

Demographic Consequences of Changed Pupping and Hauling Sites of the Hawaiian Monk Seal

TIM GERRODETTE*

Southwest Fisheries Science Center
Honolulu Laboratory
National Marine Fisheries Service, NOAA
2570 Dole Street
Honolulu, HI 96822, U.S.A.

WILLIAM G. GILMARTIN

Southwest Fisheries Science Center
Honolulu Laboratory
National Marine Fisheries Service, NOAA
2570 Dole Street
Honolulu, HI 96822, U.S.A.

Abstract: During the last 30 years, changes in the size of Hawaiian monk seal populations at several locations have been associated with the amount and type of human disturbance. Recreational beach activities caused monk seals to alter their pupping and hauling patterns. Survival of pups in suboptimal habitats was low, leading to gradual population declines. During the last decade at Kure Atoll, the process has been reversed: human disturbance on beaches has decreased, and traditional pupping and hauling sites have been reestablished. Subsequently, high survival rates of young seals, coupled with two successful enhancement programs for female pups, have led to dramatic changes in the age and sex composition of the population. Based on these changes, the monk seal population at Kure Atoll soon should begin to increase. Apparently small behavioral changes in such vital activities as feeding and reproduction can have large demographic consequences. Therefore, monitoring of endangered species should include data on habitat use and age and sex composition, as well as estimates of abundance.

Resúmen: Durante los últimos treinta años, los cambios en el tamaño de las poblaciones de la foca de Hawai en varias localidades, han sido asociados con la cantidad y el tipo de perturbación humana. Las actividades recreativas en las playas causaron que las focas alteraran su patrones de procreación y alimentación. La sobrevivencia de los cachorros en habitats subóptimos fué muy baja originando la disminución gradual de las poblaciones. Durante la última década, en Kure Atoll, el proceso ha sido revertido: la perturbación humana en las playas ha disminuido y los lugares tradicionales de procreación y alimentación han sido reestablecidos. Subsecuentemente, los altos índices de sobrevivencia de las focas jóvenes, aparejados con dos exitosos programas para acrecentar los cachorros hembra, han producido cambios dramáticos en la composición, en edad y sexo, de la población. Basado en estos cambios, la población de la foca de Hawai en Kure Atoll debería de empezar a incrementarse pronto. Los cambios aparentemente pequeños en actividades vitales como la alimentación y la reproducción pueden tener grandes consecuencias demográficas. Por lo tanto, el monitoreo de las especies en peligro debe de incluir datos sobre el uso del hábitat y la composición en cuanto a la edad y el sexo así como cálculos estimados sobre la abundancia.

Paper submitted November 29, 1989; revised manuscript accepted July 16, 1990.

* Present address: Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, U.S.A.

"The primary cause of the decay of organic diversity is not direct human exploitation or malevolence, but the habitat destruction that inevitably results from the expansion of human populations and human activities" (Ehrlich 1988).

It is widely recognized that anthropogenic destruction of habitat is a leading cause of the loss of species diversity on Earth. Clearing of rain forests and draining of wetlands are obvious examples, but "destruction" of habitat also can be more subtle. It need not involve physical alteration of habitat. Seemingly benign human activities can cause small but important changes in a species' behavior that, by their demographic effects, can have major population consequences. This is clearly demonstrated by the recent history of Hawaiian monk seals (*Monachus schauinslandi*).

With few exceptions, Hawaiian monk seals live and breed only in the Northwestern Hawaiian Islands (Kenyon & Rice 1959; Kenyon 1981), a 1800-km string of small, mostly uninhabited islands forming the northwestern end of the Hawaiian Archipelago. The Hawaiian Islands National Wildlife Refuge includes most of the range of the Hawaiian monk seal. Because of an apparently low rate of migration between islands (Johnson & Kridler 1983), monk seals form somewhat discrete populations at eight islands or atolls. Following a general population decline in the 1960s and 1970s, the species was declared endangered in 1976 under provisions of the U.S. Endangered Species Act (Gilmartin 1983).

A particularly sharp decline has occurred in the monk seal population at Kure Atoll (28°25'N, 178°10'W), which lies at the northwestern end of the Hawaiian chain. Beach counts of adult seals declined from over 100 in the late 1950s to about 30 in the late 1970s to less than 14 in the late 1980s (Table 1). The number of pups born at Kure Atoll similarly declined from about 30 per year to 10 and then to a mean of 5 during the same period (Table 1). A low point was reached in 1986 when only a single pup was born.

