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> Preliminary analysis of mortality, immigration, and emigration of IZZex populations on the Scotian Shelf
> by
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INTRODUCTION
Ikeda and Sato (1976) and Huxley and Waldron (1978) have both used modifications of the cohort analysis to estimate mortality rates and initial population size for squid populations in the West Atlantic. Apart from the assumption that we are dealing with individuals from a single spawning (which seems supported, at least for 1978: the only year for which data were available to the author), the rates estimated in this way for the beginning and end of the season may include components of imuigration and emigration. It is postulated that we are not dealing with a closed population, but one where the population comes onto the Shelf in spring and moves offshore in fall while the fishery is still in progress.

## Analysis of Apparent Moxtality Rate

Basically, three stages may be identified during the exploited phase while at least some of the Illex population is on the Shelf, or along the edge of the Shelf.

Stage I
Immigration of immature $\theta^{*}$ and O's $^{\prime}$ and partial availability to the gear

Stage II
Fully recruited 'closed' $\rightarrow$ population on the Shelf $\rightarrow$

## Stage III

Fully recruited but emigrating adults moving off Shelf

In terms of corresponding instantaneous rates of immigration, natural and fishing mortality and emigration, we can write for the decrease in numbers on a two weekly basis (the basic unit of time used in previous analyses); ( $\Delta T=2$ weeks ) :

If $Z$ ' is the apparent mortality rate, or fitted exponential rate of decline in numbers (as evaluated, for example, by cohort analysis) on the Shelf, in theory, these rates can be decomposed as follows:

For Phase $1, Z_{1}^{\prime}=q_{1} f_{1}+M-I$
For Phase $2, Z_{Z}^{\prime}=q_{2} f_{2}+M$
For Phase $3, Z_{3}^{\prime}=q_{3} f_{3}+M+E$
Where $I=$ immigration rate

$$
\begin{array}{l}\varepsilon=\text { emigration rate } \\ \qquad q_{1-3}=\text { catchability coefficients for squid on the shelf } \\ \qquad \\ \qquad M=\text { standardized fishing effort } \\ \end{array}
$$

(For simplicity of treatment in what follows, it will be assumed that during Phases II and III, $q$ is constant so that $q_{1}=q_{2}=q_{3}$ and $F=q f$.)

If the points in time separating Phases 1, 2, and 3 can be identified to within $\ddagger 2$ weeks, the mortality rates given in the cohort analysis (calculated assuming a closed population with natural death rate, M) can be used to estimate $I$ and $E$, if catchability coefficient and fishing effort by two weekly periods is known. This can be accomplished by subtraction of equations 2-1:

$$
I=z_{2}^{\prime}-z_{1}^{\prime}+q f_{1}-q f_{2}
$$

and by subtraction of 3-2:

$$
\begin{aligned}
& Z_{3}^{\prime}-Z_{2}^{\prime}=q f_{3}-q f_{2}+\varepsilon \\
& E=Z_{3}^{\prime}-z_{2}^{\prime}-q\left(f_{3}-f_{2}\right)
\end{aligned}
$$

## Recognition of Migration Phases

Three basic approaches may be of value:

1) From examination of apparent mortality rates by two-week period Thus, the rates obtained by Hurley and Waldron (1978) show low initial apparent mortality rates at the start of the fishery and high apparent rates at the end. By plotting two weekly values of $F$ against effort units over the same period, phase II may be identified when the plot of effort versus fishing mortality is given by a straight line.
2) Some indirect biological index (eg. sex ratio data, stages of gonad maturity) can be used to estimate a significant point at which onset of emigration begins.
3) The plot of mortality rate against time in Hurley and Mohn (1979) was used to arrive at some trial values for $I$ and $\varepsilon$ given the rather unrealistic assumption that the overall mortality rate obtained for Phase II ( $M+F=-0.32$ ) applied also during Phases $I$ and III but was modified by immigration
and emigration rates; thus:

| Phase |  | Approximate dates |  | Apparent rate of decline | $\begin{aligned} & \text { Assumed } \\ & \mathbf{Z} \end{aligned}$ | I | $\varepsilon$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| I |  | May, 1977 |  | +0.98 | -0.32 | $\geq+1.30$ |  |
| II |  | May to 30 Aug., | 1977 | -0.32 | -0.32 |  |  |
| III | 30 | Aug., 1977 |  | -0.93 | -0.32 |  | <-0.61 |

Evidently, the assumed constant $z$ values for Phases I and III are incorrect since effort was much lower earlier and later in the season than during Phase II.

If this were true, then we can see that rates of emigration and (especially) immigration would have been significantly higher, and in any case, would be much larger than the true mortality rate. The significance of this observation will be discussed in the next section.

