

## USE OF DISCOVERY CURVES TO ASSESS ABUNDANCE OF HAWAIIAN MONK SEALS

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### ABSTRACT

We investigated the pattern of first sighting of individual seals over the course of a field season, or the “discovery curve,” as a means for estimating abundance of the endangered Hawaiian monk seal, *Monachus schauinslandi*. We empirically derived a criterion to determine whether or not total enumeration had been accomplished at a given site and year. When greater than 100-h field effort was expended without a new individual being identified, we concluded that total enumeration was likely achieved. To evaluate the potential for estimating abundance through extrapolation of nonlinear asymptotic functions fitted to discovery curves, we conducted simulations under a range of capture probability scenarios, including some based on observed individual variability in monk seal sighting frequencies. We demonstrated that if capture heterogeneity existed among individuals, the fitted asymptotes tended to yield biased estimates of abundance. Moreover, the levels of bias and uncertainty tended to increase inversely with the proportion of the population identified. While extrapolation shows little promise for generating unbiased abundance estimates, discovery curves have practical appeal for determining whether total enumeration has been achieved, and for optimizing field effort allocation. This is especially true for relatively small, closed populations of marked individuals.

Key words: discovery curves, abundance estimation, Hawaiian monk seal, *Monachus schauinslandi*.

Reliable abundance information is critical for the conservation and management of rare species. Precise estimates of abundance reduce the time required to detect population declines and allow more powerful evaluation of management interventions. Furthermore, the factors that drive population trends may be more readily detected when trends in abundance are better characterized.

Populations consisting, at least in part, of individually identifiable animals are especially well suited for abundance estimation. Typically, some form of capture-recapture method is used to estimate population size based on individual sighting histories (*e.g.*, Otis *et al.* 1978, Seber 1982, Schwarz and Seber 1999). Additionally, examination of “discovery curves,” the number of unique individuals identified plotted against some measure of search effort, is often used in studies of cetaceans and nesting marine turtles to judge whether total enumeration has been achieved or to indicate whether a population is open or closed (*e.g.*, Williams *et al.* 1993, Karczmarski *et al.* 1999, Wilson *et al.* 1999, Limpus *et al.* 2001). This approach is especially applicable to relatively small, localized populations comprised of readily identifiable individuals.

The Hawaiian monk seal (*Monachus schauinslandi*) is an endangered species, primarily inhabiting the remote Northwestern Hawaiian Islands (NWHI) and predominantly distributed among six subpopulations each composed of up to a few hundred seals (Fig. 1) (Ragen and Lavigne 1999). Abundance trends have historically been characterized using an index of population-size termed as “beach counts,” tallies of all seals on land at a given time (Kenyon and Rice 1959). Substantial declines in these counts led to the species being listed as endangered under the U.S. Endangered Species Act in 1976 (U.S. Department of Commerce 1976*a, b*).

The mean beach count index is useful because it is relatively easy to obtain and provides a comparable measure available over several decades. However, while beach counts seem to provide a good indication of long-term trends, they poorly reflect year-to-year changes in populations (Eberhardt *et al.* 1999). Also, total abundance

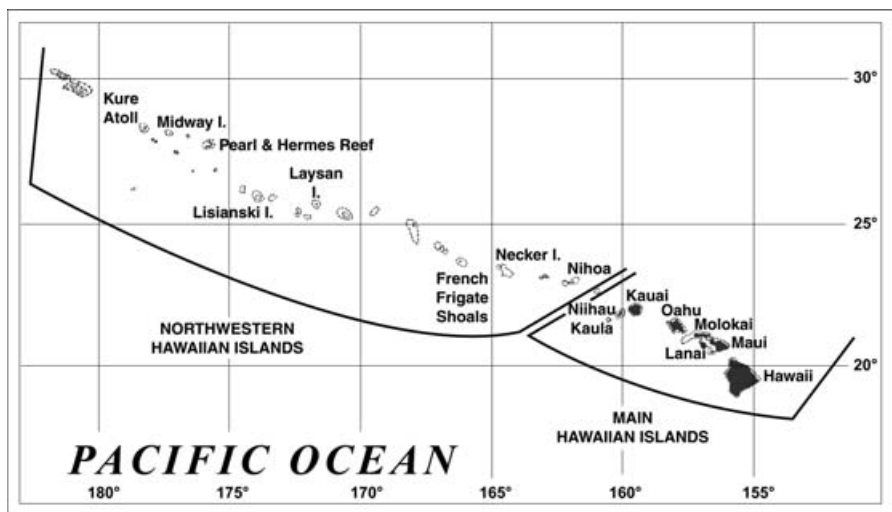


Figure 1. The Hawaiian Archipelago, showing the main Hawaiian Islands and the monk seal populations in the Northwestern Hawaiian Islands.

information is preferable to indices for various applications, including estimating sustainable incidental take levels in commercial fisheries (*e.g.*, under the Marine Mammal Protection Act, Wade 1998), and providing input to demographic (*e.g.*, Harting 2002) and bioenergetic models (Polovina 1984).

