

## USE OF COHORT ANALYSIS TO ESTIMATE ABUNDANCE, RECRUITMENT AND SURVIVORSHIP FOR NEWFOUNDLAND MOOSE

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**ABSTRACT:** The use of a fisheries computer model (CAGEAN) to perform cohort analysis of Newfoundland age-specific moose kill data was investigated. Cohort analysis was used to estimate temporal changes in moose population abundance, recruitment, and age-specific survivorship and vulnerability to hunting. Different populations displayed 1 to 3 cyclic fluctuations between 1966 and 1991 with density varying from 0.5 (1973) to 4.0 moose/km<sup>2</sup> (1990). Cohort abundance estimates generally compared favourably with aerial survey results, and indirect indices determined from hunter questionnaires. Sensitivity analysis indicated that abundance estimates were most sensitive to changes in natural mortality. Cohort analysis was less reliable as an estimator of calf recruitment and the method cannot directly measure productivity or early calf survival. Estimates of age-specific vulnerability to hunting and age-specific survivorship for males and females were compared for two time periods. Calves were least vulnerable to hunting, yearlings were the most vulnerable and vulnerability increased with age for males over 7 years old and females over 10 years old. The major age-specific differences in mortality patterns for female moose between two time periods was the low mortality rate of calves (4%) during the 1978-80 period subsequent to 7-9 years of uninterrupted population growth. Generally, the fisheries computer model provides useful demographic information for research and management purposes but important limitations exist.

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Newfoundland, like most jurisdictions in North America, has relied on a number of methods of measuring changes in moose (*Alces alces*) population abundance: (1) direct estimation of population numbers using aerial surveys (Bergerud and Manuel 1969); (2) indirect indices of abundance or hunter statistics derived from questionnaires (Ferguson *et al.* 1989); and (3) direct and indirect indices combined in a population model (Albright and Keith 1987, Ferguson 1992). Another technique of indirectly measuring changes in abundance originally developed by fisheries scientists is the cohort or virtual population analysis (Ricker 1975). More recently, cohort analysis has been applied to deer (*Odocoileus virginianus*)(Fryxell *et al.* 1991), caribou (*Rangifer tarandus*)(Eberhardt and Pitcher 1992 without effort data), and moose (Jordan *et al.* 1971 without effort data; Fryxell *et al.* 1988 with effort data).

Cohort analysis essentially requires only time series data on age-specific kills and age-specific natural mortality rate (Gulland 1965). The method does require a large cumulative mortality for completed cohorts (Pope 1972) and therefore without auxiliary information cohort analysis does not provide reliable estimates of recent population abundance. Deriso *et al.* (1985) developed a cohort analysis model (CAGEAN) that requires extra information about model parameters and additional assumptions about the dynamics of the population, to derive abundance estimates. Such additional information includes (1) hunting effort data to provide information about hunting mortality rates, and (2) the additional assumptions of a relationship between sexually mature females and calf production to provide information about year-class strength, and (3) about sources of random errors. Here, I investigate the utility of the CAGEAN model

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for moose harvest age data from Newfoundland. The age of moose killed by hunters acts as a sample of the population age structure from which age-specific survivorship can be estimated indirectly (Fryxell 1986).

The Newfoundland situation offers the opportunity to analyze the direct impact of hunting on a single species, moose. Black bears (*Ursus americanus*) are the only other major predator of moose besides humans. These results can form the essential basis for more complex and more realistic analyses that take account other relevant factors such as changes in natural environment, changes in competing species, wolf predation and food.

### STUDY AREA

In 1991, Newfoundland had 67 Moose Management Units (MMUs) but between 1973 and 1986, the number of MMUs remained relatively constant at about 38. These MMUs

are distributed among nine ecoregions (Damman 1983) according to carrying capacity of land, hunter accessibility and moose population demography (Mercer and Manuel 1974). Of 13 MMUs that had sufficient samples of aged hunter kill over a long continuous period of time, I chose 4 MMUs (3, 11, 17, 24) to test cohort analysis. These 4 MMUs represented different sample sizes, accessibility, ecoregions and two MMUs (17 and 24) had previous cohort analysis results available for comparison (Fryxell *et al.* 1988).

MMU 3, Harbour Deep (3580 km<sup>2</sup>), is located on the mostly forested part of the Great Northern Peninsula, Northern Peninsula ecoregion (Damman 1983)(Fig. 1). *Abies balsamea* predominates largely because of the infrequent forest fires. Forests go deep into valleys of the Long Range Mountains and occur up to altitudes of about 450 m. At the higher elevations *Picea mariana* becomes an

