Biological Conservation 167 (2013) 173–178

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Short communication

Integrating population and genetic monitoring to understand changes in the abundance of a threatened seabird

Catalina Vásquez-Carrillo [a], R. William Henry [b], Laird Henkel [c], M. Zachariah Peery [a,*]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA
[b] Ecology and Evolutionary Biology, University of California, Santa Cruz, Center for Ocean Health, 100 Shaffer Road, Santa Cruz, CA 95060, USA
[c] Office of Spill Prevention and Response, California Department of Fish and Wildlife, 1451 Shaffer Road, Santa Cruz, CA 95060, USA

ARTICLE INFO

Article history:
Received 10 June 2013
Received in revised form 31 July 2013
Accepted 4 August 2013

Keywords:
Dispersal
Genetic monitoring
Marbled Murrelets
Population monitoring

ABSTRACT

Population monitoring programs for threatened species are rarely designed to disentangle the effects of movements from changes in birth and death rates on estimated trends in abundance. Here, we illustrate how population and genetic monitoring can be integrated to understand the cause of large changes in the abundance of a threatened species of seabird, the Marbled Murrelet (*Brachyramphus marmoratus*). Specifically, we used genetic data to test whether a large apparent population decline and subsequent recovery in central California was due to a population collapse followed by dispersal from larger populations to the north (the "rescue hypothesis"), or whether it was due to local changes in distribution where resident individuals dispersed from and then returned to surveyed areas (the "distribution hypothesis"). An alternative explanation, that rapid population recovery was the result of positive local population growth, was not supported by demographic data. The post-recovery population was more similar genetically to the pre-decline population than it was to northern populations. In addition, both pre-decline and post-recovery populations had a similar proportion and number of individuals of migrant ancestry, as determined with genetic assignment tests. Thus, pre-decline and post-recovery samples appear to come from the same population and our results support the distribution hypothesis. By conducting concurrent genetic and population monitoring, we were able to understand observed changes in the abundance in a threatened species, which would not have been possible by only monitoring abundance.

1. Introduction

Assessing whether changes in abundance are the result of alterations in birth and death rates or individual movements is essential for understanding population trends in threatened species. Population monitoring programs, however, typically yield estimates of population trends that incorporate both local demographic processes and movements among populations implicitly, and are therefore unable to disentangle the effects of movements from changes in birth and death rates (e.g., Saracco and DeSante, 2008; Miller et al., 2012). Pairing population and genetic monitoring programs constitutes an appealing approach for understanding the extent to which changes in abundance are due to changes in birth and survival rates, changes in immigration and emigration among populations, or smaller scale movements by residents across study area boundaries (Schwartz et al., 2007). While, in practice, such programs are rarely combined into a unified framework, population and genetic monitoring approaches can be integrated in a number of different ways. For example, in cases where the target population is genetically differentiated from potential source populations, declines in genetic population structure could indicate that a stable or recovering population is being sustained by an increase in immigration rather than local recruitment. In addition, genetic assignment methods that identify migrant individuals can be used to determine if population increases or declines are associated with changes in the number of migrants recruiting from other populations (Paetkau et al., 1995).

Here, we combine at-sea population and genetic monitoring to understand observed changes in the abundance of a population of Marbled Murrelets (*Brachyramphus marmoratus*) in central California that is classified as Threatened under the US Endangered Species Act. While this population is moderately genetically differentiated from larger populations to the north (Friesen et al., 2005), previous studies indicated that dispersal, largely by temporary influxes of nonbreeding individuals, into central California does occur (Hall et al., 2009; Peery et al., 2010). We used genetic methods to determine whether a short-term (⩽5-year), large (~4-fold) decline in at-sea abundance and subsequent rapid rebound (~1-year) in numbers were due to: (i) temporary dispersal and subsequent return to areas covered by at-sea surveys (i.e., the "distribution hypothesis"), or (ii) an actual decline in

* Corresponding author. Tel.: +1 (608) 890 2766.
E-mail address: mpeery@wisc.edu (M.Z. Peery).

