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Yield-per-recruit Analysis of Short-finned Squid on the Scotian Shelf by Simulation

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Abstract

A yield-per-recruit model for short-finned squid, *Illex illecebrosus*, indicates that the cannibalism may be a major component of natural mortality. Two methods of estimating mortality due to cannibalism indicated that this component may be as high as 0.6 per 2-week period. The analyses showed that squid should be harvested early in the season to obtain the highest yields.

Introduction

The traditional yield-per-recruit models are based on three types of data: fishing mortality and natural mortality as functions of age. For the short-finned squid, information on growth patterns during their occurrence on the Scotian Shelf (NAFO Divisions 4V, 4W and 4X) in 1977–79 have been reported by Amaratunga (MS 1980a). Estimates of fishing mortality may be derived from trawl selectivity (Amaratunga *et al.*, MS 1979) and historical patterns of fishing effort (Amaratunga, pers. comm.). However, the remaining component of total mortality, i.e. all causes of removal from the population except catch, may be broken down into three parts: migration, cannibalism, and all other natural factors termed "natural mortality". In this paper, the sources of mortality are investigated and their implications concerning yield-per-recruit of short-finned squid are explored. Whenever the name "*Illex*" is used, it implies *Illex illecebrosus*.

Methods

The analysis involves a simulation of the life cycle of short-finned squid from their presumed arrival on the Scotian Shelf in April (week 14) until spawning is presumed to occur at the end of the year. Units of time for the simulation are 2-week periods. The catch equation with three components of non-catch mortality was the basic relationship used:

$$C = FN\ (1-e^{-Z})/Z$$

where C = catch in numbers during a time period,

N = population size (numbers) at the beginning of a time period,

$Z = F + M$ = total mortality coefficient,

F = fishing mortality coefficient,

and $M = M_c + M_m + M_n$

where M_c = mortality due to cannibalism,

M_m = mortality due to migration,

and M_n = natural mortality.

Growth

The relationship between *Illex* growth and bottom temperature on the Scotian Shelf was noted by Scott (1978). Also, O'Dor *et al.* (1980) reported an increase in growth rate of *Illex* with temperature for animals maintained in the laboratory. The parameters of von Bertalanffy growth curves for *Illex* in 1977, 1978 and 1979 were considered in relation to average bottom temperatures from bottom-trawl surveys on the Scotian Shelf in July (Mohn, MS 1981). The mean bottom temperature in 1978 (5.8° C) was lower than those for 1977 and 1979 (6.4° and 6.5° C respectively). Consequently, the growth parameters (L_∞ = asymptotic length, t_o = hypothetical age at zero length, and K = growth coefficient) for 1978 were compared with the average values for 1977 and 1979 in relation to the difference in bottom temperature (Table 1). The parameter differences ($\triangle P$) for males and females showed similar patterns. In the simulation, each of the growth parameters was assumed to behave in a linear fashion:

$$P(T) = P(5.8) + (T - 5.8)\ (\triangle P/\triangle T)$$

where the function $P(T)$ represents variation in L_∞, t_o and K when bottom temperature (T) varies between 5° and 7° C.

The mean lengths of males and females for each two-week period were calculated from the temperature-dependent von Bertalanffy equation. These were then averaged and converted to weight at the onset of each period by the following relationship

TABLE 1. Changes in growth parameters of *Illex* with bottom temperature for 1977-79.

Sex		Average 1977+1979	1978	ΔP	ΔP/ΔT
Male	L_∞	239.9	278.0	−38.1	−58.6
	T_o	9.3	−0.1	9.4	14.5
	K	0.090	0.036	0.054	0.083
Female	L_∞	294.0	347.0	−53.0	−81.5
	T_o	6.8	−2.5	9.3	14.3
	K	0.054	0.025	0.029	0.045
Temperature (°C)		6.45	5.80	0.65 (ΔT)	—

TABLE 2. Changes in mean length of *Illex* by maturity stage with bottom temperature, 1978-79.

