Evidence for substock dynamics within whiting (Merlangius merlangus) management regions

Carlos de Castro1,2, Peter J. Wright1, Colin P. Millar1,3, and Steven J. Holmes1*

1Marine Scotland Science, Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen, AB11 9DB, UK
2Calle Dalia Portal 60, 28109, Alcobendas, Madrid, Spain
3European Commission, Joint Research Centre, Institute for the Protection and Security of the Citizen/Maritime Affairs Unit, 21027 Ispra (VA), Italy
*Corresponding author: tel: +44 1224 295 507; fax: +44 1224 295 511; e-mail: s.holmes@marlab.ac.uk


Whiting in the North Sea and Eastern Channel is currently assessed as a single management unit. However, several studies suggest that this stock may be comprised of more than one subpopulation within a larger metapopulation. A key characteristic of metapopulations is asynchrony in the dynamics of component subpopulations. In this study, indices of recruitment and spawning–stock biomass (SSB) were developed to test for asynchrony across putative subpopulations in the North Sea and west of Scotland. Differences in SSB and recruitment trends were detected, consistent with expectations from metapopulation dynamics. At least three different subpopulation components (southern and northern North Sea, and west of Scotland) were indicated on the basis of differing trends. Analysis of spatial distribution suggested that the boundary between the northern and southern North Sea subpopulations was associated with the change in bathymetry that extended from the coast of Norfolk in England to the southern tip of Norway. The current management system for whiting in the North Sea assumes a unit stock, which is contrary to current sources of biological evidence and seems inappropriate. Consideration of a north–south split along the boundary detected should be beneficial for both assessment and management of the resource.

Keywords: Merlangius merlangus, metapopulation, recruitment, smoothers, SSB, survey indices.

Introduction

There is increasing evidence that fishery management units often do not reflect the population structure of marine fish. An understanding of such structuring is essential for devising effective fishery strategies, both in terms of delineating appropriate spatial scales for management, and avoiding local depletion (Fogarty and Botsford, 2007). Whiting (Merlangius merlangus) is one of the most abundant and widely distributed gadoids in the North Sea (Knijn et al., 1993). Spatial distribution of landings in recent years suggests that there are three major concentrations in the North Sea: (i) around the Northern Isles, (ii) off the eastern English coast, and (iii) in the southern Bight and English Channel (ICES, 2005). These areas correspond to the major areas of whiting eggs found in an ichthyoplankton survey in 2004 of the entire North Sea (Munk et al., 2009). Whiting stock abundance in the North Sea generally began to decline in the early 1990s, reaching an historic low in spawning–stock biomass (SSB) in 2007 (ICES, 2012a). The whiting stock west of Scotland has also experienced a significant decline in SSB beginning in the mid-to-late 1990s, with an historic low in 2005 (ICES, 2012b).

The assessment of whiting in the North Sea, Irish Sea, and west of Scotland has been problematic for many years. Estimates of stock dynamics derived from different sources, such as reported landings, estimated discards, and research vessel surveys, were often contradictory, making coherent assessments extremely difficult. Since 1996, whiting in the North Sea and Eastern Channel (ICES Subarea IV and ICES Division VIIId, respectively) have been assessed as a single management unit. A review group proposed that the apparently contradictory dynamics might be explained if the North Sea whiting stock were comprised of more than one population unit (ICES, 2005).

There are several sources of evidence consistent with the segregation of whiting aggregations between the northern and southern North Sea. Vertebral counts (Roessingh, 1957; Hislop and McKenzie, 1976), anal fin-ray counts (Hislop and McKenzie, 1976), and parasite load (Kabata, 1967; Lang, 1990) differ...
between the northern and southern North Sea. There is also evidence for very limited exchange between the north and south based on tag-recapture experiments (Knudsen, 1964; Hislop and McKenzie, 1976; Tobin et al., 2010). Evidence for genetic differentiation is less clear. Although microsatellite DNA studies (Rico et al., 1997; Charrier et al., 2007) have suggested segregation between the northern and southern aggregations, both studies found very low levels of diversity, and the results were confounded by the use of microsatellites that deviated significantly from Hardy–Weinberg equilibria. Hence, any existing structure is unlikely to reflect substantial genetic drift, but rather limited exchange. Whilst the physical barriers involved in this apparent structuring are not known, changes in bathymetry, currents, jets that cross the North Sea (Brown et al., 1999), and the position of freshwater-influenced frontal zones (Munk et al., 2002) could potentially limit egg and larval exchange. Some intermixing between the northern North Sea (ICES Subarea IV) and the Scottish west coast (ICES Division Vla) occurs during the juvenile phase, although the magnitude of this exchange is unknown (Tobin et al., 2010).

