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Annual egg production estimates of cod (*Gadus morhua*), plaice (*Pleuronectes platessa*) and haddock (*Melanogrammus aeglefinus*) in the Irish Sea: The effects of modelling choices and assumptions

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ABSTRACT

The annual egg production (AEP) of cod (*Gadus morhua*), plaice (*Pleuronectes platessa*) and haddock (*Melanogrammus aeglefinus*) in the Irish Sea during the 2008 spawning season was estimated using generalized additive models (GAMs that further developed previous applications of the annual egg production method to Irish Sea stocks by including 2-D spatial smoothing, automatic selection of the degree of smoothing and precision estimates. The estimates of AEP from the GAMs were compared to those from a stratified mean method and the sensitivity of the estimates to different model specifications, outliers, boundary effects and prediction period was assessed. The influence of outlying large observations was notable but overall the estimates of AEP were robust to the factors studied, with effect sizes comparable to the estimates' coefficients of variation.

1. Introduction

Egg production methods (EPMs) provide spatially resolved, fishery-independent estimates of spawning stock biomass (SSB). The choice of EPM depends on how mature females develop and spawn batches of eggs throughout the spawning season (Armstrong and Witthames, this issue). In the Irish Sea, the annual egg production method (AEPM) is applied to study the spatio-temporal spawning patterns of a range of species that are 'determinate' spawners (Murua and Saborido-Rey, 2003) such as plaice (*Pleuronectes platessa*), cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), for which all the eggs to be spawned in the forthcoming season are identifiable in the ovaries prior to spawning. This paper studies a central step in the AEPM, converting observations of egg density from plankton samples collected on a series of surveys into estimates of daily and total egg production over the whole spawning period and area. This step of estimating annual egg production (AEP) is often the component of the AEPM with the poorest precision (Armstrong et al., 2001). If the surveys are designed using stratified random or systematic sampling grids and sampling coverage is good then a stratified average of egg density, together with assumptions that allow extrapolation to the density of eggs at spawning (i.e. egg production) can be used to estimate daily and annual egg production. However, the precision of estimates can potentially be improved by applying models that make use of the strong temporal and spatial patterns that are often observed in the data, even within strata. Model-based approaches can also take into account the variance in estimating the egg production curve and help to resolve difficulties in imputing production if parts of the survey grid have missing data (Augustin et al., 1998).

The presence of smooth underlying trends in the spatial and temporal patterns of spawning allows the use of generalized additive models (GAMs) (Hastie and Tibshirani, 1990), from which abundance maps and daily production estimates can be created. Further, if there is a tendency for the spatial distribution of spawning to be stable throughout the spawning season then the GAMs can be defined as a smoothed spatial pattern of egg production together with a smooth seasonal egg production cycle that appropriately scales the spatial pattern through the spawning season. Since their introduction, GAMs have been widely used for Daily EPM and AEPM surveys (Borchers et al., 1997; Augustin et al., 1998; Bernal et al., 2011a) and in mapping spawning grounds (Fox et al., 2008). For Irish Sea stocks, GAMs have been applied to estimate annual production of the earliest developmental stage (stage 1A) of cod, sole (*Solea solea*) and plaice eggs using data from the ichthyoplankton survey programme in 1995 (Fox et al., 2000), and to model production of all stages of plaice eggs from the 1995 and 2000 survey programmes in order to investigate plaice egg mortality (Dickey-Collas et al., 2003). These applications were generally successful but difficulties were experienced when high concentrations of eggs occurred close to coastlines (Fox et al., 2000) and

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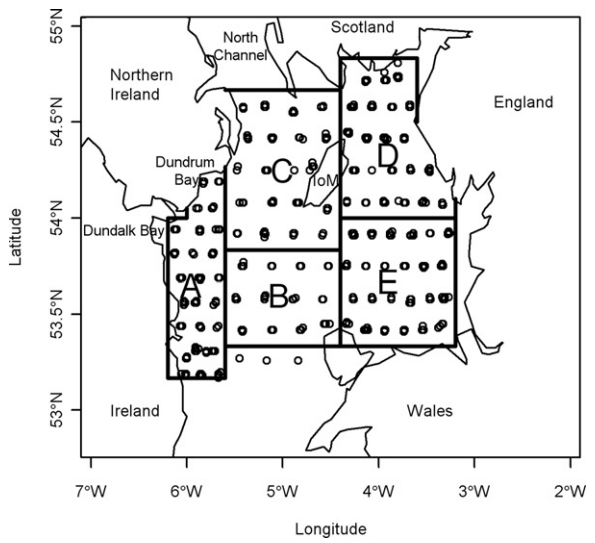

Fig. 1. Sampling locations from all five Irish Sea ichthyoplankton surveys in 2008 and sampling strata (A–E). IoM is Isle of Man.

sometimes potentially unrepresentative multi-modal production curves were predicted.

