MARINE MAMMAL SCIENCE, 5(1):1–16 (January 1989) © 1989 by the Society for Marine Mammalogy

MANAGING THE EXPLOITATION OF PACIFIC WALRUSES: A TRAGEDY OF DELAYED RESPONSE AND POOR COMMUNICATION¹

FRANCIS H. FAY

BRENDAN P. KELLY

Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99775

JOHN L. SEASE²

Biological Sciences Program, University of Alaska, Fairbanks, Alaska 99775

ABSTRACT

The Pacific walrus population has been depleted and subsequently allowed to recover three times in the past 150 yr. As we see it, the population has been made to fluctuate like an r-selected species, rather than being maintained at a high, stable level, as befits a K-selected species. The latest depletion began in the 1930s but was not recognized until 25 yr later, by which time the population had been reduced by at least half. Without benefit of communication, the U.S.S.R. and the State of Alaska put similar protective measures into place by 1960, and in the next two decades the walrus population recovered again, at least doubling in size. By 1980, it already was showing density-dependent signs of having approached or reached the carrying capacity of its environment. As productivity and calf survival declined sharply in the late 1970s and early 1980s. the catches more than doubled. We believe that the combined effects of natural curtailment and human intervention may be bringing the population down again rather rapidly. With the present, crude monitoring methods, delayed management responses, and poor international communications, however, the downward trend may not be acknowledged for at least another decade, by which time the unilateral Soviet and American corrective measures are likely to be too much, too late. Walrus management needs to be based less on response to immediate crisis and more on long term prediction than it has been in the past. Because the U.S.A. and U.S.S.R. are trying to manage the same walrus population, without sufficient communication or consensus and sometimes to opposite ends, an international joint management program needs to be implemented.

Key words: walrus, Odobenus rosmarus, population dynamics, management.

¹ This paper is based on a presentation in Plenary Session II, "Science and Marine Mammal Conservation," of the Vancouver meetings of the Society. Other papers from that Session have been published in other issues of *Marine Mammal Science*. Publication costs have been provided by grants to the Society from the National Marine Mammal Laboratory (NOAA/NMFS) and the Marine Mammal Commission. The convenor, G. Carleton Ray, also wishes to acknowledge Dr. Shiela S. Anderson of the Sea Mammal Research Unit, Cambridge, U.K. for her skillful chairing of the Session.

² Present address: NOAA, National Marine Fisheries Service, Box 1668, Juneau, Alaska 99802.

Development of an understanding of the population dynamics of living organisms has contributed heavily to management of the world's renewable resources. For a number of species, however, especially those with a length of life approaching our own, the full range of dynamic responses to environmental factors still is not understood sufficiently for implementation of effective, farsighted management (Estes 1979, DeMaster 1984b). A case in point is the Pacific walrus (Odobenus rosmarus divergens), whose population has undergone marked fluctuations in size in the past 150 yr, partly as a consequence of no management at all and partly due to insufficient understanding of its population ecology by the managers. Perceiving a need to improve on that situation through increased understanding, we began a thorough compilation of the documented history of the Pacific walrus population, feeling that the events of the past needed to be placed into a long-term, dynamic perspective to appreciate how the population has responded to alternating perturbation and protection. We still are engaged in that process and in the analysis of archived data. While many of the details remain to be clarified, the overall picture is sufficiently complete and striking to warrant presentation at this time. Additional supporting data can be found in Fay et al. (1986), Sease (1986), Sease and Fay (1987), and Sease and Chapman (1988).

HISTORICAL ASPECT

The walrus populations of the world have been exploited by man for thousands of years, most of that time without any management at all or any need for it, for the greatest proportion by far of that exploitation was by primitive men with primitive means. That kind of exploitation probably was more or less constant and in small amounts, and it probably had no more effect on the walrus populations than any other kind of natural predation.

In the present millennium, however, walruses have been exploited in a different way, principally by civilized men with technically advanced means and primarily to obtain large quantities of tusks, hides, and oil that could be sold or traded on the world market. We call this "commercial exploitation" and note that its only limits are those of the resource itself and the demand for the goods. Commercial exploitation of the Pacific walrus population apparently began in a small way in the middle of the 17th century. It was expanded a hundred years later, when the hunters and trappers of the Russian merchant companies swept eastward across the Bering Sea into Bristol Bay and northward toward Bering Strait. Along the way, they took walruses primarily for the ivory of the tusks (Berkh 1823). The impact of that exploitation on the Pacific walrus population probably was insignificant, however, for the quantity was comparatively small, and most of that taking was done in the southeastern part of the Bering Sea, where it was aimed principally at adult male walruses, rather than at females. The average export of tusks from the region at the peak of this exploitation was only about 4,800 kg per year (Tikhmenev 1861-63), which would have amounted to between 900 and 990 animals per year (at 2.54 kg/per tusk, SD = 0.565, n = 83). At least one-third of that ivory was acquired

as tribute and in barter from the indigenous natives of the region, whose total annual catch probably was no more than about 3,000 walruses. Together, these catches could have been sustained easily without adverse effects by a walrus population exceeding 200,000 individuals (Fay 1957).

