Recent Snowy Plover population increase arises from high immigration rate in coastal northern California

Mark A. Colwell[1]*, Elizabeth J. Feucht[1], Matt J. Lau[1], David J. Orluck[1], Sean E. McAllister[2] & Amber N. Transou[3]

[1] *Wildlife Department, Humboldt State University, Arcata, CA 95521, USA*
[2] *Sean E. McAllister & Associates, Eureka, CA 95503, USA*
[3] *California State Parks, North Coast Redwoods District, Eureka, CA 95503, USA*
Corresponding author: mark.colwell@humboldt.edu

The Pacific coast population of the Snowy Plover *Charadrius nivosus nivosus* is listed as threatened under the U.S. Endangered Species Act, which requires demographic data to inform management directed at increasing the population. Accordingly, we summarized a 16-year dataset on population size and growth, return rates, and productivity of a color-marked breeding population in coastal northern California, one of six recovery units for the listed population. The geographically isolated population varied annually in size (19–74 breeding adults), with an early nine-year decline ($\lambda = 0.92 \pm 0.30$) followed by a seven-year increase ($\lambda = 1.22 \pm 0.19$). Overall, productivity averaged 0.85 ± 0.29 chicks fledged per male, which is well below that identified by viability analyses to maintain the population. Adult return rates, an index of survivorship, varied greatly among years (30–95%). Immigrants comprise $63 \pm 5\%$ of the population over the past 12 years when we have marked approximately 95% of breeding adults. We conclude that the northern California population is a demographic sink, and that management actions currently are insufficient to increase the population; recent growth stems from immigration.

INTRODUCTION

Conservation of biodiversity, whether at the level of ecosystem, community or species, requires detailed knowledge derived from monitoring to inform management decisions. Of the world's ~10,600 species of bird (Clements 2007), 220 are shorebirds; 59 of these shorebird species require conservation action based on IUCN criteria (e.g., Near Threatened, Vulnerable, Endangered or Critically Endangered; *http://www.iucnredlist.org/*); many (17) are plovers (Charadriidae). The causes of this extinction risk are varied, but most are associated with humans. For instance, the Spoon-billed Sandpiper *Calidris pygmaea* population is estimated to be several hundred; hunting in the species' winter range is a principal cause of its Critically Endangered status (Zöckler *et al.* 2010). For endemic shorebirds of New Zealand (e.g., Black Stilt *Himantopus novaezelandiae*, Wrybill *Anarhynchus frontalis*), populations are imperiled owing to introduced predators that have increased adult mortality and lowered reproductive success (Dowding & Murphy 2001). In many cases, monitoring of individually-marked birds has provided valuable data to inform conservationists of population genetic structure (Koenig 1988), or to evaluate captive-rearing efforts (Neuman *et al.* 2016) or actions to lethally remove predators to bolster populations (Dinsmore *et al.* 2014, 2017).

