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The effect of age and sex selective harvest patterns for baleen whales

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ABSTRACT

The taking of calves and females accompanied by calves is prohibited under the original and current forms of the Schedule of the International Whaling Commission. Proposed regulations under the Revised Management Scheme would reduce catch limits according to the proportion of females in the landings when females make up more than one-half of the landings. The implications of regulations on age, sex and reproductive status were explored by examining the relative impacts of baleen whale harvests with different age, sex and female reproductive status selectivity patterns using a matrix population model. The effects of 11 harvest patterns with varying selectivity for females and calves were measured by computing the fraction of the population that would have to be killed to reduce the growth rate of the population model to zero and the corresponding fraction of the population that would be landed (harvest fraction). The harvest impact per whale landed was measured for each selectivity pattern by expressing the harvest fraction as a percentage of the value of that fraction for a harvest random across age, sex and reproductive status. The harvest impacts per whale landed of the 11 patterns ranged from 64% greater to 29% lower than a random harvest. The patterns with the lowest harvest impact per whale landed were the pattern consistent with the IWC Schedule of prohibiting harvest of calves and females accompanied by calves, and the pattern of harvesting only calves. The harvest selectivity patterns which increased the vulnerability of females had the greatest impact. Relative to the IWC's Revised Management Procedure, this increased female vulnerability was roughly compensated for by the decrease in catch limits as the proportion of females in the catches increased.

KEYWORDS: MODELLING; DIRECT CAPTURE; SUSTAINABILITY; MSY RATE; MANAGEMENT PROCEDURE; GROWTH; ATLANTIC OCEAN; NORTHERN HEMISPHERE; HUMPBACK WHALE; BALEEN WHALE

INTRODUCTION

Bartholomew (1974) argued that accurate knowledge of the natural history of an exploited population is needed for effective management. In particular, he argued that knowledge of the population's sex ratio and reproductive strategy should be used to set regulations for the sex, age and reproductive status composition of the harvest. He described the life history of northern fur seals (*Callorhinus ursinus*) as an ideal example because its polygynous mating system, spatial distribution by age and sex on rookeries and sexual dimorphism allow for easy selection of animals by sex, age and reproductive status in a land-based harvest. The history of the Pribilof Islands fur seal harvest clearly illustrates the utility of regulating sex and age composition of harvests. During the Russian harvest of fur seals in the mid-1800s, the prohibition against killing females allowed for some recovery (Busch, 1985). In addition, the harvest of 2-6 year old males which began in 1918 proved to be a successful management strategy (see Smith and Polacheck, 1981). These are contrasted by the mixed (and sometimes female dominated) pelagic harvest of the late 1800s and early 1900s that, combined with the land-based harvest, brought the species to near extinction (Busch, 1985).

The use of such sex, age and female reproductive status specificity in historical whaling is illustrated by the Oxford English Dictionary's (OED) (Simpson and Weiner, 1999) definition of 'bay whaling', where they draw on Ommaney's (1933, p.243) description of the New Zealand right whale (*Eubalaena australis*) fishery:

> Much of the right whale industry was carried on by the method known as 'bay whaling'. This branch of the fishery derived its name from the Right whales' habit of entering shallow bays and inlets of the coast for the purpose of giving birth to their calves.

The OED goes on to note the effect of bay whaling in New Zealand in terms of Clark (1947, p.32):

> The large numbers of fur seals and bay whales (i.e. the right whales) which once frequented the island are now virtually extinct.

There are a number of baleen whales where the composition of the harvest by sex, age and female reproductive status could be controlled by using differences in behaviour and spatial distribution. Humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*) calve in shallow waters like right whales (*Eubalaena* sp.), making differential harvests of calves and females accompanied by calves possible. Although less pronounced, the sex ratio of catches of common minke whales (*Balaenoptera acutorostrata*), Bryde's whales (*Balaenoptera edeni*) and sei whales (*Balaenoptera borealis*) have often shown a latitudinal gradient. For example, in recent decades the catches of common minke whales in the Northeastern Atlantic have favoured females (Øien *et al.*, 1987); the whales seem to segregate geographically and temporally by sex, with females occurring earlier and farther north around Greenland (Larsen and Øien, 1988) and in certain areas of the Barents Sea (Øien *et al.*, 1987) and the North Sea (Øien, 1988). Northeastern Atlantic common minke whales also show geographic segregation by age; for example, Vestfjorden is an area

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where calves spend much of the summer (Øien, 1988). In addition to baleen whales, sperm whales (*Physeter macrocephalus*) exhibit latitudinal segregation by sex, and historic harvests were predominantly male due to the whalers' preference for the larger animals (Best, 1974).

