POPULATION VITAL RATES FOR COMMON MURRES (*URIA AALGE*) OF SOUTHEAST FARALLON ISLAND, CALIFORNIA

A REPORT TO THE CALIFORNIA DEPARTMENT OF FISH AND GAME - OFFICE OF SPILL PREVENTION AND RESPONSE

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EXECUTIVE SUMMARY

We used state-of-the-art capture-mark-recapture methods to estimate annual and age-specific probabilities of survival, recruitment, and breeding success for Common Murres (*Uria aalge*) of the Farallon Islands, California. These estimates are suitable for use in population modeling and simulation exercises. Age-specific values were determined for birds banded as nestlings. Annual variation in survival, breeding propensity, and breeding success was determined for birds marked as adults. We ranked models of temporal environmental covariates for adult survival, breeding propensity, and breeding success. We found age effects on survival, recruitment, and breeding success. We found that survival of adult Common Murres was diminished during years of warmer sea surface temperatures (SST). Breeding propensity was reduced during the El Niño phase of the El Niño-Southern Oscillation phenomenon. Breeding success was variable, with extremely low values in three years characterized by El Niño conditions, but we found no correlation between breeding success and ocean climate indices. Temporal variation in adult parameter values co-varied positively, a situation conducive to rapid population change. The age-specific vital rates estimated in this report and our estimates of interannual variation in those rates are appropriate for use in population dynamics modeling efforts for Common Murres in the highly variable California Current System. We suggest incorporating variance into any simulation modeling, especially the positive covariation among demographic parameters.

INTRODUCTION

The Office of Spill Prevention and Response (OSPR) of the California Department of Fish and Game (CDFG) uses a population dynamics modeling approach to estimate damages and long-term impacts on seabird populations affected by oil spills. Key demographic parameters necessary for a seabird population model include: (1) juvenile survival, (2) recruitment (the probability that a bird that has never bred before breeds), (3) breeding propensity (the probability that experienced adult breeds), (4) breeding success, and (5) adult survival, (Nur and Sydeman 1999a). PRBO Conservation Science (formerly Point Reyes Bird Observatory, hereafter PRBO) was contracted to provide estimates of these demographic parameters for Common Murres (*Uria aalge*) breeding at the Farallon Islands. The Farallon Islands, in the California Current System (CCS), host the largest seabird breeding colony in the continental United States south of Alaska, and the largest murre breeding colony in California. The CCS, an eastern boundary current upwelling domain, is one of the most productive areas in the world ocean. However, primary and secondary productivity is highly variable due to high- and low- frequency temporal environmental variability. High frequency perturbations include the El Niño Southern Oscillation (ENSO) phenomenon (Goericke *et al.* 2004). Low frequency perturbations include the Pacific Decadal Oscillation (Mantua and Hare 2002).

Herein, we summarize 19 years of capture-mark-recapture data and 32 years of breeding success data to examine age-specific and annual variation in demographic rates for Common Murres of the Farallon Islands, California. We estimate age-specific survival and recruitment for birds aged from fledging to adulthood (defined by first breeding attempt), and annual rates of adult breeding propensity, breeding success, and over-winter survival.

METHODS

The Common Murre is a medium-sized seabird (*Alcidae*) that breeds throughout the Holarctic, laying an invariate 1-egg clutch (Harris and Wanless 1988, Boekelheide *et al.* 1990). The mating strategy of the Common Murre is monogamous, with presumed high natal and breeding site fidelity. In the central CCS, murres feed omnivorously on krill, anchovies, squid, and juvenile rockfish (Ainley *et al.* 1996, Sydeman et al. 1997, 2001, Miller and Sydeman 2004, Mills et al. in press).

Common Murres on Southeast Farallon Island (SEFI), California (37°42’N, 123°00’W) have been under study since 1972 (Boekelheide et al. 1990). The population was estimated to contain ~180,000 birds in 2005 (PRBO unpublished data). The capture-mark-recapture (CMR) data for this study were collected from 1985-2004, with capture and marking occurring from 1985 to 2001. Adult birds were banded at two sub-colonies: Shubrick Point and Upper Upper. These sub-colonies are located on opposite sides of SEFI (Sydeman 1993). Birds were marked with a metal band and three color bands, sorted to provide individual identification. Nestlings (dependent young-of-the-year) were captured and marked each year from 1986 to 2001 at only the Upper Upper sub-colony.

Each year from ~15 April through ~15 June, efforts were made to resight banded birds upon their return to the colony. Resighting efforts were made daily throughout the breeding season using binoculars and a spotting scope from a blind located approximately 10 m above each colony; individual color band combinations and occasionally metal band numbers were easily read. Birds were confirmed as "resighted" if their color-band combination was recorded at least 3 times during each season. Each resight of an individual was accompanied by determination of its breeding status as "breeder" or "non-breeder" based on whether an egg was laid at its nesting site. Annual records of resighted birds were compiled to form individual encounter histories. Breeding success of birds that attempted to breed was determined. Breeding success (0 or 1) was coded depending on whether offspring survived to at least 16 days post-hatching.

Birds banded as nestlings constituted a known-age sample that we used to estimate age-specific parameters (juvenile survival and recruitment – age at first breeding). Birds banded as adults were used to examine annual variation in vital rates (adult survival, breeding propensity, and breeding success). We analyzed adults from the two sub-colonies separately because previous work had shown that each sub-colony had different survival probabilities and sources of mortality (Sydeman 1993).

Age-specific vital rates

We classified each known age bird each year according to its breeding "state" (non-breeder = *N*, breeder = *B*). When data from both pre-breeders and breeders are available, it is possible to use multi-state models (e.g., Brownie *et al.* 1993, Nichols *et al.* 1994, Nichols and Kendall 1995) to address recruitment and survival while accounting for age- and state-specific recapture probabilities (e.g., Cam *et al.* 2002, 2003). Multi-state models allow estimation of age- and state-specific survival probability (e.g. $S^N{}_i$, the probability that a non-breeding individual survives between age *i*-1 and age *i*), and age-specific transition probability (Ψ) from non-breeder state to breeder state (e.g. $\Psi^{NB}{}_i$, the probability that an individual in state *N* at age *i* and that survives to age *i* + 1 is in state *B* at that age (Nichols *et al.* 1994)). $\Psi^{NB}{}_i$ for young birds corresponds directly to age-specific recruitment probability at age *i*. Therefore, we used multi-state models to infer age-specific survival and recruitment probabilities for SEFI murres.

Recruitment is a probabilistic event conditional on three different, potentially independent components (Clobert *et al.* 1993): (1) survival probability from birth to age *i* - 1, (2) fidelity to the natal area, and (3) the "transition probability" that an individual alive and in the "prebreeder" state at age *i* - 1 survives to age *i* and transitions to a "breeder" state at age *i*. Hereafter, when we refer to "recruitment probability" we mean the transition probability from non-breeder to breeder from one year to the next (Pradel and Lebreton 1999). As emphasized by Clobert *et al.* (1993), unless relevant data from colonies within the plausible range of natal dispersal are available, the two first components cannot be separated and their product is "local apparent survival" (*S*). Local apparent survival is biased low due to permanent dispersal. Since there is no resighting data from nearby colonies and a small number of individuals were banded, we will deal only with apparent survival in this analysis.

These models also estimate the parameter $\Psi^{BN}{}_i$ which is the probability of transitioning from breeder to non-breeder, also called "skipping" probability. The complement of this parameter $\Psi^{BB}{}_i$ is "breeding propensity," the conditional probability that an individual that bred in year $i - 1$ will breed in year i, given that it has survived to that year. Breeding propensity is a parameter that is difficult to measure and is often ignored.

The parameter p is "recapture probability." The recapture probability of species with high natal site fidelity, such as seabirds, is interesting for young, non-breeding birds because it incorporates the probability that birds of a given age will return to their natal area to prospect for mates and nest sites. Recapture probability of breeders in this model is essentially a nuisance parameter, but necessary to provide estimates of survival and transition probabilities unbiased by differential recapture probability.

Previous studies on marine birds have documented the age-specific survival curve as a constant (Potts, Coulson and Deans 1980), a negative linear function (Dunnett and Ollason 1978; Spear *et al.* 1987), a constant that exhibits senescent decline in oldest ages (Buckland, Rowley, and Williams 1983; Bradley *et al.* 1989; Aebischer and Coulson 1990; Croxall *et al.* 1990), a constant with elevated survival in the oldest birds (Ainley *et al.* 1990), or a quadratic curve, where survival increases with age to a midlife optimum, then declines as the oldest birds senesce (Rattiste and Lilleleht 1987; Frederiksen and Bregnballe 2000). Age-specific breeding success in seabirds has been described as a positive linear relationship (Sæther 1990; Mills 1989), a quadratic curve (Wooller *et al.* 1989; Forslund and Pärt 1995), or steadily increasing to an asymptote, then constant (Wooller *et al.* 1992; Mauck, Huntington and Grubb 2004). Age-specific breeding propensity has been infrequently described for seabirds, but varying patterns have been observed: a linear increase with age (Ollason and Dunnet 1988; Thomas and Coulson 1988), steadily increasing to an asymptote, then constant (Wooller *et al.* 1989), or linearly decreasing with age (Mills 1989; Nur and Sydeman 1999b).

With these previous studies in mind, our *a priori* model set for age functions included S, p, and Ψ parameters modeled separately for each state (N and B), and the rs parameter: (1) as constants; (2) as linear trends with age ("linear age"); (3) as quadratic trends with age (age + age^2; "age^2");(4) as natural log trends (ln age); and (5) as inverse age trends (1/age). Data from known age birds was analyzed for age-specific rates only; data were too sparse to examine annual variation in addition to age-specific rates. Annual variation was examined using birds banded as adults (see below).

To obtain age-specific survival, recapture, and transition probability estimates, we used multi-state capture-mark–recapture models in program MARK (White and Burnham 1999). A fully age-specific model with 15 age classes was run to obtain age-specific estimates and assess goodness of fit. Age classes >14 years were pooled due to small sample sizes in the oldest age classes. We used the bootstrap approach available in program MSSURVIV (Hines 1994) to estimate an overdispersion parameter ($\hat{c}$) based on 100 simulations. The variance inflation factor ($\hat{c}$) quantifying data overdispersion, was calculated as the observed model deviance divided by the mean bootstrapped deviance.

Model selection was subsequently based on QAICc (Akaike's information criterion corrected for small sample sizes, based on quasi-likelihood; Burnham and Anderson 2002) with program MARK (White and Burnham 1999). All estimates were generated using a time-independent model. The general model {*S*(*state* * *age15*) *p*(*state* * *age15*) *Ψ*(*state* * *age15*)} fit the data well, as assessed by a bootstrap goodness-of-fit test. The value of $\hat{c}$ was 1.464, indicating minimal overdispersion (Cooch and White 1998).

We also examined known-age bird breeding success (fledglings pair^{-1}) from 1989-2004. Breeding success (*rs*) in relation to age was assessed using a generalized linear model (GLM) in program STATA 8.2 (Stata Statistical Software: Release 8.2, College Station, TX: StataCorp LP, 2005). Because the reproductive output as the dependent variable included failed breeding attempts, but has a maximum of 1 fledgling pair^{-1}, a binomial error structure and log link function were used (Nielsen and Drachmann 2003).

