STUDIES OF THE POPULATION LEVEL EFFECTS OF ENTANGLEMENT ON NORTHERN FUR SEALS

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ABSTRACT

Recent studies have focused on entanglement among the juvenile male northern fur seal, *Callorhinus ursinus*, as a means of evaluating the effects of entanglement at the population level. Most entanglement-related field studies were conducted on St. Paul Island, Alaska, in the 1980's but the analyses include relevant data from the late 1970's. Reported here are the results of recent studies on monitoring of entanglement, estimates of entanglement-caused mortality, and the effects entanglement may have on the chances an animal is observed on the breeding islands.

The observed proportions of seals entangled in 1985 and 1986 were consistent with those observed during the last few years of the commercial harvest (about 0.4%). The proportion observed in 1988 was 0.29%, the lowest observed since 1970. The change reflects a drop in the numbers of animals entangled in fragments of trawl webbing. The frequency of occurrence of trawl webbing among the entangling debris was about half the former levels whereas the proportion of seals entangled in other types of debris did not change.

These studies confirm earlier estimates indicating that, after 1 year, the survival of seals entangled in debris light enough to permit the animals to return once to land is about half of the survival of nonentangled seals. Data indicate that the main factor contributing to the success of entangled animals that do survive is escapement from the debris.

Rates at which entangled animals are resighted indicate that the proportion of animals resighted drops with an increase in the size (weight) of debris.

Data from radio-tagged seals confirm that entangled seals go to sea for longer periods of time than do controls.

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INTRODUCTION

Entanglement in marine debris, specifically in plastics associated with the commercial fishing industry, has been documented for a number of species of seals and sea lions (Fowler 1988). The effects of entanglement in such debris have been the subject of a number of studies, especially as related to the impact on the northern fur seal, *Callorhinus ursinus*. Many of these studies have examined effects at the population level (Fowler 1982, 1985, 1987; Swartzman 1984; French and Reed 1990; Swartzman et al. 1990). Others have studied the effects at the level of the individual (Fowler 1988).

Entanglement of northern fur seals in marine debris has been a concern for several decades. The first sightings of entangled seals occurred just after World War II. Records of entanglement among young males taken in the commercial harvest or seen in juvenile male roundups have been maintained since 1967. Concern about the potential role of entanglement-caused mortality has given rise to research focused on determining as clearly as possible the extent to which entanglement contributes to a reduction in survival and to declining trends in the population (Swartzman 1984; Fowler 1985, 1987; French and Reed 1990; Swartzman et al. 1990).

This paper reports on recent field work to assess the effects of entanglement on the population of northern fur seals breeding on St. Paul Island, Alaska. The objectives of this work are: (1) continued monitoring of the proportion of seals entangled, (2) determination of the nature of entangling debris, (3) determination of the mortality caused by trawl webbing, especially as related to effects at the population level, and (4) assessment of the relative rates at which entangled and control animals are resighted. Part of the study of relative rates of resighting addresses the question of whether or not an animal's chances of being seen again are altered by being, or having been, entangled.

METHODS

Most of the data treated in this study deal with young male fur seals of the size (roughly 105 to 125 cm in total length) formerly taken in the commercial harvest on St. Paul Island. The commercial take of fur seals, which ended in 1984, was the earliest source of data on entanglement. Other data, as the main focus of this paper, were collected during 1985, 1986, and 1988 from animals of the same size (and same approximate age) to ensure comparability with historical data. Males of this size are usually between the ages of 2 and 5 years, mostly 3-year-olds.

The studies reported here involved roundups, a procedure conducted during the breeding season. A total of 63 roundups were conducted in July and early August 1985. Sixty-one were conducted in July and early August 1986; 66 were completed during July 1988.

During roundups, young males are herded together to be examined for debris or tags and for applying tags. To conduct a roundup, field biologists approach an area (called a hauling ground) near a breeding rookery where young males come ashore in large numbers. Avoiding disturbance to the rookeries, the members of the research team position themselves between the hauling ground and the water. The males on the hauling ground are then surrounded and herded away from the rookery but close to the water's edge. Care is taken to minimize the movement required of the animals and to allow them sufficient space to prevent crowding and overheating.

Once the seals are in a controlled group, field workers then allow small numbers of animals to leave the group and file toward the water. Once one or more seals begin moving toward the water, other seals follow. This movement is controlled (to ensure that tagged flippers will be seen) by the field crew. While moving toward the water, seals pass between observers, some of whom are engaged in counting seals while others watch for tags and entangling debris. Others of the field crew remain prepared to capture seals, while the remainder work to assure that the main group of seals remains in place.

When an entangled or tagged seal is seen among those leaving, the movement of seals from the main group is stopped. If tag numbers cannot be read, if tags are to be applied, or if a detailed examination of the debris is required, the seal is captured with a wooden pole fitted with a rope noose (<2% of these seals escape to the water without being captured). If tags are to be applied, or the debris examined in detail, the seal is placed on a restraint board (Gentry and Holt 1982) for a few minutes. Tags are applied on the trailing edge of each foreflipper, about 2-3 cm distal from the hairline.

If the captured animal is entangled, the nature of the entanglement is recorded (and tags applied if not previously tagged). Data recorded at the time of tagging include the tag number; the color, size, and type of debris; mesh size (if it is a net fragment); and the extent of the wound the debris has caused. A sample of the debris is removed (if there is enough) to be used later for measuring twine size and for any analysis necessary for identification of the plastics involved.

