Distribution patterns of ichthyoplankton communities in different ecosystems of the Northeast Atlantic.

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ABSTRACT

Results are presented of an extensive ichthyoplankton survey that covered the continental slope, the offshore banks and oceanic regions west of Ireland. Oceanographic measurements revealed domes of cold less saline water over the Porcupine, Rockall and Faroese Banks, constituting Taylor columns. The most species rich stations were those found on and close to the offshore banks and the shelf edge. Larvae found in these areas were mainly from demersal fish species including some commercial species such as haddock *Melanogrammus aeglefinus,* lemon sole *Microstomus kitt* (Walbaum, 1792), ling *Molva molva* (L.) and witch *Glyptocephalus cynoglossus* (L.). The deep water stations of the Rockall Trough and the north and west stations off the Rockall and Hatton Banks were characterised by a low number of species and high numbers of individuals of mesopelagic species such as *Maurolicus muelleri* and *Benthosema glaciale*. Results from multivariate statistical analysis confirmed that species compositions varied significantly at different sites and were related to environmental conditions, whereby sites of similar temperature, salinity and bottom depth harboured similar species assemblages. Generalised additive mixed modelling was used to model the relationship between species richness and environmental variables and confirmed that there was a significant negative relationship between species richness and bottom depth indicating that the offshore banks and the slope stations present favourable habitats for a large number of species.

Key words: GAMM, Ichthyoplankton; Rockall; Mesopelagic; Submarine Banks, *Maurolicus muelleri*

INTRODUCTION

Consistent oceanographic mechanisms of transport or retention from a spawning into a juvenile area are necessary to maintain fish populations in the longterm (Heath, 1992). Demonstrated links or entrainments have been shown to include Taylor column circulation over banks (Saville, 1956); tidal fronts (Lough and Manning, 2001) and onshore Ekman transfer (Alvarez *et al*., 2001). These entrainments are often characterised by high diversity and productivity, thus providing a beneficial environment for larval survival.

This paper describes the results of an extensive ichthyoplankton survey that covered the shelf, offshore region and a number of important offshore banks in the northeast Atlantic. The objective of the survey was to assess spawning activities of commercial and non-commercial fish species in the offshore regions west and north of Ireland and to relate the distribution patterns of fish larvae to prevailing oceanographic conditions. The underlying questions in this paper are (i) whether particular environmental conditions are associated with in higher ichthyoplankton abundance and diversity and (ii) at a different level, whether different environmental conditions result in changes of species composition.

MATERIALS AND METHODS

The three-week ichthyoplankton survey was carried out on the MFV "*Atlantean*", between 28 May and 16 June 2002 and covered the Northeast Atlantic from the Porcupine Bank at 53.15°N across the Rockall Trough, the Rockall Bank including parts of the Hatton Bank from 8.15 °W to 19.45 °W and south of the Faroese waters up to 61.15°N (Fig.1). Samples were collected with a Gulf 7 high-speed plankton sampler to a maximum depth of 200m and a spatial resolution of half a degree longitude. A real time CTD sensor (PRO-NET) was attached to the GULF to record depth, temperature and salinity profiles for each deployment. Further details on sample collection and processing are given in Dransfeld *et al.* (2005). Attempts were made to identify all fish eggs and larvae using the appropriate ichthyoplankton keys (Fahay, 1983; O'Brien, 1986; Olivar and Fortuno, 1991 & Russell 1976). The numbers of fish eggs and larvae removed from each sample were standardised to m^2 according to the formula described by Smith and Richardson (1977). For visualisation and statistical analysis geographical regions were categorised into submarine bank stations <1000m: 'P'-Porcupine Bank, 'R'-Rockall Bank, 'H'-Hatton Bank, 'F'-Faroese Plateau, 'M'- Anton Dhorn Seamount; 'S'-shelf stations <1000 m depth and 'O'-offshore stations ≥1000m. To test for spatial correlation, geographical positions of sampling stations were converted from longitudes and latitudes to true distance x,y coordinates using the Universal Transverse Mercator coordinate system.