The most intensive commercial exploitation of the Pacific walrus population took place following the American purchase of Alaska from Russia in 1867. That exploitation was by American whalers, who harvested walruses in addition to bowhead whales (Balaena mysticetus) in the northern Bering and southern Chukchi seas (Bockstoce and Botkin 1982). Those harvests took place during the spring and early summer, while the whalers waited for the pack ice to retreat, and the catches were primarily of adult females (Clark 1887). From those walruses, the whalers took only the oil and ivory, as those were the only marketable parts. For a time between 1869 and 1879, their catches averaged more than 12,000 walruses per year, and perhaps nearly as many more were destroyed but lost through sinking and wounding. Such destructive losses were related to the new method of hunting. Before 1868, the hunting had been done mainly with harpoons and lances, and virtually every animal that was struck was retrieved. After the American Civil War, however, the whalers began to use firearms for hunting walruses, and the average proportion of animals retrieved varied widely from less than one-third to more than two-thirds of the animals that were shot (Allen 1880, Bockstoce and Botkin 1982). By killing mainly the adult females, the whalers not only depleted the productive segment of the population but probably caused the death by starvation of most of the young that had accompanied them (Clark 1887).

In retrospect, it is clear that the Pacific walrus population was being over-exploited by the American whalers as early as 1870, but their depletion of it apparently went unnoticed for about 10 yr. By that time, the whalers were judged to have reduced the population by half (Nelson and True 1887). The effects of that reduction on the coastal natives was unmistakable: one-third of the Eskimos in the Bering Strait region were said to have starved to death in 1878–79 (Allen 1895), and that proportion was much higher on the islands, where the resource base was narrowest and the dependency on walruses was greatest (Nelson and True 1887, Muir 1917). Fortunately for the walruses and for the dependent natives, the whalers' catches practically ceased after 1880, presumably due in part to the scarcity of walruses and in part to the declining price of walrus oil (Bockstoce and Botkin 1982). The aboriginal catch also was greatly reduced by then, for not only were the walruses scarce but the natives were, as well.

With the hunting pressure lowered, the walrus population apparently recovered somewhat in the 20 yr between 1880 and 1900, as was indicated by the reappearance of animals in peripheral parts of the range (Fay et al. 1986). By the turn of the century, however, the walrus population was exposed again to commercial exploitation, this time by a small number of arctic traders, mainly Americans, Canadians, and Norwegians, who were engaged in bartering with the natives of Chukotka and Alaska for furs. To supplement their profits from that activity, they also set native crews to work harvesting walruses for the ivory

and hides. The amount of that exploitation apparently went unrecorded, but it is said to have been great enough to have had a noticeable impact again on both the walruses and the dependent natives, reaching its maximum about 1920 and declining thereafter (Nechiporenko 1927, Brooks 1953). The degree of depletion from that period of exploitation apparently was not as great as from the previous one, for recovery of the walrus population already was evident by the 1930s, as the animals reappeared in parts of their former range from which they had been absent for several decades (Ognev 1935, Murie 1936, Zenkovich 1938, Belopol'skii 1939, Nikulin 1941). This may not have been a full recovery, but it was enough that the Soviet Union was able to mount a major commercial assault on the walrus population in the 1930s. That exploitation, as before, was primarily for hides, oil, and ivory (Zenkovich 1938). As it got underway, Soviet catches were as high as 8,000 animals per year (Krylov 1968). At the same time, however, the American government was trying to conserve the walrus population by prohibiting commercial killing. This American action was in delayed response to the earlier depletion, but it was obviously too late, for the Soviets were harvesting walruses again intensively by that time. Since neither the American nor the Soviet government was aware of what the other was doing, and neither of them was really capable of monitoring the status of the population, they did not know that it was being depleted. They could not have detected any change in the walrus population, unless the change was very large. Thus, the depletion continued unabated for 25 yr (Fay 1957, Geller 1957, Kleinenberg 1957), and by the mid-1950s, the walrus population again had been reduced by about half. As before, its depletion caused food shortages among the dependent natives (Hughes 1960, Fay 1982).

Finally, about 1960, the U.S.S.R. and the newly established State of Alaska responded by putting protective measures into place, intending to restore the Pacific walrus population. This was done more or less concurrently on both sides of the international boundary, though still without benefit of communication. By regulation, the catches on both sides were reduced markedly, and their overall composition was shifted from being about 60% females to about 75% males (Burns 1965, Krylov 1968). Furthermore, the coastal sites where the animals hauled out to rest were given almost complete protection. On the Soviet side, shooting of animals in the water also was prohibited, in an effort to reduce the waste from wounding and sinking.

THE PRESENT SITUATION

As a result of that protection, the walrus population was restored, probably to its pre-exploitation level. Between 1960 and 1980, it increased steadily in size, as documented by the results of more than a dozen censuses conducted by Americans and Soviets (Fig. 1). The steady increase was indicated also by the fact that the animals gradually reoccupied nearly all of their former range, including some areas that had been vacant for up to 100 yr (Fay et al. 1986). Because the censuses were beset by potentially huge, uncontrollable sampling errors, however, the population estimates derived from them were useful only

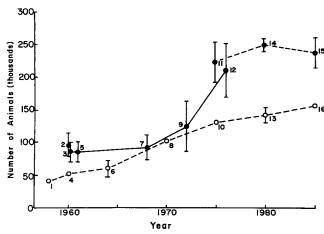


Figure 1. Estimated size of the Pacific walrus population, based on aerial censuses conducted by the U.S.S.R. and the U.S.A. Open symbols and dashed line indicate Soviet estimates for animals west of the Russian-American Convention Line in autumn only, 1958 to 1985; solid symbols and solid line represent American estimates of the entire population wintering in the Bering Sea, 1960 to 1976; solid symbols and dotted line represent joint American-Soviet estimates of the entire population in autumn, 1975 to 1985. Vertical bars are the reported 95% confidence limits (U.S.A.) or range of estimates (U.S.S.R.). Numbers adjacent to the symbols refer to sources: 1—Nikulin in Fedoseev 1962, 2 and 3—Kenyon 1960, 4—Fedoseev 1962, 5—Kenyon in Fay 1982, 6—Gol'tsev 1968, 7—Kenyon in Fay 1982, 8—Gol'tsev 1972, 9—Kenyon 1972, 10—Gol'tsev 1976, 11—Estes and Gol'tsev 1984, 12—Krogman et al. 1986, 13—Fedoseev 1984, 14—Johnson et al. 1982, 15—Gilbert (1989), and 16—Fedoseev and Razlivalov (1986).