Sex	Maturity stage	Mean length (mm) 1978	Mean length (mm) 1979	ΔP
Male	1	156	146	-10
	2	209	188	-21
	3	220	228	8
Female	1	174	195	21
	2	250	258	8
	3	271	267	-4
Temperature (°C)		5.8	6.5	—

for males and females combined, derived from data for 1978 and 1979 (unpublished data, Resource Branch, Dept. of Fisheries and Oceans, Halifax, Nova Scotia):

$$W = 0.00000843\ L^{3.16}$$

where W is total weight (g) and L is mantle length (mm).

Migration

The onset of maturity stage 3 in *Illex* (Amaratunga and Durward, 1979) was assumed to be associated with migration for spawning. The same approach, as used above for growth, was attempted with data reported by Amaratunga (MS 1980a) to relate the onset of maturity to temperature changes (Table 2), but no consistent pattern was found.

To approximate the emigration pattern, a sigmoid curve was used, which is the integral of a normal distribution with its mean on 1 December and a standard deviation of one 2-week period. Thus, the emigration rate was assumed to be half of its maximum value on 1 December. The maximum was chosen to be an instantaneous rate of 0.2 per 2-week period. This value was considered to be reasonable in the light of a late-season rate (including cannibalism) of 0.31 per 2-week period derived by Hurley and Beck (MS 1979) for *Illex* in the Newfoundland area, and a late-season total mortality rate (Z) of 0.68 per 2-week period derived by Waldron (MS 1979) from catch and effort data for the squid fishery on the Scotian Shelf (weeks 42-52). Migration was treated as a component of mortality because it removes animals from the population on the Scotian Shelf without contributing to the catch. The loss due to migration was assumed to be proportional to abundance.

Cannibalism

Two approaches were used to estimate the effects of cannibalism. One is based on a preliminary analysis of mortality in *Illex* by Caddy (MS 1979), in which the loss due to cannibalism was estimated from the efficiency of food utilization for growth. The second approach is simpler and requires estimates of the feeding frequency of squid instead of the metabolic efficiency. Estimates of the rate of cannibalism were derived from studies by Amaratunga (MS 1980b) and by Ennis and Collins (1979) which give the percentage occurrence of squid in the stomach contents of squid throughout the period of their occurrence on the continental shelf. The percentages were converted into mortality rates for simulating the two approaches.

In the first approach, mortality due to cannibalism (M_c) over a time period is given by the following relationship (see Appendix for derivation):

$$M_c = ln\ KE\overline{W}/(KE\overline{W} - \Delta\ \overline{W}H)$$

where E = efficiency of conversion of food to somatic growth,

H = proportion of squid in the stomachs (varies as the animal grows),

K = ratio of mean prey weight to predator weight,

W = average weight of predator during a time period.

and $\Delta\overline{W}$ = weight gain of predator during a time period.

The value for conversion efficiency (E) was set at 0.25 throughout the simulation. Because the weight of prey squid in the laboratory studies by O'Dor *et al.* (1980) was less than 25% of the predator's weight, the value of K, which reflects the size difference between prey and predator, was set at 20%. These two parameters were assigned lower values than those indicated by O'Dor *et al.* (1980) (25–36% for E and 25% for K) because food is presumably less abundant in nature than was the case in the laboratory studies and more energy is required for hunting and maintenance. The final version of the above relationship used in the simulation was:

$$M_c = ln\ (0.05W/(0.05W - \Delta WH)$$

The second approach is conceptually and mathematically simpler, but it requires a value for the feeding rate of squid. In the absence of other sources of mortality, if one animal unit enters a feeding period and Y of them are alive at the end of the period, HY of which were eaten by members of their cohort, the result is:

$$1 = Y + HY \text{ or } Y = 1/(1+H)$$

As noted above, estimates of H as a function of size were based on data reported by Amaratunga (MS 1980b) and Ennis and Collins (1979). In the model, H was set at zero for animals less than 125 mm (mantle length) and increased to a maximum of 0.4 for animals greater than 325 mm. In a simulated period, each animal will feed, on the average, P times. Consequently, the mortality due to cannibalism over a time period is given by the relationship:

$$M_c = P \, ln \, (1+H)$$

The feeding rate of *Illex* is less well known than the efficiency of conversion, and neither is well defined for natural populations. The feeding rate was assumed to decrease throughout the season, based on the increased incidence of empty stomachs observed in the latter part of the season (Amaratunga, MS 1980b) and the observation by O'Dor *et al.* (1980) that the actual growth rate declines relative to the theoroetical rate, a consequence of starvation as suitable-sized prey animals become scarce. Therefore, in the simulation, the number of feeding times per 2-week period was chosen to have a maximum value of 5 in the early part of the season and to diminish to 3 by the end of December.

