



Unravelling the stock structure of blue whiting in the Northeast Atlantic: navigating contradictions towards resolution

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Abstract Understanding population structure is fundamental to the sustainable management of marine fish. Blue whiting (*Micromesistius poutassou*) plays a key ecological role in the Northeast Atlantic as a mid-trophic species linking zooplankton to top predators, while also supporting major commercial fisheries. This review synthesises available evidence on its population structure, revealing a complex metapopulation composed of resident and migratory subpopulations. Although currently assessed as a single stock,

this management unit does not account for underlying biological structure, potentially limiting the effectiveness of assessment and management strategies. Our synthesis supports the presence of partial migration, with both migratory and resident contingents contributing to spatial complexity in population structure. Genetic, otolith, parasite, and life-history data indicate the existence of relatively discrete northern and southern subpopulations, mixing zones, and resident groups. We highlight the importance of adaptive, spatially explicit management approaches that account for temporal variability, support stakeholder engagement, and foster regional cooperation. Key knowledge gaps remain in fine-scale population structuring, life-history stage characterisation, and connectivity mechanisms. Addressing these will require integrative approaches using genomics, otolith chemistry, and biophysical modelling. While current stock boundaries encompass the species' range, integrating internal biological structure into assessments and management strategies will enhance their effectiveness and contribute to sustainable exploitation.

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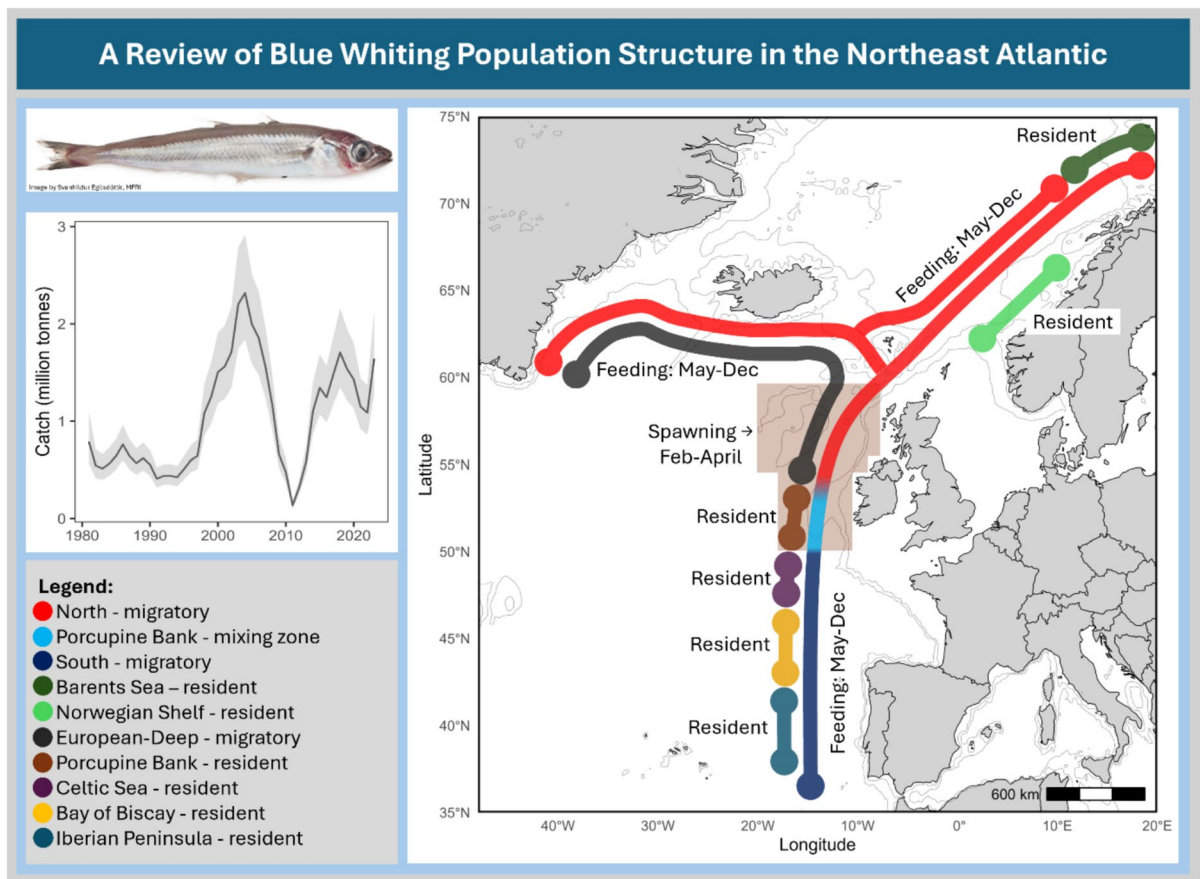
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Graphical abstract



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Introduction

Pelagic fish, such as capelin (*Mallotus villosus*), mackerel (*Scomber scombrus*), herring (*Clupea harengus*), and blue whiting (*Micromesistius poutassou*), are critical components of the Northeast (NE) Atlantic marine ecosystem, linking primary production to higher trophic levels and supporting diverse marine food webs (Trenkel et al. 2014). These species also support global food production and play central roles in the supply of fishmeal, and oil for agriculture and aquaculture (Hidalgo and Browman 2019; Peck

et al. 2021). Within this group, blue whiting presents particular challenges to fisheries management due to its transboundary migrations and unresolved population structure.

Blue whiting is a highly mobile species, widely distributed along the continental shelf-break and upper slope (200 to 600 m depth) of the NE Atlantic (Bailey 1982; Johnsen and Godø 2007) (Fig. 1). It undertakes diel vertical migrations and broad-scale seasonal movements between spawning grounds west of the British Isles and feeding areas in the Norwegian Sea, Iceland, Bay of Biscay, and the Iberian Peninsula (Hátún et al. 2009b; Miesner and Payne 2018). This broad geographic distribution is coupled with a central ecological role in NE Atlantic food webs. Blue whiting occupies a mid-trophic position, feeding on high-energy zooplankton and mesopelagic fish

(Dolgov et al. 2010; Petursdottir et al. 2012; Bachiller et al. 2016; Mir-Arguimbau et al. 2020; Post et al. 2021), while serving as prey for sharks, marine mammals, seabirds, and commercially important fish such as mackerel, hake, and cod (Hillgruber et al. 1997; Cabral and Murta 2002; Santos and Pierce 2003; Pálsson and Bjarnasson 2011; Gosch et al. 2014; Biais et al. 2017; Day et al. 2019; Church et al. 2019). Through these interactions, it mediates energy transfer from surface waters to the deep sea and across broad latitudinal gradients, contributing to functional connectivity of NE Atlantic ecosystems (Bakun 2006; Irigoien et al. 2014; Trenkel et al. 2014; Cavan et al. 2019; Pershing and Stamieszkin 2020).

Blue whiting has undergone dramatic shifts in exploitation, reflecting both biological variability and evolving management strategies. Annual landings increased dramatically during the 1990s, peaking at over 2.4 million tonnes in 2003–2004, coinciding with strong recruitment and high stock biomass (ICES 2023). However, fishing mortality exceeded F_{MSY} between 2005 and 2009, resulting in stock decline and subsequent recommendations to close the fishery in 2011 (Payne et al. 2012; ICES 2023). Responding to these fluctuations, management measures have been adapted over time, but catches have stabilised between 1.1 and 1.7 million tonnes annually from 2014 to 2023, supported by relatively strong recruitment. Nonetheless, fishing mortality has generally remained above levels recommended by scientific advice.