If corrected effort data had been available, I would have used it to arrive at a better estimate of $I$ and $E$ from the above table, given that an estimate of $M$ has been suggested $(M=0.02-0.05: ~ A v 0.03)$.

Thus: Phase II: $\quad Z^{\prime}=M+q \vec{f}_{2}$
(numerical example: $0.32=0.03+q \bar{f}_{2}$ )

$$
\therefore q=0.29 / \bar{f}_{2}
$$

where $\bar{f}_{2}$ is mean effort per two-week period in Phase II.
Phase I: $\quad Z^{\prime}=M+q \bar{f}_{1}-I$

$$
\begin{align*}
(+0.98 & \left.=0.03+q f_{1}-I\right) \\
\therefore I & =-0.95+q f_{1}
\end{align*}
$$

where $\bar{f}$ is mean effort level per two-week period in Phase 1 .
Phase III: $\quad Z^{\prime}=M+q \overline{\mathbf{f}}_{3}+\varepsilon$

$$
\begin{aligned}
(0.93 & \left.=0.03+\mathrm{qf} \mathbf{f}_{3}+E\right) \\
\therefore E & =0.90+q f_{3} \quad \ldots \ldots \ldots .3
\end{aligned}
$$

RESULTS
Modelling of a Fishery With Seasonal Availability
A first attempt at modelling some of the processes involved in a threestage fishery has been made which makes the assumptions (admittedly difficult to substantiate at this stage) that $M, I$, and $E$ are constant duxing each of the two-week periods they are expected to apply. A Ricker type of format was used in which all rates are assumed annual, and where the stock is divided

- into two components, one on, one off the Shelf, and where the outputs from
each time period are fed in as inputs to the next: equations being developed for movement of animals between on- and off-Shelf areas between successive time periods (see Figure 2). Apart from Phase II (which is assumed to be a closed population), during each two-week period of Phase I, survivors moving on-Shelf during the interval are added to those already on-Shelf from the previous interval(s). During Phase III, survivors off-Shelf that arrived off-Shelf in previous interval(s) are added to those that arrived in the current interval, to contribute to the final spawning population.


## Equations Used in the Model

Assuming the three phases described in the test (immigration, residence, on-Shelf, emigration), with fishing restricted to on-Shelf areas in all phases, we may consider the fate of the number of individuals ( $N_{1}$ ) off-Shelf at the start of the immigration phase in each of a series of intervals of length $\Delta T$ (two weeks) :

## Phase I

The number remaining off-Shelf at the end of $\Delta T$ if natural mortality were not a factor, is given by $N^{\prime}=N_{1} e^{-I \Delta T}$.
a) However, the number remaining off-Shelf at the end of $\Delta T$ is
determined by both immigration and natural mortality rates (both assumed constant) :

$$
\begin{aligned}
N_{2} & =N_{1} e^{-I \Delta T} \cdot e^{-M \Delta T} \\
& =N e^{-(M+I) \Delta T}
\end{aligned}
$$

b) The number of individuals that would have arrived on-Shelf by the end of $\Delta T$ if natural mortality were not a factor is given by:

$$
N^{\prime \prime}=N_{1}\left(1-e^{-I \Delta T}\right)
$$

Evidently, since $\Delta T$ is a small but finite interval, not all of those arriving on-Shelf by the end of $\Delta T$ will be available for capture on-Shelf throughout the interval, although we must assume that natural mortality occurs throughout; and without evidence to the contrary, natural mortality rate is assumed constant. As a first approximation, it is assumed that the removals due to fishing at a rate $F$ from those individuals that arrive onShelf at different times during the interval, are approximately the same as the numbers that would be removed by fishing at the same rate, if all those finally arriving by the end of $\Delta T$ were available for the last half
of the interval only. This assumption (which is similar to that used in Pope's cohort analysis) can best be expressed graphically (figure 3).

If it is assumed that the fraction of the off-Shelf population that eventually survives to arrive on-Shelf by the end of $\Delta T$ is subject to natural mortality by $\Delta T / 2$, then the number subject to fishing for the last half of $\Delta T$ is given by:

$$
N^{\prime \prime}=N_{1}\left(1-e^{-I \Delta T}\right) e^{-M \Delta T / 2}
$$

and is then fished at rate $F$ for a further $\Delta T / 2$, The number of survivors $\mathrm{N}_{2}^{\prime \prime}$ is then given by:

$$
N_{2}^{\prime \prime}=N^{\prime \prime} e^{-(F+M) \Delta T / 2}
$$

and substituting for $\mathrm{N}^{\prime \prime}$ and simplifying we have:

$$
\begin{aligned}
N_{2}^{\prime \prime} & =N_{1}\left(1-e^{-I \Delta T}\right) e^{-M \Delta T / 2} e^{-(M+F) \Delta T / 2} \\
& =N_{1}\left(1-e^{-I \Delta T}\right) e^{-(M+F / 2)}
\end{aligned}
$$

To this is added the number of survivors that arrived in previous intervals, given by:

$$
N_{2}^{\prime \prime} '=N_{2}^{\prime \prime}+N_{1}^{\prime \prime} e^{-(M+F) \Delta T}
$$

where $N_{1}^{\prime \prime}$ is the total number left on-Shelf at the end of the previous interval.