The metapopulation concept may have some value in interpreting marine fish population dynamics in stocks comprised of more than one subpopulation (see for example Smedbol et al., 2002; Grimm et al., 2003; Kritzer and Sale, 2004). Although marine fish metapopulations do not fit the classical extinction and recolonization concept defined by Levins (1969, 1970), physical limits to the dispersal of early life stages and local adaptation can lead to aggregations of fish that are largely demographically independent, whilst not genetically isolated.

Despite the extensive evidence for segregation of whiting aggregations, there has been no attempt to compare demography among putative subpopulations. In this study, spatial and temporal trends of SSB and recruitment for the different areas of the North Sea and west coast were derived from survey data and compared, following Holmes et al. (2008). As asynchrony in population dynamics is important to metapopulation persistence, it may be expected that northern and southern North Sea whiting aggregations would differ with respect to trends in spawning-stock size and recruitment, if they represented different subpopulations. Conversely, if there is frequent exchange between the northern North Sea and west of Scotland, at least during the juvenile phase (Tobin et al., 2010), then these two managed regions may be expected to exhibit similar dynamics. The suitability of the current management units and assessment practices is discussed, with a view to providing a better framework for the management of whiting fisheries in the North Sea and west of Scotland.

Methods

Definition of subpopulation areas

The density distribution of North Sea and west of Scotland whiting was examined using a geospatial smoothing technique (Lindgren et al., 2011) fitted in R using the INLA library (Rue et al., 2009) applied to the quarter 1 (Q1) International Bottom Trawl Survey (IBTS). Numbers-at-age per statistical rectangle for 1986–2011 for the North Sea and Division Vla were downloaded from the ICES “DATRAS” web-based database (http://datras.ices.dk/Home/Default.aspx). Smoothers were fitted to recruitment (age 1 numbers h⁻¹) and spawning biomass (kg h⁻¹) per haul. The resultant plots made it possible to visualize the evolution of SSB and recruitment trends in the area of study, and allowed for refinement of the borders between putative subpopulation areas. This allowed testing of the sensitivity of results to the exact location of boundary. For the SSB trends, the objective was to consider indices at the time when whiting are spawning and hence aggregated in their natal areas. The ideal time would be a Q2 survey, but there are only seven years with such data in the North Sea (and none for Division Vla). The Q1 surveys at least correspond to the early part of the spawning period. Time-series from quarters 3 and 4 are also short, and it is feasible that some mixing may occur outside the long spawning period of this species.

An initial division of the North Sea stock area was placed consistent with previous studies of whiting segregation (Gamble, 1959; Rout, 1962; Williams and Prime, 1966; Kabata, 1967; Hislop and McKenzie, 1976; Pilcher et al., 1989; Rico et al., 1997; Charrier et al., 2007; Tobin et al., 2010), where the North Sea and Eastern Channel management unit for whiting (ICES Subarea IV and ICES Division VId) was divided approximately along the 50-m depth contour north of Dogger Bank (Figure 1a).

The region west of Scotland, as defined by ICES for the current Division Vla stock assessment, has not received the same degree of attention as the North Sea region, and any division of the area was based solely on results from the smoothers. The Eastern Channel (ICES Division VId) was excluded from the analysis. To date, only three years of data for this area were available within the IBTS framework. Data from surveys other than the IBTS, with different gears and procedures, would not be comparable and could eventually lead to erroneous interpretations.

