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Range-wide Patterns in Hawaiian Monk Seal Movements Among Islands and Atolls



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Cover: Hawaiian monk seals and green sea turtles hauled out at Necker Island (Mokumanana). Photograph by Mark Sullivan, courtesy of the Hawaiian Monk Seal Research Program, Pacific Islands Fisheries Science Center, National Marine Fisheries Service.



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ABSTRACT

Most Hawaiian monk seals reside in the Northwestern Hawaiian Islands (NWHI) where population abundance is declining. A small and growing number also occur in the main Hawaiian Islands (MHI), and rare sightings have been documented at Johnston Atoll, south of the Hawaiian Archipelago. Until recently, it was thought that there was essentially no movement of seals between the NWHI and MHI. Here, we present a new analysis of movements throughout the species range based on sightings of tagged seals over a 30-year period. The proportion of seals observed away from their natal sites varied with location but increased until adulthood, when 14% of seals were at non-natal sites. Females at non-natal sites accounted for 10% of all births. No sex differences were found. Annual movements declined rapidly with distance, with very little interchange between locations separated by over 400 km. The highest movement was observed among the relatively closely grouped MHI. In general, the likelihood of seals moving between sites in any given year increased with age class. While relatively rarely observed, at least 10 seals made 14 trips between the NWHI, the MHI, and Johnston Atoll. Due to incomplete and uneven sampling, actual movement probabilities were not estimated. However, the observed age- and distance-related movement patterns, along with confirmation that monk seals freely disperse throughout the Hawaiian Archipelago, will help inform measures to manage and conserve this critically endangered species.

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INTRODUCTION

Connectivity between subpopulations is critical to understanding and conserving meta-populations. The degree of interchange strongly influences the level of demographic asynchrony amongst subpopulations, also affecting probabilities of local extinction and recolonization (Levins, 1969; Hanski and Simberloff, 1997; Matthiopoulos et al., 2005). In the long term, isolation by distance determines genetic population structure (Wright, 1943). Another important consideration for conservation and management associated with movement is the probability and speed of disease transfer (Fulford et al., 2002).

Approximately 1200 Hawaiian monk seals (*Monachus schauinslandi*) remain scattered throughout the Hawaiian Archipelago (Fig. 1, Carretta et al., 2012). The species is listed as endangered under the U.S. Endangered Species Act and critically endangered according to the International Union for Conservation of Nature (IUCN, 2012). Previous movement analyses focused on interchange among the six most well-studied NWHI sites (defined here at single islands or atolls), from Kure Atoll southeast to French Frigate Shoals (Wirtz, 1968; Johnson and Kridler, 1983; Harting, 2002; Schultz et al., 2011). During an opportunistic tagging and re-sighting study conducted in 1966–1972, 8% of seals were resighted at least once away from their tagging location, with the proportion varying from 3 to 15% by location (Johnson and Kridler, 1983). And, as expected, the exchange of seals tended to be higher among nearby sites compared to more distant locations (Johnson and Kridler, 1983; Harting, 2002).

Although there has been some descriptive analysis of monk seal movement beyond the six most studied NWHI sites (Schultz et al., 2011), little detailed information has been available on interchange within the MHI or between the NWHI and MHI. Until recently, it was thought that there was essentially no movement of seals between the NWHI and MHI, a perception that influenced the scope of past conservation efforts. However, a lack of genetic population structure within the species' range indicates that sufficient dispersal occurs to maintain panmixia (Schultz et al., 2011). Here, we present a new analysis of movements throughout the species range based on sightings of tagged seals over a 30-year period. This paper is already published as a Note (Johanos et al., 2014) which is nearly identical yet lacks some additional detail, and is re-published here due to the importance of documenting additional detail deemed extraneous to the Note.

METHODS

Study Site

Most Hawaiian monk seals reside on low-lying islands and atolls in the NWHI; the 6 most-studied breeding sites occur at Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island, and French Frigate Shoals (Fig. 1). In 2010, an estimated 893 seals remained in these 6 areas (approximately 50–225 seals per site), where overall abundance has been declining by 4% per year (Carretta et al., 2012). Necker (Mokumanamana) and Nihoa Islands, high rocky islands at the eastern end of the NWHI, also host a total of roughly 150 seals.

Prior to the 1990s, monk seals were rarely seen in the MHI, but the population is estimated to have expanded to at least 150, at an estimated growth rate of 7% per year (Baker and Johanos, 2004; Baker et al., 2011*b*). Outside the Hawaiian Archipelago, rare monk seal sightings (including a single birth) have been confirmed only at Johnston Atoll, which lies approximately 850 km southwest of French Frigate Shoals (Schreiber and Kridler, 1969; Amerson and Shelton, 1976; NMFS, 2007).

Data Collection

We used visual sightings of marked seals collected over a 30-year period (1981–2011) to evaluate movement patterns. Weaned pups were marked with plastic tags on each rear flipper, and older seals were tagged or retagged on an opportunistic basis. Consistent tagging commenced at Kure Atoll in 1981, at Lisianski in 1982, at Laysan and Pearl and Hermes in 1983, and at French Frigate Shoals in 1984. Tagging began in 1988 at Midway Atoll, where births did not consistently occur until 1987, and in the MHI, where weaned pups were available for tagging beginning in 1988. Difficulty in landing small boats and accessing seals at Necker and Nihoa Islands, and high ecological and archeological sensitivity, has allowed for only a few seals to be tagged sporadically at these sites. Since 1991, seals were also routinely marked with implanted Passive Integrated Transponder (PIT) tags.

Identities of individual seals were maintained using a combination of flipper tags, PIT tags, natural features (scars or other) and temporary applied bleach marks, aided by a comprehensive digital photography database (Harting et al., 2004). Only absolutely certain sightings of individual seals were used in analyses of movement patterns. However, unusual sightings of unidentified seals were also tallied in areas that lacked an established population, as evidence of movement to that area from an unknown location. Re-sighting effort was highly uneven throughout the archipelago, and regional patterns are described below.