Baker (2004) evaluated a variety of closed capture-recapture estimation methods and determined that they generally produced negatively biased estimates of Hawaiian monk seal abundance, likely due to capture heterogeneity. Among the models examined, the estimators available in Program CAPTURE (Otis *et al.* 1978, White *et al.* 1982, Rexstad and Burnham 1991) tended to be least negatively biased.

Total enumeration is a possible alternative to estimating abundance using capture-recapture methods. Individual monk seal subpopulations are relatively small, and field seasons last for several months. Throughout the field season, effort is made to identify individual seals using natural and applied marks, generating an accumulating list of identified animals. At some sites and years, continued effort no longer results in the sighting of individuals not previously identified in that season at that site, suggesting that all animals in the subpopulation may have been counted. Yet, no criteria exist for distinguishing with confidence when total enumeration may have been achieved.

The species accumulation and species-area literature addresses issues relating to the form of curves representing either the discovery of new species with field effort within a designated area, or the relationship between the number of species and size of area sampled. Fisher *et al.* (1943) and Good and Toulmin (1956) are classic papers in this area, and Flather (1996) and Tjørve (2003) examined a suite of nonlinear functions proposed to represent species accumulation and species-area relationships. Others have specifically focused on using such relationships to estimate the total number of species by extrapolation (Soberon and Llorente 1993, Colwell and Coddington 1994, Ugland *et al.* 2003).

In this paper, we develop an empirically derived criterion based on discovery curves to determine whether a population has been fully enumerated. We also explore the potential for estimating abundance of partially enumerated populations using observed patterns of accumulation of new individuals within field seasons. Specifically, we test whether models used in species accumulation analyses can produce reliable estimates of population abundance through extrapolation.

## METHODS

### *Individual Identification*

The six main Hawaiian monk seal subpopulations in the NWHI are either single islands (Laysan and Lisianski) or atolls containing two to nine islets where monk seals come ashore to rest and rear offspring (French Frigate Shoals, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll, Baker 2004, Fig. 1). This study focuses on the six NWHI subpopulations where most of the species occurs and where, throughout field seasons typically lasting from 2 to 5 mo or more, seals were identified during shoreline surveys. Most of these seals were identifiable by unique alphanumeric colored plastic tags on each hind flipper. Photographic and hand-drawn records of natural markings (shark bite and other scars, permanent natural pelage patterns) were also collected and updated annually (Harting *et al.* 2004). Finally, to facilitate resighting seals and to provide a unique mark for those without tags or distinguishing natural marks, most seals were given temporary marks by bleaching their pelage.

As field seasons progressed, the list of uniquely identifiable individual seals was incremented. This process was straightforward for tagged seals and untagged seals once they were bleach marked, but is more complicated for others. Unknown seals were often assigned "temporary" identities during individual surveys to facilitate their ultimate identification, and sometimes an individual seal received more than one temporary identifier. Thus, the number of unique seals in a subpopulation is less than the total number of identifiers assigned. For this investigation, we used only data from years and sites where rigorous protocols were followed to determine the unique status of seals with temporary identities.

True population abundance is variable as animals are born and die so that the time period to which an abundance estimate is being ascribed should be explicit. For example, the total number of individuals alive in a calendar year is greater than the highest number alive at any one time. Because it is impossible to instantaneously estimate abundance in the field, we designate a time period during which animals must be alive to be considered part of the population. We have adopted the convention that only seals seen during March to August are considered members of a Hawaiian monk seal population. Most field effort has historically occurred within this period, so this criterion can be consistently applied to all years and sites, while taking advantage of as much available data as possible. The few pups born outside March to August and their mothers are also counted. Additionally, some individuals move between subpopulations and are identified at more than one site per year. To avoid double-counting individuals when subpopulation abundances are tallied, each seal is assigned to a single subpopulation in a given year using the following conventions. Adult females are assigned to the subpopulation where they gave birth that year, if known. Pups are assigned to the subpopulation where they were born. If neither of the preceding conditions applies, seals are assigned to the subpopulation where they undergo molt. Finally, if molt is not observed, seals are assigned to the subpopulation where they were seen closest to 15 May.

### *Discovery Curves*

The cumulative number of unique seals identified in a given subpopulation within a given year plotted against cumulative field effort is called the discovery curve. Observers recorded when they began and ended daily surveys so that the number of person-hours of survey time expended was used to characterize effort for both systematic censuses and nonsystematic surveys. To uniformly sample the accretion of new seals throughout a field season, the total number identified was tallied, as closely as possible, at 10-h intervals.

Our goal was to determine how informative the observed accumulation patterns were for revealing the true number of seals in the population. We expected that the number of new individuals would increase rapidly at the beginning of the season and, if field effort was sufficient, an asymptote would eventually be attained, representing total abundance. One objective was to develop criteria for determining when saturation sampling had occurred and all individuals in the population had been identified. Another aim was to determine whether we could extrapolate to reliably predict total abundance when the asymptote was not reached during a field season. The validity of such an approach requires a few simple assumptions: (1) observers continuously attempt to identify new individuals throughout the field season; (2) there is no "un-catchable" segment of the population, meaning that there are no seals

that either never land or cannot be identified; and (3) there are no additions to the population during the season that would cause true abundance to climb. This also means that the rate at which new individuals are discovered per unit effort should generally decline as the season progresses. We also assume that the number of seals that die during March to August prior to being identified is negligible.