Natural mortality

The remaining contributing factors to mortality (starvation, disease, predation by other species, etc.) are pooled into this parameter (M_n). The Z-values from catch/effort data for the past four years do not give any indication of the magnitude of M (See Fig. 1). With an assumed life span of about one year, and considering the mortality rates reported by Hurley and Beck (1979) and Waldron (MS 1979) (M = 0.06 and 0.062 per 2-week period respectively), the value of M = 0.06 per 2-week period was used for the simulations.

Fishing mortality

The fishing mortality rates used in the model represent the product of three factors: an average effort pattern, a selectivity pattern, and a level of fishing intensity. The average effort pattern (Table 3) was derived from effort data for the non-Canadian fleets fishing for squid on the Scotian Shelf during 1978–80. The data were averaged over the years by 2-week periods and normalized so that the largest was equal to unity. The selectivity pattern was that for 60-mm mesh codends (Amaratunga *et al.*, MS 1979) with 50% retention length of 122 mm. The levels of fishing intensity ranged from 0.02 to 0.40 per 2-week period.

TABLE 3. Effort pattern used in the simulated effects of cannibalism on yield of *Illex*.

Week	Effort	Week	Effort	Week	Effort
14	0.00	28	0.54	42	0.55
16	0.00	30	0.93	44	0.52
18	0.00	32	1.00	46	0.21
20	0.00	34	0.78	48	0.10
22	0.20	36	0.72	50	0.10
24	0.20	38	0.69	52	0.00
26	0.21	40	0.56		

Results

The simulation model is an extension of the method of Thompson and Bell (Ricker, 1975). A cohort of 1 million recruits was assumed to be present on 1 April and was subjected to the mortalities described above for 20 two-week periods. The parameters controlling the yield were temperature variation, choice of cannibalism model, and the insensity and pattern of fishing.

The results of simulating the two approaches of estimating mortality due to cannibalism are shown in Table 4, with all other input parameters being constant. Mortality due to cannibalism in the early part of the season was higher for the "conversion efficiency" approach than for the "feeding frequency approach", but the trend was reversed after week 22. By the start of fishing in week 28, the numbers surviving in each case (about 97,000) had declined to approximately 10% of the original population size. The sustained higher cannibalistic mortality from the second approach resulted in less total yield than that from the first approach where mortality gradually declined after week 24 (Table 4). Consequently, the escapement was much higher in the first case than in the second.

The results of yield-per-recruit analyses for three combinations of bottom-temperature effects and method of estimating cannibalistic mortality are given in Table 5 for increasing levels of fishing mortality. In all cases, yield-per-recruit was highest in the first time period and increased with increasing fishing intensity. Yield-per-recruit estimates were lower for the higher of the two bottom temperatures with mortality due to cannibalism based on the conversion efficiency method, and were lower still for the higher bottom temperature with mortality due to cannibalism based on frequency of feeding.

Analogous to the yield-per-recruit analyses given in Table 5, the calculated escapements for spawning

TABLE 4. Simulation of effect on population size and yield of *Illex* with mortality due to cannibalism estimated from (**A**) conversion efficiency and (**B**) feeding frequency. (Bottom temperature at 6.5°C.)

