

Use of Pup Counts in Indexing Population Changes in Pinnipeds

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A series of population simulations were used to test the accuracy of estimating the discrete rates of population change (RPC) from annual pup counts. The simulations indicate that pup counts can give a biased estimate of RPC, and that the magnitude and direction of bias depends on which life history parameters are density dependent and on the maximum rate of population change. In general, if pre-census pup survival is density dependent the estimated RPC using pup counts is too low. If post-census pup survival is density dependent, the estimated RPC is too high. If adult survival is density dependent, there is very little bias in the estimate. The results indicate that pup counts can be reliable indicators of population growth, but caution should be used in interpreting the results unless density feedback mechanisms have been identified.

Les auteurs utilisent une série de simulations démographiques pour vérifier la précision des estimations des taux discrets de variation d'une population (TVP) effectuées à partir des recensements annuels de nouveaux-nés. Les simulations révèlent que ces dénombrements peuvent fournir une estimation biaisée du TVP et que les paramètres vitaux dépendant de la densité et le taux maximum de variation d'une population influent sur l'ampleur et la direction de la tendance. En général, le TVP calculé en fonction des recensements de nouveaux-nés est trop faible si la survie de ceux-ci avant le dénombrement dépend de la densité. Par contre, le TVP est trop élevé si la survie après le dénombrement dépend de la densité. L'estimation est très peu biaisée si la survie des adultes dépend de la densité. Les résultats révèlent que le recensement des nouveaux-nés constitue un indice fiable de la croissance démographique; on doit toutefois interpréter les résultats avec prudence à moins d'avoir trouvé des mécanismes rétroactifs liés à la densité.

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For many species of pinnipeds, annual counts of pups provide the best available censusing method. These counts are used to estimate the rate of population change (RPC) by comparing percentage change in counts from year to year as in the case of California sea lions, *Zalophus californianus* (DeMaster et al. 1982); northern elephant seals, *Mirounga angustirostris* (Antonelis et al. 1981; Cooper and Stewart 1983); and Antarctic fur seal, *Callorhinus ursinus* (Chapman 1961; Eberhardt 1981; Fowler 1982). Recently, methods that rely on pup counts have also been developed to estimate whether the population is above or below the maximum net productivity level (MNPL), the point where the net growth rate of the population is maximized (DeMaster et al. 1982).

In this paper, an age structured simulation model is used to evaluate the accuracy of predicting population trends from a time series of pup censuses. We have assumed that the sex ratio of pups at birth does not change with population size, and therefore, models that utilize female pups only are suitable for predicting the direction and magnitude of bias in using pup counts to estimate the RPC. Possibly, biases in estimating RPC's with pup counts exist, and these biases may differ under different life history scenarios. If we can understand these biases and their causes, we can increase the predictive powers of the pup counts, or at least be aware of the limits when using pup counts to manage resources.

In the simulations we use life history parameters that are

representative of most populations of pinnipeds (Eberhardt and Siniff 1977). The number of individuals in the first age class (1) is defined as the number of female pups at the time the census is made. In developing the model, three mechanisms of density dependence were investigated: density-dependent post-census pup survivorship, dependent on the number of pups in the population; density-dependent pre-census survivorship, dependent on the number of births in the population; and density-dependent adult survivorship, dependent on the number of non-pups in the population. Both types of pup survival are considered to be the most likely types of density dependence in the wild (Eberhardt 1977). Adult survival was selected because the population growth rate is most sensitive to its change (Goodman 1978, 1984). Fecundity and age at maturation were not investigated in depth because, as will be shown, they would provide the same sort of bias as does density dependence in pre-census pup survival. For simplicity, all types of density dependence were treated as linear functions.

Methods

Our age structure population models were written in the FORTRAN programming language. Initial parameters were selected to produce either an 8% or a 4% growth rate. These RPC's were considered reasonable for recovering populations of pinnipeds (Eberhardt and Siniff 1977). The model was

TABLE 1. Selected pinniped life history parameter values of given age classes (*denotes minimum values).