0006-3207/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2013.08.008

abundance followed by immigration from larger populations to the north (the "rescue hypothesis"). Under the rescue hypothesis, we expected that genetic differentiation between central California and northern populations would decline, and that the proportion and number of migrants in central California would be significantly greater after the recovery. In contrast, we predicted little change in genetic differentiation or the proportion and number of migrants in central California under the distribution hypothesis. Because murrelets produce a single young per year and reproductive success was very low during the recovery, the large increase in abundance could not have been the result of a local demographic recovery (Appendix A, Supplementary methods 1; Peery et al., 2004a, 2007; Peery and Henry, 2010).

2. Methods

2.1. Population monitoring

We conducted visual surveys of Marbled Murrelets at sea from a small vessel between Half Moon Bay and Santa Cruz, California (Fig. 1) from 1999 to 2003 and from 2007 to 2011 following methods described in detail in Peery et al. (2006). Note that surveys in inland breeding habitats do not provide rigorous estimates of population size because of the murrelet's secretive nesting behavior high in the canopy of old-growth forests. At-sea surveys were not conducted from 2004 to 2006 due to funding constraints. Surveys were conducted from June to August in waters adjacent to the Santa Cruz Mountains which contain all known murrelet nesting habitat for the genetically distinct and geographically isolated (~300 km) central California population. Detailed banding and radio-telemetry studies indicate that murrelets occurring within the survey area largely represent locally breeding individuals (Peery et al., 2004a,b, 2008). The survey area and design were established based on extensive pilot surveys conducted in the central California region (Becker et al., 1997) and encompassed 89% of all locations of radio-marked murrelets observed for this population (Peery et al., 2007). Surveys were conducted along approximately 100-km line transects that were delineated in a zigzag manner from 200- to 2500-m from shore. We randomized the starting point of each transect with respect to distance from shore such that a unique transect was followed for each survey. This sampling design was shown to have high statistical power to detect declines in abundance for the central California population (Rachowicz et al., 2006). We randomly determined whether the transect was drawn starting in the north or south, because surveys drawn from the south tend enter small bays more frequently than surveys from the north, and tend to yield higher murrelet densities because can congregate in such habitats (Peery et al., 2006). However, transects were only delineated from the north in 1999 and 2000 and abundance in these 2 years may have been underestimated compared to subsequent years when transects were drawn in both directions (in equal proportions; Peery et al., 2006). Therefore, we corrected estimates in 1999 and 2000 by adding half of the average difference in abundance between transects drawn from the north and south after 2000 (76 individuals). A detailed description of the analytical methods used to estimate murrelet abundance from the survey data is provided in Appendix A (Supplementary methods 2).

2.2. Genetic monitoring

We captured and took blood samples from 249 Marbled Murrelets in Año Nuevo Bay, central California from 1999 to 2003 and an additional 23 samples at this same location in 2010 and 2011 following methods described in Peery et al. (2010; Fig. 1). Año Nuevo Bay is near the middle of the at-sea transect and harbors approximately half of the central California murrelet population from April through October (Peery et al., 2008). Sampling in central California from 1999 to 2003 was conducted from April through October, whereas sampling in 2010 and 2011 was conducted only in September, but the proportion of migrant murrelets in central California does not change significantly from April through October and is approximately 0.07 throughout this period (Hall et al., 2009). Moreover, while our sample size was considerably smaller in the pre-recovery period, statistical power to detect a change in the proportion of migrants under the "rescue hypothesis" was very high because of the large expected effect size even with 23 samples (see below). To sample potential source populations, we also captured and took blood samples from 316 murrelets in northern California ($n = 80$), central Oregon ($n = 27$), the north coast of Washington and southern British Columbia ($n = 147$), and southeast Alaska ($n = 62$) from 1997 to 2007 (Fig. 1). Murrelets at all sampling locations were captured at sea from an inflatable vessel using a dipnet. Estimates of the proportion of migrants and the level of genetic population structure using samples collected in central California from 1999 to 2003 and from northern populations have been presented elsewhere (Hall et al., 2009; Peery et al., 2010); the objective here was to determine if a change in population genetic structure or the proportion and number of migrants occurred between pre-decline and post-recovery sampling periods in central California.