The first assumption was met by confirming that, for all data sets analyzed, appropriate field protocols were in place such that observers regularly attempted to identify all seals present. Regarding the second assumption, all monk seals are believed to come ashore to give birth, molt, socialize, or rest. Thus, given sufficient field effort, all should eventually be available on shore to be identified either by tags, natural marks, or bleaching. Most monk seal births occur during spring and summer (Johanos *et al.* 1994), which contradicts the third assumption. Therefore, this analysis was restricted to animals older than pups. Pup production was assessed by documenting births that occurred during field seasons and tagging weaned pups present when teams arrived. Because field seasons occurred during the pupping season and pups typically remain near their birth site for approximately 2 mo post-weaning (Henderson and Johanos 1988), pup production estimates are probably near complete.

To develop criteria for determining when, for practical purposes, total population enumeration had been achieved, we calculated the number of additional seals discovered following effort intervals of varying length when no new seals were identified. For each data set, we determined the duration of these flat intervals with no new seals, then counted any new seals seen during the remainder of the field season. This indicates the likelihood that uncounted seals remain, given the amount of field effort expended with no new sightings. This approach is valid only if sufficient field effort is conducted following the start of a flat interval, so that yet-undiscovered seals would have a high likelihood of being detected if present. We therefore considered only cases when at least 100 additional hours of effort were expended following the start of flat periods.

To explore abundance estimation using sighting accumulation data, we fit a variety of asymptotic nonlinear functions commonly found in the species accumulation (and species-area) literature (reviewed in Flather 1996, Tjørve 2003, Table 1<sup>1</sup>). This approach was evaluated using both simulated and field data. For simulations, we defined a hypothetical population consisting of 200 seals subdivided into as many as 20 groups, each group having a unique capture probability and comprising a specified proportion of the total population. At each simulated field effort time step, the status of each "un-captured" seal in the population was tested by comparing a number between 0 and 1 randomly drawn from a uniform distribution against the specified capture probability for the group to which the seal belonged. If the random number was greater than or equal to the operative capture probability, the seal was "captured." With each capture, the cumulative number of seals detected at that effort step was incremented.

To test how the functions performed given different levels of field effort, curves were fit to simulated detection of varying portions of the total population. First, to simulate field situations where the population is enumerated and effort continues with no new discoveries, curves were fit to simulated data sets with all 200 seals captured plus 500 h additional effort after the last seal was identified. Next, to simulate incomplete sampling, we fit curves to the same simulations truncated when

<sup>1</sup> We also explored some alternative function forms implemented in CurveExpert software (CurveExpert 1.38 by Daniel Hyams, [www.curveexpert.webhop.net](http://www.curveexpert.webhop.net) 1698 Chadwick Court, Hixson, TN 37343).

Table 1. Candidate asymptotic functions fitted to discovery curve data. Functions were drawn from those proposed for species accumulation and species-area analyses as reviewed in Flather (1996) and Tjørve (2003).

Model	Type	Function
Negative exponential	Convex	$y = a(1 - e^{-bx})$
Asymptotic regression	Convex	$y = a - bc^{-x}$
Rational function	Convex	$y = (a + bx)/(1 + cx)$
Monod	Convex	$y = a(x/(b + x))$
Weibull <sup>a</sup>	Sigmoid	$y = a(1 - e^{-bx^c})$
Weibull <sup>b</sup>	Sigmoid	$y = a(1 - e^{-b(x-c)^d})$
Weibull <sup>c</sup>	Sigmoid	$y = a - be^{(-cx^d)}$
Morgan-Mercer-Flodin <sup>a</sup>	Sigmoid	$y = ax^b/(c + x^b)$
Morgan-Mercer-Flodin <sup>c</sup>	Sigmoid	$y = (ab + cx^d)/(b + x^d)$
Cumulative beta-P distribution	Sigmoid	$y = a(1 - (1 + (x/c)^d)^{-b})$
Chapman-Richards	Sigmoid	$y = a(1 - e^{-bx^c})$
Lomolino	Sigmoid	$y = a/(1 + b^{\ln(c/x)})$
Gompertz	Sigmoid	$y = ae^{-e^{-(b-cx)}}$
Extreme value	Sigmoid	$y = a(1 - e^{-e^{-(b+cx)}}$
Logistic	Sigmoid	$y = a/(1 + be^{-cx})$

<sup>a</sup>Formula used by Tjørve (2003).

<sup>b</sup>Formula used by Flather (1996).

<sup>c</sup>Formula used in CurveExpert 1.38 by Daniel Hyams (1995–2003).