QAICc Weights are a measure of the strength of evidence for a given model (Mi). QAICc Weight = exp(-1/2 * ΔQAICc of Model Mi) / [sum for all models of exp(-1/2 ΔqAICc)]. Due to model selection uncertainty, information from all models in the set with qAICc Weight > 0 should be considered when making inferences (Burnham and Anderson 2002). When evaluating our models, we used qAICc Weights as importance values to indicate the descriptive power of that model relative to the others in the set (Burnham and Anderson 2002). The model with the largest qAICc Weight is considered the most important, and the model with the smallest qAICc Weight is considered to be the least important. The ratio of qAICc Weights between 2 models computes how many times better the evidence that the numerator model is best compared to the denominator model (Burnham and Anderson 2002). We computed model-average parameters using qAICc Weights as the weighting factor.

We performed model selection on each parameter sequentially, obtaining model ranks and weights and computing model average curves in this order: p^N, p^B, $\Psi^{N\text{-}B}$, $\Psi^{B\text{-}N}$, S^B, and S^N (superscript denotes state: *N* = non-breeder, *B* = breeder). In each sequential step, we kept previously modeled parameters in their most parsimonious form (Lebreton *et al.* 1992). We selected models for each parameter individually, but also examined the evidence for equality of survival in breeders and non-breeders using all possible age functions. We used the logit link function throughout, and 2nd part variance estimation procedure.

Model selection for *rs* was performed in STATA 8.2 (2005) using the age models described above, as well as models that controlled for El Niño years in 1992 and 1998 because island-wide productivity was known to be >1 SD lower than average in those years (PRBO unpublished data).

Annual variation in adult vital rates

Accurate estimates of annual local survival probability (*Φ*) and recapture probability (*p*) are best obtained from analysis of capture-recapture data from populations with models that estimate survival and recapture probabilities separately (Lebreton *et al.* 1992).

Accurate annual breeding success data are also best obtained from a marked population where nests are monitored frequently during the breeding season (Mayfield 1975). In this model structure, the recapture probability of species with high breeding site tenacity, such as seabirds, is biologically interesting because it incorporates the conditional probability that an individual will breed in a particular year given that it has survived to that year (Lebreton *et al.* 1990; Clobert *et al.* 1994). Thus, capture-recapture data may be used to infer breeding propensity, the proportion of the experienced adults attempting to breed each year. In this model structure, recapture probability is composed of breeding propensity and recapture rate, but due to high breeding site fidelity in this species, recapture rate is nearly 1, so the parameter p is dominated by breeding propensity. Simultaneous estimation of age- and year-specific demographic parameters reduces potential biases associated with estimation of one that does not control for the other. In the adult data, age was minimum age, because birds were banded as adults. Age curves in the adult data were included merely to control for nuisance bias associated with age-like effects, including true age effects, and more importantly, trap dependence.

To obtain annual estimates of survival and recapture we used capture-mark–recapture models implemented in program MARK (White and Burnham 1999). We used the bootstrap approach available in program MARK to estimate an overdispersion parameter ($\hat{c}$) based on 100 simulations. The variance inflation factor ($\hat{c}$) quantifying data overdispersion, was calculated as the observed model deviance divided by the mean bootstrapped deviance. Model selection was subsequently based on QAICc (Akaike's information criterion corrected for small sample sizes, based on quasi-likelihood; Burnham and Anderson 2002) with program MARK (White and Burnham 1999). The general model $\{\Phi(year + age15)\ p(year + age15)\}$ fit the data well, as assessed by a bootstrap goodness-of-fit test. The value of $\hat{c}$ was 1.394 for Shubrick Point colony, and 1.233 for Upper Upper colony, indicating minimal lack of model fit given the data (Cooch and White 1998).

We performed model selection on each parameter sequentially, obtaining model ranks and weights first for age-like effects on p, then temporal models of p, then age-like effects in Φ, and finally temporal models of Φ. In each sequential step, we kept previously modeled parameters in their most parsimonious form (Lebreton *et al.* 1992). We used the logit link function throughout, and 2nd part variance estimation procedure

The *a priori* model set for age functions included Φ and p parameters modeled: (1) as constants; (2) as linear trends with age (A); (3) as quadratic trends with age (age + age^2; (A^2); (4) as natural log trends (*ln age*); and (5) as inverse age trends (*1/age*). These functions were chosen as the most likely shapes for age-specific parameters because they have been previously described or theorized for other species.

The *a priori* model set for temporal covariates included Φ and p parameters as functions of: (1) a constant; (2) over-winter values (October-March) of the Multivariate El Niño Index (*MEI*) (see below); (3) over-winter values of the Northern Oscillation Index (*NOI*) (see below); (4) over-winter values of sea-surface temperature at SEFI (*SST*). Over-winter values of each parameter were calculated using monthly averages from October-

March. The winter season was considered because seabird mortality is believed to occur primarily during winter (Gaston 2003; Jenouvrier *et al.* 2003; Votier *et al.* 2005). MEI is an index of the ENSO phenomenon that includes measurements from the eastern tropical Pacific for sea level pressure, the east-west and north-south components of the surface wind, SST, surface air temperature, and cloud cover combined in a multivariate empirical orthogonal function analysis (Wolter and Timlin 1993). MEI is not a physical forcing mechanism, but strongly reflects the El Niño and La Niña pattern. NOI is the difference in sea level pressure (SLP) between the North Pacific High off the California coast and the Equatorial Pacific low off Darwin, Australia. NOI represents a physical forcing mechanism and indicates the prevailing wind patterns for the northeast Pacific. High NOI values indicate stronger northerly winds that drive springtime upwelling in the California Current System near SEFI. SST is local sea surface temperature at SEFI expressed as a monthly mean of daily measurements.

We examined annual breeding success (fledglings pair^{-1}) from 1972-2004. Breeding success (*rs*) was assessed using a generalized linear model (GLM). Because breeding success as the dependent variable included failed breeding attempts, we used a binomial error structure and log link function (Nielsen and Drachmann 2003). Model selection for *rs* was performed using STATA 8.2 (Stata Statistical Software: Release 8.2, College Station, TX: StataCorp LP, 2005) using the temporal models as above for Φ and p. We also included terms for colony differences. AICc was used as the model selection criteria and to compute model weights. We computed the significance of, and percentage of variation explained by covariate models using analysis of deviance (ANODEV, Skalski *et al.* 1993).

We computed the pairwise correlation coefficients, Spearman rank correlation coefficients, and probability values of correlations between annual estimates of p, Φ, and *rs* for both colonies during the years of overlap. We used p and *rs* in year x, and Φ from year x -1 to year x. Computation was performed using STATA 8.2.

RESULTS

Age-specific parameters

From 1986 to 2001, PRBO biologists marked and released 375 Common Murre chicks (age 0) at the Upper Upper colony; only chicks that fledged were considered as released. Model selection results for recapture, transition, and survival probabilities are given in Table 1. The only strong age effects were found in recapture probability of non-breeders (Fig. 1), and the transition from non-breeder to breeder (Fig. 2). The recapture probability of non-breeders indicates return to the natal colony to prospect for a breeding site and find a mate. The transition from non-breeder to breeder indicates the recruitment probability of young birds. Both these parameters were most parsimoniously modeled by an inverse age function.

The recapture probability of non-breeders climbed to an asymptote at age 7 years. Recapture probability of breeders was nearly constant at 0.964 ± 0.034 (mean ± SE), but may have declined slightly with age (Fig. 1). The transition probability from non-breeding to breeding remained near zero until age 3 indicating 3 is the youngest age of first breeding. The transition probability from non-breeding to breeding then climbed to 0.51 at age 9 (Fig. 2) and remained constant through the older age classes. By age 9, an average of 91% of murres have recruited into the breeding population. The transition probability from breeder to non-breeder (B to N; skipping probability) was nearly constant at 0.037 ± 0.037 (mean ± SE), but there was a slight increase as birds aged. Due to the very high breeding site fidelity in this species, it is logical that the recapture rate of breeders (true recapture probability + breeding propensity), and the transition probability from breeder to non-breeder are complementary.

Figure 3 depicts the model average age curve for local apparent survival of breeders. Non-breeder survival is essentially constant at 0.667 ± 0.058 (mean ± SE).

Multiple models of breeding success received high qAICc weight, but the top-ranked model was again the inverse age model (Table 2). The model average curve shows an increase in breeding success as birds aged, and a slight decrease in the oldest age classes, possibly indicating senescence (Fig.4).

Annual variation in adult vital rates

From 1986 to 2001, PRBO biologists marked and released 150 adult Common Murres at Shubrick Point, and 205 at Upper Upper. Model selection results for survival probability and breeding propensity at Shubrick Point and Upper Upper colonies are given in Tables 3 and 4.

At the Shubrick Point colony, local over-winter survival probability was negatively correlated with winter *SST* (Table 3; Fig. 5). However, the *SST* model explained only 13% of the variation in over-winter survival (r^2=.13), and ANODEV determined that SST was not a statistically significant covariate ($F_{1,17}$ = 2.73, P = 0.116). Mean adult survival at Shubrick Point was 0.924 ± 0.061 (mean ± SD). Breeding propensity at Shubrick Point was best modeled as a constant (Fig. 6), with some evidence that winter *MEI* affects breeding propensity (Table 3). Mean breeding propensity of Shubrick Point adults was 0.899 ± 0.041 (mean ± SD).

At Upper Upper, survival was best modeled as a constant (Table 4). This model was ranked far superior to competing models, being 2.3 times better supported by the data than the next best models; the 3 ocean climate models all with similar weights. Mean survival of Upper Upper adults was 0.904 ± 0.054 (mean ± SD). The best model of breeding propensity at Upper Upper was as a function of winter *MEI* (Table 4). This model accounted for 11% of the annual variation in breeding propensity (Fig. 7), but was not statistically significant (ANODEV: $F_{1,17}$ = 2.09, P = 0.166). Mean adult breeding propensity at Upper Upper was 0.856 ± 0.054 (mean ± SD).

When data were pooled from 1986-2004, and the two colonies were analyzed together, annual survival probabilities varied considerably (Fig. 8), but the best model of survival was constant with a colony effect (Shubrick Point > Upper Upper). The best model of breeding propensity was a function of winter MEI, with a colony effect (Shubrick Point > Upper Upper).

Adult breeding success from 1972 to 2004 was best modeled by a model including annual variation (Table 5). The *year* + *colony* model (Shubrick Point > Upper Upper) was nearly equally weighted compared with the top-ranked model, indicating that either model could be the best. The outstanding feature of this time series are the extremely low values for the 1983, 1992, 1995 (Upper Upper sub-colony only) and 1998 breeding seasons. All four values are far below 1 standard deviation from the overall mean (Fig. 9). None of the ocean climate covariate models came close to competing with the annual model for top rank (Table 5). Mean breeding success was 0.740 ± 0.205 (mean ± SD), but rose to 0.798 ± 0.078 (mean ± SD) when the lowest *rs* years were excluded.

Table 6 gives the pairwise correlation coefficients, Spearman rank coefficients, P-values, and number of observations for annual estimates of demographic parameters during the period of temporal overlap (1986-2004). Correlation coefficients were a mixture of positive and negative, but all the significant coefficients were positive (Table 6). Significant positive coefficients were found between all three demographic parameters: survival, breeding propensity and breeding success.