We genotyped sampled individual Marbled Murrelets at 12 of the 13 tetranucleotide microsatellite loci described in Hall et al. (2009; excluding GATA553) following laboratory methods in Hall et al. (2009). None of these loci deviated from Hardy–Weinberg or linkage equilibrium in the pre-decline central California sample or northern populations (Hall et al., 2009; Peery et al., 2010). The same was true for the post-recovery central California sample after applying the correction described by Narum (2006) for conducting 12 tests of Hardy–Weinberg disequilibrium (significance level = 0.016) and 61 tests for linkage disequilibrium (significance level = 0.011). We estimated pairwise differentiation between all six sampling locations/occasions using Wright's F_{ST} with program ARLEQUIN v3.5 (Excoffier et al., 2005). We also tested for genetic population structure with samples pooled into the following three groups: central California prior to the decline (1999–2003), central California after the recovery (2010 and 2011), and all four "northern populations" since previous analyses indicate that northern populations are not, or only very weakly, genetically differentiated (Friesen et al., 2005; Piatt et al., 2007; Hall et al., 2009; Peery et al., 2010). *P*-values for tests of the null hypothesis that F_{ST} was equal to zero were estimated using 10,000 permutations in ARLEQUIN. We used the approach of Narum (2006) to calculate significance levels that accounted for conducting multiple tests, which yielded a significance level of 0.027 when northern populations were pooled ($n = 3$ tests) and a significance level of 0.015 when northern population were treated independently ($n = 15$ tests).

We used program STRUCTURE v2.2 to estimate the number of genetically distinct populations (K) in our sample and to estimate the probability of membership in inferred populations for each sampled Marbled Murrelet (Pritchard et al., 2000). If murrelets sampled in central California following the recovery largely represented immigrants, we expected post-recovery individuals to generally be classified in the same genetic population as individuals sampled in northern populations. If murrelets sampled in California after the recovery represented resident individuals, we expected post-recovery individuals to be assigned to the same genetic population as pre-decline individuals. While we had an *a priori* expectation of two genetic populations based on previous work (Hall et al., 2009), we ran STRUCTURE for $K = 1$–6 populations (6 representing the number of sampling locations/occasions) and

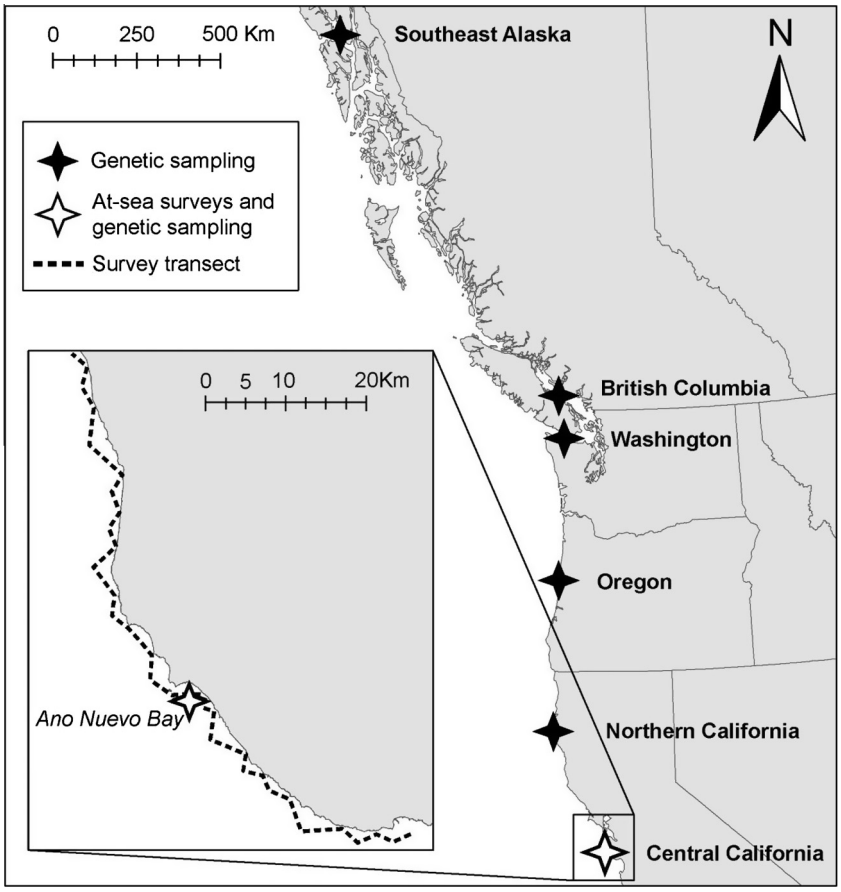

Fig. 1. (a) Locations of genetic sampling and population monitoring for Marbled Murrelets. The inset depicts a typical zigzag line transect used to estimate population size with at-sea surveys in central California. The white star represents the location of genetic sampling in central California and black stars represent the locations of genetic sampling in northern populations.