In 1993, the United States government listed the Pacific coast population of the Snowy Plover *Charadrius n. nivosus* as threatened (United States Fish & Wildlife Service 1993; hereafter USFWS) based on numerous factors, including evidence of a small and declining population (Page & Stenzel 1981, Page *et al.* 1991). The recovery plan (USFWS 2007) specified that delisting for this species hinges on two demographic metrics: (1) population exceeding 3,000 breeding adults sustained for 10 consecutive years; and (2) per-capita reproductive success exceeding 1.0 fledged young (per male) for five years. Since the species' listing almost a quarter century ago, a number of studies have been initiated to provide data necessary to evaluate these criteria. For example, in 2005 USFWS personnel began an annual, coordinated, range-
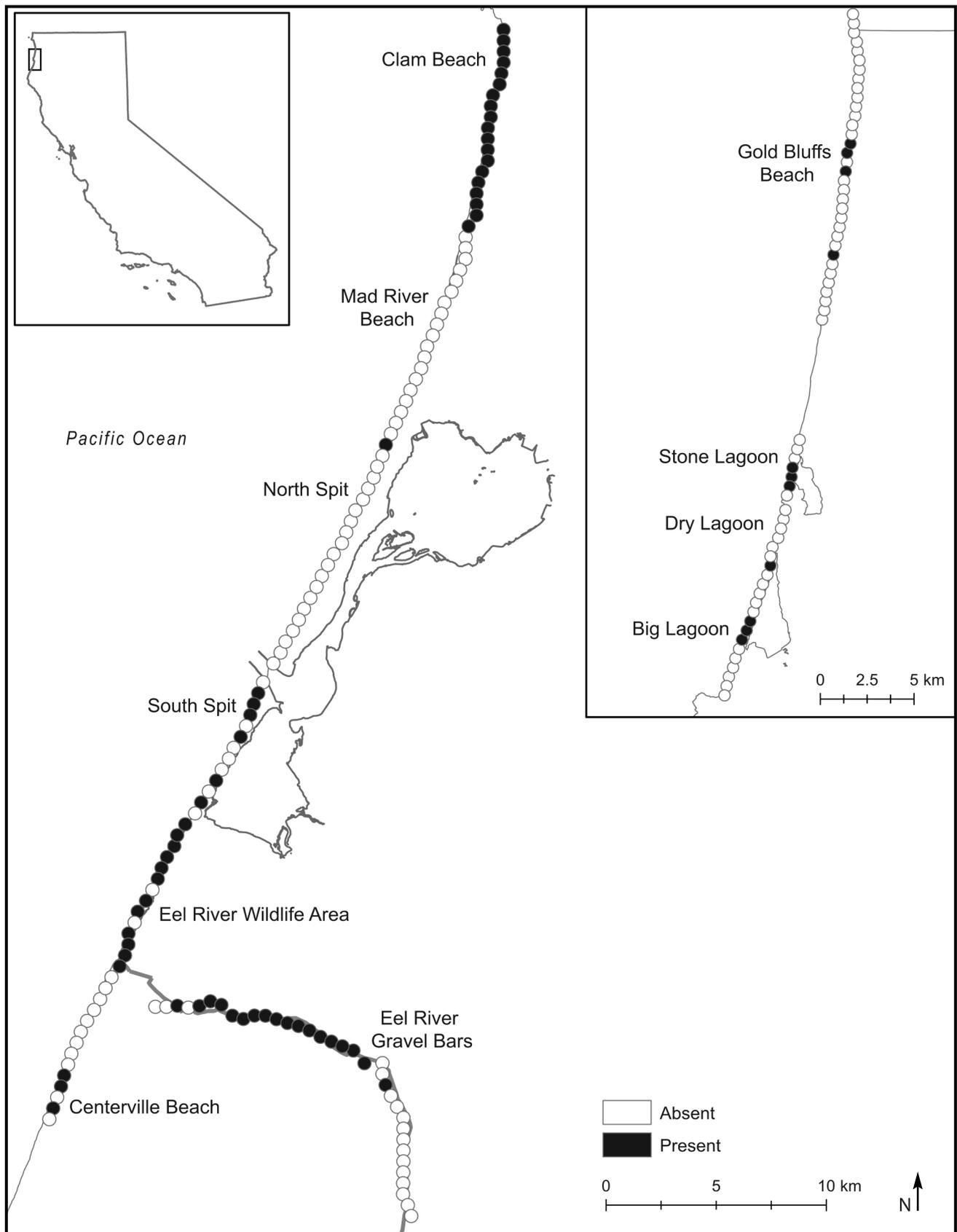
Fig. 1. Breeding locations of Snowy Plovers along ~80 km of ocean-fronting beaches and ~15 km of gravel bars along the Eel River in coastal northern California. Filled and open circles (500 m radius) represent the presence or absence, respectively, of breeding based on at least one nest over 16 years (n = 917 nests; 2001–2016 in Humboldt County). Some stretches of rocky intertidal habitat were not surveyed owing to unsuitability of habitat for breeding. Occasional nesting occurred in Mendocino (n = 9) and Del Norte (n = 3) counties (not shown).

wide effort to estimate population size, which has provided insight into population growth in relation to management actions (Eberhart-Phillips *et al.* 2015). At a finer spatial scale, research across the Pacific coast range of the plover is required to quantify vital rates (e.g., apparent survivorship, annual and lifetime reproductive success) necessary to predict population growth (Stenzel *et al.* 2007, 2011, Mullin *et al.* 2010, Herman & Colwell 2015), as well as to evaluate effectiveness of management actions aimed at ameliorating factors that limit population recovery (e.g., Dinsmore *et al.* 2014, 2017, Eberhart-Phillips *et al.* 2015). Here, we provide details on the vital rates of a small, geographically-isolated subpopulation of Snowy Plovers that we have monitored for 16 years (2001–2016).

METHODS

Study area

We studied Snowy Plovers in Del Norte, Humboldt and Mendocino counties, California (Fig. 1), which is Recovery Unit 2 of the species' recovery plan (USFWS 2007). The delisting criteria for the northern California subpopulation are 150 breeding adults maintained for 10 years and 1.0 fledgling per male for 5 years (USFWS 2007). This is the smallest subpopulation within the listed population segment (USFWS 2007, Eberhart-Phillips *et al.* 2015). Plovers bred in two types of habitat. Throughout the 16 years, plovers have bred on ocean-fronting beaches characterized by fine, homogeneous (i.e., sandy) substrates sparsely vegetated with native (e.g., *Leymus mollis, Abronia* spp., *Umbellata breviflora*) and invasive (*Ammophila arenaria, Carpobrotus* spp.) plants. Early in the study, plovers also bred on coarse, heterogeneous (i.e., gravel) substrates of the lower Eel River, amidst sparse vegetation dominated by willow (*Salix* spp.) and white sweet clover *Melilotus albus*. Detailed descriptions of habitats are provided elsewhere (Colwell *et al.* 2010, Brindock & Colwell 2011, Herman & Colwell 2015). These two habitats differ markedly in habitat quality as gauged by per-capita reproductive success (Colwell *et al.* 2010, Herman & Colwell 2015), with riverine substrates affording greater crypsis, and hence survival, of eggs and chicks (Colwell *et al.* 2007a, 2011).

