

# FORAGING BIOGEOGRAPHY OF HAWAIIAN MONK SEALS IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

The extant population of Hawaiian monk seal (*Monachus schauinslandi*) numbers around 1,300 distributed among six island atolls in the remote Northwestern Hawaiian Islands (NWHI) and at several small, emerging colonies on the Main Hawaiian Islands. Demographic studies have identified poor juvenile survival as the ultimate primary cause of substantial declines at all colonies and of slow recent recovery at some. Variable foraging success may be a key proximate effect, but the knowledge of habitat needs of foraging monk seals has not been adequate to test that hypothesis nor to provide management with the necessary information to address resource conservation issues. We documented the geographic and vertical foraging patterns of 147 Hawaiian monk seals from all six NWHI breeding colonies from 1996 through 2002 to describe the marine habitats that may be key to the species' viability. We found that seals foraged extensively within barrier reefs of the atolls and on the leeward slopes of reefs and islands at all colony sites. They also ranged away from these sites along the Hawaiian Islands Archipelago submarine ridge to most nearby seamounts and submerged reefs and banks. Most dives were less than 150 m deep, though dives of some seals exceeded 550 m. Suitable foraging habitat may be a resource limiting the population of monk seals in the NWHI. Moreover, the foraging biogeography of Hawaiian monk seals may vary spatially and temporally with variation in the extent of physical substrate, prey community composition and species' abundance, and demographic composition of seal colonies.

## INTRODUCTION

The Hawaiian monk seal is endemic to the Hawaiian Island Archipelago. It was listed as "Endangered" in 1976 (U.S. Department of Commerce, 1976) under the U.S. Endangered Species Act (ESA) of 1973<sup>3</sup> owing to substantial declines in abundance during the previous several decades throughout its range in the Northwestern Hawaiian Islands (NWHI). In 2003, the species was estimated to number around 1,300 seals (ca 30% to 40% of recent historic abundance; NOAA Fisheries, unpub. data), virtually all occurring in the NWHI at six breeding colonies (Kure, Midway, and Pearl & Hermes

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atolls, Lisianski and Laysan islands, and French Frigate Shoals; Fig. 1; Ragen and Lavigne, 1999; Baker and Johanos, 2004). These six locations consist of all above-sea-level habitats in the NWHI west of Necker Island (Fig. 1). Movement of seals among colonies is evidently limited (Harting et al., 2002). Consequently, each breeding colony has been considered to be a relatively distinct subpopulation. The greatest affiliations among these colonies are apparently among subpopulations within three regional areas: (1) the western NWHI (Kure-Midway-Pearl & Hermes atolls); (2) the central NWHI (Lisianski-Laysan islands); and (3) the eastern NWHI (French Frigate Shoals). Nonetheless, the demography and trends in abundance of each colony appear to be independent (Harting, 2002). However, the ultimate factor accounting for declines at some colonies and limited or slow recovery at others appears to be poor survival of juvenile seals (e.g., Craig and Ragen, 1999; Harting, 2002; Ragen and Lavigne, 1999). The posited proximate cause of poor survival of juveniles has been poor foraging success<sup>1</sup> from fluctuations or reductions in prey population assemblages. Our strategic objective was to document the geographic and vertical components of foraging habitats of Hawaiian monk seals in the NWHI as a key element in developing conservation and management plans for this critically endangered marine mammal.

## METHODS AND MATERIALS

From 1996 through 2002, we monitored the movements of 147 Hawaiian monk seals (about 10% of the extant species range-wide abundance) for several months or more using satellite-linked radio transmitters that communicated data on their geographic and vertical (dive depth) locations to earth-orbiting satellites (Table 1). The age and sex composition of the instrumented seals was chosen to provide a reasonable sample of males and females in each age category (weaned pups [ca 4 to 6 months old when tagged], juveniles [1 to 4 years old], adults [> 4 years old]) relative to the size of the subpopulation that would allow general characterization of habitat use and permit comparisons among colonies. All transmitters were glued to the seals' dorsal pelage with quick-setting epoxy, and the seals were then monitored remotely through the Argos Data Collection and Location Service (DCLS) until the transmitters were shed in spring and summer when seals molted, the batteries expired, or transmissions ended because of transmitter failure or antenna breakage. Most of the seals were outfitted with transmitters between October and early January (see Stewart and Yochem, 2004a, 2004b, 2004c; Stewart, 2004a) except those at French Frigate Shoals, which were instrumented in spring (cf. Abernathy and Siniff, 1998; Abernathy, 1999).

