

Abundance and movements of spinner dolphins off the main Hawaiian Islands¹

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ABSTRACT

Collaborative photo-identification data were used to calculate minimum abundance estimates and to analyze movements of individuals for three spinner dolphin (*Stenella*

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longirostris longirostris) stocks within the main Hawaiian Islands. Island-specific photographic catalogs range from 11 to 215 individuals (median=49). Mark-recapture analyses produced six closed capture estimates of minimum seasonal abundance for leeward portions of Kaua‘i – 559 (CV=0.19) in Oct-Nov 2005; O‘ahu – 149 (CV=0.12) in Jun-Jul 2002 and 330 (CV=0.05) in Jul-Sep 2007; and Hawai‘i Island – 733 (CV=0.15) in May-Jul 2003, 260 (CV=0.20) in Jan-Mar 2005, and 190 (CV=0.15) in Jan-Mar 2006. Although negatively biased due to unmodeled survey effort variability and individual heterogeneity, the estimates suggest inter-island variation in abundance and seasonal variation in dolphin numbers along leeward coasts. Movement analyses quantified individual travel distances and rates at all islands and site fidelity (using standard distance deviations) at O‘ahu and Hawai‘i Island. Findings indicate that 1) inter-island movements occur but are infrequent, particularly between stocks; 2) observed travel distances and rates vary by island; and 3) O‘ahu individuals exhibit higher site fidelity than Hawai‘i Island individuals. This study demonstrates the value of using collaborative photo-identification data to explore the complex population characteristics of spinner dolphins in the main Hawaiian Islands.

INTRODUCTION

The Gray’s spinner dolphin (*Stenella longirostris longirostris*) occurs worldwide in the coastal waters of the tropical and subtropical oceans (Perrin and Gilpatrick 1994) and throughout the Hawaiian archipelago from Kure Atoll at the northern end of the archipelago to the southernmost tip of the Big Island (Hawai‘i Island) (Norris and Dohl

1980, Shallenberger 1981, Norris *et al.* 1994). The spinner dolphins in Hawaiian waters are genetically distinct from those found elsewhere in the world (Galver 2000, Andrews *et al.* 2010). Based on recent genetic analyses (Andrews *et al.* 2010) spinner dolphins in Hawaiian waters were redefined from a singular management stock that spanned the entire Hawaiian Exclusive Economic Zone (EEZ) into six separate stocks. Five of the stocks occupy waters within 18.5 km (10 nmi) of shore, including stocks at Kure/Midway and Pearl & Hermes in the Northwestern Hawaiian Islands and Ni‘ihau/Kaua‘i, O‘ahu/4-Islands (Moloka‘i, Lana‘i, Maui and Kaho‘olawe), and Hawai‘i Island in the main Hawaiian Islands (Fig. 1). A sixth “offshore” stock includes all other spinner dolphins found farther than 18.5 km from shore in waters adjacent to these defined island stocks and at all other Northwestern Hawaiian Island locations (Carretta *et al.* 2011).

A 2002 shipboard line transect survey within the Hawaiian EEZ indicated that spinner dolphins are concentrated near the main Hawaiian Islands and rarely encountered outside this stratum (Barlow 2006). Aerial surveys within the main Hawaiian Islands found spinner dolphins at all eight islands (from west to east: Ni‘ihau, Kaua‘i, O‘ahu, Moloka‘i, Lana‘i, Maui, Kaho‘olawe, and Hawai‘i) (Norris and Dohl 1980, Mobley *et al.* 2000). Previous studies that included spinner dolphin abundance and movements in the main Hawaiian Islands were primarily focused on animals located off the Kona Coast of Hawai‘i Island (Norris and Dohl 1980, Norris *et al.* 1994; Östman 1994, Östman *et al.* 2004) and the leeward coasts of O‘ahu (Lammers 2004). No previous studies have looked at the interisland movements of spinner dolphins within the main Hawaiian Islands.

The Pacific Islands Photo-Identification Network (PIPIN) was formed as a collaborative effort of researchers, working within the Hawaiian Islands, who were either directly focused on or opportunistically taking photos of spinner dolphins. The PIPIN project was initiated to organize the existing photo data to create a main Hawaiian Islands photo-identification catalog of spinner dolphins that could be used to address relevant questions about spinner dolphin life history and to identify existing data gaps. The objectives of this study were to estimate the abundance of the three main Hawaiian Islands stocks using mark-recapture methods and to analyze the intra- and inter-island movements of the cataloged individuals within the main Hawaiian Islands. Mark-recapture estimates of spinner dolphin abundance in the main Hawaiian Islands presently do not exist, but are important for managing the newly defined spinner dolphin stocks. Information on the movements of individuals can be used in conjunction with the existing genetic data to further refine the current stock boundaries.

METHODS

PIPIN Data and Spinner Dolphin Catalogs

Seven organizations (Cascadia Research Collective, Hawai'i Association for Marine Education and Research, Hawai'i Institute of Marine Biology, Hawai'i Marine Mammal Consortium, Kula Nai'a Foundation, Pacific Islands Fisheries Science Center, and The Dolphin Institute) contributed approximately 16,000 photos from over 200 sightings of spinner dolphins within all the main Hawaiian Islands, except Moloka'i, between 2001 and 2009 (Table 1; Fig. 2). From these photos, catalogs of individuals

were created for each island. Each cropped photo of a unique dorsal fin was given a quality rating (1-3; 1=highest, 3=lowest) based on the angle of the fin and the focus, clarity, and contrast of the image. In addition, each dorsal fin was given a distinctiveness rating (1-3; 1=very distinct, 3=not distinct) based on the number and size of nicks and notches (*i.e.*, features considered to be permanent) on both the leading and trailing edges. These two ratings are independent of one another (see Read *et al.* 2003). An individual was entered into the catalog under the following conditions: 1) an associated photo had a quality rating of 1 and a distinctiveness rating of 1-2, or 2) an associated photo had a quality rating of 2, a distinctiveness rating of 1-2, and the individual was seen more than one time. Both left and right sides of fins were used. Only sightings of cataloged (*i.e.*, distinctive) individuals with a quality rating of 1 or 2 were utilized in subsequent analyses.