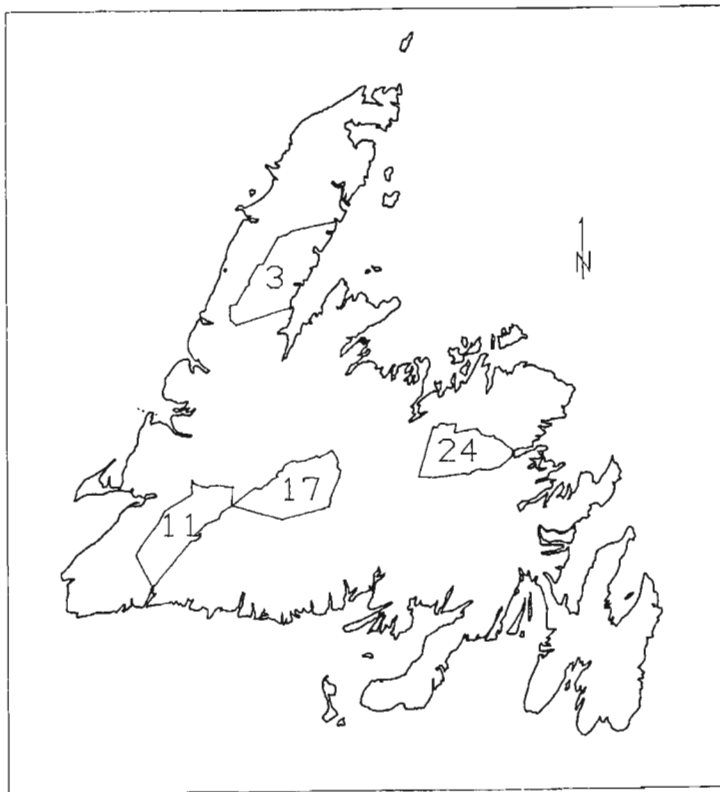


Fig. 1. Location of four Moose Management Units on the island of Newfoundland where moose abundance was investigated.

important part of the less productive fir forests. The more open areas include numerous bogs and exposed, rock dwarf shrub barrens. The climate is characterized by a growing season of 110-150 days, a long frost-free season for this area, lower than average precipitation for the island, uninterrupted winter snow cover of about 150-180 days.

MMU 11, Dashwoods (2844 km<sup>2</sup>), is unusual because the area is divided into two halves, the Central (north) and Southern Long Range Barrens (south) ecoregions (Damman 1983)(Fig. 1). The northern half of this MMU is heavily forested with rugged topography, hills rising above the tree line and underlain by bedrock. Vegetation is boreal with *Abies balsamea* covering most of the area. The southern half of the MMU is mostly barrens of dwarf shrub heaths, shallow patterned peatlands, areas of 'tuckamoor' (stunted *Picea mariana*) and small patches of forests occur in some sheltered valleys. Climate is continental with high snowfall (>5 m), permanent snow cover during winter months, snow cover stays into late spring (June) and snow drifting is extreme during the winter with snow storms exposing sites practically all winter.

MMU 17, Millertown (2800 km<sup>2</sup>) is located in the Central Newfoundland ecoregion (Damman 1983) and is heavily forested (primarily *Abies balsamea*) with gently rolling to hilly topography (150-450 m) and underlain by bedrock (Fig. 1). Continental climate is characterized by cooler summers, more precipitation and shorter growing season than MMU 24 within the same ecoregion.

MMU 24, Northwest Gander-Gambo (2111 km<sup>2</sup>) of the Central Newfoundland ecoregion (Damman 1983) is mostly covered by boreal forest predominated by *Abies balsamea* with a dense moss carpet in areas not disturbed by fire (Fig. 1). The highest forest fire frequency of the island has resulted in stands of *Picea mariana*, and to a lesser extent *Betula papyrifera*, covering large areas. The continental climate in this area has

the highest summer temperatures and lowest winter temperatures of the island. This area receives lower rainfall than other subregions with occasional dry spells. Growing season is 140-160 days based on a threshold temperature of 42° F. Precipitation and snowfall is average relative to most of the island in winter with reliable winter snow cover.

## METHODS

Lower mandibles were collected from hunters at check stations, via the mail, or from hand deliveries. Aged samples varied for MMU 3 (19 years, 299 females (15.7 ± 12.3 (mean ± standard deviation), CV=78.3, min=2, max=46) and 932 males (49.1 ± 28.3, CV=57.6, min=10, max=112)), MMU 11 (19 years, 502 females (26.4 ± 14.0, CV=52.9, min=6, max=73) and 1149 males (60.5 ± 23.4, CV=38.7, min=11, max=103)), MMU 17 (26 years, 1548 females (59.5 ± 41.2, CV=69.3, min=12, max=175) and 2141 males (81.6 ± 41.6, CV=51.0, min=12, max=193)), and MMU 24 (23 years, 1882 females (81.8 ± 34.1, CV=41.7, min=37, max=152) and 2695 males (117.2 ± 28.1, CV=24.0, min=79, max=180)).

Age of moose was determined from tooth eruption pattern for calves and yearlings and by counting cementum annuli on the first incisor from older animals (Sergeant and Pimlott 1959). Problems occurred with ageing moose incisors (>2-years-old) during two periods, 1974-78 and 1981-84. Therefore, I used the adjustments calculated by Ferguson *et al.* (1990) that were based on a proposed relationship between morphological and demographic measures. Hunters were less likely to return a calf than an adult mandible and therefore I adjusted the number of calves in the aged sample according to hunter questionnaire results. I used a correction factor of 1.58 based on a reported harvest of 5.8% calves:adults (n=36,252) relative to a 3.7% calf:adult mandible ratio (n=10,464) for 1986-91 data.

To evaluate accuracy, indirect and direct indices of abundance were compared with cohort analysis results. The indirect indice of moose abundance, unweighted Moose Seen Per Day hunted (MSPD), was smoothed using a 3-year-running-average and had the advantage of covering the same period of annual fall estimates as cohort analysis results. Although calves in the harvest better correlated with moose densities estimated from aerial surveys (Ferguson *et al.* 1988), the presence of sample sizes of 0 limited the use of this measure as a trend indice. I chose not to use Kill Per Unit Effort (KPUE) as a comparable estimate of abundance since cohort analysis incorporates estimates of both kill and effort and therefore a high correlation results (see Fryxell *et al.* 1988). Aerial moose surveys provided the direct indices of abundance and were conducted using primarily helicopters to count moose on 4 km square quadrants with systematic-random block sampling. All block surveys were adjusted for sightability bias after Oosenbrug and Ferguson (1992).

