Simulating the Development of Pilchard Eggs using a Stochastic Compartmental Model

Neil R. Sumner[a] and W.J. Fletcher[b]

[a]Fisheries Department of W.A. P.O. Box 20, North Beach, WA 6020
[b]Fisheries Research Institute, N.S.W. Fisheries P.O. Box 21, Cronulla NSW 2230

Abstract It is difficult to estimate the stock size for schooling pelagic fish, such as pilchards (*Sardinops sagax*). Many stocks of pelagic fish are monitored using techniques based on egg/larval abundance rather than fishery dependant methods, such as catch per unit effort, which give unreliable estimators since alterations to the schooling behaviour and migration patterns influence catch rates. Fishery independent techniques such as the daily egg production method (DEPM) and distribution indices are now used. The DEPM requires the precise classification of eggs into developmental stages related to age. This is then used for the estimation of egg mortality from which the total number of eggs released at the time of spawning can be estimated. A stochastic compartmental model is developed to simulate the development of pilchard eggs through twelve morphological stages. Parameters determining the transition rates between consecutive stages are estimated. Once calibrated the model predicts the time when spawning occurred so eggs of different stages can be separated into the present or previous days spawning event. When used in conjunction with egg staging the model computes the probability of eggs of a given stage occurring. This provides a useful check on the staging procedure particularly when training new staff. The model is also useful for infilling missing data for periods at night where sampling may not have occurred.

1. INTRODUCTION

The pilchard fishery off the south coast of Western Australia has expanded rapidly over the past fifteen years and now forms the largest volume finfish fishery of this state with the annual value of catch in the vicinity of six million dollars. Information on both the size and number of pilchard stocks along this coast is required to determine if the level of exploitation in the established fisheries is sustainable.

It is difficult to estimate the stock size for schooling pelagic fish, such as pilchards (*Sardinops sagax*). Their schooling behaviour makes the examination of commercial catch and effort data unreliable and the capture of adults for purposes of research difficult. Many stocks of pelagic fish are monitored using techniques based on egg/larval abundance rather than fishery dependant methods such as catch per unit effort which give unreliable estimators since alterations to the schooling behaviour and migration patterns influence catch rates. Fishery independent techniques such as the daily egg production method (DEPM) and distribution indices are now used.

The DEPM [eg. Lasker, 1985; Fletcher et al., 1996a] provides an absolute measure of spawning biomass from the daily egg production. The method requires the precise classification of eggs into developmental stages so they can be related to a spawning event, and the sampling of adult fish to determine batch fecundity and spawning frequency. This method uses the number of eggs (P_t) present at time t to estimate the total number of eggs produced at the time of spawning (P_0) and rate of mortality (z).

$$P_t = P_0 e^{-zt} \tag{1}$$

The eggs developmental stage must be identified (staged) to determine whether they originated from the last or previous nights spawning event and to determine whether they are live or occluded (dead at time of capture possibly due to not being fertilised). The staging needs to be done as accurately as possible to minimise any bias in the estimates.

A number of studies have examined the egg development rates of pilchards, both Sardinops and Sardina [eg. Sette, 1943; Miller, 1952; King, 1977; Miranda et al., 1990]. All were laboratory based with eggs cultured at different temperatures from which relationships between the speed of development and temperature were developed. These studies observed the development and mortality rates for individual eggs.

In the field it is not possible to observe growth and mortality rates for individual eggs, rather samples of the population are taken at various times. Due to evident spatial heterogeneity individual samples give a poor indication of abundance. A large number of

samples from different locations must be taken to estimate the abundance of eggs.

2. MATERIALS AND METHODS

2.1 Data collection

Samples were collected from Fremantle in Western Australia to Adelaide in South Australia. Eight surveys were completed over a three year period from July 1992 to July 1995. All tows were conducted with a bongo net arrangement fitted with either 300um or 500um mesh nets [Fletcher et al., 1996b]. Nets were deployed over the side of the vessel and winched to the surface at a speed of approximately one metre per second, thereby obtaining a vertical profile of the water column. A complicating factor was that sampling was generally restricted to the hours of 0600 to 1800 hr. Thus the night time period was only sampled during the cruise on the RV Franklin in July 1994.

