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Cover: Seals on Tern Island, July 1985. Photo: Julie Eliason

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Executive Summary

The endangered Hawaiian monk seal (Neomonachus schauinslandi) requires terrestrial habitat for critical life functions, such as parturition and nursing. Islands also provide monk seals with resting space that is both safe from shark attack and within commuting distance to their marine foraging habitat. Terrestrial habitat in the Northwestern Hawaiian Islands (NWHI), where some 1,100 of the remaining 1,400 monk seals reside, is threatened by manifestations of global climate change, primarily sea-level rise. French Frigate Shoals currently hosts approximately 20% of the monk seals in the NWHI and for many decades accommodated the species' single largest subpopulation. The several sand islets used by seals throughout the atoll have been decreasing in size for at least several decades. Whaleskate Island was once the second largest in the atoll and for several years the site of the greatest number of monk seal pup births within French Frigate Shoals. By 2000, Whaleskate Island had completely eroded away. Female monk seals subsequently began to give birth most commonly at Trig Island, the nearest to where Whaleskate Island had been. Trig Island had previously accounted for a small fraction of births, and it proved to be suboptimal habitat for rearing pups, as Galapagos sharks (*Carcharhinus galapagensis*) have been able to approach sufficiently close to the island to kill a large portion of the pups born there each year. In 2018, the two remaining primary birth sites, Trig and East Islands, washed away. Trig succumbed to progressive erosion in September 2018, and East Island was obliterated by Hurricane *Walaka* in October 2018. Throughout the rest of the NWHI, pup survival from birth to weaning, a period of five to seven weeks, averages 95%. At French Frigate Shoals in 2018, only 57% of pups born survived to weaning. This high mortality of young pups was attributable to shark predation and drowning due to birth islands being inundated by storms or high tides.

The foraging ranges of monk seals residing in the various NWHI are documented in previouslypublished satellite telemetry studies. Seals commute to marine foraging areas adjacent to their terrestrial resting sites, but also swim to submerged features offering foraging habitat up to approximately 250 km from shore. Seals based at French Frigate Shoals access 42% of the total NWHI foraging habitat (defined as areas with depths less than or equal to 200 m). Excluding the bank surrounding Necker Island, foraging seals from French Frigate Shoals likely have near exclusive access to 31% of the available foraging area in the NWHI. If French Frigate Shoals were to become uninhabitable by seals due to total loss of terrestrial habitat in the future, this significant portion of foraging habitat would likely also become virtually inaccessible to seals, thereby limiting potential for the species recovery.

Tern Island now accounts for about three-quarters of the remaining terrestrial habitat area at French Frigate Shoals. Due to its relatively higher elevation and semi-hardened shoreline, it is likely the most resilient of the remaining islets to future inundation. Relationships between historical maximum counts of seals at all NWHI subpopulations and the respective amount of terrestrial and marine habitat accessible to seals residing at each site, suggest that seal subpopulation abundance is constrained more by foraging habitat availability than by terrestrial habitat area. That being the case and based on historical counts when the seal population of French Frigate Shoals was near its peak, Tern Island could hypothetically accommodate the entire current population if all the remaining islets in the atoll were to subside. Whether Tern Island would provide sufficient quality pup rearing habitat to sustain the population is not known. Moreover, potential competition among seals, Hawaiian green sea turtles (*Chelonia* *mydas)*, and seabirds for limited space could become a significant limiting factor for these taxa, which all require terrestrial habitat for successful reproduction. Notwithstanding these uncertainties, Tern Island will undeniably play an increasingly crucial role in the persistence of monk seals at French Frigate Shoals.

Unfortunately, Tern Island in its current condition actually poses serious threats to monk seals. The island's human-built infrastructure has been largely destroyed by storm events since 2012, leaving the island strewn with various debris. The greatest threat is the remnant of a decaying steel double seawall bordering a portion of the island. Monk seals, primarily weaned pups, as well as green sea turtles and seabirds, make their way between the parallel walls and become entrapped. Since 1989, a total of 70 monk seal entrapment cases have been documented, 25 of which occurred just during 2017 to 2019. When people are present on the island, seals can be rescued that would otherwise likely perish. However, since 2012, Tern Island is no longer permanently staffed. As such, seals and other trapped wildlife can only be freed from seawall entrapment during the few months of the year when NMFS monk seal staff are present.

In less than two decades, three major islands previously used by French Frigate Shoals monk seals for giving birth and rearing their pups have been greatly diminished or completely lost, and the remaining islets have also contracted. These facts indicate that the French Frigate Shoals monk seal population may not persist in the long term without intervention to improve the quality, if not quantity, of terrestrial habitat. Man-made hazards on Tern Island should be eliminated and, in the meantime, the island should be staffed sufficiently to mitigate seawall entrapment of seals and other wildlife. In the longer term, efforts to preserve, and ideally restore, terrestrial habitat will likely be essential to ensure the French Frigate Shoals monk seal population remains viable and contributes to the species ultimate recovery.

Background

This document is intended to provide resource managers, scientists, and other stakeholders with information regarding how terrestrial habitat loss and degradation at French Frigate Shoals, Northwestern Hawaiian Islands (NWHI), has impacted the resident Hawaiian monk seals as well as the implications for the species' conservation. It is further hoped that the findings presented here will help inform any future efforts to improve and restore terrestrial habitat at French Frigate Shoals for the benefit of monk seals and other species.

Hawaiian monk seals (*Neomonachus schauinslandi*) require terrestrial habitat for several critical functions. All seal species must give birth on land (or on ice in some cases); therefore, suitable habitat for parturition is a prerequisite for the species to perpetuate themselves. Terrestrial habitat also provides monk seals with resting space that is both safe from attack by their predators (large sharks) and within commuting distance to their marine foraging habitat.

The Hawaiian monk seal metapopulation comprises multiple subpopulations distributed throughout the Hawaiian Archipelago (Fig. 1). NWHI monk seals sometimes swim between atolls and islands, but predominantly remain within their natal subpopulations and forage in benthic habitats (Johanos et al. 2014). Tracking studies have revealed that the foraging grounds include the shoals and slopes immediately adjacent to their terrestrial resting sites, as well as numerous submerged banks and seamounts within commuting distance (Stewart et al. 2006). Further, it has been determined that the vast majority of foraging occurs at the sea floor at depths less than 200 m (though some seals occasionally dive much deeper, in excess of 500 m) (Parrish et al. 2000).