Field methods

Intensive monitoring began in 2001. Each subsequent year, we attempted to capture and band unmarked adults or those wearing non-unique color band combinations (i.e., juveniles from previous years or those that had lost bands; Colwell *et al.* 2007a, Mullin *et al.* 2010). Also, we marked virtually all chicks at hatch with a brood-specific color band that facilitated monitoring brood survival (Colwell *et al.* 2007b). Over the 16 years, the population consisted of an average of 87 ± 11% (annually) of individuals with unique color band combinations. We base our demographic description of the population on these individuals, as well as a few unmarked birds each year. We conducted research under federal (USFWS recovery

permit TE-73361A-1; USFWS banding permits #23844 and #10457, HSU IACUC 14/15.W.07-A), and state (CA Dept. Fish & Wildlife Scientific Collecting permit #SC0496; CA Dept. Parks & Recreation research permit #16-635-017) permits.

In the field, observers surveyed habitat for breeding plovers from March into September. We surveyed most sites once per week, but visits increased (often 2–3 a week) when we detected breeding adults. The last date on which chicks fledged varied annually (mid-Aug to mid-Sep), which determined our last survey, and, hence, duration of breeding season. Observers worked mostly alone to survey suitable habitat (e.g., sandy ocean-fronting beaches or gravel bars; not rocky intertidal habitats) by walking slowly, stopping occasionally, and using binoculars and a spotting-scope to scan for plovers. At a few sites occupied consistently by more plovers, observers often surveyed in pairs. Occasionally observers used all-terrain vehicles to survey long stretches of beach. When observers detected plovers, they observed them from a distance to evaluate their breeding status (e.g., courting, copulating, scraping, incubating, brooding). Also, we routinely scanned sandy substrates for plover tracks and courtship scrapes in dry, sand substrates to indicate the presence of breeding activity. This was not possible on riverine gravel bars.

In 2005, we began using a personal data assistant (PDA) equipped with a global positioning system (GPS) to record locations of adults, nests, and broods. We summarized the presence of plover breeding activity (Fig. 1) based on the occurrence of at least one nest within an array of 500 m radius circles established in a systematic-random fashion using a geographic information system (GIS). Observers routinely determined the reproductive status by observing adults courting or tending eggs or chicks. When we did not detect an adult incubating a clutch, we approached to a distance where we could determine with binoculars whether eggs were present. We categorized a nest as successful if at least one egg hatched. We determined that a clutch failed if eggs disappeared, were buried or abandoned prior to the predicted hatch date based on the sequence of egg laying or egg flotation (Westerkov 1950). Observations of adults re-nesting often confirmed our determination that a reproductive attempt had failed. For failed nests, we categorized the cause of egg loss as predation based on direct observation or video recording; in other cases, we used tracks of predators at nest, egg shells and yolk in nest cup to conclude that predation was the cause of failure. Similarly, humans occasionally caused nest failure (e.g., video placed near nest recording activity; tracks at nest), tides sometimes over-washed nests (e.g., eggs out of nest cup and debris around nest moved after recent high tide), and windy conditions caused sand to cover eggs. Finally, eggs occasionally were untended for multiple days and adults often observed re-nesting, in which case we characterized the nest as abandoned. We categorized all other causes of failure as 'unknown'. We monitored all broods (each
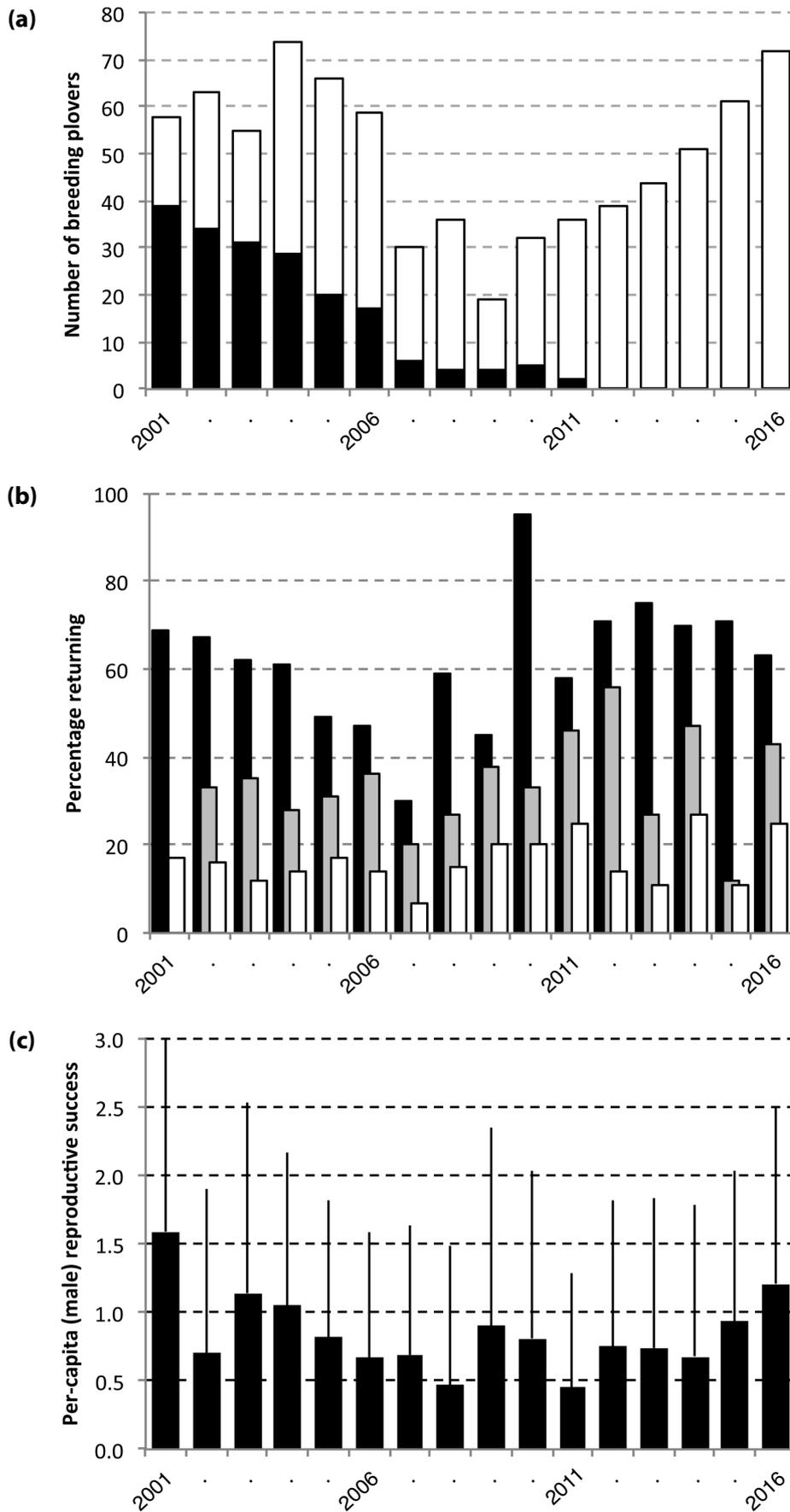
Fig. 2. Annual variation in Snowy Plover **(a)** population size categorized by those breeding on riverine gravel bars (■) and sandy, ocean-fronting beaches (□); **(b)** percentage of returning adults (■), fledglings (■) and chicks (□); and **(c)** average (± SD) male per-capita fledging success. Return rates are the percentage of marked individuals in year$_t$ observed in year$_{t+1}$.

