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The North Atlantic subpolar gyre regulates the spawning distribution of blue whiting (Micromesistius poutassou Risso)

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1   **The North Atlantic subpolar gyre regulates**

2   **the spawning distribution of blue whiting (*Micromesistius poutassou* Risso)**

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24   **Abstract:** The spawning stock of blue whiting, an economically important pelagic gadoid in the

25   North Atlantic Ocean, increased threefold after 1995. The reproductive success of the stock is

26   largely determined during the very early stages of life, but little is known about the spawning

27   dynamics of this species. We here show that the spawning distribution of blue whiting is variable,

28   regulated by the hydrography west of the British Isles. When the North Atlantic subpolar gyre is

29   strong and spreads its cold and fresh water masses east over the Rockall Plateau, the spawning is

30   constrained along the European continental slope and in a southerly position near the Porcupine

31   Bank. When the gyre is weak and conditions are relatively saline and warm, the spawning

32   distribution moves northwards along the slope and especially westwards covering the Rockall

33   Plateau. The apparent link between the spawning distribution and the subpolar gyre is the first

34   step towards understanding the reproduction variability, which currently is the main challenge for

35   appropriate management of the blue whiting stock.

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37   Keywords: Long-term, Climate variability, North Atlantic Subpolar gyre, Fisheries, Spawning

38   distribution.

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Introduction

49   The northern blue whiting (*Micromesistius Poutassou* Risso) is a pelagic gadoid mainly

50   occupying the waters between the spawning grounds west of the British Isles and the feeding

51   areas in the Norwegian Sea (Bailey 1982). The spawning stock of blue whiting has increased

52   dramatically in the late 1990s (Fig. 1) due to a succession of strong or extremely strong year

53   classes (ICES 2007). The fishery intensified correspondingly and has in recent years been one of

54   the largest fisheries in the North Atlantic Ocean (ICES 2007). Concurrent large changes have

55   occurred in the ocean circulation in the north-eastern Atlantic (Hakkinen and Rhines 2004),

56   resulting in a rapid temperature and salinity increase west of the British Isles after the mid-1990s

57   (Hatun et al. 2005; Figs. 1 and S1). Noting the tight temporal correlation between these events,

58   we here ask whether the changes in marine environment and the blue whiting stock are causally

59   related.

60   Possible causal relations are probably complex as the environment influences many ecological

61   components simultaneously. Blue whiting are sensitive to temperatures and salinities during the

62   spawning period (Schmidt 1909), and the main spawning grounds are located west of the British

63   Isles (Fig. 2), where large oceanographic changes are known to take place (Holliday 2003).

64   The water-masses of the north-eastern Atlantic at different depths have different origins with

65   their own recognizable planktonic fauna or flora, according to their physical, chemical,

66   biochemical or biological features (Fraser 1961). The subpolar gyre controls the flow trajectory

67   of the North Atlantic Current (NAC) in the north-eastern Atlantic. When the gyre is strong and

68   extends far eastwards, a branch of the NAC peels off into the Rockall Trough, dragging cold and

69   low-salinity subarctic waters over the Rockall Plateau (Fig. 3a). When the gyre weakens and

70   shifts westwards, it allows subtropical water to spread north and west (Fig. 3b), resulting in much

71   warmer and more saline conditions. The strength of the subpolar gyre, and thus the hydrographic

72   conditions in the Rockall region, has been represented by a so-called *gyre index* (Hatun et al.

73   2005; Fig. S1)

74   Since blue whiting are sensitive to hydrography while spawning in a region characterized by

75   large water mass exchanges, one might expect that the marine climate must influence the

76   spawning distribution of blue whiting. The blue whiting fishery has historically been most

77   intensive along the European continental slope, primarily near the Porcupine Bank, but also west

78   of the Hebrides, as illustrated in Fig. 2. These areas are typically thought of as the main spawning

79   grounds of blue whiting (Monstad 2004). However, investigations of blue whiting larvae before

80   the fishery commenced in the late 1970s indicated, on the other hand, that the Rockall Plateau

81   was the principal spawning ground, as opposed to the Porcupine Bank (Henderson 1957; Fig. 2).

82   Thus, there are apparent conflicting statements about the spawning areas of blue whiting and only

83   limited explanations for their spawning dynamics (Bartsch and Coombs 1997; Skogen et al.

84   1999).