In 2019, the total estimated abundance of Hawaiian monk seals throughout the Hawaiian Archipelago was approximately 1,400 (NMFS unpublished data). Roughly 1,100 seals reside in the Northwestern Hawaiian Islands (NWHI) and 300 in the main Hawaiian Islands (MHI) (Fig. 1), respectively (Carretta et al. 2020). Within the NWHI, seals occur in eight subpopulations from Kure Atoll in the west to Nihoa Island in the east (Fig. 1). The seals use all suitable landing areas available to them in the NWHI (Norris et al. 2017, Stewart et al. 2006). These subpopulations currently range in size from roughly 70 to 230 individuals.

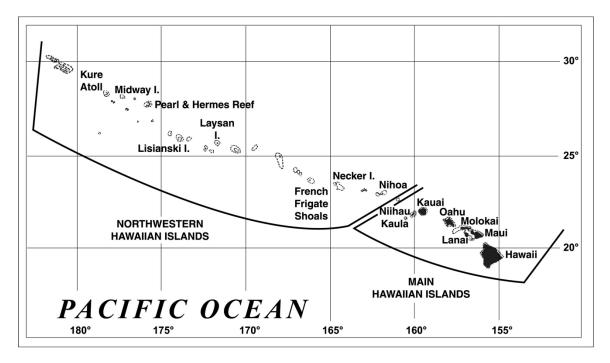


Figure 1. The Hawaiian Archipelago

French Frigate Shoals is the largest atoll in the NWHI; its longest axis extends more than 30 km and encompasses several small islets (Fig. 2). Over the past 100 years, the islets at French Frigate Shoals have been the setting for a variety of human activities that likely impacted monk seals and other wildlife (Ragen 1999). The seal subpopulation at this atoll has exhibited the greatest variability in abundance observed among the six most closely monitored in the NWHI (Johanos et al. 2020a, Fig. 3). Prior to a peak in abundance in the late 1980s, the French Frigate Shoals seal population had grown rapidly for at least the preceding two decades (Fig. 4). Although total abundance estimates are only available going back to 1997 (when the population was twice as large as it is now), beach counts (an index of abundance) were four times higher at French Frigate Shoals in the mid-1980s than the current level. This suggests that more than 800 seals may have lived at the atoll less than forty years ago. For three decades prior to 2008, French Frigate Shoals was the most populous monk seal subpopulation (Fig. 3). In 2019, despite the prolonged decline, French Frigate Shoals still hosted the second largest NWHI monk seal subpopulation with 223 seals, just shy of the 231 residing at Laysan Island.

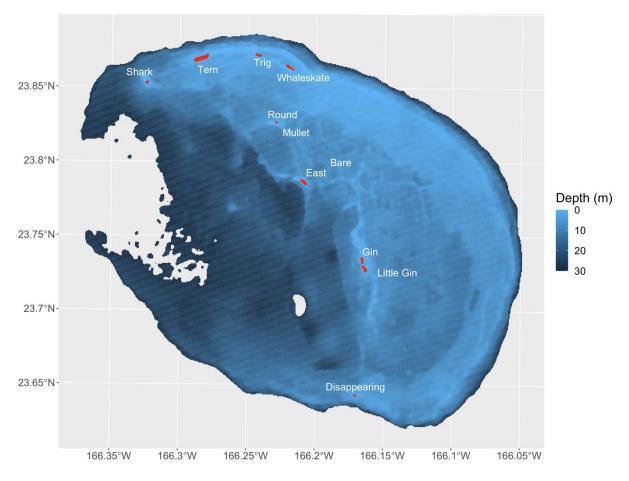


Figure 2. Islets of French Frigate Shoals. Labels indicate approximate former location of Mullet and Bare Islands, and red shapes indicate the former location of some islets (Trig, Whaleskate, East), which had been completely or virtually submerged prior to 2019.

The reasons for the dramatic boom and bust of the French Frigate Shoals monk seal population are not entirely known, but it is likely that the growth was at least partially due to a reduction of human activity and disturbance on shore that had previously excluded seals from much of their terrestrial habitat in the atoll. As depicted in Figure 4, during the 1930s and through the end of WWII, the U.S. Navy was active at French Frigate Shoals, including a project to enlarge Tern Island with dredged material so that the island could serve as a naval air station. In 1944, a long-range navigation (Loran) station was established and staffed at East Island and was then moved to Tern Island in 1952, where it remained until 1979. Additionally, shore-based commercial fishing occurred at French Frigate Shoals from 1946 to 1959. It was only after all these activities ceased, except the operation of the Tern Island Loran station, that the monk seal population began to rapidly recover. However, the population crashed following 1989, and it is well-documented that this was due to a severe reduction in survival of juvenile seals (Craig and Ragen 1999). This was accompanied by the observation that juvenile seals were generally in very poor to emaciated body condition, indicating that inadequate prey availability was driving the population decline (Craig and Ragen 1999).

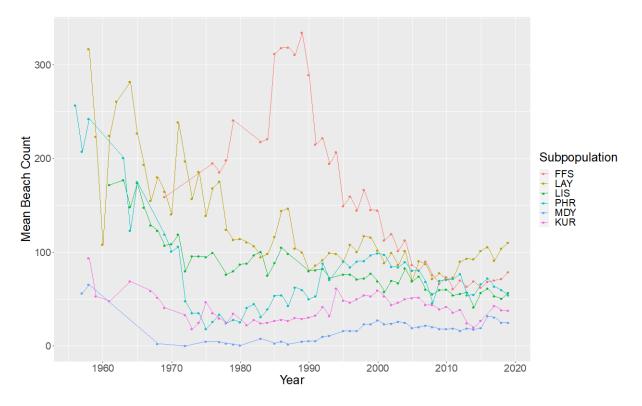
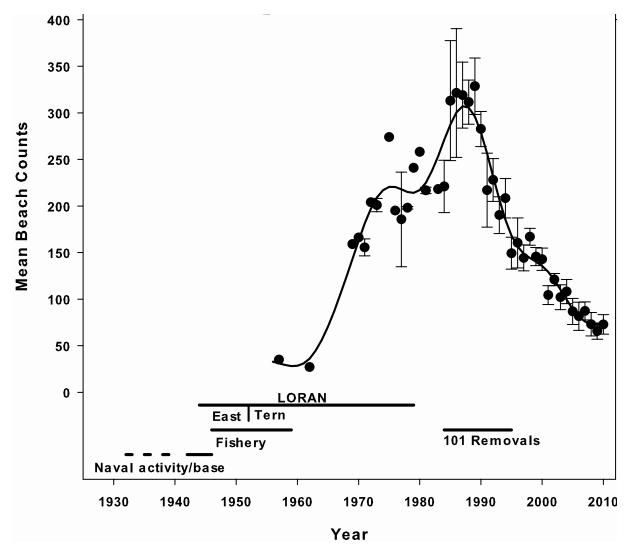
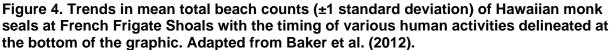