Northwestern Hawaiian Island Observations

Nearly every year since 1982, research field camps have been established at most NWHI sites, with the exception of Necker and Nihoa Islands. Camps at French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll were typically 2–5 months in duration (ranging from a few days to year-round), usually timed to coincide with the spring–summer breeding season. In some years, data collected at French Frigate Shoals, Laysan, Midway and Kure were augmented by incidental observations recorded by collaborators at other times of the year. During the field season, systematic surveys of all island and atoll shorelines were conducted every 4–7 days on average, typically with partial or complete shoreline surveys occurring daily (Baker et al., 2006). Researchers identified as many seals as possible at each site while also collecting reproductive and other life history data (Johanos et al., 1994; Harting et al., 2007). Variability in the duration of camps and ease of re-sighting among sites meant that identification of all seals was usually not achieved (Baker et al., 2006). Nevertheless, analysis of seal sighting histories indicates that the probability that a tagged seal is seen at least once during a field season at one of these six sites typically exceeded 90% (Baker and Thompson, 2007). In

contrast, the probability of detecting a seal at each location it may have visited, however briefly, during a given field season, was surely much lower and more variable among sites. Further, there was typically no field effort during the majority of each year, so that many (perhaps most) movements among these 6 sites were likely not detected.

Nihoa and Necker Islands were usually surveyed from 0 to only 2 days a year. When conditions permitted, researchers went ashore, tagged pups and identified seals. Boat surveys were also occasionally conducted at Gardner Pinnacles, where only a small number of seals (typically fewer than 6 individuals) were observed and no evidence of pupping was found. Individual seals were not identifiable as researchers did not typically land at this site.

Main Hawaiian Island Observations

Re-sighting effort differed in several ways between the NWHI and MHI. Previously, seals were rare in the MHI so few re-sightings were available until the mid-1990s. Whereas a relatively large number of seals is concentrated on very small and mostly accessible islands in the NWHI, in the MHI a small number of seals is distributed over extensive and often inaccessible coastlines and offshore islets. Furthermore, MHI monitoring is spatially uneven but occurs year-round; in the NWHI, monitoring is largely seasonal.

MHI monk seal data were derived from multiple sources. Weaned pups were tagged as in the NWHI and data collected during directed research and stranding response activities; however most re-sighting information was supplied by an informal network comprised by volunteers, collaborators, and the public (Baker et al., 2011*b*). Sightings were verified by trained observers. Occasional systematic surveys were also conducted at remote sites not regularly covered by the sighting network. Aerial surveys of all MHI shorelines were conducted in 2000, 2001, and 2008 (Baker and Johanos, 2004; Wurth and Johanos, 2009) and represent the only systematic complete shoreline counts of monk seals in the MHI. These and other single-island aerial surveys include some photographic identification of individual seals. MHI monk seal surveillance has increased in recent years but remains highly biased toward areas frequented by people, whereas inaccessible parts of even heavily populated islands may be underrepresented. Further, no tagging and little re-sighting information was available from Niihau, a privately owned island situated closest to the NWHI, which typically yields the highest single-island count during aerial surveys. Similarly, inaccessible Lehua Island and Kaula Rock, small islands at the western end of the MHI, are regularly used by monk seals but were only very rarely surveyed (Fig. 1).

Although the Hawaiian Archipelago comprises the entire established range of the Hawaiian monk seal, reports of confirmed and unconfirmed sightings were opportunistically collected from Johnston Atoll (the closest atoll to the south of the Hawaiian Archipelago, and considered within the species range) and from other areas in the Pacific. Johnston Atoll was populated by the U.S. military, U.S. Fish and Wildlife Service, and other government and civilian personnel since the beginning of our study until the completion of base closure in 2004 and has been infrequently visited since.

Data Analysis

For this study, movements were defined as sequential sightings of an individual seal at two different island/atoll sites, and a “round-trip” was treated as a series of independent movements in which a seal transited from one site to another, later returning to the first site. In the NWHI (from Kure Atoll southeast to Nihoa Island), interchange between the distinct islands or atolls were counted as movements, whereas much shorter transits along a single-island shoreline or amongst islets within atolls were excluded. In contrast to the small and relatively far apart NWHI, the MHI consists of 8 large islands, many of which are relatively near each other (Fig. 1). As in the NWHI, we also excluded within-island transits in the MHI but treated any interchange between the 8 MHI as a movement. None of the following analyses reference the duration of the movements, e.g., a seal which transited to another site for a day is counted the same as one having a longer residence at the destination. Because the movement data were incomplete, we did not attempt to attribute biological significance to most observed movements. For example, movements may involve giving birth, mating, foraging or simply briefly resting at different sites, but in most cases we cannot reliably determine the relationship between movement and these activities.

Movement analyses were based primarily on seals tagged as weaned pups at their natal sites to allow investigation of age-related trends and to reduce the likelihood of missed detection of seals with less-apparent identifying marks. Weaned pups were tagged at all sites within the species range with the exception of Lanai, Niihau, Lehua Rock, Kaula Rock, Gardner Pinnacles, and Johnston Atoll. Tagged seals were re-sighted at all sites except Kaula Rock and Gardner Pinnacles. Some seals were brought into captivity for rehabilitation or translocated between islands or atolls for management purposes. Data from such seals were excluded following the captivity or translocation action to eliminate biases associated with the unknown effects of those actions on subsequent seal movements. The only exception to reliance on this subset of seals tagged as pups was the inclusion of observations from other seals when describing relatively rarely observed cross-regional movements among the MHI, NWHI, and Johnston Atoll.

As a result of both spatial and temporal gaps in the observational data, many movements were likely undetected. Consequently, we report minimum observed, rather than actual movement rates. These minimum observed rates are distinct from true movement probabilities which cannot be estimated with the available data. Typically, no observations were made at the 6 most-studied NWHI sites between the end of one field season and the beginning of the next the following year (a gap roughly from at least September to April in most years). For the purposes of describing within-year movement patterns, we assumed that seals remained where last seen in a calendar year until the beginning of the subsequent year. Thus, when the first sighting in one year differed from the final sighting of the previous year, we assumed that the movement occurred in the latter year, at some time prior to the initiation of field observations.

Our analysis of movement data is mostly descriptive and usually not amenable to statistical testing as a result of unequal marking and re-sighting effort. However, in some cases where these issues were not expected to be influential (e.g., comparing age and sex related trends), statistical testing was conducted. A Friedman analysis of variance (ANOVA) was used to determine whether the annual proportion of seals observed to move varied by size class. A *t*-test was conducted to determine whether the proportion of seals of each age that were observed at non-natal sites differed between the sexes.