marked with a brood-specific color band) at approximately 2–5 day intervals (Colwell *et al.* 2007b), and based per-capita (male) fledging success on direct observations of the number of young that reached 28 days of age, which is the average fledging age (Page *et al.* 2009, Herman & Colwell 2015).

Data summary and analysis

We summarized population growth (λ) based on the ratio of breeding adults present in consecutive years (i.e., N_{t+1}/N_t, where N is number of breeding adults and t is year). We report annual adult site-fidelity and philopatry of local chicks based on the return of color-marked individuals to breed (i.e., at least one nest found) in a subsequent year in the study area. We marked virtually all chicks at hatch. Given our survey and banding effort, the high percentage of adults marked each year, and average adult longevity of 2.3 ± 1.8 years (Herman & Colwell 2015), we categorized the composition of the population as follows. We apportioned the annual number of breeding adults into percentages that represent local recruits (i.e., those we marked as chicks in our study population), immigrants banded elsewhere along the Pacific coast, or unmarked plovers, which we assumed to be immigrants. This latter assumption was based on the observation that, on average, 95% of individuals each year were marked. Consequently, unmarked birds likely originated elsewhere. For each year, we estimated adult sex ratio as the total number of breeding males divided by the total breeding population based on our tally of color-marked individuals and a few unmarked plovers (Stenzel *et al.* 2011). We report apparent hatching success as the percentage of nests each year that hatched at least one chick. We report averages (± SD) and provide descriptive statistics for most comparisons.

RESULTS

Population size

From 2001–2016, the number of breeding adults varied between 19 and 74 (Fig. 2a), with two distinct intervals of growth. From 2001–2009, the population declined dramatically ($\lambda = 0.92 \pm 0.30$) from 74 to a low of 19, after which it grew for seven consecutive years at an annual rate of 22% ($\lambda = 1.22 \pm 0.19$). Coincident with the early population decline was a shift in distribution away from high quality (Fig. 2a) riverine gravel bars to sandy ocean beaches; by 2011 all plovers bred on beaches.

Over 16 years, we kept detailed histories for 353 marked individuals (159 males, 194 females) that bred locally. One third (33%; *n* = 115) were chicks that hatched in the study population and recruited to breed (i.e., had a nest) for at least one year. The remainder were immigrants marked elsewhere along the Pacific coast (*n* = 107; 41 males and 66 females) or originally unmarked and presumed to be immigrants (*n* = 131; 52 males and 79 females). Of marked immigrants, 79 (74%) arrived from natal sites several hundred km north in Oregon; the

other 28 (26%) marked immigrants came from California sites south of the study area. In the latter seven years when the population grew steadily, immigrants comprised an average of 62 ± 4% of breeding adults. Overall, adult sex ratio was slightly male-biased (0.51 ± 0.03), with (1–4) extra males in nine years and (1–6) surplus females in three years.