Two control seals about the same size as the entangled animal are also tagged to compare rates of return in succeeding years. The choice of tagging two control seals is arbitrary. Tagging more controls than entangled seals ensures a larger sample of returns to be used in comparing the relative rates of return of the two groups. It also aids in the study of the frequency of resighting rates and the locations (for study of intermixture) of resighted seals.

In most cases, seals that are not handled and seals released after being tagged or examined return directly to the water. By the end of the roundup, all seals have returned to the water.

Some of the animals seen in the first roundup are seen again in later roundups. The resulting sampling scheme is one of sampling with replacement, and the data for both the control animals and the entangled animals are treated accordingly.

Other sets of the data reported in this paper are from similar studies prior to 1985 in which animals were sighted in the commercial harvest prior to 1985. During the harvests, animals were herded together and moved to special areas where they were killed. These data from harvests, therefore, are treated as samples without replacement.

In previous studies of fur seal entanglement, two approaches have been used to categorize debris on seals according to its size (weight). For continuity and comparison, both are used in this study with distinction depending on the terms used. The first approach divides the debris into "light" or "heavy" categories depending on whether it is light enough for the entangled seals to return (at least once) to the breeding islands or so heavy that they cannot return. This definition suffers from lack of precision because the two categories are not discrete; their overlap is dependent on factors such as how far the seal has to swim to haul out on land. The upper limit of the light category is about 400 g, since over 90% of the entangled seals observed on land are in debris that weighs <400 g (Fowler 1987).

The second approach uses three distinct weight categories. The debris seen on animals is either weighed (after being removed) or subjectively evaluated (when entangled animals are released with debris intact). The weight of debris is classified as small (<150 g), medium (between 150 and 500 g), and large (>500 g).

To study the behavior of entangled animals, and the influence of entanglement on the chances of being resighted, radio transmitters (weighing about 40 g) were attached to 16 control and 16 entangled animals to monitor their presence and absence in the vicinity of the hauling grounds or rookeries. A radio transmitter was attached with epoxy glue to the back of the animal's head while the animal was restrained following procedures described in Loughlin et al. (1987). Each radio-tagged seal was also marked with bright paint applied to the radio and glue. Each radio was a 3.5-V transmitter, manufactured by Advanced Telemetry Systems, Inc. All radios transmitted within the frequency range of 164 to 166 MHz.

Data on the behavioral effects of entanglement were all collected in 1988. After attaching radios early (17 to 26 July), observers, using hand-held receivers, listened for radio-tagged seals during a daily visit to each haulout site until 29 August. A computer attached to a receiver was set up at the southern end of St. Paul Island (Reef Point) to scan for and record radio signals from each of the radio-tagged animals within receiving distance (approximately 5 km).

The amount of time the seals spent on shore was estimated in two ways. Detailed data for seven animals (three control and four entangled) were available from the computer at Reef Point. The computer scanned for the presence of these animals for 10 sec every 15 min, 24 h/day. We estimated the duration of intervals spent on land or at sea to the nearest quarter hour. Because the signals occasionally were blocked by the animals lying on the transmitters, and because the animals frequently entered the near-shore water without going to sea, we considered an animal to be at sea only when its transmitter had not been heard for at least an hour. Hence, by this definition, trips to sea could never be shorter than 1 h.

The second method for estimating the time ashore involved the use of data obtained from observers with hand-held receivers. If the radio on a given animal was heard during a survey, the seal was considered to have been on land all day. If the signal from that radio was not heard, the seal was considered to have been at sea all day. When the signal from a given animal was heard one day but not on the next day, we assumed that the animal had departed halfway between the two observations. This gave us an onshore estimate to the nearest half day for all 32 animals.

Standard methods were employed in conducting the usual statistical tests (e.g., chi-square tests) where noted. The level of significance chosen for statistical tests was P = 0.05, unless otherwise noted. The analysis of data resulting from the resighting of tagged animals involved both standard approaches (e.g., the Seber-Jolly method; Seber 1973) and a regression analysis specifically designed for this study. The latter was developed to make use of all the existing data to address questions unique to this study. The specifics of the procedure used in this analysis, with the assumptions involved in estimating survival from entanglement-caused mortality, are presented in the Appendix.

RESULTS

During 1985, 1986, and 1988, 22,211, 22,572, and 24,519 (respectively) male seals of the size conventionally taken in the harvest were sampled. As will be presented in more detail below, about 25% of these totals were repeated sightings. Table 1 shows the numbers of seals that were tagged each year and percentage resighted in subsequent years.

Of the 49 tagged animals released in 1985 and resighted in 1986, 12 (24%) were originally tagged as entangled animals. The change from a ratio of 85:172 (85/172 = 0.494, entangled to controls) tagged in 1985 to 12:37 (12/37 = 0.324) resighted in 1986 is not statistically significant (chi-square test). There was no field effort in 1987, so no samples were collected in that year. Of the 14 seals tagged in 1985 and resighted in 1988, 1 (7.7%) had been tagged as entangled. The change in ratio from 85:172 (85/172 = 0.494) to 1:13 (1/13 = 0.077) between 1985 and 1988, and from 12:37 to 1:13 (12/37 = 0.324 to 1/13 = 0.077) between 1986 and 1988 are statistically significant (binomial probability tests).

Of the 407 animals tagged in 1986, 128 (31.4%) were entangled. Of 46 seals tagged in 1986 and resighted in 1988, 6 (13%) were tagged as entangled seals in 1986. The change from a ratio of 128:279 (128/279 = 0.459) to 6:40 (6/40 = 0.150) between 1986 and 1988 is also statistically significant (chi-square test).