The sample obtained per tow was standardised to number of eggs per $200m^3$ of water using flowmeter readings. The eggs from each tow were preserved in a 3% solution of buffered formalin. Later in the laboratory, using a dissecting microscope, eggs from each tow were classified into one of twelve morphological stages of development (staged) based on the drawings of Baker, [1972] and later White and Fletcher [in press].

When staging eggs the number of occluded eggs for each stage was recorded. Unfertilised eggs only develop through the initial stages, they do not complete all the egg stages and develop into larvae [Masanobu and Knoishi, 1996]. Since occluded eggs are opaque the morphological features are considerably more difficult to identify. It is likely that occluded eggs sink rather than float in the water column [Masanobu and Knoishi, 1996] and hence are less likely to be caught in the nets than live eggs. Since occluded eggs originated from the spawning process they were included when estimating the abundance of eggs at each stage.

For most trips sea temperatures were taken by scooping a bucket of water from the sea surface and placing a mercury thermometer in the bucket, when available a electronic thermometer deployed over the side of the vessel was used. The data for all cruises were divided into three groups based on sea surface temperature at the location of capture. Since laboratory studies have shown that the rate of development is related to water temperature [Miranda et al., 1990] the data was divided into three temperature groups: less than 17.5, 17.5 to 19.4 and greater than or equal to 19.5 degrees Celsius. The number of samples for each temperature group are 339, 861 and 782 respectively. A separate model was applied to each temperature group.

2.2 Stochastic compartment model

Compartmental analysis [Jacquez, 1985] assumes a system can be divided into homogenous components, or 'compartments'. The characteristics of the system are usually determined by observing the movement of material. The compartmental model developed represents the approximate theoretical background for the observed biological phenomena. It employs an abstraction of the transition of eggs from one stage of development to the next without specifying a detailed causative theory responsible for the development mechanism.

We use a stochastic compartmental model to simulate the development of pilchard eggs through twelve physiological stages of development. The model is stochastic since the behaviour of the eggs is probabilistic. The egg development is modelled using a system of twelve compartments and transition rates that describe the rate of development from one stage to the next. Let $N_i(t)$ specify the number of eggs in stage i at time instant t. We assume, as an initial condition, that when spawning occurs (t=0) all eggs will be in stage one ($N_i(0) = 0$, i=2,3,...,12). The transition intensity or 'development rate' from stage i to stage i+1 is determined by the positive constants k_i, i=1,2,...,12. Then, by definition, k_i is the probability that a particular egg develops from stage i to stage i+1 in the time interval Δt.

The steady state compartment analysis approach adopted assumes that: (1) the k_i are independent of time and (2) each of the $N_i(t)$ compartments acts independently. The fundamental differential equations are

$$\frac{dN_1}{dt} = -k_1 N_1$$
$$\frac{dN_i}{dt} = k_{i-1} N_{i-1} - k_i N_i \qquad i = 2,3,\ldots,12 \tag{2}$$

With general solutions of the form

$$N_i = c_{i,1} e^{-k_{i-1} t} + c_{i,2} e^{-k_i t} \quad i = 1,2,\ldots,12 \tag{3}$$

Where $c_{i,1}$ and $c_{i,2}$ are determined by the initial conditions. The overall process may be summarised graphically as

$$N_1 \xrightarrow{k_1} N_2 \xrightarrow{k_2} N_3 \xrightarrow{k_3} N_4 \xrightarrow{k_4}$$
$$N_5 \xrightarrow{k_5} N_6 \xrightarrow{k_6} N_7 \xrightarrow{k_7}$$
$$N_8 \xrightarrow{k_8} N_9 \xrightarrow{k_9} N_{10} \xrightarrow{k_{10}}$$
$$N_{11} \xrightarrow{k_{11}} N_{12} \xrightarrow{k_{12}} \text{larvae}$$

The eggs progress through the twelve egg stages eventually developing into larvae. Once they have reached the larval stage it is not possible to relate them to a spawning event.