All annual estimates and their standard errors are provided in Appendix I.

DISCUSSION

Age-specific parameters

Herein, we provide the first estimates of age-specific variation in survival, age of first breeding, breeding propensity, and breeding success for Common Murres in the Pacific Ocean. Our model selection of age functions of these demographic parameters indicates that the inverse age function best characterized the relationship between age and the probability of transitioning from non-breeder to breeder state (recruitment). The transition from non-breeder to breeder indicates the probabilistic age of first breeding, controlling for age-specific recapture probability and survival. Our results suggest that the point of maximum inflection in the age of first breeding curve occurs at age 6 years. At age 6 years, almost 60% of the individuals in any cohort that are still alive will have begun breeding, and by age 10 years over 95% have begun breeding. Our estimates of the age of first breeding for Common Murres from SEFI closely resemble estimates made at colonies in Great Britain (Harris *et al.* 1994; Swann and Ramsay 1983; Birkhead and Hudson 1977).

Our results also show that murres rarely skip a year once they have initiated breeding. The probability of transitioning from breeder to non-breeder (skipping probability) is ~4%, meaning 96% of birds that bred the previous year remain in the breeder state the following year. This result was similar to, but slightly lower than, estimates from North Sea colonies (5-10%, Harris and Wanless 1995; Harris et al 1996b). Generally, birds that skip a year of breeding have lost a mate, lost their breeding site, or suffered breeding failure in the previous year (Harris et al 1996b, PRBO unpublished data). Beyond age 10 years, we see a nearly constant transition probability of non-breeder to breeder at ~50%. This transition parameter represents birds that previously bred, then failed to breed for a year, and returned to breeding once again in subsequent years. So, the ~4% of birds that skip breeding in any given year have a ~50% probability of returning to breeder state the next year. The positive trend in skipping probability with age may indicate some senescence in breeding effort, or may indicate that its takes more time to acquire new mates or sites when one member of the breeding pair disappears at older ages. That the probability of recapturing non-breeders was also an inverse age function reflects the same range of phenotypes in age of first breeding as we are seeing in age of first breeding, since recapture of non-breeders indicates the age-specific probability of returning to the natal colony to prospect for mates and nest sites, a prerequisite for first breeding attempts.

Crespin *et al.* (2006) showed that recruitment of cohorts in this species varies in relation to ocean climate conditions, such that murres begin breeding at earlier ages when conditions are favorable (presumably due to enhanced prey availability). Unfortunately, we could not examine annual variation in recruitment due to small sample size of our cohorts. Colony size may also influence recruitment if young birds are forced to wait longer for a breeding site in dense colonies (Swann and Ramsay 1983).

Breeding success was another parameter from the known-age bird data that showed large age-specific effects; the inverse age function was most parsimonious. However results were equivocal, as other age functions performed nearly as well. The model average curve indicates low *rs* for the youngest breeders (age 4) that increases to a peak at ages 10 – 11 years. There was some evidence for decreasing breeding success after age 11.

Survival of known-age breeders compares well with survival estimates of murres banded as adults at SEFI. Moreover, recall that local apparent survival is composed of true survival and site fidelity. However, because of high breeding site fidelity of this species, we interpret variation in local survival to be largely due to mortality, rather than dispersal or permanent emigration from the study site. Observations of banded birds around the Upper Upper sub-colony also indicate very low rates of movement or dispersal among closely situated sub-colonies (PRBO unpublished data). However, the presence of any permanent emigration would bias our survival estimates lower than the true survival probability. This bias could be more pronounced in the survival estimates for the youngest age non-breeders, where site fidelity is not well established. Pre-breeding murres often prospect at their natal colony before dispersing to other sites (Halley *et al.* 1995, Harris et al 1996a; Crespin *et al.* 2006), and that emigration would be confused with mortality in the estimates of young non-breeder survival in this study, resulting in underestimates.

Annual variation in adult parameters

We provide the first estimates of annual variation in adult survival, breeding propensity, and breeding success based on capture-mark-recapture analyses for adult Common

Murres in the California Current System. Previously, Sydeman (1993) reported simple resighting probabilities. Our results for over-winter survival of adult murres are similar to Sydeman's previously reported values for this population. We also document that survival is negatively affected by warmer ocean temperature. Positive winter MEI (indicating warm El Niño-like conditions) also negatively affected the probability of breeding the following spring. Reproductive success showed substantial inter-annual variability, but we found no significant relationship with any ocean climate indices. Other seabirds breeding on the Farallon Islands have exhibited negative demographic responses to El Niño conditions (Nur and Sydeman 1999b, Lee, Sydeman and Nur, in review). Similarly, recent studies of Atlantic populations of murres have documented a negative correlation between adult over-winter survival and the North Atlantic Oscillation (NAO; Sandvik *et al.* 2005, Votier, *et al.* 2005); higher NAO indices indicate warmer, wetter, and windier conditions in northern Europe (Hurrell 1995) which could affect the murre's prey base.

Our mean adult survival estimates were within the range of those previously reported for this species (Table 7). Our estimates of mean survival and breeding propensity and their variances update those of Sydeman (1993). Comparing our estimates of mean survival with Sydeman's (1993), our Shubrick Point estimate was slightly lower, and our estimate for Upper Upper was much higher. During Sydeman's study, Peregrine Falcon mortality of Upper Upper murres was very high. It is possible that peregrine-related mortality has decreased in recent years leading to the higher estimates of survival. Sydeman also calculated return rates, while in this study we used modern CMR methods (program MARK) to estimate recapture probabilities and survival separately. This latter method is better. Estimates of survival based on simple return rates analyses are generally biased low because "unresighted" birds are mistakenly recorded as dead.

Our mean estimate for Shubrick Point is not significantly different from the average survival probability of European colonies, but estimates for Upper Upper were lower (Table 7). Our variance estimate (SD) for Shubrick Point is similar to that calculated by Sydeman (1993), but our variance estimate for Upper Upper is lower (Table 7), possibly due to the different methods employed, and the longer time span of this study. Our estimates of breeding propensity are likely under-estimates because we do not know true recapture probability, independent of breeding propensity, but it is likely less than unity. Breeding propensity estimated from multi-state models for murres banded as chicks at Upper Upper was 96.5%, much higher than our estimates of those banded as adults, but similar to those of Sydeman (1993) and Harris and Wanless (1995).

Our estimates of annual adult breeding success update those of Boekelheide *et al.* (1990) and Sydeman et al. (2001). The fact that breeding success was best modeled by annual variation, with none of our climate models receiving any weight whatsoever is likely because we modeled winter ocean climate status, while breeding success is determined by conditions in spring and summer. Apparently, winter and spring/summer climate is sufficiently decoupled that winter models were not good descriptors of annual variation in breeding success. Alternatively, the climate indices used (NOI, MEI, SST) are not reflective of wintertime conditions that affect murre breeding success. For example, wintertime (January-March) Southern Oscillation Index is correlated with murre breeding success at SEFI (Sydeman, unpublished). Moveover, the significant co-variation described between annual estimates of survival and breeding success indicate that winter climate does affect breeding success. Therefore, we conclude that our model set did not include a suitable covariate for breeding success.

As noted above, low survival value in 1989 at Upper Upper colony was previously explained by Peregrine Falcon predation (Sydeman 1993). Falcon predation may also be responsible for other years when Upper Upper colony survival was unusually low compared to Shubrick Point colony (i.e. 1992, 1994, and 1996). Peregrine Falcons specializing on Murres at the Upper Upper colony have been observed to take up to 11% of the marked population of that colony in a single winter (Sydeman 1993), and eagle predation on Tatoosh reduced murre survival there (Parrish *et al.* 2001).

It is not surprising that we did not find mechanistic relationships between biological parameters and overall ocean climate indices examined. The ocean climate indices chosen (averaged over 6 months) may have been too coarse to detect fine scale variation. Although overall trends were not apparent, there were obvious years of reduced survival, breeding propensity and reproductive success that may be explained indirectly by anomalous ocean climate conditions. The years 1997-99, and to a lesser extent 2001-02, stand out as having especially low survival for both colonies relative to the remaining years, when there is no evidence of substantial Peregrine predation. Rather, fall 1997 marked the beginning of a strong ENSO event which lasted through late spring to early summer 1998 (Chavez *et al.* 1999; Marinovic *et al.* 2002); 1997 and 1998 were also characterized by reduced breeding propensity. Another explanation is oil pollution. During winter 1997-98 oil leaking from the sunken vessel *S.S. Jacob Luckenbach* caused extensive mortality of murres in the Gulf of the Farallones (Hampton et al. 2004).

Temporal co-variation in vital rates

All significant temporal correlations between demographic parameters were positive. Covariation among demographic parameters has rarely been addressed in the literature. Saether and Bakke (2000) demonstrated that where data were available, large temporal covariation among demographic parameters was often found. For marine birds, Jenouvrier *et al.* (2003) recently found that adult survival, recruitment and breeding propensity were positively correlated for fulmars in the Southern Ocean. Lee et al. (in review) found positive co-variation in Cassin's Auklet survival, recruitment, breeding propensity, and breeding success. Co-variation among demographic parameters should be expected when fluctuations in different demographic parameters are governed by the same external variable, such as ocean climate. When demographic parameters co-vary in a positive fashion, population fluctuations can be much larger than when parameters vary inversely (Caswell 2001, Burgman *et al.* 1993).

Recommendations for population dynamics modeling

The age-specific vital rates estimated in this report and our estimates of interannual variation in those rates are appropriate for use in population dynamics modeling efforts for Common Murres in the California Current System. We suggest incorporating variance into any simulation modeling efforts, especially the positive covariation among demographic parameters. The basics of accomplishing this in a Leslie matrix framework is to have multiple matrices (e.g. a mean matrix, a +1 SD matrix, and a -1 SD matrix). Then, use historical climate data and predictions for future climate change to create a stochastic model that produces a sequence of environmental states. Next, create a function that associates one of the matrices of demographic parameters with each environmental state. The result would be a series of population vectors that results from applying the series of matrices to an initial population vector. This, or some permutation with more matrices and different thresholds for utilizing a given matrix, would be a reasonable approach. Addressing different levels of autocorrelation in SST or MEI, and how this affects Murres would be important, and interesting, in light of climate change scenarios.

(1) Age-specific parameters were estimated from the Upper Upper sub-colony where adult survival is known to be lower than at Shubrick Point. It is reasonable to assume that juvenile survival probabilities and breeding success from Upper Upper is also lower than at other sub-colonies. Therefore, we recommend that adjustments be made to all age-specific estimates to account for this difference in demography between sub-colonies.

(2) We recommend using model-average estimates for age-specific survival, recruitment and breeding success (see Appendix I) for population dynamics modeling. A preliminary Leslie matrix population model of Upper Upper sub-colony that was parameterized using model-average estimates yielded a finite rate of population growth (lambda) that was nearly identical to the lambda calculated from the observed population trajectory of that sub-colony (PRBO unpublished data).