There also exists a potential for sex, age and reproductive status selectivity based on epimeletic (care-giving) behaviour of whales. For example, historical accounts of blue whales (*Balaenoptera musculus*) indicate that to harvest both whales in a male/female pair, the female should be killed first since the male will 'stand by' the female but not *vice versa* (Caldwell and Caldwell, 1966). In addition, historical descriptions of whaling include numerous accounts of whalers intentionally wounding or tethering a calf with the hope of luring the accompanying female within range. This has been reported for right, humpback and sperm whales (Caldwell and Caldwell, 1966). Due to the difficulties of harvesting humpback whales, whalers often targeted calves on the breeding/calving grounds due to the shallower locations and the ease of harvesting the accompanying female once the calf was tethered (Mitchell and Reeves, 1983; Reeves *et al.*, 2001). However, whalers were inconsistent as to whether the calf was landed or cut free. Price's analysis of the Bequia humpback fishery from 1958 to 1980 based on interviews with whalers indicated that in most years a single female and calf was harpooned (Price, 1981). On the other hand, whalers also reported avoiding harpooning gray whale calves until after killing the accompanying female because female gray whales were known to attack if their calf was harpooned, earning them the name of 'devil fish' (Caldwell and Caldwell, 1966).

From the beginning of the International Whaling Commission in 1946, the Schedule prohibited taking baleen whales both below certain lengths and calves or females accompanying calves (IWC, 1950). The value of such size, age, sex and female reproductive status selective regulations do not appear to have been initially debated within the Commission, but rather were assumed to be the right thing to do (and indeed were included in earlier international attempts to manage whaling – see Tønnessen and Johnsen, 1982). More recently, the IWC developed a Revised Management Procedure (RMP) to set commercial catch limits for baleen whale fisheries. The RMP was designed to be more robust to uncertainties than previous management approaches, and specific to the focus of this paper, included a provision to decrease catch limits when the proportion of females landed exceeds one-half (IWC, 1999). To explore the likely value of the prohibitions on harvesting calves and females accompanied by calves as specified in the IWC Schedule and the restrictions specified in the RMP, some calculations are presented of the relative impact of a range of harvest selectivity patterns in terms of the proportions of the population killed and landed and the impact per whale landed relative to a random harvest.

METHODS

Eleven harvest selectivity patterns were considered (Table 1) with males age 1 and older, females accompanied by calves (hereafter referred to as cows), females age 1 and older without calves (hereafter referred to as females) and both male and female calves vulnerable to harvest or protected by geographic segregation, behavioural differences or regulations. In addition, in patterns which harvest both cows and calves, the harvests were either linked so that both were taken if one was, or made independent so that either one or both could be taken randomly. Following Mitchell and Reeves (1983), it was assumed that orphaned calves died in all cases, as suggested by their rapid growth over the first months of life (Stevick, 1999) and their extended nursing period (Clapham *et al.*, 1999). For selectivity patterns involving orphaned calves, the indirect mortality of calves was accounted for by increasing the relative vulnerability of calves proportional to the harvest mortality of cows.

Patterns 1-7 are implementable in baleen whale populations. Patterns 8-11 parallel Patterns 1-4, but are not generally implementable in baleen whale populations because of a lack of sexual dimorphism. However, Patterns 8-11 represent extremes of the geographic segregation by sex which is seen in some populations; for example, common minke whales in the Barents Sea. Pattern 3 produces direct harvest mortality that is random across age, sex and reproductive status but also includes additional indirect mortality of orphaned calves. In contrast, Pattern 2 produces random harvest mortality and is numerically random, but would not be random in practice due to the association of cows and calves.

