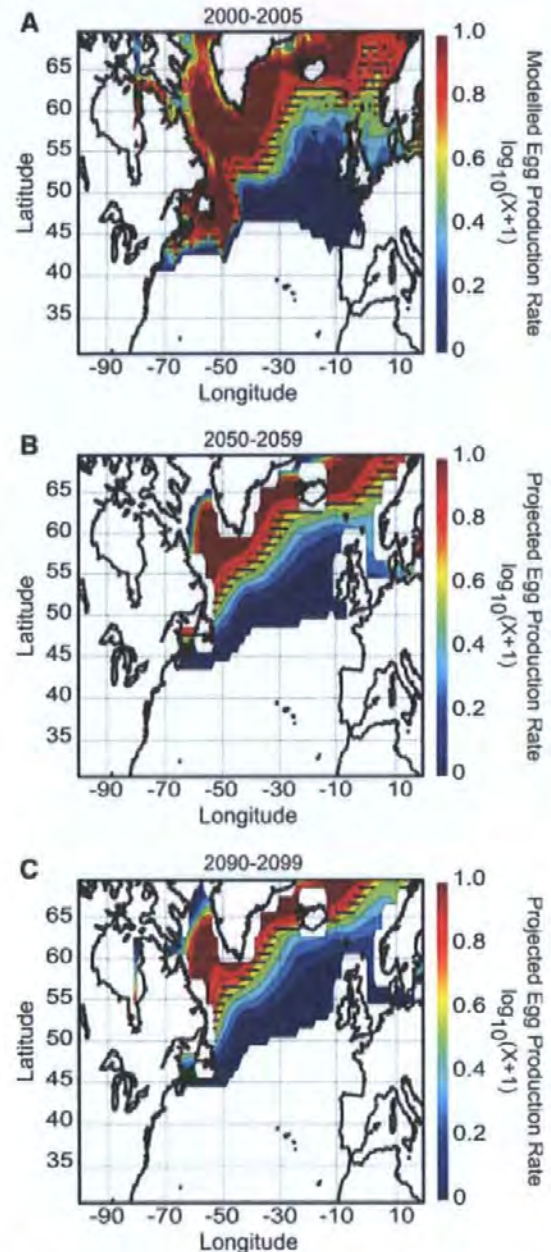


Figure 5. **A** Spatial distribution of EPR of *C. finmarchicus* based on observed SST data for the period 2000–2005. **B** Projected spatial distribution of EPR based on scenario A2 of SST change for the period 2050–2059. The EPR is used here as a proxy to evaluate future changes in spatial distribution of the abundance of *C. finmarchicus* with global climate change. **C** Projected spatial distribution of EPR based on scenario A2 of SST change for the period 2090–2099. Scenario B2, which gives very similar results, is not presented. The isotherm 9–10°C is represented by asterisks (Beaugrand and others 2008).

migration. Indeed, the spatial distribution of *C. finmarchicus* clearly matches the subpolar gyre and is limited by the Oceanic Polar Front (Dietrich

1964) and associated oceanic currents (Krauss 1986; Helaouët and Beaugrand 2007). Second, the link between egg production and spatial distribution may be explained by the fact that an expatriated population is unlikely to persist and therefore to be detectable at the scale of our study. Pulliam (2000) stressed that a population may persist as long as the immigration rate from source regions nearby is sufficient. Dispersion from source habitats (region where local reproduction exceeds mortality; Pulliam 1988) seems to be rapidly counteracted by mortality related to physiological stress, which might in turn be worsened by interspecific competition, parasitism and predation in sink habitats (regions where mortality exceeds local reproduction; Pulliam 1988).