(3) Interannual variation in vital rates was substantial. Therefore, annual variation in parameters must be included in population dynamics models. Although mean (i.e., constant) models were occasionally the most parsimonious, there were clear annual signals in all parameters, and, importantly, this variation exhibited temporal co-variation. Therefore, in a given year all parameters could be on the same side of the mean (positive or negative). Covariance among parameters is easily modeled by allowing an environmental state to select an entire matrix from a specified set of matrices reflecting different environmental conditions. Serial autocorrelation of environmental signals should also be determined, but is beyond the scope of this report. Survival should be modeled as a function of SST, with additional negative departures from the mean due to unexplained causes. Large amplitude catastrophic breeding failure could be modeled by including threshold functions. Smaller amplitude annual variation in breeding propensity and breeding success related to warmer water MEI conditions could be included. Annual variation in recruitment, although not examined here due to data limitations, should be included in modeling efforts because this effect was found in other murre populations.

Finally, mean SST and annual variation is expected to increase due to global climate change (IPCC 2002).

(4) The estimates of survival in this report are apparent local survival, which includes permanent emigration as a component of local mortality. Due to the extremely high site fidelity of this species, it is likely that permanent emigration rates are very low, but reasonable levels of emigration should be incorporated into any simulation modeling that uses these estimates. Differing levels of emigration should be inversely related to mortality to determine what effect different levels of emigration may have on observed population trajectories.

Some comments on observed SEFI population trends

There has been dramatic growth of the SEFI Common Murre population since the late 1990s. Starting in 1999 and lasting through 2002, a major change in ocean climate to cooler, more productive conditions, was observed. Given that we observed no obvious increase in breeding success or survival during these years and in 2003-2005 when the SEFI population continued to grow rapidly, we surmise that positive changes in juvenile survival (and recruitment) determined recent population growth.

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LITERATURE CITED

Aebischer, N. J., and J. C. Coulson. 1990. Survival of the Kittiwake in relation to sex, year, breeding experience and position in the colony. Journal of Animal Ecology 59:1063-1071.

Ainley, D. G., L. B. Spear, S. G. Allen, and C. A. Ribic. 1996. Temporal and spatial patterns in the diet of Common Murres in California waters. Condor 98:691-705.

Birkhead, T. R., and P. J. Hudson. 1977. Population parameters for the Common Guillemot (*Uria aalge*). Ornis Scandinavica 8:145-154.

Boekelheide, R. J., D. G. Ainley, S. H. Morrell, H. R. Huber, and T. J. Lewis. 1990. Common Murre. Pages 245-275 in Seabirds of the Farallon Islands: Ecology, Structure and Dynamics of an Upwelling-System Community (D. G. Ainley and R. J. Boekelheide, Eds.). Stanford University Press, Palo Alto, CA.

Bradley, J. S., R. D. Wooller, I. J. Skira, and D. L. Serventy. 1989. Age-dependent survival of breeding Short-tailed Shearwaters *Puffinus tenuirostris*. Journal of Animal Ecology 58:175-188.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173-1187.

Buckland, S. T., I. Rowley, and D. A. Williams. 1983. Estimation of survival from repeated sightings of tagged galahs. Journal of Animal Ecology 52:563-573.

Burgman, M.A., S. Ferson, and H.R. Akçakaya. 1993. Risk Assessment in Conservation Biology. Chapman and Hall, London.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Cam, E., W. A. Link, E. G. Cooch, J. Y. Monnat, and E. Danchin. 2002. Individual covariation in life history traits: seeing the trees despite the forest. The American Naturalist 59:96–105.

Cam, E., L. W. Lougheed, R. Bradley, and F. Cooke. 2003. Demographic assessment of a Marbled Murrelet population from capture-mark-recapture and radio-telemetry data. Conservation Biology 17:1118-1126.

Caswell, H. 2001. Matrix Population Models: Construction, analysis and interpretation, (2nd edition). Sinaur Associates, Sunderland, Massachussetts.

Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley, M. J. McPhaden. 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997-98 El Niño. Science 286:2126-2131.

Clobert, J., R. Julliard, and R. H. McCleery. 1993. The components of local recruitment. Pages 281-293 in The Study of Bird Population Dynamics Using Marked Individuals (J. D. Lebreton and P. North, Eds.). Birkhauser Verlag, Basel.

Cooch E., and G. White. 1998. Program MARK: A gentle introduction. http://canuck.dnr.cornell.edu/misc/cmr/mark/docs/.

Crespin, L., M. P. Harris, J. D. Lebreton, M. Frederiksen, and S. Wanless. 2006. Recruitment to a seabird population depends on environmental factors and on population size. Journal of Animal Ecology 75:228–238.

Croxall, J. P., P. Rothery, S. P. Pickering, and P.A. Prince. 1990. Reproductive performance, recruitment and survival of Wandering Albatrosses *Diomedea exulans* at Bird Island, South Georgia. Journal of Animal Ecology 59:775-796.

Dunnett, G. M., and J. C. Ollason. 1978. Survival and longevity in the Fulmar. Ibis 120:124-125.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds—hypotheses and tests. Trends in Ecology and Evolution 10:374–378.

Frederiksen, M., and T. Bregnballe. 2000. Evidence for density-dependent survival in adult cormorants from a combined analysis of recoveries and resightings. Journal of Animal Ecology 69(5):737-752.

Gaston, A. J. 2003. Synchronous fluctuations of thick-billed murre (*Uria lomvia*) colonies in the eastern Canadian Arctic suggest population regulation in winter. Auk 120:362-370.

Goericke, R., S. J. Bograd, G. Gaxiola-Castro, J. Gomez-Valdes, R. Hooff, A. Huyer, K. D. Hyrenback, B. E. Lavaniegos, A. Mantyla, W. T. Peterson, F. B. Schwing, R. L. Smith, W. J. Sydeman, E. Venrick, and P. A. Wheeler. 2004. The state of the California Current 2003–2004: a rare "normal" year. California Cooperative Oceanic Fisheries Investigation Report 45:27-60.

Halley, D. J., M. P. Harris, and S. Wanless. 1995. Colony attendance patterns and recruitment in immature Common Murres (*Uria aalge*). Auk 112:947-957.

Harris, M. P., and S. Wanless. 1988. The breeding biology of Guillemots *Uria aalge* on the Isle of May over a six year period. Ibis 130:172-192.

Harris, M. P., D. J. Halley, and R. L. Swann. 1994. Age of first breeding in Common Murres. Auk 111:207-209.

Harris, M. P., D. J. Halley, and S. Wanless. 1996a. Philopatry in the Common Guillemot *Uria aalge*. Bird Study 43:134-137.

Harris, M. P., and S. Wanless. 1995. Survival and non-breeding of adult Common Guillemots *Uria aalge*. Ibis 137:192-197.

Harris, M. P., S. Wanless, and T. R. Barton. 1996b. Site use and fidelity in the Common Guillemot *Uria aalge*. Ibis 138:399–404.

Hines, J. E. 1994. MSSURVIV User's manual. Patuxent Environmental Science Center. Laurel, Md.

Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. Journal of Animal Ecology 72: 576-587.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118.

Marinovic B. B., D. A. Croll, N. Gong, S. R. Benson, and F.P. Chavez. 2002. Effects of the 1997-1999 El Niño and La Niña events on the zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system. Progress in Oceanography 54:265-277.

Mauck, R. A., C. E. Huntington, and T. C. Grubb Jr. 2004. Age specific reproductive success: evidence for the selection hypothesis. Evolution 58:880–885.

Mayfield, H.F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Miller, A., and W. J. Sydeman. 2004. Rockfish response to low-frequency ocean climate change as revealed by the diet of a marine bird over multiple time scales. Marine Ecology Progress Series 281:207-216.

Mills, J. A. 1989. Red-billed gull. Pages 387-404 in Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

Nichols, J. D., J. E. Hines, K. H. Pollock, R. L. Hinz, and W. A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. Ecology 75:2052–2065.

Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835–846.

Nielsen, J. T., and J. Drachmann. 2003. Age-dependent reproductive performance in Northern Goshawks *Accipiter gentilis*. Ibis 145:1-8.

Nur, N., and W. J. Sydeman. 1999a. Demographic processes and population dynamic models of seabirds. Curent Ornithology 15:149-188.

Nur, N., and W. J. Sydeman. 1999b. Survival, breeding probability, and reproductive success in relation to population dynamics of Brandt's Cormorants Phalacrocorax penicillatus. Bird Study 46:2-13.

Ollason, J. C. and G. M. Dunnett. 1988. Variation in breeding success in Fulmars. Pages 263-278 in Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems (T. H. Clutton-Brock, Ed.). Chicage University Press, Chicago.

Olsson, O., T. Nilsson, and T. Fransson. 2000. Long-term study of mortality in the Common Guillemot in the Baltic Sea: Analysis of 80 years of ringing data. Rapport Naturvardsverket, 5057. Swedish Environmental Protection Agency, Stockholm.

Parrish, J. K., M. Marvier, and R. T. Paine. 2001. Direct and indirect effects: interactions between bald eagles and common murres. Ecological Applications 11:1858-1869.

Potts, G. R., J. C. Coulson, and I. R. Deans. 1980. Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. Journal of Animal Ecology 49:465-484.

Pradel, R., and J. D. Lebreton. 1999. Comparison of different approaches to study the local recruitment of breeders. Bird Study 46:74–81.

Rattiste, K., and V. Lilleleht. 1987. Population ecology of the Common Gull *Larus canus* in Estonia. Ornis Fennica 64:25–26.

Sǽther, B. E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642-653.

Skalski, J.R., A. Hoffmann, and S.G. Smith. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. Pages 9–28 in Marked Individuals in the Study of Bird Populations (J.-D. Lebreton and P.M. North, Eds.). Birkhäuser-Verlag, Basel, Switzerland.

Spear, L. B., H. R. Carter, T. M. Penniman, J. F. Penniman, and D. G. Ainley. 1987. Survivorship and mortality factors in a population of Western Gulls. Studies in Avian Biology 10:44-56.

Stata Corporation. 2005. Intercooled Stata 8.2 for Windows. Stata Corporation, College Station, Texas.

Swann, R. L., and A. D. K. Ramsay. 1983. Movements from and age of return to an expanding Scottish Guillemot colony. Bird Study 30:207-214.

Sydeman, W. J. 1993. Survivorship of Common Murres on Southeast Farallon Island, California. Ornis Scandinavica 24:135-141.

Thomas, C. S., and J. C. Coulson. 1988. Reproductive succes of kittiwake gulls, Rissa tridactyla. Pages 251-262 in Reproductive Success: Studies of Individual

Variation in Contrasting Breeding Systems (T. H. Clutton-Brock, Ed.). University of Chicago Press, Chicago.

Votier, S. C., B. J. Hatchwell, A. Beckerman, R. H. McCleery, F. M. Hunter, J. Pellatt, M. Trinder, and T. R. Birkhead. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. Ecology Letters 8:1157-1164.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120-139.

Wolter, K., & Timlin, M.S. (1993) Monitoring ENSO in COADS with a seasonally adjusted principal component index. *Proceedings of the 17th. Climate Diagnostic Workshop*, 52-57.

Wooller, R.D., J. S. Bradley, and J. P. Croxall. 1992. Long-term population studies of seabirds. Trends in Ecology and Evolution 7:111–114.

