FINAL REPORT

ABUNDANCE AND POPULATION STRUCTURE OF HUMPBACK WHALES IN THE NORTH PACIFIC BASIN

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EXECUTIVE SUMMARY

This project examined the abundance and population structure of humpback whales in the North Pacific and was the result of the collaboration of researchers from 16 independent studies. Locations sampled included three wintering regions (Mexico, Hawaii and Japan) and feeding areas from California to the Aleutian Islands. Photographs taken between 1991 to 1993 (later expanded to include 1990 for Mexico) were selected because samples throughout the entire North Pacific were the largest and the most complete during this period. Of the 6,414 photographs, 3,650 were selected based on photographic quality for the sample used in the comparison (including photographs from Mexico from 1990). Two matching teams made independent comparisons of the entire collection to identify resightings of the same whale. Several methods to evaluate their success in finding photographic matches revealed that 93-99% of matches were correctly found. A total of 2,712 (2,993 without inter-regional duplicates) different individual whales were determined to be present in the sample.

The study provided new insights into the movements and population structure of humpback whales in the North Pacific. Although there was some interchange among the three wintering regions, it occurred only at a very low rate. While there was considerable mixing among the three subareas sampled off the Hawaiian Islands, interchange was more structured among the subareas in Mexico and Japan. In all three wintering regions, migrations from multiple feeding areas were documented. Whales identified at some feeding areas showed a clear preference for particular wintering regions (whales that fed off southeastern Alaska tended to migrate to Hawaii and whales that fed off California to Mexico) while at other feeding areas, animals tended to travel to multiple wintering areas. Whales identified off British Columbia, for example, showed a similar rate of interchange with all three wintering regions. Whales showed a strong site fidelity to specific feeding areas, although the near continuous distribution of whales along their feeding range and the limited sampling of most areas makes defining these feeding areas difficult.

Abundance estimates were determined using several geographically stratified capture-recapture models. Two models (Darroch and Hilborn) that incorporate migration rates among wintering areas, yielded estimates of approximately 6,000 humpback whales (4,000 for Hawaii, 1,600 for Mexico, and 400 for Japan). Probable sources of downward bias to these estimates included a skewed sex ratio towards males sampled on the wintering areas and other sources of heterogeneity of capture probabilities such as from geographic sampling bias. Alternate Petersen capture-recapture estimates of the abundances of humpback whales in the wintering areas using whales initially captured on the feeding areas yielded slightly higher estimates for Hawaii (5,200) and dramatically higher estimates for Mexico (4,200). The disparity in the estimates for Mexico are likely the result of the uneven sampling among the three subareas and the stratification of movements among them. The true abundance for Mexico may be between these values which would be consistent with the estimates of 2,200-2,800 from other studies using a larger time period (Urban *et al.* 1994, In prep.). The best estimate of the humpback whale population in the North Pacific using data from this study was 6,010 (SE=474) based on the average of the estimates from the Darroch method. Adjustments for the effects of sex bias and use of the

alternate estimate for Mexico suggests that true abundance could be as much as 2,000 whales higher (to a total of 8,000). Expansion of this methodology to a more representative sampling of the North Pacific would improve this estimate. Nevertheless, this study shows that the North Pacific humpback whale population is well above the rough estimates of 1,400 that were made at the end of whaling in the 1960s.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) were depleted due to commercial exploitation and remain listed as endangered today. North Pacific populations were thought to have numbered about 15,000 prior to commercial exploitation in the twentieth century (Rice 1978), although this was only a rough calculation based on whaling data that may have been inaccurate. There are few precise estimates of abundance after the end of commercial whaling for humpback whales in 1966. Rough estimates have included about 1,400 (Gambell 1976) and 1,200 (Johnson and Wolman 1984), although the methods used for these estimates are uncertain and their reliability questionable.

More recently, capture-recapture (or mark-recapture) techniques using photographically identified individuals have been used to estimate the population size of humpback and other large whales (Hammond 1986). This has allowed estimates of humpback whale abundance in Hawaii (Darling and Morowitz 1986, Baker and Herman 1987, Cerchio 1994, In prep.), Mexico (Alvarez *et al.* 1990, Urban *et al.* 1994), southeastern Alaska (Baker *et al.* 1992, Straley 1994), and California, Oregon, and Washington (Calambokidis *et al.* 1990, 1993, Calambokidis and Steiger 1995). Capture-recapture techniques have not been employed in the North Pacific using data from multiple regions to estimate the abundance in the entire North Pacific basin.

Information on the geographic structure of populations is critical to assess the status and recovery of humpback whales from past exploitation. These data form an integral part in geographically stratified mark-recapture estimates and also are essential for interpreting overall estimates of population abundance. Past information on the geographic structure of humpback whale populations in the North Pacific have come from a number of sources including: 1) accounts from commercial whaling based on where whales were killed (Kellogg 1928, Tomilin 1957, Berzin and Rovnin 1966) and movements based on Discovery tags (Nishiwaki 1966, Omura and Ohsumi 1964, Ohsumi and Masaki 1975, Ivashin and Rovnin 1967), 2) movements determined from photographically identified humpback whales beginning in the late 1970s and early 1980s (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1988, Darling and Mori 1993, Urban *et al.* 1987, Calambokidis *et al.* 1989, 1996, Steiger *et al.* 1991, Darling and Cerchio 1993, Darling *et al.* 1996), 3) geographic differences in genetic patterns of humpback whales based either on mtDNA (Baker *et al.* 1990, 1994, Medrano *et al.* 1995) or nuclear DNA (Baker *et al.* 1993, In prep., Palumbi and Baker 1994), 4) geographic differences in the songs of humpback whales sung primarily on the wintering areas (Cerchio 1993, Helweg *et al.* 1990, Payne and Guinee 1983), and 5) differences in the proportion of whales with different fluke coloration patterns (Baker *et al.* 1985, 1986, Allen *et al.* 1994, Pike 1953, Rosenbaum *et al.* 1995).

Despite these studies, no clear consensus exists on the structure of humpback whale populations in the North Pacific. The International Whaling Commission considers humpback whales in the North Pacific as one "stock" for management purposes (Donovan 1991). The mounting evidence of at least some intermixing among all three wintering regions has led some researchers to suggest these are one or at most two "stocks" (Darling and McSweeney 1985, Darling and Cerchio 1993, Darling *et al.* 1996). Baker *et al.* (1994) concluded that humpback whales in the eastern North Pacific could be divided into at least two groups or "stocks" based on genetic evidence: a central stock that feeds in Alaskan waters and migrates predominantly to Hawaii, and an “American” stock that feeds along the coast of California and winters off Mexico. Barlow (1994) concluded that, based on the information available and the need to define conservative population units, humpback whales in the North Pacific should be divided into four populations.

Photographic identification research has proved valuable in describing movements of animals among some wintering or feeding areas as well as describing the dynamics of movement and interchange within a region. Unfortunately, these comparisons have often been limited to a few regions and not been conducted in a way that provides a quantitative assessment of the success rate of finding matches or the rates of interchange. A centralized database and photographic archive has been established for the North Pacific humpback whales (Mizroch *et al.* 1990) which includes humpback whale identification photographs from a broad range of regions and years. It has not, however, been used to generate abundance estimates.

We report the population size and related population structure and movements of humpback whales in the North Pacific based on a large collaborative effort among 16 research groups that collected identification photographs throughout the North Pacific from 1990 to 1993. The years and collections used were designed to provide a sample distributed across the entire North Pacific Ocean that was as broad as possible. These data were used to 1) examine population structure by comparing interchange rates among regions and 2) calculate abundance estimates with capture-recapture models. Because not all areas were sampled equally and humpback whales do not move randomly among regions, we primarily employed geographically stratified capture-recapture models that took into account the complex population structure of North Pacific humpback whales.

METHODS

Selection and matching of photographs

This project was the result of the collaboration of researchers from 16 independent photo-identification studies that encompassed all regions of the North Pacific where this type of work has been done. The locations represented (Table 1, Figure 1) included three wintering regions (Mexico, Hawaii and Japan), each with two or three subareas, and feeding areas that extend from southern California to the Aleutian Islands. The years 1991 to 1993 were selected because samples throughout the entire North Pacific were the largest and the most complete during this period (whales identified in Mexico in 1990 were later added, see below). Photographs of calves, where known, were excluded because it was difficult to obtain reliable identification photographs from these animals and because markings on calf flukes have the potential to change. In all of the studies, the natural marks on the ventral side of the flukes were photographed. Field methods of most of these studies have been described (*e.g.*, Calambokidis *et al.* 1996b, Cerchio 1994, Dahlheim and Waite 1993, Darling and Mori 1993, Ladrón de Guevara 1995, Salinas *et al.* 1993, Straley 1994, Uchida *et al.* 1993, Urbán *et al.* 1987, von Ziegesar 1992, Yamaguchi *et al.* 1995).

Selection of photographs

Photographs of each individual whale identified were provided as black-and-white prints or negatives, color slides, or, in one case, access to their collection at the National Marine Mammal Lab (NMML). Custom black-and-white prints (2.5 x 3.5 in) were made for all the negatives. Internal within-year duplicates within each collection were removed when present. We began with a sample of 6,414 photographs.

Each photograph was graded and a uniform set of criteria used to select the sample of photographs used for the comparison. We also evaluated our success in finding matches with these selected photographs (described later in “Matching success”). The quality of the photograph was graded based on: the proportion of the fluke that was visible in the photograph, fluke angle (*i.e.*, how perpendicular it was to the water), the lateral angle of the photographer, the sharpness and grain, fluke size on print, and the photographic quality (lighting, exposure, and contrast). Because some of these measures were clearly subjective, photograph archetypes for the different codes were used during the grading process. Additionally, the distinctiveness of flukes (marks along the trailing edge and ventral surface) and presence of killer whale scars was also scored.

Quality and distinctiveness categories and codes were as follows:

Proportion of fluke visible
1- 100%
2- 75-99%
3- 50-74% (base of notch still visible)
4- <50%
5- right/left side only

Fluke angle:
1- perpendicular to the water
2- short of perpendicular but no loss in visibility
3- short of perpendicular w/ some loss in quality but ridging easily visible
4- low angle, ridging only partially visible
5- low angle, ridging and markings not visible or very distorted

Photographer lateral angle:
1- straight behind
2- not directly behind but minimal distortion
3- angled about 45° to side
4- angled >45° but markings still visible
5- angle so extreme most markings obscured

Focus/sharpness:
1- excellent focus with clear grain
2- good focus and grain with only minimal loss in quality
3- okay focus and grain with some loss in ability to discern marks and edges
4- fair to poor focus in grain with significant loss in clarity
5- soft focus/grainy with extreme loss in detail

Fluke size on print:
1- > 3 inches wide
2- 2.7 - 3 inches wide
3- 2.3 - 2.7 inches
4- 2.0 - 2.3 inches
5- < 2.1 inches wide
For partial flukes, imagine what size would be for whole fluke.

Lighting/contrast/exposure:
1- excellent lighting and contrast, any marks present would be seen
2- good but with some loss in contrast on ventral surface
3- fair, some marks might not be seen at all but most would likely be visible
4- fair to poor with significant backlighting or exposure problems
5- poor (*e.g.* back lit or gray), likely many marks would not be visible

Distinctiveness - fluke trailing edge (separate from quality):
1- very distinctive gouges and bites
2- deep fringing
3- clear ridges and bumps
4- ridges and bumps present but not very distinctive
5- smooth trailing edge, hard to use ridging
Fluke tips should be considered part of trailing edge (*e.g.* missing tips from orca bites)

Distinctiveness - scars:
1- distinctive and numerous scars and markings
2- either a few distinctive marks or numerous not very distinctive marks
3- marks present but neither distinctive nor numerous
4- only a few faint and not distinctive scars or markings
5- no marks visible

Rake marks:
1- rake marks with missing parts
2- 3 or more sets of rake marks
3- 1-2 clear, obvious sets of rake marks
4- possible rake marks
5- no rake marks

Of the initial 6,414 photographs, 3,650 were selected as the sample used for the comparison (including photographs from Mexico from 1990). After review of the limited information available from mainland Mexico for 1991-1993 (Table 1), we decided to expand the sample from this region to include 1990 photographs from both mainland Mexico and Baja. These additional 131 photographs from mainland Mexico and 43 from Baja were of acceptable quality and were included in the sample; a comparison of these photographs was made after the completion of the primary comparison of all other photographs.

Comparison of photographs

Before the comparison began, all photographs from each collection were divided into five categories based on the coloration of the flukes: Category 1- all white with no medial line; Category 2 - mostly white; Category 3 - half white and half black; Category 4 - mostly black; and Category 5 - all black. Categories 2-5 were further subdivided by light to dark pigmentation; black flukes (Category 5) were divided by types of scars (missing pieces, rake marks, scratches, and circles. The matcher was aware of all potential subcategories the picture could occur and thoroughly checked to ensure that no matches were missed systematically. Matchers compared each photograph to its own subcategory and to the two adjacent subcategories. Photographs were also compared to additional subcategories if the matcher felt the coloration was ambiguous (*e.g.*, a photograph in category 3B would be compared with 3A and 3C; it could also be compared with 4A or 2C at the discretion of the matcher).

Two separate matching teams made independent comparisons of the entire collection. Photographs were compared using the coloration, trailing edge, scars and other markings on the flukes of the actual photographs. At least one member of each team compared each photograph to all other photographs.

Another redundancy built into the process was that all photographs, once compared, were returned to the sample. This ensured that each team searched for match from both photographs of the matched pair. An exception to this was when a match was found with a photograph of lesser quality then the one being compared; here, the lower quality photograph was not compared to the rest of the sample. Matches were recorded independently and were not discussed amongst the matchers.

When the comparison was complete, all matches found by only one team were verified. A second check was made by verifying all matches found between two regions where migratory destinations were not previously determined. The comparison began in April and was completed in November 1996, the supplemental comparison of the photographs from Mexico in 1990 was completed in January 1997.

Matching success

In the primary comparison, the two independent teams found 1,036 and 1,032 matches, respectively (Table 2). The combined matches found by either team was 1,098 with each team finding about 94% of this total. A simple Peterson capture-recapture calculation (using total matches found by each team as n_1 and n_2 and the number of these found in common by both teams as m_{12}) yielded an estimate that revealed that over 99% of the matches would have been found by at least one team (Table 2). This estimate, however, was unrealistically high. The matches found by each team were not truly independent events because some whales were easier to match to than others making some matches more likely to be found by both teams.

A second method to measure matching success was to determine the proportion of matches that were known by the contributors that we also found. These were mostly inter-year matches within their collections to which our matchers were blind. The contributors generally identify these matches with a high degree of success because of their familiarity with their smaller collections. Of the 563 matches provided to us by the contributors (involving whales in our initial comparison), 546 (97%) were found by one or both teams (Table 2). This is a more unbiased assessment of our matching success rate.

The success rate in the supplemental comparison (1990 Mexico) was lower (93%) (Table 2). This probably reflected the reduced opportunity for each team to find these matches. Supplemental photographs were compared to the original catalog but photographs in the original catalog were not compared to the supplemental (which were not yet incorporated when that was conducted). This resulted in only a single opportunity for a match to be found by each team compared to the two opportunities for most photographs. This slightly lower success rate only affected the small (174) number of whales in the 1990 sample and was still high enough (93%) to not warrant any adjustment of the data.

The rate of matching success in our comparison was much higher than expected. Because it was high, no corrections were made to account for missed matches in our calculations. Reasons for even the low number of matches that were missed were varied (Table 3). Different categorization of the coloration type of multiple photographs of the same whale was one of the primary reasons for the matches that were missed (Table 3).

Statistical Methods

Index of interchange

An Index of Interchange was calculated to quantify the degree of interchange among two samples (among years or regions) that accounted for sample size:

$$\text{Index of Interchange} = (m_{12}/(n_1 * n_2)) * 1000$$

Where:
n_1 = Whales identified (captured) in sample 1
n_2 = Whales identified in sample 2
m_{12} = Captured whales from sample 1 recaptured in sample 2

This is basically the inverse of the Petersen capture-recapture index and has been used to examine rate of interchange of humpback whales among areas by several other researchers (Baker *et al.* 1985, Cerchio *et al.* 1994). A high value in this index reflects a small population with a high probability of the same individual being recaptured in both samples while a low value reflects a low probability of recapture due to either a large population or an unlikely interchange of animals between the two samples (years or regions).