Calculation of indices

Spawning–stock biomass and recruitment indices for each of the defined putative areas were calculated from research vessel survey data. Although there are North Sea data available for 1967–1974, the IBTS area coverage has changed over time, and during the first years, the survey was restricted to the central and southern North Sea. The entire North Sea, Skagerrak, and Kattegat have only been surveyed since 1974 (ICES, 2010).

SSB and recruitment indices for each of the putative areas were obtained by the same procedure used by ICES to produce indices for its stock assessment areas, i.e. as arithmetic means over the statistical rectangles within a particular area. Ages 1–6 were included (numbers of whiting at older ages are negligible and not included). SSB, defined as the total weight of the fish in a stock that are able to spawn, was calculated according to the following equation:

\[
SSB_y = \sum_{a} U_{a,y} \times W_{a,y} \times Mat_{a,y}
\]

where \(U_{a,y}\), \(W_{a,y}\), and \(Mat_{a,y}\) are the numbers, stock weight, and maturity, respectively, for whiting at age \(a\) and year \(y\). Stock weights were taken from the North Sea whiting assessments, as were the time-invariant maturities-at-age, i.e. proportion mature of ages 1 and 2, which were taken as 0.11 and 0.92, with all older fish being mature (ICES, 2012a).

Recruitment \((R)\) was taken to be numbers at age 1 according to the definition of recruits in the whiting assessments:

\[
R_y = U_{1,y}
\]
Statistical analysis
To investigate the degree of synchrony of SSB and recruitment trends between the different subpopulation areas, the modelling approach of Holmes et al. (2008) was used, although paired tests were used this time because only a limited number of areas were being considered. For each paired test, SSB and recruitment indices were log-transformed, and the resultant trends for the different areas were compared by fitting a generalized additive model (Wood, 2006) to the ratio between them. The resulting fit was then compared to a constant fit of this ratio by a standard $F$-test. Model fitting was carried out using the “mgcv” package in R (R version 2.12.1; http://www.r-project.org/). The comparisons were visualized using reference bands (Bowman and Azzalini, 1997). The figures indicate trends that are non-parallel (with 95% certainty) when the results of the smoother pass outside the reference bands. A more detailed explanation can be found in Youngson et al. (2002). For simplicity, figures relating to the indices and the reference band comparisons are shown in relation to the initial geographic boundary between the component North Sea areas only (Figure 1a).

Results
Spawning–stock biomass
Spatial distribution
The geospatial smoothing indicated bands of persistently low density at the boundary between ICES Divisions IVa and VIa, and in the North Sea (Figure 2) in a line that roughly equated to that of the 50-m depth contour (see Figure 1a). However, the width of this latter band of low density varied, and the orientation shifted between years. Nevertheless, the full year-to-year sequence suggested a boundary starting south of the 50-m depth contour in the west (at the Norfolk coast) and keeping the 50-m depth contour in the southern area in the east (Figure 1b; see Supplementary material).

Within the three areas (west of Scotland, northern North Sea, and southern North Sea), there has been considerable temporal variation in patterns of abundance. However, persistent or recurring areas of high adult whiting density are apparent in the northern North Sea (in an area east of Orkney and an area towards the northeast English coast), and in the southern North Sea (in an area off the Dutch coast and in the area of the English Channel). (Figure 2 shows years selected at 5-year intervals; see Supplementary material for figures containing all years).

Temporal trends
There were highly significant differences in SSB trends from the northern and southern North Sea (Table 1). In the northern North Sea, SSB increased to a peak in 1991 and then fell to levels lower than at the beginning of the time-series. In contrast, SSB in the southern North Sea exhibited oscillation around a slowly increasing underlying trend. Only the underlying trend in the southern North Sea is reflected by the fitted smoother (Figure 3a). The reference band figure (Figure 3b) clearly shows the smooth for each region passing outside its reference band.