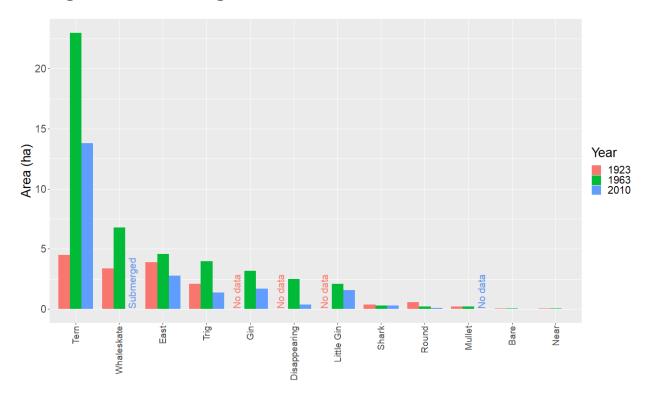
Figure 3. Mean annual beach counts of Hawaiian monk seals at the six most-studied Northwestern Hawaiian Islands subpopulations. FFS = French Frigate Shoals, LAY = Laysan I., LIS = Lisianski I., PHR = Pearl and Hermes Reef, MDY = Midway Atoll, KUR = Kure Atoll.

Partly in response to the population decline and poor condition of juveniles, a total of 101 female seals were removed from French Frigate Shoals from 1984 to 1995. The seals were rehabilitated in captivity and released at other NWHI subpopulations where their survival chances were judged to be much more favorable (Gilmartin et al. 2011). Primarily undersized weaned pups and starving juveniles with poor survival prospects were removed for rehabilitation. Consequently, simulation modeling indicated that the removals likely only lowered the total population at French Frigate Shoals by a small amount (Gilmartin et al. 2011).





As context for evaluating the current status and threats to the French Frigate Shoals monk seal population, it is noteworthy that the past observed dramatic population fluctuations, at least until the 1990s, were likely unrelated to changes in the *amount* of terrestrial habitat at the atoll. Rather, the monk seal population was suppressed during much of the 20th Century by their *exclusion from* that habitat by human occupation and activities. When released from this constraint, the population soared (Gerrodette and Gilmartin 1990, Ragen 1999). The subsequent decline, as evidenced by the poor condition of juvenile seals, appears to have been driven by factors in the marine, rather than the terrestrial realm (Craig and Ragen 1999). However, as described below, reduction in amount and quality of terrestrial habitat has now become an important factor influencing current population trends and the prospects for long-term viability of the French Frigate Shoals monk seal population.



Changes in French Frigate Shoals terrestrial habitat

Figure 5. Area (in hectares) of individual islets at French Frigate Shoals in 1923, 1963, and 2010. Sources: Amerson (1971), Reynolds et al. (2012). No measurements of Gin, Little Gin, or Disappearing Islands were available from 1923. No measure of Mullet Island was available for 2010. Whaleskate Island subsided by the late 1990s, such that its area was zero in 2010.

Land area measurements of individual French Frigate Shoals islets are available from three sources during roughly the past 100 years. Palmer (1927) provided acreage of several of the islets as surveyed during the Tanager expedition in 1923. Amerson (1971) reported on results of the Smithsonian Institution's Pacific Ocean Biological Survey Program (POBSP), which began in 1963. There were multiple POBSP expeditions that landed at French Frigate Shoals, at least until 1967. As it was unclear in which year(s) the acreage of islands was measured, 1963 was used here as the reference for this period. We used 1923 acreages from Palmer (1927) as reported by Amerson (1971). The third survey was conducted in 2010 and reported in Reynolds et al. (2012). The 2010 survey used lidar, whereas the survey methods used in 1923 and 1963 are not described; thus, the comparability of estimates is uncertain, but can assist with a basic evaluation of general land mass trends over time. The large increase in the size of Tern Island between the first two time points was attributable to the expansion of the island to accommodate an airfield constructed by the U.S. Navy in 1942. All of the other islets with the exception of tiny Shark Island decreased by varying amounts between 1963 and 2010 (Fig. 5). Most notably, Whaleskate Island, once the second largest land area in the atoll, was entirely inundated by the late 1990s and thereafter has only occasionally appeared as a small ephemeral sand spit.

In the two decades following the disappearance of Whaleskate Island, other remaining islets probably continued to erode. Although this has not been systematically documented, monk seal researchers have anecdotally reported various islands diminishing in size, being washed over, and in the case of Trig Island, being temporarily bisected. What had been a gradual erosive process became acute in 2018, when two of the remaining larger islets were lost. Trig Island finally succumbed to progressive erosion in September, and East Island was obliterated by Hurricane *Walaka* in October 2018. In 2019, these islets reappeared only as small sand spits. Figure 6 starkly demonstrates the alteration of Whaleskate, Trig, and East Islands through photographs taken at various time points.



Figure 6. Changes in appearance of Whaleskate, Trig, and East Islands over time. All three were once relatively large and vegetated and are now continually submerged (Whaleskate) or ephemeral small remnants (Trig and East). Photo credit: Whaleskate 1962—appeared in Amerson (1971) attributed to Hawaii Division of Fish and Wildlife, David B. Marshall. Whaleskate 2002, Trig 2017 and 2019—NOAA staff. East Island photos—U.S. Fish and Wildlife Service.

Impacts of habitat loss on distribution of Hawaiian monk seal births and pup survival

The loss of Whaleskate, Trig, and East Islands has profoundly altered the location of monk seal births and coincided with anomalously low survival of pups during the five to seven weeks from birth to weaning. The total number of pups born at French Frigate Shoals declined from a high of 127 in 1988 to an average of about 38 per year since 2008 (Fig. 7). This trend reflects the overall population crash due to poor post-weaning juvenile survival described above (Fig. 3).