The differences in the effect of these harvest selectivity patterns were investigated using a linear, density-independent, age, stage and sex structured matrix population model (Caswell, 2001). Here, model A, includes 100 age-sex-stage classes and is shown in Fig. 1. C_F and C_M

Table 1

Definition of 11 harvest selectivity patterns targeting All individuals, Females only or Calves only with exceptions as noted. Females, cows, calves and adult males are either Vulnerable (V) or Protected (P) by geographic segregation, behavioural differences or regulations. Harvest of calves is either linked to or independent of harvest of cows. The existence of orphaned calves varies, and when present are assumed to die.

Pattern #	Harvest Selectivity Pattern	Females (1+)		Calves		Males (1+)
		Females	Cows	Males & Females	Orphans	
1	All: Protecting Cows and Calves	V	P	P	No	V
2	All: Harvest of Cows and Calves Linked	V	V	V	No	V
3	All: Harvest of Cows and Calves Independent	V	V	V	Yes	V
4	All: Protecting Calves	V	V	P	Yes	V
5	Calves Only	P	P	V	No	P
6	Female: Cows and Calves Only	P	V	V	No	P
7	Female: Cows Only	P	V	P	Yes	P
8	Female: Protecting Cows and Calves	V	P	P	No	P
9	Female: Harvest of Cows and Calves Linked	V	V	V	No	P
10	Female: Harvest of Cows and Calves Independent	V	V	V	Yes	P
11	Female: Protecting Calves	V	V	P	Yes	P

denote the number of female and male calves, age 0 to one year, respectively. X_M denotes the numbers of males age X, and X_F and X_L denote the number of females and cows, respectively. Animals are denoted age X from calendar age X to X+1, where X runs from one to 34. The survival rates between age classes in Fig. 1 are denoted P_C for age 0-1, P_J for age 1-2 and P for females age 2-4 and for males age 1-34. The transfers to calving states are denoted R_i for animals in non-calving states and R_{iL} for animals in calving states. P_{iL} denotes the rate of transfer from calving to non-calving states, and P_i denotes the rate between non-calving states. A 50:50 sex ratio at birth was assumed so that the fecundity rates for females producing female calves were the same as the fecundity rates for females producing male calves. Survival rates for females and males were assumed to be the same, and all animals die before age 35. For simplicity, Barlow and Clapham's (1997) density-independent, female-only, age-structured population model, and the life history parameters they estimated for humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine were used as a basis to determine parameter values for the model in this paper.

The yearly time step for Barlow and Clapham's (1997) matrix model began roughly six months after the calving season, and the first age class was 0.5 to 1.5 years of age. To model an instantaneous harvest, which may include calves during the calving season, their yearly time step was shifted back six months, making the first age class from birth to one year. Since the survival rate from birth to 0.5 years of age (S_0) was not estimated by Barlow and Clapham (1997), two values were explored: the square root of their non-calf survival and the square root of their calf survival. Both values produced similar results, and results for the square root of their non-calf survival are given here.

Due to the shift in the time step, three stage-classified survival rates (P_C, P_J, P) were used rather than the two ($P_{0.5}$, $P_{1.5}$) used by Barlow and Clapham (1997, table 2):

survival from new born to age 1:

$$P_C = S_0 * \text{sqrt}(P_{0.5}) = 0.898$$

survival from age 1-2:

$$P_J = \text{sqrt}(P_{0.5}) * \text{sqrt}(P_{1.5}) = 0.917$$

survival for all other age classes: $P = 0.960$

Since females of age five and above were divided into classes with (cows) and without (females) accompanying calves, transition probabilities into these age classes were a function of Barlow and Clapham's (1997) fecundity rates ($F_{4.5:34.5}$) and their estimated probability of a one year calving interval ($C_1 = 0.043$) as well as the adult survival rate (P). Barlow and Clapham's (1997) fecundity rates ($F_{4.5:34.5}$) were for a female-only matrix and were multiplied by two, assuming the calf sex ratio is at parity, for incorporation into the current model. These rates also included the survival rate for the first six months of life (S_0) and were divided by this rate (($F_{i.5}/S_0$) for i = 4.5 to 34.5). Thus, the transitions from an age 4 female to an age 5 cow (R_4) or female (P_4) were defined as:

age 4 female to age 5 cow: $R_4 = P * (2F_{4.5}/S_0)$
age 4 female to age 5 female: $P_4 = P * (1 - (2F_{4.5}/S_0))$