85   The dominance of the Rockall Plateau as a spawning ground was particularly pronounced

86   during the warm early 1960s, but the spawning distribution shifted southwards towards the

87   Porcupine Bank during the late 1960s (Bainbridge and Cooper 1973) when temperatures

88   decreased in the region (Fig. 1). The stark contrast between the spawning distributions reported

89   during the mid-nineteenth century warm period and the cold early 1990s (Fig. 2) suggests a link

90   between the marine environment and the spawning dynamics of blue whiting. Bainbridge and

91   Cooper (1973) postulated that the source of this variable distribution probably involved

92   environmental variables; that the source of this variability might be found in regions remote from

93   the spawning areas and that they might affect the stock after a considerable time lag. They also

94   stated that further progress on this topic had to await better environmental data over a longer run

95   of years.

96   Since that work was published, we have witnessed the large mid-1990 changes in both the

97   recruitment (and stock size) of blue whiting and also in the marine climate. Additionally, physical

98   time series are now available that link the previous (1960s) warm period to the recent (post-1995)

99   warm period. It is therefore timely to look at the previous and the present spawning distributions

100   and to collectively examine these in light of the oceanographic changes that have taken place.

101   In trying to approach the fundamental question of a causal link between marine climate and

102   blue whiting reproduction, we here limit the aim to document a link between the spawning

103   distribution of blue whiting and the variable marine environment in this region. The working

104   hypothesis we explore here is that the spawning distribution is predominately controlled by the

105   marine climate conditions to the west of Great Britain and Ireland, moving north along the

106   European continental slope and west over the Rockall Plateau during (saline and warm) periods

107   when the subpolar gyre is weak, and south towards the Porcupine Bank during (fresh and cold)

108   periods when the gyre is strong.

109

110   **Material and Methods**

111   **The NISE hydrographic database**

112   A comprehensive hydrographic (temperature and salinity) dataset has been compiled in

113   association with the project *Norwegian and Iceland Seas Experiment* (NISE). The basis of this

114   dataset is the public database maintained by the International Council for the Exploration of the

115   Seas (ICES) (www.ices.dk). This database is then supplemented by data from the Marine

116   Research Institute, Iceland; Institute of Marine Research, Norway; the Faroese Fisheries

117   Laboratory; the Arctic and Antarctic Research Institute, Russia and Geophysical Institute,

118   University of Bergen, Norway and the World Ocean Circulation Experiment

119   (WOCE)(www.woce.org). The data used here (post-1980) are generally measured by CTD

120   (Conductivity, Temperature, Depth) sondes, but data from the Argo float array

121   (www.usgodae.org) have also been included. Data quality control has been performed by each

122   data contributor, but some additional data cleaning has been applied to the dataset by NISE

123   (Nilsen et al. 2008).

124

125   **Acoustic biomass survey data**

126   Acoustic abundance estimates of blue whiting in the spawning areas from 1981 and onwards

127   were obtained from the annual blue whiting surveys reported in the ICES "Northern Pelagic and

128   blue whiting Working Group" reports (ICES 2007) as biomass (tons) averages over 0.5° latitude

129   x 1° longitude (1981-2001).

130   During the standardized surveys, continuous acoustic recordings of fish and plankton were

131   collected along the cruise tracks using calibrated 38 kHz echo sounder systems. The acoustic

132   recordings (area backscattering by each nautical mile, s_A) were allocated to blue whiting based on

133   the composition of the trawl catches taken whenever needed to identify the acoustic scatterers as

134   well as by visual scrutiny of the echo recordings, whereafter biomass estimates were calculated

135   by multiplying abundance in numbers by the average weight of the fish in each statistical square

136   (Foote 1987; Toresen et al. 1998).

137   The annual surveys were carried out from mid-March to mid-April with less than two weeks

138   difference in timing. The error introduced by a variable timing in relation to the spawning

139   progress should be minor compared to the large spatial shift revealed by these data. The surveys

140   are widely regarded as representing the actual spawning distribution and not the pre or post-

141   spawning migrations. The most recent data (after 1995) originate from joint international surveys,

142   while the older data are obtained predominately from Norwegian surveys, with two years from

143   Russian surveys.

144   Furthermore, the fish present in the area at spawning time are mostly actively spawning blue

145   whiting. The proportions of immature fish in the spawning area varied in most of the years

146   between nil and 10%, with some exceptions, e.g. around 15% in 2001, 1998, and 1989, mainly

147   due to rich year-classes contributing as young fish (1 or 2 group) in the area (ICES 2007). The

148   survey coverage included the Porcupine Bank area, the shelf edge west of the Hebrides all years

149   except in 1982, 1997 and 2001. The Rockall Plateau area has been regularly covered since 1998,

150   but only occasionally during the 1980s and early 1990s (Fig. 4a).