Abundance Estimation

Both open and closed mark-recapture models can be used for abundance estimation (see Nichols 1992 for overview), with the latter requiring that births, deaths, immigration, and emigration do not occur in the population during the study period. Given that the sighting data for some islands span up to six years (Table 1), it is unrealistic to assume population closure for a study period of this length. However, the continuous and variable occurrence of sighting data within and between years did not provide a cohesive framework for open population modeling. Further, closed capture estimates of abundance are generally less biased and more precise because heterogeneity

in capture probability can be accounted for in closed models (Kendall *et al.* 1995). Therefore, closed models were employed to estimate spinner dolphin abundance for periods of sightings spanning one to three months. Study periods of these lengths allowed for a sufficient number of accrued sightings, while remaining consistent with spinner dolphin life history and other dolphin abundance studies (*e.g.*, Wilson *et al.* 1999, Read *et al.* 2003) in terms of population closure.

A preliminary assessment of the spatial and temporal distribution of survey effort and dolphin sightings indicated that the available data would not support estimating island-wide abundance for each time period and island represented in the study. However, an adequate number and concentration of sightings were available to pursue abundance estimation for the leeward portions of three islands encompassing six time periods: 1) Kaua'i in October-November 2005, 2) O'ahu in June-July 2002 and July-September 2007, and 3) Hawai'i Island in May-July 2003, January-March 2005, and January-March 2006 (Fig. 3). While survey effort in the abundance estimation study areas was not systematic, there was wide-ranging coverage of these areas. Additionally, a qualitative examination of dolphin resightings in each area revealed that movements of at least some individuals spanned the length of the area over daily timescales (consistent with the quantitative movement analyses; see Table 4). Given the broad spatial extent of survey effort and individual dolphins, these areas were considered suitable for abundance estimation. Nonetheless, the estimates were expected to be impacted by variability in effort characteristics and individual movement patterns.

A sensitivity analysis was conducted to determine an appropriate estimation framework for the sighting data in terms of the number and duration of capture occasions (*i.e.*, the time interval over which an individual is recorded as sighted or not sighted). To achieve precise and reasonable results, Otis *et al.* (1978) recommended that the number of capture occasions within the period of closure be maximized, while ensuring high capture probability of individuals. The sensitivity analysis indicated that capture probabilities associated with each of the six abundances remained above a minimum threshold of 0.1 (Otis *et al.* 1978) with at least three capture occasions, but not more than three, if occasion duration was less than approximately 20 days. Thus, although the estimation framework was determined retrospectively, a single systematic approach was applied to all islands.

The abundance estimation relied on the following assumptions: 1) the estimated population portion was closed to births, deaths, immigrants, and emigrants within the study period; 2) individual dolphins were correctly identified at each capture occasion and their identification marks were not lost; 3) photo-identification efforts in one occasion did not affect capture probability in future occasions; and 4) capture probability of individuals was equal over all occasions. The last assumption is commonly violated in cetacean mark-recapture studies due to various sources of heterogeneity (Hammond 1986), including survey effort and individual behavior (*e.g.*, space use, movements, social affiliations). Not accounting for heterogeneity in capture probability leads to underestimates of abundance. Data were not available to quantify metrics of survey effort and dolphin behavior that could be used in explicit models of capture probability.

Finite mixture models offer a tool for modeling unspecified individual heterogeneity in capture probability (Pledger 2000). However, a preliminary analysis revealed that these models did not perform well in any of the six estimations, presumably because the number of available capture occasions was less than recommended (Conn *et al.* 2006).

Consequently, analysis was restricted to comparison of models incorporating time variation by capture occasion to models of constant capture probability. Thus, for each of the six study periods, two maximum likelihood estimates of abundance were obtained, one for each capture probability model. The models were weighted according to values of Akaike's Information Criterion corrected for small sample size (AICc). The weights were used to produce model-averaged estimates of abundance, which accounted for model uncertainty. The analysis was conducted using Program MARK (White and Burnham 1999), as interfaced through the RMark package (Laake 2011). As the resulting estimates applied only to distinctive individuals, total abundance was estimated as:

$$\hat{N}_{total} = \frac{\hat{N}_{dist}}{\hat{\theta}}$$

where \hat{N}_{total} is the estimated abundance of all individuals (distinctive and non-distinctive) associated with the study area during the study period, \hat{N}_{dist} is the model-averaged mark-recapture estimate of distinctive individual abundance, and $\hat{\theta}$ is the estimated proportion of distinctive individuals. As \hat{N}_{dist} and $\hat{\theta}$ are independent estimates, the variance of \hat{N}_{total} was estimated using the delta method as follows:

$$\text{var}(\hat{N}_{total}) = \hat{N}_{total}^2 \left(\frac{\text{var}(\hat{N}_{dist})}{\hat{N}_{dist}^2} + \frac{1 - \hat{\theta}}{n\hat{\theta}} \right)$$

where n is the total number of individuals used to estimate $\hat{\theta}$ (see below). Lognormal 95% confidence intervals (Burnham *et al.* 1987) for \hat{N}_{total} were then computed.

The proportion of distinctive individuals, $\hat{\theta}$, was estimated using the method of Wilson *et al.* (1999). That is, for each group, all high quality photographs were used to determine the numbers of distinctive and non-distinctive individuals, which were then summed over all groups. Secondary and ephemeral identification features such as scars, scratches, and skin coloration were utilized to differentiate non-distinctive individuals within a group. The summed value of distinctive individuals was divided by the sum of distinctive plus non-distinctive individuals (n) to produce $\hat{\theta}$. Ideally, a separate $\hat{\theta}$ would have been determined for each island and study period (*e.g.*, Wilson *et al.* 1999). However, a comparison of group size estimates to the number of photographs taken per group suggested that not all individuals present in each group were photographed, a requirement of the $\hat{\theta}$ estimation method (Wilson *et al.* 1999). In order to ensure that $\hat{\theta}$ was estimated as accurately as possible, only groups where the number of photographs taken was approximately four times the estimate of group size were incorporated, a level providing a high assurance that all individuals present were documented (Würsig and Jefferson 1990). A total of 38 groups (Kaua‘i: 13, O‘ahu: 23, Hawai‘i Island: 2; 27.3% of groups available for the three islands) met this criterion. Given the limited number of representative groups, only one $\hat{\theta}$ was computed and applied to each of the six estimates of \hat{N}_{dist} .