Of the eight seals resighted in 1988 after having been tagged as entangled in earlier years (including one tagged prior to 1985), six had lost their entangling debris. No seals have been resighted as entangled after originally having been tagged as controls.

Table 1.--Comparison of numbers of tags applied (in parentheses) and resighted (percent resighted shown in brackets below the numbers resighted) by year for entangled and nonentangled seals, each row corresponding to the tags released in the first year for that row (from Fowler et al. 1989).

	Year			
Controls	1985	1986	1987	1988
Nonentangled	(172)	37	--	13
		[21.5]	--	[7.6]
		(279)	--	40
			--	[14.3]
			--	--
			--	--
				(104)
Entangled	(85)	12	--	1
		[14.1]	--	[1.2]
		(128)	--	6
			--	[4.7]
			--	--
			--	--
				(52)

Table 2 presents the percentage of juvenile male seals found entangled, by year, for 1981 to 1988 in terms of the kinds of debris in which they were entangled. More detailed presentations of the data for 1988 are available in Fowler et al. (1989). Figure 1 illustrates the percentage of entangled seals observed in the harvests since 1967 and in the roundups since 1985. Table 2 also shows the composition of the debris found on animals in terms of proportions entangled. The proportion entangled in 1988 was the lowest observed since 1970 and was about half of the mean proportion observed from 1981 to 1986.

The frequency distribution of the size of debris seen on the animals per year is shown in Table 3. The numbers and percentages of those animals resighted in subsequent years, in relation to the size of debris, are presented in Table 4. None of the seals entangled in large pieces of trawl webbing were resighted more than 1 year subsequent to their being tagged,

Table 2.--Debris found on juvenile male fur seals in 1988 compared to 6 earlier years, expressed as the observed percent of juvenile male seals entangled by debris category.

	Entanglement (%)						
Type of debris	1981	1982	1983	1984	1985	1986	1988
Trawl net fragments	0.29	0.24	0.30	0.22	0.36	0.27	0.15
Monofilament net fragments	0.00	0.01	0.01	0.02	0.01	0.01	0.00
Plastic packing bands	0.08	0.10	0.07	0.09	0.05	0.06	0.07
Cord, rope, string	0.04	0.04	0.02	0.05	0.08	0.07	0.05
Miscellaneous items	0.03	0.01	0.03	0.01	0.01	0.01	0.01
Total	0.43	0.41	0.43	0.39	0.51	0.42	0.28
Sample size	102	102	112	87	76	70	53

Table 3.--Annual percentage frequency distribution of the size of debris on entangled seals that were tagged and released.

Year	n	<150 g(%)	150-500 g(%)	>500 g(%)
1983	84	63	23	14
1984	57	81	12	7
1985	78	72	20	8
1986	128	72	21	7
1988	53	72	15	13
Total	400	71	19	10

whereas seals in small debris were resighted up to 5 years later. The resighting rate of animals in medium-size debris was intermediate to those for large and small debris.

A summary of the results of the radio tagging study using hand-held radio receivers is presented in Table 5. The table contains data from both full and partial records because the study was of insufficient length to encompass an entire long feeding trip for all of the tagged seals. Furthermore, almost no seal completed a full cycle, from departure on a trip to sea followed by a return and an on-land interval until departure for the next feeding trip. For that reason, the estimated percentages of time spent on land during the course of this study may be different from those over an entire season spanning several full cycles. However, the entangled seals spent more time at sea than did controls. Twelve of sixteen entangled

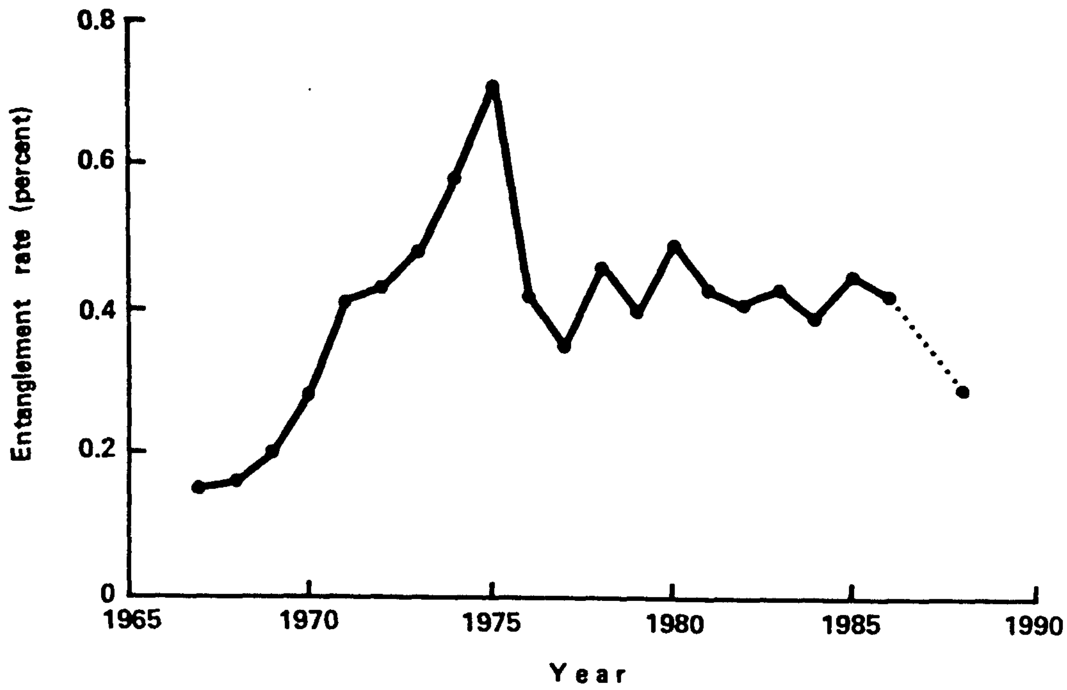

Figure 1.--The percentage of juvenile male seals found entangled in the commercial harvest from 1967 to 1984 and in research roundups from 1985 to 1988, on St. Paul Island, Alaska.