	Weddell seal ^a	Antarctic fur seal ^b	NW Atlantic harp seal ^c	Gray seal ^d
Annual survival rates of given age classes				
Birth-weaning		0.85		0.73
Weaning - age 1				0.90
Birth - age 1	0.76-0.82*	0.76-0.92	0.50-0.97	
Juvenile	0.48-0.50*	0.95		0.93
Adult	0.66-0.76*	0.92-0.95	0.90	0.94
Annual fecundity rates of given age classes				
Age 3	0.27	0.28		
Age 4	0.27	0.38		0.08
Age 5	0.27	0.42		0.28
Age 6 and older	0.40	0.45	0.46	0.42

^aStirling (1971).
^bPayne (1977, 1979).
^cLett et al. (1981).
^dHarwood (1981).

designed to handle a population with 25 year-age classes (Eberhardt and Siniff 1977). The probability of surviving through age class 25 was set at 0. A sample of life history parameter values reported for pinnipeds is listed in Table 1. The range of life history values used in the simulations is listed in Table 2.

The age classes followed a trajectory based on the following equations:

$$N_{1,t+1} = \sum_{x=1}^{25} N_{x,t} \cdot M_x$$

$$N_{x+1,t+1} = N_{x,t} \cdot P_x \quad x = 1, 2, \dots, 24$$

where P_x = the probability of survival from census at age x until census at age $x + 1$ and M_x = the probability of a female age x at year t having a female offspring at year $t + 1$.

For each case, the population level was initially set at 25% of the carrying capacity and allowed to continue to equilibrium. The RPC at time t was estimated by calculating

$$\text{RPC (total population)} = N_t / N_{t-1}$$

$$\text{RPC (pups)} = N_{\text{pups}_t} / N_{\text{pups}_{t-1}}$$

The net population change was calculated as

$$\text{Delta (total population)} = N_t - N_{t-1}$$

$$\text{Delta (pups)} = N_{\text{pups}_t} - N_{\text{pups}_{t-1}}$$

The bias of estimating the RPC by the pup growth rate was calculated as

$$\text{Bias} = \frac{\text{RPC (pups)} - \text{RPC (total population)}}{\text{RPC (total population)}}$$

The three types of density dependence were tested with initial RPC's of 8 and 4% to see if changing the rate at which equilibrium is achieved changes the bias. Density-dependent post-census survival was calculated in the following way:

$$P(1, t) = P(1, k) + [P(1, i) - P(1, k)] \times \left[1 - \frac{N(1, t) - N(1, i)}{N(1, k) - N(1, i)} \right]$$

TABLE 2. Parameter values used in density dependence simulations.

	Model 1 (post-census pup survival)	Model 2 (pre-census pup survival)	Model 3 (adult survival)
Annual survival rates of given age classes			
Birth-census	1.00	0.40-1.00	1.00
Census - age 2	0.30-0.75	0.75	0.75
Age 2	0.85	0.85	0.85
Age 3	0.90	0.90	0.90
Age 4 - age 24	0.94	0.94	0.84-0.94
Annual fecundity rates of given age classes			
Age 4	0.10	0.04-0.10	0.09-0.10
Age 5	0.20	0.08-0.20	0.18-0.20
Age 6	0.30	0.12-0.30	0.27-0.30
Age 7 - age 24	0.40	0.16-0.40	0.36-0.40

where $P(1, t)$ = survival of age class 1 at time t , $N(1, t)$ = population of age class 1 at time t , k = time at which population is at carrying capacity, and i = time at which population is initially started.

Density-dependent pre-census survival was calculated in the following way:

$$G(t) = G(k) + [G(i) - G(k)] \cdot \left[1 - \frac{N(B, t) - N(B, i)}{N(B, k) - N(B, i)} \right]$$

where $G(t)$ = pre-census survival rate at time t and $N(B, t)$ = number of births at time t calculated by

$$N(B, t) = \sum_{x=1}^{25} F(x) \cdot N(x, t) \cdot P(x)$$

where $F(x)$ = fecundity for age class x conditional on female survival, $N(x, t)$ = population in age class x at time t , and $P(x)$ = survival of age class x .