Our results show that *C. finmarchicus* could be abundant in the North Sea as the model forecasts high reproductive potential. This paradox has already been noted by Heath and others (1999). The species is not observed throughout the year because it typically requires bathymetry greater than 500 m to overwinter in diapause (Hirche 1996). The North Sea is thought to be invaded each spring by adults from deeper oceanic regions (Heath and others 1999). Not only the magnitude of the spring invasion has been reduced due to a warming of the Norwegian Sea Deep Water (Heath and others 1999), but our results also suggest that the potential for this remaining population to reproduce and grow during the season has been considerably reduced. Year-to-year changes between the abundance of *C. finmarchicus* and the modelled egg production rate in this region are highly correlated ($r = 0.66$, $P < 0.001$, 45 years). The parallelism between decadal changes in both egg production and abundance (see Figure 4) indicates that a reduction of offspring quickly propagates to the level of species population. The concomitant changes between level of abundance and egg production rate suggests that an approach based on physiological rule combined with biogeographical information enables better projections of change in spatial distribution to be made (Parmesan 2005). Overall, we found a very close link between abundance and potential EPR. However, at a regional scale, local hydrodynamics such as the volume of Norwegian Sea Deep Water and its influence on spring invasion (Heath and others 2000) on the eastern side of the North Atlantic or the state of the NAO, and its impact on the Labrador Sea Water may have a strong influence (Greene and others 2003).

Modelled sea surface temperature (SST) data from the ocean-atmosphere general circulation model (ECHAM4 scenarios A2 and B2) and ob-

served sea surface temperature (COADS) data are highly positively correlated in the area covered by this study, showing that we can be confident in the use of the two scenarios of changes in SST for our projection of spatial patterns in egg production rate (Beaugrand and others 2008). Modelled changes in the egg production rate for the period 2050–2059 and 2090–2099 show a substantial poleward movement of the species of about one degree of latitude per decade (Figure 5). Regions characterized by high abundance and high reproduction rates, observed (Figure 4) or modelled (Figure 5), are just below the isotherm 9–10°C. This isotherm represents a biogeographical boundary between the Atlantic Arctic and Atlantic Westerly Winds Biome (*sensu* Longhurst 1998) (Beaugrand and others 2008). Beaugrand and others (2008) linked a change in the location of this boundary to an abrupt ecosystem shift affecting the food web from phytoplankton to zooplankton to fish. As a key structural species (Planque and Batten 2000; Speirs and others 2004), *C. finmarchicus* is one of the most abundant copepods in subarctic waters of the North Atlantic Ocean (Conover 1988). This species transfers energy from phytoplankton to upper trophic levels (Mauchline 1998) and represents a key-prey for at least some stages of exploited fish (for example, cod (Sundby 2000)). Its biogeographical movement might therefore reveal major ecosystem changes that will propagate northwards if climate warming continues (Intergovernmental Panel on Climate Change W.G.I 2007). The expected changes in the abundance of the species might impact the trophodynamics of pelagic ecosystems, altering predator–prey relationships (Cushing 1997) and some biogeochemical cycles (Beaugrand 2009).

The current knowledge of the spatial distribution of species up to now is limited in the pelagic realm, which covers 71% of the earth surface. With the establishment of a link between physiology, ecological niches and species distribution, our study opens a new avenue for predicting the potential response of species and ecosystems to global climate change. Further investigations of regions and species, for which information on physiology and distributional patterns are known, would make it possible to generalize this link to other realms. Such a validation might bring new empirical evidence to the ongoing debate on the redefinition of the fundamental and realized niches (Araújo and Guisan 2006).

ACKNOWLEDGMENTS

We are grateful to all the past and present members and supporters of the Sir Alister Hardy Foundation

for Ocean Science whose sustained help has allowed the establishment and maintenance of the CPR data-set in the long-term. Consortium support for the CPR survey is provided by agencies from the following countries: United Kingdom, USA, Canada, Faroe Islands, France, Ireland, Netherlands, Norway and the European Union. We thank the owners, masters and crews of the ships that towed the CPRs on a voluntary basis. This research is part of the European network of Excellence EUR-OCEANS.