The following account of the decline of monk seals

and their potential recovery at Kure Atoll draws on seal counts and observations over several decades. Numerous beach counts of monk seals have been made annually at Kure Atoll since 1981 by the National Marine Fisheries Service (NMFS) using a uniform methodology. Earlier counts by various researchers at less regular intervals used procedures that varied somewhat. Because the number of seals hauled out varies by time of day and time of year, in this report we have made pre-1981 data comparable by selecting only beach counts begun between 1200 and 1500 hours of each day and 1 March and 30 September of each year. Unless noted otherwise, seal counts include all seals counted on the beach except pups of the year.

Causes of the Decline

The emergent land at Kure Atoll consists of a single, permanent, vegetated island, Green Island, and several much smaller sand islets. Before human occupation, Green Island was the favored site for pupping and hauling out. The number of seals hauling out on Green Island declined after 1960 when the U.S. Coast Guard (USCG) built a loran station there (Fig. 1). Dogs and recreational beach activities of the 20–25 men at the station, primarily beachcombing for Japanese glass fishing floats, caused the seals to abandon the preferred Green Island beaches and haul out on the sand islets instead (Kenyon 1972). The converse effect has been observed on Tern Island at French Frigate Shoals, a multi-island atoll 1,350 km to the southeast. For more than two decades while a loran station was in operation on Tern Island, few seals were ever seen, but the number of seals using the island increased sharply after the USCG vacated the station in 1979 (Fig. 1). In 1988, the highest of the weekly seal counts on Tern Island was 118, and the March–September mean was 61.4.

The immediate effect of human beach activity on the choice of monk seal hauling sites is thus clear, but the

Table 1. Numbers of pups born, mean adult beach counts, and relative pupping rates (ratio of pups to adult beach count) at Kure Atoll for selected years, 1957–1988 (* = incomplete pup count; ** = single adult beach count).

Year	Number of pups born	Mean adult beach count	Relative pupping rate	Reference
1957	23*	79**	0.29	Kenyon & Rice 1959
1958	25*	107**	0.23	Rice 1960
1964	32			Wirtz 1968
1965	30			Wirtz 1968
1977	10	31.0	0.32	Johnson et al. 1982a
1978	10	33.0	0.30	Rauzon 1978
1985	5	14.1	0.35	Reddy & Griffith 1988
1986	1	11.5	0.09	NMFS unpublished data
1987	6	11.8	0.51	Reddy 1989
1988	8	13.1	0.61	Henderson & Finnegan 1990

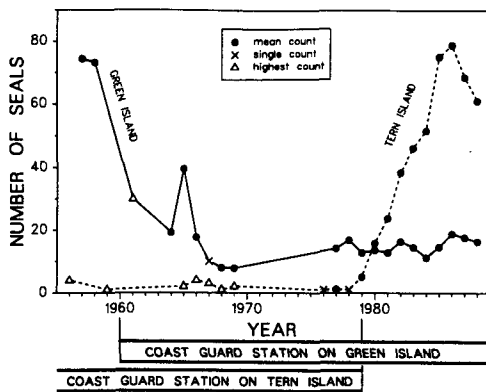


Figure 1. Number of Hawaiian monk seals bauled out on Green Island, Kure Atoll, and Tern Island, French Frigate Shoals, 1956–1988. Filled circles indicate a mean count, triangles a maximum of several counts, and x's a single count. The U.S. Coast Guard built a loran station on Green Island in 1960 and vacated a loran station on Tern Island in 1979. The U.S. Fish and Wildlife Service took over the Tern Island station in 1979 and has operated it as a field research station since. (Sources: Svibla 1957; Udvardy & Warner 1964; Amerson 1971; Kenyon 1972; Schulmeister 1981; DeLong et al. 1976; Fiscus et al. 1978; Rauzon 1978; Johnson et al. 1982b; Gilmartin 1983; Gilmartin et al. 1986; Reddy & Griffith 1988; Reddy 1989; NMFS unpublished data.)

demographic effects of changed pupping and hauling sites are less obvious and require a longer time to express themselves. In the absence of human disturbance, seals use the optimal sites available for their activities; a change to suboptimal sites may lead to higher mortality, lower fecundity, or both. After the establishment of the loran station on Green Island in 1960, fecundity, as indicated by number of pups per adult, did not decline (Table 1). However, pup mortality was very high (Wirtz 1968), and few immature seals were seen (Johnson et al. 1982a). There are no data on nonpup mortality rates. The virtual lack of immature seals, together with the steady decline in beach counts and number of births over several decades, is consistent with the hypothesis, first advanced by Kenyon (1972), that changed pupping and hauling sites lead to high postnatal mortality, low recruitment, and a gradually senescent population.