Table 4.--The numbers and percentages of tagged animals listed in Table 3 that were resighted by year in relation to size of entangling debris and year.

Year tagged	Year resighted	Size of debris <150 g(%)	150-500 g(%)	>500 g(%)
1983	1984	18(34)	3(16)	2(17)
1983	1985	4(8)	1(5)	0(0)
1983	1986	3(6)	0(0)	0(0)
1983	1988	1(0)	0(0)	0(0)
1984	1985	14(30)	2(29)	0(0)
1984	1986	9(16)	0(0)	0(0)
1984	1988	0(0)	0(0)	0(0)
1985	1986	9(16)	3(19)	0(0)
1985	1988	1(2)	0(0)	0(0)
1986	1988	6(7)	0(0)	0(0)
Combined years		65(23)	9(12)	2(5)

Table 5.--Comparison of the percent of time spent on land (present) and at sea (absent) for entangled and control seals fitted with radio tags. Data are from daily surveys with hand-held receivers on all hauling areas on St. Paul Island.

Seals[a]		Percent of time: Present	Percent of time: Absent
Entangled-fr	(N = 4)	35	65
Controls-fr	(N = 13)	28	72
Entangled-pr	(N = 12)	13	87
Control-pr	(N = 3)	10	90
Entangled-t	(N = 16)	19	81
Control-t	(N = 16)	25	75

[a]fr = males with full records, pr = males with partial records, and t = all males combined.

seals had not returned to land by the end of the study, whereas only 3 of 16 control seals had not returned (chi-square test, $P < 0.005$, or 0.001 with continuity correction). Typically, both entangled and control seals made several short trips while in the vicinity of St. Paul, and then departed on one long feeding trip. Selecting this longest trip to sea for each seal, we found that the entangled seals had significantly longer trips (30.9 days) than did controls (24.3 days). For seals that did not return from their long trips, the time from departure until the end of the study was used. Therefore, these were actually minimum estimates of their trip lengths.

The hand-held receivers could not detect the short trips taken between daily scans. Thus, the proportion of time on land (Table 5) actually estimates the time when the seals were in the vicinity of St. Paul, but not necessarily ashore. However, the data collection computer, which was able to detect short trips for seven seals, provided estimates of the time actually spent ashore at Reef Rookery. These data indicated that the four entangled animals spent a smaller proportion (44.8%) of their visit to St. Paul on land than did the controls (55.3%), but the difference is not statistically significant. The mean time between the application of tags and the departure to sea for a long feeding trip for entangled animals was 7.59 days; that for the controls was 6.17 days (no significant difference).

In 1988, 7 of 16 entangled seals fitted with transmitters were resighted in subsequent roundups. Four of sixteen controls with transmitters were resighted. There is no significant difference between these rates of resighting (chi-square test).

Analyses of the data in Table 1 are possible through the application of two very similar methods described in Brownie et al. (1978) and the Seber-Jolly method (Seber 1973). These methods result in estimates of survival of both categories of seals (entangled and controls). The annual survival of entangled seals estimated by these two methods (the same for each) is 0.22 (0.95 confidence limits of ±1.00, assuming a Poisson distribution for the resightings), and 0.51 (0.95 confidence limits of ±0.446) for controls. Although not statistically significant, the estimated survival for the entangled animals given by these results is 42% that of the controls. The estimated survival for the controls (0.51) is lower than the estimates of survival produced by Lander (1981) for juvenile males (about 0.8, including the effects of unobserved entanglement), but the difference is within the confidence limits shown above.

We also used the data in Table 1 in a regression analysis to estimate the ratio of the probabilities of being resighted for entangled and control animals and the survival factor associated with entanglement in light debris. The basis of the regression analysis is demonstrated in Figure 2, which shows the declining rate at which entangled animals were resighted relative to the controls. Each data point is corrected for the ratio of entangled to nonentangled animals, as shown in Table 6.