Statistical analysis

To summarise the large number of species with a diversity index, the Shannon index and Margalef's richness index (Begon *et al.*, 1996) was used. Data exploration techniques were applied as described in Zuur *et al,* (2007). Analysis included Cleveland dotplots and conditional boxplots to identify large values, and pairplots, coplots and variance inflation factors (VIF) to detect collinear explanatory variables. Initial data exploration revealed that a.) the two diversity indices Shannon and Margalef were highly correlated (r^2=0.9) and subsequent analysis only included Margalef's index of richness; b) the correlation between explanatory variables was relatively small, indicating that there were no obvious problems with collinearity between bottom depth, salinity and temperature (VIF values >5) and c.) richness vs bottom depth exhibited a non linear relationship.

In order to model the relationship between species richness and multiple explanatory variables, the following general additive model (GAM) was applied to the data:

$$\mathbf{Richness}_i = \alpha + f_1(\mathbf{Depth}_i) + f_2(\mathbf{Temp}_i) + \mathbf{f3}(\mathbf{Sal}_i) + \varepsilon_i \qquad \mathbf{(1)}$$

Where i refers to the site (location), $Depth_i$ is the bottom depth at sample i, and $Temp_i$ and Sal_i the corresponding temperature and salinity values. The term ε_i is independently normally distributed noise. The notation $f_j()$ stands for smoothing function. In this model, the residuals showed a clear spatial correlation structure and therefore the model was extended from a GAM to a general additive mixed model (GAMM) by allowing for a spatial residual correlation structure. Using the AIC (Akaike Information Criteria) as a model selection tool, the Gaussian correlation structure (implemented with the corGaus function in R) was selected. Using the spatial correlations structure, the optimal structure in terms of the smoothers was explored. The least significant explanatory variables were dropped and then the model was fitted until all terms were significant. Models with 2-dimensional smoothers (allowing for interaction between two continuous smoothers) were also tried but these models were not better, as judged by the AIC.

The partial Mantel test was applied in order to test whether sites that had similar species composition, also had similar environmental conditions, while filtering out any spatial effects (Legendre and Legendre, 1998 & Zuur *et al*., 2007). The Bray-Curtis index was used to calculate the similarity between the sites in terms of species composition. To calculate a dissimilarity matrix between the sites in terms of environmental conditions, surface salinity, surface temperature and bottom depth was standardised and the Euclidean distances calculated. The third matrix, required for filtering out the spatial effects, is based on Euclidean distances between spatial coordinates of the sites. The partial Mantel test calculated the Pearson correlation between the elements of the first matrix, while partialling out the effects of the third. A permutation test was used to assess significance with results based on 1000 permutations.

All statistical calculations were carried out in the software Brodgar (www.brodgar.com), the gamm function from the mgcv library in R (R core team, 2007), and the vegan library in R.

RESULTS AND DISCUSSION

Environmental description of the study area

The ichthyoplankton survey presented in this study covered environments of distinct hydrographical characteristics in the northeast Atlantic. Sea surface temperatures obtained from the CTD profiles, ranged between 9 ºC and 12 ºC and salinity between 35.1 to 35.5. Lowest values of temperature and salinity were found above the Rockall, the Faroe and the Hutton Banks, while highest sea surface temperatures and salinities were measured in the Rockall Trough and along the shelf edge. Across the Faroese plateau, cold less saline water domed over the eastern part and also close to the shelf edge leaving the isotherms to form a V-shape across the Wyville-Thompson ridge. Isotherms also domed over the shallowest part of the Porcupine Bank and over the Rockall Bank where water temperatures decreased by more than a degree compared to surrounding waters (Fig. 2). These cold water domes have previously been documented for the Porcupine Bank (Mohn *et al.*, 2002 & White *et al*., 1998) and the Rockall Bank (Dooley, 1984 & Mohn and White 2007) and constitute Taylor columns, which are formed when isopycnals slope over isolated or quasi-isolated bathymetries.