All satellite-linked radio transmitters that were used consisted of an ARGOS-certified transmitter (PTT = Platform Transmitter Terminal) for determining geographic locations of foraging seals. Most of the transmitters also included a microprocessor-controlled event recorder to monitor use of vertical marine habitats (diving behavior). They (SLDRs = Satellite-Linked Dive Recorders) were capable of either about 20,000

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<sup>1</sup>Poor foraging success of weaned pups and juveniles and perhaps poor provisioning of nursing pups owing to limited body reserves of lactating females. Poor prepartum foraging success may lead to fat deposits insufficient to support lactation.

transmissions (all weaned pups and some juveniles) or about 60,000 transmissions (some juveniles and all adults) because of differences in battery supplies (less battery capacity on the instruments on pups to reduce instrument size and mass). Whenever seals were at sea, transmissions were suppressed when the PTTs and the SLDRs were below the sea surface owing to an electrical conductivity circuit that closed whenever there was continuous saltwater contact between two or three electrodes mounted on the surface of the SLDR. This feature extended tracking duration by conserving power, and it also maximized the probability that adequate transmissions would reach an orbiting satellite when seals surfaced. To further conserve battery power and extend tracking, the SLDRs were programmed to be active only during periods of the day when orbiting ARGOS system satellites were expected to pass within radio view of the NWHI. The SLDRs were also programmed to shift from a transmission rate of around 1/40 s to around 1/90 s once a seal was hauled out constantly for 6 to 10 minutes. Moreover, if the seal remained hauled out for about 70 minutes, transmissions ceased until it reentered the sea for more than 1.5 minutes. The latter feature also ensured that most of the locations that were obtained likely occurred when seals were foraging.

The ARGOS DCLS uses many criteria to generate predictions on the distance error that may be associated with a location, and the DCLS assigns an index of accuracy to each one. The best locations (LC = 1, 2, 3) are predicted to be within a kilometer or less of the true transmitter location. Other locations are made available to wildlife tracking community users (LC = 0, A, B, Z). The Argos DCLS does not provide users with a prediction of the error that may be associated with these locations. The assignment of these indices to locations does not strictly imply that they have large error, only that the criteria used to assign indices with associated predictions of errors were not all satisfied by the transmissions received during satellite passes when the location estimates were made. Of those locations, we considered only locations of LC = 0 and A for analysis. All locations were filtered and outliers were rejected based on knowledge or assumptions about reasonable travel speeds and distances between serial locations.

The SLDRs also recorded and stored information on diving patterns (vertical habitat use). Maximum depth of dive, duration of dive, and time at depth were summarized by 6-hour periods and then transmitted as frequency histograms. The depth of the deepest dive made during each 24-hour period was also recorded and transmitted separately. Locations were determined several times each day by the ARGOS DCLS, as described in detail elsewhere (e.g., Fancy et al., 1988; Harris et al., 1990; Stewart et al., 1989; Stewart, 1997), whenever two or more transmissions reached an orbiting satellite during a single overpass.

We used a probabilistic model (fixed kernel density estimate method; e.g., Kernohan et al., 1996; Worton, 1989) to estimate the extent of monk seal foraging areas. We chose this model because it is relatively assumption free, is less sensitive to outliers, can calculate multiple centers of activity, is relatively robust to sample size variation, and accommodates irregular location distributions relative to other models. In general, it is arguably the most appropriate model for assessing patterns of spatial distribution (cf. Kernohan et al., 1996; White and Garrott, 1990; Worton, 1987, 1989). We calculated 95% and 75% probability distributions as two general estimates of the areas that seals

actually used to forage, out of all locations they visited. We also calculated the 50% probability distributions to estimate core areas of foraging activity, as have been routinely used in studies of wildlife populations (e.g., Harris and Leitner, 2004; Kernohan et al., 1996; White and Garrott, 1990).

## RESULTS AND DISCUSSION

The median duration of monitoring varied among age and sex classes from 1.3 to 3.5 months overall. Monitoring of individual seals lasted from 1 to 351 days. Monitoring of seals at French Frigate Shoals (FFS) was substantially shorter than at the other colonies (Table 2), owing primarily to seals at FFS being tagged closer to when they molted. If patterns of geographic dispersion of seals at the FFS colony are similar during the rest of the year, then the foraging ranges derived from the brief tracking samples should be relatively unbiased indicators of foraging ranges of adult males and females there. If seals actually disperse less during other parts of the year, then the actual foraging ranges (i.e., probability distributions as measured here) may be more constricted.