Hunting effort (total days hunted by hunters) was partitioned into male and female components according to the licence type (either sex, male only, calf only, female only or nonresident licence). I used an averaging procedure (Gulland 1983:70) to estimate effort over a period approximately one-half the life span used in cohort analysis. I took the average effort over the current year plus 5 and 4 previous years for female and male moose respectively. Life span of moose used in cohort analysis was 12 for females and 9 for males based on the age sample having less than 5% of moose aged greater than 12 or 9 respectively.

Total catch (harvest) was calculated from hunter success information obtained from hunter questionnaires. Follow-up questionnaires were used to make adjustments for the lower success of non-respondents and then to estimate total harvest from the licence quota. Corrections were made assuming 20% crip-

pling loss. The aged sample was increased proportionately to estimate the total age-specific harvest. Generally one in every 2-6 successful hunters returned a mandible and variation in the rate of return occurred as a result of area (lower return for hunters hunting in inaccessible Moose Management Units; MMUs), sex of kill (lower return of males killed) and over time (lowest return during the mid-1960s and highest during the mid-1970s). I used Hatter and Bergerud's (1991) definition that at the completion of the population survey (fall hunt, September to December) calves are recruited into the moose population. Offspring that die of causes unrelated to hunting before the end of the hunting season are simply not counted.

Caughley (1966) lists the assumptions for life tables as the population having a stable age distribution, known rate of increase and known differential vulnerabilities to hunting. Fluctuations in the rate of increase violate the assumption of a stable age distribution, but to minimize this bias I chose two time periods from MMU 24 data for comparison: one when the population was relatively stable following a population decrease, 1969-71, and the other prior to a population increase, 1978-80. Adjustments for rate of population growth were made.

Age-specific vulnerability to hunting was measured for males and females for both time periods as age-specific hunting rate divided by population hunting rate. Age-specific hunting rate was calculated as the number of moose shot by hunters divided by total moose in the age class estimated from cohort analysis. For comparison between time periods the values were standardized to an overall mean of 1. For example, a value of 2 means an animal of this age class was twice as likely to be killed by hunting compared to an average animal of this population.

The cohort analysis model developed by Deriso *et al.* (1985) has the following characteristics:

1. Hunting mortality rate ( $F(t,a)$ ) is separable into an age-dependent factor (age-specific selectivity coefficient;  $s(a)$ ) and a year-dependent factor (hunting mortality rate;  $f(t)$ ) as suggested by Pope (1974) and originally modelled by Doubleday (1976):

$$F(t,a) = s(a)f(t)$$

2. Hunting mortality is proportional to hunting effort. The  $f(t)$  parameter is replaced by one catchability coefficient  $q$  while  $h_1$  adjusts the relationship between hunting effort and mortality. This weighting term adjusts the amount of influence of the auxiliary information (i.e. hunting effort) such that a high  $h_1$  results in a deterministic relationship and  $h_1 = 0$  results in no relationship. Deriso et al. (1985) recommended medium levels of  $h_1$  of about 0.5 (cohort 1 used  $h_1 = 0.5$ ).

3. Catch (kill) is given by a Baranov catch equation:

$$C(t,a) = u(t,a)N(t,a)$$

$$\text{where } u(t,a) = \frac{F(t,a) [1 - \exp(-Z(t,a))]}{Z(t,a)}$$

$C(t,a)$  = total hunting harvest at year  $t$  for aged  $a$ -year-olds;  $N(t,a)$  = population abundance at year  $t$  for aged  $a$ -years-old;  $F(t,a)$  = hunting mortality rate in year  $t$  for  $a$ -year-olds;  $Z(t,a)$  = total mortality rate of  $a$ -year-olds at year  $t$  (natural + hunting mortality rate).

4. Recruitment is based on a Ricker spawner-recruit function with log-normal departures (Fournier and Archibald 1982) and age-specific fecundity. Estimates used here (cohort 1) are from Pimlott (1959:389, Table 6) of 0.27 female calves per female yearling and 0.50 female calves per female adult. As with  $h_1$ , a large  $h_2$  forces recruitment to become a deterministic function of the number of females (cohort 1 used  $h_2 = 0.5$ ).
5. To estimate more recent data with incomplete cohorts all three parameters, hunting

effort, kill and recruitment are estimated by statistical procedures so as to minimize the sum of squares between observed and expected values. The CAGEAN program uses a method introduced by Doubleday (1976) of analyzing catch-at-age data by linearized least squares which analyzes various cohorts simultaneously thereby taking into account stochastic variability in the observed catch data. The algorithm used is based on logarithms of effort (see no. 2), catch (see no. 3) and recruitment (see no. 4) ratios to provide starting values for an iterative procedure which applies standard least squares to the resulting linear approximations in an iterative manner until two successive estimates of all parameters differ by less than  $10^{-2}$ .

6. Natural mortality is fixed at assumed age dependent values and variance ratios ( $h_1$  and  $h_2$ ) are fixed at assumed values. I used the estimates of natural mortality from Cederlund and Sand (1991; 1% mortality for 0.5 to 1.5-year-olds and 5% for >1.5-year-olds) since this moose population in Sweden also lived without wolves (*Canis lupus*). The effects of violating the assumption of constant natural mortality are likely small if fluctuations in natural mortality are random but if there is systematic variation in natural mortality (e.g. with time, age or year-class size) then Ulltang (1977) argues that significant biases in parameter estimates will result. Terminal mortality of 0.16 was used in the CAGEAN analysis (cohort 1) reported here.

## RESULTS

I compared cohort analysis results with other direct and indirect indices of moose abundance for 4 MMUs (3, 11, 17, and 24; Fig. 2 and 3). Estimates of moose abundance by cohort analysis showed no marked annual fluctuations compared to MSPD (3-year-running-average). Overall density estimates compared favourably with aerial survey estimates.