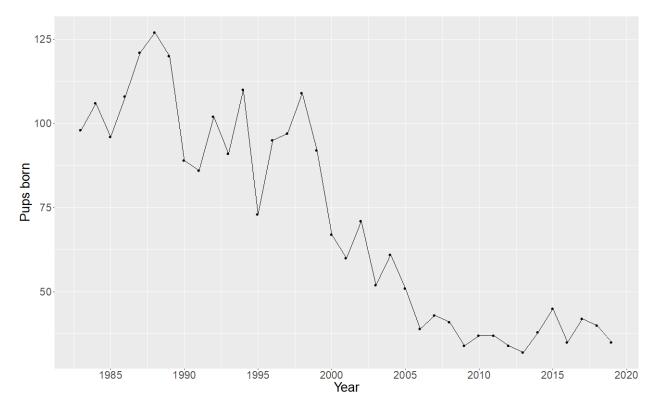
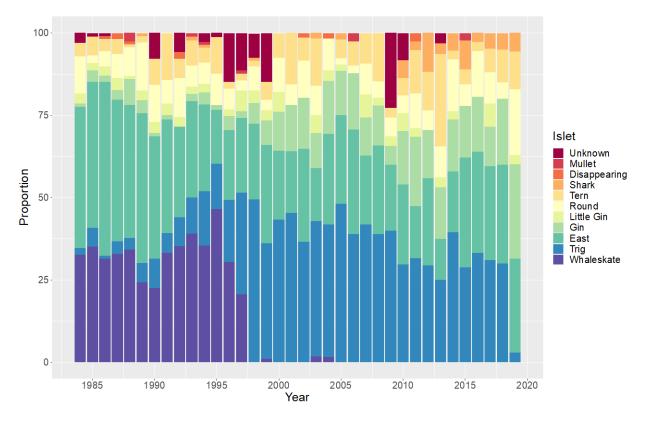


Figure 7. Trend in the number of monk seal pups born at French Frigate Shoals.

While the number of births was declining, their distribution around the atoll also changed (Fig. 8). Monks seal mothers are selective with regard to where they give birth, showing a distinct preference for beaches adjacent to very shallow, protected waters (Westlake and Gilmartin 1990). Prior to the late 1990s, the majority of mother seals gave birth on either Whaleskate or East Islands. After 1990, there was a diminishing proportion born at East Island, perhaps due to the increasing number of nesting green sea turtles present on that island. An abrupt and near complete cessation of births at Whaleskate Island occurred in 1998. The island was first observed completely washed over in November 1996, after the pupping season. In 1997, the island washed over only during the highest high tides. In 1998–1999, Whaleskate Island was frequently awash and was completely submerged by 2000. The reduction in seal births at both East and Whaleskate in the 1990s was accompanied by a marked increase in the percentage of births occurring at Trig Island, which previously had accounted for only a small fraction of births (Fig. 8). There was also an increase in births occurring at Gin Island.





The degradation of Whaleskate Island and consequent shift in births to Trig Island corresponded to unprecedented high mortality of pups during the five to seven weeks between birth and weaning. During this period, monk seal mothers nurse their pups and typically remain close by. At other NWHI subpopulations, 95% of pups on average survive until weaning. This was also the case at French Frigate Shoals in the 1980s. In contrast, only 75% of pups at French Frigate Shoals have survived to weaning since the mid-1990s, coincident with the decline of Whaleskate Island and shift in distribution of births (Fig. 9). Most of the increased mortality of monk seal pups prior to weaning is attributable to predation by Galapagos sharks (*Carcharhinus* galapagensis). The phenomenon whereby Galapagos sharks patrol shallow waters adjacent to islets where monk seals are born and target pups is unique to French Frigate Shoals and was very rare at the atoll until the mid-1990s. Since that time, some 15–30% of pups born each year at the atoll are killed by Galapagos sharks (Gobush et al. 2012, Johanos 2020e). The majority of these pups are killed before weaning, but some fraction of weaned pups also succumbs to predation. Further, the vast majority of pup losses to Galapagos shark predation occurred at Whaleskate and Trig Islands, though the phenomenon eventually spread to other islets in the atoll. A thorough description of this issue and efforts to mitigate it are available in Gobush et al. (2012). One plausible hypothesis is that the eroding islands of Trig and Whaleskate provided unprecedented access for Galapagos sharks to approach closely enough to access young pups playing in the nearshore waters. Regardless, the anomalous rise in early pup mortality due to predation was undeniably coincident with monk seals using increasingly eroded, sub-optimal habitat. In recent years, deaths of dependent pups have also been attributable to drowning when the islands they inhabited were subject to inundation from storms, high tides, and strong currents (Johanos 2020e).

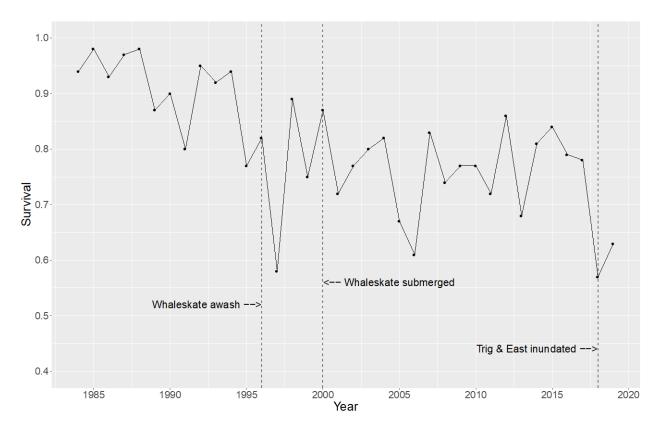


Figure 9. Trend in monk seal pup survival at French Frigate Shoals from birth until weaning. Vertical dashed lines indicate notable changes in island morphology.

In 2018, the year in which both Trig and East Islands disappeared, pup survival to weaning dropped to 57%, the lowest level ever recorded (Fig. 9). In 2019, the distribution of pupping shifted dramatically again, as only one pup was born at the remnant of Trig Island (Fig. 8). Ten pups were born at the East Island remnant. Survival to weaning improved only slightly in 2019 (69%). In both years, the causes of death prior to weaning that were known or inferred from circumstantial evidence were shark predation and drowning due to the birth island being inundated by storms or high tides. Twenty-five pups died prior to weaning in 2018–2019, 16 due to shark predation and 8 or 9 from drowning (one of the latter cases may have involved a congenital defect). Further, in 2019, two pups that survived to weaning died soon thereafter from egregious shark bite wounds, and two others were also bitten. Tern Island was the only 2018–2019 birth site where no pups were documented to have died prior to weaning. Galapagos shark attacks on pups born on Tern have never been documented (Gobush et al. 2012, Johanos 2020e). For this reason, NMFS staff have, for many years, translocated weaned pups from all other islets to Tern Island as soon as possible following weaning.

