FALSE KILLER WHALES AROUND THE MAIN HAWAIIAN ISLANDS: AN ASSESSMENT OF INTER-ISLAND MOVEMENTS AND POPULATION SIZE USING INDIVIDUAL PHOTO-IDENTIFICATION

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Summary

The current best estimate of population size for false killer whales within Hawaiian waters is only 268 individuals (Barlow 2003), though the estimate is not very precise (CV = 1.08). False killer whales are considered a "strategic" stock by the National Marine Fisheries Service, as "takes" in the Hawai'i-based swordfish and tuna long-line fishery exceed the "Potential Biological Removal" (PBR) level. We studied false killer whales as part of small-boat based surveys for odontocetes around the main Hawaiian islands from 2000 through 2004, and in this report we assess inter-island movements, examine "mark" change over time on individual animals, estimate the proportion of marked individuals within the population, and provide a mark-recapture population estimate. Dedicated surveys for odontocetes were undertaken around all the main Hawaiian islands, and all groups of false killer whales encountered were approached and attempts made to photographically identify all individuals present. False killer whales were encountered on 14 occasions in directed surveys (2.9% of all odontocete sightings), in eight of the 10 months of the year surveyed, and in three of the four island-areas surveyed. Encounters were in a wide range of water depths (37 to 3,950 m). Photographs from seven opportunistic encounters were also available. Seventy-seven percent of individuals photographed were considered to have markings that could be recognized in the long-term (between-years). Seventy-six individuals with such long-term markings were documented, 47 of which were seen on two or more occasions. Ten individuals were documented with mark changes, though the rate of mark change was low (approximately one change every six years). Re-sighting analysis suggest that there are considerable inter-island movements of individuals (for example, 19 of 21 individuals identified off O'ahu have been recorded off the island of Hawai'i or around the "4-islands"). A multi-site mark-recapture analysis, taking into the proportion of marked individuals in the population, resulted in an estimate of 123 individuals in the population (CV = 0.72). This estimate applies to a population of false killer whales that used the study area; however the geographic range of that population is not known. Also, we assumed population closure and homogenous capture probabilities among individuals. The degree to which these assumptions may have been violated and the resulting estimate biased remain unclear.

Introduction

Information on false killer whales in Hawaiian waters is limited. Shallenberger (1981) reported anecdotal sightings and strandings of this species throughout the main Hawaiian islands, noting that they can be found in both shallow (<200 m) and deep (>2000 m) waters. Two population estimates exist, both from line transect surveys, and one short survey was undertaken to provide a minimum count of false killer whales around the main Hawaiian islands. Leatherwood and Reeves (1989) undertook aerial surveys on eight days in June and July 1989 within 55 km of shore off the lee coasts of the islands of Hawai'i, Lana'i and O'ahu, specifically to provide a minimum count of false killer whales. Their survey resulted in 14 sightings of false killer whales (16% of all sightings), with estimated minimum counts of 460 and 470 individuals on two different days. Mobley et al. (2000) undertook aerial line-transect surveys for humpback whales within 46 km of all the main Hawaiian islands, approximately 16 days per year in each of 1993, 1995 and 1998 (in February through April). False killer whales were seen on 21 occasions (5.8% of all odontocete sightings), and the population size was estimated at 121 individuals (CV = 0.47). In similar surveys in 2000 and 2003 no false killer whales were sighted (J. Mobley, pers. comm.). In the summer and fall of 2002, Barlow (2003) undertook a ship-based line transect survey covering areas both around the main Hawaiian islands and out to approximately 360 km offshore (the entire Hawaiian Exclusive Economic Zone). False killer whales were seen on two occasions (approximately 1% of all odontocete sightings), and the population was estimated as 268 individuals, though the precision of the estimate was low (CV = 1.08). Using Barlow's (2003) estimate of population size, the Hawaiian stock of false killer whales is considered "strategic" under the Marine Mammal Protection Act, as the rate of mortality and serious injury in the Hawai'i-based swordfish and tuna long-line fishery is higher than the "Potential Biological Removal" (PBR) level (Carretta et al. 2004).

Since 2000 we have undertaken small-boat based surveys for odontocetes around the main Hawaiian islands, for the purposes of examining stock structure and for population estimation (see e.g., Baird et al. 2002, 2003). Combined with samples collected elsewhere in the Pacific, genetic samples collected from these efforts have been used to suggest that false killer whales around the main Hawaiian islands are reproductively isolated from false killer whales elsewhere in the tropical Pacific, though the boundaries of populations are not known (Chivers et

al. 2003). Photographs of false killer whales obtained during these surveys have also been used to suggest that animals around the main Hawaiian islands may be part of the same population as those interacting with the long-line fishery offshore of the main islands (Baird and Gorgone 2005). This report utilizes photographic identifications of false killer whales from these studies to: 1) assess false killer whale inter-island movements within the main Hawaiian islands; 2) examine "mark" change over time on individual animals; 3) estimate the proportion of marked individuals within the population; and 4) provide a preliminary mark-recapture population estimate for false killer whales around the main Hawaiian islands.

Methods

Field methods

Photographs of false killer whales around the main Hawaiian islands used in this study were collected in two ways: 1) opportunistically, incidental to studies of humpback whales or during commercial whale or dolphin watching; and 2) during directed surveys of odontocetes. Opportunistic photographs used in this study were collected by DJM, DRS, MHD, and also provided (photos of 1-2 individuals each) by P. Colla, T. Cullins, A. Frankel and D. Perrine.

Directed surveys of odontocetes were undertaken each year from 2000 through 2004, using research vessels ranging in size from 6-18 m. Surveys were undertaken off Kaua'i and Ni'ihau, off O'ahu, in the "4-island" area (Moloka'i, Lana'i, Maui, Kaho'olawe), and off the island of Hawai'i. During 2002 and 2003 we often used two research vessels simultaneously, though maintained a distance of several kilometers between vessels to cover different parts of the study area. Survey speeds were generally between 16 and 30 km/h, and two to five observers scanned 360 degrees around the survey vessel. Search locations were logged every five minutes on a GPS. Search effort was concentrated in areas where sea conditions were less than Beaufort 4; nearly all sampling was in leeward (SW) waters. We searched non-systematically both near-shore and out to approximately 42 km from shore, attempting to cover as much of the study area as possible, given sea conditions and fuel constraints. All groups of odontocetes observed were approached for species identification and recording of location and group size. For false killer whales, efforts were made to obtain multiple photographs of both the left and right sides of all individuals present in each group, and from some groups we collected genetic samples for

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examining stock structure (see Chivers et al. 2003). Photographs were taken using Canon cameras (film in 2000-2002, digital in 2003-2004) with 100-300 mm lenses.