Incorporating the estimated probability of a one year calving interval along with the estimated fecundities is slightly more difficult. First, because Barlow and Clapham's (1997) estimated rate included survival over the year time step, it was divided by the adult survival rate (C_1/P). Thus, the transitions from cow age classes were constrained by the one year calving interval as follows:

age i cow to age (i+1) cow:

$$R_{iL} = P\,(C_1/P) = C_1 \quad \text{for } i \text{ 5 to 33}$$

age i cow to age (i+1) female:

$$P_{iL} = P\,(1 - (C_1/P)) \quad \text{for } i \text{ 5 to 33}$$

Second, the transition probabilities from the female stages to the cow stages for ages five and above (R_i = for i 5 to 33), were increased by a factor, a, such that the resulting

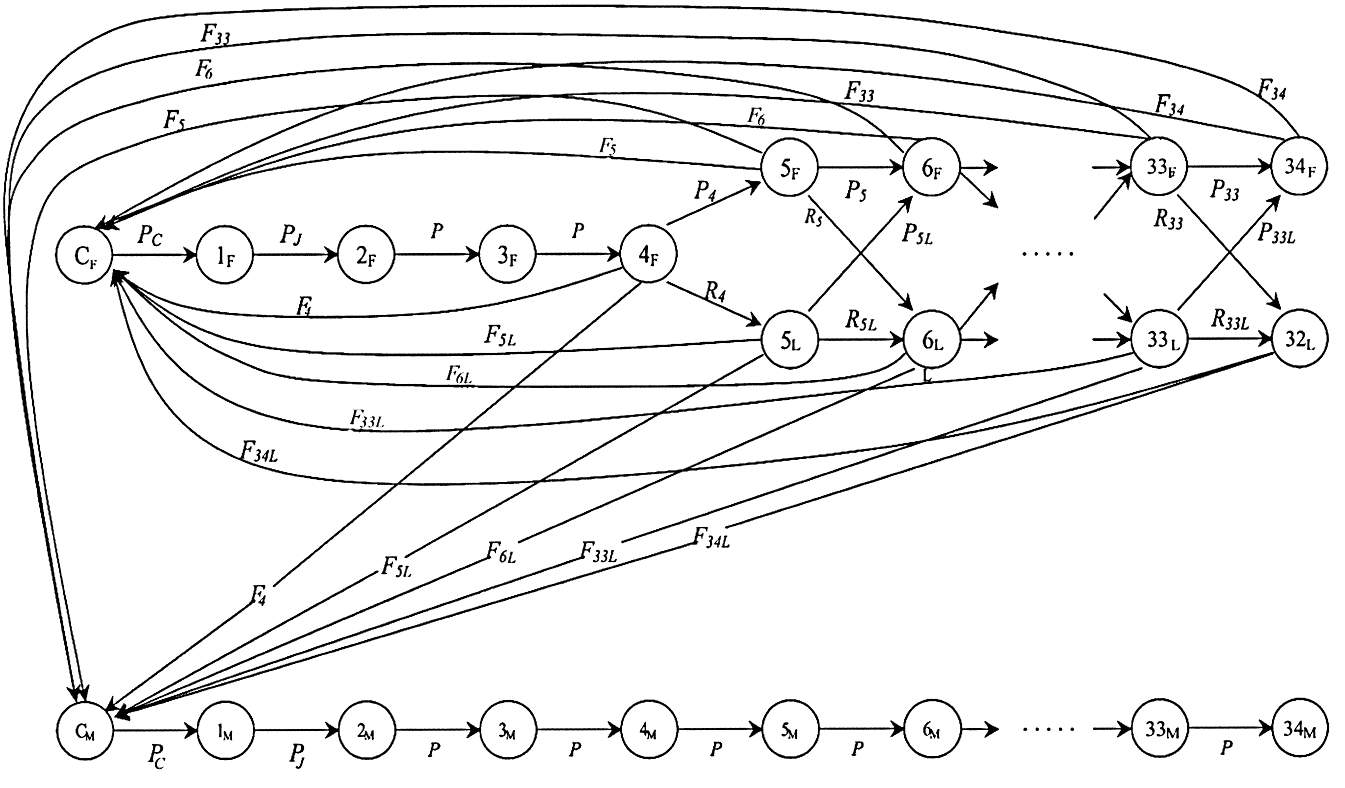

Fig. 1. Life cycle graph for the age, sex- and stage-structured model of a baleen whale population based on Barlow and Clapham's (1997) female-only, age-structured model of the Gulf of Maine portion of the North Atlantic humpback whale population.