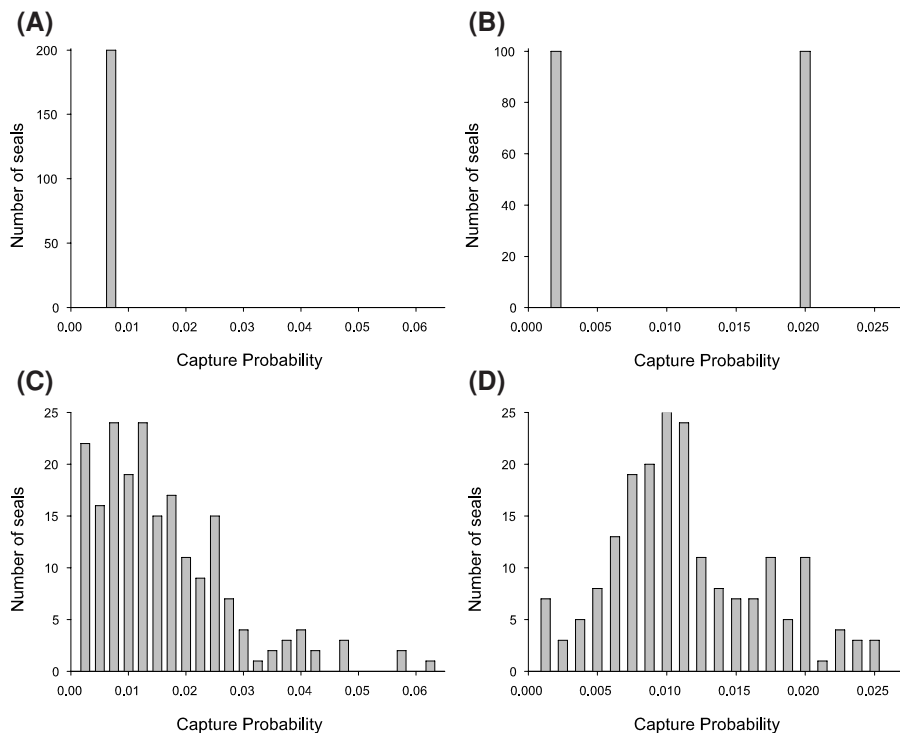
90% and 80% of the true population had been captured (that is, the effort steps at which the cumulative number of seals reached 180, and 160 seals).

Candidate functions were then fit to the resulting points (cumulative number of seals at effort intervals of 10 h) using the Levenberg-Marquardt algorithm (Levenberg 1944, Marquardt 1963), for nonlinear least squares regression, as implemented in IMSL Fortran subroutines (Visual Numerics 1999). In a simulation context, the automation of nonlinear curve fitting frequently presents difficulties associated with nonconvergence or unreasonable results from local minima or other data anomalies. To minimize these problems, we began by fitting each function in Table 1 to the mean of 1,000 simulated discovery curves under each capture probability scenario. Performance was assessed using the percent relative bias in the estimated asymptote ( $100 \times [\text{estimated abundance} - \text{true abundance}]/[\text{true abundance}]$ ). In this way, we screened the 15 functions to identify those that tended to provide the least biased estimates of abundance, and subsequently proceeded with automated fitting of the best performing functions to new sets of simulated discovery curves. In this latter process, we filtered out extreme outliers that would likely be rejected by a reasonable researcher dealing with real field data. Manual inspection of curve fits revealed that very high asymptotes typically reflected poor fits to the data with very high regression error terms. We conservatively stipulated that any asymptote exceeding twice the true population size (400 seals) should be rejected. The simulations were repeated until 1,000 acceptable realizations were obtained for each scenario.

Four different capture probability scenarios were explored. In the simplest case, all individuals were assigned the same capture probability. We next considered a

relatively extreme case of heterogeneity, whereby two capture probabilities differing by a factor of 10 were each operative for half the population. While this may be unrealistic, it demonstrates the influence of a high degree of heterogeneity. Moreover, one might encounter an analogous situation where two groups of animals, one resident and the other far ranging, overlap in the same study area.

To more realistically explore capture heterogeneity observed in monk seals, we extracted distributions of the number of times individuals were identified during a single field season as a proxy for capture heterogeneity. Two representative distributions, one from a single island subpopulation and another from a multi-islet atoll, were selected. To convert these distributions of the number of occasions observed to capture probabilities for simulations, we simply rescaled the  $y$ -axis. In this way, we maintained the shape of the distributions while obtaining capture probability values that were convenient for simulations. In all simulations, capture probabilities were scaled such that the entire simulated population of 200 individuals would be identified after 1,000–3,000 h of effort (Fig. 2). Thus, in scenarios based on observed



*Figure 2.* Distribution of capture probabilities operative for simulating discovery curve data sets for populations of 200 individuals under scenarios of (A) equal capture probabilities, (B) high capture heterogeneity, and reflecting the observed relative sighting frequencies of individuals at (C) Pearl and Hermes Reef in 2002 and (D) Lisianski I. in 2003. Capture probability units are per hour of effort.

sighting frequencies, the capture probabilities do not estimate true values, rather they represent the relative range and frequencies observed.

Curves were likewise fitted to two real data sets (Laysan Island in 1997 and Lisianski Island in 1999), for which the total populations had almost certainly been identified (based on criteria developed here). As with the simulations, nonlinear functions were fitted to the full data sets (all individuals identified), and to discovery curves truncated when 90% and 80% of the individuals had been identified.