The following descriptive analyses were conducted to reveal broad patterns in monk seal movement. Age-related natal site fidelity was investigated by calculating the proportion of seals at each age that were observed at other than their natal site. Minimum annual interchange between specific sites was calculated as the proportion of seals (all ages pooled) per year observed to move from site X to site Y per year. This analysis was not limited to seals born at each site—all seals observed at a site were included in the sample for that site. Minimum annual movements by age were calculated as the proportion of seals that were observed to move, again irrespective of natal site. This was analyzed for four age classes: Weaned pups, juveniles (ages 1–2 yr), subadults (ages 3–4 yr), and adults (ages 5 yr and over). The data were pooled over all available data years so that, for each age class, the sample consisted of all individuals that belonged to that class in one or more years. Accordingly, an individual seal could, depending on its longevity, contribute to the sample for multiple age classes. Finally, we evaluated individual variability in movement histories for adult seals (ages ≥ 5 yr), including the number of observed movements of individual seals per year, and the number of within-year round trips (from site X to another site, and later returning to site X regardless of route).

RESULTS

Natal Site Fidelity

Study animals ($n = 4,438$ seals; 4,320 NWHI and 118 MHI) were re-sighted throughout their lifetimes, allowing detection of 1161 movements by 373 individuals. The proportion of seals observed away from their natal sites varied with location but, in general, increased from weaning to adulthood. There was no significant difference between males and females in the proportion of seals of each age that were observed at non-natal sites (paired *t*-test on arcsin square root transformed proportions, $t(25) = -1.57321$, $P = 0.13$); Fig. 2a). The pattern became more variable among older ages represented by small sample sizes. Overall, 14% of surviving seals (94 of 694 seals) were not at their natal site by age 10, an age by which nearly all females have attained full maturity as evidenced by adult size and reproductive performance (Harting et al., 2007). Also, because seals ventured away from and then returned to natal areas, roughly twice as many (28%) had been observed at a non-natal site at least once by age 10 yr. Of 1621 births by females whose natal sites were known ($n = 349$), 10% were females giving birth at sites other than where they were born. Although mating was rarely observed, some information on natal and breeding dispersal may be inferred from pupping sites: 11% of first pups were born to females at non-natal sites, and 95% of subsequent pups were born at the same island or atoll as the female's first

pup. Observations of seals from a given natal site decreased with distance from the natal site (see below, Fig. 2b).

Inter-site Movement and Distance Effects

Observed movements were most common among neighboring islands, while movements across regions (the 6 well-studied NWHI to MHI or the reverse) were rarely observed (Table 1). Seals were observed to move between the atolls at the western end of the chain (Kure, Midway, and Pearl and Hermes) more than between other NWHI sites. For example, annually 15% of seals seen at Midway were later observed at Kure. A lower amount of interchange was observed between Lisianski and Laysan Islands, and still less between Laysan and French Frigate Shoals. Relatively more movement was observed between islands in the MHI.

Although movements involving Nihoa and Necker were poorly characterized as a result of minimal field effort at these locations, observed movements between Nihoa, Necker, and nearby French Frigate Shoals were fairly high, as were movements between Nihoa and the MHI. Annually, 2% of seals seen on Nihoa were later seen in the MHI (ca. 250 km away); a higher level of movement than was observed between Laysan and French Frigate Shoals (ca. 600 km apart).

To evaluate the influence of proximity on interchange, we measured the straight-line distance between each pair of sites and plotted the observed proportion that moved against these distances. Observed annual movements declined rapidly with distance, with relatively high movement between sites separated by 100 km or less, and very little observed interchange between locations separated by more than 400 km (Fig. 3).

Age and Regional Effects

Minimum annual movement varies by age and region. The proportion of seals observed to move annually differed significantly among the age groups [Friedman ANOVA, Chi Sq ($n = 11$ sites, $df = 3$) = 28.418; $p < 0.001$], was progressively higher for older seals, and consistently higher in the MHI (Figs. 4a, b). Movements of pups were rarely observed, whereas 8% and 53 of adults move annually in the NWHI and MHI, respectively.

Although adults generally had the highest movement, there was considerable individual variability in the frequency of observed movement among seals. The distributions for number of observed movements per year and number of round trips observed per year were highly right skewed, with most individuals having no or few annual movements, but a small number of seals engaging in more frequent movements, including round trips. In the MHI, where distances are close, most adults were seen on multiple islands over the course of the year, with several seen on as many as 4 islands. As with natal site fidelity, there was no significant difference between sexes in either the proportion of individuals that moved (chi-square, $P = 0.51$, $df = 1$), the mean number of annual movements per individual (t -test, $P = 0.53$, $df = 1209$, $F = 1.099$) nor in the number of round trips per individual ($F = 1.43$, $P = 0.92$, $df = 1209$).

Cross-region Movement Patterns

Minimal surveillance at Necker and Nihoa hinders characterization of movements to and from these islands. Even less surveillance at Johnston Atoll and other Pacific islands limits characterization of monk seal movements outside the Hawaiian Archipelago to anecdotal observation. Based on the paucity of data, we utilized all documented movements, including trips by seals tagged at older ages and a previously translocated seal, to describe relatively rarely observed cross-regional movements.