Individual Movements

Two methods were used to analyze the movement patterns of individual spinner dolphins in the main Hawaiian Islands. These methods include the measurement of straight-line distances between sighting locations and the estimation of standard distance deviations around mean sighting locations.

For each individual seen on more than one occasion, straight-line distances between sightings locations were measured (in km) within ArcGIS 9.3. The time (in days) and movement rate (km/day) between sightings were then calculated. The movement rate is therefore the straight-line distance between two sighting locations divided by the period of time between those sightings and is not intended to represent the actual rate of travel of the individual. Both intra- and inter-island movements were measured when appropriate.

To assess the site fidelity of particular individuals, measurements of standard distance deviations were computed using ArcGIS 9.3. The standard distance deviation (S_{XY}) measures the dispersion of an individual's positions from their mean center as follows:

$$S_{XY} = \sqrt{\frac{\sum (X_i - \bar{X})^2 + \sum (Y_i - \bar{Y})^2}{N - 2}}$$

where X_i and Y_i are the coordinates of the projected location (in meters) of each individual dolphin, \bar{X} and \bar{Y} are the means of each coordinate, and N is the total number of times an individual animal was sighted. Larger values of S_{XY} indicate higher dispersal of individuals and therefore lower affinity to a particular area. Only those individuals seen four or more times and in multiple years were used in the assessment of S_{XY} .

RESULTS

PIPIN Data and Spinner Dolphin Catalogs

The resulting 2001-2009 photographic catalog of spinner dolphins in the main Hawaiian Islands consists of 673 individuals. The sizes of the catalogs at each island range from 11 to 215 individuals (Table 1). The largest catalogs are from O‘ahu, Hawai‘i Island, and Kaua‘i (>150 individuals in each). The greatest effort (days on the water) and number of resights of individuals also occurred at these three islands (Table 1).

Table 1. Summary of the cataloged spinner dolphins by main Hawaiian island including the number of individual sightings, the years sightings occurred, the number of days spinner dolphins were photographed, and the PIPIN contributors (CRC-Cascadia Research Collective, HAMER-Hawai‘i Association for Marine Education and Research, HIMB-Hawai‘i Institute of Marine Biology, HMMC-Hawai‘i Marine Mammal Consortium, KNF-Kula Nai‘a Foundation, PIFSC-Pacific Islands Fisheries Science Center, TDI-The Dolphin Institute).

Island	# Cataloged Individuals	# Individual Sightings	Years	Days on Water	PIPIN Contributors
Ni‘ihau	34	37	2003, 2005, 2007	6	CRC, PIFSC
Kaua‘i	153	221	2003-2006	22	CRC, HAMR
O‘ahu	196	524	2001-2003, 2005-2007, 2009	34	CRC, HIMB, PIFSC, TDI
Lana‘i	11	13	2001, 2003, 2006-2007	5	CRC, HAMR
Maui	49	68	2003-2004, 2006-2007	14	HAMR, TDI
Kaho‘olawe	15	15	2001	1	CRC
Hawai‘i	215	460	2003-2007	50	CRC, KNF, HMMC

Abundance Estimation

Study periods for the six estimations ranged in duration from 29 to 87 days (median=57), with most periods encompassing only three capture occasions (Table 2). The number of individuals identified in each study period ranged from 50 to 146 dolphins (median=84; Table 3) and did not appear to level off substantially for any of the study periods (Fig. 4). Models of time-varying capture probability generally received the highest AICc weights during the estimation process, but data associated with two study periods (O‘ahu in 2002 and Hawai‘i in 2005) did not support the added model complexity (Table 3). The proportion of distinctive individuals for all study periods was estimated as $\hat{\theta} = 0.46$ (SE=0.01), which was applied to each \hat{N}_{dist} to produce the following values of \hat{N}_{total} for leeward portions of Kaua‘i – 559 (CV=0.19) in October-November 2005; O‘ahu – 149 (CV=0.12) in June-July 2002 and 330 (CV=0.05) in July-September 2007; and Hawai‘i Island – 733 (CV=0.15) in May-July 2003, 260 (CV=0.20) in January-March 2005, and 190 (CV=0.15) in January-March 2006 (Table 3).

Table 2. Summary of study periods and capture occasions (CO) used for spinner dolphin abundance estimation on leeward portions of three main Hawaiian Islands.

Island	Year	Study period (mm/dd- mm/dd)	Period duration (days)	No. CO	CO duration (days)	No. surveys	No. Individuals Identified
Kaua‘i	2005	10/12-11/10	29	3	10	9	107
O‘ahu	2002	06/23-07/27	34	3	11	11	50
O‘ahu	2007	07/12-09/12	62	3	21	10	135
Hawai‘i	2003	05/04-07/30	87	4	22	18	146
Hawai‘i	2005	01/08-03/03	54	3	18	8	60
Hawai‘i	2006	01/27-03/28	60	3	20	9	60

Table 3. Closed capture estimates of seasonal spinner dolphin abundance (\hat{N}_{total}) for leeward portions of three main Hawaiian Islands. \hat{N}_{dist} is the mark-recapture estimate of distinctive individuals that resulted from averaging over constant (.) and time-varying (time) models of capture probability (p). $\hat{\theta}$ is the estimated proportion of distinctive individuals.

Island	Year	Months	Selected model	AICc Weight	\hat{N}_{dist}	SE	95% CI	$\hat{\theta}$	SE	\hat{N}_{total}	SE	95% CI
Kaua'i	2005	Oct-Nov	$p(\text{time})$	0.999	256	47	187-384	0.46	0.01	559	105	388-804
O'ahu	2002	Jun-Jul	$p(\cdot)$	0.708	68	8	57-94	0.46	0.01	149	18	117-189
O'ahu	2007	Jul-Sep	$p(\text{time})$	0.898	151	6	143-167	0.46	0.01	330	16	300-362
Hawai'i	2003	May-Jul	$p(\text{time})$	1.000	336	49	260-462	0.46	0.01	733	110	547-984
Hawai'i	2005	Jan-Mar	$p(\cdot)$	0.737	119	23	87-188	0.46	0.01	260	52	177-382
Hawai'i	2006	Jan-Mar	$p(\text{time})$	1.000	87	12	71-126	0.46	0.01	190	28	143-252