dominant eigenvalue (λ) equalled the dominant eigenvalue from Barlow and Clapham's (1997) female-only, age-structured model ($\lambda = 1.065$). The value of the factor a depends on the transition probabilities R_{iL} and R_i as well as the numbers of animals in the female and cow states ($a = 1 + (1 - (R_{iL} / R_i)) * (X_L / X_F)$), and so cannot be solved for analytically. Thus, the transitions from these female classes were defined as follows:

age i female to age (i+1) cow:

$$R_i = P * (2aF_{i.5}/S_0) \qquad \text{for } i \text{ 5 to 33}$$

age i female to age (i+1) female:

$$P_i = P * (1 - (2aF_{i.5}/S_0)) \qquad \text{for } i \text{ 5 to 33}$$

Finally, fecundity rates were equal for females producing male and females calves and were defined as half of the R_i and R_{iL} values:

fecundity for age four females:

$$F_4 = (R_4)/2 = P * (F_{4.5}/S_0)$$

fecundity for age i cows:

$$F_{iL} = (R_{iL})/2 = (P\,(C_1/P))/2 = C_1/2 \qquad \text{for } i \text{ 5 to 33}$$

fecundity for age i females:

$$F_i = (R_i)/2 = P * (aF_{i.5}/S_0) \qquad \text{for } i \text{ 5 to 33}$$

The model assumed that there are always enough males to fertilise all the females. Thus, the male contribution to fecundity was ignored; this limits evaluation of complex selectivity patterns involving males.

A diagonal matrix (ψ_h) of the relative vulnerability of each age-sex-stage class to direct harvest mortality was constructed for each harvest pattern (h). The relative vulnerabilities were zero or one indicating whether the class was vulnerable to harvest. For the indirect harvest mortality of orphaned calves, an additional fractional vulnerability was added to the calf classes to account for the number of cows harvested without the calf they were accompanying. This harvest mortality matrix was multiplied by a scalar (α) and the product subtracted from the identity matrix (I) to create a harvest survival matrix, $S = (I\text{-}\alpha\psi_{\boldsymbol{h}})$, which defined the probability of surviving the harvest for each class.

Energetic costs of lactation are likely greater than the energetic costs of gestation for large whales (Boyd *et al.*, 1999). Thus, if a calf is harvested on the mating grounds without its accompanying cow (as in Patterns 3, 5 and 10), the cow is likely to have a higher probability of producing a calf in the following year than if its calf had not been lost. To model this dynamic, a third projection matrix, T, was created which transferred cows to the corresponding female class in the same year. For Patterns other than numbers 3, 5 and 10, T is the identity matrix (I). For Patterns 3, 5 and 10, T is the same as the identity matrix, but with $T[iF, iL]$ equal to the proportion of cows which lost their calves and $T[iL, iL]$ equal to $1 - T[iF, iL]$. For Patterns 3, 5 and 10, the effect of this increase in fecundity was explored by defining T as the identity matrix; thus turning off this dynamic.

Combining the three projection matrices defined above results in the following:

$$n_{t+1} = (TSA)n_t = (T(I\text{-}\alpha\psi_{\boldsymbol{h}})A)n_t$$

where n is the age-sex-stage distribution vector. The value of α was iteratively determined such that the dominant eigenvalue of TSA equalled one.

The fraction of the population killed due to the harvest (K), which included landed whales and orphaned calves, was calculated, $\sum_{i=1}^{100} (\alpha\psi_{\boldsymbol{h}}w)_{\boldsymbol{i}}$, where w was a column vector representing the stable age distribution of the 100 age-sex-stage classes and was scaled to sum to one. The harvest fraction, H, was the fraction of the population landed and was computed as K less the orphaned calves as a fraction of the total population size.