151

152   **Blue whiting larvae data**

153   Blue whiting larvae data were obtained from the Continuous Plankton Recorder survey (CPR)

154   (Reid et al. 2003). The survey is a monitoring programme using a high-speed plankton sampling

155   machine that is towed at 10-m depths behind ships of opportunity on standard routes each month

156   of the year. The data presented here are obtained from tows performed by Ocean Weather Ships

157   patrolling the waters west of the British Isles from 1951 to 1970 (Bainbridge and Cooper 1973).

158   These data have kindly been reworked and made available to us by Sir Alister Hardy Foundation

159   for Ocean Science (www.sahfos.ac.uk).

160

161   **Fisheries catch statistics**

162   Under the NEAFC (North Eastern Atlantic Fisheries Commission, www.neafc.com) scheme,

163   vessels report to their respective (national) Contracting Parties and this information is shared via

164   the NEAFC Secretariat's database. The blue whiting catch statistics applied here are obtained

165 from this database. The data are available as monthly values of the total catch gridded onto 0.5º

166 latitude x 1º longitude rectangles and differentiated for each national fleet. Data are exclusively

167 used from the Norwegian fleet, as the spatial distribution of this fleet was not limited by political

168 regulations. The other major fishing nations for blue whiting, the Faroe Islands and Russia had

169 only limited or no access, respectively, to European Union waters during most of the period from

170 1980 to 2007. The fishery in spring is focused on spawning blue whiting. We assume that the

171 figures given represent catches of adult spawning blue whiting with proportions of immature fish

172 comparable to those in the surveys reported above, as the fishery tend to selectively concentrate

173 on large (adult) and thus mature fish.

174

175 **Regional gyre index**

176 A regional gyre index, based on simulated sea surface height, has been produced here. This is

177 done by repeating the analysis of Hatun et al. (2005), while limiting the analysis to a

178 geographical region in the north-eastern Atlantic Ocean (54-66°N, 30-0°W). The regional index

179 presented here is similar to the one presented by Hatun et al. (2005), except from a dip in the

180 mid-1980s, which is largely ascribed to dynamics in the Irminger and Labrador Seas. The

181 employed numerical Ocean General Circulation Model (OGCM) is the Nansen Center version

182 (Bentsen et al. 2004; Drange et al. 2005) of the MICOM (Miami Isopycnal Coordinate Ocean

183 Model) (Bleck et al. 1992), forced with daily mean NCEP/NCAR (Kalnay et al. 1996) reanalyses

184 of fresh water, heat, and momentum fluxes for the period 1948-2003. Since this model system

185 terminated in 2003, the gyre index has been extended to 2006 using satellite altimetry (Hakkinen

186 and Rhines 2004, updated).

187

188

189   **Use of spatial data transformations**

190   The biological and physical data sets described above are generally scattered in both time and

191   space, with variable resolution, making direct comparisons difficult. The survey biomass and the

192   hydrographic data are most densely distributed along the European continental slope (roughly

193   meridional) (Fig. 4), while the CPR larvae data are most densely distributed along track lines

194   fanning out westwards from the continental slope towards Hatton Bank (Bainbridge and Cooper

195   1973). To enable meaningful comparisons, each dataset has been transformed onto a common

196   axis, following the regions with densest data coverage.

197   To illustrate meridional shifts in the survey biomass and the hydrography along the European

198   continental slope, these data have been transformed onto a curvilinear axis (*s*-axis) tracking the

199   high density of observations along the continental shelf-edge, starting within the Porcupine

200   Seabight in the south (50.5°N), and continuing with points along the slope north to 61°N, west of

201   Shetland (Fig. 4). To illustrate blue whiting larvae distribution shifts on-off the Rockall plateau,

202   the CPR larvae data are transformed onto a rectilinear axis (*r*-axis) extending from the

203   continental slope north-westward towards the Hatton Bank (Fig. 8a).

204   The value at a given position *x* along these axes is calculated as a weighted average of the

205   available observations within a truncation radius (r_0) around this position. If too few observations

206   are available near a position *x*, the truncation leaves the transformed value void, instead of having

207   it represented by only a few too remotely positioned observations. The transformed value at

208   position *x* can be written as:

209

210   (1)
$$\hat{D}(x) = \frac{\sum_i^N D_i w(d_i)}{\sum_i^N w(d_i)}$$

211

212   where N is the number of observations (D_i) within the truncation radius r_0, and w is a weight,

213   which is a function of the distance d_i from position x. A Gaussian weighting function was used,

214   as it gives a smooth distribution and its properties are easily understood. This weight is given by:

215

216   (2)
$$w(d) = \exp\left(\frac{-d^2}{2\tau^2}\right)$$

217

218   where d is the distance between position x and the location of the observation, and τ is the width

219   of the filter. Since we are interested in shifts in distributions more than the inter-annual

220   abundance variations, the biological observations have been normalized by the annual along-axis

221   mean.