Several proximate causes of high postnatal mortality in Hawaiian monk seals are probable. First, preferred pupping sites have a calm nearshore area where pups, which are weak swimmers, develop their swimming ability (Westlake & Gilmartin 1990); however, the sand

islets at Kure Atoll change size and shape frequently, and large waves may wash over them entirely. At other locations, we have observed pups swept out to sea and not returning. Second, sharks, especially large tiger sharks (*Galeocerdo cuvier*), are common near shore during the seal pupping season, apparently attracted by fledging albatross (*Diomedea immutabilis* and *D. nigripes*) chicks, which are unable to fly out of the water after swimming offshore or landing in the water. Shark predation is indicated by wounds on seals (Kenyon 1973), seal remains in shark stomachs (Taylor & Naftel 1978), and direct observation (Balazs & Whitrow 1979; Alcorn & Kam 1986; Johanos & Kam 1986; Johanos & Austin 1988). Pupping locations on Green Island have shallow nearshore waters that probably offer some protection from sharks, but the sand islets do not.

Finally, the phocid pattern of maternal care makes the postnatal period a particularly vulnerable stage in the life cycle. Phocids (true seals) have a high rate of energy transfer from mother to pup during a short nursing period, terminated by an abrupt weaning (Oftedal et al. 1987). Hawaiian monk seal pups nurse for 35–40 days, during which the mother is in constant attendance to her pup and does not feed. The amount of energy transferred to the pup during the nursing period is critical since, after weaning, the pup must live on its fat reserves until it learns to feed on its own. Immature survival rates are positively correlated with weaning size in the Hawaiian monk seal (unpublished data) and other phocids (Coulson & Hickling 1964; Hill 1987). Repeated interruption or stress during the nursing period reduces the amount of milk the pup receives and its subsequent likelihood of survival. Disruption of normal maternal care has been a factor in the decline of many threatened and endangered mammals (Oldfield 1988).

Similar factors related to human disturbance have altered monk seal population sizes at two other atolls, Midway Islands and French Frigate Shoals, although data are less complete than at Kure Atoll. Midway Islands became an active U.S. naval base in the early 1940s. If monk seals there reacted to human activity as they did at Kure Atoll, the seal decline was well under way when the first detailed counts were made in the late 1950s (Kenyon & Rice 1959). The rate of abortions, stillbirths, and preweaning deaths was a very high 46% at that time (Rice 1960). By the late 1960s, only a few seals were seen (Kenyon 1972), a situation that continues to the present. Thus, the monk seal decline at Midway Islands apparently took about 25–30 years, the same length of time as the decline at Kure Atoll and, not coincidentally, about the apparent lifespan of these seals (Kenyon 1981; unpublished data).

On the other hand, the monk seal population at French Frigate Shoals increased substantially between the late 1950s and the late 1970s (Johnson et al. 1982a), a puzzling anomaly against the general decline

at most locations during this period. However, the increase makes sense if we consider the pattern of human disturbance. The primary pupping site at French Frigate Shoals is East Island (Westlake & Gilmartin 1990). A USCG loran station was located on East Island from 1944 to 1952 (Amerson 1971). East Island is much smaller than Green Island, and the disruption of pupping was undoubtedly greater. The loran station was moved to Tern Island in 1952, and monk seals avoided that location until the station ceased operation in 1979 (Fig. 1). Because Tern Island is not used for pupping, it is possible that pupping at the atoll returned to nearly normal once human activity around East Island stopped. Thus, the 1956–1958 seal counts at French Frigate Shoals were probably made at a low point, and with decreased human disturbance at the primary pupping island, the population recovered over the next two decades. The lack of juvenile and subadult seals at French Frigate Shoals in 1958 and the high proportion of them in 1977 (Johnson et al. 1982a) are consistent with this explanation.