evaluated support for each value of K using the log-likelihood of the data given K [$\ln \Pr(X|K)$]. We used 30,000 "burn-in" iterations followed by a simulation of 50,000 iterations for analyses in STRUCTURE.

We used genetic assignment methods implemented in program GENECLASS v2.2 (Piry et al., 2004) to identify migrants and compare the proportion and number of migrants in central California before the decline and after the recovery. To identify migrants in central California, we first used the "detection of first generation migrants" option in GENECLASS using only pre-decline central California and northern population samples, and then repeated the same analysis using post-recovery central California and northern population samples. These analyses were conducted treating the four northern sampling sites as independent populations and with these four sampling sites pooled into a single population in separate analyses. Murrelets sampled in central California were considered migrants from northern populations if their multi-locus genotype had less than a 0.05 probability of originating from central California based on the simulation approach developed by Paetkau et al. (2004) implemented in GENECLASS. This significance level is expected to result in approximately 2 Type I errors and 2 Type II errors in the pre-decline sample, and <1 of each type of error in the post-recovery sample given error rates estimated by Hall et al. (2009). We tested for a difference in the proportion of migrants between the pre-decline and post-recovery periods using a χ^2-test. We estimated the number of migrants in the pre-decline and post-recovery periods by multiplying the proportion of migrants by the mean estimate of abundance derived from at-sea surveys during the corresponding period.

We conducted statistical power analyses to assess our ability to detect potential increases in the proportion of migrants in central California under the rescue hypothesis given the modest sample size of 23 individuals in the post-recovery period. To do so, we first estimated effect size as the expected increase in the proportion of migrants from the pre-decline to the post-recovery period if the entire recovery from 2008 to 2010/2011 was due to immigration. We used the following formula to estimate the expected effect size:

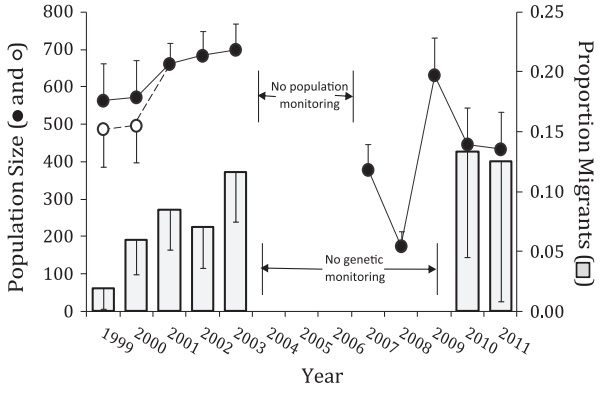

Fig. 2. Annual estimates of Marbled Murrelet population size in central California derived from at-sea surveys, and the proportion of migrant individuals derived from genetic assignment tests conducted in program GENECLASS (Piry et al., 2004). White and black circles represent estimates of population size that are "uncorrected" and "corrected", respectively, for differences in survey methodology between 1999–2000 and 2001–2011. Error bars represent standard errors.