Darroch's method

Darroch's (1961) method is an extension of the simple Petersen capture-recapture method for populations stratified geographically (Seber 1982, ch. 11; Quinn and Deriso, *In press*, ch. 10). The extension is also based on two time points for release and capture, only that releases and captures are recorded by geographical strata. Let
a_i = number of marked releases (whales identified) at time 1 in region i, $i = 1, \dots, R$,
n_j = number examined for marks (whales identified) at time 2 in region j,
$m_{i\to j}$ = marked recaptures in region j originally marked (identified) in region i,
p_j = probability of capture in region j,
$\theta_{i\to j}$ = probability that a whale identified from region i moves to region j.

It is assumed that: (1) the population is closed, (2) all individuals in region j have the same probability p_j of being captured; (3) each whale behaves independently of others in regard to movement and capture; (4) movement and capture are independent; (5) the matrix $\mathbf{\Theta}$ of the θ's is non-singular.

If $\underline{\rho}$ is the column vector of the inverses of the capture probabilities ($\rho_j = 1/p_j$), maximum likelihood estimates of $\underline{\rho}$ and $\theta_{i\to j}$ are:
$\underline{\hat{\rho}} = \mathbf{M}^{-1}\underline{a}$ and $\hat{\theta}_{i\to j} = m_{i\to j}\hat{\rho}_j / a_i$,
where $\mathbf{M}$ is the matrix of the $m_{i\to j}$, $\underline{a}$ is the column vector of the a_i, and D is a diagonal matrix with entries corresponding to the given symbol. The variance-covariance matrix for $\underline{\hat{\rho}}$ is in Seber (1982), and the estimated variance of $\hat{\theta}_{i\to j}$ is in Quinn and Deriso (*In press*).

Estimated abundance at the time of recapture is

$\hat{N}_j = n_j \hat{\rho}_j = n_j / \hat{p}_j$.

If $\mathbf{\Theta}$ applies equally to marked and unmarked, then estimated abundance at time when the whale was identified is

$\underline{\hat{N}}^* = \left(\hat{\mathbf{\Theta}}^{-1}\right)' \underline{\hat{N}}$, where $(\ )'$ denotes transpose.

Further information about the Darroch method in Seber (1982) and Quinn and Deriso (*In press*) includes discussion of validity of assumptions, consideration of variable number of strata, description of hypothesis tests, generalization of the method to account for natural mortality in an open population, and discussion of additional references.

Our analyses using Darroch's method were done with only winter data; the more complex situation of summer / winter data was better analyzed by Hilborn's method. The 1991 data set had insufficient data from Mexico to estimate parameters. Data from Mexico in 1990 was pooled with 1991 data. Then pairwise analyses of 1990/91, 1992, and 1993 data were undertaken. To reduce variability in the estimates, only three geographic areas were used: Mexico (MX), Hawaii (HI), and Japan (JP).

Hilborn's method

A general framework for estimating movement and population parameters from capture-recapture data (Hilborn 1990) synthesizes several earlier approaches. This framework has proven to be a versatile one used by several authors (e.g. Heifetz and Fujioka 1991, Deriso *et al.* 1991, Anganuzzi *et al.* 1994, see Quinn and Deriso, *In press*). The framework consists of a population dynamics model for groups of marked individuals, an observation model for recaptured animals, and maximum likelihood theory to estimate parameters.

Our application of Hilborn's method is a simpler version than given in his paper; we assume that there is no mortality (natural or human-induced) during the study period. The group of marked (or captured) individuals is defined as the number of individuals identified at a given time t_0 and place i; by convention we denote this M_{i,j,t_0}. Let $M_{i,j,t}$ be the number of identified individuals of group i in recovery area j at time t after initial sampling and $\mathbf{M}_t$ be the matrix of the $M_{i,j,t}$. As in Darroch's method, we let $\mathbf{\Theta}$ be the matrix of movement probabilities. The population equation which redistributes the population at each subsequent time period is then

$\mathbf{M}_{t+1} = \mathbf{\Theta}' \mathbf{M}_t, \ t = t_0, t_0 + 1, \ldots$.

The observation model specifies the recapture process for identified whales. If the probability of capture $p_{i,j}$ is assumed constant for all animals from identified group i in recovery area j, the predicted number of marked (identified) recaptures from the model can be written:

$m_{i,j,t} = M_{i,j,t} p_{i,j}$.

The likelihood component of the model specifies a suitable error structure for observations of mark-recoveries. Hilborn presented both the Poisson and multinomial error structures. For a given marked recapture observation $m'_{i,j,t}$ following the Poisson distribution, the likelihood can be written

$$\mathcal{L}(m_{i,j,t}|m'_{i,j,t}) = e^{-m_{i,j,t}} m_{i,j,t}{}^{m'_{i,j,t}} / m'_{i,j,t}! \ ,$$

and the total likelihood is the product of the individual likelihoods. The total likelihood (or its logarithm) is then maximized as a function of parameters to obtain MLE's. Following Cormack and Skalski (1992), an index of dispersion δ (essentially the square root of a chi-square statistic divided by degrees of freedom) was calculated to validate the Poisson distribution. If δ is close to 1, then the Poisson distribution is valid.

Total abundance was estimated by assuming that the number of captures $n_{j,t}$ followed a binomial distribution with parameters $N_{j,t}$ and p_j. The estimator of abundance is then $\hat{N}_{j,t}$ = $n_{j,t} / \hat{p}_j$. Since the calculation is done using the recapture data, it is not necessary to assume that identified and unidentified animals have the same movement rates, only that they have the same probabilities of capture. This procedure can also be followed with animals from a particular release group *i*.

Our analyses using Hilborn's method were done with winter data and with summer / winter data. For the winter data, a single analysis was done with the three regions and three years. Logit transformations (Schnute and Richards 1995) were used to constrain parameter estimates between 0 and 1 and to force migration rates to sum to 1.

Standard errors were obtained from the bootstrap procedure of Efron and Tibshirani (1993). Observed mark-recaptures were generated parametrically from the Poisson distribution using the predicted mark-recaptures. The total number of captures $n_{j,t}$ was generated from the binomial distribution given $\hat{N}_{j,t}$ and $\hat{p}_j$. The bootstrap procedure was repeated 100 times following the recommendation in Efron and Tibshirani (1993) for calculating standard errors.

For the summer/winter analysis, the application needed to be modified in some ways. The two primary summer areas were Alaska (AK) and California (CA). First, the $\mathbf{\Theta}$ matrix was redefined to represent movement from winter to summer areas, and a new matrix $\mathbf{\Psi}$ was defined to represent movement from summer to winter areas. Second, it appeared during analysis that some whales particularly those in Japan, were not as observable in the summer as whales from Mexico and Hawaii. This was modeled by defining a mystery area (labeled "??" in tables), where whales from any area could move in the summer time but not be observed. Third, separate sets of capture probability parameters were used for each season. It also became apparent that whales identified in the summer were more observable in the summer, than whales identified in winter areas, a result of the site fidelity of whales to feeding areas (see Discussion). An additional set of capture probabilities was incorporated based on release area.

Sensitivity to sex ratio

The capture probability of whales may differ by gender, because whales of a particular sex may be more available to being sighted in particular areas. We investigate the sensitivity to differences in capture probability by constructing a movement model and then showing how estimates of abundance can be obtained.

The following abundance model is for a migratory, closed population for which the capture probabilities of whales differ by gender, so that the number of captured whales also differs by gender. The movement rates are assumed to be the same across sexes. Let χ be the proportion of originally captured population that is female, let *f* denote females, and let *m* denote males. Absence of a subscript denotes summation over that subscript. If a_i is the number captured at time 1 in area *i*, then the numbers of females and males captured are

$$a_{if} = a_i\chi \text{ and } a_{im} = a_i(1-\chi).$$

Assume that the capture probability for sex x in area j is p_{jx}. If Θ is the matrix of movement probabilities, then the number captured in area *j* after movement is

$$b_{jx} = \sum_i a_{ix}\theta_{i\to j}.$$

and the expected number captured is

$$m_{jx} = b_{jx}p_{jx}.$$

The average capture probability over sex is then

$$\overline{p}_j = \left(b_{jf}\,p_{jf} + b_{jm}p_{jm}\right)/\,b_j.$$

If it is assumed that the ratio of the probabilities of capture by sex is the same as in the original population, then

$$p_{jf}\,/\,p_{jm} = \chi\,/\,(1-\chi).$$

Since b_{jf} is proportional to χ and b_{jm} is proportional to $(1 - \chi)$, then the average capture probability becomes

$$\overline{p}_j = \left(\chi\frac{\chi}{1-\chi}p_{jm} + (1-\chi)p_{jm}\right) = \frac{2\chi^2 - 2\chi + 1}{1-\chi}p_{jm}.$$

Solving for the male capture probability yields

$$p_{jm} = \frac{1-\chi}{2\chi^2 - 2\chi + 1}\overline{p}_j,$$

and hence the female capture probability is

$$p_{jf} = \frac{\chi}{2\chi^2 - 2\chi + 1}\overline{p}_j.$$

If the population has a 50:50 sex ratio, then the true average capture probability is $p_j^* = (p_{jf} + p_{jm})/2$. An unbiased estimate of abundance is then $N_j^* = n_j\,/\,p_j^*$. This must be applied to the total number captured and not the number of unmarked captured, because the unmarked populations by sex are not the same.

Summer-winter Petersen capture-recapture methods

As an alternate approach to estimating the abundance of humpback whales on the Mexico and Hawaii wintering areas, we used the animals identified on two feeding areas as the marked samples. Humpback whales identified on feeding areas in southeastern Alaska were found to almost exclusively migrate to the three subareas of the Hawaii wintering area (all 63 southeastern Alaska whales that matched a wintering area were to Hawaii). Similarly, humpback whales identified off California, Oregon, and Washington almost exclusively migrated to the Mexican wintering areas (48 of 50 animals from this feeding area matching a wintering area were to Mexico). California-Washington and southeastern Alaska areas were also the two best sampled feeding areas together accounting for almost 75% of the identifications from feeding areas.

Capture-recaptures estimates were generated separately using each of the three sample years as captures and recaptures on the wintering area for the previous and following season (approximately 6 months before and after). This yielded five separate estimates (two for each year except the final year where there was no winter season after the last feeding area sample). For this estimate the partial Mexico sample from 1990 was again pooled with 1991 to provide a single fairly complete sample of this region.

Capture-recapture estimates were conducted using the Petersen estimate with the Chapman modification for sampling without replacement (Seber 1982, Hammond 1986). Each individual was only counted as a mark or recapture once in a sample making the sampling effectively without replacement (Hammond 1986).

RESULTS

Total matches and unique whales

Of our sample of 3,650 photographs, 2,712 were unique whales (2,993 without inter-regional matches). This is the result of 1,241 different matches that were found (by the two teams plus the 21 collaborator matches that were missed). Table 4 summarizes both the internal and inter-region matches found among all regions.

Matches within an area were more common than those between regions and accounted for 808 (65%) of the 1,241 pairs of matches. Because catalogs from each area had been already internally compared and duplicate photographs eliminated, most of these matches were of whales seen in different years in the same area. A disproportionate number of these resightings of the same whale were made at feeding areas (550) compared to wintering areas (258). The rate of resightings within an area (as measured by the interchange index) varied among the areas (Figure 2) with highest resighting rates at the two areas off Japan and most feeding areas (Prince William Sound, southeastern Alaska, British Columbia, and California-Washington). Whales identified off Kodiak and western Gulf of Alaska were the only feeding-area samples with low resighting rates. These rates of inter-year resightings within regions reflect the size of the overall population being sampled and the degree of regional fidelity. In general, these findings show that regional fidelity is higher on the feeding areas. The exceptions probably reflect the abundance of animals using the region. Feeding areas off Kodiak and in the western Gulf of Alaska are probably used by large numbers of whales while wintering regions off Japan appear to be used by a relatively small number (see Abundance Estimates).

Population Structure and Movements

Interchange among and within wintering regions

Within-region movements

Within each wintering region, the degree of interchange among the subareas varied by region (Tables 5-8). For all three regions, the highest interchange index was within the same subarea in different years indicating whales were more likely to return to the same subarea compared to being seen in a different subarea. The magnitude of this pattern was very different for each region, however, with interchange among subareas high off Hawaii and limited in the waters off Japan.

Movements and interchange among the three Hawaii subareas was extensive (Table 4 and 5). The same whales were seen in multiple subareas both in the same year and in different years. The mean interchange index for whales at the same subarea in different years (0.306) was only slightly higher but not statistically different (t-test, $p>0.05$) than that for different subareas in different years (0.264). This indicates that whales are equally likely to return to a different subarea as they are the same subarea in successive years. Only between-subarea interchange in the same year was lower (0.138) indicating whales are not as likely to travel to multiple subareas in the same year as they are to return to the same or a different subarea in a different year.

Interchange among the Mexico subareas was less extensive and showed some clear preferred directions for interchange, although sampling among subareas and years was incomplete (Table 6). The highest interchange index values were obtained for whales returning to the same subarea in different years (0.95). No interchange was seen between the mainland Mexico and Revillagigedo subareas although this comparison was confined to a good sample from only a single year for each of these subareas. Interchange among subareas was most common between mainland and Baja, both for the same year (0.355) and between years (0.380). Interchange between the Revillagigedos and Baja was only slightly lower (0.221 and 0.241). This indicates that Baja serves as an area where whales from both Revillagigedo and mainland occur. This makes the Baja subarea more representative of the Mexico wintering area as a whole than either of the other two subareas. The sample from Baja is larger and includes four years (1990-1993) compared to only large single-year samples from the other two subareas.

Interchange among the two subareas off Japan was different than off Mexico and Hawaii (Table 7). The index of interchange for different years in the same subarea was much higher than seen off Mexico and Hawaii. This was especially true for Okinawa where the index was four times higher than off Ogasawara (11.6 vs. 2.9). Although interchange between these two subareas was seen in both the same year and in different years, the index of interchange was more than order of magnitude lower than for the same subarea in different years. Though interchange occurs frequently among these two subareas, whales are far more likely to return to the same subarea.

Interchange between regions

Interchange between wintering regions was uncommon. A total of five individual whales were seen in both Mexico and Hawaii and three individuals in both Hawaii and Japan (Figures 3). None of these were seen in more than one wintering region in the same year. No exchange was found between Mexico and Japan. The interchange index among the three broad wintering regions was very low (Table 8). The index of interchange between any two wintering regions were one to two orders of magnitude lower than the between-year rate for the same region (Table 8). Clearly, most whales return to the same wintering region.

Interchange among feeding areas

There was little interchange among different feeding areas (Figure 4). For five of the eight feeding areas, no matches were found with any other feeding area. Interchange among feeding areas was found for only four whales and these were whales among seen among the southeastern Alaska, Prince William Sound, and Kodiak Island areas (Figure 4). Of the 287 whales photographed in southeastern Alaska, two were seen in Prince William Sound (87) and one was seen off Kodiak (69). Additionally, a single whale was seen both off Kodiak and in Prince William Sound. In all but one case, these matches were of whales seen in different years. One animal moved between Prince William Sound and southeastern Alaska in the same year (July and November 1992).

Migratory movements

Whales from the three wintering regions were found at multiple feeding areas in the North Pacific. This is shown in both the number of whales moving between wintering and feeding areas (Figures 5-7) and the interchange index (Figure 8) among these areas. Whales photographed off Mexico tended to be resighted off California (interchange index=0.208) although they were also seen off northern and southern British Columbia, Kodiak and the Aleutian Islands (Figure 6). All but one of these whales were identified off either mainland or Baja Mexico. Of the 159 individuals photographed off the Revillagigedo Archipelago, only one was seen at any feeding region (off California).