Impacts of terrestrial habitat loss on Hawaiian monk seal distribution

Changes in island habitat at French Frigate Shoals not only influenced the distribution of births, but also altered habitat use patterns of the seal population-at-large. Full atoll beach counts are systematic surveys of all seals on all islands within the atoll conducted during one or two days. These provide a representation of the proportional use of each island by seals. Figure 10 shows the mean percentage of seals counted during atoll-wide beach counts (16 counts per year on average) at each island since 1985.

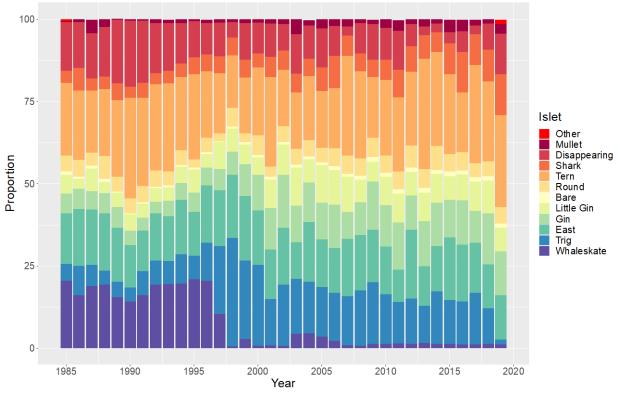
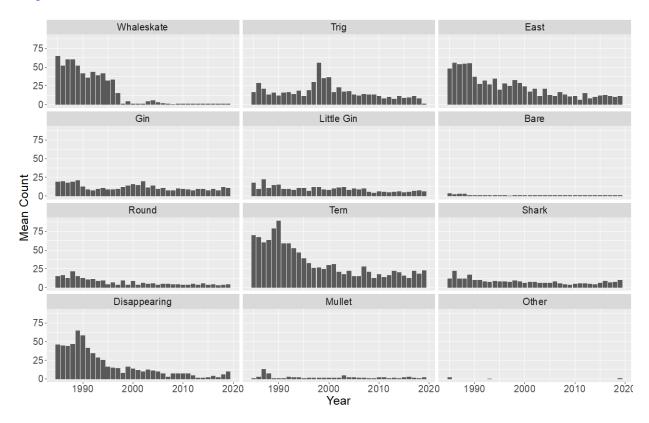


Figure 10. Percentage of seals counted during atoll counts at French Frigate Shoals islets, 1985–2019.

The entire seal population has been more evenly spread amongst islands than mothers and pups. Yet the same patterns are evident whereby use of Whaleskate in the late 1990s, and use of Trig Island in 2019, dropped abruptly (Fig.10), coinciding with the aforementioned virtual disappearance of these islands. Some seals have continued to land at ephemeral, tiny sand spits such as Bare, Mullet, and Whaleskate Island remnants. Because seals older than young pups are not subject to Galapagos shark predation or drowning, these small emergent sand features apparently remain suitable for resting.

Another illustrative aspect of the historical atoll count data is that they show just how many seals could be accommodated on the various islands at a time when the population was several-times larger than at present. The islands that have virtually vanished (Whaleskate, Trig, and East) each hosted an average of 50–60 seals in the past (Fig. 3). Remarkably, Tern Island at times averaged



between 70–90 seals, more than have been counted on shore in the entire atoll in recent years (Fig. 3).

Figure 11. Mean number of monk seals counted, by islet, during atoll counts at French Frigate Shoals, 1985–2019.

Hawaiian monk seal terrestrial and marine habitat in the NWHI

In the context of the entire NWHI, French Frigate Shoals contains less land area than all other sites except Necker Island (Fig. 12). However, both Necker and Nihoa Islands are tall, steep, rocky volcanic remnants, and most of their area is unsuitable for monk seal use. Given this perspective, French Frigate Shoals actually has the third lowest amount of monk seal terrestrial habitat in the NWHI.

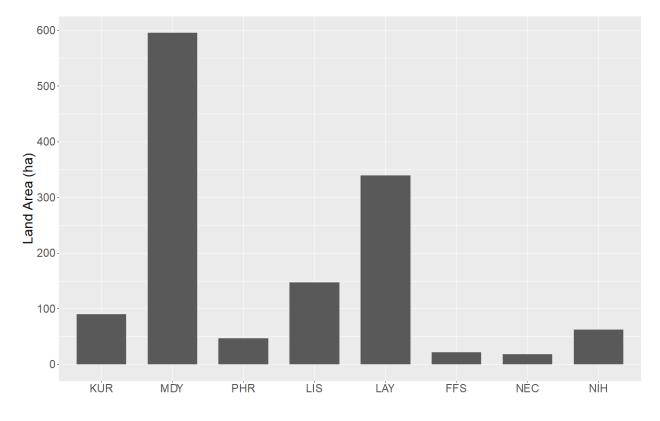


Figure 12. Land area of the Northwestern Hawaiian Islands in 2010 (from Reynolds et al. 2012). FFS = French Frigate Shoals, LAY = Laysan I., LIS = Lisianski I., PHR = Pearl and Hermes Reef, MDY = Midway Atoll, KUR = Kure Atoll, NEC = Necker Island, NIH = Nihoa Island.

Despite this limited space, French Frigate Shoals currently hosts a relatively large seal population and once was several-fold larger. Figure 13 plots each NWHI subpopulation's maximum mean annual beach count going back to the late 1950s against its land area. One would expect a positive correlation between these two variables if the amount of terrestrial habitat constrained the number of seals that could be accommodated. In fact, there clearly is no such relationship (r = -0.09). French Frigate Shoals has the highest mean beach count recorded at any subpopulation yet contains one of smallest amounts of land. In stark contrast, Midway Atoll boasts by far the largest land area but one of the smallest seal populations.