Return rates

There was substantial annual variation in site-fidelity (Fig. 2b). In total, we marked 718 chicks of which 16% (*n* = 115) returned to breed in any subsequent year. Annually, the percentage of hatched chicks that returned to breed averaged 16.6 ± 5.6%; this rate doubled (34.0 ± 11.1%) when we based our calculation on total number of fledglings. The difference, in part, represents mortality in the chick stage. Assuming an equal sex ratio at hatch, slightly more males (18.4%) than females (13.4%) were philopatric (Chi-square test; $\chi^2 = 2.95$, df = 1, $P = 0.09$).

For adults, average percentage of site-faithful males (66.6 ± 13.3) was significantly higher (*z*- test; $z = -2.59$, *n* = 16, $P = 0.01$) than for females (57.8 ± 18.0). Overall, more adult males returned than females in 13 of 16 years. Return rates of adults and yearlings were not similar ($r_s = 0.03$, $P = 0.90$) across the years. Lowest return rates (for both yearlings and adults) occurred in several years (2007–2009) preceding and including the population nadir.

Productivity

Plovers exhibited low reproductive success in most years. Apparent hatching success averaged 32.8 ± 14.5% across years; most (50.8 ± 16.9%) clutches failed owing to predation (including unknown category). Average per-capita (male) fledging success varied greatly (Fig. 2c). Fledging success exceeded 1.0 in three of the first four years, when two thirds of the population bred on gravel bars (Colwell *et al.* 2010, Herman & Colwell 2015). In most (12 of 16) years, however, fledging success was below 1.0, which is the benchmark identified in a population viability analysis to maintain the population (Nur *et al.* 1999, Hudgens *et al.* 2014).

DISCUSSION

Monitoring provides demographic data that is critical to evaluating population growth in the context of evaluating the success of management; it also provides necessary data for meeting recovery objectives that serve in the decision to delist threatened and endangered species. The most noteworthy results from our 16-year effort are that the plover population in northern California: (1) remains well below criteria (population size and per-capita reproductive success) used to delist the population as outlined in the recovery plan (USFWS 2007); (2) routinely produces fewer fledglings than are necessary to maintain the population; (3) exhibits occasional years of low survivorship; and (4) has increased recently, owing to immigrants from elsewhere along the Pacific coast.

Population size and growth

The northern California subpopulation is managed as a distinct recovery unit (#2), with a delisting objective of 150 breeding adults maintained for 10 years (USFWS 2007). Over 16 years, the population has varied three-fold (19–74); it currently is approximately 50% of this objective.

Our estimates of breeding population size are based on intensive monitoring of a color-marked population conducted over a six-month breeding season. Each year since 2005 the USFWS has coordinated a region-wide survey to census the listed population (see Eberhart-Phillips *et al.* 2015). This survey occurs during a one week 'window' at the end of May, coincident with the peak of plover breeding. In our study area, the number of breeding adults detected during this 'window survey' is always lower (65 ± 12%; range 50–87% of annual total) than the population totals (based on marked birds) provided here. As a result, the USFWS applies a correction factor (x1.3) to adjust upward the region-wide population estimate. Our dataset (1.60 ± 0.29; range: 1.15–2.00) suggests that this multiplier is conservative. Differences between our counts of individually-marked plovers with known breeding records and the window survey may stem from several factors, some methodological and others related to the plover's breeding system. First, poor survey (e.g., weather) conditions may cause observers to fail to detect some individuals during one-time visits to a site. Second, although a survey protocol exists (USFWS 2009), inexperienced observers who lack prior knowledge of plovers breeding at a site may miss birds. Third, the one-week survey represents a brief interval in the long breeding season (clutches are initiated from early March to late July). Some individuals, especially females, move widely among breeding sites along the Pacific coast (Stenzel *et al.* 1994, Colwell *et al.* 2007a). As a result, our tally of the total number of breeding adults includes individuals that were not present during the window survey.

Return rates

The return rates of adults and yearlings, which are related to estimates of apparent survival reported elsewhere (Mullin *et al.* 2010), provide a minimum estimate of survivorship. For this paper, we did not conduct a formal survival analysis because we have marked virtually all individuals in the population and monitor them intensively. As a result, return rates parallel and are the basis for results reported elsewhere (Mullin *et al.* 2010, Eberhart-Phillips & Colwell 2014). Instead, we use return rates to index annual variation in survival of adults and juveniles. These indices exhibit sequences of multiple years of high return (or survival; e.g., 2010–2016) punctuated by a year (2007) of substantially lower return (or higher mortality; Mullin *et al.* 2010, Eberhart-Phillips & Colwell 2014). This pattern is also evident in the plover population at Monterey Bay, California (Stenzel *et al.* 2007, 2011), and is detectable in region-wide analyses of population change (Eberhart-Phillips *et al.* 2015). The cause of low survival in some years may be weather-related because the effect shows up across a range of latitudes encompassing the plover's Pacific coast distribution. For example, population sizes at the northern extent of the species' range exhibited a synchronous decline in one of eight years, and data from regional weather stations suggested that this coincided with a winter in which cold temperatures occurred for extended periods (Eberhart-Phillips *et al.* 2015).