Considering the northern North Sea and west of Scotland (ICES Division VIa), it is clear that both areas experienced a steep increase in SSB up to a peak in the 1990s before a rapid decline towards the end of the time-series. SSB levels west of Scotland were generally lower than those in the northern North
Sea. There appeared to be a temporal lag between trends, suggesting the trend west of Scotland was delayed relative to that in the northern North Sea (Figure 4a). The pairwise test for non-parallelism was significant at the 1% level (Table 1), and the smooths for each region passed outside the reference bands (Figure 4b). The revised boundary (Figure 1b) did not greatly alter the significance of the pairwise comparison between the northern and southern North Sea (Table 1).

**Figure 2.** Geospatial smooth of whiting SSB (kg h$^{-1}$) and recruitment at age 1 (no. h$^{-1}$) using IBTS quarter 1 survey data. Surface estimated on the log scale by linear interpolation assuming a Matérn spatial covariance function on the sphere. Top panels show recruitment and SSB scales and irregular grid of smoothing method, respectively.

**Recruitment**

**Spatial distribution**

Spatial plots of age 1 whiting indicated that concentrations were less stable in time than for SSB, although a general trend was still discernible. In the northern North Sea, there was a tendency for age 1 whiting to concentrate in coastal areas off the east coast from England to the north of Scotland, with higher densities registered in the areas around Moray Firth and the Firth of Forth.
(Figure 2). In the southern North Sea, age 1 whiting concentrations were persistently found in an area in the middle of the southeastern North Sea off the Dutch, German, and Danish coasts. West of Scotland, the highest densities of age 1 were present in the Clyde Estuary area and lesser concentrations in the waters between the Scottish mainland and the Hebrides known as the North Minch.

Temporal trends
In the northern North Sea, recruitment varied considerably throughout the period of study. The indices suggest a succession of highs and lows, with two noteworthy peaks in the late 1980s and early 1990s. In the southern North Sea, recruitment has oscillated with no obvious trend and considerable noise, although the fitted smoother indicates a long-term decreasing trend (Figure 5a).

As for SSB, recruitment trends in the northern and southern North Sea were significantly non-parallel (Table 2); therefore, their dynamics seem to be asynchronous. The fitted smoothers moved outside the reference bands in the pairwise comparison (Figures 5b). This remained the case when using the alternative north–south boundary. Similarly, significant results were obtained when comparing the northern North Sea to west of Scotland. While recruitment in the northern North Sea declined from early in the time-series, that for west of Scotland peaked in the middle part of the time-series (Figure 6a). Again, the fitted smoothers moved outside the reference bands (Figure 6b).

Comparison of northern North Sea and west of Scotland, assuming a time-lag
The indices generated for the northern North Sea and west of Scotland suggested the same temporal pattern in metrics, albeit separated by a time-lag. In order to explore this further, the northern North Sea data were shifted five years, such that, for example, west of Scotland data for 1995 were compared to northern North Sea data from 1990. With the time-lag applied, recruitment trends in the northern North Sea and west of Scotland tested as parallel, with a $p$-value of 0.52, and the fitted smoothers remained inside their respective reference bands throughout the time-series (Figure 7a).

Figure 7b shows how the fitted smoothers for SSB are surprisingly similar prior to 2005 (albeit outside of their respective reference bands briefly). The $F$-test analysis on SSB, however, yielded a result similar to that obtained when comparing the original trends ($p = 0.0006$). The significance of the result can be attributed to the sharp decline in SSB estimation in Division VIa in the last four years of the time-series.

<table>
<thead>
<tr>
<th>Area</th>
<th>Northern North Sea</th>
<th>Southern North Sea</th>
<th>VIa (west of Scotland)</th>
</tr>
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<td>0.003</td>
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<td>VIa (west of Scotland)</td>
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<td>0.0039</td>
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The numbers give the resultant $p$-value for each comparison when the northern and southern North Sea regions are as defined in Figure 1a (values in lower left cells); as defined in Figure 1b (values in upper right cells).