Once $G(t)$ was calculated, it was used in the following equation to calculate the effective fecundity (Goodman 1984) for

TABLE 3. Results of density dependence simulations with three models. (RPC = rate of population change, MNPL = maximum net productivity level, EPL = equilibrium population level).

	Model 1 (post-census pup survival) initial growth rate		Model 2 (pre-census pup survival) initial growth rate		Model 3 (adult survival) initial growth rate	
	8%	4%	8%	4%	8%	4%
	Percentage of EPL at true MNPL	68	58	67	58	52
Percentage of EPL at predicted MNPL	78	63	48	47	49	50
Percentage of EPL at predicted MNPL minus percentage of EPL at true MNPL	10	5	-19	-11	-3	-2
Bias in RPC at true MNPL	0.009	0.002	-0.018	-0.005	-0.002	-0.001
Largest bias in RPC	0.011	0.002	-0.027	-0.006	-0.002	-0.001
Time lag in years between true MNPL and predicted MNPL	-3	-3	+6	+7	+1	+1
Largest time lag in years	-4	-4	+15	+12	+3	+1

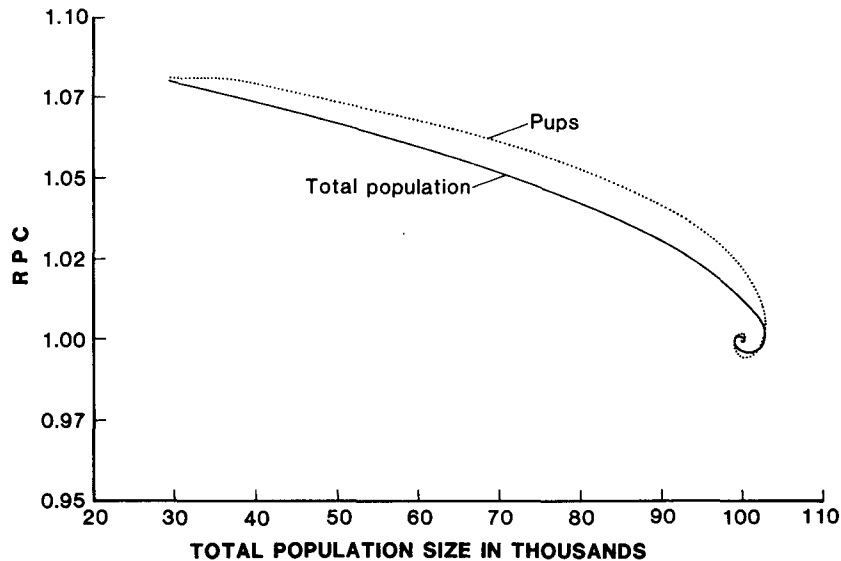


FIG. 1. Relationship of the RPC and the total population size when post-census pup survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

use in the Leslie matrix:

$$M(x, t) = F(x) \cdot P(x) \cdot G(t)$$

where $M(x, t)$ = effective fecundity of age class x at time t .

Density-dependent adult survival was calculated in the following way:

$$P(A, t) = P(A, k) + [P(A, i) - P(A, k)] \times \left[1 - \frac{N(NP, t) - N(NP, i)}{N(NP, k) - N(NP, i)} \right]$$

where $P(A, t)$ = survival of adult age classes at time t (adult age classes are 4 through 25) and $N(NP, t)$ = number of non-pups in the population at time t calculated by

$$N(NP, t) = \sum_{x=2}^{25} N(x, t)$$

The adult survival rate at time t was used to calculate $M(x, t)$ at each iteration of the simulation.

Results

Results of the six different simulations indicate that biases in estimating the RPC depends on the type of density dependence and the magnitude of the maximum RPC. Additionally, biases found in estimating the time when the MNPL is reached also depend on the type of density dependence and the magnitude of the RPC. Simulation results are discussed in three sections: density-dependent post-census pup survival (model 1), density-dependent pre-census pup survival (model 2), and density-dependent adult survival (model 3). A summary of results is provided in Table 3.