Species distribution related to environmental parameters

A total of 11,636 larvae were removed from the 172 plankton samples taken in this study and divided into 71 species groupings. The most abundant species larvae was *Maurolicus muelleri* (Gmelin, 1788), a mesopelagic fish of the Sternoptychidae family. *Maurolicus muelleri* larvae were found in all but nine of the sampling stations, with highest abundances being recorded in deep waters such as the Rockall Trough, and lowest abundance in the shallow waters above the Rockall Bank, the Porcupine Bank and the continental shelf (Fig.3). Just over 35% of all larvae found on the survey were lantern fishes (Family *Myctophidae). Benthosema glaciale* was the most abundant of myctophids and its distribution pattern was very similar to that of *M. muerlleri* with high concentrations found in deep waters, decreasing in the shallow waters over most of the banks (Fig. 3). Larvae of both species have previously been recorded in deeper waters off the Irish coast at high abundances (Acevedo *et al.,* 2002, Horstman and Fives, 1994 & O' Brien and Fives, 1995). Other abundant lantern fish larvae recorded in this study were those belonging to the myctophid genus *Lampanyctus*; which were also concentrated in the deeper waters of the Rockall Trough. Myctophidae and Sternopychidae are not commercially exploited but, their importance in the ecosystem should not be underestimated. They are mesopelagic species which undergo diel vertical migrations, and are thus an important link between the upper euphotic layers of the water column and the deeper aphotic zones (Torgersen and Kaartvedt, 2001). Deepwater fisheries inhabiting the continental slope as well as seamounts feed on these species and it is believed that this energy contribution is critical to the maintenance of their populations (Gordon, 1979 & Koslow,1997).

Larvae of demersal fish species had a very different distribution to those of the mesopelagic groups, being mainly concentrated along the shelf edge and above the submarine banks. The Rockall Bank presented an important spawning and larval ground for species such as witch *Glyptocephalus cynoglossus* (L.). *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809)*, Sebastes vivipaous* (Kroyer, 1845), *Callyonomys* sp. as well as gadoids such as *Gadiculus argenteus thori* and *Melanogrammus aeglefinus,* while the lemon sole *Microstomus kitt* (Walbaum, 1792) was concentrated along the slope and the Rockall Bank (Fig.3). The Partial Mantel statistic, based on Pearson's product-moment correlation using depth, salinity and temperature was r =0.1682 ($p< 0.001$) indicating that the similarity between sites in terms of species composition was significantly correlated to the similarity between sites in terms of environmental conditions also when the spatial correlation was filtered out. Results further showed that reapplying the partial Mantel test with different subsets of explanatory variables (Table 2) gave similar results, suggesting that the habitats characterised by temperature, salinity and bottom depth influence species composition. This test confirmed the results that that there was a strong species association with different environmental variables whereby oceanic areas had high numbers of individuals from a small number of mesopelagic fish species, while offshore marine banks were characterised by species rich larval assemblages from primarily demersal fish species.

Species richness related to depth

The relationship between species richness and environmental variables was further explored with GAMM, which showed that bottom depth had a negative effect on larval species richness and that this relationship was highly significant [significance of smooth terms s(Bottom Depth): edf = 1.975, F =6.692 and p-value = 5.05 e-05]. Highest levels of species richness were found on the offshore banks, ie the Rockall Bank and the Porcupine Bank followed by the slope stations, while the deep water stations of the Rockall Trough and the Hutton Bank were characterised by lower species richness (Fig. 3).

The prevailing oceanographic conditions, in particular the Taylor columns, are believed to be important factors in the creation of these larval diversity hotspots above the Porcupine and Rockall Banks. Taylor columns occurring above the banks cause anticyclonic circulation patterns (Kloppmann et al., 2001; Mohn et al., 2002 & Mohn and White, 2007), which in turn can cause the entrapment of plankton. For both banks it has been demonstrated in *in situ* studies and model simulations (Bartsch and Coombs, 1997, Kloppmann et al., 2001 & Mohn and White 2007) that fish eggs spawning above are subsequently retained in the area. Furthermore, elevated nutrient levels persist over the banks (White et al., 1998) and chlorophyll concentrations on the Porcupine Bank and particularly on the Rockall Bank are much higher compared to the surrounding waters

(Mohn and White, 2007). It can therefore be assumed that an effective entrainment system coupled with enhanced productivity has resulted in diverse larval assemblages above these offshore banks. These larval assemblages are part of isolated and self-sustaining demersal fish populations, some of which are commercially exploited (Newton et al. 2008).