as indicators of relative numbers and trends, not of absolute population size (Estes and Gilbert 1978). The trend of increase appeared to be documented most reliably by the censuses in Soviet waters, where the numbers were estimated in the same way each time and were based mainly on counts from aerial photographs of herds on the coastal haulouts. In both the Soviet and the American census data, the relative increase of the population appeared to be at least 100% between 1960 and 1975.

Already by the late 1970s, however, there were signs of other changes that could be interpreted as density-dependent responses of the population to the carrying capacity of its environment (Fay and Kelly 1980, Fay 1981, Fay et al. 1986). Walrus populations are presumed to be food-limited, and the events that transpired in the late 1970s and early 1980s appeared to confirm that presumption. In 1976, the Alaskan Eskimos began to report that the harvested walruses were much leaner than they had been a few years earlier. They also reported that the stomach contents increasingly included unusual items such as seal flesh, suggesting that the normal prey (bivalve mollusks) were becoming scarce. Our investigations of those claims disclosed that:

(a) The animals were significantly leaner in the 1980s than they had been in the late 1950s to early 1970s (Table 1; Kruskal-Wallis test, P < 0.02). This

Sex	Statistic	1958–72 (Jan–Sept)	1980 (May–Jun)	1981 (Feb–Mar)	1983 (Jul–Aug)
Males	n	8	22	85	56
	Range	25–76	4–60	15–54	10–37
	Mean	49.6	27.4	32.6	24.4
	SD	14.08	11.73	7.70	5.76
Females	n	18	122	87	321
	Range	30–102	12–75	24–68	13–59
	Mean	57.3	38.9	39.6	29.5
	SD	21.61	10.81	8.98	7.83

Table 1. Comparative sternal blubber thickness (mm) of Pacific walruses, 1958-83.a

suggested that either the food supply had diminished or the animals were expending more energy than before to get it (or both).

(b) The occurrence of seal flesh in the stomach contents of animals taken in the Bering Strait region in spring was unusually high in the late 1970s (Lowry and Fay 1984), and we found that other alternate prey such as fishes, anemones, and polychaetes, also occurred more frequently than before (Fay and Stoker 1982a, b; Fay et al. 1984). Seal flesh diminished in frequency of occurrence in the samples after 1979, but the presence of parasites acquired from eating fishes remained high. From 1975 to 1982, the bivalves found in the walruses' stomachs were of diminishing size in each successive sample, suggesting that selective predation was changing the structure of the prey populations. That is, having expanded into essentially "virgin" range, some of which had been unoccupied for more than a century, the walrus population finally appeared to be exerting a detectable effect on its primary food supply in the central part of the range and was taking increasing amounts of alternate prey.

Further evidence of the walrus population having increased greatly was seen in the steadily rising use of traditional haulouts on islands in the Bering Strait region during the 1960s and 1970s. At first, this amounted to increased use during seasonal migrations, but it later changed to prolonged (up to 6-mo) occupancy from spring to fall (Fay et al. 1986). At St. Lawrence Island, native residents expressed great concern that the numbers of walruses using the Punuk Island haulout was becoming too large, for the amount of natural mortality there had risen markedly in the 1970s. Our investigations confirmed that the mortality was higher there in 1978 than it had been for at least the previous 30 yr (Fay and Kelly 1980). Data acquired since then indicate that it has declined again.

At the villages on St. Lawrence Island where the annual harvest of meat and hides of newborn walrus calves is of primary importance for subsistence, the Eskimos began to report times of severe scarcity of calves in the late 1970s and early 1980s. Although the adults were more abundant than they had been for

^a From Fay *et al.* (1986). Sources per year: 1958–72 by J. J. Burns, F. H. Fay, and E. Muktoyuk; 1980 by T. E. Smith; 1981 by F. H. Fay and R. R. Nelson; 1983 by F. H. Fay, R. R. Nelson, and J. L. Sease.

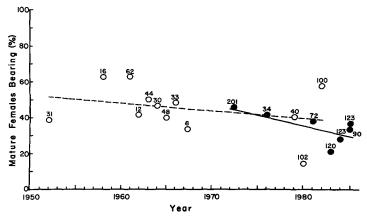


Figure 2. Proportion of mature females bearing a calf per annual sample from the Alaskan native catch in the vicinity of Little Diomede Island, Bering Strait (open symbols, dashed line) and from the Soviet ship-based catch (solid symbols, solid line) in the Bering and Chukchi seas. Sample size is indicated adjacent to each symbol. Data from Little Diomede by J. W. Brooks, J. J. Burns, F. H. Fay, K. W. Kenyon and J. L. Sease, and from Soviet catch by IU. A. Bukhtiiarov, J. J. Burns, F. H. Fay, V. N. Gol'tsev, A. A. Kibal'chich and J. L. Sease.

a long time, the proportion of them with newborn young was reported to be down markedly from previous levels. Samples drawn from the Alaskan and Soviet harvests at that time confirmed that the fecundity of adult females had declined and, furthermore, that it had become highly variable from year-to-year (Fig. 2). The lowest fecundity on record was in 1980, when instead of about 40% of the cows bearing calves, the proportion was about 15%.