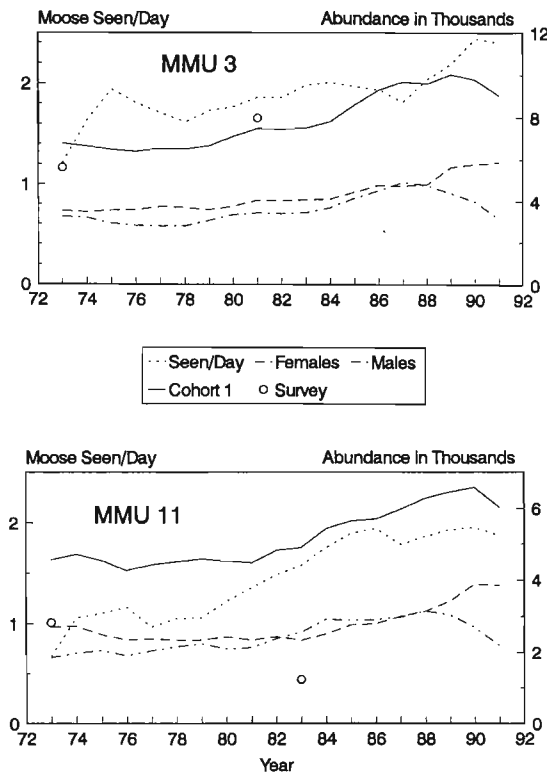


Fig. 2. Comparison of direct and indirect measures of moose abundance for two MMUs (MMU 3 upper panel and MMU 11 lower panel). The indirect indice, MSPD shows a 3-year-running-average. Cohort analysis estimates shown include males, females and total moose (Cohort 1).

For the two MMUs considered inaccessible to moose hunters (MMU 3, moose reported shot were a mean distance of 17.1 km to nearest road; MMU 11, mean 9.8 km to road; overall mean for island = 7.1), the cohort analysis results tracked the MSPD pattern over time ( $r=0.54$ ,  $P=0.017$  and  $r=0.84$ ,  $P=0.0001$  for MMU 3 and 11 respectively) but for MMU 11, the abundance estimates were considerably higher than aerial survey estimates. Another problem with the results from cohort analysis was a generally higher estimated number of males than females when the opposite is expected. The pattern of more males than females calculated for inaccessible MMUs was reversed for the two accessible MMUs (MMU 17, mean 1.8 km to nearest

road; MMU 24, mean 1.6 km to road).

Two methods of cohort analysis were used to estimate moose density in MMUs 17 and 24: Cohort 1 (CAGEAN program; Deriso *et al.* 1985) and Cohort 2 (Fryxell *et al.* 1988). Cohort 1 tracked the changes in population abundance shown by the indirect indice MSPD better than Cohort 2 (MMU 17:  $r=0.63$  vs.  $r=-0.12$ ; MMU 24:  $r=0.88$  and  $r=-0.28$  for Cohort 1 and Cohort 2 respectively) although Cohort 1 had the advantage of estimating moose abundance during the consistent population growth period of the 1980s. For MMU 24, both cohort analysis methods, severely underestimated the population increase during the mid-1970s that was shown by both aerial surveys and the hunter statistic MSPD.

To investigate the robustness of the CAGEAN method, I varied (high, medium,

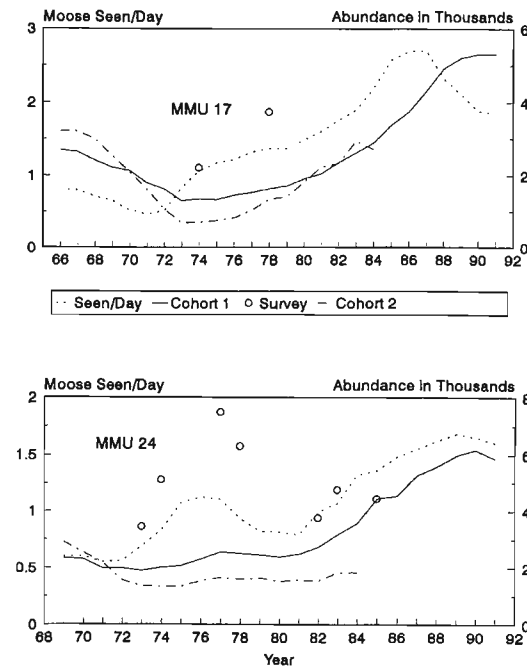


Fig. 3. Comparison of direct and indirect measures of moose abundance for two MMUs (MMU 17 upper panel and MMU 24 lower panel). The indirect indice, MSPD shows a 3-year-running-average. Cohort analysis estimates shown include estimates from CAGEAN program (Deriso *et al.* 1985)(Cohort 1) and Fryxell *et al.* (1988)(Cohort 2).

Table 1. Influence of high, medium and low parameter estimation of natural mortality, terminal mortality, fecundity schedule and two weighting terms ( $h_1$  and  $h_2$ ) on CAGEAN cohort analysis results for central Newfoundland moose (MMU 24), 1969-1991.