Wooller, R.D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1989. Short-tailed Shearwater. Pages 405-417 in Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

Table 1. Table of model selection results for age-specific effects on recapture (*p*), transition (*Ψ*), and survival (*S*) probabilities of non-breeder (*N*) and breeder (*B*) Common Murres banded as chicks on Southeast Farallon Island, California from 1986-2004. $\hat{c}$ = 1.464.

Parameter	Model	qAICc	ΔqAICc	qAICc Weight	k	qDeviance
p^N	**1/age**	875.99	0	**0.97**	77	327.97
	ln(age)	883.19	7.20	0.03	77	335.17
	age^2	893.93	17.94	0	78	343.26
	linear age	897.86	21.87	0	77	349.85
	age categorical	903.20	27.21	0	90	319.84
	constant	942.08	66.09	0	76	396.71
p^B	**constant**	845.35	0	**0.50**	63	333.44
	linear age	847.73	2.39	0.15	64	333.31
	ln(age)	847.77	2.42	0.15	64	333.35
	1/age	847.80	2.45	0.15	64	333.38
	age^2	850.20	4.85	0.04	65	333.25
	age categorical	875.99	30.65	0	77	327.97
$\Psi^{N\text{-}B}$	**1/age**	824.21	0	**0.65**	50	344.16
	age^2	825.84	1.63	0.29	51	343.40
	ln(age)	828.93	4.72	0.06	50	348.88
	linear age	838.27	14.06	0	50	358.22
	age categorical	845.35	21.14	0	63	333.44
	constant	866.86	42.65	0	49	389.20
$\Psi^{B\text{-}N}$	**constant**	795.47	0	**0.43**	36	348.05
	1/age	797.32	1.86	0.17	37	347.64
	ln(age)	797.35	1.88	0.17	37	347.66
	linear age	797.35	1.89	0.17	37	347.67
	age^2	799.62	4.16	0.05	38	347.65
	age categorical	824.21	28.74	0	50	344.16
S^B	**constant**	773.81	0	**0.35**	22	357.43
	linear age	774.94	1.13	0.20	23	356.39
	ln(age)	775.08	1.27	0.19	23	356.53
	1/age	775.19	1.38	0.18	23	356.64
	age^2	776.80	2.99	0.08	24	356.08
	age categorical	795.47	21.65	0	36	348.05
S^N	**constant**	753.00	0	**0.43**	8	366.15
	ln(age)	754.90	1.90	0.17	9	365.98
	1/age	754.93	1.93	0.16	9	366.01
	linear age	754.96	1.96	0.16	9	366.05
	age^2	756.47	3.47	0.08	10	365.49
	age categorical	773.81	20.81	0	22	357.43

Table 2. Model selection results for age-specific breeding success (*rs*) of Common Murres banded as chicks on Southeast Farallon Island, California from 1986-2004. EN controls for El Niño effects in 1992 and 1998 breeding seasons.

Model	qAICc	ΔqAICc	qAICc Weight	k	qDeviance
EN+1/age	156.22	0.00	**0.28**	2	76.06
EN+ age^2	156.63	0.41	0.23	3	75.22
EN	156.65	0.43	0.22	1	77.31
EN+ln(age)	157.47	1.25	0.15	2	76.69
EN+ linear age	158.31	2.09	0.10	2	77.11
1/age	162.97	6.75	0.01	1	80.47
age^2	164.06	7.84	0.01	2	79.98
ln(age)	164.17	7.95	0.01	1	81.07
linear age	165.20	8.98	0.00	1	81.58
EN+ age categorical	169.37	13.15	0.00	13	70.06
age categorical	175.51	19.29	0.00	12	74.38

Table 3. Table of model selection results for recapture (*p*) and survival (*Φ*) probabilities of adult Common Murres from Shubrick Point colony on Southeast Farallon Island, California from 1985-2004. Variance inflation factor (ĉ) = 1.394.

Year model of *Φ*	qAICc	ΔqAICc	qAICc Weight	k	qDeviance
SST	1165.73	0	**0.38**	5	1155.67
NOI	1166.13	0.40	0.31	5	1156.07
constant	1166.80	1.07	0.22	4	1158.76
MEI	1168.60	2.87	0.09	5	1158.54
year	1182.36	16.64	0.00	23	1135.30
Age model of *Φ*					
ln(age)	1182.36	0	**0.31**	23	1135.30
1/age	1182.69	0.32	0.26	23	1135.62
A	1183.09	0.73	0.21	23	1136.03
constant	1183.94	1.58	0.14	22	1138.97
A2	1185.03	2.67	0.08	24	1135.87
age	1210.53	28.17	0	40	1127.33
Year model of *p*					
constant	1212.53	0	**0.45**	41	1127.16
MEI	1213.87	1.33	0.23	42	1126.32
SST	1214.54	2.01	0.17	42	1127.00
NOI	1214.70	2.17	0.15	42	1127.16
year	1239.78	27.25	0	60	1112.47
Age model of *p*					
1/age	1239.78	0	**0.73**	60	1112.47
ln(age)	1242.23	2.45	0.21	60	1114.92
A	1246.06	6.28	0.03	60	1118.76
constant	1246.50	6.72	0.03	59	1121.44
age	1270.46	30.68	0	77	1104.27
A2	1555.60	315.82	0	61	1426.05

Table 4. Table of model selection results for recapture (p) and survival (Φ) probabilities of adult Common Murres from Upper Upper colony on Southeast Farallon Island, California from 1985-2004. Variance inflation factor ($\hat{c}$) = 1.233.

Year model of Φ	qAICc	ΔqAICc	qAICc Weight	k	qDeviance
constant	1158.54	0	**0.46**	4	1150.49
SST	1160.23	1.69	0.20	5	1150.16
NOI	1160.56	2.02	0.17	5	1150.49
MEI	1160.56	2.02	0.17	5	1150.49
year	1166.63	8.09	0.01	22	1121.44
Age model of Φ					
1/age	1166.63	0	**0.44**	22	1121.44
ln(age)	1167.24	0.61	0.33	22	1122.04
A	1168.73	2.10	0.16	22	1123.53
A2	1170.57	3.94	0.06	23	1123.27
constant	1173.51	6.88	0.01	21	1130.42
Year model of p					
MEI	1183.97	0	**0.36**	36	1108.76
constant	1184.52	0.55	0.27	35	1111.49
SST	1185.23	1.27	0.19	36	1110.03
NOI	1185.28	1.31	0.18	36	1110.08
year	1199.66	15.69	0	53	1086.63
Age model of p					
constant	1199.66	0	**0.35**	53	1086.63
A2	1200.56	0.91	0.22	55	1082.98
A	1201.17	1.51	0.16	54	1085.87
1/age	1201.30	1.64	0.15	54	1086.00
ln(age)	1201.92	2.27	0.11	54	1086.62
age	1211.48	11.83	0	68	1063.75

Table 5. Model selection results for breeding success (*rs*) of adult Common Murres on Southeast Farallon Island, California from 1972-2004.

Model	qAICc	ΔqAICc	qAICc Weight	k	qDeviance
year	4688.50	0	**0.56**	32	2312.03
year + colony	4689.02	0.52	0.44	33	2311.28
SST	5106.64	418.14	0	1	2552.32
NOI	5110.77	422.27	0	1	2554.39
MEI	5190.28	501.78	0	1	2594.14
colony	5297.75	609.25	0	1	2647.87
constant	5304.47	615.97	0	0	2651.23

Table 6. Temporal correlation between adult annual survival (Φ), breeding propensity (p), and breeding success (rs) for Common Murres from sub-colonies Upper Upper (UU) and Shubrick Point (SP) on Southeast Farallon Island, California between 1986 and 2004. Pairwise correlation coefficients are below the diagonal, Spearman rank coefficients above the diagonal and number of observations (n) are within parentheses. Significant correlations are in bold. Significance levels are indicated by symbols: 0.10 > † ≥ 0.05 > * ≥ 0.01 > ** ≥ 0.001.

	SP p	UU p	UU Φ	SP Φ	SP rs	UU rs
SP p	1	+0.26	+0.08	-0.02	+0.30	+0.37
		(18)	(18)	(19)	(19)	(17)
UU p	+0.29	1	**+0.49***	+0.07	+0.07	+0.05
	(18)		(18)	(18)	(18)	(17)
UU Φ	+0.11	**+0.55***	1	**+0.58***	+0.18	+0.20
	(18)	(18)		(18)	(18)	(17)
SP Φ	-0.05	+0.11	**+0.63****	1	**+0.43†**	**+0.51***
	(19)	(18)	(18)		(19)	(17)
SP rs	+0.35	-0.06	-0.09	+0.21	1	**+0.59***
	(19)	(18)	(18)	(19)		(17)
UU rs	+0.38	+0.09	-0.03	+0.27	**+0.79****	1
	(17)	(17)	(17)	(17)	(17)	

Table 7. Mean survival, breeding propensity, and breeding success for adult Common Murres (*Uria* aalge) at Southeast Farallon Island 1986-2004 compared with some other colonies. Values of survival (Φ), its standard deviation (SD) and breeding propensity (p) are given as percentages, *rs* is chicks fledged per pair per year. SP = Shubrick Point, UU = Upper Upper sub-colonies.

Colony	years	Φ (local survival)	SD	p (breeding propensity)	*rs* (chicks/pair)	ref.
SE Farallon Island, California, USA	1986-2004	SP 92.4 UU 90.4	SP 6.1 UU 5.4	SP 89.9 UU 85.6 (96.3)	0.74	this study
SE Farallon Island, California, USA	1986-1991	SP 93.9 UU 77.2	SP 5.2 UU 20.0	95.5		Sydeman (1993)
SE Farallon Island, California, USA	1972-1983				0.80	Boekelheide *et al.* (1990)
Tatoosh Island, Washington, USA	1992-1999				0.35	Parrish *et al.* (2001)
Canna, Scotland, UK	1984-1996	93.9				Harris *et al.* (2000b)
Colonsay, Scotland, UK	1991-1996	96.4				Harris *et al.* (2000b)
Isle of May, Scotland, UK	1986-1997	95.2				Harris, Wanless & Rothery (2000a)
Isle of May, Scotland, UK	1982-1992	94.9		92.6		Harris & Wanless (1995)
Stora Karlso, Gotland, Sweden	1962-1997	85.9				Olsson, Nilsson & Fransson (2000)
Hornoya, Finmark, Norway	1989-2003	96.1				Sandvik *et al.* (2005)
	avg (non-SEFI)	93.7				
	se	1.6				

Appendix I. Tables of estimates and standard errors.

a. Model average age-specific estimates and standard errors for probability of transitioning from non-breeder to breeder state (recruitment).

Age	Estimate	SE
1	0.0001	0.0001
2	0.0009	0.0013
3	0.0109	0.0078
4	0.0546	0.0206
5	0.1472	0.0388
6	0.2703	0.0733
7	0.3840	0.1038
8	0.4650	0.1228
9	0.5088	0.1521
10	0.5175	0.2048
11	0.5049	0.2587
12	0.4970	0.2928
13	0.5044	0.3146
14	0.5186	0.3269
15+	0.5323	0.3343

b. Model average age-specific estimates and standard errors for probability of survival of breeders.