Understanding the population structure of blue whiting is essential for effective and sustainable management. In fisheries science, population structure refers to the boundaries and structure of biological populations—groups of interbreeding individuals that are reproductively isolated—whereas stocks are operational units defined for management and assessment purposes (Waples and Gaggiotti 2006; Cadrin 2020). Populations may exhibit varying degrees of spatial complexity (Kritzer and Sale 2004; Ciannelli et al. 2013; Kerr et al. 2017; Cadrin et al. 2023). At one end of the spectrum, populations may be panmictic with extensive mixing; at the other, they may form metapopulations—networks of connected subpopulations that persist through local reproduction, dispersal, and limited exchange of individuals through migration and dispersal.

In blue whiting, this complexity is further compounded by persistent evidence for partial migration—where only a portion of the population undertakes migratory behaviour while others remain resident (Kloppmann et al. 2001; Was et al. 2008). Partial migration is a behavioural strategy increasingly recognised in marine fishes, and plays a central role in metapopulation dynamics (Kerr et al. 2009; Chapman et al. 2012a, b; Gillanders et al. 2015; Peller et al. 2023). It facilitates demographic buffering, spatial heterogeneity in vital rates, and ecological plasticity, but also complicates stock delineation and assessment. These features are crucial for understanding population resilience and dynamics, but difficult to incorporate into conventional management frameworks (Fig. 2).

The alignment of management unit (stock) with biological population structure is a foundational principle of effective fisheries governance (Russell 1931; Reiss et al. 2009; Hawkins et al. 2016). Most stock assessment models assume static boundaries, homogeneous vital rates, and extensive within-stock mixing (Cadrin 2020; Cadrin et al. 2023). Such simplifications infer demographic independence of parameters like age structure, recruitment, and mortality, which may not reflect biological realities. Moreover, preserving diversity within structured populations supports ecological stability and resilience (Hilborn et al. 2003; Schindler et al. 2010), identifies vulnerable subpopulations, and enables spatially explicit management strategies, such as marine protected areas (Liu et al. 2018; Chollett et al. 2022). For highly migratory species like blue whiting, these considerations also foster international coordination of research and governance (Standal and Grimaldo 2021).

The transboundary nature of blue whiting fisheries necessitates coordinated international management. The species is jointly managed by five coastal states (Faroe Islands, European Union, Iceland, Norway, and the United Kingdom) alongside the Northeast Atlantic Fisheries Commission (NEAFC) for international waters. Scientific advice, including the delineation of management units, is provided by the International Council for the Exploration of the Sea (ICES). This complex jurisdictional framework makes resolving questions of population structure particularly important for sustaining cooperation and aligning policy with biological evidence. While blue whiting also occurs in the Northwest Atlantic (NAFO/

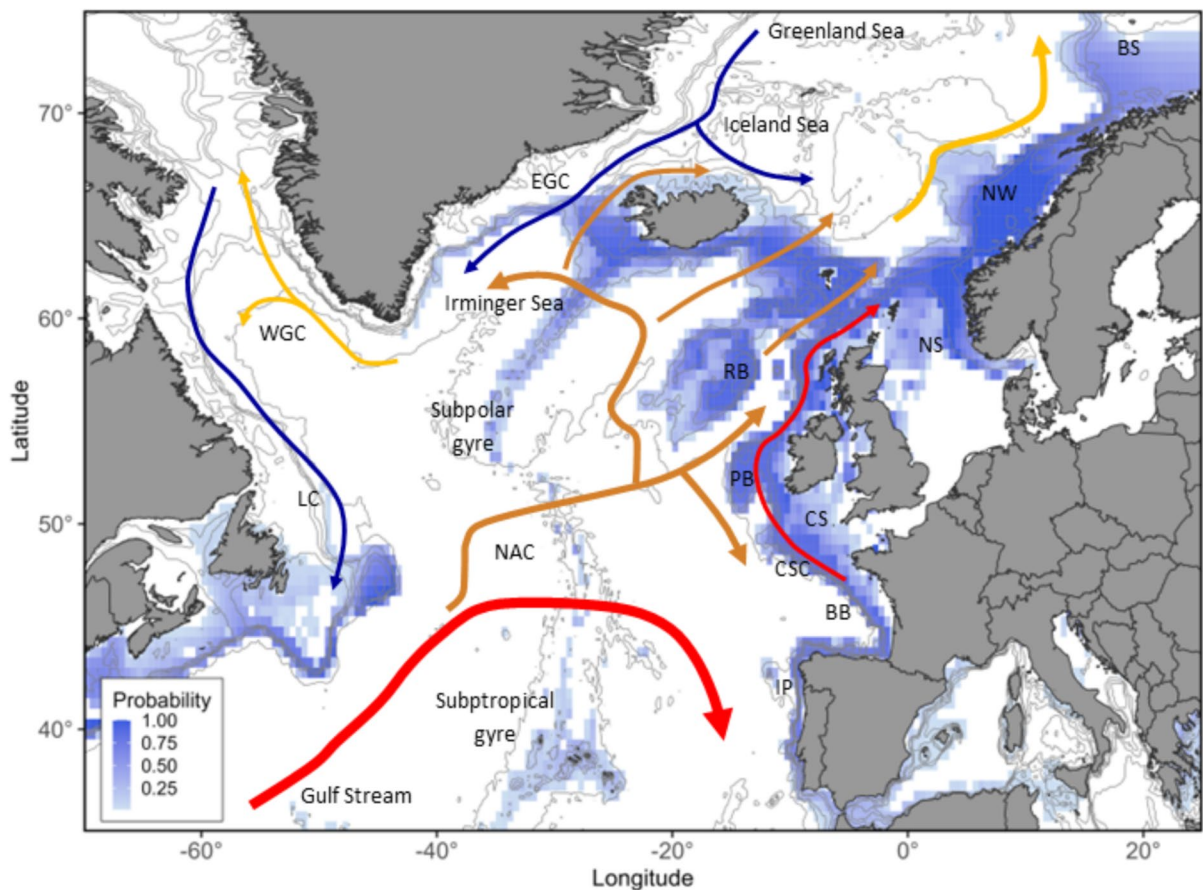


Fig. 1 Predicted year-round probability of occurrence for blue whiting (*Micromesistius poutassou*) in the North Atlantic, overlaid with key surface currents. Distributions were generated from FishBase (Froese and Pauly 2023), which uses occurrence data (including OBIS) and environmental preferences. To reflect shelf-slope habitat use, input parameters were adjusted (depth: 150–1000 m; “pelagic” set to false), producing a more realistic benthopelagic distribution. Arrows indicate

major surface currents, coloured by relative temperature: warm (red), intermediate (orange), cool (yellow), and cold (blue). NAC North Atlantic Current, WGC West Greenland Current, EGC East Greenland Current, CSC Continental Shelf Current, LC Labrador Current, BS Barents Sea, NW Norwegian Sea, NS North Sea, RB Rockall Bank, PB Porcupine Bank, CS Celtic Sea, BB Bay of Biscay, IP Iberian Peninsula

FC Doc. 10/9), that population is geographically and jurisdictionally distinct from the NE Atlantic population (Miller 1966; ICES 2023), and is not considered further in this review.

Management approaches for blue whiting have evolved as scientific understanding has progressed, yet key uncertainties persist. When formal stock assessments began in 1981, blue whiting was managed as two stocks: a dominant northern stock (Hebrides-Norwegian) and a smaller southern stock (Bay of Biscay and the Iberian Coast) (ICES 2023). In 1988, the stock boundary was moved southward from 52.5 to 48°N to include the mixing zone

at Porcupine Bank. A major shift occurred in 1995 when genetic studies (Mork and Giæver 1993, 1995) supported a single-stock framework (Skogen et al. 1999; ICES 2023). However, contemporary research using advanced field, laboratory and analytical techniques continues to highlight complexities that challenge this simplified model (Skogen et al. 1999; Brophy and King 2007; Was et al. 2008; Keating et al. 2014; Pointin and Payne 2014). Uncertainties remain concerning the extent of resident versus migratory contingents, the role of peripheral subpopulations, and the degree of connectivity between regions. Blue whiting has thus become a well-recognised example

of the tension between biological evidence and management practices (Reiss et al. 2009).

