Fisheries Research 117–118 (2012) 121–129

Contents lists available at ScienceDirect

Fisheries Research

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

Revised concepts for estimation of spawning fraction in multiple batch spawning fish considering temperature-dependent duration of spawning markers and spawning time frequency distribution

Yutaka Kurita*

Tohoku National Fisheries Research Institute, Fisheries Research Agency, Shinhama 3-27-5, Shiogama, Miyagi 985-0001, Japan

ARTICLE INFO

Article history:
Received 10 June 2010
Received in revised form 13 May 2011
Accepted 14 May 2011

Keywords:
Spawning fraction
Temperature
Spawning time
Spawning marker
Japanese flounder

ABSTRACT

A generalized method to accurately estimate the spawning fraction (S) of multiple batch spawning fish considering the duration of histological spawning markers over a wide range of ambient temperature, spawning time frequency distribution of the population, and sampling time was developed. The concept of the variable "fraction of the daily spawning females with spawning markers at a sampling time t ($FDSM_t$)", which varies diurnally in relation to the duration of the spawning markers and the spawning time frequency distribution, was introduced. Spawning fraction can be calculated as $S = Psm_t \times (1/FDSM_t)$, where Psm_t is the observed fraction of active females with signs of previous or imminent spawnings, referring to various spawning markers, at a sampling time t. Simulations suggested the following two methods were robust when the spawning time frequency distribution was long and uncertain. The first refers to sampling females evenly throughout the 24 h period, whilst the second is based on selecting a single or combination of spawning markers so that the total temperature-adjusted marker duration at sampling sums to around 24 h and applying, if necessary, a correction factor. With these methods, the influence of sampling time and spawning time frequency distribution can be ignored. The utility of the second method was evaluated with field data for Japanese flounder *Paralichthys olivaceus*. In all cases, accurate validation of the temperature-dependent duration of spawning markers is essential for accurate estimation of S.

1. Introduction

The daily egg production method (DEPM) has a long history of applications to estimate stock size of indeterminate multiple batch spawning fish species following its introduction in 1980 (Parker, 1980; Lasker, 1985). The following equation shows the variables required to determine spawning stock size (SSB) with the DEPM:

$$SSB = \frac{P_d \times A}{R \times S \times F}, \qquad (1)$$

where P_d = daily egg production per unit area of sea surface determined by ichthyoplankton survey, A = sea surface area surveyed, R = sex ratio, S = fraction of mature females spawning per day, F = batch fecundity per g female released in a spawning event.

The S in Eq. (1) refers to the prevalence of daily spawning females in the target population. The target population varies among studies; *e.g.* only active females which are within the batch spawning cycle, both active and regressing females, or all females including immature individuals (Stratoudakis et al., 2006). In this study active females are adopted as the target population. Daily spawning females are identified by the presence of histological spawning markers, *i.e.* oocytes at migratory nucleus (MN) and hydrated (HD) stages indicate imminent spawning whilst postovulatory follicles (POF) recent spawning (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985; Stratoudakis et al., 2006; Ganias, 2012). S is also the most problematic variable because it is believed to be the largest source of biased error (Stratoudakis et al., 2006).

The daily egg production method has so far been applied mainly to those clupeid stocks (Stratoudakis et al., 2006) that spawn synchronously as a spawning cohort during a restricted period of a few hours in the early night (Hunter and Macewicz, 1980). By adopting a daily sampling strategy that covers a short period just after each evening's spawning, the spawning cohort is easily and accurately identified by the presence of POFs 0, 1, or 2 days old because the morphology of each POF cohort changes rapidly as they age and the age of POFs appears intermittently. In the situation of northern anchovy *Engraulis mordax* (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985), day-0 POF was actually 0–5 h old and day-1 POF actually 19–28 h old. In many studies DEPM has been applied to fish species that spawn synchronously during a restricted few hours

* Tel.: +81 22 365 9931; fax: +81 22 367 1250.
E-mail address: kurita@affrc.go.jp

0165-7836/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2011.05.010

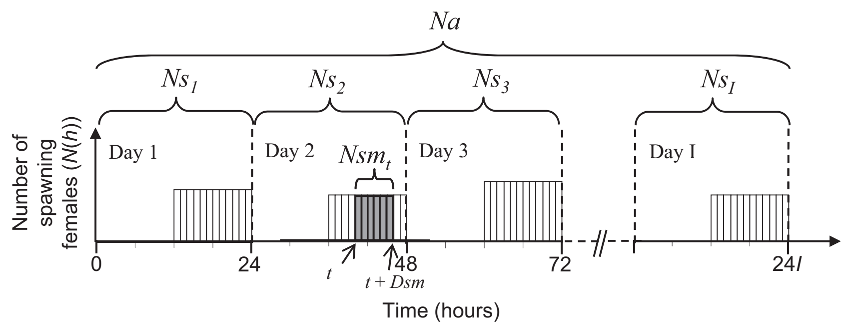

Fig. 1. Illustration showing the terminology used to describe the spawning dynamics in a simulated population of active spawning females including the appearance of associated spawning markers at a sampling time. The number of spawning females per daily hours ($N(h)$) within each day constitutes each daily cohort of spawners (Ns_1, Ns_2, . . ., Ns_I) which spawn between 1200 and 2400 h. The sum of daily spawners for spawning interval (I days) is the number of active females (Na). The shaded area of $N(h)$ corresponds with the number of females (Nsm_t) with a pre-spawning marker (such as hydrated oocytes) at sampling time (t) which depends on this time in relation to the daily spawning period and the duration of the spawning marker (Dsm).