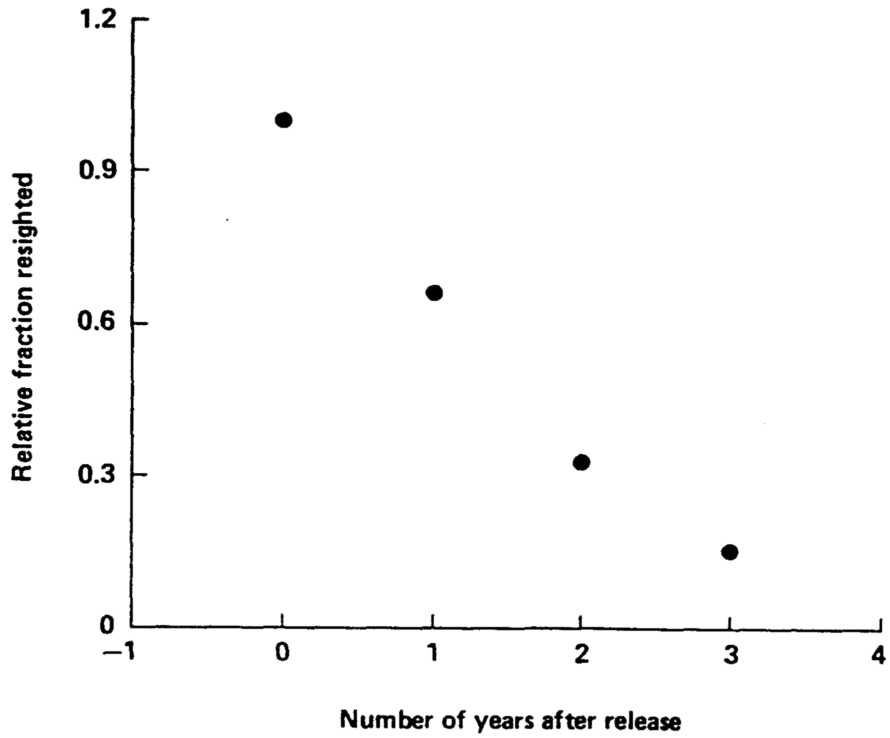

Figure 2.--Relative rates of return for entangled juvenile male fur seals compared to controls (nonentangled tagged seals) for varying time intervals. The relative rate of return is $F*(C/D) = p_{i,k}(N_{c,i}/N_{e,i})$ and the time interval is $x = (k-i)$, from Table 6 and Appendix. The point at time zero, with an adjusted ratio of entangled to control animals of one, was not used in the regression analysis.

Table 6.--List of data as extracted from Table 1 for regression analysis to estimate entanglement related survival; for a linear model of y = a + bx. See Appendix for details.

A Year i	B Year k	C $N_{c,i}$	D $N_{e,i}$	E $\ln(N_{c,i}/N_{e,i})$	F $p_{i,k}$	G $\ln(p_{i,k})$	y E+G	x B-A
1985	1986	172	85	0.7048	0.3243	-1.1260	-0.42	1
1986	1988	279	128	0.7792	0.1500	-1.8971	-1.12	2
1985	1988	172	85	0.7048	0.0769	-2.5649	-1.86	3

The results of the regression analysis, with the assumptions involved in estimating survival from entanglement-caused mortality, are presented in the Appendix. The estimated annual survival of seals entangled in light debris is about half (0.49) that of nonentangled seals. The probability of resighting an entangled seal was estimated to be about 1.35 times as great as the probability of resighting a control (given that they are both alive). However, this estimate is not significantly different from 1.0 (the case where the probabilities of seeing a seal from either group are the same).

It should be made clear that the total annual survival among entangled animals (including the effects of other sources of mortality along with those due to entanglement) is the product of natural survival and survival from entanglement. If we use the survival for juvenile males from Lander (1981)--about 0.8--the overall survival for seals entangled in light debris would be about 0.4 (i.e., about 0.8 × 0.5 = 0.4 for 3-year-old males). This is a higher survival rate than that from the Seber-Jolly analyses presented above (0.22).

Table 7 contains data on the frequency of resighting tagged seals during the season when tags were applied. These data show that the fraction of resighted control animals is nearly the same as the fraction of resighted entangled animals (both being about 25%). No statistically significant differences were found between the rates of resighting for entangled and control animals for any year or for the total (chi-square tests).

DISCUSSION

Although there is insufficient information to draw conclusions, the data collected in 1988 on St. Paul Island suggest a decline in the proportion of juvenile male northern fur seals that are entangled. Most of the change seems to be associated with a reduction in entanglement in trawl webbing, possibly a reflection of reduced occurrence of trawl webbing among pelagic debris as reported in 1988 by Japanese scientists (Fowler et al. 1989). The proportion of seals entangled in other forms of debris seems to be about equal to the proportion observed in the past 7 years. The differences between 1988 and previous years may be a result of changes in the

Table 7.--Comparison of numbers of tags applied to entangled and control juvenile male fur seals in 1985, 1986, and 1988 with the numbers in each category resighted the same season. The numbers in parentheses are the percent of the tags applied that were resighted.

	Number of tags			
	Controls		Entangled	
Year	Applied	Resighted	Applied	Resighted
1985	170	35(20.6)	76	21(27.6)
1986	165	54(32.7)	70	19(27.1)
1988	104	21(20.2)	52	15(28.8)
Total	439	110(25.1)	198	55(27.8)

rate of loss and discard of net fragments. Various education programs at national and international levels have been in place for several years, and international regulations prohibit the discard of such debris.

Severe wounds caused by prolonged entanglement in light debris contribute to death. Bengtson et al. (1988), demonstrated that pups become entangled in net fragments with mesh sizes much smaller than those seen on the subadult males in the roundups. The subsequent growth of those seals caught in debris light enough for them to survive the effects of drag in the water then results in wounds and death. Seals remaining entangled in debris often suffer from wounds that increase in size as a result of the seals' growth (DeLong et al. 1990). The degree to which wounds and resulting infections contribute to mortality in comparison to other sources of mortality caused or accentuated by entanglement (such as starvation, strangulation, and predisposition to predation) cannot be determined from existing data.

Some seals survive because they escape from the debris. Escape has been reported for animals resighted in other studies (Scordino 1985; Fowler 1987), some within the season during which animals were tagged. Of the total of eight seals resighted in 1988 after having been tagged as entangled in earlier years, six had lost their entangling debris. How this affects estimates of survival of seals in light debris has not been determined; conceivably, individuals that have lost their debris would be resighted with the same probability as control animals.