Photographic matching

Within encounters, photographs were sorted by individual using a variety of characteristics. Clearly distinct individuals were sorted using body scars, notches on or immediately adjacent to the dorsal fin, and major dorsal fin disfigurements (see Baird and Gorgone 2005). Other individuals were identified within encounters using subtle differences in dorsal fin shape, and/or relative size (i.e., animals that are obviously small calves or neonates based on relative size in photographs). Individual neonates or small calves were distinguished based on proximity to a recognizable putative adult female (presumably the mother). In these latter cases, if two distinctive adult-sized animals both were accompanied by small (unmarked) calves, two unmarked animals were tallied for the group. Each individual identified within an encounter was assigned a "distinctiveness" coding, to determine the proportion of "marked" individuals. Distinctiveness codes were: 1 = not; 2 = slightly; 3 = average; 4 = very. Individuals with a distinctiveness of 1 could usually be identified within an encounter, but not between an encounter. Code 2 animals typically had one or two small notches on the trailing edge of the dorsal fin. Those with a code > 1 could be identified both within and between encounters with a photograph (taken from either side) of sufficient quality. The program *Finscan* (Hillman et al. 2003) was used to assist in matching individuals between encounters. All photographs were used to assess inter-island movements and examine mark change.

Mark-recapture analyses

Photographs from both directed surveys and opportunistic photographs collected during the same period (2000-2004) were used in mark-recapture population estimation. Because of spatial and temporal variations in survey effort (see Results), we used photographic re-sightings of individuals between island areas to estimate abundance, following the approach of Durban et al. (2005). Using only good quality photographs of distinctiveness 3 and 4, a list was compiled of all individuals identified in each of the three island areas where photographic encounters occurred (O'ahu, the 4-islands and Hawai'i). The re-sightings of individuals between areas were then presented in a simple contingency table, where the cells of the table referred to the discrete categories formed by combinations of the study sites. We used log-linear models to describe

these count data and project an estimate into the missing cell depicting the number of individuals not identified in any of the three areas (e.g. Durban et al. 2005). In particular, these models aimed to account for dependencies that may have existed between the areas due to geographical distance effects, in addition to population ranging patterns. A suite of different log-linear models were fit to the data, each containing a variety of terms describing the dependence between pairs of sites. We used the Bayesian Markov chain Monte Carlo (MCMC) approach of Durban et al. (2005) to estimate the probability associated with each model, and base inference on a model-averaged estimate of population size that incorporated model selection uncertainty.

Because this mark-recapture approach only used the reliable between-island re-sightings of distinctive individuals, the abundance estimate only referred to the number of individuals N that possessed distinctive markings. To produce estimates of overall abundance P, it was necessary to re-scale the estimate of the abundance of distinctive whales to include animals that were not distinctive. This required an estimate of the proportion of individuals that were reliably distinctive, π. Only photographs from directed surveys were used in estimating the proportion of reliably distinctive individuals in the population. To calculate π, good quality photographs were used to determine the number of distinctive whales in each encounter from the total number of whales of all distinctiveness levels in that encounter. This involved the assumption that all whales could be distinguished within an encounter from good quality photographs, even though only a distinctive subset of these could be distinguished between encounters. The number with reliable markings was then treated as a binomial sample from the total sample size in each encounter, and the proportion of individuals that possessed reliable markings (π) was estimated as the binomial probability. Estimation of the posterior distribution for the rescaling proportion π was conducted in the same Bayesian MCMC run as estimation of the number of individuals N in the mark-recapture model. These two components were then linked to form a single probability model, by defining the overall abundance P to be a function of N and π:

$$P = N / \pi$$

By embedding this mark-type rescaling step into the full probability model with the mark-recapture component, we incorporated the uncertainty from both the mark-recapture and mark-

type rescaling components directly into the inference about *P*.

It should be noted that due to the relatively sparse nature of the data, we adopted a "closed" population model for estimating abundance, which did not require estimation of additional parameters for survival and movement. Therefore, although the study period spanned five calendar years, we assumed that changes to the population through birth, death or permanent migration were minimal over this period. However, we anticipated that individuals would have moved to and from the near-shore study area during the study period, and it is important to note that our abundance estimates therefore corresponded to the number of animals that *used the study area during the sampling period*, and we make no explicit assumption as to how this estimate relates to the total population to which these animals belong, or the amount of time that they spent within the study area. We assumed that every whale using the study area had some probability of being photographed over the course of the study period, although individual whales might not have spent all their time in the surveyed areas, and the probability of identification varied between island areas. Homogenous capture probabilities among individuals within a particular area were assumed.

Results

Encounters and group size

Between 2000 and 2004, directed odontocete surveys were undertaken around all the main Hawaiian islands, though survey effort varied between years and island areas, as well as seasonally (Table 1; Figure 1, Figure 2). False killer whales were encountered on 14 occasions (2.9% of all odontocete sightings; the 6th most frequently encountered species of odontocete), off three of the island areas (O'ahu, the 4-islands, and Hawai'i), and in eight of the 10 months of the year surveyed (Figure 2). Sighting depths ranged from 37 m to 3,950 m (mean = 1,079 m; SD = 1,385 m). Group size estimates ranged from 3 to 41 individuals (mean = 17.5, SD = 12.3, median = 15). However, it is likely that some group size estimates are negatively biased because some groups were encountered in unfavorable sea conditions (i.e., Beaufort 4 or greater), or were left after short periods due to fuel constraints or time of day. Encounter duration ranged from 0.83 to 7.93 h (mean = 3.14 h, SD = 1.98 h). There was a significant positive relationship between encounter duration and group size (regression, p = 0.047, r^2 = 0.29). If we exclude encounters

less than two hours in duration, group size ranged from 12 to 41 individuals (mean = 24.7, SD = 10.9, median = 21.5, n = 8). Groups were often spread over large areas, with distances between individuals and sub-groups of up to several kilometers. During longer encounters we were more likely to spot distant sub-groups, or sub-groups would merge and group size estimates would increase over the duration of the encounter.