Monk seal populations have declined at other locations in the Northwestern Hawaiian Islands (Johnson et al. 1982a), where human activity has been less intense. All of the islands, however, have suffered various degrees of human disturbance from a combination of shipwrecks; visits by fishermen; military activity; scientific research, including collections; and, in the more distant past, sealers, turtle hunters, guano miners, and seabird egg and feather collectors (Amerson 1971; Woodward 1972; Amerson et al. 1974; Clapp & Kridler 1977; Clapp et al. 1977; Ely & Clapp 1973; Clapp & Wirtz 1975). Other known sources of mortality include disease (Gilmartin et al. 1980), shark predation (Alcorn & Kam 1986), adult male aggression (Johnson & Johnson 1981; Johanos et al. 1987; Alcorn 1984; Johanos & Austin 1988), and entanglement in debris (Henderson 1984, in press). Data are insufficient to assess the relative contribution of these sources of mortality to the population declines at the other islands.

Changes Leading to Recovery

After the Hawaiian monk seal was declared an endangered species in 1976, management actions were undertaken to assist its recovery. The USCG modified its regulations at Kure Atoll to reduce disturbance to seals. Dogs were banned from the station, recreational driving of vehicles on the beaches was eliminated, and seal refuge areas with restricted access were established at the north end of Green Island and on the sand islets. The immediate effects of these changes on seal behavior are difficult to quantify since no data are available from the early 1970s. The biggest documented changes occurred

after 1981, when NMFS began an annual research program there. Seals began pupping on Green Island again (Fig. 2); in fact, since 1982, 33 of the 35 births at Kure Atoll have occurred on Green Island. Also, seals once again began using Green Island as the main haul-out area (Fig. 2). The fraction of seals presently using Green Island for hauling out (about 0.60–0.65) is far above the figure of 0.16 recorded in 1968 when disturbance was high, but is still below the figure of 0.72 in the late 1950s before the station was built (Kenyon 1972). The fraction of seals using Green Island is significantly higher after 1980 for both hauling out ($P < 0.05$) and pupping ($P < 0.005$, rank-sum test, two-tailed). We believe these changes in the seals' behavior result from changes in the behavior and attitude of USCG personnel toward monk seals; the latter changes, in turn, result from (1) restrictions on beach activities beginning in 1976; and (2) an increased awareness of and concern for the plight of the monk seals beginning in 1981, coincident with the NMFS research presence.

Beach counts have indicated that there are about three adult male seals for each adult female at Kure Atoll. The reasons for this excess of males, which also occurs at some but not all other locations, are a current focus of research. Because of the declining number of females and the unbalanced sex ratio, two programs aimed at increasing the number of female seals were initiated in recent years at Kure Atoll. The first project, "Headstart," was begun in 1981 and continues to the present. Female pups have been collected after weaning, tagged on the rear flippers, and placed in a large (ca. 40

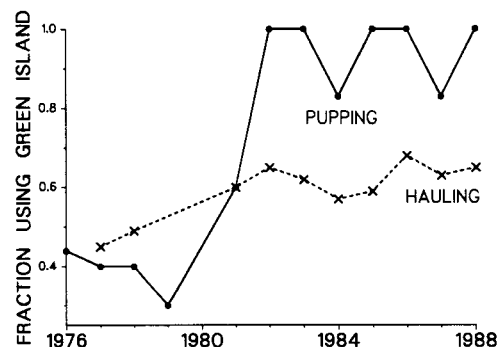


Figure 2. Fraction of Hawaiian monk seals at Kure Atoll using Green Island for pupping (●) and hauling (x), 1976–1988. (Sources: DeLong et al. 1976; Fiscus et al. 1978; Rauzon 1978; Rauzon et al. 1978; Johnson et al. 1982a; Johnson et al. 1982b; Gilmartin et al. 1986; Reddy & Griffith 1988; Reddy 1989; NMFS unpublished data.)

m × 60 m) fenced beach enclosure with equal areas of sand and water (Gilmartin et al. 1986). The enclosure is stocked with live fish trapped on nearby reefs. Female pups are kept in the enclosure throughout the summer months and released in September of each year, at 3–7 months of age. Male pups are similarly tagged after weaning but not placed in the enclosure. Survival rates from weaning to one year have been higher for the protected females ($14/15 = 0.93$) than for the unprotected males ($14/17 = 0.82$). The difference is not significant based on a chi-square test ($= 0.05$), but with this small sample, the probability of detecting such a difference is low ($1 - < 0.2$) (Cohen 1988). The median annual survival rate of all seals from 1 to 4 years of age has been 0.94 (Gilmartin et al. 1987). These high survival rates since 1981, even for male pups not given the extra protection of the enclosure, coincide with the shifts in pupping and hauling sites (Fig. 2).