The catch during $\Delta T$ of those arriving in $\Delta T$ :
This is given by $C_{2}=N^{\prime \prime} E\left[\left(1-e^{-(M+F) \Delta T / 2}\right)\right]$. Substituting for $N^{\prime \prime}$, and simplifying:

$$
C_{2}^{\prime}=E\left[N_{1}\left(1-e^{-I \Delta T}\right) e^{-M \Delta T / 2}\right]\left[1-e^{-(M+F) \Delta T / 2}\right]
$$

where $E$ is the exploitation ratio, $F /(F+M)$.
To this is added the number caught of those arriving in earlier intervals; namely:

$$
C_{2}^{\prime \prime}=N_{1}^{\prime \prime \prime} \quad E\left[1-e^{-(F+M) \Delta T}\right]
$$

Thus, $C_{2}=C_{2}^{\prime}+C_{2}^{\prime \prime}$ which is added to the cumulative yield (after multiplying by the age-specific weight).

## Phase II

This begins when all individuals are on-Shelf (in practice, this is programmed in the HP model to begin when the number left off-Shelf is $0.01 \%$ of the initial number of recruits).

Calculations during this phase are those for a fully available stock; thus:

Number of survivors at end of $\Delta T: \quad N_{2}=N_{1} e^{-(M+F) \Delta T}$
Catch during $\Delta T: \quad C_{1}=N_{1} E\left[1-e^{-(F+M) \Delta T}\right]$
(The duration of this phase can either be preset, or probably more realistically, detemined by the mean size attained in the population.)

## Phase III

Emigration from the Shelf begins at a constant rate $\varepsilon$, so that:
a) The number surviving on-Shelf is:

$$
N^{\prime \prime}=N_{1} e^{-(\varepsilon+M+F) \Delta T}
$$

b) The number caught on-Shelf is:

$$
C_{2}=\frac{N_{1} F}{(\varepsilon+M+F)}\left[1-e^{-(\varepsilon+M+F) \Delta T}\right]
$$

c) If no natural mortality were to apply, the number moving off-Shelf would be given by:

$$
N_{2}^{\prime}=N_{1}\left(1-e^{-\varepsilon \Delta T}\right)
$$

The final numer arriving off-Shelf and surviving natural mortality by end of $\Delta T$ is then:

$$
N_{2}^{\prime}=N_{1}\left(1-e^{-\varepsilon \Delta T}\right) e^{-M \Delta T}
$$

Add to this the number surviving off-Shelf from the previous intervals:

$$
\begin{aligned}
N_{2} & =N_{2}^{\prime \prime}+N_{2}^{\prime} \\
\text { where } N_{2}^{\prime \prime} & =N_{1}^{\prime \prime} e^{-M \Delta T}
\end{aligned}
$$

Adding these, we get total survivors off-Shelf.

## Calculations With the Squid Immigration/Emigration Model

The model can be used as a yield/recruit calculation to predict the overall yield to the fishery given input such as that in Appendix $I$. (This appendix also gives the HP model listing.)

An array of total catches for the model used in this way, for a combination of through-season F's, and progressive delays in onset of the fishery is given in Table 1. The delay in onset of the fishery after time zero when growth begins, and squid begin to come on-Shelf, is in effect the same as imposing a knife-edge selection curve at the mean size attained at the start of that time period. The overall yield in weight from $10^{6}$ squid initially is shown in Table 1 , scaled on the $y$ axis for increasing F, and along the $x$ axis for the delay from the start of imnigration and growth to the onset of fishing. Numbers on- and off-Shelf, and catch in
weight on-Shelf are shown in Figures 4 and 5.

The (Knife-Edge) HP Model with Lagged Onset of Fishery
The HP model with knife-edge recruitment was run for the parameters given and a delay in onset of fishing up to 12 weeks after growth begins (Figures 6 and 7) for a range of $F$ 's from 0.1 (over a 2-week time period) to 0.6. The growth curve used (from Hurley and Waldron, 1977) reaches 50 gm (approxiactely the mean size at which the fishery was taking squid in 1978, at the end of April), 6 weeks after the start of the simulation. The maximum yield at this lag occurs at an $F=0.3$; close to the value obtained from cohort analysis in 1977. Reducing the $F$ value at this lag to $F=0.2$ will somewhat increase yield. Postponing fishing by at least a further 4 weeks is predicted to result in increases in yield. This delay may be seen as equivalent to increasing mean size at first capture to at least 106 g . Further increases with greater delays are foreseen, but an attempt to define these increments is postponed until the next section, when mesh selectivity factors are incorporated into a rather more realistic model.