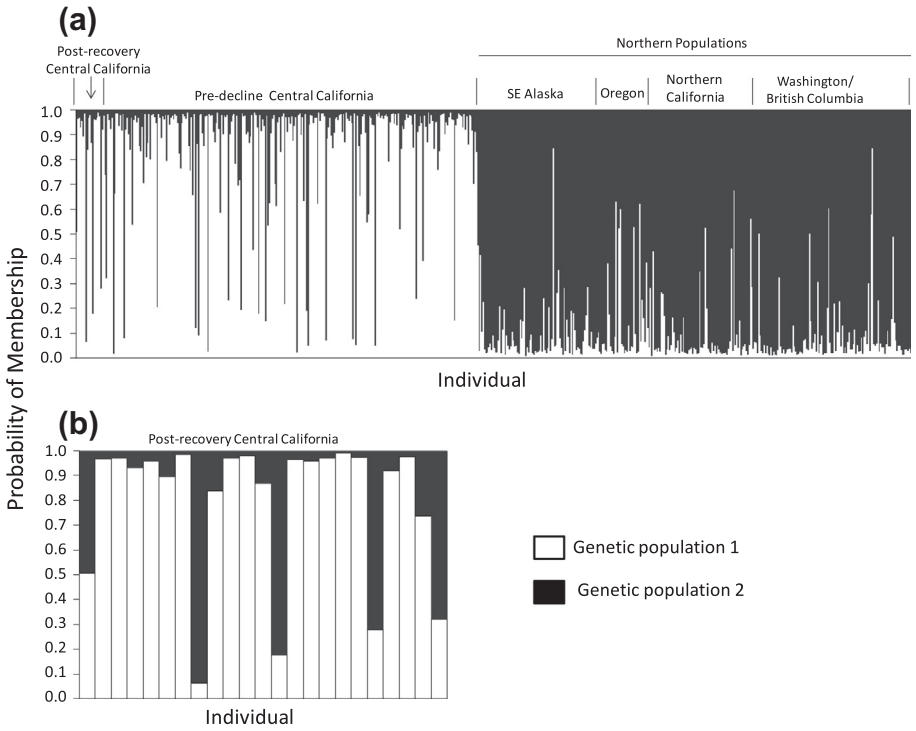

Fig. 3. Probability of membership for 588 Marbled Murrelets genotyped at 12 microsatellites in each of two "genetic populations" based on program STRUCTURE (Pritchard et al., 2000). (a) Probability of membership for all individuals and (b) probability of membership for individual sampled in central California after the population recovery.

effect size = $(1 - N_{pre\text{-}decline}/N_{post\text{-}recovery})$, where $N_{pre\text{-}decline}$ and $N_{post\text{-}recovery}$ were the mean pre-decline and post-recovery population sizes estimated with at-sea surveys. This equation gives the expected effect size if the recovery was entirely due to immigration; we also estimated the effect size (and statistical power) assuming that two- and one-thirds of the recovery were due to immigration by multiplying the "full" effect size by 0.667 and 0.333, respectively. We then used Monte Carlo simulations to generate migrant–resident data for central California for each of these effect sizes, where $n = 249$ and 23 for the pre-decline and post-recovery samples, respectively. We tested for an increase in the proportion of migrants in each of 1000 simulated data sets using a χ^2-test and estimated power as the proportion of significant tests.

3. Results

3.1. Population monitoring

The abundance of Marbled Murrelets in central California averaged 635 individuals from 1999 to 2003 (range: 563–699; Fig. 2, Table A1). A 41% reduction in abundance down to 378 individuals (95% CI: 238–518) was recorded in 2007 following the 3 years without surveys. Abundance further declined to 174 individuals (95% CI: 91–256) in 2008, a decline of 72% from the mean estimate from 1999 to 2003. However, a marked recovery to 631 individuals (95% CI: 449–885) occurred in 2009, with abundances declining to 446 (95% CI: 339–553) and 433 (95% CI: 340–585) in 2010 and 2011, respectively (Fig. 2, Table A1). We consider the post-recovery population size to be 440, the average of 2010 and 2011 abundance estimates, given that genetic samples were not collected in 2009.

3.2. Genetic monitoring

Both the pre-decline and post-recovery central California populations were significantly differentiated from pooled northern populations (pre-decline: $F_{ST} = 0.025$, $p < 0.001$; post-decline $F_{ST} = 0.028$, $p < 0.001$). Moreover, F_{ST} between pre-decline and post-recovery central California populations was considerably lower than F_{ST} between each of these populations and northern populations, and was not statistically significant greater than zero ($F_{ST} = 0.004$; $p = 0.063$). F_{ST} between both of the central California samples and northern populations was similar when northern populations were treated independently (Table A2).