222

223   **Results**

224   **Meridional shifts**

225   *Survey biomass and the subpolar gyre*

226   Meridional shifts in the concentration of spawning blue whiting along the European

227   continental slope (s-axis) are seen to co-vary with the dynamics of the subpolar gyre (Fig. 5a).

228   For transforming the survey data onto the s-axis, these biomass observations are regarded as data

229   points located in the centre of each 0.5° latitude x 1° longitude square, as presented in the ICES

230   reports. The Gaussian filter width (τ) and the truncation radius (r_0) were both 100 km, as this is

231   comparable to the size of each data square. The denominator in equation (1) removes the effect of

232   high or low survey coverage in an area, and the obtained value is thus consistent and comparable

233   along the entire s-axis. This gives a normalized Gaussian-weighted mean-density of blue whiting

234   observed within a 200-km wide swath along the s-axis, including the spawning period every year

235   since 1981 (Fig. 5a).

236   The regional gyre index is plotted onto the survey biomass map (black curve Fig. 5a), together

237   with the salinity (red curve) observed along a section (Ellett Line; Fig. 4b) extending from the

238   continental shelf towards the Rockall Bank across the northern Rockall Trough (Holliday et al.

239   2000). The salinity is averaged over depth range 0-800 m, and the time series illustrates the

240   strong subpolar gyre related exchanges of water masses around Rockall, as previously

241   demonstrated (Hatun et al. 2005). Salinity is shown since this is a more conservative tracer than

242   temperature, and thus a better indicator for oceanic advection.

243   The gyre was relatively weak in the early 1980s, the salinities were high and whilst survey

244   coverage is incomplete during this time, the available observations suggest that spawning has a

245   northerly orientation, taking place on the shelf edge west of the Hebrides (~58°N) (Fig. 5a). The

246   gyre intensified appreciably in the early 1990s, resulting in very low salinities and the largest

247   spawning concentrations in the Porcupine Seabight, to the far south. The sudden weakening of

248   the subpolar gyre after 1995 enforced a rapid increase in salinities and a clear northward shift of

249   spawning activity. Since about 2003 the gyre has intensified slightly, salinities have again

250   decreased and the spawning distribution has retracted somewhat toward the south. Statistical

251   analysis shows significant correlations between the location of the maximum spawning

252   concentrations on the s-axis and both the gyre index ($r = -0.56$, df $=15$, $p = 0.021$) and the

253   average salinity on the Ellett Line ($r = 0.62$, df $= 15$, $p = 0.007$). Similar correlations are seen

254   using the centre of mass of the distribution as the dependent variable instead of the location of the

255   maximum.

256

257 *Hydrographic threshold*

258   The largest concentrations of spawning blue whiting are observed within specific salinity (Fig.

259 5b) and temperature (Fig. S2) ranges. Demonstrating this requires considerable hydrographic data

260 distributed along the southward migration route of the pre-spawners. This data material is not

261 available over the open ocean areas (Fig. 4b), and the analysis has therefore been done along the

262 *s*-axis, bearing in mind that this might not entirely represent the environment experienced by the

263 migrating fish.

264   The hydrographic data from the spawning period (March to June) were first interpolated onto

265 300-m depths using the software Ocean Data View (Schlitzer 2007). The salinity at 300 m,

266 considered as representative of the environment experienced by spawning blue whiting (Bailey

267 1982), was then transformed onto the *s*-axis. The result was, however, not sensitive to the choice

268 of depth, since the water column is rather homogeneous after winter convection. The Gaussian

269 filter width (τ) and the truncation radius (r_0) were both 50 km (see Fig. 4b). This gives salinities

270 at 300-m depths, along the continental slope from 50°N to 61°N, for the spawning period every

271 year since 1981, as shown in the time-longitude (Hovmüller) plot in Fig. 5b.

272   The isohalines move south until 1995, followed by a subsequent northwards shift, resembling

273 the variability of the subpolar gyre and the survey biomass (Fig. 5a). This shift is clearest for the

274 35.35 to 35.45 psu isohalines (black curves in Fig. 5b). A second point to note is that the

275 anomalies occur in pulses – one around 1990, one around 1997 and one around 2003. The two

276 latter pulses have their counterpart in the gyre dynamics, while the pulse around 1990 does not.

277   A similar analysis has been performed using temperatures (Fig. S2), leading to similar

278 conclusions: Blue whiting prefers to spawn within relatively narrow ranges of salinity (35.35-

279   35.45 psu) and temperature (9-10°C), in gross agreement with previous findings (Henderson

280   1957; Schmidt 1909).

