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Research paper

Utility of mixed effects models to inform the stock structure of whiting in the Northeast Atlantic Ocean

Alexander Barrios[a], Bruno Ernande[b], Kelig Mahé[b], Verena Trenkel[a], Marie-Joëlle Rochet[a,*]

[a] Ifremer, rue de l'Ile d'Yeu, Nantes, France
[b] Ifremer, 150 quai Gambetta, Boulogne-sur-Mer, France

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ABSTRACT

Stock structure of whiting (*Merlangius merlangus*) in the North East Atlantic is unclear. This study uses mixed effects models to analyse growth variability as a way to investigate stock identification. Growth trajectories for 634 individuals and length-at-age data for 78,686 individuals were analysed for spatial coherence and temporal synchrony in the parameters of the von Bertalanffy growth model. Growth was found to differ among most ICES divisions, and temporal fluctuations were poorly synchronized between areas. This study illustrates how growth analyses can contribute to stock identification, in addition to other data.

1. Introduction

Stock structure of whiting (*Merlangius merlangus*) in the North East Atlantic is unclear. Biological, stock assessment and fisheries management units do not coincide for whiting (Fig. 1) (Reiss et al., 2009). The general genetic structure of whiting in the area seems to be indistinct, suggesting a single wide-ranging population, except in the North Sea where distinct sub-populations have been reported (Charrier et al., 2007). Meanwhile, the species is assessed by the International Council for the Exploration of the Sea (ICES) as eight separate stocks, one of which includes the North Sea and Eastern English Channel (Reiss et al., 2009). In contrast, the Celtic Sea, Irish Sea and Bay of Biscay are considered separate stock units whereas available genetic evidence suggests they might belong to a single stock, while the North Sea, for which more genetic structure has been reported, is assessed as a single unit. However, genetic analyses are not always sufficient to delineate stock units for management (Lowe and Allendorf, 2010), especially those based on neutral markers (Nielsen et al., 2009), which were used by Charrier et al. (2007). Moreover, the practice of stock identification nowadays relies on multiple multidisciplinary analyses. Further, phenotypic differences can be relevant for management (Cadrin et al., 2014), even if they are hardly detectable using genetic methods (Nielsen et al., 2009).

Life history traits can contribute to identify stock structure, either at an early stage when no other data are available, or to provide context for stock structure dynamics (McBride, 2014). Growth characteristics have been used for a long time to help identify stock structure (e.g., Abaunza et al., 2008; Macdonald et al., 2013; McBride, 2014; Sequeira et al., 2012). Since growth, as other life history traits, is determined by genetics, demographics, and the environment, the responses of population components to environmental drivers can also contribute to delineation of stock units (Heino, 2014; McBride, 2014). Environmental drivers are taken here in a broad sense, as opposed to intrinsic, inherited chararcteristics. For whiting these drivers may include temperature and population density (Baudron et al., 2014; Hunter et al., 2016; Lauerburg et al., 2015).

Calcified structures such as scales or otoliths are often used for ageing fish. Growth at the population level is then analysed from age-length relationships. Moreover, measuring daily or annual growth increments on otoliths allows individual growth trajectories to be reconstructed to better appraise scales of variability (Panfili et al., 2002).

Mixed effects models are increasingly used in fisheries biology (Thorson and Minto, 2015). Recently, they have been applied to

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* Corresponding author at: Ifremer, B.P. 21105, 44311 Nantes Cedex 03, France.
E-mail address: mjrochet@ifremer.fr (M.-J. Rochet).

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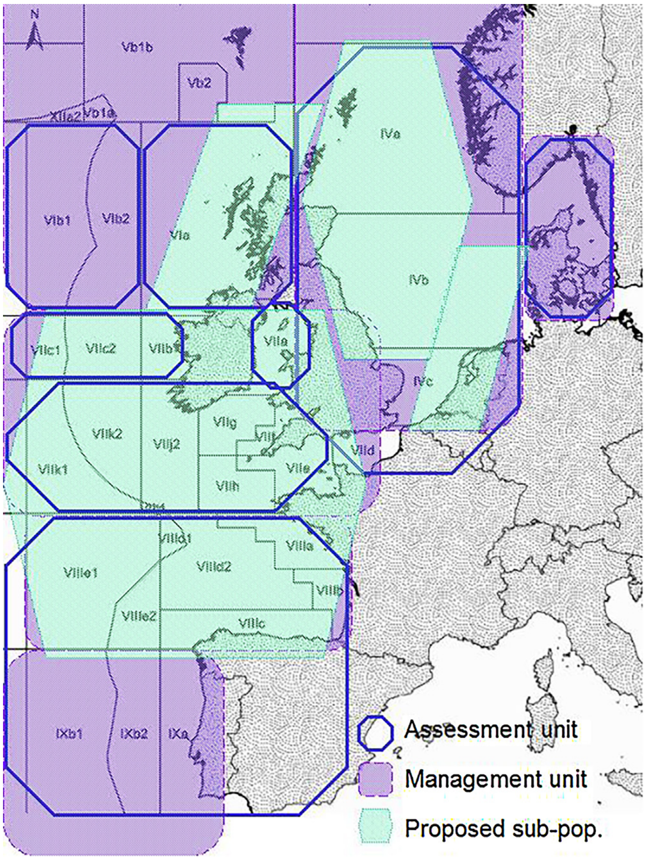