The most likely number of genetic populations was $K = 2$, where the log-likelihood of two populations exceeded the log-likelihood of $K = 4$ (the second most likely K) by 60, using program STRUCTURE. Most individuals sampled in central California, both before the decline and after the recovery, had a high probability of belonging to the first genetic population whereas individuals sampled in northern populations generally had a high probability of belonging to the second genetic population (Fig. 3a). Four individuals sampled in central California after the recovery had a membership probability of >0.70 in the second genetic population, and a fifth individual had a membership probability of 0.50 in the second population (Fig. 3b).

Assignment tests implemented in GENECLASS were somewhat sensitive to whether northern populations were pooled or treated separately (Table 1). Prior to the decline, 8.4% (21 of 249) and 11.2% (28 of 249) of murrelets sampled in central California were classified as migrants when northern populations were treated independently and pooled, respectively (Table 1, Fig. 2). By comparison, 13.0% (3 of 23) and 17.4% (4 of 23) of murrelets sampled in central California after the recovery were classified as migrants when northern populations were treated independently and pooled, respectively (Table 1, Fig. 2). While the proportion of migrants increased nominally from the pre-decline to the post-recovery period regardless of how northern populations were treated, neither increase was significant (independent: $\chi^2_1 = 0.56$, $p = 0.456$; pooled: $\chi^2_1 = 0.56 = 0.77$, $p = 0.381$). Moreover, the estimated *number* of migrants (abundance × *proportion* of migrants) was very similar in the pre-decline and post-recovery periods (Table 1). Fi-

Table 1
Estimated proportion and number of migrants in central California prior to the decline in abundance (1999–2003) and after the recovery (2010 and 2011) based on program GENECLASS (Piry et al., 2004).

Northern populations	Proportion migrants in central California		Number of migrants/residents in central California[a]		% of abundance increase explained by migration[b]
	Pre-decline (n = 249)	Post-recovery (n = 23)	Pre-decline	Post-recovery	
Treated individually	0.112	0.130	71/560	57/383	0
Pooled	0.084	0.174	53/588	77/363	9

[a] Number of migrants calculated by multiplying estimated abundance (pre-decline N = 631; post-recovery N = 440) by the estimated proportion of migrants. Number of residents calculated by subtracting the number of migrants to estimated abundance.
[b] Percentage of the increase in abundance from N = 174 in 2008 to N = 440 in 2010/2011 that was due to an increase in the number of migrants.

nally, the estimated percentage of the increase in abundance from 2008 to 2010/2011 (i.e., from 174 to 440 individuals) that was due to an increase in the number of migrants in the post-recovery period was small (0–9%; Table 1).

We estimated that we had >99% power to detect an increase in the proportion of migrants if the entire increase in abundance from 2008 to 2010/2011 (i.e., from 174 to 440 individuals) was due to immigration (expected effect size = 0.60). Power was also >99% if two-thirds of the increase was due to immigration (expected effect size = 0.40). Even if only one-third of the increase was due to immigration, we would still have had a 77% probability of detecting the expected difference in the proportion of migrants (expected effect size = 0.20).

4. Discussion

The low level of genetic differentiation between the post-recovery and pre-decline central California samples, coupled with the much greater population genetic structure detected between both central California samples and northern populations, supports the distribution hypothesis as the primary explanation for the sudden "recovery" of the central California population. Had the population recovered via large-scale dispersal from northern populations, we would have expected genetic differentiation between central California and northern populations to have declined between pre-decline and post-recovery sampling. Perhaps more importantly, the proportion and number of migrants in central California did not increase significantly, and the majority of individuals present in central California following the recovery were resident individuals (Table 1). Had the recovery largely been due to immigration from northern populations, we would have witnessed a much greater increase in the proportion and number of migrants. While a small amount of the recovery may have been due to immigration (i.e., up to 9%; Table 1), the stability in genetic population structure coupled with the Marbled Murrelet's low fecundity in central California (Peery et al., 2004a; Appendix A) leaves the dispersal and subsequent return of resident birds to the at-sea survey area as the most likely explanation for observed changes in abundance.