281

282   **On-off the Rockall Plateau**

283

284   *Hydrography*

285   The above analysis suggests that a salinity range of 35.35-35.45 psu, a temperature range of 9-

286   10°C, or similar water mass characteristics related to these hydrographic ranges, govern the

287   spawning distribution of blue whiting. If this result is generally valid, we would expect to see

288   evidence of spawning activity throughout these water bodies, not just within the relatively narrow

289   range covered by the ICES acoustic surveys considered here (Fig. 4a).

290   The mid-1990s weakening of the subpolar gyre (Hakkinen and Rhines 2004) (Fig. 5a)

291   represents, as mentioned, a particularly pronounced shift from a subarctic influenced regime to a

292   subtropical influenced regime. This period is thus used to depict the variable dynamics of the

293   system. Composite maps of salinities at 300 m for the low-saline pre-1995 decade (Fig. 6a) and

294   the saline post-1995 decade (Fig. 6b) illustrate that the salinity changes are even larger around the

295   Rockall Plateau than near the continental shelf. The salinity interval (35.35-35.45 psu) in which

296   most spawning is observed near the continental slope (Fig. 5b), does not cover the Rockall

297   Plateau before 1995 (Fig. 6a), but does during the decade thereafter (Fig. 6b). A similar statement

298   can be made based on temperatures (Fig. S3). Does this mean that blue whiting also spawned

299   near the bank after 1995?

300

301

302

303   *Fisheries*

304   The distribution of the spawning-fishery provides some insight into this question. A marked

305   westward shift occurred in the fishing location of the Norwegian fleet during the mid-1990s (Fig.

306   7). No catches of blue whiting are reported west or south-west of the Rockall Bank before 1996

307   (Fig. 7a), while very large catches are reported there after 1996 (Fig. 7b). The Norwegian fleet

308   was not greatly-limited by political regulations in the Rockall region, and should therefore be a

309   reasonably unbiased proxy for the distribution of spawning fish in this region. In the absence of

310   more reliable biological observations of blue whiting, this data is an indication of significant

311   spawning west of the Rockall Plateau after the 1995 hydrographic shift.

312

313   *Rockall-continental slope larvae distribution and sea surface temperature (SST)*

314   Historical observations of larvae from the CPR survey also provide insight into the presence of

315   spawning over the Rockall Plateau. CPR larvae data from the northern Rockall Trough during the

316   period 1951-1970 have been transformed onto a linear axis (r-axis) from the continental slope at

317   57°N extending north-westwards towards the Hatton Bank (Fig. 8a), using the Gaussian

318   transformation scheme described above (eqs. 1 and 2). The Gaussian filter width (τ) and the

319   truncation (r_0) radius were both 100 km (see Fig. 8a), in order to encompass a sufficient number

320   of tows without spanning too wide. Only data from the spawning period March-June have been

321   used. Currents in this region generally flow northwards parallel to the continental shelf (Fig. 3)

322   (Ellett et al. 1986) and thus perpendicular to the r-axis, so that drift between spawning and the

323   observation of larvae is not expected to greatly alter the east-west distribution. The analyzed data

324   shows a clear east-west meandering of the larvae concentration evident in the longitude-time

325   (Hovmüller) plot in Fig. 8b.

326   Data regarding salinity in this region are sparse during this early period, and we are forced

327   instead to use SST as a proxy of oceanographic conditions. Comparison with the simulated gyre

328   index in recent times shows that SST represents to first order the oceanographic changes in the

329   region (Fig. S1). However, due to the spin-up period of the numerical ocean model (whose

330   integration started in 1948), the SST time series is considered to be a more reliable measure of

331   oceanographic conditions for the early 1950s-1960s period.

332   When the SST time series is plotted onto the larvae map (red curve in Fig. 8b), good

333   qualitative agreement is seen between the east-west distribution of the larvae and the average

334   SST in this region. Warmer temperatures are seen to cause a westward shift in the larval

335   distribution towards the Rockall Plateau. Statistical analysis shows a significant correlation

336   between the location of the maximum larvae concentrations on the r-axis and the SST ($r = -0.50$,

337   df $= 18$, $p = 0.024$). A similar correlation is seen using the centre of mass of the distribution as

338   the dependent variable.