The fact that these offshore banks are larval diversity hotspots and that their resident fish populations are dependant on the prevailing oceanographic conditions has important implications for their fisheries management. Firstly, if it can be assumed that the larvae are primarily derived from resident populations, then the residing demersal fish communities are species rich. In the Rockall mixed demersal fishery the non-commercial species, contributing to this high biodiversity, are caught as bycatch and can be subsequently discarded (Newton et al. 2008). To maintain diversity, management needs to take account not only of the target species but of the whole fish community. Secondly, retention of the planktonic life stages is dependant on the circulation pattern. As a consequence, recruitment variability of fish populations on isolated marine banks is often higher than that of nearby shelf populations; and this has been shown to be the case for Rockall haddock (Myers and Pepin 1994). This could explain the wide fluctuations of abundance and catches of haddock populations residing at Rockall in surveys and the fishery as noted by Newton et al. (2008). This variability needs to be taken into consideration when assessing and managing such stocks.

In conclusion, this study has shown that there are distinct larval communities in different habitats oft the Northeast Atlantic which are closely associated with prevailing oceanographic conditions. Water depth is an important factor in determining species composition and contributing to species richness. Particular favourable environments for species richness of fish larvae seem to be the offshore banks such as Rockall and

Porcupine. For their sustainable management it is important to recognise the distinctness of their habitats and communities and to manage activities at this scale.

ACKNOWLEDGEMENTS

The authors would like to thank the skipper and the crew from the MFV "Atlantean" for their assistance during the survey. The survey was funded by the Northwest Pelagic Management and Advisory Committee.

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Expl. Variable	Mantel statistic r	Significance:
"Depth","Temp","Sal"	0.1682	< 0.001
"Depth","Temp"	0.1339	< 0.001
"Depth","Sal"	0.108	0.009
"Temp","Sal"	0.1736	< 0.001
"Depth"	0.06428	0.059
" Temp"	0.1348	0.002
"Sal"	0.09256	0.012

Table 1. Statistical parameters for the mantel test

FIGURE HEADINGS

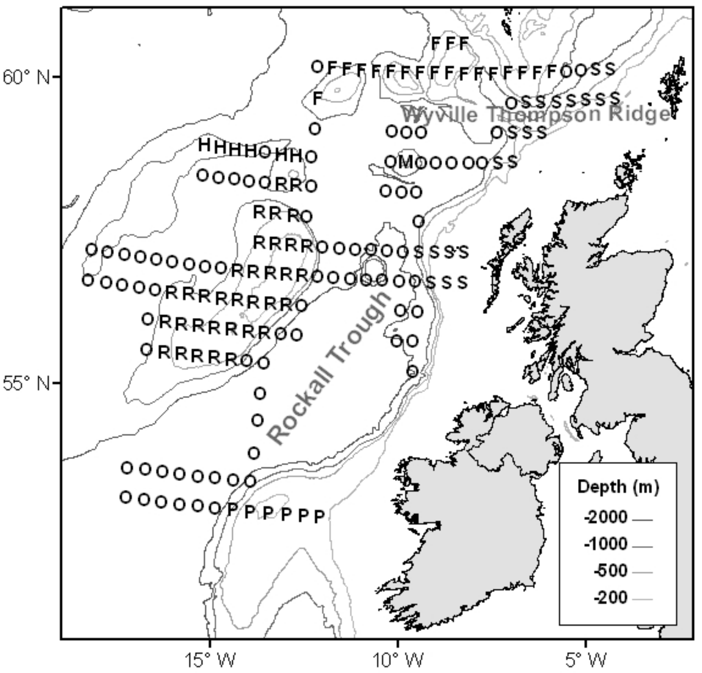
Fig. 1. Sample stations of 2002 survey and geographical locations (Submarine bank stations <1000m: 'P'-Porcupine Bank, 'R'-Rockall Bank, 'H'-Hatton Bank, 'F'-Faroese Plateau, 'M'- Anton Dhorn Seamount; 'S'-shelf stations <1000 m depth and 'O'-offshore stations ≥1000m).

Fig. 2. Vertical temperature and salinity profiles along the transects 60.45°N (upper panel); 57.15°N (middle panel) and 53.15°N (lower panel) with temperature (°C, left) and salinity (right) contour plots at selected stations.