Whales identified off Hawaii tended to be seen off southeastern Alaska (interchange index=0.208)(Figures 5 and 8). Most of the Alaskan migratory destinations, consisted of whales that had been identified at all three of the Hawaiian subareas that were sampled. Whales identified off Hawaii were also observed off California, northern British Columbia, southeastern Alaska, Prince William Sound, Kodiak Islands, and the Aleutian Islands (Figure 5). Of the 11 whales that were found to move between Hawaii and the easternmost feeding areas from California to British Columbia, none were from Kauai (the westernmost site sampled along the Hawaiian Island chain).

Only three whales were documented moving between the Japan wintering regions and feeding areas; these consisted of single matches to southern British Columbia, northern British Columbia and Kodiak Island (Figure 7-8). All three of these whales were identified off Ogasawara; we found no matches for whales that had been seen off Okinawa.

Whales identified in a specific feeding area sometimes showed a clear preference for a wintering region (Figure 8). Whales identified in southeastern Alaska showed a high interchange index with Hawaii and were not identified in any other wintering area. Whales identified off California, Oregon, and Washington were almost exclusively identified in Mexico with only a few matches to Hawaii. For most other feeding areas, however, migrations were documented to multiple wintering areas. Whales identified off British Columbia, for example, showed a similar interchange index with all three wintering areas.

Differences in color patterns among regions

There were significant differences in the distribution of fluke coloration types by region (chi-square, $p<0.001$). The most dramatic differences were between wintering and feeding areas (Figure 9) where these differences were highly significant (chi-square, $p<0.001$). There was a higher proportion of all black-fluked animals on the feeding area (38%) compared to the wintering areas (24%). Conversely, the proportion of animals with half to mostly white flukes was lower on the feeding areas compared to the wintering areas (40% vs. 51%).

Among wintering areas, there were significant differences in the fluke coloration patterns (chi-square, $p<0.001$). For the two areas off Japan, dark flukes were predominant (Figure 10). The three Mexico subareas had the highest proportion of animals with all white flukes, although the proportion of other coloration types were more mixed. An unusual spread of coloration types was seen for the Maui area of Hawaii which had the highest proportion of coloration 4 (mostly black flukes) and the lowest proportion of coloration 5 (all black flukes). This finding may be an artifact of the photographic processing. This subarea is the only one where photographs were originally taken as slides and then duplicated to black and white negatives. This affected the appearance which caused greater contrast and possibly biased the coding process.

There were also significant differences in coloration types among the feeding areas (chi square, $p<0.001$). Whales photographed in Prince William Sound deviated the most from the other areas and showed a higher proportion of all white flukes and a dramatically lower proportion of all black-fluked animals (Figure 11). Overall, whales from southeastern Alaska had the darkest flukes, with the highest proportion of all black and mostly back flukes (total of 73% of whales). There were no clear east to west or north to south patterns to the coloration differences among feeding areas.

Abundance estimates

Darroch's Method

Data and parameter estimates from Darroch's method were calculated using wintering area release-recovery data for three pairs of years (Tables 9a, 9b, and 9c) for 1990/91–1992, 1990/91–1993, and 1992–1993. The estimates of capture probability, migration, and population size were fairly consistent among the three analyses, with some indication of inter-annual variability in migration rates. Average capture probabilities were 4.5%, 10.4%, and 38.4% for Mexico (MX), Hawaii (HI), and Japan (JP), respectively. The only relatively large average migration rates were about 7% from MX to HI and 7% from JP to HI. Average estimated population sizes were about 1,600 (MX), 4,000 (HI), and 400 (JP), for a total of 6,000. The abundance estimates did not vary widely among the three pairs of years (5,654-6,617).

Petersen estimates of population size (without any geographic stratification) shown in Tables 9a–9c are generally smaller than the Darroch estimates. It is well known that heterogeneity in capture probabilities can lead to underestimation of abundance (Seber 1982). For the whale data, there appear to be clear differences in capture probabilities among areas. Chi-square tests (not shown) did not indicate any support for pooling the data to obtain the Petersen estimates, so the Darroch estimates are preferred.

Hilborn's Method

Results from the analysis of winter release and recovery data using Hilborn's method were calculated using all three years of data (Table 10a). The estimates of migration rates and capture probabilities were nearly identical to Darroch's. Average capture probabilities were 4.5%, 9.9%, and 37.4% for MX, HI, and JP, respectively. The only relatively large average migration rates were about 7% from MX to HI and about 6% from JP to HI. The main advantage of Hilborn's method is that it can assimilate the data across years to obtain parameter estimates. Standard errors were similar to Darroch's method, as expected. The index of dispersion δ was 0.90, suggesting that the Poisson distribution was valid.

Estimates of abundance from the Hilborn method by wintering region, totaled for all regions, and averaged across years are given in Table 10b. The abundance estimates were variable by region across the two years, but total abundance was remarkably consistent between the years at about 6,000 (5,937-6,077) with a cv of about 8% and was in close agreement with the Darroch estimates. The average abundances by region were about 1,800 (MX), 3,800 (HI), and 400 (JP) with larger cv's of 19%, 12%, and 9%, respectively (Table 10b). The individual standard errors were somewhat lower than for the Darroch method, perhaps due to performing a unified analysis rather than pair-wise analyses.

Results of analyses using the combination of both wintering and feeding areas were more complex and variable. Estimates of migration rates and capture probabilities from four analyses of winter and summer data are presented in Table 11. There were three years and two seasons for a total of 6 different release/recapture matrices. Model 1 is a baseline model with the three winter regions (MX, HI, JP), 2 pooled summer areas (CA-BC and AK), and constant capture probabilities for whales within each recovery area. Model 2 is the same as model 1, except that the mystery area (labeled "??" in the tables) is included in the summer only for Japan whales the previous winter. Model 3 is the same as Model 2, but all winter areas can contribute whales to the mystery area the following summer. Model 4 is the same as Model 3 except that capture probabilities are different for animals released in the summer (denoted **p**(s)) than in the winter (**p**).

Based on log-likelihood values, each successive model in Table 11 represents a significant improvement. The largest improvement comes from having separate capture probabilities for summer and winter releases. The results show many differences in migration rates depending upon what model is used. There is also variability in capture probabilities. It seems that without further data collected from more complete coverage of all major feeding (summer) areas, the models incorporating data from both winter and summer areas are problematic.

For comparative purposes, however, estimates of abundance were calculated using data from winter and summer areas (Table 11b). For the winter captures, estimates were similar to those in Table 10b using only winter data and yielded estimates of total abundance of about 6,200. For the summer captures, the estimates of abundance were obtained by adding the number of marked whales to an estimate of the number of unmarked whales. Two sets of estimates were calculated, the first assuming that the probability of capture is **p** and the second assuming **p**(s). No estimate could be made of the abundance of whales outside CA and AK, because the capture probability is 0. The estimates of abundance for CA-BC and AK were quite variable across years and depended strongly on the capture probability assumption; the range for the two areas combined is from 1588 to 9392. Because of this lack of consistency, we did not calculate standard errors, because the prime sources of variability were not due to sampling variability.

Because of the variability and problems with the summer-winter data, we consider the estimate based solely upon winter areas (Table 10b) to be superior.

Sensitivity to sex ratio

We illustrate the bias caused by differences in capture probability by sex and the correction approach derived in the methods section. A hypothetical population of 6000 whales distributed with a 1:1 sex ratio across two areas is constructed, for which 20% of the population is marked at time 1 and 33% of the originally marked population is female. Other population parameters are shown in Table 12a. The expected number marked and unmarked by sex after movement are also given in Table 12a. If data are available by sex, then the Darroch method will clearly provide approximately unbiased estimates of abundance (Table 12b). If the recapture data are not available by sex, then biased estimates will occur by applying the Darroch method to the pooled data (Table 12b). Table 12b shows the details of correcting the estimates as described in the methods section. Application of these calculations to two possible sex biased scenarios of a 2:1 and 3:1 male:female sampled sex ratio, revealed that a correction factor of 1.11 and 1.25, respectively, would need to be multiplied by the abundance estimate to obtain an estimate of the abundance of the entire population. This assumes that the true population, even if not all present on the wintering region at one time, has a sex ratio of 1:1.

Petersen estimates from winter-feeding areas samples

Petersen capture-recapture estimates using whales identified in southeastern Alaska as marks and Hawaii as the recapture locations yielded abundance estimates slightly higher than those obtained for Hawaii using the geographically stratified models for wintering areas described above (Table 13). The five estimates for Hawaii ranged from 3,603 to 8,055 with an average of 5,151 (S.D.=1,804). This is higher than the 4,000 estimates for Hawaii from the models using only winter region data (Table 14).

Estimates for Mexico were generally much higher using animals seen off California as the marked sample (Table 13). The five estimates ranged from 2,976 to 5,879 with an average of 4,220 (S.D.= 1,225). This is more than twice as high as the 1,600 estimate using only wintering areas (Table 14).

DISCUSSION

Population structure and movements

Site fidelity and movement among wintering areas

Humpback whales show some degree of site fidelity to specific feeding areas and wintering regions although the extent of this varies. The higher interchange indices within wintering regions (compared to those found between them) show that whales usually return to the same region. Some movement between wintering regions was seen in this study and has been reported previously between Hawaii and Japan (Darling and Cerchio 1993) and Mexico and Hawaii (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1990). Although not found in this study, one whale has been documented moving between Hawaii and Mexico in the same season (North Pacific Humpback Whale Working Group, Unpubl. data). Exchange among wintering areas occurred at a dramatically lower rate than the return to the same wintering area.

The degree of interchange and movement of whales among the sampled areas within each of the three wintering regions was also variable. Interchange among subareas of the Hawaiian Islands found in this study and reported previously (Baker and Herman 1981, Darling and Morowitz 1986, Darling and McSweeney 1985, Cerchio *et al*. 1994, In prep.) supports our study design, that treats the Hawaiian Islands as one wintering region. For Mexico, movements among subareas were more stratified. Samples from this study were consistent with the larger sample analyzed by Urban *et al.* (1994, In prep.) showing only a low rate of interchange between whales wintering along the mainland and those around the offshore Revillagigedo Islands. The Baja Peninsula, however, may serve as a migratory corridor for animals from both these subareas (Urbán *et al*. 1994, Ladrón de Guevara 1995). Interchange among the two subareas sampled off Japan, reported previously (Darling 1991a, 1991b, Darling and Mori 1993, Uchida *et al*. 1993, Yamaguchi *et al.* 1995) and found in this study, occurred at a lower rate than what would be expected if whales mixed randomly throughout the region.

The more limited interchange among subareas for the wintering areas off Mexico and Japan are problematic for the abundance estimates if the samples from these subareas are not proportional to whale abundance. This would be most extreme where there were wintering regions (or subareas) that were not sampled at all. Humpback whales were hunted during the winter months at numerous other locations in the western North Pacific, even though whale occurrence off Taiwan, the Mariana Islands and the Marshall Islands is currently uncommon or unknown (Darling and Mori 1993). Humpback whales also winter at scattered locations along the Mexican mainland south of the subareas that have been sampled (Urban and Aguayo 1987).

One known wintering region not included in our sample is the coastal waters of Central America, especially Costa Rica and Panama. This region has recently been documented as a area where humpback whales from the North Pacific breed and give birth to calves (Steiger *et al.* 1991, Rasmussen *et al.* 1995, Calambokidis 1997), although no photographs were available from 1991-1993. These areas off Central America appear to be used by a relatively small number of humpback whales, that almost exclusively migrate from feeding areas off California and with some interchange with whales wintering off Mexico.

Site fidelity and movement among feeding areas

Site fidelity was strongest at the feeding areas. Resighting rates among years at most feeding areas were high and only limited movements were seen between areas. The low rate of inter-year resightings for a few feeding areas such as off Kodiak and western Gulf of Alaska are probably an indication of the large number of whales of which relatively few have been sampled. Currently, it is impossible to evaluate the number and nature of the division among most of these feeding areas. The areas in the North Pacific where whales feed is large and often remote.

Some interchange has been documented between feeding areas in the North Pacific by past research and the current study including: interchange between California and both British Columbia and southeastern Alaska (Calambokidis *et al.* 1996a, North Pacific Humpback Whale Working Group Unpubl. data), British Columbia and southeastern Alaska (Darling and McSweeney 1985, Straley and Ellis Unpubl. data), and southeastern Alaska and the western Gulf of Alaska including Prince William Sound (Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1990, von Ziegesar 1992, Waite and Dahlheim In prep., J. Straley Unpubl. data), and among areas in the western Gulf of Alaska (North Gulf Oceanic Society Unpubl. data, Waite and Dahlheim In prep., Dahlheim and Waite 1993).

Consistent with this study, the interchange among feeding areas documented in past have been at very low rates involving just a few whales. A relatively distinct feeding aggregation of humpback whales has been documented along the coast of California, Oregon, and Washington with little interchange with feeding areas farther north (Calambokidis *et al.* 1996a). Although there was a steep drop in interchange at the Washington-British Columbia border, interchange rates also declined with distance within the aggregations that range off California, Oregon, and Washington (Calambokidis *et al.* 1996a).

Migratory movements of whales

Despite the site fidelity of humpback whales to specific areas, migrations between feeding areas and wintering regions have not generally followed a simple pattern to allow definition of an integrated wintering/feeding area population structure. Results of photo-identification studies conducted in the North Pacific over the past 20 years provide additional insight into migratory destinations of these whales.

The findings in this comparison, combined with those from other comparisons, confirm the dichotomy in the migratory destinations of whales wintering in the different subareas of Mexico. Humpback whales from the Revillagigedos, for which we had only a limited sample and only a single match to a feeding area (California) have been previously documented migrating to feeding areas off California, British Columbia, southeastern Alaska, Prince William Sound, and the Kodiak Island area (Urban *et al.* In prep., Gabriele *et al.* 1996, Calambokidis *et al.* 1996b). Consistent with this study, the rate at which whales from the Revillagigedos were seen at these different feeding areas was extremely low and suggests that other unsampled feeding areas are likely the primary migratory destination of these whales. Whales wintering off mainland and Baja Mexico, however, have a high rate of interchange with feeding areas especially California-Washington where over 100 matches have been documented; whales have also been seen off British Columbia, southeastern Alaska, Prince William Sound and the western Gulf of Alaska (this study, Baker *et al.* 1986, Urban *et al.* 1987, In prep., Calambokidis *et al.* 1989, Calambokidis and Steiger 1995). Movements between mainland or Baja Mexico and southeastern Alaska were not found in this study but a few have been reported in other comparisons (Urban *et al.* In prep., Perry *et al.* 1990, Baker *et al.* 1986).

Our findings of humpback whales migrations between Hawaii and most of the feeding areas sampled were consistent with past reports. The close connection between whales feeding in southeastern Alaska and those wintering in Hawaii has been documented in several past studies (Darling and McSweeney 1985, Baker *et al.* 1986). A migration time of as short as 39 days has been recorded between these two areas (Gabriele *et al.* 1996). One of the migratory transits between Hawaii and Alaska documented in this study was also very short (36 days) between Kauai and southeastern Alaska.

Some of the migratory destinations of humpback whales wintering in the western North Pacific found in this study have not previously been documented with identified individuals but are consistent with the past findings showing extensive migrations of these animals. A whale documented in this study that migrated between the Ogasawara, Japan, and a feeding area off southern British Columbia is the same individual reported by Darling *et al.* (1996). Our finding of a second whale that migrated between Ogasawara and northern British Columbia indicates such east-west migrations may not be uncommon. Other migrations of whales from these wintering areas have come from whaling records. Discovery tag recaptures have indicated movement of whales between Ogasawara and Okinawa and feeding areas in the Bering Sea, on the southern side of the Aleutian Islands, and in the Gulf of Alaska (Nishiwaki 1966, Omura and Ohsumi 1964, Ohsumi and Masaki 1975). One whale tagged off Ogasawara in March was captured in June of the same year west of northern Japan, possibly indicating movement up towards the Kuril Islands (Nishiwaki 1966). Given these movement patterns, the movements to feeding areas near Kodiak Island and northern British Columbia found in this study are not surprising.