REFERENCES

Araújo MB, Guisan A. 2006. Five (or so) challenges for species distribution modelling. *J Biogeogr* 33:1677–88

Batten SD, Clark R, Flinkman J, Hays G, John E, John AWG, Jonas T, Lindley JA, Stevens DP, Walne A. 2003. CPR sampling: the technical background, materials, and methods, consistency and comparability. *Prog Oceanogr* 58:193–215

Beaugrand G. 2004. I. Introduction and methodology. In: Beaugrand G, Edwards M, Jones A, Stevens D, Eds. Continuous plankton records: a plankton atlas of the North Atlantic Ocean (1958–1999). Marine Ecology Progress Series

Beaugrand G. 2009. Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Res II* 56:656–73

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC. 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–4

Beaugrand G, Edwards M, Brander K, Luczak C, Ibañez F. 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol Lett* 11:1157–68

Beaugrand G, Helaouët P. 2008. Simple procedures to assess and compare the ecological niche of species. *Mar Ecol Prog Ser* 363:29–37

Beaugrand G, Ibañez F, Lindley JA. 2001. Geographical distribution and seasonal and diel changes of the diversity of calanoid copepods in the North Atlantic and North Sea. *Mar Ecol Prog Ser* 219:205–19

Begon M, Townsend CR, Harper JL. 2006. Ecology. From individuals to ecosystems. Bath: Blackwell Publishing

Bucklin A, Astthorsson OS, Gislason A, Allen LD, Smolenack SB, Wiebe PH. 2000. Population genetic variation of *Calanus finmarchicus* in Icelandic waters: preliminary evidence of genetic differences between Atlantic and Arctic populations. *ICES J Mar Sci* 57:1592–604

Carlotti F, Radach G. 1996. Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model. *Limnol Oceanogr* 41:522–39

Chase JM, Leibold MA. 2003. Ecological niches—linking classical and contemporary approaches. Chicago/IL: The University of Chicago Press

Conover RJ. 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167(168):127–42

Cushing DH. 1997. Towards a science of recruitment in fish populations. Oldendorf/Luhe: Ecology Institute

Dietrich G. 1964. Oceanic polar front survey. *Res Geophysic* 2:291–308

Greene CH, Pershing AJ, Consersi A, Planque B, Hannah C, Sameoto D, Head E, Smith PC, Reid PC, Jossi J, Mountain D, Ben eld MC, Wiebe PH, Durbin E. 2003. Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Prog Oceanogr* 58:310–2

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009

Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecol Modell* 135:147–86

Heath MR, Astthorsson OS, Dunn J, Ellertsen B, Gaard E, Gislason A, Gurney WSC, Hind AT, Irigoien X, Melle W, Niehoff B, Olsen K, Skreslet S, Tande KS. 2000. Comparative analysis of *Calanus finmarchicus* demography at locations around the Northeast Atlantic. *ICES J Mar Sci* 57:1562–80

Heath MR, Backhaus JO, Richardson K, McKenzie E, Slagstad D, Beare D, Dunn J, Fraser JG, Gallego A, Hainbucher D, Hay S, Jonasdottir S, Madden H, Mardaljevic J, Schacht A. 1999. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fish Oceanogr* 8(suppl 1):163–76

Helaouët P, Beaugrand G. 2007. Statistical study of the ecological niche of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Mar Ecol Prog Ser* 345:147–65

Hirche H-J. 1990. Egg production of *Calanus finmarchicus* at low temperature. *Mar Biol* 106:53–8

Hirche H-J. 1996. Diapause in the marine copepod, *Calanus finmarchicus*: a review. *Ophelia* 44:129–43

Hirche H-J, Kwasniewski S. 1997. Distribution, reproduction and development of *Calanus* species in the northeast Atlantic in relation to environmental conditions. *J Mar Syst* 10:299–317

Hirche H-J, Meyer U, Niehoff B. 1997. Egg production of *Calanus finmarchicus*—effect of temperature, food and season. *Mar Biol* 127:609–20

Hirzel AH, Hausser J, Chessel D, Perrin N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83:2027–36

Hirzel AH, Le Lay G, Heller V, Randin C, Guisan A. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecol Modell* 199:142–52

Huggett RJ. 2004. Fundamentals of biogeography. London: Routledge

Hutchinson GE. 1957. A treatise on limnology. Geography, physics, and chemistry 1. New York: Wiley, p 555