	Week	Population number	Length (mm)	Weight (g)	Catch (No.)	Yield (kg)	M_c	M_m	M_n	F
A.	14	1,000,000	81	9	—	—	—	—	0.06	—
	16	940,270	106	21	—	—	0.05	—	0.06	—
	18	843,541	127	38	—	—	0.29	—	0.06	—
	20	592,981	145	58	—	—	0.38	—	0.06	—
	22	382,279	161	81	—	—	0.40	—	0.06	—
	24	240,240	174	104	—	—	0.40	—	0.06	—
	26	151,437	186	127	—	—	0.38	—	0.06	—
	28	97,130	196	150	4,179	673	0.36	—	0.06	0.05
	30	60,483	205	172	4,456	812	0.33	—	0.06	0.09
	32	37,237	212	193	2,974	601	0.30	—	0.06	0.10
	34	23,428	219	212	1,492	329	0.28	—	0.06	0.08
	36	15,497	224	229	933	222	0.25	—	0.06	0.07
	38	10,585	229	246	616	156	0.22	—	0.06	0.07
	40	7,439	233	260	355	95	0.20	—	0.06	0.06
	42	5,422	237	273	258	72	0.18	—	0.06	0.05
	44	4,022	240	285	179	52	0.16	0.03	0.06	0.05
	46	2,970	243	296	53	16	0.14	0.10	0.06	0.02
	48	2,150	245	305	18	6	0.13	0.17	0.06	0.01
	50	1,493	248	314	12	4	0.11	0.19	0.06	0.01
	52	1,023	249	322	—	—	0.10	0.20	0.06	—
		Total (average)			15,525	3,038	(0.23)	(0.03)	(0.06)	(0.03)
B.	14	1,000,000	81	9	—	—	—	—	0.06	—
	16	941,317	106	21	—	—	0.02	—	0.06	—
	18	868,543	127	38	—	—	0.18	—	0.06	—
	20	683,264	145	58	—	—	0.30	—	0.06	—
	22	474,656	161	81	—	—	0.40	—	0.06	—
	24	299,408	174	104	—	—	0.47	—	0.06	—
	26	175,363	186	127	—	—	0.53	—	0.06	—
	28	97,103	196	150	3,795	611	0.57	—	0.06	0.05
	30	48,872	205	172	3,190	581	0.60	—	0.06	0.09
	32	22,971	212	193	1,591	322	0.62	—	0.06	0.10
	34	10,515	219	212	570	126	0.63	—	0.06	0.08
	36	4,865	224	229	246	58	0.64	—	0.06	0.07
	38	2,252	229	246	109	27	0.64	—	0.06	0.07
	40	1,047	233	260	41	11	0.63	—	0.06	0.06
	42	496	237	273	19	5	0.62	—	0.06	0.05
	44	236	240	285	9	2	0.61	0.03	0.06	0.05
	46	111	243	296	2	1	0.59	0.10	0.06	0.02
	48	51	245	305	—	—	0.57	0.17	0.06	0.01
	50	23	248	314	—	—	0.55	0.19	0.06	0.01
	52	10	249	322	—	—	0.53	0.20	0.06	—
		Total (average)			9,572	1,744	(0.49)	(0.03)	(0.06)	(0.03)

TABLE 5. Yield-per-recruit analyses for *Illex* with different combinations of cannibalistic mortality and bottom temperature.

Method of estimating cannibalism	Onset week	Yield (kg) per 10^6 recruits for different F				
		0.02	0.05	0.10	0.20	0.40
Conversion efficiency (5 8°C)	24	1,336	3,131	5,654	9,403	3,888
	28	1,144	2,683	4,851	8,070	1,867
	32	686	1,625	2,986	5,100	7,762
Conversion efficiency (6.5°C)	24	867	2,037	3,695	6,205	9,344
	28	715	1,678	3,037	5,072	7,523
	32	414	980	1,798	3,064	4,652
Frequency of feeding (6.5°C)	24	564	1,361	2,571	4,631	7,742
	28	386	928	1,745	3,114	5,107
	32	140	338	640	1,157	1,933

are given in Table 6. These values represent the sum of the migrating animals and those left after the last period of simulation. The escapement declines with increasing F and the trend is quite pronounced when F increases from 0.2 to 0.4.

Discussion

The application of this model represents an attempt to coordinate biological and environmental information in order to provide some insight into the effects of different factors on the life cycle of *Illex* and the management of the stock. In the absence of a

TABLE 6. Escapement-per-recruit analyses for *Illex* with different combinations of cannibalism mortality and bottom temperature.

