



A maximum likelihood method for obtaining incubation temperature of eggs of synchronous spawning fishes

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ARTICLE INFO

Article history:

Received 17 July 2009

Received in revised form 11 January 2010

Accepted 19 January 2010

Keywords:

Anchovy

Bay of Biscay

DEPM

Egg ageing

Incubation temperature

ABSTRACT

The Daily Egg Production Method (DEPM) used to estimate the Spawning Stock Biomass for many fish species requires that eggs classified into morphological stages are converted into daily cohorts. Since the development of the eggs is dependent on the temperature, the ageing process requires the temperature at which the eggs have been incubated. For the Bay of Biscay anchovy the incubation temperature is usually considered to be the observed temperature at 10 m depth, where maximum concentrations of eggs are typically reported. However, this temperature cannot always be recorded. In cold years, this can sometimes produce cohorts that are older than expected. Physical transport of the eggs could be one of the explanations: as the eggs are transported from one area to another, they follow an unknown gradient of temperatures. In this paper we present a method to calculate the incubation temperature by station corresponding to the maximum probability of finding the number of eggs by stages in the station, given sampling time and daily distribution of spawning time. The algorithm sweeps a range of temperature values below the sea surface temperature (SST) recorded at each station, and gives both the global maximum and the local maximum closest to SST as potential solutions. We analyze the effect of the temperature on the ageing, and assess the expected variations in the final estimates of the Daily Egg Production.

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1. Introduction

The Daily Egg Production Method (Hunter and Lo, 1997; Lasker, 1985; Lo et al., 1996; Parker, 1980) is yearly applied for the estimation of egg production of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay (Somarakis et al., 2004). The Spawning Stock Biomass (SSB) is consequently calculated as the population responsible of that production. The daily egg production rate P_0 is estimated, together with the daily mortality rate z from the following equation:

$$P_a = P_0 \exp(-za), \quad (1)$$

where P_a is the density of eggs at age a .

This requires that the eggs sampled at sea and allocated into morphological stages (Moser and Ahlstrom, 1985) are classified into daily cohorts. The egg development depends, among other factors, on the incubation temperature (Pepin, 1991), which is usually studied through egg incubation experiments (Bernal et al., 2008;

Ibaibarriaga et al., 2007; Lo, 1985). Both, previously used ageing methods (Bernal et al., 2001; Lo, 1985) and recently developed Bayesian ageing methods (Bernal et al., 2008; Bernal, 2008; ICES, 2004) make use of temperature dependent egg development models, and therefore they require that the incubation temperature is known. Usually, it is assumed that the incubation temperature of all the eggs found at the station is known without error and equal to the sampled temperature recorded at the survey.

However, these assumptions about the incubation temperature can be questioned. On the one hand, there is no unique modal depth for the egg vertical distribution. For instance Sundby (1983) and Boyra et al. (2003) found surface peaks of egg distribution for high salinity areas, and sub-surface peaks with low salinity. On the other hand, the incubation temperature of all the eggs found at the station has likely not been constant throughout the whole development of the eggs. There is a certain amount of transport of eggs by the water masses (Stauffer and Picquelle, 1980), and the seasonal trend in temperature should also be considered; waters get warmer in general during this survey carried out in spring time (Motos et al., 1996).

The implications of the selected incubation temperature and the underlying assumptions have been little discussed until recently. Several publications have concentrated on the effects of the temperature in the development and survival of eggs (Mendiola et al., 2006; Pepin, 1991; Portilla et al., 2007), but to our knowledge, the

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estimation of the temperature itself has not been the focus yet. The estimation differs between areas and species, but the value is usually chosen *ad hoc*, and not always detailed in the reports. A related work carried out in Portugal (Manuel et al., 2008) showed how the stability of the water column in this area eliminated the temperature variability with depth; the incubation temperature is nonetheless prone to change with time due to possible transport and seasonal variation.

The main objective of this work is to propose and evaluate a method to estimate the incubation temperature that maximizes the egg stage distribution observed at sea. We firstly introduce the new method to estimate incubation temperatures. The method is first tested on simulated data. Real data using a vertical plankton sampler at different depths are used to compare different incubation temperature estimates. Finally, the incubation temperature estimation method is applied to the DEPM time series from 1995 to 2007 and the associated changes in total egg production estimates are studied.

2. Materials and methods

2.1. Incubation temperature method

At each station, let $n_I, n_{II}, \dots, n_{XI}$ be the number of eggs in each stage, τ the sampling time and t the incubation temperature. Assuming independence of eggs concerning their actual spawning time (conditioned to the same probability density function spawning time), but a common incubation temperature, the probability of observing $n_I, n_{II}, \dots, n_{XI}$ eggs at stages I, II, ..., XI, given the sampling time τ and temperature t is given by

$$P(n_I, n_{II}, \dots, n_{XI} | \tau, t) = \prod_{i=1}^{XI} p(i | \tau, t)^{n_i} \quad (2)$$

where $p(i | \tau, t)$ denotes the probability that an egg is in stage i given the sampling time τ and temperature t . This marginal probability can be computed as:

$$p(i | \tau, t) = \int_a p(i, a | \tau, t) da = \int_a p(i | a, \tau, t) p(a | \tau, t) da, \quad (3)$$

where $p(i | a, \tau, t)$ and $p(a | \tau, t)$ are both terms used in the Bayesian ageing process (Bernal et al., 2008; Bernal, 2008; Ibaibarriaga et al., 2007; ICES, 2004).