All debris on entangled animals that was later lost had been judged to weigh <150 g at its first sighting; otherwise it was similar to commonly observed debris. One possible explanation for this pattern is that the animals in small debris are the most likely of the entangled animals to return to the breeding islands. There they can come into contact with substrates (such as rocks) where the debris can abrade or otherwise wear to the point of breaking and falling off. Such wear is noted on the debris on many of the seals seen in the roundups, and on a few occasions debris has broken and fallen off during the handling of entangled animals. In view of the small numbers of animals resighted as entangled and the low survival of entangled animals, it would appear that most animals that remain entangled eventually die as a result of the debris.

The relative rate of resighting of animals originally tagged as entangled varies with the size of debris. A statistically significant (chi-square) decline in the rate at which seals are resighted with increasing size of debris is seen in Table 4. Corresponding information reported by DeLong et al. (1990) shows that of 17 females experimentally entangled in 200-g fragments of trawl net, 2 (12%) returned to the same rookery to give birth 1 year later. This is equal to the 12% resight rate of the seals entangled in medium-sized debris (Table 4). Thus, factors such as exhaustion, starvation, and drowning (likely acute factors at sea) appear to be increasingly important in the causes of death due to entanglement as debris size increases. If the survival of seals in large debris is proportional to the rate at which they are resighted, the survival of those in debris weighing just over 500 g would be about one-fourth (5/22) the survival of those in small debris. Therefore, survival resulting from the effects of entanglement alone would be about 0.11 ($(5/22) \times 0.49 = 0.11$; using the 0.49 from the Appendix). Assuming survival from natural causes is 0.8 (Lander (1981), whose results may include some mortality due to entanglement), the total survival for this large-debris group is calculated as 0.09 ($0.8 \times 0.11 = 0.088$). This implies a turnover in the population of about 2.4 times per year (turnover meaning the number of entangled seals that die for every entangled seal occurring in the population, and being equivalent to the instantaneous mortality rate, or the negative natural log of survival; $-\ln 0.09 = 2.42$). Presumably, following the trend in Table 4 to even larger debris, the turnover rate continues to increase with the size of entangling debris. If the estimated survival for controls from the Seber-Jolly analyses presented above were used (0.51 in place of 0.8), this estimated turnover would be even more rapid.

Seals that are entangled in large debris may find it impossible to return to land. Seals are seen entangled at sea in debris that is clearly large enough to prevent their returning to land (Fowler 1987). This is important in interpreting the information in Table 4. The number of seals entangled in large debris resighted on land may be small not because the seals thus entangled have died soon after entanglement, but because the debris prevents them from returning to the islands to haul out. This effect would be greater with increasing size of entangling debris. Such a trend would affect estimates of entanglement-related mortality. However, failure to return has the same effect on the population as mortality; an animal that does not return to its breeding colony is removed from the reproductive population.

Whether or not a seal is entangled may affect its chances of being seen in roundups. This is important in estimating the proportion of seals entangled and their survival rates. Factors that may affect estimates include: 1) time spent on land and at sea, 2) entangling debris or scars attracting the attention of observers, 3) relative proportions of the two groups which remain at sea for the entire season, a factor about which nothing is known, and 4) probability of seeing seals that have lost entangling debris compared with the probability of seeing entangled seals.

Entanglement results in prolonged at-sea portions of the feeding cycles for northern fur seals. Previous work on radio-tagged entangled male seals showed that the pelagic phase of feeding cycles was about twice as long for entangled seals as for controls (Bengtson et al. 1989). The results of this study are consistent with this effect of entanglement. Similar results have been noted for females (DeLong et al. 1990). It has not been possible to produce accurate estimates of the effects of entanglement on the portion of time spent on land. As a consequence, the relative time spent on land (as a fraction of the complete feeding cycle) remains undetermined. Thus, it is not possible, with the data from radio tagging, to quantify the effect of altered feeding cycles on the chances of a seal being seen.

Other data concerning the probability of resighting a seal are inconclusive. Based on data in Table 7, it would appear that once seals return to the islands, entanglement does not significantly affect their chances of being seen at least twice. Such a comparison can also be made with the smaller sample of radio-tagged animals (these seals being more visible with the bright paint). In 1988, no significant difference was found in the rates of resighting entangled and control seals fitted with transmitters in subsequent roundups.

Based on conventional mark-recapture analyses and results presented in the Appendix, seals entangled in light debris experience an annual survival that is about half (0.41 to 0.49) that for control seals. Previous estimates are very similar (0.42, Fowler 1987; 0.46, Fowler 1985.)

Regardless of a seal's probability of being resighted, it is obvious that entangled seals suffer higher mortality than do controls (Fig. 2). We have considered whether the reduced relative rates of resighting between initial release and the first resighting (e.g., the change between the first two points in Fig. 2) could have been due only to differences between the probabilities of seeing entangled or control seals. Both groups would have experienced similar survival, and the change would have been entirely due to a higher probability of seeing control animals. If this were the case there would be no further changes in the ratios over time. A level relationship would emerge between the points for years 1-3, all of which would be lower than the ratio at year 0, the time of release. The continued decline is indicative of the predominate effect of lowered survival among entangled seals.

Combined with other factors, the mortality caused by entanglement in light debris lowers the total survival for juvenile males entangled in light debris to about 0.39, assuming independence of the causes of mortality and a natural survival of 0.8. Each year, then, the number of seals in light debris that die would be about the same as the number of seals in light debris that are estimated to be alive in the population at the time of sampling (94% as many, based on a turnover of 0.94 from -ln(0.39) = 0.94, as the instantaneous rate of mortality).