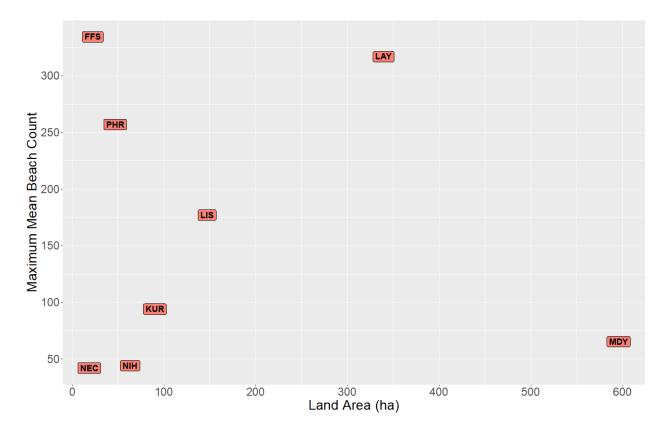


Figure 13. Maximum total mean annual (since 1956) atoll-wide beach counts of Hawaiian monk seals plotted against land area of Northwestern Hawaiian Islands (from Reynolds et al. 2012). FFS = French Frigate Shoals, LAY = Laysan I., LIS = Lisianski I., PHR = Pearl and Hermes Reef, MDY = Midway Atoll, KUR = Kure Atoll, NEC = Necker Island, NIH = Nihoa Island.

The foraging ranges of monk seals traveling from the various islands and atolls of the NWHI are shown in Figure 14 (based upon Norris et al. 2017, Stewart et al. 2006). Seals generally foraged near where they were captured and fitted with tracking devices, but some also made trips to other areas, including submerged features offering foraging habitat. Distances traveled from shore ranged up to approximately 250 km, possibly indicating that the cost of ranging further exceeds any benefit of reaching more distant foraging areas. Bathymetry data¹ were analyzed to calculate the amount of foraging area (defined as sea floor 200 m or less in depth) accessed by monk seals from each subpopulation. No seals have been tracked from Necker Island, so it was assumed that seals from that site use the banks surrounding that island.

¹ https://catalog.data.gov/harvest/object/552924b8-6d32-44ab-9141-fb7725a9a5a8/html

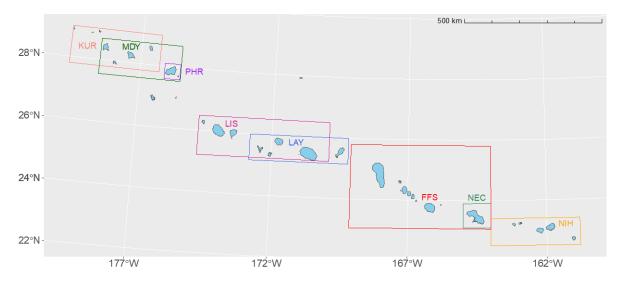


Figure 14. Foraging areas (light blue shaded areas indicating depths 200 m and less) of Hawaiian monk seals in the NWHI. The boxes encompass the foraging areas known to be used by seals traveling from the various atolls and islands. FFS = French Frigate Shoals, LAY = Laysan I., LIS = Lisianski I., PHR = Pearl and Hermes Reef, MDY = Midway Atoll, KUR = Kure Atoll, NEC = Necker Island, NIH = Nihoa Island. Box color matches the abbreviation for the location it represents.

Monk seals from French Frigate Shoals utilize 42% (5,750 km²) of the available foraging area in the NWHI. This exceeded the area used by seals from all other NWHI subpopulations. Seals from French Frigate Shoals appear to enjoy near exclusive use of their foraging range. The known exception is that French Frigate Shoals seals travel to, and forage at, the extensive bank adjacent to Necker Island. It may be that some individuals from the relatively small population of seals at Necker Island also travel to French Frigate Shoals and forage there (Johanos et al. 2015). Excluding the bank surrounding Necker Island, foraging seals from French Frigate Shoals likely have near exclusive access to 31% of the available foraging area in the NWHI. If French Frigate Shoals becomes uninhabitable by seals due to total loss of terrestrial habitat in the future, this significant portion of foraging habitat would likely also become virtually inaccessible to seals. Only Necker Island, which as noted previously has limited landing space for seals, is within 250 km of French Frigate Shoals and Brooks Banks. The nearest island with ample haulout area is Laysan Island, which lies 350 km from the nearest feature (Gardner Pinnacles) currently exploited by French Frigate Shoals seals. Given that observed movements from land have not exceeded 250 km, it seems unlikely that seals from Laysan Islands would travel 350 km or further to reach areas currently exploited by French Frigate Shoals seals. Lack of access to the significant amount of foraging habitat currently available to French Frigate Shoals seals would limit the potential for the species to recover.

There is a positive correlation (r = 0.63) between the maximum mean annual beach count and the amount of foraging area accessed by seals from each subpopulation (Fig. 15). Pearl and Hermes Reef is somewhat of an outlier from this otherwise consistent trend. Pearl and Hermes Reef has a mean maximum beach count of 257 seals, whereas a study conducted in 1997–1998 found that seals from Pearl and Hermes Reef only foraged at the atoll and a nearby bank to the southeast. Pearl and Hermes Reef seals may actually forage more broadly; it is not uncommon to observe

tagged natives of that atoll on beaches at neighboring Midway and Kure Atolls (Johanos et al. 2014). Tracking studies were not conducted at any of the sites when the populations were near their maxima, and the full extent of seal foraging ranges was likely not represented by the individuals tracked at each site. However, those studies likely captured typical foraging behavior. Figures 13 and 15 are consistent with the concept that NWHI monk seal populations may be limited in size by accessible foraging habitat rather than the amount of terrestrial habitat. That being the case, if only a modest amount of terrestrial habitat were preserved at French Frigate Shoals, it may allow for a sizeable seal population to persist.

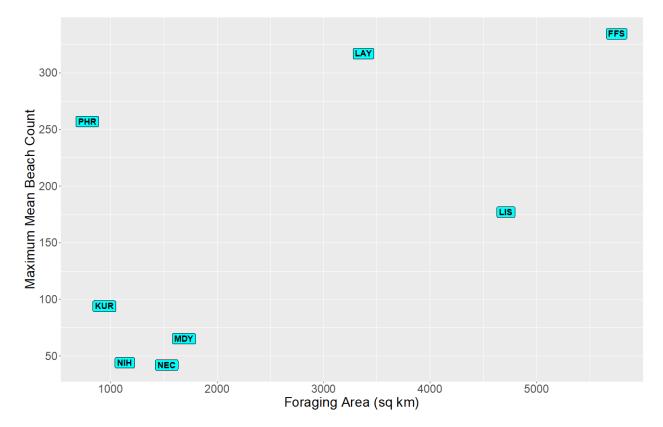


Figure 15. Maximum total mean annual (since 1956) atoll-wide beach counts of Hawaiian monk seals plotted against the amount of foraging area (Figure 14) utilized by seals from the various Northwestern Hawaiian Islands subpopulations. FFS = French Frigate Shoals, LAY = Laysan I., LIS = Lisianski I., PHR = Pearl and Hermes Reef, MDY = Midway Atoll, KUR = Kure Atoll, NEC = Necker Island, NIH = Nihoa Island.