Age	Estimate	SE
0-1	0.5958	0.4197
1-2	0.6712	0.3674
2-3	0.7543	0.2615
3-4	0.8028	0.1622
4-5	0.8306	0.1038
5-6	0.8487	0.0695
6-7	0.8620	0.0504
7-8	0.8728	0.0421
8-9	0.8820	0.0404
9-10	0.8901	0.0415
10-11	0.8975	0.0439
11-12	0.9041	0.0470
12-13	0.9099	0.0504
13-14	0.9149	0.0534
14-15	0.9191	0.0557

c. Year-specific estimates and standard errors for adult recapture probability (recapture + breeding propensity) of Common Murres at Shubrick Point and Upper Upper sub-colonies.

	Shubrick Point			Upper Upper	
Year	Estimate	SE	Year	Estimate	SE
1986	0.9754	0.0524			
1987	0.9352	0.0544	1987	0.4374	0.1449
1988	0.8950	0.0558	1988	0.8610	0.1010
1989	0.8720	0.0545	1989	0.9476	0.0398
1990	0.8993	0.0499	1990	0.7989	0.0632
1991	0.8960	0.0515	1991	0.8910	0.0511
1992	0.8566	0.0553	1992	0.9183	0.0434
1993	0.8473	0.0555	1993	0.8787	0.0564
1994	0.8903	0.0491	1994	0.8220	0.0632
1995	0.8798	0.0508	1995	0.7751	0.0758
1996	0.8857	0.0500	1996	0.8790	0.0513
1997	0.8284	0.0621	1997	0.7588	0.0639
1998	0.8496	0.0663	1998	0.7816	0.0615
1999	0.9244	0.0533	1999	0.8897	0.0514
2000	0.9219	0.0537	2000	0.8422	0.0609
2001	0.8729	0.0693	2001	0.8671	0.0560
2002	0.9514	0.0457	2002	0.9204	0.0492
2003	0.9480	0.0479	2003	0.8821	0.0616
2004	0.9478	0.0479	2004	0.8316	0.0696

d. Year-specific estimates and standard errors for adult local survival probability of Common Murres at Shubrick Point and Upper Upper sub-colonies.

Year	Shubrick Point Estimate	SE	Year	Upper Upper Estimate	SE
1985-86	0.9464	0.0537			
1986-87	0.9596	0.0445	1986-87	0.9573	0.0888
1987-88	0.9588	0.0416	1987-88	0.9591	0.0762
1988-89	0.9735	0.0321	1988-89	0.9487	0.0354
1989-90	0.9878	0.0248	1989-90	0.8473	0.0522
1990-91	0.9607	0.0321	1990-91	0.9540	0.0357
1991-92	0.9535	0.0346	1991-92	0.9858	0.0251
1992-93	0.9326	0.0395	1992-93	0.8593	0.0577
1993-94	0.9285	0.0408	1993-94	0.9328	0.0407
1994-95	0.9237	0.0411	1994-95	0.8768	0.0449
1995-96	0.9740	0.0297	1995-96	0.9778	0.0300
1996-97	0.9187	0.0476	1996-97	0.8329	0.0494
1997-98	0.8045	0.0668	1997-98	0.8388	0.0499
1998-99	0.8037	0.0718	1998-99	0.8235	0.0567
1999-2000	0.8135	0.0725	1999-2000	0.8434	0.0524
2000-01	0.9679	0.0414	2000-01	0.9082	0.0446
2001-02	0.8599	0.0698	2001-02	0.9177	0.0470
2002-03	0.8965	0.0646	2002-03	0.8776	0.0599
2003-04	1.0000	0.0500	2003-04	0.9270	0.5000

e. Age-specific estimates and standard errors of breeding success of Common Murres from Upper Upper sub-colony.

Age	Estimate	SE
4	0.4286	0.1870
5	0.6945	0.1323
6	0.6786	0.1210
7	0.7384	0.1111
8	0.9333	0.0644
9	0.7045	0.1281
10	0.6541	0.1423
11	0.7500	0.1250
12	0.8711	0.1789
13	0.7500	0.2191
14	0.7500	0.2165
15+	0.6667	0.1870

f. Year-specific estimates of breeding success of Common Murres from Shubrick Point and Upper Upper sub-colonies.

	Shubrick Point	Upper Upper
1972	0.7759	
1973	0.7923	
1974	0.9034	
1975	0.9051	
1976	0.7654	
1977	0.8197	
1978	0.6585	
1979	0.8444	
1980	0.8958	
1981	0.8904	
1982	0.9000	
1983	0.0444	
1984	0.7333	
1985	0.7983	
1986	0.7946	
1987	0.8525	
1988	0.8943	0.9722
1989	0.8667	0.8605
1990	0.8248	0.9118
1991	0.8815	0.8684
1992	0.0825	0.0435
1993	0.7480	0.7429
1994	0.8298	0.6562
1995	0.8322	0.3529
1996	0.6064	0.9412
1997	0.7584	0.7879
1998	0.3694	0.3810
1999	0.8231	0.8491
2000	0.8235	0.6842
2001	0.8176	0.6512
2002	0.7895	0.6250
2003	0.5897	0.8889
2004	0.8494	0.9509

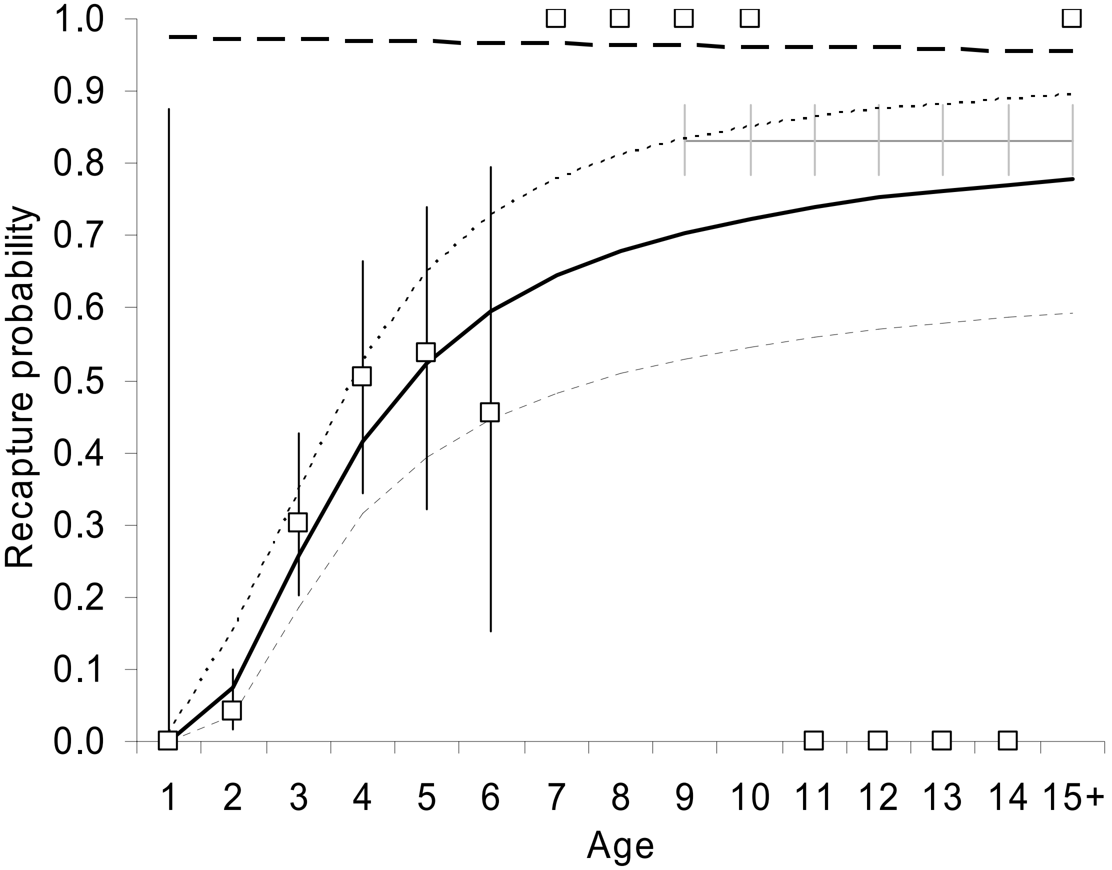

Fig. 1. Age-specific estimates (squares) of recapture probability for non-breeding Common Murres fledged at UU colony of Southeast Farallon Island, California 1986-2001. Recapture probability of non-breeders indicates probability of returning to the colony to prospect for mates and nest sites, a prerequisite to primiparity. Error bars indicate 95% confidence intervals of estimates. Solid black line indicates model average age curve for non-breeders; dotted black lines are 95% confidence interval of model average curve for non-breeders. Dashed black line is model average recapture probability of breeders. Grey line is recapture probability of birds banded as adults at the same site, grey error bars indicate 95% confidence interval.

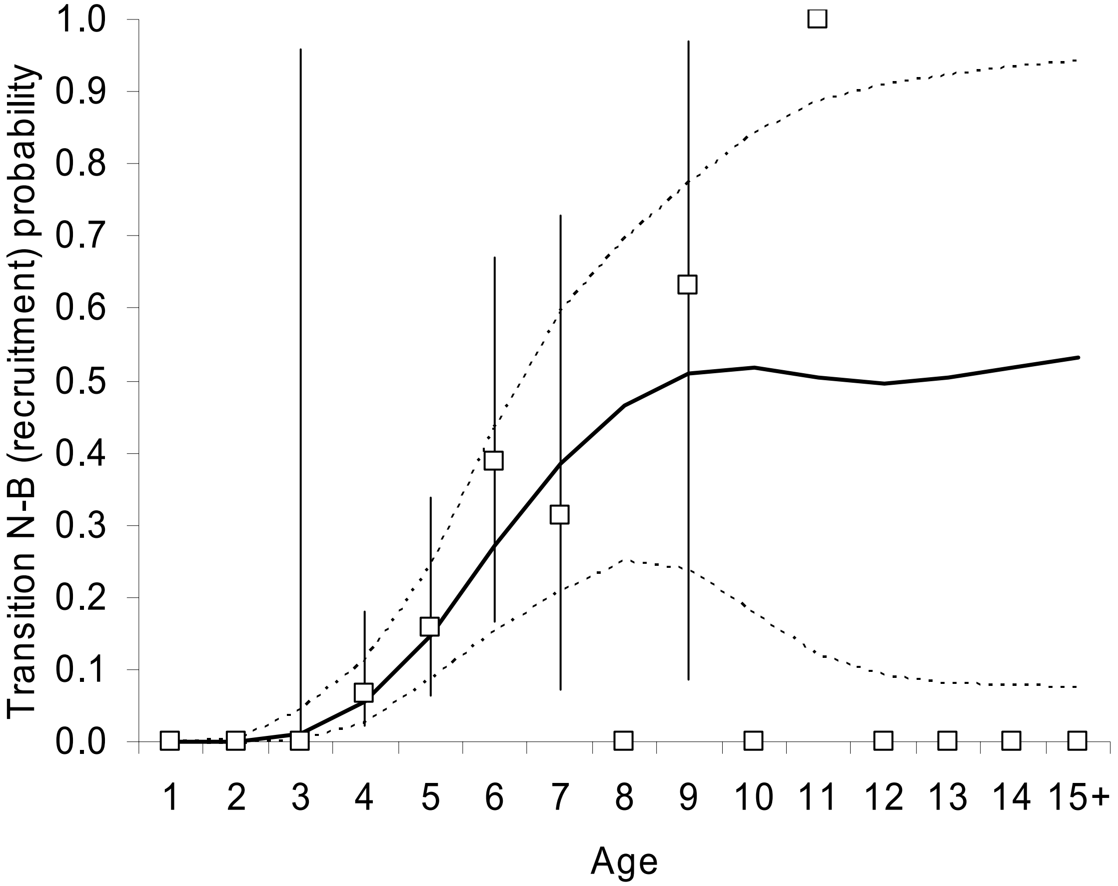

Fig. 2. Age-specific estimates (squares) of transition probability from non-breeding to breeding state for Common Murres fledged at Upper Upper colony of Southeast Farallon Island, California 1986-2001. Transition probability from non-breeding to breeding state indicates probabilistic age of first breeding (recruitment). Error bars indicate 95% confidence intervals of estimates. Solid black line indicates model average age curve; dotted black lines are 95% confidence interval of model average curve.