From 1981 to 2011, at least 68 seals were observed to make 132 trips among the 6 most closely monitored NWHI sites, Necker and Nihoa, the MHI, and Johnston Atoll (Table 2). Most of these trips occurred between Necker or Nihoa Islands and French Frigate Shoals, the nearest major NWHI site to the west, with several seals making one or more round trips. However, 10 seals made 14 trips between the NWHI, the MHI, and Johnston Atoll; 8 trips occurred between Necker/Nihoa and the MHI, 5 trips occurred between more distant NWHI and the MHI, and one trip occurred between the NWHI and Johnston Atoll. An adult male, originally translocated from Laysan to the MHI (Johanos et al., 2010), made 2 round trips from the MHI to Nihoa. Another male born at Laysan Island traveled to French Frigate Shoals and on to Nihoa and Kauai as a subadult, later returning to French Frigate Shoals as an adult. One female seal born at Midway Atoll traveled to Laysan as an adult and then on to the MHI where she was first seen on Molokai. She subsequently traveled to the southernmost MHI, Hawaii Island, and has remained within the MHI to date. Thus, this female was documented to transit approximately 2400 km, nearly the entire span of the Hawaiian Archipelago. She produced the first recorded pup on Hawaii Island in 2001, and subsequently pupped on Niihau and Oahu for a total of 8 MHI births recorded as of 2011. Another adult female, born at French Frigate Shoals, traveled to Johnston Atoll and remained there for about a year before disappearing. Other than at Johnston Atoll, no sightings of Hawaiian monk seals have been confirmed by photos or other tangible evidence on any Pacific island external to Hawaii, and unconfirmed sightings may have been of other Pacific pinnipeds. That said, we have received unconfirmed reports at Palmyra Atoll and Wake Atoll (Westlake and Gilmartin, 1990; Ragen and Lavigne, 1999) and in the Marshall Islands at Bikini Atoll and Mejit Island; areas ca. 1700–2500 km away from the NWHI.

DISCUSSION

Interpreting observed monk seal movements using sighting records is complicated by biases resulting from unequal marking, unequal re-sighting effort, and likely unequal sightability at different locations. These issues greatly undermine the ability to assess either the true or relative rates of movement between sites but allow us to describe the minimum annual movement among sites. Other aspects of monk seal movement patterns were likely not affected by these sampling difficulties. For example, the findings that adult seals move more frequently than younger animals and that there was no difference in the minimum movement among sexes are credible because there was no difference in relative effort to re-sight seals by age or sex among sites, and we have not found any evidence of bias in our ability to detect movement by age or sex over the course of this study.

If sites with disparate interchange rates were disproportionately made up of adults or either gender, then spurious age- and sex-related results might be obtained. French Frigate Shoals has had an age structure distinct from other locations. Based on prolonged poor juvenile survival leading to low recruitment, this subpopulation has been made up of relatively more adults than other sites for approximately two decades (NMFS, unpublished data). Because observed movement from French Frigate Shoals was relatively low (Table 1), likely based on relative geographic isolation from other closely monitored sites, the over-representation of adults at French Frigate Shoals would, if anything, tend to negatively bias estimates of adult movement. This is contrary to the observation that adults are the most mobile age class. Sex ratios are roughly even at monk seal breeding sites, with the exception of Laysan and Lisianski Islands, which have at times had male-biased adult sex ratios (Johanos et al., 2010). We know of no plausible scenario by which the adult sex ratio imbalance at these sites could mask a real gender difference in movement frequency.

A common pattern in animal movement is that juveniles have a greater tendency to disperse while adults exhibit greater site fidelity (Baker, 1978). We found the seemingly contradictory result that adult monk seals dispersed more widely among islands and atolls than did young animals. This finding is difficult to interpret because we lack complete information on the duration or function of the observed movements. The age-related pattern we observed may simply reflect size-related biological capacity and foraging patterns, whereby larger adults have more knowledge and greater swimming and diving capabilities, allowing them to exploit broader regional habitats.

Male-biased dispersal occurs in the majority of mammals, possibly because of a suite of selective factors that remain to be fully explicated (Greenwood, 1980; Lawson Handley and Perrin, 2007). Our results suggest that monk seals may depart from the mammalian norm, although the extent to which observed movement correlates with actual breeding dispersal is uncertain. It is also possible that monk seal movements vary between the sexes, but on a smaller geographic scale (e.g., along an island perimeter or between islets within an atoll), or in a manner that can only be captured using a finer-grained approach. For example, males have a more generalized distribution and ‘cruise’ or seek out females along the shoreline of Laysan Island (Johanos et al., 2010), and future telemetry studies may show that males similarly seek females between islands in the MHI.

The finding that seals tend to more readily move between nearby sites than more distant ones, while intuitive, could well be influenced by sampling inequities among sites. For example, there are year-round (albeit largely nonsystematic) observations in the MHI but not in the NWHI, and the MHI are situated more closely to one another. This could have biased the rate of movement such that short-distance transits were relatively more likely to be detected. However, when we examine just the NWHI, we also see a decline in movement with distance (Fig. 3). The most proximate NWHI sites represented in Figure 3 are Kure Atoll, Midway Atoll, and Pearl and Hermes Reef, and these atolls have relatively high minimum observed movement. However, over the course of the study years, these sites had, on average, relatively lower field effort compared to sites such as Laysan Island and French Frigate Shoals (which are more distant from other well-studied locations). Therefore, the relatively high interchange seen between the western three sites is not likely a result of sampling bias. We conclude that while the precise

shape of the declining curve in Figure 3 may be somewhat distorted by sampling bias, the finding that movements decline with increasing distance is likely correct. The dearth of direct movements exceeding 400 km may be a useful consideration when planning translocations or planning response to disease outbreaks. While relatively rarely documented, long-distance movements were observed and these confirm that monk seal subpopulations, even between the NWHI and MHI, are not demographically isolated. Our findings of range-wide connectivity are consistent with Schultz et al. (2011), who found no genetic stock structure within the species range.

Because seals are most likely to travel between adjacent sites, distance is likely a major determinant of monk seal movements to other land masses. Thus, the relatively high observed interchange among the western atolls in the NWHI and even higher movement between islands within the main Hawaiian Islands may be attributed to geographic opportunity. The closest distance between adjacent atolls in the western NWHI (Midway to Kure, a little over 100 km) is comparable to the greatest distance between adjacent MHI (Kauai to Oahu), and we see a similar pattern of relatively free movement between these adjacent sites.

Our findings based on land-based tag sightings are corroborated by satellite telemetry studies that show monk seals foraging extensively near their island of origin but also traveling freely to other sites within the MHI (Littnan et al., 2006; Cahoon, 2011) and using nearby extra-colony banks and seamounts within the NWHI (Abernathy, 1999; Stewart et al., 2006). Telemetry studies show that foraging ranges near colonies tend to increase slightly with age (Stewart, 2004), and that monk seals are capable of undertaking long forays up to 322 km (Stewart et al., 2006), orienting near or over the NWHI submarine ridge when traveling to and from extra-colony foraging sites (Abernathy, 1999; Stewart et al., 2006).