Method of estimating cannibalism	Onset week	Escapement per 10^6 recruits for different F				
		0.02	0.05	0.10	0.20	0.40
Conversion	24	3,920	3,188	2,258	1,134	287
efficiency	28	3,951	3,251	2,349	1,227	336
(5.8°C)	32	4,068	3,496	2,717	1,641	600
Conversion	24	3,051	2,475	1,747	871	217
efficiency	28	3,076	2,526	1,820	945	255
(6.5°C)	32	3,168	2,719	2,108	1,267	459
Frequency	24	49	40	29	15	4
of feeding	28	50	41	30	16	4
(6.5°C)	32	51	44	34	21	8

stock-recruitment relationship, simulation for more than a single season is meaningless. A significant effect appears to be mortality due to cannibalism. Except in the early part of the season when squid grow rapidly, the frequency of feeding approach to cannibalism showed much higher mortality than the approach based on data from studies of food conversion efficiency. This was evident even late in the season when the frequency of feeding in the model was reduced from five to three times per 2-week period. Feeding less often than once every 4 days seems to be a long period for an animal as active as the squid. However, Ennis and Collins (1979) reported that up to 70% of the squid examined late in the season had empty stomachs. Similar data reported by Amaratunga (MS 1980b) indicated that only 20–30% of the squid examined late in the season had significant amounts of food in their stomachs. Wallace *et al.* (1981), from laboratory observations, suggested that squid may take up to 36 hours to completely digest a large meal. The inference then is that the estimates of food conversion efficiency are too high or that the feeding rate is too high. It appears that the efficiency of food conversion to growth, as measured in the laboratory (O'Dor *et al.*, 1980), is not directly applicable to the wild population. The level of conversion efficiency in the wild population would have to be considerably lower than the 25% value used in the model, in order to achieve similar results from the two approaches of estimating mortality due to cannibalism.

Another implication of the simulation is that total mortality is dominated by the mortality due to cannibalism (Table 4). This dominance increases with increasing temperature, resulting in a faster rate of decline in abundance in warmer years. An indication of this prediction is evident from the catch-per-unit-effort trends for 1977 and 1979 (Fig. 1) when bottom temperatures on the Scotian Shelf in summer were higher than normal. The other sources of non-catch mortality (migration and residual natural) are poorly known but are presumably of reasonable magnitude. The sum of the three mortalities considered in the model exceeds the slopes of lines representing the commercial catch-per-unit-effort trends shown in Fig. 1. This implies that either a portion of the model is in error or the stock exploited by the offshore fleet on the Scotian Shelf cannot be considered a closed stock which is recruited as a unit. In reality, recruitment is likely to be protracted, and catch rates may thus be maintained at higher levels relative to those implied from the model. Other possibilities to be explored are the effects of schooling and the fishing practices of the fleet in keeping the catch rates from declining as rapidly as the decline in abundance predicted by the model.