For a strictly random harvest, H would be obtained by setting all the values of ψ to unity. Then, the value of α that satisfied the equation would be $1\text{-}1/\lambda = 0.061$. Harvest patterns that result in a lower harvest fraction have a correspondingly greater effect on the population per whale landed. The harvest impact ($\%H$) was expressed as the percentage difference between $H = 0.061$ for a strictly random harvest value and H for each harvest selectivity pattern. A positive value denotes a proportionately greater impact per whales landed, while a value of zero indicates that the harvest pattern has an impact equivalent to a strictly random harvest. Finally, the RMP multiplicative adjustment was computed; this reduces the catch limit when the majority of the landed catch is female. When the proportion of females in the landed catch is 0.5 or less, there is no adjustment and the catch multiplier equals one. When the proportion of females is greater than 0.5, the catch multiplier equals 0.5 divided by the female proportion in the landed catch.

RESULTS

The computed harvest fractions and associated statistics are shown for the 11 selectivity patterns in Table 2. The harvest fractions ranged from 0.022 for the selectivity pattern that allowed only cows to be harvested (Pattern 7) to 0.079 for the pattern that allowed only calves to be harvested (Pattern 5). The harvest impact of the selectivity patterns ranged from 64.4% more to 28.7% less than a strictly random harvest. The proportion of the population killed under the 11 harvest patterns differed from the harvest fractions because of the assumed death of orphaned calves, and ranged from 0.029 to 0.079. Selectivity Pattern 2, where the harvest of cows and calves were linked, had an impact that was numerically identical with a strictly random harvest, as expected. Both harvest selectivity patterns with the greatest harvest impacts per landed whales (Patterns 7 and 11) also had the highest level of additional calf mortality due to orphaned calves.

The harvest selectivity patterns targeting females had substantially greater impact per landed whales than any of those patterns where all animals or calves were targeted. The patterns where only calves were harvested (Pattern 5) and where both cows and calves were protected (Pattern 1), as specified in the IWC Schedule, had the lowest impacts.

The sex composition of the landed animals ranged from 42.8% to 100% female. The RMP multiplicative catch limit adjustments implied by these sex ratios ranged from 1.00 to 0.50 and resulted in decreases in the catches of up to one-half. The RMP adjustments decreased the catch limit more for those selectivity patterns with greater harvest impacts per whale landed.

The computed harvest fractions and associated statistics are shown for Patterns 3, 5 and 10 in Table 3 when the cows which lost their calves do not experience an increase in the probability of reproducing in the next year. Differences between this scenario and when there was an increase in fecundity were negligible for Pattern 10 when females were harvested randomly with cows and calves harvested independently. For Pattern 3 when whales were harvested randomly with cows and calves independent, lack of an increase in fecundity reduced the harvest fraction (H) by 1.7%. However, there was a significant effect for Pattern 5 where only calves were harvested which decreased H by

Table 2

The harvest patterns in order of increasing harvest fractions (*H*) are presented with the harvest impacts per whale landed (*%H*), the fraction of the population killed (*K,* landed whales plus orphaned calves), the percentage of the animals killed and landed that were female and the RMP multiplicative adjustment to the catch limits implied by the percentage of females landed.

Pattern #	Harvest Selectivity Pattern	*H*	% *H*	*K*	% Female Killed	% Female Landed	RMP Adj.
7	Female: Cows Only	0.022	64.4	0.044	75.0	100.0	0.50
11	Female: Protecting Calves	0.027	55.6	0.034	89.9	100.0	0.50
8	Female: Protecting Cows and Calves	0.029	53.0	0.029	100.0	100.0	0.50
10	Female: Harvest of Cows and Calves Independent	0.032	47.1	0.038	83.6	89.9	0.56
9	Female: Harvest of Cows and Calves Linked	0.034	44.4	0.034	89.9	89.9	0.56
6	Female: Cows and Calves Only	0.044	28.7	0.044	75.0	75.0	0.67
4	All: Protecting Calves	0.054	11.2	0.061	50.0	50.0	1.00
3	All: Harvest of Cows and Calves Independent	0.058	4.8	0.064	50.0	50.0	1.00
2	All: Harvest of Cows and Calves Linked	0.061	0.0	0.061	50.0	50.0	1.00
1	All: Protecting Cows and Calves	0.067	-9.9	0.067	42.8	42.8	1.00
5	Calves Only	0.079	-28.7	0.079	50.0	50.0	1.00

Table 3

Harvest fractions (*H*), harvest impacts per whale landed (*%H*), the fraction of the population killed (*K*, landed whales plus orphaned calves), the percentage of the animals killed and landed that were female and the RMP multiplicative adjustment to the catch limits implied by the percentage of females landed for Patterns 3, 5 and 10 when the increase in fecundity due to the loss of a calf is not modelled.