Using icythoplankton survey data from 2008 for plaice, cod and haddock in the Irish Sea, we aim to develop the previous models in several ways. Making use of advances in GAM methodology (ICES, 2004; Wood, 2006), 2-D spatial smoothers are included to improve model fit, formal tests of spatial stratification are incorporated and simulation based confidence intervals are provided. The estimates also incorporate technical improvements in the identification of the morphologically very similar early-stage eggs of gadoid species (Fox et al., 2005; Goodsir et al., 2008), which allow estimates of egg production for haddock and remove a potential source of bias in earlier estimates of cod egg production.

It is important to consider the effect of methodological changes on the results as for any modelling process the final result depends on a range of choices made by the analyst and variance estimates are generally conditional on these choices (Elith et al., 2002). To be of use in decision-making, such as fisheries management, results should be robust to plausible changes in input data and model details (McAllister et al., 1999). Therefore, our second aim is to investigate the sensitivity of the annual egg production estimates to the choice of method, the assumptions within a method, such as alternative error distributions, and properties of the data, particularly outliers. Considering these results provides insights into the fitted models, a guide to the importance of different assumptions and an indication of areas for further developments.

2. Materials and methods

The study area covered the Irish Sea from 53.33°N to 54.83°N (Fig. 1). This region is known to contain two spatially discrete spawning sites for cod and plaice, in the coastal areas of the western Irish Sea (WIS) and eastern Irish Sea (EIS) (Armstrong et al., 2001). A deep water channel (>100 m) runs through the WIS and is considered an important migration pathway for adult cod (Bendall et al., 2009) while the seasonal establishment of an anti-cyclonic gyre in the WIS (Hill et al., 1997) is considered an important larval retention feature (Dickey-Collas et al., 1997). The spawning sites in the EIS are in an area of generally shallow water (<50 m). The North Channel, St George's Channel (approx. 52.17°N, 6.37°W to 51.90°N, 5.32°W) and the areas north and south of the Isle of Man are tidally very dynamic and generally unsuitable as spawning sites, and historical egg surveys show much lower egg abundances than in the coastal bights. Spawning patterns of haddock were previously poorly known due to the difficulty in identifying early-stage eggs and the relatively low abundance of this species prior to the mid 1990s. However, trawl surveys show that mature haddock are confined mainly to the WIS with some spill-over into the EIS.

2.1. Sample collection and processing

Five ichthyoplankton surveys of up to 10 days duration were carried out at intervals during the spawning season in 2008. The survey grids comprised of around 100 stations based on a stratified, systematic design (Fig. 1 and Table 1). Station spacing was reduced in the coastal areas where the between-station variance in egg abundance was expected to be highest based on previous surveys. At each station, a Gulf-VII plankton sampler (Nash et al., 1998) was deployed in a double-oblique tow to as close to the seabed as was deemed safe given the topography. Sampler deployment and filtering efficiency were monitored using a depth sensor mounted on the sampler and flowmeters mounted inside and outside the net. These data were analysed together with data on ship speed and shooting/retrieval times to compute the total volume of water filtered during the tow, using standard formulae for double-oblique plankton tows. A temperature sensor mounted on the sampler provided continuous data from which depth-integrated temperatures were derived for predicting egg development rates at each station. Due to a failure in the sampler electronics in Survey 5, it was only possible to collect surface temperatures using the through-flow seawater system on board the vessel. Egg abundance was very low by Survey 5, so this is likely to have caused negligible bias in estimates of daily egg production. The pattern of increasing temperature in Survey 5 was similar to the pattern in the equivalent surveys in 2006 when depth-integrated values were available for all surveys.

The fish eggs from each station were separated and quantified as follows:

1. A subsample of up to 100 stage 1 'cod-like' eggs (defined as eggs of diameter 1.1–1.75 mm and lacking oil globules or other distinguishing features) was removed from each sample immediately after capture and preserved in ethanol for genetic analysis ashore. The diameter range was specified to include effectively all eggs of cod and haddock (Russell, 1976). The total number of eggs taken for genetic analysis comprised 6–13% of the total catches of stage 1 cod-like eggs in each survey (Table 1).
2. The remaining plankton sample was preserved in 4% buffered formaldehyde and sorted on shore into the residual cod-like eggs, and those identifiable to species. Unsegmented eggs >1.75 mm in diameter, with no oil globules and no large perivitelline space were classified as plaice. Samples with large quantities of plankton were split if required and the raising factors recorded. All eggs in the sorted fractions were measured and allocated to an embryonic development stage using criteria described by Simpson (1959), Riley (1973) and Thompson and Riley (1981), and the numbers recorded.

The eggs in the ethanol-preserved samples were identified as cod, haddock, whiting or 'other' using TaqMan Real-Time PCR analysis as described by Goodsir et al. (2008). The accuracy of the method was continuously evaluated by processing hatchery-reared control eggs interlaced anonymously with the field-caught eggs. Sub-samples of the field-caught eggs not identified as cod, whiting or haddock were re-analysed using gene-sequencing equipment to determine if the eggs were of another species or failed to provide enough DNA for species identification.