This review addresses the need for a multidisciplinary synthesis of blue whiting population structure to guide evidence-based fisheries management. (1) We begin by reviewing contemporary information on blue whiting population structure, summarising conclusions from various disciplines. (2) Next, we synthesise results across these disciplines to highlight areas of scientific consensus and variability. (3) We then explore the management implications of these findings, focusing on challenges and opportunities for sustainable fisheries management. (4) Finally, we identify remaining knowledge gaps and propose innovative approaches for resolving uncertainties. By integrating diverse lines of evidence, this review seeks to bridge the gap between biological complexity and practical management for this ecologically and economically important species.

Evidence for population structure

North Atlantic oceanographic context

Although this review focuses on blue whiting in the NE Atlantic, understanding their population

structure requires a basin-wide oceanographic perspective. Large-scale physical processes across the North Atlantic shape key biological patterns such as spawning, larval dispersal, migration, and habitat use (Fig. 1).

The circulation of the North Atlantic is dominated by the subpolar gyre (SPG)—a large counter-clockwise system of subarctic and Atlantic water masses (Hátún et al. 2009a, b). The southern boundary of the SPG is defined by the eastward-flowing North Atlantic Current (NAC), an extension of the Gulf Stream, which transports relatively warm, saline waters to the European slope, over the Porcupine Bank—one of the most important blue whiting spawning grounds (Sko-gen et al. 1999). Even warmer, more saline waters also flow northward along the continental shelf via the Continental Shelf Current (CSC), contributing to the formation of a mixing zone west of the British Isles. This zone is thought to play a key role in shaping spawning habitats and larval transport pathways (Trenkel et al. 2014).

Further north, Atlantic inflows influence water mass properties across the Barents, Norwegian, Iceland, Irminger, and Greenland Seas (Holliday et al. 2008). Simultaneously, the Arctic exports cold, low-salinity water into the North Atlantic via the East Greenland Current (EGC), which combines with

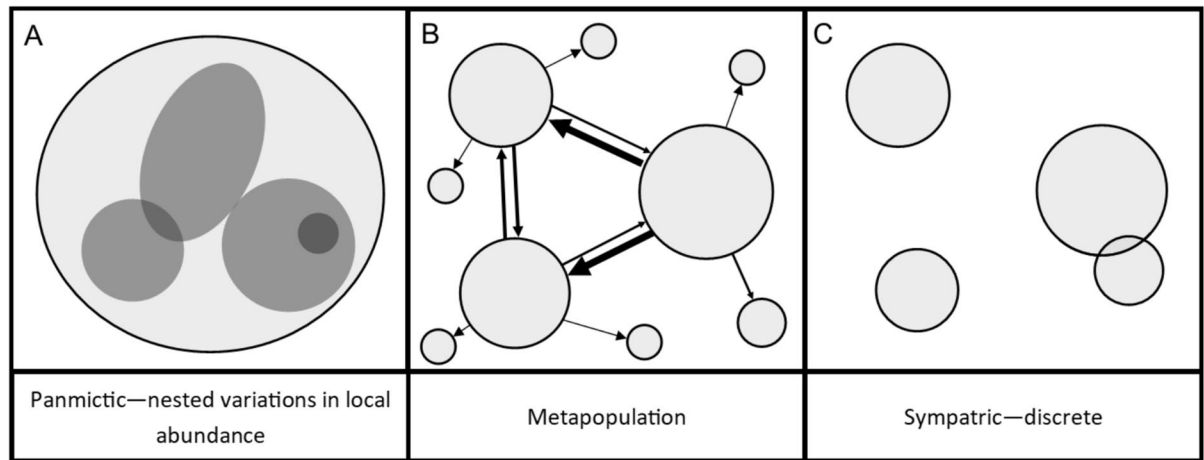


Fig. 2 Conceptual representation of three general population structure scenarios (adapted from Ciannelli et al. 2013). **A** Panmictic population: individuals belong to a single interbreeding population with spatially variable local abundance; shading indicates nested gradients in density rather than demographic structuring. **B** Metapopulation: a network of demo-

graphically distinct but connected subpopulations; circles represent subpopulations, and arrows indicate direction and relative strength of connectivity (e.g. dispersal or migration). **C** Sympatric discrete populations: coexisting but reproductively isolated populations with limited or no gene flow; overlaps in space do not imply demographic or genetic exchange

West Greenland and East Iceland Currents. These northern inflows interact with deeper layers of over-flow water, which transport cold water masses southward and contribute to the formation of the Labrador Current (LC) (Myers 2005). Collectively, these surface and deep currents connect the eastern and western basins and shape both the physical environment and potential biological connectivity across the range of blue whiting.

Early multidisciplinary approaches

Early efforts to investigate blue whiting stock structure drew on a combination of international survey data, technical cruise reports, and unpublished scientific material. From 1965 to 1979, the Soviet Union conducted 54 specialised expeditions to investigate the biology and ecology of blue whiting throughout its distribution in the NE Atlantic (Zilanov 1980). Based on differences in distribution, spawning and feeding areas, size-age composition, morphometric features, and parasite assemblages, two distinct stocks were inferred: a northern component in the Hebrides-Norwegian region and a southern component in the Bay of Biscay (Zilanov 1980). The northern stock exhibited divergent migratory pathways through the Faroes-Shetland Channel and Faroes-Iceland Sill, though this variation was not directly linked to substructure. Observations of advanced maturation schedules on the Porcupine Bank indicated that the area likely served as a spawning ground for both northern and southern stock components, with temporal separation in spawning events (Schöne 1979). Morphometric and meristic analyses further supported this stock division, showing a gradient in vertebrae and gill raker counts from the Barents Sea to Portugal, with a potential separation zone at 52°N (Sahrhage and Schöne 1975; Schultz et al. 1978). Multivariate analyses identified three northern subpopulations: one in the Barents Sea north of 72°N, a group northeast of the Faroes, and a deep-water subpopulation from the Faroes to west of Ireland (Andersen and Jákupsstovu 1978).

These early efforts were synthesised in a comprehensive review, which described a largely continuous distribution along the shelf-slope of the NE Atlantic, undertaking seasonal north–south migrations (Bailey 1982). Temporal separation was identified between northern and southern spawning components, with

two seasonal peaks: an earlier event on the Porcupine Bank and a later peak further north. Blue whiting were also observed year-round across much of their range, including adult and juvenile occurrences southwest and west of Ireland, in the Celtic Sea, and on Rockall Bank. (Bailey 1982). Further, the presence of adult fish in northern areas during the spring spawning period, including over the Faroe-Iceland Ridge, along the Norwegian coast, and in the Barents Sea, prompted suggestions of residual or resident subpopulations. Subsequent studies expanded on these early findings. Analyses of otolith structure and maturation schedules indicated the presence of two northern spawning subpopulations separated at 56°N: a dominant group spawning on the Hebrides Shelf and migrating northeast into the Norwegian Sea, and a second West European deep-sea subpopulation spawning on the Porcupine Bank and migrating offshore to the northern Reykjanes Ridge, southwest of Iceland (Isaev and Seliverstov 1989). These early multidisciplinary approaches established the foundational understanding of blue whiting population structure, identifying key spatial and temporal patterns that would guide subsequent research efforts using more specialized methodological approaches (Fig. 3).

Genetic variation

Blue whiting exhibits traits that may impede clear genetic differentiation, including large population sizes, high fecundity, pelagic eggs and larvae subject to passive dispersal, and significant migratory behaviour. Despite these challenges, genetic analyses have provided valuable insights. Early allozyme studies (IDHP-2 and PGM-1) indicated limited genetic differentiation across the NE Atlantic, suggesting panmixia across the central distribution and separate reproductive units in the Barents Sea and an inshore Norwegian Fjord (Romsdalsfjord) (Mork and Giæver 1993, 1995; Giæver and Stien 1998).