Individual Movements

Multiple individual spinner dolphins moved between sighting locations along island coastlines and between islands within stock boundaries (Fig. 5), although no movements of individuals were observed (*i.e.*, no photo-identification matches were made) between O'ahu and any of the other islands within the 4-Islands region. The mean, minimum, and maximum values of straight-line distances between sighting locations of individuals are reported in Tables 4 (intra-island) and 5 (inter-island). Off all islands in which multiple sightings occurred, some individuals were re-sighted within 1 km of a previous location, with the exception of Ni'ihau (Table 4). The maximum distance between intra-island sighting locations of any individual was 58 km along the

coast of Hawai‘i Island. A total of 18 individuals were observed moving between islands (Table 5). Four of these individuals moved between stock boundaries (Fig. 6). The maximum distance between inter-island sighting locations of any individual was 305 km (over 823 days) between O‘ahu and Hawai‘i Island (Table 5; Fig. 6). The shortest timespan between inter-island sightings was one day (spanning 43 km) between Kaua‘i and Ni‘ihau.

Table 4. Intra-island straight-line movement measurements (mean, minimum, and maximum) of spinner dolphins in the main Hawaiian Islands. Measurements used to calculate the minimum and maximum movement rates are listed in the brackets. Note that some individual dolphins are represented more than once in the calculations. A zero timespan indicates a resighting of an individual on the same day.

Island	# Individuals		Distance (km)	Movement Rate (km/day)
Ni‘ihau	3	mean:	26.00	0.03
				0.02
		min:	15.97	[26.0/1411]
		max:	36.45	[36.5/869]
Kaua‘i	55	mean:	8.03	1.89
				<0.01
		min:	0.55	[0.6/244]
		max:	33.66	[9.2/0]
O‘ahu	126	mean:	8.16	0.44
				<0.01
		min:	0.12	[0.3/2241]
		max:	37.22	[6.3/0]
Maui	10	mean:	7.56	0.35
		min:	0.00	[0.0/13]

Island	# Individuals		Distance (km)	Movement Rate (km/day)
				4.12
		max:	20.62	[1.3/88]
		mean:	0.65	<0.001
Lana'i	2	min:	0.65	<0.001 [0.7/1834]
		max:	0.65	<0.001 [0.7/1834]
		mean:	16.22	0.35
Hawai'i	142	min:	0.00	0 [0.0/33]
		max:	57.54	23.17 [46.3/2]

Table 5: Individual inter-island straight-line movement measurements (mean, minimum, and maximum) of spinner dolphins in the main Hawaiian Islands. Note that some individual dolphins are represented more than once in the calculations. Measurements used to calculate the minimum and maximum movement rates are listed in the brackets.

Islands	# Individuals		Distance (km)	Movement Rate (km/day)
		mean:	50.80	6.25
Kaua'i-Ni'ihau	6	min:	36.77	0.08 [72/868]
		max:	72.15	42.86 [43/1]
		mean:	198.85	0.31
O'ahu-Ni'ihau	1	min:	198.85	0.31 [199/640]
		max:	198.85	0.31 [199/640]
		mean:	39.60	0.04
Kaho'olawe- Maui	5	min:	39.31	0.02 [39/1833]
		max:	39.67	0.05 [40/786]
		mean:	24.82	0.02
Maui-Lana'i	3	min:	13.13	0.01 [13/1080]
		max:	40.80	0.03 [41/1414]

Islands	# Individuals		Distance (km)	Movement Rate (km/day)
		mean:	156.22	0.24
Hawai'i-Lana'i	1	min:	154.63	[155/1031]
		max:	157.80	[158/493]
		mean:	289.91	0.29
Hawai'i-O'ahu	2	min:	275.68	[290/1500]
		max:	304.93	[287/745]
		mean:		0.19

The criterion for the measurement of the standard distance deviation (*i.e.*, 4 or more sightings per individual over multiple years) limited the analysis to O'ahu and Hawai'i Island. Forty four O'ahu individuals and 29 Hawai'i Island individuals met the criterion. Measurements of standard distance deviation (S_{XY}) demonstrated that the majority (89%; n=39) of the 44 individuals used in the analysis off O'ahu had a S_{XY} of 10 km or less from their mean center location, 56% (n=25) had a S_{XY} of 5 km or less, and none of the individuals had a S_{XY} of 15 km or greater (Fig. 7). Of the 29 individuals used in the analysis from Hawai'i Island, 34% (n=10) had a S_{XY} of 5 km or less from their mean center location, 59% (n=17) had a S_{XY} greater than 10 km, and 45% (n=14) of the individuals had a S_{XY} of 15 km or greater (Fig. 8).

DISCUSSION

PIPIN Data and Spinner Dolphin Catalogs

The PIPIN project is the first collaborative photo-identification study of spinner dolphins in the main Hawaiian Islands. The compilation of sighting data and the creation of the island photo-identification catalogs from multiple research groups increased the

scope of the study area and time period that could be addressed by any single group. This type of collaborative effort was the only means by which the inter-island movements of spinner dolphins could presently be investigated.

The spinner dolphin photo-identification catalogs for some of the islands are small (Table 1), which is most likely a reflection of the amount of survey effort around those islands rather than the actual number of distinctive individuals. More than half of the photos are off of O‘ahu and Hawai‘i Island, where five of the seven PIPIN contributors are based. Research effort was focused on the leeward (west and southwest) sides of the islands (Fig. 2), where the waters are typically calmest. The predominant winds are northeast trade winds and are relatively constant year-round, making sighting and working conditions less favorable on the north and east coasts. Currently, no data exist in the PIPIN catalog for the island of Moloka‘i.

It is clear from aerial surveys that spinner dolphins are found on all coasts of the main Hawaiian Islands (Norris and Dohl 1980, Norris *et al.* 1994, Mobley *et al.* 2000). Concerted photo-identification effort is needed along all shores of all islands in order to increase the number of individuals within the main Hawaiian Islands catalog, which would allow for assessments of abundance and movement over broader spatial scales.