Fig. 3. Conditional box plots of species richness and the 11 most abundant larval species on geographical area, areas are coded as follows: 'F'-Faroese Plateau, 'H'-Hatton Bank,, 'M'-Anton Dhorn Seamount, 'O'-offshore stations ≥1000m, P'-Porcupine Bank, 'R'-Rockall Bank, and 'S'-shelf stations <1000 m depth.

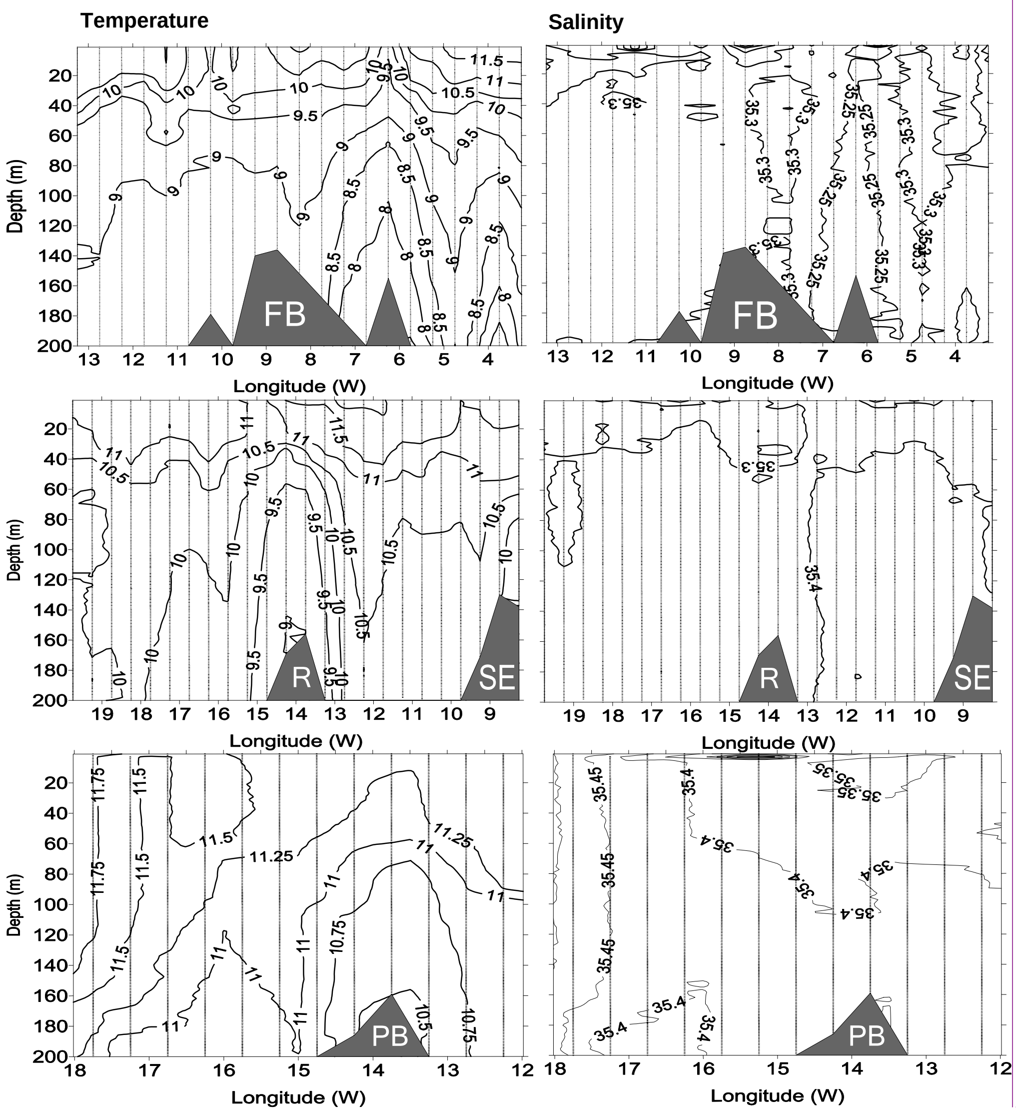
Figures

Fig.1)