Photographs were available from seven opportunistic encounters (Table 3), five during the time frame of the dedicated surveys (2000 through 2004), and two pre-study (one from 1990 and one from 1999). Five of the opportunistic encounters were during the same months as sightings in dedicated surveys, while two were in months when no false killer whales were encountered in dedicated surveys (April and July). All opportunistic encounters were in areas surveyed in dedicated survey efforts.

Mark types and distinctiveness categories

A total of approximately 4,000 false killer whale photographs were taken during dedicated surveys. For all categories of distinctiveness, there were 172 identifications (including re-sightings) from dedicated surveys. Of those, 29 were considered not distinctive, and 14 were considered slightly distinctive. Individuals in the slightly distinctive category had between 1 and 3 notches (mean = 1.8, SD = 0.8). While it was possible to match slightly distinctive individuals between encounters within a year, there was only one match of these individuals between years, and this match was based on a body scar, rather than on dorsal fin markings. Individuals in the average distinctiveness category had between 0 and 8 notches (mean = 4.25, SD = 1.3), as this category included one individual completely missing the dorsal fin (see Baird and Gorgone 2005). Those considered very distinctive had between 2 and 9 notches (mean = 5.74, SD = 1.6).

Mark change

For the purposes of examining mark change we included only those individuals with a distinctiveness coding of 3 (average) or 4 (very) that were seen on two or more occasions. Opportunistic photographs, including three individuals observed prior to the initiation of our study (two in 1990 and one in 1999), were included in these analyses. Time intervals between each re-sighting ranged from 6 to 4,306 days (mean = 504 days, SD = 713 days). Forty-seven individuals were seen on two or more occasions, for a total of 116 sighting occasions. Ten of

these were documented with mark changes; six had only a single mark change, three had two changes, and one had four changes. Mark changes included new leading edge notches or dents (2), changes in trailing edge notch size/shape (7), and new tip or trailing edge notches (7). The average rate of mark change was calculated using 16 mark changes and the sum of all intervals (34,782 days), as one mark change per 2,173 days (5.95 years).

Inter-island movements

For examination of inter-island movements, both directed and opportunistic photographs were used, including those from prior to the initiation of our study. Twenty-six individuals were documented moving between islands. Twenty-four were documented moving once (6 movements between the 4-islands and Hawai'i, and 18 between O'ahu and Hawai'i), and two were documented moving twice; one individual was photographed off the 4-islands in March 2000, off Hawai'i in March 2001, and off the 4-islands in April 2003, while another was photographed off Hawai'i in July 1990, off the 4-islands in March 2000, and off O'ahu in September 2003. Thus there were a total of 9 movements documented between the 4-islands and Hawai'i (8 individuals), 19 between O'ahu and Hawai'i (19 individuals), and 1 between the 4-islands and O'ahu. All inter-island movements were between years, although the likelihood of detecting within-year inter-island movements was small, given the distribution of sightings among areas and years (Table 2, Table 3). In only one year (2003) were there false killer whales identified off all three island areas. Straight-line distances moved between the sighting locations off the furthest islands (O'ahu to Hawai'i) ranged from 254 to 283 km.

Seasonal distribution of repeated sightings

As field efforts varied seasonally among the different island areas (e.g., work off O'ahu in April and May only, off the 4-islands primarily in fall/winter, etc; Table 1), we qualitatively assessed the possibility that individual false killer whales might use the study area only during particular times of the year (e.g., some individuals might use the area only during spring, while other individuals might use the area only during the fall), introducing bias into our population estimates. Oceanographic seasons for Hawai'i based on sea surface temperature (Flament 1996) are: winter (Feb-Apr); spring (May-Jul); summer (Aug-Oct); and fall (Nov-Jan). Seventeen percent of the re-sightings spanned three seasonal periods (e.g., between "spring" and "fall"), while an additional 42% spanned two seasonal periods (e.g., between "fall" and "winter"),

suggesting that individuals have no strong seasonal preference for use of the area.

Population estimation

In total, 76 "distinctive" individuals were included in the mark-recapture analysis[1]. The overlap of individuals between island areas is represented in Table 5. Parameter estimates from the log-linear models described well the sample sizes of individuals identified in each area and the overlap of individuals between areas (Table 6). Specifically, there was a larger main effect estimated for Hawai'i, reflecting a larger capture probability in this area where the greatest number of individuals were identified. In contrast, the smallest effect was for O'ahu, where fewest individuals were documented. The interaction effects indicated that interactions were present between the geographically-stratified samples. Specifically, because the numbers of individuals matching between the 4-islands and Hawai'i (6), and between the 4-islands and O'ahu (1) were relatively low given the sample sizes in these areas, a negative dependence was estimated between each of these two areas and the 4-islands. In contrast, the relatively high number (17) of individuals identified from both O'ahu and Hawai'i, but not the 4-islands, resulted in a positive dependence between O'ahu and Hawai'i, although this interaction was relatively weak.

The need to incorporate these interactions was further supported by calculations of model probabilities (Table 7). The strong negative interactions had a high probability of remaining in the model, with probability of 0.67 for models with the 4-islands/Hawai'i interaction and 0.73 for the 4-islands/O'ahu interaction. In contrast, the weaker interaction between O'ahu and Hawai'i was only included in the models selected during 56% of MCMC iterations, implying a probability of only 0.56. However, there was uncertainty about the specific model form to use for inference, and estimates of abundance were highly dependent on the chosen model. For example, without any interactions the estimate for the number of distinctive individuals was approximately 127, but there was negligible probability associated with this model. The most probable model, with a probability of 0.44, included the two negative interaction terms between the 4-islands and Hawai'i and the 4-islands and O'ahu. Such negative dependencies result in a lower re-sight rate between areas than expected by the no-interaction model, and therefore we obtained a smaller

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[1] Baird and Gorgone (2005) report 80 distinctive individuals, though their sample included individuals with a distinctiveness coding of 2, and only identifications from 11 of the 14 encounters reported here.

estimate of 84 when the model incorporated these interactions. In contrast, positive interactions result in a higher re-sighting rate than expected by the no-interaction model, and therefore the model that accounted for the positive O'ahu and Hawai'i interaction produced an estimate of around 253 distinctive whales. This was the second most probable model, with a model probability of 0.23.