Parameter		Year					
		1969	1973	1977	1980	1985	1991
natural <sup>a</sup> mortality schedule	low	1067	777	1012	979	1841	3795
	med.	1362	1126	1502	1603	2834	5389
	high	2327	2366	3243	3755	6004	10297
$h_1$ <sup>b</sup> hunting effort	low	1334	1071	1396	1418	2437	4340
	med.	1362	1126	1502	1603	2834	5389
	high	1499	1440	1827	2212	3437	6144
$h_2$ <sup>b</sup> recruitment	low	1364	1128	1505	1601	2827	5353
	med.	1362	1126	1502	1603	2834	5389
	high	1403	1274	1805	2217	4310	8925
terminal <sup>c</sup> mortality	low	1367	1136	1519	1629	2882	5491
	med.	1362	1126	1502	1603	2834	5389
	high	1357	1116	1489	1588	2810	5325
fecundity <sup>d</sup> schedule	NONE	1364	1128	1505	1601	2828	5353
	low	1362	1128	1505	1607	2843	5413
	med.	1362	1126	1502	1603	2834	5389
	high	1362	1126	1501	1602	2831	5381

<sup>a</sup>natural mortality schedule: low ( $q_x=0.001$  for calves and  $q_x=0.005$  for >1-year-olds); medium (0.01 and 0.05 respectively; Cederlund and Sand 1992); and high (0.05 and 0.10)

<sup>b</sup> weighting factor for hunting effort and recruitment: low (0.001); medium (0.5); and high (1000)

<sup>c</sup> terminal mortality: low (0.01); medium (0.16) and high (1.0)

<sup>d</sup>fecundity schedule: low ( $m_x=0.01$  for yearlings and  $m_x=0.1$  for >2-year-olds); medium (0.27 and 0.52 respectively; Pimlott 1959); and high (0.5 and 0.8)

low) the five parameters using female age data for MMU 24 (Table 1). Adjusting terminal mortality and fecundity schedules resulted in less than 1% change in estimated abundance. The cohort analysis was most sensitive to changes in estimated natural mortality (31% decrease and 2.06 times increase) followed by changes in the  $h$ s (19% decrease, 1.14 times increase and 1% decrease, 1.66 times increase for  $h_1$  and  $h_2$  respectively)(Fig. 4). Decreasing the effect of effort  $h_1$  or  $h_2$  did not always result in a decrease in estimated population size but rather the estimated abundance some-

times increased (data on file).

I found no significant correlation between the percent calf cohort calculated from CAGEAN cohort analysis and percent calves seen by hunters for the four MMUs ( $r=0.34$  MMU 3;  $r=-0.11$  MMU 11;  $r=0.21$  MMU 17;  $r=-0.16$  MMU 24). I consider percent calves seen by hunters a good indicator of fall calf recruitment since this measure correlated with calves seen on winter aerial classification surveys ( $r=0.27$ ,  $p=0.012$ ,  $n=88$ ). Also, cohort results from Fryxell *et al.* (1988) were not correlated to either the CAGEAN cohort calf

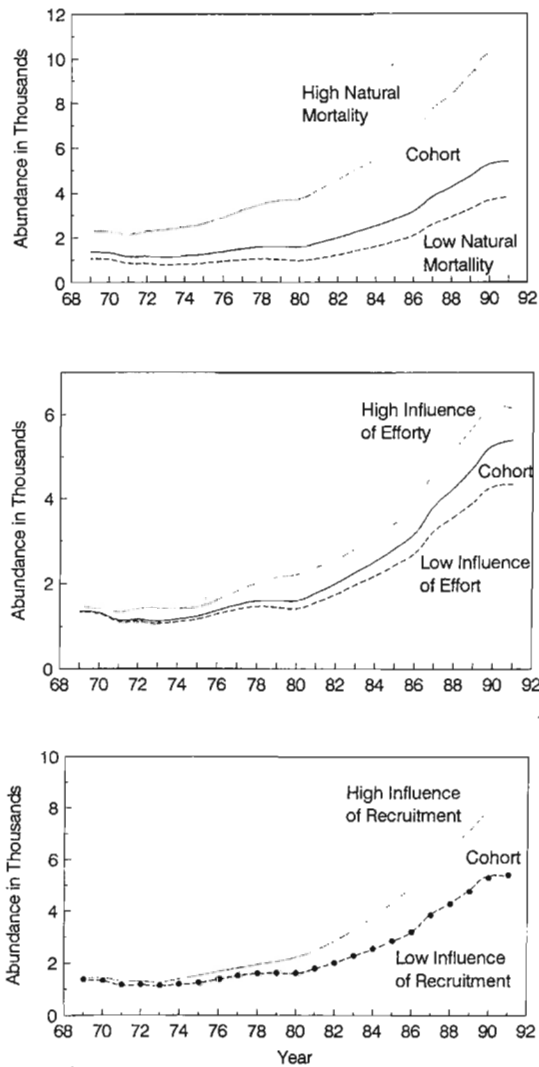


Fig. 4. Influence of high, medium and low parameters of natural mortality (upper panel), catch-effort (middle panel) and recruitment (lower panel) information for female moose of central Newfoundland, MMU 24.

estimates ( $r=-0.63$  MMU 17;  $r=-0.25$  MMU 24) nor calves seen by hunters ( $r=-0.02$  MMU 17;  $r=0.21$  MMU 24). The lack of correlation of calf estimates may be related to the low vulnerability of calves to hunters and suggests that the cohort analysis calf measure may not be a good indicator of calf recruitment. In comparison, yearlings were the age class most vulnerable to hunters and therefore had the largest sample size.

Vulnerability of moose to hunting varied with age and period of time for MMU 24 (Table 2). Calves were least vulnerable to hunting (.4 to .7), yearlings were the most vulnerable (1.7 to 1.9) and vulnerability increased with age for males over 7 years old and females over 10 years old. The pattern of age-specific vulnerability of males did not change between time periods. For females, not only did overall vulnerability decrease from 22% of all females harvested in 1969-71 to 12% in 1978-80, but also the pattern of age-specific vulnerability varied with a greater vulnerability of calves and yearlings during the 1969-71 period (Fig. 5).