339

340   **Discussion**

341   **Blue whiting distributions during a century**

342   We here show that the spawning distribution of blue whiting is determined by the

343   oceanographic conditions to the west of Great Britain and Ireland, which in turn are regulated by

344   the North Atlantic subpolar gyre. A century after Schmidt (1909) made the first mapping of the

345   blue whiting distribution, we have now begun to understand how climate and large-scale

346   oceanography shifts and warps this distribution. The first mapping was made during the coldest

347   years (1904-1908) of the twentieth century and Schmidt (1909) observed a "striking absence" of

348   fry west of the Rockall Bank, while significant amounts of fry were observed near the Porcupine

349   Bank. The distribution of fry observed with the CPR during the rapidly warming period from

350   1948 to 1955 contrasted with Schmidt's findings, as no fry were observed near the Porcupine

351   Bank, while large concentrations were observed around the Rockall Plateau (Henderson 1957).

352   The larvae concentrations decreased in the north and increased further south during the late

353   1960s, when the climate again deteriorated and temperatures declined (Bainbridge and Cooper

354   1973).

355   Using acoustic survey data along the continental slope, we have shown that spawning fish

356   were aggregating at a northerly position during the early 1980s, but shifted again southwards

357   towards the Porcupine Bank during the late 1980s and especially during the very fresh and cold

358   early 1990s. After the dramatic decline of the subpolar gyre in 1995, the fish concentrations

359   shifted about 1400 km northwards along the continental slope. The spawning distributions of blue

360   whiting reported here and in the literature, can therefore be better understood by putting them in a

361   century-long hydro-climatic perspective. These hydro-climatic changes have been attributed to

362   the subpolar gyre dynamics for the post-1960 period (Hatun et al. 2005), but the gyre forcing

363   might also have been dominating during the pre-1960 period, although data are too scarce to

364   show this.

365

366   **On-off Rockall**

367   In this study, we especially want to draw attention to rapid changes in the spawning

368   distribution to include the Rockall Plateau. Coverage by the acoustic surveys is inconsistent in

369   this area, and no larvae data are available to document a possible sudden increase in spawning

370   near Rockall after 1995. The fishery catch statistics, however, do indicate a marked shift after

371   1995.

372   Re-analyzing the blue whiting data presented by Bainbridge and Cooper (1973), while

373   focusing on the Rockall Plateau-continental slope dimension, we showed marked on-off Rockall

374   shifts during the two decades 1951-1970. Comparing this with the sea surface temperatures (SST)

375   in the region revealed consistent near-Rockall distributions during warm years, and a near-slope

376   distribution during colder years. This result is consistent with our hypothesis of intensive

377   spawning near Rockall during the warm post-1995 period. The apparent conflicting depictions of

378   the spawning distribution of blue whiting presented by Henderson (1957) and Monstad (2004)

379   can thus be explained by the fact that they represent warm and cold regimes, respectively.

380

381   **Hydrographic escort**

382   We have discussed the spawning dynamics in relation to temperature and salinity mostly

383   because these parameters are widely available and facilitate a century-long perspective on the

384   marine environment-blue whiting link. Henderson (1957) stated that a hypothesis of too high

385   temperatures for spawning near the Porcupine Bank during the 1950s was hardly tenable

386   considering that the same fish species also spawns in the much warmer Mediterranean Sea. In

387   this regard, it is important to understand that SST and salinity changes in the north-eastern

388   Atlantic are proxies for large water mass exchanges. Such redistribution of water masses not only

389   alters temperatures and salinities, but also chemistry and plankton contents in the ocean. The

390   indication that most spawning occurs within narrow ranges of salinities (35.35-35.45 psu) and

391   temperatures (9-10°C) could therefore be an expression of pre-spawning fish seeking the

392   chemical clues or the plankton composition contained by water masses with this temperature-

393   salinity signature.

394   The spawning distribution must, irrespective of the actual guidance mechanism, be determined

395   during the late winter period when the fish is migrating southward. An instructive example of

396   how this may work is that of mackerel (*Scomber scombrus*), a pelagic species with spawning

397   migration dynamics that resemble that of blue whiting. For this species it has been demonstrated

398   that the southward migrating fish swim fast when they are in cold water, but slow down when

399   they encounter warmer waters (Reid et al. 1997). This characteristic has been called

400   *enviroregulation* (Neill 1984). An evolutionary process may have 'programmed' this fish species

401   to deliver their eggs in a specific marine climate and fauna which maximizes the survival of their

402   offspring. If enviroregulation also governs the southward migration of blue whiting, this can

403   explain the association between hydrography and spawning distribution. For example, the

404   preferred hydrographic range does not encompass the Rockall Plateau during the low-saline and

405   cold pre-1995 decade, so pre-spawners located near the bank will continue to swim

406   southeastwards along the salinity/temperature gradient, and thus towards the Porcupine Bank.

407   Alternatively, during the post-1995 period the preferred hydrographic conditions cover the

408   Rockall Plateau, so ripe fish first entering this region will not continue to swim southward, but

409   rather start spawning.