Males returned at a higher rate than females, which may stem from greater site-fidelity associated with mating system and parental investment (Greenwood 1980), higher mortality of females (Stenzel *et al.* 2007, 2011), or both. The plover mating system along the Pacific coast is characterized as sequential polygamy, with females often dispersing long distances between breeding attempts within and between years (Colwell *et al.* 2007a, Stenzel *et al.* 2007, Pearson & Colwell 2014). Males share incubation with females but typically have sole responsibility for chicks (Stenzel *et al.* 2011). Greenwood (1980) argued that site-fidelity was favored owing to advantages of familiarity with an area accrued by individuals of the sex (i.e., male plovers) investing more in parental care. By contrast, female plovers benefit more from dispersing in search of mates. This latter observation is confirmed by lower encounter probabilities for females than males in an interior population of Snowy Plovers (Paton 1994); higher male encounter rates have been reported for two other plovers (Kentish Plover *C. alexandrinus*, Sandercock *et al.* 2005; Semipalmated Plover *C. semipalmatus*, Badzinski 2000). Our data are in line with the mating systems hypothesis (Greenwood 1980). The unequal contribution of males and females sets the stage for an increasingly biased operational sex ratio (*sensu* Emlen & Oring 1977), with more females available at any one time owing to greater male parental care. Consequently, females experience greater intra-sexual competition, including a greater tendency to disperse (Stenzel *et al.* 2007, 2011).

Sex ratios

Higher return rates indicate that adult males survive better than females (Mullin *et al.* 2010), although this difference may simply stem from the mating system. In an earlier paper (Colwell *et al.* 2007a), we reported that philopatry (percentage of yearlings that bred locally) was male-biased (17% vs. 12% of females), although the pattern was not significant. With additional years, the pattern remains, with 18% and 13% of males and females, respectively, returning to breed locally. In most years, however, we observed slightly more males in the population than females. The average sex ratio was 0.51 but there was considerable annual variation (0.47–0.56). Stenzel *et al.* (2011) estimated that there were slightly more males (0.530; annual range: 0.502–0.547) at Monterey Bay, California. A population of Kentish Plovers breeding in Turkey had more males (0.54), which Sandercock *et al.* (2005) attributed to higher encounter rates of males rather than differences in survival. A skewed adult sex ratio (ASR) may arise

from differential mortality between the sexes at three stages: as embryos (e.g., primary sex ratio), at hatch (secondary sex ratio), or later (Liker *et al.* 2013). Evidence indicates no bias in secondary sex ratio for Kentish Plovers (Székely *et al.* 2004, 2006), which suggests that biases in ASR result from differential mortality or sex differences in encounter rates. In several *Charadrius* plovers, survival analyses show higher female mortality of chicks (Saunders & Cuthbert 2015), juveniles (Stenzel *et al.* 2007), and adults (Paton 1994, Foppen *et al.* 2006, Mullin *et al.* 2010, Stenzel *et al.* 2011).

Productivity

Two viability analyses have been produced for the listed population segment (Nur *et al.* 1999, Hudgens *et al.* 2014). Based on the initial analysis, the recovery plan set 1.0 fledged chick per male as the minimum that must be exceeded for five consecutive years in order to delist the population (USFWS 2007). Over 16 years, the study population exceeded this minimum value for three of four early years, when a large percentage of the population bred in high quality habitats of the lower Eel River (Fig. 2a). For much of our study, however, productivity was well below 1.0 when the population occurred on ocean beaches; a notable exception was 2016. Elsewhere, we have shown that heterogeneous (i.e., gravel bar) substrates of the river increase crypsis for eggs (Colwell *et al.* 2011). As a result, nests and chicks survive better on gravel substrates compared with sandy, ocean-fronting beaches (Colwell *et al.* 2007b). Moreover, individual males breeding on gravel substrates have higher annual (Colwell *et al.* 2010) and lifetime reproductive success (Herman & Colwell 2015). The loss of breeding plovers from high-quality, riverine gravel bars is perplexing. It may have stemmed from an interaction between low population size (<10 for five consecutive years: 2007–2011), high river flows that precluded settlement during early spring, and the absence of wintering flocks in this habitat. This hypothesis remains to be explored.

Role of immigration

Elsewhere, we derived estimates of λ (based on per-capita fledging success, and survival of juveniles and adults) to show that the subpopulation in northern California was a sink (Mullin *et al.* 2010), although immigration was important. Population viability analysis confirmed the characterization of the population as a sink (Eberhart-Phillips & Colwell 2014); specifically, reproductive success was consistently low and insufficient to maintain the population. Why, then, has the population grown at a rate of 22% annually for the past seven years? Since our population is small, nearly all breeding plovers are marked each year (95%; 87% with unique combinations). With knowledge of the contribution of local recruits vs. immigrants, we conclude that the recent steady growth in the population is attributable to immigration. Specifically, immigrants from sites elsewhere along the Pacific coast have consistently comprised 63 ± 4% of the population in northern California.

Conservation implications

The Snowy Plover subpopulation in coastal northern California (Recovery Unit 2) is the smallest and most isolated of six designated in the recovery plan. Our results show conclusively that, unlike other recovery units to the north and south, the subpopulation breeding in northern California remains well below criteria for delisting (i.e., 150 breeding adults and per-capita fledging success exceeding 1.0; USFWS 2007), although recent growth has been steady (λ = 1.22). Immigration is the principal cause of this growth, with 62% of the population originating from elsewhere along the Pacific coast in the seven years of positive growth.

