UNIVERSITY OF ALBERTA

THE SIGNIFICANCE OF WOUNDING TO THE SURVIVAL OF THE HAWAIIAN MONK SEAL, *Monachus schauinslandi*

BY

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Abstract

The significance of wounds to the Hawaiian monk seal (Monachus schauinslandi) population was assessed by examining their effect on female reproductive success and population dynamics. Six major categories of injuries, observed on monk seals at Laysan Island and French Frigate Shoals (FFS) in the Northwestern Hawaiian Islands, were described. At both locations, injuries inflicted by adult male seals during mobbing incidents, in which several males attempt to mate with one seal, were observed more frequently than other types of injuries. Adult males injured adult females more often than other size classes of seals.

Injuries did not appear to affect a female monk seal's reproductive success if the female was able to recover from her injury before parturition and lactation. Pup production, parental investment and survival of pups of females injured in the previous year were not significantly different from those of uninjured females. Females injured before the pup was born or during lactation had slightly lower pup survivorship than uninjured females. Immature females entering the reproductive population (age 4-7 years) were injured by adult male seals significantly more frequently than females aged 0-3 years but at a similar frequency to adult females, indicating that adult males injure females throughout their breeding lifespan.

Injuries inflicted by adult male monk seals on females occurred mor frequently at Laysan Island, where the adult sex ratio is skewed towards males, than at FFS, where the adult sex ratio is 1:1. The relationship between adult sex ratio and the development of mobbing behaviour was discussed.

Mortality of female monk seals as a result of adult male-inflicted injuries increased over the study period. High adult female mortality reduced the net recruitment of new females to the population. The combination of shark predation and injuries inflicted by adult males may further increase the mortality of female monk seals.

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1. General Introduction

Injuries are generally considered detrimental to animals. The survival of an injured animal may be reduced (Congdon et al. 1974; Willis et al. 1982) or maturation of an injured immature animal can be delayed (Maiorana 1977). Injuries can affect reproductive success in a variety of ways. Reproduction may be suppressed both in the year of the injury (Maiorana 1977) and in the following year, if the animal does not recover from its injury (Clutton-Brock et al. 1979) or if it does not mate (LeBoeuf et al. 1982). The reproductive output, in terms of the size of eggs or number of young, may be reduced in the year of injury (Dial and Fitzpatrick 1981; Maiorana 1977), or an injured parent may not be able to raise its young to independence (LeBoeuf et al. 1982). An injured animal can lose rank in a dominance hierarchy, resulting in lower reproductive success (Clutton-Brock et al. 1979; LeBoeuf and Reiter 1988).

Fresh injuries on an animal can be classified by the context in which they are inflicted. Injuries can indicate an escape from predation, levels of intraspecies aggression in the population, or injury from the environment. Predators larger than the animal may inflict severe and potentially fatal injuries (Smith 1966; Carrick and Ingham 1962; Siniff and Bengtson 1977; Randall et al. 1988). Other injuries from attempted predation are less severe. Predators smaller than the animal may inflict relatively minor injuries (Van Utrecht 1959; Jones 1971; LeBoeuf et al. 1987), or attacks by predators can result in injury such as tail autotomy in salamanders (Maiorana 1977), lizards (Dial and Fitzpatrick 1981) and snakes (Willis et al. 1982).

Injury due to the environment of the animal can range in severity from small scratches to large wounds. Weddell seals (Leptonychotes weddelli) sustain small cuts from scraping against ice (Smith 1966). Red howler monkeys (Alouatta seniculus) may be cut by thorny vegetation, and may sustain more serious injuries if they fall from the canopy (Crockett and Pope 1988).

Levels of aggression within populations of animals can be indicated by the frequency of occurrence of injuries (Christian 1971; Rose 1979). Aggression between males usually occurs within the context of territoriality or competition for mates during the breeding season. For example, injuries to mountain goats (Oreamnos americanus, Geist 1964), red deer (Cervus elaphus, Clutton-Brock et al. 1979) and northern elephant seals (Mirounga angustirostris, LeBoeuf 1974; Cox 1981) occur when two males fight in competition for groups of females. Male Belding's ground squirrels (Spermophilus beldingi) often injure each other severely when fighting in the presence of a sexually receptive female (Sherman and Norton 1984). Male sea lions and fur seals bite each other in boundary displays during territory defense (Gentry 1975). Aggression between females is usually in the context of defense of young (Christenson and LeBoeuf 1978), although aggressive Weddell seal females occasionally charge and bite other females if they approach too closely (Kaufman et al. 1975). Solitary female red howler monkeys attempting to join an established group are chased and bitten by resident females (Crockett and Pope 1988).

Aggression between males and females also occurs during the breeding season. Females are aggressive towards males when defending their young (Christenson and LeBoeuf 1978; Boness et al. 1982). Males sometimes inflict injuries on females during mating. The male may bite the female while mounting her (Siniff et al. 1979; Hatler 1972), or the injuries may be inflicted when the male attempts to approach or subdue the female (e.g. subadult male orangutans, Pongo pygmaeus, "grab, bite or slap" females while positioning them for copulation, Mitani 1985; Galdikas 1985). Male macaques and baboons usually attack and wound estrous females more often than anestrous females (Smuts 1987). Female crabeater seals may bite males during mating as well (Siniff et al. 1979).

In this thesis, I examine the significance of injuries to the population dynamics and survival of the endangered Hawaiian monk seal, Monachus schauinslandi. The Hawaiian monk seal is the most abundant of the three species of monk seals, with a population size estimated at 1500 to 1700 seals (Gerrodette 1985; Gilmartin 1988). The Mediterranean monk seal (M. monachus) population is estimated at 500 to 1000 seals (Ronald 1973; Sergeant et al. 1978), and the Caribbean monk seal (M. tropicalis) is extinct (Kenyon 1977; LeBoeuf et al. 1986). The Hawaiian monk seal is found only in the Northwestern Hawaiian Islands (NWHI), where it breeds on small coral sand islands (Figure 2.1).

Since Kenyon and Rice's (1959) landmark life history study of the Hawaiian monk seal, various aspects of the morphology (King 1964), population dynamics (Rice 1960; Johnson et al. 1982), juvenile growth and development (Wirtz 1968), age determination (Kenyon and Fiscus 1963) and evolutionary origin (Repenning and Ray 1977) of the Hawaiian monk seal have been documented. More intensive studies of monk seal abundance and behaviour have been conducted since 1977 (e.g. Gilmartin et al. 1980; Johnson and Johnson 1984a,b; Alcorn 1984; Stone 1984).

The number of Hawaiian monk seals counted on beaches in the NWHI has declined from approximately 1000 seals in the 1950s to about 580 in 1987 (Johnson et al. 1982; Gilmartin 1988). Several factors, including harassment by humans (Kenyon 1972, Gerrodette and Gilmartin in press), natural toxin concentrations in the reef fish population (Gilmartin et al. 1980), shark predation (Taylor and Naftel 1978; Alcorn and Kam 1986), and mobbing behaviour of adult male monk seals (Gilmartin and Alcorn 1987), are thought to be possible causes for this decline. Injuries caused by sharks and by the mobbing behaviour of adult males are the focus of this study.

Mobbing behaviour, in which several males attempt to mate with a lone adult female seal or an immature seal of either sex, has been observed regularly in Hawaiian monk seals since 1978 (Johnson and Johnson 1981). Though mobbing behaviour was not recognized prior to 1978, injuries typical of adult male harassment were first reported in 1964 and 1965 (Wirtz 1968), indicating the presence of this behaviour in earlier years. A male bites the back of a seal when mounting it, and may inflict puncture and tear wounds. When several males attempt to mate with a lone seal at the same time, these dorsal wounds are enlarged and in extreme cases can cover up to two thirds of the dorsal surface of the seal (Alcorn 1984). The mobbed individual may die or disappear after receiving such wounds (Alcorn 1984, Johanos et al. 1987 Johanos and Austin 1988). Mobbing incidents have been observed primarily at islands where the adult sex ratio is skewed in favor of males (Gilmartin and Alcorn 1987), although seals with injuries characteristic of mobbing incidents have been observed at islands where the adult sex ratio is even (M.P. Craig, pers. comm.). The number of seals that have died after sustaining wounds inflicted in mobbing incidents has increased in recent years so that it is possible that mobbing behaviour has become a significant cause of mortality and population decline in some monk seal populations.

Wounding of Hawaiian monk seals by sharks can be fatal. Tiger sharks (Galeocerdo cuvier) have been documented to attack and eat monk seals (Taylor and Naftel 1978; Alcorn and Kam 1986). However, the significance of injuries inflicted by sharks relative to injuries inflicted by adult males is not well known.

The aim of this thesis is to assess the significance of injuries to the Hawaiian monk seal population. In Chapter 2, I first describe the different types of injuries sustained by monk seals and quantify their frequency of occurrence. I then assess the significance of wounding on the reproductive success of injured female Hawaiian monk seals in Chapter 3. Finally, in Chapter 4 I evaluate the importance of injuries to Hawaiian monk seal population trends.

1.1. Literature cited

Alcorn, D.J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-41. 37 p.

Alcorn, D.J., and A. Kam. 1986. Fatal shark attack on a Hawaiian monk seal (Monachus schauinslandi). Marine mammal sci. 2(4):313-315.

Boness, D.J., S.S. Anderson and C.R. Cox. 1982. Functions of female aggression during the pupping and mating season of grey seals, Halichoerus grypus (Fabricius). Can. J. Zool. 60(10):2270-2278.

Carrick, R. and S.E. Ingham. 1962. Studies on the southern elephant seal, Mirounga leonina (L.) V. Population dynamics and utilization. CSIRO Wildl. Res. 7, p. 201-209.

Christenson, T.E. and B.J. LeBoeuf. 1978. Aggression in the female northern elephant seal, Mirounga angustirostris. Behaviour 64:158-162.

Christian, J.J. 1971. Fighting, maturity and population density in Microtus pennsylvanicus. J. Mammal. 52(3):556-567.

Clutton-Brock, T.H., S.D. Albon, R.M. Gibson and F.E. Guiness. 1979. The logical stag: Adaptive aspects of fighting in red deer (Cervus elaphus L.). Anim. Behav. 27:211-225.

Congdon, J.D., L.J. Vitt and W.W. King. 1974. Geckos: adaptive significance and energetics of tail autotomy. Science 184:1379-1380.

Cox, C.R. 1981. Agonistic encounters among male elephant seals: frequency, context and the role of female preference. Amer. Zool. 21:197-209.

Crockett, C.M. and T. Pope. 1988. Inferring patterns of aggression from red howler monkey injuries. Amer. J. Primatol. 15:289-308.

Dial, B.E. and L.C. Fitzpatrick. 1981. The energetic costs of tail autotomy to reproduction in the lizard Coleonyx brevis (Sauria: Gekkonidae). Oecologia (Berl.) 51:310-317.

Galdikas, B.M.F. 1985. Subadult male orangutan sociality and reproductive behavior at Tanjung Puting. Amer. J. Primatol. 8:87-99.

Geist, V. 1964. On the rutting behavior of the mountain goat. J. Mammal. 45(4):551-568.

Gentry, R.L. 1975. Comparative social behavior of eared seals. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 169:189-194.

Gerrodette, T. 1985. Estimating the 1983 population of Hawaiian monk seals from beach counts. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii. SWFC Admin. Rep. H-85-5. 13 p.

Gerrodette, T. and W.G. Gilmartin. in press. Demographic consequences of changed pupping and hauling sites of the Hawaiian monk seal. Conserv. Biol.

Gilmartin, W.G. 1988. The Hawaiian monk seal: population status and current research activities. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii. SWFC Admin. Rep. H-88-17. 14 p.

Gilmartin, W.G., and D.J. Alcorn. 1987. A plan to address the Hawaiian monk seal adult males "mobbing" problem. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rep. H-17-12. 24 p.

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. In: R.W. Grigg and R.T. Pfund (eds.), Proceedings of the symposium on status of resource investigations in the Northwestern Hawaiian Islands, University of Hawaii, Honolulu, Hawaii, April 24-25, 1980. p.32-41. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-04.

Hatler, D.F. 1972. The coastal mink on Vancouver Island, British Columbia. Ph. D. Thesis, University of British Columbia. 360 p.

Johanos, T.C., and S.L. Austin. 1988. Hawaiian monk seal population structure, reproduction, and survival on Laysan Island, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-118. 38 p.

Johanos, T.C., A. Kam, and R.G. Forsyth. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-70. 38 p.

Johnson, A.M., R.L. Delong, C.H. Fiscus, and K.W. Kenyon. 1982. Population status of the Hawaiian monk seal (Monachus schauinslandi), 1978. J. Mammal. 63:415-421.

Johnson, B.W. and P.A. Johnson. 1981. The Hawaiian monk seal on Laysan Island: 1978. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va. PB-82-109661. 17 p.

Johnson, B.W., and P.A. Johnson. 1984a. Observations of the Hawaiian monk seal on Laysan Island from 1977 through 1980. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-49. 65 p.

Johnson, P.A., and B.W. Johnson. 1984b. Hawaiian monk seal observations on French Frigate Shoals, 1980. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-50. 47 p.

Jones, E.C. 1971. Isistius brasiliensis, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. Fish. Bull. 69(4):791-798.

Kaufman, G.W., D.B. Siniff and R. Reichle. 1975. Colony behaviour of Weddell seals, Leptonychotes weddelli, at Hutton Cliffs, Antarctica. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 169:228-246.

Kenyon, K.W. 1972. Man versus the monk seal. J. Mammal. 53:687-696.

Kenyon, K.W. 1977. Caribbean monk seal extinct. J. Mammal. 58:97-98.

Kenyon, K.W., and C.H. Fiscus. 1963. Age determination in the Hawaiian monk seal. J. Mammal. 44(2):280-282.

Kenyon, K.W., and D.W. Rice. 1959. Life history of the Hawaiian monk seal. Pac.Sci. 8:215-282.

King, J.E. 1964. The monk seal of the Pacific. Z. Saugetierkunde. 29:37-42.

LeBoeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. Amer. Zool. 14:163-176.

LeBoeuf, B.J., K.W. Kenyon and B. Villa-Ramirez. 1986. The Caribbean monk seal is extinct. Marine mammal sci. 2(1):70-72.

LeBoeuf, B.J., J.E. McCosker and J. Hewitt. 1987. Crater wounds on northern elephant seals: the cookiecutter shark strikes again. Fish. Bull. 85(2):387-392.

LeBoeuf, B.J. and J. Reiter. 1988. Lifetime reproductive success in northern elephant seals. In: T.H. Clutton-Brock (ed.), Reproductive success. Chicago: University of Chicago Press. p.344-362.

LeBoeuf, B.J., M. Riedman and R.S. Keyes. 1982. White shark predation on pinnipeds in California coastal waters. Fish. Bull. 80(4):891-895.

Maiorana, V.C. 1977. Tail autotomy, functional conflicts and their resolution by a salamander. Nature 265:533-535.

Mitani, J.C. 1985. Mating behaviour of male oranutans in the Kutai Game Reserve, Indonesia. Anim. Behav. 33:392-402.

Randall, B.M., R.M. Randall and L.J.V. Compagno. 1988. Injuries to jackass penguins (Spheniscus demersus): evidence for shark involvement. J. Zool. Lond. 214:589-599.

Repenning, C.A., and C.E. Ray. 1977. The origin of the Hawaiian monk seal. Proc. Biol. Soc. Wash. 89(58):667-688.

Rice, D.W. 1960. Population dynamics of the Hawaiian monk seal. J. Mammal. 41:376-385.

Ronald, K. 1973. The Mediterranean monk seal, Monachus monachus. In: SEALS, 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 of IUCN, 18-19 August 1972, University of Guelph, Ontario, Canada. IUCN Publ. New Ser., Suppl. pap. 39.

Rose, R.K. 1979. Levels of wounding in the meadow vole, Microtus pennsylvanius. J. Mammal. 60(1):37-45.

Sergeant, D, K. Ronald, J. Boulva and F. Berkes. 1978. The recent status of Monachus monachus, the Mediterranean monk seal. Biol. Conserv. 14:259-287.

Sherman, P.W. and M.L. Morton. 1984. Demography of Belding's ground squirrels. Ecology 65(5):1617-1628.

Siniff, D.B. and J.L. Bengtson. 1977. Observations and hypotheses concerning the interactions among crabeater seals, leopard seals, and killer whales. J. Mammal. 58(3):414-416.

Siniff, D.B., I. Stirling, J.L. Bengtson and R.H. Reichle. 1979. Social and reproductive behaviour of crabeater seals (Lobodon carcinophagus) during the austral spring. Can. J. Zool. 57(11):2243-2255.

Smith, M.S.R. 1966. Injuries as an indication of social behaviour in the Weddell seal. Mammalia. 30:241-246.

Smuts, B.B. 1987. Gender, Aggression and Influence. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.). Primate Societies. Chicago: University of Chicago Press. pp. 400-412.

Stone, H.S. 1984. Hawaiian monk seal population research, Lisianski Island, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-47. 33 p.

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. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va. PB-285-626. 34 p.

Van Utrecht, W.L. 1959. Wounds and scars in the skin of the common porpoise, Phocaena phocaena (L.). Mammalia 1959:100-122.

Willis, K., S.T. Threlkeld and C.C. Carpenter. 1982. Tail loss patterns in Thamnophis (Reptilia: Colubridae) and the probable fate of injured individuals. Copeia 1982:98-101.

Wirtz, W.O., II. 1968. Reproduction, growth and development, and juvenile mortality in the Hawaiian monk seal. J. Mammal. 49:229-238.

2. Wounding in the Hawaiian monk seal

2.1. Introduction

A variety of scars and fresh injuries are seen on Hawaiian monk seals (Kenyon and Rice 1959; Wirtz 1968; Alcorn 1984; Johanos et al. 1987). Interest has increased recently in fresh injuries, because of the possibility they have a detrimental effect on the reproduction and survival of individual seals (Gilmartin and Alcorn 1987; Taylor and Naftel 1978). Consequently, it is important to describe and quantify the types of wounds in a way that will facilitate monitoring their occurrence and assessing their significance to injured animals.

Most injuries noted have been attributed to attacks by sharks, and to what has been termed "mobbing" behaviour of adult male monk seals, which occurs when several males try to mate with one seal at the same time (Johanos et al. 1987; Gilmartin and Alcorn 1987). During normal mating in monk seals, the male mounts the female and takes a purchase on her back with his teeth. Occasionally puncture wounds and abrasions, which are usually of little consequence, are inflicted on the back of the female during mating. However, when several males try to mate with a female at the same time, the biting becomes intense, resulting in the initial formation and subsequent enlargement of the dorsal wounds. In extreme cases, the resulting wound can become an open wound exposing up to two-thirds of the dorsum of the seal (Alcorn 1984). Because of the apparent severity of wounds inflicted by adult male monk seals and large sharks, the survival of injured seals may be significantly affected (Gilmartin and Alcorn 1987; Taylor and Naftel 1978; Wirtz 1968).

In this paper, I describe the major categories of injuries observed on Hawaiian monk seals in two populations in the Northwestern Hawaiian Islands (NWHI). I also test the hypothesis that injuries inflicted by adult male monk seals occur more frequently than would be expected if injuries of different types occur with the same frequency. Because wounds inflicted by large sharks and by adult males appear severe enough to be important to the survival and reproduction of individuals, I examine these injuries in greater detail than other types of wounds.

2.2. Methods

Injury and census data on Hawaiian monk seals at Laysan Island (lat. 25° 42'N, long. 171° 44'W; Figure 2.1) were collected by me and personnel from the National Marine Fisheries Service Marine Mammal and Endangered Species Program (NMFS MMESP) from 28 February 1988 to 21 June 1988 and from 28 March 1989 to 17 July 1989. The majority of the field work was done at Laysan Island, but data were also collected on French Frigate Shoals (FFS, lat. 23° 45'N, long. 166° 10'W; Figure 2.1), another location in the NWHI chain, by NMFS MMESP biologists from 13 April 1988 to 24 August 1988 and from 28 March 1989 to 31 August 1989. I also analysed census and injury data collected from 1982 to 1987 at Laysan Island, and from 1985 to 1987 at FFS by NMFS MMESP personnel as part of an ongoing study of the population dynamics of the Hawaiian monk seal.

Laysan Island is a low coral sand island about 2.8 km long and 1.7 km wide, with a hypersaline lagoon in its center (Figure 2.1). The island is surrounded by submerged coral reefs. Ely and Clapp (1973) give an extensive description of the geography and natural history of the island. In 1989, the monk seal population was 258 seals (excluding pups), and the ratio of adult males to females was about 1.6:1 (B.L. Becker, pers. comm.), based on the number of identified seals.

French Frigate Shoals (FFS) is a coral atoll with a crescent-shaped fringing reef, approximately 32 km long and 9.6 km wide (Figure 2.1). There are 12 permanent sand islets, several sandspits which vary in size and location through the year, and two volcanic remnants in the atoll. Amerson (1971) describes the geography and natural history of FFS in detail. The monk seal population at FFS was estimated to be 664 animals (excluding pups) in 1987, and the ratio of adult males to females was 0.67:1, based on beach counts of seals (Gilmartin 1988).

2.2.1. Identification of animals

Laysan Island

Individual seals were marked with identifying numbers using commercial bleach (Stone 1984) in all years except 1982, 1986 and 1987. In 1985, only adult and subadult males were marked with bleach. Some of these marks persisted until the seals molted in 1986. In all years, distinctive scars and natural markings were also recorded to aid in the identification of individuals (Alcorn 1984). Weaned pups of the year were tagged on both hind flippers with plastic Temple cattle ear tags (Gilmartin et al. 1986) each year from 1983 to 1989. Adult male seals were tagged with metal Monel tags from 1983 through 1988, and with plastic Riese tags and Temple tags in 1988. Seals with distinctive marks (e.g. large scars, flipper tags or natural markings) were easily identified between years, but seals known only by marks applied with bleach were not consistently identified between years.

French Frigate Shoals

Individuals were not marked with bleach at FFS. In 1987, females on East Island were marked with Nyanzol D dye as part of another study (Boness 1990). Whenever possible, distinctive scars and natural markings were recorded to help identify animals. Weaned pups of the year were tagged with plastic Temple tags from 1984 to 1989. No adult animals were tagged during the study period.

Size and sex classes

Seals were assigned to a size class based on known age (e.g. nursing pup, weaned pup), reproductive state (adult female with nursing pup), or estimated size (Stone 1984). Seals were classified into three estimated size classes, independent of known age: 1) juveniles - immature seals from one to 3 years old; similar in length or slightly longer than weaned pups, but thinner and with brown pelage; 2) subadults - immature seals estimated to be 3 to 5 years old, less robust and with lighter pelage than adults, and 3) adults - reproductively active seals, or seals approximately the same size as known breeding seals, with dark brown pelage, sometimes extensively scarred. Stone (1984) and Johnson and Johnson (1981) give more detailed criteria for size estimation.