Subsequent research employing DNA mini- and microsatellite loci, identified low but detectable genetic structure, comparable to patterns observed in demersal gadoids such as cod, hake, and haddock (Ryan et al. 2005; Was et al. 2008). Significant genetic heterogeneity was confirmed among samples from the Barents Sea, as well as the Porcupine Bank,

Hebrides Shelf (Ryan et al. 2005), and Rockall Bank (Was et al. 2008), providing robust evidence of complex population structure in the main spawning area. In the south, three genetic barriers were identified (Was et al. 2008). A distinct separation of the Bay of Biscay from northern sites indicated a stable, isolated population with possible recruitment from Portuguese waters. Additionally, isolation between southern (CS) and northern (PB/IS) Celtic Sea sites, and broader separation of the Celtic Sea from all other northern regions, suggest self-contained populations in these areas (Fig. 4).

Temporal variation in genetic heterogeneity, particularly in the main spawning grounds and the Barents Sea, complicates delineation of population boundaries. This variability may arise from additional structural complexities, limitations in sampling resolution, or temporal changes in life-history traits affecting connectivity. The underlying causes remain unresolved (Giæver and Stien 1998; Ryan et al. 2005; Was et al. 2008).

Early life stage dispersal

Simulations of larval dispersal from spawning areas west of the British Isles highlighted significant retention driven by anti-cyclonic circulation, with rates of 78–86% over Rockall Bank and 45–69% over Porcupine Bank (Bartsch and Coombs 1997; Skogen et al. 1999). Dispersal pathways included northward movement into the Norwegian Sea, northern North Sea, and Shetland Islands, and southeastward into the Celtic Sea and Bay of Biscay, while no dispersal was predicted into Iceland, northern Norway, or the Barents Sea (Bartsch and Coombs 1997). A distribution gap over the Porcupine Bank (53–54°N) delineated northern and southern zones, consistent with early evidence of two spawning components. Subsequent research identified a separation line at approximately 54.5°N, with a transition zone northeast of the Porcupine Bank facilitating stock mixing (Skogen et al. 1999). Dispersal patterns displayed high annual variability influenced by localised oceanographic conditions (Bartsch and Coombs 1997), with shifts of the transition zone of up to 200 km along the shelf break (Skogen et al. 1999). Uncertainties in predictions, particularly over longer time scales, stem from unknowns in larval behaviour and ontogenetic

changes, which may modulate dispersal dynamics (Bartsch and Coombs 1997; Skogen et al. 1999).

Studies of egg and larval distributions confirmed the Porcupine Bank as a critical stock boundary zone, with anti-cyclonic flow supporting a self-sustaining resident population (Kloppmann et al. 2001). Retention was strongest along the western and northwestern slopes of the bank, with a north–south population boundary identified at 53.5°N. The lateral boundaries of the retention zone were defined by northward flow along the eastern shelf edge (12.5°E) via the Shelf Edge Current (SEC) and offshore flow through a secondary SEC to the west. Severe weather could disrupt this retention, enhancing southward dispersal. This zone of connectivity appears to support gene flow between the Porcupine, Hebrides, and Biscay subpopulations, positioning the Porcupine Bank as both a retention area and mixing ground within the broader NE Atlantic metapopulation.

Spatial–temporal distribution

Several sources provide spatial data on blue whiting distribution, but differ in continuity, resolution, and underlying assumptions. A modelled species range map from FishBase utilises occurrence data from OBIS and GBIF alongside environmental tolerances to depict a continuous transatlantic distribution (Froese and Pauly 2023; OBIS 2023). However, this model likely overestimates habitat use by assuming fully pelagic behaviour, extending into deep offshore areas not typically associated with the species' benthopelagic ecology. In contrast, raw occurrence records used in this approach show a more fragmented distribution, particularly between the NE and NW Atlantic (OBIS 2023). Commercial catch records reveal apparent discontinuities even within the NE Atlantic, although these patterns are influenced by spatial variability in fishing effort, fleet access, and reporting standards (ICES 2023). These differences reflect the limitations inherent in presence-only spatial datasets and highlight the importance of integrating multiple indicators when interpreting population structure.

Research has focused on the spatial–temporal variability of the dominant spawning aggregation and their implications for blue whiting stock delineation. Continuous plankton recorder (CPR) surveys have been instrumental in mapping the scale, location, and

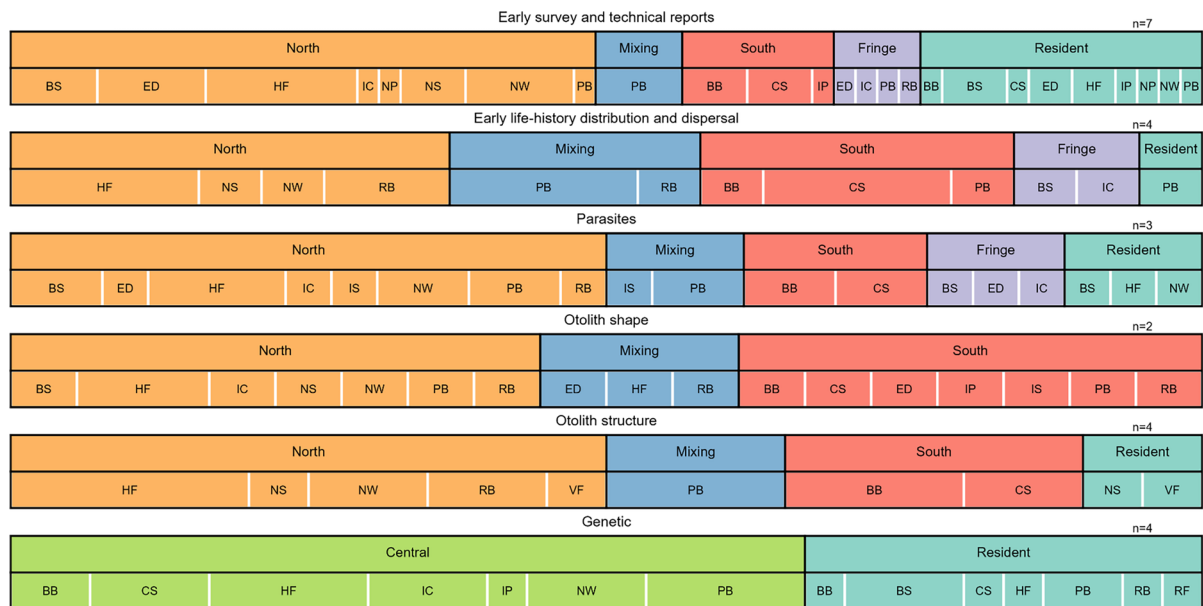


Fig. 3 Summary of research on population structure for blue whiting in the Northeast Atlantic organised by methodological approach. Upper bars show geographic structures; lower bars show study zones within each structure, with larger bars indicating greater allocation to the respective structure. Sample sizes (n) indicate number of studies per approach. *NS* North

Sea, *NW* Norwegian Shelf, *HF* Hebrides-Faroes Shelf, *ED* West European Deep, *PB* Porcupine Bank, *CS* Celtic Sea, *BB* Bay of Biscay, *BS* Barents Sea, *NP* North of Porcupine Bank, *IP* Iberian Peninsula, *RB* Rockall Bank, *IC* Iceland, *IS* Irish Shelf, *VF* Vestfjorden, *RF* Romsdalsfjord

structure of the spawning population, using eggs and larvae to infer adult distribution (Bartsch and Coombs 1997; Corten and Lindley 2003; Pointin and Payne 2014; Miesner and Payne 2018). However, CPR surveys under-sample the full vertical range of blue whiting eggs, which occur from the surface down to 600 m (Ådlandsvik et al. 2001).