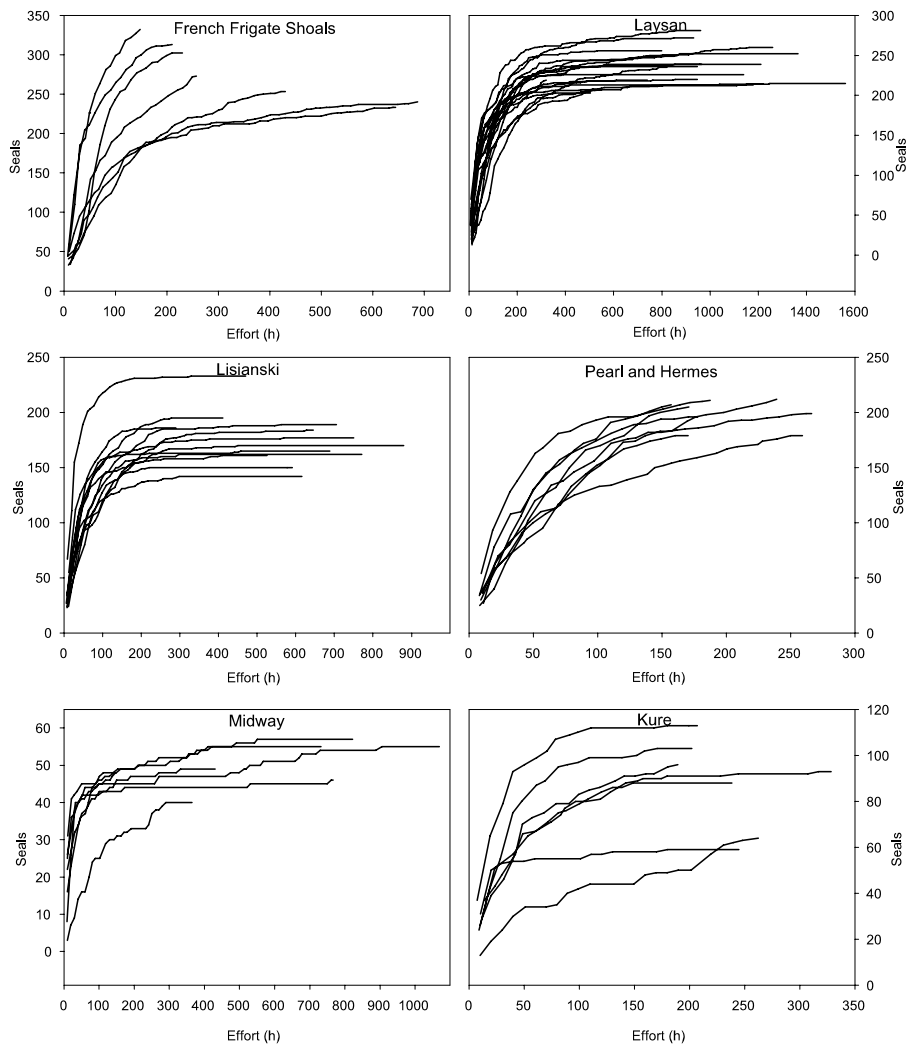
## RESULTS

### *Discovery Curves and Total Enumeration*

Patterns in discovery curves varied markedly among the six sites examined (Fig. 3). At Laysan and Lisianski Islands, an asymptote was usually attained. While this was not the case at other sites, the curves always showed a decline in the rate of accumulation, suggesting that extrapolation to an asymptote might provide a useful abundance estimate. The amount of field effort varied from less than 200 h to over 1,500 h per season, differing greatly among subpopulations. The single island subpopulations (Laysan and Lisianski) consistently had more effort than the multi-islet atolls, except at Midway atoll where there was extensive effort in some years. These differences resulted from variability in both duration of field seasons and accessibility. For example, while all shorelines were accessible daily at single island subpopulations, inter-islet travel time and weather conditions that precluded boating sometimes limited the amount of effort that could be expended per day at multi-islet sites.

Because of the long field seasons at Laysan and Lisianski Islands, these sites provided most of the empirical data for determining when total enumeration was accomplished. Periods with no new sightings were too rare at Kure Atoll and Pearl and Hermes Reef to reveal patterns. At Laysan and Lisianski, an average of less than one additional seal was discovered following periods of at least 100 h with no new sightings (Fig. 4). This finding was not simply an artifact of the requirement that there should be a minimum 100 h of subsequent effort. This rule had little influence as it excluded relatively few cases. There were no flat periods of 100 h at French Frigate Shoals, but the pattern emerging from shorter periods suggests that this criterion might reasonably apply. At Midway atoll, the observed pattern was similar, with the exception of two cases from 1999 where flat periods between 150 and 200 h duration were followed by the discovery of several new seals (circled points in Fig. 4). This seems to have been an artifact of unequal sampling effort and lack of population closure. Seals from the adjacent subpopulations at Pearl and Hermes Reef and Kure Atoll frequently visit Midway Atoll (Harting 2002). In 1999, field effort was year round at Midway Atoll, but lasted only about 1.5 mo at Kure Atoll and Pearl and Hermes Reef allowing animals moving between these sites a greater opportunity to be seen and counted as members of the Midway Atoll population. The new seals observed at Midway Atoll after prolonged periods with no new sightings probably represent relatively recent migrants from the other atolls. Had field effort been as great at these other sites, those migrants would likely have already been counted as members of the other subpopulations.