Concurrent with this change in overall fecundity, we found (Table 2) that the females in recent years have been reaching maturity later than before (Kolmogorov-Smirnov 2-sample test, 2-tailed P < 0.005). Whereas in previous decades, the average female gave birth to her first calf at 8 yr of age, the mean age at first birth in recent years has been about 10 yr. Such a change is regarded as a good indicator that a population has reached or is approaching carrying capacity (Eberhardt 1977, Eberhardt and Siniff 1977). Presumably, this change is the result of slower body growth (Laws 1956), which is likely to be a product of lowered nutrient intake.

Field samples of herd composition gathered by us and by some of our colleagues in the early 1980s (Fay and Kelly 1988) also indicate that the survival of calves had been very low for several years, probably since the mid- to late 1970s (Fay et al. 1986). In 1980, in addition to the low production, the postnatal survival of calves appeared to have been no better than 20% (Fay et al. 1986). Formerly, it was judged to have been as high as 80% during the time when the population was increasing (Fay 1982).

In recent years, we and the Alaskan Eskimos also have observed a remarkably high proportion of animals in the population with extremely worn, blunted tusks. Since this condition is characteristic of very old animals (Fay 1982), it suggests that there is an unusual abundance of old individuals in the population.

Table 2. Comparative frequencies per age class and cumulative frequencies of ages at first birth for female walruses in the 1952–72 and 1975–82 periods.^a

			Age (yr) at first birthh											
Sample	n		4	5	6	7	8	9	10	11	12	13	14	15
1952–72 Cum. freq. Cum. rel. freq.	61	f	0 0 0	1 1 2	6 7 12	19 26 43	14 40 66	9 49 80	3 52 85	3 55 90	2 57 93	2 59 97	2 61 100	0 61 100
1975–85 Cum. freq. Cum. rel. freq.	48	f	0 0 0	0 0 0	3 3 6	3 6 12	6 12 25	8 20 42	6 26 54	7 33 69	6 39 81	2 41 85	0 41 85	7 48 100

^a Data from Alaska Department of Fish and Game, U.S. Fish and Wildlife Service, Alaska Eskimo Walrus Commission, and University of Alaska.

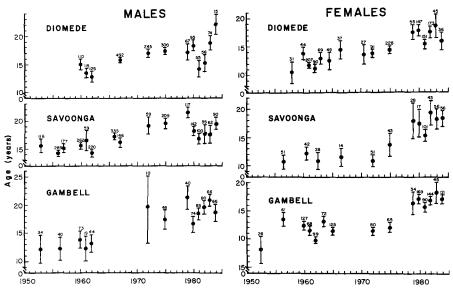


Figure 3. Mean age (excluding calves) of samples from the annual spring catches of male (*left*) and female (*right*) walruses at the three principal locations in Alaska. Vertical bars indicate 95% confidence intervals. Sample size is indicated above each symbol. Data from F. H. Fay 1952–57, Alaska Department of Fish and Game by S. J. Harbo 1960–61 and J. J. Burns 1962–75, and U.S. Fish and Wildlife Service by F. H. Fay 1979–84.

We found that the age composition of the Alaskan catch had changed, with a significant increase in mean age of both males and females since the 1960s (Fig. 3). Although the results from the Alaskan catch are not necessarily representative of the population because of hunter selection, we also found an increase in mean age in ostensibly non-selective samples taken during Soviet-American research cruises (Krylov 1965, 1968; Fedoseev and Gol'tsev 1969; Fay et al. 1986; Sease 1986). Furthermore, an increase in mean age was indicated even in the natural mortality of walruses on the Punuk Islands haulout (Fay et al. 1986).

The decreased fatness, change in diet, increased natural mortality, decreased productivity and calf survival, increased age at first pregnancy, and change in age composition appeared after the increase in population size had been underway for at least 15 yr. These conditions indicated that a significant change in status had taken place in the late 1970s, probably related to the population having reached or approached K and begun to have an adverse impact on its food supply. Perhaps, the population may even have exceeded the carrying capacity of its environment by the early 1980s, for the animals still are very lean, their reproductive performance still is highly erratic, and the survival of calves still seems very low. We believe that the probability of the population having overshot carrying capacity is very high, because its expansion was into a range that had been unused for as much as a century. That is, we suspect that the momentum gained by the walrus population in its expansion was comparable to that of an exotic species expanding into virgin habitat, where the population exceeds carrying capacity before its density-dependent regulators can come into

full operation. A classic analogy is the sea otter's (*Enhydra lutris*) increase, then decrease, following reinvasion of some parts of its former range (Kenyon 1969).

Reduced recruitment, coupled with high survival of adults, would be expected to lead to increasing average age of the population. This would be self-reinforcing, for the older females are less productive than the younger ones (Burns 1965, Krylov 1966, Fay 1982). Judging from the very low production and survival of calves since the mid-1970s, recruitment into the adult population will be very poor in the 1980s and 1990s. Presumably, this mechanism would have controlled the growth of the population, putting it into a natural decline and eventually bringing it into equilibrium with its environment. Because the catches have been rising steadily since the mid-1970s (Table 3), however, the stabilizing effect of that natural process probably has been exacerbated. Although the higher catch may have prevented the population from greatly exceeding K, we suspect that the population is being depressed more rapidly by the increased catch, and that the depletion could become severe if the catches on both sides of the Bering Sea are not moderated very soon. A simple arithmetic model of the population (Table 4), which begins with a population size based on Gilbert's (1989) mean estimate for 1980, suggests that, even if the catches were reduced immediately, the population might continue to decline into the next decade before any reversal could take place.