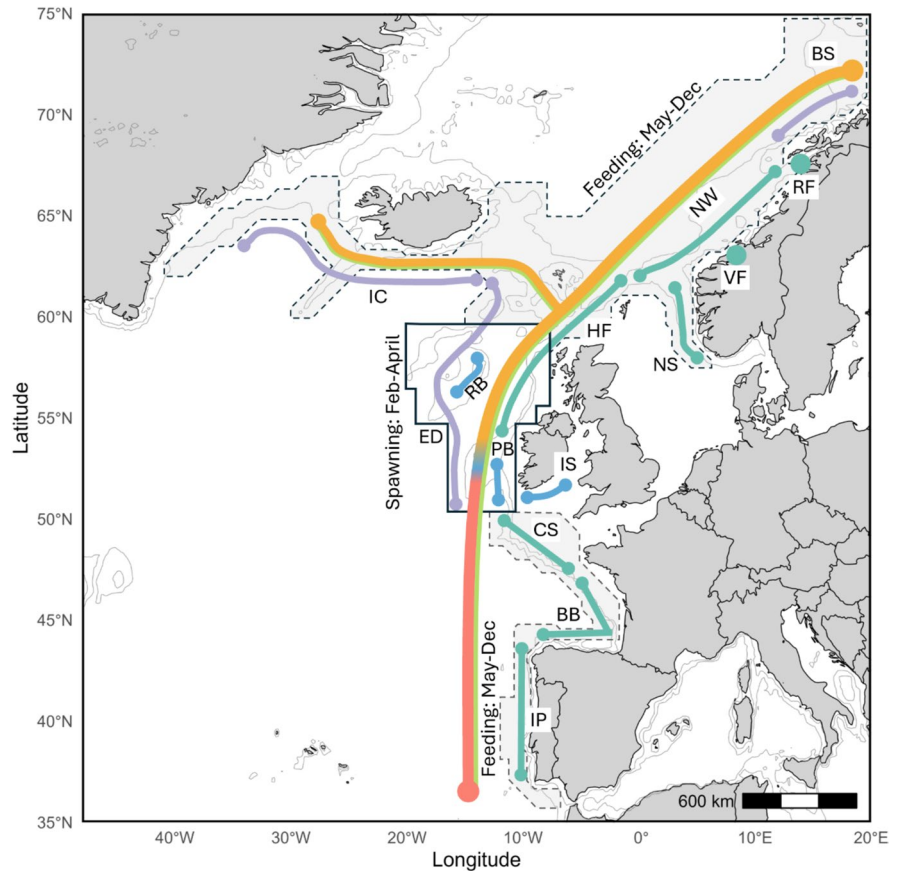
CPR egg and larval data (1948–2005) revealed two high-density aggregations: one in the Rockall Trough and another in the Porcupine Seabight, separated by a minimum at 52–54°N (Pointin and Payne 2014). The northern aggregation exhibited a more protracted spawning period, occurring 30–45 days later than the southern component. Interannual dynamics revealed greater abundance in the north, consistent with earlier studies showing ~90% of the spawning biomass was concentrated in the north and ~7% in the south (Bartsch and Coombs 1997; Pointin and Payne 2014).

The spatial extent of spawning is influenced by interactions between subarctic and subtropical water masses in the NE Atlantic (Heino et al. 2008; Hátún et al. 2009a, b; Miesner and Payne 2018; Post et al. 2019; Miesner et al. 2022). Spawning is limited to

narrow salinity (35.3–35.5 psu) and temperature (9–10 °C) ranges, tightly linked to the strength of the SPG (Fig. 1) (Hátún et al. 2009b; Miesner and Payne 2018; Miesner et al. 2022). A strong SPG spreads cold, freshwater masses over the Rockall Plateau, restricting spawning to the northern European continental slope and Porcupine Bank. A weakened SPG, characterised by warmer and more saline conditions, shifts spawning northwards over Rockall Plateau and Hatton Bank, while reducing reproductive activity in the southern zone (Hátún et al. 2009b; Miesner and Payne 2018). These regime shifts likely influence dispersal pathways, nursery grounds, and feeding areas, which in turn shape migratory behaviour and population connectivity through mechanisms such as site fidelity.

Fringe subpopulations in the Barents Sea and Greenland exhibit distinct ecological patterns. In the Barents Sea, fisheries-independent surveys (1981–2006) showed that higher abundances and expanded northerly ranges were associated with strong recruitment from the main NE Atlantic stock, whereas reductions in mean body length suggested

Fig. 4 Northeast Atlantic distribution of blue whiting, illustrating population structures—central (light-green), northern (orange), mixing (blue), southern (red), fringe (purple), and resident (green)—as described in studies reviewed in the text. Main spawning areas are shown as solid lines; seasonal migratory routes as dashed lines. Abbreviations: *NS* North Sea, *NW* Norwegian Shelf, *HF* Hebrides–Faroes Shelf, *ED* West European Deep, *PB* Porcupine Bank, *CS* Celtic Sea, *BB* Bay of Biscay, *BS* Barents Sea, *IP* Iberian Peninsula, *RB* Rockall Bank, *IC* Iceland, *IS* Irish Shelf, *VF* Vestfjorden, *RF* Romsdalsfjord



density-dependent effects (Heino et al. 2008). During warm, saline phases, migrants from the core population dominated, while during weak recruitment years, local subpopulations expanded their spatial range. Off east Greenland, age-dependent spatial–temporal patterns suggest that the area may function as both a juvenile nursery and adult summer feeding ground (Post et al. 2019). However, it remains unresolved whether individuals in these regions are migrants from the main NE Atlantic spawning stock, residents of local subpopulations, or a mixture of both. Together, these findings underscore the ecological significance of migratory subpopulations in fringe areas such as the Barents Sea and Greenland, as well as the persistence of resident subpopulations, highlighting the need for further research into their roles in shaping overall population structure.

Life-history traits

Research into blue whiting life-history traits reveals a clear north–south divide, with evidence of a mixing zone and heterogeneous subpopulation structures (Pawson et al. 1978; Monstad 1990; Bailey and Heath 2001; Brophy and King 2007). Fish from northern areas west of Great Britain exhibit poorly defined otolith growth zones, in contrast to the clear, seasonal patterns found in fish from southern regions below 53°N, particularly in the Bay of Biscay (Pawson et al. 1978). These differences likely reflect distinct environmental conditions and suggest the presence of spatially structured subpopulations.

Consistent growth patterns between the Hebrides and the Norwegian Sea support the idea of a shared northern spawning–migratory stock (Monstad 1990). In contrast, only minor differences with individuals on the Porcupine Bank suggest this area may represent either a transition zone involving some degree of mixing with a southern component or the presence

of a partially resident subpopulation (Monstad 1990). Supporting this, faster larval growth rates were recorded in blue whiting spawning south of the Porcupine Bank (49–52°N) compared to those in northern spawning (Rockall Bank, Hebrides Shelf) and foraging (Norwegian Sea) areas (Brophy and King 2007). Fish spawning in an intermediate zone (northern Porcupine Bank, 53–54.5°N) exhibited slower larval growth than those in the south. Larval otolith growth rates in the Bay of Biscay were significantly faster than those from all other areas. These findings suggest that fish from northern and southern regions do not mix randomly, and that larval dispersal may influence the spatial distribution of spawning adults. Collectively, these results support the separation of blue whiting into at least three demographically distinct stocks or subpopulations, rather than a single homogenous unit.

In addition, larger body sizes observed in the Norwegian coastal, Vestfjord, and North Sea suggest the presence of local subpopulations that may not participate in the main northern spawning migration (Monstad 1990). Along the Hebrides Shelf Edge, latitudinal variation in larval growth was observed, with faster growth occurring in warmer southern areas (Bailey and Heath 2001). Southern spawning areas also produced larvae with smaller otolith radii at hatching, suggesting smaller egg and larval sizes. However, no clear latitudinal trends were detected in length–weight relationships. Back-calculated hatch dates revealed a narrow, six-day spawning period across a wide geographic area, supporting the conclusion of structured subpopulations within the broader northern spawning stock.