(Ganias et al., 2003) or whose spawning time can be practically presumed to be short (Alheit et al., 1984; Motos, 1996; Somarakis et al., 2004). For those fish species the prevalence of each daily class of POFs is supposed to be equal to the daily spawning fraction.

In contrast, some fish species spawn throughout the day at the population level and do not display synchronised spawning among individuals. For example, Atlantic mackerel *Scomber scombrus* spawn throughout the daily cycle (Ferraro, 1980; Walsh and Johnstone, 1992; Nichols and Warnes, 1993), and the Australian population of sardine *Sardinops sagax* spawn for 12 h (2100–0900 h; Ward et al., 2001). For these species, prevalence of females with a spawning marker does not necessarily equal the daily spawning fraction. For example, if the duration of a spawning marker is 12 h, only females which spawn within 12 h before (in the case of POF) or after (in the case of HD and MN) a given sampling period would be detected, whilst those spawning during the remaining 12 h would be missed. A correction factor "24/*Dsm*" was proposed to estimate spawning fraction of Atlantic mackerel to solve this problem,

$$S = Psm \times (24/Dsm) \tag{2}$$

where *Psm* is prevalence of a spawning marker and *Dsm* is the duration of the marker (Priede and Watson, 1993; Murua et al., 2003). If the spawning time frequency distribution of the population is constant over a 24 h period, Eq. (2) should be completely correct. However, in some cases, spawning time frequency distribution would not be constant and the corrected estimate of *S* by Eq. (2) is still biased. For example, let us consider a species that evenly spawns during 1800–2400 h and has a new POF duration of 12 h. If this population is sampled at 1800 h, no fish among those that will spawn on the current day will have new POFs. Thus, the proportion of the current-day spawners with new POFs is 0 at 1800 h and increases with time and reaches 1.00 at 2400 h. This proportion is constant at 1.00 between 0000 and 0600 h, and then decreases to 0 at 1200 h. As such, the proportion of the current-day spawners with the spawning marker varies through 24 h depending on the spawning time frequency distribution, and none or only a part of the daily spawners could be monitored with the spawning marker during part of the day (*e.g.* 0600–2400 h in the example above). In addition, many multiple batch spawning fish spawn at a wide range of water temperatures because they have a long spawning season (*e.g.* Beare and Reid, 2002) or a wide distribution (*e.g.* Takasuka et al., 2005; Kurita, 2006). The duration of spawning markers (*i.e.* POF; Fitzhugh and Hettler, 1995; Ganias et al., 2007: MN and HD; Kurita et al., 2011) varies depending on the ambient temperature. Therefore, a proper approach to estimate *S* requires that the spawning time frequency distribution and the temperature-dependent duration of spawning markers are all taken into account in relation to sampling time.

The objective of this study is to develop a generalized method to accurately and robustly estimate the *S* of a multiple batch spawning fish considering temperature-dependent duration of histological spawning markers and spawning time frequency distributions. For this purpose, first, a concept of "the fraction of daily spawning females with spawning markers at a given sampling time", which varies diurnally and the inverse number of which is a correction factor taking the place of "24/*Dsm*" in Eq. (2), has been introduced. Second, the diurnal changes in the fraction of daily spawning females with spawning markers was simulated under varying durations of spawning marker due to temperature and three population spawning scenarios (population spawning time lasting either for 3, 12, or 24 h of the daily cycle). Third, an appropriate method to estimate the *S* of all these scenarios was established and then, the method was applied to Japanese flounder *Paralichthys olivaceus*.

The flounder is a commercially important bottom fish, which inhabits coastal areas <150 m. Tank experiment shows that the most active fish spawn every day and individual females typically show a spawning period of 3 months (Hirano and Yamamoto, 1992) whilst the spawning season of the population lasts 4–5 months (Takeno et al., 1999). The flounder experience temperatures of 7–19 °C during their spawning season at the sampling area (Joban area, eastern coast of Japan between 37 and 38°N) of this study. Duration of spawning markers (MN, HD, and POF) decreases exponentially with increasing water temperature (Kurita et al., 2011). Spawning also occurs throughout 24 h periods at the population level (Kurita et al., unpublished data). Such reproductive characteristics and information are suitable to develop a generalized method for estimating spawning fraction in multiple batch spawning fish considering temperature-dependent duration of histological spawning markers and spawning time frequency distribution. The method developed for this flounder will be applicable to many other fish species with a long duration of population spawning time and spawning in a wide range of water temperature.

2. Materials and methods

2.1. The concept of the variable "the fraction of daily spawning females with spawning markers (FDSM) at a certain sampling time"

The fraction of daily spawning females with spawning markers (FDSM) at a certain sampling time is the key concept of the generalized method to estimate spawning fraction. The basic concept is that only a part of females which spawn in a day could be monitored at a sampling time with spawning markers by field survey and the fraction would change diurnally according to the duration