In the second program, begun in 1984 at French Frigate Shoals where the population is larger, severely underweight female pups are collected after weaning, treated and fed in Honolulu, and released as yearlings at Kure Atoll the following spring (Gilmartin & Gerrodette 1986). Six of the eight seals so treated and released through 1987 were alive at Kure Atoll in 1988, one had emigrated to Midway Islands, and one was not seen in 1988.

The female pup enhancement programs, while involving a small number of animals, have thus been extremely effective at a critical stage in the life cycle. Equally important, the shifts in pupping and hauling sites have resulted in high survival rates for all immature seals since 1981. The cumulative demographic effect on this small population has been substantial. Although the number of seals at Kure Atoll remains low, the decline has been halted. The total number of seals has not changed much since 1981, but a large shift in the age and sex composition has occurred (Fig. 3). Before 1981 immature seals (approximately ages 1–5 for females, 1–6 for males) were rarely seen; now they constitute half the population. Moreover, in contrast to adults, the sex ratio in the immature portion of the population is 2:1 in favor of females. The number of births is increasing after reaching a low of a single pup in 1986. All eight seals who gave birth at Kure Atoll in 1988 were identified; five of them are known to have first pupped in 1987 or 1988, a sixth first pupped in 1984, and the ages of the other two mothers are unknown. Because monk seals may live to 25 years or more, the breeding population as well as the total population is now quite young. The high pupping rates in 1987 and 1988 (Table 1) may be the result of a young and more fecund breeding population, but the sample sizes are small and the high pupping rates could have occurred by chance alone. In any case, if fecundity remains at least at its historical level and sur-

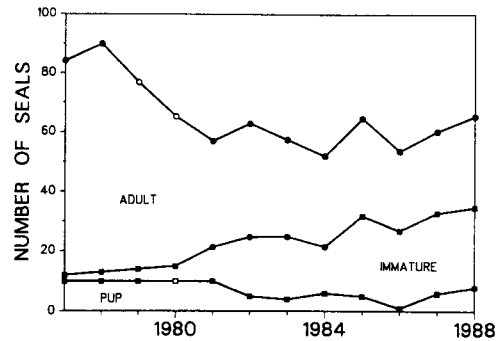


Figure 3. Number of Hawaiian monk seals in each of three age categories at Kure Atoll, 1977–1988. Pups are seals born in that year; immatures are seals 1 year and older but less than adult size; adults are seals of full adult size or observed breeders. Squares indicate a completely known cohort of tagged or individually recognizable seals. Circles indicate number of seals estimated from a mean beach count based on the mean observed haul-out fraction of immature seals from 1985 to 1988. Open symbols indicate points estimated from partial data. (Sources: Rauzon 1978; Johnson et al. 1982a; Johnson et al. 1982b; Gilmartin et al. 1986; Reddy & Griffith 1988; Reddy 1989; NMFS, unpublished data.)

vival remains as high as it has been since 1981, the population soon should begin to increase.

Conclusions

We are cautiously optimistic for growth of the monk seal population at Kure Atoll in the near future. The causes of the seals' decline were reversible, and the seals' responses to changes in human behavior have been dramatic and well documented. Monk seals and humans can coexist on these islands if humans do not disrupt the seals' vital activities of hauling out, pupping, and feeding. This has been clearly demonstrated by the seals' increased use of Tern Island after 1979 when the USCG Ioran station was replaced by a USFWS field station (Fig. 1; Schulmeister 1981). Under the USFWS, access to the beach at Tern Island, as well as elsewhere in the atoll, has been strictly limited to necessary research, and the researchers make special efforts to avoid disturbing the seals (USFWS 1986).

Our findings have applications to a related endangered species, the Mediterranean monk seal (*M. monachus*). That species is declining rapidly in abundance, and exists only as small scattered colonies around islands in the Mediterranean Sea and eastern subtropical

Atlantic Ocean (Sergeant 1984). Habitat loss, pollution, and shootings by fishermen are thought to be primary causes of the decline, but indirect human effects may be operating as well, as in the Hawaiian case. It is clear from their remaining distribution in only the most remote locations that Mediterranean monk seals avoid human activity. Because of this avoidance, the seals may be using suboptimal pupping, hauling, and feeding sites. In the past, the Mediterranean monk seal apparently used sandy beaches (Ronald & Yeroulanos 1984), as the Hawaiian species does, but now hauling and pupping are confined to caves. Lower fecundity and survival rates at such sites could be contributing to the population decline. On the positive side, the success of the Hawaiian monk seal pup relocation program from French Frigate Shoals to Kure Atoll has shown that seals will tend to remain at a new location if moved when young and held in semicaptivity before release. If sanctuary areas with suitable habitat could be identified for the Mediterranean monk seal (Avella 1984; Biscoito 1984; Ronald & Yeroulanos 1984), it might be possible to establish or increase populations at these sanctuaries by moving young seals from areas where conflicts with humans are a problem.