### Geographic Dispersion of Monitored Seals

Of approximately 54,000 locations that we considered suitable for analysis, 69% were of  $LC = 0$  and  $LC = A$ ; no error predictions for distance between calculated and true locations are available for those locations. Most of them were likely determined when seals were actively foraging and consequently spending little time at the surface between dives.

Overall, all seals remained within waters under exclusive jurisdiction of the U.S. (i.e., the U.S. Exclusive Economic Zone [EEZ]; waters from the NWHI and exposed atolls out to 370 km) while foraging during the periods they were monitored. Virtually all the seals foraged extensively within atoll lagoons or around the island colonies where they were tagged, including the outer slopes of those atolls and islands (Fig. 1). Core foraging areas (i.e., 50% probability distributions) were generally centered over areas of high bathymetric relief (e.g., submerged banks, seamounts) or focal areas within atoll lagoons (Fig. 1). When foraging around the colonies, 95% of the locations were within 38 km of the center of the atoll or island, except at French Frigate Shoals where the ranges for adult females extended up to 50 to 58 km (Table 3). Seventy-five percent of those locations were within 20 km of the colony centers, with minor exceptions (Table 3). The ranges of weaned pups were smaller than those of adults at Kure Atoll and Midway Atoll, but similar at Lisianski Island and Laysan Island (Table 3).

Seals at all colonies also foraged at other extra-colony sites (Tables 4, 5, 6). There was no consistent pattern of extra-colony site use by adult males, adult females, juveniles, or weaned pups among the colonies.

Overall, seals tagged at Kure Atoll, Midway Atoll, Laysan Island, and French Frigate Shoals used four extra-colony sites near each colony (Table 6). At Pearl and Hermes Atoll, all but two seals (adult males) foraged exclusively within the barrier reef or on the immediate seaward slopes.

Weaned pups tagged at Kure Atoll and Midway Atoll did not use extra-colony sites. Pups tagged at Lisianski Island used one additional site. Pups tagged at Laysan used two additional sites. Juveniles tagged at Kure Atoll, Midway Atoll, Pearl and Hermes Atoll, and Laysan Island did not use extra-colony sites. Juveniles tagged at Lisianski Island used two extra-colony sites.

The distances from colonies to extra-colony foraging sites varied from around 24.1 to 322 km (Table 3). Those extra-colony sites were at or near shallow reefs and submerged banks (e.g., Maro Reef, St. Rogatien Bank, Raita Bank, Brooks Bank) or seamounts (e.g., Nero, Ladd, Northampton) (Table 4; Fig. 1). Seals oriented near or over the NWHI submarine ridge system when traveling to those sites.

#### Vertical Dispersion of Monitored Seals: Dive Depth Patterns.

Analyses of frequency-histogram data (6-hour periods for each day; i.e., based on all dives each day) have been reported for Pearl and Hermes Atoll (Stewart, 2004a) and for French Frigate Shoals (Abernathy, 1999). About 90% of dives at Pearl and Hermes Atoll were less than 40 m deep, which correspond to water depths within the atoll lagoon where virtually all seals focused their foraging efforts during the monitoring periods. Most (ca 60% – 80%) dives of seals at French Frigate Shoals were to depths of 4 to 40 m, though there was considerable variation in dive patterns among seals. Many seals dove considerably deeper (e.g., 10% to 25% of dives exceeded 40 m) with additional modal depths of dives at 60 to 80 m, 100 to 120 m, 120 to 140 m, and 140 to 160 m, and a few dives of some seals exceeded 500 m (1,605 ft) (Abernathy, 1999). The maximum depths of dives (i.e., one dive per day) that we report here for seals at Kure and Midway atolls and Laysan and Lisianski islands indicate that a substantially large number of dives were deeper than 40 m, relative to those at Pearl and Hermes Atoll and French Frigate Shoals (Fig. 2). A secondary mode in maximum daily depth occurred at 100 to 150 m at Kure and Midway atolls and at Laysan Island; a third mode occurred at 200 to 400 m at Midway Atoll and Laysan Island; and there was a fourth mode at around 500 m at Kure Atoll.