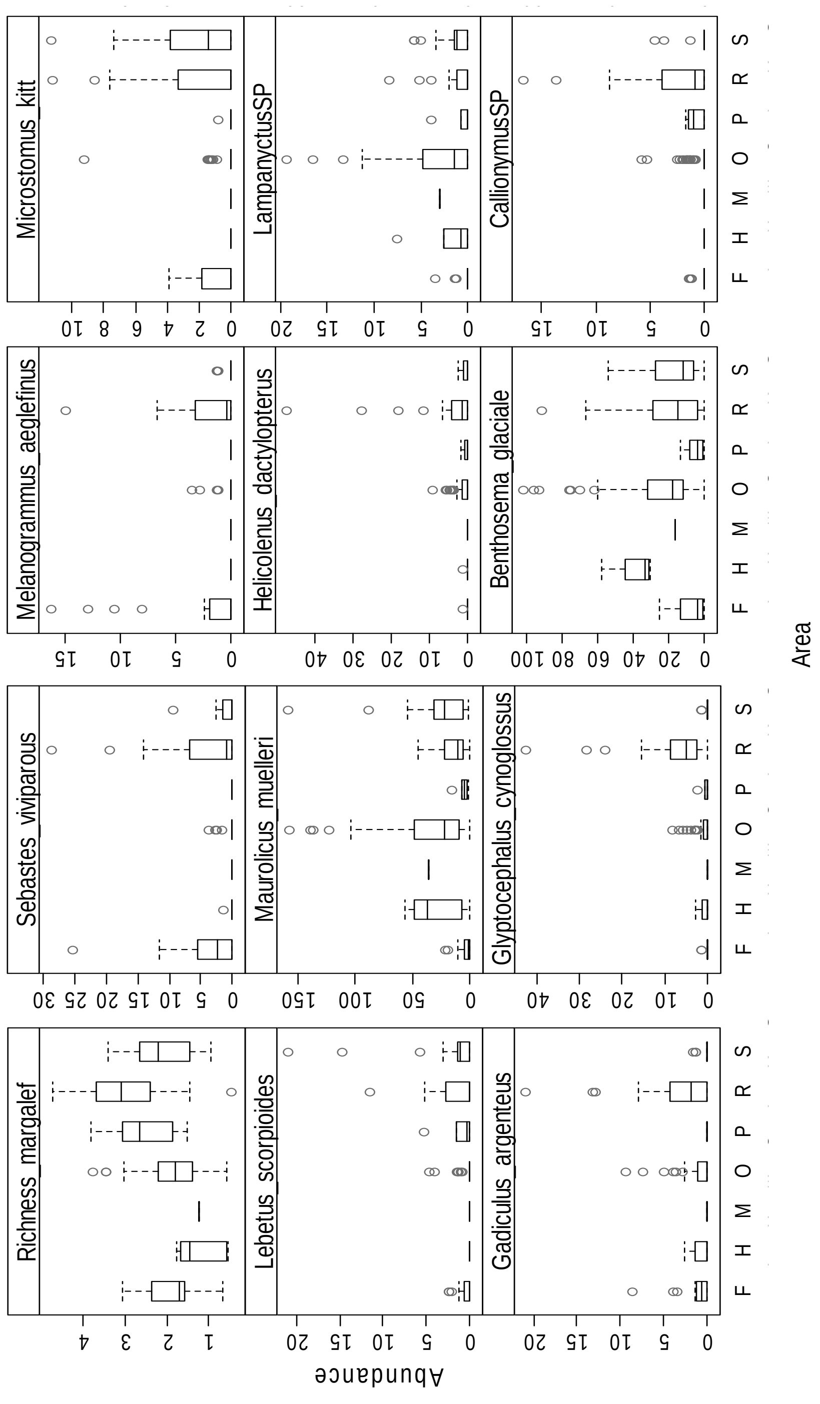
Comment [BP1]: Can this be of nicer graphical quality?

Fig. 2.)



Comment [BP2]: Need to include temperature and Salinity headings

Fig.3)


Richness_margalef
Sebastes_viviparous
Melanogrammus_aeglefinus
Microstomus_kitt
Lebetus_scorpioides
Maurolicus_muelleri
Helicolenus_dactylopterus
LampanyctusSP
Gadiculus_argenteus
Glyptocephalus_cynoglossus
Benthosema_glaciale
CallionymusSP
Abundance
Area
F H M O P R S