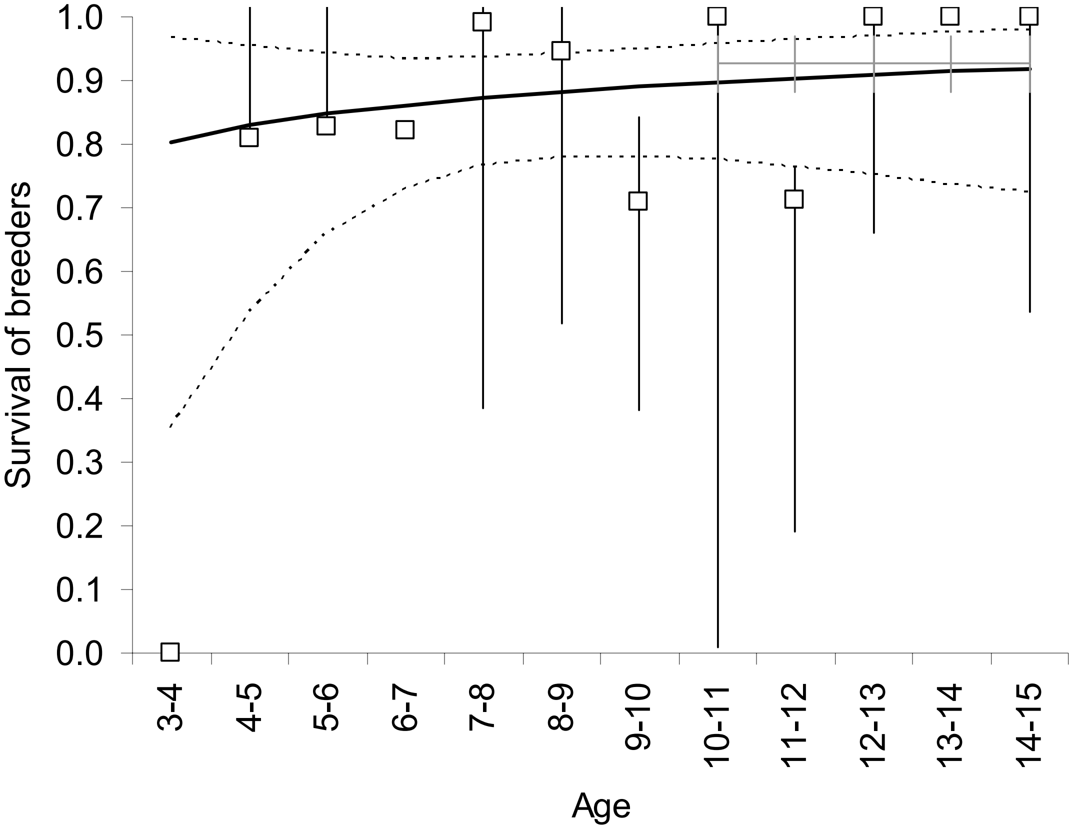

Fig. 3. Age-specific estimates (squares) of local survival probability for breeding Common Murres fledged at UU colony of Southeast Farallon Island, California 1986-2001. Error bars indicate 95% confidence intervals of estimates. Solid black line indicates model average age curve; dotted black lines are 95% confidence interval of model average curve. Grey line is mean local survival probability of birds banded as adults at the same site, grey error bars indicate 95% confidence interval.

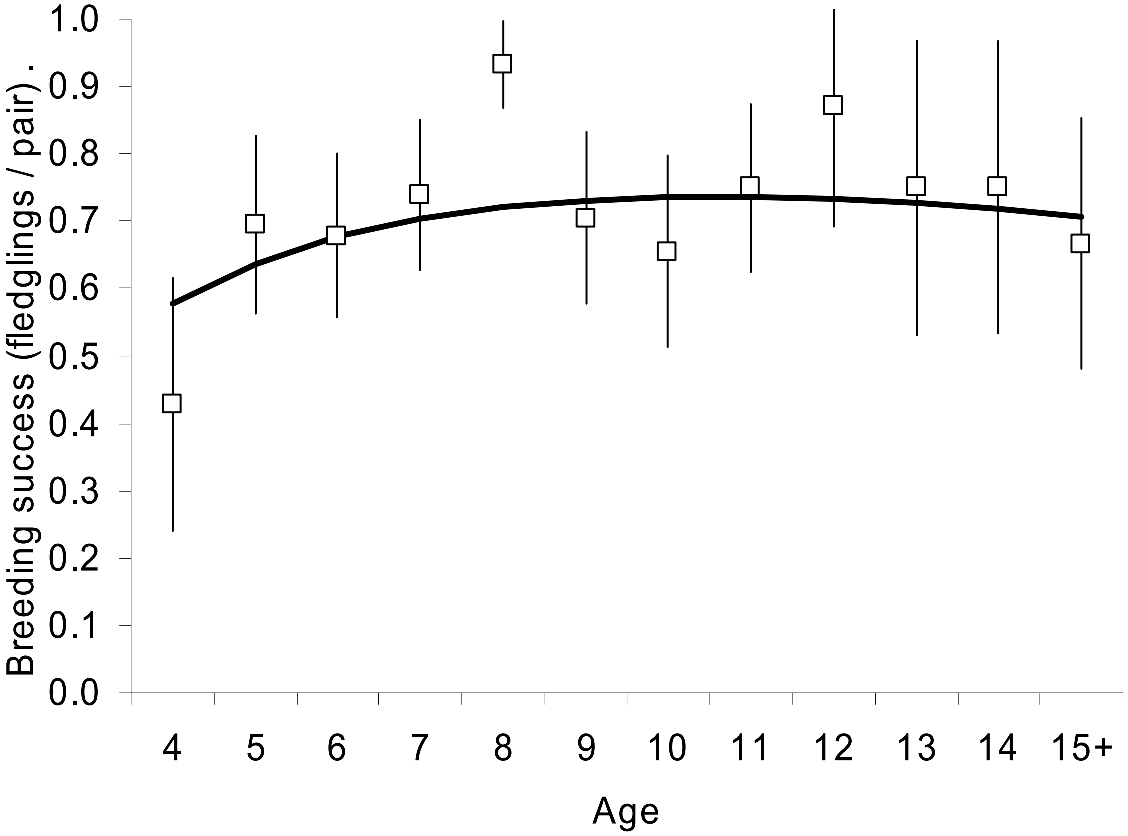

Fig. 4. Age-specific estimates (squares) of breeding success for Common Murres fledged at UU colony of Southeast Farallon Island, California 1986-2001. Error bars indicate 95% confidence intervals of estimates. Solid black line indicates model average age curve for breeding success.

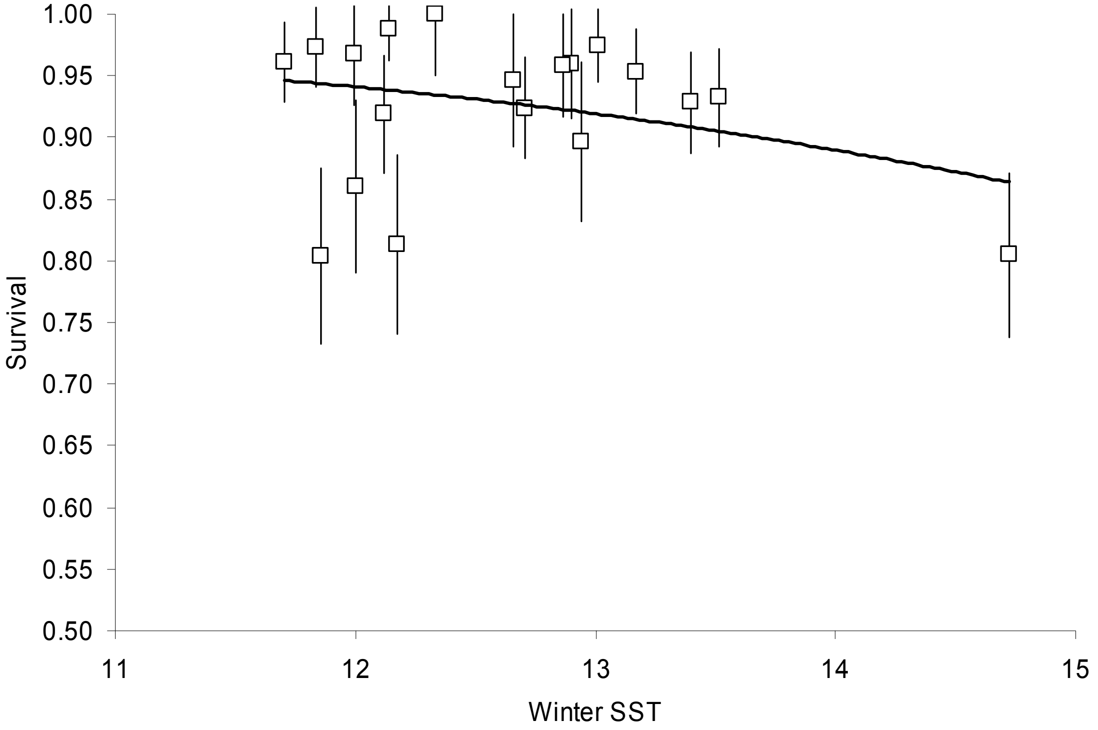

Fig. 5. Annual estimates of local survival probability relative to winter SST for adult Common Murres at Shubrick Point colony of Southeast Farallon Island, California 1985-2003. Open squares are year-specific estimates. The solid black line indicates the relationship between survival and SST (13% of variation in survival explained by SST). Error bars indicate standard errors of estimates.