Because of this uncertainty over choice of model, we produced model-averaged estimates of population size by MCMC sampling across candidate models (e.g. Durban et al. 2005). The estimate of population size was therefore composed of MCMC samples from the different models, with the proportion of samples originating from each model corresponding to the relative model probabilities. The estimate of the number of distinctive individuals *N* using the study area was then 93 (95% Probability Interval 78-437). The posterior probability distribution for this abundance estimate was positively skewed, indicating greater uncertainty about the upper bound of abundance than the lower bound.

Only a small proportion of the individuals were judged to be non-distinctive, with 77% (95% Probability Interval 70-82%) estimated to be "average" or "very" distinctive. Therefore the model-averaged abundance estimate was rescaled to incorporate non-distinctive individuals, with an estimate of total abundance of 123 individuals. Note that the uncertainty about the rescaling factor has been incorporated into this estimate along with the uncertainty from the mark-recapture component, and as a result the posterior probability distribution for the overall abundance *P* covers a wide range of values (95% PI = 99-574). Coefficient of variations (CV) assume normality, while our estimates are realistically skewed. However, for the purpose of comparison with other estimates, we calculated CV (0.72).

Discussion

False killer whales are only infrequently encountered around the main Hawaiian islands. Our surveys covered areas off all the main islands, in water depths from near-shore out to over 4,600 m, and spread out over 10 months of the year, but resulted in only 14 sightings of this species (2.9% of all odontocete sightings). While the depths surveyed varied between island areas (Figure 1), false killer whales were sighted over a very broad depth range (from 37 to 3,950

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m), one of the broadest depth ranges of any species of odontocete in Hawai'i. The animals are relatively large, are frequently surface-active (splashing or leaping), groups are often spread out over wide areas (several kilometers or more), and dive times are typically short.

We used our photo-identification studies of false killer whales around the main Hawaiian islands to produce a mark-recapture estimate of abundance that accounted for the re-sighting of individuals in different geographic areas. This analysis resulted in a model-averaged estimate of approximately 123 individuals using the area during our study. However, estimates from individual mark-recapture models ranged widely, and therefore the model-averaged estimate was subject to considerable uncertainty (95% CI = 99-574; CV=0.72). Although we sacrificed precision by adopting the model-averaging method, this represents real model selection uncertainty that we cannot omit at this stage. Given the spatial and temporal variability in our survey effort, the use of this method seems more appropriate than more traditional mark-recapture methodologies using temporal sampling. However, given the temporal variability in effort (Table 1) and sightings (Table 2), our no interaction model (Table 7) is analogous to a 3-sample Schnabel mark-recapture model. However, this model had negligible probability compared to some of the others (Table 7), highlighting the importance of dependencies between areas.

The benefit of this spatially-explicit approach to mark-recapture analysis is that we can also use estimates of interactions between study areas to make inferences about population structuring. Specifically, we estimated negative interactions between the 4-islands area and Hawai'i, and between the 4-islands and O'ahu, and a possible positive dependence between O'ahu and Hawai'i. Because these do not appear to represent logical geographic distance effects, it indicates possible site fidelity of individuals in the 4-islands region, with more regular movement of individuals between the more extreme parts of the study areas. Alternatively, this may reflect the temporal aspects of sampling, with encounters in the 4-islands region occurring primary in 2000-2001 compared to encounters in the other areas primarily in 2003-2004. Such temporal differences in the identity of animals identified may result from temporary movement of individuals into and away from the study area as a whole, such that some individuals were only available for sampling at some times. Future studies incorporating simultaneous (or near-simultaneous) sampling off all the major island areas could help address this issue.

It is interesting to note that our mark-recapture estimate of the number of false killer whales using these coastal waters is very similar to the line transect estimate of 121 (CV = 0.47) produced by Mobley et al. (2000) for the waters within 46 km of all the main Hawaiian Islands. In contrast, the larger-scale line-transect survey of Barlow (2003) estimated a larger number of approximately 268 whales (CV = 1.08) using a larger area including the leeward Hawaiian islands and waters up to 360 km offshore of all the islands. However, our mark-recapture confidence intervals (99-574) clearly overlap with this estimate. Further work is needed to assess the degree of mixing of false killer whales between the nearshore and offshore waters of the Hawaiian Exclusive Economic Zone, and establish if the whales using the coastal waters close to the islands are a discrete population. Estimates of temporary migration to and from the coastal study area could be made by extending the duration of this mark-recapture dataset and using open population mark-recapture models (e.g. Whitehead 1990).

The robustness of the mark-recapture estimate is contingent on meeting the assumptions of the mark-recapture approach. Mark-recapture models typically assume that all individuals have equal probabilities of capture. In reality, variation in the likelihood that individuals may be recaptured (heterogeneity of capture probabilities) may be due to a variety of factors, including spatial sampling bias (spatial heterogeneity) and individual differences, for example, in approachability or likelihood of being marked. In terms of approachability, false killer whales showed no obvious avoidance of the research vessel. Individuals would frequently ride the bow wave of the research vessel, and even those engaged in high-speed travel would eventually slow and could be approached and photographed. Unlike many other species of small odonotocetes in Hawai'i (e.g., rough-toothed dolphins and bottlenose dolphins), false killer whale groups were never lost except in extremely rough sea conditions (Beaufort 4 or higher). Since we did not sample all areas at the same time of the year, it is possible that temporal heterogeneity in sampling has influenced our results. However, our analysis of seasonal distribution of re-sightings, with the majority of re-sightings (59%) spanning two or more seasons, suggests that temporal heterogeneity may not be important.