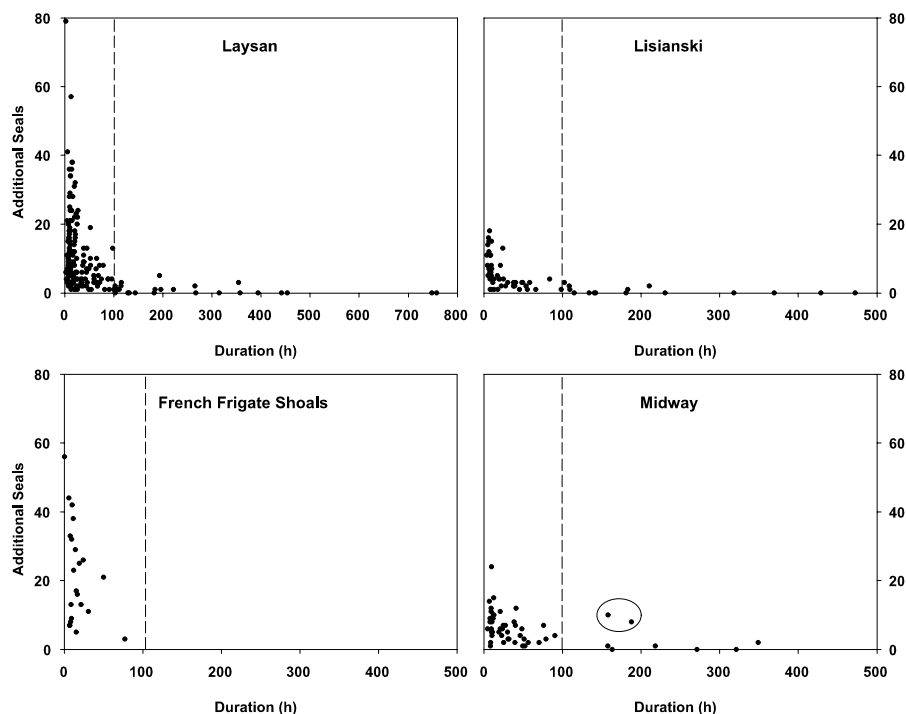
Based on the preceding analysis, we conclude that a zero slope sustained for at least 100 h indicated that the population was very likely identified. Zero slopes sustained for somewhat less than 100 h suggest near total enumeration. Total enumeration was



*Figure 3.* Discovery curves for several years at each of six Hawaiian monk seal populations. Cumulative total individuals (older than pups) identified is plotted against total hours of field effort. Years presented are those which were adequate for constructing discovery curves, including French Frigate Shoals and Midway Atoll (1997–2003), Pearl and Hermes Reef (1996–2003), Laysan (1983–1985, 1988–2003), Lisianski (1983, 1992–1993, 1995–2003), and Kure (1985, 1990, 1995, 1997–2003).

achieved in most years at Laysan Island, Lisianski Island, and Midway Atoll. In contrast, the French Frigate Shoals, Pearl and Hermes Reef, and Kure Atoll populations were not fully enumerated.

To graphically represent whether a zero slope was achieved and, if so, how long it was sustained, we plotted the slope of the line connecting each sequential point



*Figure 4.* Number of additional new seals identified following varying duration intervals of field effort within which no new identifications were obtained. Few or no new seals were seen following such periods of at least 100-h (dashed vertical line) duration. The circled points on the Midway Atoll figure indicate two notable exceptions at this site in 1999, which are apparently artifacts of sampling effort and lack of population closure.

on the discovery curve from the beginning of the field season to the fixed point at the end of effort. The slopes obtained allowed us to place the accumulation curves into three informative categories. First, in many cases the slope never reached zero, indicating that new animals were still being discovered at the end of the field season and that the population was not totally enumerated (Fig. 5A). On the other extreme were cases when a zero slope asymptote was attained and no new seals were observed even after hundreds of hours of additional effort, indicating that the population had been enumerated (Fig. 5B). Finally, there were intermediate cases where a zero slope was attained, but not sustained for sufficient time to convincingly indicate total enumeration (Fig. 5C).

### *Simulations*

Bias in estimated abundance using asymptotes fitted to the means of 1,000 simulated discovery curves varied greatly depending upon which function was used, the capture heterogeneity scenario, and the proportion of the population that had been identified. The overall relative performance of the various functions was evaluated by averaging the absolute value of each function's biases for all scenarios. Based on this criterion, two distinct groups emerged, with four functions performing better than

