Fisheries Research 117–118 (2012) 35–47

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Developments in understanding of fecundity of fish stocks in relation to egg production methods for estimating spawning stock biomass

Michael J. Armstrong*, Peter R. Witthames

Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, Suffolk, NR33 0HT, United Kingdom

ARTICLE INFO

Article history:
Received 17 September 2010
Received in revised form
18 December 2010
Accepted 24 December 2010

Keywords:
Egg production surveys
Annual egg production method
Daily egg production method
Spawning
Fecundity
Atresia

ABSTRACT

The use of egg production methods to estimate the spawning stock biomass (SSB) of fish depends critically on establishing the biological basis underpinning the methods. In this paper we review recent developments in knowledge of several key aspects of reproductive biology relevant to the estimation of annual egg production and daily specific fecundity at the individual and population level, as required in particular for application of the Annual and Daily Egg Production Methods respectively. The parameters to be estimated include spawning frequency, potential annual fecundity or batch fecundity, and rates of atresia prior to and during the spawning season. The initial development of egg production survey methods led to a significant growth in understanding of the reproductive biology of the target fish species. Drivers for further developments have come from the extension of the surveys to more species and areas, an increasing interest in evaluating time-series of reproductive potential in stocks, and the needs for research and development in support of marine aquaculture. A growing number of studies on field-caught and captive fish since the 1990s have led to important advances in our understanding of the triggering of maturation and gametogenesis, the subsequent processes of oocyte (follicle) growth and vitellogenesis, regulation of fecundity through atresia, batch spawning dynamics, and the influence of extrinsic factors such as day length, temperature and feeding. We conclude that the biological basis for egg production survey methods is now extremely well established for the main species being surveyed. However, the extension of the methods to a wider range of species has highlighted the practical difficulties in obtaining sufficiently precise and unbiased estimates of key parameters such as spawning fraction or sex ratio that are influenced by spatial distribution or catchability of several population components (e.g. mature, immature active spawning or spent). The definition and validation of spawning markers also remains a challenge, particularly for new species being surveyed. Given the often high cost of egg production surveys, particularly the annual method, there is a need for simulation studies to determine the relative performance of simpler and less expensive approaches to tracking SSB from egg surveys for use in stock assessment. Developments that expand the quantity and utility of the information yielded by the surveys, including integration of the surveys into broader ecosystem studies, could also be considered a way to improve cost-effectiveness.

1. Introduction

Estimates of spawning stock biomass (SSB) are widely used in the formulation and implementation of fishery management strategies for commercially exploited species. The most common use of SSB time-series is to define the shape of stock-recruit curves, to define biological reference points such as the SSB below which recruitment is impaired, and to estimate trends in SSB relative to these. In the majority of cases, SSB estimates are derived from stock assessment models using fishery and survey data or in some cases obtained directly from trawl and acoustic surveys. Such approaches can be extended to derive time-series of spawning potential, by computing the total population egg production (TEP) from maturity and fecundity data (Marshall et al., 1998), or using predictors of TEP such as total lipid energy (Marshall et al., 1999). However, the most direct estimates of SSB for fish species that have planktonic eggs are obtained by combining estimates of egg production from ichthyoplankton surveys with estimates of fecundity per unit biomass from representative sampling of mature fish at the appropriate time (Hunter and Lo, 1993). Egg production methods have also been applied to fish such as herring (*Clupea harengus*) that lay demersal eggs (Hunter and Lo, 1993).

Egg production survey methods have the advantage of providing SSB estimates for spatially discrete spawning sites, and avoid the bias in fishery-dependent SSB estimates associated with assumptions regarding maturity ogives, fishery selectivity patterns, sex

* Corresponding author. Tel.: +44 1502 52 4362.
E-mail address: mike.armstrong@cefas.co.uk (M.J. Armstrong).

0165-7836/$ – see front matter. Crown Copyright © 2011 Published by Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2010.12.028

ratio, natural mortality, stock mixing and especially the accuracy of fishery data. However there are many steps leading to the final SSB estimates from egg production methods, each with potential biases. To eliminate or sufficiently reduce these errors requires careful attention to survey design and technical aspects of data collection, and to choosing methods appropriate to the reproductive biology and behaviour patterns of the target species. Hunter and Lo (1993) noted that estimation of egg production from plankton surveys is straightforward, but that fecundity estimates "continue to be the Achilles heel of ichthyoplankton-based biomass estimation". Their main concern was the poorly tested assumption that estimates of annual or batch fecundity obtained from ovary tissue samples are exactly equivalent to the numbers spawned and successfully fertilised (procedures used to test these assumptions were described by Hunter et al., 1992).

There has been a notable growth in studies of reproductive biology of fish, and associated methodological development since the time of Hunter and Lo's (1993) summary. This has been driven by the development of egg production survey methods for a greater range of fish stocks, an increasing interest in developing time-series of stock reproductive potential, and a need to improve cost-effectiveness of surveys and sample processing. The knowledge gained in aquaculture and the associated technology transfer to scientific studies has also been an important driver. The formation of a number of large collaborative research programmes on fish reproductive biology has facilitated development of methods and understanding – examples include the 3-year EU 5th Framework project *Reproduction and Stock Evaluation for Recovery* (RASER: contract no. Q5RS-2002-01825; http://raser.imr.no) (Kjesbu et al., 2010a), the North Atlantic Fisheries Organisation Working Group on Reproductive Potential http://www.iim.csic.es/pesquerias/NAFOWGRP/intro.htm and the Cost Action *Fish Reproduction and Fisheries* (http://www.fresh-cost.org).