#### Generalized Foraging Habitats

The collective patterns of dive depths and geographic dispersion for monk seals throughout the NWHI are partially consistent with the hypothesis that Hawaiian monk seals may often forage in relatively shallow demersal habitats. However, the geographic extent of potential demersal foraging habitats within 500 m of the surface (the maximum vertical extent of virtually all dives) is substantially less than the geographic extent of the dispersion of foraging seals (Stewart, 2004b). This suggests that a substantial number of dives may have been in the water column, rather than to the seafloor, regardless of geographic location. In any event, the information that we collected on diving patterns (6-hour histogram summaries of depth) are difficult to link with more temporally resolved geographic locations of foraging seals and, consequently, with fine-scale bathymetry.

Geographic patterns of foraging were complex and varied among colonies by season and age and sex of seals. For example, seals at Pearl and Hermes Atoll foraged



almost exclusively within the barrier reef of the atoll, compared with other colonies where seals ranged various distances away from islands and atoll lagoons (Table 3). Moreover, core foraging areas within the atoll varied seasonally for some seals but not others. We think that these differences among colonies may reflect important differences in community structure and abundance of prey species, but we recognize that further multidisciplinary research is needed to construct and test these trophic-structure hypotheses.

Because the studies at the six breeding colonies were not conducted simultaneously, we cannot determine whether the variation documented in foraging dispersion among colonies and among adults, juveniles, and pups near colonies, and use of extra-colony sites, might be mostly related to differences in prey availability at and near each colony, colony size and composition, or temporal environmental variability. Foraging ranges and diving patterns are likely dynamic and may vary with environmental conditions, such as abundances and compositions of prey assemblages, and abundances and age structures of monk seal colonies.

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Table 1. Hawaiian monk seals outfitted with satellite-linked data recorders and transmitters at the Northwestern Hawaiian Islands, 1996-2002<sup>1</sup>.

| Colony   | Males         |                  |                    |              | Females       |                  |                    |              | TOTAL      |
|--|---------------|------------------|--------------------|--------------|---------------|------------------|--------------------|--------------|------------|
|  | <i>Adults</i> | <i>Juveniles</i> | <i>Weaned pups</i> | <i>Total</i> | <i>Adults</i> | <i>Juveniles</i> | <i>Weaned pups</i> | <i>Total</i> |            |
| French Frigate Shoals <sup>2</sup> (1996-1997) | 17            | 0                | 0                  | <b>17</b>    | 10            | 0                | 0                  | <b>10</b>    | <b>27</b>  |
| Laysan Island <sup>3</sup> (2001-2002)         | 5             | 5                | 5                  | <b>15</b>    | 5             | 5                | 5                  | <b>15</b>    | <b>30</b>  |
| Lisianski Island <sup>4</sup> (2000-2001)      | 4             | 7                | 4                  | <b>15</b>    | 5             | 2                | 4                  | <b>11</b>    | <b>26</b>  |
| Pearl & Hermes Atoll <sup>5</sup> (1997-1998)  | 9             | 5                | 0                  | <b>14</b>    | 9             | 1                | 0                  | <b>10</b>    | <b>24</b>  |
| Midway Atoll <sup>6</sup> (2000-2001)          | 2             | 5                | 2                  | <b>9</b>     | 3             | 2                | 2                  | <b>7</b>     | <b>16</b>  |
| Kure Atoll <sup>7</sup> (2001-2002)            | 4             | 7                | 1                  | <b>12</b>    | 4             | 4                | 4                  | <b>12</b>    | <b>24</b>  |
| <b>TOTAL</b>                                   | <b>41</b>     | <b>29</b>        | <b>12</b>          | <b>82</b>    | <b>36</b>     | <b>14</b>        | <b>15</b>          | <b>65</b>    | <b>147</b> |

Table 2. Summary of duration of monitoring Hawaiian monk seals at the Northwestern Hawaiian Islands (Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, Kure Atoll = Colony Group 1; French Frigate Shoals = Colony Group 2) from 1996 through 2002.

| Age | Sex | Median monitoring duration (months) | Maximum tracking duration (months) | Number of Seals | Colony Group |
|-----|-----|-------------------------------------|------------------------------------|-----------------|--------------|
| WP  | F   | 3                                   | 7.5                                | 15              | 1            |
| WP  | M   | 3.5                                 | 8.1                                | 12              | 1            |
| JUV | F   | 5.2                                 | 8.9                                | 15              | 1            |
| JUV | M   | 4                                   | 9.6                                | 29              | 1            |
| AD  | F   | 6.2                                 | 11.1                               | 25              | 1            |
| AD  | M   | 7.8                                 | 11.7                               | 24              | 1            |
| AD  | F   | 1.3                                 | 4.2                                | 10              | 2            |
| AD  | M   | 2.9                                 | 4.5                                | 17              | 2            |