Density-Dependent Post-Census Pup Survival

When post-census pup survival is density dependent, the total population reacts more quickly than the pup population to the effects of the density dependence. Density-dependent post-census pup survival affects the number of individuals in the first

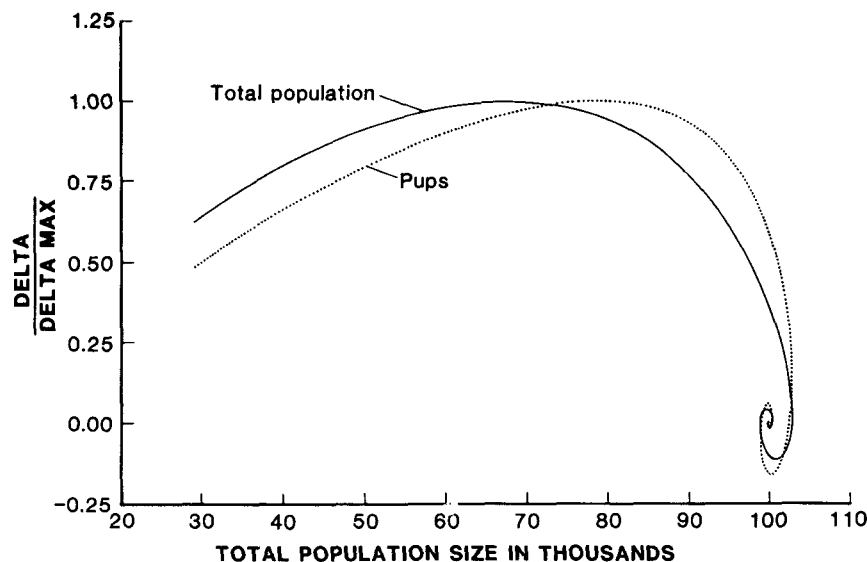


FIG. 2. Relationship of predicted and true production curves to total population size when post-census pup survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

age class that survive to the second age class. Therefore, any drop in survivability immediately acts on the number of individuals entering the second age class and, in doing so, acts on the total population as well. The first age class does not respond to the effects of the density dependence until the cohort that originally entered the second age class becomes capable of reproducing. Thus, the dynamics of the pup population lag behind the total population as the RPC declines (Fig. 1).

For the same reason, the production curve determined by pup counts lags behind the production curve of the total population (compared by measuring delta/delta max in both curves) (Fig. 2). In this case, delta max is the maximum change in the production curve.

In both the 8 and 4% growth simulations, the RPC of the pups lags behind the RPC of the total population. The time lag between the pups and the total population is the same in both simulations. However, the high initial RPC simulated population grows much larger during the time lag than the low initial RPC population. The difference between the true MNPL and the MNPL as indicated by the pup counts is larger for those simulations using higher initial rates of increase.

Density-Dependent Pre-Census Survival

In the case of density-dependent pre-census survival, the bias is in the opposite direction from that in the case of density-dependent post-census pup survival. Once again this bias can be explained to be a result of density dependence acting on a specific part of the age structure. Any decrease in pre-census survival immediately acts on the population in the first age class. The effect of this decreased survival is an immediate decline in the RPC of the number of pups. The RPC of the total population also declines but to a lesser degree, due to the buffering of the 24 unaffected age classes (Fig. 3). Once again the production curves also show this time lag (Fig. 4).

The 4% initial growth simulation again shows the same direction of bias as found in the 8% simulation. The magnitude

of the bias in terms of time lags in the two production curves is similar, although in the 4% simulation it is slightly less than in the 8% simulation. This translates into a smaller population difference between the two peaks of the production curves, due again to the lower population increase in the same amount of time as seen in the simulation with 4% initial growth.

Density-Dependent Adult Survival

In the case of density-dependent adult survival, the decreasing survival rate affects both the adult age classes (5–25) and the pup age class (1). Therefore, a much smaller bias is created. This is because adult survival affects the number of pups entering the first age class the following year. Any given decrease in adult survival affects all age classes other than the juveniles (ages 2, 3, and 4) in the next time step. Having three age classes with unchanging survival rates in turn causes the total population's RPC to decline slightly behind the pup population's RPC (Fig. 5). The magnitude of this bias is much smaller than is seen in the previous two types of density dependence. Once again, the production curves follow this same pattern (Fig. 6).