The present paper provides a broad overview of developments in knowledge arising from methodological advances concerning fish reproductive biology and focusing on fecundity estimation, based on a key note speech from the March 2010 Fresh-Cost Workshop in Athens from which papers in this Special Issue of *Fisheries Research* are mostly derived.

2. Egg production survey methods

Three egg production methods have been developed for fish with planktonic eggs. These are the Daily Egg Production Method (DEPM) developed initially for northern anchovy *Engraulis mordax* off California (Parker, 1980), the Annual Egg Production Method (AEPM) developed for NE Atlantic mackerel *Scomber scombrus* (Lockwood et al., 1981, based on the concept of Saville, 1964) and the Daily Fecundity Reduction Method (DFRM) developed for Dover sole *Microstomus pacificus* by Lo et al. (1992, 1993). The basic equations for estimation of SSB of female fish are given in Table 1. The main difference between the three methods is in the estimation of fecundity (see Fig. 1 for an illustration of the fecundity production process and associated terminology), and in the time period over which egg production is estimated. Stratoudakis et al. (2006) provide a summary of the biological characteristics distinguishing the ichthyoplankton methods described by Hunter and Lo (1993).

The primary estimate of biomass from an egg production survey is the average biomass of mature females that have spawned during the survey period. Extension of the method to include other population components such as mature males, immature females or skipped spawners (Rideout et al., 2005) requires an appropriate sampling survey design to estimate the biomass of these components relative to the biomass of spawning females. It is important

Table 1
Summary of egg production methods for estimating biomass of mature female fish. Extension to include other population components (e.g. SSB of males) requires additional parameters (not shown).

Method	Calculation of SSB of females	No. of surveys per year
DEPM	$\dfrac{(P_0 \times \text{Area} \times W_f)}{\text{FB} \times S}$	One plankton survey to estimate mean daily egg production per m^2 (P_0), and contemporaneous sampling of adult fish to estimate mean weight of mature females (W_f), mean batch fecundity (FB) and daily spawning fraction (S). Area = area of spawning grounds in m^2
AEPM	$\dfrac{\sum_{t=\text{start}}^{t=\text{end}} P_{0,t} \times \text{Area}}{(F_p - \text{AT})}$	A series of plankton surveys covering spawning season to estimate annual egg production (integration of estimates of P_0 over time t from start to end of spawning season); sampling of pre-spawning adults to estimate potential annual fecundity F_p per unit body weight; sampling of adults during season to estimate loss of fecundity due to atresia (AT, per unit body weight)
DFRM	$\dfrac{(P_0 \times \text{Area} \times W_f)}{\text{d}(F \times G)/\text{d}t}$	One or more plankton surveys to estimate mean daily egg production P_0 during part of the spawning season, and contemporaneous sampling of adult fish to estimate mean W_f and rate of decline of product of mean residual fecundity F (numbers of vitellogenic oocytes) and proportion of fish (G) that are active spawners (i.e. in the batch spawning cycle)

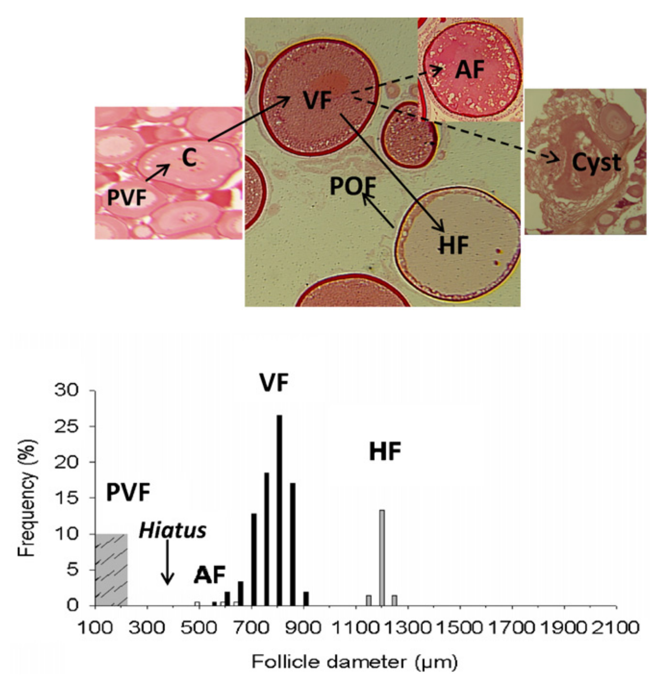

Fig. 1. Pictorial illustration of the fecundity production process, shown in histological section (top panels) and as a follicle size frequency distribution for a determinate annual spawner (bottom panel). In the main route of development (solid arrows), pre-vitellogenic follicles (PVF) develop through cortical alveoli (C) to form vitellogenic follicles (VF), which grow rapidly and become hydrated follicles (HF) just before spawning. Post-ovulatory follicles (POF) remain after ovulation. Down-regulation of fecundity or skipped spawning may occur when VF turn into atretic follicles (AF) or remain in the ovary as cysts (dashed arrows). A pronounced hiatus may form between the PVF and VF in the follicle size frequency of determinate annual spawners as the VFs mature.