Table 3. Foraging ranges of Hawaiian monk seals from colonies where they were tagged with satellite-linked transmitters.

| Colony                          | Total number of foraging sites used <sup>1</sup> | 95% of locations (km) <sup>2</sup> | 75% of locations (km) <sup>3</sup> | Distances (km) to extra-atoll/island foraging sites |
|---------------------------------|--|------------------------------------|------------------------------------|---|
| <b>Kure Atoll</b>               | 5  |                                    |                                    |   |
| AD M                            | 5  | 16 to 20                           | 10 to 13                           | 62.7, 64.4, 67.6, 133.5                             |
| AD F                            | 1  | 13 to 15                           | 8 to 12                            |   |
| JUV                             | 1  | 8 to 12                            | 3 to 6                             |   |
| WP                              | 1  | 5 to 12                            | 1 to 3                             |   |
| <b>Midway Atoll</b>             | 5  |                                    |                                    |   |
| AD M                            | 4  | 20 to 30                           | 15 to 17                           | 66, 74, 96.5  |
| AD F                            | 2  | 18 to 20                           | 12 to 13                           | 80.4  |
| JUV                             | 1  | 6 to 20                            | 3 to 10                            |   |
| WP                              | 1  | 3 to 8                             | 1 to 5                             |   |
| <b>Pearl &amp; Hermes Atoll</b> | 2  |                                    |                                    |   |
| AD M                            | 2  | 10 to 20                           | 5 to 20                            | 33.8  |
| AD F                            | 1  | 8 to 17                            | 3 to 13                            |   |
| JUV                             | 1  | 5 to 15                            | 3 to 12                            |   |
| <b>Lisianski Island</b>         | 7  |                                    |                                    |   |
| AD M                            | 1  | 8 to 20                            | 3 to 5                             |   |
| AD F                            | 2  | 17 to 28                           | 8 to 27                            | 56.3  |
| JUV                             | 3  | 25 to 38                           | 20 to 23                           | 164.1, 220.4  |
| WP                              | 1  | 6 to 28                            | 3 to 12                            |   |
| <b>Laysan Island</b>            | 5  |                                    |                                    |   |
| AD M                            | 3  | 25 to 30                           | 17 to 20                           | 80.4, 235   |
| AD F                            | 2  | 20 to 30                           | 15 to 20                           | 123.9   |
| JUV                             | 1  | 20 to 23                           | 13 to 15                           |   |
| WP                              | 3  | 21 to 27                           | 15 to 17                           | 54.7, 90.1  |
| <b>French Frigate Shoals</b>    | 5  |                                    |                                    |   |
| AD M                            | 3  | 27 to 30                           | 17 to 20                           | 67.6, 210.8   |
| AD F                            | 4  | 50 to 58                           | 38 to 43                           | 115.8, 201.1, 217.2                                 |

<sup>1</sup> Including colony atoll or island

<sup>2</sup> This is the radial distance from center of colony atoll or island to perimeter boundary that encloses 95% of the locations determined for the seals when they were foraging near the colony atoll or island.

<sup>3</sup> This is the radial distance from center of colony atoll or island to perimeter boundary that encloses 75% of the locations determined for the seals when they were foraging near the colony or atoll.

The centers of the atolls or islands are: Kure Atoll, 28.42°N, 178.31°W; Midway Atoll, 28.24°N, 177.37°W, Pearl & Hermes Atoll, 27.87°N, 175.83°W; Lisianski Island, 26.1°N, 173.97°W; Laysan Island, 25.75°N, 171.74°W; French Frigate Shoals, 28.80°N, 166.21°W.