Figure 3. Comparison of northern and southern North Sea (area definitions as in Figure 1). (a) Log indices of spawning–stock biomass. Solid lines represent the fitted smoothers with 95% confidence bands shown by shaded areas. (b) Pairwise comparison reference bands with lines representing the fitted smoothers, as in frame (a).
Figure 4. Comparison of northern North Sea and west of Scotland (area definitions as in Figure 1). (a) Log indices of spawning–stock biomass. Solid lines represent the fitted smoothers with 95% confidence bands shown by shaded areas. (b) Pairwise comparison reference bands with lines representing the fitted smoothers, as in frame (a).

Figure 5. Comparison of northern and southern North Sea (area definitions as in Figure 1). (a) Log indices of recruitment. Solid lines represent the fitted smoothers with 95% confidence bands shown by shaded areas. (b) Pairwise comparison reference bands with lines representing the fitted smoothers, as in frame (a).
Discussion

Demographically divergent trends were evident between the two putative subpopulations in the North Sea. In the north, SSB peaked in the 1990s and then sharply declined, whilst SSB levels in the southern North Sea oscillated throughout most of the time-series. Recruitment trends were also found to be non-parallel with a high probability. However, recruitment trends were noisier than SSB, and the differences were not as clear on a visual basis. According to Rothschild (2007), recruitment time-series contain internal non-linearities that challenge stationary assumptions and, therefore, are difficult to use to discriminate among stocks. SSB seems to be a better stock differentiator as it acts as a natural filter that integrates or averages recruitment.

The differences between North Sea regions were consistent with expectations from a metapopulation of largely demographically independent subpopulations (Hanski, 1999; Kritzer and Sale, 2004), supporting the segregation indicated by biological studies of population structuring in North Sea whiting. The density distribution of adults was consistent with the previously proposed sub-population boundary corresponding to the 50-m depth contour between eastern England and southern Norway (Pilcher et al., 1989). The tests for synchrony were not significantly affected by shifting the boundary from the 50-m depth contour to the centre of the low adult whiting concentration band indicated by the 3D smoothing. Accordingly, the exact choice of boundary coordinates between northern and southern North Sea subpopulations does not seem critical for assessment purposes.

The comparison of SSB and recruitment trends in the northern North Sea and west of Scotland (ICES Division VIa) suggests that population dynamics in these areas are asynchronous and, therefore, to a certain extent, independent from each other. Whilst tag–recapture experiments do not indicate any appreciable exchange of adult whiting between the northern North Sea and west of Scotland, otolith microchemistry does indicate the potential for some mixing at the juvenile phase (Tobin et al., 2010). However, based on the survey indices, any such mixing does not appear to be sufficient to homogenize dynamics; therefore, whiting west of Scotland and in the northern North Sea should not be treated as a single population unit. Despite the detected asynchrony, SSB trends in both areas show certain similarities, albeit with generally lower indices west of Scotland. There may be some interconnection between the dynamics west of Scotland and those in the northern North Sea, given that a 5-year lag resulted in parallel trends for recruitment. One interpretation is that abundance of whiting in the northern North Sea may, to a certain extent, determine abundance west of Scotland a few years

Table 2. Recruitment: results from pairwise comparisons between northern North Sea, southern North Sea, and west of Scotland (VIa).

<table>
<thead>
<tr>
<th>Area</th>
<th>Northern North Sea</th>
<th>Southern North Sea</th>
<th>VIa (west of Scotland)</th>
</tr>
</thead>
<tbody>
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<td>0.0015</td>
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<td>VIa (west of Scotland)</td>
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The numbers give the resultant p-value for each comparison when the northern and southern North Sea regions are as defined in Figure 1a (values in lower left cells); as defined in Figure 1b (values in upper right cells).

Figure 6. Comparison of northern North Sea and west of Scotland (area definitions as in Figure 1). (a) Log indices of recruitment. Solid lines represent the fitted smoothers with 95% confidence bands shown by shaded areas. (b) Pairwise comparison reference bands with lines representing the fitted smoothers, as in frame (a).
Whether that interpretation is justified, and if so, what the underlying cause is should be explored further. Visual inspection of SSB trends in the three areas, especially the southern North Sea, suggests they might be following a cyclic behaviour. These oscillations could be the result of internal dynamics driven by density-dependent processes that, according to Ray and Hastings (1996), are difficult to detect when densities are averaged over larger scales than the local population.