There was considerable spatial heterogeneity in our survey effort, but evidence from inter-island movements suggests our mark-recapture samples provided coverage of the full coastal population. For example, of the 21 individuals documented off the island of O'ahu, 19

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have been recorded at other islands, and more than half (26 of 45) of the individuals documented off the island of Hawaiʻi have been recorded off other islands (Table 4). The multi-site mark-recapture approach we have employed does explicitly account for spatial dependencies (Durban et al. 2005) between geographical mark-recapture samples, and for spatial difference in effort and resultant capture probability. However, individual differences in movements and behavior may still be present. We attempted to minimize the effect of individual differences in approachability by attempting to photograph all individuals present in each encounter. As the duration and quantity of mark-recapture data increases, we hope to be able to fit mark-recapture models with more parameters, to account for heterogeneous movement and capture probabilities. We also assumed population closure, but sampling over a five-year period is too long for complete closure to have been achieved. Some births and deaths will have occurred, and this will bias estimates. However, this bias will be small compared to the overall imprecision of the model-averaged estimate.

Additionally, mark-recapture methods assume that individuals can be correctly identified, and that marks are not lost. Our analyses indicate that a large proportion (an estimated 77%) of individuals in this population have distinctive long-term markings which can be used in photo-identification and mark-recapture analyses. Based on known mark change, the rate of mark acquisition/change is low, estimated at only one mark change per individual approximately every six years. It is certainly possible that some matches in our dataset were missed due to substantive mark change, but we restricted our analyses to exclude individuals with just one or two small marks (those considered "slightly" distinctive) to minimize this probability, and it is unlikely that many matches were missed, given the five-year time frame of our study. If matches were missed, this would mean that our mark-recapture population estimate would be positively biased.

It does not appear that false killer whales are "resident" to particular island regions, as opposed to bottlenose dolphins, which appear to resident to specific island areas (Baird et al. 2002, 2003). This is supported by the frequent inter-island movements (Table 4) and the lack of sightings in areas that have been extensively surveyed over an extended period (e.g., Kauaʻi/Niʻihau in 2003, the 4-islands in 2002 or 2003, or Hawaiʻi in 2002), as well as by movement patterns within encounters (groups would often travel long distances within an encounter). Assessing between-year capture probabilities within a particular area (e.g, off the

island of Hawai'i) is limited by the temporal and spatial distribution of our encounters (and number of identifications). For example, off the island of Hawai'i, 58 of the 66 identifications of marked individuals were in one year. While off the 4-islands identifications are spread more evenly between two years (21 identifications in 2000 and 25 in 2001), most survey effort in that area in those years were concentrated in the same "season" (November 2000 to March 2001), thus the high number of between-year re-sightings documented in the 4-islands (Table 4) reflect within-"season" re-sightings.

While we were able to estimate the number of false killer whales using our study area during our study period, the total range of this population is unknown. Deployment of satellite or VHF radio tags on individuals in this population could help determine the population boundaries (in the case of satellite tags) as well as provide information on the rate of movements between islands, and facilitate re-locating groups for photo-identification (in the case of VHF tags). Expansion of the geographic scope of photographic sampling would also be of value in helping determine the boundaries of the population, as well as increasing the precision and reducing the bias in our estimate. This could include the leeward Hawaiian islands as well as waters further offshore, and areas where we have previously sampled but have had no encounters (i.e., Kaua'i/Ni'ihau). Given the sample size of sightings from dedicated survey effort (n=14), it is unclear whether the tendency towards a higher number of sightings per unit effort suggested during certain months (Figure 2) is a reflection of an actual increase in use of the islands in the fall/winter, or just an artifact of small sample size. Survey effort during months of the year where little or no effort is currently available (e.g., July, August) would also be informative, in terms of assessing seasonal use of the area. As our time series grows, we recommend the use of open population models needed to estimate survival and assess population trends (e.g. Caswell et al. 1999). More years, and open population mark-recapture approaches could also be used to quantify residency of these animals around the islands, and use estimates of temporary emigration to estimate the size of the "parent" population to which these individuals belong (e.g. Whitehead, 1990).

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Table 1. Distribution of dedicated search effort by area and year.

Island area	Year	Dates	# boat days	# km	# hours
Kaua'i/Ni'ihau	2003	5/30-6/12	24*	3,222	195
Kaua'i/Ni'ihau	**Sub-total**		**24**	**3,222**	**195**
O'ahu	2002	4/23-5/1	9	860	57
O'ahu	2003	5/22-5/29	13*	1,789	111
O'ahu	**Sub-total**		**22**	**2,649**	**168**
4-islands	2000	2/26-4/18, 11/22-12/31	54	3,578	304
4-islands	2001	1/2-3/24	18	2,202	182
4-islands	2002	4/13-4/21	9	785	64
4-islands	2003	5/13-5/21	16*	1,659	107
4-islands	**Sub-total**		**97**	**8,224**	**657**
Hawai'i	2002	4/3-4/13, 9/24-10/5	30*	2,738	229
Hawai'i	2003	5/4-5/12, 10/8-10/20	39*	3,286	281
Hawai'i	2004	9/12-10/8, 11/18-12/9	42	4,656	290
Hawai'i	**Sub-total**		**111**	**11,680**	**800**
All			**254**	**25,775**	**1,820**

*Two vessels operated on most days, at least several kilometers apart.