Given the scale at which our at-sea surveys were conducted (100-km transects, 200- to 2500-m from shore), it is possible that small-scale movements by locally breeding murrelets to locations outside of at-sea surveys areas could have significantly reduced our estimates of population size in 2007 and 2008, even though such behavior has not previously been observed in radio-marked individuals (Peery et al., 2007, 2008, 2009). The observed decline in 2007 and 2008 could also have been the result of the abandonment of breeding activities at a regional scale, coupled with larger-scale movements further offshore or north/south of waters adjacent to the nesting habitat in the Santa Cruz Mountains. Indeed, radio-marked murrelets have been observed dispersing long distances (~300 km) from the at-sea survey area during both the breeding and non-breeding seasons, and then return to breed in central California in subsequent years (Peery et al., 2008). Low murrelet numbers followed a warm temperature anomaly in the California Current in 2005 that persisted into 2006, profoundly impacted the biomass and composition of zooplankton (Mackas et al., 2006), and was responsible for record-low numbers of juvenile rockfish in central California from 2005 to 2007 (Field et al., 2010). Moreover, increases in rockfish abundance observed in 2008, followed by greater increases in 2009 and 2010 (Partnership for Interdisciplinary Studies of Coastal Oceans, *unpubl. data*), are concordant with the murrelet recovery in 2009.

Similar to this study, a combination of genetic and population monitoring was used to show that the recovery of Common Terns on Bermuda following a bottleneck was due to local recruitment rather than immigration (Szczys et al., 2012). Distinguishing between the distribution and the rescue hypotheses to explain the cause of observed changes in the abundance in both studies was possible because concurrent population and genetic monitoring were conducted before and after the change. We suggest that population monitoring programs for threatened populations and species, at least in some cases, can benefit by incorporating genetic monitoring (Schwartz et al., 2007). Effective integration of genetic and population monitoring programs requires careful consideration of the limitations associated with using genetic data to infer population connectivity (Lowe and Allendorf, 2010). Assignment tests can be used to identify migrants with confidence when sufficient genetic population structure exists between the target and the source populations, but do not perform well in weakly structured populations and when gene flow is high (Hall et al., 2009). When migration into the target population is high, genetic kinship approaches can be effective for quantifying the effect of connectivity on population change (Palsbøll, 1999). While implementing concurrent genetic and population monitoring programs requires additional investments in effort and resources, the benefits of understanding mechanisms behind observed changes in abundance can outweigh costs. Moreover, investments in genetic monitoring can be reduced by collecting baseline samples at the beginning of a population monitoring program and then conducting additional sampling after significant changes in abundance have occurred.

Acknowledgements

We thank Ben Becker, Steve Beissinger, and Per Palsboll, Kim Nelson, Richard Golightly, Laura McFarlane-Tranquilla, and Martin Raphael for their contributions throughout this project. We thank Robin Waples and four anonymous reviewers for their comments. Funding was provided by the Command Oil Spill Trustee Council.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.08.008.

References

Becker, B.H., Beissinger, S.R., Carter, H.R., 1997. At-sea density monitoring of Marbled Murrelets in central California: methodological considerations. Condor 99, 743–755.

Excoffier, L., Laval, G., Schneider, S., 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evol. Bioinformatics Online 1, 47.

Field, J., MacCall, A., Bradley, R., Sydeman, W., 2010. Estimating the impacts of fishing on dependent predators: a case study in the California Current. Ecol. Appl. 20, 2223–2236.

Friesen, V.L., Birt, T.P., Piatt, J.F., Golightly, R.T., Newman, S.H., Hebert, P.N., Congdon, B.C., Gissing, G., 2005. Population genetic structure and conservation of Marbled Murrelets (*Brachyramphus marmoratus*). Conserv. Genet. 6, 607–614.

Hall, L.A., Palsbøll, P.J., Beissinger, S.R., Harvey, J.T., Berube, M., Raphael, M.G., Nelson, S.K., Golightly, R.T., McFarlane-Tranquilla, L., Newman, S.H., 2009. Characterizing dispersal patterns in a threatened seabird with limited genetic structure. Mol. Ecol. 18, 5074–5085.

Lowe, W.H., Allendorf, F.W., 2010. What can genetics tell us about population connectivity? Mol. Ecol. 19, 3038–3051.

Mackas, D.L., Peterson, W.T., Ohman, M.D., Lavaniegos, B.E., 2006. Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. Geophys. Res. Lett. 33, L22S07.