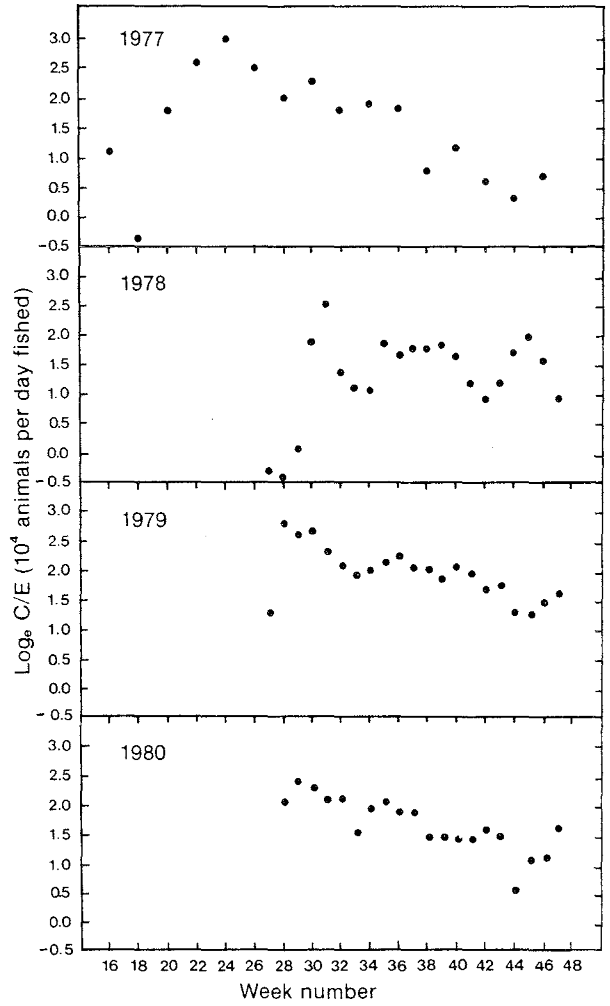

Fig. 1. Trends in commercial catch rates for *Illex* on the Scotian Shelf, 1977–80.

The yield-per-recruit results (Table 5) show increasing yield with increasing fishing intensity. From the results of a simulation with growth data associated with the 6.5° temperature and cannibalistic mortality based on the efficiency of food conversion, no F_{max} could be found with fishing mortality values per 2-week period up to F = 10, and the optimum fishing mortality was unrealistically high at $F_{0.1} = 1.6$. This is because the mortality rate is higher than the growth rate throughout the season, implying that the sooner the squid are harvested the better the yield.

Depending on the approach used in the model, the yield-per-recruit is predicted to be 50–170% higher when fishing commences in early July (week 28) than in early August (week 32). The impact of changes in the commencement of fishing on the predicted escapement is less pronounced, the difference being less than 30% for all but the highest F-values used. These results are expected because the F to Z ratio is small and the Z to growth rate ratio is large.

With the recruiting cohort of animals constant and appearing as a unit prior to the start of fishing, the model indicates that yield-per-recruit is less in warm years than in cool years. This is contrary to trends in recent catch statistics, because recruitment appears to be greatly enhanced in years when bottom temperatures are higher than normal (Mohn, MS 1981).

The management implication of this study from a yield-per-recruit point of view can be expressed as "It is better to catch them before they die". Since the $F_{0.1}$ level appears to be unrealistically high, less damage to the stock may be done per ton caught early in the season.

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APPENDIX

Determination of Mortality Due to Cannibalism Given the Efficiency of Food Utilization

Consider a unit of squid of weight W_1 at the beginning of a 2-week period. At the end of this period a portion Y of these have survived and weight W_2. During the period, a proportion of the squid have squid in their stomachs, and the efficiency of conversion to somatic growth is E. Mortality is portioned into two components, M_c for cannibalism and M_x for all other sources.

$1 - Y$ = proportion lost through all causes.

$\frac{(1-Y)\,M_c}{M_x + M_c}$ = proportion cannibalized.

$\frac{(1-Y)\,M_c K\overline{W}}{M_x + M_c}$ = biomass cannibalized, where W is the mean weight of survivors and K is a factor relating to the smaller size of the prey.

$\frac{(1-Y)\,M_c K\overline{W}}{(M_x + M_c)\,H}$ = total biomass consumed.

$$\frac{(1-Y)\,M_c K\overline{W}}{(M_x + M_c)\,HY} = \Delta W = W_2 - W_1 = \text{weight gain per survivor.} \qquad (1)$$

$$\frac{(1+Y)}{Y} = \frac{\Delta W\,(M_x + M_c)\,H}{M_c K\overline{W}E} \qquad (2)$$

$$Y = \frac{M_x K\overline{W}E}{M_x K\overline{W}E + \Delta WH\,(M_x + M_c)} \qquad (3)$$

$$M_c = ln\left[\frac{M_x K\overline{W}E}{M_x K\overline{W}E + \Delta WH\,(M_x + M_c)}\right] - M \qquad (4)$$

This is a non-linear equation for M_c and requires a numerical solution. The expression can be simplified by assuming $M_x < M_c$, which leads to the following approximation:

$$M_c = ln\left(\frac{K\overline{W}E}{K\overline{W}E + \Delta WH}\right) \qquad (5)$$

The mean weight (W) is the average of W_1 and W_2.

With $K = 0.2$, $W_1 = 50$, $W_2 = 60$, $E = 0.25$, $H = 0.15$, and $M_x = 0.06$, equation (4) results in $M_c = 0.42$, and equation (5) results in $M_c = 0.44$.