Otolith shape

Otolith shape analysis has been instrumental in delineating subpopulation structure within blue whiting spawning grounds across the NE Atlantic (49–58°N) (Keating et al. 2014). Two distinct otolith morphotypes were identified: (1) a northern morphotype, associated with fish from the Hebrides Shelf, Rockall Bank, and northern Porcupine Bank; and (2) a southern morphotype, found in fish from offshore areas west and south of Porcupine Bank. Limited mixing was observed in the intermediate zone north and offshore of the Porcupine Bank, supporting the presence

of spatially structured subpopulations with distinct feeding grounds.

A broad-scale study across the NE Atlantic (37–75°N, 20–25°W) identified two major subpopulations, northern and southern, with a mixing zone on the Hebrides Shelf and Rockall Bank (54–60°N, 4–11°W) (Mahe et al. 2016). The northern subpopulation ranged from the Faroe Shelf and northern North Sea through to the Norwegian and Barents Seas, while the southern subpopulation extended from Porcupine Bank to the Portuguese and Spanish Shelves. Despite clear spatial structure, temporal variability and misclassification of individuals indicate partial connectivity, suggesting incomplete reproductive isolation between the subpopulations.

Parasite assemblages

Geographic variation in parasite assemblages provides additional insight into blue whiting population structure, particularly at ecological scales. Differences in *Anisakis* sp. larval infections revealed three broad zones: northern (Barents Sea), central (Norwegian Sea), and southern (Faroe Shelf), with infection intensity increasing from south to north (Dumke 1988). While these patterns may reflect underlying subpopulation structure or distinct ecological conditions, parasite data are limited in their ability to distinguish reproductively isolated populations. Instead, they are best interpreted as indicators of spatial or trophic separation that may align with stock or subpopulation boundaries.

Using *Myxobolus aeglefini* as an indicator, separate subpopulations were identified in northern (Hebrides-Norwegian and Porcupine Bank) and southern (Irish Shelf, Celtic Sea, Bay of Biscay) regions (Karasev 1989). The northern subpopulation was further divided into three components: (1) the Porcupine Bank and Irish Shelf as an intermediate mixing zone, (2) the Rockall and Hebrides Shelf spawning and Faroes-Norwegian feeding areas, and (3) fringe subpopulations in Iceland and the Barents Sea (Karasev 1990). Southern subpopulations were characterised by parasites of benthopelagic, warm-temperate habitats and lacked species typical of temperate systems, such as *Hemiurus leviseni* (trematode fluke), and *Diphyllbothrium* sp. (tapeworm), suggesting limited ecological interaction with copepods, the intermediate hosts. These

findings suggested limited northerly migrations and minimal mixing with northern subpopulations.

More recent parasite studies remain sparse. In northwest Spain, parasite diversity was low, with most individual (90% of 400 fish) hosting fewer than 20 parasites (Fernández et al. 2005; MacKenzie and Hemmingsen 2015). Infections were dominated by *Anisakis simplex* larvae and *Stephanostomum lophii* metacercaria. These findings contrasted with richer parasite communities observed in other NE Atlantic regions and likely reflect geographic variation in blue whiting abundance and host community composition rather than discrete subpopulation structure (Fernández et al. 2005; MacKenzie and Hemmingsen 2015).

Integration of current evidence

Significant progress has been made in understanding the population structure of blue whiting in the NE Atlantic. The primary goal of these studies is to accurately estimate the productivity and abundance of individual components, essential for integration within stock assessment models and making informed management decisions. The research spans from the inception of the fishery and the establishment of an initial management framework (pre-1982) through the iterative refinement of strategies via adaptive management approaches (1983–1994), to the present-day management structure (post-1995). Extensive evidence suggests that a panmictic population structure across the NE Atlantic is improbable. Instead, indications point towards a complex metapopulation structure, comprising a central, dominant highly migratory subpopulation, surrounded by several smaller migratory and resident subpopulations, each exhibiting varying degrees of ecological and evolutionary connectivity. Research across diverse scientific disciplines underscores that the current single stock management approach does not reflect the spatial complexity of blue whiting's biological population structure. However, how best to incorporate this complexity into assessment and management frameworks remains unresolved (Reiss et al. 2009; ICES 2023).

An interdisciplinary examination of historical and contemporary biological information consistently reflects the existence of a dominant central population, with spawning on the Hebrides Shelf to the west

and north of Scotland, and annual feeding migrations into the Norwegian Sea (Hebrides-Norwegian stock). This conclusion is supported by genetic homogeneity among the proposed spawning and feeding grounds (Ryan et al. 2005; Was et al. 2008), a spatially and temporally discrete spawning aggregation (Pointin and Payne 2014), and northward larval dispersal pathways (Bartsch and Coombs 1997; Skogen et al. 1999). Further corroboration is provided by the convergence of early life-history growth rates in mature fish across both spawning and feeding areas (Brophy and King 2007), consistent patterns in otolith shape (Keating et al. 2014; Mahe et al. 2016), and uniform parasite assemblages (Karasev 1989, 1990). Remaining knowledge gaps in the context of stock identification for the dominant Hebrides-Norwegian stock centre around two critical areas: systematically identifying and characterizing recruitment and feeding areas within the stock's habitat and investigating the persistence of connectivity pathways between key life-history stages, such as hatching to recruitment, recruitment to feeding, and feeding to spawning locations. Understanding these pathways helps delineate distinct stock boundaries and identify areas of overlap, clarifying population structure.

The southern boundary of the Hebrides-Norwegian stock consists of a spatially and temporally variable intermediate zone of mixing, primarily located over the northern edge of the Porcupine Bank. The precise demarcation of the boundary between northern, and southern blue whiting subpopulation, has been a subject of considerable investigation. Genetic research proposed a barrier to the south of the Porcupine Bank at 51–53°N, indicating a clear genetic divide between northern and southern populations (Was et al. 2008). Similarly, parasite studies suggest a separation point south of the Porcupine Bank, typically around 51.5°N (Karasev 1989, 1990). In contrast, analyses of otolith shape reveal a broader zone extending across the entire main spawning area, spanning approximately 54.5–60.5°N, indicating a more diffuse boundary (Mahe et al. 2016). Spatial-temporal distribution models suggest a distinct area of reduced spawning activity between 52 and 54°N, generally north of the Porcupine Bank (Kloppmann et al. 2001; Pointin and Payne 2014). Dispersal dynamics studies also indicate potential separation zones, with suggested boundaries between 53–54°N (Bartsch and Coombs 1997) or 54.5°N (Skogen et al. 1999), both

situated at the northern extent of the Porcupine Bank. Similarly, variability in larval otolith growth histories suggests a southern stock boundary at the northern extent of the Porcupine Bank at 54.5°N. Despite these insights, uncertainties persist regarding the precise location and nature of the boundary between the Hebrides-Norwegian stock, and southern blue whiting subpopulations.

The southern component of the blue whiting stock appears to be further structured into multiple resident subpopulations found on the southern Porcupine Bank, the Celtic Sea, and the Bay of Biscay and Spanish/Portuguese Shelf. The existence of distinct southern subpopulations is supported by several lines of evidence. Genetic studies have revealed strong heterogeneity among regions, indicating the presence of distinct populations (Ryan et al. 2005; Was et al. 2008). Additionally, these populations exhibit an earlier spawning period with spatially discrete spawning areas over the southern Porcupine Bank (Pointin and Payne 2014) and northern Portuguese Shelf (Gonçalves et al. 2017). Furthermore, observations of significantly faster larval growth patterns in the southern Bay of Biscay suggest that these subpopulations do not form a randomly mixing unit through large-scale migrations into the areas of the Hebrides-Norwegian stock (Brophy and King 2007). Remaining knowledge gaps related to the genetic structure and ecological dynamics of these southern subpopulations need to be addressed to better understand their connectivity and interactions. Additionally, the alignment of the subpopulation over the Iberian Peninsula with the Bay of Biscay and Mediterranean population, or as an independent unit, remains unclear and requires further investigation.