2.3 Estimation of transition rate parameters

Given the $N_i(t)$ independent units in stage i at time t, the probability that a single unit moves from stage i to stage i+1 in Δt is determined by the binomial distribution. Applying the maximum likelihood method we need to determine the values of k_i i=1,2,...,12 that maximise

$$\ell(k_i) = \binom{N_i}{x_i} k_i^{x} (1-k_i)^{N_i - x_i} \qquad (4)$$

over all stages and time steps where x_i is the number of eggs successfully developing from stage i to i+1. Since the values of k_i that maximises (4) will also maximise (5) it is more convenient to use the following

$$L(k_i) = \ln\binom{N_i}{x_i} + x_i \cdot \ln k_i + (N_i - x_i) \cdot \ln(1-k_i) \qquad (5)$$

Optimal development rates were estimated by fitting the modelled to observed egg distributions. The initial number of eggs ($N_1(0)$) is set to 100 and the number of eggs in each stage calculated from the observed distribution of eggs among the 12 stages. (5) is summed across all stages and time steps to obtain the objective function to maximise

$$S(\hat{\mathbf{k}}) = \sum_{t=1}^{m} \sum_{i=1}^{12} L\left(\hat{k}_i\right) \qquad (6)$$

where m is the number of time steps from the time of spawning until all eggs have developed into the larval stage. (5) was constrained so that the number of successful transitions from stage i to i+1 cannot exceed the number of eggs previously in stage i $(x_i \le N_i)$. Although not theoretically possible this occurred because of variability between tows due to spatial heterogeneity.

A simulated annealing algorithm [Sumner et al., in press] was used to search the parameter space maximising (6). Simulated annealing is more effective than local search methods because it is more likely to find the global maximum of a multivariate function that has many extraneous local maxima. Since there appeared to be only one local maximum a direct search method [Hooke and Jeeves, 1961] was adequate. The method of moments was used to provide a reasonable initial estimate.

3. RESULTS

The model coped extremely well with poor quality data, particularly for some of the middle stages of development. However, it was not possible to estimate the first transition rate k_1 for the temperature groups since no stage one eggs were found in any tows. The second transition rate could not be estimated for the between 17.5 and 19.4 degree Celsius temperature group due to inadequate data for stage two. There was only three tows with stage two eggs. Eleven transition rates were estimated for the other two temperature groups.

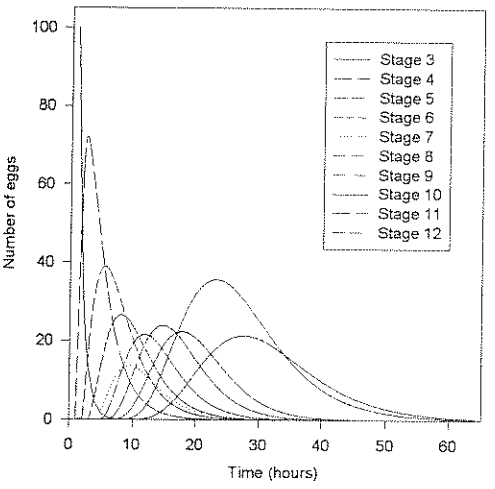

Figure 1. Predicted development of pilchard eggs from stage 3 to 11 at 17.5 to 19.4 degrees Celsius.

The 17.5 to 19.4 degrees Celsius group is used to highlight some of the difficulties that may be encountered in satisfying the statistical assumptions. There was a reasonable number of observations, however only ten of the transition rates could be estimated. The model predicted the number of eggs in each stage of development for each of the one hourly time steps used (Figure 1). The progression of the eggs from stages three to twelve can be readily seen as can the proportion of eggs in each stage. The kurtosis of the distribution for each stage is related to the

transition rates for that stage. The distribution is more peaked for stages with a high transition rate.

The plot of the observed subtract expected number of eggs for the 17.5 to 19.4 degrees Celsius group (Figure 2) illustrates problems with both the data and model. It cannot be assumed that the available data is a random sample of the population. More tows were taken during the day than at night which has placed more emphasis on fitting stages present at these times. There is considerable variability in the data which could not be accounted for by the model. This may be due to staging error or samples (usually with a very small number of eggs) missing the stage or stages that were expected at the time. This is evident as patterns in the negative residuals particularly for the early stages. Figure 2 also shows high autocorrelation which was not taken into account by the model. It is also assumed that eggs from the same spawning were sampled from one time period to the next. Data from several trips was combined to obtain an adequate number of observations for model calibration. However, if the spawning time is different for these trips or different nights on the one trip this may compromised the results.