Coloration differences

Coloration differences among regions could indicate phenotypic variations among regions and provide insight to population structure. Coloration differences between northern and southern hemisphere populations of humpback whales have been reported from whaling data (Pike 1953). Rosenbaum *et al.* (1995) examined differences in fluke coloration of humpback whales from northern and southern hemisphere humpback whales including a sample (smaller than used in this study) from the three primary wintering regions in the North Pacific. They found significant differences between northern and southern hemisphere populations but no significant differences among the three North Pacific wintering areas. Despite the lack of significance in their sample, they found a similar pattern for the North Pacific as we found here (generally darker flukes for Japan and lightest flukes for Mexico).

The differences in fluke coloration patterns between wintering and feeding areas we found may reflect the higher proportion of males than females being sampled on the wintering areas (see Results and Discussion sections on sex ratio). Pike (1953) reported that male humpback whales caught in commercial whaling off British Columbia tended to have more white on their flukes than females. In the North Atlantic, animals with all dark flukes tended to disproportionately be females and those with light flukes tended to disproportionately be males (Allen *et al.* 1994). This supports our assumption that males were over-represented in out wintering-region sample. Although Allen *et al.* (1994) found significant differences in fluke coloration between males and females, they did not find significant differences between wintering and feeding areas in the North Atlantic. It was unclear if there was a strong bias towards males in their wintering area sample.

Our incomplete sampling of feeding areas also may have contributed to the differences between wintering and feeding areas. This would have occurred if unsampled feeding areas were used by whales with a predominate fluke coloration different than whales in the feeding areas we did sample.

Although we found differences among regions in fluke coloration, they did not follow the clinal patterns that have been reported in the past. Baker *et al.* (1986) reported a longitudinal cline in fluke coloration among feeding areas in the North Pacific with western-most locations had the highest proportion of white flukes and eastern-most areas had the most dark flukes. Sample sizes for the regions that were farthest east and west were very small (8 and 15 animals, respectively) and without these two locations, there would not have been a significant cline. In our sample, the proportion of flukes in the western-most regions (Kodiak-Bering Sea, n=101) tended to be no lighter than the eastern-most region (California-Washington, n=694).

Genetic differences

Patterns of mtDNA and nuclear DNA in North Pacific humpback whales have also differed among whales from different regions, particularly among feeding areas. Significant differences in mtDNA haplotypes were found between 38 humpback whales biopsied in southeastern Alaska and 20 from central California, suggesting a long-term migration rate of less than one female per generation (Baker *et al.* 1990, 1994). However, differences in nuclear DNA were not found between humpback whales off California and southeastern Alaska (Baker *et al.* 1993, Palumbi and Baker 1994), suggesting some reproductive interchange, recent or historical. A larger analysis of samples from 205 humpback whales from an expanded number of areas in the North Pacific revealed highly significant differences in mtDNA among both feeding and wintering areas and weaker, although still significant differences in nuclear actin intron alleles (Baker *et al.* In prep.). The differences in alleles were significant when tested based on two presumed “stocks” which compared the wintering and feeding areas of the eastern North Pacific (Mexico and California) against those from the central North Pacific (Hawaii and Alaska). Medrano *et al*. (1995) reported weak but significant differences in mtDNA haplotypes between humpback whales wintering off the Revillagigedos and those off the Mexican coast.

The occurrence of distinct feeding aggregations, as indicated by photographic identification and mtDNA, does not necessarily indicate an absence of some interbreeding among whales from these different groups. Because mtDNA is maternally transmitted, mtDNA differences among feeding grounds may only indicate that offspring return to their mothers' feeding ground. Mattila *et al.* (1989) and Clapham *et al.* (1993) have reported that breeding groups in the West Indies have included males and females from different feeding areas. Similarly, humpback whales from feeding areas in both Alaska and California migrate to both Hawaii and Mexico although with very different frequencies (Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1990, Urbán *et al.* 1987, Calambokidis *et al.* 1989), hence, the opportunity exists for whales to interbreed. Although the frequencies of mtDNA haplotypes on Mexican and Hawaiian wintering regions are significantly different, they are not as marked as between California and Alaska (Baker *et al.* 1994). This may reflect the mixing of whales from different feeding areas on the wintering regions or migration from as yet unsampled feeding areas (Medrano *et al.* 1995).

Population structure

An understanding of population structure of humpback whales in the North Pacific is crucial to determining and interpreting abundance estimates. Unfortunately, the population structure of humpback whales in the North Pacific is complex. The limited movements and genetic differences (both mtDNA and nuclear DNA) among whales utilizing different feeding areas as well as less dramatic but still significant differences among wintering regions make it inappropriate to treat the North Pacific as a single population.

Humpback whales appear to show a greater degree of site fidelity to feeding areas; movements among these areas are often limited and genetic differences are most pronounced. Although the boundaries and nature of one distinct feeding ground in the North Pacific has been defined off California, Oregon, and Washington (Calambokidis *et al.* 1996a) these boundaries may not be as easily defined in other areas. The nearly continuous distribution of humpback whales along their feeding range around the North Pacific, may make setting exact borders for feeding aggregations impossible even though animals might show a high degree of site fidelity. The pattern of decreasing interchange with distance seen among the sampled subareas along the coast of California, Oregon, and Washington (Calambokidis *et al.* 1996a) may be a typical pattern all along their feeding range and there may be few clear borders. Genetic and photographic identifications have only been conducted in a few limited feeding areas. Very little research has been conducted on humpback whales at some of their major feeding areas in the Gulf of Alaska and along the Aleutian Islands.

Defining populations based on wintering grounds is less ambiguous than for feeding areas because they interbreed in these regions, are separated geographically by large distances, and most of these areas have been sampled and compared by photo-identification and genetic methods. Movements between wintering regions were uncommon in this study and significant differences in mtDNA exists at least for whales off Hawaii and Mexico. We conclude that there are at least three populations of humpback whales in the North Pacific (those wintering off Hawaii, Japan, and Mexico); the data from subareas of Mexico and Japan were not substantial enough to assess the possibility of further dividing populations wintering in these regions. The abundance calculations we conduct are based on this premise.

The complexity of defining the population structure of humpback whales results from the difficulty in integrating the wintering and feeding areas into a single population structure. This is problematic currently because of the varied and sometimes unusual pattern of migratory destinations and the lack of information from many feeding areas. Even though defining populations based on wintering regions is the most defensible currently, it is important to not lose sight of the strong site fidelity to specific feeding grounds. Commercial whaling off California and Washington in the early 1900s provided a demonstration of the management implications of this fidelity. During an eight-year period, 2,473 humpback whales were killed from three stations off California and Washington (Clapham *et al.* 1997). Even though this depleted the population in this feeding area as evidenced by a dramatic decline in catch rates, such a decline was not as apparent off Mexico because that wintering region is the migratory destination of whales from multiple feeding areas (Clapham *et al.* 1997).

Abundance estimates

Heterogeneity of capture probabilities due to sex proportion

Males were probably more likely to be sampled on the wintering regions than females. Migrations of humpback whales to wintering areas off Australia were biased toward males by 2.4:1 apparently as a result of some females not migrating to the wintering areas every year (Brown *et al.* 1995). Chittleborough (1965) reported that early whaling catches on several wintering areas in the Southern Hemisphere were predominately males, although the ratio changed over time as males were depleted from these populations. Using genetically tagged humpback whales (*i.e.*, whales with known gender) sampled in the West Indies, Palsboll *et al.* (1997) obtained higher abundance estimates for males than females. Humpback whales identified at several locations in Hawaii had an apparent sex ratio of 1.8:1 to 2.7:1 (Mizroch *et al.* 1996). Biopsy samples from five wintering areas in the North Pacific including whales off Mexico, Hawaii, and Japan showed a 2.8:1 ratio of males to females (n=96) with males outnumbering females in all five samples (Baker *et al.* In prep.).

Other factors specifically related to photographic identification could also bias identifications toward one gender. Male and female humpback whales exhibit different behaviors, affiliations, and arrival and departure times on the wintering regions (Gabriele 1992). Active surface groups of whales on the wintering grounds are often easier to spot and identify photographically; these groups are typically composed of mostly males (Medrano *et al.* 1994). This could easily result in preferential sampling of males.

The samples from the wintering regions used in this study are likely skewed towards males by perhaps 2:1 to 3:1. The degree of bias introduced by a disproportionate number of males in the sample would depend partly on the dynamics of the female migrations. If females only made the migration or were photographed in alternate years, this would bias inter-year estimates upward. If they were absent only for a series of consecutive years while they were not sexually mature, it could bias the estimate downward because they would be largely excluded from the estimated population. Estimates based on feeding to winter areas matches would not be as affected by this bias and this may be one reason those estimates yielded higher abundances than estimates based solely on wintering area samples.

The magnitude of the bias introduced to the abundance estimates relying on inter-year winter region samples is relatively small (25%) even for the most extreme 3:1 skewed sex ratio. Effects of these ratios and how they may account for some of the differences in abundance estimates are discussed below (see Total estimate of abundance). Additionally, research will be needed on the degree and dynamics of sex bias in photo-identification samples to determine a more accurate correction factor.

Heterogeneity of capture probabilities due to geographic sampling bias

While whales (in the sample used for this study) photographed off Hawaii showed almost random mixing among subareas between years, this was not the case for the subareas off Mexico and Japan. Humpback whales wintering off Mexico have been sampled in three primary subareas; the Mexican mainland, Baja Peninsula, and the Revillagigedo Archipelago (Urban and Aguayo 1987). Most samples used in this study came from Baja; samples from the other two subareas were limited primarily to only one year. Humpback whales were more likely to return to the same subarea than be seen in a different subarea. The lowest rate of interchange among these subareas was between the Revillagigedo Archipelago and mainland Mexico (Landron 1995, Urban *et al.* 1994). Similarly, interchange among the two sampled subareas off Japan was more limited than the inter-year return rate at either site.

For this study, we pooled subareas into three primary wintering areas (Mexico, Hawaii, and Japan). Because the photographs from Baja dominated the sample from Mexico, the abundance estimates (based on inter-year samples of wintering areas) could be biased downwards. This would be due to the increased probability of resampling whales off Baja. Conversely, the single-year samples from mainland Mexico and the Revillagigedos may have reduced the chance of recaptures and biased the estimates for Mexico upwards. If there were unsampled subareas off Japan (in addition to the ones that were included in this study), the results would underestimate of the abundance of animals using these waters.

Other sources of bias

A variety of other factors potentially alter the “catchability” of some whales and create heterogeneity of capture probabilities. These include behavioral differences that might alter an animal’s chance of being seen during a boat survey or being successfully photo-identified if seen. The degree of bias introduced by these factors is also a function of the sampling strategy employed, which varied among the different researchers who provided photographs for the current study.

The Petersen estimates of abundance using animals marked on specific feeding areas and recaptured on wintering regions may be biased upward by the movement of some of these animals to secondary wintering areas. That estimate assumed that all whales from southeastern Alaska migrated to Hawaii and all whales from California-Washington migrated to Mexico. Although this was the principal trend, it was not universally true; some southeastern Alaska whales migrate to Mexico and not Hawaii (see Discussion section on migratory movements) and similarly, some humpback whales that feed off California migrate to Hawaii. Whatever portion of the whales treated as marked from these feeding areas that migrated to the secondary wintering areas would be unavailable for recapture and would bias the estimate upward by a similar proportion. This probably contributed to the higher abundances obtained from those estimates compared to the wintering area models.

Comparison to previous estimates of abundance

There have been relatively few estimates of humpback whale abundance for the entire North Pacific Basin. This species was thought to have numbered approximately 15,000 in the North Pacific prior to commercial exploitation in the twentieth century (Rice 1978), although this was determined using a rough back-calculation based on animals killed and estimates of life history parameters. At the end of commercial whaling for humpback whales in 1966, estimates were about 1,400 (Gambell 1976) and 1,200 (Johnson and Wolman 1984). These were based on either crude estimates from censuses of wintering areas or on sighting rates on feeding areas and rough estimates of line transect parameters. Most of the past estimates of abundance have been for specific regions and recently have been based primarily on capture-recapture techniques using photographically identified individuals. Barlow (1994) concluded that the North Pacific humpback whale population was greater than 3,000 based on separate minimum assessments of different wintering areas.

A number of past estimates of abundance have been made for the Hawaii wintering region and these have generally been considerably lower than our estimates of 4,000-5,000. Rice and Wolman (1980) estimated 550-790 humpback whales using the shallow waters around the Hawaiian Island chain based on line transect surveys from 1976 to 1979. Darling and Morowitz (1986) estimated that 1,000 (single season) and 2,100 (over five seasons) humpback whales inhabited Hawaii waters based on capture-recapture of identified whales from 1977-81 off Maui. Baker and Herman (1987) considered this estimate high and concluded more reasonable estimates were 635-1,536 based on analysis of their similar though separate dataset from off Maui for 1980-83. These estimates were lower than those made here, probably because of both an increase that has occurred over the 10 years separating these estimates, as well as the reliance of those samples on a single subarea. It would require a relatively high rate of increase of 7% per year for humpback whale abundance to double in a ten-year period. The use of samples from a single subarea of Hawaii for these past estimates may have resulted in heterogeneity of capture probabilities biasing the estimates downward (Hammond 1986). However, because we did not see a noticeable tendency for whales to return to the same subarea of Hawaii between years this bias was probably not large. Though an increase in whale abundance over time and biases in the earlier estimates may not individually explain the differences among the estimates they might in combination account for the difference.

A more contemporaneous estimate to those reported here was based on samples from Kauai for 1989-93 that yielded estimates of 2,500-5,000 (Cerchio 1994). The sample we used in this study for Kauai for 1991-93 period was the same included in that analysis. The primary differences between our analysis and that reported by Cerchio (1994) was the smaller number of years included in this study, our inclusion of three different sub-areas of Hawaii, and our use of a geographically stratified model. Despite these differences, our estimate of abundance for Hawaii was within the range reported by Cerchio (1994).

Although past estimates for the Mexico wintering area were more limited, recent estimates by Urban *et al.* (1994, In prep.) may provide a more accurate abundance estimate than this study. The 1990-93 sample for Mexico used for our estimates did not provide good coverage of the different subareas in most years. This is likely the reason for the highly variable estimates of 1,600 to 4,200 in our study. Urban *et al.* (In prep.) estimated approximately 2,700 humpback whales for the combined mainland and Revillagigedo Archipelago in 1991-92. This estimate is still likely biased downward from the bias toward males in samples from the wintering areas.

The number of whales killed during several periods of commercial whaling whales in the waters off Ogasawara and Okinawa indicates these populations were certainly larger than the current estimates from this study. A total of 3,277 humpback whales were reported killed in commercial whaling in the coastal waters of Japan between 1910 and 1965 (Rice 1978, Nishiwaki 1959). Of these, 970 were taken in the waters around the Okinawa (Ryukyu Islands) with the majority (764) in a four year period between 1958 and 1961. A total of 817 whales were killed in the waters around Ogasawara (Bonin Islands) though these were taken primarily from 1924 to 1944.

Estimates of the abundance of humpback whales have also been made for a number of feeding areas although these are not as easy to compare to the results of the current study. Estimates of the abundance of humpback whales off California have ranged from 300 to 700 based on capture-recapture of identified whales and line-transects methods (Dohl *et al.* 1993, Barlow *et al.* 1995 Barlow 1995, Barlow and Gerrodette 1996, Barlow and Calambokidis 1995, Forney *et al.* 1995, Calambokidis *et al.* 1990, 1993, Calambokidis and Steiger 1995). Abundance in southeastern Alaska has been estimated at 270-372 for 1979-83 (Baker *et al.* 1985), 547 for 1986 (Baker *et al*. 1992), and 404 for 1985-92 (Straley 1994). A minimum estimate (uncorrected for animals missed on the transect line) of 1,247 (SE=392) humpback whales was made from vessel surveys in 1987 in the northwestern Gulf of Alaska encompassing shelf waters from the Kenai Peninsula west to Unimak Pass (Brueggeman *et al.* 1988). Estimates from these feeding areas total far less than our estimates of wintering areas and reflect the lack of data from many feeding areas used by humpback whales in the North Pacific.

Total estimate of abundance

The Darroch and Hilborn methods yielded virtually identical estimates of abundance (Table 14). We consider the estimate from the Darroch method as the best estimate because its variance estimates were lower by region and for the total (Table 14). This makes the best estimate of the North Pacific humpback whale population, as determined from our data, to be 6,010 (SE=474).