Table 2. False killer whale sightings from dedicated survey effort, by year and island area, with number of identifications of marked individuals (shown in parentheses)

Island area	2000	2001	2002	2003	2004	Total
O'ahu			1 (1)	1 (20)		2 (21)
4-islands	4 (21)	2 (25)	0	0		6 (46)
Hawai'i			0	1 (5)	5 (57)	6 (62)
Total	**4 (21)**	**2 (25)**	**1 (1)**	**2 (25)**	**5 (57)**	**14 (129)**

Table 3. Opportunistic sightings of false killer whales by year and island area, with number of identifications of marked individuals (shown in parentheses)

Island area	1990	1999	2001	2003	2004	Total
O'ahu				1 (1)		1 (1)
4-islands		1 (2)		2 (10)		3 (12)
Hawai'i	1 (2)		1 (1)		1 (1)	3 (4)
Total	**1 (2)**	**1 (2)**	**1 (1)**	**3 (11)**	**1 (1)**	**7 (17)**

Table 4. Number of marked (distinctiveness > 2) individuals by area[1]

Island area	# IDs of marked individuals	# individuals (excluding re-sightings)	# within-area within-year re-sightings	# within-area between year re-sightings	# matches with other island areas[2] (# individuals matched)
O'ahu	22	21	n/a	1	20 (19)
4-islands	58	38	3	17	10 (9)
Hawai'i	66	45	20	1	28 (26)
Overall		**76**			

[1]Totals include all opportunistic identifications, including those prior to 2000. [2]Matches with other island areas counted both directions (e.g., an individual matched between O'ahu and Hawai'i counted under the totals for both rows).

Table 5. A contingency table for the multi-area identification data from 2000 through 2004, where the cells of the table refer to the number of individuals that appear in each distinct combination of study areas (overlap information)[1].

		O'ahu	
		Identified in area	**Not identified in area**
Hawai'i - identified	4-islands - identified	0	6
Hawai'i - identified	4-islands - not identified	17	20
Hawai'i - not identified	4-islands - identified	1	30
Hawai'i - not identified	4-islands – not identified	3	?

[1]Differences in values between Table 4 and Table 5 due to the inclusion of pre-2000 opportunistic identifications in Table 4.

Table 6: Estimates of log-linear model parameters for the full model incorporating main effect for each area (around Hawai'i (H), 4-islands (4I) and O'ahu (O)), and interaction terms between each pair of areas. Estimates are presented as the mean and standard deviation (SD) of the marginal posterior distribution for each parameter. For description of model, see Durban et al. (2005).

Term	Mean	SD
Main effect H	0.12	0.17
Main effect 4I	-0.71	0.38
Main effect O	-1.01	0.35
Interaction H-4I	-0.70	0.54
Interaction H-O	0.14	0.51
Interaction 4I-O	-0.78	0.48

Table 7: Posterior model probabilities (to 2 decimal places) and summary statistics for the number of distinctive individuals, *N*, and overall population size, *P*. Estimates are presented for 8 models corresponding to the inclusion of different sets of interaction terms between study areas around Hawaiʻi (H), 4-islands (4I) and Oʻahu (O), along with an estimate of population size averaged across all models in a joint MCMC run (e.g. Durban et al. 2005). Data are presented for the posterior median and the 95% credibility interval (CI) displaying the interval of values encompassing 95% of the posterior density.

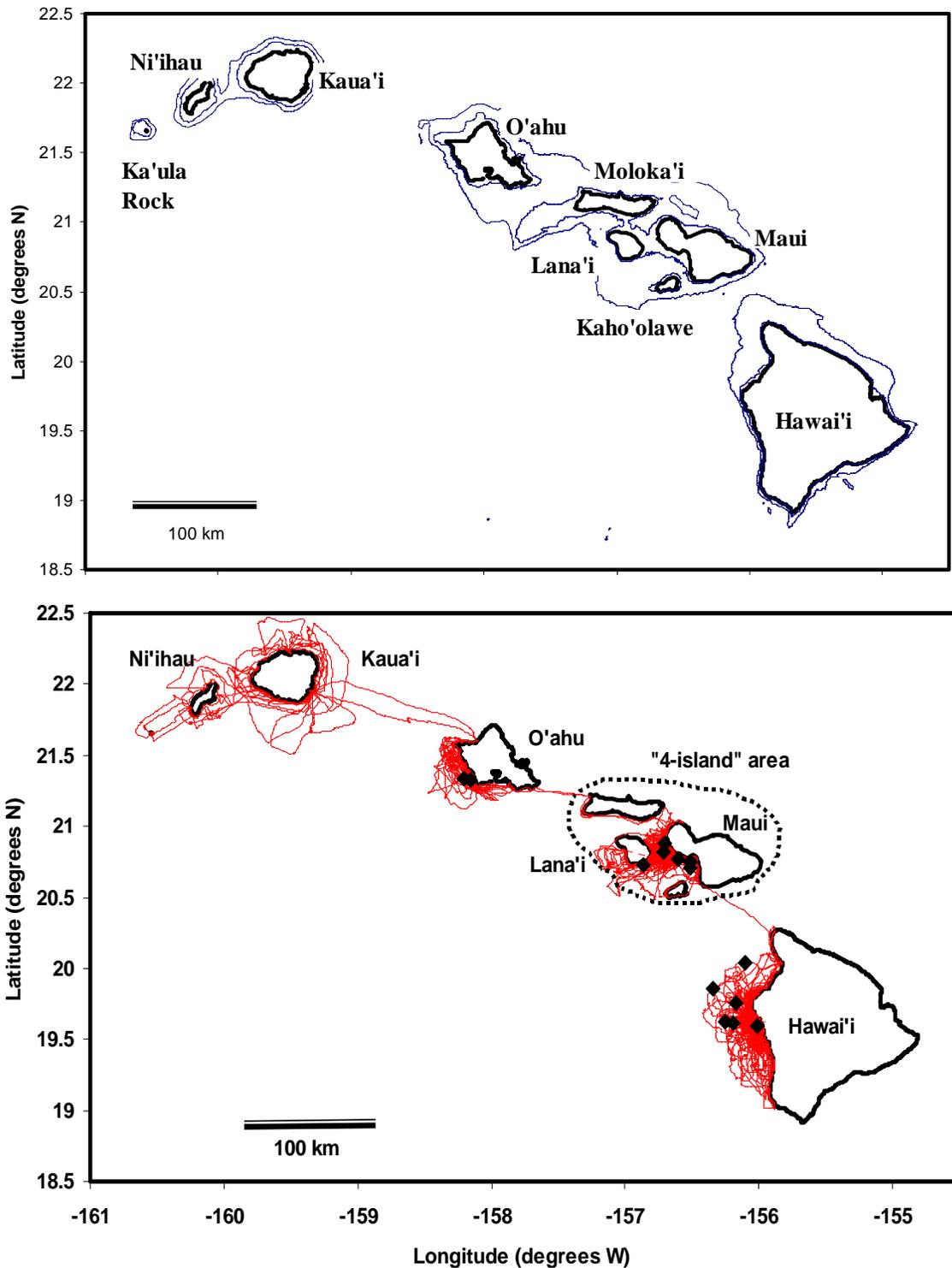| Model	Model Probability	N	P
No Interactions	0.00	127 (97-174)	166 (125-229)
H/4I	0.00	89 (78-112)	116 (100-149)
H/O	0.23	253 (149-581)	333 (193-771)
4I/O	0.04	112 (87-146)	146 (113-194)
H/4I + H/O	0.00	141 (84-736)	184 (109-968)
H/4I + 4I/O	0.44	84 (78-101)	111 (98-135)
H/O + 4I/O	0.10	189 (115-405)	246 (150-529)
H/4I + H/O + 4I/O	0.19	90 (78-250)	119 (99-329)
Average		**93 (78-437)**	**123 (99-574)**