Pattern #	Harvest Selectivity Pattern	*H*	% *H*	*K*	% Female Killed	% Female Landed	RMP Adj.
10	Female: Harvest of Cows and Calves Independent	0.032	48.2	0.038	83.6	89.9	0.56
3	All: Harvest of Cows and Calves Independent	0.057	6.9	0.063	50.0	50.0	1.00
5	Calves Only	0.068	-10.6	0.068	50.0	50.0	1.00

13.9%. The decrease for Pattern 5, resulted in an *H* of 0.068 which is only 1.5% greater than Pattern 1 where both cows and calves were protected.

DISCUSSION

The range in harvest impacts for the harvest selectivity patterns considered was large, and the proportional adjustment based on sex ratio in the RMP roughly compensated for such differences. The selectivity pattern corresponding to the IWC Schedule prohibition on the harvest of calves and females accompanied by calves (Pattern 1) had one of the two lowest impacts of all the selectivity patterns, which was a 9.9% lower impact than the strictly random harvest. The most risk adverse pattern explored was the harvest of calves (Pattern 5). However, when the probability of a cow reproducing in the next year was not increased, the impact of harvesting only calves was only 1.5% lower than the selectivity pattern protecting cows and calves. The selectivity patterns targeting females (Patterns 6-11) had the highest impacts, indicating the need to protect females. However, because of the lack of strong sexual dimorphism in baleen whale species, the only practical way to protect females is to protect animals which are accompanied by calves. These results suggest that, where operational procedures allow, consideration of harvest selectivity patterns should be given in the development of other management procedures, such as that being developed for aboriginal whaling (IWC, 2002).

The present analysis utilised a simple population model for one baleen whale species. Results would be different for other baleen whale species because of different age-specific fecundity and survival rates, and the relative order of the results might change if there are sufficient differences in the pattern of the age-specific reproductive values. Further, this simple model did not allow for any effects of males on the population reproductive rates. Thus, the calculations of impact per whale landed for harvest selectivity patterns that included males could be underestimates, if the abundance of males did have an effect on reproduction; then the relative order of harvest impacts could change. Although this would not be expected for baleen whales, it is more likely for odontocetes, especially those with strong social structures (e.g. sperm whales). Finally, the simple model is density-independent. Adding density-dependence to the model would change the absolute values of the results, but the effect of these changes on the relative pattern of the results is unclear. If harvest selectivity patterns are to be incorporated into management procedures, the sensitivity of the relative rankings to the life history parameters for other baleen whales and to density-dependence should be explored.

However, other aspects of the biology of whales not included here could be more significant. For example, this analysis does not address either the effect of size-specific harvest regulations, as also specified in the IWC’s Schedule, or the question of yield in weight. Such analyses would require incorporating a model of animal growth rate, both in length for the former question and in weight for the latter question. The question of yield in weight versus number could be important, especially for harvest patterns that take large numbers of calves. For example, the selectivity pattern which harvested only calves had the lowest impact, but because many whales grow rapidly in length over their first year of life (e.g. humpbacks more than double in length according to Stevick, 1999) and because weight tends to increase with the cube of length (e.g. Lockyer, 1979), the catch in weight using this harvest pattern would likely be much lower than that of any other pattern considered.

Finally, the high harvest impact of female and calf directed harvests should be taken into account in reconstructions of historical abundance from catch records. The historical use of bay whaling and epimeletic behaviour has the potential to result in harvest patterns focused on cows and, either directly or indirectly, on calves. The greater impact of such harvests, as shown here, including the likely death of orphaned calves and the lower oil yield from calves, would all tend to result in an underestimate of the actual numerical removals. Such downward biases were, for example, one explanation suggested for the apparent inconsistencies in the earlier assessment of gray whales (IWC, 1993; Butterworth *et al.*, 2002).

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