Abundance Estimation

The mark-recapture abundance estimation relied on several assumptions and possible violations to these assumptions merit consideration. First, the portion of the population estimated was assumed to be demographically and geographically closed

during the study period. Spinner dolphins are characterized by low reproductive rates (Perrin and Gilpatrick 1994). While spinner dolphin natural mortality rates are unknown, cetaceans generally have high rates of survival. Thus, the few, if any, births and deaths that might have occurred during the one- to three-month study periods were not likely to have biased the estimation. Given known patterns of spinner dolphin distribution and movements (Norris and Dohl 1980, Norris *et al.* 1994, Mobley *et al.* 2000, Lammers 2004, this study), it is probable that some individuals entered and left the study areas (Fig. 3) during the study periods. However, Kendall (1999) found that random movement in and out of a study area does not bias estimates from closed capture models, although precision is decreased, which suggests that geographic closure violations are not of concern in this case. To evaluate the effect of possible closure violations due to study period length, the two longest study periods (*i.e.*, O‘ahu in 2007 and Hawai‘i Island in 2003) were reanalyzed using only sightings from the first half of the study period. The resulting abundance estimates were not significantly different from the full-period estimates, but were less precise. Specifically, the O‘ahu 2007 half-period point estimate was 7% lower than the full-period estimate, but 1.4 times less precise. The Hawai‘i Island 2003 half-period point estimate was 18% higher than that of the full period, but 2.2 times less precise. Thus, the study period lengths used in this analysis did not appear to engender significant net gains or losses in individuals and the resulting estimates were regarded as robust to closure violations.

Violations of the second key assumption, that individual dolphins were correctly identified based on persistent marks, were considered unlikely given the use of only

photos with ratings of quality 1 and 2, the utilization of only distinctive individuals in the estimation, and the short durations of the study periods. Regarding the third key assumption, independence of capture probabilities, the non-invasive “capture” of individuals using photo-identification was not expected to influence subsequent capture probabilities, a determination consistent with other dolphin studies (*e.g.*, Wilson *et al.* 1999, Read *et al.* 2003). Finally, violations to the equal capture probability assumption were anticipated (Hammond 1986), but could only be minimized by employing time-varying capture probability models, which were not well supported by the data in all cases (Table 3). Even with time variation accounted for, this assumption implies that capture probabilities were equal in all other respects, which was unlikely because of heterogeneity in survey effort and dolphin behavior. Given this remaining heterogeneity, the estimated abundance of individuals associated with each of the six study periods is presumed to be negatively biased, although to what degree is unknown.

The resulting abundance estimates were strongly influenced by the estimated proportion of distinctive individuals. If the proportion of distinctive individuals is less (more) than presently estimated, then abundance was underestimated (overestimated) accordingly. While this proportion was obtained using a standard method (Wilson *et al.* 1999), available data only permitted the determination of one estimate that was applied to all study periods. Thus, if this proportion varies seasonally, or more conceivably, by island, such variation was not accounted for in the abundance estimates. The estimated proportion indicated that approximately 46% of individuals off Kaua‘i, O‘ahu, and Hawai‘i Island have distinctive dorsal fins. This percentage is similar to estimates made

for some populations of bottlenose dolphins (*Tursiops truncatus*), which generally consist of at least 50% distinctive individuals (Würsig and Jefferson 1990). However, the percentage is substantially higher than a previous estimate of 20% for Hawaiian spinner dolphins (Norris *et al.* 1994), although it is possible that mark rates have increased since the time of that study. Östman (1994) noted that the yearly average of the percent of identified individuals per school in his study increased every year and did so dramatically over a one-year period (from 29.0% to 40.7%) when he changed photographic equipment and began using a camera with an autofocus lens.

Despite the various biases and limitations, the estimates reported here offer insight into the magnitude of recent spinner dolphin abundance on three main Hawaiian Islands. For example, the estimates suggest that island stocks are currently comprised of at least several hundred individuals, with likely variation between islands. Previous estimates of abundance for the Hawai'i Island spinner population were derived from photo data that was collected from May 1979 to October 1980 and 2 weeks in June 1981 (minimum of 960; Kona coast, primarily Kealahou Bay) (Norris *et al.* 1994) and then again in 1989-1992 (2,334; north-central Kona coast) (Östman 1994) and March-November 2003 (855-1,001; western coast) (Östman-Lind *et al.* 2004). These estimates were made by the following calculation:

$$\frac{\# \textit{identified individuals}}{\textit{average \% of individuals identified per school}}$$

which does not account for unobserved individuals or uncertainty in the estimates. All of these abundance estimates are larger than those of the current study. It is unknown

whether this is related to an actual decrease in abundance or to differences in the size and location of the study areas and/or the time periods for which the estimates were made.

An abundance estimate of spinner dolphins within 46 km (25 nmi) of the main Hawaiian Islands (3,184; CV=0.37) came from aerial surveys conducted in February-April of 1993, 1995, and 1998 (Mobley *et al.* 2000). The most recent estimate of abundance for spinner dolphins in the main Hawaiian Islands (1,488; CV not provided) comes from a ship line-transect survey conducted in August-November 2002 (Barlow 2006). The estimates from the present study indicate that spinner dolphin numbers along leeward coasts vary seasonally within islands, at least for Hawai‘i Island. Of the three periods for which estimates were made, May-July 2003 was the highest (733; CV=0.15). This estimate was nearly 3 and 4 times that of the other two periods, both of which were in the winter season; 260 (CV=0.20) in January-March 2005 and 190 (CV=0.15) in January-March 2006 (Table 3). Norris *et al.* 1994 observed a shift in the distribution of spinner dolphins from the Kona (leeward) coast in summer to the south and east coasts of Hawai‘i Island in winter and related it to seasonal changes in wind and swell. Winters in the Hawaiian Islands are characterized by large swells on the north and west shores that are produced by storm systems in the northwestern Pacific. Studies in other parts of the world have demonstrated seasonal changes in spinner dolphin usage of particular bays or coastlines related to wind direction (Poole 1995) and water turbidity from runoff (Gannier and Petiau 2006, Silva and Silva Jr. 2009). Thus, the present abundance estimates may reflect the seasonal shift described by Norris *et al.* (1994).

Clearly, more accurate and comprehensive estimates of abundance are needed for main Hawaiian stocks of spinner dolphins. The estimation framework and inferences presented here can serve as a useful reference for such future efforts.