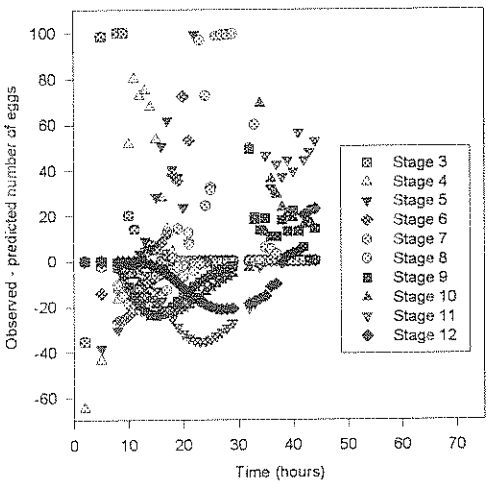

Figure 2. Observed subtract predicted number of eggs for 17.5 to 19.4 degrees Celsius.

It was not possible to discern expected differences in the transition rates due to the temperature groups (Figure 3). However, the highest temperature group had the highest transition rate on five occasions and had a higher transition rate than the 17.5 to 19.4 degrees Celsius group on eight occasions. The transition rates for less that 17 degrees Celsius have larger standard errors and show more variability due to the smaller sample size among other things. The standard errors of the transition rates are computed from the Hessian matrix. The variability between the transition rates for each of the three temperature groups is due in part to the quantity and quality of the data, particularly the small number of night time tows.

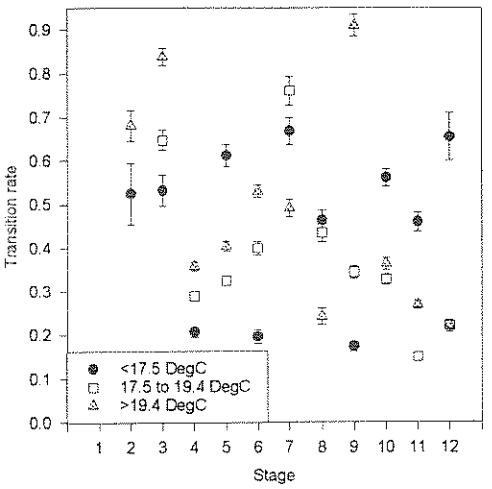

Figure 3. Estimated transition rates (+\- 2 standard errors).

4. DISCUSSION

The model predicts the proportion of pilchard eggs of each stage likely to be present given the time of spawning, time of capture and water temperature at capture. This will assist greatly with the correct staging of pilchard eggs. This is particularly important for eggs that were 'occluded' at capture where the embryo has often begun to disintegrate and shrink. Occluded eggs are often difficult to assess and in some cases they can make up to 30% of the total eggs collected in a survey [Fletcher and Tregonning, 1992]. The egg mortality information on the number of occluded eggs in each tow was not used because occluded eggs may drop through the water column rather than remain in suspension. Also it is likely that some eggs may have been damaged by the nets at the time of capture.

Stochastic models based on stage duration will be better suited to the egg development process. These models have a mean and variance for the duration in each stage. Such models are more realistic since there is a delay associated with each stage providing eggs in a stage time to develop before transferring to the next stage. However, these models require information on individual egg development times for each stage which is not available from field data. One such model is developed by Lo et al., [1995].

5. CONCLUSIONS

The study has confirmed that pilchards spawn at night with the majority of spawning probably occurring before midnight. Although not conclusive, our results are consistent with that of other laboratory based studies [Miranda et al., 1990; Lo et al., 1995]. It is likely that development time of the eggs prior to hatching is dependent upon the temperature of the water in which they live.