Discussion

The simulations we described indicate that the type of density dependence affecting a population can bias estimates of RPC based on pup counts. For example, estimates of replacement yield and MNPL that rely on pup counts are probably biased. The direction of bias, however, can be inferred if the density-dependent mechanisms are known.

Managers should be aware of these biases and should incorporate them in the development of management policy. The following comparisons of density dependence found in the wild and its effects on estimating population changes using simulations will, hopefully, illustrate this point.

To infer a direction of bias in the use of pup counts to estimate

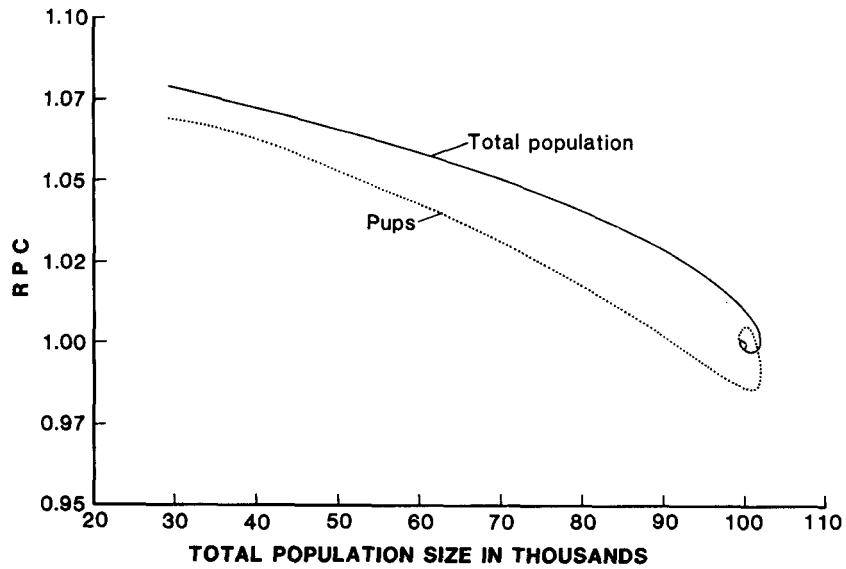


FIG. 3. Relationship of the RPC and the total population size when pre-census pup survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

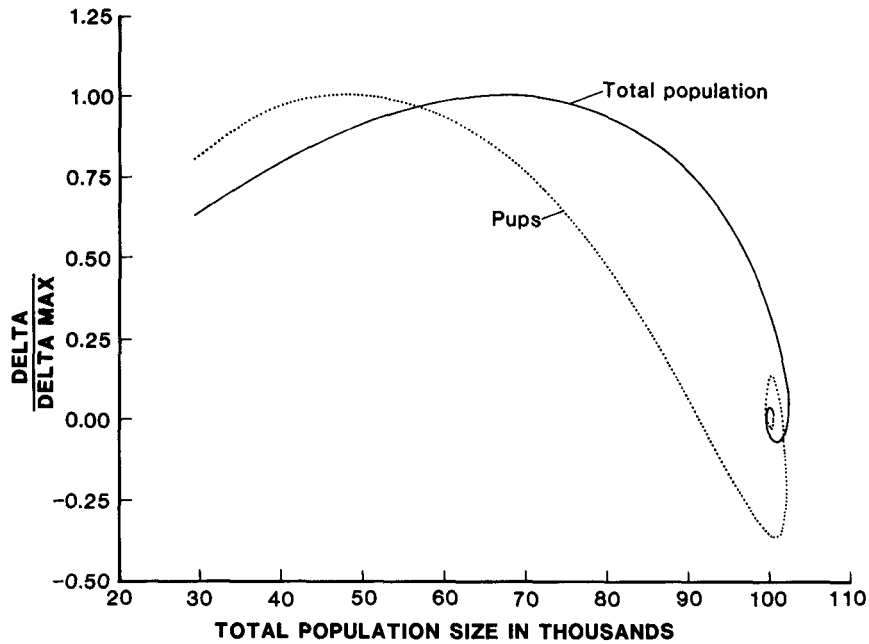


FIG. 4. Relationship of predicted and true production curves to total population size when pre-census pup survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