Figure 1. Top. Main Hawaiian islands with 1,000 m and 100 m depth contours. Bottom. Distribution of dedicated search effort and false killer whale sighting locations. Search effort was concentrated off the leeward shores due to unfavorable sea conditions elsewhere.
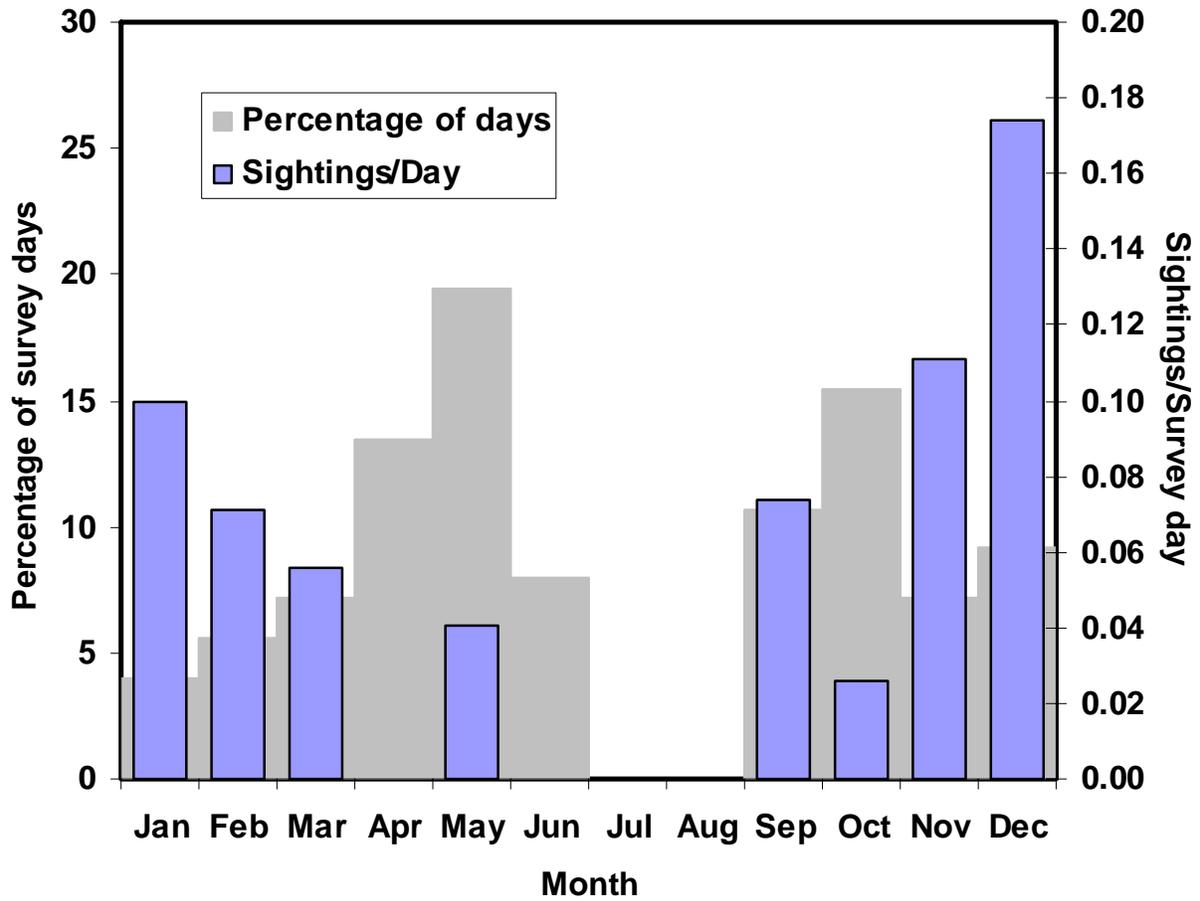
Figure 2. Distribution of directed survey effort (percentage of days) and number of sightings per survey day, by month.
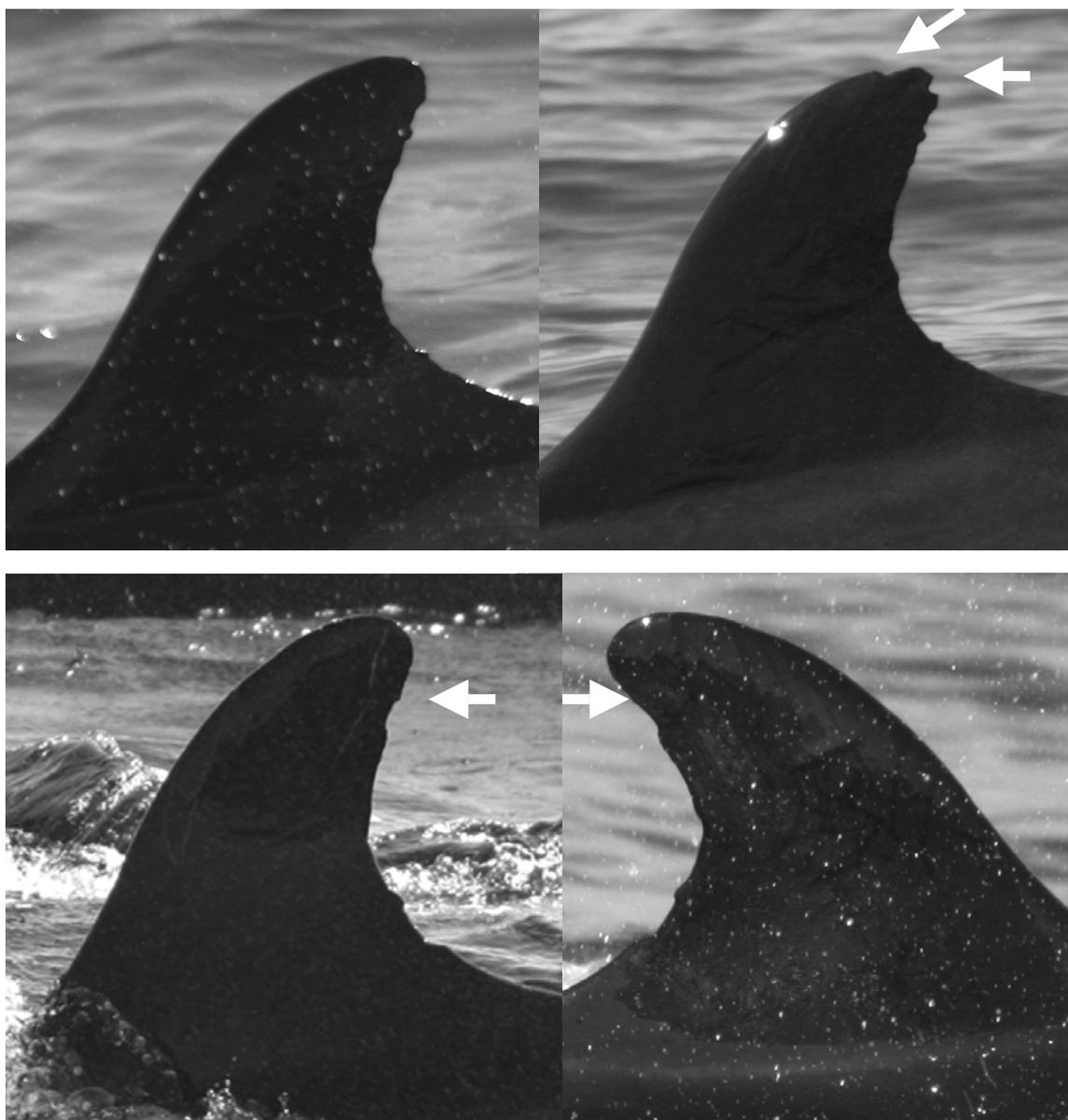