To discern patterns in age-specific survivorship, I chose to use age distribution data adjusted for population rate of increase but not smoothed by a quadratic polynomial procedure (Table 2). Survivorship rates and age-specific pattern of mortality were similar for males (68.6 and 67.4%) during the two time periods but showed differences for female moose (Fig. 6). Survivorship for female moose greater than 6 months of age were higher during the 1978-80 period (88.4%) relative to the 1969-71 period (77.8%). Both periods showed a similar age-specific mortality pattern between the ages 2 to 7 years with

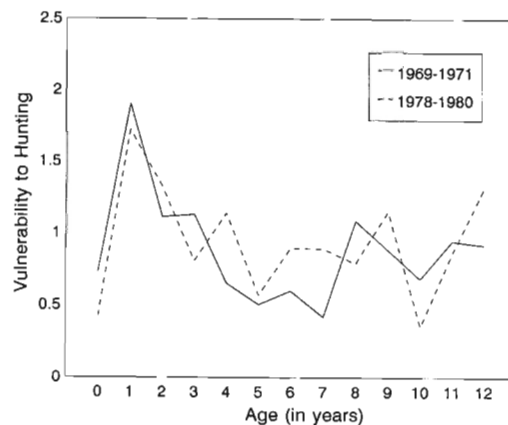


Fig. 5. Age specific vulnerability of female moose to hunting mortality calculated from cohort analysis of female moose shot in central Newfoundland, 1969-71 and 1978-80 (MMU 24).



Table 2. Life tables for male and female moose calculated from cohort analysis of harvest data from central Newfoundland (MMU 24) 1969-71 and 1978-80.

1969-1971 Females						
Age (x)	Vulnerability	Freq. Hunter Kill (F <sub>x</sub> )	Live Moose Freq. (N <sub>x</sub> )	Standing Age Distr. (S <sub>x</sub> )	Corrected (r=0.931) (N <sub>x</sub> e <sup>rx</sup> )	Mort. Rate Q <sub>x</sub>
0	0.728	124	768	1000	1000	.203
1	1.905	277	656	854	797	.175
2	1.112	143	580	755	658	.324
3	1.128	105	420	547	445	.262
4	0.652	48	332	432	328	.247
5	0.505	30	268	349	247	.189
6	0.600	31	233	303	201	.223
7	0.419	18	194	253	156	.360
8	1.085	32	133	173	100	.670
9	0.882	26	133	173	93	.256
10	0.681	16	106	138	69	.195
11	0.942	19	91	118	55	.292
12	0.915	14	69	90	39	
	0.222	883	3983			
1978-1980 Females						
Age (x)	Vulnerability	Freq. Hunter Kill (F <sub>x</sub> )	Live Moose Freq. (N <sub>x</sub> )	Standing Age Distr. (S <sub>x</sub> )	Corrected (r=0.931) (N <sub>x</sub> e <sup>rx</sup> )	Mort. Rate Q <sub>x</sub>
0	0.421	47	963	1000	1000	.035
1	1.721	183	918	953	965	.150
2	1.322	118	771	801	820	.226
3	0.805	55	590	613	635	.259
4	1.139	57	432	449	471	.182
5	0.569	23	349	362	385	.104
6	0.894	32	309	321	345	.175
7	0.891	26	252	262	285	.253
8	0.789	17	186	193	213	.184
9	1.151	20	150	156	174	.170
10	0.351	5	123	128	144	.087
11	0.856	11	111	115	132	.280
12	1.312	12	79	82	95	
	0.116	606	5233			

Table 2 cont. Life tables for male and female moose calculated from cohort analysis of harvest data from central Newfoundland (MMU 24) 1969-71 and 1978-80.

1969-1971 Males						
Age (x)	Vulnerability	Freq. Hunter Kill ( $F_x$ )	Live Moose Freq. ( $N_x$ )	Standing Age Distr. ( $S_x$ )	Corrected ( $r=0.931$ ) ( $N_x e^{rx}$ )	Mort. Rate $Q_x$
0	0.451	122	830	1000	1000	.286
1	1.709	357	641	772	714	.315
2	1.331	206	475	572	489	.413
3	1.108	109	302	364	287	.364
4	0.974	66	208	251	183	.418
5	0.539	23	131	158	106	.224
6	0.279	10	110	133	83	.261
7	0.732	21	88	106	61	.380
8	0.624	12	59	71	38	.499
9	1.055	11	32	39	19	
	0.326	937	2876			
1978-1980 Males						
Age (x)	Vulnerability	Freq. Hunter Kill ( $F_x$ )	Live Moose Freq. ( $N_x$ )	Standing Age Distr. ( $S_x$ )	Corrected ( $r=0.931$ ) ( $N_x e^{rx}$ )	Mort. Rate $Q_x$
0	0.412	111	856	1000	1000	.243
1	1.746	369	672	785	757	.353
2	1.319	187	451	527	489	.291
3	1.149	120	332	388	347	.359
4	0.950	66	221	258	223	.272
5	0.533	28	167	195	162	.308
6	0.530	20	120	140	112	.333
7	0.613	16	83	97	75	.338
8	0.781	14	57	67	50	.273
9	0.961	13	43	50	36	
	0.314	944	3002			

high mortality of 2.5 to 3.5-year-olds, low mortality of 5 year olds and higher mortality to age 7 (Fig. 7). The major age-specific differences in mortality patterns for females between the two time periods was the low

mortality of calves (0.5 to 1.5-years-old) during the 1978-80 period (4% versus 20%) leading up to the population growth of the 1980s.