There are several reasons this estimate from our study is likely an underestimate of the true population. Most violations of assumptions of capture-recapture models (such as heterogeneity of capture probabilities due to geographic sampling patterns or sex ratio) generally result in a downward bias in estimates of abundance. Several factors that cannot be evaluated with current data (such as the use of wintering areas other than those sampled) could also result in a downward bias in estimates of abundance.

Although the primary methods used in this study indicate an abundance of about 6,000 humpback whales in the North Pacific, we can calculate some alternate abundance estimates adjusting for a primary source of bias and employing the alternate estimate for Mexico made by other researchers using a larger dataset. Adjusting our estimate of Hawaii and Japan (4,400) for a 3:1 male biased sex ratio on the wintering would increase these estimates to 5,500. Abundance estimates for Mexico, which ranged from 1,600 to 4,200 in this study, are likely in between this range and perhaps near the value of 2,200-2,800 estimated by Urban *et al.* (1994, In prep.) using a wider range of years. Use of the estimates adjusted for sex bias for Hawaii and Japan and the estimates from Urban *et al.* for Mexico would yield a total North Pacific abundance of about 8,000. Although this higher estimate may be more realistic, it is based on an imprecise understanding of the degree of sex bias so it is impossible to calculate a variance estimate for this calibration. This study clearly demonstrates that the North Pacific humpback whale population is well above the rough estimates of 1,400 that were made at the end of whaling in the 1960s, although it is still half the rough estimate of 15,000 for pre-exploitation.

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Table 1. Summary of photographs received and used by region for North Pacific comparison.

Region Code	Region	Collector	Photos submitted	Photos selected	Unique IDs	Year*				Color Category				
						90	91	92	93	1	2	3	4	5
1	Revillagigedo	Jacobsen,UNAM,UABCS	250	168	159		158	10	0	11	46	26	47	38
2	Mainland Mexico	UNAM, CWR, UABCS	193	139	138	131	4	4	0	7	25	35	36	36
3	Baja	UABCS	408	255	233	43	56	100	56	30	75	39	45	66
4	Hawaii- Big Island	KBMML	1,184 **	433	401		175	74	184	20	78	120	111	104
5	Hawaii- Maui	HWRF	744	393	368		117	114	162	17	58	111	138	69
6	Hawaii- Kauai	S. Cerchio	929 **	386	375		101	137	148	17	79	103	91	96
7	Ogasawara	OMC	576	360	257		110	136	114	13	99	87	68	93
8	Okinawa	OEA, WWF	129	88	63		30	23	35	2	16	26	18	26
9	California & Washington	CRC	917	694	454		190	316	188	21	112	175	124	262
10	Southern British Columbia	CWR, CRC	17	13	14		11	0	2	1	3	1	3	5
11	Northern British Columbia	G. Ellis	76	64	59		2	23	39	2	8	14	15	25
12	Southeast Alaska	GBNP, J. Straley	670	421	287		148	158	115	17	54	43	119	188
13	Prince William Sound	NGOS	180	135	87		45	64	26	9	41	30	28	27
14	Kodiak	NMML, NGOS	116	79	76		1	43	35	3	17	16	16	27
15	Shumagin Islands	NMML	18	15	15		0	4	11	0	0	3	7	5
16	Bering	NMML	7	7	7		0	7	0	0	0	0	4	3
	Total		6,414	3,650	2,993	174	1,148	1,213	1,115	170	711	829	870	1,070
	Total Unique (after between-region matches)				2,712									

* Year code reflects 1990-93 except for some SEAK early winter sightings kept with their respective field season. Only Mexico samples added for 1990.

** Includes several hundred within-year duplicates.

Table 2. Success rate finding matches based on two independent teams and known contributor matches.

	Matches found	**Found by team 1**	**Found by Team 2**	**Found by both teams**	**Total matches***	**Missed by both teams***
Primary comparison (1991-93)						
Matches using	1098	1032	1036	970	1102	4
independent teams	100%	94%	94%	88%	100%	0%
Contributor matches	546				563	17
	97%				100%	3%
Mexico 1990 supplemental comparison						
Matches using	122	117	105	100	123	1
independent teams	99%	95%	85%	81%	100%	1%
Contributor matches	53	50	48	45	57	4
	93%	88%	84%	79%	100%	7%

*Total and missed matches for the two independent teams computed using mark-recapture.

Table 3. Evaluation of reasons why whales were missed by one or both teams. Because each missed match was compared twice (for each whale in the pair), the number of misses and explanations is double the number of matches.

			Number of times a match was missed in each category							
Team	**Matches missed**	**Times missed**	**A Photos never compared due to subcategory separating**	**B Both photos marginal**	**C Change in markings**	**D Difference in lighting**	**E No specific reason**	**F One photo poor quality**	**G Photos not compared**	**H Photo printed backwards**
Matches found by one team but missed by the other										
1	66	132	35 26.5%	10 7.6%	5 3.8%	22 16.7%	38 28.8%	18 13.6%	2 1.5%	2 1.5%
2	62	124	21 16.9%	14 11.3%	10 8.1%	22 17.7%	49 39.5%	7 5.6%	1 0.8%	0 0.0%
Total	128	256	56 21.9%	24 9.4%	15 5.9%	44 17.2%	87 34.0%	25 9.8%	3 1.2%	2 0.8%
Contributor matches missed by both teams										
Both teams	17	68	45 66.2%	0 0.0%	5 7.4%	6 8.8%	12 17.6%	0 0.0%	0 0.0%	0 0.0%

Table 4. Number of individual whales seen multiple times in the same region or in more than one region. Number of acceptable quality photographs used (Photo) and unique identifications (IDs) is shown.

Region	Abrev.	Photo	IDs	Rev.	Mnl.	Baja	Big Is	Maui	Kuai	Ogas.	Okin.	CA-WA	SBC	NBC	SEAK	PWS	Kodiak	Aleut.	Ber.
Revillagigedo	Rev.	168	159	9															
Mainland Mexico	Mnl.	139	138	0	1														
Baja	Baja	255	233	9	12	19													
Hawaii- Big Island	Big Is	433	401	1	0	2	31												
Hawaii- Maui	Maui	393	368	0	0	0	40	24											
Hawaii- Kauai	Kuai	386	375	2	0	0	19	32	10										
Ogasawara	Ogas.	360	257	0	0	0	3	1	0	82									
Okinawa	Okin.	88	63	0	0	0	0	0	0	7	22								
California-Washington	CA-WA	694	454	1	32	19	1	2	0	0	0	197							
S British Columbia	SBC	15	13	0	0	1	0	0	0	1	0	0	2						
N British Columbia	NBC	62	60	0	0	1	6	4	0	1	0	0	0	2					
Southeast Alaska	SEAK	421	287	0	0	0	25	23	18	0	0	0	0	0	97				
Prince William Sound	PWS	135	87	0	1	0	6	5	3	0	0	0	0	0	2	37			
Kodiak	Kodiak	79	76	0	0	1	3	5	3	1	0	0	0	0	1	1	3		
Shumagin Is. (Aleutians)	Aleut.	15	15	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
Bering	Ber.	7	7	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Total		3,650	2,993																
Total unique			2,712																

Table 5. Interchange indices for different combinations of years and regions for the three subareas in Hawaii 1991-93.

Samples	**n**	**Mean**	**Std. dev.**
Same area in different years	**9**	**0.306**	**0.114**
Big Island	3	0.271	0.041
Maui area	3	0.395	0.154
Kauai	3	0.253	0.094
Different areas in same year	**9**	**0.138**	**0.127**
Big Island - Maui	3	0.254	0.099
Maui - Kauai	3	0.108	0.135
Big Island - Kauai	3	0.053	0.062
Different areas and years	**18**	**0.264**	**0.183**
Big Island - Maui	6	0.306	0.250
Maui - Kauai	6	0.276	0.152
Big Island - Kauai	6	0.211	0.152
All	**36**	**0.243**	**0.164**

Table 6. Interchange indices for different combinations of years and regions for the three subareas in Mexico 1990-93.
Small samples only used for within-region calculations.

Samples	**n**	**Mean**	**Std. dev.**
Same area in different years	**9**	**0.950**	**0.676**
Mainland	2	0.954	1.349
Revillagigedos	1	0.662	
Baja	6	0.997	0.589
Different areas in same year	**2**	**0.298**	**0.081**
Mnld-Baja	1	0.355	
Rev-Baja	1	0.241	
Different areas and years	**7**	**0.258**	**0.168**
Mnld-Baja	3	0.380	0.152
Rev-Baja	3	0.221	0.059
Rev-Mnld	1	0.000	
All	**18**	**0.608**	**0.591**

Table 7. Interchange indices for different combinations of years and regions for the two subareas in Japan 1991-93.

Samples	**n**	**Mean**	**Std. dev.**
Same area in different years	**6**	**7.265**	**5.867**
Okinawa	3	11.636	5.358
Ogasawara	3	2.893	0.166
Different areas in same year			
Okin.- Ogas.	**3**	**0.167**	**0.289**
Different areas and years			
Okin.- Ogas.	**6**	**0.244**	**0.207**
All	**15**	**3.037**	**5.009**

Table 8. Interchange indices for different combinations of years and pooled wintering regions.

Samples	**n**	**Mean**	**Std. dev.**
Same region in different years			
Mexico	6	0.518	0.253
Hawaii	3	0.257	0.055
Japan	3	2.365	0.156
Different regions in same year			
Mexico-Hawaii	3	0.000	0.000
Hawaii-Japan	3	0.000	0.000
Mexico-Japan	3	0.000	0.000
Different regions and years			
Mexico-Hawaii	9	0.015	0.021
Hawaii-Japan	6	0.010	0.012
Mexico-Japan	9	0.000	0.000

Table 9a. Data and population estimates from Darroch and Petersen methods using winter releases from 1990/91 and winter recoveries from 1992.

		Recovery 1992				
	M	MX	HI	JP	$m_{i.}$	**a**
Release 1990/91	MX	18	2	0	20	375
	HI	0	38	1	39	377
	JP	0	0	55	55	140
	$m_{.j}$	18	40	56	114	892
	u	95	277	103		
	n	113	317	159	589	

p		**se(p)**
	0.0507	0.0118
	0.1015	0.0156
	0.3929	0.0413

Θ				**se(θ)**		
	0.947	0.053	0.000	0.310	0.038	0.000
	0.000	0.993	0.007	0.000	0.216	0.007
	0.000	0.000	1.000	0.000	0.000	0.149

N_i		**se(N_i)**
	2230	558
	3124	509
	405	49

N	5759	**se(N)**	744

Petersen

N	4580	**se(N)**	356

Table 9b. Data and population estimates from Darroch and Petersen methods using winter releases from 1990/91 and winter recoveries from 1993.

		Recovery 1993				
	M	MX	HI	JP	$m_{i.}$	**a**
Release 1990/91	MX	13	3	0	16	375
	HI	0	37	0	37	377
	JP	0	2	45	47	140
	$m_{.j}$	13	42	45	100	892

u	42	426	102	
n	55	468	147	670

p		**se(p)**
	0.0377	0.0104
	0.0981	0.0153
	0.3762	0.0626

Θ				**se(θ)**		
0.918	0.082	0.000		0.357	0.049	0.000
0.000	1.000	0.000		0.000	0.221	0.000
0.000	0.146	0.854		0.000	0.105	0.177

N_i	**$se(N_i)$**
1457	447
4769	773
391	70

N	6617	**se(N)**	870

Petersen

N	5932	**se(N)**	510

Table 9c. Data and population estimates from Darroch and Petersen methods using winter releases from 1992 and winter recoveries from 1993.

		Recovery 1993				
	M	MX	HI	JP	$m_{i.}$	**a**
Release 1990/91	MX	5	1	0	6	113
	HI	0	36	0	36	317
	JP	0	1	57	58	159
	$m_{.j}$	5	38	57	100	589

u	50	430	90	
n	55	468	147	670

p	0.0480	**se(p)**	0.0213
	0.1136		0.0178
	0.3795		0.0449

Θ	0.922	0.078	0.000	**se(θ)**	0.574	0.079	0.000
	0.000	1.000	0.000		0.000	0.222	0.000
	0.000	0.055	0.945		0.000	0.056	0.150

N_i	1146	**se(N_i)**	530
	4121		671
	387		52

N	5654	**se(N)**	843

Petersen

N	3919	**se(N)**	326

Table 10a. Data and parameter estimates from Hilborn's method using winter releases from 1991 and 1992 and winter recoveries from 1992 and 1993. Predicted and observed marked recaptures are shown.

Θ	MX	HI	JP	Sum
MX	0.928 (±0.033)	0.072 (±0.033)	0.000	1.00
HI	0.000	0.997 (±0.022)	0.003 (±0.022)	1.00
JP	0.000	0.057 (±0.067)	0.943 (±0.067)	1.00

p	MX	HI	JP
	0.045 (±0.008)	0.099 (±0.011)	0.374 (±0.055)
ln *L:*	−33.33		

$M_{i,j,t}$; *t*=	90-1	92			93		
j=	marked	MX	HI	JP	MX	HI	JP
MX	375	348	27	0	323	25	0
HI	377	0	376	1	0	410	1
JP	140	0	8	132	0	8	126
		348	411	133	323	442	127

92	93		
marked	MX	HI	JP
95	88	7	0
277	0	276	1
103	0	6	97
	88	289	98

Predicted $m_{i,j,t}$

t=	92			93		
j=	MX	HI	JP	MX	HI	JP
MX	16	3	0	14	2	0
HI	0	37	0	0	41	0
JP	0	1	49	0	1	47
	16	41	50	14	44	47

93		
MX	HI	JP
4	1	0
0	27	0
0	1	36
4	29	37

Observed $m'_{i,j,t}$

t=	92			93		
j=	MX	HI	JP	MX	HI	JP
MX	18	2	0	13	3	0
HI	0	38	1	0	37	0
JP	0	0	55	0	2	45
Tot	18	40	56	13	42	45

93		
MX	HI	JP
3	1	0
0	30	0
0	0	33
3	31	33

Table 10b. Estimates of abundance and corresponding standard errors from Hilborn's method using only winter releases and recoveries.

	Estimated abundance			
	MX	HI	JP	Total
1992	2,485	3,037	415	5,937
se	485	361	50	538
1993	1,210	4,483	384	6,077
se	276	548	49	576
Average	1,848	3,760	400	6,007
se	352	439	46	504

Table 11a. Data and parameter estimates from Hilborn's method using winter and summer releases and winter and summer recoveries, 1991 -- 1993.

Model 1 ln *L:* -132.87

Θ	W->S			**Ψ**	S->W			
	1(CA)	2(AK)	Sum		1(MX)	2(HI)	3(JP)	Sum
1(MX)	0.939	0.061	1.000	CA(1)	0.604	0.000	0.396	1.000
2(HI)	0.011	0.989	1.000	AK(2)	0.014	0.986	0.000	1.000
3(JP)	0.896	0.104	1.000					
	1(CA)	2(AK)			1(MX)	2(HI)	3(JP)	
p	0.097	0.045			0.075	0.098	1.000	

Model 2 ln *L:* -127.31

Θ	W->S				**Ψ**	S->W			
	1(CA)	2(AK)	3(??)	Sum		1(MX)	2(HI)	3(JP)	Sum
1(MX)	0.938	0.062	0.000	1.000	CA(1)	1.000	0.000	0.000	1.000
2(HI)	0.002	0.998	0.000	1.000	AK(2)	0.012	0.983	0.005	1.000
3(JP)	0.128	0.098	0.773	1.000	3(??)	0.000	0.000	1.000	1.000
	1	2	3			1	2	3	
p	0.095	0.044	0.000			0.045	0.098	0.489	

Model 3 ln *L:* -123.57

Θ	W->S				**Ψ**	S->W			
	1(CA)	2(AK)	3(??)	Sum		1(MX)	2(HI)	3(JP)	Sum
1(MX)	0.662	0.052	0.285	1.000	CA(1)	1.000	0.000	0.000	1.000
2(HI)	0.004	0.991	0.005	1.000	AK(2)	0.014	0.986	0.000	1.000
3(JP)	0.148	0.083	0.768	1.000	3(??)	0.000	0.000	1.000	1.000
	1	2	3			1	2	3	
p	0.154	0.045	0.000			0.071	0.099	0.483	

Model 4 ln *L:* -87.73

Θ	W->S				**Ψ**	S->W			
	1(CA)	2(AK)	3(??)	Sum		1(MX)	2(HI)	3(JP)	Sum
1(MX)	0.945	0.055	0.000	1.000	CA(1)	1.000	0.000	0.000	1.000
2(HI)	0.001	0.999	0.000	1.000	AK(2)	0.013	0.982	0.005	1.000
3(JP)	0.086	0.106	0.808	1.000	3(??)	0.000	0.000	1.000	1.000
	1(CA)	2(AK)	3(??)			1(MX)	2(HI)	3(JP)	
p	0.064	0.039	0.000			0.045	0.098	0.462	
p(s)	0.304	0.109	0.000						

Table 11b. Estimates of abundance from Model 4 in Table 3b.