Individual Movements

During the period of this study, individual spinner dolphins within the main Hawaiian Islands moved between most of the surveyed areas along island coastlines (Fig. 5). The measured distances between dolphin sighting locations are considered minimum distances because the true path taken by each individual is unknown and the shapes of the coastlines were not taken into consideration (Table 4; Fig. 5). Individuals radiotagged off the Kona Coast of Hawai‘i Island in 1979 and 1980 traveled distances of 20-70 km along the shore over periods of two to six days (Norris *et al.* 1994).

It is probable that individual spinner dolphins at all islands travel to other sides of the islands as was observed in this study at Ni‘ihau, Kaua‘i and O‘ahu (Fig. 5). Norris *et al.* 1994 documented the movement of one individual from the Kona Coast of Hawai‘i Island to the east coast of the island south of Hilo (~200 km). It is also possible that some individuals may circumnavigate an island (particularly the smaller islands). During his study on the Island of Mo‘orea in French Polynesia, Poole (1995) observed all but 2 of the identified and most frequently sighted spinner dolphins (n=41) along all sides of the island. Mo‘orea’s coastline is a total distance of 60 km, which is similar to that of Kaho‘olawe.

A small number of individuals (14) moved between islands within current stock boundaries (Fig. 5). No movements were observed between O‘ahu and the 4-Islands

region, which is considered to encompass one stock. It is possible that individuals were moving between these islands but the existing data did not capture the movements. No data were available from Moloka'i and the data were limited from Maui, Lana'i, and Kaho'olawe. Each of these photo-identification catalogs has fewer than 50 individuals. An increase in the catalog sizes at these islands would help to elucidate the degree to which movement occurs between O'ahu and the 4-Islands region. Andrews *et al.* 2010 observed that the highest spinner dolphin gene flow within the Hawaiian Islands occurred at the smallest islands (e.g., Ni'ihau, Kaua'i, O'ahu) and suggested that this may be related to fewer available resources, increased competition and therefore increased movement between islands.

An interesting finding of this study was the movement of two individuals between the islands of O'ahu and Hawai'i (Fig. 6). One of these individuals was seen in both May and July 2003 off of Hawai'i Island and was then seen twice in August 2007 off of O'ahu (a distance of ~300 km). The other individual was seen first in July 2003, seen again in January 2005 off of Hawai'i Island and later seen in August and September 2007 off of O'ahu (a distance of ~290 km). The two animals were never seen together and there is no record of either returning to their original sighting locations. It is unknown whether these two individuals moved between these islands at a greater frequency. Given the movement of the individual that traveled 43 km in one day between Kaua'i and Ni'ihau, it is reasonable to speculate that a spinner dolphin could travel the 300 km distance over a period of a week. Spinner dolphins tagged in the eastern tropical Pacific traveled 20 km in 16 hrs (Perrin and Gilpatrick 1994). A spinner dolphin radiotagged off the Kona Coast

of Hawai'i Island traveled 30 km along the coastline in less than 24 hr (Norris *et al.* 1994). However, this individual, as well as two other radiotagged individuals traveled no more than 14 km from shore (Norris and Dohl 1980, Norris *et al.* 1994). The significant genetic differentiation between the spinner dolphins of O'ahu and those of Hawai'i Island (Andrews *et al.* 2010) suggests that the occurrence of movements between these islands is low, or at least genetic exchange between travelling individuals and local individuals is rare. A study on the movements (using photo-identification) and genetics of Gray's spinner dolphins within the Society Archipelago, French Polynesia demonstrated low levels of interchange between neighboring islands resulting in genetic distinctions between islands as close as 17 km (Oremus *et al.* 2007)

The results of the standard distance deviation calculations suggest that those spinner dolphins used in the analysis off of O'ahu have higher site fidelities than those off Hawai'i Island (Fig. 7 and 8). Overall there were a greater number of resights of individuals along the O'ahu coast compared to Hawai'i Island. Twenty-nine O'ahu individuals and 11 Hawai'i Island individuals were seen at least five times. Of the 29 and 11 individuals, 10 (34%) and 3 (27%), respectively, had S_{XY} of 5 km or less. There were 8 O'ahu individuals and no Hawai'i Island individuals that were seen 8 or more times over the course of the study period. Of the 8 O'ahu individuals, 4 (50%) had S_{XY} of 5 km or less. Additional evidence of the higher site fidelity of O'ahu spinners comes from the measurement of the mean distance between sighting locations at each island, which includes all individuals seen more than once. Off of O'ahu, the mean distance between resight locations was 8 km while that off of Hawai'i Island was 16 km (Table 4).

It is possible that the reported results are an artifact of sampling given the larger span of the study area along the coast of Hawai'i Island. The effort (days on the water) was greater and the spinner dolphin sighting rate was higher (1.9/day) off Hawai'i Island than off O'ahu (1.4/day). The greater access to dolphin movement and more individuals off Hawai'i Island may have translated into lower resights of individuals and lower estimates of site fidelity.

From a photo-identification analysis of 38 cataloged individuals that were resighted 27 times Norris and Dohl (1980) concluded that spinner dolphins off the Kona Coast of Hawai'i Island were not resident to any particular location. The data from the radiotagged individuals also demonstrates the spinner dolphin's tendency to move between locations along the Kona Coast (Norris *et al.* 1994). In addition, Norris *et al.* 1994 described the dynamics of the Hawai'i Island spinner dolphin population as fluid, in which individuals move into and out of groups and group sizes change regularly. Lammers (2004) observed this same phenomenon off the coast of O'ahu while visually tracking spinner dolphin groups as the composition of groups changed over a period of a few hours.

Along O'ahu's Waianae (west) Coast, Lammers (2004) observed a diurnal pattern in the distribution of spinner dolphin sightings. In the early mornings, spinner dolphins were concentrated along the northern and southern portions of the coast, but the dolphins spread out along the coast as the day progressed. A different pattern was observed along the south shore of O'ahu in which dolphin's showed no preference for a particular site during the day (Lammers 2004). On both O'ahu coasts spinner dolphins displayed an

affinity for a depth contour of 10 fathoms (18.3 m). In this study, the photo-identification effort was concentrated along the west coast of O‘ahu. Greater coverage along the south shore may reveal a similar pattern of site fidelity, as was observed off of Hawai‘i Island.