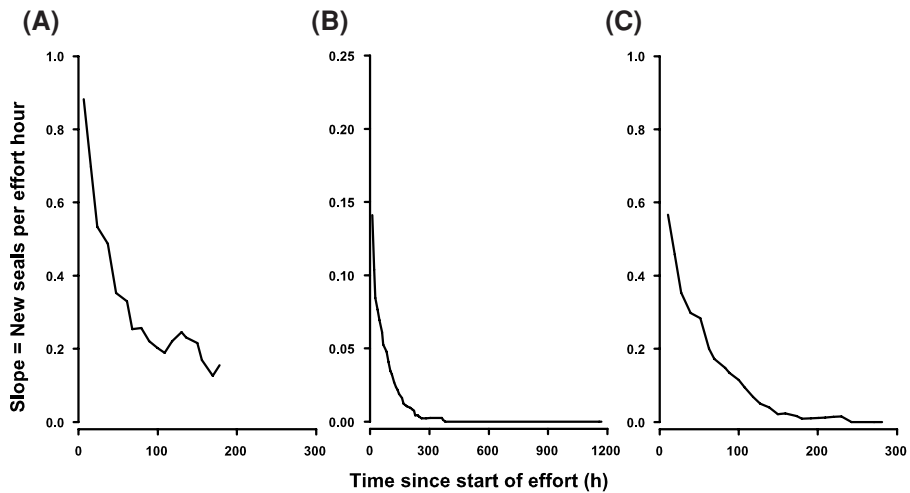


Figure 5. Three characteristic results showing the average slope of the line connecting each sequential point on the discovery curve from the beginning of the field season to the fixed point at the end of effort, plotted against the start point in the field season for each calculated slope (time since start of effort). (A) Zero slope not attained, indicating the population was not been completely enumerated (Pearl and Hermes Reef 2001), (B) zero slope sustained for several hundred hours indicating total enumeration (Laysan 1996), (C) intermediate result where zero slope was attained not long before field effort ceased, indicating at least near total enumeration (Lisianski 1993). Note that y-axis scales differ among the graphs.

the rest. The average percent bias for the negative exponential, asymptotic regression, the Weibull (three formulae), and the Chapman-Richards was three times smaller than that of the remaining functions (5.9% vs. 17.4%).

The distribution of estimated asymptotes revealed that these four functions performed quite well even with truncated data sets as long as capture probabilities were equal among animals. However, there was a slight tendency for positive bias and a large penalty in precision when less than 100% of the seals were identified (Fig. 6A). The functions also yielded low bias and high precision when fitted to complete data sets (100% identification) under all capture heterogeneity scenarios. However, when capture probabilities were unequal and all seals had not been identified (Fig. 6B–D), negatively biased and less precise estimates were usually obtained. An exception was that two of the Weibull functions yielded positive bias in the high heterogeneity scenario. In general, however, the magnitude of bias tended to increase with the degree of modeled heterogeneity and both bias and uncertainty increased inversely with the percentage of the population identified. The high heterogeneity scenario had the greatest bias, homogeneity resulted in no or low positive bias, while intermediate bias resulted from our scenarios based on observed variability in monk seal capture probabilities.

Curves fit to the field data sets (Fig. 6E, F) were essentially unbiased using all data available, relatively mild bias when truncated at 90%, and quite large bias at 80%. Unlike the typical pattern seen in the simulations, several functions produced large overestimates for the Laysan Island data set truncated at 80% (Fig. 6F). In this case, 80% of the population was identified in less than 80 h of effort, so the functions