	Estimated abundance			
Winter	MX	HI	JP	Sum
1992	2517	3220	344	6081
1993	1225	4754	318	6297
Average	1871	3987	331	6189

Using capture probabilities **p**

Summer	CA-BC	AK	Sum
1992	3696	5696	9392
1993	1512	4126	5638
Average	2604	4911	7515

Using capture probabilities **p**(s)

Summer	CA-BC	AK	Sum
1992	911	2154	3065
1993	247	1341	1588
Average	579	1748	2326

Table 12a. Model for a hypothetical two-area, two-sex population of 6,000 animals where 20% of the population is marked. The population has a 1:1 sex ratio but samples are biased 2:1 male to female. Model serves as basis for calculation of population size (Table 12b).

N	6000	(total population)
	0.2	(proportion of population marked)
χ	0.333	(proportion of marked whales that were females)

	Marked					Unmarked			
	Males:	800	Females:	400		Males:	2200	Females:	2600
	Area 1	Area 2	Area 1	Area 2		Area 1	Area 2	Area 1	Area 2
	0.7	0.3	0.7	0.3		0.7	0.3	0.7	0.3
N_i, time 1	560	240	280	120	U_i, time 1	1540	660	1820	780
Migration									
Θ	0.4	0.6	0.4	0.6	Θ	0.4	0.6	0.4	0.6
	0.6	0.4	0.6	0.4		0.6	0.4	0.6	0.4
N_j, time 2	368	432	184	216	U_j, time 2	1012	1188	1196	1404
Probability of capture									
p_{jx}	0.15	0.25	0.075	0.125	p_{jx}	0.15	0.25	0.075	0.125
Captures									
m	55.2	108	13.8	27	u	151.8	297	89.7	175.5

Table 12b. Estimates of abundance for the hypothetical population (Table 12a) using Darrochs' method.

Darroch method by sex (unbiased)

	(area 1)	(area 2)	(Total)
p_{jm}	0.15	0.25	
p_{jf}	0.075	0.125	
True $\overline{p}_j$	0.1125	0.1875	

Darroch method pooled by sex

	(area 1)	(area 2)	(Total)
$\overline{p}_j$	0.125	0.208	
$\hat{U}_j$	1932	2268	4200
True U_j	2208	2592	4800

Correction of $\overline{p}_j$

	(area 1)	(area 2)	(Total)
p_{jm}	0.15	0.25	
p_{jf}	0.075	0.125	
n_j	310.5	607.5	
$\hat{N}_j$	2760	3240	6000
True N_j	2760	3240	6000

Table 13. Peterson mark-recapture estimates for wintering areas using marks at feeding areas.

Feeding area		Winter area				
Year	n	Year	n	Match	Estimate	SE
California - Mexico						
1991	189	1990-91	375	23	2,976	538
1991	189	1992	113	5	3,609	1,307
1992	314	1992	113	6	5,129	1,738
1992	314	1993	55	2	5,879	2,847
1993	187	1993	55	2	3,508	1,693
Average					4,220	800
SE Alaska - Hawaii						
1991	142	1991	377	14	3,603	835
1991	142	1992	317	7	5,683	1,818
1992	151	1992	317	5	8,055	2,956
1992	151	1993	468	17	3,959	837
1993	113	1993	468	11	4,454	1,154
Average					5,151	769

Table 14. Summary of abundance estimates by wintering region for the different models employed.

Years/samples	**Mexico**		**Hawaiii**		**Japan**		**Total**	
	N	**SE**	**N**	**SE**	**N**	**SE**	**N**	**SE**
Darroch method (winter areas only)								
1991*-1992	2,230	558	3,124	509	405	49	5,759	744
1991*-1993	1,457	447	4,769	773	391	70	6,617	870
1992-1993	1,146	530	4,121	670	387	52	5,654	843
Average	1,611	297	4,005	381	394	33	6,010	474
Hilborn method (winter areas only)								
1992	2,485	485	3,037	361	415	50	5,937	538
1993	1,210	276	4,483	548	384	49	6,077	576
Average	1,848	352	3,760	439	400	46	6,007	504
Hilborn method (feeding areas and winter areas)								
1992	2,517	--	3,220	--	344	--	6,081	--
1993	1,225	--	4,754	--	318	--	6,297	--
Average	1,871	--	3,987	--	331	--	6,189	--
Correction for male biased sampling on winter area								
Uncorrected abundance	1,800		4,000		400		6,200	
Corrected for 2:1 male bias	1,998		4,440		444		6,882	
Corrected for 3:1 male bias	2,250		5,000		500		7,750	
Petersen (using CA and SEAK as marks for Mexico and Hawaii recaptures)								
Average	4,220	800	5,151	769				

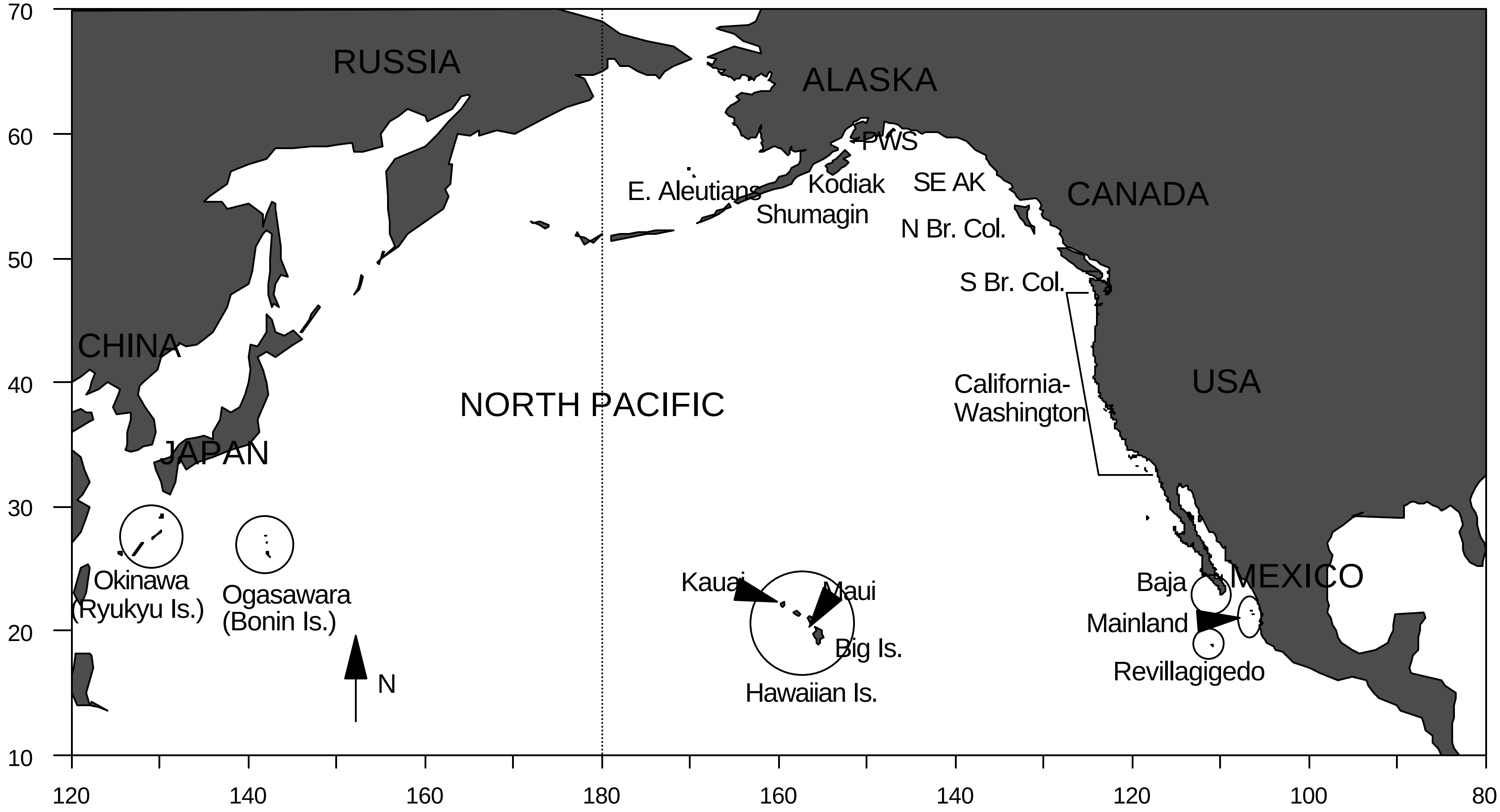

Figure 1. Locations where photographic identification data were collected.

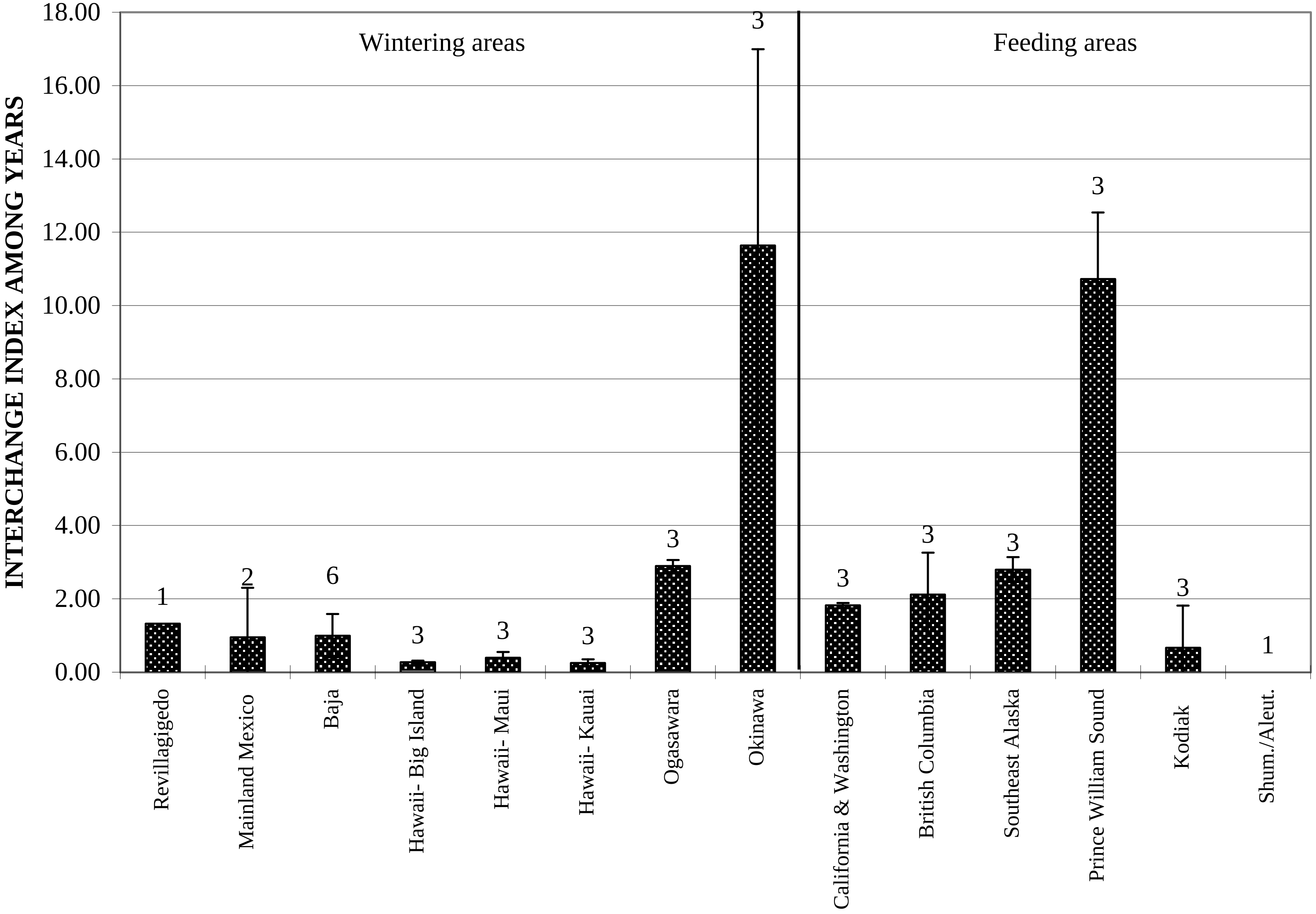

Figure 2. Interchange indeces for inter-year resightings at the same area. Numbers show pairs of years, bars show SD.

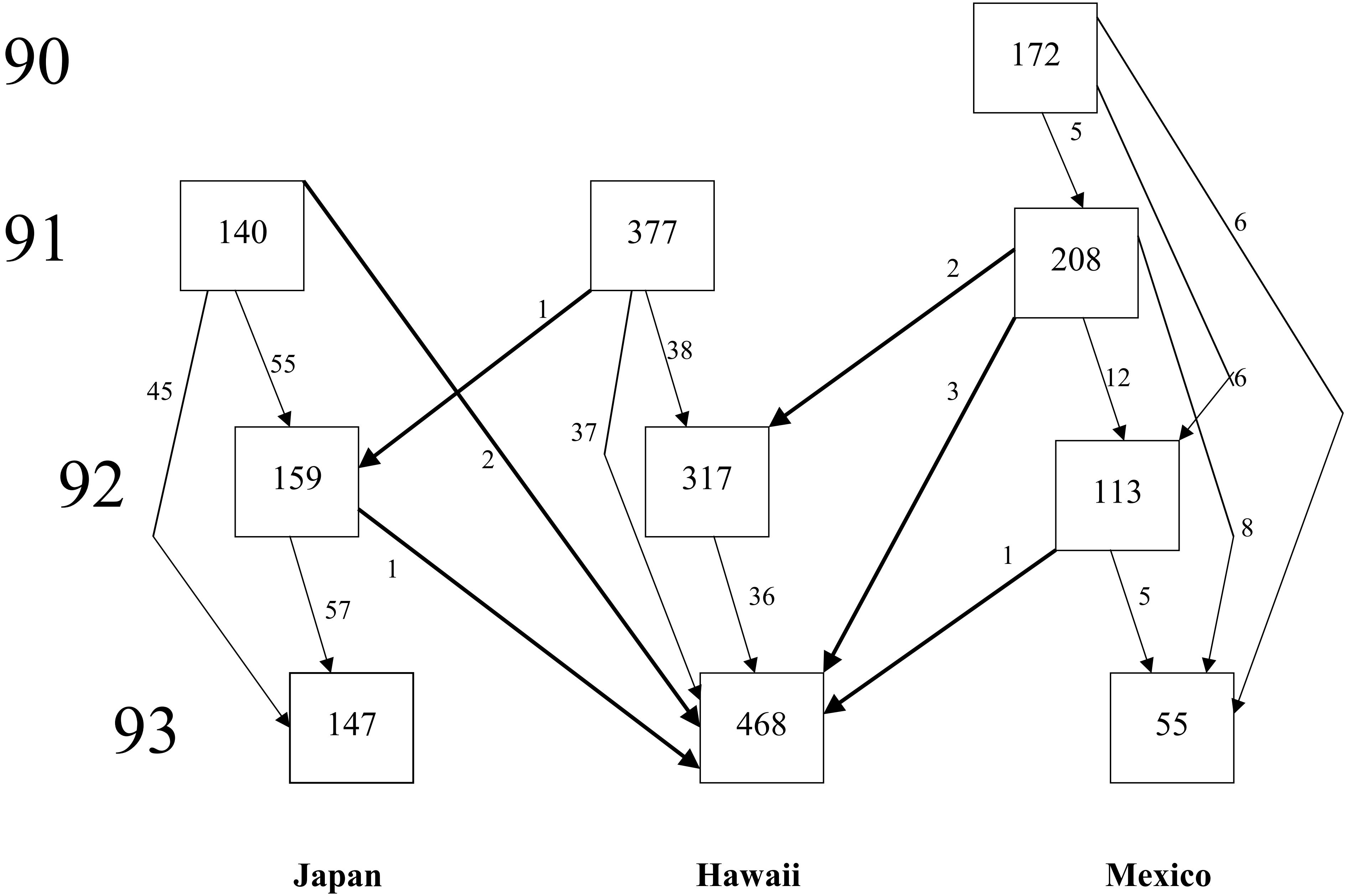

Figure 4. Inter-year and inter-region matches between the wintering areas off Japan, Hawaii, and Mexico. Numbers in boxes show number of individuals and numbers next to lines show number of whales that matched between years or regions.