Table 4. Generalized radial distances from centers of reefs, banks, and seamounts to the boundaries of zones that encompassed 95% of the foraging locations of Hawaiian monk seals at those sites.

| <b>Extra-colony foraging site<sup>1</sup></b> | <b>Coordinates of center of zone encompassing 95% of foraging locations at the site</b> | <b>Generalized radial distance (km) from center of zone to zone boundary encompassing 95% of foraging locations at the site</b> |
|---|---|---|
| Un-named Kure seamount 1 (1)                  | 28.9°N, 179.57°W  | 10.1  |
| Un-named Kure seamount 2 (2)                  | 28.8°N, 178.86°W  | 10.6  |
| Un-named Kure seamount 3 (3)                  | 28.9°N, 178.62°W  | 9.3   |
| Nero seamount (5)                             | 27.96°N, 177.97°W   | 16.7  |
| Ladd seamount (7)                             | 28.55°N, 176.66°W   | 26.4  |
| Un-named Pearl and Hermes seamount (9)        | 27.73°N, 175.57°W   | 2.5   |
| Pioneer Bank (11)                             | 25.96°N, 173.42°W   | 7.2   |
| Northampton seamount W (12)                   | 25.53°N, 172.41°W   | 8.4   |
| Northampton seamount E (13)                   | 25.37°N, 172.03°W   | 8.8   |
| Un-named Laysan seamount (15)                 | 25.42°N, 171.00°W   | 16.6 (merged) and 16.3 (budded)   |
| Maro Reef (16)                                | 25.44°N, 170.61°W   |   |
| Raita Bank (17)                               | 25.5°N, 169.46°W  | 7.2   |
| Gardner Pinnacles (18)                        | 24.8°N, 168.01°W  | 42.7  |
| St. Rogatien Bank (19)                        | 24.6°N, 167.29°W  | 22.0  |
| Brooks Banks (20)                             | 24.2°N, 166.85°W  | 29.9  |
| Necker Island (22)                            | 23.46°N, 164.46°W   | 48.3  |

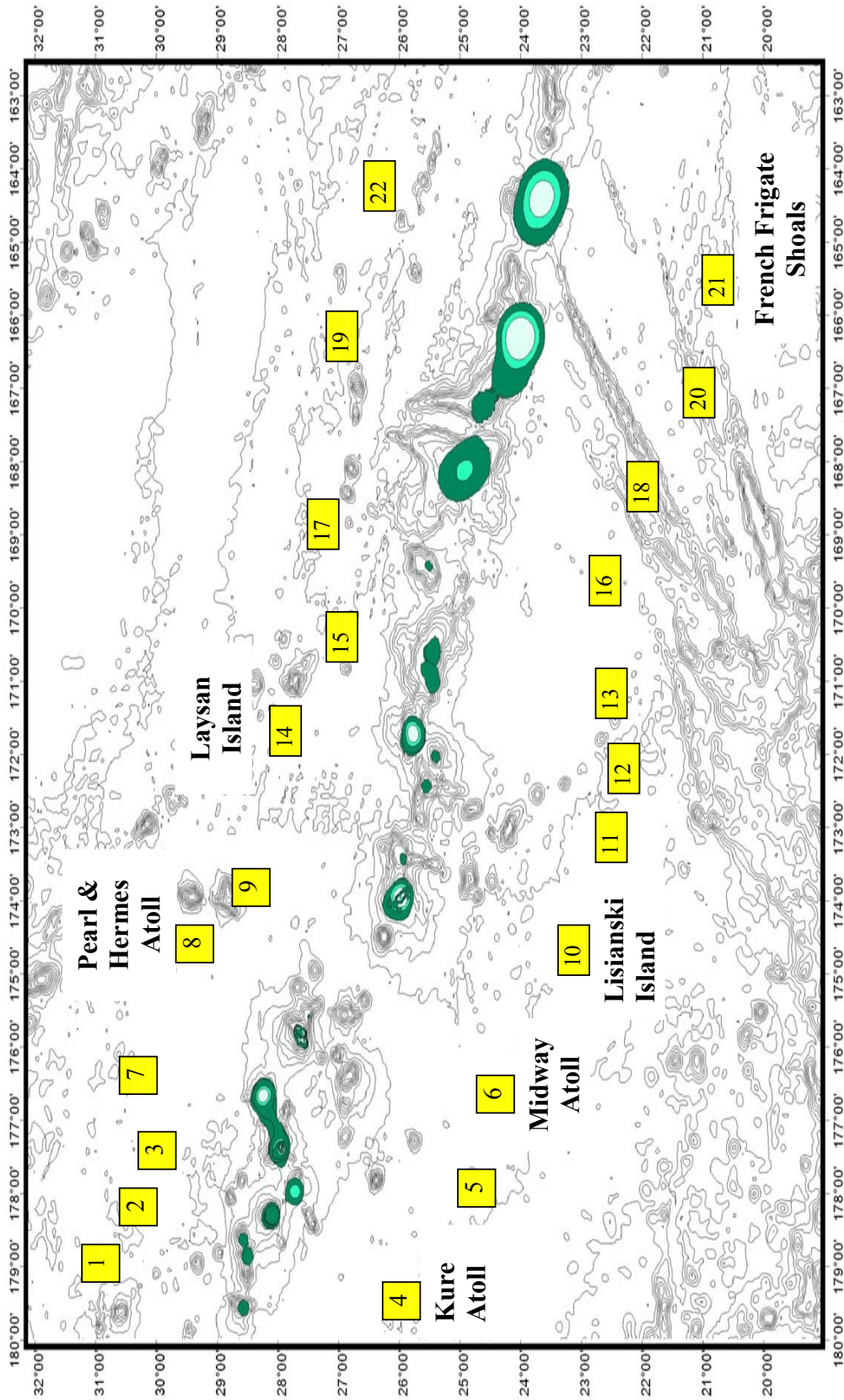
<sup>1</sup> Numbers in parentheses refer to the site locations on Figure 1.

