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Effects of temperature on development and mortality of Atlantic mackerel fish eggs

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Abstract

The development of Northeast Atlantic mackerel (*Scomber scombrus*) eggs, obtained from artificial fertilisation during the spawning season in the Biscay Bay area, was monitored at five temperatures (ranging from 8.6 to 17.8 °C). The times to intermediate stages (III–V) and total hatching, obtained in this study, agree with the results of previous studies undertaken some years ago. However, the times over stages IA, IB and 50% hatching indicate that development rates differed significantly between the studies; this could be related to an effect of the previous thermal history of the eggs, or to experimental biases. Daily mortality (Z) during the embryonic period was found to vary between 0.17 and 0.38, using traditional exponential decay models. The estimates of mortality rate were found to range consistently with those derived from previous studies on Northwest Atlantic mackerel eggs without predation. However, the shape of the survivorship-curve during the development pursued in this study has indicated that mortality is not constant in time. Similarly, the suitability of an exponential model to describe daily mortality should be considered.

Keywords: Atlantic mackerel; *Scomber scombrus*; Eggs; Development; Mortality; Temperature models; Stock assessment

1. Introduction

High mortality in the embryonic and larval stages is an important factor in determining the success of a year-class, and thus, the recruitment to the fishery (Hjort, 1914; Blaxter, 1974). Small differences in instantaneous mortality rates (Z) during the early life stages can generate large differences in final abundance or survivorship (Houde, 1987; Chambers et al., 2001); but these changes in the magnitude of Z are often difficult to quantify from field estimates of abundance (Dickey-Collas et al., 2003); this is mainly because of magnitude and variability of the factors involved (Pepin and Myers, 1991).

Proper estimates of egg mortality in the field require accurate ageing of the eggs, which implies a good knowledge of the egg developmental rates at different temperatures. Many studies have examined the influence of temperature on the development and mortality rates of fish embryos (Lasker, 1964; Lo, 1985; Pauly and Pullin, 1988; Pepin, 1991; Van der Land, 1991; Le Clus and Malan, 1995), but these temperature-related mechanisms remain unclear for many species (Legget and Deblois, 1994). In this way, only limited information is available for the southern spawning component of the Northeast Atlantic mackerel, *Scomber scombrus* L. (herein NEA mackerel). Only Lockwood et al. (1977) have described the development of NEA mackerel eggs from the Bay of Biscay, Celtic Sea and West of Ireland at temperatures ranging from 7.4 to 17.8 °C. Similarly Thompson (1989) fitted mortality curves to NEA mackerel egg counts, from the northern spawning components of the Bay of Biscay and Celtic Sea. However, both studies have limitations, since Lockwood's experimental design might not be optimal for the study of development; as such, Thompson (1989) concluded that erro-

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Nomenclature

a	parameter of temperature
A	total mortality
b	parameter of scale
$h(t)$	hazard function of the Weibull distribution (i.e. age-specific instantaneous mortality rate)
i	egg stage ($i = 1, \ldots, N_{stages}$)
I	egg incubation time to reach the end of each stage of development
N_t	number of surveyed eggs
N_0	initial number of eggs fertilised successfully and incubated per temperature treatment
S	survival
$S(t)$	survival function of the Weibull distribution (i.e. probability that an individual survives longer than an age)
t	incubation time (i.e. h, days)
T	egg incubation temperature (°C)
Z	instantaneous rate of mortality, derived through exponential models fitted in log scale

Greek letters

α	scale parameter, in units of event observations
$\boldsymbol{\beta}$	vector parameter, defining the age range within stage and temperature for the event analysis
γ	shape parameter of the event analysis equation

neous stage identifications may have affected their results on mortality. In turn, the Northwest Atlantic mackerel embryonic period was studied from temperature controlled conditions by Worley (1933) and Lanctot (1980), who used eggs of mature individuals from fish populations inhabiting close to Woods Hole, Massachusetts and St. George's Bay, Nova Scotia areas, respectively. The development of mackerel eggs, between both localities, was shown to be very similar; however, the temperature range over which development took place was greater in the study of Worley (1933).

Since 1977, independent estimates of the spawner biomass of NEA mackerel have been based on direct eggs surveys. These estimates of biomass are derived from the total annual egg production method (TAEP) (Gunderson, 1993), and then, they are used as inputs for the assessment with the integrated catch at age analysis (ICA) (Patterson and Melvin, 1996). An important requirement of this method is that spawned eggs of the target species can be aged (Stauffer and Picquelle, 1985). Age determination requires precise information on the effect of temperature on the rate of development of a large number of egg stages (Moser and Ahlstrom, 1985). Lockwood et al. (1977) modelled the temperature dependent development rate for each of the egg stages of NEA mackerel. Nowadays, such rates are being used to apply the method of assessing abundance of mackerel fishes in the Bay of Biscay.

Egg production in many surveys is estimated by fitting a mortality exponential decay model to the data for each stage, extrapolating back to the number of eggs at the time of spawning, then calculating the area under the seasonal production curve (Bunn et al., 2000). However, there are indications that eggs without predation do not die at a constant rate (Cameron et al., 1992; Makhotin et al., 2001; Dickey-Collas et al., 2003). Thus, to assume a constant mortality rate, through all egg developmental stages could not be always appropriate. Daily egg production methods were developed for the Atlantic mackerel (Priede and Watson, 1993). Likewise, mortality estimates generated from the abundance of stage IA eggs, were already successfully integrated in the TAEP method of 1996 for this species (Anon, 1996); this is consistent with the concept of the number of eggs spawned at sea is closer to the abundances of stage IA. However, neither stage-specific mortality estimates, nor curves of population decay from laboratory controlled conditions, have ever been described for the NEA mackerel egg stage.

The aim of this study was to check the influence of temperature on development and mortality of artificially fertilised eggs of NEA mackerel, from stages I to V. The hatching time was included for comparison with previous studies. Moreover, we examined the suitability of the traditional exponential models and we explored the event analysis, to estimate embryonic mortality.

2. Materials and methods

2.1. Incubation

Adult mackerel, *S. scombrus*, were captured in March 2004 during the spawning season in the Biscay Bay area at 45°47′N 2°25′W; sperm and eggs were collected from 84 ripe female and 60 running male mackerels. Only females that yielded eggs freely (i.e. with little or no pressure on the vent) were used in these experiments. Eggs and sperm were combined in filtered seawater at ambient temperature. After 1 h of incubation the temperature was lowered to 5 °C to keep the gametes at the basal metabolic activity level, during transportation to culture tanks (see, Table 1). After approximately 6 h from fertilisation, at the laboratory, 300 eggs were sampled and individual diameters measured to the nearest 0.1 mm, using a dissecting microscope. Fertilised eggs were selected and organised as follows: around 40 000 eggs were separated and incubated into five black cylindro-conical 200 l tanks (35–40 ind l^{-1}); 250 eggs were placed in five 1 l jars (50 ind l^{-1}); 150 viable eggs were separated into individual 35 ml sterile vials. Thirty of these vials were transferred to each of five tanks, maintained at 8, 11, 13, 15 and 17 °C water baths (Table 1). Seawater in each vial was replaced every day, throughout the experiment. Every bath was filled with UV-sterilised filtered (1 μm) seawater and temperature conditions were controlled by the combined function of an air-conditioning device and flow-through water