Divergent trends in subpopulation dynamics may arise from differences in environmental conditions, exploitation regimes, and even internally driven dynamics. In the North Sea, whiting are caught in mixed demersal roundfish fisheries, fisheries targeting flatfish, *Nephrops norvegicus*, and Norway pout (ICES, 2012a). Jennings et al. (1999) and Greenstreet et al. (1999, 2009) analysed the spatial trends in trawling effort in the North Sea and concluded that fishing effort in the North Sea is clearly patchy. Some areas are intensively fished, while others remain relatively lightly fished. Most otter trawling effort was confined to the northeast coast of the UK and east of the Shetland Islands, while the beam trawl effort is largely confined to the southern and eastern North Sea. Areas subject to the greatest fishing intensity roughly matched high adult whiting concentration areas identified in the present study. Although there has been a steep decline in SSB levels in the northern North Sea since the beginning of the 1990s, these levels have only reached values comparable or slightly smaller than those registered at the beginning of the time-series in the early 1970s. This recent drop in SSB levels in the northern North Sea is not obviously connected to changes in fishing activity. After a long period with relatively little change (1960–2000), there has been a marked reduction in overall fishing effort since 2001. This reduction is partly explained by a decrease from 2000 to 2004 in trawl and seine gear types (primarily within the northern North Sea) (Greenstreet et al., 2009). Data collected from all EU nations has also shown a decline in trawl and seine gear effort within ICES Subarea IV between 2000 and 2011, particularly in gear of larger mesh size associated with the whitefish catch. Spatially resolved effort data for these gears for 2003–2011 showed a relatively constant pattern of fishing effort. (STECF, 2012).

The presence of a metapopulation structure has important biological and management implications. A failure to recognize and account for complexity in population structure may lead to erosion of spawning components and have unexpected ecological consequences (Kell et al., 2009). If whiting populations in the North Sea are to be managed effectively, measures should be taken to acknowledge this structuring. Fishery management advice relies strongly on abundance indices formed from arithmetic means across large areas that are considered homogeneous in terms of their stock dynamics (Holmes et al., 2008). If management areas comprise more than one substock with different dynamics, apparent trends may deviate significantly from the real trends leading to inappropriate management advice (Daan, 1991). Consequently, a first and obvious consideration arising from the results is that the current management unit defined for the assessment of whiting in the North Sea may be inappropriate for management purposes because it does not consider the proposed structure of whiting populations in the North Sea. Spawning–stock biomass trends differ considerably between the putative subpopulation areas compared to the entire North Sea.

![Figure 7. Comparison of northern North Sea (5 years +) and west of Scotland (area definitions as in Figure 1). Pairwise comparison reference bands, (a) recruitment, (b) SSB. Lines in the vicinity of the bands represent fitted smoothers to the log indices for the associated area.](https://academic.oup.com/icesjms/article-abstract/70/6/1118/633552)
area, the current North Sea SSB trends reflect those from the northern region, leading to an erroneous perception of the southern subpopulation trends. Therefore, management advice derived from assessments of the entire North Sea could lead to fishing levels inappropriate for either of its constituent subpopulations.

The detected asynchrony between northern North Sea and west of Scotland suggests that, for assessment purposes, these subpopulations should, as is currently done, be considered as different management units. If the suggested population structure in the North Sea is to be acknowledged, new management units should be defined. Any boundary located along the low adult whiting concentration band identified in the present study could be considered suitable for management purposes.

**Supplementary material**

Supplementary material is available at the ICES Journal of Marine Science online version of the paper. It contains figures showing a time-series of results from a geospatial smoother of whiting SSB (kg h⁻¹) and resulting recruitment at age 1 (no. h⁻¹) for 1987–2011 using IBTS quarter 1 survey data. The surfaces were estimated on the log scale by linear interpolation assuming a Matérn spatial covariance function on the sphere. Top panels show recruitment by linear interpolation assuming a Matérn spatial covariance function on the sphere. Top panels show recruitment and SSB scales and the irregular grid of smoothing method, respectively.

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