A great deal of progress has been made in understanding the extent and effects of entanglement in marine debris on northern fur seals. However, precise estimates of the contribution of entanglement to the survival and trends at the population level have yet to be produced. Several studies indicate that young fur seals are more likely to become entangled than larger seals. Pups can become entangled even before leaving land (DeLong et al. 1988). Pups have been observed entangled or becoming entangled in large fragments of debris. Groups of pups often become entangled together or in succession (Fowler 1987; DeLong et al. 1988). Experiments show that pups are susceptible to entanglement in about four times as much debris as older animals because they can pass their heads through net fragments of smaller mesh size (Fowler 1987; Bengtson et al. 1988). A greater proportion of entangled animals among the young (also less experienced) seals is also consistent with the view that immature seals are more curious than older seals and are, therefore, more likely to be attracted to debris in which they may become entangled.

Research continues to show that mortality rates are quite high for seals that become entangled in larger debris. The results of the studies reported here indicate an annual survival (from the effects of entanglement) of about 0.09 for seals in debris weighing just over 500 g. Combined with the potential that larger net fragments have a higher probability of attracting seals and the fact that seals have been observed entangled in groups in large debris (Fowler 1985; DeLong et al. 1988), entanglement in large debris obviously deserves attention. However, logistic and financial constraints have made such studies impossible.

The need for studies to examine this problem is emphasized by the implications of previous attempts to account for the effects of large debris. Trawl webbing accounts for about two-thirds of the light debris (Table 2), so the portion of the juvenile male population entangled in light pieces of trawl webbing has been (before 1988) about 0.003 (0.66 × 0.004 = 0.00264; 0.004 being the proportion entangled in light debris of all kinds). On beaches, at sea, and on entangled animals seen away from the breeding colonies, the frequency of occurrence of pieces of heavy trawl webbing is about five times that of light (Fowler 1987). Assuming, that for every piece of light debris on an entangled seal there are five pieces of heavy debris also entangling seals, then entanglement in heavy debris involves about 1.5% of the juvenile male population (0.003 × 5 = 0.015).

As mentioned above, pups during their first few months at sea may be four times more susceptible to entanglement than juvenile males. If so, 6% of their numbers become entangled each year (4 × 0.015 = 0.06). Accounting for the turnover from mortality of seals in large debris (estimated earlier as 2.4 times per year for debris just over 500 g) produces the implication of an entanglement-caused mortality of over 14% (2.4 × 0.06 = 0.14). This does not account for the mortality in light debris. Entanglement in heavier debris has been observed to involve more than one animal per piece (Fowler 1985, 1988; DeLong et al. 1988). This, combined with the greater attraction large debris must have for seals (the larger pieces presumably being more easily seen because of their size), could result in higher rates of entanglement and mortality.

If, as indicated by field observations (Fowler 1988; DeLong et al. 1990), entanglement involves both sexes (especially among the younger age classes), entanglement and resultant mortality may have contributed significantly to the declining trends among fur seal populations (Fowler 1985, 1988). Such implications are consistent with recently observed population trends, and models consistent with such trends have been constructed (Swartzman 1984; French and Reed 1990; Swartzman et al. 1990). These observations emphasize the need for better studies to clarify our estimates of the degree to which entanglement has caused these trends. Feasible field studies to verify the role of entanglement in large debris have yet to be designed and conducted.

CONCLUSIONS

The 1988 results of field research on entanglement of northern fur seals through roundups of juvenile males on St. Paul Island, Alaska, showed:

1. A reduction of the proportions observed entangled on land from about 0.4 to 0.29%.

2. Entanglement in fragments of trawl webbing in 1988 was about half of entanglement levels observed for this kind of debris in previous years.

3. The rate of resighting for animals tagged in 1985 and 1986 and resighted in 1988 showed that entangled animals tagged in those years were seen at rates that were significantly less than the rate at which controls were resighted.

4. The pelagic portion of the feeding cycle of entangled seals is greater (and a larger portion of their time may be spent at sea) than that of control seals, but the extent of the difference is unknown.

Analysis of these data in combination with data from previous studies (data on resighted animals collected in 1986, also on St. Paul Island, and data on debris collected from 1967 through 1988) showed that:

5. The estimated survival due to being entangled in light debris ranged from 0.41 to 0.49, close to estimates of about 0.5 or less from previous work.

6. Combined with natural survival, the total survival of entangled seals is probably <0.39, with the equivalent of nearly a complete turnover in the population of juvenile males entangled in light debris each year.

7. Mortality increases with the size of entangling debris based on the observation that survival for seals entangled in large debris is less than for those in small debris.

8. The probability of resighting entangled seals (or seals that once were entangled), compared to that of nonentangled seals, has yet to be clearly evaluated.

9. A great deal has been learned about the specifics of mortality caused by entanglement in debris weighing <500 g. Implications for effects at the general population level are serious. However, the main result of this progress is a continuing emphasis on the need to refine estimated mortality rates caused by large debris, especially pieces much larger than 500 g.

10. More studies will be required to better understand the interacting factors associated with the probability of entangled seals being resighted in the roundups.

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APPENDIX

ESTIMATION OF ENTANGLEMENT-RELATED SURVIVAL AND THE RELATIVE PROBABILITIES OF ENTANGLED AND CONTROL FUR SEALS BEING RESIGHTED

To make use of the data on the returns of male fur seals (i.e., those resighted) as shown in Table 1, we make a set of assumptions and define the following terms. Let

$N_{c,ik}$ = the number of control seals tagged in year i and resighted in year k, where k > i (i = 1985,1986, k = 1986,1988).

$N_{e,ik}$ = the number of seals tagged in year i as entangled animals and resighted in year k (regardless of whether or not they were entangled when resighted), where k > i (i = 1985,1986, k = 1986,1988).