Although the population has grown steadily in the past seven years, the impetus for this growth is unlikely to have been management in northern California. The USFWS (2007) identified three factors that limit recovery of the Pacific coast population via negative impacts on productivity and survival: (1) habitat loss and degradation owing to human development and invasive plants; (2) human disturbance; and (3) predation. Each of these limiting factors acts principally on reproductive success; there is limited mention in the recovery plan of survivorship. Over the 16 years we studied plovers, local management to affect plover population growth has varied. Restoration to enhance coastal dunes for plovers and other biota has been extensive, and plovers have responded by breeding in some restored habitats (Leja 2015). However, the effect of restoration on per-capita reproductive success has not been evaluated. Moreover, large stretches of suitable habitat remain unoccupied, probably because the population is small and new immigrants tend to establish themselves at sites occupied by older birds (Nelson 2007). If recent growth continues, restored areas may accommodate a growing population. Management of human recreational use of plover habitats is most effective on federal and state lands where enforcement also occurs. Currently, no predator management occurs despite evidence that predation is the main cause of low reproductive success (Colwell *et al.* 2007b, 2011, Burrell & Colwell 2012, Herman & Colwell 2015). Importantly, most immigrants in recent years have originated from areas where active predator management, including lethal removal, has resulted in consistently high productivity (Dinsmore *et al.* 2014, 2017). In summary, the population we studied is growing because of predator management in these areas to the north (Dinsmore *et al.* 2014, 2017). Consequently, we urge agencies responsible for the Snowy Plover in northern California to redouble their efforts to expand predator management to recover the species.

REFERENCES

Badzinski, D.S. 2000. *Population dynamics of Semipalmated Plovers (Charadrius semipalmatus) breeding at Churchill, Manitoba.* MSc. thesis, Trent University, Peterborough, Ontario.

Brindock, K.M. & M.A. Colwell. 2011. Habitat selection by Western Snowy Plovers during the nonbreeding season. *Journal of Wildlife Management* 75: 786–793.

Burrell, N.S. & M.A. Colwell. 2012. Direct and indirect evidence that productivity of Snowy Plovers *Charadrius nivosus* varies with occurrence of a nest predator. *Wildfowl* 62: 204–223.

Clements, J.F. 2007. *The Clements checklist of birds of the world, 6th edition.* Cornell University Press, Ithaca, NY.

Colwell, M.A., S.E. McAllister, C.B. Millett, A.N. Transou, S.M. Mullin, Z.J. Nelson, C.A. Wilson & R.R. LeValley. 2007a. Philopatry and natal dispersal of the Western Snowy Plover. *Wilson Journal of Ornithology* 119: 378–385.

Colwell, M.A., S.J. Hurley, J.N. Hall & S.J. Dinsmore. 2007b. Age-related survival and behavior of Snowy Plover chicks. *Condor* 109: 638–647.

Colwell, M.A., N.S. Burrell, M.A. Hardy, K. Kayano, J.J. Muir, W.J. Pearson, S.A. Peterson & K.A. Sesser. 2010. Arrival times, laying dates, and reproductive success of Snowy Plovers in two habitats in coastal northern California. *Journal of Field Ornithology* 81: 349–360.

Colwell, M.A., J.J. Meyer, M.A. Hardy, S.E. McAllister, A.N. Transou, R.R. LeValley & S.J. Dinsmore. 2011. Western Snowy Plovers *Charadrius alexandrinus nivosus* select nesting substrates that enhance egg crypsis and improve nest survival. *Ibis* 153: 303–311.

Dinsmore, S.J., D.J. Lauten, K.A. Castelein, E.P. Gaines & M.A. Stern. 2014. Predator exclosures, predator removal, and habitat improvement increase nest success of Snowy Plovers in Oregon, USA. *Condor* 116: 619–628.

Dinsmore, S.J., E.P. Gaines, S.F. Pearson, D.J. Lauten & K.A. Castelein. 2017. Factors affecting Snowy Plover chick survival in a managed population. *Condor* 119: 34–43.

Dowding, J.E. & E.C. Murphy. 2001. The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. *Biological Conservation* 99: 47–64.

Eberhart-Phillips, L.J. & M.A. Colwell. 2014. Conservation challenges of a sink: the viability of an isolated population of the Snowy Plover. *Bird Conservation International* 24: 327–341.

Eberhart-Phillips, L.J., B.R. Hudgens & M.A. Colwell. 2015. Spatial synchrony of a threatened shorebird: regional roles of climate, dispersal and management. *Bird Conservation International* 26: 119–135.

Emlen, S.T. & L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215–223.

Foppen, R.P.B., F.A. Majoor, F.J. Willems, P.L. Meininger, G.C. van Houwelingen & P.A. Wolf. 2006. Survival and emigration rates in Kentish *Charadrius alexandrinus* and Ringed Plovers *Ch. hiaticula* in the Delta area, SW-Netherlands. *Ardea* 94: 159–173.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140–1162.

Herman, D.M. & M.A. Colwell. 2015. Lifetime reproductive success of Snowy Plovers in coastal northern California. *Condor* 117: 473–481.

Hudgens, B., L. Eberhart-Phillips, L. Stenzel, C. Burns, M. Colwell & G. Page. 2014. *Population viability analysis of the Western Snowy Plover.* Report prepared for the U.S. Fish & Wildlife Service, Arcata, CA.