Intergovernmental Panel on Climate Change W.G.I2007. Climate change 2007. The physical science basis. Cambridge: Cambridge University Press, p 996

Krauss W. 1986. The North Atlantic current. *J geophys res* 91:5061–74

Lam NSN. 1983. Spatial interpolation methods: a review. *Am cartogr* 10:129–49

Legendre P, Legendre L. 1998. Numerical ecology. 2nd edn. The Netherlands: Elsevier Science BV, p 853

Leibold MA. 1995. Niche concept revisited: mechanistic models and community context. *Ecology* 76:1371–82

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. Sunderland: Sinauer Associates Inc, p 845

Longhurst A. 1998. Ecological geography of the sea. London: Academic Press, p 390

- Mauchline J. 1998. The biology of calanoid copepods. San Diego: Academic Press
- Parnesan C. 2005. Biotic response: range and abundance changes. New Haven CT: Yale University Press
- Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12:361–71
- Peterson AT. 2003. Predicting the geography of species' invasions via ecological niche modeling. *Q rev Biol* 78:419–33
- Planque B, Batten SD. 2000. *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES J Mar Sci* 57:1528–35
- Provan J, Beatty GE, Keating SL, Maggs CA, Savidge G. 2008. High dispersal potential has maintained long-term population stability in the North Atlantic copepod *Calanus finmarchicus*. *Proc R soc Lond B* 276:301–7
- Pulliam HR. 1988. Sources, sinks, and population regulation. *Am Nat* 132:652–61
- Pulliam HR. 2000. On the relationship between niche and distribution. *Ecol Lett* 3:349–61
- Reid PC, Beaugrand G. 2002. Interregional biological responses in the North Atlantic to hydrometeorological forcing. In: Sherman K, Skjoldal H-R, Eds. Changing states of the large marine ecosystems of the North Atlantic. Amsterdam: Elsevier Science, p 27–48
- Reid PC, Colebrook JM, Matthews JBL, Aiken J, Barnard R, Batten SD, Beaugrand G, Buckland C, Edwards M, Finlayson J, Gregory L, Halliday N, John AWG, Johns D, Johnson AD, Jonas T, Lindley JA, Nyman J, Pritchard P, Richardson AJ, Saxby RE, Sidey J, Smith MA, Stevens DP, Tranter P, Walne A, Wootton M, Wotton COM, Wright JC. 2003. The continuous plankton recorder: concepts and history, from plankton indicator to undulating recorders. *Prog Oceanogr* 58:117–73
- Richardson K, Jonasdottir SH, Hay SJ, Christoffersen A. 1999. *Calanus finmarchicus* egg production and food availability in the Faroe-Shetland channel and northern north sea: october-march. *Fish Oceanogr* 8:153–62
- Roeckner E, Arpe K, Bengtsson L, Christoph M, Claussen M, Dumenil L, Esch M, Giorgetta M, Schlese U, Schulzweida U. 1996. The atmospheric general circulation model ECHAM-4: Model description and simulation of present-day climate. Hamburg: Max-Planck Institut für Meteorologie. 90p
- Schmidt-Nielsen K. 1990. Animal physiology: adaptation and environment. New York: Cambridge University Press. p 602
- Soberon J, Peterson AT. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers Informatics* 2:1–10
- Speirs D, Gurney WSC, Holmes SJ, Heath MR, Wood SN, Clarke ED, Harms IH, Hirche H-J, McKenzie E. 2004. Understanding demography in an advective environment: modelling *Calanus finmarchicus* in the Norwegian Sea. *J Anim Ecol* 73:897–910
- Sundby S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* 85:277–98
- Woodruff S, Slutz R, Jenne R, Steurer P. 1987. A comprehensive ocean-atmosphere dataset. *Bull Am meteorol soc* 68:1239–50

Copyright statement

This copy of the thesis has been supplied on condition that anyone who consults it is understood to recognise that its copyright rests with its author and that no quotation from the thesis and no information derived from it may be published without the author's prior consent.