Miller, S.L., Raphael, M.G., Falxa, G.A., Strong, C., Baldwin, J., Bloxton, T., Galleher, B.M., Lance, M., Lynch, D., Pearson, S.F., Ralph, C.J., Young, R.D., 2012. Recent population decline of the Marbled Murrelet in the Pacific Northwest. Condor 114, 771–781.

Narum, S.R., 2006. Beyond Bonferroni: less conservative analyses for conservation genetics. Conserv. Genet. 7, 783–787.

Paetkau, D., Calvert, W., Stirling, I., Strobeck, C., 1995. Microsatellite analysis of population structure in Canadian polar bears. Mol. Ecol. 4, 347–354.

Paetkau, D., Slade, R., Burden, M., Estoup, A., 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Mol. Ecol. 13, 55–65.

Palsbøll, P.J., 1999. Genetic tagging: contemporary molecular ecology. Biol. J. Linn. Soc. 68, 3–22.

Peery, M.Z., Henry, R.W., 2010. Recovering the Marbled Murrelet via corvid management: a PVA-based assessment. Biol. Conserv. 143, 2414–2424.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Burkett, E.B., Williams, T.D., 2004a. Applying the declining population paradigm: diagnosing causes of poor reproduction in the Marbled Murrelet. Conserv. Biol. 18, 1088–1098.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Becker, B.H., Burkett, E., Williams, T.D., 2004b. Individual and temporal variation in inland flight behavior of marbled Murrelets: implications for population monitoring. Condor 106, 344–353.

Peery, M.Z., Becker, B.H., Beissinger, S.R., 2006. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. Ecol. Appl. 16, 1516–1528.

Peery, M.Z., Becker, B.H., Beissinger, S.R., 2007. Age ratios as estimators of productivity: testing assumptions on a threatened seabird, the Marbled Murrelet. Auk 124, 224–240.

Peery, M.Z., Henkel, L.A., Newman, S.H., Becker, B.H., Harvey, J.T., Thompson, C., Beissinger, S.R., 2008. Effects of rapid flight-feather molt on post-breeding dispersal in a pursuit-diving seabird. Auk 125, 113–123.

Peery, M.Z., Newman, S.H., Storlazzi, C.S., Beissinger, S.R., 2009. Meeting reproductive demands in a dynamic upwelling system: foraging strategies of a pursuit-diving seabird, the Marbled Murrelet. Condor 111, 120–134.

Peery, M.Z., Hall, L.A., Sellas, A., Beissinger, S.R., Moritz, C., Bérubé, M., Raphael, M.G., Nelson, S.K., Golightly, R.T., McFarlane-Tranquilla, L., 2010. Genetic analyses of historic and modern Marbled Murrelets suggest decoupling of migration and gene flow after habitat fragmentation. Proc. Roy. Soc. Biol. Sci. 277, 697–706.

Piatt, J.F., Kuletz, J.K., Burger, A.E., Hatch, S.A., Friesen, V.L., Birt, T.P., Arimitsu, M.L., Drew, G.S., Harding, A.M.A., Bixler, K.S., 2007. Status Review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. U.S. Geological Survey Open-File, Report 2006-1387.

Piry, S., Alapetite, A., Cornuet, J.M., Paetkau, D., Baudouin, L., Estoup, A., 2004. GENECLASS2: a software for genetic assignment and first-generation migrant detection. J. Hered. 95, 536–539.

Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155, 945–959.

Rachowicz, L.J., Hubbard, A.E., Beissinger, S.R., 2006. Evaluating at-sea sampling designs for Marbled Murrelets using a spatially explicit model. Ecol. Model. 196, 329–344.

Saracco, J.F., DeSante, D.F., 2008. Identifying Proximate Causes of Population Trends in Migratory Birds. The Institute for Bird Populations, Point Reyes Station, CA.

Schwartz, M.K., Luikart, G., Waples, R.S., 2007. Genetic monitoring as a promising tool for conservation and management. Trends Ecol. Evol. 22, 25–33.

Szczys, P., Nisbet, I.C.T., Wingate, D.B., 2012. Conservation genetics of the Common Tern (*Sterna hirundo*) in the North Atlantic region; Implications for the critically endangered population at Bermuda. Conserv. Genet. 13, 1039–1043.