The sex of a seal was only recorded if its ventrum was observed, or if the seal was identified by scars, marks applied with bleach, or tags. The only exception to the above criteria was when an adult seal was seen with a black nursing pup. In this case, the adult was always classed as female (Johnson and Johnson 1984). At Laysan Island, because all adult and untagged immature seals were individually identified by marks applied with bleach (except in 1982, 1986 and 1987) and most immature seals were tagged, the sex of most seals seen was known. Thus, the sex ratio recorded for each size class was accurate. In contrast, at FFS, animals were not marked for individual identification (except for a small number of females in 1987), and the sex of one third of the animals counted could not be recorded. Thus, the counts for each size and sex class were considered to be minimum counts. The large number of animals for which the sex could not be recorded probably biased the determination of the adult sex ratio at FFS (Johnson and Johnson 1984). Adult females were more likely to be identified than adult males, because adult seals accompanied by black pups were always identified as female. Thus, the female biased adult sex ratio was probably not the true sex ratio. Johnson and Johnson (1984) corrected for the mother-with-pup bias by estimating the number of moulting seals of each sex outside of the pupping season. By this method, the ratio of adult males to females was estimated to be 1:1 at FFS in 1980.

2.2.2. Census data

On censuses, the information recorded for each animal observed included location of the seal on the island, size class, sex, individual identification (e.g. tag number or mark applied with bleach), and any association with other seals (Johanos et al. 1987). Only seals on land (with 50% or more of the body out of the water) were censused, as animals in the water might be counted more than once during a census.

Slightly different procedures were used in conducting censuses at Laysan Island and FFS. At Laysan Island, censuses commenced between 1200 and 1300 Hawaiian standard time, and two observers walked in opposite directions around the island until they met at the other side of the island (Johanos et al. 1987). Censuses were conducted every two to four days, and took about 2.5 hours to complete. At FFS, because of safety considerations in travel from islet to islet, censuses of all islets within the atoll were conducted over a two day period by one or two observers. At islets which were too small for an observer to land without disturbing the seals, the number of seals on the island was counted from the boat. Weather permitting, atoll censuses were conducted at least once a week. The number of complete censuses at FFS was therefore fewer than at Laysan over the same time period.

2.2.3. Data collected on injuries

Injuries were recorded as the observer walked around the perimeter of the island (at Laysan Island) or islet (at FFS). Data were collected both on census and non-census days. Data collected from each injured seal included identification number, size class, sex and location of the seal, and a standardized description of the injury. Six types of injuries were commonly recorded, based on physical characteristics:

1) puncture - a hole of small diameter created by a sharp pointed object piercing the skin.
2) abcess - a swollen blister-like area under the skin.
3) abrasions and lacerations - scratches or tears in the skin. The depth of lacerations ranged from surface scratches (not breaking the skin) to deep tears into the muscle tissue.
4) gaping wound - an open wound where flesh was removed from the injury. The shape of these wounds was oval or irregular.
5) circular wound - a wound ranging from semicircular cuts through the skin to circular wounds with flesh removed.
6) amputation of limb - all or part of a limb removed from the body.

Injuries recorded in 1988 and 1989 were classified by the observer. I classified injuries recorded by NMFS MMESP personnel from 1982 to 1987 by examining drawings and photographs taken at the time of observation.

2.2.4. Data analysis

Only data from 1988 and 1989 were used to examine the frequencies of occurrence of all types of injuries because wounds were recorded more often and more systematically during those years. From 1982 to 1987, only major injuries were usually recorded (e.g. Alcorn and Buelna 1989). Consequently, when comparing frequencies of wounding between all years, only records of major injuries were used.

The number of seals counted during a census varies with the season (Gerrodette 1985). To minimize this variation at each location, I used the average number of seals counted in May and June of 1988 and 1989 as an index of the relative size of the population. The frequency of injuries inflicted by large sharks and by adult male seals for each month was divided by these indices to compare the frequency of injuries between Laysan Island and FFS in 1988 and 1989.

The distribution of injuries inflicted by adult male seals and by large sharks over the size and sex classes of the population at each island were compared to the distribution that would be predicted from the census data if these injuries were distributed randomly among size and sex classes. Injured animals of unknown sex were excluded from the analysis.

To determine if my data, collected in 1988-89, were comparable to data collected by others in 1982-87, I compared the two data sets (G-test: Sokal and Rohlf 1981). When no significant differences were detected, the data sets were combined. For all statistical comparisons of observed frequencies to expected distributions, a G-test with the Williams correction (Sokal and Rohlf 1981; p.736) was used. To compare two proportions, a 2x2 G-test of independence was used. All tests were evaluated at the 0.05 level of significance.

2.3. Results

2.3.1. Causes of injuries

The shape of an injury and its location on the seal's body were often indicative of its origin. Six characteristic types of injuries for which the cause could be determined were observed.

1) *Injuries inflicted by adult male monk seals during mating attempts*

These wounds consisted of abrasions on the dorsum of the injured seal, caused by adult males attempting to secure a hold on the seal with their teeth and foreflippers while mounting it (Plate 2.1a,b). Often the dorsum of the injured seal was dark because of fluids leaching from the abrasions. Some seals sustained more severe gaping wounds, usually located in the mid-body to posterior dorsal area, in addition to these abrasions. The gaping wounds ranged from small (ca. 2 cm diameter; Plate 2.2a) to large open areas covering up to two thirds of the injured animal's back (Plates 2.1c, 2.2b; Alcorn 1984). Often, the injured seal was initially observed shortly after the wound was inflicted. The injury was moist from body fluids and the seal was usually associated with one or more adult male seals. Mobbing incidents in which these injuries have been inflicted have been observed in several years (Alcorn 1984; Johanos and Kam 1986; Johanos et al. 1987; Johanos and Austin 1988; Alcorn and Buelna 1989).

2) *Injuries inflicted by large sharks*

The large shark most likely to attack monk seals in the NWHI is the tiger shark (Galeocerdo cuvier). Tiger sharks are often seen close to shore at islands in the NWHI. Injuries inflicted by large sharks included shallow punctures in the skin, deep lacerations, gaping wounds or amputated limbs (Plates 2.2c, 2.3a-c). The characteristic U-shape of these wounds reflected the shape of a shark's jaw (Plates 2.2c, 2.3c). Attacks by sharks are rarely observed (Alcorn and Kam 1986; Johanos and Austin 1988). However, similar injuries, attributed to large sharks, have been seen on other species of pinnipeds (e.g. LeBoeuf et al. 1982).

3) *Injuries inflicted by Isistius brasiliensis*

Isistius brasiliensis, the cookiecutter shark, is a small squaloid shark, 14 to 50 cm in length, that inhabits the deep water of tropical and subtropical areas of the Atlantic, Pacific and Indian Oceans (Castro 1983; Compagno 1984a). Injuries inflicted by Isistius included open crater-like wounds 3-7 cm in diameter, 1-2 cm in depth, circular or semi-circular cuts through the skin, or round open wounds with a circular plug of skin and tissue attached to the edge of the wound (Plate 2.4a). The shape of these injuries was similar to those attributed to Isistius that were seen on northern elephant seals, other marine mammals and large fish (LeBoeuf et al. 1987; Jones 1971).

4) *Injuries inflicted by other seals during aggressive interactions*

Seals inflicted abrasions and bite wounds on each other during jousting interactions. Jousting interactions often occur when two seals interact aggressively. Open mouth threats and sparring, where the two seals lunge at one another with open mouths, and occasionally biting characterize these jousts (Kenyon and Rice 1959). Injuries inflicted during jousts were usually inflicted around the head and the hindflippers.

5) *Injuries due to contact with coral reef or debris*

A group of abrasions, close together and parallel to each other (Plate 2.4b) and single scratches were sustained by a seal when it scraped past a coral reef or possibly sharp pieces of debris such as rusted metal or broken glass.

6) *Injuries due to entanglement in netting*

Hawaiian monk seals become entangled in fragments of netting and marine debris which wash up on the beach in the NWHI (Balazs 1979; Henderson 1985). When a seal is entangled in netting or a plastic ring for a considerable length of time, injuries may result from the constricting item. These injuries were deep, linear wounds, usually around the neck of the animal (Plate 2.4c). Often the netting or plastic ring was still present on the seal.

7) *Other injuries and unknown causes*

Injuries due to known causes which were infrequently seen, such as a case in which a monk seal had ingested a toxic fish (Alcorn 1984), were classed as "other". Any injuries for which the cause was uncertain were classed as "unknown".

2.3.2. Frequency of injuries

For injuries for which the cause could be determined, there were differences in the distribution at Laysan Island and FFS (Figure 2.2). At Laysan Island, adult male-inflicted mating injuries (n=80/201, 39.8% of total injuries), seal-inflicted injuries (n=37/201, 18.4%) and shark-inflicted injuries (n=25/201, 12.4%) were most frequently seen. Of these injuries, only the frequency of adult male-inflicted injuries was significantly greater than would be expected if injuries of different types occurred at equal rates (G=25.63, d.f.=1, $p<0.005$). At FFS, adult male-inflicted injuries (n=21/68, 30.9%) and shark-inflicted injuries (n=19/68, 27.9%) were most frequently observed. Injuries inflicted by seals in aggressive incidents were infrequently observed. Both adult male-inflicted injuries (G=8.30, d.f.=1, $p<0.005$) and shark inflicted injuries (G=6.12, d.f.=1, $0.025<p<0.05$) occurred significantly more frequently than expected if injuries from different causes occurred at the same rate. At both locations, the proportion of injuries which were of unknown origin was high (Laysan: 20.9%, FFS: 29.4%).

Seal inflicted injuries due to aggressive interactions

At Laysan Island, the frequency of seal-inflicted injuries was high in comparison to FFS. Adult male seals sustained this type of injury significantly more frequently than other size and sex classes of seals (n=27/37; G=23.52, d.f.=1, $p<0.005$). At FFS, two of the 3 seal inflicted injuries were sustained by adult males.

Adult male-inflicted wounds

Injuries were inflicted by adult male monk seals earlier in the year at Laysan Island than at FFS (Figure 2.3). The frequency of injuries inflicted by adult male seals in April and May was three to four times higher at Laysan Island than at FFS. In June and July, the rates from both areas were similar. At both Laysan Island and FFS, the distribution of injuries inflicted by adult male seals over the size and sex classes of monk seals differed significantly from a distribution of injuries relative to the numbers of seals in each size and sex classes counted on the beach (G=172.65, d.f.=8, $p<<0.005$, Figure 2.4a; G=53.38, d.f.=8, $p<0.005$, Figure 2.4b). Significantly more adult females were injured by adult male seals at both Laysan Island and FFS than could be expected from their relative numbers in the population (Laysan: G=52.76, d.f.=1, $p<0.005$; FFS: G=7.48, d.f.=1, $0.005<p<0.01$). At FFS, the distribution of adult male-inflicted injuries over size and sex classes should be interpreted conservatively because adult females were more likely to be identified than adult males, which biased the adult sex ratio. Even so, the proportion of adult male-inflicted injuries in the adult and subadult female size classes was much higher than in any of the other size classes.

Shark-inflicted injuries

For the period from March through July, the frequency of injuries inflicted by large sharks at Laysan Island was highest from April through June (Figure 2.3). At FFS over the same period, the frequency of shark-inflicted injuries was high for April and May, then dropped in June. The frequency of large shark-inflicted injuries at FFS was lower than at Laysan Island in most years.

At Laysan Island, adult seals were injured significantly more frequently by large sharks than were subadult and juvenile size classes ($G=15.83$, d.f.=2, $p<0.005$, Figure 2.5a). Adult male seals were injured significantly more frequently than all other classes of seals ($G=15.95$, d.f.=1, $p<0.005$). At FFS, the distribution of large shark-inflicted injuries over size classes did not differ significantly from random ($G=0.369$, d.f.=2, $p>0.9$; Figure 2.5b). Adult male seals did not sustain a significantly greater proportion of injuries than expected ($G=1.67$, d.f.=1, $0.5<p<0.1$).

2.4. Discussion

2.4.1. Injuries inflicted by adult males during mating

Adult males inflicted the greatest proportion of injuries on other seals at both Laysan Island and FFS. At both locations, female seals were wounded most often (Figure 2.4). Because of their frequency of occurrence and apparent severity (Plates 2.1c, 2.2b), injuries inflicted by adult male monk seals may have a significant effect on the survival of individuals in other size and sex classes.

The injuries inflicted on females by males during mating and attempted mating, especially severe gaping wounds, look dramatic and appear to be detrimental to the injured seals. However, males also inflict injuries on females during courtship and mating in other species. In some cases, apparent negative effects on the females involved are absent. Male crabeater seals (Lobodon carcinophagus) usually bite the female on the neck while attempting to mount her (Siniff et al. 1979), resulting in considerable light wounding and superficial bleeding. Male sea otters (Enhydra lutris) apparently inflict wounds on the female during mating when the male takes a purchase on the female's nose (Foott 1970). Male southern elephant seals (Mirounga leonina) commonly inflict scars on the female's neck during mating (McCann 1982). In other cases, wounds inflicted during the mating period may have more serious consequences for the injured female. Hatler (1972) found that in a wild population of mink (Mustela vison) on Vancouver Island, nearly every female mink observed during the mating season had extensive neck wounds. These injuries became enlarged if the female mated with several males, each of which aggravated the wounds, over a short period of time. Occasionally, females died from these wounds (Hatler 1972). Male macaques and baboons often attack and wound estrous females (Smuts 1987; Enomoto et al. 1979).

Many males also pursue and attempt to mate with one female in other species. Harassment of females by a group of males has been recorded in the Australian sea lion (Neophoca cinerea; Marlow 1975) and in the northern elephant seal (Mirounga angustirostris; Mesnick and LeBoeuf in press), where groups of subordinate males harass females as they arrive at or leave the breeding colony. Groups of male squirrel monkeys (Saimiri oerstedi) often chase a single female extensively during the breeding season to evaluate her estrus condition (Boinski 1987). In many species of waterfowl, forced extra-pair copulatory behaviour, in which one or several males pursue and attempt to mate with one female, has been widely documented (e.g. McKinney et al. 1983; Bailey et al. 1978; Titman and Lowther 1975). Female white-fronted bee-eaters (Merops bullockoides) are often chased by as many as 12 males during forced copulation attempts (Emlen and Wrege 1986). As well, groups of male dugongs (Dugong dugon) and manatees (Trichechus manatus) often pursue a single estrus female and attempt to copulate with her (Preen 1989; Hartman 1979).

When harassed by groups of adult males, females are sometimes injured or killed. Female northern elephant seals may sustain injuries serious enough to be killed during mating (LeBoeuf and Mesnick in press). Female dugongs are often scarred by males attempting to mate with them (Anderson and Birtles 1978) and are sometimes mounted by several males until the female appears very tired (Preen 1989). Female toads (Bufo bufo) and woodfrogs (Rana sylvatica) that are involved in mating struggles in areas of high density may be drowned at the center of a ball of struggling males (Arak 1983; Howard 1980). Female waterfowl that are harassed by males are occasionally killed (McKinney et al. 1983). Thus, the phenomenon of severe injuries inflicted on females by males during the mating season is not unique to monk seals and may be important to the population only if a significant number of females die as a result of these wounds.

2.4.2. Injuries inflicted by seals during jousts

Injuries inflicted by other seals during jousts or aggressive interactions occurred more frequently at Laysan Island than at FFS during 1988 and 1989 (Figure 2.2). These seal-inflicted injuries were observed mostly on adult male seals, which may indicate a higher level of intrasexual competition and aggressive behaviour between males at Laysan Island in comparison to FFS. Males of many species often wound each other when competing for females (e.g. northern elephant seals, LeBoeuf 1974, Cox 1981; crabeater seals, Siniff et al. 1979; Weddell seals (Leptonychotes weddelli), Smith 1966; red deer (Cervus elaphus), Clutton-Brock et al. 1979; mule deer (Odocoileus hemionus) and white-tailed deer (O. virginianus), Geist 1985). Usually, injury is the result of escalated interaction, since most conflicts are resolved by non-injurious threatening displays (e.g. Clutton-Brock et al. 1979; Geist 1964). Thus, the frequency of occurrence of injuries inflicted by seals at Laysan Island might indicate a high level of escalated jousts between male seals.

2.4.3. Shark-inflicted injuries

Of the sharks commonly seen in the Northwestern Hawaiian Islands, tiger sharks have the most potential to affect the monk seal population, as they are known to attack and eat monk seals (Balazs and Whittow 1979; Taylor and Naftel 1978; Alcorn and Kam 1986). Hammerhead sharks (Sphyrna lewini) and mako sharks (Isurus glaucus) have also been observed in the NWHI (Rice 1960), but there is no evidence that they attack monk seals. The tiger shark, 3 to 5.5 m in size, is common in all the warm oceans of the world (Johnson 1978; Compagno 1984b). This inshore, nocturnal species is the most frequently caught shark in longlining sets in the NWHI (Taylor and Naftel 1978; Johnson 1978; Tricas et al. 1981). It has a catholic diet and is both a scavenger (Gudger 1949) and a predator (Dodrill and Gilmore 1978; Johnson 1978).

Subadult seals are generally considered to be more vulnerable to shark attack than adult seals (Brodie and Beck 1983; LeBoeuf et al. 1982; Ainley et al. 1985). This could be due to lack of experience with sharks, or because their smaller size makes it easier for sharks to kill them (Ainley et al. 1985). Brodie and Beck (1983) suggested that since juvenile grey seals are free of scars typical of shark attacks, they rarely escape when they are attacked by sharks. Ainley et al. (1985) found that subadult pinnipeds were injured more often than adults at the Farallone Islands. Cockcroft et al. (1989) found that relatively few bottlenose dolphin (Tursiops truncatus) juveniles and calves had shark bite scars, and suggested that the predominance of young dolphin remains in shark stomachs indicated that juveniles were more vulnerable than other size classes to shark attack.

At Laysan Island, large shark injuries were recorded more frequently on adult monk seals than on other size classes (Figure 2.5a). This may indicate either that juveniles are not injured by large sharks or, more likely, that juveniles are less likely to survive attacks by large sharks. Juvenile seals also disappear at a much higher rate than adults (Chapter 4, Figure 4.5). Although the cause of disappearance of an apparently healthy seal is difficult to determine, some of these disappearances probably result from shark predation (Balazs and Whittow 1979; Alcorn and Kam 1986).

Among adult seals, males were injured more frequently than females by large sharks. Most of the injuries inflicted by large sharks occurred in April and May (Figure 2.3), which coincides with the peak of the pupping season (Kenyon and Rice 1959; Kenyon 1981). Nursing females stay on land or in shallow water until their pups are weaned (Kenyon and Rice 1959). During the same period, adult males spend the majority of their time in the water patrolling the shore and searching for receptive females. Thus, adult males are probably more vulnerable than adult females to injury from sharks.

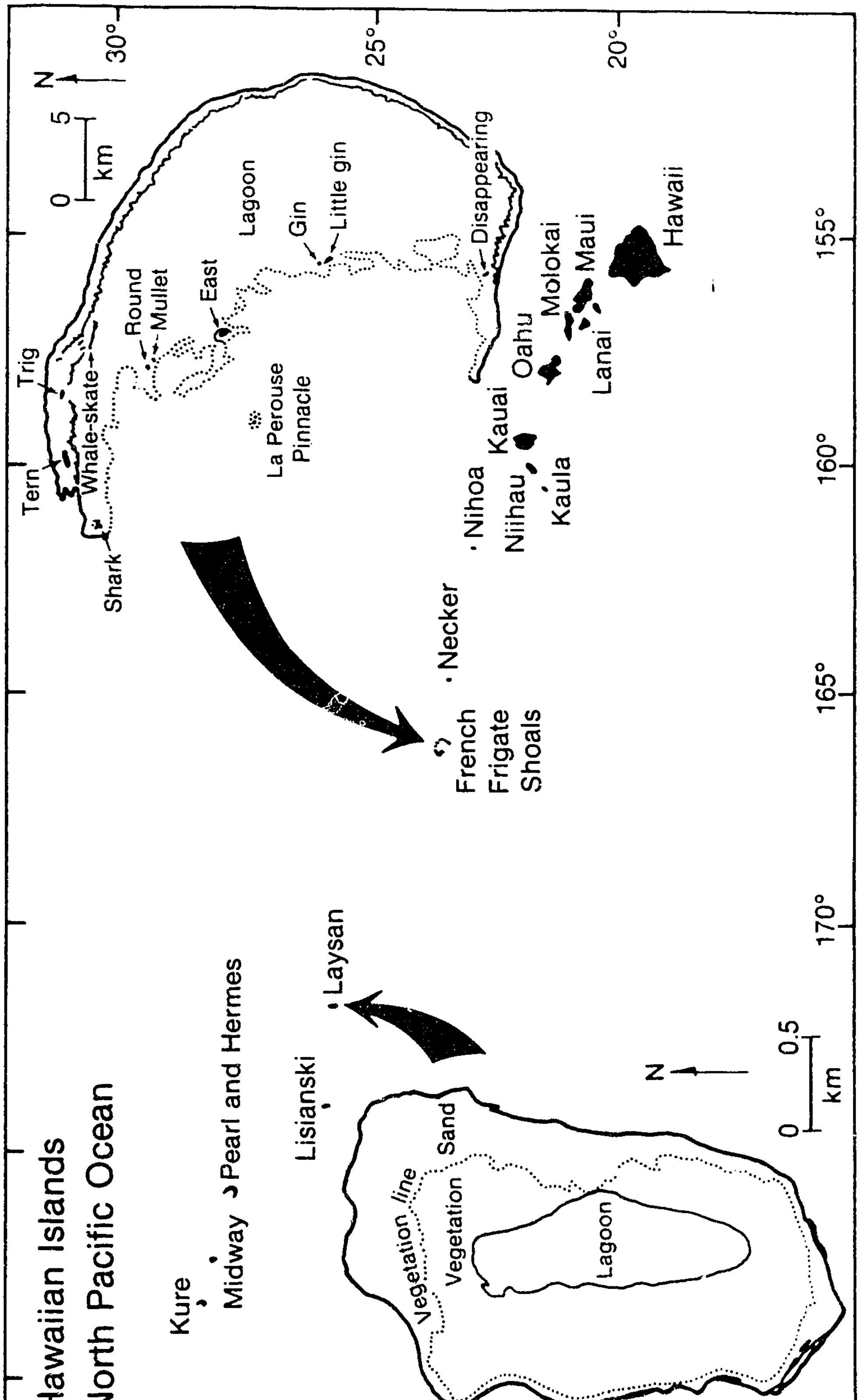
At FFS, adult seals were not injured by sharks more frequently than other size classes (Figure 2.5b). No data are available on mortality of adult seals at FFS, but the rate of disappearance of juveniles at FFS is the same as that at Laysan Island (NMFS MMESP unpub. data; T.C. Johanos-Kam, pers. comm.; Appendix A). Although it seems that all age classes at FFS are being injured with equal frequency, juveniles may be fatally attacked by sharks more often than are adult seals.