In addition to the broader separation into central and southern subpopulations, consensus findings point towards the existence of a distinct resident subpopulation in the Barents Sea. Evidence for this includes the identification of limited gene flow (Giæver and Stien 1998; Ryan et al. 2005), unique parasite assemblages (Dumke 1988) and annual concentrations of blue whiting individuals in the Barents Sea region during the spawning migration of the main northern subpopulation to the west of the British Isles (Schultz et al. 1978; Bjørke 1983; Heino et al. 2008). It is important to note that during periods of heightened recruitment and abundant years, this local stock is known to mix with foraging components of

the primary northern subpopulation, particularly to the west of the region, where these periods of abundance dominate the population dynamics (Heino et al. 2008). Further investigation is warranted to elucidate various aspects of this resident subpopulation, including the identification of areas where key life-history stages occur, connectivity pathways that link these, and biological characteristics such as maturation schedules, spawning areas, age, and growth.

Anecdotal evidence suggests a north-western subpopulation of blue whiting, hypothesised to spawn in the deep waters of West European regions, with subsequent feeding migrations through the western Faroes Shelf into Icelandic and Greenlandic waters. While direct evidence is limited, genetic studies indicate variability in spawning grounds off the north of Rockall Bank (Was et al. 2008), the Hebrides, and Porcupine Bank (Ryan et al. 2005). Age-defined spatial patterns support this hypothesis, with indications of recruitment occurring off Greenland and Iceland (Sveinbjörnsson 1975; Post et al. 2019), suggesting a separate spawning source from those of the Hebrides-Norwegian Stock. Additionally, analyses of otolith shape reveal an offshore-inshore separation in the main spawning area, possibly indicating a deep-spawning aggregation (Keating et al. 2014). The evidence for this distinct north-western subpopulation remains indirect and unclear. One explanation may be the westward dispersal of eggs and larvae from the Rockall and Hatton Banks, with those spawned along the eastern shelf edge drifting northwards, and those on the Porcupine Bank area drifting southwards. Further investigations are needed to identify potential areas for key life-history stages and connectivity pathways of the West-European Deep subpopulation.

Our interdisciplinary review of stock structure research on blue whiting in the NE Atlantic highlights the transitional nature of the boundaries between the proposed Hebrides-Norwegian, Barents Sea, West-European deep, and southern subpopulations. Evidence for dynamic boundaries is supported by temporally variable genetic structure among regions (Ryan et al. 2005; Was et al. 2008), predicted interannual shifts in larval dispersal boundaries by up to 200 km (Bartsch and Coombs 1997; Skogen et al. 1999), high interannual variability in the distribution patterns of mature fish over the main spawning area (Pointin and Payne 2014; Miesner and Payne 2018), and strong overlap

in larval growth histories (Brophy and King 2007). Additionally, variability in the stock boundaries is captured in the large area of overlap in otolith shape analyses (Mahe et al. 2016), reflecting environmental conditions across the full life history of the fish. This variability is closely linked to oceanographic factors, particularly the strength of the SPG (Hátún et al. 2009a, b), which influences the location of spawning, the direction and extent of larval dispersal, and the extent of feeding migrations through temperature and salinity gradients. These various factors further play a pivotal role in defining the abundance of the dominant subpopulation and potentially influencing other subpopulations. During periods of high abundance, there is a noticeable increase in mixing across subpopulation components, leading to blurred boundaries. Conversely, high recruitment years could alternatively lead to increased intraspecific competition, pushing individuals out of optimal spawning areas and creating opportunities for egg and larval dispersal that bring blue whiting from the same subpopulation to different areas sporadically. Despite fluctuations in identified boundaries, these findings collectively underscore the significance of transitional zones in mediating subpopulation interactions and emphasise the role of oceanographic dynamics in shaping population structure. Further research is needed to elucidate the specific mechanisms driving boundary dynamics and their implications for population dynamics and management strategies. A focus should be applied to the main transit areas to the west and east of the Faroe Islands to identify whether migratory profiles from the spawning to feeding areas occur as discrete yet overlapping pathways, or as a well-mixed randomly migrating population.

The presence of both resident and migratory contingents in blue whiting, along with regionally distinct migratory pathways, suggests that the species exhibits behaviours consistent with partial migration (Chapman et al. 2012a). Partial migration often arises as an adaptive response to spatial environmental heterogeneity, density-dependent pressures, and life-history trade-offs (Peller et al. 2023). In blue whiting, persistent local contingents in regions such as the Barents Sea, Porcupine Bank, and Icelandic waters may reflect evolved strategies to optimise fitness across variable environments and to

buffer the population against ecological uncertainty, such as fluctuations in the SPG. The population structure emerging from this review – dominated by a central migratory contingent and surrounded by smaller, more resident contingents – aligns with the partial migration paradigm commonly observed in other marine species (Chapman et al. 2012b). This framework provides a powerful lens through which to interpret observed spatial complexity and demographic connectivity in blue whiting, including overlap zones, seasonal migrations, and the resident contingents. Recognising partial migration as a core feature of blue whiting population dynamics reinforces the view that its spatial structure is not a management artefact, but rather an ecologically meaningful and potentially adaptive configuration. As such, it should be explicitly considered in future stock assessment models and transboundary management strategies.

Management implications

Considering population structure

Reconciling complex biological population structure with the current single-stock assessment framework remains a significant challenge. Uncertainty persists regarding how to appropriately account for spatial population complexity within the existing single-stock assessment and management framework for blue whiting in the NE Atlantic. Identifying adaptive management strategies that account for spatial and temporal variability in population dynamics is essential for sustainable fisheries management. Given the current uncertainty in population structure, a pragmatic approach would prioritize monitoring and protecting areas where research has identified complex population dynamics—including mixing zones and potential subpopulations—within the existing stock assessment framework.

Effective management strategies for blue whiting in the NE Atlantic require careful consideration of the strong evidence indicating a clear division between the northern and southern stock boundaries over the Porcupine Bank. However, the intermediate zone of mixing, primarily located over the Porcupine Bank, complicates this task. This evidence highlights the need to account for spatial population structure

in assessment and management, through spatially stratified data collection, modelling, and catch allocation, rather than assuming a single homogenous stock. While blue whiting exhibits features consistent with partial migration and metapopulation structure, this does not necessarily imply fully independent stock units. Rather, it underscores the need for stock assessment frameworks that accommodate spatial connectivity, subpopulation-specific dynamics, and differential mixing—potentially through spatially explicit assessment models, subpopulation monitoring, and spatially allocated management measures (Cadrin et al. 2023). To address these complexities, it is crucial to: (1) identify stock boundaries using robust markers such as genetic, ecological, or movement data; (2) develop methods to monitor and quantify stock mixing within the intermediate zone; and (3) allocate catches appropriately to either the northern or southern stocks, ensuring alignment with biological realities. This allocation should be guided by stock discrimination markers and improved scientific understanding of mixing dynamics. Additionally, assessment and management strategies must account for potential temporal variability in mixing patterns, as these may influence the effectiveness of management measures. The current evidence delineating the Hebrides-Norwegian and West-European deep stocks remains insufficient to make definitive management recommendations, underscoring the need for further research in this area. Enhanced monitoring and data collection are necessary to establish clear boundaries and better understand population connectivity.

Recognising the existence of resident subpopulations underscores the importance of incorporating appropriate management measures to protect and maintain their viability. Given the limited gene flow and unique ecological characteristics associated with these subpopulations, targeted conservation efforts are essential to ensure their long-term survival. Specifically, protecting critical spawning habitats and nursery grounds—such as shallow coastal areas, fjords, or localised regions with suitable substrate and hydrodynamic conditions—is vital for these subpopulations. Seasonal or area closures during critical spawning periods can minimize fishing pressure and disturbance, while measures to limit habitat degradation (e.g., by reducing bottom-trawling activities in sensitive areas) can preserve essential ecological features.