## Fortran Model With Partial Selection at Size

The same calculation (in Fortran IV) allows a gear selection routine (linear segmented approximation to a selection curve) to be incorporated in the model, in which the proportion retained by the gear in each biweekly period is interpolated for a given mean size, assuming all individuals passing through the gear survive (i.e. initial $F$ is scaled for selection at size, and $F_{t} \nleftarrow P_{t} F$, where $P_{t}$, the proportion retained at the mean size during interval $t$, is assumed to be a measure of availability at size). The results from this procedure are shown for three mesh sizes ( $60,90,100 \mathrm{~mm}$ ) in Tables 3-8, the mesh selection parameters for which are given in Table 2, and other input variables as shown in the Appendix.

With the procedure described earlier for terminating Phases I and III, the duration of the simulation increases unduly for low values of $F$, thus making the results of different runs less easy to compare. The results presented in Tables $3-8$ were therefore run for a fixed duration of fishing of 26 weeks from the time at which a mean size of 50 g was present in the
fishery ( 6 to 8 weeks from the start, and roughly corresponding to the end of April, in the 1977-78 fishery). After week 32, when fishing ceased (roughly equivalent to late November when the fishery was largely over in 1977-78), the model was allowed to continue to run with $\mathrm{F}=0$, and only M operating, to determine the predicted number of survivors off-Shelf one year after the start of the simulation. The figures resulting may be then considered representative of the potential spawning stock available for the next season for each strategy, and are shown in Tables 4, 6, and 8 for 60,90 , and 100 mm mesh sizes.

From mesh selection experiments by Amaratunga et al. (1979) (and pers. comm.)
the values input for mesh selection appear to show relatively little difference between 60 and 90 mm mesh so that the results are also quite similar, although with $\mathrm{F}=0.2$, and $\operatorname{lag}=8$, the yield and number of survivors are slightly greater for 90 than 60 mm . The similarity of 60 and 90 mm is contrasted with that for 100 mm , which appears much different than would be expected from geometric considerations alone. Certainly, maximum yield with 100 mum occurs with higher $F^{\prime} s$ and a shorter lag than at 90 mun. Further attempts to establish availability and selection with mesh size would seem warranted here before detailed conclusions from the model are pursued, although the general conclusions presented in 1) to 2) above would seem to remain valid.

Attempting to place the model roughly in a realistic time frame, it is noted that $40-60$ gm was approximately the mean size in the early fishery in late April, 1978. This size occurs after week 7 in the simulation. Thus, $t=0$ occurs roughly at the beginning of February as presently conceived.

## 60 mm Mesh Size

Peak yield with an 8 -week lag ('77-' 78 condition) occurred at $F=0.3$. Yield was, however, increased progressively by a delay in the fishexy of up to 10 weeks (initial mean wt. 148 g ). This also doubles the number of survivors reaching the end of the year. Reduction in $F$ necessitated a smaller delay for the same effect, and vice versa (Figure 8).

## 90 man Mesh Size

With the selection parameters given, 90 mm is closely similar to 60 mm
in effect, except that the optimum yield at a given lag occurs at slightly higher $F^{\prime} \mathrm{s}$.

## 100 mun Mesh Size

Included mostly for reference, peak yield at this mesh size occurs at the highest $F$ levels considered $(F=0.6)$ and the benefits of delaying the fishery are reduced, presumably because availability is postponed until later in the fishery anyway, at this higher mesh size.

## DISCUSSION

## Some Points of Relevance to Management of Squid Stocks

Two key observations can be made as a result of the foregoing that may be relevant to management of this fishery.

1) In terms of ensuring a "safe" level of population for an annual species to reproduce the stock in the following year, the key control point seems to be to ensure that an adequate number of animals ( $N$ ) survive until the time at which emigration begins. After that point in time, the proportion of $N$ available to the fishery will not exceed $F /(F+M+\varepsilon)$. (For values postulated earlier, this means that the proportion caught subsequent to Phase III beginning will not much exceed $30 \%$.) The actual proportion surviving to spawn is, of course, unknown since the time between the end of the fishing period and onset of spawning is unknown at present. However, the proportion surviving to the end of the fishery will probably not exceed $E /(F+M+E)$ (or for the same parameter values above, roughly 60\%). In the simulation, the number of survivors of fishing are reduced further by natural mortality, to give the number still alive at the end of one year, as the best measure of spawning potential.
2) The question of what is the best method of ensuring adequate survival may be rephrased in terms of the strategy that results in a given number surviving to onset of Phase III. Postponing onset of the fishery or controlling fishing intensity seem the two obvious options, and these two measures have roughly equivalent effects (i.e. for a low $F$, the fishery need not be postponed as long).