Fledging, the time of first flight, of Laysan albatrosses (Diomedia immutabilis) and black-footed albatrosses (Diomedea nigripes) occurs from mid-June to August (Rice 1984). Tiger sharks begin to swim near the shore of several islands in the NWHI in mid-June, apparently to prey on albatross chicks as they land in the water to rest between initial flights (Rice 1960; W.R. Strong pers. comm.). The seasonal predation on albatross chicks by tiger sharks in the NWHI may also influence the frequency of shark attacks on monk seals (Rice 1960; Fisher 1975; W.R. Strong pers. comm.). The decrease in wounding rate for shark-inflicted injuries at both Laysan Island and FFS in June and July (Figure 2.3) may result from tiger sharks shifting their focus to albatross chicks.

2.4.4. Interactions between wounding by adult male monk seals and sharks

In April and May, the frequencies of injuries by both adult males and large sharks were relatively high (Figure 2.3). The overlap in peak periods of adult male-inflicted injury and shark inflicted injury may be related. Body fluids leaching from a seal's injuries probably attract sharks. A wounded seal may be less vigilant and less mobile in the water, both of which could increase its vulnerability to a shark attack. Activity in the water can attract sharks; tiger sharks have been seen patrolling underneath aquatic mobbing incidents (Johanos and Austin 1988) and have subsequently attacked injured female seals (Alcorn and Kam 1986) as well as males involved in the mobbing incident (Johanos and Austin 1988). The combination of wounding by adult male monk seals and sharks may thus increase the mortality rate of injured seals.

Figure 2.1. Northwestern Hawaiian Island chain, showing Laysan Island and French Frigate Shoals in detail. Note the difference in scales.


Hawaiian Islands
North Pacific Ocean
Kure
Midway
Pearl and Hermes
Lisianski
Laysan
French Frigate Shoals
Necker
Nihoa
Niihau
Kaula
Kauai
Oahu
Molokai
Lanai
Maui
Hawaii
30°
25°
20°
155°
160°
165°
170°
N
0 5 km
0 0.5 km
Shark
Tern
Trig
Whale-skate
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Mullet
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La Perouse Pinnacle
Lagoon
Gin
Little gin
Disappearing
Vegetation line
Vegetation
Sand
Lagoon

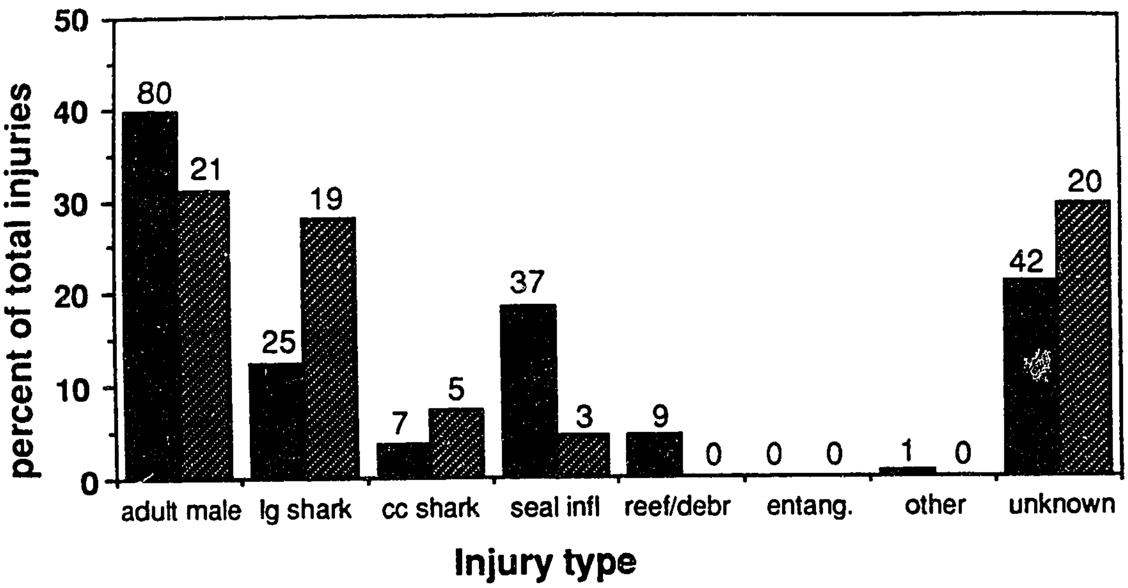

Figure 2.2. Frequencies of different types of wounds recorded from April through June, 1988-89, at Laysan Island and French Frigate Shoals, NWHI. Solid bar: Laysan Island; hatched bar: FFS. See text for description of wound types. Number of seals in each class indicated above bars.

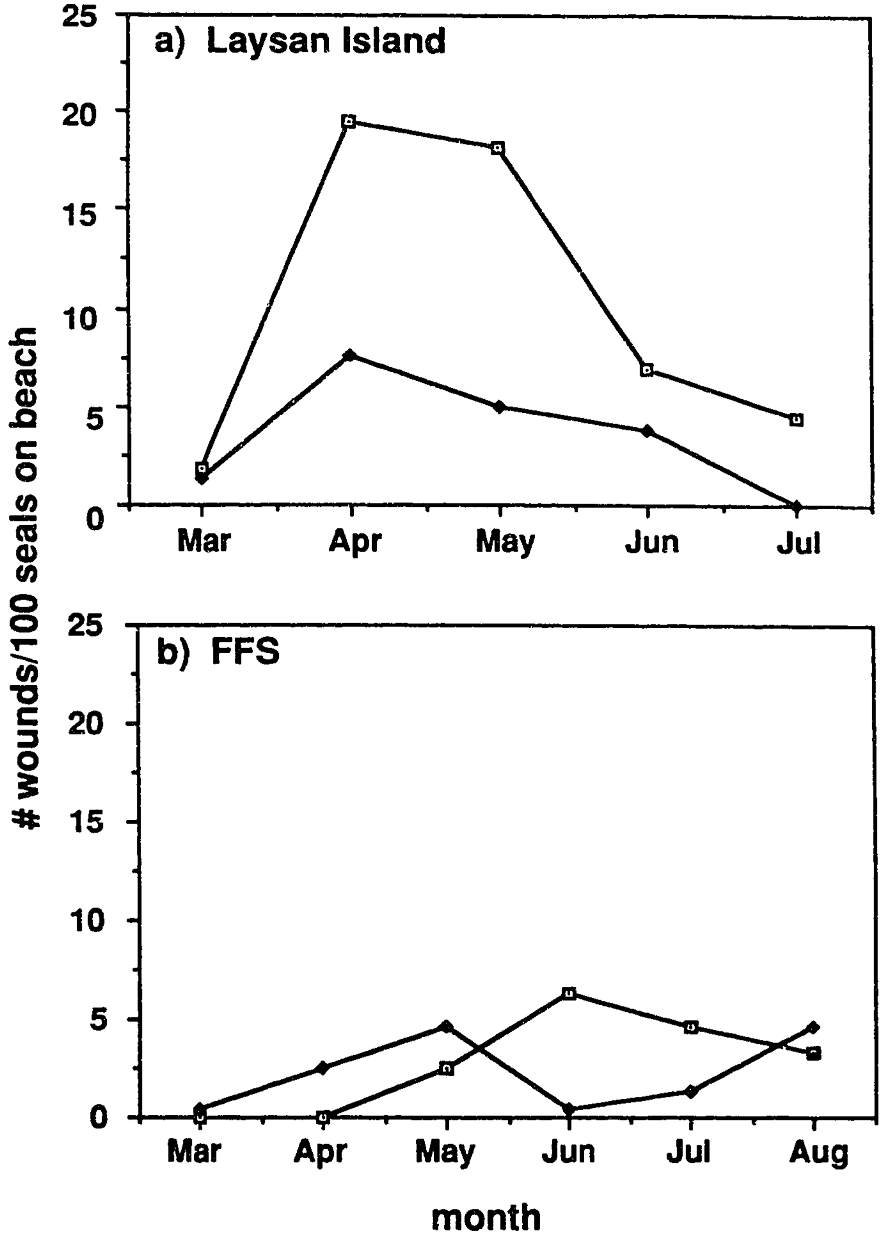

Figure 2.3. Frequency of wounding by month on Hawaiian monk seals for injuries inflicted by adult male monk seals and large sharks at a) Laysan Island and b) French Frigate Shoals, NWHI, 1988-89. All size and sex classes of seals are included. Open square: injuries inflicted by adult male monk seals; closed square: injuries inflicted by large sharks.

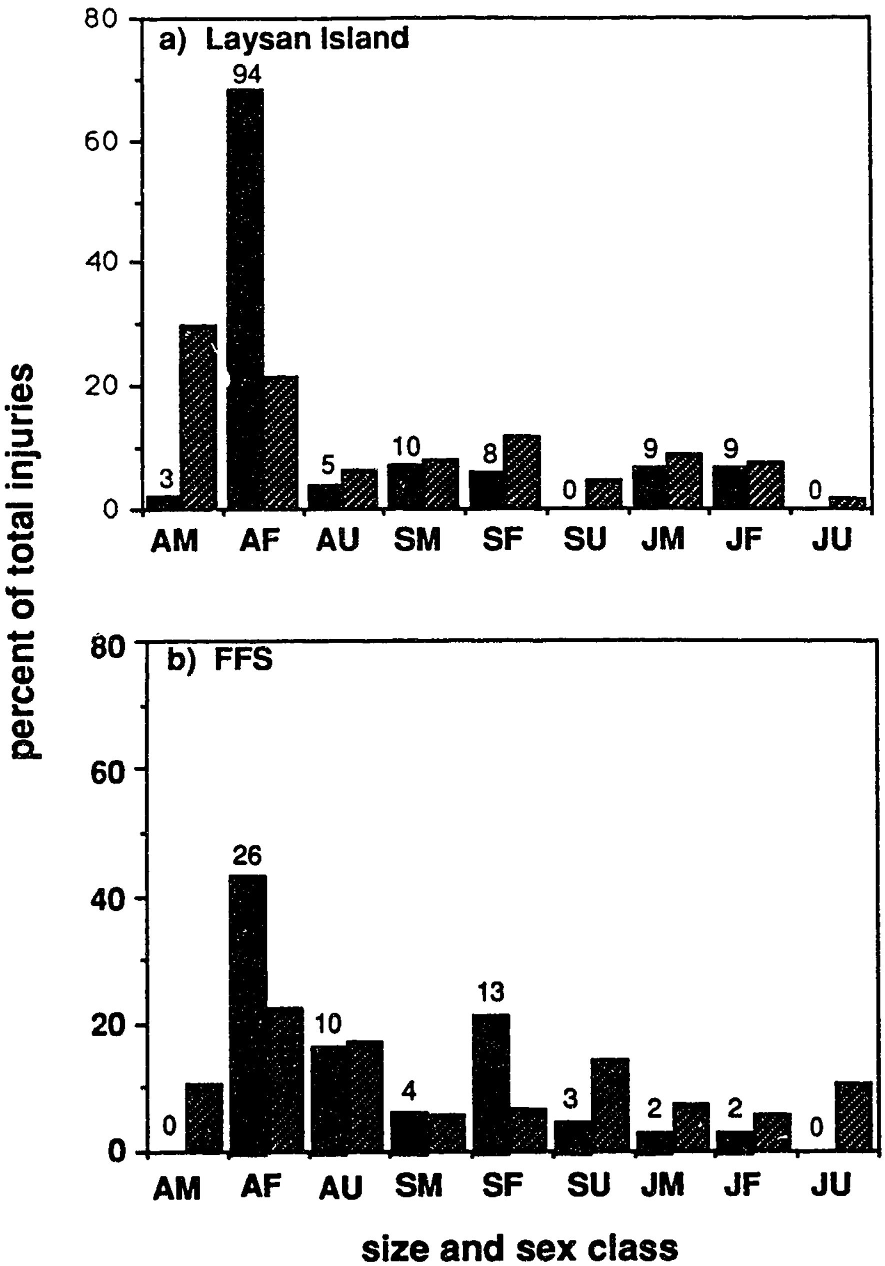

Figure 2.4. Injuries inflicted by adult male Hawaiian monk seals on different size and sex classes of seals at a) Laysan Island and b) French Frigate Shoals, NWHI, 1982-89. Expected frequencies are based on mean censuses from May and June 1982-89. Solid bar: observed frequency of injury; hatched bar: expected frequency of injury. Number of seals in each class indicated above bars.

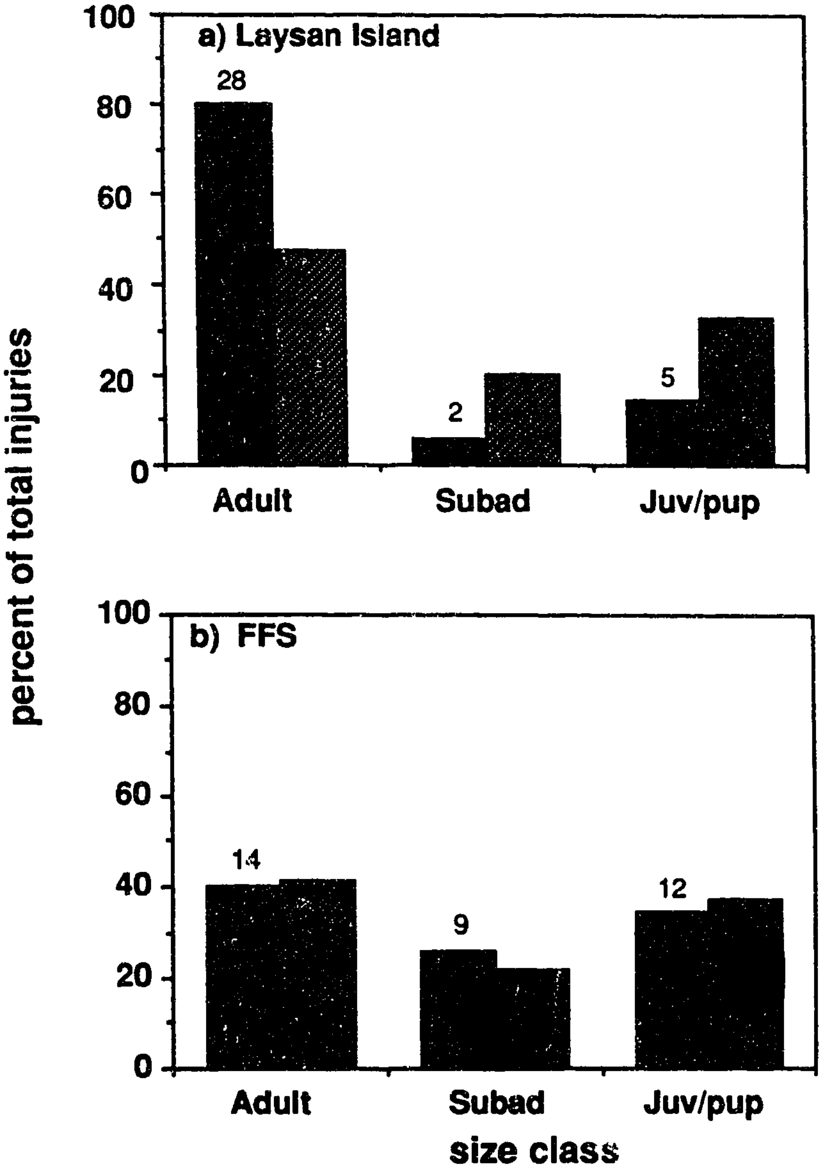

Figure 2.5. Injuries inflicted by large sharks on different size classes of Hawaiian monk seals at a) Laysan Island and b) French Frigate Shoals, NWHI, 1982-89. Expected frequencies are based on mean censuses from May and June 1982-89. Solid bar: observed frequency of injuries inflicted by large sharks; hatched bar: expected frequency of injuries. Number of seals in each class indicated above bars.

Plate 2.1. Injuries observed on Hawaiian monk seals. a), b) dorsal abrasions inflicted by adult male monk seals; c) gaping injury inflicted by adult male monk seals during mobbing incidents.

A

B

C

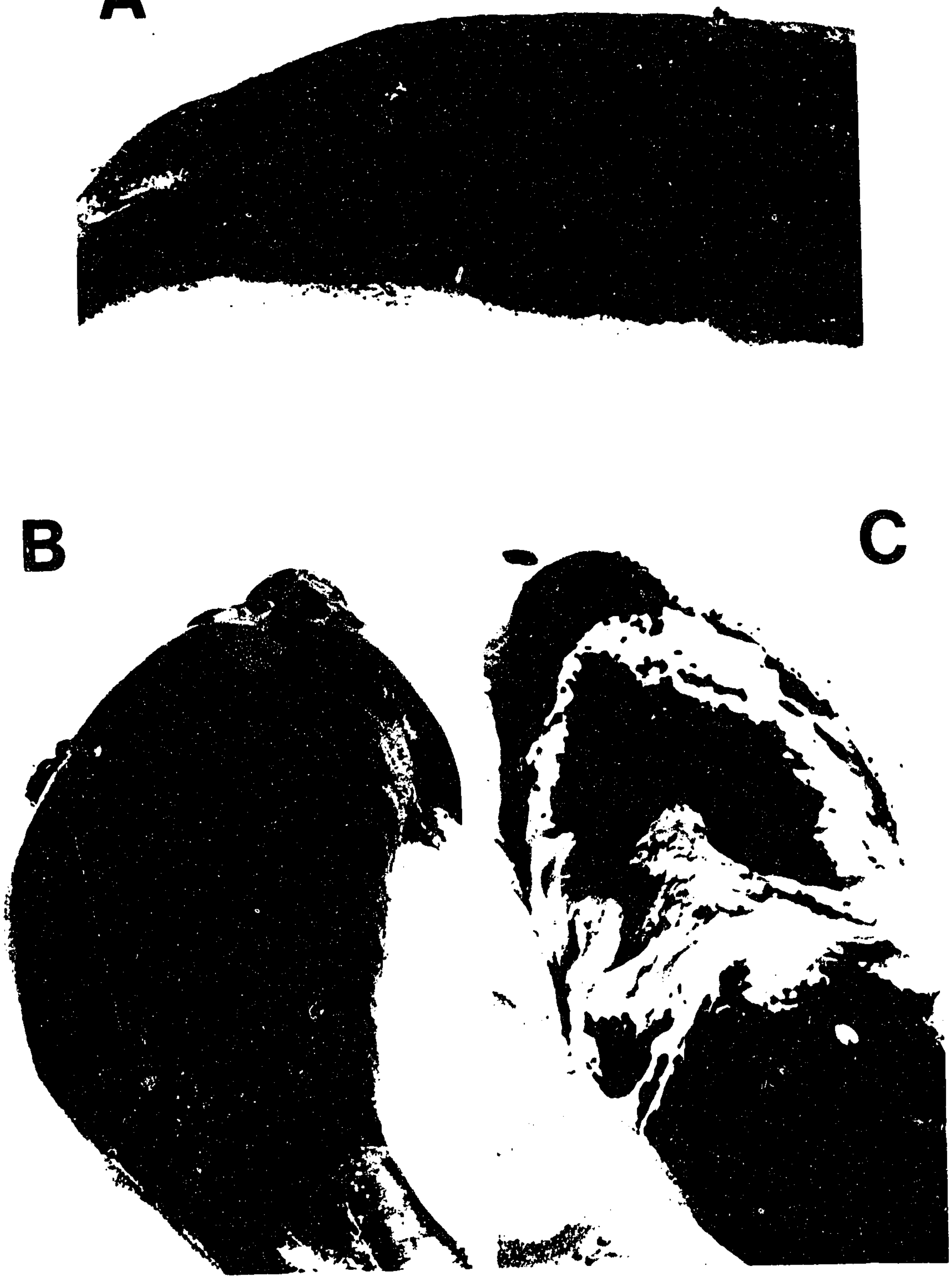

Plate 2.2. Injuries observed on Hawaiian monk seals. a) small gaping wound and dorsal abrasions inflicted by adult male monk seals; b) large gaping wounds inflicted by adult male monk seals; c) shark–inflicted injury.

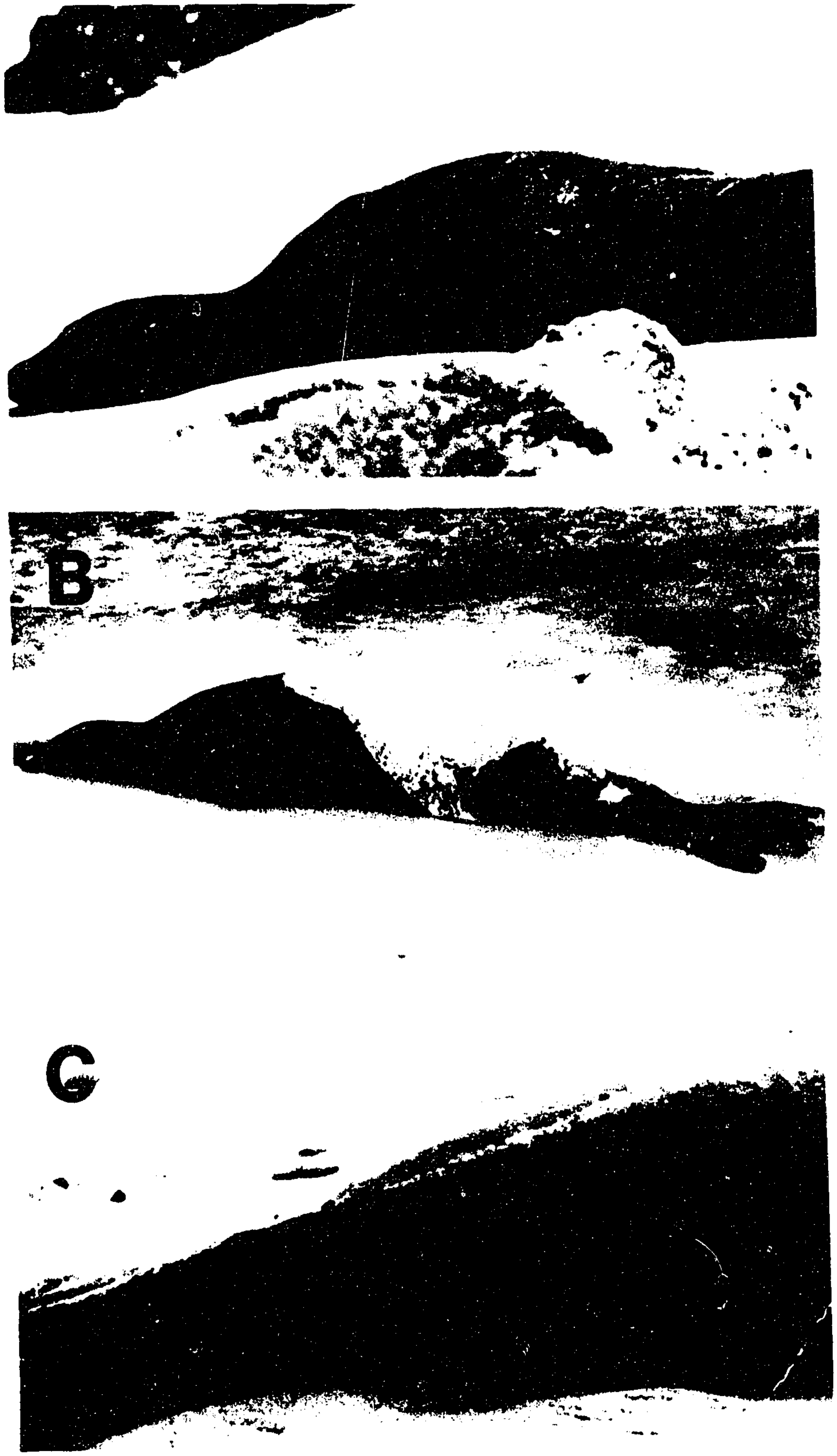
B
C

Plate 2.3. Injuries observed on Hawaiian monk seals. a) lacerations inflicted by a large shark; b) amputated hindflipper, caused by a large shark; c) large U–shaped gaping wound inflicted by a large shark.