Individual seals made exceptionally long journeys, including a NWHI-born seal (Midway) that eventually transited nearly the entire length of the Hawaiian Archipelago (ca. 2400 km) and produced the first recorded pup on Hawaii Island, and a French Frigate Shoals-born female that traveled to Johnston Atoll, an area outside the established species range. Additionally, at least 4 tagged seals from French Frigate Shoals and Laysan Island, including one confirmed to be Laysan-born, traveled to Johnston Atoll during a previous study (Schreiber and Kridler, 1969; Johnson and Kridler, 1983), and an untagged female pupped there in 1969 (Amerson and Shelton, 1976). Unconfirmed reports suggest that vagrant monk seals may wander even farther afield and ultimately haul out on far-flung Pacific Islands. Although difficult to evaluate, movement to new areas may prove advantageous to both individual and species survival, especially during periods of climate change or environmental stress. Based on preliminary findings, seals translocated to areas with higher survival probability may experience improved survival-to-reproductive age (Baker et al., 2011a). On a species level, most if not all subpopulations in the NWHI have undergone depletion/or near elimination at one time or another because of harvesting, human disturbance, and other factors, followed by periods of recovery (NMFS, 2007), likely aided in part by migration to the depleted site from adjacent locations, and an understanding of range-wide movement patterns is essential when evaluating the risk of extinction.

Although some Hawaii community members view the monk seal as endemic to the NWHI and not to the MHI, monk seal bones have been recovered from two pre-European contact archeological sites on Hawaii Island and another on Maui (Rosendahl, 1994; Kittinger et al., 2012), rare sightings of monk seals were documented in the MHI during the early 20th Century (Kenyon and Rice, 1959), and MHI sightings were documented each year during the current study. These seals may have been members of an established though very sparse MHI subpopulation or nonresident transients venturing from the NWHI and outside the established range of the time (the first successful pupping was not recorded in the MHI until 1988, and puppings and sightings increased sharply beginning in the mid-1990s (Baker and Johanos, 2004)). Regardless, our findings confirm that there is no barrier to movement between regions within the Hawaiian Islands and lead us to conclude that monk seals have been present in the MHI (or the predecessors of the MHI) at some level throughout the species history.

A prolonged decline in monk seal abundance in the NWHI, coupled with robust growth of what had until recently been an incipient seal population in the MHI, has profoundly altered the landscape of Hawaiian monk seal conservation and management (Baker et al., 2011a). In the remote and protected NWHI, where most recovery effort has historically been focused, human presence and activities (e.g., fishing) are greatly restricted. The advent of the MHI monk seal population has raised a host of new opportunities and challenges. The MHI potentially represent habitat that can sustain a sizeable number of seals, thus acting as a buffer against extinction. However, MHI monk seals face threats that are largely or entirely absent from the NWHI. These include exposure to novel pathogens, fishery interactions (hooking and entanglement in active gear), human disturbance and, more recently, intentional killing (Baker et al., 2011b).

Translocation has been successfully used to enhance monk seal survival and reduce the potential for human-seal conflict in the MHI (Baker et al., 2011a). With a growing seal population and increasing rates of conflict with beach and ocean users, there will likely be more demand for such intervention. The design of successful translocations depends on characterization of natural patterns of movement of individual monk seals between island habitats.

Other threats facing MHI seals also require an understanding of monk seal movements within the MHI and between the MHI and NWHI. For example, while monk seals have been isolated from terrestrial mammalian diseases during millions of years of evolutionary history, humans have introduced numerous terrestrial mammals to the MHI. Furthermore, satellite monitored seals in the MHI spent substantial amounts of time in shallow coastal waters near sources of land-based water runoff and sewage dispersal and may be at risk of exposure to disease agents associated with terrestrial animals that are known to cause disease in marine mammals (Littnan et al., 2006). Epidemic disease could jump from these nonnative mammal vectors to naïve monk seals in the MHI, thus affecting the local subpopulation. More alarming, depending in part on movement patterns, epidemic diseases could spread to the NWHI and devastate seal subpopulations.

While the NWHI and MHI sites were once thought to be effectively isolated from each other, we have documented seals moving across these geographic regions and described observed age- and distance-related movement patterns within regions. The deployment of additional satellite transmitters and other technologies will eventually help to fill gaps in our understanding of movement and how it relates to recovery issues. Greater movement between regions increases

the threat of natural disease transmission to the NWHI from the MHI, yet it might also give the species greater resiliency, allowing recolonization of depleted areas. The observed age- and distance-related movement patterns, along with the confirmation that monk seals move freely throughout the Hawaiian Archipelago, will help inform ongoing measures to manage and conserve the species.

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TABLES

Table 1A. – Minimum annual observed movement rates among 8 Northwestern Hawaiian Islands (NWHI) sites and from the NWHI to main Hawaiian Islands (MHI). The *n* value is the number of tagged seals seen annually at each site, summed over all years. Proportions in individual rows sum to 1, whereas proportions in columns do not. Shaded values indicate the proportions of seals that were only observed at the site where they had been the previous year. French Frigate Shoals and Pearl and Hermes Reef are abbreviated FFS and PHR, respectively. One seal from FFS was observed at Johnston Atoll (annual proportion = 0.0001).

Original Site	<i>n</i>	Destination Site								
		MHI	Nihoa	Necker	FFS	Laysan	Lisianski	PHR	Midway	Kure
Nihoa	92	0.0218	0.8913	0.0000	0.0870	0.0000	0.0000	0.0000	0.0000	0.0000
Necker	69	0.0000	0.0000	0.5072	0.4928	0.0000	0.0000	0.0000	0.0000	0.0000
FFS	7035	0.0001	0.0024	0.0065	0.9888	0.0020	0.0000	0.0000	0.0000	0.0000
Laysan	4909	0.0004	0.0000	0.0000	0.0037	0.9635	0.0312	0.0012	0.0000	0.0000
Lisianski	3145	0.0000	0.0000	0.0000	0.0010	0.0471	0.9450	0.0054	0.0010	0.0006
PHR	3022	0.0000	0.0000	0.0000	0.0003	0.0030	0.0076	0.9500	0.0271	0.0119
Midway	887	0.0000	0.0000	0.0000	0.0000	0.0011	0.0000	0.0676	0.7768	0.1545
Kure	2067	0.0000	0.0000	0.0000	0.0000	0.0000	0.0010	0.0155	0.0745	0.9090

Table 1B. – Minimum annual observed movement rates among 8 sites within the main Hawaiian Islands (MHI) and from the MHI to Northwestern Hawaiian Islands (NWHI). The *n* value is the number of tagged seals seen annually at each site, summed over all years. Proportions in individual rows sum to 1, whereas proportions in columns do not. Shaded values indicate the proportion that was only observed at the site where they had been the previous year. Kahoolawe and Molokai are abbreviated KAH and MOL, respectively. No seals were recorded moving between the MHI and Johnston Atoll.