The case of the Hawaiian monk seal at Kure Atoll also has lessons for monitoring endangered species in general. First, monitoring should include more than estimates of population size. Estimating population size (or an index of population size) over time is a necessary but insufficient condition for monitoring. Factors that indicate the condition of a population can alert wildlife managers to incipient problems at an earlier stage (Eberhardt & Siniff 1977; Gerrodette & DeMaster 1990). Such factors could include individual physiological condition (growth rate, size, weight, and disease), behavioral observations (mating, nesting, feeding, and social interactions), and demographic characteristics of the population (age, stage, size, and sex composition). The decline of the monk seal population at Kure Atoll would have been detected earlier if, for example, the size composition of the population had been recorded as well as total seal count. Even today, after more than a decade of effort at restoring the population, total counts of monk seals at Kure Atoll have not changed very much. Our optimism for the future growth of the population comes from a more detailed consideration of the changing age and sex structure of the population (Fig. 3).

Second, monitoring requires a long-term commitment. Many "charismatic" endangered species are characterized by long lives and low rates of reproduction. For animals and plants with such life histories, changes in population size may occur slowly—excepting, of course, catastrophic mortality or rapid habitat destruction. Changes in the monk seal population at Kure Atoll are clear from the perspective of several decades, but

less clear at other locations where fewer counts have been made.

Third, a species' habitat may be made unsuitable in subtle ways. Recent declines of Hawaiian monk seals in the presence of humans were not caused by malevolence or even by habitat alteration in the usual sense. Apparently benign human activities caused small behavioral changes that had large population effects. Beachcombing, jogging, and similar activities may have seemed innocuous, yet there is little question that Hawaiian monk seals would have been extirpated at Kure Atoll had changes not been made. Every species requires suitable habitat to carry out its vital activities, and the denial of access to such critical habitat kills as surely as direct exploitation.

Acknowledgments

We thank the U.S. Coast Guard, 14th District, for transportation and logistical support at Kure Atoll. The U.S. Fish and Wildlife Service provided support at Tern Island and allowed use of their seal counts. Comments by Ancel Johnson, Karl Kenyon, Leslie Williams, and the reviewers improved the manuscript. Special thanks are due to the many volunteers who assisted NMFS staff in all aspects of this work. The pup rehabilitation program was partially supported by the Center for Marine Conservation.

Literature Cited

- Alcorn, D. J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFC-42. 37 pp.
- Alcorn, D. J., and A. K. H. Kam. 1986. Fatal shark attack on a Hawaiian monk seal (*Monachus schauinslandi*). *Marine Mammal Science* 2:313–315.
- Amerson, A. B., Jr. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. *Atoll Research Bulletin* 150. 383 pp.
- Amerson, A. B., Jr., R. B. Clapp, and W. O. Wirtz II. 1974. The natural history of Pearl and Hermes Reef, Northwestern Hawaiian Islands. *Atoll Research Bulletin* 174. 306 pp.
- Avella, J. 1984. A plan for the reintroduction of the monk seal (*Monachus monachus*) in the Archipelago of Cabrera, Balearic Islands, Spain. Pages 92–101 in K. Ronald and R. Duguy, editors. *Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Société des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.*
- Balazs, G. H., and G. C. Whittow. 1979. First record of a tiger shark observed feeding on a Hawaiian monk seal. *'Elepaio* 39:107–109.