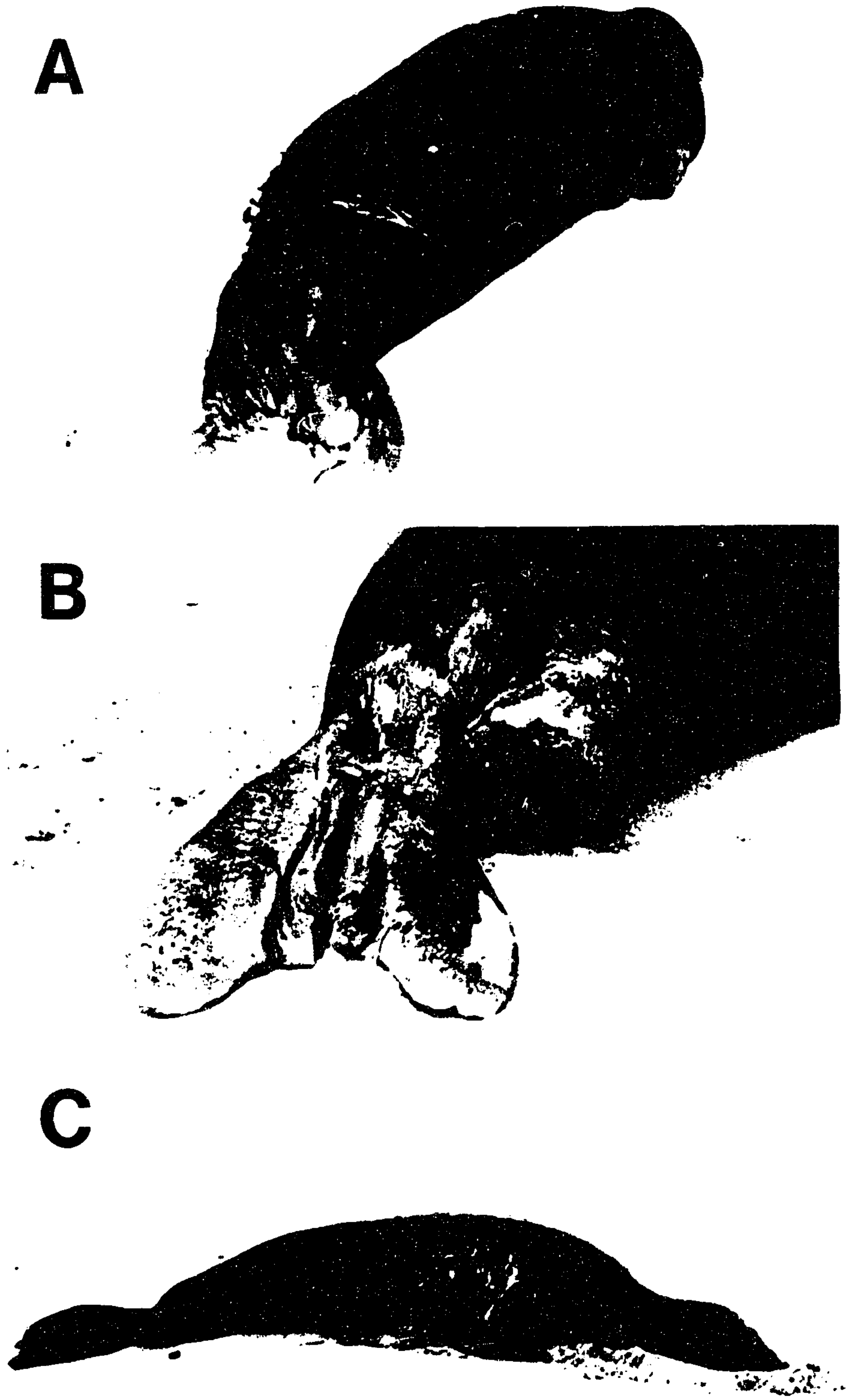
A
B
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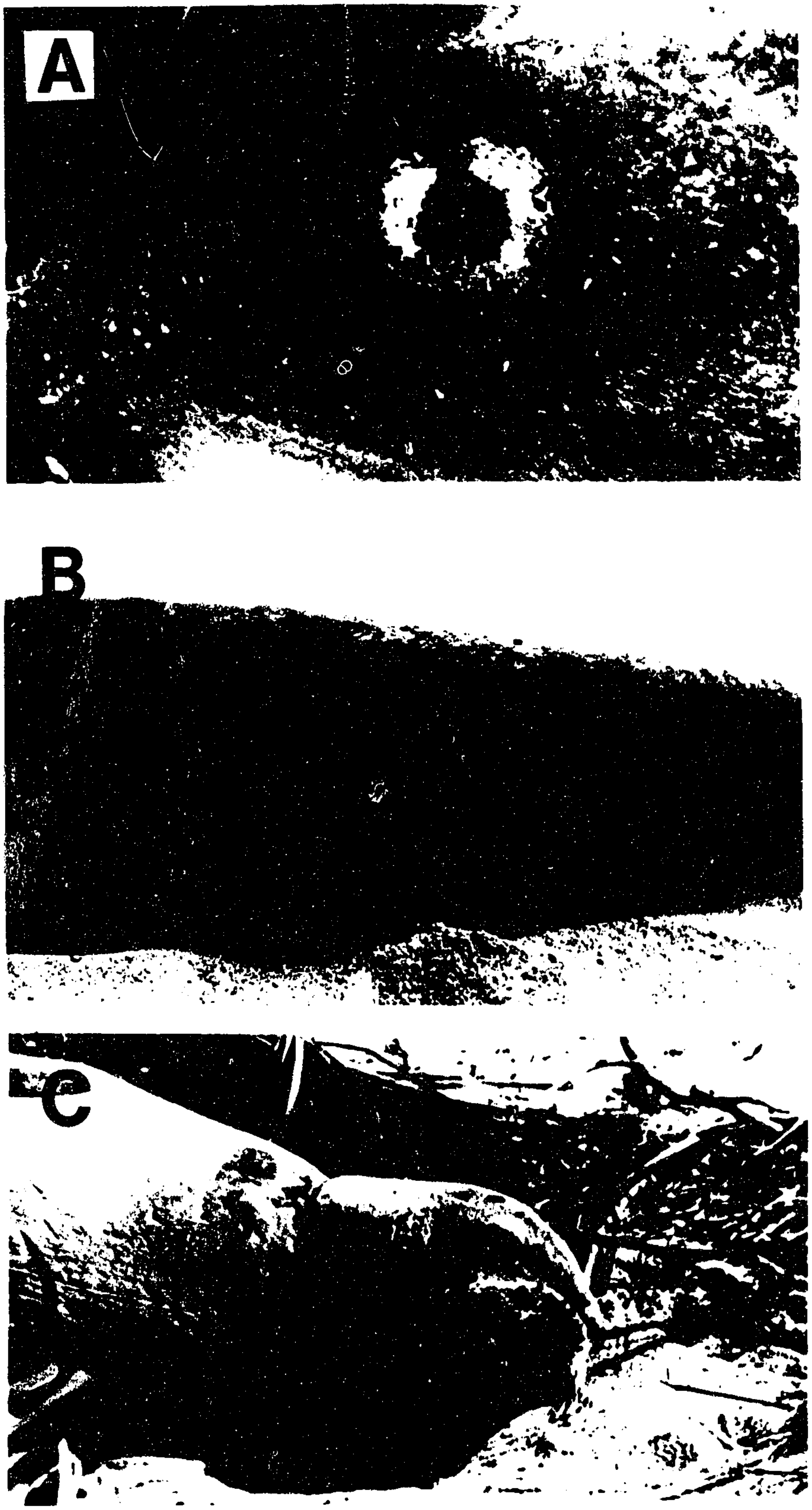
Plate 2.4. Injuries observed on Hawaiian monk seals. a) circular wound inflicted by _Isistius brasiliensis_, the cookiecutter shark; b) abrasions caused by contact with a coral reef; c) entanglement scar caused by constriction from netting around seal's neck.


A
B
C

2.5. Literature cited

Ainley, D.G., R.P. Henderson, H.R. Huber, R.J. Boekelheide, S.G. Allen and T.L. McElroy. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. So. Ca. Acad. Sci. Mem. 9:109-122.

Alcorn, D.J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM- NMFS-SWFC-42. 37 p.

Alcorn, D.J. and E. Buelna. 1989. The Hawaiian monk seal on Laysan Island, 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-124, 46 p.

Alcorn, D.J. and A. Kam. 1986. Fatal shark attack on a Hawaiian monk seal (Monachus schauinslandi). Marine Mammal Sci., 2(4):313-315.

Amerson, A.B. Jr. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. Atoll Research Bulletin 150.

Anderson, P.K. and A. Birtles. 1978. Behaviour and ecology of the dugong, Dugong dugon (Sirenia): observations in Shoalwater and Cleveland Bays, Queensland. Aust. Wildl. Res. 5:1-23.

Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. In: Bateson, P. (ed). Mate Choice. Cambridge University Press. Cambridge. p. 181-210.

Bailey, R.O., N.R. Seymour and G.R. Stewart. 1978. Rape behavior in blue-winged teal. Auk 95:188-190.

Balazs, G. 1979. Synthetic debris observed on a Hawaiian monk seal. 'Elepaio 40(3):43-44.

Balazs, G. and C. Whittow. 1979. First record of a tiger shark observed feeding on a Hawaiian monk seal. 'Elepaio 39(9):107-109.

Boinski, S. 1987. Mating patterns in squirrel monkeys (Saimiri oersted) - implications for seasonal sexual dimorphism. Behav. Ecol. Sociobiol. 21:13-21.

Boness, D.J. 1990. Fostering behavior in Hawaiian monk seals: is there a reproductive cost? Behav. Ecol. Sociobiol. 27:113-122.

Brodie, P. and B. Beck. 1983. Predation by sharks on the grey seal (Halichoerus grypus) in eastern Canada. Can. J. Fish. Aquat. Sci. 40(3):267-71.

Castro, J.I. 1983. The sharks of North American waters. Texas A & M University Press. College Station, Texas.

Clutton-Brock, T.H., S.D. Albon, R.M. Gibson and F.E. Guinness. 1979. The logical stag: adaptive aspects of fighting in red deer (Cervus elaphus L.). Anim. behav. 27:211-225.

Cockcroft, V.G., G. Cliff and G.J.B. Ross. 1989. Shark predation on Indian Ocean bottlenose dolphins Tursiops truncatus off Natal, South Africa. S. Afr. J. Zool. 24(4):305-310.

Compagno, L.J.V. 1984a. Sharks of the World - FAO Species Catalogue Part 1. FAO Fish Synopsis No. 125, Vol. 4, Part 1, FAO, Rome.

Compagno, L.J.V. 1984b. Sharks of the World - FAO Species Catalogue Part 2. FAO Fish Synopsis No. 125, Vol. 4, Part 2, FAO, Rome.

Cox, C.R. 1981. Agonistic encounters among male elephant seals: frequency, context, and the role of female preference. Amer. Zool. 21:197-209.

Dodrill, J.W. and R.G. Gilmore. 1978. Land birds in the stomachs of tiger sharks Galeocerdo cuvieri (Peron & LeSuer). Auk 95:585-586.

Ely, C.A. and R.B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Research Bulletin 171. 361 p.

Emlen, S.T. and P.H. Wrege. 1986. Forced copulations and intra-specific parasitism: two costs of social living in the white-fronted bee-eater. Ethology 71:2-29.

Enomoto, T., K. Seiki and Y. Haruki. 1979. On the correlation between sexual behavior and ovarian hormone level during the menstrual cycle in captive Japanese monkeys. Primates 20:563-570.

Fisher, H.I. 1975. Mortality and survival in the Laysan albatross, Diomedia immutabilis. Pac. Sci. 29(3):279-300.

Foott, J.O. 1970. Nose scars in female sea otters. J. Mammal. 51(3):621-622.

Geist, V. 1964. On the rutting behavior of the mountain goat. J. Mammal. 45(4):551-568.

Geist, V. 1985. New evidence of high frequency of antler wounding. Can. J. Zool. 64:380-384.

Gerrodette, T. 1985. Estimating the 1983 population of Hawaiian monk seals from beach counts. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii. SWFC Admin. Rep. H-85-5. 13 p.

Gilmartin, W.G. 1988. The Hawaiian monk seal: population status and current research activities. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rept. H-88-17. 14 p.

Gilmartin, W.G. and D.J. Alcorn. 1987. A plan to address the Hawaiian monk seal adult male "mobbing" problem. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rept. H-87-12. 24 p.

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. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-59. 9 p.

Gudger, E.W. 1949. Natural history notes on tiger sharks, Galeocerdo tigrinus, caught at Key West, Florida, with emphasis on food and feeding habits. Copeia 1949:39-47.

Hartman, D.S. 1979. Ecology and behavior of the manatee (Trichechus manatus) in Florida. The American Society of Mammalogists, Spec. Pub. No. 5.

Hatler, D.F. 1972. The coastal mink on Vancouver Island, British Columbia. Ph. D. Thesis, University of British Columbia. 360 p.

Henderson, J.R. 1985. A review of Hawaiian monk seal entanglements in marine debris. In: R.S.Shomura and H.O.Yoshida (eds): Proceedings of the workshop on the fate and impact of marine debris, 26-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54.

Howard, R.D. 1980. Mating behaviour and mating success in woodfrogs, Rana sylvatica. Anim. Behav. 28:705-716.

Johanos, T.C. and S.L. Austin. 1988. Hawaiian monk seal population structure, reproduction, and survival on Laysan Island, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM0NMFS-SWFC-118, 38 p.

Johanos, T.C. and A.K.H. Kam. 1986. The Hawaiian monk seal on Lisianski Island: 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-58. 37 p.

Johanos, T.C., A. Kam and R.G. Forsyth. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-70. 38 p.

Johnson, B.W. and P.A. Johnson. 1981. Estimating the Hawaiian monk seal population on Laysan Island. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., No. PB-82-106113, 29 p.

Johnson, P.A. and B.W. Johnson. 1984. Hawaiian monk seal observations on French Frigate Shoals, 1980. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-50. 47 p.

Johnson, R.H. 1978. Sharks of Polynesia. Les Editions du Pacifique, Papeete. 170 p.

Jones, E.C. 1971. *Isistius brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. Fish. Bull. 69(4):791-798.

Kenyon, K.W. 1981. Monk seals - *Monachus*. In: S.H. Ridgway and R.J. Harrison (eds.), *Handbook of marine mammals*. Vol. 2, *Seals*. London: Academic Press. p. 195-220.

Kenyon, K.W. and D.W. Rice. 1959. Life history of the Hawaiian monk seal. Pac. Sci. 31:215-252.

LeBoeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. Amer. Zool. 14:163-176.

LeBoeuf, B.J., J.E. McCosker and J. Hewitt. 1987. Crater wounds on northern elephant seals: the cookiecutter shark strikes again. Fish. Bull. 85(2):387-392.

LeBoeuf, B.J. and S.L. Mesnick. in press. Sexual behavior of northern elephant seals: I. Lethal injuries to adult females. Behaviour.

LeBoeuf, B.J., M. Riedman and R.S. Keyes. 1982. White shark predation on pinnipeds in California coastal waters. Fish. Bull. 80(4):891-895.

Marlow, B.J. 1975. The comparative behaviour of the Australasian sea lions, *Neophoca cinerea* and *Phocarctos hookeri* (Pinnipedia: Otariidae). Mammalia

39:159-230.

McCann, T.S. 1982. Aggressive and maternal activities of female southern elephant seals (Mirounga leonina). Anim. Behav. 30:268-276.

McKinney, F., S.R. Derrickson and P. Mineau. 1983. Forced copulation in waterfowl. Behaviour 86:250-293.

Mesnick, S.L. and B.J. LeBoeuf. in press. Sexual behavior of male northern elephant seals: II. Female response to potentially injurious encounters. Behaviour.

Preen, A. 1989. Observations of mating behavior in dugongs (Dugong dugon). Marine Mammal Sci. 5(4):382-387.

Rice, D.W. 1960. Population dynamics of the Hawaiian monk seal. J. Mamm. 41:376-385.

Rice, D.W. 1984. Albatrosses. In: Haley, D. (ed). Seabirds of eastern north Pacific and arctic waters. Pacific Search Press, Seattle, WA.

Siniff, D.B., I. Stirling, J.L. Bengtson and R.H. Reichle. 1979. Social and reproductive behaviour of crabeater seals (Lobodon carcinophagus) during the austral spring. Can. J. Zool. 57(11):2243-2255.

Smith, M.S.R. 1966. Injuries as an indication of social behaviour in the Weddell seal (Leptonychotes weddelli). Mammalia 30:241-246.

Smuts, B.B. 1987. Gender, Aggression and Influence. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds.). Primate Societies. Chicago: University of Chicago Press. pp. 400-412.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd ed. W.H. Freeman and Company. New York.

Stone, H.S. 1984. Hawaiian monk seal population research, Lisianski Island, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-47, 33 p.

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. Natl. Tech. Info. Serv., Springfield, Va. No. PB-285626. 34 p.

Titman, R.D. and J.K. Lowther. 1975. The breeding behavior of a crowded population of mallards. Can. J. Zool. 53:1270-1283.

Tricas, T.C., L.R. Taylor and G. Naftel. 1981. Diel behaviour of the tiger shark, Galeocerdo cuvier, at French Frigate Shoals, Hawaii. Copeia 1981(4):904-908.

Wirtz, W.O., II. 1968. Reproduction, growth and development, and juvenile mortality in the Hawaiian monk seal. J. Mammal. 49:229-238.

3. The significance of wounding to the reproductive success of the female Hawaiian monk seal

3.1. Introduction

In recent years, efforts to identify factors contributing to decreased survival and productivity have increased as part of an overall monk seal recovery plan (Gilmartin 1988). Counts of monk seals have declined from 1300 seals in 1959 to approximately 580 in 1987 (Johnson et al. 1982, Gilmartin 1988). In this situation, even a slight decrease in female productivity could have a significant negative impact on population dynamics, as the net growth of a population is dependent on, and most sensitive to, female reproductive success and survival (Eberhardt 1985). Consequently, the occurrence of injuries to female Hawaiian monk seals and their potential effect on reproductive success have become a matter of concern (Gilmartin and Alcorn 1987).

Female reproductive success can be subdivided into several components, such as survival to breeding age, reproductive life span, productivity and survival of offspring (Clutton-Brock 1988), all of which could be influenced by injuries. In long-lived animals, such as monk seals that can reproduce up to 25 years of age or more (Johanos et al. 1990), longevity is a significant component of female lifetime reproductive success (LeBoeuf and Reiter 1988; Thomas and Coulson 1988), especially if only one offspring is produced per year. If injuries increase the mortality of female monk seals, their lifetime productivity will be reduced.

Injuries to adult female monk seals could affect the production of pups in several ways. A wounded female might be less likely to breed simply because she needs her resources to ensure her own survival, or if she does breed, her pup may be aborted. Injured female northern elephant seals (Mirounga angustirostris) did not copulate in the year that they were injured, and thus did not have a pup in the year following the injury (LeBoeuf et al. 1982). Suppression of a female's productivity for one or more years because of injury would decrease her overall reproductive success.

Injuries may also reduce the survival of pups born to wounded females. If an injured female has a pup, the amount of energy she is able to invest in it during the nursing period may be less than an uninjured female could invest. Energy stored for lactation or for development of her pup might be redirected towards recovery from the injury (Ainley et al. 1981). Similarly, a pregnant female that recovered from an injury might not be in as good condition at parturition as a female that was not injured. Female Hawaiian monk seals fast during the entire nursing period (Kenyon and Rice 1959), as do most other phocid seals (King 1983; Riedman 1990). If a female monk seal is in poor condition when her pup is born, she may be more likely to have a smaller pup or to wean her pup prematurely due to energy constraints, because she is not feeding and cannot replenish her energy stores during lactation. A light weaning weight may reduce the pup's probability of survival through its first year of life.

In this paper, I examine the influence of injuries on four areas of female reproductive success: pup production, maternal investment, survival of pups, and mortality of adult females. I test the hypothesis that injuries inflicted on females by adult males have a negative impact on their survival and reproduction. Three specific predictions are considered: 1) production of pups is lower for injured females than uninjured females; 2) injured females invest less energy in their pups than uninjured females; and 3) the survival of pups through their first year of life is lower for pups of injured females than for pups of uninjured females. I also examine the ages of immature females that are injured by adult males and evaluate the significance of injury to recruitment of young females into the population.

3.2. Methods

Female Hawaiian monk seals were observed on Laysan Island, a low coral sand island located northwest of the main Hawaiian Islands (lat. 25° 42'N, long. 171° 44'W; Figure 2.1), from 28 February 1988 to 21 June 1988, and from 30 March 1989 to 14 July 1989 (Chapter 2) by me and personnel from the National Marine Fisheries Service Marine Mammal and Endangered Species Program (NMFS MMESP). In addition to the data collected in 1988 and 1989, I analysed data on female reproductive histories and injuries, collected by NMFS MMESP biologists on Laysan Island from 1983 to 1987.