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TABLE 1. Cumulative weight of the catch with the HP "knife-edge" simulation. (X-Axis is F , Y - Axis is the onset of the fishery, progressively delayed by up to 12 weeks from the start of growth. The second column refers to the weight of the squid at the start of the fishery.)

| Delay <br> (weeks) | Weight <br> (kgs) | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 0.002 | $[51482.29]$ | 50050.89 | 41508.90 | 33815.29 | 28028.65 | 23798.67 |
| 2 | 0.009 | 53288.92 | $[53495.71]$ | 45700.76 | 38255.64 | 32509.76 | 28244.93 |
| 4 | 0.023 | 56314.11 | $[61.345 .50]$ | 55693.39 | 49178.00 | 43785.96 | 39624.04 |
| 6 | 0.041 | 59863.71 | $[69820.50]$ | 67139.98 | 62168.48 | 57555.20 | 53789.68 |
| 8 | 0.062 | 62378.11 | $\boxed{77274.65}$ | $[77971.48]$ | 74960.34 | 71452.26 | 68327.86 |
| 10 | 0.084 | 63502.53 | 82925.48 | $[87134.08]$ | 86350.83 | 84193.17 | 81894.80 |
| 12 | 0.106 | 63092.94 | $\underline{86358.94}$ | 94023.96 | $[95639.75]$ | 95030.52 | 93721.99 |

KEY: Bracketed values are eumetric yields for each delay period: Underlined values are maximum yields at each $F$ level.
Dashed line is first estimate of onset of fishery in 1977-78.
values in box are tentative estimates of 1977-78 position.

TABLE 2. Mean weight of squid at 5 percentile points ( kg ) for each of 3 mesh sizes. (Data from Amaratunga, pers. comm.)

| \% Retention | Mesh size (mm) |  |  |
| :---: | :---: | :---: | :---: |
|  | 60 | 90 | 100 |
| 0 | 0.019 | 0.019 | 0.081 |
| 25 | 0.031 | 0.030 | 0.116 |
| 50 | 0.047 | 0.054 | 0.148 |
| 75 | 0.081 | 0.098 | 0.199 |
| 100 | 0.137 | 0.160 | 0.445 |

TABLE 3. Number surviving off-Shelf at the end of the squid population simulation with a mesh size of 60 mm.*

| Delay (weeks) | Weight (kgs) | 0.0 | 0.1 | $0.2{ }^{\text {F }}$ | 0.3 | 0.4 | 0.5 | 0.6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 0.002 | 352923.9 | 143139.4 | 58898.8 | 24537.8 | 10330.7 | 4388.2 | 1878.0 |
| 2 | 0.009 | 352923.9 | 143139.4 | 58898.8 | 24537.8 | 10330.7 | 4388.2 | 1878.0 |
| 4 | 0.023 | 352923.9 | 143139.4 | 58898.8 | 24537.8 | 10330.7 | 4388.2 | 1878.0 |
| 6 | 0.041 | 352923.9 | 143141.7 | 58900.7 | 24538.9 | 10331.4 | 4388.5 | 1878.2 |
| 8 | 0.062 | 352923.9 | 146729.9 | 61889.4 | 26429.3 | 11405.4 | 4965.7 | 2178.2 |
| 10 | 0.084 | 352923.9 | 154263.6 | 68406.6 | 30711.4 | 13933.1 | 6377.2 | 2940.7 |
| 12 | 0.206 | 352923.9 | 166289.8 | 79488.1 | 38468.0 | 18812.3 | 9281.5 | 4613.4 |
| 14 | 0.128 | 352923.9 | 179352.5 | 92466.6 | 48264.1 | 25457.0 | 13546.5 | 7262.3 |
| 16 | 0.148 | 352923.9 | 193536.6 | 107670.4 | 60644.0 | 34516.7 | 19820.0 | 11465.9 |
| 18 | 0.167 | 352923.9 | 213912.6 | 131535.4 | 81885.3 | 51513.3 | 32694.1 | 20904.7 |
| 20 | 0.184 | 352923.9 | 236433.4 | 160690.0 | 110567.0 | 76879.3 | 53930.0 | 38113.8 |
| 22 | 0.199 | 352923.9 | 261325.7 | 196306.7 | 149294.9 | 114736.7 | 88960.2 | 69489.1 |
| 24 | 0.213 | 352923.9 | 288838.6 | 239817.8 | 201587.9 | 171235.9 | 146744.1 | 126693.8 |
| 26 | 0.225 | 352923.9 | 219247.9 | 292972.7 | 272197.0 | 255556.4 | 242061.6 | 230990.1 |
| 28 | 0.235 | 352923.9 | 335842.1 | 322084.1 | 310924.6 | 301807.6 | 294305.3 | 288087.9 |