Table 5. Generalized area (km<sup>2</sup>) of foraging zone encompassing 95% of foraging locations of Hawaiian monk seals around the center of the island, atoll, reef, bank, or seamount.

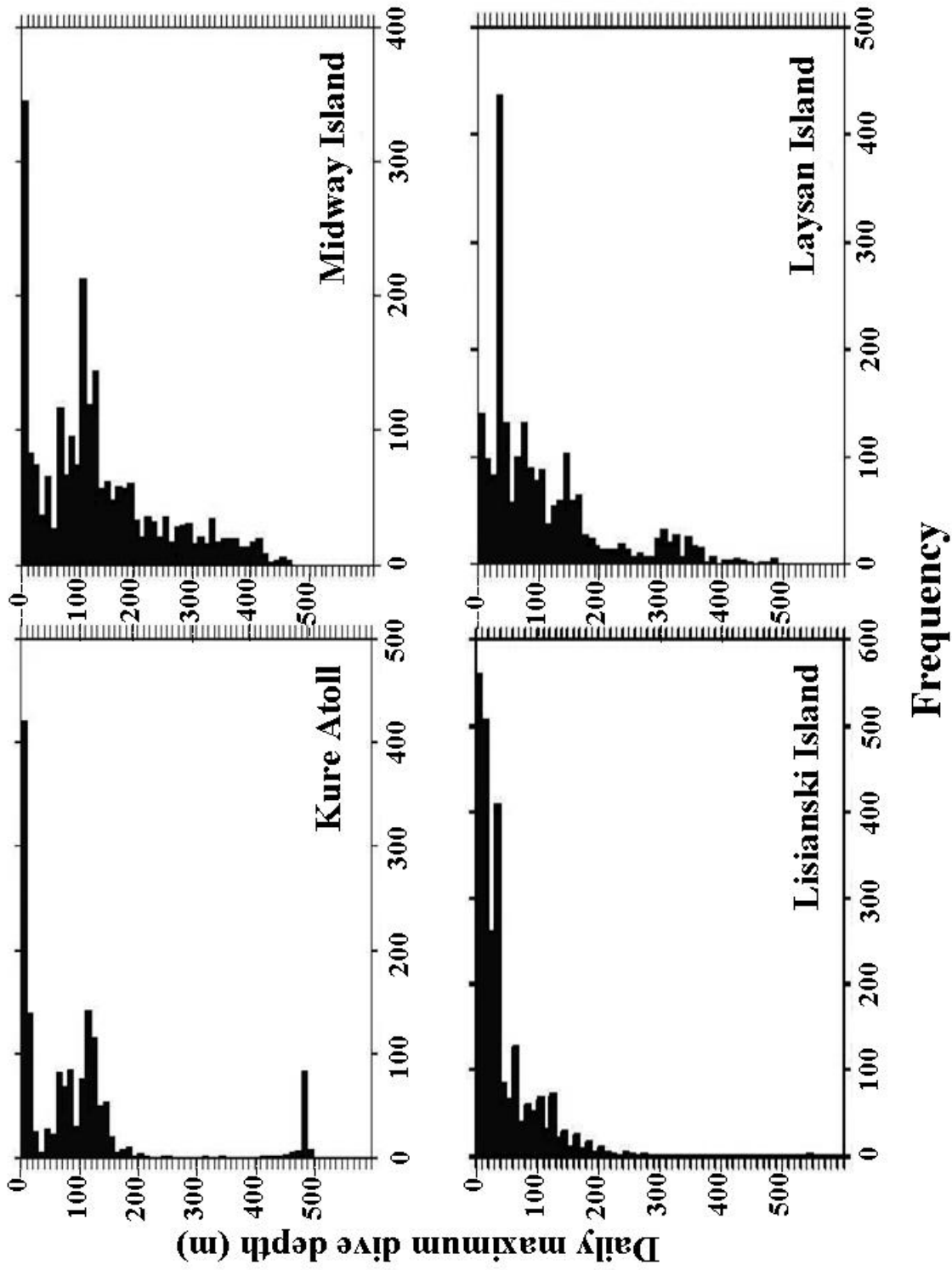
| <b>Colony and extra-colony foraging sites<sup>1</sup></b> | <b>Coordinates of center of zone encompassing 95% of foraging locations at the site</b> | <b>Generalized area of foraging zone encompassing 95% of foraging locations around site center (km<sup>2</sup>)</b> |
|---|---|---|
| Un-named Kure seamount 1 (1)                              | 28.9°N, 179.57°W  | 321   |
| Un-named Kure seamount 2 (2)                              | 28.8°N, 178.86°W  | 353   |
| Un-named Kure seamount 3 (3)                              | 28.9°N, 178.62°W  | 272   |
| Kure Atoll (4)  | 28.42°N, 178.31°W   | 878   |
| Nero seamount (5)   | 27.96°N, 177.97°W   | 876   |
| Midway Atoll (6)  | 28.24°N, 177.37°W   | 1562  |
| Ladd seamount (7)   | 28.55°N, 176.66°W   | 2187  |
| Pearl and Hermes Atoll                                    | 27.87°N, 175.83°W   | 707   |
| Un-named Pearl and Hermes seamount (9)                    | 27.73°N, 175.57°W   | 20  |
| Lisianski Island (10)                                     | 26.1°N, 173.97°W  | 2043  |
| Pioneer Bank (11)   | 25.96°N, 173.42°W   | 163   |
| Northampton seamount W (12)                               | 25.53°N, 172.41°W   | 222   |
| Northampton seamount E (13)                               | 25.37°N, 172.03°W   | 243   |
| Laysan Island (14)  | 25.75°N, 171.74°W   | 2240  |
| Un-named Laysan seamount (15)                             | 25.42°N, 171.00°W   | 810 (merged) and 835 (budded)   |
| Maro Reef (16)  | 25.44°N, 170.61°W   |   |
| Raita Bank (17)   | 25.5°N, 169.46°W  | 163   |
| Gardner Pinnacles (18)                                    | 24.8°N, 168.01°W  | 5730  |
| St. Rogatien Bank (19)                                    | 24.6°N, 167.29°W  | 1521  |
| Brooks Banks (20)   | 24.2°N, 166.85°W  | 2809  |
| French Frigate Shoals (21)                                | 23.8°N, 166.21°W  | 6420  |
| Necker Island (22)  | 23.46°N, 164.46°W   | 7331  |