$p_{i,k}$ = $N_{e,ik}/N_{c,ik}$, or the ratio of numbers of seals resighted in year k that were entangled when first tagged in year i to the numbers of nonentangled (control) seals tagged in year i and resighted in year k.

$s_{c,j}$ = the annual survival of control animals, or the animals tagged without debris in year j, for j from i to k (i.e., $s_{c,j}$ = survival from j to j+1). This is the probability of surviving from natural causes of mortality.

s_e = the annual survival of animals entangled in light debris (debris light enough to return to the breeding islands), and is assumed not to vary from year to year. This is the probability of surviving entanglement given that an animal has survived natural causes of mortality and is assumed to be independent of $s_{c,j}$ (so their total annual survival is $s_{c,j}s_e$).

$N_{e,i}$ = the number of seals tagged as entangled animals in year i (i = 1985, 1986), and

$N_{c,i}$ = the number of seals tagged as controls in year i (i = 1985, 1986).

Different proportions of entangled seals may return to the islands to be seen when compared to controls. Once in the vicinity of the islands, entangled seals may be seen at different rates than the controls for various reasons. These include the possibility of different fractions of time spent on land and entangled seals being seen more readily than controls because of their entanglement, or the effects of having been entangled. Thus we define

f_{ek} = the probability of resighting a seal in year k given that it was entangled when tagged and that it is alive. This probability is expressed on the basis of a unit of searching effort that is the same as applied in looking for control animals. It is assumed to vary from year to year but not in relation to f_{ck} (below), and

f_{ck} = the probability of resighting a control animal in year k given that it is alive in the population, again as based on the unit of effort spent in searching for both control and entangled seals. This is also assumed to vary from year to year but not in relation to f_{ek} (f_{ek}/f_{ck} is assumed constant).

With these terms, the expected number of seals that were entangled when tagged and sighted in year k after being tagged in year i, for one unit of effort is

$$E(N_{e,ik}|N_{e,i}) = f_{ek}ß_k s_e^{(k-i)} N_{e,i}$$

(i = 1985,1986, k = 1986,1988, and $ß_k$ is the product of $s_{c,j}$ for j from i to k), and the expected number of controls for the same circumstances is

$$E(N_{c,ik}|N_{c,i}) = f_{ck}ß_k N_{c,i}$$

($ß_k$ is the product of $s_{c,j}$ for j from i to k).

Substituting the observed for the expected values we have the following moment estimators:

$$N_{e,ik} = f_{ek}ß_k s_e^{(k-i)} N_{e,i} \quad \text{and} \quad N_{c,ik} = f_{ck}ß_k N_{c,i}.$$

The ratio of these two equations, then, is

$$N_{e,ik}/N_{c,ik} = p_{i,k} = (f_{ek}/f_{ck})(N_{e,i}/N_{c,i})s_e^{(k-i)}$$

which can be used to estimate f_{ek}/f_{ck} and s_e.

We note that variability in natural survival (i.e., the survival of the controls and that part of the survival of entangled animals from natural effects) can occur over time and not affect the calculation since these terms cancel in the formulation of the equation above. We also note that the probability of resighting animals from each of the two groups can vary from year to year as long as their ratio remains the same, as assumed above. Effort spent in resighting entangled and control seals is the same (the same roundups) but the number of roundups can vary from year. This is because effort for each of the two groups influences the above relationships only as a ratio in f_{ek}/f_{ck} (i.e., it cancels and need not be defined).

By rearranging terms we have

$$p_{i,k}(N_{c,i}/N_{e,i}) = (f_{ek}/f_{ck})s_e^{(k-i)},$$

and taking the natural log of this equation results in the following linear equation which can be used for regression analysis and the estimation of relevant parameters as defined above:

$$\ln[p_{i,k}(N_{c,i}/N_{e,i})] = \ln(f_{ek}/f_{ck}) + \ln(s_e)(k-i).$$

Using this equation and the data from Table 6, the estimated parameters determined from regression analysis for the above equation are

$$\ln(f_{ek}/f_{ck}) = 0.307 \text{ and } \ln(s_e) = -0.720 \ (R^2 = 1.00,\ p = 0.011).$$

These results imply that the ratio of the probabilities of being resighted is about 1.35 (calculated as $e^{0.307}$, with 95% confidence limits of 0.95 to 1.95). Thus, the chances of being resighted after being tagged as an entangled animal, given that the animal has survived, are estimated to be about 1.35 times that of being resighted as a control, but this does not differ significantly from 1 or an equal probability. The estimated survival of entangled animals from the effects of entanglement is 0.49 (calculated as $e^{-0.720}$ with 95% confidence limits of 0.41 to 0.57).

In addition to the small sample size, other factors prevalent in this analysis need noting. The data points for the 1- and 3-year time intervals are not independent. A random difference between the mean (here assumed constant) survival from entanglement in the first year will be seen as a bias in the same direction in the third. With this set of data, this does not affect the estimate of entanglement-related survival as much as it does the estimated ratio of probabilities of being resighted. This is because the slope of the line as seen in Figure 2 (the estimate of survival) depends more on a rotation about the point for the 2-year time interval than the distance the line is above or below the second point. The height of the line will be affected by the interdependence of the two end points.

The effect of assuming that the survival from risks caused by entanglement is independent from surviving the risks of other, natural, causes has not been explored. The same holds for the assumption that the ratio of the probabilities of being resighted for the two categories remains the same over time. However the various steps in the derivation of the linear equation used in this analysis might contain hidden assumptions, or sources of statistical error, have yet to be examined.