Integrating scientific monitoring programs to assess population vital rates, reproductive success, and habitat utilization of these resident populations is paramount. Such monitoring will guide adaptive management strategies, enhancing the resilience and sustainability of the broader blue whiting population in the NE Atlantic ecosystem.

Strengthening local and regional stakeholder engagement

Involving stakeholders, including industry representatives, local communities, fisheries managers, and the scientific community in the co-production of knowledge and decision-making processes is critical for effective fisheries management. Bridging the gap between scientific research and stakeholder perspectives can enhance the relevance and legitimacy of management measures. The wide distribution and extensive migratory behaviour of the blue whiting population highlight the importance of developing regional partnerships. Cooperation between countries with vested interests in blue whiting fisheries is crucial for gathering comprehensive data across its distribution range. International collaborations can facilitate data sharing, standardize research methodologies, and establish a unified management approach. In the current context, this can be linked to the development of regional and local projects aimed at improving the understanding of population structure for blue whiting across the NE Atlantic and Mediterranean (ICES 2023).

Knowledge gaps, uncertainties, and future research

Fine-scale population structuring

Current population genetic studies on blue whiting utilised a limited number of neutral markers, such as microsatellites (e.g. Ryan et al. 2005; Was et al. 2008), which may lack the resolution to detect subtle population structuring at finer spatial scales. The prevalence of cryptic or subpopulations within proposed management units remains poorly understood. However, the advent of more affordable high-throughput sequencing or genotyping make it possible to identify and target thousands of single nucleotide

polymorphisms (SNPs) in areas of the genome under positive selection, increasing the capacity to detect potentially subtle patterns in population structuring related to gene flow and adaptive processes. Additionally, advancements in otolith chemistry and quantitative techniques offer opportunities to accurately delineate stock boundaries and assess population connectivity (see Sect. 4.3.3).

Identification and characterisation of life-history stages

The dynamic nature of blue whiting population boundaries poses challenges in defining discrete management units. Temporal shifts in key life-history stages, influenced by environmental variability and ecological dynamics, contribute to the uncertainty surrounding population structure. Research efforts should focus on identifying areas where these stages occur, characterising their temporal persistence, and determining the environmental and ecological drivers. The three primary life-history stages—spawning, recruitment, and feeding—must be thoroughly characterised and studied to accurately map the life cycle and connectivity potential of various populations. Understanding whether key life-history stages occur as discrete units or expansive zones of connectivity is crucial for defining local and regional population boundaries.

Considerable research has been devoted to understanding the spatial and temporal delineations within the principal spawning grounds situated west of the British Isles and the environmental factors influencing their distribution and abundance (Hátún et al. 2009b; Pointin and Payne 2014; Miesner and Payne 2018; Miesner et al. 2022). Future investigations can further develop this understanding through an extended time series of fisheries-independent surveys, the expansion of acoustic monitoring surveys southward, and technological innovations facilitating the acquisition of higher-resolution oceanographic data (The Copernicus Marine Environment Monitoring Service). These advancements are underpinned by developments in computational power driving the development and application of more powerful quantitative models. Based on these earlier studies, there exists a compelling imperative to systematically identify and characterise the primary recruitment and

feeding areas for the dominant population throughout the region.

Maintaining biocomplexity in the blue whiting population structure requires targeted research across fringe areas or resident subpopulations in the Barents Sea, Icelandic Waters, the Spanish-Portuguese Shelf, and the Bay of Biscay (Heino et al. 2008; Gonçalves et al. 2017; Post et al. 2021). Many fringe areas lack fundamental life-history information, such as maturity schedules, identification of spawning areas, and growth rates. Notably, the unique demographic characteristics observed in the northern North Sea and the genetic heterogeneity identified in Norwegian inshore areas underscore the complexity of blue whiting population dynamics. Further investigation is warranted to determine whether these groups occur in isolation or represent specific life-history stages associated with other stock components.

Connectivity, dispersal, and partial migration

While multiple lines of evidence suggest the presence of distinct subpopulations, the degree of connectivity among them, and the extent to which they reflect partial migration, remains uncertain. Knowledge gaps include larval dispersal pathways, the timing and scale of individual movement, and the ecological mechanisms underlying population mixing. Addressing these gaps is critical to resolving blue whiting's stock structure and informing spatial management.

Integrating biophysical modelling with natural tagging approaches such as otolith chemistry and parasite assemblages can offer significant insights. In particular, improving our understanding of oceanographic transport—especially the variability across key boundaries such as 51–60°N—is crucial for assessing larval dispersal and retention. Existing data and samples from fisheries-independent surveys can be leveraged to identify larval retention zones, predict spawning areas, and improve estimates of larval duration by back-calculating hatching and settlement periods, thereby enhancing the accuracy of dispersal models.

Otolith microchemistry is a powerful, underutilised tool for blue whiting. Because otoliths grow continuously and incorporate trace elements from the surrounding water, they archive an individual's environmental history (Campana 1999; Campana and Thorrold 2001; Izzo et al. 2016). Chemical line

transects from the core (birth) to the otolith edge (capture) can reveal movements across different life-history stages, including during early or offshore periods that are difficult to sample directly (Wells et al. 2020; Rooker et al. 2021; Lee et al. 2024). This makes otolith chemistry especially well-suited to detecting partial migration, by distinguishing resident and migratory life histories across spatially structured contingents. Despite its potential, this approach has not yet been applied to blue whiting across their range.

Parasite assemblages also offer promise for understanding spatial structure and host connectivity. Past efforts were limited by low taxonomic resolution (MacKenzie and Hemmingsen 2015), but recent advancements in molecular diagnostics (Nadler and Pérez-Ponce De León 2011; Catalano et al. 2014) now allow higher-resolutions assessments of cryptic parasite diversity (Nadler and Pérez-Ponce De León 2011). These methods may further support inferences about trophic separation and site fidelity in different contingents thus expanding the potential utility of parasites in elucidating blue whiting population structure.

Conclusion

Our interdisciplinary review indicates that the current single stock management unit for blue whiting in the NE Atlantic does not fully capture the species' underlying biological population structure. The paradigm of partial migration offers a compelling framework for interpreting the coexistence of migratory and resident contingents in blue whiting and reinforces the need for spatially nuanced management approaches. The primary spawning component on the Hebrides Shelf and the northern extent of the Porcupine Bank appears strongly connected to the Norwegian Sea feeding area. Additionally, a distinct local population seems to exist in the Barents Sea. Regions south of the Porcupine Bank, including the Celtic Sea, Bay of Biscay, and Iberian Peninsula, appear to consist mainly of localised populations with varying degrees of mixing.

These findings highlight the need to explore ways of incorporating spatial population structure into the current single-stock assessment framework. However, significant uncertainty remains around how best

to operationalise such an approach. Future research should adopt an interdisciplinary approach to fill these gaps. Incorporating life-history data, genetic analyses, otolith-derived information, variations in parasite assemblages, and spatial-temporal modelling will provide a more holistic understanding of the factors influencing population dynamics. This integration will help elucidate the complex interactions between individual movement patterns and environmental factors shaping the various blue whiting populations.

Given the substantial uncertainty in stock identification, a precautionary approach should prioritise monitoring and protecting areas where research has identified complex population structure—including mixing zones and potential subpopulations—within the existing stock assessment framework. Rather than waiting for definitive stock boundaries, management should focus on maintaining the biological processes that support population resilience and connectivity. This includes protecting critical spawning and nursery areas, implementing spatial measures in mixing zones like the Porcupine Bank and developing monitoring programmes for putative resident subpopulations. While spatially explicit assessment models represent the long-term goal, immediate management priorities should ensure the sustainability of population complexity through targeted conservation measures that complement the broader regional management framework.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no conflict of interest.

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