[^0]TABLE 4. Yield per recruit with a mesh size of 60 mm.*

| Delay (weeks) | Weight (kgs) | 0.0 | 0.1 | 0.2 | $\mathrm{F}$ $0.3$ | 0.4 | 0.5 | 0.6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 0.002 | 0.0 | 60650.1 | 78172.2 | [80689.9] | 78373.1 | 74839.6 | 71312.7 |
| 2 | 0.009 | 0.0 | 60650.1 | 78172.2 | [80689.9] | 78373.1 | 74839.6 | 71312.7 |
| 4 | 0.023 | 0.0 | 60650.1 | 78172.2 | [80689.9] | 78373.1 | 74839.6 | 71312.7 |
| 6 | 0.041 | 0.0 | 60650.7 | 78174.0 | [80692.7] | 78376.7 | 74843.9 | 71317.4 |
| 8 | 0.062 | 0.0 | 61278.0 | 80333.1 | [84164.7] | 82821.9 | 80003.7 | 77021.7 |
| 10 | 0.084 | 0.0 | 61772.3 | 83352.9 | 89430.7 | [89725.8] | 88055.4 | 85891.5 |
| 12 | 0.106 | 0.0 | 61334.3 | 85936.0 | 94988.8 | [97529.8] | 97436.2 | 96367.8 |
| 14 | 0.128 | 0.0 | 59718.0 | 86589.9 | 98309.0 | 103025.2 | 104532.9 | [104610.1] |
| 16 | 0.148 | 0.0 | 56954.2 | 85258.2 | 99231.1 | 105974.6 | 109058.0 | [110296.7] |
| 18 | 0.167 | 0.0 | 51851.8 | 80782.0 | 97039.6 | 106196.7 | 111331.4 | [114168.9] |
| 20 | 0.184 | 0.0 | 45297.5 | 73387.3 | 91035.1 | 102245.7 | 109430.6 | [114064.9] |
| 22 | 0.199 | 0.0 | 37345.8 | 62864.0 | 80572.4 | 93037.4 | 101925.0 | [108334.8] |
| 24 | 0.213 | 0.0 | 28039.7 | 48918.7 | 64723.0 | 76872.7 | 86348.4 | [93836.1] |
| 26 | 0.225 | 0.0 | 17405.3 | 31148.7 | 42162.0 | 51117.0 | 58501.4 | [64672.7] |
| 28 | 0.235 | 0.0 | 8852.3 | 16070.5 | 22005.8 | 26928.5 | 31047.2 | [34523.5] |

*(For key to table, see Table 1.)

TABLE 5. Number surviving off-Shelf at the end of the squid population simulation with a mesh size of 90 men

| Delay (weeks) | Weight (kgs) | 0.0 | 0.1 | 0.2 | 0.3 | 04 | 05 | 06 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 0.002 | 352923.9 | 150321.2 | 64957.0 | 28419.0 | 12564.7 | 5604.7 | 2518.9 |
| 2 | 0.009 | 352923.9 | 150321.2 | 64957.0 | 28419.0 | 12564.7 | 5604.7 | 2518.9 |
| 4 | 0.023 | 352923.9 | 150321.2 | 64957.0 | 28419.0 | 12564.7 | 5604.7 | 2518.9 |
| 6 | 0.041 | 352923.9 | 150323.2 | 64958.6 | 28420.1 | 12565.4 | 5605.1 | 2519.1 |
| 8 | 0.062 | 352923.9 | 154098.9 | 68261.4 | 30614.1 | 13874.5 | 6344.0 | 2922.4 |
| 10 | 0.084 | 352923.9 | 162001.1 | 75440.9 | 35567.9 | 16945.6 | 8145.0 | 3944.2 |
| 12 | 0.106 | 352923.9 | 170396.4 | 83462.5 | 41389.0 | 20740.6 | 10485.6 | 5340.7 |
| 14 | 0.128 | 352923.9 | 183718.7 | 97023.6 | 51875.3 | 28027.9 | 15277.6 | 8389.7 |
| 16 | 0.148 | 352923.9 | 198191.4 | 112912.0 | 65125.6 | 37959.1 | 22320.9 | 13223.2 |
| 18 | 0.167 | 352923.9 | 213912.6 | 131535.4 | 81885.3 | 51513.3 | 32694.1 | 20904.7 |
| 20 | 0.184 | 352923.9 | 236433.4 | 160690.0 | 110567.0 | 76879.3 | 53930.0 | 38113.8 |
| 22 | 0.199 | 352923.9 | 261325.7 | 196306.7 | 149294.9 | 114736.7 | 88960.2 | 69489.1 |
| 24 | 0.213 | 352923.9 | 288838.6 | 239817.8 | 201587.9 | 171235.9 | 146744.1 | 126693.8 |
| 26 | 0.225 | 352923.9 | 319247.9 | 292972.7 | 272197.0 | 255556.4 | 242061.6 | 230990.1 |
| 28 | 0.235 | 352923.9 | 335842.1 | 322084.1 | 310924.6 | 301807.6 | 294305.3 | 288087.9 |