Discussion

Tern Island: Refuge within a Refuge?

Reynolds et al. (2012) created the first high resolution maps of NWHI topography using airborne lidar in 2010. At that time, Tern Island represented 62% of the total land area at French Frigate Shoals (excluding La Perouse Pinnacle, which is not suitable habitat for monk seals). We can approximate that Tern Island now accounts for 77% of the land area at the atoll by assuming Trig and East Islands are virtually gone and that the remaining islands have not changed substantially. Because the islands have not been re-measured since 2010, this value may be biased either low or high, depending on the evolution of both Tern and the remaining islands. Regardless, Tern Island is almost certainly the most resilient of the remaining monk seal habitat at French Frigate Shoals. Reynolds et al. (2012) report that most of Tern Island is above 2 m elevation, whereas the remaining islands have elevations predominantly lower than 2 m. The semi-hardened shorelines of Tern Island also likely provide some protection against sea level rise and erosion due to high seas and tidal flooding. Thus, it seems likely that Tern Island represents the most precious terrestrial feature for monk seals and all other species that require terrestrial habitat at French Frigate Shoals.

Hypothetically, if Tern Island were to remain intact in the future and all other low-lying islands were lost to sea-level rise and other factors, Figure 11 suggests that at least the current population of monk seals at French Frigate Shoals could be accommodated solely at Tern Island. As noted previously, 70–90 seals on average used to bask together on that island, and recent atoll counts have averaged from 60 to 70 seals on all islands. Further, based on shoreline alone, far more seals could presumably "fit" on Tern Island. On the other hand, sufficiency of good habitat for giving birth to and rearing pups could be limited. Other species, such as green sea turtles and seabirds, may be vying for the same limited space. One may speculate about how these factors will interplay in a future French Frigate Shoals; nevertheless, it seems plausible that Tern Island will likely play a crucial role in the long-term viability of a monk seal population at the atoll.

Unfortunately, Tern Island, in its current condition, actually poses serious threats to seals that land or are translocated there to mitigate shark predation (Fig. 16). The island's human built infrastructure had been degrading, then was severely damaged by a microburst storm in 2012, and further damaged by Hurricane Walaka in 2018. Beaches where monk seals rest are strewn with various debris, including collapsing cisterns and rusting metal. The greatest threat, however, is posed by the remnants of a decaying steel double seawall bordering a portion of the island. Monk seals, primarily weaned pups, as well as green sea turtles and seabirds, make their way between the parallel walls and become entrapped. The first documented monk seal entrapment in the seawall occurred in 1986. There has been a total of 70 such cases documented, but seawall entrapments have become more common recently, with 25 documented just during 2017 to 2019. When people are present on the island, seals can be rescued that would otherwise likely perish. Only one entrapped seal has been confirmed dead, in 1991. However, since the microburst in 2012, Tern Island is no longer permanently occupied by either U.S. Fish and Wildlife Service or National Marine Fisheries Service staff. As such, trapped seals and other wildlife can only be detected and freed from seawall entrapment during the few months of the year when NMFS monk seal staff are present. Making matters worse, because of the imminent threat of Galapagos shark predation at the other islands, all pups are typically translocated to Tern Island after they

wean. Thus, at the end of the field season, nearly the entire surviving new cohort of seals is left to their own devices on Tern Island. Some portion may needlessly die in the seawall. These deaths are unlikely to be detected when staff return several months later due to decomposition and scavenging of carcasses, and because the seawall is exposed to heavy wave action that would tend to flush out remains over time.

After some 25 years of population decline, the French Frigate Shoals monk seal population has been slowly increasing since 2015. This increase is due to a marked upturn in juvenile survival rates beginning about a decade ago; the precise timing of the improvement varying with seal age (Fig. 17). During the preceding decline, survival to at least age three years was severely depressed; in recent years, the period of low survival has largely been restricted to the first year of life. The far left panel of Figure 17 demonstrates that even survival from weaning to age one year has been quite favorable for some cohorts. Visually assessed body condition scores of juveniles are generally good in contrast to the emaciation witnessed during the decline. However, the high mortality of pups from birth until weaning is constraining population growth (Fig. 9). Ironically, just when it appears that foraging conditions in the seals' marine habitats are favorable for juvenile survival, the diminishing quality and quantity of terrestrial habitat is threatening the population's recovery.



Figure 16. Scenes from Tern Island in 2019. Top left: Decaying seawall section. Top right: A healthy weaned monk seal pup (inside red circle) wedged between parallel seawalls and pinned beneath an I-beam. The pup was freed by NMFS staff with great difficulty, requiring excavation of sand beneath the pup. The rescue was urgent as the tide was rising and the pup would have otherwise drowned. Lower left: Monk seals resting amidst debris from Tern Island infrastructure. Lower right: Sample of metal debris. All are NOAA photographs.

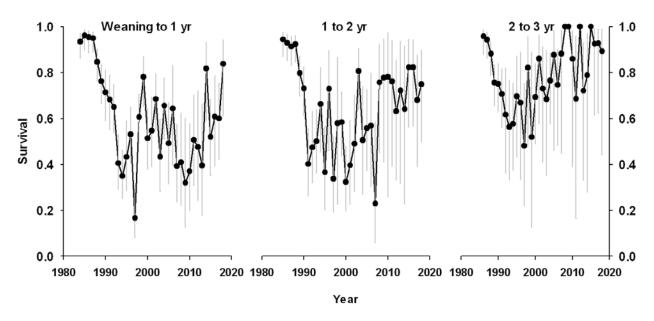


Figure 17. Trends in age-specific survival rates of juvenile Hawaiian monk seals at French Frigate Shoals (gray bars encompass 95% confidence intervals).