Conclusion

Catches of walruses in Alaska have grown since the early 1970s from an average of less than 1,700 per year to more than twice that amount by the 1980s (Table 3). Meanwhile, the Soviet Union has more than quadrupled its catch from less than 1,000 to about 4,000 walruses per year. In the same period, the overall proportion of adult females in the catch also has risen sharply. The increases on both sides of the international boundary have been due mainly to relaxation of restrictions, which took place when the population was recognized as having become very large. The best estimate of the overall kill since 1980, which includes both the catches and the losses (from sinking and wounding), suggests that the removal rate by exploitation is now around 10,000 to 15,000 per year or about 4 to 6% of the population. Furthermore, to this must be added the natural mortality, which is unknown but thought to be at least 3% per year (DeMaster 1984a). Judging from the low productivity and the low survival of young in recent years, we believe that the recruitment could now be as low as 1% per year, and that it is far exceeded by the rate of removal. If so, the population could be halved again within a decade. Removal rates in excess of 10,000 per year have caused such depletion at least twice in the past. Unfortunately, with the present, crude monitoring methods, neither the U.S.A. nor the U.S.S.R. will be able to identify a decline with certainty until long after it has taken place.

Depletion, of course, is not irreversible, but the basic problem in this situation, as we see it, is that the Pacific walrus population is being made to fluctuate like

Table 3. Size of annual catches of Pacific walruses and proportion of each catch made up of adult females, 1960–85.^a

Year	Soviet catch	Alaskan catch	Total catch	Percent adult females
1960	2,866	2,300	5,166	18.4
1961	2,537	1,860	4,433	17.6
1962	1,818	1,690	3,508	17.8
1963	1,249	1,725	2,974	19.9
1964	1,500	975	2,475	9.9
1965	891	1,739	2,630	19.5
1966	909	2,808	3,717	21.2
1967	940	1,347	2,287	5.8
1968	939	1,436	2,375	13.9
1969	965	882	1,847	10.1
1970	988	1,422	2,410	17.7
1971	897	1,915	2,812	9.1
1972	1,518	1,325	2,843	12.1
1973	1,291	1,581	2,872	8.1
1974	1,205	1,410	2,615	10.1
1975	1,265	2,378	3,643	17.8
1976	1,271	2,989	4,260	21.2
1977	1,461	2,377	3,838	17.3
1978	2,120	2,224	4,344	15.2
1979	1,526	2,745	4,271	16.1
1980	2,653	2,900	5,553	24.7
1981	2,574	4,096	6,670	26.3
1982	3,569	2,809	6,378	17.4
1983	3,422	2,413	5,835	21.3
1984	4,286	5,986	10,272	26.7
1985	4,306	4,611	8,917	32.3

^a Data from Soviet Ministry of Fisheries, Alaska Department of Fish and Game, and U.S. Fish and Wildlife Service.

an *r*-selected species, whereas it should be maintained at a high equilibrium with its environment, as befits a *K*-selected species (Estes 1979, Ray 1981). The fluctuations up to now have been mainly the result of excessively delayed responses by the management agencies in both the U.S.A. and the U.S.S.R., which still take action only when stimulated by immediate crisis, rather than through foresight. "Crisis-management" is not appropriate for a long-lived species, because each perceived crisis is the product of processes that were begun a decade or more before (Laws 1981). Crisis-management simply is a mismatch with the walrus' life history; by the time each crisis is recognized, the conditions that caused it already are historical rather than current events.

Effective management for such a long-lived, slowly maturing mammal must be planned far ahead, and regulations must be enacted well in advance, to head off any prospective crisis. The lack of foresighted planning thus far has been partly the result of the methods used for biological monitoring of the population, which do not provide sufficient warning about potential demographic problems ahead. Present monitoring methods reveal only general trends in population size,

MARINE MAMMAL SCIENCE, VOL. 5, NO. 1, 1989

Table 4.	Optimistic hypothetica	I model of	the Pa	acific w	valrus	population,	based or	1
recent data a	nd with catch reduced l	у 10% ре	r year a	after 19	986.ª			

Year	Population 1 January	Recruits at 6 yr	Total catch	Estimated kill (catch + losses)
1980	246,140	11,322	5,553	8,531
1981	232,918	10,192	6,670	9,853
1982	225,427	8,975	6,378	9,125
1983	224,947	7,805	5,835	8,355
1984	215,959	6,385	10,272	14,620
1985	204,135	3,812	8,917	13,516
1986	197,268	2,510	7,985	11,663
1987	189,270	4,336	7,263	10,497
1988	183,519	5,611	6,537	9,447
1989	179,245	5,494	5,883	8,502
1990	176,400	5,388	5,295	7,652
1991	174,840	6,173	4,765	6,887
1992	174,437	6,973	4,289	6,198

^a Assumed parameters: 1980 population size based on Gilbert (1989); structure 73% "adults" 6 yr old and older (27% male, 46% female: after Fay 1982); survival rate 0.97 for adults (after DeMaster 1984a), 0.95 for 1- to 5-yr-olds, and 0.2 for calves in 1980 (after Fay and Kelly 1988), increasing by 0.025 per year thereafter; fecundity follows Figure 2 to 1985, constant thereafter at 1980–85 mean of 0.31; recruitment based on relative strength of immature cohorts in 1981–84 samples (Fay and Kelly 1988); kill with ratio of catch: loss at 7:3 and overall kill of calves at 0.4 × kill of adult females, to allow for hunter selection.

and because of large sampling errors and wide confidence limits, the trends are believable only in retrospect, a decade or more after any change has taken place (Fay et al. 1986). Even the density-dependent changes recognized by the walrus hunters, who are closest to the resource, although useful are historical, for they are the climax of processes begun several years before. They usually are perceived too late to be the basis for appropriate remedial action.