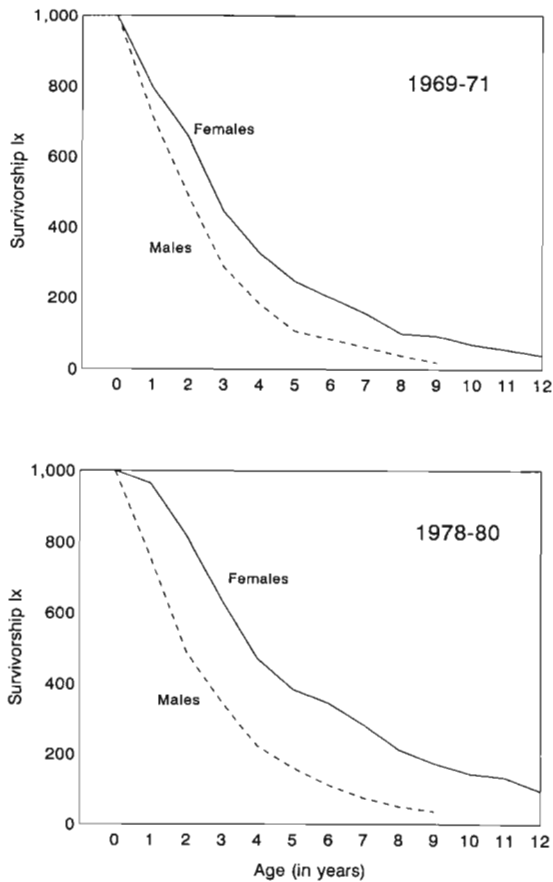


Fig. 6. Survivorship calculated by cohort analysis of male and female moose harvested from central Newfoundland 1969-71 (top) and 1978-80 (bottom).

### DISCUSSION

Cohort analysis can help in making management decisions that require estimates of moose abundance, recruitment and survivorship. A major management limitation in the method is that abundance estimates in the more recent years are less accurate and there may be a tendency for annual assessments to overestimate (Sinclair *et al.* 1991). Therefore the method is best suited to demographic studies over long periods of time and management theory that is developed from the lessons of history.

The cohort analysis method requires a long time series (15-20 years) of well sampled kill data (20-40 ages for each sex each year)

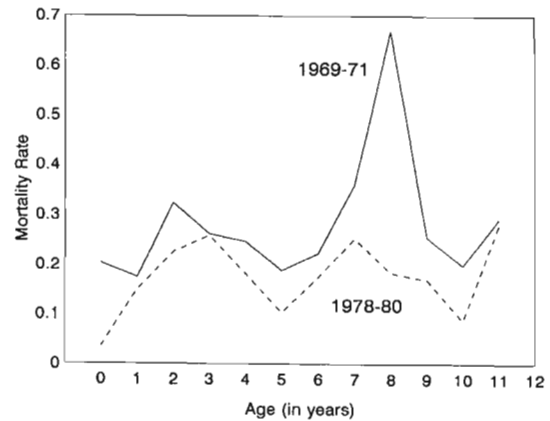


Fig. 7. Female mortality rates calculated from moose shot in central Newfoundland (MMU 24), 1969-71 and 1978-80 estimated from cohort analysis.

during which recruitment rate has not changed greatly. The method also performed less well for inaccessible MMUs due to lower sample sizes and possible misreporting by hunters. In Newfoundland, more males than females are generally harvested and therefore cohort analysis results for males usually better reflect population abundance patterns. If cohort analysis results indicate more total males than females, when the opposite is expected, then the results should be viewed cautiously. This problem occurred for inaccessible MMUs and for previous analyses of accessible MMUs (Fryxell *et al.* 1988; results on file). Possible explanations include misreporting of sex of kill by hunters or different natural mortality of males and females.

Before using cohort analysis, biologists should know if hunting methods and technology have changed over the period of time data has been collected. Cohort analysis (CAGEAN) can compare different moose harvesting strategies by calculating the relationship between effort and catch (selectivity) for each period. If a trend in catchability over time is not accounted for then a possible result is a biased estimation of change in effort or KPUE. For example, if in later years the effort

statistics underestimate mortality and KPUE, then an overestimation in abundance relative to earlier years will result. Patterns of changes in catchability can occur as a result of (1) changes in distribution of hunting effort; (2) trends in catchability over a period of years due to an increasing efficiency of hunting (e.g. hunting partners could increase KPUE); and (3) interference or cooperation between hunters. The distribution of hunting is seldom uniform and the average moose density in hunting areas differs from the true average density because hunters tend to hunt in more accessible areas. Interference can have two effects: (1) KPUE could decrease while abundance remains the same and catchability decrease with an increase in number of hunters; and (2) effect of hunting (increased number of hunters) on abundance is that KPUE of all hunters decreases proportionately to decreases in abundance.

Moose have been traditionally managed according to the convenient concept of maximum sustainable yield (MSY) which provides a useful description of population behaviour as harvest increases. A major problem with the MSY concept is the occurrence of time lags. Although productivity changes little during a population increase, at high densities recruitment can decrease dramatically. Because of their size, moose live longer and mature later and these characteristics create time delays in effects due to food limitation. The estimation of recruitment from cohort analysis can be used to investigate these time lags (see Fryxell *et al.* 1991).