- Biscoito, M. 1984. On the creation of a natural reserve in the Desertas Islands, Madeira—Portugal. Pages 88–91 in K. Ronald and R. Duguy, editors. Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Société des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.
- Clapp, R. B., and E. Kridler. 1977. The natural history of Necker Island, Northwestern Hawaiian Islands. Atoll Research Bulletin 206. 102 pp.
- Clapp, R. B., E. Kridler, and R. R. Fleeter. 1977. The natural history of Nihoa Island, Northwestern Hawaiian Islands. Atoll Research Bulletin 207. 147 pp.
- Clapp, R. B., and W. O. Wirtz II. 1975. The natural history of Lisianski Island, Northwestern Hawaiian Islands. Atoll Research Bulletin 186. 196 pp.
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates, Publishers, Hillsdale, New Jersey.
- Coulson, J. C., and G. Hickling. 1964. The breeding biology of the grey seal, *Halicobaeus grypus* (Fab.), on the Farne Islands, Northumberland. Journal of Animal Ecology 33:485–512.
- DeLong, R. L., C. H. Fiscus, and K. W. Kenyon. 1976. Survey of monk seal (*Monachus schauinslandi*) populations of the Northwestern (Leeward) Hawaiian Islands. Northwest Fisheries Center Processed Report. 36 pp.
- 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.
- Ehrlich, P. R. 1988. The loss of diversity: causes and consequences. Pages 21–27 in E. O. Wilson and F. M. Peter, editors. Biodiversity. National Academy Press, Washington, D.C.
- Ely, C. A., and R. B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Research Bulletin 171. 361 pp.
- Fiscus, C. H., A. M. Johnson, and K. W. Kenyon. 1978. Hawaiian monk seal (*Monachus schauinslandi*) survey of the Northwestern (Leeward) Hawaiian Islands, July 1978. Northwest and Alaska Fisheries Center Processed Report. 27 pp.
- Gerrodette, T., and D. P. DeMaster. 1990. Quantitative determination of optimum sustainable population level. Marine Mammal Science 6:1–16.
- Gilmartin, W. G. 1983. Recovery plan for the Hawaiian monk seal, *Monachus schauinslandi*. U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Southwest Region, Terminal Island, California. Various paging.
- Gilmartin, W. G., R. L. DeLong, A. W. Smith, L. A. Griner, and M. D. Dailey. 1980. An investigation into unusual mortality in the Hawaiian monk seal, *Monachus schauinslandi*. Pages 32–41 in R. W. Grigg and R. T. Pfund, editors. Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24–25, 1980, University of Hawaii, Honolulu, Hawaii. UNIHI-SEAGRANT-MR-80-04.
- Gilmartin, W. G., and T. Gerrodette. 1986. Hawaiian monk seal population status and recovery potential at Kure Atoll. Southwest Fisheries Center Honolulu Laboratory, Honolulu, HI. Southwest Fisheries Center Administrative Report H-86-16. 26 pp.
- Gilmartin, W. G., T. C. Johanos, and T. Gerrodette. 1987. Preliminary assessment of juvenile Hawaiian monk seal survival. Southwest Fisheries Center Honolulu Laboratory, Honolulu, HI. Southwest Fisheries Center Administrative Report H-87-16. 11 pp.
- Gilmartin, W. G., R. J. Morrow, and A. M. Houtman. 1986. Hawaiian monk seal observations and captive maintenance project at Kure Atoll, 1981. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service. NOAA-TM-NMFS-SWFC-59. 9 pp.
- Henderson, J. R. 1984. Encounters of Hawaiian monk seals with fishing gear at Lisianski Island, 1982. Marine Fisheries Review 46:59–61.
- Henderson, J. R. In press. Recent entanglements of Hawaiian monk seals in marine debris. Second International Conference on Marine Debris, Honolulu, Hawaii.
- Henderson, J. R., and M. R. Finnegan. 1990. Population monitoring of the Hawaiian monk seal, *Monachus schauinslandi*, and captive maintenance project at Kure Atoll, 1988. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-150. 23 p.
- Hill, S. E. B. 1987. Reproductive ecology of Weddell seals (*Lepidonychotes weddelli*) in McMurdo Sound, Antarctica. Ph.D. thesis. University of Minnesota, 106 pp.
- Johanos, T. C., and S. L. Austin. 1988. Hawaiian monk seal population structure, reproduction, and survival on Laysan Island, 1985. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-118. 38 pp.
- Johanos, T. C., and A. K. H. Kam. 1986. The Hawaiian monk seal on Lisianski Island: 1983. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-58. 37 pp.
- Johanos, T. C., A. K. H. Kam, and R. G. Forsyth. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-70. 38 pp.
- Johnson, A. M., R. L. DeLong, C. H. Fiscus, and K. W. Kenyon. 1982a. Population status of the Hawaiian monk seal (*Monachus schauinslandi*), 1978. Journal of Mammalogy 63:415–421.
- Johnson, A. M., and E. Kridler. 1983. Interisland movement of Hawaiian monk seals. *Elepaio* 44:43–45.
- Johnson, A. M., J. Ruehle, K. W. Kenyon, and M. Rauzon. 1982b. Hawaiian monk seal studies, summary report, 1977–1980. Unpublished report. 76 pp. (Available from Marine Mammals and Endangered Species Program, National Marine Fisheries Service Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822).