Original Site	<i>n</i>	Destination Site								
		Hawaii I	KAH	Maui	Lanai	MOL	Oahu	Kauai	Niihau	NWHI
Hawaii I	38	0.7368	0.0000	0.1053	0.0263	0.0526	0.0789	0.0000	0.0000	0.0000
KAH	23	0.0435	0.6522	0.1304	0.0000	0.1739	0.0000	0.0000	0.0000	0.0000
Maui	39	0.1026	0.1282	0.4103	0.0000	0.3077	0.0513	0.0000	0.0000	0.0000
Lanai	4	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
MOL	208	0.0096	0.0096	0.0817	0.0096	0.7548	0.1154	0.0192	0.0000	0.0000
Oahu	100	0.0200	0.0000	0.0100	0.0000	0.2400	0.6500	0.0700	0.0100	0.0000
Kauai	125	0.0160	0.0000	0.0000	0.0000	0.0320	0.1120	0.8320	0.0000	0.0080
Niihau	2	0.0000	0.0000	0.0000	0.0000	0.0000	0.5000	0.0000	0.5000	0.0000

Table 2. – All documented movements of Hawaiian monk seals between the 6 most closely monitored Northwestern Hawaiian Islands (NWHI), Necker, Nihoa, the main Hawaiian Islands (MHI), and Johnston Atoll from 1981 to 2011. Most documented trips occurred among Necker, Nihoa, and French Frigate Shoals, the nearest major NWHI subpopulation to the west. However, 10 seals were observed to make 14 trips between the NWHI, the MHI, and Johnston Atoll. Individual seals may contribute to information on multiple rows. French Frigate Shoals is abbreviated FFS. Table does not include 3 tagged seals (1 from FFS and 2 from Laysan) that traveled to Johnston Atoll prior to the current study.¹

Original Site	Destination Site	Total Trips	Seals	Notes
FFS	Necker	51	41	All seals tagged at FFS
Necker	FFS	39	33	All but two seals tagged at FFS (2 identified at Necker)
FFS	Nihoa	18	17	All but one seal tagged at FFS (1 born at Laysan)
Nihoa	FFS	10	9	All but one seal tagged at FFS (1 tagged at Nihoa)
Laysan	MHI	1	1	Destination Molokai, seal born at Midway
FFS	MHI	2	2	Destinations Lehua and Hawaii I. (1 born at FFS, 1 tagged FFS)
MHI	FFS	2	2	Traveled from Kauai (1 identified on Kauai, 1 born at Laysan)
FFS	Johnston	1	1	Seal born at FFS
Nihoa	MHI	6	5	Destinations Kauai (seal born at Laysan), Hawaii I. (seal identified at Nihoa) and Oahu (4 trips; 2 trips by seals either born/ first identified on Nihoa, and 2 trips by a single male translocated to the MHI from Laysan, tagged on Laysan).
MHI	Nihoa	2	1	The same translocated male as above originated travel from Oahu and Hawaii I.
Total		132		Trips made by 68 individual seals

¹ Reported in Schreiber and Kridler (1969), Amerson and Shelton (1976), Johnson and Kridler (1983).

FIGURES

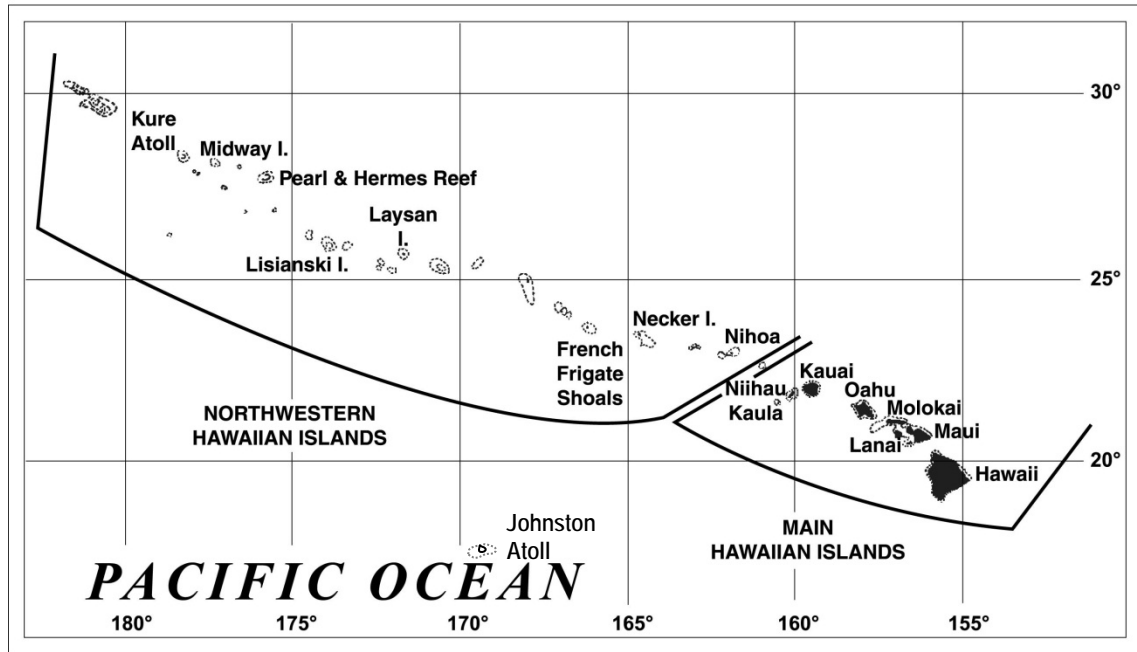


Figure 1. –The Hawaiian Archipelago (spanning ca. 2500 km) is grouped into two regions, the Northwestern Hawaiian Islands (NWHI) and the main Hawaiian Islands (MHI). Johnston Atoll is situated approximately 850 km southwest of French Frigate Shoals, its closest neighbor in the Hawaiian Archipelago.