<sup>1</sup> Numbers in parentheses refer to the site locations on Figure 1.





**Figure 1.** Locations of breeding colonies of Hawaiian monk seals and probability distributions of foraging areas of 147 Hawaiian monk seals. (Lighter to darker shades of green = 95%, 75% and 50% of locations within boundaries; 1 = Unnamed Kure seamount 1; 2 = Unnamed Kure seamount 2; 3 = Unnamed Kure seamount 3; 4 = Kure Atoll; 5 = Nero Seamount; 6 = Midway Atoll; 7 = Ladd seamount; 8 = Pearl & Hermes Atoll; 9 = Unnamed P&H seamount; 10 = Lisianski Island/Neva Shoals; 11 = Pioneer Bank; 12 = Northampton seamount W; 13 = Northampton seamount E; 14 = Laysan Island; 15 = Unnamed Laysan seamount; 16 = Maro Reef; 17 = Raita Bank; 18 = Gardner Pinnacles; 19 = St. Rogatien Bank; 20 = Brooks Banks; 21 = French Frigate Shoals; 22 = Necker Island [Mokumamama])



**Figure 2.** Daily maximum depth of dives of Hawaiian monk seals near Kure Atoll, Midway Island, and Lisianski Island, and Laysan Island (histogram intervals = 10m).

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