410

411   **A coherent picture from vague components**

412   To illustrate both the long-term and the large-scale changes in the spawning distribution of

413   blue whiting, it has been necessary to utilize many, widely-differing data sources. While each

414   individual source does not provide conclusive evidence supporting our hypothesis, taken

415   together, this material gives a consistent picture of the spawning dynamics.

416   The acoustic survey biomass is associated with uncertainties due to the acoustic method itself

417   and the timing and spatial coverage of the cruises. Although individual years and details of the

418   survey distribution might be unreliable, the characteristic southward shift until the mid-1990s,

419   followed by a northward shift is probably a real signal.

420   The similar pattern seen in the meridional shifts of isohalines along the continental slope are

421   also believable, although data from both near-shelf and more off-shore locations have been

422   included. The data coverage is sparse until 1987, but relatively good thereafter as shown with the

423   black crosses in Fig. 5b. The basic patterns discussed are not greatly influenced by data limitation

424   after 1987. Aliasing due to the seasonal cycle is found to be insignificant since the seasonal

425   salinity variability at 300 m is much smaller than the interannual variability. Only using data

426   during late spring-early summer (March to June) further alleviates the aliasing problem.

427   The mid-1990 salinity changes at 300-m depths were illustrated by lumping scattered

428   observations into a pre-1995 decade and a post-1995 decade, and applying an objective mapping

429   technique (Bohme and Send 2005). Although this is a crude depiction, it probably illustrates the

430   northward flush of high-salinity water in a realistic way, due to the large extent of the mid-1990s

431   salinity changes. We also feel that the extent of the mid-1990s changes in the fishery must be

432   caused by a real shift in the spawning stock, despite the fact that fishery statistics often are

433   strongly biased by mis-reporting, and that the number and efficiency of the trawlers increased

434   greatly during the mid-1990s.

435   Some doubt has been cast on how well larvae data represent spawning distribution since the

436   larvae can have drifted considerable distances since spawning (Bainbridge and Cooper 1973).

437   Furthermore, the larvae data are sampled at 10-m depths and can be significantly influenced by

438   aperture avoidance. The sampled routes towards the weather ships vary somewhat, and the

439   approach of decomposing these data onto an axis (r-axis) could therefore be questioned

440   (Henderson 1957). But the close co-variability between SST and the east-west meandering of the

441   larvae distribution still lends credibility to the result. However, the very low larvae counts near

442   the continental slope during warm years do probably not reflect an absence of spawning there. It

443 more likely reflects a northerly spawning distribution and that the eggs may have been either

444 spawned to the north of the *r*-axis, or already drifted north prior to the time of sampling.

445

446 **Outlook and recruitment**

447 Our ability to link the spawning distribution of blue whiting to the dynamics of the subpolar

448 gyre is perhaps the most promising result in this study. Using realistic numerical ocean models,

449 oceanographic databases and satellite-based observations (Hakkinen and Rhines 2004; Hatun et

450 al. 2005), it is now possible to better understand the dynamics of this gyre and its atmospheric

451 forcing mechanisms (Eden and Willebrand 2001). These issues are not further elaborated here,

452 but will constitute the basis for future work aiming at a better understanding of the blue whiting

453 stock dynamics.

454 Having established a link between the spawning distribution and the marine climate, the next

455 challenges are to explain how the changeable spawning distribution might influence the

456 recruitment to the blue whiting stock. The large shifts in the marine environment will probably

457 influence larvae growth conditions both near the continental slope and near the Rockall Plateau.

458 Assuming that the on-off Rockall Plateau variability of blue whiting spawning activity is the

459 most important mechanism underlying the pronounced recruitment variability, we suggest the

460 following causal relations. Firstly, that eggs and fry starting on the plateau will follow different

461 drift paths from those starting on the shelf, which would enlarge and diversify their nursery area

462 and thereby improve growth/survival opportunities of the larvae. Secondly, that a potentially

463 strong retention of water masses near the Rockall Bank during warm low-gyre index years

464 (Dooley 1984) might provide good local growth conditions. Thirdly, that larval development near

465 Rockall might be in closer synchrony with production cycles of key prey types (zooplankton),

466 than nearer the continental slope (Bainbridge and Cooper 1973).

467   Differentiating between these competing hypotheses is a challenging task which should be

468   validated by i) applying hydrographic drift modeling to investigate how the initial position of

469   eggs and larvae might influence the downstream spread of larvae and the environment they

470   encounter, ii) establishing regular field studies to sample larvae growth/size and feeding

471   intensity/food content simultaneously in the spawning areas and in the downstream larval feeding

472   areas, and relate this to the ambient prey availability and the hydrographic environment and iii)

473   examining expected east-west shifts in the distribution of 0 and 1-year-old blue whiting, by using

474   annual demersal trawl surveys on the Icelandic, Faroese, and North Sea Plateaus (cf. Heino et al.