the RPC, it is reasonable to look at the available data on what parameters are density dependent in pinnipeds. Eberhardt (1977) suggested that pup survival (both pre- and post-census) is more likely to be density dependent than either adult fecundity or adult survival. Adult fecundity would cause the same direction of bias as pre-census pup survival, since both act on the first age class. However, because pre-census pup survival is

more likely to be density dependent than adult fecundity (Eberhardt 1977), it was chosen for modeling.

Density-dependent pup production has been described in many pinniped species (for summary see Fowler et al. 1980). For gray seal, *Halichoerus grypus*, this mechanism has been described to act on pups between the age of birth and weaning (Coulson and Hickling 1964; Bonner 1975; Harwood 1981).

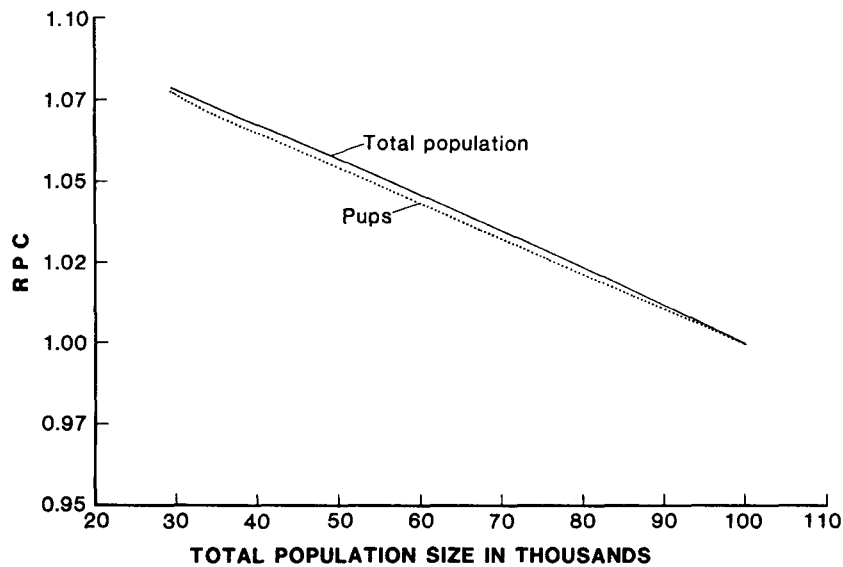


FIG. 5. Relationship of the RPC and the total population size when adult survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

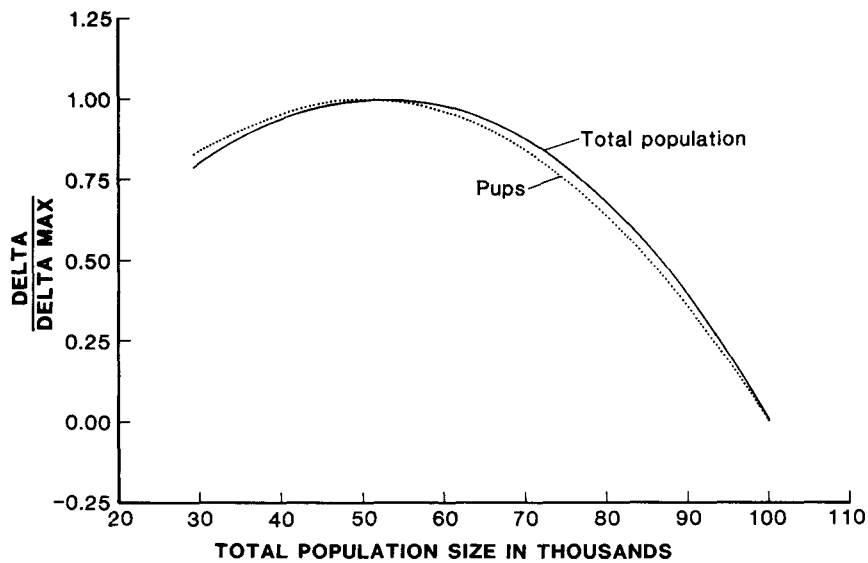


FIG. 6. Relationship of predicted and true production curves to total population size when adult survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