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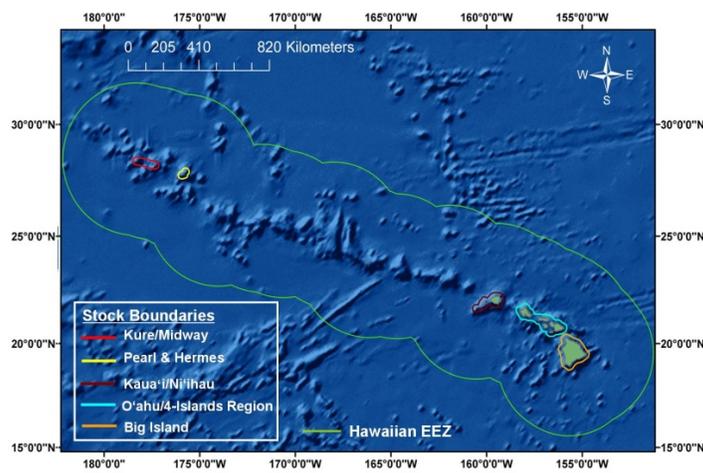


Figure 1. Newly defined insular Hawaiian spinner dolphin stocks based on genetic analyses of Andrews *et al.* 2010. A sixth stock encompasses animals in the same areas but more than 18.5 km (10 nmi) offshore and animals at all other locations within the Northwestern Hawaiian Islands.

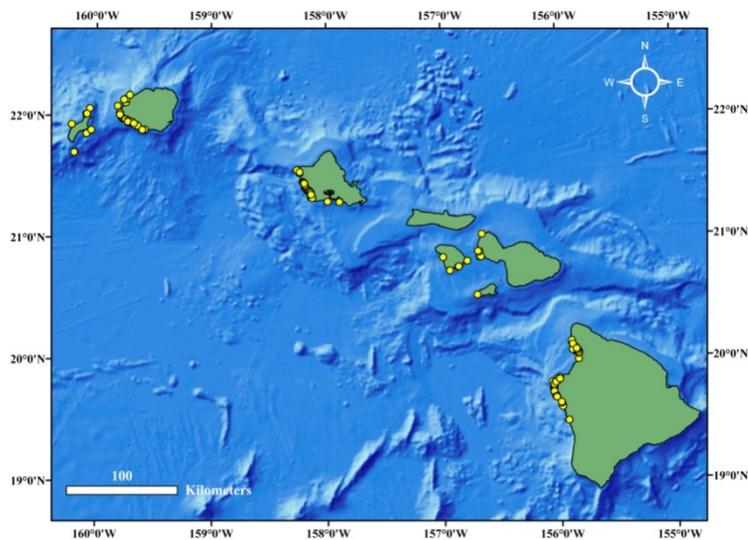


Figure 2. The locations of PIPIN spinner dolphin sightings (yellow dots) within the main Hawaiian Islands in which photographs were collected. The islands from west to east are Niʻihau, Kāuaʻi, Oʻahu, Molokaʻi, Lanaʻi, Maui, Kahoʻolawe, and Hawaiʻi.

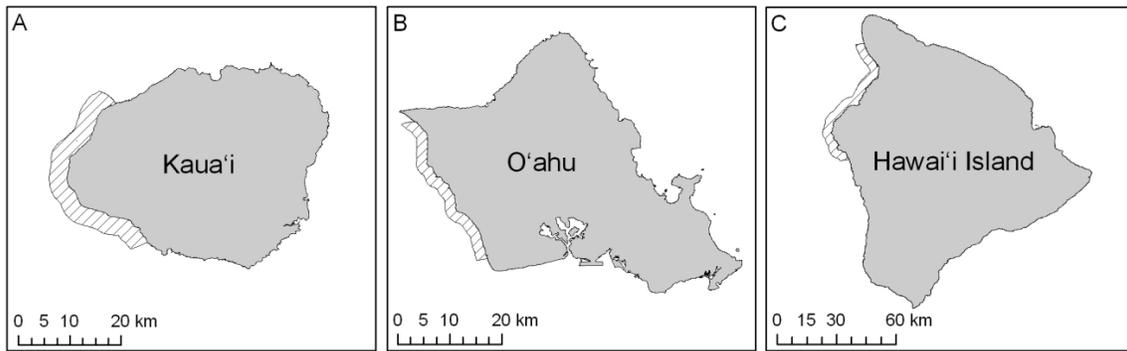


Figure 3. Abundance estimation study areas (denoted by hatched lines) on leeward portions of Kaua'i (A), O'ahu (B), and Hawai'i Island (C). Study areas were defined spatially by the extent of sighting concentrations and are characterized by broad spatial coverage of survey effort and individual dolphins. Resulting abundances apply only to these areas and should not be considered island-wide estimates.

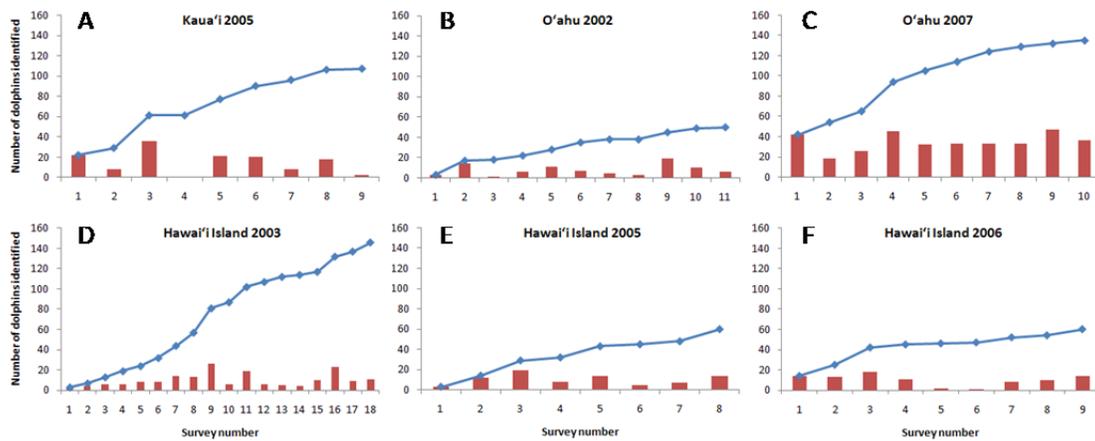


Figure 4. Number of individual dolphins sighted per survey (bars) and cumulative number of individuals identified (lines) on Kaua'i in Oct-Nov 2005 (A), O'ahu in June-July 2002 (B) and July-September 2007 (C), and Hawai'i Island in May-July 2003 (D), January-March 2005 (E), and January-March 2006 (F).