Biologists have speculated on both a 10-year lag in moose cycles (R.O. Peterson pers. comm. 1992) and a 9-11 year moose cycle (H.R. Timmermann pers. comm. 1992). Cycles appear to have characterized the moose population of MMU 17 over the past 40+ years with highs occurring approximately every 9 years, 1950 (Pimlott 1959), 1960, 1966 (Bergerud and Manuel 1968), 1978 and 1986 (MSPD, Fig. 3 and KPUE on file). A

study of the variation in recruitment as a result of density dependent changes for this MMU would test if this is the main mechanism in determining how populations maintain themselves at around a density level rather than continuously decreasing or increasing. Considerable theoretical and practical work is needed before we can manage moose in Newfoundland without creating or following cycles in density.

I recommend discretion in using cohort analysis as a method of estimating productivity because the smaller calves experience greater natural mortality before becoming part of the hunted population. Extrapolating back from observed harvest involved in the cohort analysis procedure will underestimate absolute numbers of calves although the relative number in different hunting seasons will be unaffected. Cohort analysis only uses information from the fall hunt and therefore the method does not account fully for productivity and recruitment changes as a result of variation in conception, fetal survival, birth success, early neonatal mortality (primarily due to black bear predation in Newfoundland) and survival to 6 months of age.

Caughley (1977) cautions against calculating the full life table from the age distribution without knowing the rate of mortality over the first 6 months of life (results used here and Boer 1988). The methods outlined by Taylor and Carley (1988:371, Census C) for calculating life tables for a population censused following breeding (fall hunt) require an estimate of natality (defined as production of embryos), adult female survival and survival of offspring to time of census. Although reasonable estimates of natality (Pimlott 1959) and adult female survival (Albright and Keith 1987) are available for Newfoundland, estimation of early juvenile survival is difficult to obtain and also shows great variation (Ballard 1992). Mortality rate of radio-collared calves in central Newfoundland were 0.30 to 0.50 for the first 6 months of



life (data on file; Albright and Keith 1987). Calf mortality (0.5 to 1.5 years of age) calculated for MMU 24 varied from 4 to 18% for females and 24-29% for males although these estimates do not include early hazard mortality (0-6 months).

Caughley (1977) recommends using life tables to discern the life history strategies of an animal. Age-specific survivorship adjusted for rate of increase, but not 'smoothed', allowed interpretation of the life history characteristics of young moose (0.5- to 3.5-year-olds). Using a smoothing procedure or calculating 1.5- and 2.5-year-old vulnerability to hunting (e.g. arcsine transformation; Simkin 1965 following Pimlott 1959; Newfoundland data on file) resulted in removal of the variation in mortality required to determine life histories. Unsmoothed survivorship estimates indicated differences in calf mortality between different time periods and a general higher mortality of 2.5- and 3.5-year-old female moose which coincides with age of first reproduction.

Calculations of vulnerability to hunting have shown variation between areas and temporally within the same area. Vulnerability factors calculated for 1.5- and 2.5-year-olds have varied from 2.5 and 1.3 respectively in Quebec (Crête et al. 1981) 1.8 and 2.1 for female moose in New Brunswick (Boer 1988), 1.4 and 1.2 in central Newfoundland (Fryxell et al. 1988:18) and in this study, 1.9 and 1.1 during 1969-71 and 1.7 and 1.3 during 1978-80 for female moose in central Newfoundland. Also Pimlott (1959:396) used 1.8 and 1.4 vulnerability factors for yearling moose in Newfoundland and Simkin (1965) calculated 1.6 for yearlings in Ontario. Comparing age-specific vulnerability per unit hunting effort calculated by Fryxell *et al.* (1988; Fig. 4) during a period of population decline (1966-73, mean= $1.7 \times 10^{-4}$ ) with results here from one of the same populations (MMU 24) during a phase of population increase (1981-85, mean= $5.4 \times 10^{-5}$ ; data on file) suggests that

overall vulnerability to hunting is 3 times greater for all age classes during the period of population decline. Also, the distribution of vulnerability among age classes changed with population increase and decrease. During the population increase, yearling and 2.5-year-olds were the most vulnerable to hunting. In contrast, the same population during a period of decline showed less of a difference in vulnerability between immature and mature age classes and generally a greater vulnerability of prime aged moose.

The life table results calculated from cohort analysis fit the expected differences in pattern between hunted and unhunted and increasing and decreasing moose populations (Fig. 8). Differences in survival occur between hunted and unhunted moose populations (Isle Royale; Peterson 1977), particularly in the decreased survival of mature animals with hunting. The moose population studied here (MMU 24, 1978-80) before entering a period of population growth showed a better survival of young moose (1.5- to 4.5-year-olds) relative to stationary hunted populations with wolves (northcentral Ontario; Snider 1976)

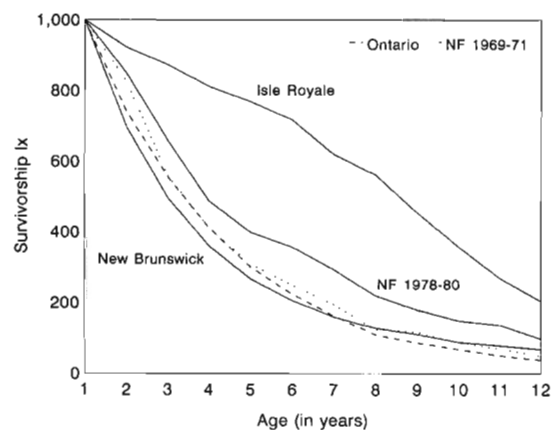


Fig. 8. Comparison of survivorship estimates for moose from New Brunswick (Boer 1988, n=422 females), Isle Royale (Peterson 1974, n=482), north central Ontario (Snider 1976, n=1360), and Newfoundland (MMU 24; 1969-71, n=366 females; 1978-80, n=295 females).

and without wolves (New Brunswick; Boer 1988)(MMU 24, 1969-71).

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