Individual female seals were identified by temporary marks applied with commercial bleach at the beginning of the field season, by natural markings or scars, or by flipper tags applied in previous years, as described in Chapter 2. Only seals with distinctive scars, natural markings, or flipper tags were easily identifiable between years. Seals that were known only by minor scars or marks applied with bleach were not consistently identified between years.

Data were recorded on the reproductive status (i.e. whether the female had a pup or not) and injuries sustained by each female seal. For all female seals with pups, the date of parturition, date of weaning of the pup, and the permanent identification number assigned to the pup after it had been tagged were recorded. From 1983 through 1989, all pups were tagged after they were weaned (Alcorn and Buelna 1989, Johanos et al. 1987, Johanos and Austin 1988, Johanos et al. 1990). For all injured female seals, the data recorded were as described in Chapter 2.

Because birthrate usually varies with age in pinnipeds (e.g. northern elephant seals, Huber 1987; Weddell seals, Leptonychotes weddelli, Testa 1987), I divided female seals into two classes based on estimated age, so that seals that matured during the study period were not compared to adult seals. Adult female seals were defined as seals that were classed as adults in 1983 according to criteria of seal length, girth, pelage appearance and scarring (Stone 1984), or if the female had a pup in 1983 or earlier. Immature seals were defined as seals that were seen as juveniles or subadults in 1983 or 1984, or that were born in 1983 or later.

To evaluate the relative importance of injuries on reproductive success, adult female monk seals were divided into three categories in each year:

uninjured - females that did not sustain any injuries prior to parturition or in the previous year;

currently injured - females injured before parturition or while still nursing the pup; and previously injured - females that were injured in the previous year, usually after weaning the pup of that year. This category also includes the females that were injured in the previous year and were not observed with a pup.

I divided immature seals into two classes, based on the reproductive maturity and age of the seals in 1988 and 1989. Seals aged 0 to 3 years were classed as pre-reproductive, based on the knowledge that the youngest observed age of first reproduction for Hawaiian monk seals is 5 years (Johanos et al. 1990). The minimum age of first estrus is therefore 4 years, since female monk seals mate the year before they give birth. Seals aged 4 to 7 years were classed as reproductive. Seals born in 1983 and after were tagged as pups, and thus were classed on their known age. Since the minimum age in 1988 of untagged, unknown age females seen as juveniles or subadults in 1984 was greater than 4 years, they were classed as reproductive.

Injuries were classified as minor or major wounds. Minor wounds were circular wounds inflicted by cookiecutter sharks (Isistius brasiliensis), wounds inflicted by seals in jousting incidents, or those inflicted by the seal contacting a coral reef or debris (Chapter 2). Major wounds were those inflicted by adult male seals (dorsal lacerations or gaping wounds) or large sharks (Chapter 2). Some of the wounds inflicted by adult males did not appear to be severe externally. However, because superficially minor abrasions and lacerations (Plate 2.1a,b) may mask significant subcutaneous damage (Johanos and Austin 1988), and females die after sustaining seemingly minor wounds from adult male monk seals (Johanos et al. 1990; pers. obs.), these injuries were classified as major wounds.

3.2.1. Pup production

I defined pup production as the proportion of females that had a pup in a particular year. The pup production of females that were injured in the previous year was compared to the pup production of uninjured females. Because the definition of currently injured females ensures that all currently injured females have pups, this class of females was excluded from the analysis of pup production.

3.2.2. Parental investment

The parental investment period (the number of days that a female nurses and defends her pup) was calculated from the birth and weaning dates of each pup. If a range of dates was recorded for the birth date or weaning date (e.g. Mar. 1-Mar. 3), the last day of the range (Mar. 3) was used to calculate the parental investment period. Although monk seal births have been recorded in every month, most pups are born between late December and mid-August with a peak in occurrence of births between mid-March and May (Kenyon and Rice 1959; Kenyon 1981). Because of the protracted length of the pupping season, the duration of field camps did not always coincide with the whole period. Consequently, some females gave birth to pups before the start of the field camp for that year, and some females weaned their pups after the camp had ended. The length of completed parental investment periods of currently and previously injured females were compared, as were those of injured and uninjured females. If a female's parental investment period was cut short because her pup died or because she lost her pup to another female and did not gain another, the record was excluded from the analysis. Females with major and minor injuries were compared independently to uninjured females.

3.2.3. Pup survivorship

Pup survivorship was measured in two ways: 1) the proportion of pups alive at the end of the nursing period, and 2) the proportion of pups alive after their first year. Survivorship of pups of currently and previously injured females were compared to each other, and independently to pups of uninjured females. Pups of females with major and minor injuries were compared independently to pups of uninjured females.

3.2.4. Frequency of injury

I examined the reproductive history of all permanently identified adult female seal in relation to the number of major injuries sustained per year in 1988 and 1989. The distribution of major injuries within years (number of injuries per year for each seal) was compared to a Poisson distribution to determine if some females received a disproportionate fraction of injuries.

3.2.5. Immature females

To determine the age class of immature females that adult male seals attack most frequently, I compared the proportion of animals injured by adult males in the pre-reproductive (age 0-3 years) and reproductive (age 4-7 years) classes of immatures in 1988 and 1989.

3.2.6. Mortality

The number of identified female seals that died or disappeared from Laysan Island from 1983 to 1989 was examined to determine how many were known to have sustained adult male-inflicted injuries.

3.3. Results

Data were available on 56 individually identified adult female seals, 14 untagged immature females and 99 tagged immature female seals from 1983 through 1989. Thirteen adult and two untagged immature female seals were identified in all years from 1983 through 1989. Only partial records were available for the remaining 43 adult and 12 untagged immature females. All tagged animals were consistently identified between years.

3.3.1. Pup production

The severity of the injury did not appear to affect pup production of injured females (Table 3.1). Both those with major injuries ($G=0.722$, $d.f.=1$, $p>0.25$) and those with minor injuries ($G=0.015$, $d.f.=1$, $p>0.9$) had pup production similar to that of uninjured females.

3.3.2. Parental investment

Major injuries

Injured females did not appear to invest significantly less in their pups than did uninjured females. The parental investment period of previously injured females with major injuries was similar to uninjured females ($\bar{x}=41.1$ days, $n=74$; Mann-Whitney normal approximation, $t=0.918$, $0.1<p<0.25$). Currently injured females with major injuries invested the same amount of time in their pups ($\bar{x}=40$ days, $n=2$) as females injured the previous year ($\bar{x}$=38.8 days, n=6; Mann-Whitney U-test: U=6.5, p>0.5). When both current and previous classes were combined, females with major injuries invested a similar amount of time in their pups ($\bar{x}$=39.13 days, n=8) to uninjured females (Mann-Whitney normal approximation, t=0.981, 0.1<p<0.25).

Minor injuries

The parental investment period of currently injured females with minor injuries ($\bar{x}$=41.8 days, n=6) did not differ significantly from that of previously injured females ($\bar{x}$=41.5 days, n=2; Mann-Whitney U-test: U=11, p>0.05). Injured females (current and previous classes combined, $\bar{x}$=41.75, n=8) and uninjured females had similar investment in their pups (Mann-Whitney normal approximation: t=0.723, 0.1<p<0.25).

3.3.3. Pup survivorship

Survival to weaning

Of six pups that died prior to weaning, 2 had uninjured mothers, 2 had mothers with a major injury, and 2 had mothers with a minor injury. Pup survival to weaning was similar for pups of females with major injuries (n=18/20, 90%) and those with minor injuries (n=9/11, 82%; G=0.361, d.f.=1, p>0.5). Within the females with major injuries, survivorship to weaning of pups of currently injured (n=7) and previously injured (n=13) females was not significantly different (G=0.25, d.f.=1, p>0.5). When the major and minor injury classes were pooled, the pup survival to weaning (n=27/31, 87%) was significantly lower than that of uninjured females (n=119/121, 98%; G=5.53, d.f.=1, 0.01<p<0.025).

Survival through the first year

Major injuries

Pups of currently injured females with major injuries had similar survivorship to pups of previously injured females (G=1.98, d.f.=1, p>0.1, Table 3.1), but slightly lower survivorship than pups of uninjured females (G=2.92, d.f.=1, 0.05<p<0.1), though the trend was not significant. Pups of previously injured females with major injuries had the same survivorship as pups of uninjured females (G=0.002, d.f.=1, p>0.95). Pups of injured females (current and previous classes pooled) had similar survivorship to those of uninjured females (G=1.01, d.f.=1, p>0.25).

Minor injuries

Survivorship of pups was the same for pups of current and previously injured females with minor injuries ($G=0.045$, d.f.=1, $p>0.5$). Females with minor injuries (currently and previously injured females pooled) had the same pup survivorship as uninjured females ($G=2.56$, d.f.=1, $p>0.1$).

3.3.4. Frequency of injury

Thirty-seven of 58 adult female seals (64%) did not sustain a major injury in 1988 or 1989 (Table 3.2). The distribution of the number of major injuries per year for adult female seals did not differ significantly from a Poisson distribution ($G=1.87$, d.f.=1, $p>0.1$).

3.3.5. Immature females

In 1988, adult male seals injured similar proportions of reproductive female seals aged 4 to 7 years (n=4/27) and pre-reproductive females aged 0 to 3 years (n=4/50; $G=0.78$, d.f.=1, $p>0.25$; Table 3.3). Although the difference between the two classes was not significant, wounding of reproductive females was almost double that of pre-reproductive females, which is consistent with the results from 1989, when a greater proportion of reproductive than pre-reproductive immatures was injured (n=12/32 and 3/44 respectively; $G=10.86$, d.f.=1, $p<0.001$). Moreover, many females in the reproductive class were injured more than once, whereas all injured pre-reproductive females were only wounded once (Table 3.3). The number of injuries per female for the reproductive class was significantly greater than for the pre-reproductive class in both 1988 and 1989 (1988: $G=4.16$, d.f.=1, $0.025<p<0.05$; 1989: $G=16.56$, d.f.=1, $p<0.001$). The proportion of immature females in the reproductive class that sustained adult male-inflicted injuries in 1988 and 1989 (n=16/59, Table 3.3) was similar to that of adult females (n=18/55, Table 3.2; $G=0.42$, d.f.=1, $p>0.5$).

3.3.6. Mortality

Eight of 56 permanently identified adult female monk seals died between 1983 and 1989. These females all sustained injuries inflicted by adult male monk seals prior to their deaths. During the same period, no uninjured adult females were known to have died, although two uninjured females in 1983 and one uninjured female in

1988 that were easily identified by natural bleach marks were not seen in any subsequent years. Eight unidentified females died between 1983 and 1989; all of these females sustained injuries inflicted by adult male monk seals.

One untagged immature female, and 4 of 26 females between 3 and 6 years old died after sustaining injuries from adult male seals. Two immature females identified from flipper tags disappeared after sustaining adult male-inflicted injuries, and were not seen in subsequent years.

3.4. Discussion

The predictions considered in testing the hypothesis that injuries inflicted by adult male monk seals had a negative effect on female reproductive success were not all supported. Injured females did not have lower parental investment and pup production than uninjured females. However, their pups appeared to survive less well than those of uninjured females. Pups of injured females (all classes pooled) had significantly lower survivorship to weaning than pups of uninjured females. Pups of currently injured females with major wounds had slightly lower survival through the first year than pups of uninjured females, although the difference was not significant, possibly because the sample size of the former group was small (Table 3.1).

The timing of an injury to a female could influence the amount of energy she has during lactation, which in turn could affect the pup's survival through its first year. Lactation is energetically costly for females (Young 1976). Because female phocid seals generally do not feed during lactation (e.g. monk seals: Kenyon and Rice 1959; grey seals, Halichoerus grypus: Anderson and Fedak 1987; northern elephant seals: Riedman and Ortiz 1979; harp seals, Phoca groenlandica: Lavigne et al. 1982), they use a significant proportion of their energy reserves to feed their pups. For example, female grey seals use 85% of their stored energy resources while nursing their offspring (Fedak and Anderson 1982), northern elephant seals use 58% (Costa et al. 1986), and hooded seals (Cystophora cristata) use 33% (Bowen et al. 1987). A female in poorer condition because of a recent injury may have a lower than normal supply of stored fat available for lactation, resulting in reduced survival of the pup. The survival of pups of currently injured females was lower than those of uninjured females, although the difference was not significant (Table 3.1). Because currently injured females were wounded shortly before parturition or during lactation, they may have used energy, otherwise allocated for lactation, in order to recover from injuries. Two female monk seals that sustained severe injuries inflicted by sharks shortly prior to pupping at French Frigate Shoals (lat. 23° 45'N, long. 166° 10'W; Figure 2.1) could not nurse their pups, and eventually abandoned them (M.P. Craig, pers. comm.). Stewart and Lavigne (1984) suggested that poor condition of females before parturition may reduce the survival of their offspring. Female harp seals with lower energy reserves at the beginning of the lactation period have smaller, lighter newborn pups than females with higher energy reserves (Stewart and Lavigne 1984). Female northern elephant seals arriving for the breeding season with fresh shark wounds were less successful at pupping and breeding than uninjured females (Ainley et al. 1981; LeBoeuf et al. 1982). The pups of injured female elephant seals were stillborn or abandoned soon after birth, or wounded mothers allowed other females to nurse her pup. The injuries sustained by elephant seals affected their ability to successfully wean their pups. Ainley et al. (1981) found that females that had raised pups successfully to weaning age prior to their injury were less successful in raising their pup during the year in which they were injured. Thus, wounds that result in the condition of females being poorer than normal appear to cause reduced survival of offspring.

A pup may need a minimum amount of energy from the nursing period in order to survive, since it fasts for a number of weeks after it is weaned. The postweaning period is critical because the pup is relatively defenseless, inexperienced, and must live on its stored energy until it learns to feed on its own (Reiter et al. 1978). Hawaiian monk seal pups lose approximately 15-30% of their weaning weight in the postweaning fast (Kenyon and Rice 1959). Other phocid seal pups also lose a significant proportion of their weight in the first few weeks after weaning. Hooded seal pups lose about 29% of their weaning weight before beginning to feed 30 days after weaning (Bowen et al. 1987). Weddell seal pups lose approximately 0.75 kg per day during the postweaning fast (Lindsey 1937, Bryden et al. 1984).

Most of the energy used during the postweaning fast appears to be from blubber accumulated during nursing. About 94% of the energy required by grey seal pups during the first month of their postweaning fast comes from blubber stored during the nursing period (Nordoy and Blix 1985; Worthy and Lavigne 1987). Similarly, harp seal pups obtain 80-90% of their energy from blubber acquired in the nursing period (Worthy and Lavigne 1983, 1987). Because of the high energetic cost of the postweaning fast, a pup weaned at a lighter than normal weight would probably be less likely to survive its first year. Consequently, the survival of pups of currently injured females may be detrimentally affected by their mothers' wounds.

In contrast to currently injured females, females injured in the year previous to the birth of their pups appear to have recovered sufficiently from their injuries to store normal energy reserves before parturition. Pup production, mean parental investment period, and pup survivorship of previously injured females were not significantly different from those of uninjured seals. Most pregnant grey seals do not start increasing in weight until the time of implantation of the blastocyst (approximately 3 to 4 months after copulation; Boyd 1984). Johnson and Johnson (1978) found that many Hawaiian monk seal females had regained most of the weight lost during lactation in 42 to 66 days before undergoing an extended stay on shore (20 to 30 days) for their moult. Monk seals appear to fast or eat very little during the moult (Kenyon and Rice 1959). If female Hawaiian monk seals do not begin storing energy for lactation until after they moult, a previously injured female would have several months to recover from her wound before starting to deposit fat reserves in anticipation of lactation, and her pup would be more likely to receive the full nutritional benefit of lactation than the pup of a currently injured mother.

A female monk seal's reproductive success is influenced by the severity of her injuries. Minor injuries had no detectable effect on the reproductive success of female monk seals. Pup production, mean parental investment period, and survivorship of the pups of currently and previously injured females with minor wounds were the same as those of uninjured females. Major injuries negatively affected the reproductive success of currently injured females with respect to their pup survivorship (Table 3.1). LeBoeuf et al. (1982) monitored eleven female elephant seals with "moderate to severe" fresh wounds and suggested that the injured females that were successful in raising their pups appeared to have the least severe injuries.

Adult male monk seals injured reproductively mature females most frequently, and sometimes fatally (Chapter 2; Figure 2.4). Most of the female seals that died at Laysan Island sustained injuries inflicted by adult males before they died. Some of the females that died did not appear to have injuries that were serious enough to be fatal (Chapter 2; Plate 2.1a,b). In these cases, it may have been the continued harassment of the males during a mobbing incident which resulted in sufficient wounding to cause death. The abrasions and lacerations on the back of the female, although not severe enough to be fatal, may mask subcutaneous damage which was not obvious (Johanos and Austin 1988). Some female seals are reinjured often enough in the same year by adult males (Table 3.2) that the cumulative effect may result in the death of the female. Similarly, female northern elephant seals sometimes die after being harassed by groups of subordinate males (LeBoeuf and Mesnick in press). A female elephant seal departing from the harem may be chased by several subordinate males, all of which attempt to mount her. During this time, she receives over 20 times more blows, mounts and copulations than normal, and males sometimes compete over her carcass even after death (LeBoeuf and Mesnick in press). Female mink (Mustela vison) have also been known to die after being pursued by, and mating with, several males (Hatler 1972). The female sustains neck injuries during mating, but these are often not severe enough to be fatal (Hatler 1972). Hatler suggests that because the males pursue her frequently, she probably cannot hunt and replenish her energy reserves, and thus she dies as a result of continued harassment.

Immature females were injured more often by adult male monk seals as they entered the reproductive population than when they were pre-reproductive (Table 3.3). As well, the proportion of immature females aged 4 to 7 years that were injured was similar to that of adult females. Thus, adult male seals wound females throughout their breeding lifespan. Immature females sometimes die from these injuries; 4 of 26 females between 3 and 6 years old in 1988 and 1989 sustained fatal injuries. Mortality of young females is a serious concern with respect to population growth, as their potential productivity is never realized, thus reducing future recruitment into the population.

In summary, the major consequence of injuries on female reproductive success results from the increase in female mortality, which in turn shortens their reproductive lives. The timing and severity of injuries can affect the survivorship of pups of injured females if the female does not have sufficient time to recover from her injury before parturition and lactation. However, if a female has sufficient time between sustaining the injury and parturition, there appears to be no major effect on the survival of her pup to weaning and through the first year of life.

Table 3.1. Survivorship through the first year of pups of injured and uninjured female Hawaiian monk seals, Laysan Island, NWHI. current: seals injured before or during parental investment; previous: seals injured in the previous year after the end of parental investment or during a year in which they were not seen with a pup. Numbers in brackets represent percentages.

	Females with major injuries		Females with minor injuries		Uninjured females
	current	previous	current	previous	
# pups that survived	2 (29)	9 (69)	3 (43)	2 (50)	79 (65)
# pups that did not survive	4 (57)	4 (31)	4 (57)	2 (50)	33 (27)
# pups whose fate was unknown	1 (14)	0 (0)	0 (0)	0 (0)	9 (8)
TOTAL # PUPS	7	13	7	4	121
total # females	7	25	7	7	203
% females with pup	100	52	100	57	60

Table 3.2. Number of major injuries per year for adult female Hawaiian monk seals, Laysan Island, in 1988 and 1989. Expected frequencies are generated from a Poisson distribution.

<table>
<tr><th></th><th colspan="3"># of female monk seals</th><th></th></tr>
<tr><th># injuries per yr</th><th>1988</th><th>1989</th><th>pooled</th><th>expected frequency</th></tr>
<tr><td>0 injuries</td><td>25</td><td>12</td><td>37</td><td>34.28</td></tr>
<tr><td>1 injury</td><td>5</td><td>7</td><td>12</td><td>16.21</td></tr>
<tr><td>2 injuries</td><td>1</td><td>3</td><td>4</td><td rowspan="2">4.43</td></tr>
<tr><td>3 injuries</td><td>2</td><td>0</td><td>2</td></tr>
<tr><td></td><td>33</td><td>22</td><td>55</td><td></td></tr>
</table>

Table 3.3. Number of immature female Hawaiian monk seals injured in the reproductive (age 4-7 years) and pre-reproductive (age 0-3 years) classes at Laysan Island, NWHI, in 1988 and 1989. rep= reproductive class (age 4-7 years); pre= pre-reproductive class (age 0-3 years). Numbers in brackets indicate the total number of injuries inflicted; other numbers indicate the number of seals in each class. * denotes a significant difference between reproductive and pre-reproductive classes.

	1988		1989		pooled	
	pre	rep	pre	rep	pre	rep
# females injured	4	4	3	12*	7	16*
total # injuries	(4)	(7)*	(3)	(15)*	(7)	(22)*
# females not inj.	46	23	41	20	87	43
TOTAL # FEMALES	50	27	44	32	94	59

3.5. Literature cited

Ainley, D.G., C.S. Strong, H.R. Huber, T.J. Lewis, and S.H. Morrell. 1981. Predation by sharks on pinnipeds at the Farallon Islands. Fish. Bull. 78(4):941-945.

Alcorn, D.J. and E. Buelna. 1989. The Hawaiian monk seal on Laysan Island, 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-124, 46 p.

Anderson, S.S. and M.A. Fedak. 1987. Grey seal, Halichoerus grypus, energetics: females invest more in male offspring. J. Zool. Lond. 211:667-679.

Bowen, W.D., D.J. Boness, and O.T. Oftedal. 1987. Mass transfer from mother to pup and subsequent mass loss by the weaned pup in the hooded seal, Cystophora cristata. Can. J. Zool. 65:1-8.

Boyd, I.L. 1984. The relationship between body condition and the timing of implantation in pregnant grey seals (Halichoerus grypus). J. Zool. Lond. 203:113-123.

Bryden, M.M., M.S.R. Smith, R.A. Tedman and D.W. Featherston. 1984. Growth of the Weddell seal, Leptonychotes weddelli (Pinnipedia). Aust. J. Zool. 32:33-41.

Clutton-Brock, T.H. 1988. Introduction. In: T.H. Clutton-Brock (ed.), Reproductive success. Chicago: University of Chicago Press. p. 1-6.

Costa, D.P., B.J. LeBoeuf, A.C. Huntley, and C.L. Ortiz. 1986. The energetics of lactation in the northern elephant seal, Mirounga angustirostris. J. Zool. Lond.(A) 209:21-33.

Eberhardt, L.L. 1985. Dynamics of wild populations. J. Wildl. Manage. 49(4):997-1012.

Fedak, M.A., and S.S. Anderson. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (Halichoerus grypus). J. Zool. Lond. 198:473-479.

Gilmartin, W.G. 1988. The Hawaiian monk seal: population status and current research activities. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rept. H-88-17. 14 p.