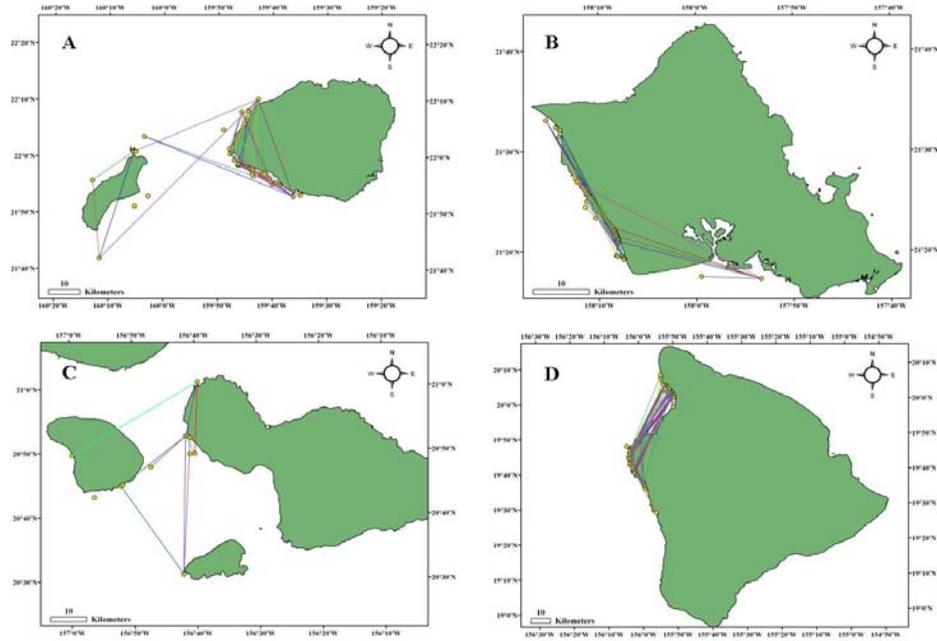


Figure 5. Intra- and inter-island spinner dolphin movements within main Hawaiian stock boundaries: (A) Ni‘ihau and Kaua‘i; (B) O‘ahu; (C) Lana‘i, Maui and Kaho‘olawe; (D) Hawai‘i Island. Spinner dolphins off O‘ahu (B) Lana‘i, Maui and Kaho‘olawe (C) are the same stock. Lines connecting sighting locations may represent more than one individual.

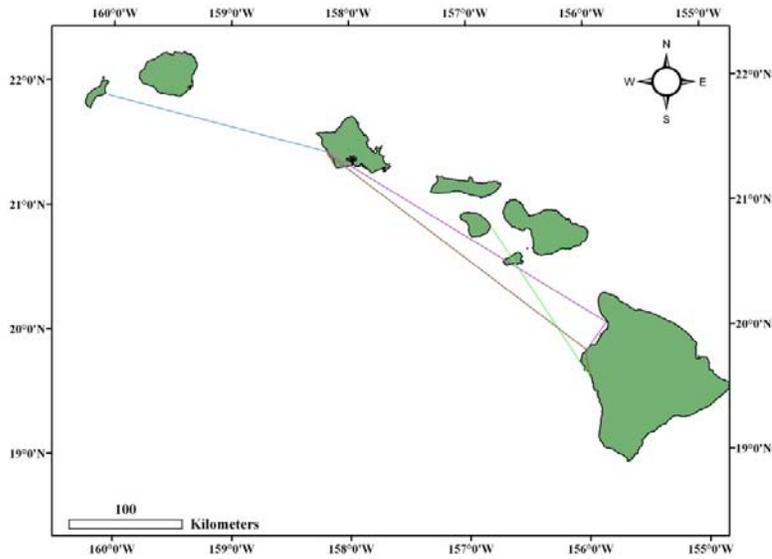


Figure 6. Movements of four individuals between stock boundaries. Each individual is represented by a different colored line.

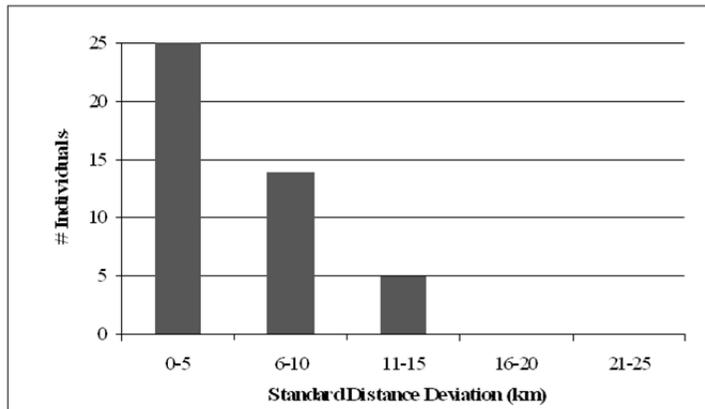


Figure 7. Standard distance deviations of individual spinner dolphins (n=44) from their mean sighting locations off O‘ahu.

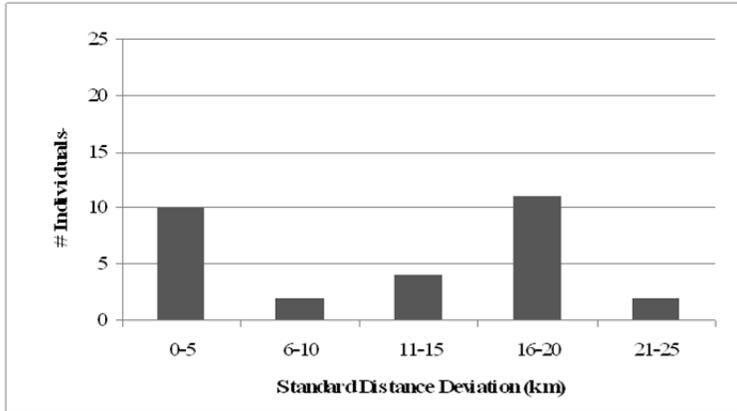


Figure 8. Standard distance deviations of individuals spinner dolphins (n=29) from their mean sighting locations off Hawai'i Island.