- Johnson, B. W., and P. A. Johnson. 1981. The Hawaiian monk seal on Laysan Island: 1978. U.S. Department of Commerce, National Technical Information Service, PB82-109661. 17 pp.
- Kenyon, K. W. 1972. Man versus the monk seal. *Journal of Mammalogy* 53:687-696.
- Kenyon, K. W. 1973. Hawaiian monk seal (*Monachus schauinslandi*). Pages 88-97 in proceedings of a working meeting of seal specialists on threatened and depleted seals of the world, held under the auspices of the Survival Service Commission, 18-19 August 1972, at the University of Guelph, Ontario, Canada. International Union for Conservation of Nature and Natural Resources, 1110 Morges, Switzerland.
- Kenyon, K. W. 1981. Monk seals *Monachus* Fleming, 1822. Pages 195-220 in S. H. Ridgway and R. J. Harrison, editors. Handbook of marine mammals. Volume 2: Seals. Academic Press, London, England.
- Kenyon, K. W., and D. W. Rice. 1959. Life history of the Hawaiian monk seal. *Pacific Science* 13:215-252.
- Oftedal, O. T., D. J. Boness, and R. A. Tedman. 1987. The behavior, physiology, and anatomy of lactation in the Pinnipedia. Pages 175-245 in H. H. Genoways, editor. Current Mammalogy. Volume 1. Plenum Press, New York.
- Oldfield, M. L. 1988. Threatened mammals affected by human exploitation of the female-offspring bond. *Conservation Biology* 2:260-274.
- Rauzon, M. J. 1978. Hawaiian monk seal studies at Kure Atoll, 8 March to 19 April 1978. Unpublished report. (Available from Marine Mammals and Endangered Species Program, National Marine Fisheries Service Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822).
- Rauzon, M. J., K. W. Kenyon, and A. M. Johnson. 1978. Observations of monk seals, French Frigate Shoals, 17 February to 27 May 1977. Unpublished report. (Available from Marine Mammals and Endangered Species Program, National Marine Fisheries Service Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822).
- Reddy, M. L. 1989. Population monitoring of the Hawaiian monk seal, *Monachus schauinslandi*, and captive maintenance project for female pups at Kure Atoll, 1987. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-123. 37 pp.
- Reddy, M. L., and C. A. Griffith. 1988. Hawaiian monk seal population monitoring, pup captive maintenance program, and incidental observations of the green turtle at Kure Atoll, 1985. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-101. 35 pp.
- Rice, D. W. 1960. Population dynamics of the Hawaiian monk seal. *Journal of Mammalogy* 41:376-385.
- Ronald, K., and M. Yeroulanos. 1984. A conservation plan for *Monachus monachus* on Greek islands and coasts. Pages 31-40 in K. Ronald and R. Duguy, editors. Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Société des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.
- Schulmeister, S. 1981. Hawaiian monk seal numbers increase on Tern Island. *'Elepaio* 41:62-63.
- Sergeant, D. E. 1984. Review of new knowledge of *Monachus monachus* since 1978 and recommendations for its protection. Pages 21-30 in K. Ronald and R. Duguy, editors. Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Société des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.
- Svihla, A. 1957. Observations on French Frigate Shoals, February 1956. *Atoll Research Bulletin* 51. 2 pp.
- Taylor, L. R., and G. Naftel. 1978. Preliminary investigations of shark predation on the Hawaiian monk seal at Pearl and Hermes Reef and French Frigate Shoals. U.S. Department of Commerce, National Technical Information Service, PB-285-626. 34 pp.
- Urdvardy, M. D. F., and R. E. Warner. 1964. Observations on the birds of French Frigate Shoal and Kure Atoll. *Atoll Research Bulletin* 103. 3 pp.
- U.S. Fish and Wildlife Service. 1986. Hawaiian Islands National Wildlife Refuge, Master plan/environmental impact statement. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Region One. Various paging.
- Westlake, R. L., and W. G. Gilmartin. 1990. Hawaiian monk seal pupping locations in the Northwestern Hawaiian Islands. *Pacific Science* 44:366-383.
- Wirtz, W. O., II. 1968. Reproduction, growth and development, and juvenile mortality in the Hawaiian monk seal. *Journal of Mammalogy* 49:229-238.
- Woodward, P. W. 1972. The natural history of Kure Atoll, Northwestern Hawaiian Islands. *Atoll Research Bulletin* 164. 318 pp.