To overcome this excessive delay in managerial responses, there is a need for more sensitive, more reliable monitoring that can provide information not only about the *status quo* but about the processes in motion that could have a significant effect several years in the future. For example, a means to measure the survival rates of the young and the recruitment into the adult population could contribute the kind of complementary information needed for prediction and far-sighted management.

Compounding the problems of the mismatched management system is the mismatch of political systems and consequent shortage of constructive communication between the U.S.A. and the U.S.S.R., the two nations that are mutually responsible for managing the Pacific walrus population. Walruses are a shared resource of considerable economic value to both countries, but management of them continues to be separate and unilateral. In the past, this has sometimes worked to the other country's disadvantage and often to the walrus' detriment. An obvious solution to this part of the problem is to implement an

international agreement that would require communication, consensus, and joint management by the two countries.

ACKNOWLEDGMENTS

The work on which this paper is based was supported primarily by the U.S. Department of Interior, Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration under the Outer Continental Shelf Environmental Assessment Program. Partial support was received also from the Division of Polar Programs, National Science Foundation, through grant number DPP-8520912, as well as from contractual arrangements between the University of Alaska, the U.S. Fish and Wildlife Service, and the Alaskan Eskimo Walrus Commission, and lastly from the University of Alaska's funding for Organized Research. We are indebted also for assistance from the Alaska Department of Fish and Game, especially via J. J. Burns, S. J. Harbo, R. R. Nelson and T. E. Smith; from the U.S. Fish and Wildlife Service via A. W. Johnson, R. D. Jones and K. W. Kenyon; from the Eskimo Walrus Commission via A. Akeya, E. Apatiki, M. Iya and K. R. Lourie; and from the Soviet All-Union and Pacific Research Institutes of Fisheries and Oceanography via L. A. Popov, IU. A. Bukhtiiarov, G. A. Fedoseev, V. N. Gol'tsev and A. A. Kibal'chich. We thank J. W. Brooks, J. J. Burns, E. H. Miller and G. C. Ray, who allowed us to analyze some of their unpublished data and to incorporate them into our assessment. We also thank J. J. Burns, L. L. Eberhardt, J. R. Gilbert, G. C. Ray, D. Wartzok and two anonymous reviewers for constructive comments on earlier drafts of the manuscript.

LITERATURE CITED

- ALLEN, J. A. 1880. History of North American pinnipeds: a monograph of the walruses, sea-lions, sea-bears and seals of North America. Miscellaneous Publications No. 12, U.S. Geological and Geographical Survey of the Territories, Washington, DC. 785 pp.
- Allen, J. A. 1895. A synopsis of the pinnipeds, or seals and walruses, in relation to their commercial history and products. Pages 367–391 in Fur seal arbitration, Vol. 1. 53rd Congress, 2nd Session, Senate Executive Document 177. Government Printing Office, Washington, DC.

 Belopol'skii, L. O. 1939. On the migrations and the ecology of reproduction of the
- Belopol'skii, L. O. 1939. On the migrations and the ecology of reproduction of the Pacific walrus (*Odobaenus rosmarus divergens* Illiger). (Fisheries Research Board of Canada Translation Series No. 246) Zoologicheskii Zhurnal 18:762–774.
- Berkh, V. N. 1823. A chronological history of the discovery of the Aleutian Islands, or the exploits of Russian merchants, with a supplement of historical data on the fur trade. (Translated by D. Krenov) Materials for the study of Alaska history, No. 5. The Limestone Press, Kingston, Ontario, 1974.
- 5. The Limestone Press, Kingston, Ontario, 1974.

 BOCKSTOCE, J. R., AND D. B. BOTKIN. 1982. The harvest of Pacific walruses by the pelagic whaling industry, 1848 to 1914. Arctic and Alpine Research 14:183–188.
- Brooks, J. W. 1953. The Pacific walrus and its importance to the Eskimo economy. Transactions of the North American Wildlife Conference 18:503–510.
- Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Department of Fish and Game, Juneau, AK. 48 pp.
- CLARK, A. H. 1887. The Pacific walrus fishery. Pages 313–318 in G. B. Goode, ed. The fisheries and fishery industries of the U.S., Vol. 2, Sec. 5. Government Printing Office, Washington, DC.
- DeMaster, D. P. 1984a. An analysis of a hypothetical population of walruses. Pages 77–80 in F. H. Fay and G. A. Fedoseev, eds. Soviet-American cooperative research on marine mammals, Vol. 1—Pinnipeds. NOAA Technical Report NMFS 12.