Density-dependent birth rates have been described in northwestern Atlantic harp seals, *Phoca groenlandica* (Lett and Benjaminsen 1977; Lett et al. 1981). Northern fur seals were the first of many pinniped species to have shown evidence of density-dependent age at maturation (Scheffer 1955). In all three types of density dependence described, the density dependence is assumed to act on the first age class and would cause the pup population to lead the total population both in the decline of the RPC and in passing the peak on the production curve as shown in the pre-census pup survival model.

The results of the two simulations where pre-census survival

is density dependent indicate that pup counts provide a conservative estimate of the RPC. This absolute value of bias can be as high as 3% in the case of an initial growth rate of 8%. In addition, using pup counts to determine whether a population is above or below the MNPL is not conservative. That is, pup counts (under this type of density dependence) indicate that a population is above the MNPL before the population actually reaches the MNPL.

Density-dependent juvenile survival has been reported in pinnipeds, as in the northwestern Atlantic harp seal (Lett and Benjaminsen 1977; Lett et al. 1981). In this case, density

dependence acts on the juvenile age classes rather than on the first age class. This would cause the pup counts to trail the total population both in the decline in the RPC and in passing the peak on the production curve as demonstrated above in the post-census simulation.

In both simulations where post-census pup survivorship is density dependent, pup counts lag behind the total population, or in other words, pup counts overestimate the true RPC of the population and are late in estimating the time at which peak productivity occurs. The largest bias in the RPC is one percentage point; it occurs in the vicinity of the MNPL. The bias in estimating peak production is -3 yr. This means that if post-census survival is density dependent, pup counts are conservative in indicating whether or not a population is above or below its MNPL.

Evidence of density-dependent adult survival in pinnipeds is difficult to obtain, if it does exist, due to the complications in obtaining accurate data. For those species where it is demonstrated to occur, pup counts would be accurate in predicting the population RPC and the relative position on the production curve as was seen in the adult survival model.

Possibly more than one type of density dependence may be operative (Smith and Polacheck 1981). Given the mechanisms we have proposed in this paper (i.e. pre-census pup survival and post-census pup survival) the resultant bias would be a combination of the two independent biases and would self-cancel to some extent.

Possibly, nonlinear density dependence is a more reasonable mechanism than linear density dependence (Fowler 1981). The difference in bias between models with linear and nonlinear density dependence would clearly be in magnitude rather than direction. The difference in resulting bias is unknown at this time. Future work will address these issues.

In order to use the predictions of this paper, managers need to know the type of density-dependent mechanisms acting on the population. If the density dependence acts on the pups, either through adult fecundity, age at maturation, or pup survival prior to census, the bias would cause the pup population to lead the total population both in the decline of the RPC and in passing the peak on the production curve. If the density dependence acts on the pups after census, the pup population would trail the total population both in the decline of the RPC and in passing the peak on the production curve.

We conclude with a particular example of how the results of our study can be used to determine the status of a stock from pup counts. It has been suggested that the San Miguel Island population of California sea lions is above the MNPL (DeMaster et al. 1982). Based on data from the years 1975 to 1981 on San Miguel Island (DeMaster et al. 1982), a regression of the survival rate of pre-census pups versus number of pups born did not show a slope significantly different from zero. In addition, most of the sea lions that are "salvaged" by rehabilitation centers each spring are yearlings in an emaciated condition. This was particularly evident in the spring of 1983, when winter storms were unusually severe. If we can assume that post-census survival is density dependent and that pre-census survival is not affected by density, then we can increase our confidence in this status assessment based on the conclusions of our model. In this case, the population should be even closer to the equilibrium population level than is indicated by the pup counts.

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