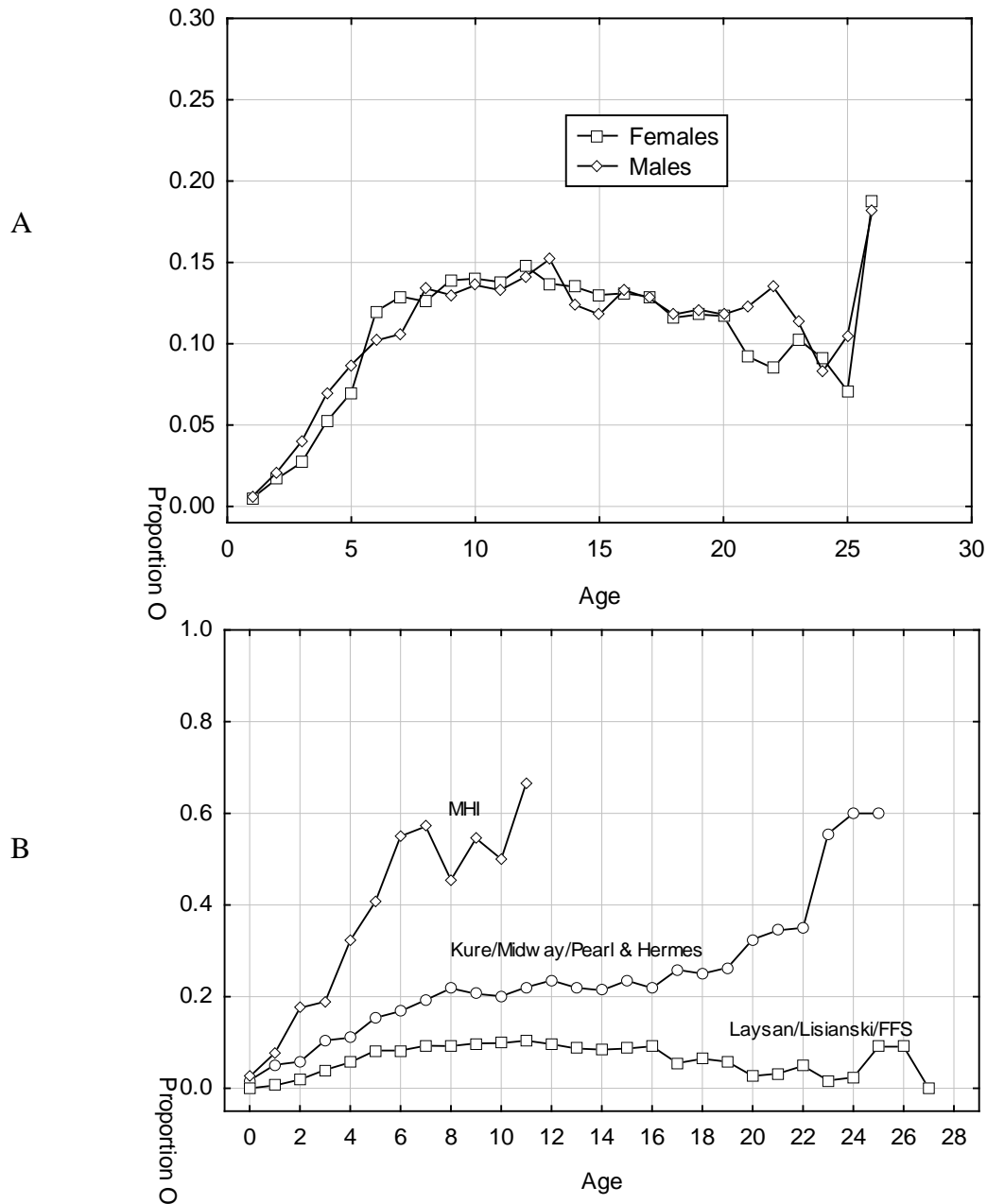


Figure 2. The proportion of Hawaiian monk seals observed away from their natal site at each age. A) By sex, showing no differences between the sexes, B) By location, combining natal areas into 3 groups based on their distance to the next adjacent site: 1) the MHI, where distances are generally closest and < 200 km), 2) the western NWHI sites (Kure, Midway, and Pearl and Hermes), also < 200 km to the next site, and 3) the eastern NWHI sites (Lisianski, Laysan, and French Frigate Shoals), which are > 200 km to the next well-surveyed site). French Frigate Shoals is abbreviated FFS.