- DeMaster, D. P. 1984b. A review of density dependence in marine mammals. Pages 139–148 in B. R. Melteff and D. H. Rosenberg, eds. Proceedings of the workshop on biological interactions among marine mammals and commercial fisheries in the southeastern Bering Sea. Alaska Sea Grant Program, University of Alaska, Fairbanks, AK.
- EBERHARDT, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation 4:205–212.
- EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.
- Estes, J. A. 1979. Exploitation of marine mammals: *r*-selection of *K*-strategists? Journal of the Fisheries Research Board of Canada 36:1009–1017.
- ESTES, J. A., AND J. R. GILBERT. 1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). Journal of the Fisheries Research Board of Canada 35:1130–1140.
- Estes, J. A., and V. N. Gol'tsev. 1984. Abundance and distribution of the Pacific walrus, *Odobenus rosmarus divergens*: results of the first Soviet-American joint aerial survey, autumn 1975. Pages 67–76 in F. H. Fay and G. A. Fedoseev, eds. Soviet-American cooperative research on marine mammals, Vol. 1—Pinnipeds. NOAA Technical Report NMFS 12.
- FAY, F. H. 1957. History and present status of the Pacific walrus population. Transactions of the North American Wildlife Conference 22:431–443.
- FAY, F. H. 1981. Modern populations, migrations, demography, trophics, and historical status of the Pacific walrus. Environmental Assessment of the Alaskan Continental Shelf, Annual Reports of Principal Investigators for the year ending March 1981 1: 191–233. NOAA, National Ocean Service, Anchorage, AK.
- FAY, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North American Fauna 74:1–279.
- FAY, F. H., AND B. P. KELLY. 1980. Mass natural mortality of walruses (*Odobenus rosmarus*) at St. Lawrence Island, Bering Sea, autumn 1978. Arctic 33:226–245.
- FAY, F. H., AND B. P. KELLY. 1988. Development of a method for monitoring the productivity, survivorship, and recruitment of the Pacific walrus population. Final report, order no. 14908. Minerals Management Service, Anchorage, AK. 62 pp.
- FAY, F. H., AND S. W. STOKER. 1982a. Analysis of reproductive organs and stomach contents from walruses taken in the Alaskan native harvest, spring 1980. Final report, contract 14-16-0007-81-5216. U.S. Fish and Wildlife Service, Anchorage, AK. 86 pp.
- FAY, F. H., AND S. W. STOKER. 1982b. Reproductive success and feeding habits of walruses taken in the 1982 spring harvest, with comparisons from previous years. Final report. Eskimo Walrus Commission, Nome, AK. 91 pp.
- FAY, F. H., IU. A. BUKHTHAROV, S. W. STOKER AND L. M. SHULTS. 1984. Foods of the Pacific walrus in winter and spring in the Bering Sea. Pages 81–88 *in* F. H. Fay and G. A. Fedoseev, eds. Soviet-American cooperative research on marine mammals, Vol. 1—Pinnipeds. NOAA Technical Report NMFS 12.
- FAY, F. H., B. P. KELLY, P. H. GEHNRICH, J. L. SEASE AND A. A. HOOVER. 1986. Modern populations, migrations, demography, trophics, and historical status of the Pacific walrus. U.S. Department of Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program, Final Reports of Principal Investigators 37: 231–376. NOAA, National Ocean Service, Anchorage, AK.
- FEDOSEEV, G. A. 1962. [On the status of the stocks and the distribution of the Pacific walrus]. Zoologicheskii Zhurnal 41:1083–1089.
- Fedoseev, G. A. 1984. [Current status of the population of walruses (*Odobenus rosmarus*) in the eastern Arctic and Bering Sea]. Pages 73–85 *in* V. E. Rodin, A. S. Perlov, A. A. Berzin, G. M. Gavrilov, A. I. Shevchenko, N. S. Fadeev and E. B. Ku-