Gilmartin, W.G. and D.J. Alcorn. 1987. A plan to address the Hawaiian monk seal adult male "mobbing" problem. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rept. H-87-12. 24 p.

Hatler, D.F. 1972. The coastal mink on Vancouver Island, British Columbia. Ph. D. Thesis, University of British Columbia. 360 p.

Huber, H.R. 1987. Natality and weaning success in relation to age of first reproduction in northern elephant seals. Can. J. Zool. 65:1311-1316.

Johanos, T.C., and S.L. Austin. 1988. Hawaiian monk seal population structure, reproduction and survival on Laysan Island, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-118. 38 p.

Johanos, T.C., B.L. Becker, M.A. Brown, B.K. Choy, L.M. Hiruki, R.E. Brainard and R.L. Westlake. 1990. The Hawaiian monk seal on Laysan Island, 1988. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-151, 44 p.

Johanos, T.C., A. Kam, and R.G. Forsyth. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-70. 38 p.

Johnson, A.M., R.L. DeLong, C.H. Fiscus and K.W. Kenyon. 1982. Population status of the Hawaiian monk seal (Monachus schauinslandi), 1978. J. Mammal. 63(3):415-421.

Johnson, B.W. and P.A. Johnson. 1978. The Hawaiian monk seal on Laysan Island: 1977. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., No. PB-825-428, 38 p.

Kenyon, K.W. 1981. Monk seals - Monachus. In: Ridgway, S.H. and R.J. Harrison (eds.), Handbook of marine mammals. Vol. 2, Seals. London: Academic Press. p. 195-220.

Kenyon, K.W., and D.W. Rice. 1959. Life history of the Hawaiian monk seal. Pac. Sci. 8:215-252.

King, J.E. 1983. Seals of the world. Oxford: British Museum (Natural History) and Oxford University Press. 2nd ed.

Lavigne, D.M., R.E.A. Stewart and F. Fletcher. 1982. Changes in composition and energy content of harp seal milk during lactation. Physiol. Zool. 55(1):1-9.

LeBoeuf, B.J. and S.L. Mesnick. in press. Sexual behavior of northern elephant seals: I. Lethal injuries to adult females. Behaviour.

LeBoeuf, B.J. and J. Reiter. 1988. Lifetime reproductive success in northern elephant seals. In: T.H. Clutton-Brock (ed.), Reproductive success. Chicago: University of Chicago Press. p. 344-362.

LeBoeuf, B.J., M. Riedman, and R.S. Keyes. 1982. White shark predation on pinnipeds in California coastal waters. Fish. Bull. 80(4):891-895.

Lindsey, A.A. 1937. The Weddell seal in the bay of Whales, Antarctica. J. Mammal. 18:127-44.

Nordoy, E.S. and A.S. Blix. 1985. Energy sources in fasting grey seal pups evaluated with computed tomography. Am. J. Physiol. 249:R471-R476.

Reiter, J., N.L. Stinson and B.J. LeBoeuf. 1978. Northern elephant seal development: transition from weaning to nutritional independence. Behav. Ecol. Sociobiol. 3:337-367.

Riedman, M. 1990. The Pinnipeds - seals, sea lions and walruses. Berkeley and Los Angeles: University of California Press.

Riedman, M. and C.L. Ortiz. 1979. Changes in milk composition during lactation in the northern elephant seal. Physiol. Zool. 52:240-249.

Stewart, R.E.A. and D.M. Lavigne. 1984. Energy transfer and female condition in nursing harp seals, Phoca groenlandica. Holarctic Ecology. 7:182-194.

Stone, H.S. 1984. Hawaiian monk seal population research, Lisianski Island, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-47. 33 p.

Testa, J.W. 1987. Long-term reproductive patterns and sighting bias in Weddell seals (Leptonychotes weddelli). Can. J. Zool. 61:447-456.

Thomas, C.S. and J.C. Coulson. 1988. Reproductive success of kittiwake gulls, Rissa tridactyla. In: T.H.Clutton-Brock (ed.), Reproductive success. Chicago: University of Chicago Press, p. 251-262.

Worthy, G.A.J. and D.M. Lavigne. 1983. Energetics of fasting and subsequent growth in weaned harp seal pups, Phoca groenlandica. Can. J. Zool. 61:447-456.

Worthy, G.A.J. and D.M. Lavigne. 1987. Mass loss, metabolic rate, and energy utilization by harp and gray seal pups during the postweaning fast. Physiol. Zool. 60(3):352-364.

Young, R. 1976. Fat, energy and mammalian survival. Am. Zool.16:699-710.

4. The importance of wounding in population dynamics of the Hawaiian monk seal

4.1. Introduction

In recent years, concern about the future of the Hawaiian monk seal has increased because the total number of seals counted on beaches at all islands in the Northwestern Hawaiian Islands (NWHI) declined to about 580 in 1987 from approximately 1000 in 1957 (Gilmartin 1988; Johnson et al. 1982). The decline was unexpected since pup survival is high in monk seals (Gilmartin et al. 1987), and females have a long reproductive life (Johanos et al. 1990). Furthermore, monk seal numbers dropped only at certain islands in the western part of the NWHI (Johnson et al. 1982). Eberhardt and Siniff (1977) and Eberhardt (1985) showed that in long-lived mammals with low reproductive rates, the most important factor related to the survival and growth of a population is the survival of adult females. Because monk seal populations at the western islands in the NWHI were small to start with (beach counts ranged from 26 to 113 seals in 1978; Johnson et al. 1982), any increase in female mortality could be detrimental to the maintenance of viable populations.

Since 1977, when intensive study of the monk seal was initiated, injuries to Hawaiian monk seals from sharks and adult male monk seals have been documented (e.g. Johnson and Johnson 1978; Alcorn 1984; Johanos et al. 1987; Johanos and Austin 1988). Injuries and scars were also noted in earlier studies (Kenyon and Rice 1959; Wirtz 1968; Kenyon 1973). The effect of these injuries on the monk seal population is unknown, but if they increase the mortality rate of adult females, decrease their productivity, or both, there could be a significant negative effect on the population.

Tiger sharks (Galeocerdo cuvier) attack Hawaiian monk seals (Balazs and Whittow 1979; Alcorn and Kam 1986), and monk seal remains have been found in their stomachs (Taylor and Naftel 1978; pers. obs.). Scars and fresh injuries thought to be inflicted by sharks have been observed on monk seals (Kenyon and Rice 1959;

Wirtz 1968; Kenyon 1973), and shark predation is thought to be an important cause of mortality (Kenyon 1973). However, there are inadequate data to confirm if this hypothesis is correct.

Particular attention has focussed on what has been termed "mobbing" behaviour, during which several adult males try simultaneously to mate with a lone seal, usually an adult female (Gilmartin and Alcorn 1987). During normal mating, the male takes a purchase on the female's back with his teeth while copulating. When several males attempt to mount a female simultaneously, each male bites the back of the female to maintain his position. Males mounted on the female are often challenged and displaced by other males. As a result, the female can be harassed for several hours (Johanos and Austin 1988). Consequently, the victims are often injured and sometimes die in these incidents (Johanos et al. 1987). Because mobbing injuries are predominantly inflicted on adult and subadult female seals, they are potentially of demographic significance.

Gilmartin and Alcorn (1987) suggested that mobbing behaviour occurs more often on islands where the adult sex ratio is skewed in favour of males. If true, this is a serious concern because a positive feedback loop could result whereby female mortality increases as a result of mobbing and the sex ratio becomes further skewed in favour of males, thereby aggravating the problem.

In this paper, I test the hypothesis that the frequency of occurrence of injuries inflicted by adult male monk seals is higher in a population with an adult sex ratio skewed towards males than in a population with an even sex ratio. I also examine the effects of wounding by sharks and adult male seals on monk seals in the same two populations to evaluate their potential significance to the numbers and productivity of adult females.

4.2. Methods

Injury and census data on Hawaiian monk seals were collected by myself and National Marine Fisheries Service Marine Mammal and Endangered Species Program

(NMFS MMESP) personnel at Laysan Island (lat. 25° 42'N, long. 171° 44'W; Figure 2.1) and French Frigate Shoals (FFS, lat. 23° 45'N, long. 166° 10'W; Figure 2.1) in the Northwestern Hawaiian Island (NWHI) chain in 1988 and 1989 (Chapter 2). I also analysed census, injury and mortality data collected by NMFS MMESP biologists from 1982 to 1987 at Laysan Island, and from 1985 to 1987 at FFS.

4.2.1. Census data

Identification of animals and census methods are detailed in Chapter 2. The entire population at Laysan Island was identified in 1984, 1988 and 1989 by marking individuals with commercial bleach. The average number of seals counted at Laysan Island and FFS in May and June of each year was used as an index of the relative size of each population. In addition to the mean number of all seals sighted, the mean number of seals in each size (juvenile, subadult and adult) and sex class were examined for trends over the study period. The number of seals of unknown sex counted in each size class was also noted. Because the average number of seals on the beach is an index of relative abundance of seals in different size and sex classes rather than the total number of individuals in the population, I examined the number of seals identified in each size and sex class at Laysan Island. The number of females recruited into the reproductive population at Laysan Island from 1987 to 1989 was also examined.

4.2.2. Wounding rates

Because of differences in the way data were collected at Laysan Island and FFS (Chapter 2), observations on injuries were standardized to facilitate a comparison of wounding rates at the two locations. Because of their size, gaping wounds (open wounds where flesh was removed from the injury; Chapter 2) were the most obvious injuries, and were most likely to have been recorded reliably throughout the study period at both locations. Therefore, the rate of occurrence of gaping wounds was used to compare the frequency of wounding at Laysan Island and FFS from 1982 through 1989. Wounding rates were calculated by dividing the mean number of gaping wounds per month for May and June by the average census for May and June of each year. Wounding rates for injuries inflicted on all size and sex classes by adult males and sharks, and for injuries inflicted on adult and subadult females by adult males, were compared between Laysan Island and FFS. Criteria for determining the cause of an injury are detailed in Chapter 2. Because gaping injuries form a subset of severe injuries, these wounding rates were minimal estimates of the frequency of injury at these locations.

4.2.3. Mortality and disappearance

Seals found dead on the beach or seen dead offshore during the study period were classified as mortalities. Seals classified as "disappeared" were those that were not resighted after sustaining a major injury, and those that were permanently identified by tags, characteristic scars or natural markings and that were not resighted after a particular year. Seals that disappeared or died were divided into two groups, depending on whether or not they were known to have been injured by adult male monk seals. The distribution of size and sex classes of seals in these two groups was compared to an expected distribution based on the relative frequency of seals in each class in censuses conducted from 1982 to 1989.

[illegible] individuals in the seal population at Laysan Island were identified. Consequently, [illegible] with injuries were regularly resighted, recovery from the injury could [illegible]mented, and most seals that died could be identified. In contrast, injured seals at FFS were rarely resighted and only a small proportion of the adult population was permanently identified. As a result, it was difficult to ascertain if an untagged injured seal had disappeared or if its injury had healed. Thus, the mortality and disappearance data at FFS (Appendix A) were not examined.

4.3. Results

4.3.1. Population trends

Laysan Island

The numbers of immature (subadult and juvenile) male and female monk seals censused at Laysan Island from 1982 to 1989 were approximately equal and followed similar trends (Figure 4.1). The male to female ratio of identified individuals in the immature classes ranged from 0.9:1 in 1983 to 1:1 in 1988 (Alcorn and Buelna 1989; Johanos et al. 1987; Johanos and Austin 1988; Johanos et al. 1990). In the adult size class, the sex ratio was skewed towards males (Figure 4.1; Figure 4.2). Although the number of adult females counted on the beach remained fairly constant from 1983 to 1989 (Figure 4.1), the number of individual adult females identified at Laysan Island increased from 46 seals in 1983 to 74 in 1988, then decreased to 62 in 1990 (Figure 4.2). Almost all females were marked with bleach in 1983 and 1984 (Alcorn and Buelna 1989; Johanos et al. 1987), and most females in 1985 retained a mark applied with bleach from the previous year (Johanos et al. 1990). Thus, the increase from 1985 to 1988 in the number of females identified appears to be due to an increase in the number of individual seals rather than an increase in the effort of identifying seals. The decrease in adult male to female ratio at Laysan Island from 2.0:1 in 1983 to 1.62:1 in 1989 appeared to be due to the increase in the adult female population between 1985 and 1988 (Figure 4.2; Johanos et al. 1990).

Young females were being recruited into the adult population at Laysan Island. Three untagged females, seen as subadults in 1984, first gave birth to a pup in 1987, 8 (5 untagged, 3 tagged in 1983) were recruited in 1988, and 2 (1 untagged, 1 tagged in 1983) were recruited in 1989 (Table 4.1). However, despite the recruitment of young females, the number of adult females in the population dropped in 1989 and 1990 (Figure 4.2). No data were available on young females recruited into the adult population at Laysan Island from 1983 through 1986.

French Frigate Shoals

From 1985 to 1989, there were equal numbers of males and females censused in the immature size classes at French Frigate Shoals (Figure 4.3). Johnson and Johnson (1984) also reported an even sex ratio for immature seals in 1980. Census numbers and data on sex ratios from FFS should be interpreted conservatively, due to the large proportion of seals of unknown sex in each size class. In all years except 1989, the sex of over 50% of the seals counted in these size classes was not determined. However, there was no known bias in the immature size classes that would make one sex easier to identify so the available data on sex ratio are probably representative.

From the available data, the sex ratio of the adult size class at FFS appeared skewed in favour of females (Figure 4.3). However, this may have been biased because adult females were easier to identify than males (Chapter 2). Consequently, the actual sex ratio at FFS was probably closer to unity, as calculated in 1980 by Johnson and Johnson (1984) when they estimated the sex ratio using counts of moulting seals of each sex, outside the breeding season. There are few data on the recruitment of young animals. Two 5-year-old females gave birth to pups for the first time at FFS in 1989 (M. Craig, pers. comm.), but no data are available on recruitment of older seals pupping for the first time.

4.3.2. Wounding rates

Adult male-inflicted injuries

Gaping injuries inflicted by adult male seals were observed at similar rates of occurrence at Laysan Island and FFS (Figure 4.4a). The frequency of occurrence of gaping wounds inflicted by adult male seals on adult and subadult females was higher at Laysan Island than at FFS, but trends at both islands were similar during the study period, with the exception of 1989, when the wounding rate increased at Laysan Island but decreased at FFS (Figure 4.4b). Because census numbers for the adult female class at FFS should be interpreted conservatively, the wounding rate at FFS for injuries inflicted on females is probably an overestimation of the rate of occurrence of adult male-inflicted injuries. The actual rate would be lower than shown here, as a greater number of females would be used to calculate the rate.

Shark-inflicted injuries

The pattern of wounding rates for gaping injuries inflicted by large sharks was similar at Laysan Island and FFS (Figure 4.4c). At both locations, the wounding rate for injuries inflicted by large sharks was lower than for injuries inflicted by adult male monk seals.

4.3.3. Mortality and disappearance

Of 45 seals known to have died at Laysan Island from 1982 through 1989, 35 (77.8%) had been injured by adult male monk seals (Figure 4.5a). Injuries included both dorsal abrasions (Chapter 2, Plate 2.1a,b) and gaping injuries (Chapter 2, Plates 2.1c, 2.2a,b). Ten seals (22.2%) that died were not known to have been injured by adult males. About half of the seals that died (22/45) were adult females. Significantly more adult females died than was expected from a distribution of mortalities proportional to the number of seals in each size and sex class counted in censuses ($G=10.61$, d.f.=1, $p<0.005$). Most of these females (20/22, 90.9%) sustained adult male-inflicted injuries prior to dying. The number of female seals known to have died each year gradually increased through the study period, reaching a maximum of 7 in 1989, and was reflected by a slight drop in the number of identified females at the end of the study period (Figure 4.6).

Over half of the seals that disappeared between 1982 and 1989 were juveniles (43/79, 54.4%; Figure 4.5b), which was significantly higher than expected from a distribution based on relative numbers in each size and sex class counted in censuses ($G=25.37$, d.f.=1, $p<0.005$). Most of these juveniles (42/43, 95.6%) were not known to have sustained adult male-inflicted injuries prior to disappearing.

4.4. Discussion

4.4.1. The frequency of occurrence of adult male-inflicted wounds in relation to sex ratio

The size and sex classes of monk seals injured by adult males at Laysan Island (where the adult sex ratio is skewed toward males), and at FFS (where the sex ratio is close to unity or skewed toward females), were compared to test the hypothesis that the frequency of occurrence of adult male-inflicted injuries is higher in populations where the adult sex ratio is biased toward males. Overall, the rates at which adult males inflicted gaping wounds upon seals of all size and sex classes were similar at Laysan Island and FFS (Figure 4.4a). However, adult females were injured more frequently than other classes of seals at both locations (Chapter 2, Figure 2.4). Thus, I examined the rate of occurrence of gaping wounds on only subadult and adult females, and found that adult males inflicted gaping wounds at similar rates, though slightly higher at Laysan Island, except for 1989 when the difference was marked (Figure 4.4b). However, the wounding rate calculated here for females at FFS overestimated the actual rate of occurrence of adult male-inflicted injuries. The wounding rate at Laysan Island was higher even with the overestimated wounding rate at FFS, which is consistent with the prediction of the hypothesis.

Johnson and Johnson (1984) compared the number of females with extensive dorsal scars as a proportion of those females identifiable by natural markings at Laysan Island and FFS, and found the dorsal scarring rate was significantly lower at FFS. From this, they concluded the rate of male-inflicted injury was lower at FFS. Although based on smaller sample sizes collected over a shorter time period, their results are similar to those reported here. In summary, the results from the wounding data were not unequivocal but in general, they supported the hypothesis that the rate of male-inflicted injury on female seals is higher in populations where the sex ratio is skewed toward males.

4.4.2. Factors influencing the development of mobbing behaviour

The operational sex ratio (the ratio of sexually active males to sexually receptive females; Emlen 1976; Emlen and Oring 1977) of a polygynous seal species may be influenced by the spatial distribution of breeding females and how synchronously they ovulate (Trivers 1972). For example, female harp seals (Phoca groenlandica) are widely spaced in the drifting pack ice, and they have highly synchronous estrus and pupping (Sergeant 1965). Because all females ovulate within a short period of time, most males can only mate with one or a few females. In this situation, the adult sex ratio and the operational sex ratio are similar. Consequently, there is reduced intrasexual male competition for mates, and little likelihood that a group of males would compete to mate with the same female.

In contrast, female monk seals have asynchronous pupping, and give birth to a pup between late December and mid-August, although there is a peak in the occurrence of births from mid-March through May (Kenyon and Rice 1959; Kenyon

1981). Females apparently come into estrus one to two months after weaning their pups (Johnson and Johnson 1978; Johanos pers. comm.), and because pupping dates are spread out over several months, the presence of estrous females is as well. Consequently, at any point during the breeding season, the operational sex ratio when a female comes into estrus is skewed toward males, even if the sex ratio of the population is 1:1. This appears to create the potential for adult males to mob and injure females at any monk seal colony. Mobbing incidents and injuries typical of mobbing behaviour have been observed at FFS (M.P. Craig, T. Gerrodette, pers. comm.; Figure 2.4b), though less frequently than at Laysan Island. Thus, it appears that an operational sex ratio skewed towards males may increase the probability of the occurrence of mobbing incidents.

Males occasionally injure females during mating in several other species (Chapter 2). In several other species of phocid seals, males take a purchase on the upper back or neck of the female during copulation (e.g. crabeater seals, Lobodon carcinophagus: Siniff et al. 1979; Weddell seals, Leptonychotes weddelli: Cline et al. 1971; harbor seals, Phoca vitulina: Allen 1985; northern elephant seals, Mirounga angustirostris: LeBoeuf 1972, LeBoeuf and Mesnick in press; and grey seals, Halichoerus grypus: Hewer 1957). Injuries inflicted by males during mating may appear severe although they apparently occur during normal mating behaviour. Thus, the potential for injury to females during mating exists even under normal conditions.

If the operational sex ratio becomes skewed in favour of males, the intensity of intrasexual competition increases, and male competition can take the form of direct male-male interaction, resulting in a dominance hierarchy among males (Emlen and Oring 1977). Within a breeding group, the dominance hierarchy can protect the female from injury when several males are competing to mate with her at the same time (Mesnick and LeBoeuf in press). For example, in northern elephant seal colonies, breeding females are highly concentrated in harems, the dominance hierarchy is strongly developed, and a small number of dominant males do most of the mating (LeBoeuf 1972). There is a high density of subordinate males at the edges of the harem, creating an area where the operational sex ratio is skewed in favour of males

(LeBoeuf and Mesnick in press). When female northern elephant seals leave the harem after weaning their pups, groups of subordinate males at the periphery of the harem often harass and mob them (Mesnick and LeBoeuf in press). The departing female typically copulates with the most dominant male in the pursuing group, and is usually not seriously injured, although occasionally females are killed during these mobbings (S.L. Mesnick pers. comm.; Mesnick and LeBoeuf in press; LeBoeuf and Mesnick in press). Similar situations exist in southern sea lion (Otaria byronia) and Australian sea lion (Neophoca cinerea) populations, where breeding males are territorial, and nonterritorial subordinate males are concentrated outside the territories (Campagna and LeBoeuf 1988; Marlow 1975). Groups of subordinate southern sea lions often mob and injure single females as they arrive at the central breeding area (Campagna and LeBoeuf 1988). Group harassing behaviour has also been observed in the Australian sea lion (Marlow 1975). In these cases, territorial males usually drive off the subordinate males and females are generally not severely injured (Campagna and LeBoeuf 1988; Marlow 1975).

In situations where the male dominance hierarchy is absent or not well defined, the potential for serious injury to a female increases when several males compete to mate with her. If there are several males present, some of which are fully grown adults, the dominant male may not be able to prevent them from attempting to mate with the female. Consequently, the injuries normally inflicted on the female during mating are enlarged and become more serious each time another male attempts to take a purchase on her back and mate with her. Female mink (Mustela vison) sustain neck wounds inflicted by males during normal mating, which become enlarged if several males mate with her over a short period (Hatler 1972). Even if a female is not injured during mating, she may still be chased and harassed by a group of males for a considerable length of time if there is no dominant individual to deter other males (e.g. manatees, Trichechus manatus: Hartman 1979). Male Hawaiian monk seals appear to have a loose hierarchy in which certain individuals are more dominant than others (T.C. Johanos-Kam, pers. comm.). In observed mobbing incidents, however, the dominant male was usually not able to deter other males from attempting to mate with the female if several males approached at the same time (Alcorn and Buelna 1989; Johanos et al. 1987; Johanos and Austin 1988). It appears that the absence of a strong dominance hierarchy contributes significantly to the occurrence of mobbing incidents.