Koenig, W.D. 1988. On determination of viable population size in birds and mammals. *Wildlife Society Bulletin* 16: 230–234.

Leja, S.D. 2015. *Habitat selection and response to restoration by breeding Western Snowy Plovers in coastal northern California.* MSc. thesis, Humboldt State University, Arcata, CA.

Liker, A., R.P. Freckleton & T. Székely. 2013. The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications* 4: 1587.

Mullin, S.M., M.A. Colwell, S.E. McAllister & S.J. Dinsmore. 2010. Apparent survival and population growth of Snowy Plovers in coastal northern California. *Journal of Wildlife Management* 74: 1792–1798.

Nelson, Z.J. 2007. *Conspecific attraction in the breeding distribution of the Western Snowy Plover (Charadrius alexandrinus nivosus).* MSc. thesis, Humboldt State University, Arcata, CA.

Neuman, K.K., L.E. Stenzel, J.C. Warriner, G.W. Page, J.L. Erbes, C.R. Eyster, E. Miller & L.A. Henkel. 2013. Success of captive-rearing for a threatened shorebird. *Endangered Species Research* 22: 85–94.

Nur, N., G.W. Page & L.E. Stenzel. 1999. Population viability analysis for Pacific coast Snowy Plovers. Appendix D in: *Recovery plan for the Pacific coast population of the Western Snowy Plover (Charadrius alexandrinus)* (2007). U.S. Fish & Wildlife Service, Sacramento, CA.

Page, G.W. & L.E. Stenzel. 1981. The breeding status of the Snowy Plover in California. *Western Birds* 12: 1–40.

Page, G.W., L.E. Stenzel, W.D. Shuford & C.R. Bruce. 1991. Distribution and abundance of the Snowy Plover on its western North American breeding grounds. *Journal of Field Ornithology* 62: 245–255.

Page, G.W., L.E. Stenzel, J.S. Warriner, J.C. Warriner & P.W.C. Paton. 2009. Snowy Plover (*Charadrius nivosus*). In: *The Birds of North America*, no. 154 (A. Poole & F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, D.C.

Paton, P.W.C. 1994. Survival estimates for Snowy Plovers breeding at Great Salt Lake, Utah. *Condor* 96: 1106–1109.

Pearson, W.J. & M.A. Colwell. 2013. Effects of nest success and mate fidelity on breeding dispersal in a population of Snowy Plovers *Charadrius nivosus*. *Bird Conservation International* 24: 342–353.

Sandercock, B.K., T. Székely & A. Kosztolányi. 2005. The effects of age and sex on the apparent survival of Kentish Plovers breeding in southern Turkey. *Condor* 107: 583–596.

Saunders, S.P. & F.J. Cuthbert. 2015. Chick mortality leads to male-biased sex ratios in endangered Great Lakes Piping Plovers (*Charadrius melodus*). *Journal of Field Ornithology* 86: 103–114.

Stenzel, L.E., J.C. Warriner, J.S. Warriner, K.S. Wilson, F.C. Bidstrup & G.W. Page. 1994. Long-distance breeding dispersal of Snowy Plovers in western North America. *Journal of Animal Ecology* 63: 887–902.

Stenzel, L.E., G.W. Page, J.C. Warriner, J.S. Warriner, D.E. George, C.R. Eyster, B.A. Ramer & K.K. Neuman. 2007. Survival and natal dispersal of juvenile Snowy Plovers (*Charadrius alexandrinus*) in central coastal California. *Auk* 124: 1023–1036.

Stenzel, L.E., G.W. Page, J.C. Warriner, J.S. Warriner, K.K. Neuman, D.E. George, C.R. Eyster & F.C. Bidstrup. 2011. Male-biased sex ratio, survival, mating opportunity and annual productivity in the Snowy Plover *Charadrius alexandrinus*. *Ibis* 153: 312–322.

Székely, T., I.C. Cuthill, S. Yezerinac, R. Griffiths & J. Kis. 2004. Brood sex ratio in Kentish Plover. *Behavioral Ecology* 15: 58–62.

Székely, T., G.H. Thomas & I.C. Cuthill. 2006. Sexual conflict, ecology, and breeding systems in shorebirds. *Bioscience* 56: 801–808.

United States Fish & Wildlife Service. 1993. Threatened status for the Pacific coast population of the Western Snowy Plover. *Federal Register* 58: 12864–12874.

United States Fish & Wildlife Service (USFWS). 2007. *Western Snowy Plover (Charadrius alexandrinus nivosus) Pacific coast population recovery plan.* Sacramento, CA.

United States Fish & Wildlife Service (USFWS). 2009. *Protocols for Snowy Plover (Charadrius alexandrinus) breeding season survey.* Division of Migratory Bird Management, Portland, OR.

Westerkov, K. 1950. Methods of determining the age of game bird eggs. *Journal of Wildlife Management* 14: 56–57.

Zöckler, C., E.E. Syroechkovskiy & P.W. Atkinson. 2010. Rapid and continued population decline in the Spoon-billed Sandpiper *Eurynorhynchus pygmeus* indicates imminent extinction unless conservation action is taken. *Bird Conservation International* 20: 95–111.