- cheriavenko, eds. [Marine mammals of the Far-East]. Tikhookeanskii Nauchno-issledovatel'skii Institut Rybnogo Khoziaistva i Okeanografii, Vladivostok.
- Fedoseev, G. A., and V. N. Gol'tsev. 1969. [Age-sex structure and reproductive capacity of the Pacific walrus population]. Zoologicheskii Zhurnal 48:407–413.
- Fedoseev, G. A., and E. V. Razlivalov. 1986. [The distribution and number of walruses in the eastern Arctic and Bering Sea in the autumn of 1985]. Pages 93–98 in L. A. Popov, ed. [Scientific-investigative work on marine mammals of the northern part of the Pacific Ocean in 1984/85]. VNIRO, Ministerstvo Rybnogo Khoziaistva, Moscow.
- Geller, M. KH. 1957. [On the protection of harvested marine mammals of Chukotka]. Okhrana Prirody i Zapovednoe Delo v SSSR 1957:108–117.
- GILBERT, J. R. 1989. Aerial census of Pacific walruses in the Chukchi Sea, 1985. Marine Mammal Science 5:17–28.
- Gol'tsev, V. N. 1968. [Dynamics of coastal herds of the walrus in connection with its distribution and numbers]. Pages 205–215 in V. A. Arsen'ev and K. I. Panin, eds. [Pinnipeds of the northern part of the Pacific Ocean]. Pishchevaia Promyshlennost', Moscow.
- Gol'tsev, V. N. 1972. [Distribution and assessment of numbers of the Pacific walrus in the autumn of 1970]. Pages 25–28 in V. A. Arsen'ev, V. M. Bel'kovich, V. A. Zemskii, B. A. Zenkovich, V. E. Sokolov and K. K. Chapskii, eds. [Theses of reports of the 5th all-union conference of studies of marine mammals, part 1]. Akademiia Nauk SSSR, Makhachkala.
- Gol'tsev, V. N. 1976. [Aerial survey of the Pacific walrus in the Soviet sector in the autumn of 1975]. Unpublished report. Tikhookeanskii Nauchno-issledovatel'skii Institut Rybnogo Khoziaistva i Okeanografii, Magadan. 22 pp.
- HUGHES, C. C. 1960. An Eskomo village in the modern world. Cornell University Press, Ithaca, NY.
- JOHNSON, A., J. BURNS, W. DUSENBERRY AND R. JONES. 1982. Aerial survey of Pacific walrus, 1980. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK. 44 pp.
- Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25–28 April 1960. Unpublished report. U.S. Bureau of Sport Fisheries and Wildlife, Seattle, WA. 39 pp.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna 68:1–352.
- Kenyon, K. W. 1972. Aerial surveys of marine mammals in the Bering Sea, 6–16 April 1972. Unpublished report. U.S. Bureau of Sport Fisheries and Wildlife, Seattle, WA. 79 pp.
- KLEINENBERG, S. E. 1957. [On protection of the walrus]. Priroda (Moscow) 1957(7): 101–103.
- KROGMAN, B. D., H. W. BRAHAM, R. M. SONNTAG AND R. G. PUNSLEY. 1986. Early spring distribution, density, and abundance of the Pacific walrus (*Odobenus rosmarus*) in 1976. U.S. Department of Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program, Final Reports of Principal Investigators 37:471–525. NOAA, National Ocean Service, Anchorage, AK.
- Krylov, V. I. 1965. [Determination of age, rate of growth and analysis of the age structure of the catch of the Pacific walrus.] Pages 201–211 in E. N. Pavlovskii, B. A. Zenkovich, S. E. Kleinenberg and K. K. Chapskii, eds. [Marine mammals]. Nauka, Moscow.
- Krylov, V. I. 1966. [On sexual maturation of females of the Pacific walrus]. Zoolo-gicheskii Zhurnal 45:919–927.
- Krylov, V. I. 1968. [On the present status of stocks of the Pacific walrus and prospects of their rational exploitation]. Pages 189–204 in V. A. Arsen'ev and K. I. Panin,

- eds. [Pinnipeds of the northern part of the Pacific Ocean]. Pishchevaia Promyshlennost', Moscow.
- Laws, R. M. 1956. Growth and sexual maturity in aquatic mammals. Nature (London) 178:193–194.
- Laws, R. M. 1981. Large mammal feeding strategies and related overabundance problems. Pages 217–232 in P. A. Jewell, S. Holt and D. Hart, eds. Problems in management of locally abundant wild mammals. Academic Press, London.
- LOWRY, L. F., AND FAY, F. H. 1984. Seal eating by walruses in the Bering and Chukchi seas. Polar Biology 3:11–18.
- Muir, J. 1917. The cruise of the Corwin. Houghton-Mifflin, Boston.
- MURIE, O. J. 1936. Notes on the mammals of St. Lawrence Island, Alaska. Pages 337—346 in O. W. Geist and F. G. Rainey, eds. Archaeological excavations at Kukulik, St. Lawrence Island, Alaska. Miscellaneous Publications of the University of Alaska no. 2. Government Printing Office, Washington, DC.
- NECHIPORENKO, G. P. 1927. [The walrus harvest in Chukotka]. Ekonomicheskaia Zhizn' Dalnego Vostoka 5:169–177.
- Nelson, E. W., and F. W. True. 1887. Mammals of northern Alaska. Pages 227–293 in H. W. Henshaw, ed. Report upon natural history collections made in Alaska between the years 1877 and 1881 by Edward W. Nelson. No. III Arctic Series of Publications Issued in Connection with the Signal Service, U.S. Army. Government Printing Office, Washington, DC.
- Nikulin, P. G. 1941. [The Chukchi walrus]. Izvestiia Tikhookeanskogo Nauchno-Issledovatel'skogo Instituta Rybnogo Khoziaistva i Okeanografii 20:21–59.
- Ogney, S. I. 1935. Mammals of the USSR and adjacent countries, vol. III. Carnivora (Fissipedia and Pinnipedia). (Translated by A. Birron and Z. S. Cole) Israel Program for Scientific Translations, Jerusalem, 1962. 656 pp.
- RAY, G. C. 1981. The role of large organisms. Pages 397–413 in A. R. Longhurst, ed. Analysis of marine ecosystems. Academic Press, London.
- Sease, J. L. 1986. Historical status and population dynamics of the Pacific walrus. Unpublished M.S. thesis. University of Alaska, Fairbanks, AK. 213 pp.
- Sease, J. L., and D. G. Chapman. 1988. Pacific walrus, *Odobenus rosmarus divergens*. Pages 17–38 in J. W. Lentfer, ed. Selected marine mammals of Alaska: species accounts with research and management recommendations. Marine Mammal Commission, Washington, DC.
- Sease, J. L., and F. H. Fay 1987. The walrus. Pages 357–368 in R. L. DiSilvestro, ed. Audubon wildlife report 1987. Academic Press, New York.
- TIKHMENEV, P. A. 1861–63. A history of the Russian-American Company. (Translated by R. A. Pierce and A. S. Donnelly) University of Washington Press, Seattle, WA, 1978. 522 pp.
- Zenkovich, B. A. 1938. [Development of the harvest of marine mammals in Chukotka]. Priroda (Moscow) 1938(11–12):59–63.

Received: January 9, 1987 Accepted: August 19, 1988