Figure 3. Examples of mark changes. Top. Individual HIPc163 from May 2003 (left) and October 2004 (right) with two new notches (indicated by arrows). Bottom. Individual HIPc174 from May 2003 (left) and October 2004 (right) showing change in notch shape (indicated by arrows).
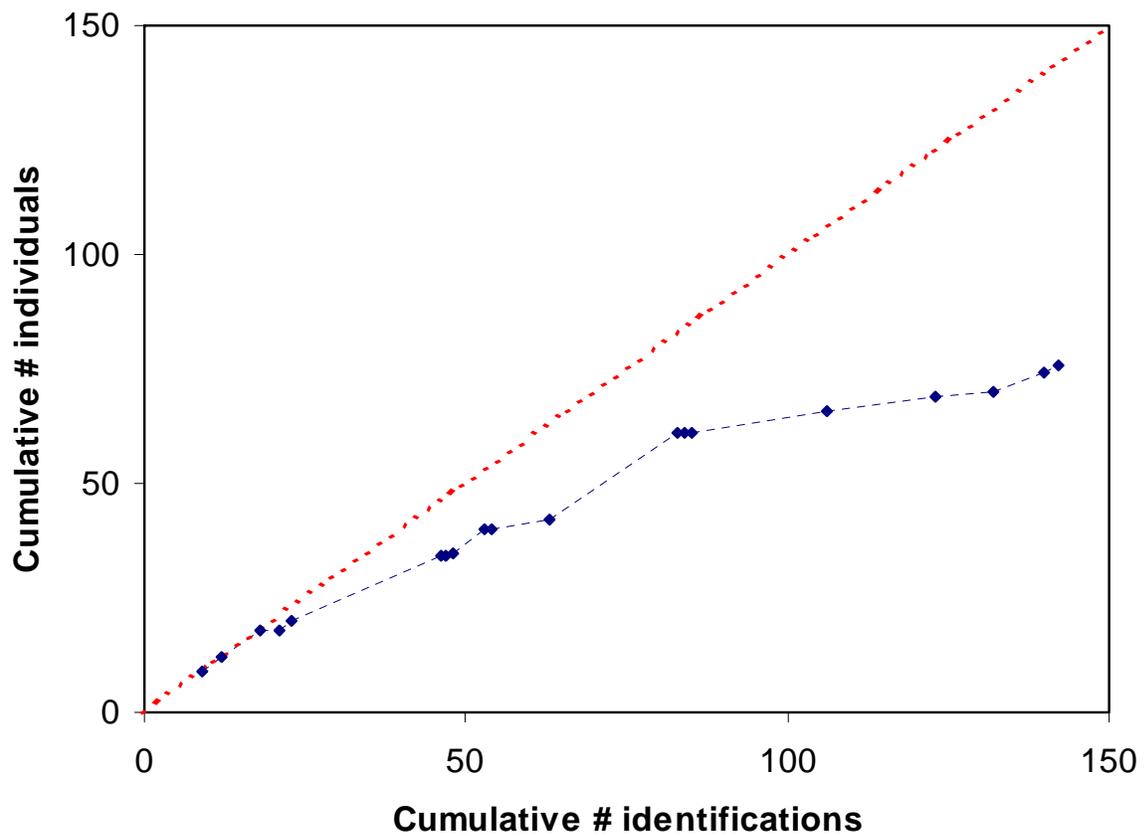
Figure 4. A "discovery" curve of new individuals. The straight dotted line represents a theoretical 1:1 ratio where all new identifications are of new individuals.