A future French Frigate Shoals conducive to Hawaiian monk seal recovery

The U.S. Navy's expansion of Tern Island to accommodate an airfield was in response to an undeniable existential threat posed by the belligerent Empire of Japan in 1942. It is ironic that almost 80 years later, this same island is poised to play a critical role in staving off an existential threat to Hawaiian monk seals; sea level rise and potentially other manifestations of climate change. Tern Island, once reshaped to serve a military purpose, could now be redesigned once more to accommodate wildlife that requires terrestrial habitat in order to persist at French Frigate Shoals. The specifics of such a transformation would be best planned by engineers working with biologists with specialized knowledge of French Frigate Shoals wildlife.

From the perspective of Hawaiian monk seal conservation and recovery, a future French Frigate Shoals would entail the following:

- Entrapment and other man-made hazards at Tern Island eliminated.
- Tern Island perimeters configured to balance preservation of land area and accessibility for monk seals. The latter would also facilitate access by green sea turtles.
- Ample terrestrial habitat for seal parturition and nursing with adjacent shallow, protected waters (Westlake and Gilmartin 1990) such that the population is not limited by the quantity and quality of terrestrial habitat.
- Ample terrestrial habitat for seals of all ages to land and rest, again such that the population is not limited by the extent of suitable land.

This work will undoubtedly require substantial funding and several years to plan and execute. In the meantime, resources should be immediately made available to staff Tern Island for most or all of the year to mitigate seawall entrapments of wildlife.

Beyond Tern Island, there may be viable options for recreating, maintaining, and improving terrestrial habitat elsewhere at French Frigate Shoals. Beach nourishment is an established method for preserving sandy shorelines, typically for human use and economic benefit, and often on a scale much larger than the small islets at French Frigate Shoals (ASBPA 2018). Beach nourishment or other methods to preserve or recover terrestrial habitat at French Frigate Shoals may be feasible.

Baker et al. (2006) and Reynolds et al. (2012) evaluated potential effects of sea-level rise on various NWHI using simple passive flooding scenarios associated with predicted future sea-level rise. Both studies recognized that many factors other than passive flooding would likely exacerbate terrestrial habitat loss. Indeed, Berkowitz et al. (2012) modeled the effect of both passive flooding and dynamic wind-driven inundation on Laysan Island, concluding that passive flooding models systematically underestimated the vulnerability of the island. Still, these authors were exploring risks of predicted sea-level scenarios on the scale of many decades to more than a century in the future. That both East and Trig Islands were already virtually annihilated in 2018 is sobering. The loss of terrestrial habitat at French Frigate Shoals is likely a harbinger of what will come to pass more broadly in the NWHI, with far more devastating consequences for the species whose persistence is so tenuously bound to a few specs of sand barely protruding from the central Pacific Ocean. French Frigate Shoals represents an opportunity to develop mitigation strategies to sustain ecosystems, Hawaiian monk seals, and other precious wildlife resources throughout the NWHI.

Methods

Hawaiian monk seal demographics

Information on Hawaiian monk seal abundance, distribution trends, and survival rates is derived from long-term demographic studies using standardized methods. Survey data (Johanos 2020a) consist of sightings records of individual seals collected either during systematic surveys or incidental observations. Mean beach counts are derived from full systematic counts of all seals on shore on a given day (or sometimes during two days at multi-islet atolls).

The number and distribution of births by islet were determined using a variety of data sources, in descending order of certainty with regard to where each pup was born. The highest certainty was obtained when the birth islet was known and recorded in the pup's annual identification records (Johanos 2020b, c). If unavailable, the islet where the mother of the pup in question gave birth was used. The next two sources were the recorded weaning islet of the pup and the mother, in that order. Lacking birth or weaning records, the first islet where a pup was recorded in survey data was assumed to be the birth islet. If no such survey line was available, the island where the weaned pup was captured and tagged was used (Johanos 2020d—handling data). Finally, if none of the foregoing data were available, the birth islet was treated as unknown.

The proportional distribution of seals of all age classes among the islets of French Frigate Shoals was calculated only from complete atoll counts. Because these counts equalize survey effort across all islets, they represent the least biased data for characterizing distribution. The proportional use of islets was calculated as the total number of individual seal census lines recorded on shore for each islet during all atoll counts in a given year, divided by the total lines recorded at all islets in that year.

Survival of pups from birth to weaning is derived from survey and seal identification data (Johanos 2020a,b). Mother seals and their pups were monitored daily or every few days during the five- to seven-week long nursing period. When possible, pelage bleach marks were applied to pups to facilitate individual identification. The annual rate of survival from birth to weaning was calculated as the number of pups that were observed to have survived to weaning, divided by the total number of pups whose fate to weaning was known. This denominator was often less than the total number of pups born because some pups were still nursing when field surveillance ceased for the year. Also, in some cases pups went missing and were presumed to have died, but whether that occurred before or after weaning was unknown. Causes of death of pups were derived from post-mortem examination and circumstantial evidence as recorded in monk seal "Survival Factor" data (Johanos et al. 2020e).

Post-weaning, age-specific survival rates were estimated based on the sightings histories of known-aged seals individually marked with rear-flipper tags and injected passive integrated transponder (PIT) tags (Wright et al. 1998). Identification was also based upon photo-identification using distinct natural marks, such as scars and pelage patterns (Harting et al. 2004). Age-specific survival rates were estimated using Cormack-Jolly-Seber capture-recapture models following Baker and Thompson (2007), using Program MARK (White & Burnham 1999) with RMark (Laake 2013) as an interface.

Spatial analysis of Hawaiian monk seal foraging habitat

The foraging ranges of monk seals from each subpopulation were inferred from satellite tracking data (Norris et al. 2017, Stewart et al. 2006). Boxes representing foraging range were drawn to include all the bathymetric features to which seals fitted with satellite transmitters traveled. Because no seals have been tracked from Necker Island, its foraging box was drawn to encompass the large bank surrounding the island. Quantification of foraging area within each box was based upon 60 m horizontal resolution rasterized bathymetry data available from the University of Hawaii at Manoa's Hawaii Undersea Research Laboratory². These data were imported for analysis in R to calculate the amount of foraging area (defined as sea floor 200 m or less in depth) accessed by monk seals from each subpopulation using the R packages *raster, sf*, and *dplyr* (Pebesma 2018, R Core Team 2019, Hijmans 2020, Wickham et al. 2020). No seals have been tracked from Necker Island, so it was assumed that seals from that site use the banks surrounding that island.

² https://catalog.data.gov/harvest/object/552924b8-6d32-44ab-9141-fb7725a9a5a8/html

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