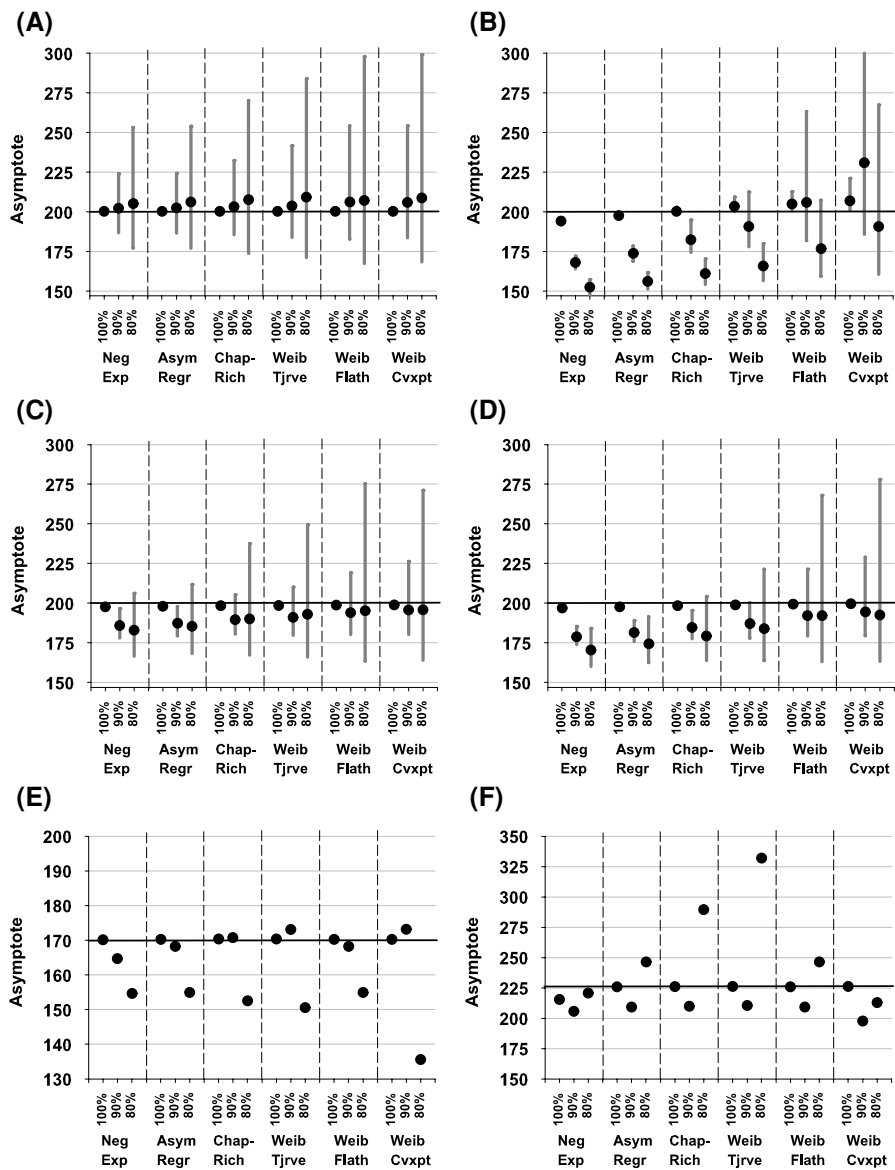


Figure 6. Estimated abundance using nonlinear asymptotic functions fitted to four simulated and two field data sets. Results for the top performing functions (negative exponential, asymptotic regression, Chapman-Richards, and three Weibull formulae) are depicted under simulated scenarios with (A) equal capture probabilities, (B) high capture heterogeneity, reflecting the observed relative sighting frequencies of individuals at (C) Pearl and Hermes Reef in 2002, and (D) Lisianski Island in 2003. Means are indicated with solid circles and bars span the range between 5th and 95th percentiles. Estimates from the same functions fit to field data sets are shown for (E) Laysan 1997 and (F) Lisianski 1999 in which the entire populations were enumerated. Results are presented for full data sets and for truncations at 90% and 80% of individuals identified.

(some with four parameters) were fitted to just seven data points, perhaps explaining the atypical bias.

## DISCUSSION

We found that discovery curves were useful for diagnosing when an entire population had been identified. The determination that all seals had been identified is based on an empirically derived criterion and involves no formal characterization of uncertainty. While this is less than ideal from a statistical perspective, we believe this approach is practically very reliable, given the wealth of data available on NWHI monk seal discovery curves. In our study it was fairly easy to distinguish between data sets where saturation sampling was attained and those where new seals continued to appear. We also found it useful to acknowledge an intermediate category of “nearly enumerated” populations, because while we could not say whether all seals had been counted, the negative bias was likely quite low. If applications of this method to other species yield less clear distinctions, a more or less arbitrary decision can be made, weighing both one’s tolerance for underestimation and the reliability of alternative estimation methods. We prefer total enumeration when warranted, because we know that capture-recapture tend to be negatively biased for Hawaiian monk seals when compared with known minimum abundance (Baker 2004).

Simulations suggest that unless capture heterogeneity was negligible, an unlikely scenario in any real population, no nonlinear function examined provided unbiased estimates of abundance by extrapolating incomplete discovery curves. Because the level of bias and uncertainty increased when less of the population had been identified, we conclude that extrapolating discovery curves has little practical value for Hawaiian monk seal assessment.

An interesting parallel exists where researchers have evaluated species-area and species-accumulation curves to estimate species richness through extrapolation (Soberon and Llorente 1993, Colwell and Coddington 1994, Flather 1996, Tjørve 2003, Ugland *et al.* 2003). Flather (1996) and Soberon and Llorente (1993) evaluated the performance of various models using empirical data and found that estimates of species number varied widely among model types. Further, they found that statistical criteria (such as the coefficient of determination) did not reliably indicate the best model. A good fit to the data, therefore, does not guarantee a valid extrapolation. Soberon and Llorente (1993) stressed that models should be derived based on explicitly stated assumptions about the underlying processes that generate species accumulation curves. Likewise, Tjørve (2003) emphasized that species-area models should be based on underlying biology rather than statistics. Unfortunately, the depth of understanding required to ascertain the appropriate emergent function for any particular ecosystem or area is difficult or impossible to attain. In light of these problems, and particularly recognizing that species will have differing detection probabilities less than one, Cam *et al.* (2002) suggest using capture-recapture models with capture heterogeneity to estimate species richness.

Our analysis has yielded valuable information regarding allocation of effort and design of the monitoring program. Clearly better total abundance estimates could be obtained by allocating effort optimally. For example, field seasons could be shorter at Laysan island, Lisianski island, and Midway Atoll, without significantly compromising the identification of all individuals. It appears that a modest extension of the field seasons at Kure Atoll could yield saturation sampling. Finally, at French Frigate

Shoals and especially at Pearl and Hermes Reef, significantly longer field seasons might be necessary to identify all individuals.

Analysis of discovery curves has great practical appeal, especially for relatively small, closed populations of marked individuals. With sufficient sampling, one can develop criteria, as we have, for determining whether the whole population has been enumerated. Moreover, discovery curves can assist in the design of monitoring programs, by indicating the amount of field effort required for saturation sampling. If total enumeration is not practical, then alternative study designs, for example, to optimize capture-recapture estimates, may be more appropriate.

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