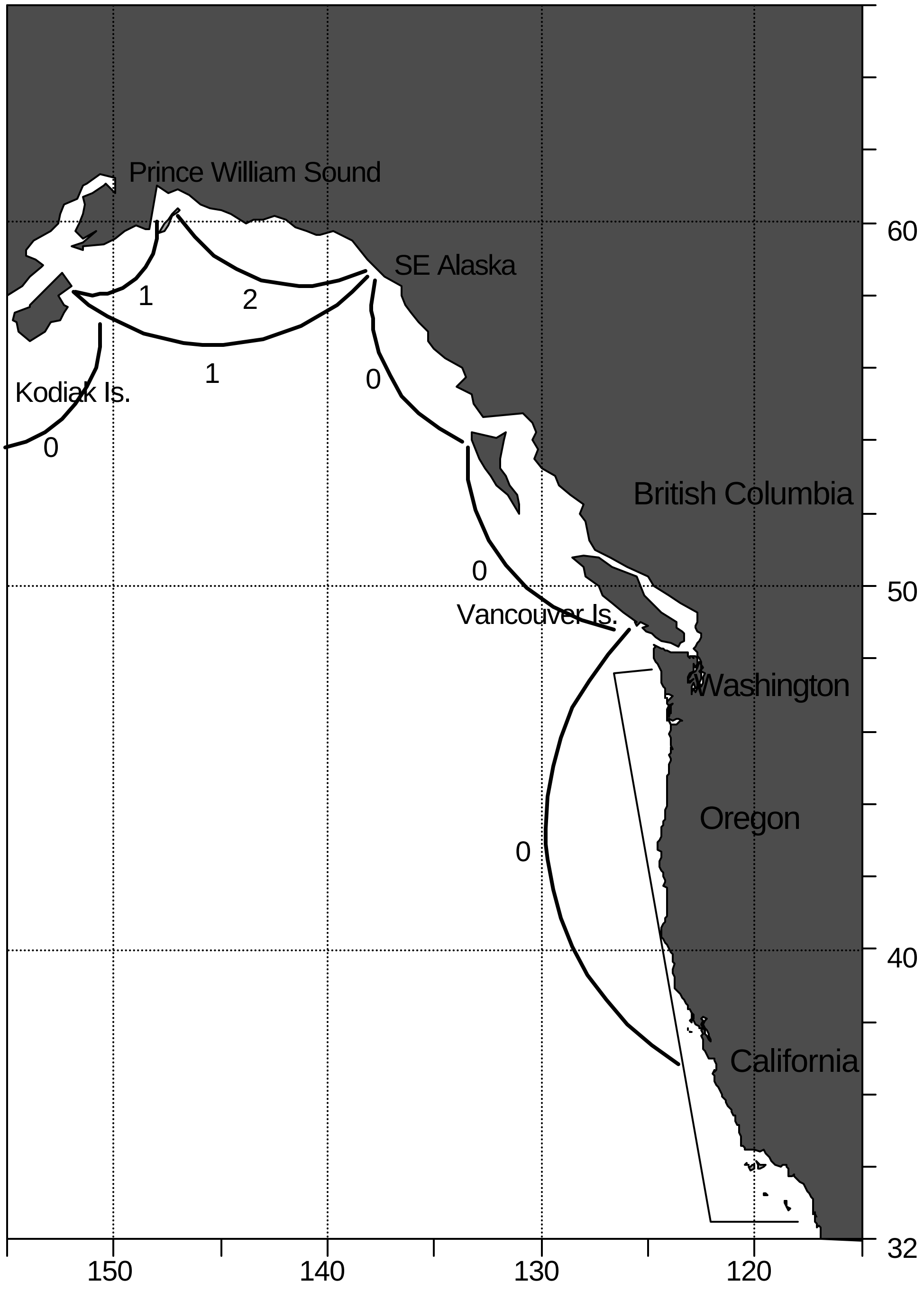

Figure 4. Number of matches found among feeding areas.

Brackets show pooled area for California-Washington.

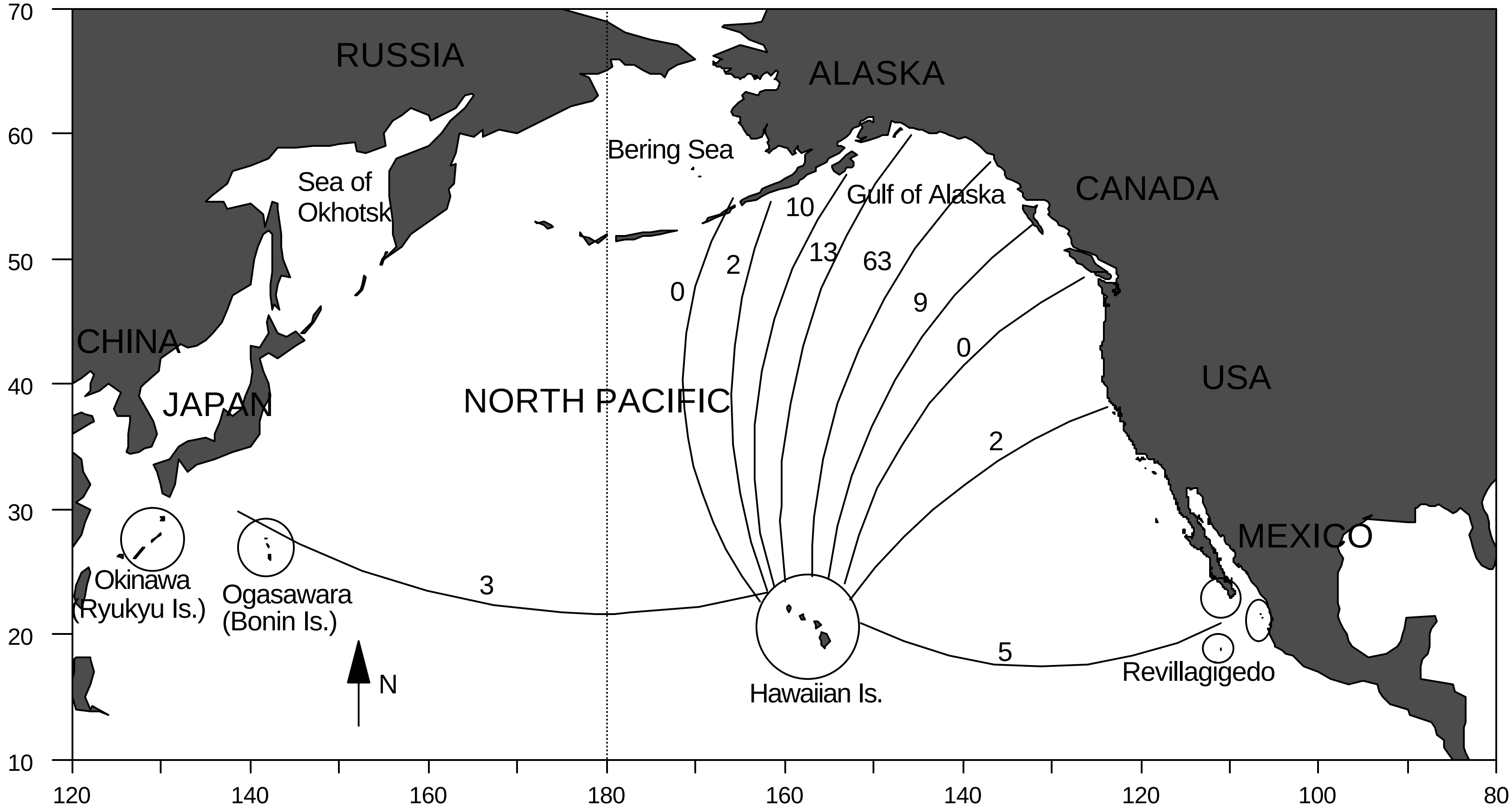

Figure 5. Migratory destinations of the 1,056 whales identified off Hawaii.

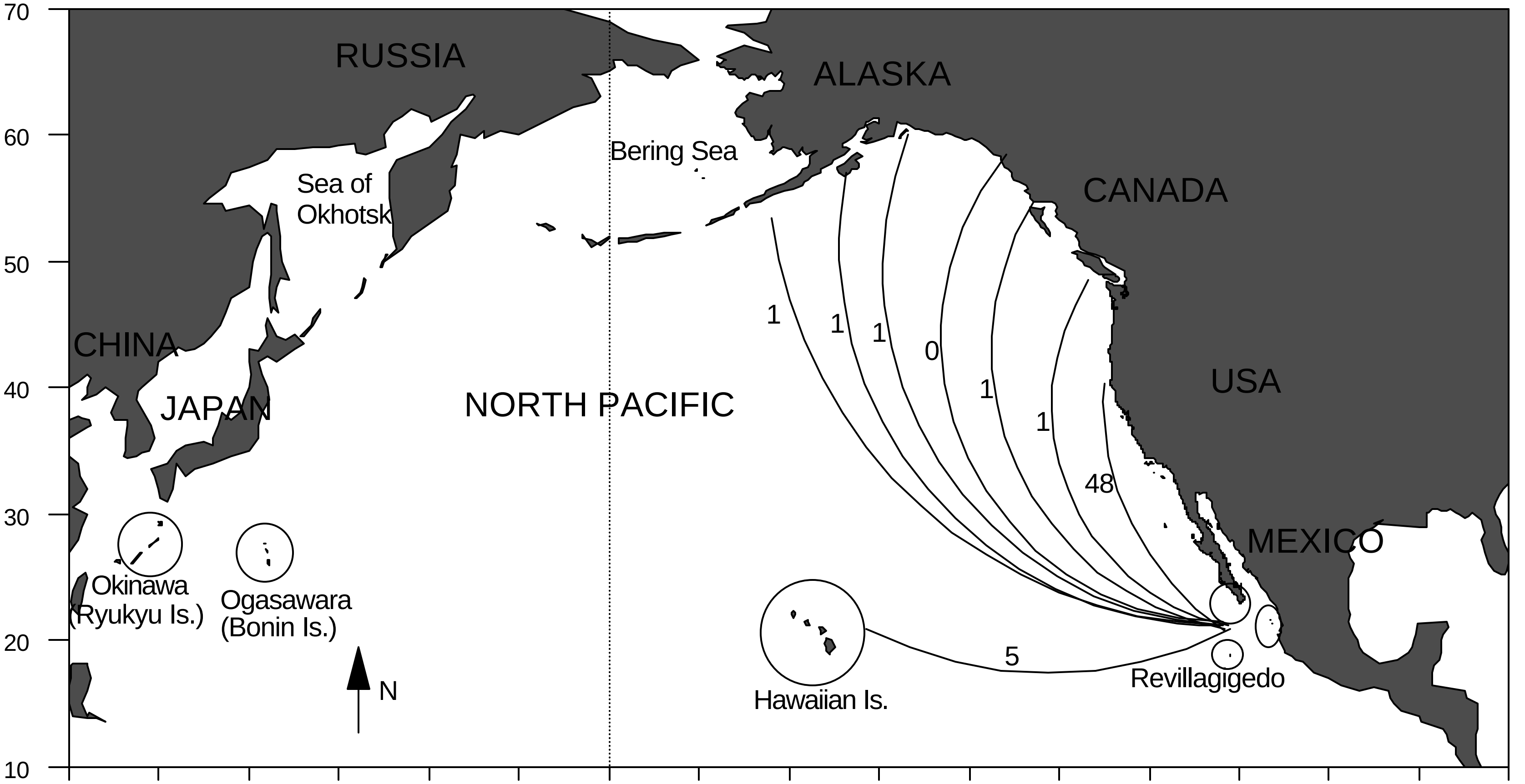

Figure 6. Migratory destinations of the 509 whales identified in Mexico.

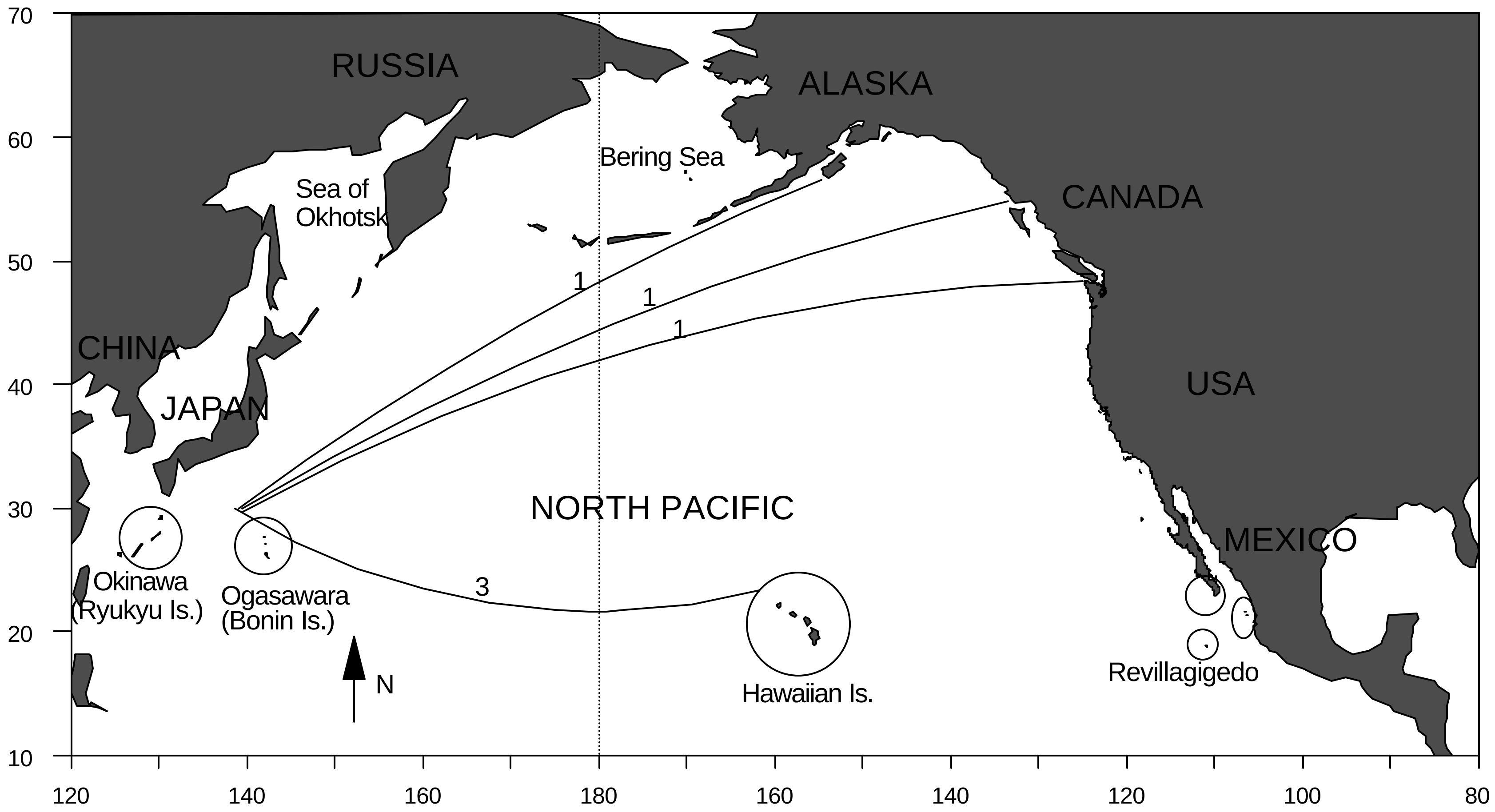

Figure 7. Migratory destinations of the 313 whales identified off Japan.