TABLE 6. Cumulative weight of the catch at the end of the squid population simulation with a mesh size of 90 mm.*

| Delay <br> (weeks) | Weight <br> (kgs) | 0.0 | 0.1 | 0.2 | $\begin{gathered} F \\ 0.3 \end{gathered}$ | 0.4 | 0.5 | 0.6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 0.002 | 0.0 | 59620.8 | 78293.7 | [81837.6] | 80102.3 | 76810.6 | 73322.9 |
| 2 | 0.009 | 0.0 | 59620.8 | 78293.7 | [81837.6] | 80102.3 | 76810.6 | 73322.9 |
| 4 | 0.023 | 0.0 | 59620.8 | 78293.7 | [81837.6] | 80102.3 | 76810.6 | 73322.9 |
| 6 | 0.041 | 0.0 | 59621.4 | 78295.2 | [81840.1] | 80105.5 | 76814.4 | 73327.2 |
| 8 | 0.062 | 0.0 | 60223.9 | 80464.6 | [85407.6] | 84740.0 | 82244.7 | 79365.5 |
| 10 | 0.084 | 0.0 | 60663.6 | 83494.5 | 90867.9 | [92059.5] | 90922.4 | 89043.2 |
| 12 | 0.106 | 0.0 | 60315.3 | 85206.2 | 94707.6 | 97577.9 | [97673.4] | 96691.7 |
| 14 | 0.128 | 0.0 | 58626.9 | 85738.4 | 97939.6 | 103061.2 | 104840.0 | [105072.6] |
| 16 | 0.148 | 0.0 | 55787.9 | 84272.7 | 98763.7 | 106010.7 | 109486.5 | [110999.5] |
| 18 | 0.167 | 0.0 | 51851. 8 | 80782.0 | 97039.6 | 106196.7 | 111331.4 | [114168.9] |
| 20 | 0.184 | 0.0 | 45297.5 | 73387.3 | 91035.1 | 102245.7 | 109430.6 | [114064.9] |
| 22 | 0.199 | 0.0 | 37345.8 | 62864.0 | 80572.4 | 93037.4 | 101925.0 | [108334.8] |
| 24 | 0.213 | 0.0 | 28039.7 | 48918.7 | 64723.0 | 76872.7 | 86348.4 | [93836.1] |
| 26 | 0.225 | 0.0 | 17405.3 | 31148.7 | 42162.0 | 51117.0 | 58501.4 | [64672.7] |
| 28 | 0.235 | 0.0 | 8852.3 | 16070.5 | 22005.8 | 26928.5 | 31047.2 | [34523.5] |

*(For key to table, see Table 1.)

TABLE 7. Number surviving off-Shelf at the end of the squid population simulation with a mesh size of 100 mun.*

| Delay <br> (weeks) | Weight (kgs) | 0.0 | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 0.002 | 352923.9 | 246360.9 | 173559.2 | 123270.0 | 88181.6 | 63478.2 | 45946.8 |
| 2 | 0.009 | 352923.9 | 246360.9 | 173559.2 | 123270.0 | 88181.6 | 63478.2 | 45946.8 |
| 4 | 0.023 | 352923.9 | 246360.9 | 173559.2 | 123270.0 | 88181.6 | 63478.2 | 45946.8 |
| 6 | 0.041 | 352923.9 | 246360.9 | 173559.2 | 123270.0 | 88181.6 | 63478.2 | 45946.8 |
| 8 | 0.062 | 352923.9 | 246360.9 | 173559.2 | 123270.0 | 88181.6 | 63478.2 | 45946.8 |
| 10 | 0.084 | 352923.9 | 246360.9 | 173559.2 | 123270.0 | 88181.6 | 63478.2 | 45946.8 |
| 12 | 0.106 | 352923.9 | 246370.3 | 173572.5 | 123284.2 | 88194.9 | 63490.3 | 45957.3 |
| 14 | 0.128 | 352923.9 | 246456.4 | 173693.8 | 123413.5 | 88318.5 | 63601.3 | 46053.8 |
| 16 | 0.148 | 352923.9 | 252739.4 | 182662.7 | 133094.7 | 97674.9 | 72132.4 | 53562.4 |
| 18 | 0.167 | 352923.9 | 259249.9 | 192194.6 | 143647.6 | 108134.9 | 81914.1 | 62392.6 |
| 20 | 0.184 | 352923.9 | 272659.9 | 212592.0 | 167111.6 | 132305.2 | 105407.8 | 84440.3 |
| 22 | 0.199 | 352923.9 | 286863.7 | 235318.4 | 194612.1 | 162104.4 | 135876.8 | 114518.8 |
| 24 | 0.213 | 352923.9 | 301902.1 | 260637.4 | 226851.4 | 198864.5 | 175427.7 | 155603.9 |
| 26 | 0.225 | 352923.9 | 325870.9 | 303665.7 | 285285.4 | 269944.6 | 257037.0 | 246091.8 |
| 28 | 0.235 | 352923.9 | 339119.4 | 327504.4 | 317688.0 | 309354.0 | 302245.8 | 296155.7 |