It is only possible to model the egg development process in a very simplistic manner using field data. It is unlikely that there is sufficient or unbiased information on egg mortality to include this process in any model. Despite these limitations the model predicts the proportion of eggs of a given stage present at any time since spawning. This will be useful for infilling missing data for periods, particularly at night, where sampling has not occurred. The model also predicts the time that spawning occurred from the transition rates.

The model is extremely robust and can be fitted even when there is no data for a stage. The transition rates for a stage can be estimated from the surrounding stages. The model can also be fitted when the data is sparse and there is only a few observations with eggs in some stages. The Hook and Jeeves method was able to calibrate the model and estimate eleven transition rates by fitting modelled to observed egg distributions.

The model provides a useful check on the staging process and has helped distinguish between eggs originating from the last and previous nights spawning event (day one and day two eggs). The model will be useful for future work estimating the spawning biomass using the egg production method. Although the simplistic modelling approach used served its intended purpose by providing the information required, the type and complexity of the model was limited by the quality of the available data. When good quality laboratory data is available stochastic models based on stage duration should be used.

ACKNOWLEDGEMENTS

Thanks are due to Ken White, Justin Chidlow, Rob Tregonning and Richard Mijat for patiently staging the eggs. Peta Calligaro prepared the final figures for publication.

REFERENCES

Baker, A.N., Reproduction, early life history, and age growth relationships of the New Zealand pilchard, *Sardinops neoplichardus* (Steindachner). Fisheries Research Division N.Z., Fisheries Research Bulletin No. 5. 64 pp., 1972.

Fletcher, W.J., Lo, N.C.H., Hayes, E.A., Tregonning, R.J. and Blight, S.J., Use of the daily egg production method to estimate the stock size of Western Australian sardines (Sardinops sagus). *Mar. Freshwater Res.*, 47, 819-25, 1996a.

Fletcher, W.J., White, K.V., Gaughan, D.J. and Sumner, N.R., Analysis of the distribution of pilchard eggs off Western Australia to determine stock identity and monitor stock size. W.A. Fisheries Department FRDC Report 92/25. 109 pp., 1996b.

Hooke, R. and Jeeves, T.A., Direct search solution of numerical and statistical problems. *J. Assoc. Comp. Mach.*, 8(2), 212-229, 1961.

Jacquez, J.A., *Compartmental Analysis in Biology and Medicine*. University of Michigan, Ann Arbor, 560 pp., 1985.

King, D.P.F., Influence of temperature, dissolved oxygen and salinity on incubation and larval development of the South West African *pilchard Sardinops ocellata*. Investigational report, Sea Fisheries Branch South Africa 114, 1-35, 1977.

Lasker, R. ed., An egg production method for estimating spawning biomass of pelagic fish: an application to the northern anchovy, *Engraulis mordax*. NOAA Technical Report NMFS 36 101 pp., 1985.

Lo, C.H.N., Smith, P.E. and Butler, J.L., Population growth of northern anchovy and Pacific sardine using stage-specific matrix models. *Mar. Ecol. Prog. Ser.* 1277, 15-26, 1995.

Masanobu, M. and Konishi, Y., Morphological characteristics of unfertilized eggs of the Japanese sardine, compared with fertilized ones. *Fisheries Science* 62(6), 855-859, 1996.

Millar, D.J., Development through the protolarval stage of artificially fertilized eggs of the pacific sardine (*Sardinops caerulea*). *Calif. Fish and Game*, 38, 587-595, 1952.

Miranda, A., Cal, R.M. and Iglesias, J., Effect of temperature on the development of eggs and larvae of sardine *Sardina pilchardus* Walbaum in captivity. *J. Exp. Mar Biol. Ecol.*, 140, 69-77, 1990.

Sette, O.E., Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 1. Structure of a research program to determine how fishing affects the resource. U.S. Fish. & Wildl. Spec. Scient. Rep. 15, 1-31, 1943.

Sumner, N.R., Flemming, P.M. and Bates, B.C., Calibration of a modified SFB model for 25 Australian catchments using simulated annealing. *J. Hydrol*, in press.

White, K.V. and Fletcher, W.J., Staging and development rates for eggs of the Australian pilchard, *Sardinops sagax*. Fisheries Research Report, Fish. Dept. WA, 20 pp., in press.