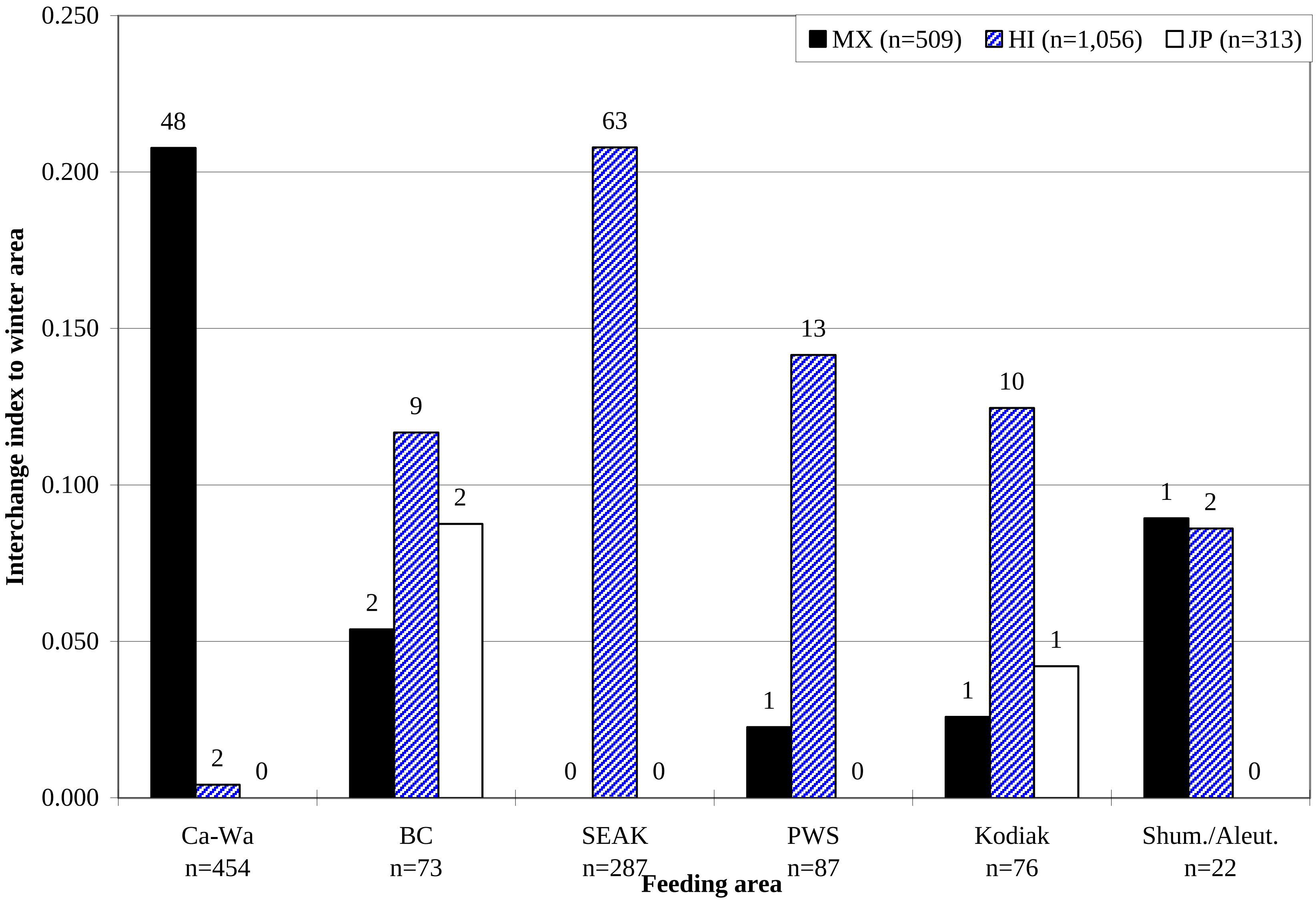

Figure 8. Interchange index between sampled feeding areas and the three main wintering regions.
Numbers above bars show number of intividuals documented migrating between areas

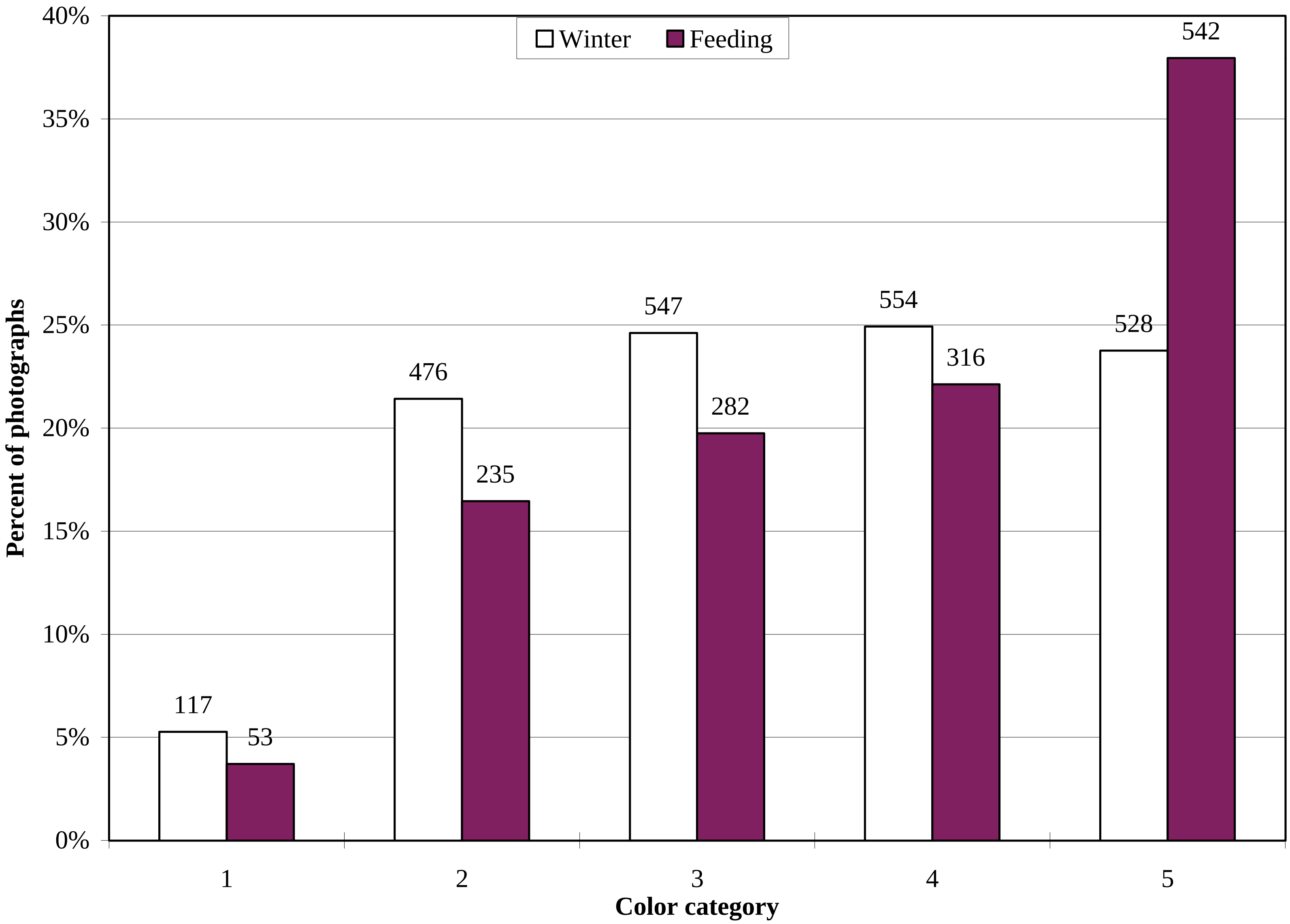

Figure 9. Differences in fluke colration patterns between wintering and feeding areas. Number of photographs are shown above the bars.

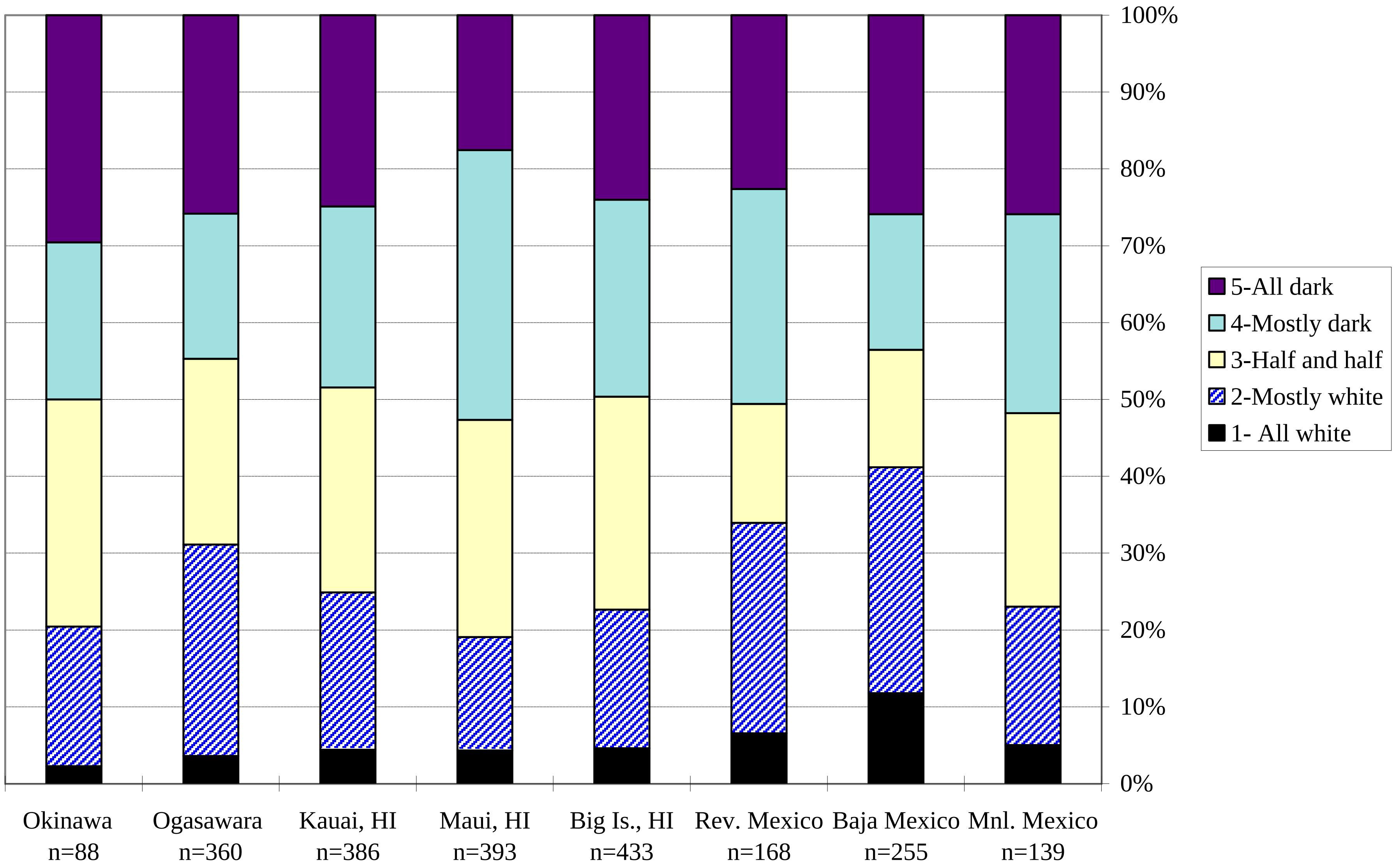

Figure 10. Percentage of flukes with different coloration types by wintering area.

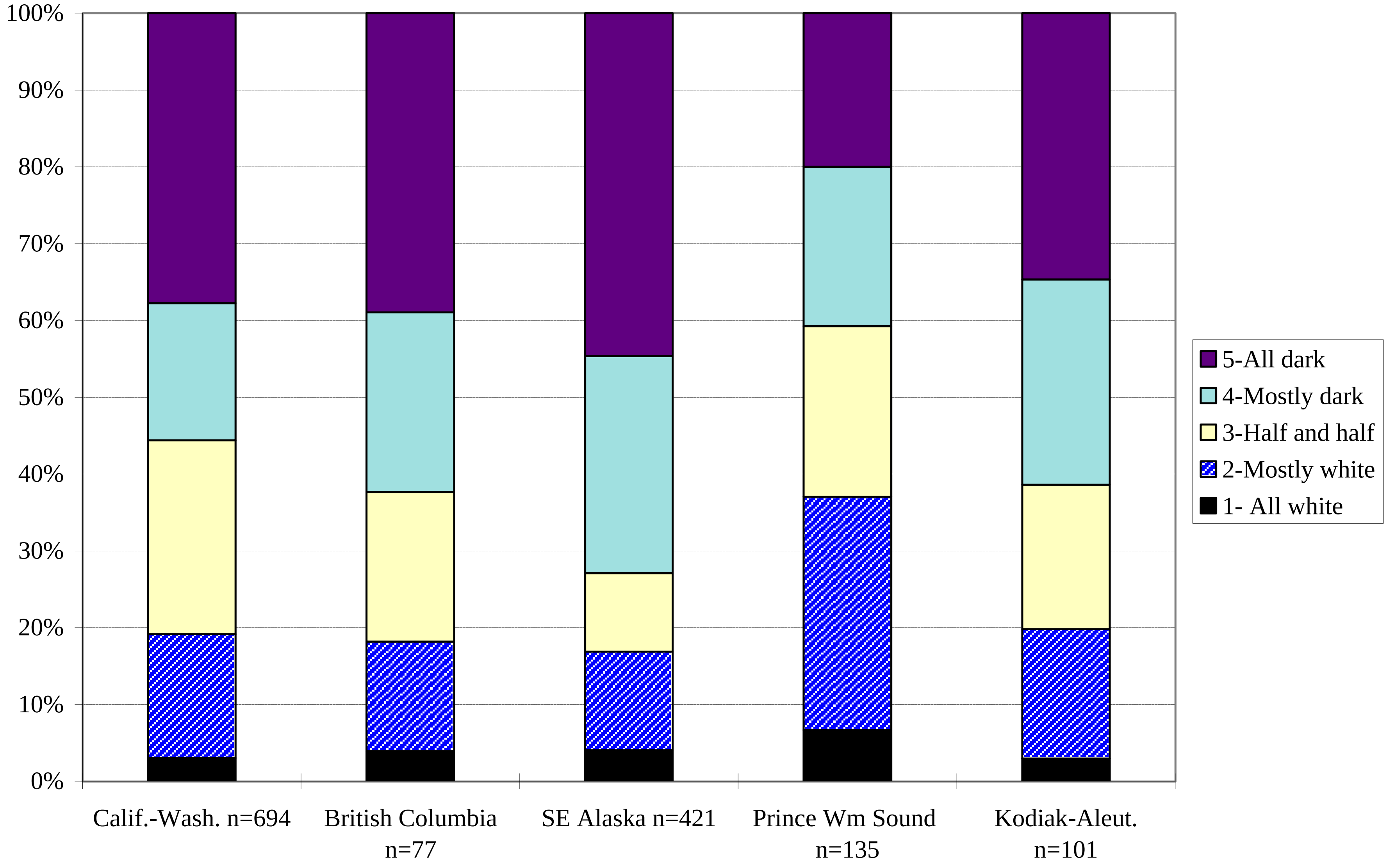

Figure 11. Percent of flukes with different coloration types by feeding area.