TABLE 8. Cumulative weight of the catch at the end of the squid population simulation with a mesh size of 100 mun.*

| Delay <br> (weeks) | Weight <br> (kgs) | 0.0 | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 0.002 | 0.0 | 39381.8 | 64868.4 | 81394.0 | 92091.6 | 98970.3 | $[103331.0]$ |
| 2 | 0.009 | 0.0 | 39381.8 | 64868.4 | 81394.0 | 92091.6 | 98970.3 | $[103331.0]$ |
| 4 | 0.023 | 0.0 | 39381.8 | 64868.4 | 81394.0 | 92091.6 | 98970.3 | $[103331.0]$ |
| 6 | 0.041 | 0.0 | 39381.8 | 64868.4 | 81394.0 | 92091.6 | 98970.3 | $[103331.0]$ |
| 8 | 0.062 | 0.0 | 39381.8 | $\boxed{64868.4}$ | 81394.0 | 92091.6 | 98970.3 | $[103331.0]$ |
| 10 | 0.084 | 0.0 | 39381.8 | $\underline{64868.4}$ | 81394.0 | 92091.6 | 98970.3 | $[103331.0]$ |
| 12 | 0.106 | 0.0 | 39380.7 | 64868.2 | 81395.6 | 92095.4 | 98976.2 | $[103339.2]$ |
| 14 | 0.128 | 0.0 | 39365.9 | 64856.3 | 81395.0 | 92109.7 | 99006.2 | $[103384.3]$ |
| 16 | 0.148 | 0.0 | 37956.5 | 63317.4 | 80354.1 | 91838.1 | 99586.2 | $[104801.9]$ |
| 18 | 0.167 | 0.0 | 36219.4 | 61121.4 | 78367.5 | 90383.7 | 98794.2 | $[104697.2]$ |
| 20 | 0.184 | 0.0 | 32191.6 | 55498.1 | 72526.6 | 85072.7 | 94385.9 | $[101345.4]$ |
| 22 | 0.199 | 0.0 | 27575.3 | 48514.5 | 64575.0 | 77010.7 | 86725.6 | $[94377.1]$ |
| 24 | 0.213 | 0.0 | 22430.4 | 40205.5 | 54439.0 | 65951.1 | 75350.9 | $[83094.9]$ |
| 26 | 0.225 | 0.0 | 13966.5 | 25534.8 | 35206.2 | 43366.6 | 50314.6 | $[56282.6]$ |
| 28 | 0.235 | 0.0 | 7145.5 | 13215.3 | 18398.3 | 22848.1 | 26689.4 | $[30023.9]$ |

*(For key to table, see Table 1.)


Fig. 1. Graph of $\log$ (C/E) versus time during the 1977 fishing season. Dashed lines fitted by eye represent hypothesized stages in migration cycle. ( $\mathrm{C}=$ catch in numbers, and $\mathrm{E}=$ effective squid effort from Hurly and Mohn, 1978.)


Figure 2. Diagramatic structure of the migration model.


Figure 3. Demonstration of method of approximation of immigration phase.


Figure 4. Log no. of individuals off (dashed line) and on (solid line) the Shelf during the course of a simulation with zero lag (knife-edge recruitment). Roman numerals indicate phase no.


Fiqure 5. Log of cumulative and hi-weetly catch in weight with delay in the onset of fishing for the simulation shown



Figure 6. Log no. of individuals off (dashed line) and on (solid line)
the Shelf during the course of a simulation with a delay in onset of fishing until the 8 th week (partial recruitment version). Roman numerals indicate phase no.


Figure 7. Log of cumulative and by-weekly catch in weight with an 8-week delay in the onset of fishing for the simulation shown in Figure 5.

## SOUID YIELD ON SHELF--MESH GOMM



Figure 8a. Yield surface for a combination of $\mathrm{F}^{\prime}$ 's and delays at onset of fishing using 60 mm mesh. (Delays are in 2-week intervals.)

SQUID SURVIVING OFF SHELF--MESH GOMM


Appendix $I$. User instructions, input values used, and HP programme listing.


C 7


[^0]:    "For key to table, please see Table 1.)