In species which have a strongly developed male dominance hierarchy as a result of male-male competition, in which a few males mate with several females, sexual dimorphism is usually marked (Bartholomew 1970; Trivers 1972; Stirling 1983). In contrast, sexual dimorphism is generally reduced in species where the mating system is monogamous or promiscuous (Stirling 1983) and where the ratio of males to females is even (Clutton-Brock and Harvey 1977). The absence of sexual dimorphism in monk seals (Kenyon and Rice 1959) suggests strongly that the adult sex ratio has been close to unity through its evolutionary history. Consequently, even though the operational sex ratio may have become temporarily skewed toward males because females ovulate over such a long period, most potential mobbing was probably prevented in most cases by the presence of a dominant male.

Removal of dominant males may cause a shift in the mating system. In a population of pronghorn (Antilocapra americana), Byers and Kitchen (1988) documented a marked change in the mating system following a year in which all mature males died. The age distribution changed to one of predominantly younger aged males and the mating system changed from territoriality to harem defense, apparently because no males were dominant enough to exclude other males from a territory (Byers and Kitchen 1988). Similarly, the instability of the dominance hierarchy created by the removal of successful males in a prairie chicken (Tympanuchus cupido) lek and a fallow deer (Dama dama) lek was the probable cause of increased disruption of copulations (Robel and Ballard 1974) and increased aggression among males (Apollonio et al. 1989; Robel and Ballard 1974).

It is possible that the dominance hierarchy of adult male seals at Laysan Island may have been disrupted in 1978 when a large number of monk seals died of ciguatera toxin (Johnson and Johnson 1981; Gilmartin et al. 1980). Over 50 seals were estimated to have died. Of the 25 seals necropsied, 9 were older adult males (Johnson and Johnson 1981). If these males were domininant individuals, their removal may have upset the dominance hierarchy, by creating a cohort of similar-aged males. Competition among these more equally-ranked males might become more intense as they approached the age of dominance, thereby increasing the probability of mobbing behaviour. Thus, the removal of dominant males from the Hawaiian monk seal population at Laysan Island during 1978 may have been the event which eventually triggered an increase in the frequency of occurrence of mobbing behaviour. If this is true, then it is also possible that hte frequency of mobbing behaviour will eventually decrease over time if a dominance hierarchy becomes re-established.

In summary, it appears that several factors may influence the development of mobbing behaviour. An operational sex ratio skewed in favour of males, the infliction of injuries during normal mating, and a weak male dominance hierarchy all affect the probability of an estrous female being injured by a group of males competing to mate with her. When all of these elements are present, as appears to presently be the case at Laysan Island, the probability of occurrence of mobbing behaviour is greatly increased.

4.4.3. Significance of male-inflicted wounding to population decline

Effects on mortality of adult females

Known mortality of adult females due to adult male-inflicted injury was relatively low from 1982 to 1987 (Figure 4.6). During this time, the number of identified females increased by 19 seals. This increase could be due to recruitment of immature females or to immigration of females from other populations. Few data are available on recruitment of immature seals to the reproductive population from 1982 to 1986, as immature seals nearing maturity were untagged and not always individually identified between years. However, 13 young females were recruited to the population from 1987 to 1989 (Table 4.1). Thus, recruitment of young seals could have accounted for some of the increase in the number of identified females.

Immigration of unmarked females from other populations may have occurred in 1986 and 1987, as not all females were individually identified. However, the number of females that immigrated from other populations in other years was usually limited to one or two females, not including a small number of adult females that move annually between Laysan Island and other populations (Alcorn and Buelna 1989; Johanos et al. 1987; Becker et al. 1989; Johanos et al. 1990). Observations of tagged seals suggest that monk seals have high fidelity for their natal island and that only a small percentage of seals immigrate to other islands (Johnson and Kridler 1983). The low level of movement between islands recorded to date suggests that the immigration of a significant number of females in 1986 and 1987 is unlikely.

In 1989, 10.3% (7/68) of the adult female population died from adult male-inflicted injuries (Figure 4.6). This is a minimal estimate, because females that disappeared after sustaining adult male-inflicted injuries are not included. It is unlikely that such high mortality of females would be compensated for by immigration of females and recruitment of immatures. DeMaster (1981), in modelling the dynamics of a Weddell seal population, found that even in his most liberal population model, the adult female population could sustain no more than a 1.7% loss (25 females harvested from a population of 1486 females) if the population was to remain at equilibrium. Similarly, polar bear (Ursus maritimus) populations cannot sustain an annual loss of adult females greater than about 1.6 percent of the total population under optimal conditions (Taylor et al. 1987). Thus, if mortality of adult female monk seals at Laysan Island continues at present levels due to adult male-inflicted injuries, monk seal numbers there will probably continue to decline.

Effects on recruitment of young seals

As subadult female seals approach maturity (5 or 6 years), adult male seals injure them more often than juvenile females (0-3 years; Chapter 3). Therefore, young females may be killed as they enter the reproductive population. All of the six subadult females that died at Laysan Island during the study period were injured by adult males before they died (Figure 4.5a). Thus, adult males not only injured adult females, but also wounded young females entering the breeding population.

Although female pups survive long enough to enter the reproductive population (Table 4.1), the adult female mortality rate resulting from injuries inflicted by adult males may be so high that it significantly reduces the net recruitment of new animals into the adult female size class. For example, in 1987 three young seals were recruited into the reproductive population (Table 4.1), and two adult females died (Figure 4.6), producing a net recruitment of only one animal. In years of high mortality, the number of seals that die may exceed the number of young animals recruited, as was the case in 1989 when 2 females were recruited but 7 died.

Relation to shark inflicted injuries

Of the sharks commonly seen in the NWHI, tiger sharks have the most potential to detrimentally affect the monk seal population, as they are known to attack and eat monk seals (Balazs and Whittow 1979; Taylor and Naftel 1978; Alcorn and Kam 1986). Sharks are probably more attracted to injured than uninjured seals, because of blood and fluids leaching from injuries. Thus, females injured by adult males may be more likely to be killed by sharks. Furthermore, females that are attacked by sharks seem to be more likely to be injured by adult male seals, possibly because they appear to be more passive than uninjured seals (T.C. Johanos-Kam pers. comm.). At least two female mortalities at Laysan Island in 1988 and 1989 involved injuries from both adult males and sharks (Johanos et al. 1990; pers. obs.). As well, several incidents have been observed in which seals injured by adult males in mobbing incidents were attacked by sharks (Alcorn and Kam 1986; Balazs and Whittow 1979). The combination of shark predation and injuries inflicted by adult males on females has the potential to negatively affect the Hawaiian monk seal population, since together they increase female mortality.

The relationship between wounds caused by adult male monk seals and female mortality is indicated by the high proportion of females that sustained adult male-inflicted injuries before dying (Figure 4.5). Recruitment of females into the breeding population is reduced by adult male-inflicted injuries on young females reaching sexual maturity. The monk seal population cannot recover while adult female mortality exceeds recruitment of females into the breeding population. In summary, it appears that mortality of adult females resulting from wounds inflicted by adult males is a significant factor in the current decline in the monk seal population.

Table 4.1. The minimum number of immature female Hawaiian monk seals recruited to the reproductive population at Laysan Island, NWHI, from 1987 to 1989. "# with no pup as of 1989" refers to the number of females in the size class without a pup but present in the population from 1987 to 1989.
a - one seal not seen in 1986 and 1987;
b - two seals not seen in 1986;
c - one seal that died in 1985 not included in total number.

size class of female	total # of females in class	Year of first pup 1987	1988	1989	# with no pup as of 1989
seen as subadult (~4-5 yr old) in 1984	8	0	3[a]	1	4
seen as subadult (~3 yr old) in 1984	4[c]	3[b]	1	0	0
seen as juvenile (~2 yr old) in 1984	1	0	1	0	0
born in 1983	6	0	3	1	2
born in 1984	11	0	0	0	11
total #	30	3	8	2	17

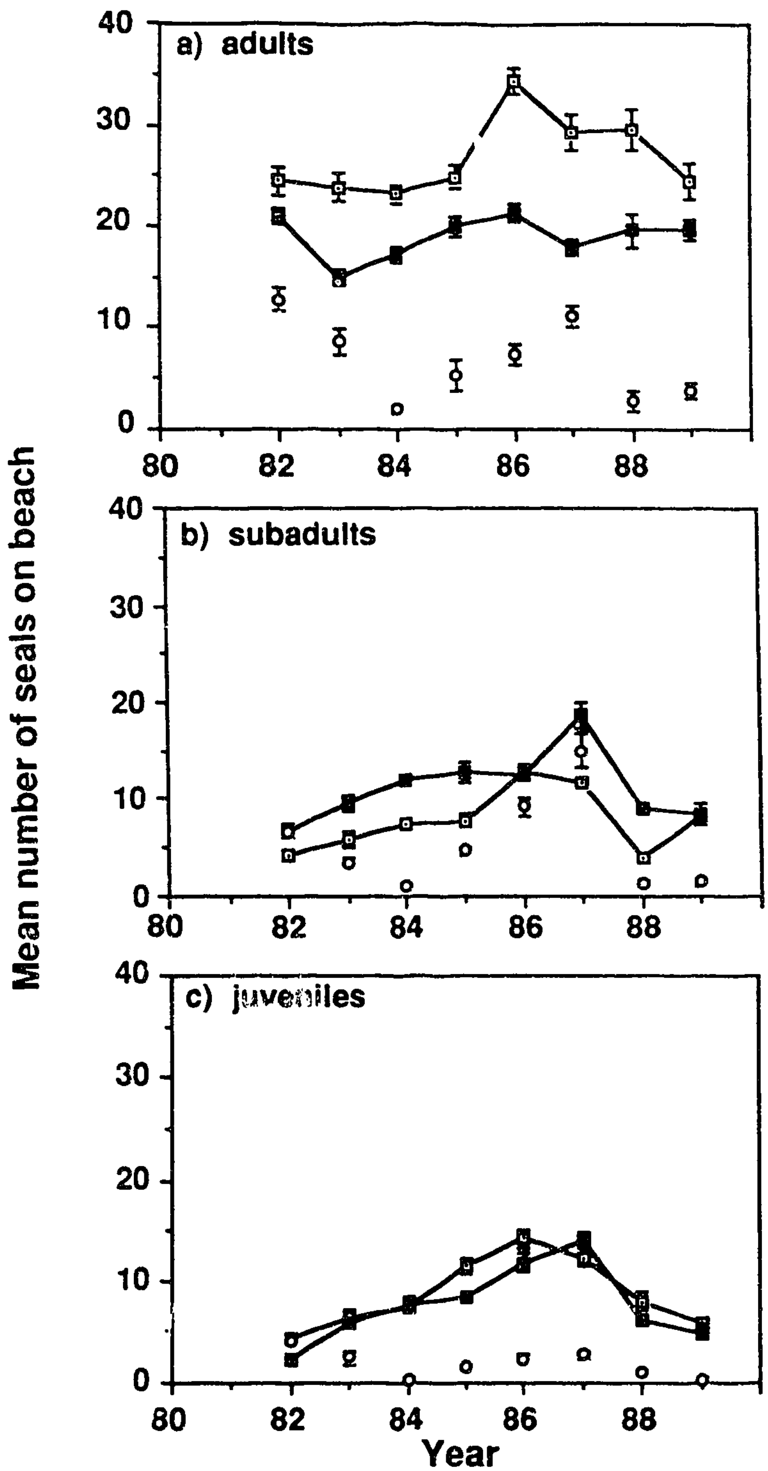


Figure 4.1. Population trends of Hawaiian monk seals at Laysan Island, NWHI, 1982-89. Censuses from May and June: a) adult seals; b) subadult seals; c) juvenile seals. Open square: male seals; closed square: female seals; open circle: unknown sex.

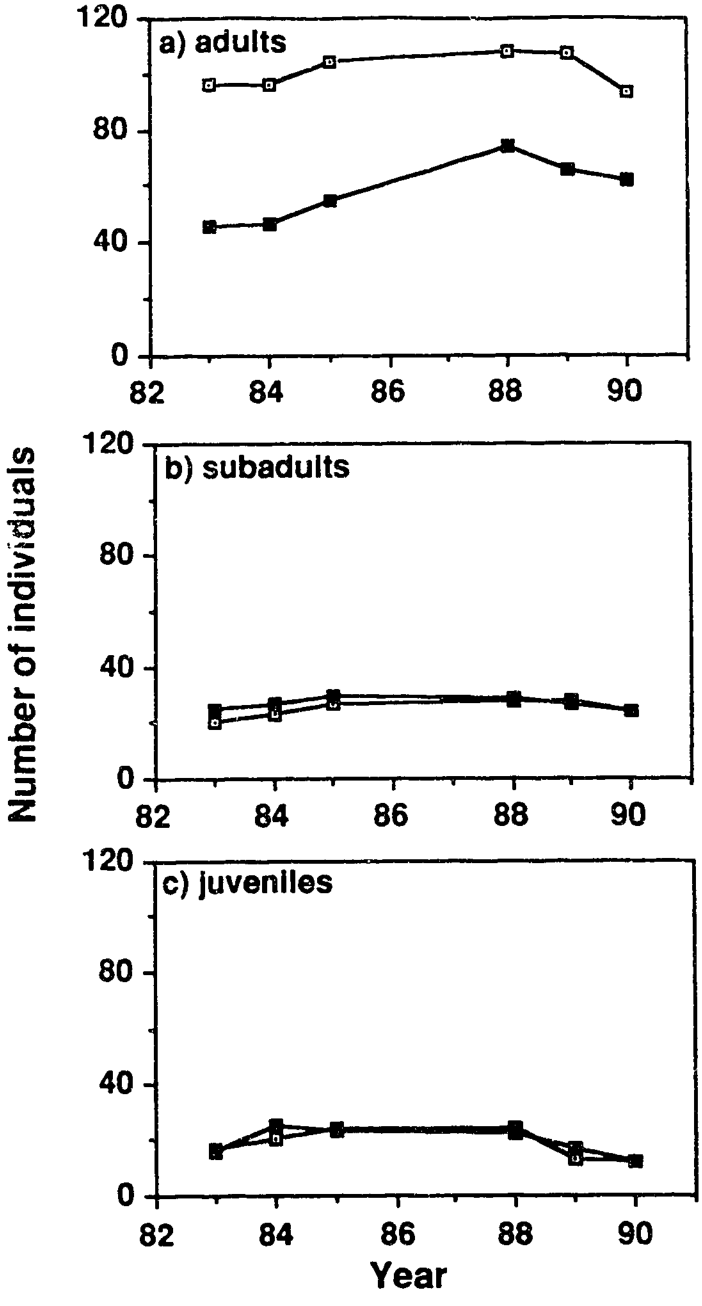


Figure 4.2. Number of identified Hawaiian monk seals at Laysan Island, NWHI, 1983-1990. a) adult seals; b) subadult seals; c) juvenile seals. Open square: male seals; closed square: female seals. Note: not all adult seals were identified in 1983 and 1985 (Alcorn and Buelna 1989; Johanos and Austin 1988). The numbers of identified Hawaiian monk seals in 1986 and 1987 were not available.

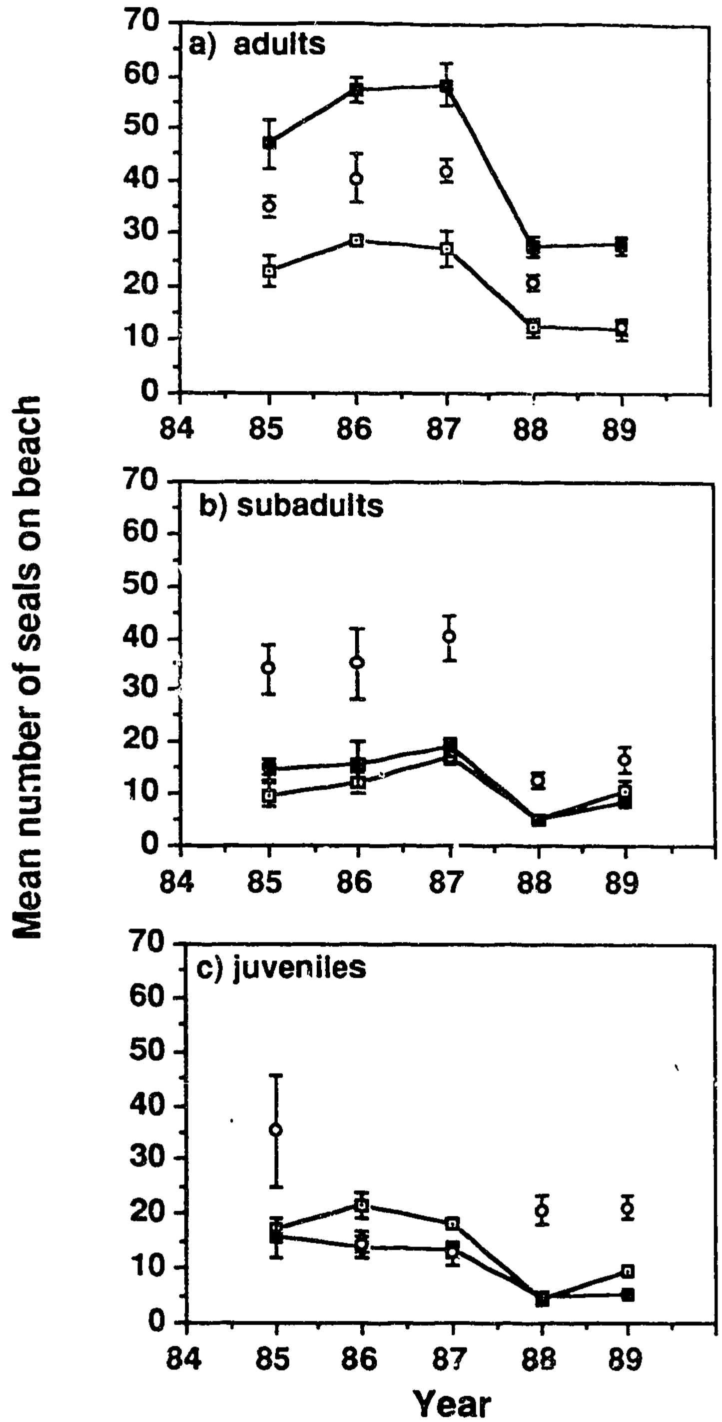


Figure 4.3. Population trends of Hawaiian monk seals at French Frigate Shoals, NWHI, 1985-89. Censuses from May and June. a) adult seals; b) subadult seals; c) juvenile seals. Open square: male seals; closed square: female seals; open circle: unknown sex.

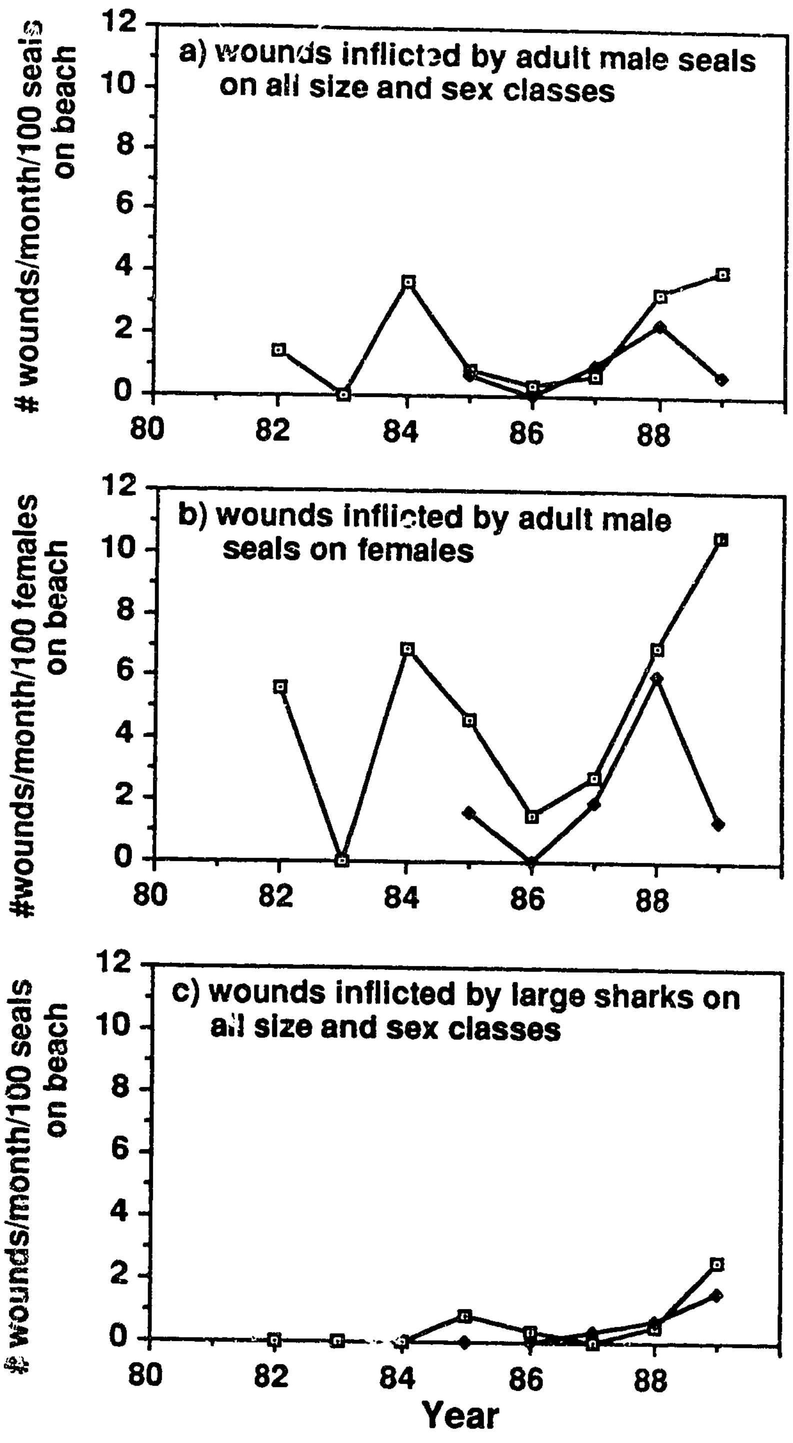


Figure 4.4. Wounding rates for gaping wounds on Hawaiian monk seals at Laysan Island (open square) and French Frigate Shoals (closed dot), NWHI, 1982-89. a) wounds inflicted by adult male monk seals on all size and sex classes of seals; b) wounds inflicted by adult male seals on adult and subadult females; c) wounds inflicted by sharks on all size and sex classes of seals.