475   2008).

476   Such questions must be understood before reasonable predictions of the dynamics of the blue

477   whiting stock in a changing environment, natural or man-made, can be made.

478

479   Acknowledgements

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485   References

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572   **Figure captions**

573   **Fig. 1.** Changes in the sea surface temperature (SST) in the north-eastern Atlantic (thin line) and

574   in the spawning stock biomass (SSB) of blue whiting (thick line). The annually averaged SST

575   time series is obtained from the Hadley Centre SST data set (HadSST2) (Rayner et al. 2006), by

576   averaging over a geographical box covering the north-eastern Atlantic (52.5-62.5°N, 27.5-

577   12.5°W). The SSB time series (ICES 2007) has been shifted three years forward in time, which

578   is the time required for new recruits to contribute to the stock biomass.

579

580   **Fig. 2.** Map of the study region, showing places referred to in the text. The gray contours show

581   the mean density of blue whiting larvae during the years 1948-1956 as reported by Henderson

582   (1961). No larvae data are available in the region west of the dashed line (southern part of the

583   Rockall-Hatton Plateau). The intensive spawning areas during the 1980s and early 1990s, as

584   reported by Monstad (2004), are shown in black along the European continental slope.

585

586   **Fig. 3.** Simplified illustration of the source flows to the Rockall Region. (*a*) A strong subpolar

587   gyre results in strong influence of cold subarctic water near the Rockall Plateau (subarctic state).

588   (*b*) A weak gyre results in a warm subtropical anomaly near the plateau (based on Hatun *et al.*

589   2005) (subtropical state). Abbreviations - RP: Rockall Plateau and PB: Porcupine Bank.

590

591   **Fig. 4.** Data coverage and the *s*-axis. (*a*) Spatial coverage of acoustic surveys (1981-2007)

592   showing the fraction coverage of each 0.5° latitude x 0.5° longitude square and (*b*) number of

593   hydrographic stations with available data at 300 meter depths during the 1981-2007 period,

594   binned into the same geographical squares. Squares with no acoustical data or fewer than five

595   hydrographic stations are colored gray. The s-axis is shown with the dots and the truncation

596   radius (r_0) is illustrated with white thin lines. EL: Ellett Line.

597

598   **Fig. 5**. (*a*) Time-latitude/distance (Hovmüller) plot of normalized biomass density of blue

599   whiting along the European continental slope (*s*-axis, see Fig 4). The thick black curve shows a

600   gyre index based on the simulated sea surface height in the north-eastern Atlantic, and the dashed

601   black line shows an extension of this index based on satellite altimetry (Hakkinen and Rhines

602   2004, updated). The red curve shows salinity averaged over depth range 0-800 m at the Ellett

603   Line (Holliday et al. 2000) (see Fig 4b). White areas indicate absence of survey data. (*b*)

604   Hovmüller plot of salinity at 300-m depths along the *s*-axis. Only data from March to June have

605   been included. The salinity range (35.35-35.45) encompassing the densest blue whiting

606   observations in (*a*) is emphasized with thick black lines. Available data points are illustrated with

607   small crosses.

608

609   **Fig. 6.** March-June temperature composites at 300-m depths for (*a*) the fresh pre-1995 years

610   (1986-1995) and (*b*) the saline post-1995 years (1996-2005). The 35.35 and 35.45 isohalines (see

611   Fig. 5b) have been emphasized with thick black dashed lines. RP: Rockall Plateau.

612

613   **Fig. 7.** Distribution of adult catches of blue whiting reported by the Norwegian fleet, averaged

614   over (*a*) the low-saline and cold years from 1989 to 1996 and (*b*) the saline and warmer years

615   from 1997 to 2005. The area of each dot is proportional to the amount of blue whiting fished

616   within a 0.5° latitude x 1° longitude rectangle centered on the dot.

617

618 **Fig. 8.** (*a*) The *r*-axis (black dots) and positions with larvae data from the CPR (red dots) during

619 the period from 1951 to 1970. The truncation radius (r_0) is shown with the blue dashed lines. (*b*)

620 Longitude-time (Hovmüller) plot of the normalized larvae counts. The red line shows the sea

621 surface temperature (SST) as described in Fig. 1. Available data points are shown with the

622 crosses.

623

624

(a)

Bottom depth
■ < 500 m
■ > 500 m

Subpolar gyre

RP

PB

North Atlantic Current

Subtropical Water

(b)

Subpolar gyre

RP

PB

Cold, fresh

Warm, saline