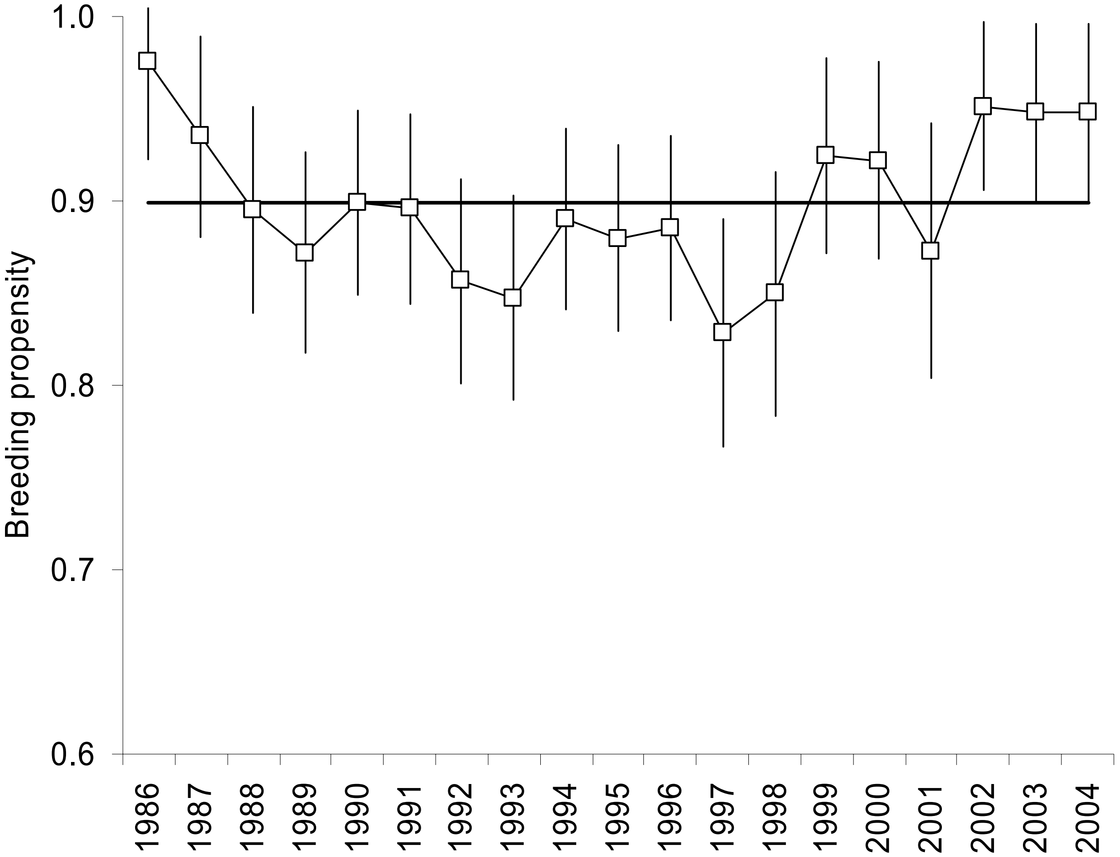

Fig. 6. Annual estimates of recapture probability for adult Common Murres at Shubrick Point colony of Southeast Farallon Island, California 1986-2004. Recapture probability indicates breeding propensity, the probability an individual will breed, given that it is alive. Error bars indicate standard errors of estimates.

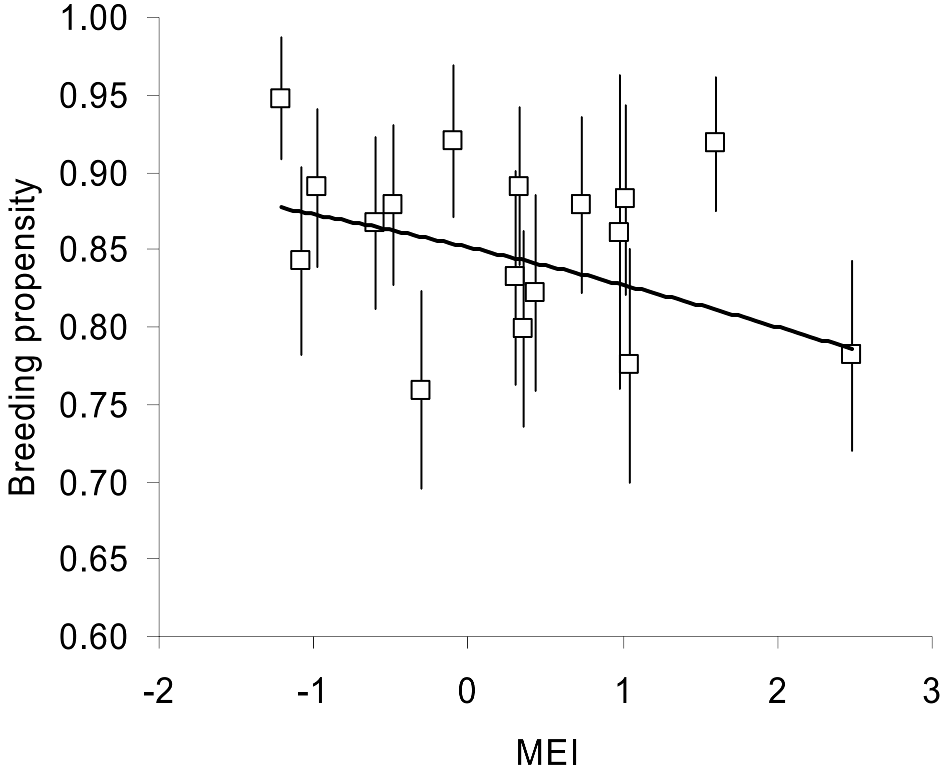

Fig. 7. Annual estimates of recapture probability relative to MEI for adult Common Murres at Upper Upper colony of Southeast Farallon Island, California 1987-2004. Recapture probability indicates breeding propensity, the probability an individual will breed, given that it is alive. The solid black line indicates the relationship between breeding propensity and MEI. Error bars indicate standard errors of estimates.

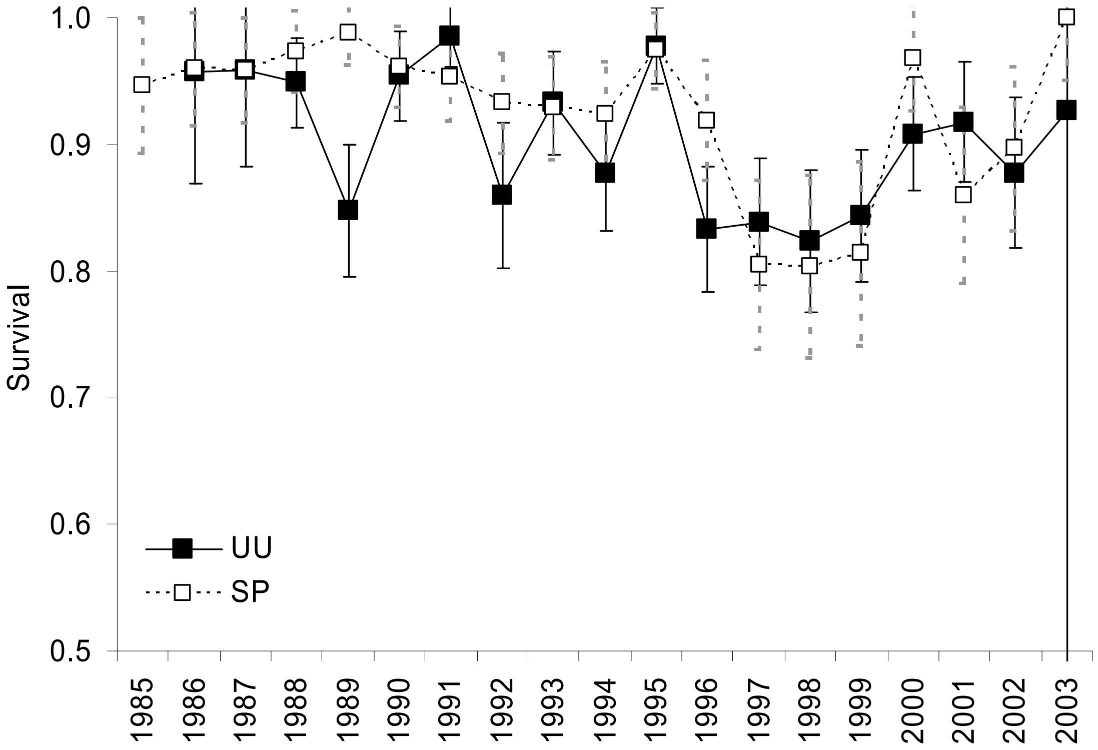

Fig. 8. Annual estimates of local survival probability for Common Murres at Upper Upper and Shubrick Point colonies of Southeast Farallon Island, California 1986-2003. Open squares are Shubrick Point, closed squares are Upper Upper. Error bars indicate standard errors of estimates.

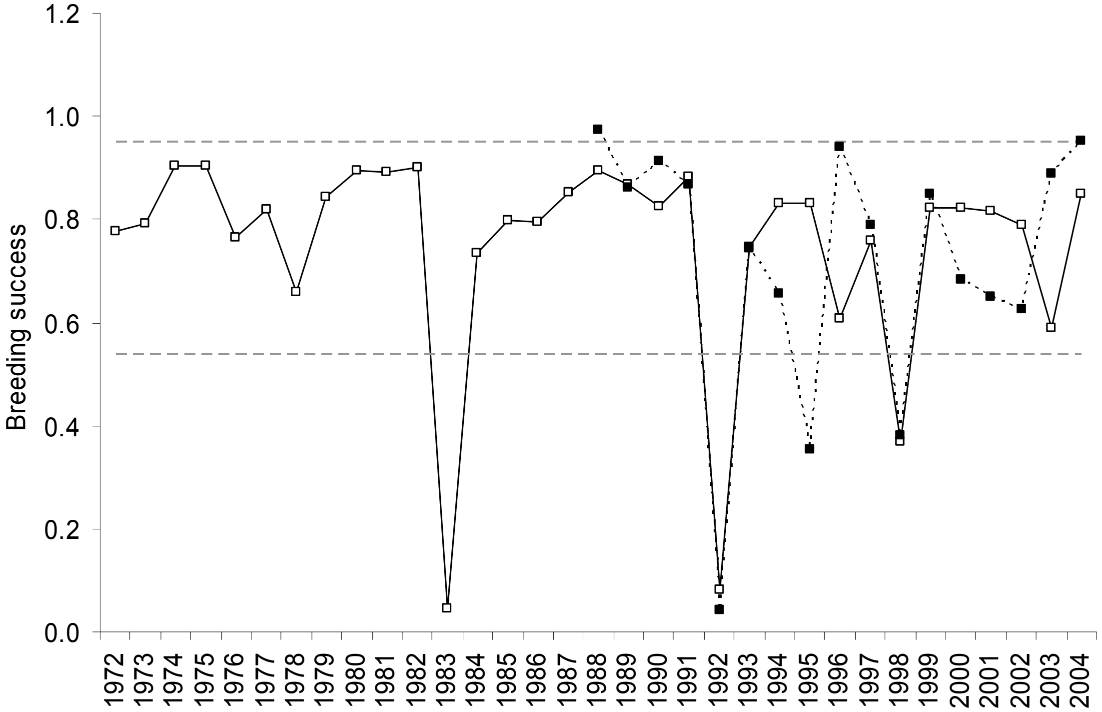

Fig. 9. Annual estimates of breeding success for Common Murres at Upper Upper (filled squares), and Shubrick Point (open squares) colonies of Southeast Farallon Island, California, 1972-2004. Dashed lines indicate ± 1 standard deviation from the overall mean (0.74) for both colonies.