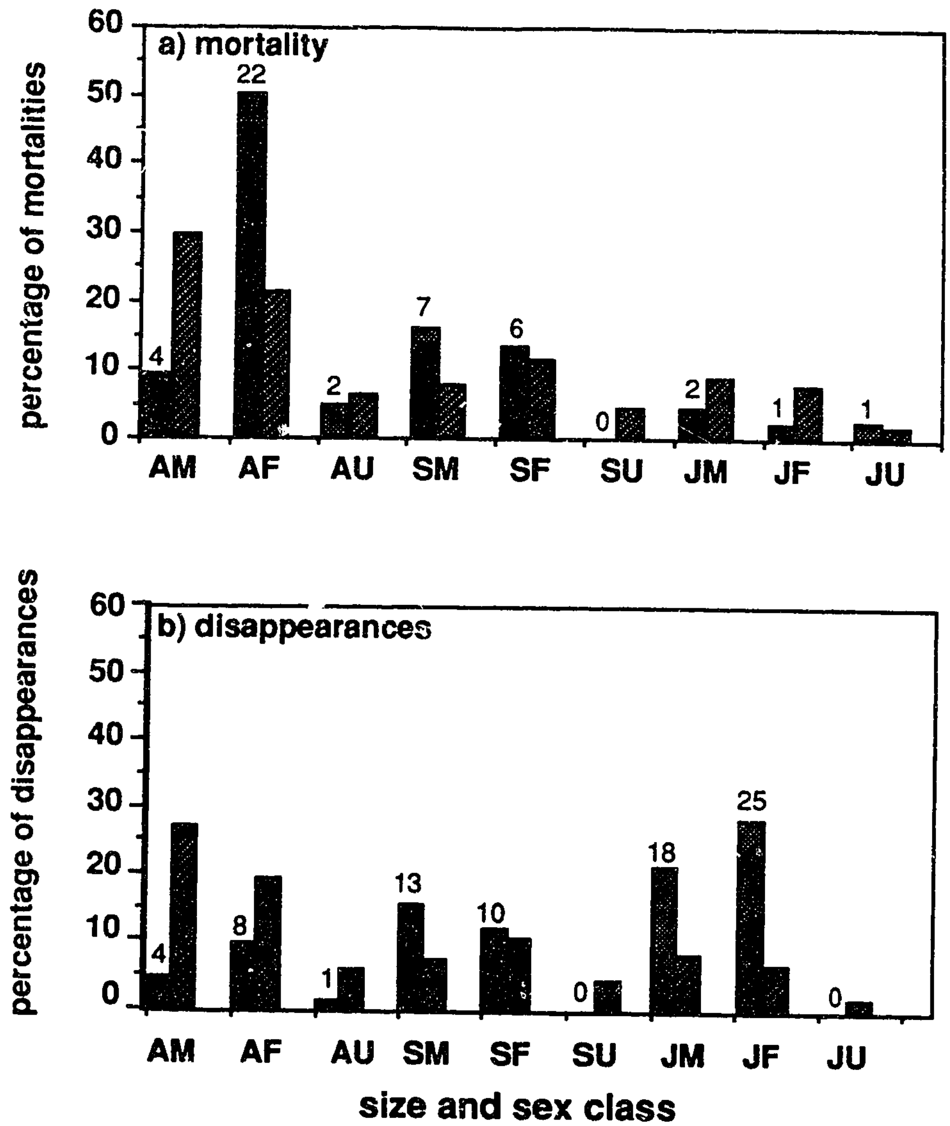


Figure 4.5. Mortality and disppearance of Hawaiian monk seals on Laysan Island, NWHI, 1982-89. Expected values for each size and sex class are based on mean censuses for May and June, 1982-89. Solid bar: instances in which the seal sustained an injury inflicted by adult male monk seals. Dotted bar: instances in which the seal was not known to have been injured. Hatched bar: expected frequency of death or disappearance. Number of seals in each class indicated above bars.

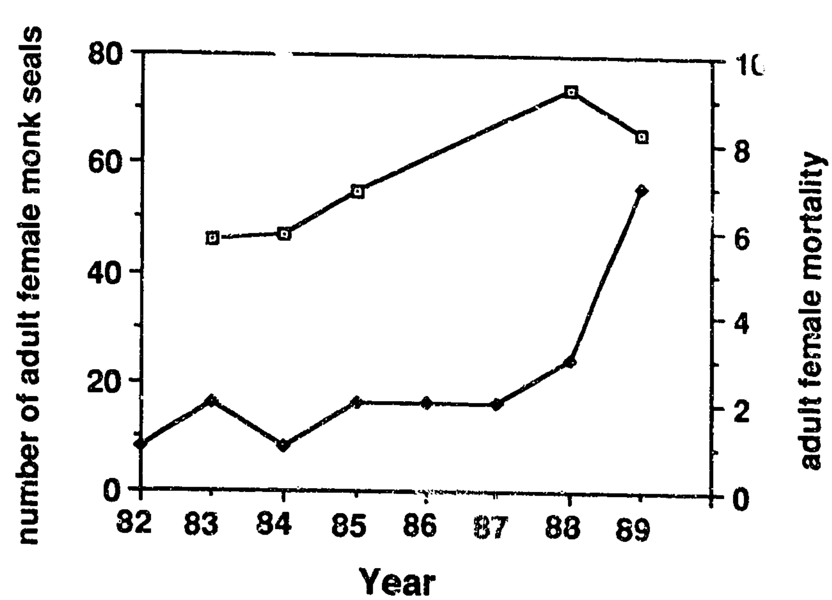


Figure 4.6. Mortality of adult female Hawaiian monk seals at Laysan Island, NWHI, compared to the number of adult females in the population. Open square: number of females in the population; closed dot: number of females that died each year.

4.5. Literature cited

Alcorn, D.J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-42. 37 p.

Alcorn, D.J. and E. Buelna. 1989. The Hawaiian monk seal on Laysan Island, 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-124, 46 p.

Alcorn, D.J. and A. Kam. 1986. Fatal shark attack on a Hawaiian monk seal (Monachus schauinslandi). Marine mammal Sci. 2(4):313-315.

Allen, S.G. 1985. Mating behavior in the harbor seal. Marine mammal Sci. 1(1):84-87.

Apollonio, M., M. Festa-Bianchet and F. Mari. 1989. Effects of removal of successful males in a fallow deer lek. Ethology 83:320-325.

Balazs, G. and C. Whittow. 1979. First record of a tiger shark observed feeding on a Hawaiian monk seal. 'Elepaio 39(9):107-109.

Bartholomew, G.A. 1970. A model for the evolution of pinniped polygyny. Evolution 24(3):546-559.

Becker, B.L., R.J. Morrow and J.K. Leialoha. 1989. Censuses and interatoll movements of the Hawaiian monk seal on Laysan Island. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-135. 25 p.

Byers, J.A. and D.W. Kitchen. 1988. Mating system shift in a pronghorn population. Behav. Ecol. Sociobiol. 22:355-360.

Campagna, C. and B.J. LeBoeuf. 1988. Reproductive behavior of southern sea lions. Behaviour 104(34):233-261.

Cline, D.R., D.B. Siniff and A.W. Erickson. 1971. Underwater copulation of the Weddell seal. J. Mammal. 52:216-218.

Clutton-Brock, T.H. and P.H. Harvey. 1977. Primate ecology and social organization. J. Zool. Lond. 183:1-39.

DeMaster, D.P. 1981. Incorporation of density dependence and harvest into a general population model for seals. In: C.W. Fowler and T.D. Smith (eds.), Dynamics of large mammal populations. New York: John Wiley and sons.

Eberhardt, L.L. 1985. Dynamics of wild populations. J. Wildl. Manage. 49(4):997-1012.

Eberhardt, L.L. and D.B. Siniff. 1977. Population dynamics and marine mammal policies. J. Fish. Res. Board Can. 34(2):183-190.

Emlen, S.T. 1976. Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1:283-313.

Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197(4300):215-223.

Gilmartin, W.G. 1988. The Hawaiian monk seal: population status and current research activities. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rept. H-88-17. 14 p.

Gilmartin, W.G. and D.J. Alcorn. 1987. A plan to address the Hawaiian monk seal adult male "mobbing" problem. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rept. H-87-12. 24 p.

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. In: R.W. Grigg and R.T. Pfund (eds.), Proceedings of the symposium on status of resource investigations in the Northwestern Hawaiian Islands, University of Hawaii, Honolulu, Hawaii, April 24-25, 1980. p.32-41. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-04.

Gilmartin, W.G., T.C. Johanos and T. Gerrodette. 1987. Preliminary assessment of juvenile Hawaiian monk seal survival. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii. SWFC Admin. Rept. H-87-16. 11 p.

Hartman, D.S. 1979. Ecology and behavior of the manatee (Trichechus manatus) in Florida. The American Society of Mammalogists, Spec. Pub. No. 5.

Hatler, D.F. 1972. The coastal mink on Vancouver Island, British Columbia. Ph. D. Thesis, University of British Columbia. 360 p.

Hewer, H.R. 1957. A Hebridean breeding colony of grey seals, Halichoerus grypus, with comparative notes on grey seals of Ramsey Island, Pembrokeshire. Proc. Zool. Soc. Lond. 128:23-66.

Johanos, T.C. and S.L. Austin. 1988. Hawaiian monk seal population structure, reproduction, and survival on Laysan Island, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-118, 38 p.

Johanos, T.C., B.L. Becker, M.A. Brown, B.K. Choy, L.M. Hiruki, R.E. Brainard and R.L. Westlake. 1990. The Hawaiian monk seal on Laysan Island, 1988. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-151. 44 p.

Johanos, T.C., A. Kam and R.G. Forsyth. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-70. 38 p.

Johnson, A.M., R.L. DeLong, C.H. Fiscus and K.W. Kenyon. 1982. Population status of the Hawaiian monk seal (Monachus schauinslandi), 1978. J. Mamm. 63(3):415-421.

Johnson, A.M. and E. Kridler. 1983. Interisland movement of Hawaiian monk seals. 'Elepaio 44(5):43-45.

Johnson, B.W. and P.A. Johnson. 1978. The Hawaiian monk seal on Laysan Island: 1977. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., No. PB-285-428, 38 p.

Johnson, B.W. and P.A. Johnson. 1981. The Hawaiian monk seal on Laysan Island: 1978. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va. PB-82-109661. 17 p.

Johnson, P.A. and B.W. Johnson. 1984. Hawaiian monk seal observations on French Frigate Shoals, 1980. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-50. 47 p.

Kenyon, K.W. 1973. The Hawaiian monk seal. In: SEALS, 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 of IUCN, 18-19 August 1972, University of Guelph, Ontario, Canada. IUCN Publ. New S Suppl. pap. 39.

Kenyon, K.W. 1981. Monk seals - Monachus. In: S.H. Ridgway and R.J. Harrison (eds.), Handbook of marine mammals. Vol. 2, Seals. London: Academic Press.

p. 195-220.

Kenyon, K.W. and D.W. Rice. 1959. Life history of the Hawaiian monk seal. Pac. Sci. 31:215-252.

LeBoeuf, B.J. 1972. Sexual behavior in the northern elephant seal, Mirounga angustirostris. Behaviour 41:1-26.

LeBoeuf, B.J. and S.L. Mesnick. in press. Sexual behavior of male northern elephant seals: I. Lethal injuries to adult females. Behaviour.

Marlow, B.J. 1975. The comparative behaviour of the Australasian sea lions, Neophoca cinerea and Phocarctos hookeri (Pinnipedia: Otariidae). Mammalia 39:159-230.

Mesnick, S.L. and B.J. LeBoeuf. in press. Sexual behavior of male northern elephant seals: II. Female response to potentially injurious encounters. Behaviour.

Robel, J.R. and W.B. Ballard. 1974. Lek social organization and reproductive success in the greater prairie chicken. Amer. Zool. 14:121-128.

Sergeant, D.E. 1965. Migrations of harp seals, Pagophilus groenlandicus (Erxleben) in the northwest Atlantic. J. Fish. Res. Bd. Canada. 22(2):433-464.

Siniff, D.B., I. Stirling, J.L. Bengtson and R.H. Reichle. 1979. Social and reproductive behaviour of crabeater seals (Lobodon carcinophagus) during the austral spring. Can. J. Zool. 57(11):2243-2255.

Stirling, I. 1983. The evolution of mating systems in pinnipeds. In: J.F. Eisenberg and D.G. Kleiman (eds.), Advances in the study of mammalian behavior. p. 489-527. Special publication, American Society of Mammalogy No. 7.

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. Natl. Tech. Info. Serv., Springfield, Va. No. PB-285626. 34 p.

Taylor, M.K., D.P. DeMaster, F.L. Bunnell and R.E. Schweinsburg. 1987. Modelling the sustainable harvest of female polar bears. J. Wildl. Manage. 51(4):811-820.

Trivers, R.L. 1972. Parental investment and sexual selection. In: B. Campbell (ed.), Sexual selection and the descent of man, p. 136-179. Chicago: Aldine.

Wirtz, W.O. 1968. Reproduction, growth and development, and juvenile mortality in the Hawaiian monk seal. J. Mammal. 49:229-238.

5. Concluding discussion

Of injuries seen on Hawaiian monk seals, wounds inflicted by adult male monk seals in mobbing incidents had the greatest influence on population dynamics. Adult male-inflicted wounds were more frequently observed than other types of injuries, and they were most often inflicted on adult females. Injuries to adult females are particularly significant to population dynamics, as they could negatively affect female productivity or survival, both of which are critical to population growth (Eberhardt 1985).

The reproductive success of wounded females was not affected by injury if there was enough time to recover from the injury before parturition or lactation. When a female was injured in the year prior to parturition, the amount of time the female invested in her pup and its survival through the first year were not negatively affected. If the female was injured shortly prior to parturition or during lactation, however, the probability of the pup surviving to weaning was reduced.

Because the growth and maintenance of a population are sensitive to changes in adult female survival (Eberhardt 1985), the increased mortality of female monk seals at Laysan Island from 1982 to 1989 due to male-inflicted injury probably limited population growth. Adult male monk seals fatally injured females throughout their breeding lives; thus, injuries affected recruitment of young females to the population as well as increasing adult female mortality. In other species, males are known to injure and sometimes kill females (northern elephant seals, Mirounga angustirostris, LeBoeuf and Mesnick in press; mink, Mustela vison, Hatler 1972; Enders 1952; sea otters, Enhydra lutris, Foott 1970). Males appear to kill females infrequently, (LeBoeuf and Mesnick in press; Carrick and Ingham 1962), and thus injuries inflicted on females do not usually have demographic significance. In contrast, because there are few females initially in the Hawaiian monk seal population, any increase in female mortality due to male-inflicted wounding has a significant negative effect on population dynamics.

Wounding of adult female Hawaiian monk seals by adult males in mobbing incidents could be responsible for (or at least related to) population decline at islands like Laysan Island, where the sex ratio is skewed toward males. An operational sex ratio skewed toward males increases the probability of groups of males attempting to mate with a single female (LeBoeuf and Mesnick in press), and thus increases the likelihood of injury to the female. At Laysan Island, where the operational sex ratio was highly skewed toward males, the rate of occurrence of adult male-inflicted wounding was higher than at French Frigate Shoals, where the sex ratio was closer to unity.

The hypothesis that an operational sex ratio skewed toward males increases the frequency of wounding by adult male monk seals can be further tested by manipulating the operational sex ratio of male biased populations. The bias toward male seals could be altered or reversed, either temporarily by using a reversible chemical treatment to suppress testicular androgen production in adult male seals (thus removing them from the breeding population for one year), or permanently by the physical removal of males (Gilmartin and Alcorn 1987). The number of females in the population could also be increased by relocating immature females born in other populations, although any change in the operational sex ratio would depend on the recruitment of these females as they matured. This method has been used successfully to alter the sex ratio of the monk seal population at Kure Atoll, in the Northwestern Hawaiian Islands (Gilmartin and Gerrodette 1986). Any decrease in the frequency of male-inflicted injury after the manipulation would suggest that the operational sex ratio contributes significantly to the occurrence of mobbing behaviour.

5.1. Literature cited

Carrick, R. and S.E. Ingham. 1962. Studies on the southern elephant seal, Mirounga leonina (L.) V. Population dynamics and utilization. CSIRO Wildl. Res. 7:201-209.

Eberhardt, L.L. 1985. Dynamics of wild populations. J. Wildl. Manage. 49(4):997-1012.

Enders, R.K. 1952. Reproduction in the mink (Mustela vison). Proc. Amer. Phil. Soc. 96, p. 691-755.

Foott, J.O. 1970. Nose scars in female sea otters. J. Mammal. 51(3):621-622.

Gilmartin, W.G. and D.J. Alcorn. 1987. A plan to address the Hawaiian monk seal adult male "mobbing" problem. Natl. Mar. Fish. Serv., NOAA, Honolulu, Hawaii, SWFC Admin. Rept. H-87-12. 24 p.

Gilmartin, W.G. and T. Gerrodette. 1986. Hawaiian monk seal population status and recovery potential at Kure Atoll. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-86-16, 26 p.

Hatler, D.L. 1972. The coastal mink on Vancouver Island, British Columbia. Ph. D. Thesis, University of British Columbia. 360 p.

LeBoeuf, B.J. and S.L. Mesnick. in press. Sexual behavior of northern elephant seals: I. Lethal injuries to adult females. Behaviour.

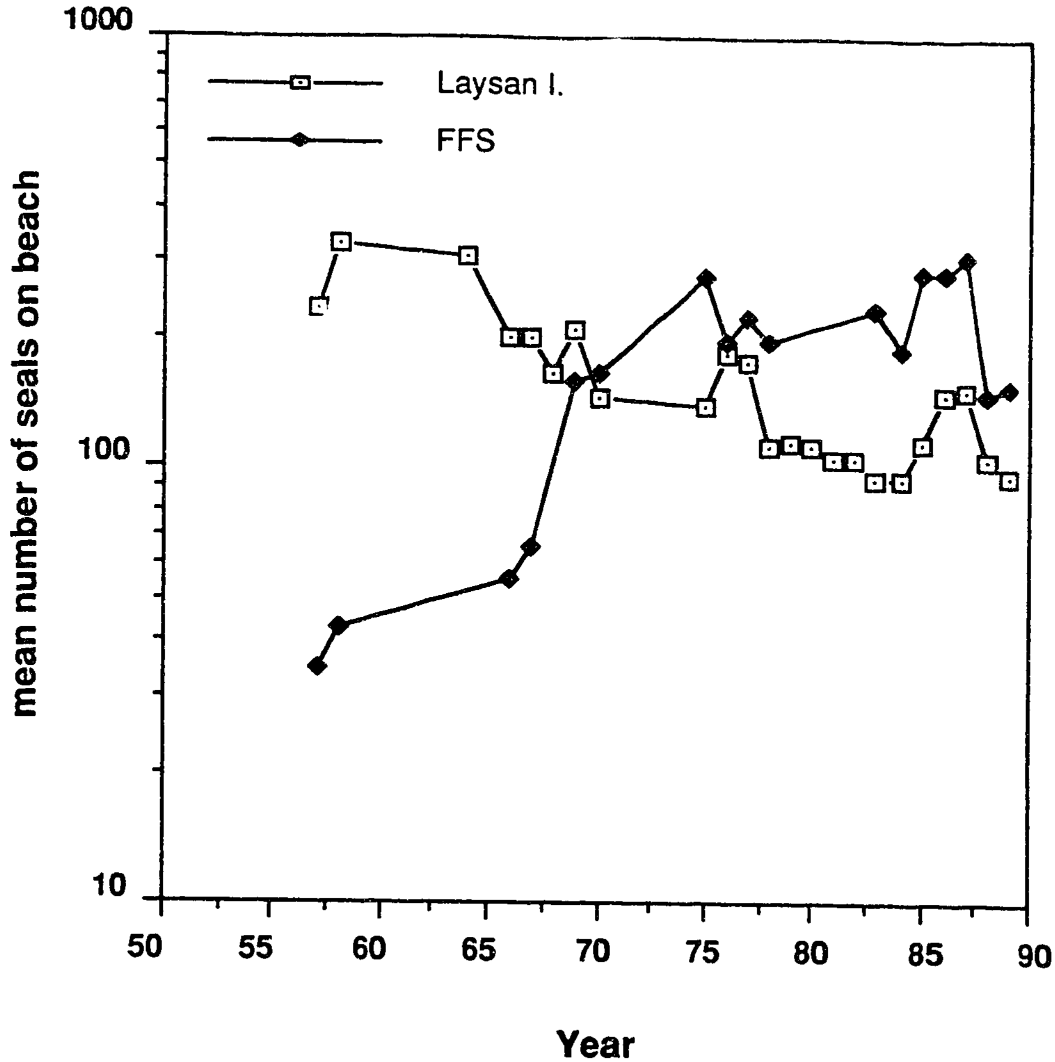
Laysan Island AGE OF SEAL

year disapp.	1 yr M	1 yr F	2 yr M	2 yr F	3 yr M	3 yr F	4 yr M	4 yr F	5 yr M	5 yr F
1984	0	0								
1985	1	2	0	0						
1986	3	4	0	1	6	1				
1987	2	5	1	1	1	0	1	0		
1988	2	2	0	0	2	0	1	2	0	0
1989	7	6	5	2	2	2	3	2	2	1
TOTAL DISAPP.	15	9	6	4	11	3	5	4	2	1
TOTAL in cohort	93 (16)	86 (22)	62 (10)	56 (7)	50 (22)	41 (7)	28 (24)	28 (14)	16 (13)	17 (6)

French Frigate Shoals AGE OF SEAL

year disapp.	1 yr M	1 yr F	2 yr M	2 yr F	3 yr M	3 yr F	4 yr M	4 yr F	5 yr M	5 yr F
1985	7	7								
1986	2	3	4	0						
1987	7	5	4	2	5	2				
1988	4	4	6	3	5	1	2	4		
1989	10	22	6	5	6	5	4	3	2	2
TOTAL DISAPP.	30	41	20	10	16	8	6	7	2	2
TOTAL in cohort	257 (12)	241 (17)	184 (11)	161 (6)	120 (13)	108 (7)	70 (9)	66 (11)	31 (6)	30 (7)

APPENDIX A. Number of tagged Hawaiian monk seals that died or disappeared from Laysan Island and French Frigate Shoals, Northwestern Hawaiian Islands. Percentages in brackets. Unpublished data from NMFS MMESP monk seal recovery team meeting, December 1990.



APPENDIX B. Population trends of Hawaiian monk seals at Laysan Island and French Frigate Shoals, NWHI, from 1957-1989.
1957 counts: Kenyon and Rice 1959. 1958 counts: Rice 1960.
1963-78 counts: Johnson et al. 1982. 1979-81 counts: Johnson and Johnson 1984. 1982 counts: Alcorn 1984. 1983 counts: Alcorn and Buelna 1989.
1984 counts: Johanos et al. 1987. 1985 counts: Becker et al. 1988.
1988 counts: Johanos et al. 1990. 1986-87, 1989 counts: NMFS MMESP unpublished data.