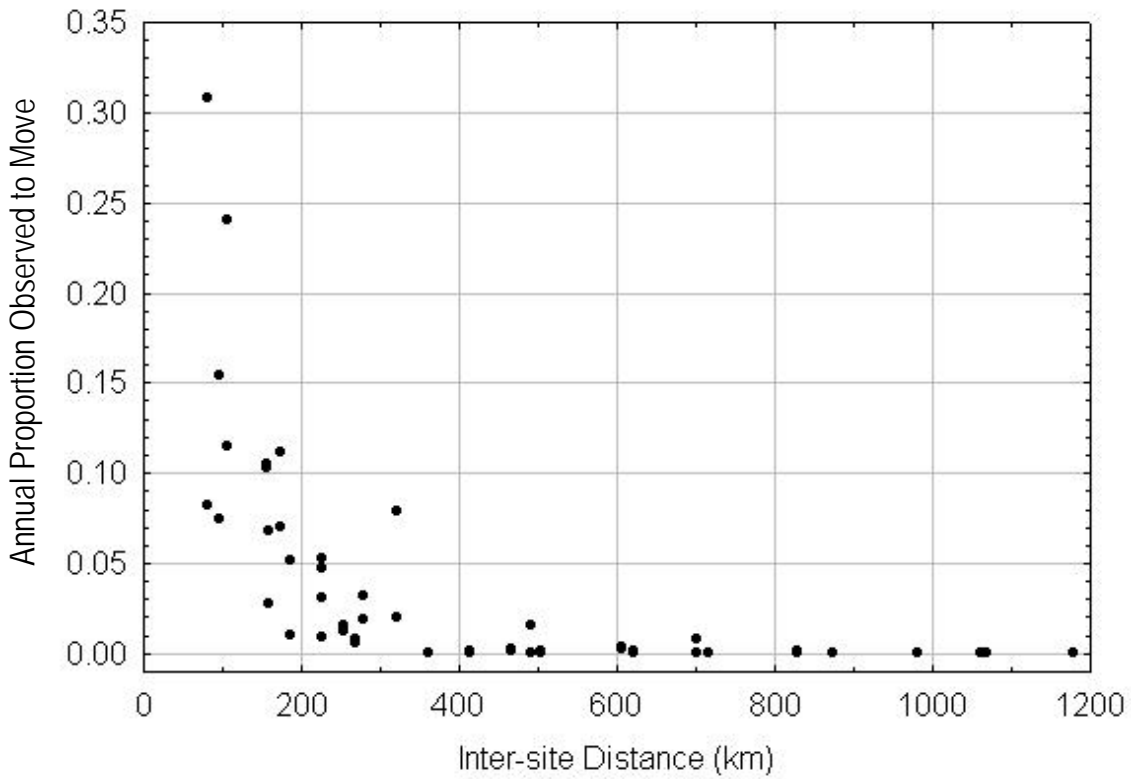


Figure 3. Relationship between inter-site distance (km) and the annual proportion of Hawaiian monk seals observed to move between locations, with each point representing directional movement between a pair of sites. This plot excludes data from Necker, Nihoa, Niihau, Lanai, Kahoolawe and Johnston Atoll based on very low field effort at these sites.

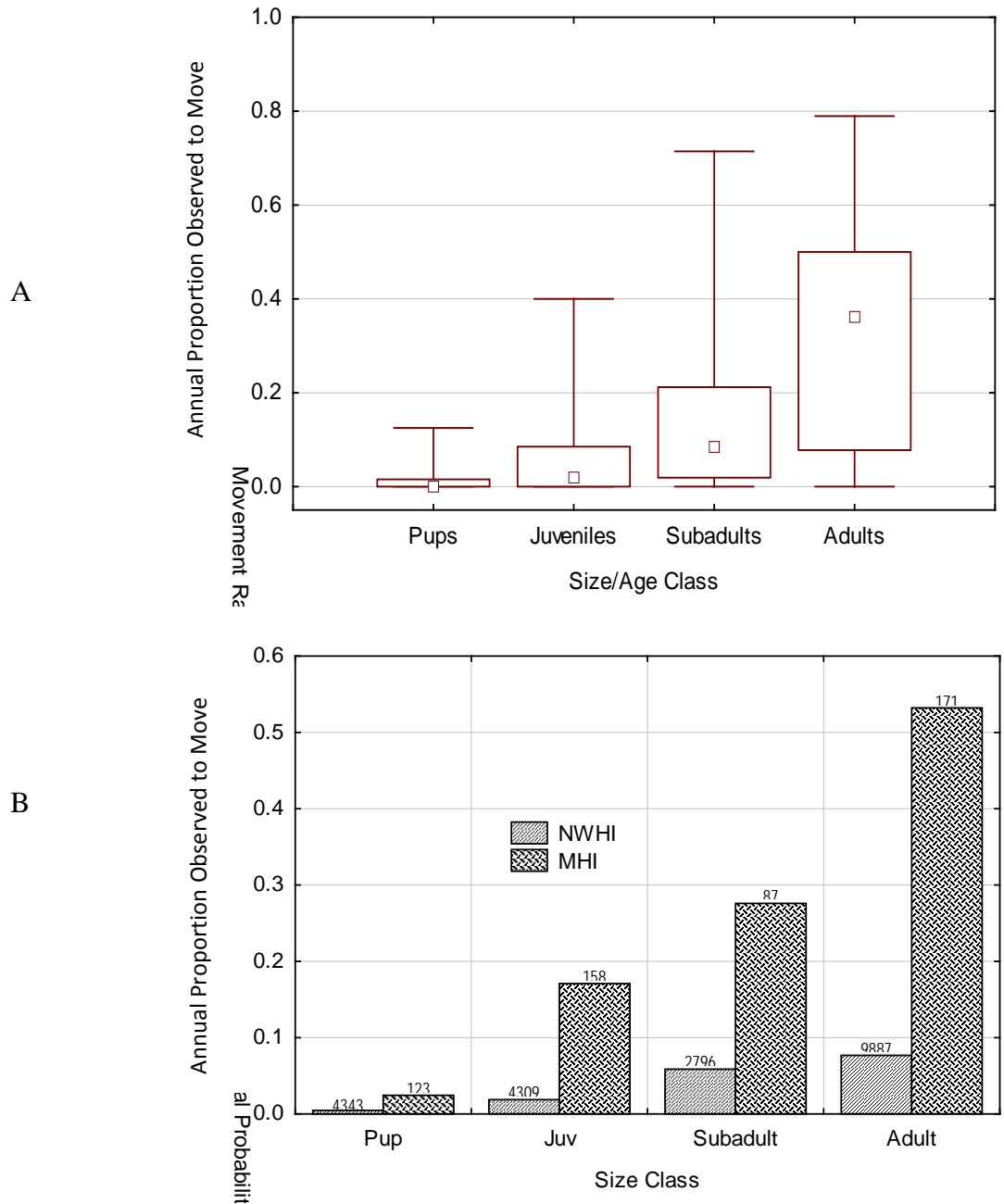


Figure 4. The proportion of seals that were annually observed to move, for four age classes (pups = birth to age 1; juvenile = ages 1–2; subadults = ages 3–4; adults = age 5 and older). Annual proportion of seals observed to move from their current site to some other location, irrespective of natal site. A) Box plot indicates mean, 25/75% quartile, and min/max, B) Bar graph, showing regional patterns in the Northwestern Hawaiian Islands (NWHI) and main Hawaiian Islands (MHI). Sample sizes are above bars and refer to the number of tagged seals of each age class and region, summed over all years.

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