The probability of an egg being in stage i conditioned on having an age a and being developed at temperature t , $p(i | a, \tau, t)$, is modeled using the incubation experiment data (Bernal et al., 2008; Ibaibarriaga et al., 2007). Note that in this case given that the spawning time is exactly known, the probability density function $p(i | a, \tau, t)$ depends only on the egg age a and the sampling time τ can be omitted $p(i | a, \tau, t) = p(i | a, t)$.

The marginal distribution of age a given the sampling time τ and the temperature t , $p(a | \tau, t)$ encapsulates the prior available information on the age distribution. For species like the Bay of Biscay anchovy with daily spawning synchronicity (i.e. that release the eggs at restricted parts of the day) this knowledge might be related to the probability density function of spawning time. In addition, given that eggs die exponentially as they get older (Eq. (1)), a survival probability term could also be included. Therefore, the marginal distribution of age a , $p(a | \tau, t)$ or simply $p(a | \tau)$ when it does not depend on the incubation temperature, can be written as:

$$p(a | \tau) = \frac{p(-a | \tau) \exp(-za)}{\int_a p(-a | \tau) \exp(-za) da}, \quad (4)$$

where $p(-a | \tau)$ is the probability that the egg was spawned a hours before given that it was sampled at time τ , $\exp(-za)$ is the

egg survival probability based on the exponential mortality decay model and the denominator is just the normalizing constant of the probability density function. For species with daily spawning synchronicity the spawning time distribution can be fitted or approximated from the distribution of stage I eggs or from the distribution of hydrated females just before spawning. In particular, for the Bay of Biscay anchovy a normal distribution with mean at 23 p.m. and standard deviation of 1.25 h is used. For species without daily spawning synchronicity a uniform distribution could be used.

Taking all this into account, we get:

$$p(i | \tau, t) = \frac{\int_a p(i | t, a) p(\tau - a) \exp(-za) da}{\int_a p(\tau - a) \exp(-za) da}. \quad (5)$$

The objective is to find the temperature t such that $P(n_I, n_{II}, \dots, n_{XI} | \tau, t)$ is maximized. The method uses a grid search algorithm, so that the joint probability function of the stages (Eq. (2)) is evaluated at all temperatures from SST to SST–5 °C, every 0.1 °C. Two different incubation temperature estimates are considered: global maximum (here onwards called T_{glob}), which would correspond to the maximum likelihood estimate, and the local maximum closest to the SST (here onwards called T_{loc}). The reason to evaluate the local maximum is explained in Section 3.1.2. Different initial mortality values were tested giving similar results (not included in this paper), so an iterative model was not necessary to estimate the right mortality, as it is the case for egg production estimates (see below).

In order to study the performance of the method, we firstly analyze the information which can be obtained from occurrence of single stages in samples, looking at the likelihood of different incubation temperatures as a function of sampling time for each stage.

2.2. Simulation study

We then apply the method to three sets of simulated data. Every day spawning is generated at 23 h (GMT) without any variability in time or the amount of eggs released, and the development follows the multinomial model of Ibaibarriaga et al. (2007). The three simulations are as follows:

1. *Simulation 1*: The first simulation considers five cohorts of eggs in a given depth with a fixed incubation temperature of 17 °C and SST equal to 18 °C. This would be the most simple option with a constant temperature, as it is commonly considered.
2. *Simulation 2*: In a second case five cohorts of eggs are located at ten depth layers with different temperatures. The vertical profile covers temperatures from 16.6 to 13.8 °C (simulating a randomly selected LHPR station from 5 to 18 m depth). Simulated sampling collects egg across depths integrating evenly all the column, as with the vertical samplers (CalVET type nets) used for the applications of the DEPM. This simulation considers the real variation of temperature with depth, but neither daily or seasonal variation nor transport of eggs is allowed.
3. *Simulation 3*: The simulation deals with two successive daily cohorts developing at different temperatures, considering a gradient of temperature of 1 °C between them. Three cases are shown: cooling of water with time, an increment in temperature, and a case where one of the cohorts includes stages I–III only. Depth is not considered in this experiment. Transport of eggs would produce these differences in gradient of temperature between eggs at the same station.

Eggs were sampled at fourteen sampling times of the fifth day throughout the 24 h day cycle (1, 2, 4, 5, 7, 9.5, 10.5, 12.5, 15, 18, 20, 21.5, 23, and 24 h) for the first two simulations. The third simulation

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