Fig. 1. Map of whiting stock structures in the North East Atlantic: management units (dotted lines, Reiss et al., 2009), assessement units (continuous lines, http://www.ices.dk/community/advisory-process/Pages/Latest-advice.aspx), and stock structure suggested by recent genetic studies (dashed lines, Charrier et al., 2007). ICES divisions are shown in black as a background: IVa Northern North Sea, IVb Central North Sea, IVc Southern North Sea, VIId Eastern English Channel, VIIf,g,h,j Celtic Sea, and VIIIab Bay of Biscay.

analyse growth at various levels and explain variability caused by environmental and/or intrinsic factors (Morrongiello and Thresher, 2015; Shelton et al., 2013; Vincenzi et al., 2014).

Here mixed effects models were used to analyse growth variability of whiting in the North East Atlantic. The main aim was to examine whether this kind of analysis could contribute to stock identification. First, individual growth trajectories for whiting collected in the southern North Sea, the Eastern English Channel, and the Celtic Sea from 2007 to 2015 were analysed. The difference between areas in estimated parameters of the von Bertalanffy growth model was examined as a potential criterion to differentiate stock units. Second, age-length data were gathered for a larger sample of individuals collected in the same areas plus the Bay of Biscay from 1996 to 2015. Again, differences in growth parameters between areas were used to identify spatial units with homogeneous growth characteristics. For the Northern and Central North Sea, for which length of time series was sufficient, time trends in growth parameters and their response to population density and temperature were also examined.

2. Materials and methods

2.1. Study area and data sources

Whiting is a small gadoid species living in temperate waters in the north-eastern Atlantic, as well as in the Mediterranean and Black Seas. Juvenile whiting feed on plankton in coastal waters (5–30 m depth), while adults are found down to 200 m depth, and also eat fish and benthic invertebrates (Pinnegar et al., 2003). Whiting live 10–20 years and can reach up to 70 cm (Cohen et al., 1990). Minimum landing size for whiting in the whole ICES area is 27 cm.

Data analysed in this study were collated from two sources: scientific bottom trawl surveys and market sampling of French landings. Trawl surveys included: the International Bottom Trawl Survey (IBTS) carried out annually in quarter 1 in the North Sea, and in quarter 4 in the Celtic Sea and Bay of Biscay, and the Channel Groundfish French Survey (CGFS) carried out in quarter 3 in the Eastern English Channel. These surveys used a stratified random design. At each station, standard 30′ hauls were carried out, and the whole catch was identified and length-measured. For selected species, sex was determined, and individuals were randomly selected from each length-class for otolith extraction (see further details on sampling protocol in ICES, 1996). Landings were sampled year-round from fish auctions covering the main ports where whiting is landed, using a métier-based sampling strategy (Leblond et al., 2008). As for surveys, individuals were randomly sampled stratified by sex and length-class. Market samples provided 0–23% of individual fish data depending on area.

Sagittal otoliths were extracted from the cranial cavity to determine fish age. The right sagittal otolith was embedded in epoxy resin and transverse sections through the core (*nucleus*) were cut with a precision saw (blade thickness: 0.3 mm). Two transverse sections were examined using ×50 magnification connected to a video camera and an image-analysis system (TNPC software, www.tnpc.fr). Yearly growth increments were assumed to consist of an opaque and a translucent band. Age was determined by counting these increments following the internationally agreed method (Easey et al., 2005; Ross and Hüssy, 2013). For a subset of otoliths, the width of annual increments was measured in addition to being counted. From both the survey and landings samples two data sets were prepared: (i) individual growth trajectories based on increment widths (see details below and Table S1) and (ii) population length-at-age using length- and age-at-capture (Table S2, Figs. S1, S2).

Environmental data used to explain variations in growth included annual average water column temperature for the whole area, from the sea surface down to 200 m depth, as predicted by hydrodynamic simulation models (Huret et al., 2013; see http://marine.copernicus.eu/). Intra-specific competition was described by whiting density averaged over the whole area, estimated from the fish trawl survey IBTS.

2.2. Data analysis

Continuous age was calculated based on the number of growth increments plus a fraction of year equal to the date of capture minus estimated date of birth. Dates of birth were set to the spawning peak in each area – 15 January in the Bay of Biscay, 15 March in the Celtic Sea, 1st of March in the English Channel, and 15 May in the North Sea (Carpentier et al., 2009; Gibb et al., 2004; Hehir, 2003; Hislop, 1984; Riley et al., 1986).

For reconstructing individual growth trajectories the relationship between total fish length L_t and otolith radius R_t at capture age t was modelled by a power function:

$$L_t = a + bR_t^c \tag{1}$$

where a, b, and c are regression coefficients.

Total length at age i could then be estimated (back-calculated) from measurements of annual otolith radii R_i as (Vigliola et al., 2000):

$$L_i = a + \exp\left[\ln(L_0 - a) + \frac{[\ln(L_t - a) - \ln(L_t - a)] \times [\ln R_i - \ln R_0]}{[\ln R_t - \ln R_0]}\right] \tag{2}$$